

# Movement of juvenile weakfish *Cynoscion regalis* and spot *Leiostomus xanthurus* in relation to diel-cycling hypoxia in an estuarine tidal tributary

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**ABSTRACT:** Fish movement and the spatial and temporal dynamics of hypoxia determine hypoxia exposure and the effect of poor water quality on nursery habitat function. Although water quality criteria for dissolved oxygen (DO) are well defined, hypoxia exposure of juvenile estuary-dependent fishes *in situ* is largely unknown. Thirty-one juvenile weakfish *Cynoscion regalis* and spot *Leiostomus xanthurus* were implanted with acoustic tags. Fish were acclimated for 5 d to either DO saturation or diel-cycling hypoxia (cycling between 11.0 and 2.0 mg O<sub>2</sub> l<sup>-1</sup>). Fish were released during summer into Pepper Creek, Delaware, an estuarine tributary. A logistic generalized additive model with generalized estimating equations was used to determine which environmental covariates significantly discriminated between movement types. Individual fish tracks were overlain on spatiotemporal contour plots of DO that highlight behavioral avoidance thresholds determined in the laboratory. Most models showed that DO, tide, and the spatial DO gradient were significant predictors of movement. Saturation-acclimated fish generally avoided DO <2.8 mg O<sub>2</sub> l<sup>-1</sup> by increasing swimming speed and using tidal flow to facilitate escape. An exception to tidally aided movement occurred when a flooding tide appeared to trap smaller fish in spatially extensive hypoxia. Diel-cycling hypoxia acclimated weakfish appeared to have a lower avoidance threshold of ~1.4 mg O<sub>2</sub> l<sup>-1</sup>. Downstream movements were far more frequent than upstream movements, possibly because late stage juveniles were moving out of the estuary. The relationship between tributary residency and the spatial extent of hypoxia suggests that there is a tradeoff between risk of hypoxic exposure and energetic benefits of remaining in productive areas.

**KEY WORDS:** Diel-cycling hypoxia · Movement · Weakfish · Spot · Acoustic telemetry · Acclimation

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## INTRODUCTION

Estuaries provide nursery habitat for many economically and ecologically important fishes (Weinstein 1979, Able 1999, Minello et al. 2003). The nursery function of estuaries derives from physical characteristics, such as proximity to freshwater runoff (Holland et al. 2004) and semi-enclosed geomorphology (Kjerfve & Magill 1989). These attributes foster an environment with higher temperatures (Day et al.

1989), higher productivity (Deegan 2002), and, often, lower predation risk (Paterson & Whitfield 2000, Manderson et al. 2004) than adjacent marine habitats. However, these same attributes create a very dynamic physicochemical environment, wherein abiotic factors such as temperature, salinity, and dissolved oxygen (DO) vary considerably both temporally and spatially (Tyler et al. 2009).

Anthropogenic impacts can disrupt natural patterns of estuarine variability to the detriment of resi-

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dent populations (Breitburg 2002). For example, human-mediated nutrient enrichment (eutrophication) can result in excessive primary production and can lead to severe hypoxia (0.1 to 2.0 mg O<sub>2</sub> l<sup>-1</sup>) or anoxia (Reckhow & Chapra 1999). Diel-cycling hypoxia occurs within the photic zone (extending to the bottom in shallow systems and above the pycnocline in deeper systems). It is driven primarily by the daytime-nighttime (diel) cycling of DO production and consumption by living algae (Kemp & Boynton 1980, D'Avanzo & Kremer 1994). DO fluctuates predictably over the 24 h period, with lowest concentrations usually occurring around dawn following nighttime respiration and highest concentrations in the late afternoon following maximum daytime photosynthesis (D'Avanzo & Kremer 1994, Tyler et al. 2009). Tyler et al. (2009) linked severe hypoxia events of greatest intensity, duration, and spatial extent with the following series of events: a pulse of rain followed by a series of sunny days followed by one or more cloudy days.

Estuarine areas of low flushing, salinity, and DO as well as high productivity are often simultaneously areas of high fish abundance and densities (Meng et al. 2001, Ross 2003, Yamashita et al. 2003, Meng et al. 2004). When dispersal and settlement are based on a simple set of rules (e.g. traverse to productive headwaters), and environmental change (e.g. eutrophication) uncouples the cues for settlement from habitat quality, then the potential for an ecological trap exists (Kokko & Lopez-Sepulcre 2006). An ecological trap is a low-quality habitat that is preferred over a higher quality habitat (Battin 2004). Any human activity such as eutrophication, and resulting diel-cycling hypoxia, may cause headwater habitats to become ecological traps.

Ultimately, if nursery areas are disproportionately used by juvenile fishes and impacted by diel-cycling hypoxia, determining how fishes utilize these areas in both space and time and on ecologically relevant scales (i.e. measurable effects on growth and mortality) is critical to assessing the impact of eutrophication on essential fish habitat (Beck et al. 2001). Many studies of fish-hypoxia interactions have utilized trawl surveys to determine presence/absence and relative abundance of fishes based on proximate DO conditions (Howell & Simpson 1994, Eby & Crowder 2002, Bell & Eggleston 2005, Tyler & Targett 2007). For example, Tyler & Targett (2007) demonstrated that juvenile weakfish *Cynoscion regalis* were absent from the upper portion of Pepper Creek, a tidal tributary of the Delaware Coastal Bays, when diel-cycling DO was below ~2.0 mg O<sub>2</sub> l<sup>-1</sup>. However,

when DO was >2.0 mg O<sub>2</sub> l<sup>-1</sup>, juvenile weakfish were disproportionately more abundant in the upper tributary than farther down the system.

Determining hypoxia avoidance mechanisms and thresholds will enhance predictive models. Basic questions remain in relation to hypoxia avoidance including: What DO levels induce the beginning of avoidance behavior, how fast do fish move during avoidance, and how far do fish move away from hypoxic zones? Fish modeling studies consistently recognize the importance of movement parameterization in calibration and validation (Tyler & Rose 1997, Railsback & Harvey 2002, Wildhaber & Lamberson 2004, Aumann et al. 2006). The scope of movement is particularly important in this regard. For example, how far a fish can move in one model time step will ultimately, in conjunction with the spatial extent of hypoxia, determine DO exposure.

Few studies have performed an explicit evaluation of individual fish movements in relation to hypoxic zones in estuaries. Emigration rates of 53 acoustically tagged summer flounder (235 to 535 mm total length [TL]) from the Mullica River-Great Bay Estuary, NJ, USA were negatively correlated with DO (Sackett et al. 2007). However, the range of DO values measured (i.e. 4.3 to 7.5 mg O<sub>2</sub> l<sup>-1</sup> at 18 to 26°C) were not lethal or even growth limiting (Stierhoff et al. 2006). Moreover, all the more direct observations of individuals in hypoxic environments have been conducted in environments with water column stratification-induced hypoxia. No study has examined the movement of individual fish in relation to diel-cycling hypoxia in shallow nursery environments.

The objectives of this study were to track juvenile weakfish and spot, 2 estuary-dependent sciaenid fishes, in an estuarine tributary nursery area in relation to abiotic variables. Specifically, we examined the degree, duration, and spatial extent of diel-cycling hypoxia that elicited an avoidance response and characterized that response. We also characterized the role of diel-cycling hypoxia acclimation in habitat use. This study utilized a gated acoustic array along the axis of a tidal tributary that is consistently hypoxic during the summer in the early morning to early afternoon (Tyler et al. 2009). The high spatial and temporal resolution of DO monitoring and passive tracking allowed a comparison of the spatial scale of fish movement with the spatial scale of hypoxic events and a determination of what environmental DO scenarios may be most problematic for estuary-dependent fishes.

## MATERIALS AND METHODS

### Study area and field data collection

This study was conducted primarily in Pepper Creek, a tributary of the Delaware Coastal Bays (Fig. 1a). Pepper Creek is a mesohaline-to-polyhaline tidal tributary with DO ranging from anoxia to supersaturation (often 300% saturation; Tyler et al. 2009). Depth at low tide ranges from 1.5 m in the channel to <0.25 m on adjacent shoals, and the tidal differential is ~0.75 m. Multiparameter sondes (YSI Model 6920 and 600XLM) were deployed along the axis of Pepper Creek, and extending into Indian River Bay (Fig. 1b,c). The multiparameter sondes measured DO, temperature, and salinity every

15 min and were changed weekly to avoid bio-fouling. Meteorological parameters that influence DO, such as wind speed, precipitation, and insolation, were collected from the Warrington Farm Site, the Bethany Beach National Guard Site, and the Lewes Marine Weather Station (Fig. 1a). Tidal amplitude data were collected from Rosedale Beach Tide Gauge (Fig. 1a).

