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Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape

N. B. FUREY*†‡, M. A. DANCE*† AND J. R. ROOKER*†

*Department of Marine Biology, Texas A&M University at Galveston, 200 Seawolf Parkway Ocean and Coastal Sciences Building, Galveston, TX 77553, U.S.A. and †Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, U.S.A.

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Habitat use of juvenile southern flounder *Paralichthys lethostigma* was examined within a shallow estuarine seascape during June and July 2011 using acoustic telemetry. Fine-scale movement and habitat use of *P. lethostigma* was investigated with an acoustic positioning system placed in a seascape that varied in habitat type, physicochemical conditions and bathymetry. The use of different habitat types was examined with Euclidean distance-based analyses, and generalized additive models were used to determine the relative importance of habitat type relative to physicochemical conditions and bathymetry. Tracks of *P. lethostigma* ranged in distance between 1477 and 8582 m and speed was $4.2 \pm 1.1 \text{ m min}^{-1}$ (mean \pm s.e.) for all *P. lethostigma* combined. Depth, slope and habitat type had the most influence on *P. lethostigma* occurrence and deep sandy areas with shallow slopes were used most frequently. In addition, depth use by *P. lethostigma* was influenced by tidal cycles, indicating habitat use varies temporally and is dynamic. Finally, temperatures $<30.5^\circ \text{C}$ were used more than warmer waters within the study area. The results successfully identify movements by juvenile *P. lethostigma*, and indicate that definitions of essential habitats need to account for dynamics in habitat use.

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Key words: acoustic telemetry; Euclidean distance-based analysis; flatfish; species–habitat relationships; VR2W positioning system.

INTRODUCTION

Habitat availability within a seascape can influence the movement of fishes by providing a mechanism for enhancing fitness by seeking optimal habitats (Kahler *et al.*, 2001). Optimal or suitable habitats are those considered to improve an individual's fitness by increasing food availability and decreasing predation risk and metabolic costs. The suitability of potential habitat types or areas can vary with time, as factors influencing fitness (*i.e.* predation, food and physicochemical conditions) are dynamic (Bowler & Benton, 2005). Furthermore, the arrangement of habitats within a seascape can influence the direction of movement and distances

‡Author to whom correspondence should be addressed at present address: Pacific Salmon Ecology and Conservation Laboratory, Centre for Applied Conservation Research, Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, V6T 1Z4 Canada. Tel.: +1 604 822 1969; email: n.b.furey@gmail.com

travelled by fishes (McIntyre & Wiens, 1999). Identifying habitats and areas that are used disproportionately is necessary for proper management of marine fishes and information regarding the movements and linkages among habitat patches remains understudied (Boström *et al.*, 2011).

Several methods have been used to investigate movement and habitat use of fishes. Traditional methods for determining movements include distributional studies, which compare abundance and size structure of fishes among areas or regions. These studies provide a snapshot of an organism's distribution within a seascape; however, information on movement or linkages across habitat types from this type of approach is limited. Conventional tagging studies can provide greater temporal resolution (depending upon the number of recaptures), but are often characterized by low tag returns and lack fine-scale resolution. The advent of electronic tags has allowed for more detailed understanding of fish movements and habitat selection (Cooke *et al.*, 2004). Passive acoustic telemetry has the ability to describe broad-scale movements of estuarine or marine fishes (Heupel *et al.*, 2004; Sackett *et al.*, 2007; Wetherbee *et al.*, 2007); however, information on specific habitat types used is limited with this approach. Although active acoustic telemetry allows for the construction of fine-scale movement patterns (Hitt *et al.*, 2011; Papastamatiou *et al.*, 2011), it is limited in duration, as animals are typically followed for a maximum of 24 h. Recently developed technology bypasses the limitations of both techniques by using multiple, closely spaced passive receivers to triangulate fish positions, generating continuous records of fine-scale movements within a seascape (Espinoza *et al.*, 2011a).

Southern flounder *Paralichthys lethostigma* Jordan & Gilbert 1884 are a recreationally and commercially important flatfish found in estuarine and coastal waters along the Gulf of Mexico and the south-east Atlantic Ocean. Recent analyses indicate a precipitous decline in the *P. lethostigma* population in the northern Gulf of Mexico (Froeschke *et al.*, 2011) as well as reduced levels of recruitment (Nañez-James *et al.*, 2009). While distributional studies (Glass *et al.*, 2008; Nañez-James *et al.*, 2009) and habitat distribution models (Furey & Rooker, 2013) have determined species–habitat relationships for newly settled and young-of-the-year (YOY) *P. lethostigma* in the northern Gulf of Mexico, understanding of fine-scale movements over short time scales is lacking. The aim of the current study was to use acoustic telemetry to describe fine-scale movements of juvenile *P. lethostigma* and to relate these movements to available habitats within an estuarine seascape.

