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# Migratory and within-estuary behaviors of adult Summer Flounder (*Paralichthys dentatus*) in a lagoon system of the southern mid-Atlantic Bight

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**Abstract**—We monitored the movements of 45 adult Summer Flounder (*Paralichthys dentatus*) between June 2007 and July 2008 through the use of passive acoustic telemetry to elucidate migratory and within-estuary behaviors in a lagoon system of the southern mid-Atlantic Bight. Between 8 June and 10 October 2007, fish resided primarily in the deeper (>3 m) regions of the system and exhibited low levels of large-scale (100s of meters) activity. Mean residence time within this estuarine lagoon system was conservatively estimated to be 130 days (range: 18–223 days), which is 1.5 times longer than the residence time previously reported for Summer Flounder in a similar estuarine habitat ~250 km to the north. The majority of fish remained within the lagoon system until mid-October, although some fish dispersed earlier and some of them appeared to disperse temporarily (i.e., exited the system for at least 14 consecutive days before returning). Larger fish were more likely to disperse before mid-October than smaller fish and may have moved to other estuaries or the inner continental shelf. Fish that dispersed after mid-October were more likely to return to the lagoon system the following spring than were fish that dispersed before mid-October. In 2008, fish returned to the system between 7 February and 7 April. Dispersals and returns most closely followed seasonal changes in mean water temperature, but photoperiod and other factors also may have played a role in large-scale movements of Summer Flounder.

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The continued degradation of estuarine environments associated with eutrophication, shoreline development, and global climate change necessitates a better understanding of how seasonal residents, like Summer Flounder (*Paralichthys dentatus*), use mid-Atlantic estuaries (Gibson, 1994; Beck et al., 2001). Estuaries provide juvenile and adult Summer Flounder with the water temperatures, food resources, and protection from predation that are necessary for their growth and survival (Stierhoff et al., 2006). Summer Flounder migrate offshore in the fall and winter to spawn over the outer continental shelf before they migrate back inshore the following spring, often returning to the same estuary in subsequent years (Sackett et al., 2007). As a result, stock abundance is influenced by local estuarine conditions (Ray, 2005). The use of estuaries as nursery habitat by Summer Flounder and the responses of juvenile Summer Flounder to estuarine conditions have been extensively examined (e.g., Malloy and Targett, 1994; Tyler, 2004; Necaise et al., 2005; Stierhoff et al., 2006, 2009). Only recently, however, have migratory and within-estuary behaviors of adult Summer Flounder been examined (Sackett et al., 2007, 2008; Henderson, 2012).

Migration timing traditionally has been determined through assessment of the abundance of fishes in an estuary over time with standard fisheries methods, such as bottom trawl surveys. However, population-level monitoring is insufficient to understand the dynamics of emigration or the variation in individual responses (DeCelles and Cadrin, 2010). In recent years, acoustic telemetry has been established as a powerful tool for observation of individual variability in behaviors (Heupel et al., 2006; DeCelles and Cadrin, 2010). A study of acoustically monitored adult Summer Flounder in the Mullica River–Great Bay estuary in New Jersey (located in the northern mid-Atlantic Bight [MAB]) indicated that a large number of fish departed the estuary in July, but the precise timing varied between years (Sackett et al., 2007).

Therefore, variation in emigration timing may exist not only by latitude but also among individual fish within a system. Some adult Summer Flounder have been known to return to the same estuary in subsequent years (Poole, 1962; Sackett et al., 2007; Henderson, 2012), but factors that influence site fidelity in Summer Flounder are not well understood.

Acoustic telemetry has also been used to identify variations in Summer Flounder within-estuary activity. For example, Summer Flounder in the Mullica River–Great Bay estuary primarily used the lower bay (near the inlet), but some fish resided in other areas (Sackett et al., 2008). Likewise, most fish remained in the Mullica River–Great Bay estuary until emigration to the outer shelf, but several adults exited and entered the system multiple times (i.e., exhibited temporary emigration). Similar patterns were observed in the Chesapeake Bay (southern MAB), where some adults remained sedentary and resided at structured sites for long periods of time, and others were more active and traveled long distances (Henderson, 2012).

The continuation of acoustic studies is necessary to identify similarities and differences in behavioral patterns between regions and to investigate the drivers behind these patterns. Our objectives for this study were to use acoustic telemetry to describe the migratory and within-estuary behaviors of adult Summer Flounder from a previously unstudied lagoon system in the southern portion of the MAB. The lagoon systems off Virginia's Eastern Shore are subject to large fluctuations in temperature typical of most MAB systems (0–30°C), but they differ from larger estuaries in that they are shallow (mean depth <3 m), well-mixed, and polyhaline areas. These lagoon systems are a nursery ground for juvenile Summer Flounder (Schwartz, 1964; Norcross and Wyanski, 1994; Desfosse, 1995; Kraus and Musick, 2001), but they also support a large number of adults and an active recreational fishery (Richards and Castagna, 1970). Previous descriptions of the use of our chosen lagoon system by Summer Flounder have been limited to descriptions of juvenile habitat preferences (Wyanski, 1990; Norcross and Wyanski, 1994) and adult migration patterns determined by traditional mark-recapture methods (Kraus and Musick, 2001; Desfosse, 1995).

We used the data from our acoustic telemetry study to determine 1) dispersal and return rates, 2) duration of residency, 3) spatiotemporal distribution, and 4) activity of fish within the system. Because tidal stage, time of day, and temperature all have been associated with flatfish activity (Olla et al., 1972; Casterlin and Reynolds, 1982; Wirjoatmodjo and Pitcher, 1984; Malloy and Targett, 1991; Szedlmayer and Able, 1993; Henderson, 2012), these factors were considered in our examination of within-estuary activity. We also analyzed the effects of seasonal temperature, photoperiod, and fish size on dispersal, returns, and residency times (Smith, 1973; Able and Kaiser, 1994).

## Materials and methods

### Study site

The estuarine lagoon system near Wachapreague, Virginia, resides behind a series of low barrier islands and primarily connects with the Atlantic Ocean through Wachapreague Inlet (Fig. 1). The 2 main channels leading from Wachapreague Inlet divide into smaller channels that cut through marsh areas (dominated by smooth cordgrass [*Spartina alterniflora*]) before they open into large, shallow tidal flats. Channels were identified as areas ~3–12 m deep, and tidal flats were identified as areas <3 m deep. As with most seaside lagoon systems in Virginia, the system near Wachapreague is characterized by restricted access to the ocean, minimal freshwater input, and a moderate tidal range (1.2–1.4 m; NOAA Center for Operational Oceanographic Products and Services, http://tidesandcurrents.noaa.gov/tides07/tab2ec2b.html#44). Strong currents are typical because of natural constrictions at the inlet and in the channels (Conrath, 2005), although currents generally dissipate with distance from the inlet. Sediment type follows the energy gradient, with coarse sand within and near the inlet, and progressively finer (muddy) sediments at greater distances from the inlet (Wyanski, 1990).

