ESTUARINE HABITAT AND BEHAVIOR OF WINTER FLOUNDER (*PSEUDOPLEURONECTES AMERICANUS*): AN APPROACH USING ACOUSTIC TELEMETRY IN BARNEGAT BAY, NJ, USA

By

JOAN H. PRAVATINER

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ABSTRACT OF THE THESIS

Estuarine habitat and behavior of winter flounder (*Pseudopleuronectes americanus*): an approach using acoustic telemetry in Barnegat Bay, NJ, USA

By JOAN H. PRAVATINER

Thesis Director: Dr. Kenneth W. Able

This study investigated habitat and movement dynamics in winter flounder (Pseudopleuronectes americanus) during estuarine residence in February-August 2009 in Barnegat Bay, a southern New Jersey estuary. Adult winter flounder (261-442 mm SL), including both males (N=16) and females (N=18), were acoustically tagged and relocated. This allowed characterization of habitat type and movement. Winter flounder burial behavior may have presented difficulties in relocation as tags proved incapable of transmission through sediment. Tag detection range also proved dependent on several environmental variables. Relocations occurred between early February and late July (N=115), with highest rates in February and March. 68.7% of total redetections were of male flounder. Few flounder were relocated after May. Relocations of winter flounder throughout the study period occurred mostly at a midrange temperature interface between warm water from a nuclear power plant and cool

ocean water. Sex explained part of habitat variation, with a correlation of 0.37 between sex and known environmental factors. Sex-based difference in water temperature was observed with females at a higher temperature during March, in the likely spawning period. There appeared to be differences in depth, substrate, and egress and spawning temperature in comparison to data from northern populations. Average movement rate was low, frequently less than 200 m d⁻¹, and with a peak in late February and early March. In a Bayesian model using the study's movement rate data, males consistently showed higher movement rates than females, particularly in February and March. Estuarine egress of some fish (N=11) occurred in April and early May, with males detected several weeks earlier than females.

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Introduction

Winter flounder (*Pseudopleuronectes americanus*), is a commercially and recreationally important demersal flatfish species occurring from Labrador to Georgia (Bigelow and Schroeder 1953). The species is most abundant in the north, from the Gulf of St. Lawrence to Chesapeake Bay (Able and Fahay 1998). Winter flounder have become less abundant in the last 30 years, with the fish south of Cape Cod, called the "Southern New England/Mid-Atlantic Bight (SNE/MAB)" stock now judged overfished (Hendrickson *et al.* 2006). In 2007, the SNE/MAB population stood at only 9% of target spawning stock biomass (Northeast Fisheries Science Center 2008).

In general, winter flounder have been assumed to follow a migration pattern of ingress into estuarine habitat in late fall, spawning in the cold months relative to temperature and so that spawning time varies with latitude, and then retreating offshore in late spring to escape warming estuarine waters (Pearcy 1962a; Crawford and Carey 1985; Scarlett 1991; Scarlett and Allen 1992; Stoner *et al.* 1999). This assumption may be overly simplistic. Year round estuarine winter flounder presence is also reported in both northern and southern populations (Howe *et al.* 1976; Phelan 1992). Likewise, mature specimens have been found in the ocean in winter (Phelan 1992; Wuenschel *et al.* 2009).

Collette and Klein-MacPhee (2002) define three different large-scale populations (i.e., north of Cape Cod, south of Cape Cod, and Georges Bank). At one point the Georges Bank population was considered a separate species (Pierce and Howe, 1977). The three stocks behave differently, with the population north of Cape Cod (Gulf of Maine/GOM) showing localized movements close inshore while the SNE/MAB population dispersed far offshore, and the Georges Bank population having little mingling with either of the others (Howe and Coates 1975). While the various large-scale stock populations may mingle offshore, there appears to be further separation into numerous smaller localized populations with a degree of natal fidelity to a spawning ground. Tagging studies support returns to a site and limited exchange of juveniles among sites (Perlmutter 1947; Saila 1961; Howe and Coates 1975; Howe et al. 1976; Phelan 1992). Furthermore, many previous winter flounder studies have focused on northern populations including early and commonly-cited studies. Results include data taken in New York (Lobell 1939, Perlmutter 1947), Rhode Island (Saila 1961), Canada (McCracken 1963), Massachusetts (Howe and Coates 1975), Newfoundland (Van Guelpen and Davis 1979), New Hampshire (Banner and Haves 1996), Maine (Brown et al. 2000) and the Gulf of Maine (Collette and Klein-MacPhee 2002). Data from the southernmost parts of the range are

comparatively sparse, particularly given population-based differences of behavior.

Population-based difference in habitat may explain why in previous studies, habitat is often broadly defined; for example, winter flounder-associated substrate has been identified as containing muddy sand, patchy eelgrass, clay, sand, and pebble/gravel (Pereira et al. 1999; and Collette and Klein-MacPhee 2002). These prior studies demonstrate a wide scope, but do not identify the relative importance or advantage of any particular type of substrate. Some indications exist on adult habitat preferences, leading to development of two models to characterize suitability of habitat areas in individual estuaries in New Hampshire (Banner and Hayes 1996) and Maine (Brown et al. 2000). These are comparatively large-scale observations (i.e., all salinities of 15 or greater are given equal suitability in Brown et al. 2000) and do not take into account finer variation. However, habitat quality appears to exhibit a profound influence over early life growth rates. Lengths of same-age specimens varied widely in different Long Island bays (Lobell 1939), as well as between areas in Great Bay/Little Egg Harbor, New Jersey (Sogard 1992; Witting 1995). Fish from Georges Bank are consistently noted as having faster individual growth rates than those of other populations (Lux 1973), while generally flounder in populations north of Cape Cod grow more slowly than those to the south

(Kennedy and Steele 1971). Numerous studies have been conducted on growth due to early life history habitat, including dissolved oxygen levels (Bedja *et. al* 1992; Stierhoff *et al.* 2006), temperature (Williams 1975; Rogers 1976), substrate (Pappel *et.* al 2009), depth and substrate (Sogard and Able 1991) and substrate, temperature and depth (Stoner *et al.* 2001). With demersal adhesive eggs (Pearcy 1962b) spawning habitat becomes incubation habitat in winter flounder. Given the importance of habitat quality to larval and juvenile survival and growth, identification of adult habitat in the estuary is an important issue. As is the case for data on differences between winter flounder populations in behaviors, data on potential differences based on sex is sparse. What is known is that males are initiators of spawning events and exhibited a wider spatial distribution during estuarine residence than females (Stoner *et al.* 1999).

The major purpose of this study was to clarify temporal, spatial, and environmental aspects of winter flounder residence in an estuary for a population in the southern part of the range (i.e., New Jersey). Specific objectives included to: 1) test the effectiveness of acoustic telemetry techniques for locating adult winter flounder throughout an estuarine residence cycle, 2) identify common abiotic characteristics of habitat during estuarine residency, 3) investigate habitat use and behavior with respect to the potential spawning cycle, and 4) investigate habitat and behavior differences with respect to sex.

Materials and Methods

Study Area

Barnegat Bay, an estuary in central New Jersey, is bounded on the east by a nearly continuous barrier island of approximately 48 km in length and ranging from 2-6.5 km wide (Marcellus 1972; Chizmadia *et al.* 1984) (Fig. 1). Exchange with the Atlantic Ocean to the east occurs at the 183 m wide Barnegat Inlet (Marcellus 1972). Further connections are to Manahawkin Bay/Little Egg Harbor/Little Egg Inlet (south of the Route 72 Causeway) to the south and the Manasquan River via the Bay Head-Manasquan Canal to the north (Chizmadia *et al.* 1984).

The depth ranges from 1.0-8.5 m and much of the estuary is shallow: 68% is <1.5 m deep, with the eastern region (<1 m) typically shallower than the central and western regions (1-4m). The deepest point is found in Barnegat Inlet (Kennish and Olsson 1975; Rogers, Golden, and Halpern Inc. 1990). Tidal range is approximately 1 m, and low tides may expose extensive shoals. NOAA bathymetric charts show at low tide, depths and proportion of available area are <1 m (37.3%), 1-2 m (25.8%), 2-3 m (28.7%), 3-4 m (7.1%), and >4 m (1.1%). Salinity ranges from 19 to 30, with lower salinities in the northern part of the bay and at the mouths of the creeks and rivers feeding into the bay, and higher salinity towards the ocean connection at Barnegat Inlet. Water temperature

ranges seasonally from -1.4°C to 28°C (Chizmadia *et al.* 1984; Kennish *et al.* 1984). Barnegat Bay is comprised of three basic substrate types: fine sand (66%) in the eastern part of the bay, and muddy sand (17%) and (17%) in the western portion (Kennish and Olsson 1975).