MATERIALS AND METHODS

The current study was conducted in Christmas Bay, a small bay within the Galveston Bay complex (GBC) along the north-west Gulf of Mexico (Fig. 1). Christmas Bay is a shallow estuary (mean depth *c.* 0.7 m), and is unique among the subbays within the GBC because it contains significant stands of seagrass, both shoal grass *Halodule wrightii* and turtle grass *Thalassia testudinum* (Pulich & White, 1991). In addition, a variety of other habitat types (sand, oyster reef and marsh edge) are in close proximity and often interdispersed in seagrass meadows making Christmas Bay an ideal system for evaluating habitat connectivity. Bare substrata within the study area generally comprised sand-sized sediments with lesser amounts of silt- and mud-sized sediments present at some locations. For simplicity, all bare substrata will be collectively referred to as sand.

Habitats within the study area were mapped using both satellite imagery and ground measurements (Table I). Orthorectified satellite images taken on 3 May 2010 (TNRIS 2010;

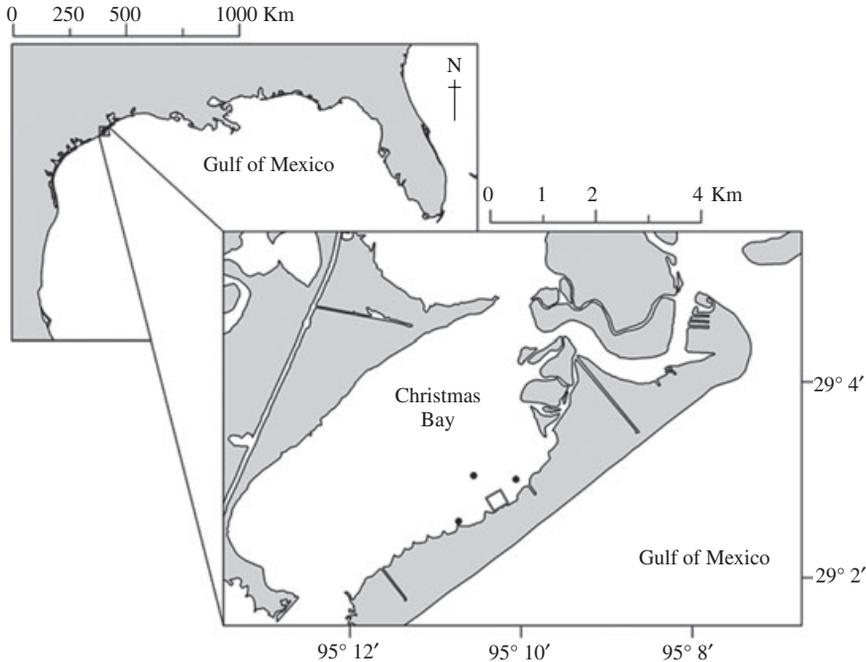


FIG. 1. Location of the study area in Christmas Bay, Texas. Coverage area of the VR2W (Vemco) Positioning System (VPS) array is denoted (\square) within the inset and the three surrounding points represent the positions of the three receivers external to the array.

<http://data.tnris.org/datadownload/quad.jsp?Quad=Christmas%20Point/>) were used to delineate salt marsh, seagrass and oyster reef boundaries. In order to verify these habitat classifications, discriminate between shoal grass and sand, and record relative depth values across the study area, 235 points (approximately half in a gridded arrangement, with the remaining strategically placed along habitat edges and in steeper substrata) within the study area were selected and examined in the field. At each point location, habitat type and relative depth (corrected for by tidal height) were recorded. Relative depths across the study area were then interpolated using universal kriging within ArcGIS's Spatial Analyst extension and substratum slope (percent slope m^{-1}) was estimated at a 5 m^2 resolution (ESRI; www.esri.com). In addition to examining relative depth use, realized depths occupied by *P. lethostigma* were estimated by correcting original recorded depths for tidal height. High and low tide predictions for Christmas Bay (NOAA, 2012) were used to fit non-linear Loess smoothers within R 2.14 (R Development Core Team; www.r-project.org). These smoothing functions were then used to predict the tidal height as a continuous variable for all times *P. lethostigma* were detected within the study area. The sum of predicted tidal height and relative depth of each location resulted in a realized depth for each *P. lethostigma* location.

Physicochemical conditions were also monitored and related to *P. lethostigma* movements. Water temperature dataloggers (Onset Inc; www.onsetcomp.com) were attached to each receiver, and temperatures were recorded every 15 min to observe fine-scale and diel temperature cycles over the duration of the study. To examine temperatures experienced by tagged *P. lethostigma*, the recorded temperature from the datalogger on the receiver closest in distance to each *P. lethostigma* location (at the closest possible time) was determined. Salinity at each receiver was measured weekly for 4 weeks during the trial to approximate salinities experienced by *P. lethostigma*.

