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Habitat dynamics of summer flounder *Paralichthys dentatus* within a shallow USA estuary, based on multiple approaches using acoustic telemetry

D. K. Sackett[1,2], K. W. Able[1,*], T. M. Grothues[1]

[1]Marine Field Station, Institute of Marine and Coastal Sciences, Rutgers University, 132/800 Great Bay Blvd., Tuckerton, New Jersey 08087, USA

[2]*Present address:* Department of Zoology, David Clark Laboratory, North Carolina State University, Raleigh, North Carolina 27695-7617, USA

ABSTRACT: A comprehensive understanding of habitat use for economically and ecologically important species in estuaries is lacking. This research, based on passive and active ultrasonic telemetry, focuses on temporal and spatial patterns of juvenile and adult (length = 268 to 535 mm) summer flounder *Paralichthys dentatus* habitat use during years, seasons, tides, and diel periods from 2003 to 2005 in the Mullica River-Great Bay estuary in southern New Jersey, USA. Annual site fidelity was demonstrated by tagged fish that returned to the study estuary and frequented locales within 550 m or less of the sites where they were located in previous year(s). Fish resided within the estuary for a mean of 86 d (range: 1 to 217 d) during summer 2004, the year of the most comprehensive tracking. Fish primarily utilized the lower bay, close to the ocean inlet. Several more mobile individuals moved along the channel of the Intracoastal Waterway in Great Bay numerous times in a single season, while others moved up the bay and into the river in a year when salinity was higher than average. Tagged fish typically used deeper areas of the estuary correlated with high, stable levels of dissolved oxygen (DO) and temperature. Over diel and tidal periods, fish resided within small (0.18 km^2) areas for 3 to 6 h but were in motion 74 % of that time. Together, these observations indicate habitat-use patterns that are stable over long periods (years) but dynamic within shorter time periods (seasons, hours).

KEY WORDS: Habitat · Estuary · Movement · Site fidelity · Dynamics · Summer flounder · Essential fish habitat · Ultrasonic telemetry

INTRODUCTION

The threat of habitat alteration and destruction to fish species of economic and ecological importance has become a major concern in the USA in the last decade (NOAA 1996). In response, the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens Act), with the cooperation of the National Marine Fisheries Service (NMFS), mandated the identification, protection, enhancement; and conservation of habitat necessary to fish growth and survival, defined as Essential Fish Habitat (EFH) (NOAA 1996). Distribution and abundance, based on static sampling, are often used to describe EFH because detailed information on fish's dynamic use of variable habitats is difficult to measure and quantify (Able 1999, Beck et al. 2001, Able et al. 2005, Dahlgren et al. 2006). This results in numerous, broad and temporally static designations of EFH that can be of limited value, or perhaps misleading, for fisheries management or for understanding the role of fishes in ecosystems (Kraus & Musick 2001, Terceiro 2001). A detailed understanding of the effect dynamic habitat characteristics have on habitat selection needs to be established to provide adequate management for economically important species and ecosystems. This is especially true for species whose growth and survival are dependent on habitats like coastal and estuarine waters, which are likely to be impacted by anthropogenic sources (Able 1999, Hoss et al. 1999, Quinlan & Crowder 1999). Furthermore, this information is critical for species that are migrants or are seasonally abundant in estuaries

*Corresponding author. Email: able@marine.rutgers.edu

because habitat loss could ecologically affect populations in other areas. One species that fit these requirements in our study area is the summer flounder *Paralichthys dentatus*.

Estuarine habitats are dynamic on tidal, diel, daily, seasonal, and yearly scales. Thus, habitat use and movement of fish in estuarine waters is likely dynamic as well. This causes problems when assessing habitat quality with classic distribution and abundance techniques. Many of these assume that fish distribution is static through the sampling period (Able 1999, NOAA 1999). Further, studies showing the effects of dynamic abiotic variables on *Paralichthys dentatus* have mostly concentrated on single parameter laboratory studies (Malloy & Targett 1994, Taylor & Miller 2001) and distributions in estuaries (Burke et al. 1991, Ross et al. 2001). Few studies have focused on the effect that several fluctuating abiotic factors, acting together in their natural environment, might have on fish habitat use, even though these dynamic factors may interact to influence growth and feeding rates (Necaise et al. 2005). Examining a process that directly influences habitat use, such as individual fish movement, provides insight into the environmental factors important to the fish (Belanger & Rodriguez 2002, Rogers & White 2007). Ultrasonic acoustic telemetry is useful for such examinations because it provides continuous relocations of individual fish. Acoustic telemetry has already successfully revealed habitat use for young-of-the-year (YOY) *P. dentatus* (Szedlmayer & Able 1993) and aspects of migratory behavior of juveniles and adults (Sackett et al. 2007).

Most of the *Paralichthys dentatus* population is located in the Mid-Atlantic Bight (MAB), from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina, USA (Smith & Daiber 1977, Grosslein & Azarovitz 1982, Packer & Hoff 1999). Fish in this region reside in estuarine waters during summer months, migrate out of the estuaries in fall or early winter (Sackett et al. 2007) to spawn and overwinter on the outer continental shelf, and return to estuarine waters in the spring (Westman 1946, Able & Kaiser 1994, Packer & Hoff 1999). Summer residence in estuarine waters is an important component of *P. dentatus* growth and survival. Fast estuarine growth of YOY (Rountree & Able 1992, Szedlmayer et al. 1992) occurs in response to appropriate temperature and food availability, according to laboratory studies (Peters & Angelovic 1973, Malloy & Targett 1991, 1994). Thus, it is important to identify the essential components of habitat use during this important growth season in estuarine waters, especially since these waters are frequently impacted by anthropogenic sources (Able 1999, Hoss et al. 1999, Quinlan & Crowder 1999).

The specific objectives of the present study were to evaluate habitat-use dynamics for large juvenile and adult *Paralichthys dentatus* within a relatively unaltered estuary in order to provide an improved understanding of estuarine fish habitat dynamics. Multiple approaches of ultrasonic telemetry, both passive and active, were applied to determine the habitat of individual fish over 2 consecutive years on annual, seasonal, diel, tidal, and hourly scales. Tagged fish densities throughout the estuary and movement of tagged individuals were compared with relevant habitat parameters, i.e. temperature, salinity, dissolved oxygen (DO), pH, depth, tide, diel category, and barometric pressure.

MATERIALS AND METHODS

Study site. The Mullica River-Great Bay portion of the Jacques Cousteau National Estuarine Research Reserve (JCNERR) (Fig. 1), in southern New Jersey, USA, was chosen for this research because: (1) the estuary is relatively unaltered (Kennish & O'Donnell 2002), (2) the JCNERR provides continuous measures of environmental variables using dataloggers (Kennish et al. 2004), (3) the infrastructure for passive ultrasonic telemetry is in place (Grothues et al. 2005), and (4) *Paralichthys dentatus* are seasonally abundant and many aspects of their life history are relatively well known (Able et al. 1990, Szedlmayer & Able 1993, Able & Kaiser 1994). This estuarine system includes more than 27 000 ha of open water consisting of Great Bay, Little Egg Harbor, the Mullica River, a few back bays and 2 smaller rivers (Bass River, Wading River). These waters are typical of a MAB estuary in that they experience a wide annual temperature range (–2 to 28°C) and moderate tidal range (<0.7 to 1.1 m) (Kennish et al. 2004). The Pinelands National Reserve includes 450 000 ha of forested area that surrounds and protects the watershed of the Mullica River-Great Bay estuary from anthropogenic sources of pollution and contributes to the relatively unaltered nature of the estuary (Good & Good 1984, Kennish & O'Donnell 2002). Downstream, the estuary is bordered by extensive salt marsh (dominated by *Spartina alterniflora*). Great Bay, approximately 41.6 km^2, averages <2 m depth. The Mullica River averages approximately 6 m deep (Kennish et al. 2004). Morphological features and currents near the inlet are complex, with sharp changes from shallow to deep water due to strong tidal flows (2 m s^{-1}).

