



Searching for Oxygen: Dynamic Movement Responses of Juvenile Spot (*Leiostomus xanthurus*) in an Intermittently Hypoxic Estuary

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Abstract

The movement responses of juvenile fishes exposed to intermittent hypoxia mediate the effects of impaired water quality on estuarine nursery habitat function. Twenty-five juvenile spot (*Leiostomus xanthurus*) were implanted with hydroacoustic tags and tracked in the Neuse River Estuary (NRE), NC during multiple hypoxic episodes (dissolved oxygen, $DO \leq 2 \text{ mg L}^{-1}$), while simultaneously monitoring environmental conditions at fish detection locations and at a representative mid-channel location. Mean swimming speed increased nearly ninefold under hypoxia, as fish traversed waters with low bottom DO over long distances (~10 km) for up to 35 h, before moving from the deeper main channel to shallow, nearshore oxygenated refuge habitats. Generalized additive models indicated that spot swimming speeds increased significantly with decreasing bottom DO and increasing depth, and were correlated with speed during the previous movement segment, though most (60–70%) of the variability in swimming speed remained unexplained. *K*-means clustering identified three behavioral modes: (1) slow swimming in deep water when DO was high throughout the NRE (normoxic behavior); (2) rapid and highly directed swimming that traversed deep waters with low bottom DO (hypoxia avoidance behavior); and (3) slow swimming in shallow, oxygenated waters while deeper waters remained hypoxic (refuge behavior). Despite comprising only 8.4% of the observed movements, hypoxia avoidance behavior resulted in highly conspicuous increases in swimming speed that led to large displacements of juvenile fish. The results help elucidate the specific behavioral responses of juvenile spot to intermittent hypoxia, as well as provide insight into the mechanisms by which variable DO conditions affect estuarine nursery habitat function.

Keywords Movement · Hypoxia · Spot · *Leiostomus xanthurus* · Neuse River estuary · Acoustic telemetry · Nursery habitat · Swimming behavior · Dissolved oxygen · Habitat use

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Introduction

Estuaries are highly productive ecosystems that serve as important nursery areas for the juvenile stages of transient marine fishes (Potter et al. 2015; Sheaves et al. 2015; Litvin et al. 2018). The value of estuaries as nursery habitats is based on favorable hydrographic conditions, abundant food resources, and refuge from predators, which promote the growth and survival of early life stages, thereby enhancing recruitment to the adult population (Craig and Crowder 2000; Nagelkerken et al. 2014; Le Pape and Bonhommeau 2015; Whitfield 2020). Fresh water and nutrients transported from coastal watersheds to downstream estuaries are important drivers of the high primary and secondary production that contribute to the value of these habitats for juvenile fishes (Peterson 2003; Mahardja et al. 2019). Even so, the high nutrient loading and salinity stratification characteristic

of riverine estuaries often causes oxygen depletion, or hypoxia (dissolved oxygen, $DO \leq 2 \text{ mg L}^{-1}$), potentially impairing fish growth (Stierhoff et al. 2009), survival (Thronson and Quigg 2008), and reproduction (Thomas et al. 2007). The effects of hypoxia on nursery habitat function are uncertain, however, due to high spatial and temporal variability in DO conditions in most estuaries, the ephemeral exposure of mobile fishes to low DO, and the multiple direct and indirect pathways by which DO can influence population and community dynamics (Rose et al. 2009; Moriarty et al. 2020).

The severity of estuarine hypoxia varies over multiple spatial and temporal scales in relation to both physical and biological processes (Costa et al. 2018; Fennel and Testa 2019). Seasonal patterns in hypoxia are typically driven by nutrient loading, freshwater flow, and temperature, which drive algal production, stratification, and microbial respiration, often leading to the most severe hypoxia during the summer months. In shallow estuaries, wind plays an important role in periodically breaking down stratification and re-aerating hypoxic bottom waters, as well as in the rapid advection of low DO water into nearshore habitats (Reynolds-Fleming and Luetlich 2004; Wang et al. 2015; Coogan et al. 2019), sometimes entrapping and killing fish and other organisms (Kelly et al. 2018). However, even in systems with severe hypoxia, some oxygenated habitat typically exists, either in surface waters above the oxycline (Craig et al. 2010; Brooks et al. 2022), in shallow waters near shore (Bell et al. 2003; Campbell and Rice 2014; Online Resource 3), or farther downstream where stratification and algal production are less intense (Buzzelli et al. 2002; Eby and Crowder 2002). Understanding the behavioral responses of juvenile fishes to dynamic DO conditions is critical to evaluating the consequences of hypoxia for estuarine nursery habitat function and the population dynamics of transient marine species.

Juvenile spot (*Leiostomus xanthurus*) are among the most abundant transient marine species in estuaries along the US Atlantic and Gulf coasts (O'Connell et al. 2004; Wingate and Secor 2008). Adult spot spawn offshore over a protracted period during fall and winter (November to March) and their larvae are transported across the continental shelf and into estuaries where they recruit to benthic habitats primarily in late winter and early spring (February to April; Weinstein et al. 1984; Flores-Coto and Warlen 1993). Small spot (up to ~50 mm) occupy shallow nursery creeks during spring and early summer (Weinstein 1983; Garwood et al. 2019) and move to deeper estuarine waters with increasing size (Weinstein and Walters 1981; Weinstein et al. 1984). Spot are highly demersal, with a laterally compressed body and sub-terminal mouth specialized for feeding on benthic prey (Deary and Hilton 2016), particularly annelid worms, copepods, and other meiofauna (Zapfe and Rackocinski

2008; Akin and Winemiller 2012; Nemerson and Able 2020). Given their movements within estuaries and their fall spawning migration, spot play an important role in the transfer of benthic production both among estuarine habitats and to offshore food webs (Currin et al. 1984; Deegan et al. 2000; Winemiller and Akin 2007; Overton et al. 2008, 2009; Christian and Allen 2014).

Exposure to low DO elicits behavioral responses in mobile organisms that vary within and among individuals and species as a function of physiological adaptations (Zhu et al. 2013), energetic state (Nelson and Lipkey 2015), prior DO exposure (Nelson et al. 2019), age and body size (Burlerson et al. 2001), ecological context (Steckbauer et al. 2018; e.g., competition and predation), and the particular spatial and temporal dynamics of DO (Bell and Eggleston 2005). When exposed to low DO, fish either increase swimming speed to facilitate escape from low DO water (active response) or decrease swimming speed to suppress metabolism in order to enhance survival during low DO exposure (passive response; Pollock et al. 2007). The avoidance response of fish is multi-faceted and complex, however, because the same individual can employ different behaviors over the course of low DO exposure. For example, juvenile weakfish (*Cynoscion regalis*) acclimated to oxygen-saturated water in the lab increased swimming speed during an initial DO decline but then decreased swimming speed at very low DO ($< 1.4 \text{ mg L}^{-1}$), while fish acclimated to low DO (diel cycling between 2.0 and 11.0 $\text{mg}\cdot\text{L}^{-1}$) had slower swimming speeds that did not change during a DO decline (Brady et al. 2009). Lab experiments indicate a variety of responses to low DO, including little change in swimming speed (Behrens and Steffensen 2007), rapid increases in swimming speed but only at extremely low DO (Cook et al. 2014), and increases (Brady and Targett 2010) or decreases (Skjaeraasen et al. 2008) in swimming speed across a broad range of DO conditions. While juvenile spot are able to detect and quickly avoid low DO in laboratory choice trials (Wannamaker and Rice 2000), little is known about their movement responses to dynamic DO conditions in the field.

Laboratory studies are useful for directly observing fish responses to low DO, but do not encompass the full range of movement behaviors and environmental conditions that fish experience in the field. Trawl surveys show that fish are typically absent from waters below a particular DO level (Eby and Crowder 2002; Bell and Eggleston 2005; Keller et al. 2017), and sometimes aggregate near hypoxic edges (Craig 2012; Craig and Bosman 2013) or in oxygenated nearshore habitats (Campbell and Rice 2014). However, the spatial and temporal scale of most field surveys is too coarse to capture the behavioral responses of mobile fishes, particularly in systems with rapidly changing DO conditions. Rather, field surveys reveal the consequences of hypoxia avoidance for spatial distributions, but provide little insight

on the particular behaviors that led to the observed changes. Biotelemetry avoids some of these limitations, but has rarely been used to investigate the movement responses of mobile fishes to hypoxia.