Barnegat Bay has experienced significant residential development over the last 50 years, particularly along Long Beach Island to the east (Lathrop and Bognar 2001; Environmental Protection Agency 2007). The Oyster Creek Nuclear Generating Station (OCNGS), located between Forked River and Oyster Creek 3.2 km inland from the bay, draws cooling water from Forked River and releases heated outflow through Oyster Creek (Danila 1978). The temperature differential between the outflow and ambient bay temperature can reach 3-5°C at times of peak station operation. The direction of the resultant plume of warm water varies according to weather and tidal influences (Kennish and Olsson 1975; Kennish *et al.* 1984).

Tagging and Telemetry

Tagging

Adult winter flounder (>250 mm SL) were collected with trawls and fyke nets between December 29, 2008 and April 14, 2009. Sex was determined by presence of a visible ovarian bulge, with a characteristic elongate triangular shape, and/or gamete expression, and relative state of spawning status by visual inspection for an ovarian bulge and/or presence of gametes. This included three classifications: "ripening" (showing gonad swelling but no gametes could be expressed), "ripe" (gametes could be expressed) or "running" (gametes running freely).

To permit tagging, two small punctures were made with a hypodermic needle through the pterygiophores of the dorsal fin at the level of the pectoral fin. An acoustic transmitter tag (CAFT 11_4 at 76.8 KHz with a five-second signal repeat rate, 11 x 55 mm, 327 day battery life; Lotek Wireless Inc., St. John's, Canada) was externally attached with plastic-coated stainless steel surgical wires shrink-wrapped to the tag. These wires, at each end of the tag, were run through the punctures and secured on the blind side of the fish with a surgeon's knot or a stainless steel crimp. A nylon shield on the blind side prevented chafing of the wires against the skin. Prior to release fish were retained for 10 to 25 minutes to allow recovery and a post-surgical health assessment for amount of bleeding from the tagging wound and signs of distress such as rapid gill flaring.

Acoustic Tracking

An acoustic tracking grid developed to cover the study area incorporated 110 points spaced 700-800 m apart where possible; restrictions of bathymetry and depth led to closer spacing in some instances. The radius of tag detection for other species in a similar tracking study of summer flounder in Great Bay/Mullica River, NJ, proved to be 500 m; this study's grid was developed from this prior data (Ng *et al.* 2007; T. Grothues pers. comm. 2009). The 800 m spacing allowed for an overlap of the detection range between points and thus minimized blind spots (Fig. 2). The tracking grid changed and coverage increased during the study. Nine eastern points were often inaccessible due to shallow water at low tide and the three points outside Barnegat Inlet required very calm conditions. Mobile tracking occurred weekly between early February and early August, 2009 (Table I). In January, several tracking efforts in Oyster Creek near the sites of the earliest releases of tagged fish used no formal protocol (Fig. 1). Tracking did not occur during inclement weather.

For each tracking event a baffled mobile LHP_1 hydrophone on a 3 m PVC pipe was employed to help determine signal directionality. This hydrophone was coupled to an SRX 400 receiver (Lotek Inc.) which detected and coded a tag signal. Upon reaching each detection point, the hydrophone was lowered from a stationary boat into the water below hull level, and turned at 90° intervals every six seconds to detect tagged fish transmitting at a five-second interval. When a signal was heard, relative direction and range were audibly gauged and the boat then moved until ideally the signal strength was at least 115 db at a gain of 15 or lower, indicating proximity to the tag of 2 m or less (Ng *et al.* 2007). The boat location and tag bearing were recorded along with the tag number, power, and gain. This standard was not always applicable. If, after 10 minutes, a tag signal could not be deciphered, other power/gain combinations were used to identify the tag.

Two stationary monitoring hydrophones (Lotek Inc., WHS_1100 and LHP_1 CAFT receivers) were also deployed in Barnegat Inlet to provide data on tagged fish movements through the inlet (Fig. 1). The first hydrophone (LHP_1) was deployed in November, 2008, and a second hydrophone (WHS_1100) in January, 2009. Coverage with the stationary hydrophones was not continuous throughout the study period, as the WHS_1100 unit was not working between April 9–15 and June 15–July 26.

Limits of Tag Detection

Tag detection limits, particularly through sediment covering a buried winter flounder, were explicitly examined in order to develop expectations for interpretation of tracking results. To test tag signal transmission through water and sediment, a lined plastic container with interior dimensions of 0.3 m x 0.3 m x 0.28 m was used to bury acoustic tags incorporating the CAFT 11_4 transmitter used on the tagged fish. Using the maximum burial depth for winter flounder (Fletcher 1977), these dimensions provided 15 cm of sediment laterally, and >15 cm beneath by placement of the container on the bottom sediments.

For each trial the container was filled with sediment and transmitters were placed at various depths (0/sediment surface, 5, 10, and 15 cm in initial trials, 1, 2, and 4 cm in subsequent trials), parallel to the sediment surface as would be found on a tagged flounder. Both sandy and muddy substrates were used during trials to examine potential effects of sediment type on signal transmission.

Trials (N=16) were conducted in February and March, 2010, with the container deployed on the bottom in Great Bay (Trials 1-10) and Barnegat Bay (Trials 11-16), at depths of 1.5-3.0 m simulating water depths in the study site (Table 2). After placement, a mobile hydrophone was used to test reception distances. The hydrophone was lowered into the water from a boat as in mobile tracking to detect either an audible tag signal or the capability to decode the tag signal via SRX from the tags in the container. Detection distance intervals as measured by GPS distance from the deployed box began at 12 m and proceeded through 25 and 50 m, with an additional 25 m added thereafter to a maximum of 900 m until both audibility (standard detection gain of 30) and coding capability (standard coding gain of 15) were lost. After exceeding the detection range of the tag on the sediment surface, it was removed to allow for potentially easier reception of any fainter buried tag signals. Current speed in km h⁻¹ during the drifting transect was estimated by GPS (taken on trials 5-16), and a handheld depth sounder read depth at each detection point (taken on trials 6-16). Average

wind speed (km h⁻¹) was also obtained on each tag testing day as a proxy for wave conditions.

Environmental Data

In order to characterize the environmental conditions experienced by tagged fish, a Professional Plus hand-held meter (Yellow Springs Instruments Inc.: Yellow Springs, Ohio) with probes for conductivity/salinity, dissolved oxygen, and temperature was used during mobile tracking. On redetection of a tagged fish a bottom reading was taken and, for depths >1.5 m, a surface reading as well. Also included in the data were depth, point in the tidal cycle (ebb, low, high, or flood), weather data, and estimated cloud cover. Comparative environmental data for Barnegat Bay during the sampling period were also obtained from several data recording stations. Oyster Creek Nuclear Generating Station provided temperature time series data from the Route 9 Bridge spanning the outflow of Oyster Creek and the Forked River intake (Fig. 1). No salinity time series data was available within the boundaries of the study area, so the closest possible location was used instead: the cooperatively managed New Jersey Department of Environmental Protection (NJDEP)/Monmouth University buoys at Seaside Park and Bonnet Island provided temperature and salinity data for regions to the north and south respectively (Fig. 1).

Data Analysis

Probability of Detection

The variation of sampled redetection (D_{act}) rates of winter flounder by week from the expected (D_{exp}) rate can be expressed as the influence of several factors: random movement of individuals out of the study area (M), blind spots due to reduction of detection range (R) from the assumed 500 m, and loss of detection due to burial (B), plus error (E): $D_{act} = D_{exp} - (M + R + B + E)$ (Equation 1). D_{exp} is derived from the number of tags expected in the study area for a tracking date after subtracting those recorded as having left via the inlet by a stationary hydrophone prior to that date.

M, the re-detection rate and distribution of tagged winter flounder was compared to expectations based on a 2-dimensional, individual-based Markov random walk model. The model was populated with 400 particles beginning at a single start point with coordinates of the fyke net where the majority of the winter flounder were tagged. Particles were free to move independently in the x and y direction as daily steps drawn from a normal distribution having the mean (100.1 m) and standard deviation (125.0) of daily movement observed from field studies of actual tagged flounder telemetered during the study. A non-absorptive hard boundary was coded for the western edge of the model domain at a distance from the release point corresponding to the shoreline of Barnegat Bay. The model was allowed to step 187 days (the duration of the telemetry study). The number of particles outside the north, south, or eastern sampling boundary area (as defined by the mobile telemetry search grid) was sampled on the daily time step, and the mean and standard deviation of that number was calculated based on six repeated model runs. The minimum movement rate used to obtain the mean and standard deviation was a straight-line movement from the previous redetection calculated by

$$r = \frac{\sqrt{[(x_c - x_l)^2 + (Y_c - Y_l)^2]}}{(T_c - T_l)}$$
(Equation 2)

where r=movement rate in m d⁻¹, X_c =current detected UTM X position, X_l =last detected UTM X position, Y_c =current detected UTM Y position, Y_l =last detected UTM Y position, T_c =current detection date and T_l =last detection date. For each tracking day (N=29) where tracking occurred, obtaining output of the number of particles inside and outside the boundaries of the model gave a ratio that was then applied to the 34 tagged flounder to find the number expected present in the study area on that date.