Tagging and telemetry methods. In 2003, 30 fish were externally tagged, following Szedlmayer & Able (1993), with ultrasonic transmitters (Model Caft16_1, 76.8 kHz, 16 × 54 mm, Lotek Wireless). This method allowed the tag to hang off the body of the fish under

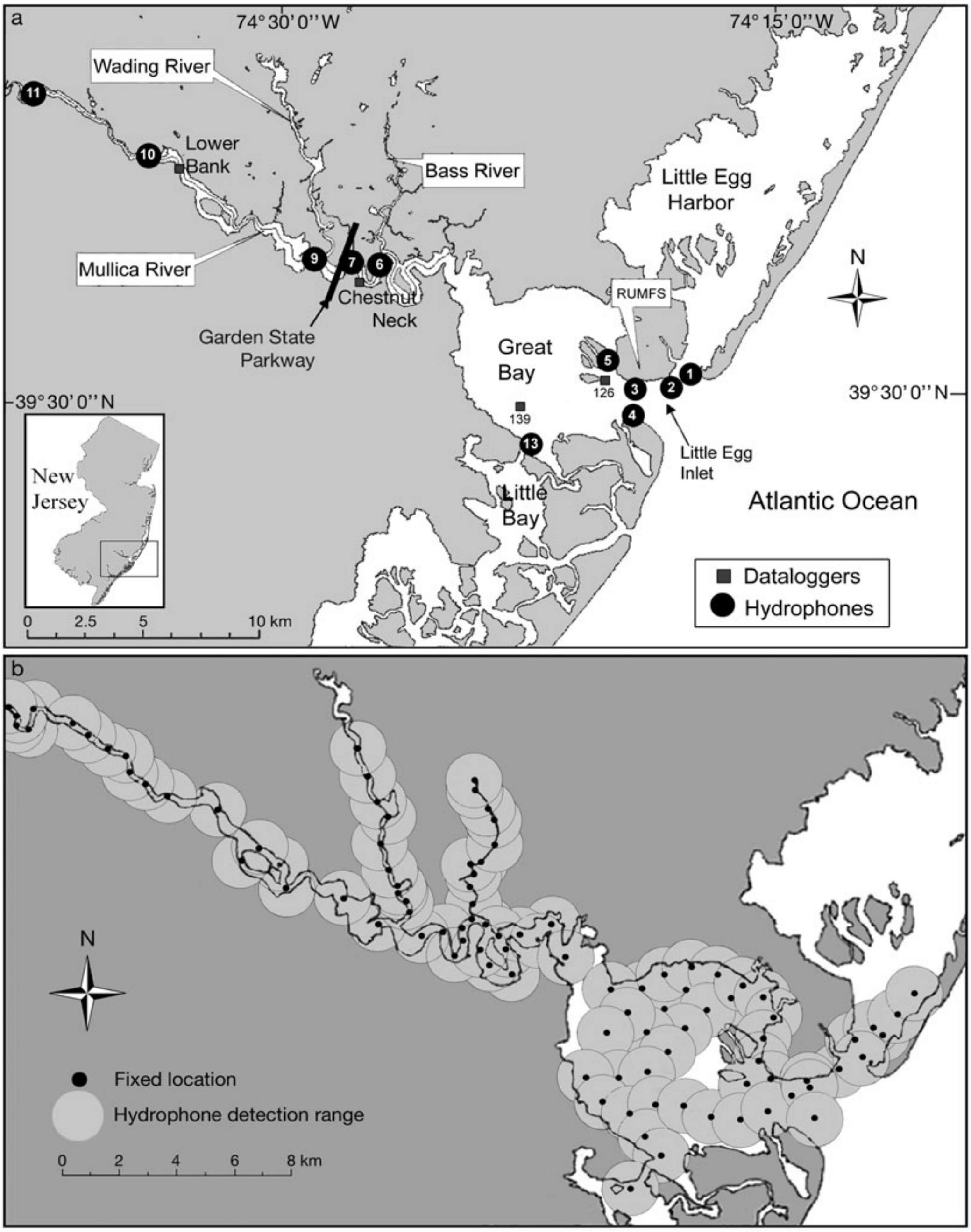

Fig. 1. (a) Mullica River–Great Bay study area in southern New Jersey, indicating locations of static, automated hydrophones, System-Wide Monitoring Program (SWMP) dataloggers and important locations mentioned in the text. RUMFS: Rutgers University Marine Field Station. (b) Fixed locations for weekly attempts to detect tagged summer flounder *Paralichthys dentatus* during June–November 2003 and March–December 2004. Each circle represents the approximate detection range (500 m radius) of a directional mobile hydrophone deployed from a boat

the dorsal fin by approximately 1 to 4 cm. In 2004, 40 fish were tagged with smaller transmitters (Model Caft11_3, 11 × 55 mm) attached to the body of the fish following Bridger & Booth (2003). In 2003, transmitters had an expected battery life of 717 d, long enough to allow tracking of these fish through 2 yr and to examine the potential return rate to the estuary. In 2004, transmitters had an expected battery life of 191 d, enabling tracking of tagged fish through the remaining year of the study (see Sackett et al. 2007 for more details). Tagging was conducted under Rutgers University Animal Use Protocol No. 88-042.

Tagged *Paralichthys dentatus* were tracked from 2003 to 2005 using both passive and active telemetry. We defined the passive telemetry approach as an array of wireless, stationary, automated hydrophones (Model WHS_1100, Lotek Wireless) set as 'gates' in the estuary to record the presence of tagged fish within an approximately 500 m radius of each hydrophone (Grothues et al. 2005, Sackett et al. 2007) (Fig. 1). Hydrophones were positioned at entrances to Great Bay at Little Egg Inlet (Hydrophones 2 to 4), Little Egg Harbor (Hydrophone 1), and Little Bay (Hydrophone 13) to identify fish migrating into and out of the estuary as well as broad-scale movements within the system (Fig. 1). Other hydrophones were moored in the Mullica River at Chestnut Neck (Hydrophones 6, 7, 9), near Lower Bank (Hydrophone 10) and at Sweetwater (Hydrophone 11) to identify estuarine movements. These data were recorded by Lotek receivers/processors (SRX_400) and logged as hydrophone number (location), time, date, and fish identity. Passive telemetry was nearly continuous; interruptions occurred only from occasional power loss or equipment damage and winter ice flows (Sackett et al. 2007).

Active telemetry included 2 techniques, fixed-location sampling and tracking, both using a mobile hydrophone (Lotek LHP_1) and processor (SRX_400) from a boat to locate tagged individuals. Fixed-location telemetry involved sampling at regular stations throughout almost the entire estuary, including Little Egg Inlet, Great Bay, Mullica River, Bass River and Wading River (Fig. 1). The proximity of the fixed locations to each other was based on the range (500 m radius) of the directional mobile hydrophone to almost completely cover the study area. When a fish was located, the boat was positioned close enough to record a signal power above 120 dB at a gain of 12 or below (approximately 2 m horizontally from the tagged fish). Fish identity, location, signal power, date, and time were recorded with a hydrophone, while bottom temperature, salinity, DO, and pH were recorded with a handheld datalogger (YSI Model 85). Fixed-location sampling was conducted 1 d per week from June to November 2003 and from March to December 2004 to locate tagged fish within the system.

