






# Southern Flounder: Major Milestones and Remaining Knowledge Gaps in Their Biology, Ecology, and Fishery Management

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## ABSTRACT

Southern flounder are an iconic coastal finfish through the Southeast U.S. Atlantic and Gulf of Mexico. Southern flounder spend the early part of their lives in coastal and estuarine habitats, later moving offshore to spawn. Several decades of research have provided much clarity to the biology, life history, and aquaculture aspects of southern flounder—this information is summarized and reviewed in this study. Despite substantial improvement in understanding the species, major questions remain about their recruitment, offshore behaviors, captive rearing, and management. Recently, southern flounder have also been in focus because of substantial synchronous population declines throughout their range with specific concerns that recruitment failure and possibly climate change may be implicated. Management of southern flounder has thus far taken place within individual states, but coming into focus is the possibility that larger coastwide management approaches may need to be considered due to both the migratory nature of the species and the possibility of population stressors acting at regional scales. Many states have already begun aquaculture and enhancement efforts, with an eye toward supplementing wild populations. Large group efforts, like the symposium that led to this study, will likely be needed to tackle the complex challenges confronting southern flounder.



## KEYWORDS

Southern flounder; life history; movement; migration; aquaculture; fishery

## Introduction

The southern flounder (*Paralichthys lethostigma*) is an iconic marine flatfish that serves an important ecological role as a benthic predator in estuarine and coastal shelf waters of the Gulf of Mexico (GOM) and southeastern U.S. Atlantic (SEUS). Esteemed as both a sport-fish and table fare, the species is targeted in commercial and recreational fisheries throughout its range. Due to

its nearshore distribution, southern flounder is among the most accessible coastal species to recreational anglers in the southeastern U.S. and thus an important component of a multi-million dollar inshore recreational fishing industry (Hall et al. 2022). Still, despite the clear ecological and economic importance of southern flounder to coastal ecosystems and communities, significant knowledge gaps remain in their ecology,

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life history, and population dynamics, which collectively limit the effectiveness of fisheries management.

Distinct populations of southern flounder are recognized in the GOM and SEUS (Wang et al. 2015); however, the complex life history of southern flounder presents several unique challenges to fisheries management. Currently, southern flounder are managed by individual states, even though flounder use both state (estuaries, rivers) and federal (continental shelf) waters to complete their life cycle and may move significant distances (potentially crossing jurisdictional lines) during their life span (Craig et al. 2015; Steffen et al. 2023). Because growth is sexually dimorphic, larger females are disproportionately harvested in fisheries that historically focus on predictable spawning migrations when individuals congregate to move through natural bottlenecks (e.g., tidal passes) between the estuary and ocean (Honeycutt et al. 2019; Smith et al. 2021). In addition to the disproportionate amount of females, the risk of potential masculinization in flounder populations is further exacerbated by the fact that southern flounder also exhibit environmental sex determination, with rising temperatures expected to lead to increasingly male-biased sex ratios (Honeycutt et al. 2019; Erickson et al. 2021).

Over the past few decades, southern flounder have experienced simultaneous range-wide declines in the GOM and SEUS, attributed to high fishing mortality (Froeschke et al. 2011; Erickson et al. 2021) and/or environmental change (Erickson et al. 2021; Anderson et al. 2023). Regulatory changes to reduce harvest have been implemented in many states to recover flounder populations; however, managers and researchers increasingly recognize the clear need to develop cooperative management strategies that transcend state boundaries (Flowers et al. 2019), and a comprehensive synthesis of the existing data relevant to the management of this species is currently lacking. The aim of this review is to synthesize the present knowledge of southern flounder biology and ecology, characterize the fishery and management approaches, and examine the role and potential of aquaculture for stock enhancement. Finally, existing data is synthesized and knowledge gaps are identified to prioritize for future research that will advance management for southern flounder populations in the GOM and SEUS.

## Species biology and ecology

### Description

Southern flounder is described morphologically by an olive to brown dorsal coloration combined with

a white ventral surface. The dorsal surface is typically characterized by non-oscillated spots that range from pale to dark in color, although the presence of spotting can vary across individuals. Southern flounder inhabit coastal waters (Reagan and Wingo 1985), estuaries (Enge et al. 1985), and rivers (Farmer et al. 2013; Nims and Walther 2014) in both the SEUS and GOM, ranging as far north as the Albemarle Sound, North Carolina, and as far west as south Texas in US waters (Ginsburg 1952; VanderKooy 2015). The GOM and SEUS populations are not contiguous; the SEUS range ends in southern Florida and the GOM range ends near Tampa Bay (Ginsburg 1952), creating a range gap where the species is absent around the tip of the Florida peninsula (Gilbert 1986).

Although earlier publications classified southern flounder as members of the Family Bothidae (Reagan and Wingo 1985), the species is now classified in the Family Paralichthyidae, which contains the sand flounders. The genus *Paralichthys* contains 18 species of relatively large left-eyed flatfishes with well-developed teeth (Gilbert 1986). Two congeners, gulf flounder (*P. albigutta*; Jordan and Gilbert 1982) and summer flounder (*P. dentatus*; Linnaeus 1766) are often co-managed with southern flounder because they share similar appearances, overlap in range, and are thus targeted by the same fisheries. Summer flounder reach larger maximum sizes than southern flounder, do not occur in the Gulf of Mexico, and can be phenotypically differentiated by the presence of at least five oscillated spots, although the spots may not always be present (Kells and Carpenter 2011). In contrast, gulf flounder have three ocellated spots and are often smaller than southern flounder. Gulf flounder overlap with southern flounder throughout most of the species range, from North Carolina to Texas, while summer flounder occur in the Atlantic Ocean from Maine to Florida, but are concentrated between North Carolina and New England (Gilbert 1986). Because all three species overlap in their distributional ranges and are closely related, gulf and summer flounders are sometimes used as congeners to inform or compare age, growth, maturity, and other biological and life history traits of each species. Interestingly, southern flounder has been studied for the parasites that it hosts, which have been documented to include multiple species that occur in specific parts of the fish (de Buron and Roumillat 2010; de Buron et al. 2011). Despite the work done on this aspect of southern flounder biology, the effects of parasite species composition or density on southern flounder ecology or the fishery remain unknown.

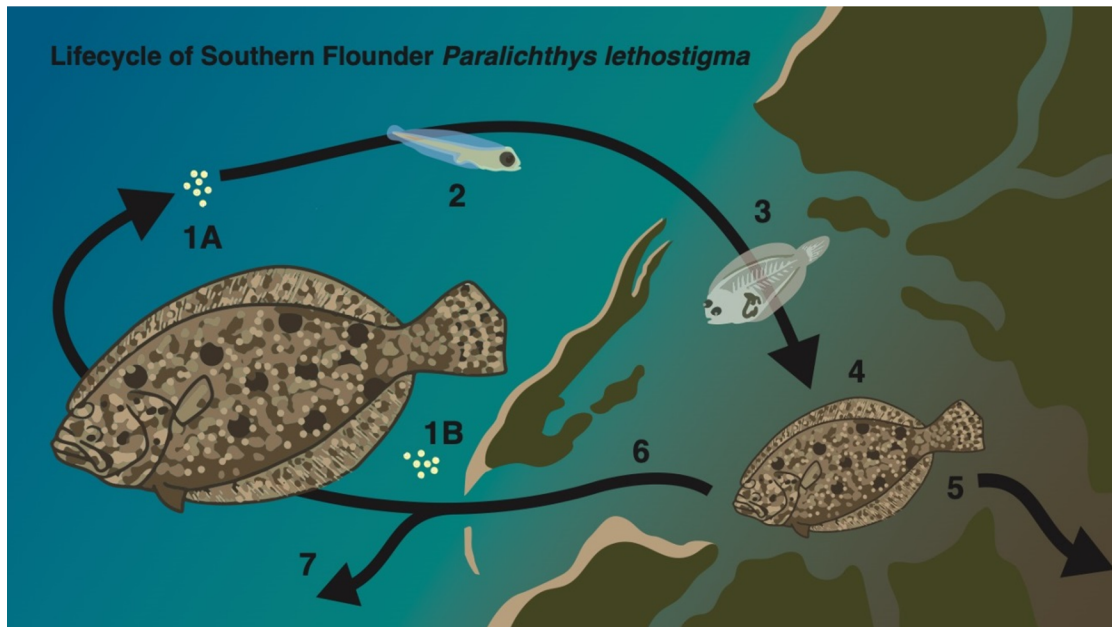
## Life history

### Reproductive biology

It is generally understood that southern flounder migrate from estuaries to offshore oceanic habitats to spawn during winter (Figure 1; Stokes 1977; Benson 1982; Wenner et al. 1990), although otolith microchemical analyses suggests the possibility of spawning in low salinity estuarine habitats (Lowe et al. 2010; Morais et al. 2012; Steffen et al. 2023). In the north-central GOM, Corey et al. (2017) estimated a November–January spawning season based on gonadosomatic index (GSI) and histological data, although no actively spawning fish were encountered in the study. The general timing of the GOM spawning season is supported by previous research (Fischer 1999). Glass et al. (2008) calculated hatch dates of larval southern flounder collected in Galveston Bay, Texas to occur between early December and early January. Along the SEUS, southern flounder with vitellogenic oocytes and elevated GSI occur from October through December in North Carolina estuaries (Midway and Scharf 2012). Powles and Stender (1978) reported the presence of paralicthyid larvae from December to March at mid-shelf locations (>40 m depths) along the SEUS from North Carolina to Florida, suggesting spawning likely occurs

in multiple locations along the shelf. Grieshaber et al. (2016) captured few vitellogenic females in SEUS estuaries after November, and Watterson and Alexander (2004) found spent stages of ovaries in southern flounder captured in March off the North Carolina coast. The spawning seasons of southern flounder in both the GOM and SEUS appear to be temporally similar.

Female southern flounder have asynchronous oocyte development (Midway and Scharf 2012; Corey et al. 2017), typical of batch spawners (Murua and Saborido-Rey 2003). Southern flounder are generally considered to be income breeders, receiving essential fatty acids from their prey, which is typical of batch spawners with indeterminate fecundity (McBride et al. 2013), but are able to switch to a capital breeder strategy when nutrient availability is limited (Burns and Fuiman 2020). Individuals in captivity have been documented spawning multiple times over several months (Arnold et al. 1977; Watanabe et al. 2006; Burns and Fuiman 2020), and Fischer (1999) estimated a spawning frequency for GOM females to be every 2.9–6.3 days. The only fecundity estimate for wild caught southern flounder ( $n=8$ ) is 14,000–68,000 eggs/batch (Fischer 1999). Fecundity of laboratory-spawned fish ranged from 510,000–897,000 eggs summed over 3–7 spawning events for groups of 4–5 females (Watanabe et al. 2006),



**Figure 1.** Depiction of the life cycle of southern flounder, *Paralichthys lethostigma* as it moves from offshore (left) to inshore (right) habitats. 1. Adults spawn offshore, with potential for outer shelf (A) and inner shelf (B) locations. 2. Larvae concentrated over outer shelf, but also found over mid and inner shelf, with 30–60d duration. 3. Larval ingress during late winter and early spring, followed by metamorphosis and settlement in estuarine habitats. 4. Juvenile and sub-adult flounder feed and grow in estuaries. Sub-adults remain in estuaries for over a year until they reach sexual maturation. 5. Some juvenile and sub-adult flounder settle and remain in oligohaline habitats to feed and grow to fresh water to feed and grow. 6. Adult males and females emigrate out of estuaries to open water to spawn in late autumn. 7. Stock mixing in the ocean facilitated by pre-spawn migration and post-spawn movements. A portion of post-spawn adults may remain in ocean habitats and not re-enter estuaries. There has been no evidence of philopatry in southern flounder.

although oocyte viability, measured as hatching success, was limited to 20–45%.

Unlike many fish species, southern flounder have indeterminate sex at hatching, with an undifferentiated gonad containing gonial cells. Perinucleolar primary oocytes are not seen until well into the juvenile life stage ( $\approx 115$  mm total length (TL)), whereas a differentiated testes is first observed at  $\approx 100$  mm TL, with meiosis not evident until  $>120$  mm TL (Luckenbach et al. 2009 in North Carolina waters). Southern flounder demonstrate strong sexual dimorphism, with females reaching considerably larger sizes (female maximum size: 60–80 cm TL) relative to males (male maximum size: 35–45 cm TL). In the wild, sex ratios of sampled adult fish are often female-dominated (VanderKoooy 2015), which may be partially related to sex-specific differences in habitat use or size-dependent gear selectivity.