We divided our study area into 4 regions (Fig. 1):

1 Wachapreague Inlet—the primary point of ingress and egress of fish characterized by depths of 6–15 m and strong currents; the inlet is about 625 m wide.
2 Upper channels—the channel leading north from Wachapreague Inlet and its divergent channels.
3 Lower channels—the channel leading south from Wachapreague Inlet and its divergent channels.
4 Tidal flats (also known locally as *bays*)—the shallowest bodies of water included in our study. Although several tidal flats are present in this area, only Swash Bay was included in our study area because we could monitor the movements of Summer Flounder into and out of this area.

We recorded environmental conditions in the inlet, channels, and tidal flat from 8 June 2007 to 29 July 2008 with 3 YSI 6920-O[1] multiparameter water-quality sondes (YSI, Inc., Yellow Springs, OH; Fig.1), which recorded temperatures and dissolved oxygen concentrations once per hour. Sondes were replaced with calibrated units every 1–2 weeks in the summer and (as fouling diminished) every 2–4 weeks thereafter. Erroneous recordings due to membrane fouling, battery failure, and calibration drift were removed from the data set. Data from the water-quality sondes confirmed that dissolved oxygen concentrations generally remained above the critical oxygen level (27.2%, 2.0 mg $O_2$ $L^{-1}$) for adult Summer Flounder at typical summer bottom-water

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

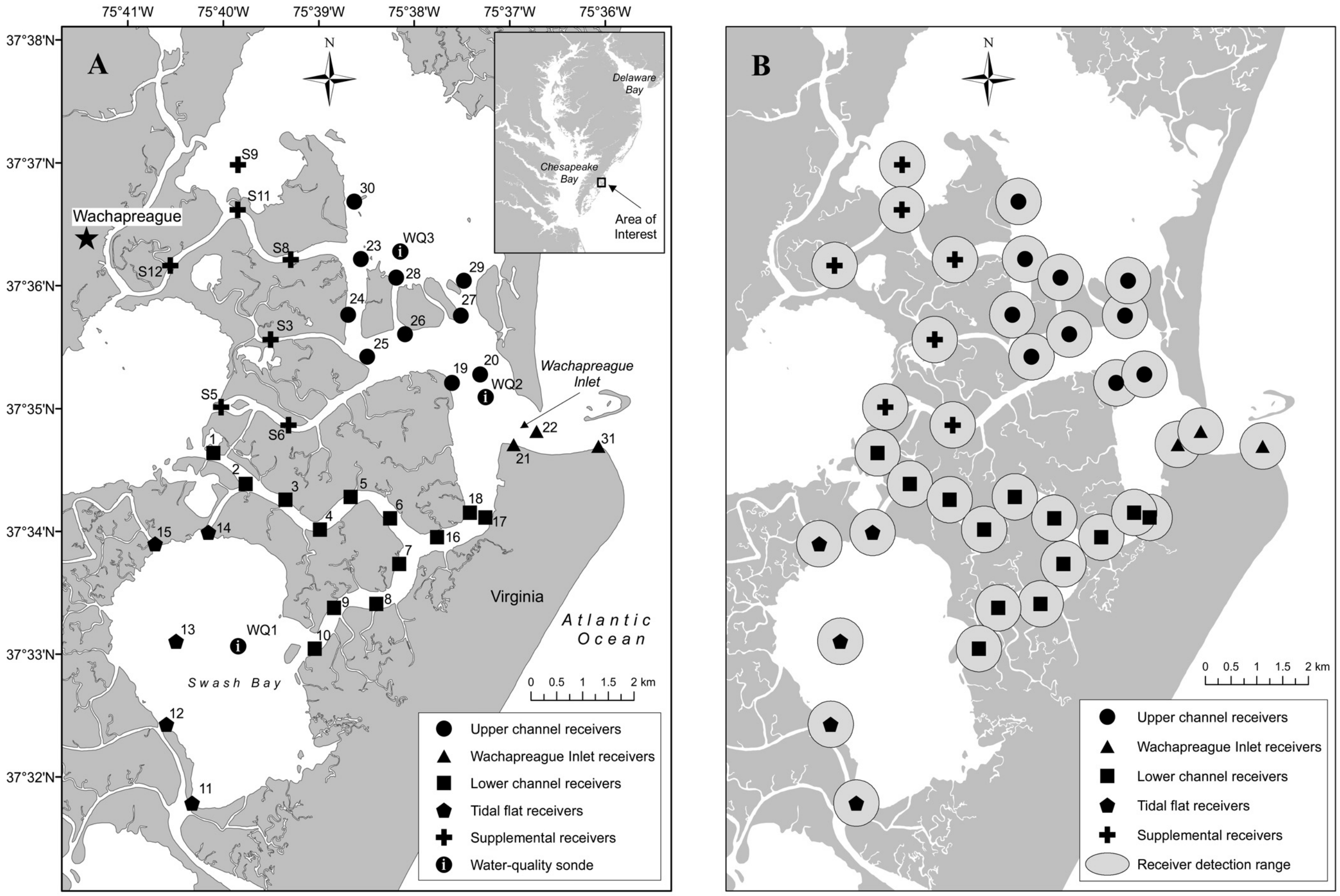


**Figure 1**

(**A**) The distribution of acoustic receivers and water-quality sondes installed in the Wachapreague lagoon system for this study of Summer Flounder (*Paralichthys dentatus*) behaviors between June 2007 and July 2008. The location of the Wachapreague lagoon system in the southern mid-Atlantic Bight is shown by the square in the smaller map. Regions specified in the text are Wachapreague Inlet, upper channels, lower channels, and tidal flat. Receivers S3, S5–S9, S11, and S12 provided supplemental data on the activity in regions outside of our study area. (**B**) In this map of acoustic receivers, each circle represents the approximate detection range (radius=350 m) of the receivers deployed in the Wachapreague lagoon system.

temperatures (Capossela et al., 2012). Photoperiod (i.e., day length) was acquired from tide prediction software (Jtides, vers. 4.9; http://www.arachnoid.com/JTides).

