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Estuarine-coastal connectivity and partial migration of southern flounder in the Gulf of Mexico

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ABSTRACT

Southern flounder *(Paralichthys lethostigma)* from an estuarine complex in the Gulf of Mexico were tagged with acoustic transmitters (n = 60) from 2016 to 2018 to assess estuarine-coastal connectivity during fall/winter spawning runs. Both egress and residency behaviors were observed for adult southern flounder caught in the Galveston Bay Complex (GBC), and individuals were classified as migrators or residents based on their maximum distance detected (MDD). Migrators (MDD >5 km; mean 13.8 km) displayed directed egress out of the GBC, with individuals moving through the tidal pass in November and December, peaking in mid to late December. In contrast, residents (MDD <5 km; mean 0.6 km) showed limited movements and were often detected in the same general area throughout the fall, winter, and spring, indicating overwintering in the GBC. Conventional tagging was also performed on over 1300 southern flounder and mean MDD for all recaptured fish was 5.7 km. Mean monthly MDD of conventionally tagged fish was also highest in December and linked to egress from the GBC. Although directed migrations into the Gulf were observed for southern flounder with both tagging approaches, a meaningful fraction of the population displayed sedentary tendencies with MDD less than 1–2 km and retention within the GBC. The coexistence of two migratory contingents with contrasting estuarine-coastal migration behaviors is symbolic of partial migration by southern flounder, which may influence the resilience and stability of the population. Given that the timing and magnitude of peak egress out of this estuarine complex did not align with management regulations intended to protect spawning adults (i.e., peak movement after reopening of fishery), our findings also indicate the need to extend future closures to protect migrators during the primary egress period.

1. Introduction

Estuaries support a variety of juvenile and adult fishes, and the population dynamics of many species are linked to seasonal and ontogenetic transitions from estuarine to coastal ecosystems (Able, 2005; Dahlgren et al., 2006; Gillanders, 2002). Although certain taxa complete their life cycles in estuaries, many species move regularly between estuarine and coastal waters, particularly as adults (Rooker et al., 2010; Secor, 2015; Goertler et al., 2021). Egress events from estuarine to coastal habitats are often associated with spawning migrations, while marine species returning to natal estuaries (homing) is another common form of estuarine-coastal connectivity (Rooker and Secor, 2005). The degree and timing of exchanges between these ecosystems are increasingly recognized as essential information to resource managers because fishing mortality varies spatially and may be elevated along common pathways used during migrations (Stephenson, 2002).

Southern flounder (*Paralichthys lethostigma*) are a key species of the inshore recreational fishery throughout the Gulf of Mexico (hereafter Gulf) and play important ecological roles in marine ecosystems through top-down regulation of estuarine communities (Matlock, 1991; Smith et al., 1999). Estuarine environments are critical habitats for southern flounder and serve as both early life and adult habitats, with adults only leaving estuaries to spawn (Hoese and Moore, 1998). During annual spawning migrations in the fall and early winter, adult southern

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flounder move into tidal passes before entering coastal waters of the Gulf, and similar types of spawning migrations to coastal waters have been reported for other flatfishes (Hunter et al., 2003; Loher and Seitz, 2006). Peak larval recruitment of southern flounder occurs in the winter or early spring when larvae are transported back into bay and estuaries, which serve as nurseries for early post-settlers and juveniles (Glass et al., 2008). Since the production and recruitment success of southern flounder appears dependent on the success of spawning migrations into the Gulf, determining the timing and magnitude of egress events is needed, particularly during the late fall and winter exodus when recreational and commercial fishing pressure is high (Froeschke et al., 2011; Smith et al., 2021).

Similar to other estuarine-dependent species that leave estuaries as adults to spawn (Adams and Tremain, 2000; Bacheler et al., 2009), migrations appear to be heavily influenced and often triggered by cold weather events (Childs et al., 2008). In the Gulf and western Atlantic Ocean (e.g., Mid Atlantic Bight), previous research suggests that conspicuous drops in water temperature may be the primary determinant of egress by southern flounder and other flatfishes from estuaries (Craig et al., 2015). As a result, the variable timing of cold weather events may alter the efficacy of regulations designed to protect spawning adults from fishing pressure during spawning migrations because individuals may migrate during periods of increased fishing activity or during periods with relaxed bag limits. Therefore, a better understanding of the timing and primary pathways used by southern flounder and the environmental drivers that initiate migrations (i.e., temperature) are critically needed by resource managers because the species is experiencing long-term population declines throughout their range (Froeschke et al., 2011; Erickson et al., 2021). These data will aid in the development of conservation strategies used by resource managers (e.g., fishery closures) for rebuilding southern flounder populations.