Juvenile *P. lethostigma* (284–370 mm total length, L_T ; Table II) were captured via hook and line in Christmas Bay. *Paralichthys lethostigma* were held in a 0.7 m^3 tank

TABLE I. Summary of habitat composition and habitat use within the VR2W (Vemco) Positioning System (VPS) array

Habitat	Available habitat (m ²)	% Available habitat	Fish locations	% Locations
Shoal grass	22 590	74.2	540	42.1
Turtle grass	3051	10.0	49	3.8
Sand	2683	8.8	692	53.9
Salt marsh	1403	4.6	0	0.0
Oyster reef	723	2.4	2	0.2

Fish locations, the number of triangulated positions of *Paralichthys lethostigma* calculated by the VPS that had a horizontal position error (HPE) ≥ 10 m that occurred after the 4 h acclimation period.

at the Texas A&M University at Galveston Wetlands Center for 4–7 days prior to tagging. During the tagging procedure, *P. lethostigma* were anaesthetized using clove oil, and V9 transmitters (Vemco Ltd, 9 × 24 mm, 69 kHz and a nominal delay of 120 s; www.vemco.com) were externally mounted on the eyed-side of each *P. lethostigma* following a protocol modified from DeCelles & Cadrin (2010). Each V9 transmitter was placed in a latex sleeve and two nickel tagging pins were passed from the blind side of the individual (held by a vinyl laminated tag; Floy Tag Inc; www.floytag.com) through both the dorsal musculature and latex sleeve. The latex sleeve and pins were secured with rubber earring backings and a small metal crimping sleeve. All *P. lethostigma* were examined for physical harm due to tagging and deemed to be healthy immediately prior to release.

Eight *P. lethostigma* were released in the study area and tracked using a Vemco VR2W Positioning System (VPS) in a section of Christmas Bay. The VPS in Christmas Bay was comprised of 10 closely-spaced (30–50 m apart) VR2W receivers, which allowed triangulation of *P. lethostigma* positions to a potential accuracy of 2–6 m (Espinoza *et al.*, 2011b). Three additional receivers were placed outside the VPS c. 600–800 m to the north, east and west of the array to track larger scale movements (Fig. 1). To ensure time synchronization of the internal clocks among VPS receivers, four sync tags (Vemco Ltd) were also placed within the VPS array. Tagged *P. lethostigma* were released on 29 June 2011 and the last detection by a single receiver occurred on 28 July 2011.

DATA ANALYSES

Prior to analyses, data were filtered by time and horizontal position error (HPE), which is a relative measure of horizontal error sensitivity (Espinoza *et al.*, 2011b). Only locations with an HPE < 10 m were included in analyses. Generally, HPE < 10 m corresponded to positional errors of < 5 m (1.4 ± 0.0 m, mean ± s.e.) when examining errors of static tags placed within the array, similar to other VPS studies (Espinoza *et al.*, 2011b). In addition, detections within the first 4 h of the study were removed from the analysis in order to account for the acclimation period of *P. lethostigma* to the study site.

Movements of tagged *P. lethostigma* were characterized by estimating step lengths between successive VPS locations using Hawth's Analysis Tools extension in ArcGIS (Beyer, 2004). Step lengths and the time elapsed between successive points were then used to calculate step speed. As missed detections could result in the underestimation of step speeds, mean step speed was calculated using only detections without missed transmissions (occurring successively within 3 min). Differences in mean step speeds among habitat types were examined with a paired *t*-test. Step lengths were summed to estimate the distance tracked within the VPS array, and VPS locations were combined with detections made by the three receivers located outside the array to estimate total tracked distance. Because of a lack of any method to determine the directionality or distance of a *P. lethostigma* detected by an individual receiver, the location of any *P. lethostigma* detection made by an outer receiver was assumed to be that of the receiver itself.

TABLE II. Summary of recorded detections for *Paralichthys lethostigma* tagged in 2011. First detection takes into account a 4 h acclimation period. Number of VPS [VR2W (Vemco) Positioning System] locations used indicates triangulated positions of *P. lethostigma* that had a horizontal position error (HPE) ≤ 10 m. The distance tracked within the VPS array (*D* tracked in VPS) was calculated as the sum of the distances between each successive VPS location. The total estimated distance tracked for each *P. lethostigma* (Total *D* tracked) includes both locations within the VPS array as well as the three Outer stations. Outer stations were labelled as being approximately East (E), North (N) or West (W) of the VPS array. Last detection refers to the last date on which *P. lethostigma* was detected by any receiver, while Last VPS detection indicates the last date on which *P. lethostigma* was detected within the VPS array

Tag identification	L_T (mm)	First detection	Last VPS detection	Last detection	Number of outer detections	Outer stations	Number of VPS locations used	<i>D</i> tracked in VPS (m)	Total <i>D</i> tracked (m)
T01	341	29 June, 2041 hours	3 July, 0717 hours	7 July	83	E, N, W	663	2414	8582
T02	350	30 June, 0405 hours	1 July, 0345 hours	25 July	58	N, W	94	528	4168
T03	315	30 June, 1644 hours	2 July, 0337 hours	5 July	7	E, N	170	1535	4269
T04	284	29 June, 2238 hours	6 July, 2159 hours	11 July	9	E, N, W	185	1303	4402
T05	347	29 June, 2129 hours	30 June, 0627 hours	30 June	7	E, N	6	220	2065
T06	370	29 June, 2217 hours	7 July, 0009 hours	16 July	1	N	99	1605	2271
T07	295	29 June, 2322 hours	29 June, 2348 hours	30 June	12	E, N	1	0	1477
T08	358	30 June, 0336 hours	30 June, 0900 hours	8 July	6	E, N, W	60	413	3588

L_T , total length.