R represented reduction of the tag detection range (from the assumed radius of 500 m) due to wind speed, current speed, and depth. With mean wind speed, mean current speed, and mean depth from the tag burial trials, a General

Linear Model (GLM) regression for expected distance of audibility was calculated in SAS v 9.2 (SAS Institute Inc.: Cary, NC). For the resulting equation $r_{det} = -30.26w + 39.03d - 70.77c + 708.76$ (Equation 3) where r_{det} is the radius of audible tag signal, w is average wind speed in km h⁻¹, d is mean depth in m, and c is mean current speed in km h⁻¹, a daily mean radius of detection was calculated for each day tracking occurred. WeatherUnderground (http://www.wunderground.com/history/) provided archived daily mean wind speed for the Atlantic City airport. The University of South Carolina's Tide and Current Predictor (http://tbone.biol.sc.edu/tide/) provided current speed estimates for all peak and slack tides within one day at Barnegat Inlet, from which a daily mean was calculated. Mean daily depth calculations came from the data of detection depths on that date; if no detections occurred a mean of 2.5 m from tag trials was used. Following calculation of r_{det} for each date, the area of the resulting detection circle was compared to the area of the standard 500 m radius circle to calculate the percentage of detection area lost. This was then multiplied by D_{exp} to determine the probable number of detections lost for that date. An R of >500 m was held as a 100% coverage of detection area. B, representing effects of signal loss due to winter flounder burial, could not be measured by the methods used in this study and was combined with E to

produce a (B + E) factor. Its value remained as the difference between D_{act} and variables D_{exp} -(M+R).

For a calculation of daily catch-per-unit-effort (CPUE) in tracking, the unit of effort was held to be 10,000 m² of area searched with tracking gear, while catch was the number of fish detected. CPUE was calculated as an equation of

$$CPUE = \frac{D_{act}}{A_{point} * P_{track}}$$
(Equation 4)

where A_{point} represents the area of the circle surrounding one tracking point determined by $\pi^* (r_{dot})^2$, and P_{track} is the points accessed each day (Table 1).

Habitat Characteristics

Each redetection had individual recorded data for bottom salinity, bottom dissolved oxygen level, bottom temperature, and depth, and data for the location on an overlay map of substrate (Kennish and Olsson 1974). Several (n=4) salinity data points had measured values of 35 or greater. For the Mid-Atlantic Bight, a salinity of 35 or higher is more characteristic of offshore conditions in the Gulf Stream rather than in an estuary. Therefore these points were judged outliers, likely due to a faulty cable on the ProPlus unit. These outlier values were replaced with the highest salinity value under 35 for analysis. Analysis of likeness for these abiotic habitat data was conducted to explore degree of similarity between individual relocations and in particular between that of fish size and of male and female flounder. First, an amongsample similarity matrix was constructed on the Euclidean distance metric. A BIOENV (Biota and/or Environment matching) analysis with a Spearman rank correlation and a normalized Euclidean distance for length-based differences and a both an Analysis of Similarities (ANOSIM) test and a 2-D non-metric Multi-Dimensional Scaling (2-D MDS) ordination for sex-based differences then used this matrix. The analysis was applied in PRIMER 6 (Plymouth Marine Laboratory: Plymouth, UK).

Comparative Movement Rates

Using positions and dates from the 12 males and 4 females with 4 or more redetections during the study period, the minimum daily movement rates were calculated using Equation 2. Following calculation of these movement rates, the data were then used as the prior distribution of a model for Markov Chain Monte Carlo (MCMC) sampling to create a posterior distribution. The MCMC sampling was conducted using BUGS (Bayesian inference Using Gibbs Sampling) programming (WinBUGS, Cambridge University: Cambridge, UK) after the principles of Gelfand and Smith (1990). Analysis for movement rates between male and female winter flounder during the periods of February, March, and April-July used a comparative model: $r_t = \beta_0 + (\beta_1 * s_x)$ (Equation 3), where r_t denotes the movement rate for the i-th numbered specimen, β_0 is the sampled movement rate, and $(\beta_1 * s_x)$ is a variable conditional on the value of s_x (0 for males, 1 for females). It was added to β_0 when the specimen was female, and multiplied by zero and thus eliminated for males. Therefore β_0 expresses movement rates for a male while the values of β_1 show differences between a rate of movement for a female from that of a male. The testing of deviance information criterion (DIC) compares the gains in posterior distribution quality by implementing a more complex model. The lower DIC value indicates the favored model (Spiegelhalter et al. 2002). DIC showed the simplified model was more advantageous for February and April-July. For March, a model incorporating separate variances for males and females proved more favorable. General Analysis

Graphing procedures and basic quantitative and statistical (percentages, correlations, etc.) operations used Excel 2008 (Microsoft: Redmond, Washington) while spatial analysis used the GIS software ArcMap 9.3 (ESRI: Redlands, California). Spatial representation of measured salinity and temperature by position and month was plotted in MATLAB 2008b (Mathworks Inc.: Natick, Massachusetts).

Results

Limitations of Tag Detection

Burial in sediment and several environmental variables had a strong effect on the ability to detect acoustic tags. During 16 trials of tags buried in sediment at depths of 1-15 cm, none were audibly detected or coded at any distance. Overall detectability of tags placed on the sediment surface ranged from 50-600 m with a mean of 188 m, while the signal audibility ranged from 100-900 m with a mean of 419 m (Table 2). There was no variation in detectability based on substrate type; a tag placed on the surface sediment in an initial comparison of muddy versus sandy substrate yielded a coding and audibility distance of 100 m in both cases, and similar power upon coding at identical distances (Table 2).

Water depth was positively correlated with tag detection distance (Fig. 3). The test transects in Great Bay had a recorded depth range of 1.3-10.2 m whereas those in Barnegat Bay had a recorded range of 1.8-3.1 m. The three trials with deepest average depths (7.8, 8.0, and 8.2 m), demonstrated higher audible/code detection distances: 150/650m, 600/900m, and 175/650m respectively (Table 2, Fig. 3). Regression analysis supported a positive depth/detection distance correlation, with a 39.0 m gain in detection for every 1 m of increased depth (Equation 1). Wind speed, and thus wave action, was negatively correlated with tag detection distance (Fig. 3). The lowest wind speed (4.8 km h⁻¹) occurred with

a 600/900m code/audible range whereas the highest wind speed (24.2 km h⁻¹) occurred with a 75/350 m range (Table 2, Fig. 3). Regression analysis supported a negative wind speed/detection distance correlation, with 30.3 m of detection distance lost with each 1 km h⁻¹ increase in wind speed (Equation 1). Current speed was negatively correlated with detection distance (Fig. 3). Currents recorded in trials 5-16 ranged from 0.2-1.8 km h⁻¹, and at the lowest speed had 600/900m range and at the highest speed had a 75/300m range (Table 2, Fig. 3). Regression analysis supported a highly negative current speed/detection distance correlation, with 70.8 m of detection distance lost with each 1 km h⁻¹ increase in current speed (Equation 1). Overall, flounder burial and reduction of detection range by environmental conditions appear to have imposed important limitations on tag redetection capability, at least under the particular estuarine conditions of this study.

Characteristics of Tagged Fish and Detections

Winter flounder (N=34) were tagged in the estuary from 35 otter trawls over 5 days between November 3, 2008 and January 12, 2009 (N=6, 17.6%), and from two fyke nets on February 2, 2009 (N=28, 82.4%). (Fig. 1, Table 3). Both males (N=18, 261-342 mm SL and mean SL 300 mm) and females (N=16, 273-442 mm SL and mean SL 322 mm) were tagged and released (Fig. 4, Table 3). Visual inspection of spawning status indicated a likely start to spawning in February. In December 2008, the females (n=3) tagged were all classified as "ripening". In January, both males (n=1) and females (n=2) were "ripening". February tagged fish included "ripening" males (n=3) and females (n=5), "ripe" males (n=2) and females (n=5), and "running" males (n=12) and females (n=1).

Finding tagged flounder used mobile tracking efforts (N=30) from February 2-August 7, 2009. The minimum redetection rate of 0 occurred on 8 different tracking days after mid-April and a maximum redetection of 16 tags occurred on February 6, the first tracking day after the release from the fyke nets $(p_{axt}$ in Table 1). Of the 34 tagged flounder, 29 were relocated at least once during the study, with redetections ranging from 1-7 (Table 4, Table 5). In total 115 individual redetections were recorded between February 2 and July 22, with detections from both trawl-tagged (N=6, 5.2%) and fyke-net tagged (N=109, 94.8%) fish. Only 2 of 6 trawl-tagged fish (33.3%) were redetected, while 27 of 28 (96.4%) of fyke-net tagged fish were redetected.

