Patterns of intra-estuarine movement of adult weakfish (*Cynoscion regalis*): evidence of site affinity at seasonal and diel scales

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Abstract—Fine-scale movements of and use of habitat space by individual marine fishes can structure broader population dynamics, yet little is known about these traits. This lack of key information applies to the economically and ecologically important sciaenid weakfish (*Cynoscion regalis*), which is seasonally distributed in estuaries and coastal habitats along the Middle Atlantic Bight, where it feeds and spawns. We examined movements of adult weakfish in a southern New Jersey estuary using acoustic telemetry at both seasonal (n=29 fish) and diel (n=9 fish) scales. From June through November 2008, a majority of tagged and redetected weakfish (12 of 20; 60%) established areas of localized residency. Several fish made excursions of varying distances (1.0–5.9 km) from these regions before returning after 1–2 weeks. At the diel scale, most weakfish (7 of 9; 78%) resided as a local aggregation during the day and made nighttime excursions beginning around sundown (1930 hours). No fish were detected within 0.5 km of their area of localized daytime residency after 2230 hours. These findings are new evidence of the affinity of adult weakfish within specific localities across ecologically relevant timescales and offer further insight into the importance of estuaries in the life history of weakfish.

Population connectivity in fishes is directed by the movements and space-use patterns of individuals in populations. We must first understand these individual behaviors to fully understand the role of population connectivity and how it informs tools used to maintain sustainable fisheries (Mittelbach et al., 2014). Fine-scale movements and related patterns of site affinity and homing have been examined extensively in terrestrial (Bright and Morris, 1991; Costello, 2010) and avian (Hoppes, 1987) species, and improvements in our ability to track marine animals with greater resolution, in both time and space, have shed light on similar behaviors (March et al., 2010). Studies of fine-scale movements of fishes have elucidated their ability to home back to relatively small geographic areas (Mitamura et al., 2009), keep restricted home ranges (McGrath and Austin, 2009), and maintain site affinity at timescales that range from daily (Humston et al., 2005) to yearly (Ng et al., 2007). Effects of scale, although important for examining ecological processes, are neglected too frequently during evaluation of animal movements (Levin, 1992; Schick et al., 2008). Therefore, obtaining ap-

propriately scaled data on the movements of exploited marine fishes is an increasingly warranted goal (Pittman and McAlpine, 2003).

Estuarine movements of adult weakfish (*Cynoscion regalis*) are poorly understood despite their relative importance within the estuarine food web, their economic contribution to both recreational and commercial fisheries (Able and Fahay, 1998), and most recent coast-wide population decline (NEFSC[1]). Weakfish range from the Gulf of Maine during some years (Collette and Klein-MacPhee, 2002) to the southwest Atlantic coast where they maintain year-round residency. They are seasonal residents in the northern portion of their range within the Middle Atlantic Bight between New York and Virginia, where migrations move south and offshore in the fall and north and inshore in the spring (Shepherd and Grimes,
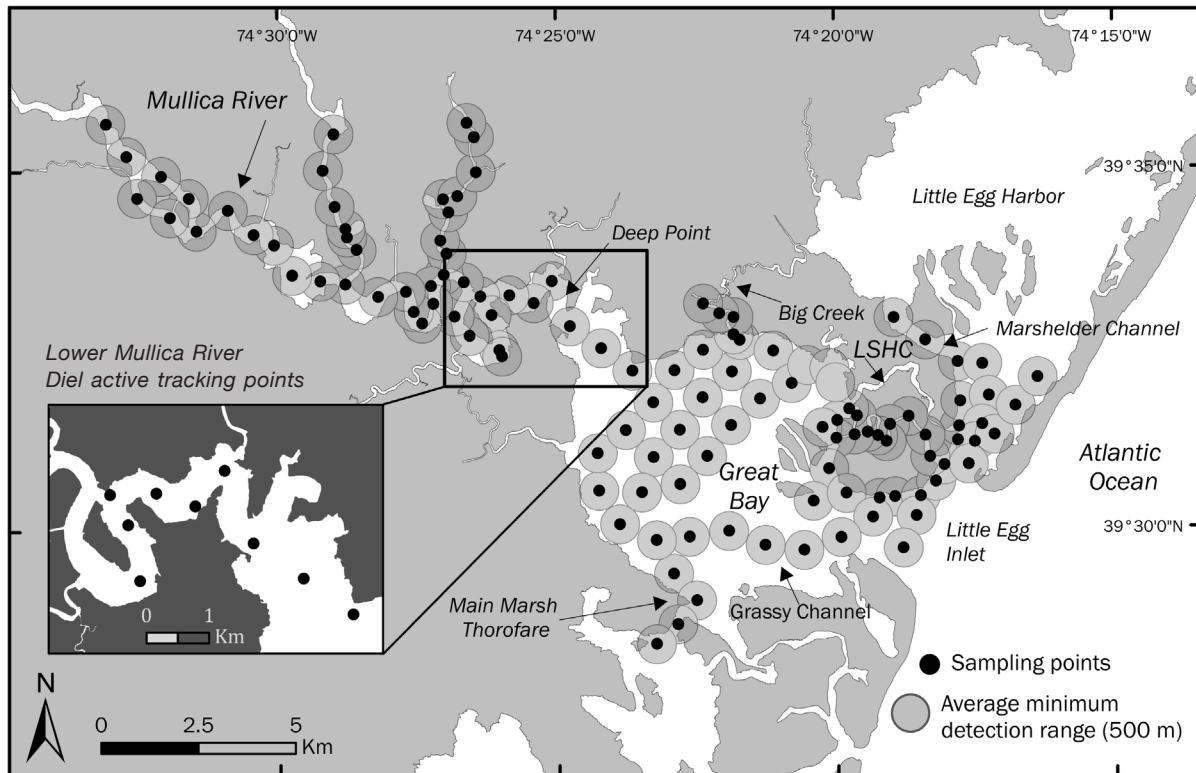
Figure 1

Study areas within the Mullica River–Great Bay estuary in southern New Jersey for the seasonal and diel scales in the study of weakfish (*Cynoscion regalis*) movement conducted in 2008. The locations of the sampling points (120) were monitored with active telemetry used to evaluate seasonal movements in 2008, including the area (shown in the inset square box) at Deep Point in the lower Mullica River surveyed for an the evaluation of diel movements. LSHC=Little Sheepshead Creek.