Vemco<sup>®</sup> VR2 hydrophone receivers along the axis of Pepper Creek detected V7-4L tags individually-coded pulse-interval transmitters (7 × 20.5 mm) configured with 40 to 120 s nominal between-signal delays. Long inactive times can increase the probability that fish will pass a receiver and not be detected; however, long nominal delays allow multiple fish to be detected at the same receiver without tag colli-

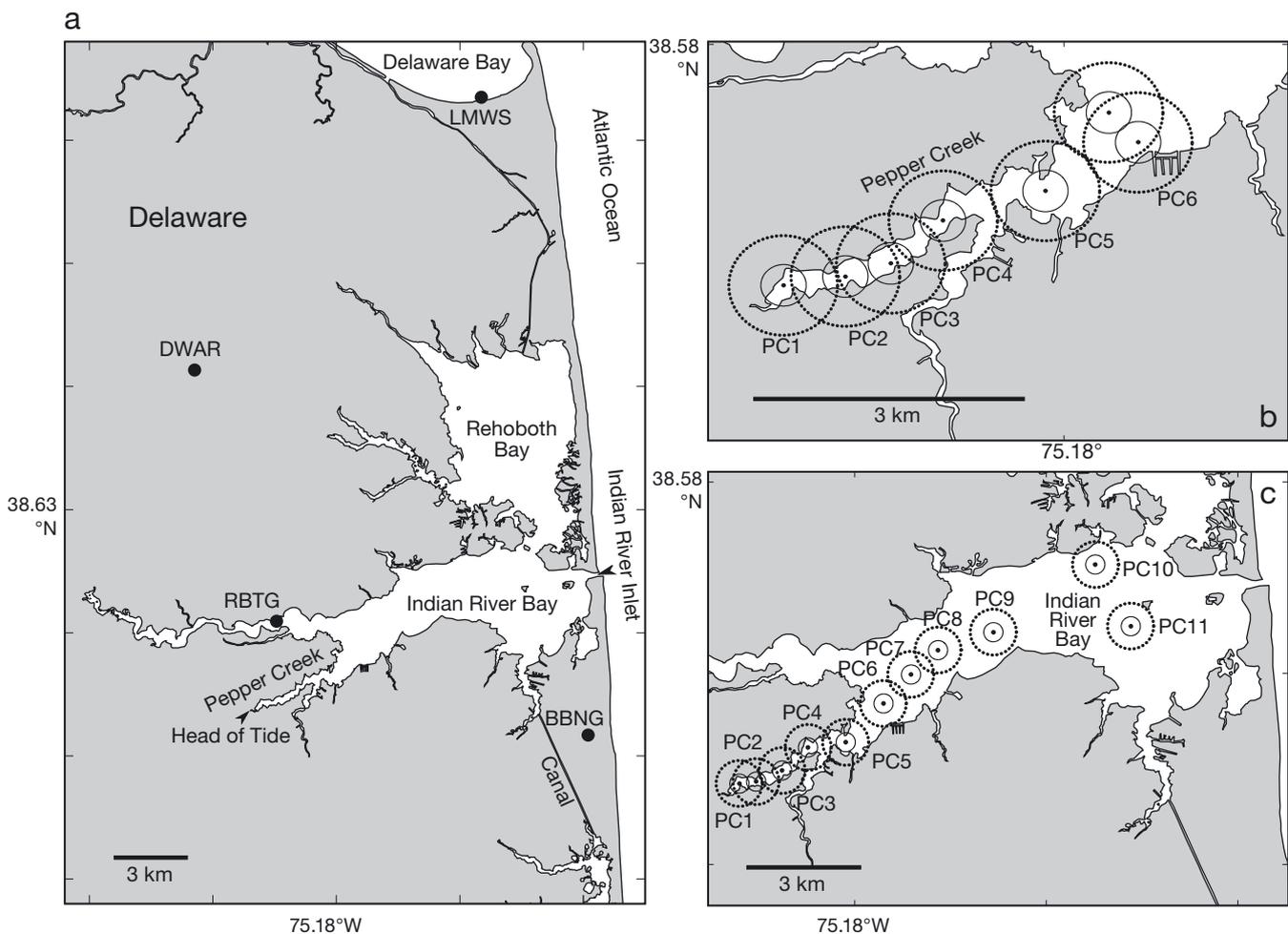


Fig. 1. (a) The Delaware Coastal Bays. DWAR is the location of the Warrington Farm Site, BBNG is Bethany Beach National Guard Station, and LMWS is the Lewes Marine Weather Station. Climatic data including wind direction, velocity, precipitation, sea level pressure, and insolation were collected from all these sites. RBTG is the location of the USGS's Rosedale Beach tide gauge where tide height data were collected. (b,c) Location of VR2 acoustic receivers and multiparameter sondes during the (b) 2005 and (c) 2006 sampling period. PC6 in 2005 (b) was monitored using 2 receivers to gate the mouth of the creek. A 200 m (solid line) and a 600 m (dashed line) buffer was added to each site to show approximate range in spatial coverage of the VR2 acoustic receivers

sions (simultaneous tag transmissions result in only one tag detection). A 40 to 120 s nominal delay was chosen to balance these 2 sources of lost detections. Range testing was conducted during the summer of 2007 at 3 sites (PC2, PC5, and PC6; Fig. 1c) over 3 consecutive days. Receiver range was within 200 m during over 90% of detections with a rare maximum of 600 m. When a fish was detected on a receiver, we assumed its location was identical to the receiver's location. Because the detection efficiency of the receiver could be up to 600 m away, there is uncertainty in the match between fish location and abiotic variable. Generally, range was negatively correlated with boat traffic (i.e. range increased at night and on low tides).

### Tagging and release

Juvenile weakfish and spot (Table 1) were collected from nursery areas in the Delaware Coastal Bays in 2005 and 2006 using an otter trawl. The mean ( $\pm$ SD) standard length (SL) of tagged fish was 137  $\pm$  16 mm (Table 1). Fish were maintained in recirculating aquaria at constant temperature (25°C), salinity (20 ppt), and a 14 h light:10 h dark photoperiod for at least 5 d before tagging. Fish were fed frozen mysid shrimp *Mysis relicta*. The protocol used to implant acoustic tags was developed by Harms (2005) and Harms & Lewbart (2000) and had been used successfully on juvenile spot by K. Craig in the Neuse River, NC, USA (pers. comm.). Fish were anesthetized in an induction bath of ~170 ppm MS-222 and were placed on a piece of seawater-saturated foam while a maintenance dose of 100 ppm MS-222 was perfused over their gills. A tag was inserted through a small incision on the ventral side midway between the anal and pectoral fins.

One objective of this study was to understand the role of diel-cycling hypoxia acclimation in habitat use. Six weakfish were acclimated to diel-cycling DO in a computer controlled DO system (Greccay & Stierhoff 2002) for 5 d before release (see Table 1) to examine the effect of diel-cycling hypoxia acclimation on the behavioral response of weakfish. Weakfish were used for the acclimation experiment because Brady et al. (2009) demonstrated that weakfish alter their behavior as a result of acclimation in the laboratory, but this had not been demonstrated *in situ*. During acclimation, minimum (2.0 mg O<sub>2</sub> l<sup>-1</sup>) and maximum (11.0 mg O<sub>2</sub> l<sup>-1</sup>) DO concentrations coincided with the beginning of the light (07:00 h) and dark (21:00 h) periods, respectively, to reflect DO

conditions observed in the field (Tyler et al. 2009). All other fish were held in the laboratory for 5 d under saturated DO conditions before being released in 6 batches of 1 to 8 fish at site PC2 (Fig. 1b,c). No fish with signs of infection near the incision were released which accounts for uneven numbers of fish in each batch release. Finally, there was no way to be certain that fish did not die during a track; however, Eguiluz & Wong (2005) reported maximum tidal flows of 0.1 m s<sup>-1</sup> in the Delaware Coastal Bays and all individuals analyzed made at least one movement greater than this velocity.

### Data analysis

Temperature, salinity, and DO were linearly interpolated, spatially and temporally, to create contour plots. The color map for DO was tuned to laboratory behavioral thresholds (Brady et al. 2009). Brady et al. (2009) exposed juvenile weakfish to a step-wise decrease in DO from 7.0 to 0.4 mg O<sub>2</sub> l<sup>-1</sup>. Maximum swimming speed occurred when DO was 2.8 mg O<sub>2</sub> l<sup>-1</sup>. Angular correlation between successive moves decreased precipitously as DO decreased from 1.4 mg O<sub>2</sub> l<sup>-1</sup> to 0.8 mg O<sub>2</sub> l<sup>-1</sup>. These 2 values were discretized in the color map as blue (>1.4 mg O<sub>2</sub> l<sup>-1</sup> and  $\leq$ 2.8 mg O<sub>2</sub> l<sup>-1</sup>) and black ( $\leq$ 1.4 mg O<sub>2</sub> l<sup>-1</sup>). Fish tracks were plotted on the DO contour plots to visualize if these laboratory-derived behavioral thresholds translated to important thresholds for activity in the field.

To associate each estimated location with its attendant abiotic conditions, increased temporal and spatial resolution was needed. Therefore, a piecewise cubic hermite interpolating polynomial (PCHIP) was used to interpolate DO, temperature, and salinity in both time and space. This interpolation technique was preferable to spline interpolation in this context because it offers smooth interpolation between points while not overshooting data to create artificial relative maximums and minimums (Kahaner et al. 1989). PCHIP was used to determine exposure if the estimated location occurred during the 15 min period between sonde measurements. Additionally, detections of the same individual by 2 acoustic receivers within less than 5 min of each other were assumed to result from overlapping receiver ranges. In this case, the fish's estimated location was assumed to be between the receivers and PCHIP interpolation was used to assign abiotic conditions to this estimated location. Overlapping receiver detections were relatively rare (on average, <5% of detections). Spatial

Table 1. *Cynoscion regalis* and *Leiostomus xanthurus*. Characteristics of tagged fish including species, acclimation history (hypoxia indicates 5 d of exposure to diel-cycling hypoxia: cycling between 2.0 and 11 mg O<sub>2</sub> l<sup>-1</sup>), length and weight and characteristics of each individual's track including time of first and last detection, duration of track and creek residency. Times are mm/dd/yy h:min