The aim of this study was to determine egress and/or residency behaviors of southern flounder in a large estuary, Galveston Bay Complex (GBC), in the northern Gulf during fall and winter spawning migrations. Egress events from the GBC were characterized using acoustic telemetry and conventional tagging, and the combination of both tagging platforms allowed us to characterize the specific timing of egress events as well as migration pathways and distances traveled by southern flounder, with conventional tags also serving to extend the geographic range of our assessment beyond the GBC acoustic array. In addition, we examined the relationship between the timing of egress with changes in water temperature under the assumption that cold weather events (fronts) affected the timing and rate of egress by southern flounder.

2. Methods

2.1. Study site

This study was conducted in the Galveston Bay Complex (GBC) located along the upper Texas coast. The GBC is one of the largest estuaries (1420 km^2) in the United States and is comprised of several smaller bay systems. The GBC includes two tidal inlets or passes that connect to the Gulf (Galveston Ship Channel, San Luis Pass), and both tidal passes represent a movement corridor that links estuarine and coastal habitats used by southern flounder and other estuarine-dependent species (Dance and Rooker, 2015; Furey et al., 2013). Average seawater temperature (°C) in the GBC from May–March (2016–2018) was obtained from Hillhouse et al. (2022).

2.2. Acoustic telemetry and conventional tagging

An array of 42 acoustic receivers (Innovasea VR2W [n = 39], and

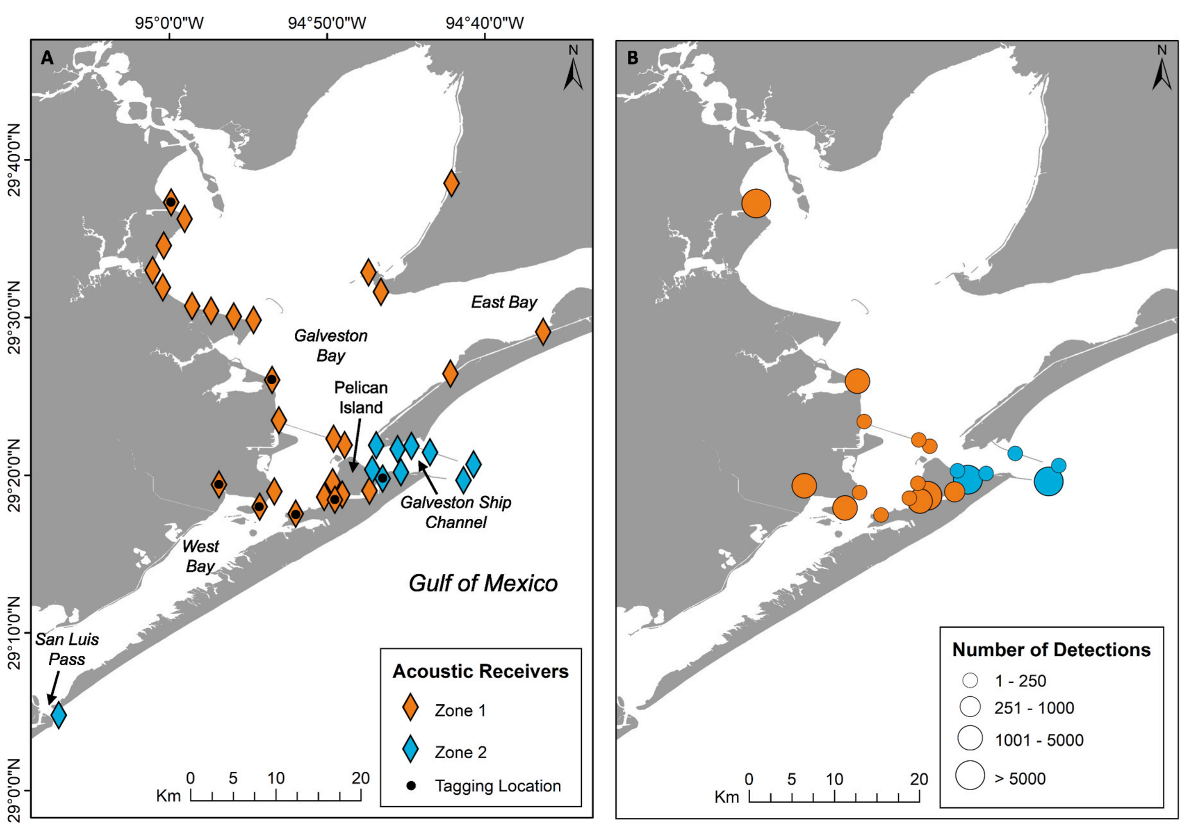

Fig. 1. A) Acoustic receiver array in the Galveston Bay Complex (GBC); filled circles within receiver symbols (diamonds) represents tagging locations of southern flounder. B) Detections of southern flounder across the receiver array denoted with bubble size related to the number of detections on each receiver. Zones 1 and 2 (shown by symbol color) represent areas in the GBC and Galveston Ship Channel (tidal pass), respectively. Entry into Zone 2 was used to denote egress from the GBC into the Gulf of Mexico. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