1984). Although weakfish occur in estuaries and inner-continental-shelf habitats, the relative importance of estuarine systems within these regions is mostly unknown (Able, 2005; Woodland et al., 2012). We do know that they establish seasonal residency in estuaries in the Middle Atlantic Bight (Turnure et al., in press; Manderson et al., 2014), where they both feed (Harfmart and Brandt, 1995) and reproduce (May–July; Connaughton and Taylor, 1994, 1995; Luczcovich et al., 1999; Able and Fahay, 2010). Previous egg and plankton sampling (Ferraro, 1980), reproductive histology (Lowerre-Barbieri et al., 1996; Nye et al., 2008), and gonadosomatic indices (Taylor and Villoso, 1994) have delineated weakfish as iteroparous nocturnal spawners, generally commencing reproductive behavior around the evening crepuscular period. In both field and laboratory passive acoustic studies, the drumming of the swim bladder of weakfish before spawning has been used to better define their location (Luczkovich et al., 1999) and the diel periodicity (Connaughton and Taylor, 1995) of their reproduction.

Because aspects of weakfish life history (e.g., reproduction and migration) occur at multiple temporal scales (i.e., seasonally and daily), it is prudent to evaluate weakfish estuarine movements within these time frames. Earlier investigations of weakfish movements within estuaries had been either too geographically coarse to resolve fine-scale patterns at biologically relevant timescales for individuals (Nesbit, 1954; Thorrold et al., 2001) or were limited to juveniles (Tyler and Targett, 2007). Previous research also has quantified homing to natal estuarine systems, suggesting that weakfish exhibit a high degree of spawning-site fidelity over broad regional areas (i.e., Chesapeake Bay and Delaware Bay; Thorrold et al., 2001), but the degree to which weakfish use small, shallow estuaries is relatively unknown, with the exception of a recent study (Manderson et al., 2014). A better understanding of weakfish movements and how extensively and intensively individuals use these estuarine habitats will clarify aspects of their complex life history and population dynamics (i.e., connectivity between estuaries and coastal habitats) and begin to delineate critical habitats for this species.

Our objectives were to characterize and quantify the fine-scale patterns of movement of individual adult weakfish at seasonal and diel temporal scales within a relatively undisturbed estuarine system (Mullica

River–Great Bay estuary, New Jersey). At the seasonal scale, active (i.e., mobile) telemetry was used to quantify estuary-wide, meter-scale movements of individually tagged animals on a weekly basis across the months from late spring to fall. At the diel scale, patterns of movement and distribution were examined on an hourly basis through the use of active telemetry during the summer months.

Materials and methods

Study areas

Seasonal movements were examined in the Mullica River–Great Bay estuary and adjacent Little Egg Harbor estuary, and diel movements were examined in a small region in the lower Mullica River known as Deep Point (Fig. 1). The Mullica River–Great Bay system is a relatively small, shallow (with depths mostly <2 m), drowned river valley dominated by salt marsh (Kennish, 2004). With the majority of its upstream portion flowing through the undeveloped Pinelands National Reserve, this watershed is considered one of the least anthropogenically disturbed estuaries in the northeastern United States (Good and Good, 1984; Kennish and O'Donnell, 2002). The adjacent Little Egg Harbor estuary is also relatively shallow, but it is characterized as a barrier island estuary with significantly fewer freshwater inputs than the Mullica River–Great Bay system (Kennish, 2001, 2004). Both estuaries are included within the NOAA Jacques Cousteau National Estuarine Research Reserve (Kennish, 2004).

Acoustic telemetry

Tagging procedure and general characteristics of tagged fish All adult weakfish (>230 mm in total length [TL], which is size at maturity based on Nye et al., 2008) examined in this study were captured by hook and line and subsequently tagged during 2008 (from 11 June to 11 September) by abdominal implantation of individually coded acoustic transmitters (CAFT and MS series[2], Lotek Wireless Inc., St. John's, Newfoundland; with a 5-s signal repeat rate) by the method of Turnure et al. (in press). After full recovery, fish were released within 100 m of their original site of capture (Table 1).

Seasonal patterns of movement were observed in 2008 for acoustically tagged fish (*n*=29; length range: 273–591 mm TL, mean: 401 mm [standard error (SE) 15) from 19 May to 4 December 2008. A subset of individuals (n=9; length range: 337–540 mm TL, mean: 456 mm TL [SE 22]) were monitored at the diel scale in the lower Mullica River at Deep Point (Fig. 1) from 30 June to 31 July 2008. Active tracking, as part of a con-

current study (Turnure et al., in press), began in May 2008 to detect weakfish (tagged in 2007) that were potentially immigrating to the estuary. However, no such immigrants were detected in 2008. All fish monitored in the study presented herein were tagged beginning in June 2008. The area used in the study of diel movements was chosen because multiple fish were tagged and released there, making it possible to examine their day–night movements as an aggregation. All fish used in these analyses were considered successfully tagged on the basis of subsequent redetections or movement from the study area (Turnure et al., in press). The battery duration of the deployed acoustic transmitters ranged from 229 to 719 days for both the seasonal and diel components of this study, allowing for monitoring of fish until final emigration from the study area in the fall (for further description of weakfish emigration, see Turnure et al., in press).

Active telemetry Active telemetry was used at both the seasonal and diel scales to examine patterns of movement in 2008. For active tracking from a small boat, a directional hydrophone (LHP_1, Lotek Wireless Inc., Newmarket, Ontario, Canada) was attached to a signal processor (SRX-400, Lotek Wireless Inc.). At each predetermined sampling location (Fig. 1), the hydrophone was lowered approximately 3 m underwater and turned in 90° increments for a full rotation. When transmitters were audibly detected, the boat was positioned to maintain close proximity (signal power >115 dB and gain <15) and fish location was recorded, with a GPS unit, together with the tag identification number, signal power (in decibels), and gain. Although variable because of ambient weather conditions, the active listening range of the hydrophone averaged approximately 500 m. For further discussion of the general active tracking procedure in this estuary, see Ng et al. (2007), Sackett et al. (2007), and Turnure et al. (in press).