Habitat use was analysed with a Euclidean distance-based analysis (EDA) according to Conner & Plowman (2001), which uses individuals as the sampling unit and thus does not require error modelling (Conner *et al.*, 2003). Even if habitat classification error occurs, the distance to the correct habitat is reduced using this approach (Conner & Plowman, 2001). Within the VPS array's coverage, 1000 random points were generated inside an area within 80 m of any three or more VPS receivers, representing the range at which conservatively the system could detect a tagged *P. lethostigma*. Distances between each random point and each habitat (salt marsh, oyster reef, sand, shoal grass and turtle grass) were determined and then averaged to generate a vector of mean distances to each habitat type. For each VPS location, the distance to all habitat types was also determined (distance to the habitat occupied by the *P. lethostigma* at the time of detection was 0) (Miller *et al.*, 2000; Conner & Plowman, 2001; Conner *et al.*, 2003). Each EDA ratio for *P. lethostigma* was based on the mean distance to each habitat type divided by the mean distance between random points of the same respective habitat type. If habitat use is random, all EDA ratios should equal 1; if habitat use is non-random, mean EDA ratios will differ from 1 (with values <1 indicating preference, and values >1 indicating avoidance). Multivariate analysis of variance (MANOVA) was used to determine if EDA ratios differed significantly from a vector where each value is 1 and the vector's length is equal to the number of habitat types investigated (5) (Conner & Plowman, 2001). Multivariate normality was tested using a Shapiro–Wilk test within the 'mvnormtest' library in R (Jarek, 2012), and the assumptions of multivariate normality were met ($P > 0.05$). If MANOVA results indicated a significant difference, univariate *t*-tests were then used to determine which habitat types were used disproportionately by comparing each habitat's EDA ratio to 1. Paired *t*-tests were also used to test for differences in the utilization of each habitat between diel periods (day or night) and between rising and falling tides. Daytime was defined as the period of time between sunrise and sunset, and night-time hours were the interval between sunset and sunrise. Type of tide was defined using the National Oceanic and Atmospheric Association Tide Predictions Program data (NOAA, 2012). For all parametric statistics, $\alpha = 0.05$.

The relative importance of species–habitat relationships for tagged *P. lethostigma* were further quantified and weighed with a habitat modelling analysis similar to that of Aarts *et al.* (2008). VPS locations from all *P. lethostigma* were pooled with an equal number of random points ($n = 1284$) generated to represent locations where *P. lethostigma* were absent. Each random point was selected from the same area used for EDA analysis, within 80 m of three or more VPS receivers. In addition, each generated point was located within 67 m of a single VPS location. This distance represents the average maximum distance observed between potential detections (based on the average observed maximum speed of 22.5 m min^{-1} and a maximum delay of 3 min between tag transmissions). These constraints were used to prevent absences from representing locations that either could not be realistically reached by *P. lethostigma* (given the previous location), or could not be reliably detected by the VPS, even if a *P. lethostigma* was present. In addition, each randomly generated point was treated as occurring at the same time as a single VPS location so that the effects of temporally dependent variables (temperature and tidal height) could be investigated. By having a pair of points at each time, however, strictly temporal variables such as diel period could not be included in the analysis. All VPS locations and randomly generated locations were linked to four covariates: habitat type, relative depth, temperature and slope (per cent change per metre). In addition, the interaction between relative depth and tidal height was investigated.

To investigate species–habitat relationships, generalized additive models (GAMs) were employed. In the case of binomial GAMs with a logit link, the following equation was used: $\ln[(1 - y) y^{-1}] = \beta_0 + \sum_k s_k x_k$, where y represents the predicted probability of *P. lethostigma* use, β_0 equals the intercept, k equals the number of covariates included in the model and s_k equals the smoothing function for the covariate x_k . Penalized cubic regression splines determined the shape of non-parametric functions, with the degree of smoothing selected automatically for models and generated within the 'mgcv' library (Wood, 2006, 2008) using R 2.14 software (R Development Core Team). To prevent overfitting, limits can be placed on the d.f. given to each response curve (Ciannelli *et al.*, 2008), and in this study the response curve for each variable was limited to a maximum of four d.f. All possible model combinations were generated and compared using percent deviance

explained and the Akaike information criterion (AIC) (Akaike, 1974). A final model was selected by minimizing the AIC score. Additional models, each with a single covariate removed from the final model, were generated to calculate the change in percent deviance explained in an attempt to understand the relative importance of covariates retained in the final model.

RESULTS

A total of 2210 locations were calculated using the VPS array, of which 1284 had an associated HPE of <10 m and occurred at least 4 h after the trial start. Because few VPS locations were detected for two *P. lethostigma* (including only one detection for fish T07; Table II and Fig. 2), these data were omitted from habitat use and movement analyses using the individual *P. lethostigma* as the sampling unit (EDA ratios, L_i values and step speeds).