In addition, tracking of individual tagged *Paralichthys dentatus* occurred from June to November 2003 and from March to December 2004 to determine habitat use on a finer scale. This tracking consisted of following a single fish for approximately 3 to 6 h while recording position and the same environmental data stated above every 15 to 25 min. All telemetry methods began with the release of the first fish in June 2003 and extended into 2005 in order to detect tagged fish that were returning from 2003 and 2004.

Environmental measures. Four System-Wide Monitoring Program (SWMP) dataloggers set along the salinity gradient in the study estuary (Fig. 1) recorded temperature, salinity, DO, and pH continuously (Kennish & O'Donnell 2002, Kennish et al. 2004). Two were set in the Mullica River (near hydrophone gates at Lower Bank and Chestnut Neck) and 2 were set in Great Bay, near the entrance to Little Bay (near hydrophone gates at Intracoastal Waterway marker buoy 139) and close to Little Egg Inlet (near hydrophone gates at marker buoy 126). Passive hydrophone records of tagged fish were associated with variables recorded by the closest SWMP datalogger by date and time. However, Hydrophones 1 and 2 were too far from a SWMP datalogger to associate environmental variables with detected fish. Highly significant correlations ($p < 0.01$) for temperature, salinity and DO were found between SWMP datalogger 126 (Fig. 1) and variables recorded with a handheld datalogger (YSI Model 85) around Hydrophones 1 and 2. These correlations provided confidence in the regression equation used to determine environmental variables for fish presence at these hydrophones (Grothues & Able 2007, Sackett et al. 2007). Handheld dataloggers were also used to record bottom temperature, salinity, DO, and pH where tagged fish were located using active telemetry methods. Barometric pressure was recorded by the Coastal Oceanic Observation Laboratory (COOL) at Rutgers University from the meteorological tower located at the Rutgers University Marine Field Station near Little Egg Inlet (Fig. 1) and from the Richard Stockton College of New Jersey by the meteorological tower located near Chestnut Neck. Photoperiod was recorded from the Astronomical Applications Department of the US Naval Observatory (http://aa.usno.navy.mil/).

Data analysis. The sampling unit (n) used in the analyses of telemetry data was an individual tagged fish because this approach places equal importance on each fish's movements (Rogers & White 2007). Therefore variables collected at tagged fish locations were averaged for each individual fish and used in analyses. Tags that were considered lost, based on no movement after tagging, were excluded from the study (2003, n = 12; 2004, n = 5).

To statistically test the relationship between the habitat/locations of individually tagged fish and the environmental variables recorded, 9 quadrants of 2 km wide and set along a transect from the mouth of the estuary to the furthest fish location upriver were classified as Regions 1 through 9 in ascending order from Little Egg Inlet (Fig. 2). The number of tagged fish per year that visited each region was standardized relative to the surface area of water (no. of fish per km^2) in that particular region. This measure was then used to

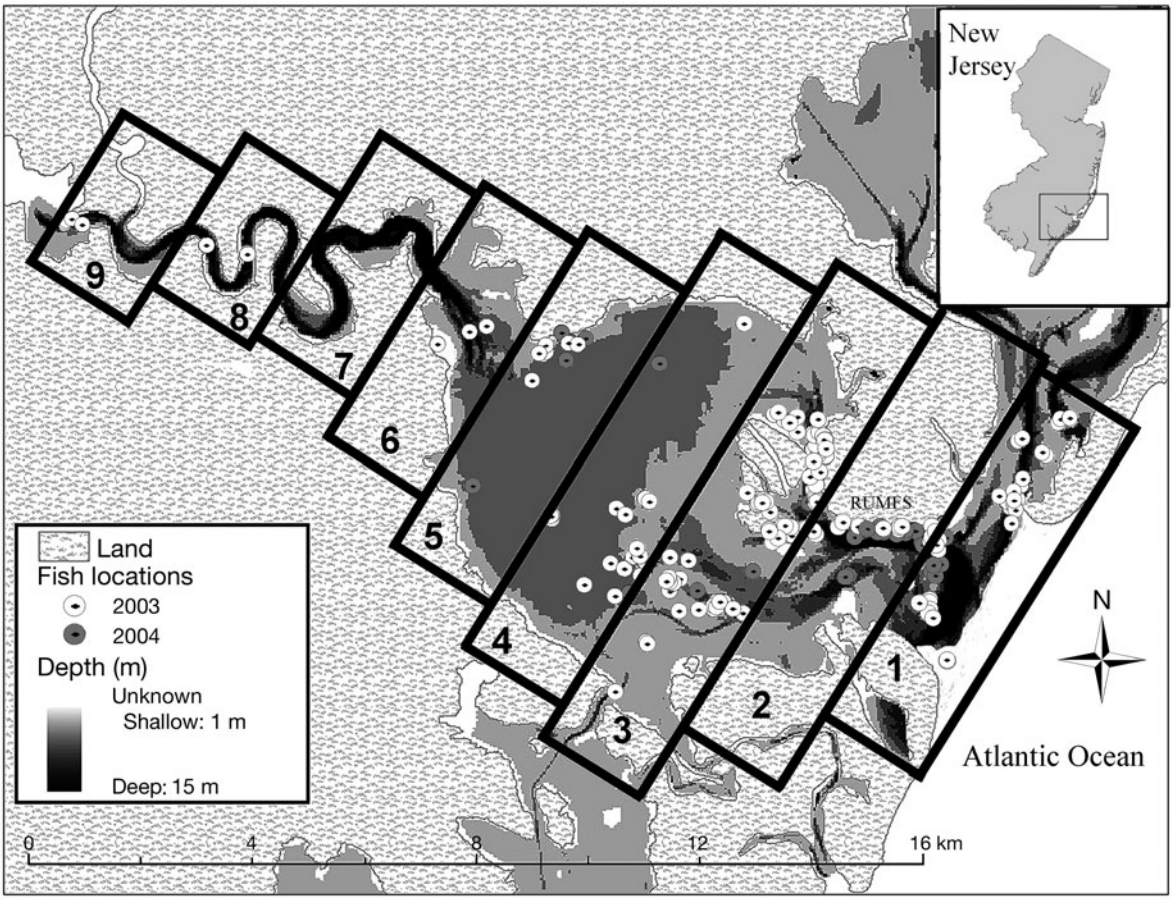

Fig. 2. *Paralichthys dentatus.* Locations of tagged fish by region (numbered quadrants) based on telemetry during 2003 and 2004. General depth contours are indicated. RUMFS: Rutgers University Marine Field Station

quantify the relationship between dynamic variables, tagged fish locations and annual distribution in the estuary.

Estuarine movements of tagged fish were determined using dates and locations recorded from passive and active telemetry to produce maps of seasonal movements for each fish in 2003 (n = 18) and 2004 (n = 42). These maps were then examined for similar patterns of residence and movement, and compared between years. Tracking data for each tagged individual was mapped with geographic information system software (GIS, Arcview 9.0) to measure the shortest possible distance a fish could have moved between individual locations. This was done to create a measure of fish movement in units of minimum displacement per hour (MDPH) (Rogers & White 2007). The environmental variables recorded at 2 consecutive fish locations were averaged and subtracted to identify the mean and change (Δ) in that variable in relation to MDPH.