VR2AR [n = 3]) was deployed throughout the GBC with receivers strategically placed near shorelines and tidal passes (Fig. 1). Receivers were mounted on channel markers and wood pilings when available, or cable tied to polyvinyl chloride (PVC) pipe driven into sediment. Acoustic release receivers (VR2AR) were placed at depth at San Luis Pass and the Galveston Ship Channel. Receivers were downloaded twice each year, and the complete array was in place for the duration of the study.

Southern flounder were collected using hook-and line techniques from November 2016 to December 2017 (Table S1). Upon collection, fish were measured (total length [TL]), and then placed in a cooler with sea water in preparation for surgical implantation of Innovasea V9–1H acoustic transmitter (69 kHz, 151 dB). Individuals were first inverted and induced into a state of tonic immobility, which places the individual in a state of torpor (Henningsen, 1994). Immediately following, a sterile surgical scalpel was used to make a small incision into the peritoneal cavity and transmitters were then inserted gently inside the cavity, with one or two uninterrupted sterile stitches (Ethicon 4–0 vicryl) to close the incision (Dance et al., 2016). A conventional tag (FLOY extra small T-bar anchor) with printed contact information was anchored in the tissue near the caudal peduncle of each individual. Following the assessment of post-surgical health, individuals were carefully released back into the GBC where initially collected. All collections and tagging were performed in accordance with institutional (Texas A&M University) animal use protocols (IACUC, 2017–0178).

Acoustic tagging generally occurred in regions of the GBC that corresponded to areas of high receiver coverage within the array (Fig. 1). A total of 60 southern flounder were tagged with acoustic transmitters, and spawning females (>40 cm TL; Fitzhugh et al., 1996) were targeted to characterize egress activity because smaller, immature fish may not participate in spawning migrations into the Gulf (Midway and Scharf, 2012; Craig et al., 2015). Transmitters were programmed with a random delay rate of 160–260 s to obtain an estimated battery life of 450 days, allowing tracking of individuals for two egress cycles.

In order to better represent the movement of individuals not implanted with acoustic transmitters, all other southern flounder collected, regardless of size, were tagged using a conventional tag (FLOY extra small T-bar anchor) with identifying information and a phone number to report recaptured individuals. These tags were anchored in the tissue near the caudal peduncle and also released back into the GBC at the initial point of capture. Recaptured individuals were reported by recreational or commercial fishers and information regarding tag identification number, total length (cm), and location of recapture was recorded.

2.3. Data analysis

Maximum distance detected (MDD) was estimated as the direct "through water" (avoiding land) linear distance in kilometers from release point to receiver or from receiver to receiver for multiple detections. MDD was estimated for each tagged individual detected within the acoustic array using ArcMap 10.2 software and Geospatial Modelling Environment (GME) (Beyer, 2012). Similar to methods defined in a previous large-scale tracking study (Moulton et al., 2017), three classifications were developed in order to characterize the movement pattern of each individual southern flounder: 1) migrator, 2) resident and 3) unclassified. Southern flounder classified as migrators were individuals with MDD estimates of greater than 5 kms away from the release point and closer to or within the tidal pass leading to the Gulf of Mexico. Residents displayed MDD estimates of less than 5 km even though tracking durations (detections within the GBC array) for all individuals classified as residents was a minimum of 30 days between release date and the last detection. Remaining individuals were categorized as unclassified because these individuals displayed limited or no movement (0–5 km) and detections for each individual spanned less than 30 days. Two individuals were never detected and not assigned to any category. Rate of movement for individuals within the array was also calculated by dividing MDD by the time elapsed (Dance and Rooker, 2015; Moulton et al., 2017). To further distinguish the specific timing of egress (i.e., individuals moving through the Galveston Ship Channel and into the Gulf of Mexico), tag detections of migrators were classified as bay detections (Zone 1) or tidal pass detections (Zone 2) as a function of time during the primary egress period (Fig. 1).