Batch release no.	Tag ID	Species	Acclimation	Standard length (mm)	Wet weight (g)	Detections	Time of first detection	Time of last detection	Duration of track (d)	Creek residency (d)	% of time in creek
1	133	<i>C. regalis</i>	Saturation	172	64.2	314	08/26/05 18:40	08/28/05 00:34	1.25	1.12	89.6
1	137	<i>L. xanthurus</i>	Saturation	132	53.0	550	08/26/05 18:40	08/28/05 15:59	1.89	0.51	26.8
1	144	<i>L. xanthurus</i>	Saturation	125	44.0	1044	08/26/05 18:47	08/30/05 07:52	3.54	0.49	13.9
1	149	<i>L. xanthurus</i>	Saturation	134	48.2	161	08/26/05 18:49	08/28/05 11:07	1.68	1.48	88.1
1	139	<i>C. regalis</i>	Saturation	180	64.8	467	08/26/05 18:58	08/28/05 08:27	1.56	1.46	93.4
1	142	<i>L. xanthurus</i>	Saturation	120	37.2	364	08/26/05 19:07	08/29/05 22:27	3.14	1.48	47.1
1	148	<i>L. xanthurus</i>	Saturation	121	39.7	637	08/26/05 19:16	08/29/05 09:14	2.58	1.47	56.9
2	140	<i>C. regalis</i>	Saturation	120	25.8	25	08/30/05 16:03	08/31/05 14:43	0.94	0.33	35.2
3	146	<i>C. regalis</i>	Saturation	161	54.9	1186	09/01/05 13:04	09/06/05 11:45	4.94	4.94	100.0
3	135	<i>C. regalis</i>	Saturation	130	27.8	25	09/01/05 13:06	09/02/05 06:45	0.74	0.74	100.0
4	131	<i>C. regalis</i>	Hypoxia	136	36.0	517	08/28/06 15:24	09/05/06 04:35	7.55	1.95	25.9
4	147	<i>C. regalis</i>	Hypoxia	126	36.6	1545	08/28/06 15:28	08/31/06 10:29	2.79	2.60	92.9
4	130	<i>C. regalis</i>	Hypoxia	180	82.8	789	08/28/06 15:35	10/03/06 03:16	35.49	0.70	2.0
4	134	<i>C. regalis</i>	Hypoxia	148	52.9	372	08/28/06 15:50	08/31/06 01:03	2.38	1.71	71.7
4	145	<i>C. regalis</i>	Hypoxia	132	40.5	1	08/29/06 00:36	08/29/06 00:36	0.00	0.00	NA
5	316	<i>C. regalis</i>	Saturation	135	44.4	189	08/31/06 11:21	09/23/06 19:32	23.34	1.36	5.8
5	305	<i>C. regalis</i>	Saturation	132	34.6	1014	08/31/06 11:21	09/13/06 01:46	12.60	2.45	19.5
5	320	<i>C. regalis</i>	Saturation	133	41.3	287	08/31/06 11:23	10/03/06 02:34	32.63	0.86	2.6
5	136	<i>C. regalis</i>	Hypoxia	135	36.2	1218	08/31/06 11:24	10/02/06 18:48	32.31	0.58	1.8
5	143	<i>C. regalis</i>	Saturation	128	32.9	17	08/31/06 11:24	08/31/06 20:58	0.40	0.35	88.2
5	321	<i>C. regalis</i>	Saturation	145	51.7	38	08/31/06 11:27	08/31/06 17:37	0.26	0.26	100.0
5	315	<i>C. regalis</i>	Saturation	137	46.3	59	08/31/06 12:55	08/31/06 21:59	0.38	0.30	78.4
5	319	<i>C. regalis</i>	Saturation	130	35.5	1275	08/31/06 13:19	09/08/06 01:11	7.49	2.26	30.2
6	308	<i>C. regalis</i>	Saturation	130	33.6	223	09/04/06 12:30	09/07/06 04:59	2.69	2.69	100.0
6	312	<i>C. regalis</i>	Saturation	133	41.0	369	09/04/06 12:31	09/06/06 09:59	1.90	1.90	100.0
6	309	<i>C. regalis</i>	Saturation	132	35.5	7	09/04/06 12:31	09/04/06 18:39	0.26	0.26	100.0
6	300	<i>C. regalis</i>	Saturation	124	29.1	670	09/04/06 12:33	09/07/06 14:35	3.08	2.43	78.7
6	307	<i>C. regalis</i>	Saturation	133	39.1	653	09/04/06 12:38	09/10/06 01:16	5.53	2.31	41.9
6	306	<i>C. regalis</i>	Saturation	132	36.2	183	09/04/06 12:38	09/10/06 16:31	6.16	2.86	46.5
6	313	<i>C. regalis</i>	Saturation	133	41.2	137	09/04/06 12:41	09/07/06 19:42	3.29	2.44	74.1
6	314	<i>C. regalis</i>	Saturation	131	35.9	775	09/04/06 12:41	09/10/06 03:36	5.62	3.54	63.0

interpolation between sites located approximately 500 m apart may also introduce an additional source of uncertainty when associating environmental covariates with estimated locations.

To characterize the local abiotic gradients that could influence fish movement, the derivative of the PCHIP at every estimated location was solved both temporally and spatially (i.e. along the axis of the creek). For example, a negative spatial gradient in DO means that DO was higher in the upper tributary than the fish's current location and a negative temporal derivative indicates DO was decreasing during a detection. Insolation at the time of each estimated location was used to detect diel-periodicity in movement patterns. The rate of tide height change was determined for each estimated location by solving for the derivative of PCHIP interpolated tidal amplitude.

Swimming speed was determined by dividing the distance between estimated locations by the time between estimated locations. There are several unknown factors which could affect estimation of swimming speed. The largest source of underestimation is the assumption that fish move in a straight line from station to station. Any deviation from a straight line path means the actual swimming speed was underestimated. On the other hand, there are also 2 unknown sources of overestimation: receiver range variability and tidal flow. The present study assumed that fish moved from the center of the range of one receiver to the center of the range of another receiver. If fish moved from edge to edge of receiver ranges, then the actual distance the fish traversed was less than estimated. Also, tidal flow can aid advection of fish if movement is tidally synchronized. Tidal flow in this system is  $0.1 \text{ m s}^{-1}$  at maximum flow (Eguiluz & Wong 2005). However, a relative comparison between individuals and groups released at the same time is instructive and whether tidally aided or not, this estimation represents the speed fish need to attain to avoid hypoxia. Additionally, the more consecutive estimated locations at different receivers observed, the more accurate the estimation of speed. Speed estimation using consecutive estimated locations at 3 receivers were used to estimate swimming speed whenever possible.

Fish movement in relation to diel-cycling hypoxia was initially characterized by Batch Release (BR; all fish released at the same time were pooled), due to the potential influence of initial conditions on fish movement. Each estimated location of a given fish was compared to its previous estimated location to determine if the fish had remained at that receiver (hereafter referred to as 'stay-put'), or moved up-

stream or downstream. A binomial-based generalized additive model (GAM) with a logit link function was used to identify environmental variables—i.e. DO, temperature ( $T$ ), salinity, the spatial and temporal gradients in DO ( $d[\text{DO}] dx^{-1}$  and  $d[\text{DO}] dt^{-1}$ , respectively) and temperature ( $d[T] dx^{-1}$  and  $d[T] dt^{-1}$ , respectively), insolation, and the rate of tide height change ( $d[\text{tide}] dt^{-1}$ )—that were predictors of movement (Diggle et al. 1995, Pirootta et al. 2011). The method of generalized estimating equations (GEEs) was used to account for correlations among estimated locations. Briefly, the GEE method uses the residuals between observations and a model that assumes independence within each fish, and then uses the correlation estimates to obtain new coefficient estimates. The process is repeated until the change between 2 successive estimates is very small. The working correlation matrix was assumed to be autoregressive; however, GEEs are relatively robust to misspecification of working correlation matrices (Pan & Connett 2002). Models were run with standardized (by the mean) and unstandardized covariates. Gradient variables were log transformed after the absolute value of the most negative gradient variable was added to all estimated locations because the derivatives of the time series and spatial gradient were extremely large when the decrease or increase was maximum. Log transformation condensed the range of values for analysis and decreased the leverage of extremely large values in the model. The distribution of residuals was checked to ensure normal distributions.

Because there were 3 categories of movement (i.e. stay-put, upstream, and downstream), 2 logistic models (i.e. upstream versus stay-put and downstream versus stay-put) were compared using stay-put as the reference outcome. Quasi-likelihood information criteria were used to determine the significance of each covariate and whether each covariate significantly improved model prediction (Pan 2001b,a, Aarts et al. 2008). The odds ratio (OR) was also used to compare the influence of multiple covariates on movement. The OR for each outcome/covariate combination (e.g.  $\text{OR}_{\text{upstream/DO}}$ ) represents the change in the probability ( $P$ ) of that outcome given a one unit increase in the covariate:

$$\text{OR}_{j/p}(a,b) = \frac{P(Y = j | x = a) / P(Y = \text{stay-put} | x = a)}{P(Y = j | x = b) / P(Y = \text{stay-put} | x = b)} \quad (1)$$

where  $j$  represents the outcome (i.e. upstream or downstream),  $p$  represents the covariate, and  $a$  and  $b$  represent 2 values of the covariate (e.g. 0 and 1 if the odds ratio is describing the change in probability for a one unit increase in the covariate). The units of gra-

dient covariates (e.g.  $d[\text{DO}] dx^{-1}$  and  $d[\text{DO}] dt^{-1}$ ) resulted in relatively small values; therefore, standardized ORs were computed for these covariates for simpler interpretation. For example, the ORs for  $d(\text{DO})/dx$  represent the increased probability of a movement for a one standard deviation (SD) change in  $d(\text{DO}) dx^{-1}$ . The 95% confidence intervals (CI) for each OR were calculated. If the CI included 1, then that covariate was assumed to have little impact on inducing movement. When  $\text{OR} = 1$ , a change in 1 unit or SD in the covariate has no influence on the outcome. Conversely, if  $\text{OR} = 0.5$  or  $2$ , a 1 unit or SD change in the covariate results in halving or doubling of the probability of that movement type, respectively. Finally, the Wald  $\chi^2$  test statistic was obtained by comparing the quasi-likelihood estimate of the coefficients ( $\beta$ s) to an estimate of the standard error. Relatively high Wald  $\chi^2$  values indicate those covariates are significant contributors to the outcome (i.e. upstream or downstream movement). All statistical analyses were performed using SAS.