Pearson's correlations were used to examine the relationship between tagged fish densities by region and MDPH with environmental variables. ANOVA and Kruskal-Wallis tests were also used to test for significant differences between tagged fish densities by region, rates of fish movement and the associated independent variables with each of these measures using the statistics program SAS. ANOVA and Bonferroni (Dunn) *t*-tests were used to make pairwise comparisons for normally distributed data, and Kruskal-Wallis and Siegel-Tukey tests were used when the data were not normally distributed. Tracking data were also organized into tidal and diel categories, and the relationship of these variables to distribution and MDPH were tested in the same way.

RESULTS

Characteristics of tagged fish

Individuals of 268 to 535 mm total length (TL), presumed to be between 1 and 2 yr old, were tagged throughout Great Bay in 2003 and 2004 (Fig. 3). In 2003 most were tagged closer to Little Egg Inlet and

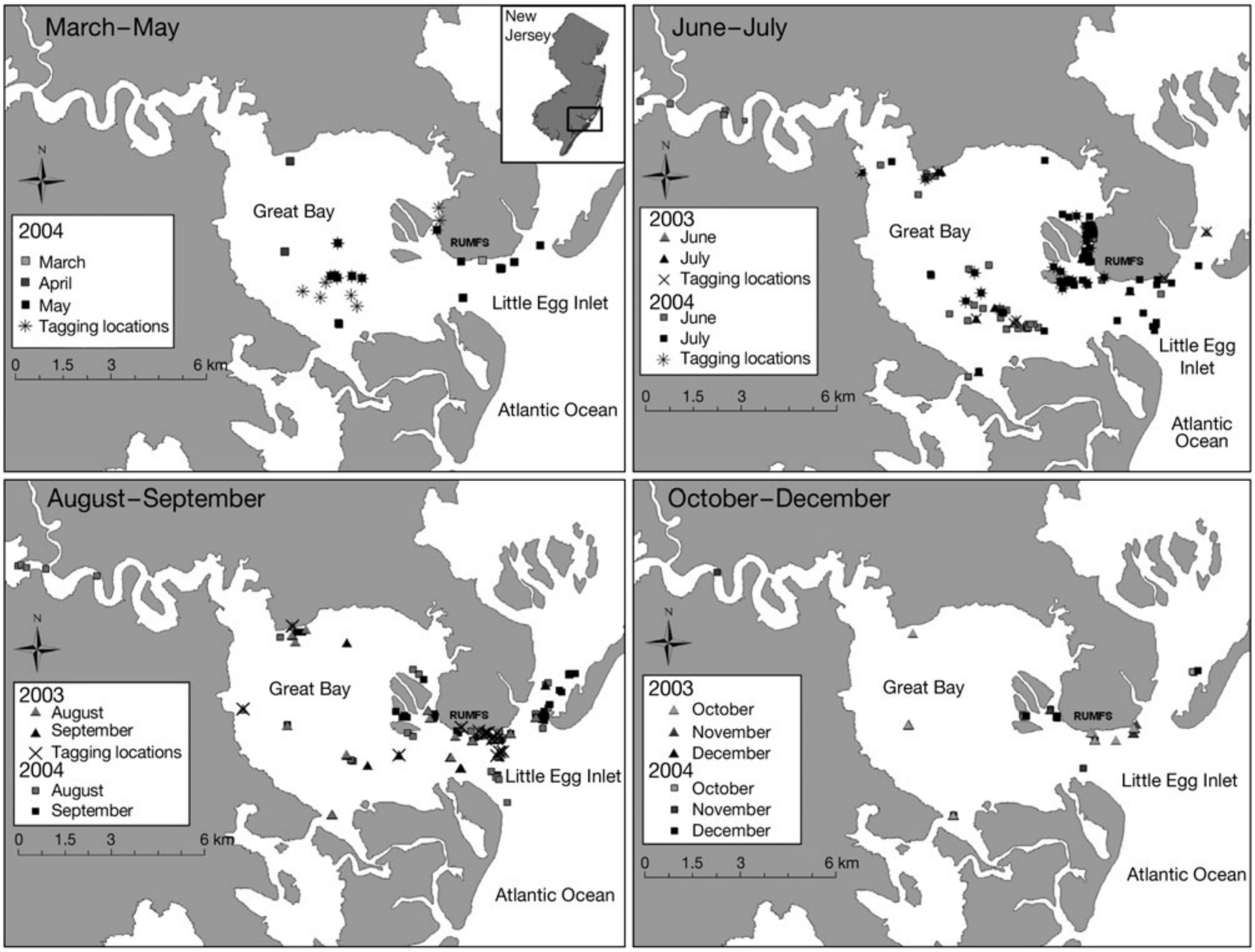

Fig. 3. *Paralichthys dentatus.* Tagging locations during 2003 and 2004 and monthly distributions of these individuals using passive and active telemetry. RUMFS: Rutgers University Marine Field Station

most were released in August. Eighteen of the 30 fish tagged (60%) in 2003 were considered successful, meaning the tag was reliably attached to the fish based on fish movement after tagging. In 2004, most were tagged across the broad mid-region of the bay during June and 35 of the 40 fish tagged (88%) were considered successful. The annual difference in tagging period, earlier in 2004 than 2003, likely influenced mean residence time and perhaps other aspects of habitat use.

The detection of tagged fish varied among techniques. Passive telemetry detected 15 tagged *Paralichthys dentatus* in 2003 and 42 in 2004; 7 of the latter were fish originally tagged in 2003. Fixed-location sampling detected 18 fish in 2003 and 35 in 2004, 7 of which were tagged in 2003. Tracking was conducted on 7 fish in 2003 and 13 fish in 2004, 2 of which were tagged in 2003. The number of passive telemetry detections was 176 099 in 2003, 29 950 in 2004, and 3037 in 2005. The number of active telemetry detections were 66 in 2003, 222 in 2004, and 11 in 2005 (see Sackett et al. 2007 for additional details). The average duration of estuarine residence for tagged *P. dentatus* was 44 d in 2003 (June to December) and 86 d in 2004 (May to December) with ranges of 1 to 150 d and 2 to 217 d, respectively. Additionally, fish tagged in 2003 and located in the estuary in 2004 (n = 7) had a mean duration of estuarine residence of 86 d and a range of 1 to 184 d (March to December).

Estuarine habitat use

Tagged fish occurred in highest densities in the lower portion of the bay (Regions 1 to 3) in both years of the study (Figs. 2 & 3). Density of tagged fish peaked in Region 2 in both years (in 2003, 2.3 tagged fish km^{-2}; in 2004, 4.4 tagged fish km^{-2}) with somewhat lower or similar densities in Regions 1 and 3 (in 2003, 1.61 and 1.04 tagged fish km^{-2}; in 2004, 2.46 and 2.98 tagged fish km^{-2}, respectively). However, the highest tagged fish density in 2004 was upriver in Region 8 (4.7 tagged fish km^{-2}). This was the result of 4 fish that moved upriver toward the end of the season in 2004. Tagged fish density was lowest in Regions 4 through 9 in 2003 (0.22, 0.63, 0, 0, 0, 0 tagged fish km^{-2}, respectively) and Regions 4 through 7 in 2004 (0.94, 0.63, 0.71, 0 tagged fish km^{-2}, respectively).