Mann-Whitney U Test was used to investigate the effect of size class (40.0–49.9 cm vs. ≥ 50.0 cm TL) on tracking duration and MDD in GBC per individual southern flounder. We also used this test to determine whether tracking duration of individuals classified as residents and migrators was significantly different. Mean MDD by conventionally tagged fish was estimated by dividing days since release date and then assigned to month based on recapture date to characterize periods of increased or significant movement by individuals. The level of significance (α) used for all statistical testing was set at 0.05 and tests were run using the statistical software package RStudio.

3. Results

3.1. Acoustic telemetry

A total of 370,918 detections were recorded in the GBC array from November 2016 to July 2018 for the 60 southern flounder tagged with acoustic transmitters. Nearly half (n = 27) of the southern flounder were detected at least 1,000 times over the course of the study, with only 7 individuals detected less than 100 times in the array (Table S1). The majority of detections were located at or near receivers where individuals were released (Fig. 1). Average total tracking duration (±1 SD) across all individuals was 51 days ± 84 days, with a maximum of 355 days (Table S1). Mean maximum distance detected (MDD) of all detected individuals was 5.7 km ± 8.4 km, ranging from 0 km to 46.0 km. The influence of size on movement was investigated, and mean MDD was statistically similar between the smaller 40.0–49.9 cm TL (9.4 km) and larger ≥50 cm TL (9.0 km) size classes of southern flounder (Mann-Whitney, U = 100, p = 0.37). No tagged southern flounder leaving the GBC (egress) were detected returning (ingress) into this bay complex.

Southern flounder classified as migrators (MDD >5 km) with acoustic tags (n = 21) accounted for 14.1% of detections, and the average MDD for these fish was 13.8 ± 9.5 km (Fig. 2, Table S1). Individuals classified as residents (MDD <5 km; n = 11) were responsible for a large fraction (79.9%) of the total detections, and mean tracking duration was significantly higher for residents (192.5 ± 107.2 days) compared to migrators (28.4 ± 28.5 days) (Mann-Whitney, U = 8, p < 0.01). Of the 28 remaining southern flounder, 26 were assigned to the unclassified category due to movement less than 5 km over tracking durations of less than 30 days; these fish accounted for only 6% of the total detections.

The timing of movement from the bay (Zone 1) into the tidal pass (Zone 2) by southern flounder in the migrator category was concentrated in December, with the majority (n = 14) of southern flounder first detected in tidal pass from mid to late December (Figs. 2 and 3). In contrast, residents typically displayed little directional movement and were often detected in the same general area of the GBC, often moving short distances between adjacent receivers. Many individuals classified as residents were detected for protracted periods of time (>6 months) and remained in the GBC through the winter and spring (Fig. 3). Even though smaller individuals (40.0–49.9 cm TL) were detected for longer periods in the GBC than larger individuals (≥50.0 cm TL) (Mann-Whitney, U = 59.5, p = 0.01), some southern flounder in the larger size category remained in the GBC through the winter.

MDD per month was used as a separate indicator of egress by southern flounder, and distance between detections was used to estimate mean monthly MDD for southern flounder. No movements between two or more receivers (MDD = 0) were detected from spring to early fall (April–October). Mean MDD peaked in November (3.2 km) and December (7.6 km) (Fig. 4A). Limiting estimates to the migrator