The objective of this study was to investigate the movements of juvenile spot in response to intermittent hypoxic episodes in the Neuse River Estuary (NRE), a large temperate riverine estuary on the Southeast US Atlantic coast. Acoustically-tagged juvenile spot were tracked for up to 8 days at relatively fine temporal (i.e., 2 h) scales while simultaneously measuring DO and other environmental conditions at the fish detection locations and in the broader NRE. The results help to elucidate the specific behavioral responses of juvenile spot to intermittent hypoxia, as well as provide insight on the direct and indirect costs that spot may incur as a result of variable DO conditions in estuarine nursery habitats.

Methods

Study Site The Neuse River estuary is a large (~70 km long × 5 km wide), shallow (mean depth of 2.7 m), wind-driven estuary located in the coastal plain of North Carolina, and draining into southwestern Pamlico Sound (Fig. 1). The NRE ranges from oligohaline to polyhaline along its

length, has a slow flushing and high nutrient retention rate, and is considered a mesotrophic to eutrophic estuary (Paerl et al. 2006; Mallin et al. 2000). The drainage basin of the NRE extends ~400 km inland and encompasses an area of ~16,000 km². A 30% nitrogen reduction target has been set for the Neuse River due to the high nutrient loading from agricultural and stormwater runoff that fuels recurrent, summertime hypoxia in the NRE (Deamer 2009). Hypoxia can extend over nearly half of the bottom of the NRE and is typically most severe in the deeper main channel and above the ~90° bend separating the upper and lower NRE (Fig. 1; Buzelli et al. 2002; Katin et al. 2019).

Telemetry Methods

Fish Collection and Tagging Juvenile spot (late age 0 and age 1; Beckman and Dean 1984) were collected by bottom trawl from the upper NRE and held in indoor 250-gal seawater (~32 psu) tanks to shed any parasites and bacteria. Twenty-five spot (mean ± standard deviation total length (TL, mm), 169.3 ± 21.4) were surgically implanted with miniature hydroacoustic coded transmitters (Sonotronics PT-2 tags, 10-day battery life; Table 1). Each tag had a unique combination of transmitter frequency and ping pattern. Surgical instruments were autoclaved, soaked overnight

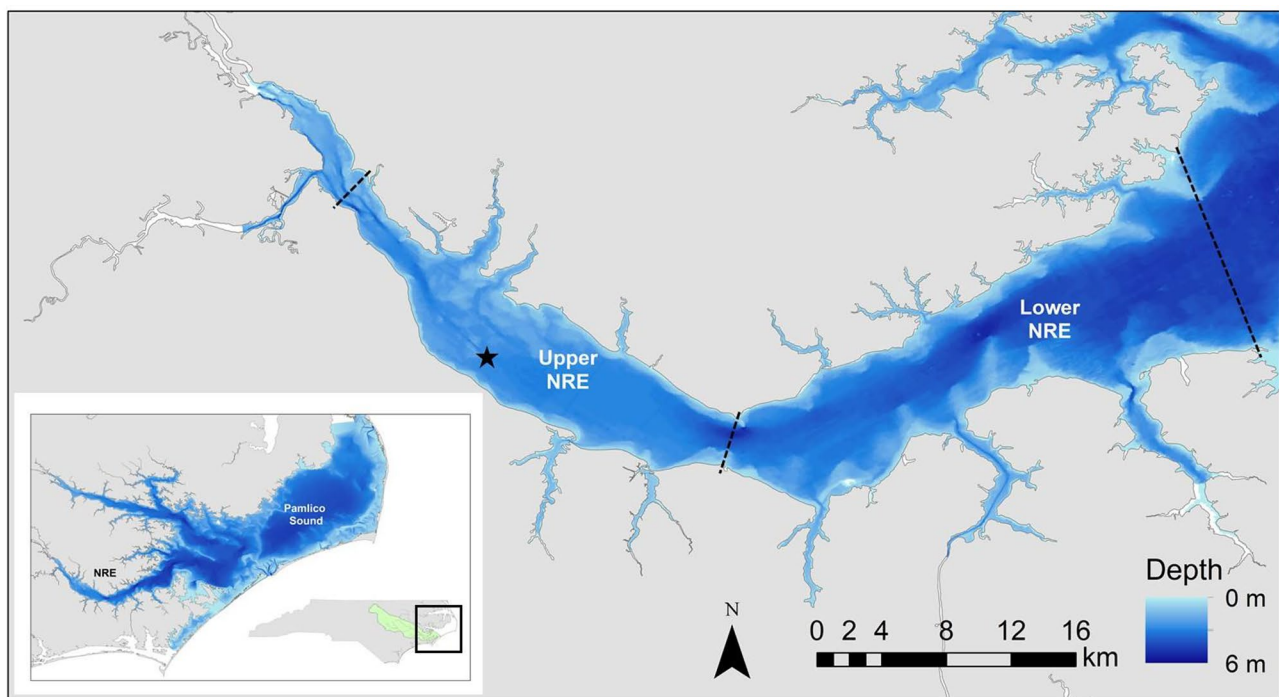


Fig. 1 The Neuse River Estuary (NRE), NC. Dashed lines delineate the upper and lower NRE separated by the near 90° bend (middle dashed line). The black star shows the location of the moored hydrolabs used to monitor surface and bottom hydrographic conditions in the system.

Blue shading indicates water depth. Green shading on the inset panel shows the Neuse River watershed and the black square delineates the Pamlico Sound system

Table 1 Summary of acoustically-tagged juvenile spot, *Leiostomus xanthurus*, in the Neuse River Estuary (NRE), NC. Fish were released and tracked in eight bouts during which environmental conditions were monitored at the fish detection locations and at a mooring in the upper NRE. “% Detections Hypoxia” is the percent of fish detection locations with bottom dissolved oxygen (DO) ≤ 2.0 mg L⁻¹

Bout	Fish ID	Total length (mm)	Release date	Track duration (d)	Number detections	% Detections hypoxia
1	1	165	9–26-02	5.1	35	0.0
1	2	162	10–2-02	1.1	11	0.0
1	3	156	10–2-02	6.7	50	0.0
2	21	172	6–20-03	1.3	21	0.0
3	22	167	7–8-03	6.5	26	0.0
3	23	178	7–14-03	3.2	22	0.0
3	25	165	7–15-03	1.9	16	37.5
3	24	173	7–15-03	2.3	14	0.0
4	5	166	10–2-03	7.7	93	16.1
4	4	165	10–3-03	6.9	80	11.3
4	6	164	10–6-03	4.5	50	16.0
5	14	152	6–6-04	2.0	20	5.0
5	15	148	6–8-04	5.3	27	7.4
6	16	139	6–21-04	4.6	44	15.9
6	20	169	6–22-04	1.1	10	0.0
6	19	168	6–28-04	0.7	9	66.7
6	17	159	6–24-04	3.7	43	25.6
6	18	134	6–27-04	2.9	26	19.2
7	8	200	7–10-05	4.9	50	24.0
7	11	157	7–10-05	2.6	29	24.1
7	7	200	7–12-05	7.6	31	31.5
7	13	151	7–14-05	5.8	23	21.7
8	10	212	7–20-05	7.2	55	3.6
8	9	200	7–20-05	6.2	51	3.9
8	12	208	7–23-05	2.1	23	0.0

in disinfectant (Cidexplus®), and rinsed with sterile saline solution. Each fish was anesthetized in a 10-L solution of 120-ppm tricaine methanesulfate (MS-222), measured (nearest mm TL), given a tetracycline injection in the dorsal musculature to prevent infection, and then placed on an anesthesia delivery system that supplied a continuous maintenance dose of anesthetic (90 ppm MS-222) perfused over the gills. A small area of the abdomen between the anus and the pelvic fins was cleaned with 10% povidone-iodine and an incision was made along the ventral surface. After implanting the tag, the incision was closed with three discontinuous monofilament sutures crimped to a 3/8 circle reverse cutting needle (Ethicon 4–0 PDS II, Somerville, NJ), and the fish revived by circulating aerated water over the gills. The surgical procedure is further described in Harms (2005) and Harms and Lewbart (2000, 2011), and has been successfully used on juvenile spot in other studies (Brady and Targett 2013; Friedl et al. 2013). Small pieces of bloodworm (*Nereis* spp.) were introduced as food 48 h after surgery. Behavioral laboratory experiments with separate fish from those tracked in the NRE found no effects of the tags on movement and feeding behavior after a 4-day recovery period (Online Resource 1).

After recovery, tagged fish were transported to the NRE in coolers with 2–3 untagged fish, acclimated for several hours by frequent water exchanges, and placed together in acclimation cages on the bottom of the NRE for 18–24 h. Acclimation cages were constructed of 0.63-cm vexar plastic mesh attached to rigid 2.5 cm PCV tubing and measured 1 m on each side. Spot form loose aggregations in the field (Stokesbury and Ross 1997), and so fish were held and released in small groups to promote normal swimming behavior.