## RESULTS

Attributing causation to a relationship between any individual environmental covariate and movement is complicated by unmeasured biotic factors such as predation and the prey field. However, an assumption supported by many laboratory studies of weakfish and spot (e.g. McNatt & Rice 2004, Brady et al. 2009, Stierhoff et al. 2009b) is that when DO approaches lethal levels (below  $2 \text{ mg O}_2 \text{ l}^{-1}$ ), fish prioritize hypoxia avoidance above other biotic and abiotic stimuli. Therefore, the analysis breaks down each batch release according to statistically relevant covariates that were correlated with movement types (i.e. upstream and downstream) and a focus on the movement of individual fish during hypoxic periods when appropriate. The average duration of a track in 2005 (BR 1–3) and 2006 (BR 3–6) was 2.23 and 8.86 d, respectively (Table 1). The track duration difference is partially attributable to increased spatial coverage in 2006 (Fig. 1).

A majority of the GAM logits included the rate of tide height change, DO, and the spatial gradient in DO (Table 2). These statistical results were corroborated by graphical analyses of tracks. Upstream and downstream movements were clearly linked to flood and ebb tides, respectively. The rate of tide height change was  $4.23 \times 10^{-5}$  and  $-8.47 \times 10^{-5} \text{ m s}^{-1}$  for all upstream and downstream movements, respectively. Additionally, fish tended to avoid DO levels below

$2.8 \text{ mg O}_2 \text{ l}^{-1}$ . Significant correlations between the spatial DO gradient and movement in most GAM logits suggest that fish may utilize this gradient as part of their avoidance mechanism. Finally, diel-cycling hypoxia acclimated fish avoided DO levels lower than saturation-acclimated fish, based on longer exposure times to DO levels in between 2.8 and  $1.4 \text{ mg O}_2 \text{ l}^{-1}$ .

### Batch releases 1 and 2

BR 1 and BR 2 occurred on August 26 and 30, 2005, respectively (Table 1). Meteorological conditions during the week following the BR 1 and 3 d of BR 2 ( $N = 5$  saturation-acclimated spot and  $N = 2$  saturation-acclimated weakfish) were hot (i.e.  $27.3^\circ\text{C}$ ) and cloudy (Fig. 2b) with calm winds (averaging only  $1.9 \text{ m s}^{-1}$ ). High temperature, low insolation, and low wind speed during BR 1 resulted in the longest lasting and most spatially extensive hypoxic conditions (Fig. 2a) of any batch release period.

Of the 3072 estimated locations during BR 1, 65 were upstream movements and 92 were downstream. The GAM logit describing upstream movements indicated that particularly important variables (in order of Wald  $\chi^2$  magnitude in Table 2) in predicting upstream movements were temperature, the spatial gradient in temperature, salinity, the spatial gradient in DO, DO, rate of tide height change, and insolation. Model results were heavily influenced by environmental conditions during a 12 h period between midnight on August 27 and noon on August 28. Almost half of upstream movements occurred during these 12 h. Hypoxia occurred throughout this time period and extended from the head of tide to near the mouth of the tributary at PC5 and PC6 (Fig. 2a). Upstream movements during this time were made by smaller spot that had recently moved 5 km downstream to avoid hypoxia ( $<2.8 \text{ mg O}_2 \text{ l}^{-1}$ ; spot nos. 137 [red squares], 144 [green squares], and 148 [cyan squares] in Fig. 2a). Spot no. 148, the smallest fish tagged, also made upstream incursions into a hypoxic zone during a flooding tide after midnight of August 28 (Fig. 2a, cyan squares & Fig. 3a).

Upstream movements outside the period between midnight on August 27 and noon on August 28 always occurred when the DO gradient was negative (higher DO in the upper tributary; Fig. 2a). For example, weakfish no. 139 moved downstream during the first night after the initial release but returned upstream as daytime DO increased throughout the tributary, especially in the upper portion, resulting in

Table 2. Results of the generalized estimating equations for each batch release of fish. Each model compares upstream and downstream movements to stay-puts. Estimates are the coefficients of the model, odds ratios (OR) for each outcome/covariate combination (e.g.  $OR_{\text{upstream/DO}}$ ) represent the change in the probability of that outcome given a 1 SD increase in the covariate, and the Wald  $\chi^2$  test statistic is the squared ratio of the estimate to the SE of the respective predictor. -: covariate was not included in the model because it did not improve model fit as calculated with the quasi-likelihood information criterion. Significance: \* $p < 0.05$ , \*\* $p < 0.01$

Batch release no.	Direction	Insolation			DO			$d(\text{DO}) dx^{-1}$		
		Estimate	OR	Wald $\chi^2$	Estimate	OR	Wald $\chi^2$	Estimate	OR	Wald $\chi^2$
1	Upstream	-0.79*	0.45	6.02	-0.59**	0.55	8.84	1.13**	3.10	8.89
	Downstream	-0.67**	0.51	6.85	0.10	1.10	0.57	0.21	0.21	0.89
3	Downstream	0.79**	2.19	435	0.96**	2.60	312	-1.02**	0.36	473
4	Upstream	0.082	1.08	0.23	-0.066	0.94	0.02	0.84**	2.32	22.3
	Downstream	0.17	1.19	1.42	-0.49*	0.61	5.29	-	-	-
5	Upstream	-	-	-	1.16**	3.20	45.0	-0.83**	0.43	27.1
	Downstream	-0.23	0.80	1.21	0.56**	1.74	34.3	-0.54**	0.58	47.8
6	Downstream	0.39*	1.47	3.72	0.099	1.10	0.86	-0.095	0.91	0.43
Batch release no.	Direction	$d(\text{DO}) dt^{-1}$			Tide			Temperature		
		Estimate	OR	Wald $\chi^2$	Estimate	OR	Wald $\chi^2$	Estimate	OR	Wald $\chi^2$
1	Upstream	-	-	-	0.69*	2.00	6.61	-1.13**	0.27	19.5
	Downstream	0.012	1.01	1.31	0.16	1.18	0.66	-0.94**	0.39	26.4
3	Downstream	-	-	-	0.65**	1.93	3568	-	-	-
4	Upstream	-0.29*	0.74	5.14	0.030	1.03	0.05	-0.54*	0.58	0.90
	Downstream	-0.13	0.87	0.74	-0.33*	0.72	4.44	-	-	-
5	Upstream	-	-	-	0.40**	1.49	83.3	-0.57**	0.57	11.65
	Downstream	-0.039	0.96	0.42	-0.24**	0.78	8.54	-	-	-
6	Downstream	-2.25**	0.10	18.4	-0.49**	0.61	9.87	-	-	-
Batch release no.	Direction	$d(\text{Temp.}) dx^{-1}$			$d(\text{Temp.}) dt^{-1}$			Salinity		
		Estimate	OR	Wald $\chi^2$	Estimate	OR	Wald $\chi^2$	Estimate	OR	Wald $\chi^2$
1	Upstream	-1.29**	0.27	15.92	-	-	-	-0.84**	0.43	10.91
	Downstream	-	-	-	-0.25**	0.78	13.00	-	-	-
3	Downstream	2.94**	18.90	37827.00	-	-	-	0.91**	2.48	3116.00
4	Upstream	0.11	1.12	0.78	-0.11*	0.89	3.95	-0.20	0.81	2.25
	Downstream	-0.28	0.75	2.65	-	-	-	-0.18	0.83	0.80
5	Upstream	-	-	-	-	-	-	-0.62*	0.54	5.10
	Downstream	-	-	-	-0.12**	0.89	130.71	-	-	-
6	Downstream	-0.33	0.72	3.05	1.57**	4.79	19.35	-0.12	0.89	0.55

a negative DO gradient (Fig. 4a,e). Ultimately, the strongest predictors of upstream movements were temperature and the spatial gradient in temperature (Table 2). The upstream GAM logit indicates that upstream movements were ~3 times (i.e. the inverse of the OR) more likely given a 1 SD decrease in the temperature gradient (i.e. the upstream location was characterized by higher temperatures; Table 2).

Overall, temperature related covariates were helpful predictors of upstream and downstream movements in BR 1. Temperature, the rate of temperature change, and insolation (in order of Wald  $\chi^2$  magnitude in Table 2) were significant predictors of down-

stream movements. Downstream movements were characterized by a  $0.44^\circ\text{C s}^{-1}$  decrease in temperature, compared to a  $0.0062^\circ\text{C s}^{-1}$  decrease observed during stay-put estimated locations, consistent with the finding that most downstream movements were made at night. A decrease in 1 SD in insolation resulted in a doubling of the probability of a downstream movement (OR = 0.51, Table 2). Another similarity between up and downstream movements was that the sign of the coefficient for  $d(\text{DO}) dx^{-1}$  was positive for all movements, suggesting that weakfish and spot use the local spatial gradient in DO to move to areas of higher DO.