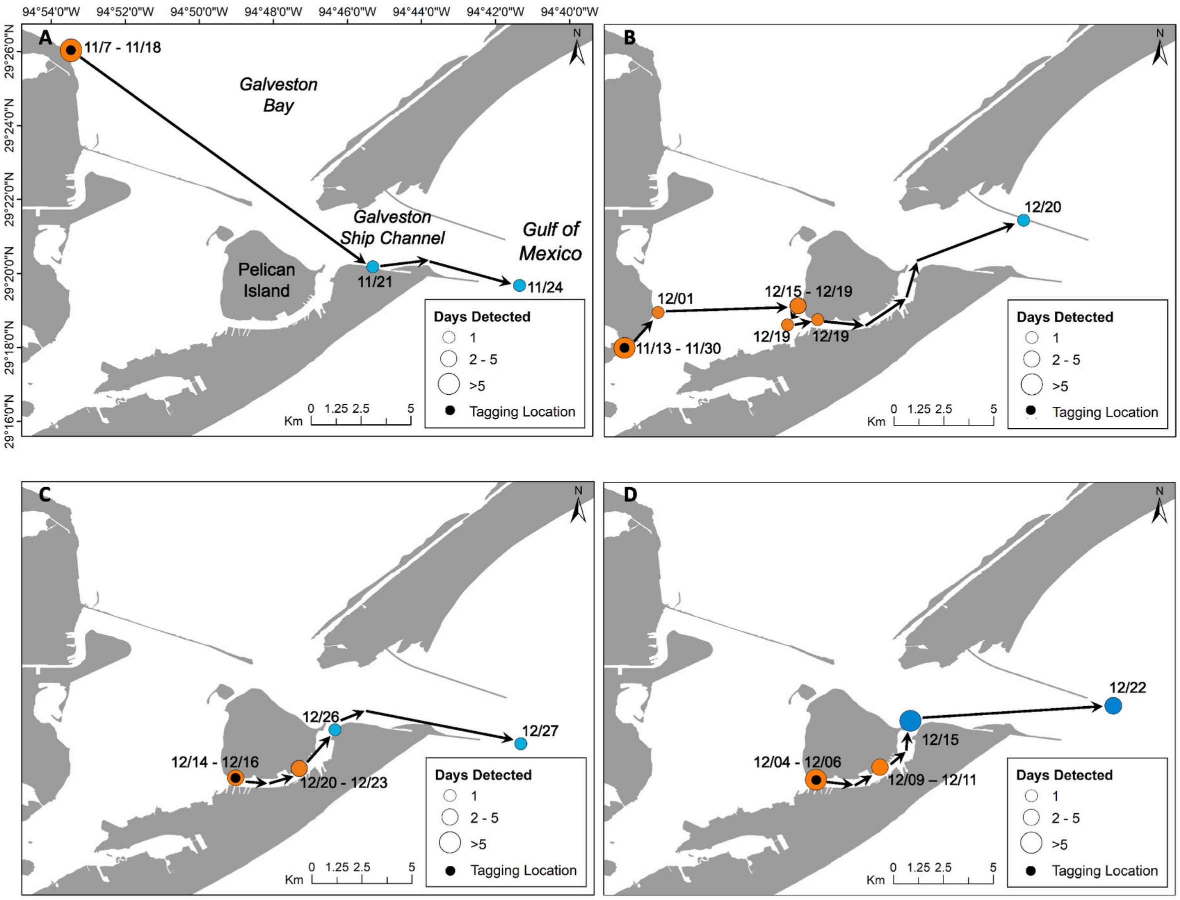

Fig. 2. Frequency plot of detections on acoustic receivers in Galveston Bay Complex over time for southern flounder classified as migrators: A) SF-21, B) SF-25, C) SF-44, and D) SF-54. Zones 1 and 2 (shown by symbol color; see Fig. 1) represent areas within Galveston Bay and Galveston Ship Channel (tidal pass), respectively. Dates (mm/dd) provided for detections and all tracks (A–D) shown were from 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

category resulted in mean MDD of southern flounder in November and December peaking at 5.1 km and 11.5 km, respectively. Mean MDDs for southern flounder after January were all less than 0.4 km even though several tagged individuals were consistently detected on receivers within the GBC into the spring. Mean daily rates of movement for individuals classified as migrators during egress—defined here as movement from receivers in GBC to a receiver at the end of the tidal pass to the Gulf of Mexico—ranged from 0.9 km/day to 5.6 km/day. The highest rate of movement observed for an individual southern flounder was 11.0 km/day on December 20, which coincided with peak rates of movement for other individuals from approximately December 17–27 (Fig. S1).

3.2. Conventional tagging

Conventional tagging was conducted on over 1,350 southern flounder in 2017 (n = 843) and 2018 (n = 510), and recapture rates of tagged individuals were similar between the two years (12.0% and 13.5%). Mean MDD for all recaptured southern flounder was 5.7 km, with one individual moving 221 km before being recaptured in a bay system to the south (Espiritu Santo Bay) in December approximately three weeks after being released in the GBC (November). Movement displayed by southern flounder with conventional tags occurred from September to February, with mean monthly MDD peaking in December (13.2 km) (Fig. 4B). From May to August, all recaptured individuals were within 1 km of the initial tagging location.

4. Discussion

Migration activity of southern flounder in the GBC was variable, ranging from resident behaviors with limited movements to directed migrations into the Gulf. The presence of different migratory contingents has been previously reported for a wide range of estuarine-dependent fishes (Jones and Wells, 1998; Kraus and Secor, 2004; Secor and Kerr, 2009; Secor et al., 2020). In accord with our findings, Craig et al. (2015) observed both resident and migratory southern flounder from estuaries in North Carolina. Similarly, other flatfishes including winter flounder (*Pseudopleuronectes americanus*) are known to migrate out of estuaries and into coastal waters during spawning runs, while some individuals overwinter in inshore systems and display resident behaviors (Sagarese and Frisk, 2011). Our findings suggest that movement patterns of southern flounder appear to be conditional with two common tendencies, migratory and resident behaviors, present in the population. This is indicative of a partial migration strategy by southern flounder in this bay system, which is ostensibly the most common type of migration displayed by marine fishes (Chapman et al., 2012, Secor and Rooker, 2005).