Fish were released in eight bouts during the summer and fall of 2002 to 2005 (Table 1). A bout consisted of a 7–14 day period during which 1–5 tagged fish were released and then tracked from a small vessel while environmental conditions were continuously monitored at a nearby mooring (see the “Environmental Monitoring” section). Fish were tracked in response to the development of short-term (i.e., days) hypoxic episodes, which were relatively frequent but also highly episodic in the NRE. Tracking was conducted by a 2-person team from a single vessel (5.5 m) powered by a 90 horsepower 4-stroke engine. Teams worked in 8-h shifts over the 24-h day, except during inclement weather. Fish were located with a Sonotronics USR 96 receiver and

DH-4 directional hydrophone. Once the tag was identified, the vessel navigated in the direction of the maximum transmitter signal strength until the amplitude was equal in all directions. The time and geographic coordinates of each fish detection location were recorded with a WAS-enabled GPS (< 3 m accuracy). Attempts to locate individual fish were made every 2 h to avoid continuous exposure of tagged fish to the tracking vessel and due to the logistical constraints of locating multiple fish that were dispersed over several kilometers. The median interval between detection locations was 2.1 h, but due to inclement weather and occasional difficulties locating tagged fish, the time between detection locations ranged up to 76.6 h. Typical distances moved by individual fish in 2 h ranged from 50 to 1000 m. Track durations ranged from 1.1 to 7.7 days (mean = 4.3 days). The average sighting accuracy based on trials where observers navigated to dummy tags hidden at unknown locations was 19.6 ± 8.2 m (mean \pm standard deviation; $n = 20$ trials).

Environmental Monitoring Surface and bottom DO, temperature, salinity, and water depth were measured at the location of each fish immediately after detection with a YSI Model 600XLM Hydrolab (“detection location DO”). Time of day was determined based on solar elevation (i.e., the angle of the sun relative to the horizon) at each detection location using the NOAA solar position calculator and R *maptools* library. In addition, two Hydrolab minisonde 5 multiprobes mounted within the bottom and the surface meter of the water column monitored water quality at a stationary channel marker (USGS station 0209262905) in relatively deep (~ 3 m) water in the upper NRE (Fig. 1). The datasondes recorded surface and bottom temperature, salinity, and DO every 15 min and were calibrated and maintained weekly (Wagner et al. 2006). Because hypoxia typically begins in the deeper main channel of the NRE, spreads vertically into the water column and laterally across the bottom, and then dissipates due to wind-mixing (Campbell and Rice 2014), the DO measurements at the mooring were considered an indicator of the development and cessation of hypoxic episodes in the upper NRE (“system DO”).

Data Analysis

Movement Data A total of 859 fish detection locations were recorded across the eight tracking bouts and 25 tagged fish (Table 1). Detection locations were converted to Universal Transverse Mercator eastings and northings (UTM 18) and then rotated 140° to obtain coordinate axes that corresponded to the along-channel (upstream–downstream) and cross-channel directions of the upper NRE. Swimming speed was computed as the straight-line distance between two successive detection locations divided by the elapsed time (nearest minute). Turning angles were computed as

the angle between the two straight-line distances formed by three successive detections. Only movement segments where the time between successive detections was from 1 to 3 h were used in the statistical analysis. Swimming speeds for longer time intervals (i.e., > 3 h) could be biased to slower values due to the assumption of straight-line swimming, and this bias would be more severe the longer the time between detections (Rowcliffe et al. 2012). Detections at time intervals < 1 h were very rare (< 0.5%) due to the tracking protocol. This filtering resulted in 682 movement segments (7 to 79 per fish; 80% of the original data) that had two successive detections measured within 1–3 h of each other. Sample sizes varied slightly among the statistical analyses described below due to the filtering process and the data requirements of each analysis (Online Resource 2, Table S1).

Environmental Drivers of Spot Swimming Behavior Generalized additive models (GAM) were used to identify environmental drivers of spot swimming speed (Wood 2017). Potential explanatory variables were surface and bottom temperature, salinity, and DO, stratification (bottom – surface salinity), and depth at the fish detection locations, time of day, day of the year (to account for seasonal or other temporal effects), and swimming speed in the preceding segment (to account for temporal autocorrelation). Each GAM term used a thin plate smoothing spline except for day of the year, which used a cyclical smoothing spline (Pedersen et al. 2019). All smoothing splines were limited to four degrees of freedom to avoid unrealistically complex shapes. The model was fit by maximum likelihood optimization using a gamma distribution and log link function. A reduced or “best fit” GAM was determined by iteratively dropping variables from the full model in order of decreasing *p*-values using a threshold of 0.01. Lower limits for the influence of the remaining variables on swimming speed were estimated as the difference in deviance explained by the reduced GAM with and without each variable included. The upper limit for the influence of each variable was estimated as the deviance explained by a GAM with only that explanatory variable included. All models were fit using the *mgcv* package in R (Wood 2017).

Identifying Behavioral Modes *K*-means clustering was used to classify movement segments from all fish into three clusters based on swimming speed and water depth (MacQueen 1967). Three clusters were specified in order to distinguish swimming behavior that was unaffected by low DO from two common responses to hypoxia, increases and decreases in swimming speed. Mann–Whitney *U* tests were used to test whether the median bottom DO at the beginning of movement segments, and thus potentially a driver of subsequent movement behavior (and not used in defining the clusters), differed among the three clusters. Separate Mann–Whitney

U tests were used to test whether the median turning angle, a measure of sinuosity (i.e., curviness) in spot swimming behavior, and the median bottom DO at the mooring, a measure of broader DO conditions in the upper NRE, differed among the three clusters. Because the GAM detected a moderate amount of temporal autocorrelation in swimming speed (see Table 2), some of the movement segments were averaged prior to statistical analysis to avoid non-independence of repeated measures on the same fish (i.e., pseudoreplication). Specifically, after classifying all movement segments, if multiple segments from the same fish occurred in the same cluster and were within the same 8-h period (starting from the time the fish was released), they were averaged prior to statistical analysis. While this approach averages over some variation in swimming behavior, it minimizes the effects of temporal autocorrelation on the statistical results.

Temporal Sequence of Movement Behaviors To quantify temporal patterns in swimming behavior in relation to DO, the number of movement segments in each of the three *K*-means clusters was compared before, during, and after hypoxic episodes, as determined by bottom DO at the mooring (“system DO”). For this analysis, hypoxia was defined as $\text{DO} < 2.8 \text{ mg L}^{-1}$ because spot swimming speed in a similar study increased when DO declined below this level (Brady and Targett 2013). The movement segments were pooled into six temporal groups: (A) prior to the first occurrence of hypoxia in the system; (B) during the first occurrence of hypoxia; (C) during subsequent periods of hypoxia; (D) 0–12 h after the end of a hypoxic episode; (E) 12–24 h after the end of a hypoxic episode; and (F) > 24 h after the end of a hypoxic episode. Segments in group “A” and groups “D” through “F” occurred when DO was $\geq 2.8 \text{ mg L}^{-1}$ at the mooring while segments in groups “B” and “C” occurred when DO was $< 2.8 \text{ mg L}^{-1}$ at the mooring during some or all of the segment. Random permutation tests were used to test whether the observed number of segments of a given cluster within a temporal group was statistically different from that expected under the null hypothesis that the behavioral modes were unrelated to the temporal dynamics of hypoxia. The number of segments for each cluster (1–3) by

temporal group (A–F) combination (18 total) was computed for 10,000 random samples drawn with replacement from the original data and compared to the observed number.

Results

Spot Movement Trajectories During Hypoxic Episodes

Spot remained within the mesohaline (10–20 psu) region of the upper NRE for the duration of the tracking bouts and used nearly the full range of depths available (Fig. 2). Tagged fish were not detected in the downstream polyhaline region of the lower NRE nor in the upstream fresh water region of the Neuse River. Two fish moved into a small tributary along the south shore for short periods (12 and 24 h) before returning to the main region of the upper NRE.

Multiple episodes of hypoxia occurred in all 4 years that spot were tracked (Fig. 3). Hypoxic episodes were characterized by a decline in bottom DO to near anoxic levels ($< 0.5 \text{ mg L}^{-1}$) over a day or more, persistent low DO for 2–5 days, sometimes interspersed with brief periods of normoxia, and a rapid (< 1 day) increase to near saturated conditions, usually due to wind-driven mixing (Fig. 3). Surface DO at the mooring was higher than bottom DO and was mostly above 4 mg L^{-1} , but occasionally declined to lower levels (Fig. 3).