All eight *P. lethostigma* were detected by both the VPS array and by at least one of the three additional receivers placed to the east, north and west of the VPS array. Three *P. lethostigma* were detected by all three of the outer receivers. The number of times individual *P. lethostigma* were detected by the outer receivers ranged between 1 and 83 (Table II). When *P. lethostigma* left the VPS array they were generally detected by the receiver east or north of the VPS array. Although four of the *P. lethostigma* were detected by the receiver west of the array, these fish were always observed by the north or east receiver first. The total tracked distances of *P. lethostigma* within the VPS array ranged between 412 and 2414 m (Table II and Fig. 2). When accounting for larger scale movements detected by the three outer receivers, the total distances tracked among *P. lethostigma* ranged between 1477 and 8582 m (3853 ± 2215 m, mean \pm s.d.). If only concurrent detections (those within 180 s of each other) were used, speed of *P. lethostigma* within the VPS array was 4.2 ± 1.1 m min⁻¹ (mean \pm s.e.), and relative speed was 12.3 ± 2.9 body lengths min⁻¹ (mean \pm s.e.). Average maximum speed observed among *P. lethostigma* was 22.5 ± 6.4 m min⁻¹ (mean \pm s.e.) and the maximum speed among *P. lethostigma* ranged between 6.4 and 52.4 m min⁻¹. Step speed was not influenced by *P. lethostigma* body size (linear regression, $F_{1,4} = 0.35$, $P > 0.05$), diel cycle (t -test, $t = -0.27$, d.f. = 5, $P > 0.05$) or habitat (ANOVA, $F_{2,12} = 1.77$, $P > 0.05$).

Areal coverage of habitats within the VPS array were shoal grass (74.2%), turtle grass (10%), sand (8.8%), salt marsh edge (4.6%; based on all salt marsh within 10 m of edge) and oyster reef (2.4%) (Table I). More than 95% of all VPS locations observed for *P. lethostigma* were located in either sand (53.9%) or shoal grass (42.1%) habitats. The proportion of VPS locations of *P. lethostigma* in the other habitats was markedly lower: turtle grass (3.8%), oyster reef (0.2%) and salt marsh (0.0%). Because of the limited number of detections in salt marsh and oyster reef, these habitat types were excluded from GAM and step speed analyses. The use of random points in EDA and GAM analyses prevents bias of habitat use based on differences in areal coverage, as the location of random points should approximate the relative availability of habitats.

Habitat use analysis based on EDA ratio indicates non-random selection of habitat types (MANOVA, $F_{5,1} = 21654$, $P < 0.01$). *Paralichthys lethostigma* locations were significantly closer to sand than random points (mean EDA = 0.36, t -test: $t = 16.59$, d.f. = 5, $P < 0.01$) and significantly farther from salt marsh than random points (mean

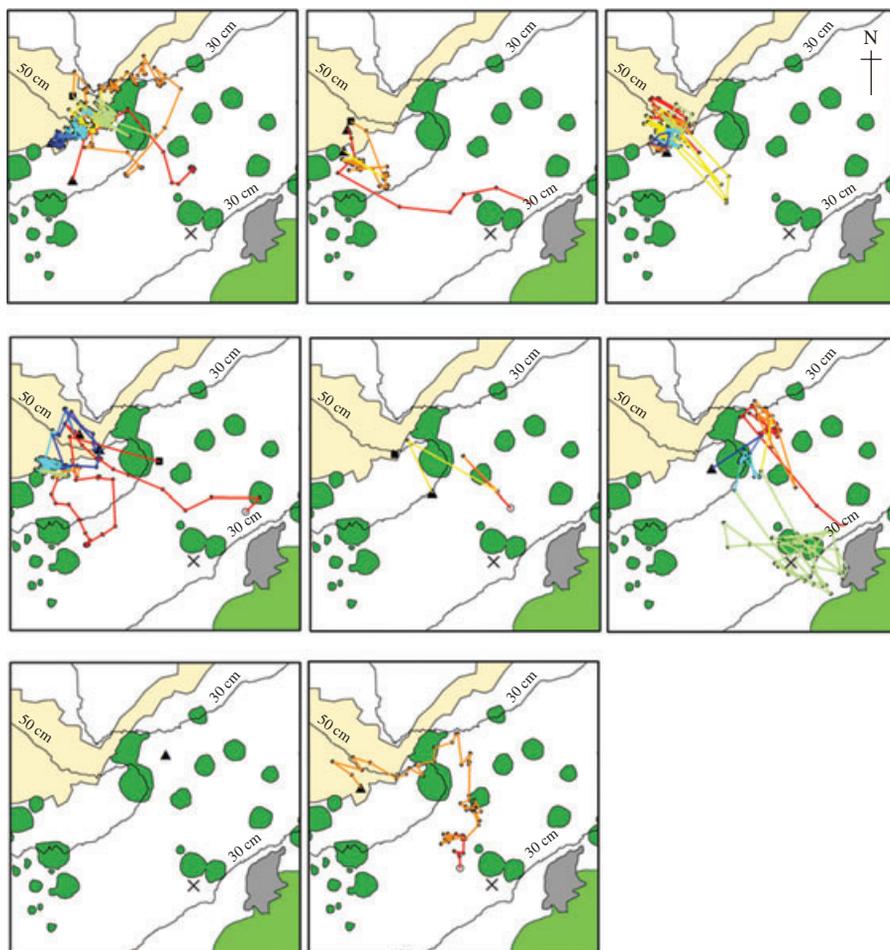


FIG. 2. Detections of juvenile *Paralichthys lethostigma* within the VPS array with habitats shown (shoal grass, □; turtle grass, ■; sand, □; oyster reef, ■; salt marsh edge, ■). Each plot represents the movements of an individual *P. lethostigma* for which initial detections (○) and subsequent detections (●) are shown, and line (movement path) colour indicates the time period, in h from trial start, during which the movement occurred (<12, —; 12–24, —; 24–36, —; 36–48, —; 48–60, —; 60–72, —; >72, —). Exits (▲) are defined as detections for which the next detection occurred on one of the three receivers exterior to the VPS array. Re-entry detections (■) were considered as those that occurred within the VPS when the previous detection occurred on one of the exterior receivers. The release location (×) was the same for all *P. lethostigma*.