Sex of tagged flounder appeared to affect frequency of redetection, with males being redetected more often than females during the period of highest redetections. 16 of 34 tagged fish were female and thus accounted for 47.1% of the tags, while 18 males accounted for the other 52.9%. However, 78 of the 115

(67.8%) total redetections were of males while 37 (32.2%) were of females. This difference in redetection by sex varied over time, with higher male rates in February-April, and more females in the few redetections in May-June (Fig. 5). Females accounted for 21 of 58 detections (36.2%) in February, 10 of 40 detections (25.0%) in March, 2 of 10 detections (20.0%) in April, 2 of 3 detections (66.7%) in May, 2 of 3 detections (66.7%) in June, and 0 of 1 detection (0.0%) in July. Males accounted for 37 of 58 detections (63.8%) in February, 30 of 40 detections (75.0%) in March, 8 of 10 detections (80.0%) in April, 1 of 3 detections (33.3%) in May, 1 of 3 detections (33.3%) in June, and 1 of 1 detection (100.0%) in July. Of the 16 flounder most frequently redetected (4 or more redetections), 12 were male and 4 were female.

Length of tagged flounder appeared to have some effect on redetection, with larger individuals being redetected slightly more often, but with redetection of smaller individuals persisting for a longer period. Small fish (261-300 mm SL) comprised 17 of 34 tags (50.0%) and 51 of 115 detections (47.0%), while larger (301-442 mm SL) flounder accounted for 17 of 34 tags (50.0%) and 64 of 115 redetections (53.0%) (Table 6). However, smaller fish were detected for a longer period than larger ones. These smaller winter flounder of <300 mm SL accounted for 25 of 58 detections (43.1%) in February, 18 of 40 detections (45.0%) in March, 4 of 10 detections (40.0%) in April, 3 of 3 detections (100.0%) in May, 3 of 3 detections (100.0%) in June and 1 of 1 (100.0%) detection in July. Flounder of 300-350 mm SL comprised 47 of 115 detections (40.9%) and 25 of 58 detections (43.1%) in February, 17 of 40 detections (42.5%) in March, 5 of 10 detections (50.0%) in April, and 0 of the 7 (0.0%)May-July detections. Flounder of 350-400 mm SL accounted for 9 of 115 total detections (7.8%), including 3 of 58 detections (5.2%) in February, 5 of 40 detections (12.5%) in March, 1 of 10 detections (10.0%) in April, and 0 of 7 (0.0%)May-July detections. Flounder <400 mm SL accounted for 5 of 115 total detections (4.4%), with this being 5 of 58 detections (8.6%) in February, and 0 of 57 detections (0.0%)in March-July (Table 6, Fig. 6).

Context for Detections

Tagged fish may not have been detected during tracking efforts due to several factors, including estuarine egress, other movement out of the tracking area, and reduction of tag detection range due to environmental conditions and burial (see *Limitations of Detection*). Multiple winter flounder (N=11) left the estuary via Barnegat Inlet between April 3 and May 4. The loss of detection potential for these fish, D_{exp} , on subsequent tracking dates particularly increased after April 24 with 5 fish leaving the estuary within the next six days (Table 1).

Several modeled parameters (Equation 1) helped account for disparities of expected detections compared to actual results. Loss of detections (M) due to movements out of the study area other than egress to the east, was a low contributor to expected lack of detections. Most of the Markov walk model test particles, representing tagged flounder, stayed inside the domain of the telemetry search grid (Fig.s 7 and 8). Almost all particles exited through the eastern edge. No particles left the grid until after day 40 (March 13). Most particles did not exit the search grid to the north and south, and only one or two did in cases where it occurred. The daily mean number of particles east of the search boundary reached a peak on the last day near 0.03, but an inflection point was reached near day 140 (June 20) when particles outside became more likely to re-enter the grid (Fig. 8). M accounts for one detection loss on February 2 due to no tracking efforts in the release area for that flounder. As calculated from Equation 1, for losses due to M from February 6 to May 19 no detection loss was expected, and from May 28 to August 7 only one detection loss per tracking day was expected (Table 1).

The number of lost tag detections due to variable environmental conditions of current speed, water depth, and wind speed/wave action (R), was highly variable and often large, particularly on earlier study dates. The calculated radius of detection capability varied from 337-554 m for a loss of detection area from the 500 m radius standard of 0 to 54.5%, with a mean loss of

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17.8%. This translated to an expected non-detection of 0-29 fish on any given date (Table 1). R loss values were higher in February through April, from 4-29 fish, than in May through August, from 2-18 fish. An R or 17 of higher, representing loss of at least 50% of detections, occurred on 10 of 16 days between February and April, and only 1 of 14 days between May and August (Table 1).

The remaining unexplained deviation from the expected daily redetections included potential losses due to flounder burial (B +E) and was also variable and often high, particularly on later study dates. B+E was from 0-21 fish on any given date (Table 1). February-April displayed typically lower values, from 0-18 fish and 5 of 16 days with a B+E value of 3 or less compared to May-July, from 4-21 fish and 0 of 14 days with a B+E value of 3 or less (Table 1).

In terms of CPUE, effort varied daily due to the radius of tag detection from conditions as well as by the number of tracking points accessed, and catch was also variable. Higher values of CPUE were found earlier in the study, with the maximum on February 6, the first initial tracking effort in a very limited area. Of larger-scale efforts, the maximum of 2.60×10^{-3} detections/10,000 m² occurred on February 11, while the minimum of 0×10^{-3} detections/10,000 m² occurred on the nine occasions of 0 detections, all April 24 or later. Higher values of CPUE occurred before April 9, with 11 of 13 tracking days showing a CPUE of 1×10^{-3} detections/10,000 m² or greater, and 5 of 13 days with a value of 2 x 10^{-3} detections/10,000 m² or greater. In contrast, CPUE values after April 9 were all below 3.0×10^{-4} detections/10,000 m², nine of which were 0×10^{-3} detections/10,000 m² due to no detections.

Habitat Characteristics

Temperature

Bottom temperatures varied seasonally, but throughout the study period most winter flounder were detected at temperatures at a midrange between the warm water from the nuclear generating station and the cold water from the inlet (Fig. 9). Measured bottom temperatures ranged from 0.5°C (February 25) to 22.5°C (July 22). Overall there was a seasonal increase in water temperature throughout the study period, particularly from early March on (Fig. 10). Average monthly bottom water temperature taken from winter flounder relocation data was: February (3.3°C), March (7.8°C), April (9.1°C), May (13.0°C), June (19.3 °C) and July (22.5 °C) (Table 7). Temperature data from the OCNGS at both intake at Forked River and outflow at Oyster Creek show an increase of $3-5 \,^{\circ}$ C at the outflow (Fig. 10). The bottom temperatures taken at redetections, when plotted against the Oyster Creek time series for February through August 2009, more closely resemble the values and seasonal trend exhibited by the

values of the intake rather than the heated outflow (Fig. 10). This may indicate avoidance of the highest available water temperatures by winter flounder, particularly as seasonal warming continued; Oyster Creek played host to several (n=2) winter flounder early in the study, where they were caught, but after March no further detections occurred there (Fig. 11 and Fig. 12). While being directly in the outflow channel may be undesirable habitat, once mixing with the waters of the open bay the heated outflow of Oyster Creek may confer some warm water influence beneficial to winter flounder in the surrounding area. Winter flounder were largely avoidant of colder areas to the north and south, and 84 of 115 (81.7%) detections were within 3 km of the mouth of Oyster Creek and the furthest detections to the south were confined to one day, February 25 (Fig.s 11 and 12). No winter flounder were detected in the colder waters near Barnegat Inlet until egress in April, and only 2 total were detected in the vicinity, although lesser focus of tracking efforts in that area prior to that point may partially explain this (Fig. 11 and 12).

Salinity

Salinity of bottom water at winter flounder redetections was typically >27, with few occurrences in the low salinity parts of the study area to the north. The bottom salinity ranged from 20.2 in the northern part of the study area to 34.3 near Oyster Creek Channel leading to Barnegat Inlet (Fig. 13). Higher salinities

occurred in the south than the north and also in the east towards the inlet compared to the west. The observed north/south gradient is supported by time series data from February to August 2009 for the two BBNEP data buoys outside the tracking area; higher salinity values consistently occurred at Bonnet Island to the south than at Seaside Park to the north. Data taken at redetections plotted against the two time series are closer to the higher-salinity waters recorded to the south at Bonnet Island than to the fresher waters north at Seaside Park although they were still higher (Fig. 14). As more winter flounder were detected to the south of the inlet than to the north and the values found at redetections were even higher than most of the Bonnet Island data due to proximity to Barnegat Inlet, this may indicate a potential preference for higher salinity waters, although influence of other habitat factors to help produce this distribution cannot be discounted (Fig. 11, Fig. 14).