The timing of female southern flounder sexual maturity can vary by region. Estimates of female  $L_{50}$  based on physiological maturity (presence of CA oocytes; Brown-Peterson et al. 2011) indicate that GOM southern flounder likely achieve sexual maturity at a smaller size and younger age than their SEUS conspecifics (Midway and Scharf 2012; Corey et al. 2017; Table 1). Furthermore, females with early CA oocytes were shown to be immature whereas those with late CA oocytes were mature, based on hormonal analyses (Grieshaber et al. 2016), which could impact estimation of the female maturity schedule. Male southern flounder have been estimated to mature at smaller sizes than females (Wenner et al. 1990), but a detailed histological description of male gonadal development is lacking. Despite concerns with using macroscopic maturity

staging and general encouragement of histology for assessment, Midway et al. (2013) found that combined GSI and TL were a useful substitute (80–90% predictive power) when compared to histology.

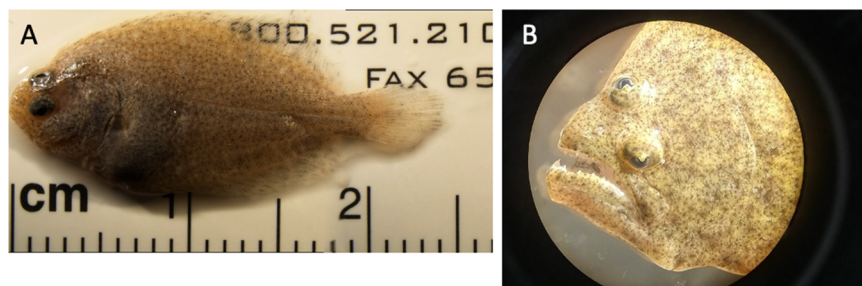
### Early life history

Offshore spawning of southern flounder has been inferred mainly from collections of larval stages (Figure 2). Encounters with *Paralichthys* spp. larvae in offshore waters were first reported by Smith et al. (1975) during winter ichthyoplankton surveys along the outer shelf of North Carolina. Both Powell and Robbins (1994) and Powles and Stender (1978) also reported *Paralichthys* spp. larvae during winter surveys in the SEUS, with peak abundances generally in February in open-shelf waters at depths  $>40$  m. Walsh (2007) observed that the smallest *Paralichthys* spp. individuals were distributed at outer shelf locations, with larval sizes increasing toward the coast. In the GOM, Hernandez et al. (2011) collected *Paralichthys* spp. larvae from December to March 18 km off the Alabama coast, and larvae have been reported congregating in the surf zones and inlets between barrier islands prior to entering estuarine waters (Gunter 1945). The observations by Hernandez et al. (2011) support the arrival timing of larvae in estuarine waters during late winter (Arnold et al. 1960; Stokes 1977; Nall 1979; Fischer 1999; Glass et al. 2008; Froeschke et al. 2011) and indicate that seasonal abundance and distribution of southern flounder larvae in GOM waters is similar to the patterns observed in the SEUS.

The timing of key early life history events (i.e., hatch and metamorphosis) can impact larval survival and

**Table 1.** Summary of size and age at 50% physiological maturity for southern flounder in the southeastern United States ( $L_{50}$  and  $A_{50}$ , respectively). GOM—Gulf of Mexico; SEUS—Southeastern US Atlantic Coast;  $L_{100}$ —100% maturity.

Sex	Region	$L_{50}$ (TL)	$L_{100}$ (TL)	$A_{50}$	Reference
Female	SEUS	408 mm		76% of age-2	Midway and Scharf 2012
	GOM	229 mm	509 mm		
Male	SEUS	303 mm	368 mm	0.96 y	Corey et al. 2017
	GOM	First maturity: 230 mm First maturity: 170 mm	310 mm		

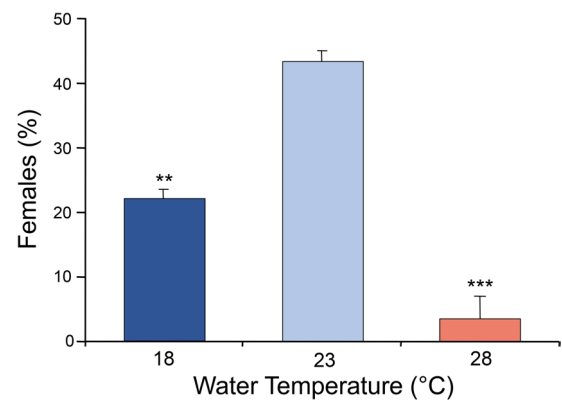


**Figure 2.** Post metamorphic young-of-year southern flounder. A. Hatchery-reared juvenile flounder, 76 days, with otolith-based age at metamorphosis of 45 days. B. Juvenile flounder captured in a bag seine from Texas waters.

juvenile recruitment success (Lapolla and Buckley 2005; Atkinson and Secor 2017). Variation in young-of-the-year (YOY, <age 1) southern flounder hatch and metamorphosis (i.e., eye migration) timing indicates that larvae and recently settled juveniles can experience a range of abiotic and biotic conditions that can influence growth and survival (Wieland et al. 2000; Rankin and Sponaugle 2014; Beeken et al. 2023). When age is not estimated, total length at capture can be used to predict age at capture, and as a result, age-based estimates (i.e., hatch and metamorphosis dates) of YOY southern flounder can be calculated (Beeken et al. 2023). Peaks in the hatch date distribution can be used to estimate the onset and duration of peak spawning (Zastrow et al. 1991), while peaks in the metamorphosis date distribution can be used to estimate peak settlement and recent recruitment to nursery habitats (Joh and Wada 2018).

Most YOY southern flounder captured coastwide in Texas showed otolith-based hatch dates from October to December and metamorphosis dates (e.g., early estuarine recruitment) in December and January (Beeken et al. 2023). This aligns with field observations of post-metamorphic YOY southern flounder (about 9–11 mm TL) that show recruitment to Texas bays from December to April (King 1971; Stokes 1977; Glass et al. 2008; Nañez-James et al. 2008) with peak recruitment in February (Stokes 1977). Similarly, along the SEUS coast (e.g., South Carolina), post-metamorphic southern flounder recruit to shallow tidal creeks starting in January with a peak in March (Wenner and Archambault 2005). YOY southern flounder showed similar average hatch and metamorphosis timing at a coastwide scale in Texas (Beeken et al. 2023), suggesting that large-scale climatic factors impact the timing of these early life history events (Sogard et al. 2001). Post-metamorphic YOY southern flounder that grew faster (on average) as larvae complete metamorphosis at an earlier age compared to individuals that grew slower (on average) as larvae (Beeken et al. 2023). Laboratory-reared southern flounder can complete metamorphosis by age 45–52 d (Arnold et al. 1977; van Maaren and Daniels 2000), which is comparable to recent otolith-based estimates of age at metamorphosis (mean 47 d; Beeken et al. 2023).

In Texas waters, earlier hatch and later metamorphosis timing have been correlated with higher water temperatures, both of which may increase recruit survival (Beeken et al. 2023). In contrast, laboratory-reared southern flounder larvae in stage 4 of development (from onset to completion of metamorphosis) complete metamorphosis earlier at higher water temperatures (van Maaren and Daniels 2001). Such information can be used to predict how future changes in water temperature could impact the hatch and



**Figure 3.** Effect of temperature on sex determination in southern flounder. Percentage of female southern flounder from replicate experiments (mean  $\pm$  SE) at temperatures of 18, 23 and 28°C ( $n=64, 53, \text{ and } 49$ , respectively, with 20–34 fish/temperature/replicate). \*\* $p < 0.01$ ; \*\*\* $p < 0.001$  represent significant deviations from a 1:1 male:female sex ratio. (Recreated from Luckenbach et al. 2003, Figure 5).

metamorphosis timing, and in turn, survival and recruitment of YOY southern flounder.

### Environmental sex determination

Southern flounder exhibit an unusual sex determination system that is dependent on both genetic and environmental influences and appears similar to that of their west Pacific congener the olive flounder (*P. olivaceus*; Tabata 1991; Yamamoto 1999). Environmental sex determination driven by temperature (temperature-dependent sex determination or TSD) was first demonstrated in paralichthyid flounders for *P. olivaceus* (Tabata 1991; Yamamoto 1999), and it appears that sex determination in southern flounder takes place similarly when juveniles settle into nearshore nursery habitats. Luckenbach et al. (2003) found rearing temperature during juvenile development of southern flounder strongly affected sex determination with approximate 50:50 male:female sex ratios at 23°C and strongly male-biased sex ratios at both lower and higher temperatures (18 and 28°C, respectively; Figure 3). It should be noted, however, that despite the clarity of effect at the temperatures used in Luckenbach et al. (2003), southern flounder occur across a wide distribution and different TSD thresholds may exist, particularly for populations living in warmer waters, such as the GOM.

Because clearly distinguishable histological markers for sex determination do not appear until southern flounder reach larger sizes (at  $\approx 100$  mm TL; Fitzhugh et al. 1996), molecular biomarkers (based on gene expression) were developed to allow female and male sexes to be assigned accurately at smaller body sizes

(<100 mm TL; Luckenbach et al. 2005; Mankiewicz et al. 2013). The female biomarkers included gonadal aromatase (*cyp19a1a*) because it is the rate-limiting enzyme in estrogen production (Luckenbach et al. 2009), and the Forkhead Box Transcription Factor (*foxl2*) given its central role in female sex determination across a range of vertebrates. The male sex determination biomarker used was Mullerian Inhibiting Substance (*mis*), because of its central role in male sex determination across a range of vertebrates (Mankiewicz et al. 2013). Sexual differentiation could be reliably discerned based on divergence in *cyp19a1a* expression in juvenile southern flounder gonads beginning at  $\approx 65$  mm TL, being validated by sexing one part of a cohort by the molecular biomarker approach and growing out other fish in this cohort for sexing at larger size by histological methods. The observed pattern was consistent with later results for *foxl2* and *mis* expression and suggests sex determination in southern flounder takes place by  $\approx 65$  mm TL (Mankiewicz et al. 2013). The timing of sex determination inferred by molecular biomarker expression was supported by a temperature shift study (Montalvo et al. 2012), whereas juveniles that shifted from a cool rearing temperature (18°C) to warmer rearing temperatures at 35–40 mm TL were effectively masculinized while those not shifted until reaching a larger body size (65–70 mm TL) did not show evidence of masculinized sex ratios.

Temperature is not the only environmental factor that can influence sex determination in southern flounder. As in many fishes, sex determination can be driven by exposure to the androgenic hormone methyltestosterone (e.g., Kitano et al. 2000; Fernandino et al. 2012) and the glucocorticoid ‘stress’ hormone cortisol (Mankiewicz et al. 2013). Using XX genotype offspring (derived from gynogenetically produced broodstock), Mankiewicz et al. (2013) showed that juveniles fed a control feed exhibited a 91% female sex ratio when reared at 23.5°C, while only 29% or 13% differentiated as females when 100 or 300 mg/kg of cortisol, respectively, was added to feed periodically during the period of sex determination. In a surprising result, Mankiewicz et al. (2013) also found that tank color had a strong effect on sex determination in hatchery-reared southern flounder juveniles. Tank color may affect sex ratios by affecting cortisol levels; juveniles in light blue tanks exhibited higher whole-body cortisol levels during the presumed sex determination window than juveniles in black tanks. It is possible that light tank colors and a resultant inability to match the background color is stressful for southern flounder, an ambush predator dependent on crypsis. Elevated cortisol may represent a common biochemical pathway under stressful conditions and evidence suggests cortisol can

inhibit aromatase expression (and therefore potentially estrogen synthesis and female sex determination; Yamaguchi et al. 2010), potentially indicating that environmental stressors could lead to masculinization in wild populations.

To investigate if temperature also affects southern flounder sex ratios in natural habitats, Honeycutt et al. (2019) used the molecular biomarkers *cyp19a1a*, *foxl2*, and *mis* to sex southern flounder juveniles from estuarine habitats in North Carolina ranging from south of the New River north to the Pamlico Sound during 2014–2017. These regions showed consistent differences in nursery habitat temperatures across years with northern sites being  $\approx 3^\circ\text{C}$  cooler than southern collection sites. Interestingly, sex ratios in juveniles also varied consistently, with collections from the northern sites exhibiting sex ratios ranging from 37–67% male across years (mean = 54% male), while the southern region collections were 81–94% male (mean = 87%) suggesting temperature differences are sufficient to produce variations in juvenile sex ratio observed in the wild.