EDA = 1.46, $t = 11.82$, $P < 0.05$) (Fig. 3). The use of other habitats, including turtle grass (t -test: $t = 2.08$, d.f. = 5, $P > 0.05$), oyster reef ($t = 5.52$, d.f. = 5, $P > 0.05$) and shoal grass ($t = 1.86$, d.f. = 5, $P > 0.05$) were found to be random using EDA ratios. These trends persist throughout the diel cycle, as paired t -tests indicated no change in EDA ratios either between day and night in all five habitats (sand: $t = 0.13$, d.f. = 5, $P > 0.05$; salt marsh: $t = -0.01$, d.f. = 5, $P > 0.05$; turtle grass: $t = 1.52$, d.f. = 5, $P > 0.05$; oyster reef: $t = -0.23$, d.f. = 5, $P > 0.05$; shoal grass: $t = 0.23$, d.f. = 5, $P > 0.05$), or between rising and falling tides (sand: $t = -1.50$, d.f. = 5,

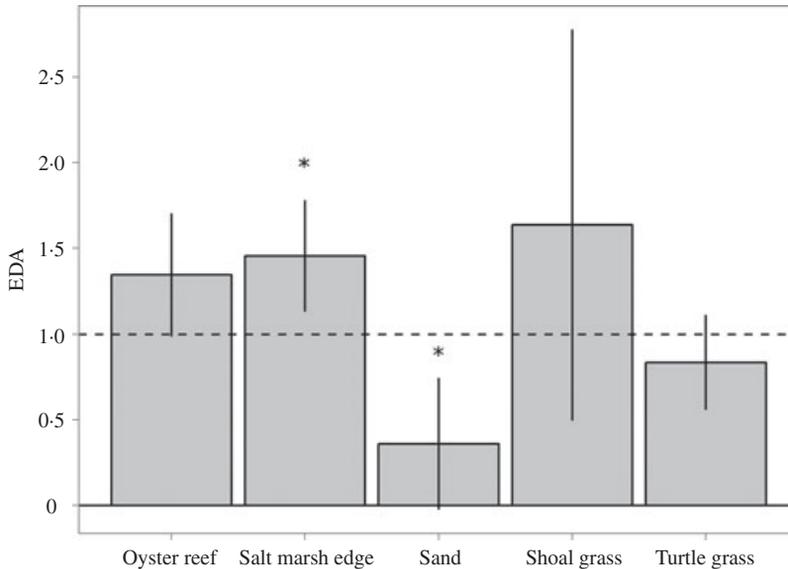


FIG. 3. Mean \pm s.d. Euclidean distance analysis (EDA) ratios of habitat types available to *Paralichthys lethostigma* within the study area. Values < 1 indicate increased use, while values > 1 indicate avoidance. *, mean EDA ratio for the habitat type was significantly different from 1 ($P < 0.05$).

$P > 0.05$; salt marsh: $t = 1.54$, d.f. = 5, $P > 0.05$; turtle grass: $t = -1.20$, d.f. = 5, $P > 0.05$; oyster reef: $t = 1.81$, d.f. = 5, $P > 0.05$; shoal grass: $t = 0.41$, d.f. = 5, $P > 0.05$).

All potential GAMs were investigated and deviance explained by the final model was 17.8% (AIC = 2945). The final model included the covariates habitat, relative depth, slope, temperature and the interaction between relative depth and tidal height. Response plots indicated that *P. lethostigma* occurrence was highest for sand habitats followed by shoal grass and turtle grass (Fig. 4). Removal of habitat type from the final GAM resulted in a 1.8% decrease in deviance explained.

Bathymetric and physicochemical variables also significantly influenced *P. lethostigma* occurrence. Relative depth, which ranged between 12 and 58 cm at mean low tide, was the most influential covariate within the final GAM and the response curve indicates increased use of depths > 50 cm by *P. lethostigma* and decreased use of depths < 50 cm (Fig. 4). Deviance explained decreased by 5.4% when depth was removed from the final GAM. Relative depth use was influenced by tide, with *P. lethostigma* using shallower parts of the study area at higher tidal heights. The removal of the interaction between relative depth and tidal height from the final GAM reduced the deviance explained slightly (1.1%). Slopes were generally shallow within the VPS array, varying between 0.0 and $1.4\% \text{ m}^{-1}$, and the occurrence of *P. lethostigma* was greatest in areas with slopes between 0.3 and $1.0\% \text{ m}^{-1}$ (Fig. 4). When slope was removed from the final model, deviance explained declined by 2.0%. The temperatures experienced by *P. lethostigma* within the VPS array ranged between 28.7 and 32.8° C , with a mean of $30.2 \pm 0.7^\circ \text{ C}$ (\pm s.d.). GAM analysis indicated a negative relationship between water temperature and *P. lethostigma* occurrence and the response plot showed that occurrence increased at