Dissolved Oxygen

Bottom water dissolved oxygen (dO) values taken at winter flounder redetections varied seasonally, though they consistently stayed above hypoxic levels and ranged from 4.8-14.3 g/mL. The maximum was observed on February 17, while the minimum occurred on June 25 (Fig. 15). Peak dO values (12 g/mL or greater) occurred in February and March (Fig. 15).
Substrate

Winter flounder were most frequently found on muddy rather than sandy substrate based on comparison with reported values for the tracking area (Fig. 16). Successful catch of winter flounder for tagging with both otter trawl and fyke net occurred in sandy mud regions. After March and the start of egress, several tagged fish occupied the fine sand regions in the eastern bay (Fig. 11, Fig. 16). Of the 115 subsequent redetections of tagged winter flounder, 10 (8.7%) occurred on fine sand, 18 (15.6%) on muddy sand, and 87 (75.7%) on sandy mud (Fig. 16). The actual-to-expected detections ratio (i.e., a measure of the percentage of detections on a substrate divided by percent of that substrate available with a value of one indicating the expected value) is therefore 0.1 for fine sand, 0.9 for muddy sand, and 4.5 for sandy mud (Fig. 16). Compared to a random distribution where the ratio of locations of flounder would equal the ratio of that habitat type (i.e., an actual-to-expected of 1), the relocations occurred at a significantly higher rate on sandy mud, close to an equal rate on muddy sand, and a much lower rate on fine sand.

Depth

Tagged winter flounder were most commonly found at water depths of 1-3 m based on data taken at redetections. From comparison to NOAA bathymetric chart values for low tide depth, 20 redetections (17.39%) were <1 m, 47 (40.87%) were 1-2 m, 43 (37.39%) were 2-3 m, 4 (3.48%) were 3-4 m, and 1 (0.87%) was >4 m (Fig. 17). By comparison, actual depths recorded at tag redetection, which occurred throughout the tidal cycle, ranged from a low of 0.9 to a high of 4.3 m. Of these, 1 (0.87%) was in <1 m, 40 (34.78%) were in 1-2 m, 64 (55.65%) were in 2-3 m, 8 (6.96%) were in 3-4 m, and 2 (1.74%) were in >4 m (Fig. 17).

The actual-to-expected ratios for depth with chart depth/measured depth values are: 0.47/0.02 for >1 m, 1.58/1.34 for 1-2 m, 1.30/1.94 for 2-3 m, 0.49/0.97 for 3-4 m, and 0.77/1.55 for >4 m. Compared to a random distribution where the ratio of locations of flounder would equal the ratio of that habitat type (i.e., an actual-to-expected of 1), the relocations occurred at much lower rates for >1 m, somewhat higher rates for 1-2 and 2-3 m, somewhat lower rates for 3-4 m, and a mixed lower (chart depth) and higher (measured depth) rate for >4 m.

Trends in Movement

Average movement rate of winter flounder was low, frequently <200 m d⁻¹, and peak movement rates occurred in late February and early March (Fig. 18). The calculated minimum movement rate was 0.9 m d⁻¹ in May-June while the maximum was 587.5 m d⁻¹ in early February (Fig. 11). Individuals remained largely in the same area for extended periods, with 67.0% of redetections within 1 km of the previous location and 49.6% within 500 m (Fig. 11).

Sex and Length Based Differences in Habitat and Behavior

Differences in male and female relocations were attributable to input from both environmental and behavioral factors, while environmental factors had little correlation with length. An ANOSIM test for similarity of sex versus distribution by environmental factors produced a global Spearman's value of 0.37 at the 0.1% alpha level, i.e, a 37% correlation. The 2-D MDS analysis produced variable distances, or dissimilarities, showing some clustering but also some overlap between males versus females, and a stress of 0.19 at the twodimensional level (Fig. 19). Therefore habitat explains some of the sex-based distribution.

Temporally, there was a difference in the bottom water temperature in redetections of males and females. In February, April, May, and June there was <1°C of difference, and <0.4 °C in February, April, and June (no females were redetected in July). However, in March, male redetections (N=30) were in cooler waters with a mean temperature of 7.5 °C, compared to a mean temperature of 9.2 °C for female redetections (N=10) (Table 7).

While sex may have a role in flatfish size with larger specimens typically being female, length had a low association with habitat variability. The BIOENV analysis run in PRIMER showed that correlation of environmental variables to explain length-based differences in distribution was highest at the single-factor level, with northing UTM position as the highest value (Table 8). Northing, in general, describes covariance of several measured environmental variables in the northern part of the study area, namely deeper (Fig. 17), fresher (Fig. 13), and cooler (Fig. 9) waters as well as the potential of further untested factors. This maximum length-to-environmental distribution correlation was low with a value of 0.039, or 3.9%. Multivariate analyses had an even lower correlation at the two or three variable level, with the highest two variable correlation of 0.027 (2.7%) for northing UTM/depth, and the highest three variable correlation of 0.009 (0.9%) for northing UTM/depth/temperature (Table 8).

Behaviorally, from February-July, male winter flounder in the Bayesian model using movement rates taken from relocation data consistently showed higher movement rates than females, with the highest difference in March during likely spawning (Fig. 20). The February model produced a β_0 , or male mean movement rate, of 152.2 m d⁻¹ and a 95% CI range of 69.8 to 228.6 m d⁻¹ and a SD of 40.3 m d⁻¹. The β_1 or female difference from the male movement rate, had a mean of -41.4 m d⁻¹ and a 95% CI range of -165.1 to 88.2 m d⁻¹and a SD of 64.9 m d⁻¹. Mean variance for February's model was 194.4 (Fig. 20). The March model had a β_0 of 75.0 m d⁻¹ with a 95% CI range of 43.9 to 104.9 m d⁻¹ and a SD of 15.5 m d⁻¹. The β_1 was -55.3 m d⁻¹ with a 95% CI range of -89.0 to -20.6 m d⁻¹ and a SD of

17.3 m d⁻¹. Mean variance for β_0 was 83.5 and 17.5 for β_1 (Fig. 20). The April-July model had a β_0 of 65.0 m d⁻¹ and a 95% CI range of 7.6 to 120.5 m d⁻¹, with a SD of 28.4 m d⁻¹. The β_1 was -8.5 m d⁻¹ with a 95% CI range of -106.9 to 91.4 m d⁻¹ and a SD of 50.2 m d⁻¹. The mean variance was 100.4 (Fig. 20).

Discussion

The successful use of acoustic telemetry in redetecting fish is subject to limitations by both behavioral and environmental factors. Burial appears to be a significant factor in detection success for winter flounder. Winter flounder habitat throughout estuarine residence in New Jersey included high salinity, midrange values of possible temperatures throughout the study period, abundant dissolved oxygen, muddy substrate, and typical depth between 1-3 m. Sex and length-based differences of habitat on a multivariate level were of low significance, but there was a sex-based difference in water temperature in March during likely spawning season. Movement rates were typically low, less than 200 m d-1, with a peak in late February during likely spawning season. Males consistently demonstrated higher activity levels than females in both number of redetections and movement rates. Males also began egress several weeks earlier than females.

Detections were sporadic in nature during mobile telemetry, indicating a variable detection potential which can be attributed to both behavioral and environmental effects. Success of signal detection in active telemetry is subject to effects of species behavior, including burial and movement from the study area. Burial in particular could have affected results. Winter flounder have been shown to bury up to 15 cm (Fletcher 1977), as a response to cold water. They also may bury in response to extreme heat (Olla *et al.* 1969). Burial as a result of posttagging stress is unlikely based on observations of winter flounder successfully spawning within hours of tagging (B. Phelan and T. Grothues unpub., 2006). Tags were effectively muted at any distance by burial in this study, even at 1 cm depth. Burial is therefore a likely explanation of the difference in expected versus actual detection rates, particularly at the coldest and warmest water temperatures. In particular, February had "missing" detections unexplained by other factors, despite tagged fish expected in closest proximity to the release sites. Burial is likely a significant factor in future telemetry studies involving winter flounder as well as other species with burial behavior.

Modeling suggests that movement out of the study area played a small role in potential non-detection in terms of intraestuarine movement out of the study boundaries. The directed effort of egress was accounted for by hydrophone detections rather than modeling. Model particles acted similar to flounder that were redetected later in the study in that the magnitude of their particle movement was determined by measured rates of actual winter flounder movement. However, the model did not include the movements of flounder that left the area in a directed, migratory movement as this movement (and the ensuing lack of redetections) necessarily removed them from consideration in the modeled-rate distribution. This provides an important bias to understanding

results. It was intended that the moored hydrophones would address this by providing data on egress. However, the periods in April and June-July where continuous hydrophone coverage of the inlet was not maintained may mean that flounder exited the estuary undetected. As egress was not recorded for 23 of the 34 flounder and thus these flounder were expected to be in the tracking area, the periods of missing egress detection likely played a role in the difference between actual versus expected detection rates later in the study. Data from the moored hydrophones rarely show consistent recording of tag signal at the expected five second interval, indicating limitation by environmental conditions likely played a role. Both hydrophones were deployed in an area of increased boat traffic in spring and summer, and propeller noise and the bubbles introduced by wake could have reduced detection capabilities (Grothues and Able 2007b). Swift current through the narrow inlet may have reduced range, as could areas of rapidly sloping bathymetry right near the dredged channel and variable wind/wave action.