Southern flounder classified as migrators displayed relatively rapid, large-scale movements during the late fall. Migrating southern flounder were generally detected within the GBC acoustic telemetry array for relatively short periods of time, often moving across multiple receivers in the bay and through the tidal passes in a few weeks. Rates of movement and MDD during egress from the estuary for southern flounder are in accord with previous studies on this species that reported daily rates of movement of approximately 1 km per day during fall with many

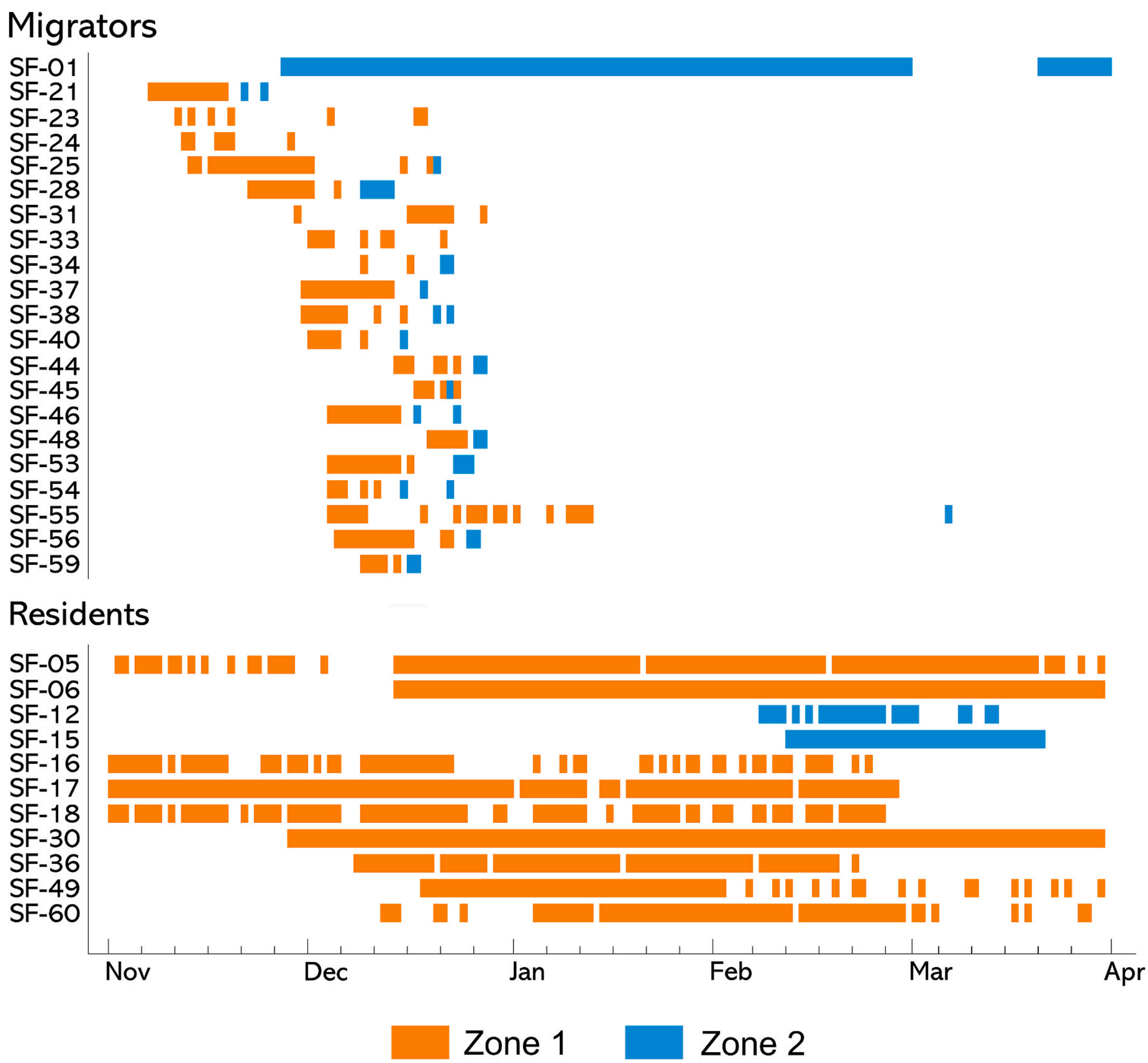

Fig. 3. Abacus plot of tag detections for southern flounder in the Galveston Bay Complex (GBC) prior to, during, and after the primary egress interval (November to December). Southern flounder classified as migrators (top) and residents (bottom) shown on plot. Zones 1 and 2 indicated with different colors and represent areas of detection within Galveston Bay and Galveston Ship Channel (tidal pass), respectively. Movement into Zone 2 was used to indicate the relative timing of egress out of the GBC and into the Gulf of Mexico. Detection data integrates two egress intervals (2016, 2017). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