Temperature, DO, depth and salinity correlated significantly with the distribution of tagged fish (Figs. 4 & 5). Tagged fish were consistently found in areas with higher mean salinity. For example, in 2004, the mean salinity up the estuary (Regions 7, 8, 9) when tagged fish were absent was 15.2 (± 4.4) and the mean salinity when fish were present in the same area was 26.4 (± 2.5). In both years, fish avoided the lowest mean temperatures available and the highest mean DO levels available. In this example, tagged fish were located in areas with mean temperatures higher than 19°C and DO levels lower than 7.5 mg l^{-1} and were consistently absent from areas with mean temperatures lower than 19°C and DO levels higher than 7.5 mg l^{-1} (Figs. 4 & 5). A few individual tagged fish were detected in temperatures as low as 7°C in spring (May) and late fall/early winter (November, December) (Fig. 5). Furthermore, during 2004 temperature showed a strong negative

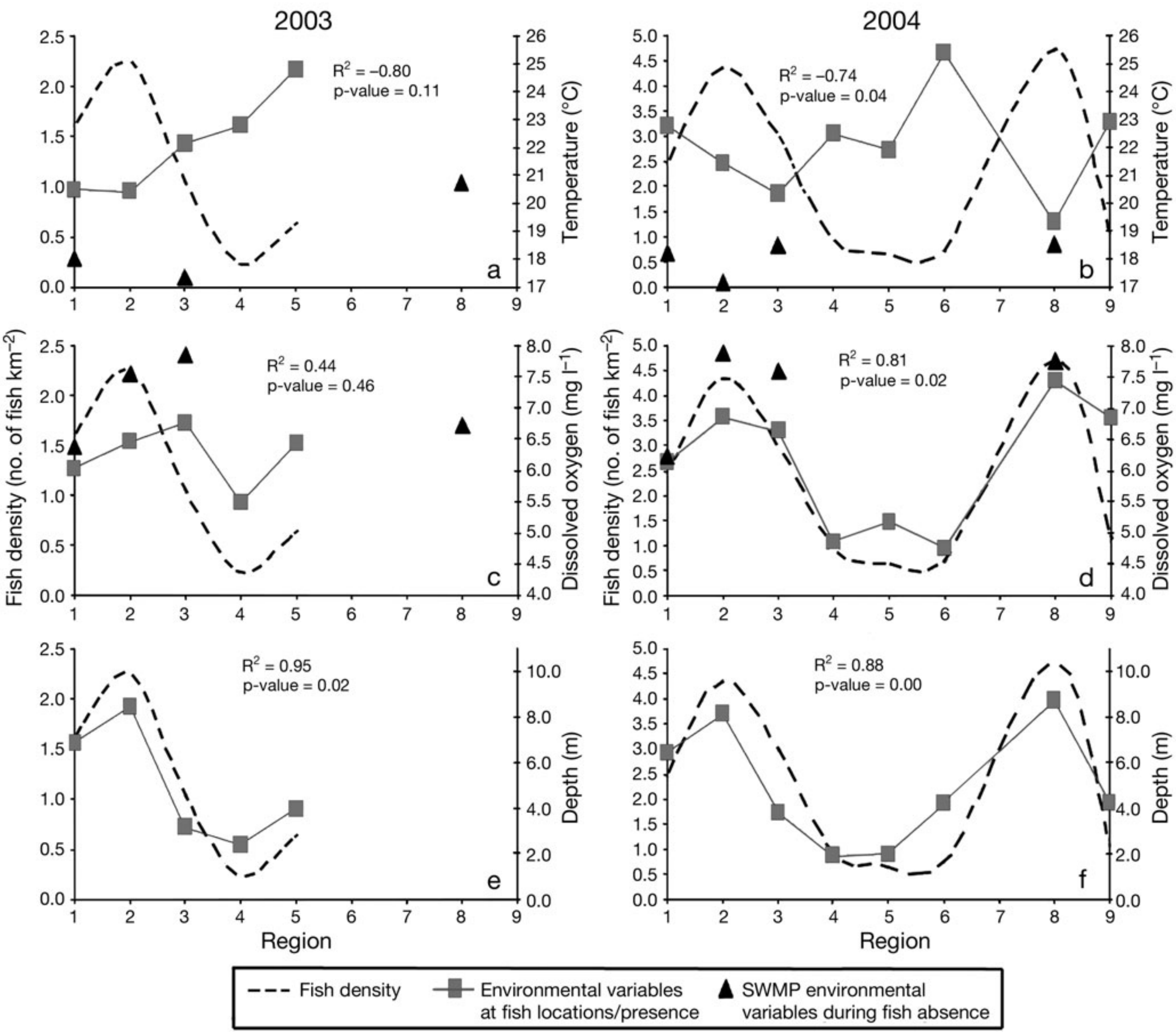

Fig. 4. *Paralichthys dentatus.* Density of tagged fish by region was significantly correlated ($p < 0.05$) to (a,b) temperature, (c,d) dissolved oxygen and (e,f) depth recorded at fish locations/presence by year. Environmental variables were recorded from the SWMP dataloggers located in the specified regions (Fig. 1)

correlation (R = –0.74) with tagged fish density (Table 1) and DO showed a strong positive correlation with tagged fish density (R = 0.81) (Fig. 4). Similar relationships applied for temperature and DO in 2003, even though the correlations were not significant ($p > 0.05$) (Fig. 4). These relationships were optimized when fish were found in areas with higher salinity and deeper water (Figs. 4 & 5). This preference is indicated by the strong significant ($p < 0.05$) correlation (2003, R = 0.95; 2004, R = 0.88) between tagged fish density and depth, and by the fact that most tagged fish used mean depths (8.5 m) much greater than the average depth of the bay (2.0 m) and the river (6.0 m) (Table 1, Figs. 2 & 4).

Habitats and environmental preferences for individual fish were also consistent across years (Figs. 5 & 6). Several tagged *Paralichthys dentatus* left the estuary and returned to the same general location in the subsequent year. Seven fish tagged in 2003 returned in 2004 and 4 of these were frequently relocated within 550 m of their location from the previous year (vicinity of Little Egg Inlet, shallow sand flats in Great Bay, silty sand substrate in the upper bay) and in similar environmental conditions. Three fish from 2003 and 2 from 2004 returned in 2005 and frequented areas within 550 m of their previous locations and these were the same general habitats revisited in 2004. The 2 fish tagged in 2004 were recorded frequently moving but were found primarily in an area within the lower bay near the marsh edge and in the Intracoastal Waterway in Little Egg Harbor (Fig. 1). These fish returned to this same area (within 200 m) the following year.

Estuarine movements

The seasonal movements of tagged fish and changes in location/habitat in the estuary were evident during the study period (Fig. 3). Tagged fish were most abundant in the middle of the bay and at the inlet from March through May. From June through July the distribution was similar, except that more fish were detected in the bay and into the river. During August and September fish were most commonly detected in the lower bay, closer to Little Egg Inlet. However, those fish that moved upriver in 2004 did so from June through September. The presence of tagged fish declined in the estuary from October to December in both years.