Every week from 19 May to 4 December 2008 (except for the week of 17 November because of inclement weather), 120 predetermined locations (Fig. 1) that covered a majority of the navigable Mullica River–Great Bay system were sampled during daylight hours (0700–1900) as described previously. For most of the tracking events, both the bay and river locations were sampled on different days within the same week (for a detailed description of tracking protocol, see Turnure et al., in press).

Active tracking also occurred from 30 June to 31 July 2008 (9 tracking events), to identify diel patterns of movement in weakfish near Deep Point in the Mullica River. During each tracking event, the sampling locations in a subset of 9 predetermined points were visited on a rotating basis (Fig. 1). After detection and subsequent meter-scale localization of individuals at a tracking point, the subsequent locations were visited until work at all 9 points was completed. Then, the rotation was repeated, beginning at point 1 until the daily tracking event was over. The average tracking event lasted 5 h and 43 min. To determine the effect

Table 1

Tagging characteristics and patterns of intra-estuarine residency for individually tagged weakfish (*Cynoscion regalis*) within the Mullica River–Great Bay estuary in 2008 (20 of 29 fish successfully tagged). Areas of localized residency (ALR) were established by 12 of 29 individuals (ALR defined as 3 or more consecutive weekly detections within 500 m of each other). No data (–) indicates fish without sufficient redetections (<3) to analyze patterns of movement (1 of 29 total fish tagged) or that did not establish an ALR, on the basis of previously described criteria (8 of 29 total fish tagged). Potential relocation events are calculated as the number of weekly tracking events in which fish were resident in the study area. An asterisk (*) indicates established ALR is the same as original tagging location. LSHCW=western side of Little Sheepshead Creek; LSHCE=eastern side of Little Sheepshead Creek; SWGB=southwestern Great Bay (for locations, see Fig. 1); NEGB=northeastern Great Bay; MMT=Main Marsh Thorofare.

Fish ID	Length (mm TL)	Date tagged	Tagging location	Total number of detections	Area of localized residency	First detection within ALR	Last detection within ALR	Size of ARL (km²)	No. of detections in ALR	Proportion of potential detections within ALR (%)
38	298	Aug 22	LSHCW	1	–	–	–	–	–	–
50	305	Aug 15	LSHCW	5	*	Sep 18	Oct 15	0.019	5	56
62	406	Jul 1	Deep Point	7	–	–	–	–	–	–
64	337	Jul 10	Deep Point	8	*	July 17	Oct 16	0.123	6	35
70	406	Jul 10	Deep Point	3	–	–	–	–	–	–
74	356	Aug 17	Grassy Channel	3	–	–	–	–	–	–
75	279	Aug 15	LSHCW	6	*	Aug 22	Sep 23	0.004	5	56
102	591	Jul 1	Deep Point	11	SWGB	Aug 22	Oct 15	0.104	6	35
103	521	Jun 21	Deep Point	3	–	–	–	–	–	–
136	540	Jul 10	Deep Point	7	*	Jul 17	Aug 12	0.029	5	50
137	489	Jul 1	Deep Point	13	*	Jul 2	Jul 23	0.028	4	24
138	432	Aug 12	LSHCW	8	NEGB	Sep 3	Oct 8	0.009	4	40
139	470	Aug 15	Big Creek	10	*	Aug 27	Oct 15	0.007	5	50
140	432	Aug 17	Grassy Channel	4	MMT	Aug 27	Sep 18	0.034	4	80
142	445	Aug 27	LSHCE	4	*	Sep 12	Sep 23	0.001	3	75
151	502	Jun 21	Deep Point	7	*	Jul 2	Aug 5	0.036	6	46
155	432	Jun 12	Big Creek	4	*	Jun 17	Jul 16	0.003	4	67
162	438	Jun 19	Deep Point	7	–	–	–	–	–	–
163	406	Sep 11	Marshelder	4	–	–	–	–	–	–
204	457	Jun 25	Deep Point	1	–	–	–	–	–	–

of the crepuscular and nighttime periods on weakfish movements, tracking occurred during and after sundown (1930 hours, 5 tracking events).

Data analysis

Seasonal movements   The sampling unit (*n*) was defined as an individual tagged fish (Rogers and White, 2007) to avoid pseudoreplication. Redetections of individual weakfish during seasonal active tracking in 2008 were first plotted with geographic information systems (GIS) software (ArcMap 9.3, Esri, Redlands, CA). Quantifying the breadth of movements in animals has traditionally been accomplished by calculating home ranges, but the lack of consecutive detections in tagged weakfish during this study precluded formal home range analyses (Rogers and White, 2007). Kernel density estimators, another technique used for home range calculation in previous studies (e.g., McGrath and Austin, 2009), would have produced bias in estimates because of low

sample size (Seaman et al., 1999) and nonconsecutive detections. Variations of these analyses were conducted but proved inadequate. For example, movement rates could not be assessed on a daily scale (kilometers per day) because sampling occurred weekly and weekly rates of movement were largely uninformative at such a large timescale and were confounded by weeks during which fish were not redetected. Movements were analyzed in relation to environmental factors, such as salinity and temperatures, but these findings were also misleading because environmental conditions in an estuarine system are highly dynamic (changing with each tidal cycle).

To characterize seasonal weakfish movements, criteria based on the spatial and temporal extent of weekly redetections were established. If 3 consecutive detections of tagged weakfish were within 500 m of each other, the fish were characterized as having established an area of localized residency (ALR; see Table 1). Only fish with 3 or more weekly detections were used in analy-

sis of estuarine movement patterns, and all detections within an ALR before or after this 3-week period were included in analysis. Patterns of weakfish movement remained consistent even at lower temporal thresholds (i.e., 2 consecutive detections within 500 m), indicating the robustness of the ALR metric for these data.

Calculation of the size of an ALR was made with the minimum convex polygon metric whereby the inner points of detection were completely enclosed by a minimum number of outer detection points that form a convex polygon. Weekly movements were calculated as minimum straight-line distances (in kilometers) from an ALR. If the original release site fell within this area, the release location was used to calculate subsequent movement distances. Otherwise, a geometric centroid of detections within the ALR was used. The total area sampled during active tracking was determined by areal analysis of active tracking points and their ranges of detection (see Fig. 1), and by excluding areas where the detection ranges fell on land. ALR differs from home range, a strictly spatial descriptor of animal activity, in that ALR incorporates a temporal component (i.e., 3 consecutive weekly detections in our study) and an explicit spatial component (detections within 500 m of one another) to describe weakfish site affinity.