The movement responses of juvenile spot to hypoxia are illustrated by three fish that were tracked prior to, during, and after a system-wide decline in bottom DO in 2003 (Fig. 4). The three fish were detected 50 to 93 times on average every 2.0–2.2 h over a 5–8-day period (Table 1, bout 4). During the tracking bout, bottom DO at the mooring declined from ~ 7.1 to $\sim 0.5 \text{ mg L}^{-1}$ over 2.5 days, followed by 2.5 days of persistent hypoxia and then a rapid return to normoxia ($> 5 \text{ mg L}^{-1}$) over about 6 h due to wind-driven remixing (Fig. 4a; Online Resource 3, Fig. S1). Additional measurements taken along cross-river transects indicated that the decline in bottom DO was spatially extensive, with DO typically $< 1 \text{ mg L}^{-1}$ across most of the upper NRE except for shallow ($< 0.5 \text{ m}$) waters close to shore (Online Resource 3, Fig. S2). Surface DO at the mooring and at the fish detection locations was generally $> 5 \text{ mg L}^{-1}$ throughout the tracking bout (Fig. 4a; Online Resource 3, Fig. S1, S3).

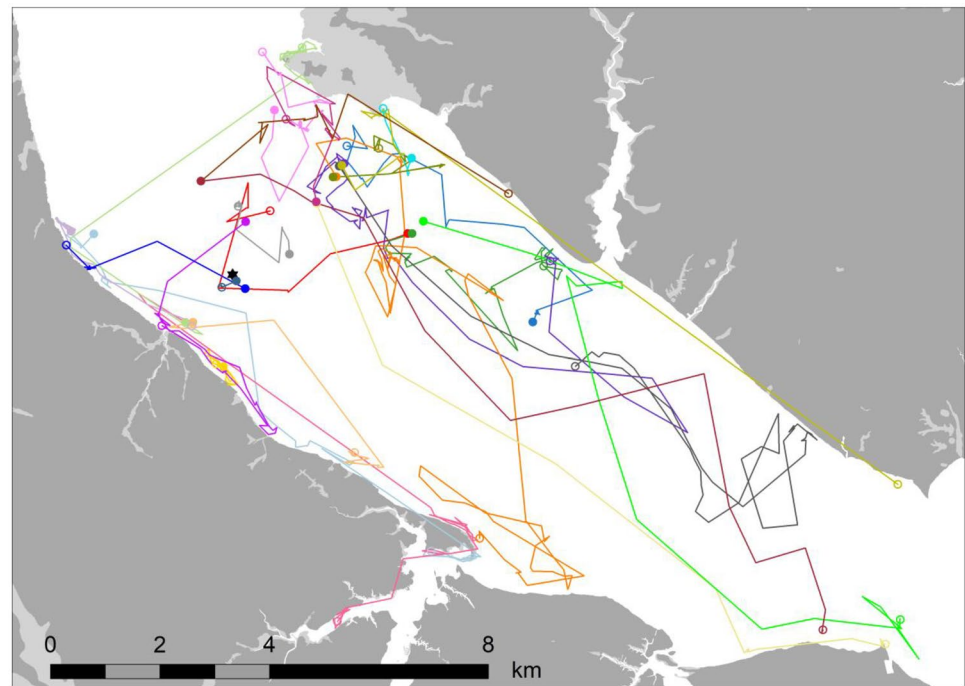
Fish 4 and fish 5 were released on Oct 2 and Oct 3, 3 and 4 days prior to a decline in DO to hypoxic levels (Fig. 4b, c). Prior to hypoxia, bottom DO at the fish detection locations was mostly above 4 mg L^{-1} (blue circles), with the exception of two detections shortly after release of fish 5 (Fig. 4c). Both fish exhibited slow swimming speeds (mean

Table 2 Results from the best fit generalized additive model (GAM) of juvenile spot swimming speed in relation to environmental variables

	EDF	Ref DF	F-statistic	Min Dev (%)	Max Dev (%)
Prior speed	2.64	2.90	15.2***	8.8	22.5
Water depth	1.61	1.97	5.19**	2.2	16.4
Bottom DO	1.0	1.01	11.0***	2.0	14.5

The model explained 29.1% of the deviance in spot swimming speed. *EDF*, estimated degrees of freedom; *Ref DF*, reference degrees of freedom; *Min Dev*, minimum deviance explained; *Max Dev*, maximum deviance explained (see text for details). *** $p < 0.001$, ** $p < 0.01$

Fig. 2 Movement trajectories of acoustically tagged juvenile spot in the upper Neuse River Estuary (NRE), NC. Each color represents the track for an individual fish ($n=25$). Filled circles indicate release locations and open circles indicate the last recorded location. The black star indicates the location of the mooring



0.028 and 0.036 m s^{-1}) during this time while remaining in relatively small regions (1.4 and 3.4 km stretch) of the deeper main channel (2.7 and 2.5 m mean depth; Fig. 4b, c). A third fish (Fish 6) was released on Oct 6, 2 h before DO at the mooring declined to hypoxic levels (Fig. 4d). When DO at the fish detection locations declined below $\sim 3 \text{ mg L}^{-1}$, all three fish began swimming downstream at greatly increased speed (mean 0.10, 0.10, and 0.18 m s^{-1} for fish 4, 5, and 6, respectively; Fig. 4b–d). Sustained rapid swimming occurred over the ensuing 16–35 h in waters with predominantly low bottom DO (Fig. 4b–d, red circles along main channel; mean detection location DO, 2.2, 1.9, and 2.7 mg L^{-1} for fish 4, 5, and 6, respectively), as well as at the mooring (Fig. 4a, gray shading). In contrast, surface waters were well-oxygenated ($> 5 \text{ mg L}^{-1}$) at both the fish detection locations and the mooring for the duration of the tracking bout (Fig. 4a, Online Resource 3, Figs. S1, S3). The three fish moved relatively large distances (7.1, 6.3, and 9.9 km for fish 4, 5, and 6, respectively) along the main channel before entering shallow (depth $\leq 1.5 \text{ m}$) oxygenated waters on the north or south shore of the upper NRE (Fig. 4b–d, blue circles near the shoreline).

After moving to shallow water, fish 4 became much less active (0.01 m s^{-1} mean speed), and remained in a small (0.3 km stretch of shoreline), normoxic (detection location $\geq 4.1 \text{ mg L}^{-1}$) nearshore area for 68 h (Fig. 4b). In contrast, upon reaching shallow water, fish 5 continued swimming for 77 h at slow speed (0.043 m s^{-1} mean speed) between shallow (0.8–1.5 m), normoxic water (detection location $\geq 4.7 \text{ mg L}^{-1}$), and nearby deeper (2.4–3.8 m) hypoxic water ($\leq 1.0 \text{ mg L}^{-1}$) along a 3.6 km stretch of

shoreline (Fig. 4c). While fish 4 and fish 5 had different swimming behaviors after moving nearshore, neither moved back to the main channel in the 48 h after the system re-mixed and deeper bottom waters were again normoxic (Fig. 4a). Fish 6 showed movement behavior similar to aspects of both fish 4 and fish 5 (Fig. 4d). After moving to shallow water, fish 6 spent 32 h swimming slowly (mean 0.012 m s^{-1}) along a 0.5 km stretch of shoreline similar to fish 4. This limited movement was followed by 28 h of swimming at moderate speed (mean 0.054 m s^{-1}) along a 2.1 km stretch of shoreline between shallow, normoxic water (detection location $> 5.5 \text{ mg L}^{-1}$), and nearby deeper hypoxic water ($< 1.5 \text{ mg L}^{-1}$). Fish 6 left shallow waters 22 h after bottom DO at the mooring had increased from $< 1.2 \text{ mg L}^{-1}$ to $> 5 \text{ mg L}^{-1}$ due to wind mixing (Online Resource 3, Fig. S1), moved back into the main channel, and traveled 3.9 km upstream over the next 29 h at slow speed (mean 0.039 m s^{-1}) in waters with high bottom DO (detection location $> 5 \text{ mg L}^{-1}$, Fig. 4d; blue circles along main channel). Surface DO was consistently high throughout the tracking bout, with the mean and minimum surface DO at the fish detection locations ranging from 7.1 to 7.3 mg L^{-1} and 4.5 to 5.9 mg L^{-1} , respectively, across the three fish tracks (Online Resource 3, Fig. S3).