Movements of individual tagged fish could be characterized as (1) local lower bay movement, (2) movement along the Intracoastal Waterway channel, or (3) movement into the river in 2004 (Fig. 7). In 2003, 83% of relocated fish were tagged in the lower portion of the bay (Regions 1, 2, 3) (Fig. 2), and 72% demonstrated local, lower bay movement (Fig. 7). In 2004,

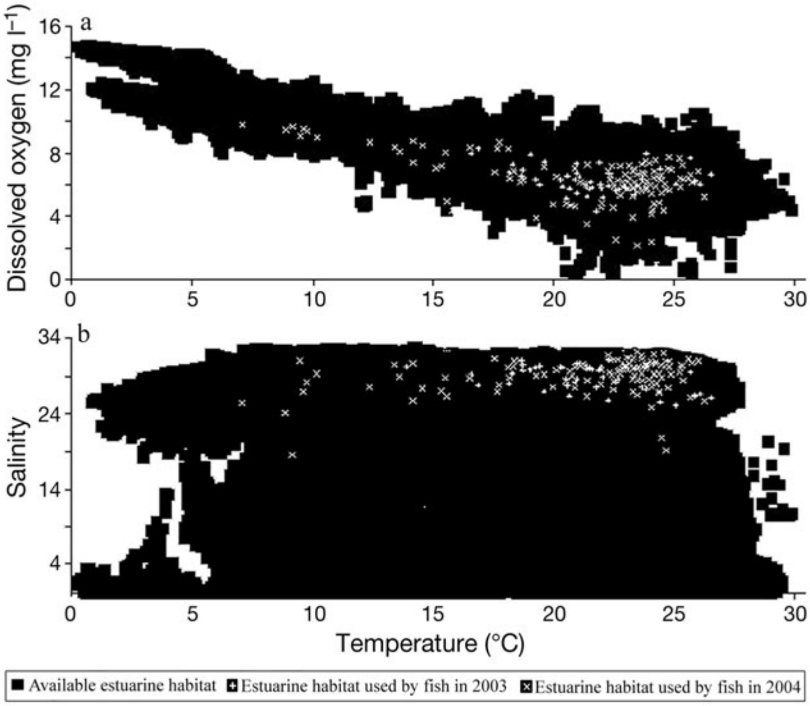

Fig. 5. *Paralichthys dentatus.* Selected versus available (a) temperature and dissolved oxygen and (b) temperature and salinity conditions for fish within the Mullica River–Great Bay estuary in 2003 and 2004. Available variables were recorded by SWMP dataloggers (Fig. 1) set throughout the estuary. Conditions selected were recorded at locations of tagged fish and averaged for individual fish by region (Fig. 2)

Table 1. *Paralichthys dentatus.* Pearson's correlation coefficients of environmental measures recorded by region during passive and active telemetry in 2003 and 2004 with fish density. See Fig. 3 for location of regions. Values in parentheses = p-value. *$p < 0.05$

Variables	2003 fish density	2004 fish density
Region	–0.79 (0.11)	–0.19 (0.66)
Temperature (°C)	–0.80 (0.11)	–0.74 (0.04)*
Salinity	0.84 (0.07)	0.24 (0.57)
Dissolved oxygen (mg l^{-1})	0.44 (0.46)	0.81 (0.02)*
Depth (m)	0.95 (0.02)*	0.88 (0.00)*
pH	–0.25 (0.68)	0.28 (0.50)

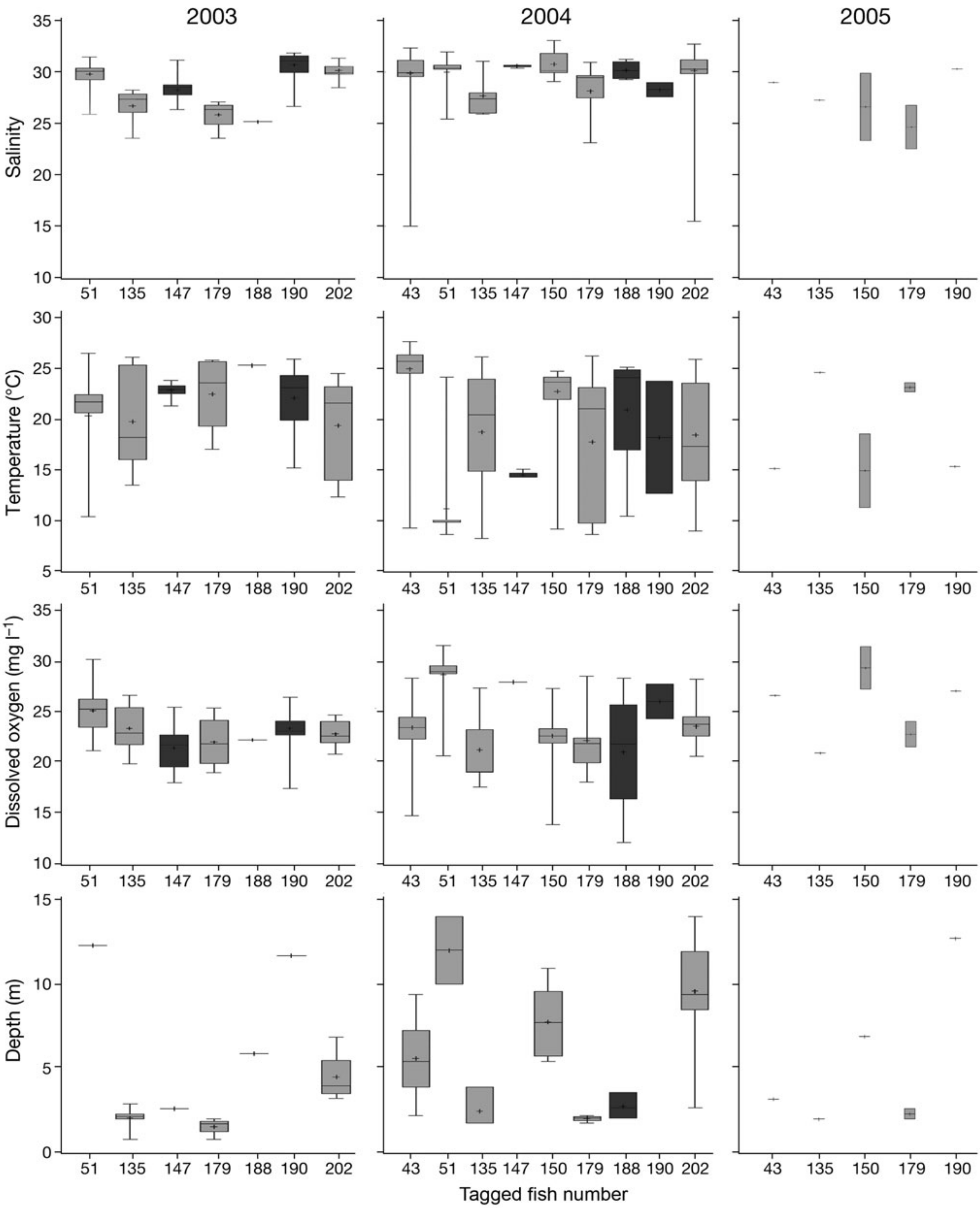

Fig. 6. *Paralichthys dentatus.* Box-and-whisker plots of salinity, temperature, dissolved oxygen and depth recorded at locations of individual tagged fish that returned to the estuary the following year(s). Light gray shaded boxes represent fish that returned to and frequented locales within 550 m or less of the sites where they were located in previous year(s) (annual site fidelity); darker shaded boxes represent fish that returned to the estuary in the following year but did not return within 550 m or less of the sites they were located in the previous year(s)