### Age and growth

Numerous researchers have studied the age and growth of southern flounder throughout their range, with a large focus on understanding juvenile growth patterns in natural systems (e.g., Guindon and Miller 1995; Fitzhugh et al. 1996; Glass et al. 2008) and laboratory settings (e.g., Taylor and Miller 2001; Luckenbach et al. 2007; Howson and Targett 2019). Glass et al. (2008) developed an exponential growth model for juveniles (9–57 mm SL; 27–78 days post hatch) in Texas estuaries that suggested an increase in size of  $2.5\% \text{ day}^{-1}$ , with an overall mean growth of  $0.40 \text{ mm SL day}^{-1}$ . Cage experiments of 37–70 mm SL southern flounder in oligohaline and mesohaline environments (0.5–8‰) showed a mean growth rate of  $0.44 \text{ mm SL day}^{-1}$  (Guindon and Miller 1995), similar to model estimates despite exposure to sub-optimal and variable environmental conditions and altered prey availability. In North Carolina, age-0 southern flounder showed a linear growth rate of  $0.65 \pm 0.28$  (mean  $\pm$  SD)  $\text{mm}\cdot\text{day}^{-1}$  across all ages and sexes (Fitzhugh et al. 1996); however, bimodal growth patterns were apparent beginning at sizes of 75–100 mm TL. Both sexually dimorphic growth as well as variation among individuals in the onset of piscivorous feeding were hypothesized to generate two size modes by the end of the first growing season. Males and undifferentiated fish contributed primarily to the smaller size mode (<200 mm TL), while females contributed to both the smaller and larger size mode (>275 mm TL), illustrating the effects of diet on juvenile

growth (Fitzhugh et al. 1996). A laboratory study of juveniles in Georgia suggested an average maximum growth rate of 1.3 mm SL day<sup>-1</sup> for fish between 76 and 93 mm SL (Reichert and van der Veer 1991), which would likely be achieved during the warmest season and when feeding on an energy rich diet of fish prey.

Several abiotic factors have also been found to contribute to the observed highly variable size-at-age of age-0 fish, including water temperature (Guindon and Miller 1995; Luckenbach et al. 2007; Del Toro-Silva et al. 2008; Howson and Targett 2019), salinity (Guindon and Miller 1995; Howson and Targett 2019), and dissolved oxygen (DO; Taylor and Miller 2001; Del Toro-Silva et al. 2008). Specific growth rate was found to increase at both higher water temperature and salinity (Guindon and Miller 1995) and decline at DO levels  $\leq 1.75$  mg L<sup>-1</sup> (Del Toro-Silva et al. 2008). There is likely an interactive effect of salinity and temperature on the growth of juvenile (45–100 mm TL) southern flounder, with growth potential (e.g., specific growth rate) and linear growth rate maximized at 24–27 °C and 14–25‰ (i.e., mesohaline conditions) and 25–28 °C and 14–24‰, respectively (Howson and Targett 2019).

Growth patterns of older life stages of southern flounder targeted by important U.S. fisheries have also been well studied (Fischer and Thompson 2004; Midway et al. 2015; Corey et al. 2017). The earliest studies investigating the age structure and growth of southern flounder relied on length frequency analysis or ages derived from scales or whole otoliths to

estimate maximum age and the size-at-age composition of fish captured in North Carolina (Powell and Schwartz 1977; Wolff 1977; DeVries 1980), Georgia (Music and Pafford 1984), Florida (Nall 1979) and Texas (Stokes 1977). These early studies identified a clear pattern of sexually dimorphic growth (Stokes 1977; Wolff 1977; DeVries 1980) and longevity (Stokes 1977; Music and Pafford 1984), with females reaching larger sizes and older ages range-wide. Recent studies have estimated the onset of sexually dimorphic growth to begin at sizes around 100 mm TL (Fitzhugh et al. 1996; Luckenbach et al. 2007) and being readily apparent by the start of their second year of life (age-1; Wenner et al. 1990); however, no clear latitudinal pattern is observed for spatial differences in maximum size (Table 2). Rather, basin-specific differences in maximum size appear to be driven by individual study sample sizes, region-specific exploitation history, gear availability and selectivity, and local environmental conditions.

Spatial variability in the lifetime growth patterns of female and male southern flounder are evident in the estimated von Bertalanffy growth relationships (Figure 4), with indications that GOM female fish grow faster (e.g., higher Brody growth coefficients, *k*) to reach their asymptotic size (Corey et al. 2017) than fish from the SEUS. Limitations of these studies include low samples sizes of smaller individuals (<200 mm TL; Stunz et al. 2000; Fischer and Thompson 2004; Corey et al. 2017), the inability to comprehensively sample offshore habitats (Wenner et al. 1990; Stunz et al. 2000), and a lack

**Table 2.** Maximum sizes of male and female southern flounder reported in various studies in the southeastern U.S. and Gulf of Mexico states.

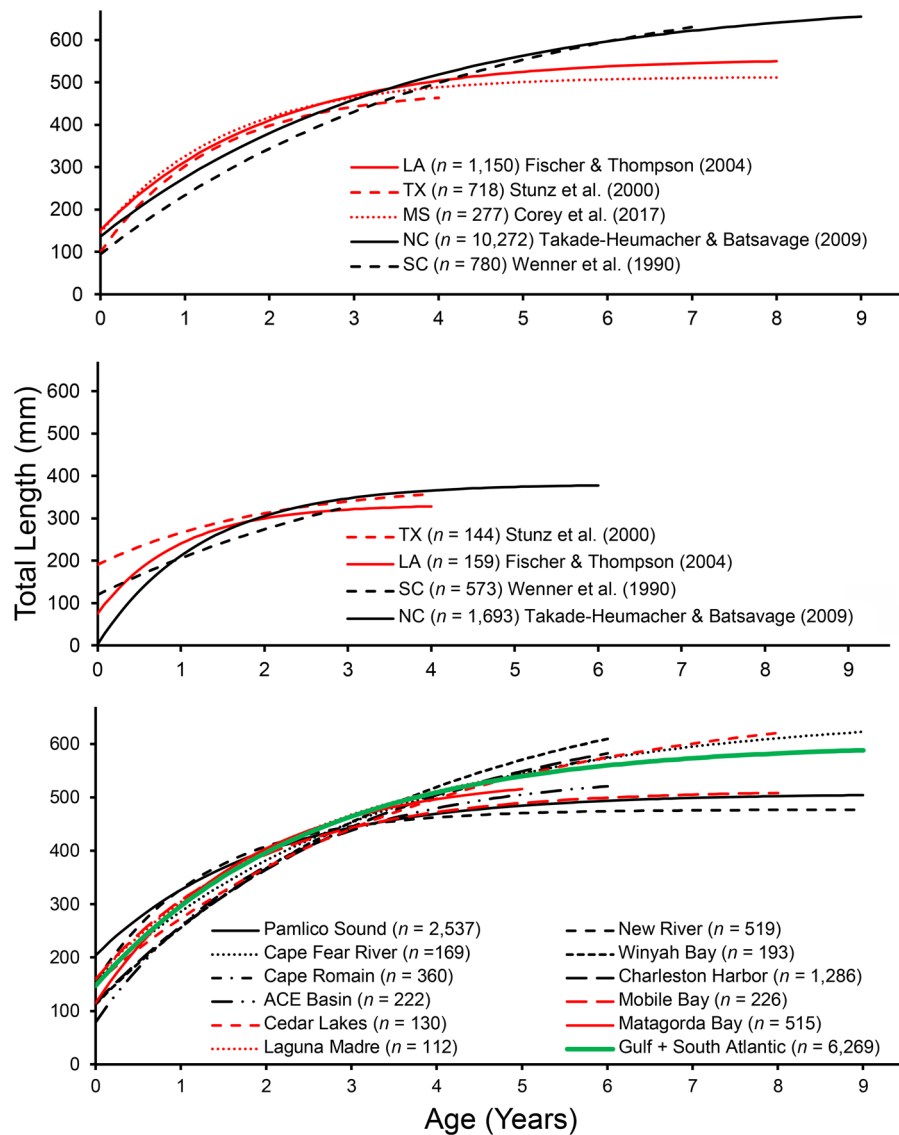
Sex	Location	Sample size	Max. size (mm TL)	Max. age (yr)	Source
Male	Texas	102	320	3	Stokes (1977)
		144	479	4	Stunz et al. (2000)
	Louisiana	146	414	4	Fischer and Thompson (2004)
	Florida	56	416	3	Flowers et al. (2019)
	Georgia	233 <sup>a</sup>	–	3	Music and Pafford (1984)
		43	464	3	Flowers et al. (2019)
	South Carolina	573	476	3	Wenner et al. (1990)
		9,912	476	5	Flowers et al. (2019)
	North Carolina	60	405 <sup>b</sup>		Wolff (1977)
		2,564	516	6	Flowers et al. (2019)
Female	Texas	162	620	5	Stokes (1977)
		718	633	4	Stunz et al. (2000)
	Louisiana	1,202	764	8	Fischer and Thompson(2004)
	Mississippi	440	576	4	Corey et al. (2017)
	Florida	399	655	5	Flowers et al. (2019)
	Georgia	233 <sup>a</sup>	700 <sup>c</sup>	6	Music and Pafford (1984)
		780	703	7	Wenner et al. (1990)
	South Carolina	2,752	777 <sup>d</sup>	6	Flowers et al. (2019)
		64	705		Wolff (1977)
	North Carolina	718 <sup>a</sup>	760		DeVries (1980)
14,934		835	9	Flowers et al. (2019)	
Sexes Combined	North Carolina	718 <sup>a</sup>	–	4	DeVries (1980)

<sup>a</sup>Sexes combined.

<sup>b</sup>Few >355 mm TL observed.

<sup>c</sup>Sexes combined maximum length as sex determination was not made, but based on sexually dimorphic growth can assume this was a female Southern Flounder.

<sup>d</sup>Reported as 696 in Flowers et al. (2019), but largest in South Carolina database is 777 mm TL (J. Ballenger, pers. comm.).



**Figure 4.** Von Bertalanffy growth functions available for specific areas in the literature for southern flounder. Top Panel: Female. Middle Panel: Male. Bottom Panel: The predicted von Bertalanffy growth curves for females based on the analysis in Midway et al. (2015). Colors represent studies in the Gulf of Mexico (Red), U.S. South Atlantic (black) or regions combined (green).

of knowledge regarding the spatial distribution of males (Stunz et al. 2000; Fischer and Thompson 2004). Regardless of region, all studies to date estimated that male southern flounder have smaller asymptotic sizes and younger maximum ages than females.

To overcome low sample sizes in regional studies, Midway et al. (2015) used a hierarchical Bayesian analysis to investigate southern flounder growth variability for fishes collected in Texas, Alabama, South Carolina, and North Carolina. They concluded that growth patterns and model parameters varied considerably, but without clear spatial patterns for females (Figure 4, bottom panel), whereas in males there was a moderate geographic effect of mean maximum length increasing with latitude, though still no basin effect. Midway et al. (2015) hypothesized two primary causes for variability

in growth patterns: small-scale environmental conditions driving individual growth rates and spatial differences in juvenile abundance leading to density-dependent growth variation. More recent work by O’Leary et al. (2021) has found the environment to play a more important role than spatial proximity in determining genomic divergence among estuaries, which may result in small-scale growth variability, among other traits.

### Natural mortality

Direct information on the natural mortality ( $M$ ) of southern flounder exists from laboratory experiments investigating the minimum thermal tolerance. One study focused on juveniles (27–40 mm TL) and adults (197–387 mm TL) from Texas (Prentice 1989), while



another focused on both younger ( $\approx 70$  mm TL) and older ( $\approx 130$ – $170$  mm TL) juveniles from South Carolina (Taylor et al. 2000). Both identified a minimum thermal tolerance limit for survival in southern flounder, though the absolute limit was affected by both the local salinity conditions and exposure length. For instance, the lower limit of thermal tolerance for southern flounder in South Carolina was  $5$ – $8^\circ\text{C}$  in oligohaline systems (Prentice 1989), while Taylor et al. (2000) concluded that southern flounder had a low temperature tolerance between  $2$ – $4^\circ\text{C}$ , which was influenced by salinity. Recently, McDonald et al. (2016) examined (simulated) cold events on pre- and post-metamorphic juveniles, in an effort to understand the sizes at which southern flounder can be safely moved to outdoor rearing facilities. A clear size effect was found, where the largest juvenile size ( $19.7$  mm TL) had high survival ( $89$ – $100\%$ ) for all treatments with the other two (smaller) sizes having low survival ( $<30\%$ ) for all treatments.

Recently, field-based estimates of natural mortality for southern flounder were generated through a combined tagging and telemetry study in North Carolina (Scheffel et al. 2020). The best model predicted a temporally constant annual rate of  $M=0.84$  for fish ranging from  $356$ – $523$  mm TL, which represents adult, legal-sized females throughout much of their range (very few males ever achieve minimum harvestable sizes). Life history-based estimators that use growth, longevity, and/or temperature to inform either age-constant or age-varying natural mortality (see Kenchington 2014 for a recent review) produce a range of mortality estimates from  $M=0.65$ – $1.38$  (age-constant) and  $M=0.47$ – $1.06$  (age-varying). The age-varying estimates of natural mortality generated by Flowers et al. (2019) and based largely on growth suggest a decline in  $M$ -at-age from relatively high levels for younger age groups (age-0  $M=2.98$ , age-1  $M=0.809$ ) to lower rates of natural mortality for the oldest ages ( $M=0.27$  for ages 8 and 9). Life history-based estimators using growth and maximum age to predict  $M$  suggest higher rates of natural mortality for male southern flounder given their faster growth rates and shorter longevity.