### Telemetry and tagging

On 22 May 2007, 50 Summer Flounder (261–558 mm total length [TL]) were captured at the study area by hook and line, identified from Murdy et al. (1997), and immediately anesthetized with 60 mg $L^{-1}$ AQUI-S (AQUI-S New Zealand Ltd., Lower Hutt, New Zealand) to allow surgical implantation of individually coded 69-kHz transmitters (V9-2L-R64K; VEMCO Division, AMIRIX Systems, Inc., Bedford, Canada) by using established procedures (Fabrizio and Pessutti, 2007). Transmitters were 30 mm long and 9 mm in diameter and had a delay time of 60–180 s and a projected 14-month battery life. All fish were tagged and released in the upper channels with the exception of a single fish that was captured, tagged, and released on the tidal flat. Before release, all fish were allowed to fully recover in an onboard aquarium that accommodated total length, and externally tagged with an individually numbered T-bar anchor tag inserted near the caudal peduncle to alert anglers to report recaptures. We considered all fish to be adults because Summer Flounder can reach maturity at 240–300 mm TL (Morse, 1981).

Summer Flounder migratory and within-estuary behaviors were examined from 8 June 2007 until the last fish departed on 17 January 2008. We chose the start date (8 June 2007), which was approximately 2 weeks after the release of tagged fish, to limit the influence of any atypical activity patterns due to recovery from capture and surgery (Knights and Lasse, 1996; Rogers and White, 2007). We recorded fish locations with 31 receivers (VR2, VR2W; VEMCO) deployed throughout the study area (Fig. 1A). Most receivers were deployed by 8 June 2007 (receivers numbered 1–27), but 4 receivers were deployed on 26 June (receivers numbered 28–30) and 16 July (receiver numbered 31) to provide additional coverage. Receivers were attached to an anchored line fitted with a buoy and positioned near the bottom of the water column (≤1 m from the bottom of the ocean floor) with the hydrophone oriented downward. Range tests conducted throughout the study area indicated an approximate detection range of 350 m.

We placed as many receivers as possible ~700 m apart in the upper and lower channels to be able to monitor fish movements on the scale of 100s of meters (Fig. 1B). Currents and boat traffic limited the placement of receivers in certain locations in the upper channels and prevented the use of a directional gate (Heupel et al., 2006) at Wachapreague Inlet. In these cases, receivers were placed in the next suitable location. The tidal flat was too shallow for extensive receiver coverage; instead, we used receivers to monitor fish as they entered and exited the tidal flat. Most receivers were retrieved on 31 January 2008, but 12 receivers (receivers numbered 5–7, 16–18, and 22–27; Fig. 1A) were left in the system to detect fish returning to the Wachapreague system the following year. To prevent receiver loss, we began retrieval of the receivers that were farthest from the inlet in mid-April. All receivers were retrieved by 29 July 2008.

A separate acoustic telemetry study conducted by researchers to examine movements of Cownose Ray (*Rhinoptera bonasus)* in the Wachapreague system overlapped with the timing of our Summer Flounder study. Receivers from the Cownose Ray study were placed mostly in small channels far from Wachapreague Inlet in an area not covered by our receivers. Receivers for that study were deployed on 26 June 2007 (receiver labeled S3) and 26 July 2007 (receivers labeled S5–S9, S11–S12; Fig. 1A) and retrieved on 17 November 2007. The receivers in the Cownose Ray study were spaced too far apart to meet the specific objectives of our study and detections from these receivers were not used in our analyses. We did note, however, the extent to which Summer Flounder were detected in these small back channels and henceforth refer to these receivers as *supplemental receivers*.

### Migratory behaviors

Data were examined over weekly intervals to examine patterns of seasonal migration. We considered a fish to have dispersed on the last day it was detected at or near Wachapreague Inlet (receivers 17–22, 31; Fig 1A). Likewise, we considered a fish to have returned when it was first redetected at Wachapreague Inlet or within the lagoon system. Weekly probabilities of dispersal and return were calculated with the Kaplan-Meier estimator, a nonparametric approach that requires no assumptions about the underlying hazard function and accommodates censored fish (Pollock et al., 1989; Bennetts et al., 2001). Fish were censored from (i.e., not included in) this analysis if they were no longer detected but did not depart from the system through Wachapreague Inlet; the fate of such fish could not be conclusively determined. Censored fish may have resided in the system undetected, been removed by fishermen or predators, or have left the system through another route.

We used a piecewise linear regression model to identify when dispersal rates changed (i.e., the *changepoint*), and we fitted the model to the data with nonlinear least-squares estimation (the NLIN procedure in SAS, vers. 9.2, SAS Institute, Inc., Cary, NC; e.g., Ryan et al., 2007). The time before dispersal rates changed was considered the *residency period*, a time during which most fish were found within the lagoon system. The time after dispersal rates changed was considered the *emigration period*, during which most fish were observed finally to have dispersed. We classified fish according to observed migratory behaviors: those fish that dispersed early (during the residency period) and those fish that dispersed late (during the emigration period). An odds ratio (Agresti, 2007) was used to test the association between the timing of dispersal (i.e., residency period vs. emigration period) and the likelihood that a fish would return to the Wachapreague system the following year.

Some fish were detected at or near the inlet (receivers 17–22, 31) but were subsequently undetected for 14 or more consecutive days before redetection. These fish were classified as *temporary emigrants* because they were presumed to have exited and re-entered the lagoon system. Such behaviors were consistent with activity reported in a previous study (Sackett et al., 2007). Tagged fish, including temporary emigrants, were considered residents until final dispersal out of the inlet, and residence time was defined as the total number of days from the start of our study (8 June 2007) until the last detection at or near the inlet before final dispersal. The residence time of uncensored fish was used to calculate a mean residence time for Summer Flounder in the Wachapreague system. The mean residence time reported throughout this article is, therefore, an estimate of least (minimum) residence time because we do not know how long tagged fish were present in the lagoon system before the start of our study. Mean residence time and other mean values are reported as mean ±1 standard error.

The effects of mean monthly temperature and mean monthly photoperiod on the percentage of fish that finally dispersed in a given month (log-transformed to improve homogeneity of variance) were examined with a multiple linear regression (general linear model [GLM] procedure in SAS). We also examined the effect of fish size on the probability of final dispersal before and after dispersal rates changed with logistic regression (LOGISTIC procedure in SAS). Goodness-of-fit sta-

**Table 1**

The total detectable area ($km^2$) that we monitored for the presence of Summer Flounder and the percentage of the total detectable area in each defined region (upper channels, lower channels, tidal flat, and inlet) of the Wachapreague lagoon system, on the basis of a 350-m detection range, for this study of Summer Flounder (*Paralichthys dentatus*) behaviors. Also included are the proportions of time Summer Flounder spent in each region and the proportions of fish found in each region over the residency and emigration periods (8 June 2007–17 January 2008). The sum of the proportion of fish that used each region exceeds 1 because a single fish could occupy more than 1 region over the study period.

| Region | Detectable area ($km^2$) | Percentage of total area (%) | Total mean proportion of time (%) | Total proportion of fish (%) |
|---|---|---|---|---|
| Upper channels | 2.75 | 39.2 | 78.1 | 97.8 |
| Lower channels | 2.21 | 31.5 | 19.4 | 28.9 |
| Tidal flat | 1.29 | 18.5 | 0.4 | 4.4 |
| Inlet | 0.76 | 10.8 | 2.1 | 67.7 |
| Total area | 7.01 | | | |

tistics were calculated to assess the fit of the model through the use of the LOGISTIC procedure in SAS.