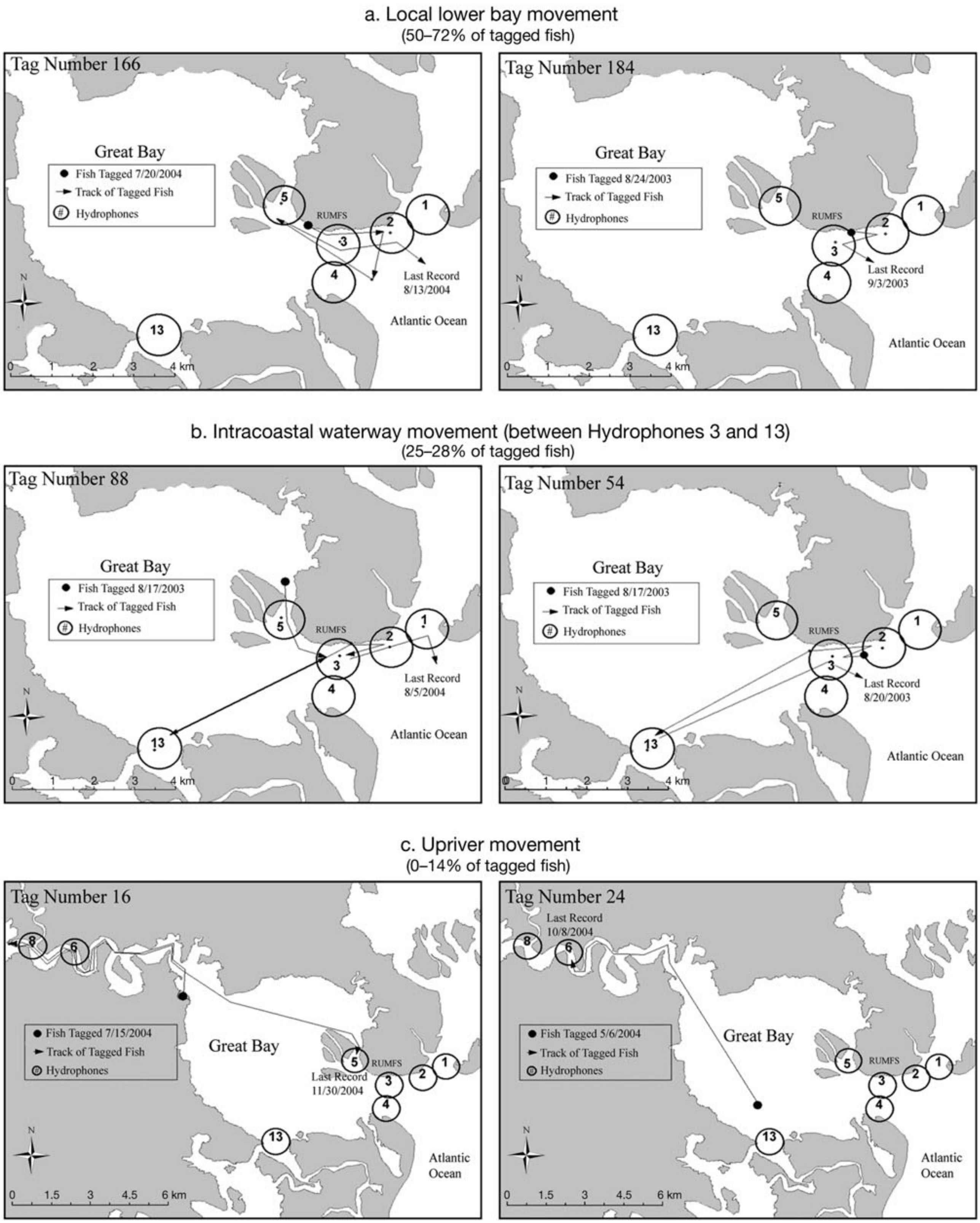

Fig. 7. *Paralichthys dentatus.* Tracks of 6 representative tagged fish during estuarine residence in 2003 and 2004 demonstrating (a) local lower bay movement, (b) Intracoastal Waterway movement (between Hydrophones 3 and 13) and (c) upriver movement, which only took place in 2004. RUMFS: Rutgers University Marine Field Station. Dates are mo/d/yr

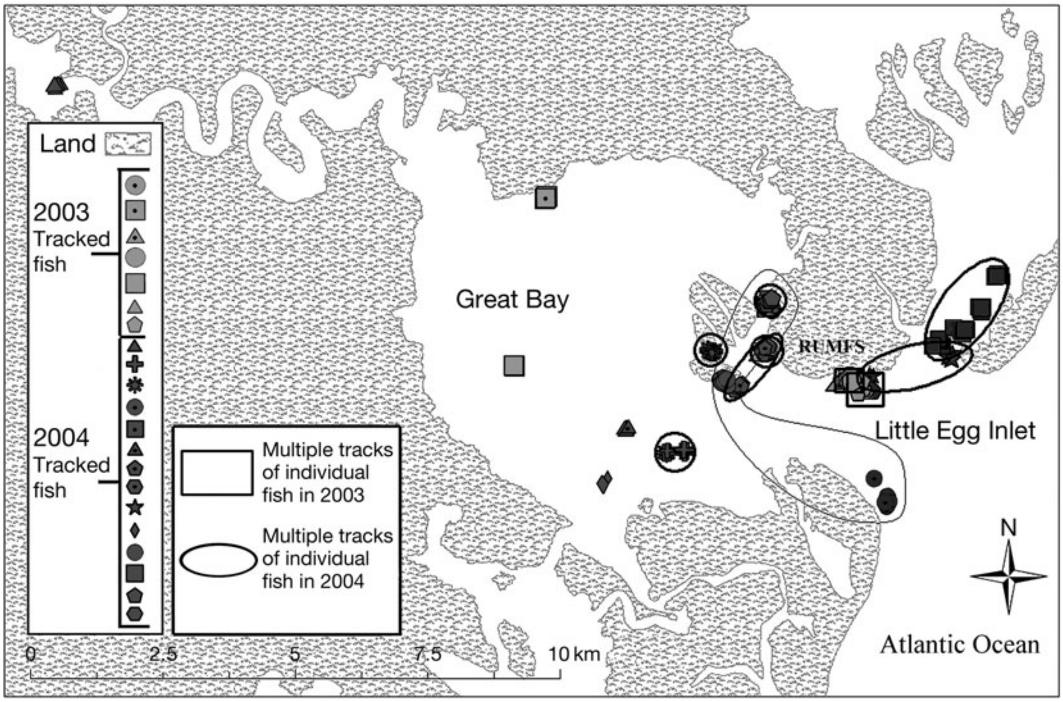

Fig. 8. *Paralichthys dentatus.* Locations of individually tracked fish (see symbols) over 3 to 6 h in 2003 and 2004. RUMFS: Rutgers University Marine Field Station

83% of relocated fish were tagged in the lower bay and 50% showed local, lower bay movement. Movement along the Intracoastal Waterway occurred for 28% of tagged fish in 2003 and 25% in 2004. A major difference between 2003 and 2004 was the movement of fish into the river in 2004 (14%). Of the 5 fish tagged that moved upriver in 2004, 4 were tagged in the lower bay between April and July and one was tagged at the mouth of the Mullica River in mid-July.

Day- and nighttime active tracking, conducted on an hourly scale, showed that fish (n = 20) frequented small locales but were often moving within these locales (Fig. 8). During all but one active track, individual fish remained within an area of 0.18 km^2 for 3 to 6 h. Additionally, 2 fish from 2003 and 7 fish from 2004 were tracked more than once in the same area. While in these locales, fish were in motion on average 74% (±19%) of the time and stationary only 33% (±15%) of the time. These values are greater than 100% because they are based on means of individual fish tracks. No measured variables (e.g. temperature, salinity, DO, depth, etc.) were found to differ significantly ($p > 0.05$) when fish were in motion or stationary. MDPH during tracking was significantly different ($p < 0.05$) between years (65.9 ± 33.7 m h^{-1} during June to November 2003; 113.8 ± 45.0 m h^{-1} during March to December 2004), but no variables measured during tracking differed significantly ($p > 0.05$) between years.

MDPH did not differ significantly ($p > 0.05$) relative to tidal or diel cycle. Environmental variables recorded during tracking were not significantly different across tidal cycles. However, mean temperature and the mean change in DO between consecutive tracking locations differed significantly ($p < 0.05$) between diel categories with higher values of DO and lower temperatures at night.