Diel movements   Redetections of individual weakfish during diel active tracking in 2008 were first plotted with ArcMap 9.3 GIS software. To characterize weakfish movements at the diel scale, we measured the minimum straight-line distance (in kilometers) across water of individual weakfish from an area of localized daytime residency (ALDR) at Deep Point in the Mullica River (Fig. 1). The location of the ALDR was determined by the previously defined seasonal ALR for individuals tagged in this region (see Table 1), with the exception of a single fish (ID 100) that did not establish an ALR. Distances of fish from their ALDR were binned into 2-h increments to observe diel movement patterns. Nighttime was defined as the period from 1 h before sundown to 1 h before sunrise (1930–0429 hours) to account for potential behavioral changes (e.g., reproduction) related to the dusk and dawn periods that have been identified previously in weakfish (Connaughton and Taylor, 1995). Daytime was defined as the period from 0430 to 1929 hours. We compared the average distance of individuals from their ALDR during daytime and nighttime detections using the nonparametric Mann-Whitney U-test (2-tailed, $\alpha=0.05$).

Results

Seasonal patterns of movement

Overall patterns of estuarine movements were variable among individual weakfish. A majority of redetected weakfish (12 of 20; 60%) established an ALR within the study area, and some redetected fish (6 of 20; 30%) with sufficient redetections for analysis did not dis-

play this localized pattern (Table 1). Of the remaining tagged fish, 9 fish were never redetected during active tracking and 2 fish were not sufficiently redetected (<3 detections) for analysis of estuarine movements. Of those fish that established an ALR, the degree of use differed between individuals. Many of the latter fish, however, were detected for a majority of the time within their ALR (mean: 51% [SE 5]; Table 1).

Weakfish established an ALR in different locations and habitats within the estuary. In general, 4 representative patterns of ALRs were observed (for examples, see Fig. 2). These ALRs were established within subtidal creeks and thoroughfares (Fig 2A; 6 of 12 locations), as well as within bay (Fig 2B; 2 of 12 locations) and river (Fig 2C; 4 of 12 locations) habitats to varying degrees, and there was an association observed between original release site and location of an ALR (9 of 12 fish; Table 1). The average size of an ALR (0.03 km^2 [SE 0.01]), based on minimum convex polygon calculations, encompassed a small proportion (0.06%) of the total area sampled during active tracking (48.4 km^2). Other tagged fish (6 of 29) that did not fit the criteria for establishment of an ALR were located within similarly localized portions of the estuary (Fig. 2D). Several individuals (IDs 62, 70, 103, and 162) were redetected for 2 consecutive weeks at locations within a range of 0.10–1.08 km from their previous locations.

The magnitude and duration of movements of fish from an established ALR differed. Several tagged fish (5 of 12) were observed at their ALR for 4–7 sampling weeks, and their final detections were at distances of 0.9–11.9 km from their ALR (Fig. 3A). Two tagged weakfish (fish IDs 140 and 155) also were observed at their ALR for 4 consecutive detections but were not detected outside that region before leaving the study area. One fish (ID 137) had the lowest proportion of potential detections within an ALR (24%; Table 1). After movement from the ALR, this individual was subsequently detected on 9 other occasions outside that region. Another small group of fish (4 of 12) were observed making excursions of varying distances (1.0–5.9 km) from their ALR, followed by a return after 1–2 sampling weeks (Fig. 3B). For both groups of tagged weakfish, detections at an ALR frequently occurred during nonconsecutive sampling weeks, indicating that fish had potentially moved outside the sampling area for short (weekly) periods. Therefore, the estimate of fish that made excursions from these areas may be low.