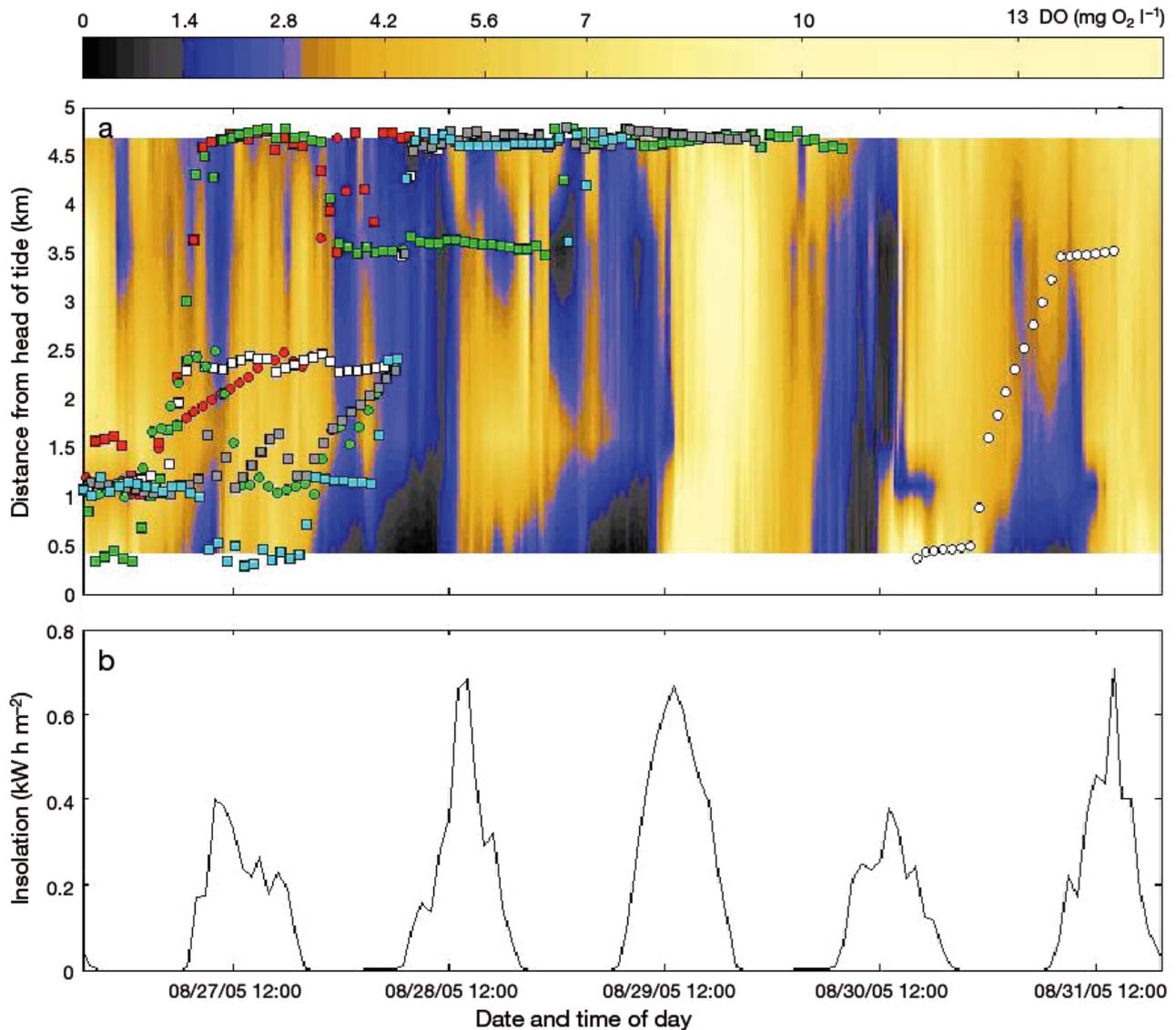


Fig. 2. *Cynoscion regalis* and *Leiostomus xanthurus*. Batch Release 1 and 2. (a) Dissolved oxygen (DO) plot and tracks of all fish and (b) insolation for 5 d following release on 08/26/2005 (dates are given as mm/dd/yy). Markers represent the hourly locations along the creek axis for weakfish nos. 133, 139, and 140 (red, green, and white circles, respectively) and spot nos. 137, 144, 149, 142, and 148 (red, green, white, gray, and cyan squares, respectively). The estimated locations have been randomly jiggered  $\pm 200$  m (approximate receiver range). The color scale for DO reflects laboratory-derived behavioral thresholds of saturation-acclimated weakfish (see 'Materials and methods'): swimming speed peaked at  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  and angular correlation between successive movements decreased markedly at  $<1.4 \text{ mg O}_2 \text{ l}^{-1}$

### Batch releases 1 and 2: hypoxia avoidance

Of the 7 fish in BR 1, 2 spot (spot nos. 137 and 144, red and green squares, respectively, in Fig. 2a) vacated the creek during the first night when DO was below  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  throughout the creek except at site PC3 ( $\sim 2 \text{ km}$  from the head of tide, Figs. 1 & 2a). Site PC3 is located at a shallower portion of the creek where mean low water is  $\sim 1 \text{ m}$ . The other 5 fish (2 weakfish and 3 spot) vacated the creek on the second night when DO

was  $\leq 1.4 \text{ mg O}_2 \text{ l}^{-1}$  along the axis of the creek and the upper portion of the tributary was severely hypoxic for over 12 h. Fish that stayed in the creek during the first night moved downstream to PC3, which was the only area in the creek with DO conditions  $>2.8 \text{ mg O}_2 \text{ l}^{-1}$  (see Fig. 4). Both fish that left the upper tributary during the first night after release remained at the mouth of the tributary until the next night, at which point they attempted to re-enter the tributary (Figs. 2a & 3e). Only spot nos. 144 and 142 (green and gray

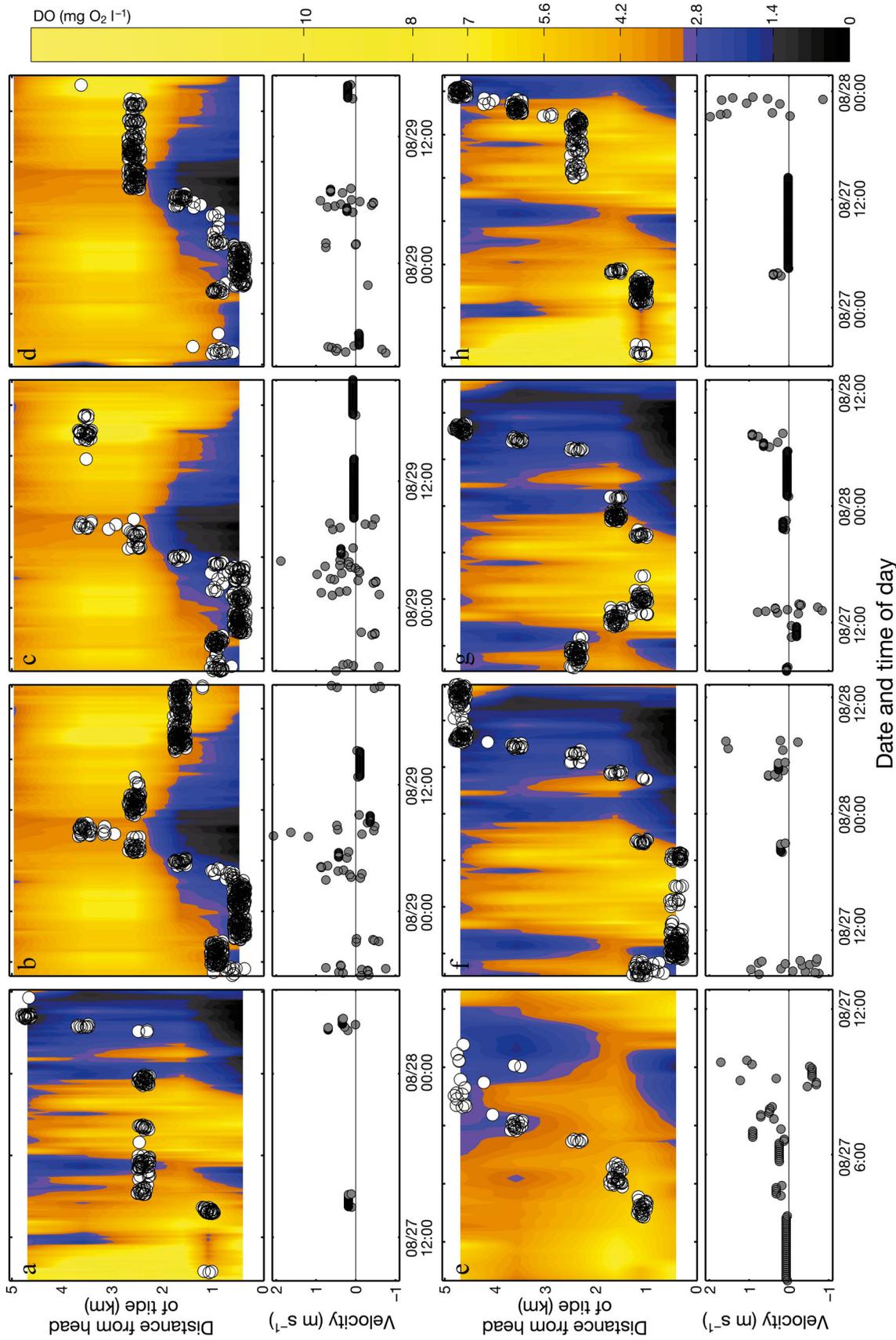


Fig. 3. *Cynoscion regalis* and *Leiostomus xanthurus*. Dissolved oxygen (DO) plot, track, and movement velocity for fish ID no. 148 [1], (b–d) weakfish nos. 147 [4], 130 [4], and 131 [4], (e) spot no. 144 [1], (f–g) weakfish nos. 139 [1] and 133 [1], and (h) spot no. 149 [1]. Tracks represent hypoxia avoidance responses at 3 consecutive receivers. The estimated locations have been randomly jittered  $\pm 200$  m (approximate receiver range). The color scale for DO reflects laboratory-derived behavioral thresholds of saturation-acclimated weakfish (see ‘Materials and methods’): swimming speed peaked at  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  and angular correlation between successive movements decreased markedly at  $<1.4 \text{ mg O}_2 \text{ l}^{-1}$