DISCUSSION

Dynamics of habitat use

The importance of estuarine habitats for this seasonally abundant species is exemplified by the annual fidelity of tagged individuals to this same estuary (Sackett et al. 2007). On a broad seasonal scale, and once in or revisiting the estuary, some tagged fish were resident in the estuary from spring (March) through early winter (December). Mean residence was approximately 86 d in 2004, when fish were tagged earlier in the year and when some returned the following year. This duration of estuarine residence is supported by other observations in the study estuary (Szedlmayer & Able 1993, Able & Kaiser 1994) and other MAB estuaries (Michels 1996, NOAA 1999). While in the estuary, distribution of tagged fish indicated that most *Par-*

alichthys dentatus used the lower bay. Of the individuals present in the lower bay, most stayed relatively close to Little Egg Inlet, although some moved between Little Bay and Little Egg Inlet, presumably along the Intracoastal Waterway (between Hydrophones 3 and 13, Fig. 1). Others have demonstrated increased catch per unit effort of adult *P. dentatus* along waterways and channels (Smith & Daiber 1977, Wilk et al. 1977, Allen et al. 1978).

In both years, few fish utilized the upper bay; however, in 2004 several fish tagged in the bay moved through the upper bay into the river. Tagging efforts were conducted in the river (only in 2004) and in the upper, mid, and lower bay; however, because upper bay and river efforts were frequently unproductive, the majority of tagging effort was focused in the mid- and lower bay. This could have elevated the lower bay preference seen in the results of this study. However, past studies have found similar lower bay distributions of *Paralichthys dentatus* in MAB estuaries (Powell & Schwartz 1977, Smith & Daiber 1977, Burke et al. 1991, Walsh et al. 1999, Miller et al. 2000), although most of these were conducted using trawl surveys.

Annual fidelity to habitats within the estuary occurred for 6 *Paralichthys dentatus* that were frequently relocated within 550 m or less of their location from the previous year(s). Four of these fish revisited locations within areas consistently used by tagged fish in both years of the study, i.e. the lower bay and the Intercoastal Waterway. The other 2 frequently visited locales were near shallow sand flats and silty/sandy portions of the upper bay. These restricted areas, during this very important growth season, could be important in essential habitat descriptions.

As a further indication of dynamic habitat use, *Paralichthys dentatus* in estuaries may undergo an age/size related shift in habitat selection. From the late larval stage to settlement, YOY juvenile *P. dentatus* (35 to 80 mm TL) make size-dependent migrations from shallow flats to deeper sandy marsh habitats (Powell & Schwartz 1977, Burke et al. 1991). Past studies conducted in the study estuary established that larger (210 to 254 mm TL) YOY *P. dentatus* reside in and use tidal currents to move up and down creeks to feed and potentially conserve energy during estuarine residence (Rountree & Able 1992, Szedlmayer & Able 1993). The larger fish (268 to 535 mm TL) examined in the present study remained in the open water of the lower bay and did not demonstrate use of tidal currents during movement. These observations suggest that YOY make use of tidal creeks more often than large juveniles and adults, perhaps due to a size-dependent shift in prey and thus habitat selection (Manderson et al. 2000) and/or protection from predators. Adult *P. dentatus* have been documented exploiting lower and mid-estuary habitats, including hard sandy substrate (Bigelow & Schroeder 1953), salt marsh creeks (Rountree & Able 1992) and sea grass beds (Bigelow & Schroeder 1953). This suggests that older individuals may exploit a broader range of habitats as they grow. There is also evidence that some, especially larger, adults may not enter estuaries at all but remain offshore all year (Festa 1977).

On a smaller temporal scale, tagged fish resided in small locales for 3 to 6 h at a time. While in these areas, fish were found to be moving most of the time they were tracked, the movement in these small areas was not significantly related to any variables tested in this study. Therefore, some other untested variable, such as feeding, competition, or territorial behavior could be responsible for this frequent movement within such small areas.

Environmental influence on habitat use

Annual distributions and movements of tagged individuals were associated with defined temperature, DO, depth, and salinity preferences. Salinity seemed to broadly influence this distribution because tagged fish consistently selected for higher-salinity areas of the estuary. This high salinity preference was the presumed response that allowed fish to move up the estuary due to higher salinities there in 2004. Several studies have attributed the spatial distributions of *Paralichthys dentatus* in other MAB estuaries to a preference for high salinity (Powell & Schwartz 1977, Able & Kaiser 1994, Gibson 1994, Miller et al. 2000), but our study was the first to confirm this with continuous tracking of individual fish.

Tagged fish demonstrated a continuous selection of optimal conditions by recurring in conditions that provided the fastest growth and feeding rates available in the natural environment, i.e. high and stable levels of temperature and DO (Peters & Angelovic 1973, Malloy & Targett 1991, 1994, Taylor & Miller 2001, Necaise et al. 2005). Tagged fish did not utilize habitat with lower mean temperatures (<19°C) and higher mean levels of DO (>7.5 mg l^{-1}) that were available in the estuary. However, at the other extreme, most fish were distributed among areas with temperatures closer to 20°C, rather than 26°C, and DO levels closer to 7 mg l^{-1}, rather than 4 mg l^{-1}. Additionally, most fish were present at depths much greater than the average depth of the bay or the river. Therefore, the probable explanation was that *Paralichthys dentatus* balanced a preference for high, stable temperatures and DO levels by distributing themselves in the deeper areas of the estuary. *P. dentatus* have been observed in the deeper areas of other MAB estuaries (Smith & Daiber 1977, Wilk et al. 1977, Allen et al. 1978). In laboratory studies, temperature and DO strongly affected *P. dentatus* and other flatfish species feeding and growth rates (Peters & Angelovic 1973, Malloy & Targett 1991, 1994). Continuously low and fluctuating DO concentrations have been determined to decrease other paralichthyid growth rates (Bejda et al. 1992, Taylor & Miller 2001), and *P. dentatus* have been documented avoiding areas of hypoxia and anoxia (Swanson & Sindermann 1979). Extreme levels of both temperature (extreme high) and DO (extreme low) have also been seen affecting *P. dentatus* mortality (Necaise et al. 2005). Thus, *P. dentatus* seem to select locations/habitat favorable to high feeding and growth rates.

As a result of the above instances of dynamic habitat use, more specific designations of EFH that take ontogenetic, annual, seasonal and tidal variables into account are needed to adequately identify EFH (NOAA 1999). This is especially true for a species, like *Paralichthys dentatus,* that have numerous obligate estuarine life-history stages (Able 2005). The results from the present found that dynamic factors such as DO, temperature, depth, and salinity can be important to habitat selection in estuarine environments. This has important implications because the currently used broad designations of EFH based on presence/absence and abundance data may be of limited value. For example, the distribution of tagged *P. dentatus* in this study changed from 2003 to 2004, when a salinity regime change allowed fish to exploit upriver habitat in 2004. Other abiotic variables (e.g. substrate, vegetation, current speed) were not tested in this study and need further evaluation. In addition, several studies have shown prey availability to influence *P. dentatus* movements and habitat use in relation to vegetation (Timmons 1995), and on tidal and fish size/age-related scales (Rountree & Able 1992, Szedlmayer & Able 1993, Manderson et al. 2000); the same is likely true for other biotic variables for this and other flatfishes (Able et al. 2005). Also, it is necessary to incorporate more details of individual habitat choice into an evaluation of EFH because there is evidence for homing to estuaries (Sackett et al. 2007) and habitats within estuaries, as in this study.

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