Diel patterns of movement

Weakfish exhibited a diel periodicity of daytime residency at Deep Point (less than 0.5 km between detections; Fig. 4A) followed by nightly movements that began around sundown (Fig. 4B)—a finding based on the locations (155) of 9 individual weakfish that were detected by focused, intensive active tracking. For several individuals (*n*=4; IDs 64, 136, 137, and 151), their ALDR at Deep Point corresponded to seasonal ALR and original tagging location. For other fish tagged at
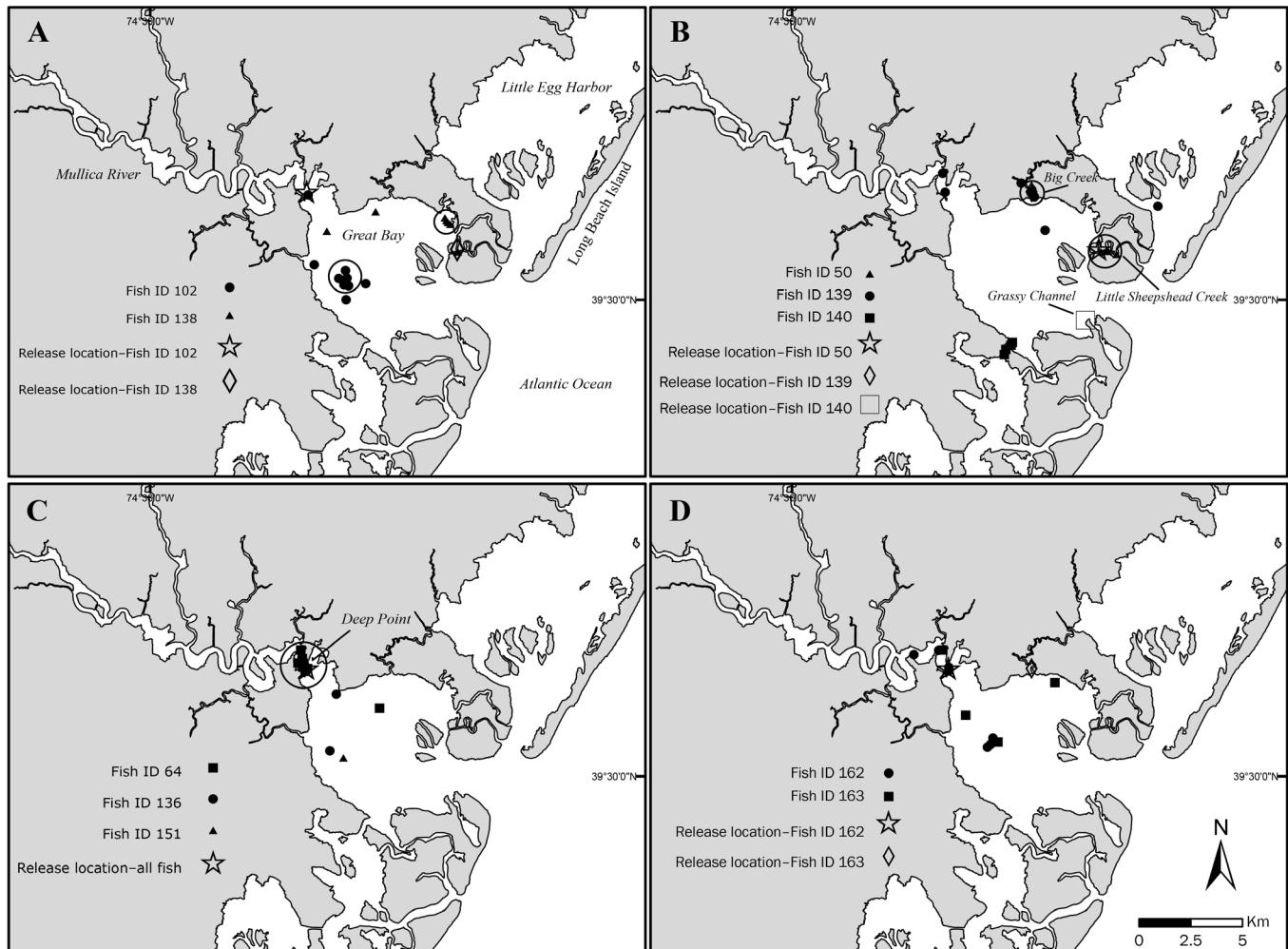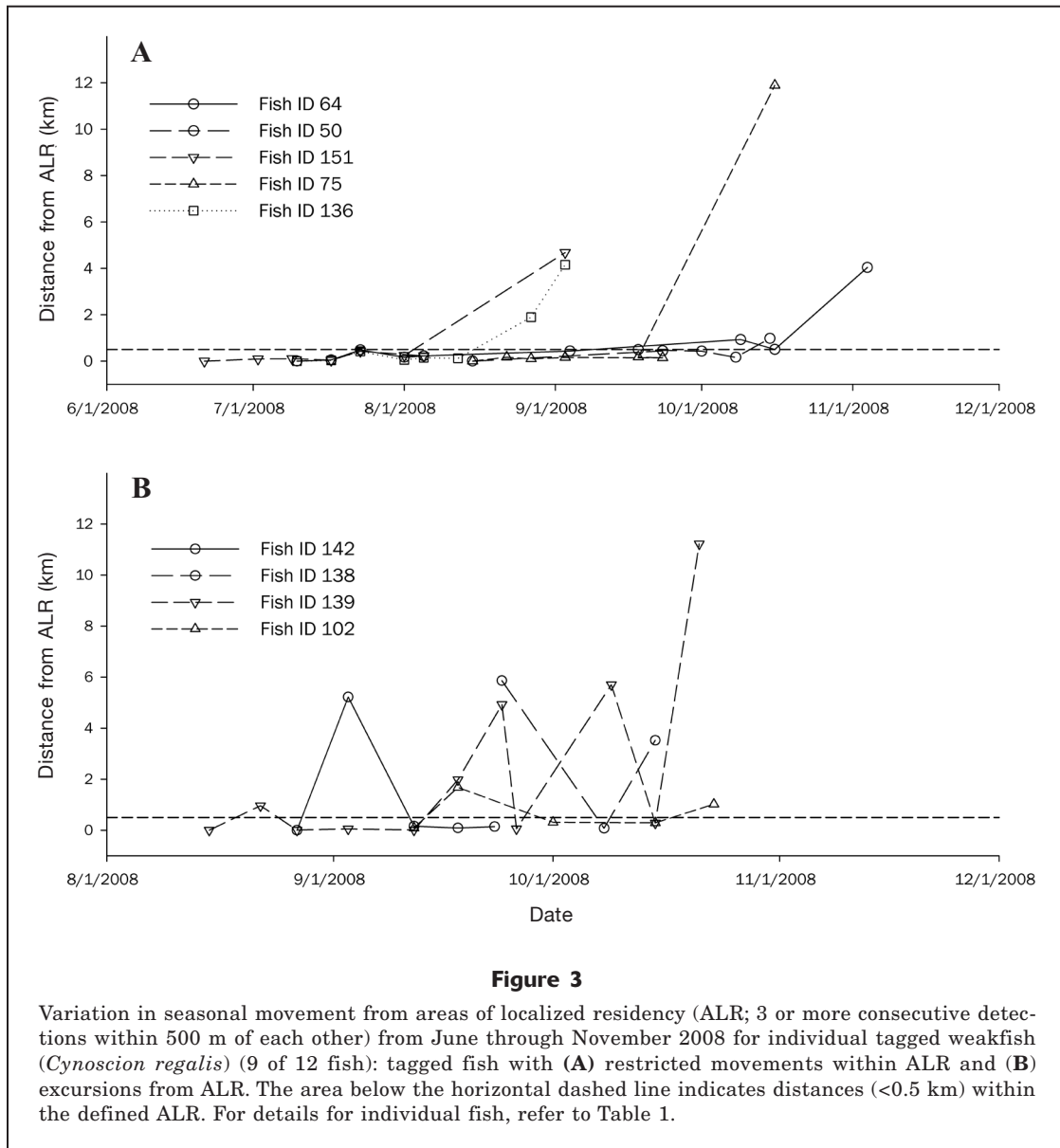
Figure 2

Release locations and representative spatial distribution patterns for weakfish (*Cynoscion regalis*) in the Mullica River–Great Bay estuary from June through November 2008: distribution of tagged fish that established areas of localized residency (ALR) in (**A**) bay, (**B**) subtidal creek, and (**C**) river habitats and (**D**) distribution of tagged fish that did not establish ALR but still used similar portions of the estuary. Circled points in panels A–C are detections that fit the criteria for localized residency (3 or more consecutive detections within 500 m of each other). For locations see Figure 1. For details for individual fish, refer to Table 1.