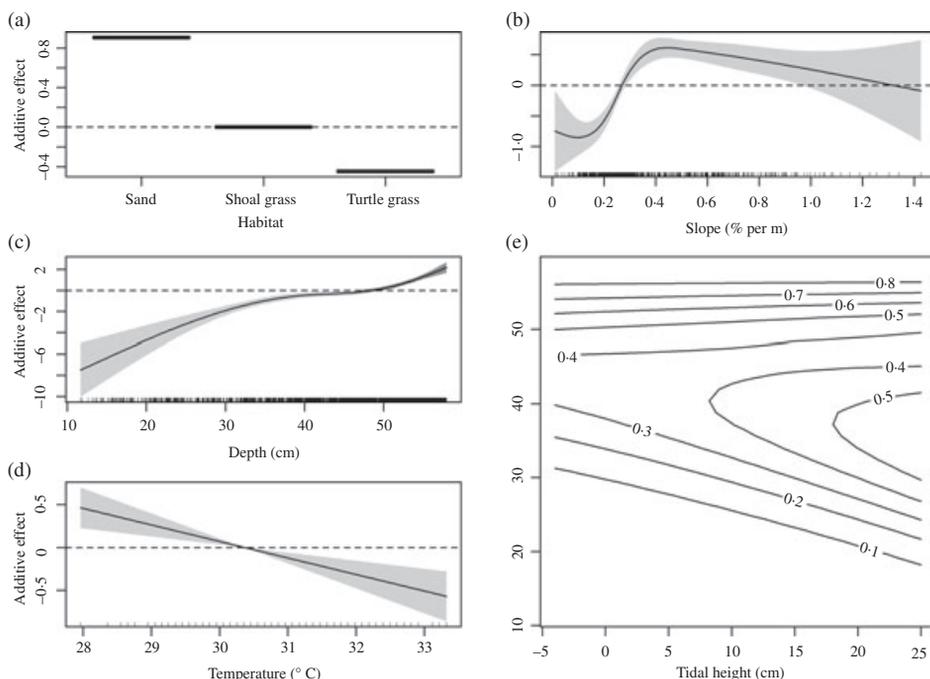


FIG. 4. Response plots of explanatory covariates (a) habitat, (b) slope, (c) depth and (d) temperature on the occurrence of *Paralichthys lethostigma* tracked with acoustic telemetry as analysed with generalized additive models (GAM). Shaded areas on each plot indicate 95% c.i. of smoothed response curves. (e) The isopleths on the contour plot indicate the additive effects of the interaction between water depth and tidal height on *P. lethostigma* position.

temperatures $< 30.5^{\circ}\text{C}$ (Fig. 4). At any given time the difference between minimum and maximum temperatures within the array was generally $< 1.0^{\circ}\text{C}$ and never $> 2.0^{\circ}\text{C}$. Temperature was considered the least important variable in the final GAM, because the removal of this variable decreased percent deviance explained by 0.4%.

DISCUSSION

This study described movement activity of juvenile *P. lethostigma* within a shallow estuarine seascape. Detections of *P. lethostigma* by receivers outside the VPS array indicated that juveniles can move up to 2 km day^{-1} and 9 km over 10 days. Because of the small spatial extent of receivers, these estimates should be considered conservative, as actual movements are probably greater. Mean overall and maximum step speeds based on VPS data (4.2 and 22.5 m min^{-1}) also demonstrate a potential for a high degree of movement on small spatial scales. The findings suggest that juvenile *P. lethostigma* remained active the majority of the time they were being tracked, but at the same time stayed within a relatively small area. Similar dispersal behaviours have been reported for other estuarine-dependent paralichthyids such as summer flounder *Paralichthys dentatus* (L. 1766) (Sackett *et al.*, 2008).

Benthic seascape structure and habitat types can influence the movements of fishes (Semmens, 2008; Farrugia *et al.*, 2011; Hitt *et al.*, 2011). Selection of habitats can change during ontogeny for flatfishes, with structurally complex habitats (*i.e.* seagrass) often used immediately after settlement followed by a transition to habitats without vegetation at larger sizes (Stoner *et al.*, 2001; Busby *et al.*, 2005; Sackett *et al.*, 2008). Similarly, distributional studies indicate that newly settled *P. lethostigma* often reside in areas near or within seagrass beds (Glass *et al.*, 2008; Nañez-James *et al.*, 2009) and then move away from these complex habitats near the end of the young-of-the-year (YOY) stage (Furey & Rooker, 2013). EDA ratio and GAM analyses of acoustic tracking data appear to support the previously reported ontogenetic shift, with juvenile *P. lethostigma* preferring habitats with limited complexity (*i.e.* sand habitat) relative to seagrass or other structurally complex habitats assumed to be important for younger, newly settled individuals. The higher occurrence of *P. lethostigma* in or near bare substrata within Christmas Bay may be because the sand substratum enhances crypsis (*e.g.* burial and camouflage), which is known to decrease predation rates (Fairchild & Howell, 2004; Ryer *et al.*, 2008) and increase foraging efficiency (Gronkjaer *et al.*, 2007; Nordstrom & Booth, 2007). Other habitat types may still be important for prey production, as invertebrate densities are often highest in seagrass beds (Beck *et al.*, 2001). Therefore, although sand substrata are deemed important, mosaics of habitat may still be necessary for optimal growth and survival.