### Within-estuary behaviors

We ascertained the temporal and spatial distributions of Summer Flounder in the upper channels, lower channels, tidal flat, and Wachapreague Inlet by examination of monthly distributions of Summer Flounder until all fish finally dispersed. Because the total detectable area that we monitored for the presence of Summer Flounder varied between regions (Table 1), our assessment of fish activity by region did not rely on continuous detection. We calculated the proportion of fish in each region by month as the number of fish detected in a region divided by the total number of fish present in the system that month. We also calculated the proportion of time the average fish resided within a region each month as the total time a fish spent in a region divided by the total time spent in all regions that month. Time in a region was defined as the total time between the first and last detection before detection in another region; receivers provided sufficient coverage to monitor fish movement into and out of the 4 regions (Fig. 1B). For fish that moved between regions, we did not use the length of time between the last region-specific detection and the next region-specific detection because we could not objectively assign fish location during that interval to a specific region. Because not all fish could be assigned objectively to a region each month, the sum of the proportions of fish using each region could be <1 for a given month. Conversely, the sum of the proportions of fish using each region could be >1 because a single fish could occupy more than one region in any given month. In addition to monthly analyses, we calculated the proportions of fish present and time spent in each region for the residency and emigration periods. The $z$ statistic was used to test for differences in the mean proportions between the residency and emigration periods (Fleiss, 1981). All proportions were expressed as percentages.

We used movement between receivers to calculate the activity index, which we defined as the total number of times an individual moved between receivers during nonconsecutive 6-h periods. We limited the data to fish in the upper channels during the residency period because the sample size was highest in this location and during this time (8 June 2007 to 10 October 2007; see the *Results* section). For each 6-h period, we assigned an activity index value of zero when a fish did not move between receivers, and a value of 1 for each arrival at a different receiver (adjacent or nonadjacent). The activity index was weighted to account for variation in distances between receivers (rounded to the nearest integer) and summarized weekly for individual fish by tidal stage (ebb, slack before ebb, flood, and slack before flood) within each time-of-day interval (day or night). Day (10:00–16:00) and night (22:00–4:00) were restricted to these nonconsecutive 6-h periods to minimize autocorrelations associated with successive observations on the same fish during day and night periods (Rogers and White, 2007). We also computed mean temperature for each period (tidal stage, time of day, and week combination).

We examined the relationship between activity indices and week, time-of-day, tidal stage, and temperature with a generalized repeated measures model (GENMOD procedure in SAS). This equation represents the statistical model fitted to the data:

$$\log(\lambda_{ijk}) = \mu + \alpha_i + \delta_j + \tau_k + \gamma,$$

where $\lambda_{ijk}$ = the mean activity in week $i$, time of day $j$, and tidal stage $k$;

$\mu$ = the overall mean activity;

α = the week effect ($i$=1, 2, 3,...32);
δ = the time-of-day effect ($j$=day, night);
τ = the tidal stage effect ($k$=ebb, flood, slack before ebb, and slack before flood); and
γ = the effect of mean temperature.

All effects in this model were considered fixed. All plausible interactions (temperature×tidal stage, temperature×time of day) were investigated and found to be insignificant (α=0.05). We modeled the repeated measures of activity (discrete count data) as a negative binomial response after verification of the superior fit of the negative binomial distribution to the Poisson distribution to these data. According to the quasi-likelihood information criterion (a modification of Akaike's information criterion applied to models fitted by generalized estimating equations; Littell et al., 2006), the independent correlation matrix best described the nature of the correlation among repeated measurements within subjects. This correlation matrix is the simplest covariance model, where the within-subjects correlation is zero (Littell et al., 2006).

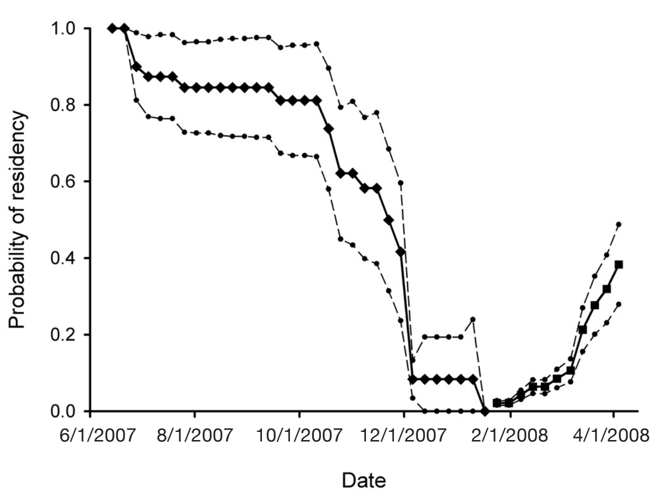


**Figure 2**

The probability that tagged Summer Flounder (*Paralichthys dentatus*) resided in the Wachapreague lagoon system from June 2007 to April 2008 on basis of the Kaplan-Meier estimator (solid lines) with 95% confidence intervals (dashed lines). Dispersal of tagged fish (◆) was monitored from 8 June 2007 until the last fish emigrated on 17 January 2008. Dispersal rates changed significantly after 11 October 2007 (change-point). The time before the change-point was considered the residency period, a time during which most fish remained within the lagoon system. The time after the change-point was considered the emigration period, during which most fish were observed dispersing from the Wachapreague lagoon system. Returns of tagged fish (■) were monitored from 18 January 2008 to 29 July 2008. The last return was detected on 7 April 2008.