Deep Point (*n*=4; IDs 62, 103, 162, and 204), where diel movement patterns were observed, no seasonal ALR was established in any estuarine location on the basis of the criteria described above. The single fish (ID 100) that was originally tagged in a different location, Big Creek (see Fig. 1) also did not fit the criteria for establishment of an ALR at any estuarine location. The duration between consecutive detections of a single individual was highly variable (12–382 min), because of the variable abundance of tagged fish, the different amount of time it took for the tracking vessel to return to the location of a previous detection, and the ability to redetect tagged fish. Redetection was reduced during the nighttime period when weakfish moved from their ALR (Table 2).

The majority of individual weakfish maintained an ALR during the day (*n*=8 fish; 119 detections; mean distance from ALR: 0.34 km [SE 0.04]) and moved significantly farther from that site during dusk and nighttime (*n*=7 fish; 36 detections; mean: 1.37 km [SE 0.17]; Mann-Whitney $U_{0.05(2),8,7}$=56, *P*=0.0015), although distances from ALR were variable between individuals (Table 2; Fig. 5). Variation was driven primarily by one tagged individual (ID 103) that maintained higher-than-average distances (2.1 and 2.2 km) from its ALR during 2 time periods (0800–1000 and 1800–2000, respectively). Overall, tagged weakfish were never detected within 0.5 km of their ALR after 2230 hours. Diel tracking also indicated a level of site affinity within a schooling aggregation because most fish during this portion of the study were detected within the same ALR.

Figure 3

Variation in seasonal movement from areas of localized residency (ALR; 3 or more consecutive detections within 500 m of each other) from June through November 2008 for individual tagged weakfish (*Cynoscion regalis*) (9 of 12 fish): tagged fish with (**A**) restricted movements within ALR and (**B**) excursions from ALR. The area below the horizontal dashed line indicates distances (<0.5 km) within the defined ALR. For details for individual fish, refer to Table 1.

Discussion

Seasonal patterns

The data presented here indicate estuarine site affinity behavior and, in conjunction with prolonged estuarine residency times (Manderson et al., 2014; Turnure et al., in press), also indicate that many adult weakfish maintain strong spatial and temporal bonds with their seasonal estuarine residence. During this period of intra-estuarine residency, weakfish are known to reproduce (Connaughton and Taylor, 1995) and feed (Harfmart and Brandt, 1995), indicating that estuaries may provide a unique and crucial role during their life history for at least a proportion of the weakfish population. The motivations and mechanisms behind

animal movements—specifically the establishment of restricted home ranges, site affinity, and homing behavior—are complex (Dingle and Holyoak, 2001; Schick et al., 2008; Lowerre-Barbieri et al., 2013; White and Brown, 2013) but are thought to occur in response to a variety of seasonal factors (Mueller and Fagan, 2008), such as patchy resource distributions (e.g., spawning habitat and prey species) and extreme water temperatures that result in physiological limitations (Pörtner, 2010).

The location and abundance of spawning aggregations and prey items are likely to influence the seasonal, intra-estuarine movements of adult weakfish. For example, the resources needed for reproductive activity could influence their site affinity patterns, as seen in other sciaenid species. In the congener spotted seat-
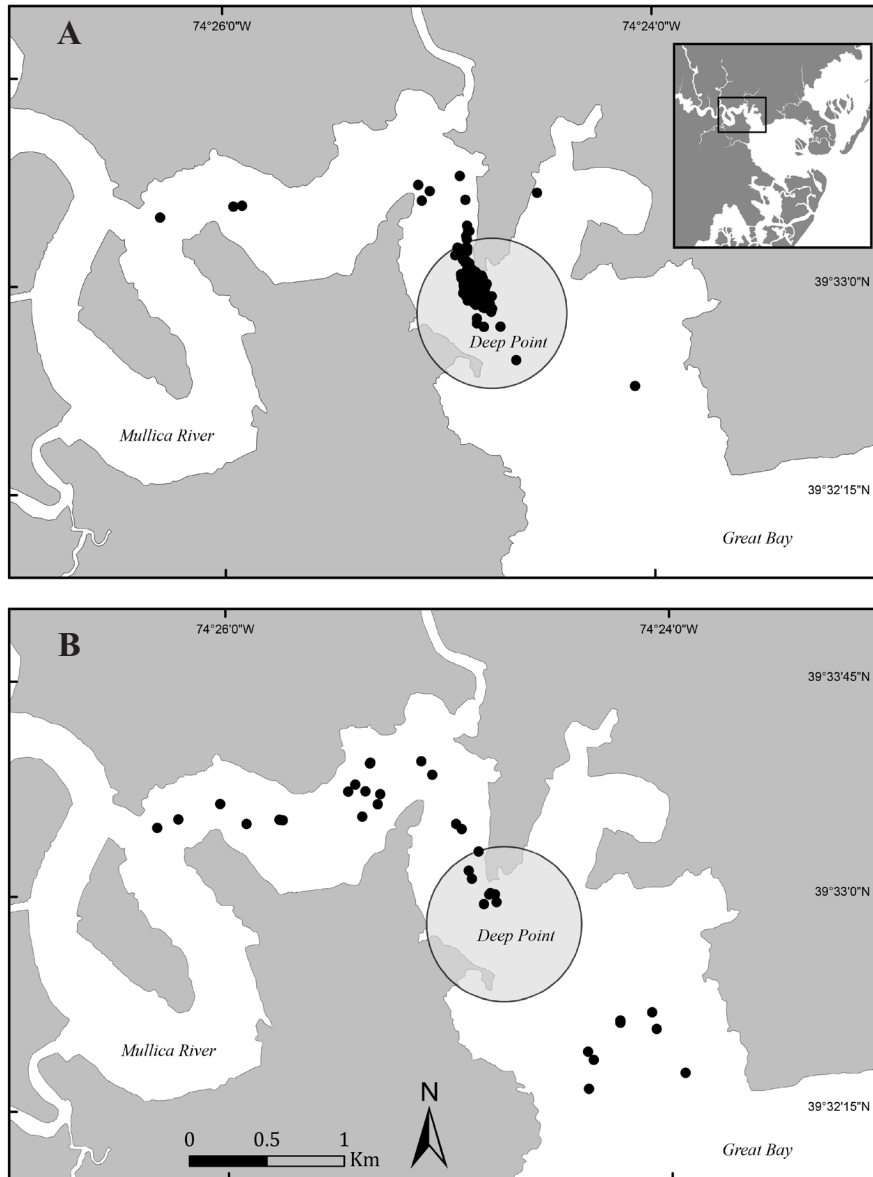
Figure 4