### **Spatial ecology and population structure**

The spatial dynamics of fish populations have long presented major challenges for fisheries science with increased recognition of their role in shaping demographics, stock connectivity, and stability. Many species of marine fish demonstrate complex life histories that include distinct spawning and nursery areas linked by larval dispersal, and often a diversity of migratory

behaviors (Secor 2015). Understanding use of specific habitats can promote successful management and conservation through appropriate habitat protections and spatial harvest control (Baltz et al. 1993; Bacheler et al. 2012), while the ability to track broad-scale movements informs connectivity and population structure that is critical for identifying the appropriate spatial scale for stock assessment, management, and putative stock enhancement (Blankenship and Leber 1995; Lorenzen et al. 2010; Goethel et al. 2011; Secor 2015). Improved understanding of spatial ecology has informed stock structure and sustainable harvest strategies for several species of flatfishes (e.g., Loher 2011; Shackell et al. 2021). For southern flounder, synthesizing knowledge of age- and size-dependent patterns and drivers of habitat use and migration dynamics will contribute to a mechanistic understanding of key population dynamic processes and foster improved management across the species range.

### **Settlement and estuarine habitat use**

Movement during early life stages is critical to population connectivity, habitat selection, and ultimately survival and recruitment success of marine fishes. Following offshore spawning and shoreward transport of larvae, post-metamorphic southern flounder have been found to inhabit freshwater to hypersaline habitats within estuaries along both Atlantic and Gulf coasts (Burke et al. 1991; Allen and Baltz 1997; Nañez-James et al. 2008). In Aransas Bay, Texas, highest densities of newly settled southern flounder were found in more saline vegetated habitats near inlets while the lowest densities of newly settled juveniles occurred in non-vegetated muddy habitats furthest from inlets (Nañez-James et al. 2008). Stokes (1977) found similar spatial patterns of newly settled juveniles in other Texas estuaries. A comprehensive assessment of juvenile habitat use across nine Texas estuaries indicated that low temperatures ( $<20^\circ\text{C}$ ), low to moderate salinities ( $\approx 5$ – $20\text{‰}$ ), and high dissolved oxygen levels ( $>5$   $\text{mgL}^{-1}$ ) were associated with high capture rates for juvenile southern flounder (Froeschke et al. 2013). Studies in both North Carolina and Louisiana found the highest densities of newly settled southern flounder in upper estuarine regions with lower salinities (Powell and Schwartz 1977; Burke et al. 1991; Allen and Baltz 1997). In North Carolina, densities of immigrating southern flounder larvae, the majority of which were in the later stages of metamorphosis, peaked during February and March (Burke et al. 1991). Time series models of annual juvenile abundance across North Carolina estuaries showed a strong effect of the timing and intensity of winter winds (+) and river discharge

(–) on juvenile settlement at river mouths and bay inlets (Taylor et al. 2010).

Post-settlement patterns of habitat use by southern flounder may also differ across regions. In Texas, Nañez-James et al. (2008) suggested that large juveniles collected in the upper estuary were older fish that moved upstream after settling near inlets. Froeschke et al. (2013) also found that distance to inlet had a parabolic relationship with juvenile capture probabilities during January–May near both barrier island inlets and at the upper reaches of estuaries, possibly supporting the hypothesis that post-settlement juveniles migrate to the upper estuary after settling near inlets. Along the Atlantic Coast, Walsh et al. (1999) found that in spring and summer, southern flounder were most abundant in middle to upper estuary habitats with mud and detritus substrate in Pamlico Sound, NC, but by autumn were only present in the lowest salinity habitats in the upper river. Other studies in Atlantic estuaries have suggested similar patterns of down-estuary movement by larger juveniles from late summer into autumn (Rogers et al. 1984; Wenner and Archambault 2005), although direct evidence of this ontogenetic shift in habitat use is limited.

Southern flounder typically remain in estuarine systems for the first 1–2 years of life, returning to estuaries outside of the spawning season throughout the adult life stage. Estuarine habitat use has been shown to be influenced by a range of environmental variables including benthic habitat features (depth, sediment composition, structured habitats), physicochemical properties of water (salinity, temperature), and biological requirements (prey distribution) that vary in both space and time. In both the SEUS and GOM, southern flounder are often associated with shallow sand/mud substrates near habitat features such as salt marsh edges, tidal creeks, seagrasses, and oyster reefs (Walsh et al. 1999; Furey et al. 2013; Dance and Rooker 2015; Hollensead 2018). Hollensead (2018) found that southern flounder densities were also positively associated with spatial patterns of abundance and diversity of prey fish assemblages. Estuarine southern flounder tend to avoid shallow habitats during the day at high summer temperatures, preferring deeper sandy habitats and then moving into shallower areas at night and also during high tides (e.g., Furey et al. 2013). During winter, southern flounder displayed less variable diel habitat partitioning and were associated primarily with mud habitats near seagrass boundaries (Dance and Rooker 2015).

Natural tracers such as otolith chemistry have provided insights into post-settlement habitat use of southern flounder across salinity gradients. For example, in the Mobile-Tensaw River Delta, Alabama, nearly one-third of age-0 juveniles appeared to move into

oligohaline habitat soon after hatching with no obvious estuarine or marine signal present near the otolith core (Lowe et al. 2010). In a subsequent study, Farmer et al. (2013) found that some juveniles making rapid migrations into oligohaline habitats could remain in low salinity habitats into their third year of life and that older juveniles continued to migrate into low salinity areas throughout their first two years of life. Working in the same system, Chrisp et al. (2023) collected southern flounder across a larger (60 km) estuarine salinity gradient (0–30 psu) including both the Mobile-Tensaw River Delta and Mobile Bay. Southern flounder collected in or near riverine habitats appeared to remain in freshwater habitats prior to offshore migrations while those in higher salinity, lower bay habitats never experienced freshwater conditions. In estuarine habitats near Port Aransas, Texas, Nims and Walther (2014) also documented a wide diversity of habitat use patterns, with more than half of the fish they examined showing no evidence of oligohaline residence, while the remainder spent some portion of time in oligohaline habitats. Time spent by southern flounder in low salinity habitats varied greatly, ranging from 5%–95% of the lifetime otolith transect (Nims and Walther 2014). Both Nims and Walther (2014) and Chrisp et al. (2023) suggested that freshwater habitat use appeared to be facultative for southern flounder. With the exception of diel habitat shifts during warmer months, temperature appears to have less influence on southern flounder habitat selection, and thermal preferences may vary among regions (Dance and Rooker 2015; Froeschke and Froeschke 2016; Hollensead 2018). Seasonal changes in temperature may provide environmental cues that initiate shifts in habitat preference (e.g., the shift from upper estuary habitats to habitats near tidal passes in fall prior to spawning)

### **Estuarine movements**

After the post-settlement period, larger juvenile and sub-adult southern flounder tend to display primarily sedentary behavior during their residence in estuarine systems. For instance, Furey et al. (2013) used electronic tags to track the movements of larger juveniles and subadults ( $n=8$ ; 284–370 mm TL) in a Texas estuary and found that bay-wide movement was limited to a small spatial range during summer, and that finer scale movements were dynamic and tide-dependent. No fish moved more than 10 km during the study period, although some were capable of moving up to 2 km per day. While these estimates represent the minimum displacement between tag detection locations, and are therefore conservative, other studies of adult southern flounder movement within estuaries corroborate their sessile nature (Scheffel et al. 2020).

Movement within the estuary is scale dependent and can be broadly classified as estuary-scale movement (>1 km) and habitat-scale movement (<1 km; Dance and Rooker 2015). At the estuary scale, southern flounder demonstrate high fidelity to preferred habitat mosaics and often remain in relatively small areas for much of the year (Craig et al. 2015; Hollensead 2018; Steffen 2019). Most individuals in large-scale tracking studies in North Carolina and Texas moved <10 km from the initial tagging site during spring and summer, with many moving <1 km (Craig et al. 2015; Steffen 2019). All individuals recaptured between May and August in Texas had moved <1 km, with one electronically tagged individual remaining in the listening area of an acoustic receiver continuously for 9 months before it was harvested by an angler (Steffen 2019). While less common outside of the spawning season, flounder are still capable of greater movement within the estuary, and rates as high as 1 km·d<sup>-1</sup> have been observed in telemetry studies (Furey et al. 2013). The likelihood and magnitude of movement increases during fall when many individuals become more active and move to the lower estuary prior to offshore spawning migrations (Craig et al. 2015; Steffen 2019). While most adults move offshore in the winter to spawn, immature fish typically overwinter in the estuary. Overwintering southern flounder also mainly remain in small areas and movements >20 km are rare (Craig et al. 2015; Dance and Rooker 2015; Hollensead 2018); however, more extensive movements are likely to be associated with shifts in environmental variables such as tidal range and temperature, with movement more likely at low tidal ranges and/or increasing temperature (Dance and Rooker 2015).

While southern flounder are characterized by relatively high site fidelity and small home range size for much of the year, movement patterns are more dynamic at smaller spatial scales. Telemetered southern flounder in a North Carolina estuary occupied a mean seasonal home range size of approximately 0.18 km<sup>2</sup> (Hollensead 2018), but comparable estimates in other regions are limited. In contrast, mean rates of movement have been calculated in estuarine seascapes in both Texas and North Carolina, with rates ranging from 0.034 to 0.07 m·s<sup>-1</sup> across multiple locations (Furey et al. 2013; Dance and Rooker 2015; Hollensead 2018). Movement within estuarine seascapes is influenced by benthic habitat, with reduced movement near structured habitat, such as seagrasses, where flounder can bury in sediment to ambush prey near habitat boundaries (Dance and Rooker 2015). Similar to other flatfish, movement rates of southern flounder at the habitat-scale are also influenced by temperature, with rates of movement decreasing at

colder temperatures potentially due to reduced metabolic rate and feeding activity in response to thermal stress (Dance and Rooker 2015).

### *Spawning migration, offshore distribution, and post-spawn movements*

Southern flounder undergo large-scale seaward movements during fall and winter (Figure 1), which presumably represent spawning emigrations from estuarine nurseries to offshore spawning grounds. Arnold et al. (1960) reported collecting southern flounder in abundance during the 'fall run' from October and November at Galveston Island, Texas with indication that movement was associated with spawning activities due to the presence of ripe fish within the samples. Similarly, Stokes (1977) reported adult southern flounder emigration from Texas bays between mid-October and mid-December, peaking in November each year which coincided with a 4–5 °C decrease in water temperature following passage of cold fronts (Anderson et al. 2023). In the SEUS, intermediate and long-term returns from conventional tagging studies also documented seaward travel during fall and winter, with individuals moving to the lower estuary before leaving through tidal passes to spawn (Wenner et al. 1990; Monaghan 1992). Multiple conventional tagging data sets showed southern flounder in North Carolina exhibited estuarine residence in spring and summer, with an increased likelihood of movements >50 km during fall for larger fish (Craig et al. 2015). Fish >450 mm TL were more than three times as likely to emigrate to the ocean than fish <375 mm TL.

Acoustic telemetry studies in both the SEUS and GOM have improved the understanding of egress patterns of southern flounder and highlight the potential for multiple migratory contingents. Hollensead (2018) documented southern flounder emigration from the New River estuary, North Carolina during five consecutive years (2012–2016), with 86% of emigrating individuals egressing between mid-October and mid-November. Individuals emigrated rapidly (system departure within 14 days) and the rate of movement during emigration was positively related to proximity to the ocean (swimming speed increased nearly 3-fold within 5 km of the ocean, (Hollensead 2018). Over the course of five years of tagging, no individuals detected emigrating from the New River, North Carolina were subsequently detected reentering the system. In the northern GOM, Steffen (2019) used both conventional and acoustic tagging methods and documented directed movements (>5 km) out of Galveston Bay, Texas from November to January, with

peak movements occurring in early December. Similar to findings in the SEUS (Hollensead 2018), Steffen (2019) observed only 25% of tagged southern flounder to be confirmed emigrants, while many individuals either overwintered within the bay complex or moved toward the lower bay but could not be classified as resident or emigrant. None of the individuals that emigrated from Galveston Bay, Texas were subsequently detected reentering the system, corroborating observations by Hollensead (2018) in the SEUS. The primary driver of southern flounder emigration behavior is believed to be declining fall water temperatures and other shifts in environmental conditions (e.g., wind, water level) associated with cold fronts (Arnold et al. 1960; Stokes 1977; Craig et al. 2015; Hollensead 2018). Using a multifactor Cox proportional hazards model, Hollensead (2018) found that the cumulative effects of temperature declines and precipitation explained the most variance in the daily probability of emigrating (vs. remaining resident) in the New River, North Carolina suggesting that the passage of several cold fronts, rather than any single event, is necessary to trigger movements toward the ocean by southern flounder. Body size, likely due to its influence on the probability of maturity, is also a key predictor of participation in annual emigration (Craig et al. 2015; Hollensead 2018). Although emigration of spawning adults in fall and the annual recruitment of southern flounder larvae to estuarine habitats in late winter/spring are well documented (Warlen and Burke 1990; Wenner et al. 1990; Burke et al. 1991; Taylor et al. 2010), the understanding of movement, distribution, and habitat use of adult southern flounder in offshore waters remains surprisingly limited. Similarly, the spatiotemporal distribution of egg and larval stages in offshore waters is not well understood. Off the North Carolina coast, the occurrence of smaller, and presumably younger, larvae in outer shelf habitats combined with more advanced larval stages found over the inner shelf (Walsh 2007) supports the hypothesis that adults migrate toward the outer shelf region for winter spawning followed by advection of larvae toward inshore nurseries. Several ichthyoplankton surveys conducted off the SEUS coast during winter (see references above in *Early Life History* section) also reported *Paralichthys* spp. larval stages in deeper waters of the outer continental shelf. In the SEUS, outer shelf regions are influenced by the Gulf Stream current, which may facilitate transport of larvae in both northward and shoreward directions. In the GOM, the annual timing of larval ingress is also well documented (Stokes 1977), but the offshore distributions of egg and larval stages remain poorly

informed. Similarly, the lack of adult movement studies in offshore regions limits understanding of spawning habitat in both the SEUS and GOM.