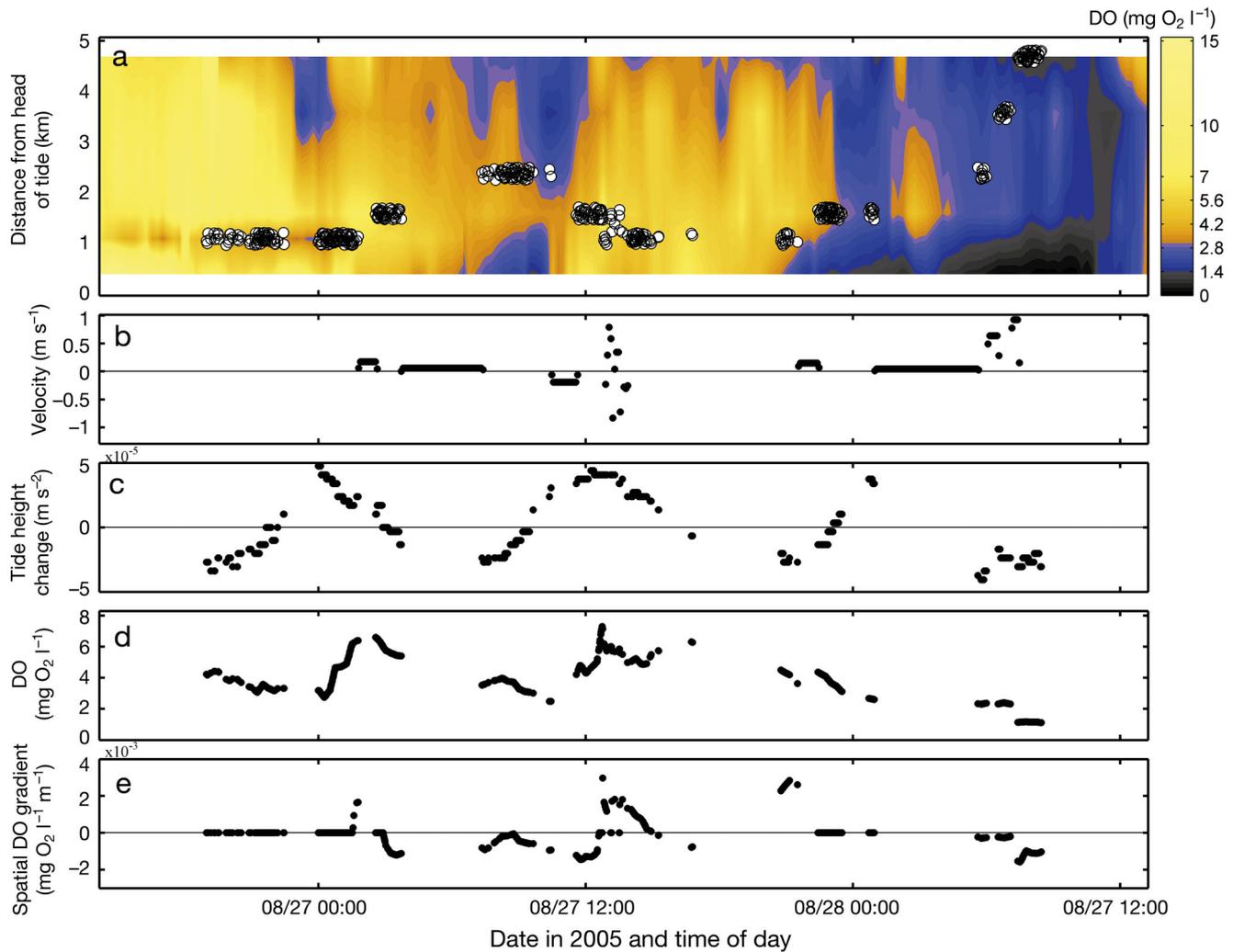


Fig. 4. *Cynoscion regalis* and *Leiostomus xanthurus*. (a) Dissolved oxygen (DO) plot and fish track for saturation-acclimated weakfish no. 139 in batch release 1, (b) movement velocity (positive for downstream speed and negative for upstream speed) (c) rate of tide height change (positive for flooding tides and negative for ebbing tides), (d) DO at the fish's location, and (e) spatial DO gradient associated with each detection (positive when DO is greater downstream and negative when DO is greater upstream). The estimated locations have been randomly jiggered  $\pm 200$  m (approximate receiver range). The color scale for DO reflects laboratory-derived behavioral thresholds of saturation-acclimated weakfish (see 'Materials and methods'): swimming speed peaked at  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  and angular correlation between successive movements decreased markedly at  $< 1.4 \text{ mg O}_2 \text{ l}^{-1}$ . Dates are given as mm/dd, times as h:min

squares, respectively, in Fig. 2a) remained in the acoustic array until the third night, which was also characterized by spatially extensive hypoxia.

Only 1 fish (weakfish no. 140, Figs. 2a [white circles] & 5b) was released in BR 2 and that fish was detected 25 times over the course of  $\sim 1$  d. The behavior of weakfish no. 140 was similar to the fish released during BR 1. Downstream movements were made during the first night when hypoxia ( $\leq 2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) extended from the headwaters to PC3 and PC4 (2 to 3 km from the head of tide; Fig. 5b). The next night was characterized by an even more extensive hypoxic zone, and weakfish no. 140 vacated the acoustic array. As in BR 1, movements were characterized by lower DO

( $4.41 \text{ mg O}_2 \text{ l}^{-1}$ ) than stay-put detections ( $6.88 \text{ mg O}_2 \text{ l}^{-1}$ ). Additionally, downstream movements were made after the spatial gradient in DO transitioned from extremely negative (higher in the upper tributary) to a neutral level and then to a positive gradient on an ebbing tide.

Swimming speed was particularly high during the avoidance of conditions that developed on the night of August 27 and early morning of August 28, where speed increased to  $1\text{--}2 \text{ m s}^{-1}$  (Fig. 3a,e-h). The most accurate determination of speed in this array is when a fish passes more than 2 receivers in one avoidance response. Both weakfish and spot consistently move between  $1$  and  $2 \text{ m s}^{-1}$  when exposed to oxygen levels