While no tag losses were recorded due to catch of tagged fish by recreational or commercial fishermen, catches may have gone unreported, despite tags being labeled with contact information and distribution of brochures with information on the study encouraging anglers to report tagged fish. One tag found on shore near the tagging site after conclusion of the study suggests that loss to fishermen was a possibility. Tags were labeled with contact information and brochures with information on the study encouraging anglers to report tagged fish were distributed. Egress might have occurred via Manasquan Inlet to the north but is unlikely as few fish were detected moving northward from the study area, and egress to the south via Little Egg Inlet was never recorded by a stationary hydrophone array there. In summary, elements of individual behavior and environmental conditions appear to play a large role in the success of tag signal detection in both active and passive telemetry, and variability in both factors should be considered in interpreting the results of this study. Burial behavior in particular is a presently unquantified factor that may carry considerable significance.

As a method of obtaining winter flounder for tagging, fyke netting proved far more efficient on a catch-per-effort-hour basis than otter trawling. A fyke net set out for 24 hours yielded the majority of the tagged fish (N=28) and observation of over a hundred mature-sized flounder in the nets, while 7.1 hours of the net in the water during otter trawling produced few tagged fish (N=6). Multiple days of otter trawling in late 2008 in two additional estuaries, Great Bay and Absecon Bay, resulted in no catch of adult winter flounder. In a concurrent study in 2009 to the north in the Navesink River, NJ, fyke netting was also a more effective method of catching winter flounder compared to otter trawl (T. Grothues, pers. comm. 2009). Fyke net caught fish were also more successfully redetected than those from otter trawl.

Tagged winter flounder exhibited sex-based differences in size and indicated a likely start to spawning in mid-January to early February. The tagged adult male winter flounder were typically smaller than females, with a male range of 261-342 mm SL and a female range of 267-442 mm SL. These results are consistent with prior studies indicating evidence for later maturation and thus larger size in adult female winter flounder (Perlmutter 1947; Saila 1962; Kennedy and Steele 1971). No males were tagged in December, but the females were classified as "ripening". Tagged males and females in January were also "ripening". On February 2, individuals in all three spawning status stages were found, with females more in the "ripening" and "ripe" stages while males were predominantly in the "running" stage. This possibly indicates spawning began sometime in February, which is consistent with a prior study of winter flounder spawning in New Jersey that determined it occurred January-March (Scarlett and Allen 1992).

Water temperatures where winter flounder were found in this study were consistent with prior data from northern populations regarding a survivable range and likely spawning temperatures, as well as indications of a temperature where flounder buried to escape warming waters also fit with the end of

detections. The relocations in this study from February to July occurred in waters ranging from 0.5-22.5 °C. The minimum survivable temperature observed in previous laboratory results was -1.4 °C (Duman and DeVries, 1974). Sources disagree on the maximum survivable water temperature for adults, though winter flounder are more vulnerable to heat shock than cold shock (Hoff and Westman 1966). Collette and Klein-MacPhee cite the lowest figure at 19.3 °C for the Gulf of Maine (2002). Pearcy cites the highest figure at 30 °C (1962a). Two sources agree on 27 °C (McCracken 1963; and Hoff and Westman 1966). In terms of activity levels, one study reports adult winter flounder going inactive and burying at water temperatures above 22 °C (Olla *et al.* 1969). Another study reports some adults were caught up to 23 °C (Howe and Coates 1975). The lack of catch at higher temperatures could be due to mortality, or potentially due to inactivity. Overall the temperature survival range is -1.4 °C with a maximum likely around 27 °C, and with a cessation of activity after 22-23 °C. As this study detected no winter flounder once water temperature reached 22.5 °C, the citation of 22 °C as a temperature where activity stopped and winter flounder buried becomes of interest given this study's finding of burial hindering detection.

Water temperature data for the probable spawning and egress period were consistent with previous findings in New Jersey but are inconsistent with data taken in northern winter flounder populations, with probable spawning

occurring at higher temperatures and egress at lower temperatures. The winter flounder spawning season in New Jersey is reported as January-March (Scarlett and Allen 1992). No water temperatures were taken in January as tracking did not occur, but monthly averages were calculated for February (3.3°C) and March (7.8°C). These findings are close to observations taken in the study area at Double Creek in 1988, for both February (4.0°C) and March (8.3°C) (Scarlett 1991). While Double Creek is more distant from the warm water influence of Oyster Creek Nuclear Generating Station than the primary redetection area, it apparently still exhibits similar temperatures compared to other regions of the bay. In northern populations, another source for the Gulf of Maine indicates a spawning temperature range of 0-3°C with a maximum of 6°C (Bigelow and Schroeder 1953). A third source reports most spawning occurs below 3.3°C with 5.6°C as an upper limit in the Gulf of Maine (Collettee and Klein-MacPhee 2002). The study data suggests spawning at temperatures higher than these supposed limits, but this may be attributed to these sources being from winter flounder populations north of Cape Cod which may experience different environmental limitations. The first recorded egress, early in April, occurred at water temperatures of 9.0°C. This agrees with previous New Jersey results indicating spawning in January-March (implying that egress after spawning should be occurring in April) and an April average water temperature of 9.3 °C in the study

area at Double Creek in 1988 (Scarlett 1991; Scarlett and Allen 1992). Other studies for northern populations report an optimal winter flounder habitat water temperature range of 12-15°C in Canada (McCracken 1963), around 11°C in laboratory study (MacIsaac *et al.* 1997), or 10-16°C in Maine (Brown *et al.* 2000), and egress at 15°C or higher in Massachusetts (Howe and Coates 1975). All of these water temperatures correspond to observations taken in May in the present study, when egress was under way for some time and the detection rate was decreasing. This disparity of temperature for egress, like that in spawning temperature, may also be due to the prior cited results being from north of Cape Cod and thus from a different population of winter flounder.

Salinity appeared to exert an influence over winter flounder location in Barnegat Bay, with fish being found in relatively high salinity waters of 27 or greater, in waters near the inlet. Polyhaline waters are said to be favored for distribution by one source from New Hampshire (Armstrong 1997). Spawning generally occurs at salinities as low as 11.4 and high as 33.0 (Collette and Klein-MacPhee 2002), while a salinity of 31-32.5 is favored for egg deposition in inshore waters and on the continental shelf for the Gulf of Maine (Bigelow and Schroeder 1953). While winter flounder may be able to tolerate more brackish waters, polyhaline or euhaline waters seem to be the most favorable habitat. Other flatfish species are also reported to have salinity-based influence over their distribution and movements, including European plaice, *Pleuronectes platessa* (Poxton and Nasir 1985), common sole, *Solea solea* (Dorel *et al.* 1991), European flounder, *Platichthys flesus* (Kerstan 1991), and summer flounder, *Paralichthys dentatus* (Sackett *et al.* 2007).

Dissolved oxygen (dO) levels measured at winter flounder locations appear higher than previously cited detrimental minimums, even as dO level decreased seasonally. The range of values (4.8-14.3 g/mL) is all above a cited sensitivity to dO levels <3 mg/L (Collette and Klein-MacPhee 2002). Two previous studies on juvenile growth rates found low dO levels had a detrimental effect at a level of 2.2 mg/L (Bedja *et al.* 1992; and Stierhoff *et al.* 2006). Flatfishes generally show a higher oxygen consumption for larger individuals (Duthie 1982), including winter flounder in a study conducted in Canada (Voyer and Morrison 1971). This finding, combined with decreased gas dissolution at higher temperatures, suggests that while it was not a factor in this study, higher water temperatures and lower dO levels found in late spring and summer may render some estuarine habitats unsuitable for larger flounder.

Substrate for winter flounder habitat appears highly variable and inconsistent between populations. Winter flounder is one of few flatfish species that possess demersal adhesive eggs (Pearcy 1962b). These eggs sink and settle below the spawning activities; therefore spawning habitat substrate becomes incubation substrate. The majority of detections in this study occurred on substrate containing a higher proportion of mud than sand (i.e., "sandy mud"). However, other researchers have found spawning or eggs on sandy bottom and algal mats in the Gulf of Maine (Collette and Klein-MacPhee 2002), soft sediments with eelgrass in New Jersey (Stoner et al. 2001), or sandy substrate in the Gulf of Maine (Bigelow and Schroder 1953). Winter flounder are also noted for having typical habitat of muddy sand when inshore (Collette and Klein-MacPhee 2002) or being on muddy bottom and burying off Georges Bank (Bigelow and Schroeder 1953). Studies in New Jersey of juveniles and young-ofthe-year cite association with sandy substrate (Able and Fahay 1998). Given this conflicting evidence for sand versus mud composition, substrate for winter flounder habitat appears highly variable. This could indicate substrate has a low influence on habitat suitability and further assessment may be necessary. Alternatively, substrate variation could indicate a population-based difference that needs to be assessed on the individual estuary level.