After spawning, the prevailing view has included the return of adult southern flounder to natal estuaries during late winter and spring (Stokes 1977), but detailed knowledge of post-spawn movements is lacking. Movements of considerable distance to non-natal estuaries have been observed in both the SEUS (Craig et al. 2015) and GOM (Steffen et al. 2023), and conventional tagging studies in the SEUS have all observed a pattern of recapture occurring in estuaries south of the tagging location, whenever fish moved an extensive (>50 km) distance (Craig et al. 2015). The absence of returns to natal estuaries following confirmed emigration during recent telemetry studies (Hollensead 2018; Steffen et al. 2023) also supports the movement of post-spawn adults to other estuarine systems. A recent study to examine southern flounder stock structure in the SEUS using otolith trace elements and stable isotopes (Wang et al. 2018; see below) concluded that the adult movements were a likely driver of the patterns they observed. The potential also exists for post-spawn southern flounder to remain in deeper coastal ocean habitats rather than reentering shallow bays and estuaries. An extensive diving survey conducted over five years off the North Carolina coast (Watterson and Alexander 2004) routinely encountered adult southern flounder occupying nearshore structured habitats throughout most of the year (except winter when fish were presumed to move to deeper mid- and outer shelf areas). The facultative use of nearshore oceanic habitats by post-spawn adults, rather than obligate return to estuaries, would have important implications for exposure of southern flounder to harvest, most of which occurs in estuarine systems (Midway et al. 2018).

### **Stock structure**

Genetic tools have become increasingly important resources for both fisheries management and stock enhancement programs. For southern flounder, several studies in the past two decades have informed stock structure at broad spatial scales, although questions remain regarding the existence of population structure at small spatial scales. Blandon et al. (2001) first examined southern flounder population structure using genetics, evaluating allozymes at nine gene loci based on adults collected in Texas, Mississippi, Alabama, Florida, and North Carolina. The analysis revealed differences between GOM and SEUS locations, as well as a break along the mid-Texas coast,

hypothesizing that offshore current patterns could result in reduced egg and larval dispersal among GOM regions and ultimately recommended that estuarine populations be considered as distinct genetic units. A mitochondrial-based genetic assessment (Anderson et al. 2012) examined tissue samples obtained from adult southern flounder across six locations from Laguna Madre, Texas to Pamlico Sound, NC. Approximately 50% of individuals represented unique haplotypes and the significant GOM and SEUS differentiation detected originally by Blandon et al. (2001) was supported. The authors suggested the potential for incipient speciation between the GOM and SEUS basins based on the high level of sequence divergence observed. The mtDNA results also suggested the potential for additional genetic barriers between eastern Texas (Galveston Bay) and eastern Louisiana (Grand Isle). Anderson and Karel (2012) evaluated a microsatellite dataset using adults primarily collected in Texas (six localities), but also included fish from Apalachicola and Jacksonville, FL, as well as Pamlico Sound, NC. The microsatellite results supported the same broad spatial pattern of stock structure, with a large divergence between fish from the GOM and SEUS, and a much lower degree of divergence and no clear spatial pattern of genetic structure within the GOM. The only genomic data set for southern flounder was studied by O'Leary et al. (2021) and largely agreed with previous work (Blandon et al. 2001; Anderson and Karel 2012; Anderson et al. 2012), all having found evidence for genetic variation at relatively small scales but with the genomic data correlating it to small-scale environmental variation.

To better define population structure within the SEUS basin, Wang et al. (2015) used both amplified fragment length polymorphism (AFLP) loci and mtDNA control region sequencing applied to southern flounder collected from several locations along the SEUS coast, and also from Sabine, Texas and Apalachicola, Florida in the GOM. The level of differentiation between the SEUS and GOM based on mtDNA was similar to the findings of Anderson et al. (2012), while the AFLP results were more closely aligned with the allozyme-based results of Blandon et al. (2001). The authors concluded that strong genetic separation between these regions was coupled with a high degree of gene flow along the SEUS coastal areas. Interestingly, the haplotype network based on the mtDNA dataset, which consisted of  $\approx 30\%$  unique haplotypes, indicated a lack of complete separation between the SEUS and GOM. Samples from South Carolina were related, although not consistently,

to fish from some GOM locations, and perhaps could be indicative of shared adaptive traits.

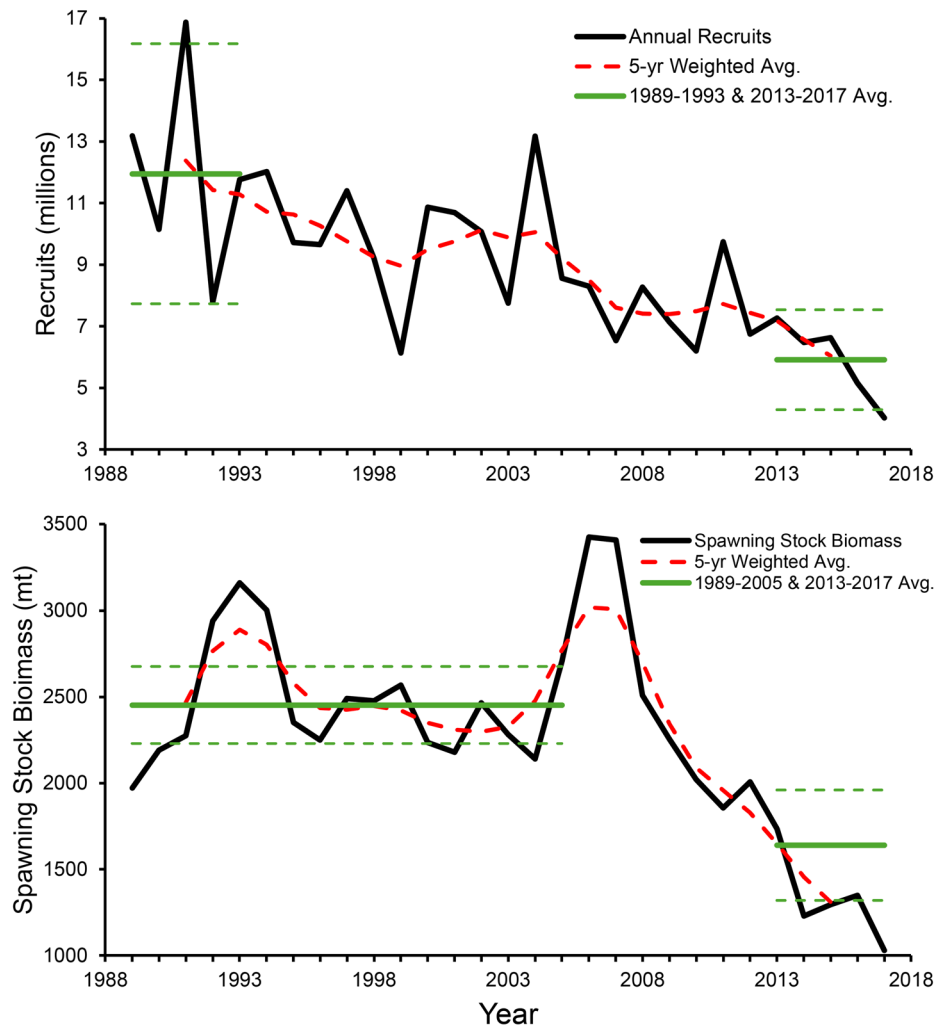
Several other studies investigating population structure of southern flounder have provided additional evidence of clear divergence between oceanic basins with more limited structure within basins, similar to the genetic analyses. Midway et al. (2014) examined otolith shape for age-1 females and detected strong evidence for differences between basins, but only minor within-basin structure that suggested extensive mixing within each basin. Wang et al. (2018) used otolith chemical signatures to examine population structure of southern flounder in the SEUS. Regional patterns were apparent in both stable isotopes and trace element composition with combined geochemical signatures differing among states; however, cross-validation classification suggested that southern flounder in the SEUS may be functioning as a meta-population, which is generally consistent with the previous genetic studies. Importantly, the otolith chemistry results pointed to the potential for mixing to occur during the adult life stages, based on post-spawning movements (Wang et al. 2018). In the northern GOM, Chrisp et al. (2023) documented both migratory and freshwater residency patterns that may contribute to the challenges in elucidating gene flow patterns at regional and local spatial scales.

In summary, genetic evidence supports two distinct stocks of southern flounder occupying the SEUS and GOM, with none of the markers evaluated providing evidence for an isolation by distance pattern within each basin. Questions remain about gene flow patterns within each region at smaller spatial scales. To address such questions with a more powerful genetic tool, researchers with the South Carolina Department of Natural Resources recently completed the development of a robust microsatellite marker panel. These emerging techniques are being combined with a collaborative annual sampling design among state agencies along the SEUS coast that includes sampling of adults during fall migration as well as YOY the following summer to obtain a clearer picture of gene flow across a broad spatial scale.

### ***Population dynamics – long-term trends and drivers***

#### ***Recruitment***

Long-term declines in recruitment of southern flounder have been occurring in both the GOM and SEUS, at both localized (Curran et al. 2021) and/or regional (Froeschke et al. 2011; Flowers et al. 2019; Erickson



**Figure 5.** Predicted annual recruits (top panel) and spawning stock biomass (bottom panel) from Flowers et al. (2019), a regional assessment of southern flounder along the U.S. South Atlantic coast. Shown is model predicted annual recruits and spawning stock biomass (heavy black line), 5-yr weighted average annual recruits and spawning stock biomass (dashed red line), and period average annual recruits and spawning stock biomass (horizontal green line) and 95% CI (dashed green line).

et al. 2021) spatial scales (Figure 5). Froeschke et al. (2011) first documented a long-term decline in recruitment in Texas based on fishery-independent surveys that estimated a rate of decline of 1.3% per year since 1979 ( $\approx 30\%$  decline overall). Similarly, Curran et al. (2021) documented a 6–7 fold decrease in abundance of juvenile southern flounder in a Georgia tidal creek between 2004–2007 and 2016–2019. Comprehensive evidence of a broad scale decline in recruitment along the SEUS coast was generated during the coastwide stock assessment (Flowers et al. 2019), which estimated a declining trend throughout the assessment time series, from an average of 11.95 million recruits per year during the earliest time period (1989–1993) to 5.91 million recruits per year during the terminal years (2013–2017).

Most recently, strong evidence for a range-wide decline in southern flounder recruitment was

generated through a comprehensive analysis of fishery-independent surveys conducted in multiple states (Erickson et al. 2021). The dataset included estimates of the relative abundance of juveniles across 31 estuaries located in four GOM states (Texas, Louisiana, Alabama, and Florida) and three SEUS states (Florida, South Carolina, and North Carolina), covering the period 1976–2018 (Erickson et al. 2021). Year was a significant predictor of annual recruitment in 23 estuaries (74%) and indicated a negative trend in juvenile abundance in 20 of 23 (87%) estuaries. The eight systems in which significant temporal trends were not detected tended to include much shorter time series. Only three estuaries suggested an increase in age-0 relative abundance, Upper Laguna Madre, Texas, Sabine Lake, Texas, and Charleston, South Carolina. The authors found that spatial proximity between estuaries did not increase the level of

synchrony in recruitment trends, suggesting that drivers of the declining trends were operating at a broad spatial scale. A plausible explanation for the observed widespread declines in recruitment was changes in climate that could influence advection of larvae into estuaries. The authors found that both wind speed and direction demonstrated an effect on recruitment of juvenile southern flounder in all estuaries with available wind data in their study (Erickson et al. 2021). Taylor et al. (2010) reported a similar effect of wind speed and direction on the recruitment of southern flounder into North Carolina estuaries. Therefore, in both the GOM and the SEUS, evidence exists to support the important role of wind speed and direction during the late winter and spring for the transport of southern flounder larvae into coastal bays and rivers. Similar to patterns observed by Taylor et al. (2010) in North Carolina systems, Erickson et al. (2021) found that range-wide declines in juvenile southern flounder recruitment could not be strongly tied to local environmental conditions within GOM estuaries; however, the impacts of local environmental conditions on cohort growth and mortality rates after settlement in estuarine habitats may modify eventual year-class strength (Taylor et al. 2010; Erickson et al. 2021). Important factors may include river discharge, estuarine warming rates, salinity, prey availability, and temperature effects on development and sex determination (Taylor et al. 2010; Erickson et al. 2021). Erickson et al. (2021) concluded that a multitude of factors, including elevated fishing mortality rates, warming water temperatures, and changing wind conditions are likely operating synergistically to affect productivity of southern flounder and contribute to the range-wide negative trends in recruitment.