## Results

### Migratory behaviors

The fish included in all subsequent analyses were the fish that were alive and detected at receivers as of 8 June 2007. As a result, 45 out of 50 tagged fish were included in the analyses (278–558 mm TL). Of the 5 fish we eliminated, 1 was assumed dead (all detections were at a single receiver). Another fish departed through the inlet before 8 June 2007 and was subsequently detected in Delaware Bay (~100 km to the north) on 9 June 2007 (Fox[2]). The remaining 3 fish were never detected by our receivers, and we assume these fish either departed undetected or were harvested by recreational anglers but not reported. All except 1 of the 45 fish included in the analyses were detected in June; the remaining fish was detected for the first time in July. Most tagged individuals accounted for <6% of the total number of detections, which was 165,003. Two fish, however, contributed 24% and 13% of the total detections. These individuals were detected continuously at receivers for long periods of time with few gaps between detections.

The mean residence time for Summer Flounder in the lagoon system was 130 ±13 days, or about 4.3 months (range: 18–223 days). Fish dispersed throughout the study period, but dispersal rates increased significantly after mid-October [change-point=week 18 (11 October 2007); $F$=212.2, $P$<0.05; Fig. 2]. On the basis of the Kaplan-Meier estimator, only 27% of tagged Summer Flounder had dispersed by 10 October 2007. Accordingly, the period from 8 June 2007 to 10 October 2007 was identified as the residency period (Fig. 2); the majority of fish that dispersed during this period did so shortly after they were tagged in June (Fig. 3). June was also the month with the highest number of censored fish (i.e., fish of unknown fate; Fig. 3). The emigration period was identified from 11 October 2007 to 17 January 2008, when the last fish departed (Fig. 2). During this period, dispersal rates increased such that 50% of fish departed by 11 November 2007, although most fish (31%) dispersed in December. Only 7 fish were classified as temporary emigrants, remaining undetected for 14 or more consecutive days (range: 14–154 days) after detection near the inlet and before redetection in the system and subsequent final dispersal.

Between 7 February and 7 April 2008, 17 Summer Flounder (36%) returned to the lagoon system (Fig. 2). Four of these fish did not disperse through Wachapreague Inlet in 2007, and, therefore, their dispersal dates were unknown. Of the returning fish with known dispersal dates, 58% (11 individuals) dispersed during the emigration

[2] Fox, D. 2007. Personal commun. Delaware State Univ., 1200 N. DuPont Highway, Dover, DE 19901.

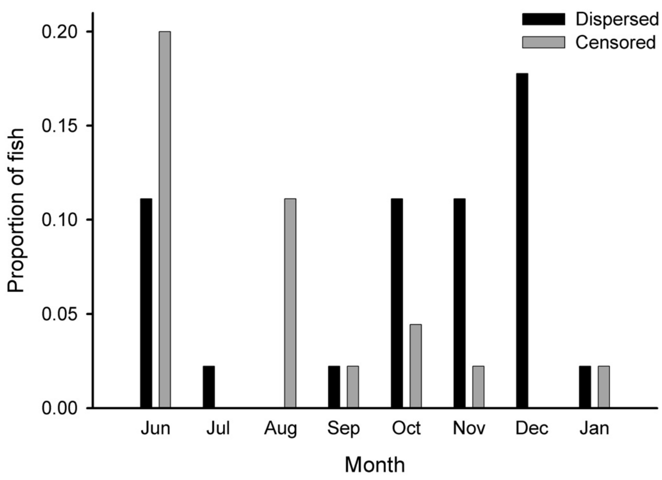


**Figure 3**

The proportion of Summer Flounder (*Paralichthys dentatus*) in each month from June 2007 to January 2008 that dispersed or was censored. Censored fish were fish that did not disperse through Wachapreague Inlet but were no longer detected by our acoustic receivers and had unknown fates. Total monthly sample sizes were 45 (Jun), 31 (Jul), 30 (Aug), 25 (Sep), 23 (Oct), 16 (Nov), 10 (Dec), and 2 (Jan).

period and 29% (2 individuals) dispersed during the residency period. Consequently, the odds of returning to the lagoon system were 3.5 times greater for fish that departed during the emigration period than for fish that departed during the residency period (odds ratio=1.4/0.4). It is possible that other fish returned undetected to the Wachapreague system because of the limited number of receivers in the system between February and July 2008; however, returning fish likely re-entered the system through the inlet and were detected by our receivers.

The emigration period was characterized by a larger seasonal variation in water temperature than that observed for the residency period (coefficient of variation [CV] $_{residency}$=9.5%, $CV_{emigration}$=46%). Dispersal followed the steep decline in temperature more closely than it did the gradual shift in day length, which (in contrast to changes in water temperature) was smooth and almost constant over time ($CV_{residency}$=7.7%, $CV_{emigration}$=5.8%; Figs. 4, 5). The multiple linear regression that included both temperature and photoperiod as predictors of dispersal was significant ($F$=20.3, $P$<0.05) and explained 89% of the variation in monthly dispersals. Temperature was a significant predictor of mean percent dispersal ($F$=6.39, $P$=0.05), but photoperiod was not ($F$=0.94, $P$=0.38). The length of time over which we observed returning fish (3 months) was inadequate to statistically examine the effects of mean monthly temperature and photoperiod on the timing of return.

The mean sizes at tagging for fish that dispersed during the residency and emigration periods were 437 ±21 mm TL and 367 ±13 mm TL, respectively. We found that the timing of dispersal was inversely related to fish size at the time of tagging ($\chi^2$=8.45, $P$<0.05). Larger fish were more likely to leave the system during the residency period (before October 11) than were smaller fish. Conversely, smaller fish were more likely to disperse during the emigration period. The goodness-of-fit of this model indicated that predicted and observed frequencies were not significantly different ($\chi^2$=3.86, $P$=0.80), indicating the adequacy of the logistic regression model as a descriptor of these data.

### Within-estuary behaviors

Summer Flounder primarily used the upper channels during the residency period, although fish were detected in all habitats (Fig. 6, A and B). Fish occupied the upper and lower channels for 78% and 19%, respectively, of the total time that fish were detected (Table 1). With the exception of the single fish released in the tidal flat, all fish were

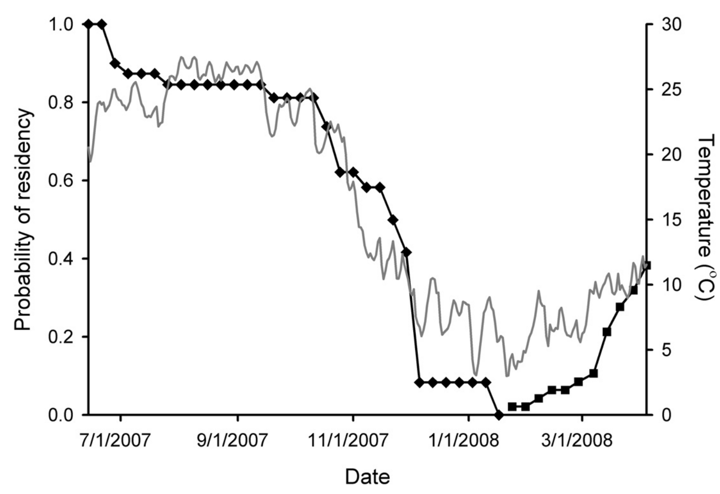


**Figure 4**

The proportion of Summer Flounder (*Paralichthys dentatus*) that dispersed from (◆) and returned to (■) the Wachapreague lagoon system from 8 June 2007 to 7 April 2008 (when the last fish was detected returning), on the basis of the Kaplan-Meier estimator. Mean daily temperature (°C; gray line) is also plotted. Confidence intervals have been omitted for clarity.