individuals moving over 50 km from initial tagging locations (Craig et al., 2015). The smaller size class of southern flounder tagged in our study were detected for a greater number of days within the GBC than individuals in the larger size class, suggesting that ranging behaviors may be size or age dependent with smaller southern flounder more likely to stay (i.e., overwinter) in the GBC. Similarly, smaller, younger winter flounder in the Gulf of St. Lawrence remained in the estuary longer than larger, older individuals (Hanson and Courtenay, 1996). Migration patterns within a population that are size- or age-dependent represent a type of partial migration commonly referred to as differential migration (Secor, 2015), and examples of shifts in residency and ranging behaviors during ontogeny have been reported for a wide range of estuarine and oceanic taxa (Jones and Wells, 1998; Secor, 1999; Kerr et al., 2009; Rooker et al., 2021).

The timing and duration of egress events by southern flounder classified as migrators was well defined, and greatest distances traveled occurred in the late fall and early winter. Both the proportion of southern flounder displaying movements >5 km and the frequency of detections on receivers in the Galveston Ship Channel (entrance into Gulf of Mexico) peaked in December. During the spring and summer months individuals exhibited little to no movement, which is generally in agreement with other studies on this species. Craig et al. (2015) reported that many of the conventionally tagged southern flounder in a North Carolina estuary were recaptured less than 1 km from their release location during spring and summer, while large-scale movements occurred in the fall and winter. Conspicuous fall and winter egress events have also been reported for a variety of other estuarine and marine fishes, including several species of flatfish (Bailey and Picquelle, 2002; Capossela et al., 2013; Henderson, 2012). The timing of fall and/or winter egress events by estuarine-dependent fishes has been linked primarily to shifts in water temperature, with pronounced drops often serving as a cue to initiate migrations out of estuaries (Peters and Angelovic, 1971; Watanabe et al., 2001; Sackett et al., 2007). Froeschke et al. (2013) demonstrated that water temperature was the most influential environmental parameter influencing the occurrence of southern flounder in Texas, which supports our finding of increased egress activity during marked declines in water temperature in the GBC during the late fall and winter.

A large portion of the tagged southern flounder were classified as residents. Individuals in this category moved less than 5 km from the

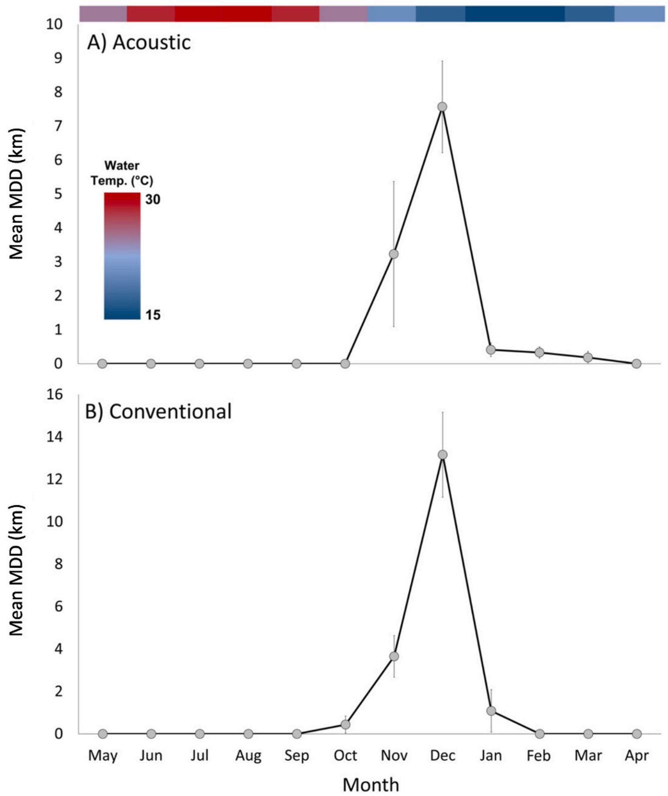

Fig. 4. Mean maximum distance detected (MDD) by southern flounder between A) acoustic receivers by all southern flounder tagged with acoustic transmitters (top panel), and B) mean distance between release and recapture location for individuals with conventional tags (bottom panel). Average seawater temperature (°C) from May–March from 2016 to 2018 in the Galveston Bay Complex is displayed by month and based on Hillhouse et al. (2022).