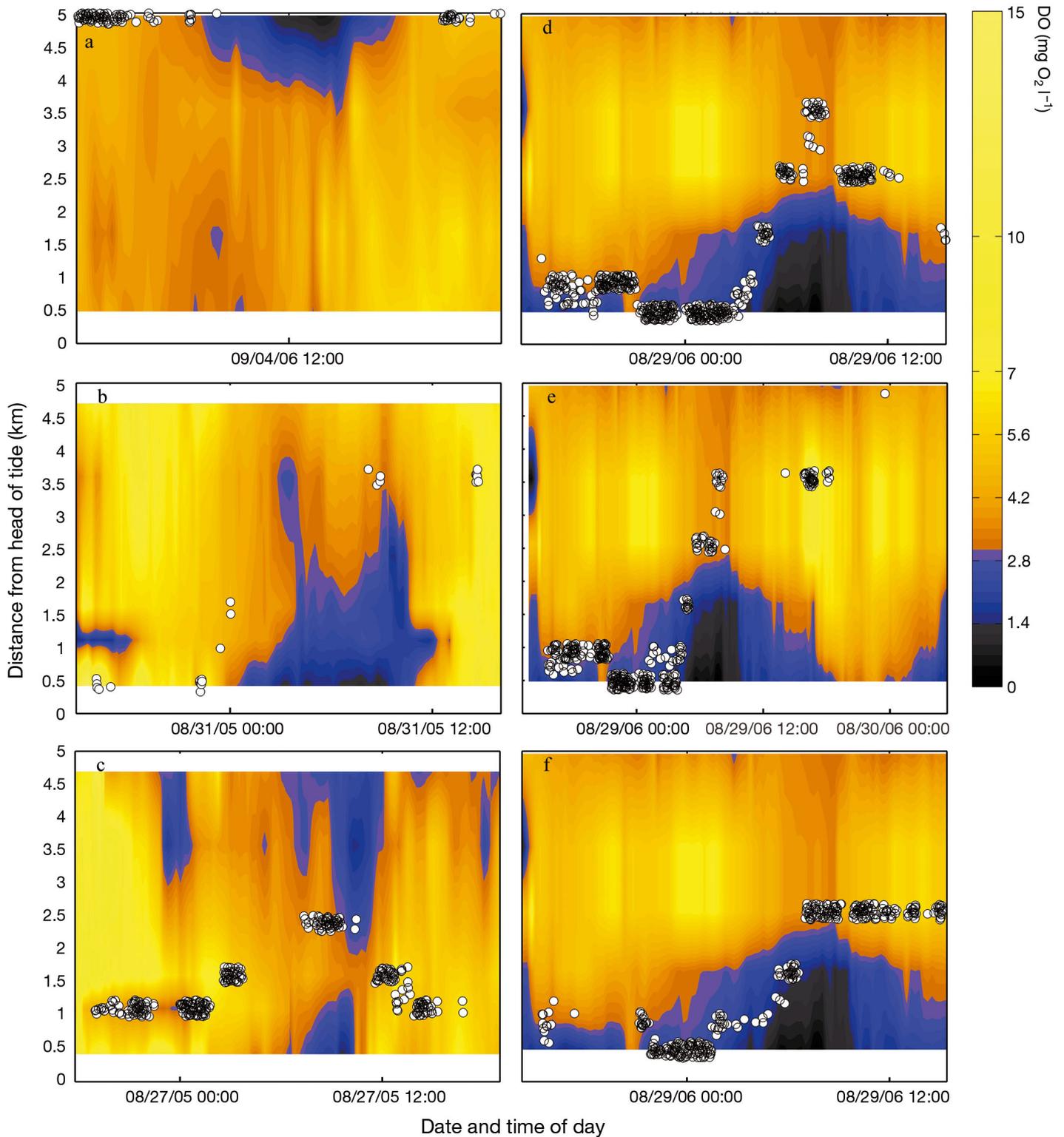


Fig. 5. *Cynoscion regalis* and *Leiostomus xanthurus*. (a–c) Dissolved oxygen (DO) plot and tracks for (fish ID no. and [batch release no.]) saturation-acclimated weakfish nos. (a) 319 [5], (b) 140 [2], and (c) 139 [1]. (d–f) DO plot and tracks for diel-cycling hypoxia acclimated (d) weakfish nos. 147 [4], (e) 130 [4], and (f) 131 [4]. The estimated locations have been randomly jiggered  $\pm 200$  m (approximate receiver range). The color scale for DO reflects laboratory-derived behavioral thresholds of saturation-acclimated weakfish (see 'Materials and methods'): swimming speed peaked at  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  and angular correlation between successive movements decreased markedly at  $< 1.4 \text{ mg O}_2 \text{ l}^{-1}$

below  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  (see Fig. 3 for 8 instances of hypoxia avoidance at 3 receivers). For a 137 mm fish (mean size of all released fish),  $1 \text{ m s}^{-1}$  converts to 7.3 BL (body length)  $\text{s}^{-1}$ .

### Batch release 3

BR 3 occurred on September 1, 2005 and consisted of 2 weakfish (Table 1). Meteorological conditions during the following week were generally unfavorable for development of spatially extensive hypoxia (i.e. high insolation). Daytime temperatures were still high,  $>28^\circ\text{C}$ . There were 1208 estimated locations, 1186 of which were from weakfish no. 146 (Table 1). Neither individual made any upstream movements and only 4 downstream movements were detected, thus only the downstream GAM logit was calculated (Table 2). Significant covariates in the downstream GAM logit were the spatial temperature gradient, rate of tide height change, salinity, the spatial DO gradient, insolation, and DO (in order of Wald  $\chi^2$  magnitude in Table 2). Downstream movements were almost 19 times more likely for a 1 SD increase in the temperature gradient (i.e. indicates movement to higher temperatures downstream).

### Batch release 3: hypoxia avoidance

Weakfish no. 146 generally stayed at the leading edge of the hypoxic zone (Fig. 6a); only making 3 downstream movements as the hypoxic zone ( $<2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) advanced. This fish moved from PC3 to PC4 during the night of September 4–5 (Fig. 6a) as the hypoxic zone advanced to PC4 likely because of poor insolation during the early morning of September 5 (Fig. 6b). In fact, the spatial gradient in DO throughout the tracking period was positive (lower DO in the upper tributary) and the fish remained at the border between hypoxia ( $\leq 2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) and more oxygenated conditions ( $\geq 2.8 \text{ mg O}_2 \text{ l}^{-1}$ ).

### Batch releases 4 and 5

BR 4 and BR 5 occurred on August 28 and 31, 2006, respectively (Table 1). Meteorological conditions changed substantially during the week of August 28 (Fig. 7). The beginning of the week (8/28/2006 to 8/31/2006) was characterized by high temperatures, low wind speed, and little precipitation (Fig. 7). A storm occurred during the end of the week (9/1/2006

to 9/4/2006) which resulted in lower temperatures and insolation, as well as high winds and precipitation (Fig. 7).

Six diel-cycling hypoxia acclimated weakfish and 7 saturation-acclimated weakfish were released and detected 6682 times (115 upstream movements and 174 downstream) during BR 4 and BR 5 (Table 1). The significant variable common to both batch releases in discriminating between upstream and stay-put estimated locations was temperature. The ORs of 0.58 for BR 4 and 0.57 for BR 5 indicate that fish were approximately half as likely to move upstream for a 1 SD increase in temperature. This temperature-linked behavior was typical of all batch releases as evidenced by negative model coefficients and ORs  $<1$  for temperature during upstream movements across all batch releases for which temperature was included in the model (Table 2).

Only DO and the rate of tide height change were significant discriminators between downstream and stay-put estimated locations for BR 4 (Table 2). A decrease in DO of  $1 \text{ mg O}_2 \text{ l}^{-1}$  increased the probability of a downstream movement by 1.3 times. Tide height decreased by  $7.0 \times 10^{-6} \text{ m s}^{-1}$  during downstream movements compared to an increase of  $3.2 \times 10^{-6} \text{ m s}^{-1}$  during stay-put periods. The  $7.0 \times 10^{-6} \text{ m s}^{-1}$  decrease in the rate of tide height change for downstream movement was the greatest rate of change observed for any detection category and was likely the result of the storm and subsequent run-off (Fig. 7c,d). The increased freshwater flow coincided with the period when fish vacated the tributary for both BR 4 and BR 5 (Fig. 7).

### Batch releases 4 and 5: hypoxia avoidance

The only night with hypoxia ( $<2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) during BR 4 was the first night (i.e. from August 28 23:00 h to August 29 13:00 h, 2006, Figs. 3b–d, 5d–f & 7). That hypoxic event was restricted to upper Pepper Creek and no fish were detected in the hypoxic headwaters (Fig. 5d–f). However, there is evidence that the diel-cycling hypoxia acclimated weakfish in this release avoided DO levels that were lower than the saturation-acclimated fish released in previous releases. For instance, weakfish no. 147 withstood several hours at DO conditions  $\leq 2.8 \text{ mg O}_2 \text{ l}^{-1}$  before ultimately avoiding the tributary headwaters when DO was  $\leq 1.4 \text{ mg O}_2 \text{ l}^{-1}$  (Fig. 5d). This pattern of latent avoidance is also apparent in weakfish nos. 130 and 131 (Fig. 5e,f). A comparison to saturation-acclimated weakfish released under similar conditions is pro-

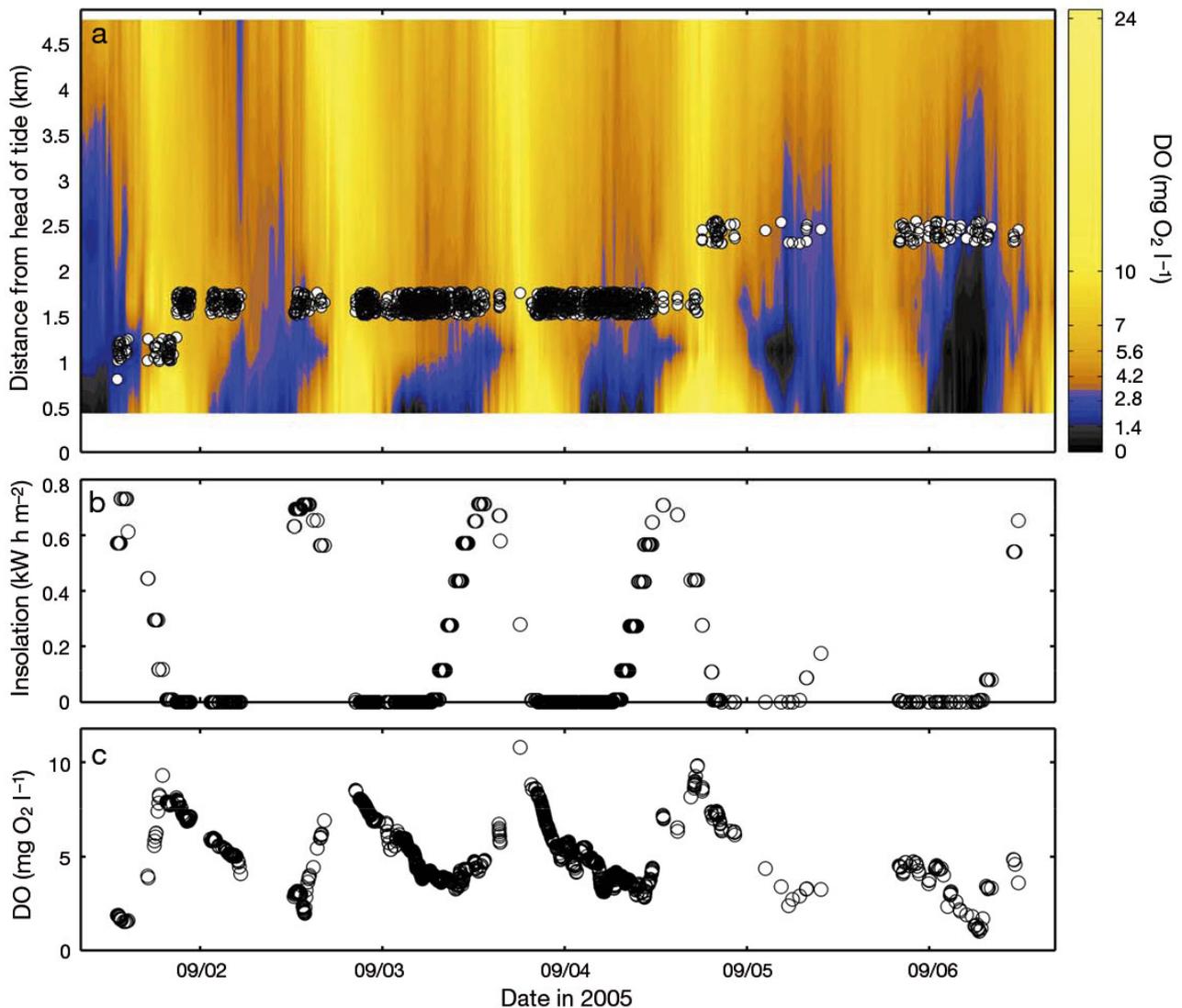


Fig. 6. *Cynoscion regalis* and *Leiostomus xanthurus*. (a) Dissolved oxygen (DO) plot and fish track for saturation-acclimated weakfish no. 146 in batch release 3, (b) insolation and (c) DO associated with each detection. The estimated locations have been randomly jiggered  $\pm 200$  m (approximate receiver range). The color scale for DO reflects laboratory-derived behavioral thresholds of saturation-acclimated weakfish (see 'Materials and methods'): swimming speed peaked at  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  and angular correlation between successive movements decreased markedly at  $<1.4 \text{ mg O}_2 \text{ l}^{-1}$ . Dates are given as mm/dd