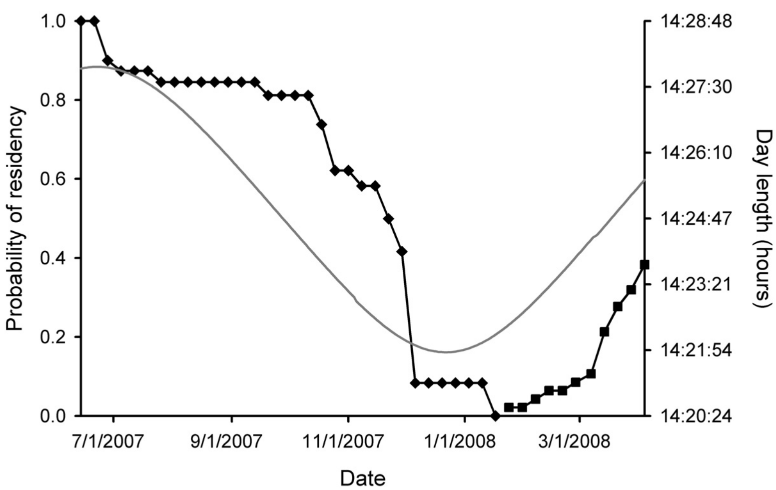


**Figure 5**

The proportion of Summer Flounder (*Paralichthys dentatus*) that dispersed from (◆) and returned to (■) the Wachapreague lagoon system from 8 June 2007 to 7 April 2008 (when the last fish was detected returning), on the basis of the Kaplan-Meier estimator. Photoperiod (day length in hours; gray line) is also plotted. Confidence intervals have been omitted for clarity.

detected in the upper channels, but only 27% (12 individuals) of the fish that were detected in the upper channels were also detected in the lower channels. This finding indicates that the majority of fish released in the upper channels (73%, 32 individuals) remained near the release site in the upper channels until dispersal.

The proportion of time and the proportion of fish in the upper channels were significantly greater during the residency period than during the emigration period (Table 2; $z_{\text{time}}$=17.0, $P$<0.05; $z_{\text{fish}}$=4.2, $P$<0.05). Use of the lower channels was greatest during the emigration period, both in terms of proportions of time spent in these habitats and the number of fish detected (Table 2; $z_{\text{time}}$=14.6, $P$<0.05; $z_{\text{fish}}$=2.6, $P$<0.05). Most fish (85%) detected in the lower channels occupied the upper channels for a mean of 132 ±14 days before they were detected in the lower channels. Fish detected in both the upper and lower channels had a later mean emigration date (15 November 2007) than that of fish that did not use the lower channels (24 August 2007).

Only 4% (2 individuals) of Summer Flounder briefly occupied the tidal flat between October and December 2007 (6 ±5 days, range: 1–11 days). Summer Flounder did not appear to regularly occupy the additional portions of the Wachapreague system monitored by the supplementary receivers. Only 7% (3 individuals) of Summer Flounder were detected by these receivers, and the mean residency was 6 ±4 days (range: 0.2–13 days). Fish presence was, however, likely underestimated because of the limited coverage and the shorter period of receiver deployment.

Although the inlet region was frequented by Summer Flounder over the course of our study (Fig. 6B), fish spent a smaller proportion of time at the inlet (2%) than in the upper and lower channels (97%; Table 1). The mean time at the inlet was 2 ±0.6 days. Not surprisingly, both the proportions of time and fish at the inlet were greatest during the emigration period (Table 2; $z_{\text{time}}$=4.9, $P$<0.05; $z_{\text{fish}}$=3.0, $P$<0.05).

Only 5 Summer Flounder in the upper channels moved between adjacent or nonadjacent receivers more than 10 times during the residency period. The mean observed activity did not vary significantly by week ($\chi^2$=19.06, $P$=0.33), but it did vary significantly with time of day; the mean activity index was significantly greater during night than during day ($\chi^2$=6.13, $P$<0.05). Individuals appeared most active during the flood tide or during the slack tide before ebb, but differences in mean activity among tidal stages were not statistically significant ($\chi^2$=6.97, $P$=0.07). Activity also was not affected by differences in mean temperature for a given tidal stage ($\chi^2$=0.46, $P$=0.55).

## Discussion

### Migratory behaviors

The observed timing of Summer Flounder dispersal from the Wachapreague system (October though January) is consistent with the established seasonal progression of spawning migration from north to south (Smith, 1973; Morse, 1981; Kraus and Musick, 2001; Sackett et al., 2007). It most closely matches the reported timing of emigration for Summer Flounder in the nearby Chesapeake Bay. Summer Flounder primarily emigrate from Chesapeake Bay from October through December, and some fish emigrate as late as February (Desfosse, 1995; Henderson, 2012). In New Jersey's Mullica River–Great Bay estuary (~250 km to the north), acoustically tagged fish generally emigrated earlier—between August and December (Able et al., 1990; Roundtree and Able, 1992b; Szedlmayer and Able, 1993). By mid-September, 75% of tagged Summer Flounder had dispersed from a study site on the inner shelf near New Jersey (Fabrizio et al.[3]). In contrast,

[3] Fabrizio, M. C., J. P. Pessutti, J. P. Manderson, A. F. Drohan, and B. A. Phelan. 2005. Use of the historic area remediation site by black sea bass and summer flounder. Northeast Fish. Sci. Cent Ref. Doc. 05-06, 95 p.

75% of tagged fish in the Wachapreague lagoon system did not disperse until early December, and mean residence time was 1.5 times longer (130 days, June–January) than the time previously reported for the Mullica River–Great Bay estuary (86 days, May–December; Sackett et al., 2008). Seasonal changes in temperature strongly influenced residence time, as indicated by the increase in dispersal rates with the seasonal decline in temperature. A similar relationship between water temperature and seasonal migration was observed in winter flounder through the use of passive acoustic telemetry (DeCelles and Cadrin, 2010).