Aside from habitat, bathymetric features, including depth and slope, can influence distributions of marine fishes. Fishes within estuaries often demonstrate depth preferences (Gibson *et al.*, 2011), and depth has been shown to influence an individual's predation risk (Ryer *et al.*, 2010). Water depth was identified as the most influential variable in the GAM analysis, with juvenile *P. lethostigma* using deeper waters (>50 cm relative depth) within the VPS array. In addition, most of the detections outside of the shallow VPS array occurred at the receiver 600 m north of the array, which had the greatest depth (*c.* 100 cm depth) when compared to the VPS array and the areas surrounding the other receivers east and west of the VPS array. Depths across the VPS array were relatively shallow (<70 cm at low tide) and the avoidance of shallow water habitats within the VPS array (<50 cm) may minimize vulnerability to avian predators (Bancroft *et al.*, 2002). In addition to depth, slope of the substratum can constrain use by fishes within riverine (Santoul *et al.*, 2005) and coastal systems (Letourneur *et al.*, 2003). Slopes throughout the array were shallow (<1.5% m⁻¹), which may allow for more efficient and complete burying than steeper areas. *Paralichthys lethostigma* occurrence was greatest in the western portion of the array adjacent to the sand bar, which contained slopes 0.4–1.0% m⁻¹.

Increased environmental variability may limit the distribution of fishes in fluvial and estuarine habitats (Love *et al.*, 2009; Beesley & Prince, 2010). Variability in temperature in Christmas Bay may be mediated by water depth, with deeper areas experiencing smaller ranges on a diel basis. Temperature dataloggers placed in deeper locations exhibited diel variations in water temperature <2.5° C, while those in the shallowest parts of the array ranged from 4.0 to 6.0° C. Reduced exposure to variations in physicochemical conditions such as temperature may reduce metabolic and physiological costs (Kieffer & Wakefield, 2009). Tides also introduce environmental variability, altering depths of estuarine systems on a

cyclical scale and potentially impacting fish movements (Sakabe & Lyle, 2010). High tides increased *P. lethostigma* use of shallower parts of the study area, indicating that suitable habitat was dynamic and varied temporally.

Physicochemical factors can act as scalars that shape the distributions of fishes at multiple spatial scales (Secor & Rooker, 2000; Attrill & Power, 2002; Selleslagh & Amara, 2008). Physicochemical conditions also influence metabolism, and decreased temperatures may mediate potentially negative impacts of low dissolved oxygen on growth rates of *P. lethostigma* (Del Toro-Silva *et al.*, 2008). In fact, temperatures of 27 and 29° C maximized growth rates of *P. lethostigma* in controlled experiments, while temperatures >30° C resulted in zero or negative growth rates (Del Toro-Silva *et al.*, 2008). Temperatures selected by *P. lethostigma* tracked with acoustic telemetry were similar; areas within the VPS array with temperatures >30° C were avoided. Although temperature is increasingly implicated as an important influence on distribution, condition and growth of flounder species (Methratta & Link, 2007; Del Toro-Silva *et al.* 2008; Vasconcelos *et al.*, 2009), it was the least important covariate in GAM analysis. Nevertheless, the ability to detect temperature's importance may be reduced because of the small spatial extent of the VPS array and corresponding low variability in water temperatures across the study area. The study occurred during a period of severe drought throughout Texas and salinity was relatively high for Christmas Bay at the trial start (36) and continued to rise throughout the study. During the week of the last fish detection (28 July 2011), salinity reached 40 at several locations. Despite the fact that salinities could not be related to *P. lethostigma* movements due to the lack of temporal resolution in the data collected, this variable is expected to influence habitat use, as salinity gradients often impact flatfish distributions, including *P. lethostigma* (Allen & Baltz, 1997; Walsh *et al.*, 1999). Reduced model fit observed with GAM analysis indicates that additional physicochemical factors may affect the movements of *P. lethostigma*. Despite the limitations of the data used here (*i.e.* sample size and spatial coverage) the approach shows promise for assessing fish-habitat relationships across estuarine seascapes.

The fine-scale movements of juvenile *P. lethostigma* within an estuarine seascape were described in the context of habitat, bathymetric and physicochemical influences and demonstrate the utility of the VPS. Of these effects, depth, slope and habitat type were most important in determining seascape use, with deeper sandy areas of shallow slopes being used most. To a lesser extent, temperature and tidal height also impacted use. In addition, results suggest that depth use may be modified by tidal cycles, demonstrating the potential dynamics of habitat use. Telemetry studies that successfully identify movements and habitat use at multiple spatial scales simultaneously will improve the understanding of the habitats required to complete the juvenile stage, which is necessary information for efficient management (Beck *et al.*, 2001). Furthermore, studies that are able to combine acoustic telemetry with other techniques to elucidate movements and trophic linkages among habitats (*i.e.* dietary tracers), will provide a more complete understanding of the relationships between habitat value and use.

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