### **Abundance trends**

**Gulf of Mexico.** Declines in adult southern flounder abundance in the GOM have been documented in both Texas (Froeschke et al. 2011; Froeschke and Froeschke 2016) and Louisiana (West et al. 2020; Smith et al. 2021). In Texas, the relative abundance of adult southern flounder decreased considerably in fishery-independent gill net surveys, with an estimated 57% decline in catch-per-unit-effort over 33 years (Froeschke et al. 2011). In Louisiana, recent stock assessments have estimated declines in both spawning stock biomass and total stock size (West et al. 2020; Smith et al. 2021). Froeschke et al. (2011) found that the magnitude of decline was more severe for adult southern flounder ( $\approx 2.5\%$  per year) compared with the juvenile life stage ( $\approx 1.3\%$  per year). Therefore, the authors concluded that

the declining adult abundance trends in Texas could not be fully explained by recruitment limitation; instead, the declines were likely attributed to increased rates of fishing and/or natural mortality on adult life stages. Froeschke and Froeschke (2016) used a boosted regression tree analysis to standardize the fishery-independent abundance index (1977–2012 time series) to account for the effects of several environmental variables and were able to confirm a steady decline in southern flounder adult abundance. They noted, however, higher relative abundance levels during the last two years of the time series (2011 and 2012), with catch rates in those years similar to observations from the early 1990s, potentially attributable to recent fishery management changes to reduce harvest. The moderate increases in abundance occurred along a north to south gradient, while the greatest declines during much of the time series occurred in the southernmost estuaries, a pattern suggesting disproportionate harvest removals of southern flounder among bay systems (Froeschke and Froeschke 2016).

**Southeastern U.S. Atlantic.** The most robust evaluation of southern flounder abundance throughout their SEUS distribution was generated as part of the regional stock assessment (Flowers et al. 2019), which estimated a region-wide decline in spawning stock biomass (SSB) beginning in 2008. During the period 1989–2007, southern flounder SSB was mostly stable with estimates ranging between approximately 2000 and 3500 metric tons, but began to decline steadily in 2008 to reach an average of 1,640 metric tons during the terminal five years (2013–2017) of the assessment (see Table 3.17 and Figure 3.63 in the assessment). The assessment concluded that fishing mortality ( $F$ ) exceeded the harvest threshold, SSB was below stock size threshold coastwide throughout the assessment time series (i.e., the stock was experiencing overfishing and was overfished), and elevated fishing mortality rates were leading to lower adult abundance throughout the SEUS. The prolonged period of overfishing caused a decline in the abundance-at-age over the time series, although truncation of southern flounder age structure is difficult to detect with the available surveys. Projections from the stock assessment predicted that total removals across the region needed to be reduced by 72% to end overfishing and rebuild the SSB to target levels within 10 years (Flowers et al. 2019). The high harvest rates in the SEUS estimated by the stock assessment model are supported by previous tagging studies in North Carolina (Smith et al. 2009; Scheffel et al. 2020), as well as earlier North Carolina state-specific stock assessments (Takade-Heumacher and

Batsavage 2009). For instance, Smith et al. (2009) estimated fishing mortality rates ( $F$ ) above 2 in both 2004 and 2005 for an estuarine gill net fishery (New River, NC). Similarly, Scheffel et al. (2020) used acoustic telemetry to estimate  $F$  as high as 1.6 in the same study system during 2014–2016. In addition, Scheffel et al. (2020) estimated the harvest rate for the entire state using conventional tag returns, with the state-wide  $F$  ranging from 0.36–0.72.

Given the high fishing mortality rates in the SEUS, Midway et al. (2018) evaluated how the complex spatial structure of southern flounder could contribute to stability in the population. They hypothesized two potential mechanisms to explain population persistence under heavy exploitation: 1) high levels of recruitment at low stock size (e.g., high steepness) or 2) considerable adult biomass remaining in offshore habitats that were much less susceptible to the fishery removal (i.e., cryptic biomass). In the simulation study, Midway et al. (2018) showed that both relatively high steepness in the stock-recruit relationship and large fractions of cryptic adult biomass were necessary to maintain even modest levels ( $\approx 25\%$ ) of unfished biomass at the high estuarine harvest rates reported in contemporary tagging studies (Smith et al. 2009; Scheffel et al. 2020) and state-specific assessments (Takade-Heumacher and Batsavage 2009). Flowers et al. (2019) estimated steepness for southern flounder within the assessment model as 0.73. Based on the harvest rate ( $F$ ) estimates from the stock assessment and the simulation by Midway et al. (2018), approximately 75% of the adult southern flounder biomass in the SEUS would have to remain cryptic to the fishery in order to maintain the SPR goals for sustainable harvest (see Figure 3 in Midway et al. 2018). Interestingly, these findings are also supported by recent telemetry studies that noted a lack of individuals returning to their natal estuaries post spawn (Hart 2018; Hollensead 2018; Steffen et al. 2023). If a large component of adult southern flounder biomass consistently occupies oceanic habitats and remains largely unavailable to the inshore fishery, this behavior would represent a mechanism of population resilience in the face of high exploitation.

## Fishery management

### History of the fishery

#### Commercial fishery

Commercial southern flounder fisheries vary greatly not only between the GOM and SEUS, but also state to

state. In the GOM, trawling was associated with approximately 80% of flounder landings prior to 1986, although it declined to approximately 29% of flounder landings across the GOM in 2010 (VanderKooy 2015). Giggling was the most popular gear type among GOM states in 2010 but varied greatly from state to state. In Louisiana, southern flounder landings associated with trawling comprised the majority of landings from 2000–2021 with fewer than 3% of commercial landings associated with giggling in any given year. In contrast, giggling accounted for 71–95% of commercial landings across three other GOM states (Texas, Mississippi, and Florida) in 2010 while trawling accounted for <5% of landings. In Alabama, 66% of 2010 flounder landings were from entanglement nets (e.g., gill nets, trammel nets), a gear that has been restricted in other GOM states since the mid-1990s. Despite the variety of methods that make up the commercial fishery in the Gulf of Mexico, the total harvest is relatively small. From 2000–2010, the entire Gulf of Mexico commercial southern flounder landings averaged only 6,530 kg per year.

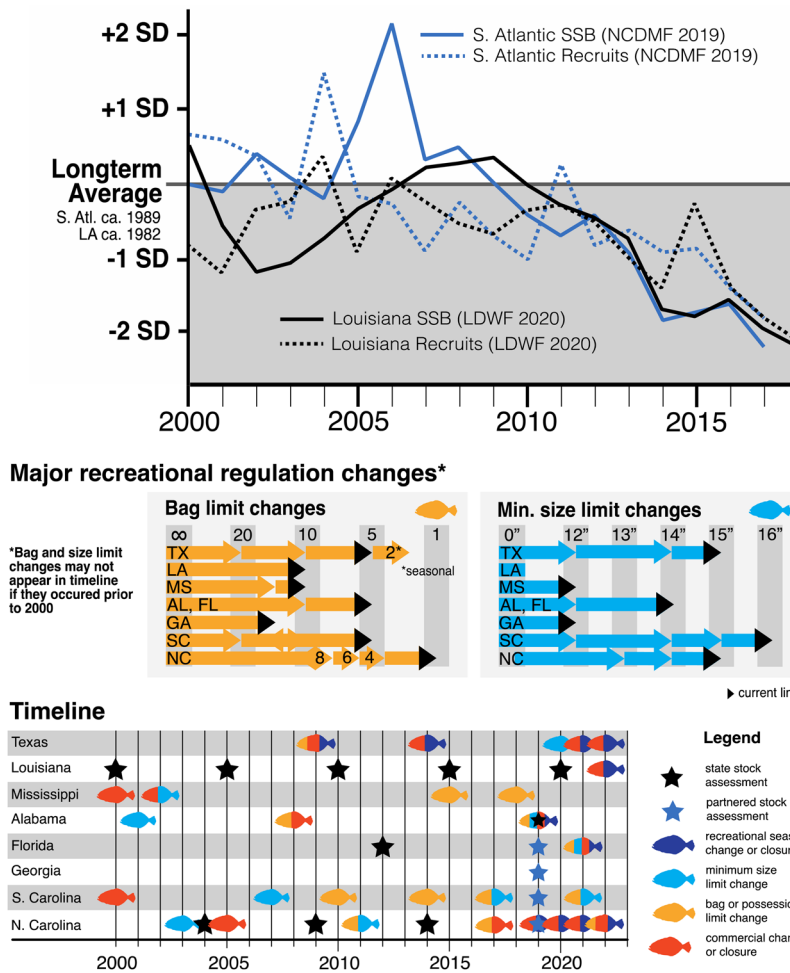
Among SEUS states, the bulk of commercial southern flounder landings come from North Carolina, with an average of over 800,000 kg per year between 2000–2021 which represents an annual average of over 94% of total SEUS landings during this time (Flowers et al. 2019). In the North Carolina commercial fishery, southern flounder are primarily landed by pound nets and gill nets; however, there has been growing percentage of fish landed by gig, accounting for as much as 14% of annual landings between 2016–2020. During the period 2000–2020, approximately 54% of North Carolina landings were by gill net, 37% by pound net, and 6% by gig (NCDMF 2022).

While commercial fishery gear usage and landings totals for southern flounder differ across states within both the GOM and SEUS, similar trends have emerged over the past two decades for both coasts, with declines in landings in nearly every state throughout their range (NOAA Fisheries Landings database). Declines can be partially attributed to more restrictive commercial southern flounder regulations in several states; however, declines are also apparent in years prior to regulatory adjustments and in states where commercial regulatory changes have not been passed. It is important to note that overall declining participation in commercial fishing may also significantly affect these trends.

#### Recreational fishery

The recreational fishery for southern flounder is popular throughout its range and commonly indicated as



**Population Dynamics of *P. lethostigma* ca. 2000**


**Figure 6.** Summary figure of major management and regulation changes for southern flounder since 2000.

one of the top three species targeted during coastal angling trips in both the GOM (Smith et al. 2022; TPWD, unpublished data) and SEUS (NCDMF 2022). Similar to commercial fisheries, declining trends in landings have occurred in state recreational fisheries throughout the range of the species. While a portion of these declines is attributable to recent changes in recreational harvest regulations among several states since 2019 (Figure 6), declining trends in harvest have occurred in nearly every state prior to regulatory adjustments (Smith et al. 2021; TPWD unpublished data; pers. comm. from the National Marine Fisheries Service, Fisheries Statistics Division, January 2023). Despite declining trends in landings, fisheries in South Carolina, for example, have seen an increase in total removals due to increased discards (and assumed discard mortality). Decreasing harvest with steady or increasing discards is thought to be attributable to a combination of factors, including shifting fisherman behavior to more of a catch-and-release fishery, an increase in regulatory discards due to regulation

changes, and increased overall fishing effort. Recreational landings and discards are imperfect data for southern flounder due to lack of reporting but represents an area where more information is needed.

In addition to traditional hook-and-line fishing, recreational gigging of southern flounder is also popular in both the GOM and SEUS. Because gigging traditionally occurs at night during hours that are not typically sampled with creel surveys, agencies have explored several alternative approaches to characterize this segment of the recreational fishery. Since 2010, NCDMF has conducted an annual mail survey to estimate harvest during nighttime gig angling and in 2017, estimates indicated that recreational gigging accounted for 11% of total recreational southern flounder harvest (NCDMF 2022). Beginning in the spring 2022, TPWD Coastal Fisheries Division has been engaged in a pilot program assessing the viability of a variety of approaches to estimate nighttime southern flounder harvest including gathering self-reported angler catch data through a smartphone application,

conducting nighttime creel surveys, and using traffic counters to gather activity data to test the viability of remote approaches. A nontraditional approach was conducted by Hall et al. (2022), where Texas guided gig fishing data was gathered from publicly archived photos on social media to reconstruct a time series of southern flounder landings. The study concluded that traditional daytime angler surveys in Texas may be missing approximately half of the total southern flounder harvest.