Winter flounder stayed primarily at shallow depths, consistent with other studies in New Jersey. Most fish were found at depths of 1-3 m; there were no detections in the deepest parts of the bay, or in the dredged channels and Barnegat Inlet, until egress. A study in the Navesink River found a mean adult winter flounder location depth of 2.6 m despite having depths of nearly 10 m available (Grothues unpublished, 2009). In northern populations deeper waters seemed more favorable. The low tide mark to 3 m depth was deemed only half as suitable habitat as the three ranges spanning 3-50 m for a study of ideal winter flounder habitat modeling in Maine (Brown *et al.* 2000). Georges Bank winter flounder occur at 46-82 m (Collette and Klein-MacPhee 2002). In the Gulf of Maine, eggs are deposited in 2-80 m depths (Bigelow and Schroeder 1953). As winter flounder did not heavily use the deeper areas available to them in Barnegat Bay, it appears that in New Jersey populations the distribution by depth is perhaps at least in part behaviorally rather than environmentally controlled. The deeper ideal ranges cited for studies north of Cape Cod in different winter flounder stocks also support a behavioral basis for depth range that may vary according to population.

Winter flounder showed quite low movement rates, up to a maximum of 587.5 m d-1 (24.5 m/hr). Similar telemetry studies of several other co-occurring Mid-Atlantic Bight estuarine species show much higher maximum movement rates. These include summer flounder, *Paralichthys dentatus*, at 4448.7 m/hr (Sackett *et al.* 2007), striped bass (*Morone saxatilis*) at 1354 m/hr (Ng *et al.* 2007), and weakfish (*Cynoscion regalis*) at 2553 m d-1 (106.4 m/hr) (J. Turnure, pers. comm., 2010). The measured movement rates appear valid: winter flounder have previously been recorded as having stayed in the vicinity of tagging sites during

estuarine residence (Lobell 1939; Perlmutter 1947; Van Guelpen and Davis 1979). Furthermore a study of acoustically tagged winter flounder in the Navesink River in 2009 found that most fish stayed within a hydrophone array with coverage of about 3 km² until egress from the estuary (T. Grothues, unpublished data, 2009). While the calculated rates represent the minimum rate required to move between two points and have some innate temporal uncertainty, they likely represent an overall low activity and movement rate in winter flounder.

Recorded tag signals of winter flounder in Barnegat Inlet in April and May indicated egress during these months. Size also plays a role in egress as smaller individuals remained in the estuary longer, by up to two months. After May, the only detections were of sub-legal (<300 mm) fish and these persisted into late July. Young-of-the-year and older immature flounder remain year round in Barnegat Bay and can tolerate the temperatures (Danila 1978). Larger specimens apparently cannot, possibly because of their higher oxygen demand as dO levels decrease with increasing water temperature (Voyer and Morrison 1971). Observed avoidance of 24.4°C water for age 1+ flounder also included speculation that with increased size, the avoidance temperature would decrease (Gift and Westman 1971). Warming waters may prompt egress by larger flounder while smaller fish that can withstand higher temperatures stay longer in the estuary.

This study found clearer indicators for behavioral than multivariate habitat differences between sexes during the spawning period, and little indication for multivariate habitat differences versus size. However, there was a sex-based difference in water temperature. In February, the difference was negligible: mean bottom water temperatures at redetection were 3.2 °C for females versus 3.4 °C for males; in March, females had a higher mean water temperature of 9.2 °C compared to 7.5 °C for males. March coincided with a sudden increase in water temperature and the period of highest movement rates and could indicate an active spawning time. Hatch time for winter flounder eggs varies inversely with temperature up to 10 °C (Williams 1975). An earlier hatching confers several potential advantages for winter flounder once they reach the juvenile stage and settlement, including less competition for food sources and decreased predation risk as a consequence of earlier growth to a larger size before many predators migrate back into the estuary. The mean female water temperature was <10°C and only one individual was in warmer water, indicating most females were perhaps in habitat advantageous for egg development. Males are known to initiate spawning events and have a wider geographic range during spawning. Males spawn far more than females (147 mean spawning events in males in a season versus 40 for females), and upon spawning of a pair other males in the area may quickly also spawn. Overall

winter flounder male spawning strategy maximizes individual genetic contribution to egg fertilization (Stoner *et al.* 1999). The use by females of temperature-favorable habitat for egg development during spawning and the low female movement and detection rates, suggests that female strategy is to settle down on ideal spawning sites waiting for males to arrive and initiate spawning, while higher male movement and detection rates suggest the male strategy is to roam from site to site seeking out numerous females. The most frequently redetected flounder (4 or more redetections) were composed of 12 males in comparison to 4 females. This lower rate of individual redectection supports a lower activity level of females, and may indicate more frequent burial behavior.

Summary

Winter flounder (*Pseudopleuronectes americanus*) is a commercially and recreationally important flatfish species; its stocks are presently both overfished and less abundant. Traditionally winter flounder are assumed to migrate inshore to estuarine waters in fall and winter for spawning, and move offshore as the waters warm. However, evidence for distinct population divisions and behavior, even down to the localized level, suggest variable patterns of estuarine residence during spawning. This study investigated habitat and movement dynamics in winter flounder during estuarine residence in February-August 2009 in Barnegat Bay, a southern New Jersey estuary. Adult winter flounder, males (n=16) and females (n=18), were acoustically tagged and relocated. This allowed characterization of habitat type and movement in the western portion of Barnegat Bay.

Winter flounder burial behavior may have presented difficulties in relocation as tags proved incapable of transmission through sediment. Tag detection range also proved dependent on depth, current, and wind/wave action, indicating a need for consideration of both site conditions and species behavior in further acoustic studies. Relocations occurred between early February and late July (n=115), with highest rates in February and March. Despite nearly equal sex ratio in tagging, 68.7% of total redetections were of male flounder, with the highest ratio difference from February-April. Few flounder were relocated after May. Relocations of winter flounder throughout the study period occurred mostly at a midrange temperature interface (from 0.5-22.5°C) between warm water from a nuclear power plant and cool ocean water even as seasonal variation increased the water temperature. Habitat of males versus females demonstrated no significant difference in the variables of dissolved oxygen level, substrate, depth, and salinity. Sex-based difference in water temperature was observed (March mean of 7.8°C for males and 9.5°C for females) during part of the spawning period.

Average movement rate of winter flounder was low, frequently less than 200 m d-1, and peak movement rates occurred in late February and early March. Individuals remained largely in the same area, with 67.0% of redetections within 1 km of the previous location and 49.6% within 500 m. In a Bayesian model using movement rate data taken from the study, males consistently showed higher movement rates than females, particularly in February and March (February mean for males: 152.2 m d-1 versus females: 107.8 m d-1, and in March males: 75.0 m d-1 versus females 19.7 m d-1). Estuarine egress of some fish (n=11) occurred in April and early May, with males observed several weeks earlier than females.

In summary, winter flounder habitat throughout estuarine residence included high salinity, midrange values of possible temperatures, abundant dissolved oxygen, muddy substrate, and typical depth between 1-3 m. The only sexually-differentiated habitat variable was water temperature in March during spawning season. Movement was typically low with a peak in late February during spawning season, and males consistently demonstrated higher activity levels than females both through number of redetections and movement rates, as well as an earlier start to egress.



Figure 1: Study area, with the location in New Jersey and in the Barnegat Bay coastal system (insets). Indicated are sites for tagged winter flounder releases, Oyster Creek Nuclear Generating Station, and sampling sites for water temperature/salinity data.



Figure 2: Winter flounder tracking grid by date of addition in 2009. Some symbols indicate conditional inaccessibility with respect to tide and weather. See Fig. 1 for additional site details.



Figure 3: Audible signal distance for an acoustic tag on sediment surface (N=16 trials) vs. mean wind speed (all), mean current speed (trials 5-16), and mean depth (trials 6-16) in February and March 2010. Trials 1-10 were in Great Bay and 11-16 in Barnegat Bay. See Table II for additional individual trial details.



Figure 4: Sex distribution by length (in 10 mm bins) for 34 tagged winter flounder in 2009.



Figure 5: Monthly detections of tagged winter flounder by sex during 2009.



Figure 6: Redetections of tagged winter flounder by date versus length (SL) at tagging in 2009. Horizontal line indicates 300 mm, the legal commercial and recreational catch size limit in New Jersey.



Figure 7: Particle (representing winter flounder) distribution on final daily time step of 187 in one run of Markov walk model, with 400 independent particles starting at coordinates marked by circled cross. Rectangle marks boundary of search area. Axis units are in m, corresponding to UTM zone 18N.



Figure 8: Mean (circles) and SD (dots) in percent of 400 particles (representing winter flounder) outside of search grid in model domain over time (187 days).



Figure 9: Bottom water temperature by position at tagged winter flounder redetections in a) February, b) March, and c) April 2009. Position by UTMs.



Figure 10: Water temperature by date in 2009 measured at tagged winter flounder redetection sites (Detections) and Oyster Creek Nuclear Generation Station sensors (Discharge and Intake, see Fig. 1 for locations)



Figure 11: Redetections for four representative tagged male winter flounder by location and date in 2009. "2/2 (R)" indicates release site on February 2. a) Tag 93 (338 mm SL): present in temperature maximums in Oyster Creek into March b) Tag 88 (304 mm SL): in southern waters only on February 25 with subsequent northern movement. c) Tag 194 (316 mm SL): most redetections near release, also only redetection in inlet waters during estuarine egress in April. d.) Tag 186 (274 mm SL): initially remained near release site then moved north, remaining until late July.