Environmental Drivers of Swimming Speed

The best fit GAM explained 29.1% of the deviance in spot swimming speed, and included bottom DO and depth at the fish detection locations, and speed during the prior

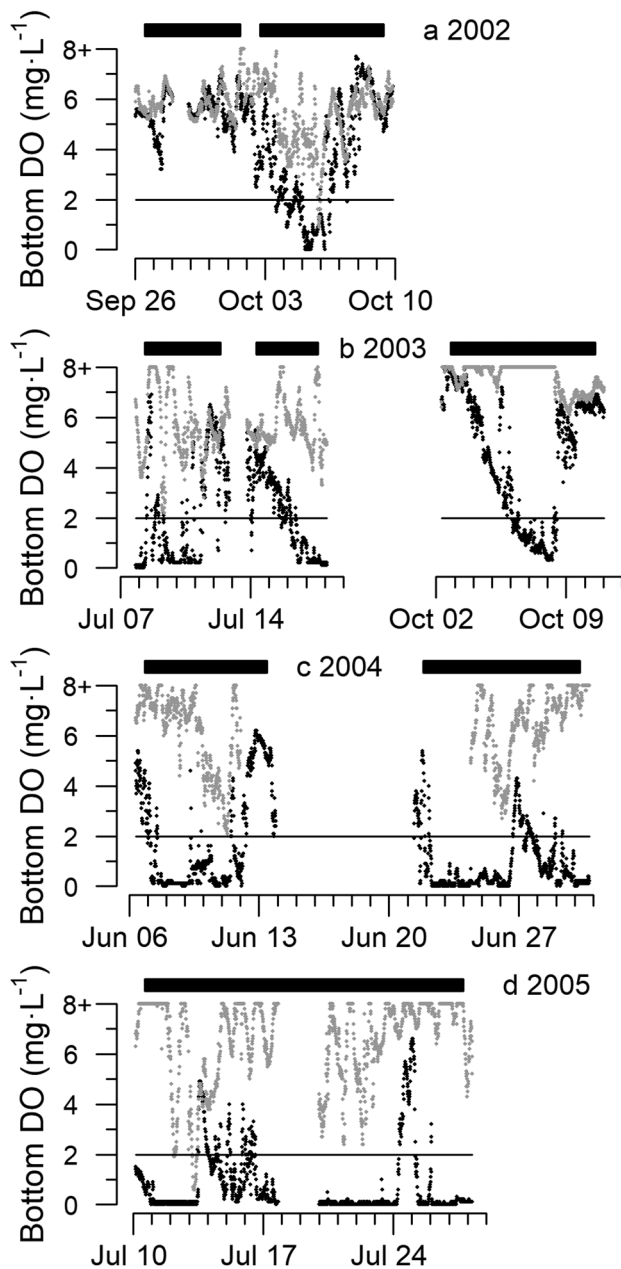


Fig. 3 Bottom (black) and surface (gray) dissolved oxygen (DO) at a stationary mooring in the Neuse River Estuary (NRE), NC. **a** 2002, **b** 2003, **c** 2004, **d** 2005. Thick horizontal black bars show the period that acoustically-tagged juvenile spot were tracked in each year. The thin solid horizontal lines show the 2.0 mg L⁻¹ DO level

movement segment (Table 2, Fig. 5). The strongest single explanatory variable was prior swimming speed, which explained 8.8–22.5% of the deviance in current swimming speed (Table 2, Fig. 5a). Swimming speed also increased with decreasing bottom DO and with increasing depth, which accounted for 2.0–14.5% and 2.2–16.4% of the deviance, respectively (Fig. 5b, c; Table 2). A GAM that included all environmental variables at both the fish detection locations

and at the mooring, as well as individual fish effects and other factors (44 predictors), gave similar results but only explained an additional 10.6% of the deviance (Online Resource 2, Table S2). Hence, 60.3 to 70.1% of the variability in spot swimming speed remained unexplained.

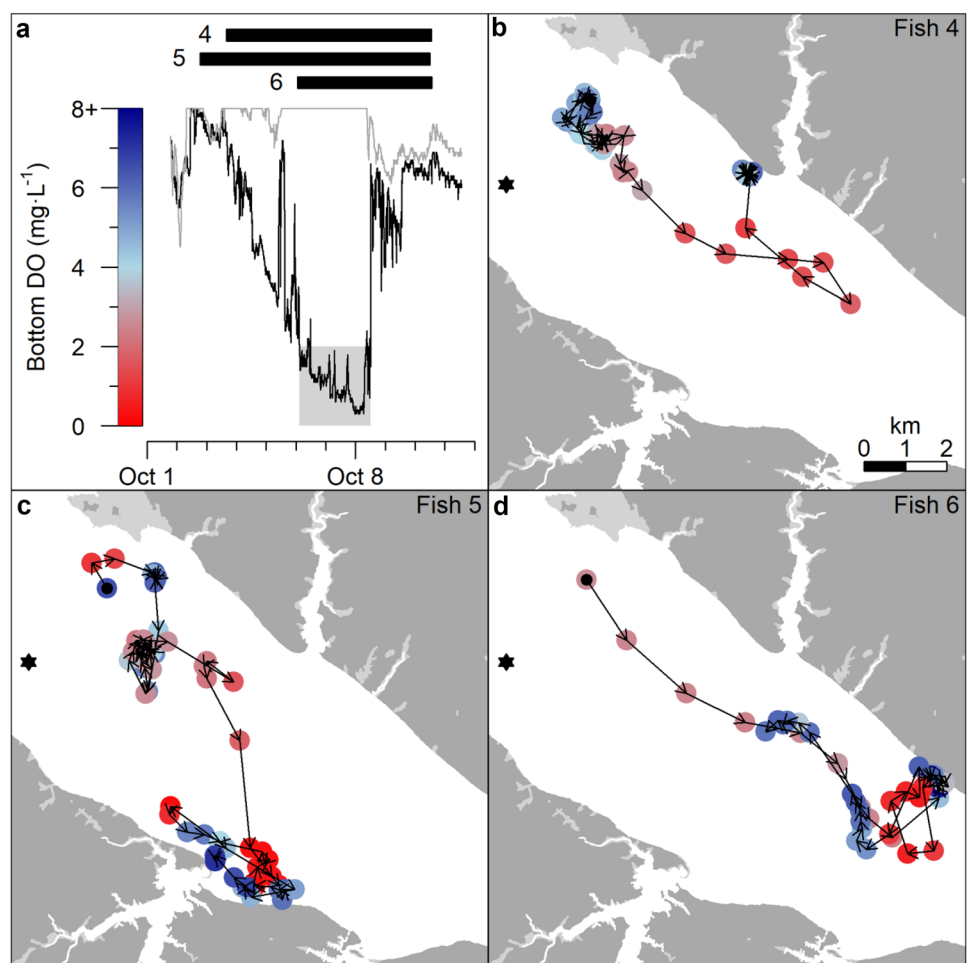
Spot Behavioral Modes in Relation to Hypoxic Episodes

Spot movement segments were classified into three groups based on swimming speed and depth using *K*-means clustering (Fig. 6). Cluster 1 (green, 52.8% of segments) was characterized by slow swimming (mean = 0.022 m s⁻¹) in shallow water (< 2 m). Cluster 2 (blue, 34.1% of segments) was also characterized by slow swimming speeds (mean = 0.025 m s⁻¹), but in contrast to cluster 1, occurred in deeper water (1.9–4.9 m). Cluster 3 was rare (orange, 8.4% of segments) and was characterized by much faster swimming speeds (mean = 0.203 m s⁻¹, range = 0.111–0.582 m s⁻¹) mostly in deep water (80% of segments in depths > 2 m). While comprising a small portion of the total observed movements, the mean swimming speed of cluster 3 was nine times greater than that of cluster 1 and cluster 2 (Fig. 6).

The three clusters differed with respect to bottom DO at the fish detection locations and at the mooring (Fig. 7a, b). Cluster 2 (slow swimming in deep water) occurred mostly under normoxic conditions, with mean bottom DO relatively high (> 4 mg L⁻¹) and similar at the detection locations and the mooring (Fig. 7a, b, blue bars). In contrast, cluster 3 (fast swimming in deep water) occurred mostly when DO was low at both the fish detection locations (mean bottom DO = 2.4 mg L⁻¹) and at the mooring (mean bottom DO = 1.7 mg L⁻¹; Fig. 7a, b, orange bars). However, for cluster 3, bottom DO at the fish detection locations extended to higher levels (~4 mg L⁻¹) compared to that at the mooring (~2.5 mg L⁻¹). Cluster 1 (slow swimming in shallow water) occurred mostly when fish occupied shallow waters with high bottom DO (Fig. 7a, green bars) while deeper waters of the NRE were hypoxic (Fig. 7b, green bars). For cluster 1, bottom DO at the fish detection locations was rarely below 4 mg L⁻¹ while bottom DO at the mooring rarely exceeded 1.5 mg L⁻¹ (Fig. 7a, b, compare green bars).