### **Current management**

To promote sustainability of the southern flounder stock and reverse the apparent region-wide decreases in abundance, state management agencies have implemented effort and harvest regulations to reduce exploitation rates. Some states have developed Fishery Management Plans for flounder whereas other states manage based on independent stock assessments or other data sources (i.e., trend analysis). Regardless of how management is derived, similar management measures have been implemented throughout the species range (Figure 6).

The timelines for implementation of southern flounder management strategies have varied by state and region. Reductions in daily bag limits, for instance, have been used by many states. Liberal bag limits from the late twentieth century, such as 20 fish per person per day in Texas and 15 fish per person per day in Mississippi, have been severely reduced in most cases. The daily recreational bag limit was reduced to 5 fish per angler in Texas in 2009 and reduced to 10 fish per angler in Mississippi by 2018. Beginning in 2022, North Carolina implemented a 1-fish bag limit for the recreational hook-and-line and gig fisheries. Recently, states such as South Carolina (2021), Florida (2021), and Alabama (2019) have reduced their daily bag limit by up to 50%. Such management measures are projected to reduce total removals (direct harvest + dead discards) by 47% in South Carolina. North Carolina recently developed amendments to their Fishery Management Plan to adopt management measures to reduce total removals of southern flounder by 72% beginning in 2020 and is investigating the possibility of managing flounder as individual species rather than as a component of a flatfish aggregate (three flounder species) for the recreational fishery.

Seasonal closures are another management measure employed by states across the southern flounder range. Louisiana closed the commercial flounder fishery from May 1996 to May 1997 due to low SPR estimates,

while North Carolina closed both recreational and commercial fisheries in 2019 for the first time based on results from the coast-wide stock assessment. Furthermore, several states have closed portions of the fishery during fall spawning migration periods. A stock assessment of southern flounder in Alabama coastal waters indicated population declines were likely due to low recruitment (Powers et al. 2018). In response, Alabama implemented seasonal closures in 2019, prohibiting commercial and recreational harvest during the month of November when spawning migrations typically occur in the coastal waters of the state. Similarly, Texas expanded seasonal closures for both commercial and recreational sectors in 2021 from November through mid-December. Florida and Louisiana also enacted recent (since 2021) regulatory changes that restrict harvest of southern flounder from mid-October through November. Many states have also adopted management measures that increase the minimum size limit for southern flounder. North Carolina increased the minimum size limit for flounder for the first time in 1988. More recently, Alabama increased the minimum size limit from 305 to 356 mm in 2019, while Florida, South Carolina and Texas all increased size limits in 2021 (305 mm to 356 mm, 381 mm to 406 mm, and 356 mm to 381 mm, respectively; Figure 5).

Commercial restrictions have also been employed as a management measure across states, although in different forms. Texas, Florida, Georgia, and Louisiana have implemented total gill net bans, while North Carolina, South Carolina, and Mississippi adopted commercial gear restrictions that include yardage reductions and soak time limits, as well as area closures. Annual catch quotas have been implemented in Mississippi since 2015 for the commercial fishery, while North Carolina implemented quotas in total removals for the commercial and recreational fisheries as recently as 2022 (Figure 5).

Current efforts to manage southern flounder on broader spatial scales are in their infancy, although progressing due to concerns about declining recruitment and abundance throughout the species range. The Gulf States Marine Fisheries Commission (GSMFC) published the Management Profile for the Gulf and Southern Flounder Fishery in the Gulf of Mexico (VanderKooy 2015) and has continued collaborative efforts between SEUS and GOM states with the “Floundering Around Symposium” held in 2022. In addition, the SEUS (North Carolina, South Carolina, Georgia, and Florida) partnered on the development of a coast-wide stock assessment and update (Lee et al. 2018; Flowers et al. 2019) to evaluate southern flounder

stock status and improve collaboration and data sharing across states (see Assessment Efforts, below). The collaboration successfully generated a coastwide stock assessment, but still does not bind individual states with implementing specific management measures. Currently, each state retains the ability to develop management measures independently in ways that fit the goals of their management programs. The SEUS collaborative group is planning on updating the coast-wide stock assessment in 2024 with data through 2022.

### Assessment efforts

The importance of southern flounder as a fisheries resource necessitates effective management to ensure the sustainability of the population for future generations. Fisheries managers typically use the results of stock assessments to guide their decisions in regulating fish stocks. In the SEUS, state-specific assessments have been conducted by both North Carolina and Florida (Takade-Heumacher and Batsavage 2009; Chagaris et al. 2012). For those assessments, the unit stock was limited to southern flounder occurring within the respective state waters. In 2014, another state-specific assessment was performed by the North Carolina Division of Marine Fisheries (NCDMF) and underwent a formal peer review by a panel of external, independent experts (L. Lee, NCDMF, pers. comm.). That stock assessment was not considered acceptable for management by either the peer review panel or NCDMF; the main limitation was the definition of the unit stock as there is clear evidence the southern flounder stock in the SEUS extends beyond North Carolina state waters (see Stock Structure in Population Dynamics section). Though the earlier North Carolina stock assessments were considered acceptable for management, it is important to note the NCDMF peer review process underwent a significant change and became more rigorous beginning in 2011.

Concern over the status of the stock prompted efforts to develop a SEUS coast-wide stock assessment that evaluated data collected in North Carolina, South Carolina, Georgia, and the east coast of Florida (Lee et al. 2018), which was promptly updated a year later (Flowers et al. 2019). The data and current southern flounder research were rigorously reviewed for consideration of inclusion into the assessment. Ultimately, the final stock assessment model incorporated landings and dead discards from three fishing fleets: commercial fishery, recreational fishery, and the commercial shrimp trawl fishery. Eight fisheries-independent surveys were also included and represented the four states in the region.

The selected data were input into a forward-projecting, statistical catch-at-age model implemented in the Age Structured Assessment Program (ASAP) software available from the NOAA Fisheries Integrated Toolbox (2014). The assessment model was used to estimate population parameters and reference points for the 1989 through 2017 time period, and results suggested declines in recruitment and female spawning stock biomass. Fishing mortality demonstrated a general increase since 2005. The predicted fisheries-independent indices of relative abundance were either flat or declining and showed no substantial evidence of strong year classes entering the population in the recent years of the time series. Overall, the results led to the conclusion that the stock was overfished and overfishing was occurring in the terminal year of the stock assessment, 2017.

Southern flounder stock assessments in the GOM have not attracted the attention that coast-wide assessment has in the SEUS; however, some GOM states are regularly conducting southern flounder stock assessments. Alabama performed a stock assessment in 2018 with results indicating a decline in overall abundance due to an extended period of low recruitment. In addition, the results showed the stock was not currently overfished, but experiencing overfishing which would result in an overfished condition in the future if management changes were not implemented (Powers et al. 2018). Louisiana has a long history of conducting southern flounder stock assessments, which they have done for over 20 years. The most recent (benchmark) assessment (West et al. 2020) uses a statistical catch-at-age model that includes female southern flounder from 1982–2018. The assessment notes an “alarming rapid downward trend in recruitment and spawning stock biomass” and since the time of the assessment, regulatory changes have taken place. To date, no coastwide assessment efforts have taken place in the GOM.

## Aquaculture and potential for stock enhancement

### History of flatfish mariculture

For several decades in Asian and European countries, flatfishes such as turbot (*Scophthalmus maximus*), sole (*Solea solea*), and the Japanese flounder have been commercially produced through aquaculture (Benetti et al. 2001). The Paralichthid species with the most potential for U.S. aquaculture development are the summer flounder (*P. dentatus*) and the southern flounder; most of the aquaculture research conducted on flounders in the last several decades has been

focused on these two species (Benetti et al. 2001). Collaborations between North and South Carolina fisheries managers led to the development of spawning and rearing protocols for southern flounder and these techniques have been incorporated into current efforts along the GOM coast in Texas and Alabama.

Southern flounder present multiple challenges for efficient production associated with the complex early life history of the species (e.g., slow growth, metamorphosis, pigmentation). The species also presents challenges in the application of Responsible Approach philosophies (Blankenship and Leber 1995; Lorenzen et al. 2010) that incorporates a broad understanding of the wild resource to best determine how a stocking program can contribute to conservation and management. Unintended masculinization of fish destined for stocking, caused by improper rearing conditions or early release, may dramatically alter the sex ratio of the local population and subsequently affect the fishery, especially considering that male flounder rarely reach sizes large enough to enter the fishery. A lack of knowledge of genotypic and phenotypic sex ratios in wild stocks is problematic for a stock enhancement program that should incorporate the understanding of how production and release of southern flounder for stock enhancement could alter wild population sex ratios. Genetic management of broodstock fish maintained in captivity is also critical; all current programs for stock enhancement (Texas, Alabama, South Carolina) are utilizing tags to identify broodstock fish and regularly rotate broodstock to increase genetic diversity of produced fish. The ability to differentiate between post-release hatchery and wild fish is necessary to measure success of a program, quantify the contribution of hatchery fish to the wild population, and adaptively manage conservation goals. As the three stock enhancement programs in the region continue to develop and advance, collaborative research will be a key component to efficiently address the numerous challenges associated with the development of successful enhancement efforts.

#### **State approaches to marine stock enhancement**

**Texas.** In 2006, the TPWD southern flounder stocking program was initiated in response to a long-term decline of southern flounder recruitment in Texas bays along with increasing water temperature coast-wide during the winter spawning season (November–February; Froeschke et al. 2011; Martinez-Andrade 2018). Annual flounder stock enhancement efforts have continued since 2009, with the primary goal of the program to develop techniques to produce flounder

on a large scale to supplement wild populations. Preliminary studies of hatchery propagation of southern flounder were developed in the SEUS (Daniels and Borski 1999; Jenkins and Smith 1999; Smith et al. 1999; Benetti et al. 2001), and transferring these rearing techniques required refinement of protocols for production of juveniles in Texas with fish from the GOM stock. Stock enhancement protocols in Texas are still being developed and refined but are based on larviculture methods developed by Daniels et al. (2010) and use Montalvo et al. (2012) sex determination temperature data to produce an expected 50:50 male-to-female ratio of hatchery-reared flounder. Since 2006, Texas has released just under 1 million post-metamorphic southern flounder fingerlings into Texas coastal waters.

**Alabama.** Southern flounder broodstock were initially acquired locally beginning in 2018 and held in temperature and photoperiod-controlled tanks at the Claude Peteet Mariculture Center. An estimated 12,200, 34,500, and 118,000 fingerlings were released to Alabama inshore waters in 2020, 2021, and 2022, respectively. In 2021, investigations began at CPMC attempting to identify and refine cryopreservation techniques for southern flounder milt to improve fertilization success and genetic diversity.

**South Carolina.** The SCDNR began the development of a South Carolina stock enhancement program for southern flounder in 2020 following a South Carolina Legislative mandate. To date, experiments continue on broodstock husbandry and spawning, live feeds production, and larviculture/juvenile production with an estimation of small-scale experimental releases to begin 2026. Tools necessary for genetic management of broodstock and evaluation of release contributions are also in development.

#### **Challenges and successes**

**Broodstock.** Due primarily to disease outbreaks, maintaining wild southern flounder in captivity over a long period of time is often difficult (Benetti et al. 2001). Flounder are susceptible to external parasites, most commonly *Argulus* sp., and secondary bacterial infections such as *Vibrio* spp. Maintaining high numbers of broodstock in recirculating aquaculture systems for spawning can allow disease outbreaks to flourish if water quality and fish health are not constantly monitored. As temperature increases in the maturation cycles used for spawning conditioning, so does the chance of disease outbreak leading to mass

mortality events. Therefore, a rigorous quarantine procedure is necessary for a successful program. In Texas, for example, flounder caught in the wild are visually inspected, and *Argulus* sp. are manually removed before exposing the fish to a three to five-minute freshwater bath. The fish are then maintained in a separate system for a minimum of one week and treated with antibiotics (if needed) to reduce secondary infections. Finally, before being moved into an established brood tank system, the fish are visually inspected again to remove any remaining *Argulus* sp., and exposed to another freshwater bath.

Weaning wild-caught southern flounder broodstock onto frozen, cut feed in a hatchery setting can also prove challenging. In Texas, newly acquired broodstock are offered live shrimp and then slowly weaned onto a diet of cut, dead feed that includes shrimp, squid, mackerel, and a prepared Mazuri™ gel diet for carnivorous fish. Flounder are ambush predators making the transition to dead and prepared feed difficult, and some fish die from not transitioning. There can also be a hierarchy in tanks where larger females outcompete smaller males for food. Feeding broodfish daily can help alleviate that competition, allowing more fish an opportunity to feed.

Volitional spawning of southern flounder is possible but impractical for large-scale hatchery production. Broodstock exposed to a 180-day photo/temperature maturation cycle mature naturally in the hatchery setting, with mature females showing signs of swelling in the abdomen as gonadal maturity increases that can be assessed using a light table (Daniels et al. 2010). In the hatchery, female southern flounder spawn over several days, releasing small batches of about 10,000 eggs/kg body weight (Daniels et al. 2010). Reliable and controlled production of a larger number of southern flounder eggs in a single batch is possible with hormone inducement to initiate oocyte maturation and spawning (Daniels et al. 2010). A synthetic analog of gonad-releasing hormone (GnRH $\alpha$ ) injected into the muscle between the dorsal fin and the lateral line (Daniels et al. 2010) results in spawning.