Cumulative active telemetric detections of tagged individual weakfish (*Cynoscion regalis*) at Deep Point in the lower Mullica River during (**A**) day (0430–19:29 hours, 119 detections of *n*=8 individuals) and (**B**) night (1930–0429 hours, 35 detections of n=6 individuals) from 30 June to 31 July 31 2008. The detection of an individual fish (ID 100) is not shown on this map. In each panel, a black circle (1 km in diameter) represents the area of localized daytime residency (ALDR) defined for individuals in the evaluation of diel movements as the seasonal area of localized residency (ALR) by weekly active tracking events (3 or more consecutive weekly detection within 500 m of each other). The ALDR also corresponds to the original release site for all fish except for one fish (ID 100). For locations of sampling points, see Figure 1. For details on individual tagged weakfish, refer to Table 2.

rout (*Cynoscion nebulosus*), strong intraseasonal site fidelity was frequently displayed (Lowerre-Barbieri et al., 2013). In red drum (*Sciaenops ocellatus*), space use significantly increased during the spawning period in Florida, presumably as a result of an enhanced search for spawning opportunities (Reyier et al., 2011). Sea ra-

ven (*Sciaena umbra*) exhibited strong site attachment outside the spawning period (Alós and Cabanellas-Reboredo, 2012), similar to the pattern observed in red drum. In contrast, results of this study indicate that weakfish maintained some degree of site affinity during the spawning season, but changes in these movements

Table 2

Detections and movements of tagged weakfish (*Cynoscion regalis*) (*n*=9) tracked on a diel basis at Deep Point (lower Mullica River) through the use of active acoustic telemetry (from 30 June 30 to 31 July 2008). For locations within study area and sampling points, see Figure 1. For tagging details on individual weakfish (except the fish (ID 100) tagged 11 June 2008 in Big Creek; 413 mm in total length), refer to Table 1. Standard errors of mean distances are given in parentheses.

Fish ID	First detection	Last detection	Number of tracking events detected	Total detections (day)	Total detections (night)	Daily mean distance from ALDR (km)	Nightly mean distance from ALDR (km)
62	July 23	July 31	5	14	1	0.20 (0.02)	1.24 (n/a)
64	July 17	July 31	6	20	4	0.21 (0.09)	1.10 (0.21)
100	July 22	–	1	–	1	–	1.36 (n/a)
103	June 30	July 30	5	25	1	0.50 (0.12)	2.27 (n/a)
136	July 17	July 31	6	19	6	0.30 (0.03)	1.49 (0.28)
137	July 10	July 22	4	5	12	0.34 (0.04)	1.24 (0.25)
151	July 10	July 31	8	24	11	0.28 (0.04)	0.86 (0.13)
162	June 30	July 10	2	2	–	0.53 (0.33)	–
204	June 30	–	1	10	–	0.34 (0.05)	–

before or after this period could not be ascertained. Interpretation of diel movements (see the following section) further corroborates the potential influence of reproductive behavior on weakfish movements.

Predator avoidance can also regulate the movements of fish species (Pittman and McAlpine, 2003) across varying scales but is most often discussed in the context of juveniles or subadults (Naesje et al., 2012). Although predation risk is greatest for juvenile fishes, adult movements may also be influenced by such factors. Seasonal occurrences of piscivorous predators, such as sandbar shark (*Carcharhinus plumbeus*; Merson and Pratt, 2005), striped bass (*Morone saxatilis*; Ng et al., 2007), and bottlenose dolphin (*Tursiops truncatus*; Toth et al., 2011) are common in the study area and may influence the movements and distribution of adult weakfish. One manifestation of a movement strategy based on predator avoidance could be periodic or long-term "stationary" behavior, as documented for Japanese croaker (*Argyrosomus japonicus*; Naesje et al., 2012) and the consistent, localized behavior observed with tagged weakfish detected weekly during this study for periods lasting up to 7 weeks. At the population level, variation in movement in contrast to prolonged stationary behavior of tagged weakfish, as observed in this study, could be explained by differences in an individual's boldness or propensity for habitat exploration (Fraser et al., 2001; Frost et al., 2013).

Maintenance of optimal environmental quality, especially in dynamic estuarine environments, is another potential predictor of weakfish movements (Manderson et al., 2014). Environmental quality, measured as water temperature, salinity, and dissolved oxygen, in relation to weakfish distribution was evaluated during a concurrent study, in which tagged weakfish were commonly detected within a relatively narrow range of environmental parameters near deep channel edges and emergent marsh banks and during all seasons (Turnure et al., in press). However, the consistency of detections within a narrow range of temperature, salinity, and dissolved oxygen may have been driven by a broader spatial restriction to the lower estuary rather than by directed movements to these areas within the estuary.

Diel patterns

The diel movements of tagged weakfish during this study could best be characterized as "commuting" behaviors (Dingle and Holyoak, 2001) because they took place on a short-term periodic basis and likely were initiated in a search for spawning or prey aggregations followed by a return to an ALDR. Although a high percentage of fish left the study area (Deep Point) used for examination of diel movements at night and were not detected until the following morning, several individuals were detected in other localized areas after movement away from their ALDR. This finding may indicate a shift to a new nightly ALR. Alternatively, the movement of some fish outside the study area may indicate ranging behavior for foraging. A previous investigation of nighttime use of subtidal creeks in the study area hinted at the possible use of these habitats by weakfish for nighttime feeding excursions on high tides (Rountree and Able, 1997). Initiation of movement from the ALDR at Deep Point (Fig. 1) corresponded to lower light levels and, more specifically, the nighttime crepuscular period. There was high variability in movements during the early nighttime crepuscular period
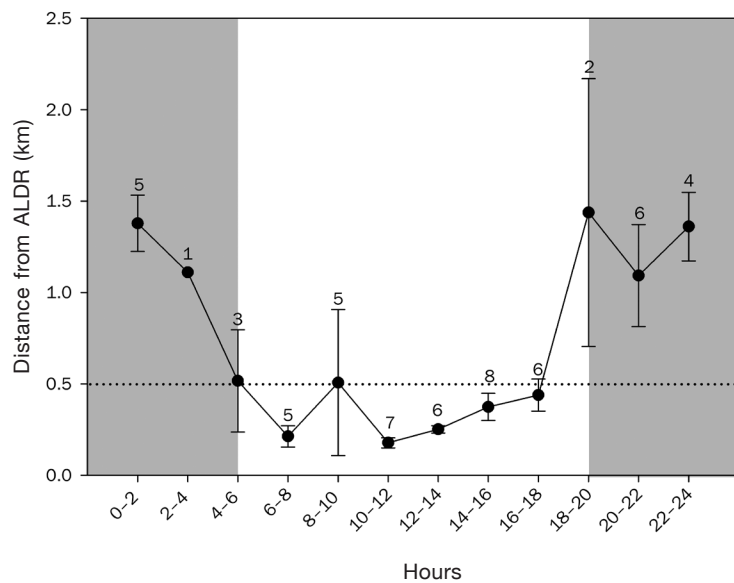
Figure 5