initial tagging location and were often detected on a single receiver or a group of adjacent receivers. These individuals displayed resident behaviors and were detected throughout the fall and winter months in the GBC, with many individuals detected for periods greater than six months and throughout the entire egress period. Deeper areas of bays and estuaries (dredged channels) are known to function as thermal refuges (Hanson and Courtenay, 1996) that are often utilized by fishes during colder periods (Blomqvist, 1986). Although the GBC is a relatively shallow system with an average depth of approximately 2 m, it also includes several channels and dredged areas that reach depths of up to 20 m deep that may maintain water temperatures above the thermal threshold of southern flounder or critical level that initiates egress into warmer, coastal waters. In support of this hypothesis, many southern flounder tagged and released near deeper channels (e.g., south of Pelican Island in or near Galveston Ship Channel) experienced less movement and higher residency, possibly due to elevated water temperatures in these deeper thermal refuges.

Both resident and migratory behaviors of southern flounder observed with acoustic transmitters were also evident with findings from conventionally tagged individuals. Reported recaptures from conventional tags indicated periods of high residency and limited movement during spring and summer months. Recapture locations were commonly in the vicinity of initial tagging locations, which is in accord with results from a similar study conducted in North Carolina estuaries (e.g., Craig et al., 2015). The proportion of conventionally tagged southern flounder classified as migrators increased considerably in fall and winter months, peaking in early December and coinciding with the timing of maximum movement observed for southern flounder with acoustic telemetry. One notable distinction between the two tagging platforms was that larger-scale movements were only detected with conventional tags, including the 230 km movement by one individual over a 23-d period. Although other acoustic arrays exist along the coast of Texas to potentially detect movements of southern flounder out of the GBC, it is not surprising that large-scale movements were observed with conventional tags because the sample size was over 20 times larger. The combined approach of acoustic and conventional tags provided important insights into the movement of southern flounder, with the latter approach and increased number of released fish offering valuable information on the capacity for large-scale movements by southern flounder.

Observed patterns of residency and egress have important implications for future management of southern flounder. Although state resource managers in Texas have closed the southern flounder fishery during the presumed migratory season (November 1 to December 15), the timing of egress and presence of overwintering by a fraction of the population in the GBC indicates that strategies currently in place may fail to meet their intended objective. Results from this study showed that significant egress occurred from early to late December, and therefore many individuals migrated during periods of increased fishing pressure (i.e., fishery open, bag limit = 5). Many of the southern flounder classified as migrators were actively moving through the GBC and into the primary tidal passes leading to the Gulf of Mexico in late December when the fishery closure was no longer in effect. Additionally, more limited movements or residency into deeper channels in the late fall and winter renders southern flounder susceptible to increased fishing pressure outside of the fishery closure. In fact, individuals that show limited movement often aggregated in specific areas (e.g., deep channels) for extended periods of time. These areas are commonly targeted by commercial and recreational fishers during fall spawning runs, leaving these individuals more vulnerable to fishing activity. Consequently, the timing of seasonal closures and shifts in bag limits may not adequately support rebuilding plans for southern flounder in Texas and other parts of their range.

The present study is the first to investigate the seasonal movements of southern flounder in Texas with acoustic telemetry, and the application of both acoustic and conventional tagging platforms significantly increases our current understanding of this species' migratory behaviors over earlier investigations (Stokes, 1977). Our study clearly demonstrates that a fraction of the adult population exhibits rapid and directed migrations into the Gulf of Mexico. The timing and range of southern flounder migrations sheds new light on the migratory behaviors of this species and extends the egress period into late December. While comprehensive receiver coverage throughout this entire large, estuarine complex was not possible, acoustic telemetry data demonstrates that a faction of the adult population overwinters in the GBC or associated channels and passes, suggesting the adult population of southern flounder displays partial migration with individuals displaying both resident and migratory behaviors. We also show that southern flounder have the capacity for large-scale movements into adjacent bay systems. Therefore, it is possible that the population(s) of southern flounder may rely on recruitment from other bay systems and inter-bay connectivity may be an important determinant of their population dynamics.

CRediT authorship contribution statement

Christopher Steffen: Writing – original draft, Methodology, Data curation. **Shane Stephens:** Writing – review & editing, Methodology, Investigation. **Michael A. Dance:** Writing – review & editing, Investigation, Conceptualization. **Daniel L. Lippi:** Writing – review & editing, Formal analysis, Data curation. **Christine C. Jensen:** Writing – review & editing, Funding acquisition. **R.J. David Wells:** Writing – review & editing, Funding acquisition, Conceptualization. **Jay R. Rooker:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jay Rooker reports financial support was provided by Texas Parks and Wildlife Department.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108545.

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