**Live feed culture.** Successful hatchery flounder production is directly tied to the intensive production of live natural feed for early grow-out stages, since larval southern flounder require small, live, but slow-moving food that provides an adequate nutritional composition (Daniels and Watanabe 2002). Rotifers (*Brachionus plicatilis*) are an excellent food source for the first prey offered to cultured larval southern

flounder because of their small size, high reproductive rates, and the ability to improve their nutritional value by adding supplements such as vitamins and fatty acids. Larval southern flounder are typically transitioned to live brine shrimp (*Artemia* spp.) as size increases.

**Larviculture.** Successful larviculture tanks vary in size, shape, and color but contain a 250- to 300-micron filter mesh over a standpipe surrounded by air stones to provide rising bubbles that will help keep the mesh clean (Daniels and Watanabe 2002). Full strength seawater (33 ppt) and temperatures between 17 to 21°C are maintained during the entire larviculture period (Daniels et al. 2010) and a photoperiod of 12-h light is recommended (Daniels and Watanabe 2002), although the growth of southern flounder larvae will increase with increasing photoperiods with no effects on larval survival (Daniels et al. 2010). After a 55-h incubation period at 17°C, flounder eggs hatch, and within 5 days they develop fins, mouths, and eyes (Daniels et al. 2010). The yolk sac is completely absorbed at 4–5 days post-hatch (dph), while the oil globule remains for several days (Daniels et al. 2010). Close monitoring of larval development is needed to ensure proper timing of first feeding with rotifers provided daily at around 20 rotifers/mL until approximately 15–20 dph, followed by transitioning to *Artemia* until metamorphosis is reached around 55 dph (Daniels et al. 2010).

Careful and precise temperature control is critical for survival and maintenance of sex ratios in hatchery-reared southern flounder (see *Environmental Sex Determination* section). Southern flounder and other Paralichthid individuals of XY genotype will develop as a phenotypic male regardless of the environmental conditions; however, based on exposure to environmental stressors, XX genetic females will differentiate into phenotypic males (XX males; Luckenbach et al. 2003; Mankiewicz et al. 2013; Honeycutt et al. 2019). Masculinized sex ratios occur when genetic females develop as males after being exposed to stressors such as cooler or warmer water temperatures (18°C and 28°C) or blue background color in tanks during critical early developmental stages (35 to 65 mm TL; Luckenbach et al. 2003; Montalvo et al. 2012; Mankiewicz et al. 2013).

Depending on the culture temperature, metamorphosis occurs as early as day 19 or as late as day 50 post-hatch. During metamorphosis, fish begin to settle on the bottom of the tank as the right eye

starts migrating to the left side of the head (Daniels and Watanabe 2002). Cannibalism has been documented as the fish begin to metamorphose if tank densities are high. Following completion of metamorphosis, fish have been successfully grown out both intensively (raceways) or extensively (outdoor rearing ponds) following weaning to dry feeds.

## Synthesis

The study of the population ecology of flatfishes has long generated broad interest due to their cosmopolitan distribution, important role in global fisheries, and unique biology. For southern flounder in particular, the last two decades have witnessed an abundance of new biological and ecological information—much of which has been driven by specific needs for fishery management and conservation. Aspects of the biology and life history of southern flounder are best understood for the estuarine life stages; in fact, most states in the SEUS and GOM have long-term monitoring programs that generate annual information on the demographics of inshore populations. In addition to monitoring trends in abundance and distribution, several targeted sampling efforts have resulted in relatively fine-scale estimates of age, growth, and reproductive biology, which have highlighted the considerable spatial variability that underlies southern flounder life history. The patterns and timing of estuarine settlement and movement have received considerable attention across the species range, promoting improved understanding of essential habitats.

The extensive long-term monitoring that has been conducted, coupled with focused life history studies, has facilitated efforts to further understanding of southern flounder population dynamics and complete additional stock assessments, including a recent multi-state assessment at a broad spatial scale that would have been unthinkable as recently as 20 years ago.

Multiple lines of evidence have supported two distinct basin stocks, one in the GOM and one in the SEUS, which has led to high confidence about the large-scale population genetic structure of the species. Differentiation within the basins has proven to be less clear, requiring new genetic tools and a well-designed sampling program to evaluate these small-scale patterns. Basin-wide similarity and estuarine-scale variability have set the stage for understanding of a fish that is also undergoing heavy commercial and recreational harvest in many locations.

## Knowledge gaps

Several outstanding knowledge gaps will shape emerging research foci for southern flounder in the next decade. A lack of understanding of the key factors contributing to recruitment variability, while shared broadly with many fishery species, is particularly acute for southern flounder. The species has experienced range-wide declines in recruitment during the past two decades, most clearly visible in multiple fishery-independent surveys across states that have varying rates of fishery removals (Froeschke et al. 2011; Lee et al. 2018; Erickson et al. 2021). The strong spatial synchrony of the decreasing trend in recruitment suggests that factors operating at regional scales are likely most critical and presents an urgent research challenge. The dependence of southern flounder sex determination on environmental stressors experienced during the juvenile post-settlement period (late spring to early summer) has already been linked to the broader potential impacts of warming coastal ecosystems. Elevated estuarine water temperatures are hypothesized to cause an increase in the proportion of males (Honeycutt et al. 2019), which given the species sexual dimorphism, contribute disproportionately little to inshore fisheries yield. Strongly male-skewed sex ratios would also be expected to reduce overall egg production within the population, limiting the supply of new recruits each year. Building on the potential effects of warming coastal water temperatures, Erickson et al. (2021) observed shorter windows for post-settlement development, based on the transition from winter to spring water temperatures, in several estuarine systems. In addition to impacting sex determination, the early onset of higher water temperatures could impact juvenile metabolism, growth, and survival rates. Lastly, the impacts of higher ocean temperatures during the winter spawning period are unknown. The aquaculture research community has demonstrated successful spawning of southern flounder under natural conditions (Watanabe et al. 2006); however, study of the factors influencing egg production and larval success has largely centered on photoperiod and salinity (e.g., Daniels et al. 1996; Moustakas et al. 2004), while controlling water temperatures within a range (14–18 °C) hypothesized to mimic ambient ocean temperatures during the Dec–Mar spawning period. It is plausible that warmer winter temperatures in presumed mid- and outer shelf regions used for spawning by southern flounder could negatively affect the stimulus for courtship behavior, fertilization rates, hatching success, and/or the growth and survival of early larvae. More focused study of

the effects of warming conditions in estuarine and coastal ocean habitats would inform hypotheses about the contribution of environmental drivers to the recent patterns of poor recruitment in southern flounder.

The dynamics of southern flounder estuarine settlement and their eventual contribution to the adult stock presents another emergent area of research. Throughout their range, the settlement of late-stage ( $\approx 30$ – $60$  days of age) southern flounder larvae has been documented to be concentrated in low salinity habitats (e.g., Wenner et al. 1990; Burke et al. 1991). Whereas down estuary movements into mesohaline habitats during the juvenile life stage have long been a presumed feature of the life history, the potential for contingents of southern flounder that remain in low salinity habitats was noted in several systems (Farmer et al. 2013; Nims and Walther 2014). Recent findings in a GOM estuary confirmed the existence of ‘freshwater residents’, found little evidence for first-year movements from settlement habitats, and estimated only a small contribution to commercial and recreational fishery landings from low salinity contingents (Chrisp et al. 2023). A study to examine sources of growth variability among post-settlement southern flounder in a North Carolina estuary observed earlier shifts to a piscivorous diet and enriched nitrogen stable isotopic signatures for fish in mesohaline compared to oligohaline habitats, and pointed to the potential for growth-mortality tradeoffs among settlement locations (Gardner et al. 2023). Further study of southern flounder settlement dynamics would inform factors impacting both recruitment variability and sex ratios, and the eventual contribution of recruits to fishery production.

The location of offshore spawning aggregations and the pathways of adult return movements to inshore habitats also remain long standing questions for southern flounder. While the data are both temporally and spatially sparse, several ichthyoplankton surveys that have reported collections of southern flounder larvae collectively point to waters over the outer portion of the continental shelf for likely spawning areas (Smith et al. 1975; Powles and Stender 1978; Powell and Robbins 1994; Walsh 2007; Hernandez et al. 2011). Further, the lack of adult southern flounder observed during inner shelf winter diving surveys (Watterson and Alexander 2004; Tucker 2011) provides additional evidence for outer shelf aggregation areas. In contrast, recent telemetry studies indicate significant numbers of non-migrating adult southern flounder remain in the lower estuary during the spawning season (Hart 2018; Steffen et al. 2023), highlighting the potential for unique

migratory contingents (i.e., partial migration) within southern flounder populations. Whether non-migrating adults spawn in the estuary or exhibit skip spawning behavior remains unresolved. A growing body of literature supports the existence of distinct populations of southern flounder for the GOM and SEUS, but has yet to show consensus regarding within-basin population structure (Anderson and Karel 2012; Anderson et al. 2012; Midway et al. 2014; Wang et al. 2015). While stock mixing for most marine species is hypothesized to occur during the early life stages that often include considerable dispersal distances, otolith chemical analyses for southern flounder suggest that post-spawning movements of adults may contribute to connectivity within oceanic basins (Wang et al. 2018). Outstanding questions remain about spawning locations, fecundity, the level of mixing among adults originating from different estuaries during ocean spawning, and the scale of post-spawning movements, including the degree to which adults return to estuarine systems compared with remaining in nearshore oceanic habitats. Coordinated tagging efforts (both traditional and electronic) across estuaries and basins, and the application of smaller archival tags (e.g., Collins 2023) should be prioritized to fill knowledge gaps about the oceanic portion of southern flounder history.

The multi-state stock assessment conducted for southern flounder along the SEUS coast applied a statistical catch-at-age model to generate estimates of stock biomass and harvest rates, with an assumption of spatially invariant life history traits within the basin. Despite this assumption, a range-wide exploration of southern flounder growth rates demonstrated the potential for considerable differences among estuarine systems (Midway et al. 2015). Similarly, recent studies which estimated southern flounder maturity schedules indicate the potential for a latitudinal gradient in the timing of maturity within the life history (Midway and Scharf 2012; Corey et al. 2017). Variability among estuarine systems in the conditions supporting southern flounder growth are likely responsible for most of the observed spatial patterning of life history traits, but differences could also have a genetic basis. In either case, growth and maturity schedules are key determinants of stock productivity and impact the ability to withstand varying degrees of harvest pressure. The incorporation of spatially-explicit life history parameters in future stock assessments will be dependent on highly resolved data to inform the existence of geographic gradients or clustering.

## Enhancement and collaborations

The range-wide patterns of low recruitment observed in the past two decades are most alarming, and importantly, seem to be independent of local environmental forcing variables and only partially explained by levels of fishing mortality. Although the mechanisms contributing to poor recruitment will need to be identified, low stock productivity may not be resolved through the application of traditional fishery management tools. For instance, if warming water temperatures due to climate change are masculinizing recruits—and possibly impacting egg production of larger females and larval growth/survival—there may be a need to either employ more conservative management actions to account for the lower productivity of the stock or take action to offset the lost productivity. The numerous stock enhancement programs for southern flounder may thus play an important role in supporting regional populations. Some of these stock enhancement programs are relatively new and still developing best practices, but the ability to supplement natural populations could be a valuable contribution to achieve sustainable fisheries for southern flounder in the future. Stock enhancement programs can serve to facilitate research in some of the emerging areas, such as recruitment failure, and may also offer potential to address future southern flounder questions that have not yet been identified. Managing a population within its natural system for a sustainable outcome is almost always the objective in resource management; however, the reality of climate change means that scientists and managers should be supportive of every potential tool available to maintain the viability of southern flounder.

## Conclusion

Southern flounder management finds itself in a tenuous position with considerations for management stretching beyond state waters, but without the resources enjoyed by federally managed species. Along with an open mindedness surrounding fishery management tools and approaches, is a continued need for collaborative efforts. Many key ecological processes for southern flounder occur during estuarine residency, but because of adult movement and potential genetic exchange within basins, states and agencies will need to work together to consider the most ecologically holistic approaches for management. The SEUS coastwide assessment was an early example of the type of management collaboration that may need to continue. In March 2022 a workshop including of 100 scientists and managers took place

(many of which had been part of the SEUS coastwide assessment), in which scientific findings and management experiences were freely shared among the southern flounder community in an effort to raise awareness of threats and mobilize ideas. For the near future, southern flounder will need to rely on synergistic research activities of the flounder community. The viability of southern flounder populations is facing major threats, and will benefit from broadly interdisciplinary groups taking a collective approach to identify and implement management and conservation solutions.

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