Spot swimming behavior under normoxic conditions involved significant meandering whether in deep or shallow water, as indicated by the relatively high and similar turning angles for cluster 1 and cluster 2 (Fig. 7c). In contrast, when bottom DO at the fish detection locations and at the mooring was low (Fig. 7a, b, orange bars), spot swimming behavior was highly directed, with the mean turning angle of cluster 3 (fast swimming in deep water) ~20% of that for other two clusters (Fig. 7c). In addition, there was much less variation in turning angles for cluster 3, with the interquartile range about one-third of that for cluster 1 and cluster 2 (Fig. 7c).

Fig. 4 Movement trajectories of three juvenile spot tracked before, during, and after a severe hypoxic episode in the Neuse River Estuary (NRE), NC, in 2003. **a** Bottom (black lines) and surface (gray lines) dissolved oxygen (DO) at a stationary mooring relative to the period over which individual fish were tracked (horizontal black bars); gray shading indicates $\text{DO} \leq 2.0 \text{ mg L}^{-1}$. **b** Fish 4 movement trajectory. **c** Fish 5 movement trajectory; **d** Fish 6 movement trajectory. Black-filled circles indicate the release location of each fish. Filled colored circles (blue to red) indicate fish detection locations color coded by the bottom DO measured when the fish was detected (see legend in panel **a**). Arrows along trajectories indicate the direction of movement. Black star indicates the location of the moored hydrolabs



Temporal Sequence of Behaviors

The number of movement segments in the three clusters varied in relation to the development and dissipation of hypoxia, as determined by bottom DO at the mooring (Fig. 8). Prior to the first occurrence of hypoxia, nearly all movement segments (91%) were in cluster 2 (slow swimming in deep water; group A, blue bars). During the first episode of hypoxia (group B) as well as during subsequent hypoxic episodes (group C), the majority of movement segments (68%) were in cluster 1 (slow swimming in shallow water, green bars), indicating a habitat shift from deep to shallow water associated with the development of hypoxia. Cluster 3 (fast swimming in deep water) comprised a small proportion of movement segments in group A (7.6%), group B (8.4%), and group C (11.3%), but was never observed after hypoxia had subsided (groups D–F). Rather, after hypoxia, the proportion of cluster 2 segments (slow swimming in deep water) increased from 19% within 12 h of hypoxia subsiding to 95% > 24 h after hypoxia, reflecting movement from the shallows back to deeper water (Fig. 8, groups D–F).

Discussion

Tracking of acoustically tagged juvenile spot revealed that swimming speed increased and movements became highly directed during hypoxic episodes, as fish shifted habitat from the deeper main channel of the NRE to shallow, nearshore oxygenated waters. The importance of DO as a driver of the short-term movements of juvenile spot was supported by multiple analyses, including the movement trajectories of individual fish that were tracked before, during, and after a single hypoxic episode, as well as regression and cluster analyses of movements pooled across fish that were tracked during different hypoxic episodes over four separate years. While the effects of hypoxia on fish swimming behavior have been investigated in the lab (Brady and Targett 2010; Cook et al. 2014), few studies have been conducted in the field, particularly in systems with highly intermittent hypoxia like the NRE. The use of acoustic telemetry to track fish for multiple days at short temporal (~2 h) and small spatial (100–1000 s m) scales, while simultaneously monitoring environmental conditions at the fish locations and in

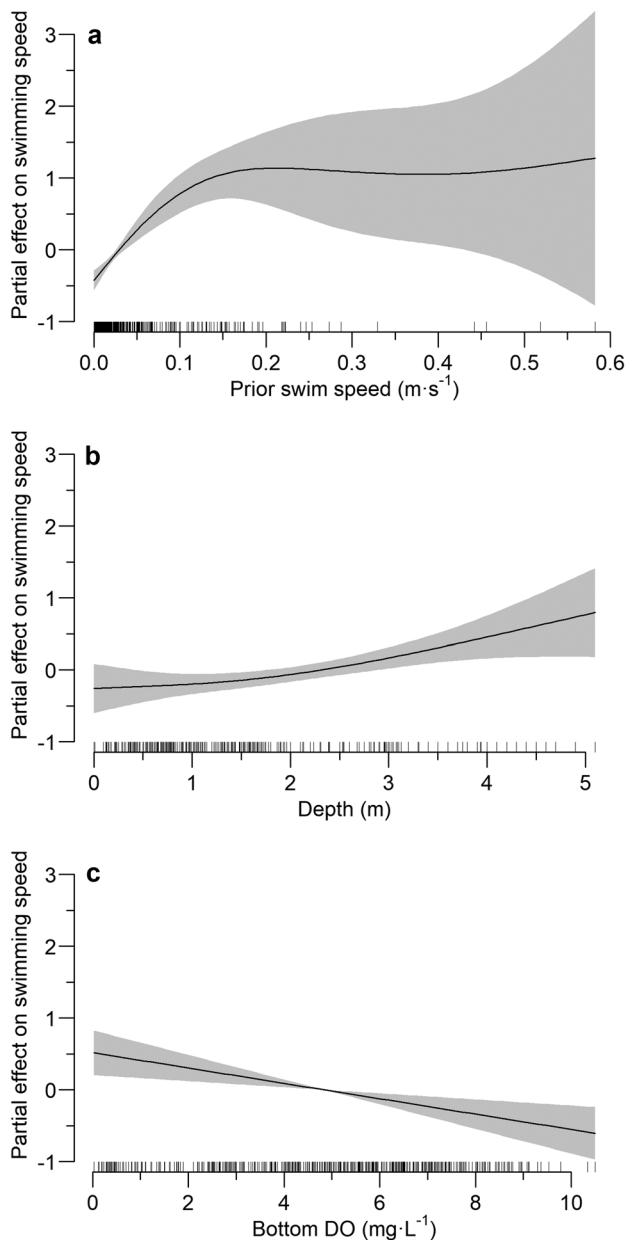


Fig. 5 Partial smoothing spline plots from the best-fit generalized additive model (GAM) of juvenile spot swimming speed in the NRE, NC. Tick marks on the *x*-axis indicate sampling intensity (i.e., number of movement segments). Shaded area represents twice the standard error around the fitted curve

the broader NRE, was critical for revealing the effects of DO on spot swimming behavior and habitat use.

The most parsimonious GAM indicated that only bottom DO, depth, and prior swimming speed had significant effects on spot swimming speed, despite consideration of several other potential environmental drivers (e.g., temperature, salinity, diel, and seasonal effects). In fact, a GAM that included all measured explanatory variables as well as individual fish effects (44 predictors compared to three in

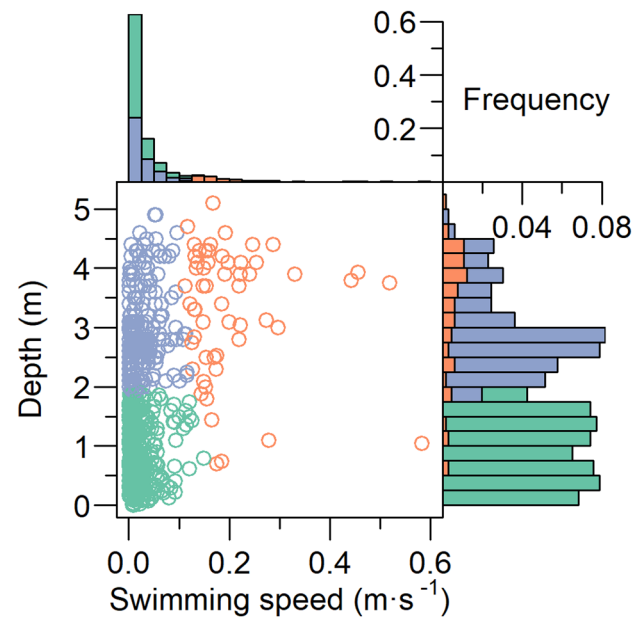


Fig. 6 *K*-Means clustering of movement segments based on swimming speed and depth for tagged juvenile spot in the Neuse River Estuary (NRE), NC. Cluster 1, green (slow swimming in shallow water); cluster 2, blue (slow swimming in deep water); cluster 3, orange (fast swimming in deep water). Circles are individual movement segments and stacked bars show the frequency of the three clusters across the range of observed depths and swimming speeds

the best-fit model) gave similar results but did not explain much additional variation (~10%), indicating that other measured factors had little influence on spot swimming speed at the spatial and temporal scales considered here. The importance of hypoxia as a driver of spot swimming behavior is not surprising given that (1) exposure to low DO is quickly lethal to spot at time scales similar to those over which fish were tracked (minutes to hours; Shimps et al. 2005); (2) juvenile spot have a well-developed capacity to detect and avoid low DO water (Wannamaker and Rice 2000); and (3) hypoxia was pervasive from summer to early fall (June–October) when spot typically occupy the upper NRE (Eby and Crowder 2002). In a similar study of juvenile weakfish and spot in a small (~4 km long) tidal creek, DO, temperature, and salinity strongly co-varied due to tidal advection that moved similar water masses up and down the axis of the creek (Brady and Targett 2013). As a result, it was not possible to disentangle the effects of low DO on fish swimming behavior from other correlated factors. In contrast, the NRE is a much larger system with low flow speeds and negligible tides that is subject to frequent mixing events (Luettich et al. 2002; Reynolds-Fleming and Luettich 2004), so that environmental gradients are less consistent than in tidal creeks. As a result, the GAM was better able to isolate the effects of DO from other factors. Even though DO and depth had significant effects on spot swimming speed, the