On the basis of the life history of Summer Flounder, fish that dispersed from the Wachapreague lagoon system during the emigration period (after 11 October 2007) were most likely moving offshore to spawn. Our study revealed that smaller fish were more likely than larger fish to leave during the emigration period, confirming previous reports that larger Summer Flounder commence spawning migrations earlier than smaller fish (Smith, 1973). Summer Flounder that dispersed from the Wachapreague system during the emigration period had significantly greater odds of returning to the system the following year than did those fish that dispersed during the residency period.

The percentage of fish returning to the Wachapreague lagoon system (36%) was similar to the percentage reported for more northern estuaries (25–35% and 39% in New York and New Jersey, respectively; Poole, 1962; Sackett et al., 2007). Unlike returns in a previous mark-recapture study (Desfosse, 1995), returns to the Wachapreague lagoon system were not detected after April, although the expected battery life of our transmitters would have permitted detection through July 2008. Summer Flounder did return to the Wachapreague lagoon system as early as February, indicating that some fish may actually remain in this system for upwards of 10 months (i.e., from February to the following December).

Acoustic telemetry permitted the identification of early and temporary emigrants from estuaries in this and a previous study (Sackett et al., 2007). It is possible that early emigrants migrate to the outer continental shelf to spawn, but the timing of these events is much earlier (typically in the early summer) than the timing reported for the spawning migration of this species. Fish that disperse early or temporarily may instead occupy habitats on the inner continental shelf or in other estuaries before final emigration to the outer continental shelf to spawn. On the basis of the confirmed observation of a single fish that was subsequently detected in Delaware Bay approximately 2 weeks after tagging, there is at least some movement of Summer Flounder between coastal estuarine systems within the same summer. Previous mark-recapture studies have also indicated that Summer Flounder move from Virginia to more northern MAB estuaries

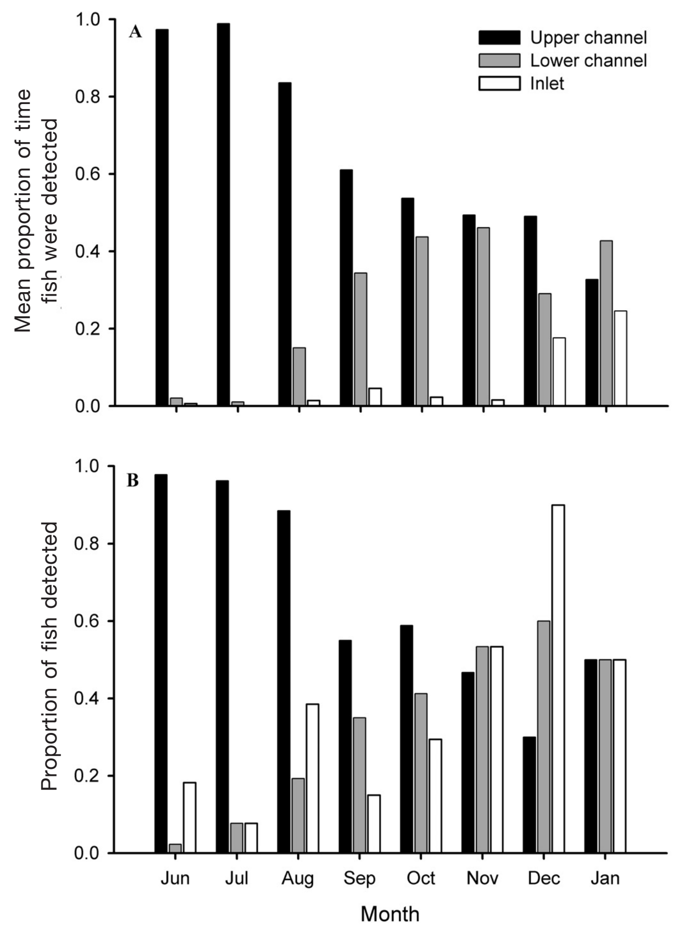


**Figure 6**

(**A**) The monthly mean proportion of time that Summer Flounder (*Paralichthys dentatus*) occupied the upper channels, lower channels, and Wachapreague Inlet in the Wachapreague lagoon system from June 2007 to January 2008. For a given month, the proportion of time that individual fish occupied each region was calculated as the ratio of the amount of time that a fish resided in a region in relation to the total time it was detected that month, with proportions for a month adding to 1. (**B**) The monthly proportion of individual Summer Flounder detected in the upper channels, lower channels, and Wachapreague Inlet. The proportion of fish that occupied a region was determined as the ratio of the number of individual fish identified in that region to the number of fish detected in the system that month. The sum of the proportions of fish in each region could be <1 if not all fish could be assigned objectively to a region in any given month. The sum of the proportions of fish that used each region could be >1 if a single fish occupied more than 1 region in any given month.

**Table 2**

Mean proportions of time Summer Flounder (*Paralichthys dentatus*) spent in each region of the Wachapreague lagoon system (upper channels, lower channels, and inlet) by month and period (residency and emigration); proportions of Summer Flounder found in each area by month and period; and numbers of fish present in the system (*N*) by month and period. The residency period was from 8 June to 10 October 2007, and the emigration period was from 11 October 2007 to 17 January 2008. Activity in tidal flats and supplementary channels was not included because of the low numbers of detections in these areas.

| | | | Mean proportion of time (%) | | | Proportion of fish (%) | | |
|---|---|---|---|---|---|---|---|---|
| | | *N* | Upper channels | Lower channels | Inlet | Upper channels | Lower channels | Inlet |
| Month | | | | | | | | |
| 2007 | June | 45 | 97.3 | 2.0 | 0.6 | 95.6 | 2.3 | 17.8 |
| | July | 31 | 98.9 | 1.1 | 0.1 | 80.7 | 6.5 | 6.5 |
| | August | 30 | 83.6 | 15.0 | 1.4 | 74.2 | 16.1 | 32.3 |
| | September | 25 | 61.1 | 34.4 | 4.6 | 44.0 | 28.0 | 12.0 |
| | October | 23 | 53.7 | 43.7 | 2.3 | 43.5 | 30.4 | 21.7 |
| | November | 16 | 49.4 | 46.1 | 1.6 | 43.8 | 50.0 | 50.0 |
| | December | 10 | 49.0 | 29.1 | 17.7 | 30.0 | 60.0 | 90.0 |
| 2008 | January | 2 | 32.7 | 42.7 | 24.6 | 50.0 | 50.0 | 50.0 |
| Period | | | | | | | | |
| | Residency | 45 | 86.3 | 11.5 | 1.5 | 97.8 | 17.8 | 40.0 |
| | Emigration | 16 | 48.9 | 14.6 | 5.6 | 50.0 | 56.3 | 87.5 |

(Lucy and Gillingham[4]), although not within the same year (as observed in our study). Early or temporary emigration from estuaries may occur in response to environmental cues not monitored in this study, such as barometric pressure or rainfall, or may simply reflect variation in migratory behavior among fish (Sackett et al., 2007; Henderson, 2012). Future research is needed to investigate the drivers of early and temporary emigration and the destination of fish that engage in these behaviors.