Diel variation in distance from area of localized daytime residency (ALDR) for individual weakfish (*Cynoscion regalis*) detected by using active telemetry (from 30 June to 31 July 31 2008). All weakfish (*n*=9), except one fish (ID 100), were originally tagged at Deep Point in the lower Mullica River and distances (km) from that site were pooled and averaged by 2-h bins for each tagged fish. Error bars represent standard error of means for individuals and sample sizes are displayed above bars. Gray boxes indicate approximate nighttime periods (1930–0430 hours). The ALDR was defined for each individual in the evaluation of diel movements as the seasonal area of localized residency (ALR) by weekly active tracking events (3 or more consecutive weekly detections within 500 m of each other). The ALDR corresponded to the original release site (Deep Point) for all fish, except one fish (ID 100). The area below the horizontal dotted line indicates distances (<0.5 km) within the defined ALDR. For sampling locations, see Figure 1. For details for individual tagged weakfish, refer to Table 2.

(1800–2000), indicating that initiation of nighttime movements was dynamic among individuals (e.g., the fish with ID 103).

Nighttime is also the period when peak weakfish spawning occurs (Taylor and Villoso, 1994). Concurrent research in the study area during active tracking events confirmed nightly weakfish drumming, indicating that spawning may have occurred during the tracking period (Turnure, 2010). These results confirm observations from previous studies of weakfish movement in Delaware Bay during the sundown period that was related to spawning activity (Connaughton and Taylor, 1994). In this study, fish facing inshore (presumably in prespawning mode) were frequently caught in gill nets during the early evening hours and in the later evening (presumably after spawning), fish were caught facing offshore. Further, few fish were caught in gill nets during the early morning and early afternoon, likely the time when weakfish decreased their movements (Connaughton and Taylor, 1994). Those authors

also examined the drumming pattern of weakfish and noted that the highest level of spawning vocalizations occurred inshore during early evening (Connaughton and Taylor, 1995).

Diel movements and day–night changes in use of space are common among other sciaenid species (e.g., red drum: Dresser and Kneib, 2007; sea raven: Alós and Cabanellas-Reboredo, 2012; and Japanese croaker: Naesje et al., 2012) and in other families (e.g., white sturgeon (*Acipenser transmontanus*): Parsley et al., 2008; red snapper (*Lutjanus campechanus)*: Topping and Szedlmayer, 2011) but this article provides the first description of similar behavior in weakfish. Juvenile weakfish movements in relation to diel-cycling of hypoxia events were observed during summer in a small tributary of the Delaware Bay (Tyler and Targett, 2007; Brady and Targett, 2013) and modeled (Brady et al., 2009). During the former study, juveniles exhibited a daily escape response (~1 km) in areas where hypoxia events occurred (dissolved oxygen <2 mg/L), indicating that movement patterns could be more dynamic in affected systems where daily fluctuations in dissolved oxygen are common. The results from the tracking study described here represent weakfish movement patterns within a relatively undisturbed estuary where low dissolved oxygen is infrequent.

The dynamics of movements in adult weakfish appear to be related to scaling over seasonal and diel time frames, and these results represent new evidence of the affinity of adult weakfish to specific estuarine localities and of their ability to return to them from relatively large distances within an estuary across ecologically relevant time scales. Although the site fidelity of other adult fishes (e.g., summer flounder (*Paralichthys dentatus*): Capossela et al., 2013), including those fishes previously studied in this system (striped bass: Ng et al., 2007; summer flounder: Sackett et al., 2007) has been observed in small estuarine systems and site fidelity has been quantified at the regional estuarine scale for weakfish (Thorrold et al., 2001), fine-scale behaviors have not been previously quantified in adult weakfish.

In further studies of weakfish estuarine movements, one step would be to reexamine the previous model of natal homing and site fidelity in adult weakfish (Thorrold et al., 2001) at smaller spatial scales. The long-term spatial memory needed to enable a fish to return back to relatively small areas (Fukumori et al., 2010) on a yearly basis was not observed in weakfish (Turnure et al., in press), but a similar ability to relocate to an

ALR from relatively large distances (~6 km) within a season was evident in several individuals in this study. With the high level of individual variation present in this study and the potential effects of intrinsic (e.g., size and sex) and extrinsic (e.g., time and location of tagging and environmental quality) variables on the observed patterns of movement, these results also indicate that a prior understanding of scale (both temporal and spatial) is necessary to formulate proper research questions about weakfish movements and likely about other estuarine species.

Inherent variability in behavior of individuals, as seen in this and in previous studies (see Bolnick et al., 2003, and citations within; Kobler et al., 2009), should not be overlooked when interpreting these patterns (Mittelbach, 2014). Explicit examination of the mechanisms that surround these temporal dynamics would provide insight into weakfish movements in relation to critical aspects of their life history (e.g., reproduction) at scales beyond the individual and could be used to scale the protection of spawning habitat and to gain insight into population-level dynamics. For example, current understanding of weakfish population genetics indicates that the western Atlantic weakfish population should be managed as one coastal stock despite the existence of geographically distinct subpopulations (Cordes and Graves, 2003). Our study, described here, further confounds the notion that weakfish maintain population connectivity through highly dispersive movements during the reproductive period. Behavioral differences among and within weakfish subpopulations, especially with regard to the phenology and location of spawning, may contribute to the genetic similarity within the coastal weakfish population.

Acknowledgments

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