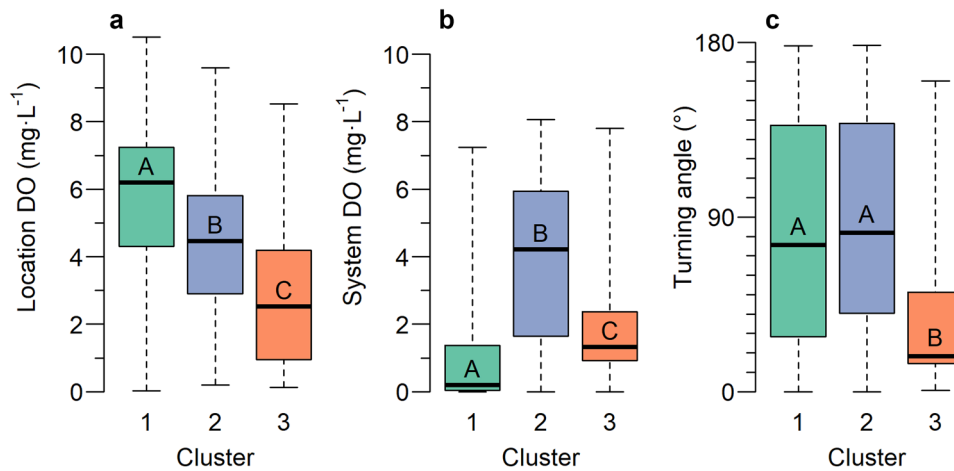


Fig. 7 Comparisons among behavioral modes determined by *K*-means clustering of movement segments for tagged juvenile spot in the Neuse River Estuary (NRE), NC. **a** Bottom DO at the fish detection locations, **b** bottom DO at a stationary mooring in the upper NRE, and **c** turning angle between consecutive movement segments. Cluster 1, green (slow swimming in shallow water); cluster 2, blue (slow swimming in deep

water); cluster 3, orange (fast swimming in deep water). Box plots represent the mean (horizontal line), interquartile range (box), and maximum and minimum values (vertical lines). Letters indicate significant differences among clusters based on separate Mann–Whitney *U* tests for each response variable ($p < 0.05$)

low amount of variability explained by each (up to ~15%) and the large amount of unexplained variability in the GAM overall (~60–70%) indicates that other unmeasured factors

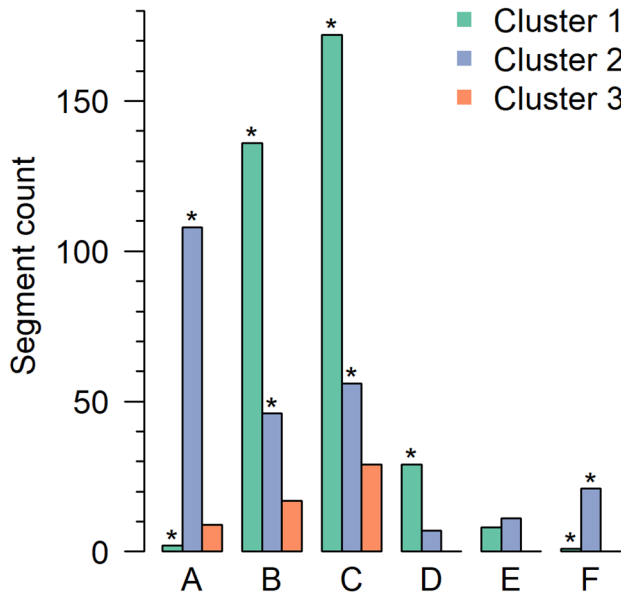


Fig. 8 Distribution of the three behavioral modes relative to the timing of hypoxic episodes in the Neuse River Estuary (NRE), NC. Cluster 1, green (slow swimming in shallow water); cluster 2, blue (slow swimming in deep water); cluster 3, orange (fast swimming in deep water). Letters on the *x*-axis indicate the different temporal periods: A=prior to the first occurrence of hypoxia, B=during the first occurrence of hypoxia, C=during subsequent periods of hypoxia, D=0–12 h after the end of a hypoxic episode, E=12–24 h after the end of a hypoxic episode, F≥24 h after the end of a hypoxic episode. * indicates that the observed number of segments of a given cluster within a temporal period was statistically different from that expected under the null hypothesis that the relative frequency of the three behavioral modes is unrelated to the temporal dynamics of hypoxia ($p < 0.05$)

(e.g., predator avoidance, foraging activity) and stochasticity had considerable influence on spot swimming behavior.

The movement and swimming behaviors of juvenile spot reflected three behavioral modes: (1) slow swimming in deep water during mostly high DO conditions (“normoxic behavior”); (2) rapid, highly directed swimming in deep water with predominantly low bottom DO (“avoidance behavior”); and (3) slow swimming in shallow waters with mostly high DO (“refuge behavior”). The three behavioral modes were relatively distinct, with normoxic and refuge behaviors overlapping little in depth distribution but similar in swimming speeds, while hypoxia avoidance behavior was characterized by rapid and mostly non-overlapping swimming speeds compared to the other two behavioral modes. During hypoxia avoidance (i.e., cluster 3), mean swimming speed of juvenile spot increased ninefold and mean turning angle was about one-fifth of that observed under normoxic conditions. The strong association between cluster 3 and low DO conditions at both the fish detection locations and at the mooring indicates that rapid and highly directed swimming is an important feature of the avoidance response of juvenile spot to hypoxia. In contrast, refuge behavior (i.e., cluster 1) was associated with high bottom DO at the fish locations, due to the diffusion and mixing of atmospheric oxygen into shallow nearshore habitats, but low DO (near anoxic) at the mooring, reflecting the severe hypoxia in the deeper main channel that spot had avoided. Importantly, *K*-means clustering classified spot movements based only on swimming speed and depth, so that the differences in local (i.e., fish detection locations) and system (i.e., mooring) DO among the clusters constitute an independent test of hypoxia effects on spot swimming behavior. The three behavioral modes

identified from movement segments pooled over all fish and hypoxic episodes are also consistent with the individual movement trajectories of juvenile spot tracked before, during, and after a single hypoxic episode, which showed localized swimming prior to hypoxia, rapid, directed swimming for 16–35 h as bottom waters became increasingly hypoxic, and then slower swimming speeds and more localized movements once fish moved to nearshore refuge habitats.

Based on trawl sampling along a cross-river transect in the upper NRE, Campbell and Rice (2014) reported that juvenile spot avoided hypoxia in the main channel by moving to the nearest shoreline ahead of a mobile low DO front, and then quickly (i.e., minutes to hours) returned to adjacent deeper waters once hypoxia subsided. This hypoxia-induced habitat compression led to temporary increases in spot densities in nearshore refuges and associated decreases in foraging success and growth rate (Campbell and Rice 2014, 2017). The telemetry results reported here also indicate that shallow nearshore habitats are important refuges from hypoxia, but differ from the trawl results in the spatial and temporal scale over which juvenile spot behaviorally respond to low DO. For example, tagged spot undertook extensive (up to 10 km) along-channel movements that traversed relatively deep, low DO water rather than moving directly to the nearest shoreline, which was often < 2 km away. In addition, after hypoxia subsided, tagged fish did not immediately return to deeper water, as inferred from trawl sampling, but remained in nearshore habitats for up to several days even after normoxic conditions had returned in the main channel. This behavior may have been due to sensory limitations in the ability of spot to detect nearby changes in DO (Bell et al. 2003), continued repayment of an oxygen debt incurred during the prior rapid swimming and hypoxia exposure (Plambech et al. 2013), or other factors influencing fish movements in shallow, nearshore habitats (Craig and Crowder 2000; Litvin et al. 2018; Whitfield 2020). Habitat compression and associated density-dependent effects are considered an important indirect mechanism by which hypoxia influences the population dynamics of mobile species (Aumann et al. 2006; Rose et al. 2009; Itakura et al. 2021). The telemetry results reported here suggest that these processes are the result of fish movements that occur over a broader spatial and longer temporal scale than previously thought. In particular, because fish remained in shallow water even after hypoxia in the main channel had subsided, the indirect effects of avoidance behavior on ecological processes in nearshore refuges, such as foraging and predation, may persist even after the NRE has returned to normoxic conditions.