Figure 12: Redetections for four representative tagged female winter flounder by location and date in 2009. "1/29 (R)" or "2/2 (R)" indicates release site on January 29 or February 2. a) Tag 6 (298 mm SL): present in temperature maximums in Oyster Creek into March b) Tag 80 (296 mm SL): most redetections near tagging site even in egress period. c) Tag 81 (357 mm SL): exhibited southern movement only until February 25 before moving northward. d) Tag 87 (382 mm SL): redetections occurred mostly near tagging site until last detection before egress on April 30.



Figure 13: Bottom water salinity by position at tagged winter flounder redetections in a) February, b) March, and c) April 2009. Position by UTMs.



Figure 14: Salinity by date in 2009 measured at redetections of tagged winter flounder (Detections) and data buoys to north and south of study area (Seaside Park and Bonnet Island, see Fig. 1 for locations)


Figure 15: Bottom water dissolved oxygen (dO) by date in 2009 at tagged winter flounder relocations.



Figure 16: Position of tagged winter flounder redetections (dots) by substrate types (from Kennish and Olsson 1975)



Figure 17: Distribution by depth (in m) of tagged winter flounder at redetections in 2009 by a) locations (dots) with NOAA bathymetric chart values and b) depth soundings by date at redetection.



Figure 18: Minimum rates of movement (measured as straight-line distance from last location) in m d-1 by date for winter flounder redetections in 2009.



Figure 19: Two-dimensional MDS plot for correlation of dissimilarities in male vs. female winter flounder distributions with environmental variables.



Figure 20: Posterior distributions for Bayesian statistical models for comparative daily movement rates between males and females in a) February, b) March, and c) April-July. beta_0 indicates daily rate of males, beta_1 difference between a male and female rate (negative indicates female rate is lower), and sigma is variance. For March, sigma[1] is for male variance and sigma[2] for female variance.

Table 1: Record of winter flounder tracking effort by date in 2009 with number of points accessed of 110 maximum (P_{track}), actual detections (D_{act}), expected detections (D_{exp}) after removal of fish with known egress, and potential removal by movement out of study area (M), reduction of detection range (R), burial and error (B + E), and flounder detections/10,000 m² tracked (CPUE).

Date	P_{track}	D _{act}	D_{exp}	М	R	B+E	CPUE
2/2/2009	3	1	6	1	4	3	5.90E-03
2/6/2009	76	16	34	0	9	9	2.18E-03
2/9/2009	76	8	34	0	18	8	1.28E-03
2/11/2009	76	9	34	0	29	0	2.60E-03
2/17/2009	81	11	34	0	13	10	1.98E-03
2/25/2009	75	9	34	0	13	12	1.46E-03
2/26/2009	78	4	34	0	23	7	9.07E-04
3/6/2009	75	3	34	0	27	4	8.78E-04
3/10/2009	79	11	34	0	25	0	2.46E-03
3/18/2009	85	7	34	0	22	5	1.81E-03
3/26/2009	69	10	34	0	23	1	2.56E-03
3/31/2009	84	9	34	0	23	2	1.90E-03
4/9/2009	101	6	32	0	26	0	1.30E-03
4/17/2009	108	2	30	0	10	18	2.26E-04
4/24/2009	99	0	30	0	26	4	0
4/30/2009	102	1	25	0	13	11	1.43E-04
5/6/2009	104	2	23	0	13	8	2.80E-04
5/12/2009	107	0	23	0	2	21	0
5/19/2009	102	1	23	0	4	18	1.20E-04
5/28/2009	104	0	23	1	13	9	0
6/2/2009	110	1	23	1	10	11	1.32E-04
6/10/2009	102	1	23	1	9	12	1.20E-04
6/17/2009	110	0	23	1	16	6	0
6/25/2009	103	1	23	1	10	11	1.18E-04
7/1/2009	101	0	23	1	6	16	0
7/8/2009	102	0	23	1	10	12	0
7/17/2009	103	0	23	1	7	15	0
7/22/2009	105	1	23	1	8	13	1.16E-04
7/29/2009	100	0	23	1	18	4	0
8/7/2009	100	0	23	1	7	15	0

Table 2: Summary of trial number, location (Trials 1-10 in Great Bay, Trials 11-16 in Barnegat Bay), substrate (mud in Trials 1 and 3-16 and sand in Trial 2) and conditions for tests on signal strength of buried tags. Wind speed is reported average for the day. Coding and audibility ranges are for a tag placed at the sediment surface. Coding range is at gain of 15 and audibility range is at a gain of 30. N/A indicates no data was taken.

	Wind Speed	Current Speed	Depth	Coding Range	Audibility	Tag Burial
Trial	(km h-1)	(km h-1)	Range (m)	(m)	Range (m)	Depths (cm)
1	6.44	N/A	N/A	100	100	0, 5, 10, 15
2	19.32	N/A	N/A	100	100	0, 5, 10, 15
3	22.54	N/A	N/A	50	100	0, 5, 10, 15
4	9.66	N/A	N/A	75	350	0, 15, 10, 15
5	24.15	1.8	N/A	75	300	0, 5, 10, 15
6	3.22	0.2	3.3-10.2	600	900	0, 5, 10, 15
7	9.66	1.5	1.3-2.0	100	325	0, 5, 10, 15
8	9.66	1.5	1.5-9.0	400	650	0, 5, 10, 15
9	8.05	1.4	2.7-9.4	150	650	0, 5, 10, 15
10	8.05	1.4	2.8-9.7	175	650	0, 2, 4
11	4.83	0.4	2.0-3.5	250	650	0, 2, 4
12	4.83	0.7	1.8-2.9	250	600	0, 2, 4
13	4.83	0.7	1.8-2.9	250	600	0, 2, 4
14	16.1	0.8	2.4-2.9	225	375	0, 1, 4
15	16.1	1	2.4-2.8	100	200	0, 1, 4
16	16.1	1.2	2.4-2.7	100	150	0, 1, 4

	Length Range	Mean Length					Fyke	
	(mm)	(mm)	Dec	Jan	Feb	Trawl	Net	Total
М	261-342	300	0	1	17	1	17	18
F	273-442	322	3	2	11	5	11	16
Total	261-442	310	3	3	28	6	28	34

Table 3: Number of winter flounder tagged in 2009 relative to sex, size, tagging month, and gear type used in collection.

Table 4: Record of winter flounder redetections in 2009 by individual tag number and tracking date. "X" indicates tagging date. Black-shaded box indicates successful redetection of that tag on that date. Grey-shaded rows indicate females while white rows indicate males.



Total	
Redetections	Number of Flounder
1	5
2	5
3	3
4	2
5	5
6	5
7	4

Table 5: Frequency of number of redetections for tagged winter flounder from February to August, 2009

Table 6: Total tags deployed and total redetections for tagged winter flounder, as well as totals by month for February-July 2009, given by length in 10 mm bins. Grey-shaded cells indicate length below New Jersey legal limit (300 mm SL) while white cells indicate legal-sized length.

Length	Tags	Redetections	February	March	April	May	June	July
261-270	3	10	5	3	0	1	1	0
271-280	6	20	9	7	2	0	1	1
281-290	3	7	2	3	2	0	0	0
291-300	5	17	9	5	0	2	1	0
301-310	3	7	2	4	1	0	0	0
311-320	4	11	5	4	2	0	0	0
321-330	0	0	0	0	0	0	0	0
331-340	5	24	15	8	1	0	0	0
341-350	1	5	3	1	1	0	0	0
351-360	1	3	1	2	0	0	0	0
361-370	0	0	0	0	0	0	0	0
371-380	1	0	0	0	0	0	0	0
381-390	1	6	2	3	1	0	0	0
391-400	0	0	0	0	0	0	0	0
401-410	0	0	0	0	0	0	0	0
411-420	0	0	0	0	0	0	0	0
421-430	0	0	0	0	0	0	0	0
431-440	0	0	0	0	0	0	0	0
441-450	1	5	5	0	0	0	0	0

	Feb	Mar	Apr	May	June	July
F	3.2	9.2	8.8	12.7	19.3	
Μ	3.4	7.5	9.2	13.4	19.4	22.5
Total	3.3	7.8	9	13	19.3	22.5

Table 7: Monthly mean bottom water temperatures taken from data collected at winter flounder redetections in 2009, by total average and by sex.

Table 8: Highest value correlations for BIOENV analysis for five environmental variables (depth, bottom temperature, bottom salinity, bottom dissolved oxygen level/dO, and substrate type) and two position variables (easting and northing UTM) against winter flounder distribution by size.

Correlation	Variables
0.039	Northing UTM
0.034	Depth
0.027	Northing UTM, Depth
0.018	Depth, Substrate
0.017	Depth, Salinity
0.014	Northing UTM, Substrate
0.013	Depth, Temperature
0.009	Northing UTM, Depth, Temperature

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