### Within-estuary behaviors

The distribution of Summer Flounder in the Wachapreague lagoon system was comparable to that observed in the Mullica River–Great Bay estuary (Sackett et al., 2008); in both studies, adult Summer Flounder were primarily detected in the lower bay near the inlet. In our 1-year study, nearly all tagged fish were released in the upper channels (where most fish remained). It is possible that tagged fish released in other regions exhibit fidelity to those regions and that the distribution of tagged Summer Flounder within the system differs by year; however, little difference was observed for Summer Flounder in the region of primary detection over the 2-year study in the Mullica River–Great Bay estuary (Sackett et al., 2008).

Although adult Summer Flounder occupy a variety of habitats in estuaries, sandier substrates enable these flatfish to bury themselves easily (Bigelow and Schroeder, 1953; Dahlberg, 1972; Orth and Heck, 1980; Roundtree and Able, 1992a). These substrates are often found in areas with high-velocity currents, such as those currents in channels near an inlet. Fishes and crustaceans compose a large portion of the adult Summer Flounder diet (Latour et al., 2008; Buchheister and Latour, 2011), and higher current velocities most likely deliver more potential prey into an area per unit of time. Summer Flounder have been observed in deeper areas (~8.5 m) of other MAB estuaries, presumably because of stable environmental conditions (Smith and Daiber, 1977; Sackett et al., 2008). For future acoustic telemetry studies in the Wachapreague lagoon system and in other estuaries, the effects of release location and year on tagged fish should be considered in order to make inferences about Summer Flounder distribution and habitat preferences within estuaries.

The coexistence of behavioral types has been noted in other species and postulated to result in approximately equal fitness among individuals (Bolnick et al., 2003; Kobler et al., 2009). Summer flounder appear to fit this pattern. In our study, the majority of Summer Flounder resided primarily in the upper channels, although a small group of fish (12 individuals) did use the lower channels. The use of the lower channels increased as the study period progressed, and these fish

[4] Lucy, J. A., and L. Gillingham. 2009. Virginia Game Fish Tagging Program annual report 2008. VIMS Marine Resource Report No. 2009-4. Virginia Sea Grant Publication No. VSG-09-03, 149 p. [Available from http://web.vims.edu/library/GreyLit/VIMS/mrr09-04.pdf.]

had a later mean dispersal date than the fish that did not use the lower channels. Divergent patterns of behavior have been observed in other acoustic telemetry studies on Summer Flounder. In the Mullica River–Great Bay estuary, up to 80% of fish remained in the lower bay near the inlet where they were tagged (Sackett et al. 2008), but several fish did move into the river system. At an artificial reef in the Chesapeake Bay, larger Summer Flounder were more likely to stay in close proximity to the reef structure than were smaller fish (Henderson, 2012).

The behavior of Summer Flounder in estuaries has been described as sedentary with only minor activity before fall emigration (Desfosse, 1995; Sackett et al., 2008; Henderson, 2012). This description characterized Summer Flounder in the Wachapreague lagoon system, where fish rarely exhibited large-scale movements (100s of meters) between receivers in the upper channels. However, passive telemetry cannot capture small-scale movements adequately, and fish may have been active within smaller areas (<100s of meters). Active tracking of Summer Flounder in the Mullica River–Great Bay estuary revealed that fish were in motion within small areas (0.18 $km^2$) for most of the time that they were observed and that small-scale movements in deeper waters (~8.5 m) were not related to tidal currents or temperature (Sackett et al., 2008). Small-scale activity was attributed to feeding, competition, or territorial behaviors (Sackett et al., 2008). We did not observe significant effects of temperature or tidal stage on large-scale (100s of meters) fish activity in the upper channels during the residency period. Fish in these regions may have an ample supply of prey delivered by the currents and, therefore, may not need to make large-scale movements or use energetically beneficial tidal conditions (e.g., Wirjoatmodjo and Pitcher, 1984; Szedlmayer and Able, 1993; Miller, 2010).

During the residency period, fish activity in the upper channels of the Wachapreague lagoon system was significantly greater at night than during the day. Laboratory-based observations revealed that Summer Flounder are more active during the day (Olla et al., 1972), but such studies considered activity on a much smaller scale (e.g., in a seawater tank that was 10.6×4.5×3.0 m). Similar large-scale (200–400 m) activity of Summer Flounder in the Chesapeake Bay also was greatest at night and influenced by lunar phase (Henderson, 2012). Although benthic foragers (such as Summer Flounder) are generally more light sensitive than are other estuarine pelagic piscivores (Horodysky et al., 2010), the foraging ability of visual predators is most likely limited at night. Therefore, night-time movements may be associated with behaviors other than prey localization and feeding.

## Conclusions

One of the benefits of acoustic telemetry is the ability to identify variation in behavior within a population that renders a species differentially vulnerable to estuarine conditions, predation, and harvesting. Differences and similarities in behavior patterns observed for a species by multiple researchers can be used to identify factors that influence such patterns. Our study confirms that, although the life history and migration dynamics of Summer Flounder are well described, individual fish are not uniform in their use of estuaries during summer residencies throughout the MAB.

Residence times vary by estuary, indicating that local conditions are important to population success. Fish size may also effect how long Summer Flounder remain in an estuarine system. As was found in a northern MAB estuary, most tagged Summer Flounder in the Wachapreague lagoon system were sedentary over 100s of meters and remained in deeper (>3 m) waters near the inlet until they undertook the spawning migration (although a small number of individuals did make use of other regions).

Further research is needed to consider the effects of release location and year on distribution of tagged Summer Flounder. Studies that combine acoustic monitoring with the distribution and availability of predators and prey may help explain observed distributions. Establishment of a network of strategic acoustic monitoring stations within multiple MAB estuaries and along the continental shelf would enable monitoring of fish in these habitats and could help clarify the fate of early or temporary emigrants (Grothues et al., 2005; Able and Grothues, 2007). A better understanding of Summer Flounder habitat preferences and behaviors in estuaries along their range of distribution is essential for protecting areas that promote year-class strength and spawning success.

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