While rapid swimming is an important component of the behavioral response of juvenile spot to hypoxia, it may not always be required to successfully avoid low DO and probably occurs in response to other factors as well. For

example, cluster 3 (rapid swimming in deep water) occurred across a broader range of DO conditions at the fish detection locations compared to the mooring, suggesting that rapid swimming, though predominant under hypoxia, also occurred under normoxic conditions. The temporal analysis of the three clusters also revealed a low incidence of rapid swimming (i.e., cluster 3) prior to the development of hypoxia. These observations may have been due to a “release effect,” however, whereby some fish temporarily increased swimming speed shortly after exiting the acclimation cage. They were retained in the analysis because inspection of individual fish tracks did not reveal a consistent pattern in swimming speed after release, fish had been acclimated to ambient conditions, and inclusion of these initial movements made the statistical analysis conservative with respect to detecting the effects of DO. Aside from these few initial observations shortly after release, cluster 3 only occurred when the NRE was experiencing hypoxia; there were no observations of rapid swimming after hypoxia had subsided. However, observations of fish movements after hypoxia were limited (11.8% of movement segments) and cluster 3 was rare (8.4% of movement segments), so that rapid swimming (i.e., cluster 3) may not have been detected due to small sample sizes. In addition, some slow swimming continued to occur in deep water when the NRE was experiencing hypoxia, suggesting that spot may have flexibility in the degree to which rapid swimming is required in order to avoid low DO. High-resolution tracking for longer durations both prior to and after hypoxic episodes, as well as under predominantly normoxic conditions, is needed to better understand the full range of conditions that induce rapid swimming in juvenile spot.

Though spot are highly demersal by nature, several lines of evidence suggest that during prolonged bouts of hypoxia avoidance behavior, they, like several other species (Craig et al. 2010; Itakura et al. 2021; Brooks et al. 2022), likely traveled in oxygenated surface waters above the hypoxic bottom layer. First, lab experiments indicate that DO levels similar to those in bottom waters of the NRE (0.5–2 mg L⁻¹) posed a significant mortality threat to juvenile spot (Pihl et al. 1991; Shimps et al. 2005). Second, because spot were actively swimming during hypoxia, the efficacy of compensatory mechanisms to maintain oxygen uptake would be severely limited if fish were also occupying low DO water near the bottom. For example, rapid sustained swimming, even in well-oxygenated water, reduces the ability of the gills to extract additional oxygen, so that fish exposed to low DO while swimming would experience more severe oxygen limitation compared to that from either low DO or swimming alone (Bushnell et al. 1984). This suggests that bottom DO conditions in the NRE may have been more lethal to actively swimming spot than suggested based on lab experiments with quiescent fish. Supporting this possibility, the

tolerance of juvenile striped bass to hypoxia decreased by a factor of five when fish were swimming at moderate speeds (50% of maximum swimming speed) compared to fish that were not swimming (Nelson and Lipkey 2015). Third, surface DO at the fish detection locations was nearly always high ($> 5 \text{ mg L}^{-1}$), and well above lethal levels ($1\text{--}2 \text{ mg L}^{-1}$; Pihl et al. 1991; Shimps et al. 2005). Given that juvenile spot can detect and respond to differences in DO much smaller ($\sim 1 \text{ mg L}^{-1}$; Wannamaker and Rice 2000) than those between surface and bottom waters in the NRE ($\sim 3\text{--}4 \text{ mg L}^{-1}$), surface waters would have provided a readily available refuge for fish evading the low DO near the bottom.

Even though spot could have avoided low bottom DO just by moving relatively short ($1\text{--}2 \text{ m}$) vertical distances, fish often moved large horizontal distances (up to 10 km) during hypoxic episodes, suggesting that there are costs to simply moving up into the water column that make this response inadequate. Spending extensive time in the upper water column separates juvenile spot from their preferred benthic food resources and may increase predation risk. Diet studies indicate that spot are almost entirely benthic foragers and rarely consume pelagic prey (Zapfe and Rackocinski 2008; Akin and Winemiller 2012; Nemerson and Able 2020), suggesting that foraging efficiency would be highly impaired for fish occupying the upper water column. In addition, gillnet sampling indicated the presence of several pelagic piscivores in the upper NRE during hypoxic episodes (bluefish, *Pomatomus saltatrix*; Spanish mackerel, *Scomberomorus maculatus*; longnose gar, *Lepisosteus osseus*; and spotted seatrout, *Cynoscion nebulosus*; Campbell and Rice 2014), suggesting that encounter rates with predators may increase for spot occupying the upper water column. Hence, even though moving vertically may be a component of the hypoxia avoidance response of juvenile spot, it is likely only a short-term strategy until suitable bottom habitat can be found, which typically involved long horizontal movements.

The rarity with which juvenile spot engaged in rapid swimming (8.4% of movement segments) suggests that it is energetically costly and reserved mostly for conditions of extreme threat. Swimming activity is a large ($\sim 40\%$) but highly variable component of fish energy budgets (Boisclair and Leggett 1989; Holker and Breckling 2002; Brodie et al. 2016). Lab experiments reported a sixfold increase in oxygen consumption of juvenile spot as sustained swimming speed increased from one to seven body lengths per second (BL/s, Horodysky et al. 2011). The mean maximum swimming speed of tagged spot in the NRE was 1.24 BL/s (range $0.24\text{--}3.41 \text{ BL/s}$ across fish), suggesting that fish may have been swimming below their maximum capacity based on lab experiments. Absolute swimming speeds are underestimated in this study, however, due to the assumption of straight-line swimming between detection locations. Even so, the relative increase in swimming speed of spot experiencing

hypoxic versus normoxic conditions in the NRE (ninefold) is comparable to the relative increase in swimming speed considered in the lab (sevenfold; Horodysky et al. 2011), suggesting that the energetic costs to spot avoiding hypoxia in the NRE may have been quite large and proportional to increases in swimming speed. Energetic costs from rapid swimming were incurred for up to $1\text{--}2$ days for some fish that made long excursions ($6\text{--}10 \text{ km}$ over $16\text{--}35 \text{ h}$) along the main channel of the NRE prior to moving shoreward. However, individual spot were tracked during only one hypoxic episode in this study, while up to 30 hypoxic episodes that average 48 h in duration have been reported during summer (June to August) in the upper NRE (Campbell and Rice 2014). Hence, recurrent periods of rapid swimming associated with the avoidance of multiple hypoxic episodes over the summer growing season may result in large cumulative energetic costs to juvenile spot.

The movement responses of juvenile fishes to low DO mediate multiple direct and indirect pathways by which hypoxia can affect fish vital rates (e.g., growth, mortality, reproduction) and ultimately influence population dynamics (Rose et al. 2017). A number of these effects have been documented for juvenile spot and other similar species, including direct mortality from exposure to low DO (Shimps et al. 2005), decreased availability or access to benthic food resources (Powers et al. 2005), decreased growth rates (McNatt and Rice 2004; Campbell and Rice 2017), density-dependent effects in nearshore oxygenated refuge habitats (Eby et al. 2005; Craig et al. 2007; Campbell and Rice 2014), and reproductive impairment (Thomas et al. 2007; Tuckey and Fabrizio 2016), in addition to the energetic and ecological costs of avoidance behavior (this study). Quantifying and integrating the diverse ways by which low DO can affect fish vital rates is necessary to understand the consequences of hypoxia for the nursery function of estuarine habitats and the population dynamics of transient marine species.

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Data Availability Data available on request from the corresponding author.

Declarations

Conflict of Interest The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. The authors declare that they have no conflict of interest. The views expressed herein are those of the authors and do not necessarily reflect the view of NOAA or any of its sub-agencies.

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