vided by Fig. 5 (panels a–c [saturation-acclimated] versus d–f [diel-cycling hypoxia acclimated]). Whereas saturation-acclimated and diel-cycling hypoxia acclimated weakfish were not released concurrently, there is no definitive evidence of differential behavioral tolerance of hypoxia. However, diel-cycling hypoxia acclimated fish were consistently in DO conditions ( $<2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) avoided by saturation-acclimated weakfish.

Hypoxia was both spatially and temporally limited during BR 5. The only time period that DO was  $<1.4 \text{ mg O}_2 \text{ l}^{-1}$  was on September 4, when a brief

period of hypoxia was located 5 km from the head of tide. Areas close to the open bay are usually not hypoxic unless hypoxia extends all the way from the upper tributary. However, the Delaware Coastal Bays can become stratified at deeper sites like PC6 (Fig. 1c) during storm events. Three weakfish of the 8 released in BR 5 left Pepper Creek on the first ebb tide after release and were not picked up in the array again even at receivers deployed in the open bay. In fact, all the BR 5 fish made downstream movements on the first ebb tide after release, an extremely strong ebb tide ( $7.0 \times 10^{-6} \text{ m s}^{-1}$ ) due to the storm. Three

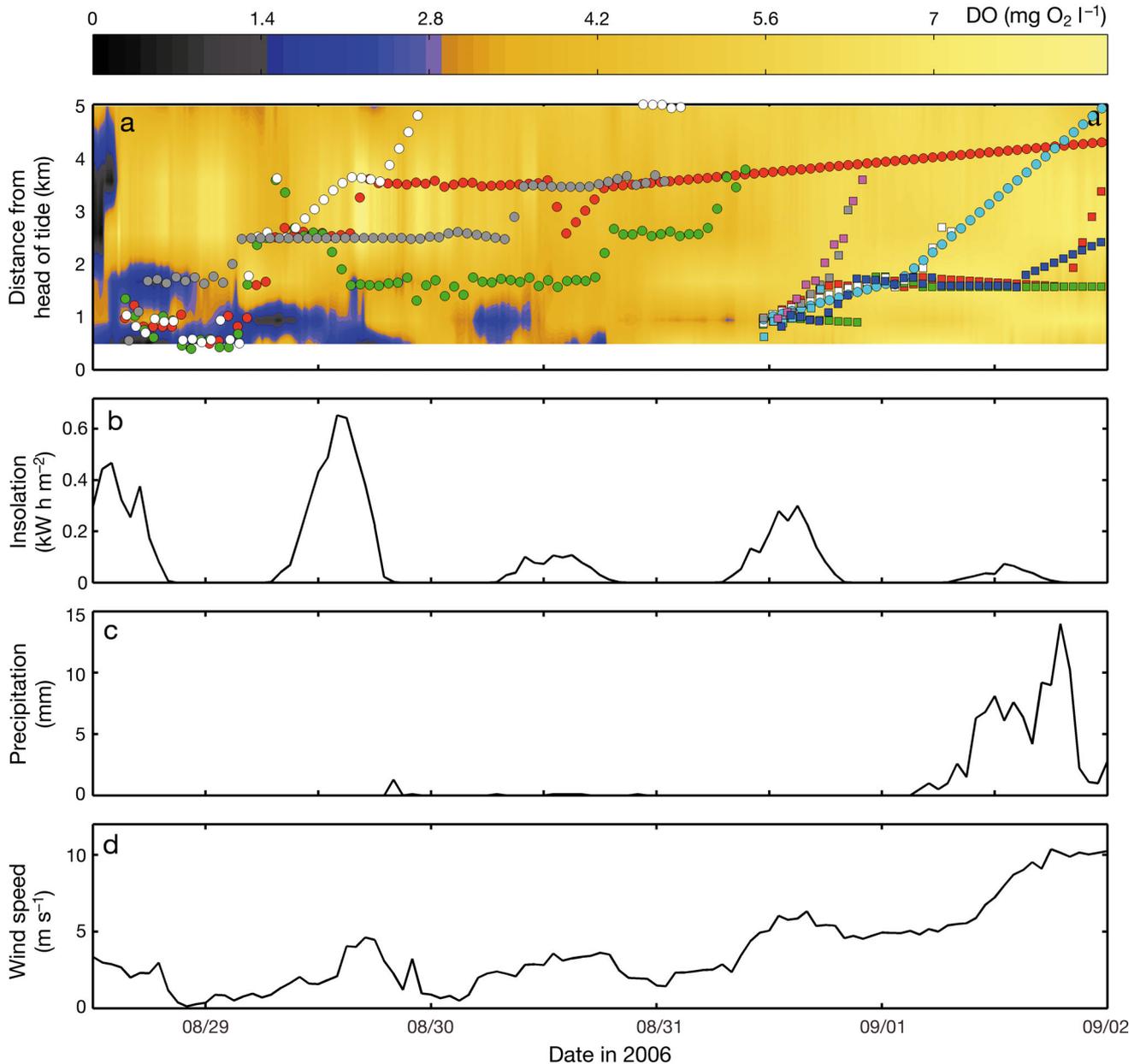


Fig. 7. *Cynoscion regalis* and *Leiostomus xanthurus*. Batch releases 4 and 5. (a) Dissolved oxygen (DO) plot and tracks of all fish, (b) insolation, (c) precipitation, and (d) wind speed for a 5 d following release on 08/28/2006. Markers represent the hourly locations along the creek axis for diel-cycling hypoxia acclimated (circles) weakfish nos. 131 (red), 147 (green), 130 (white), 134 (gray), and 136 (cyan) and saturation-acclimated (squares) weakfish nos. 316 (red), 305 (green), 320 (white), 143 (gray), 321 (cyan), 315 (magenta), and 319 (blue). The color scale for DO reflects laboratory-derived behavioral thresholds of saturation-acclimated weakfish (see 'Materials and methods'): swimming speed peaked at 2.8 mg O<sub>2</sub> l<sup>-1</sup> and angular correlation between successive movements decreased markedly at <1.4 mg O<sub>2</sub> l<sup>-1</sup>. Dates are given as mm/dd

other weakfish left Pepper Creek on the first ebb tide but were subsequently detected in the open bay until early October. Only 2 weakfish of the original 8 were in Pepper Creek during the only hypoxic period of this release, and both individuals were detected before and after this event but never within the hypoxic zone (e.g. Fig. 5a).

#### Batch release 6

The last batch release, BR 6, occurred on September 4, 2006 and consisted of 8 saturation-acclimated weakfish (Table 1) detected 2996 times (38 downstream and no upstream movements). Rain and cloudiness characterized September 5 and consequently DO at PC1

dropped below  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  for ~3 h. In general, hypoxia was limited throughout the week, likely due to low temperatures, regardless of low insolation.

Particularly important covariates discriminating downstream movements from stay-put estimated locations were (in order of Wald  $\chi^2$  magnitude in Table 2): the rate of temperature change, DO, tide height change, and insolation. Downstream movements coincided with large temperature changes, either positive or negative. The mean ( $\pm$ SD) rate of temperature change was  $-0.17 \pm 5.47^\circ\text{C s}^{-1}$  during downstream movements, suggesting that extreme temperature changes elicited movement to more stable temperature regimes in the open bay (~5 km from the head of tide). In fact, a downstream movement was almost 5 times more likely given a 1 SD increase in the rate of temperature change. Downstream movements also usually followed extreme decreases in DO as evidenced by the fact that a 1 SD decrease in the rate of DO change resulted in a 9.5-fold increase in the probability of a downstream movement (Table 2). Finally, downstream movements were more likely to occur on ebbing tides, and during the day. In contrast to BR 1, downstream movements were 8.84-fold more likely to occur for a  $1 \text{ kW m}^{-2}$  increase in insolation. Thus, in this batch release during limited hypoxia, weakfish were more active during the day, indicating that hypoxia may induce more nocturnal movement than would be expected during normoxic conditions.

#### Batch release 6: hypoxia avoidance

The only moderately hypoxic event ( $<2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) occurred in the headwaters on the night of September 5 and early morning on September 6. Most weakfish avoided this event by moving downstream from PC1 to PC2 and PC3 (~1 km from the head of tide). All fish emigrated from Pepper Creek and apparently out of the Delaware Coastal Bays since they were not detected at receivers located in the open bay during this emigration (Fig. 1c). Because this batch release was the latest batch release of any year, weakfish may have started their fall offshore migration, although 2 individuals from BR 5 were detected in the open bay in early October (Table 1).

### DISCUSSION

There are many life-history processes that contribute to the seemingly counterintuitive overlap between anthropogenically impacted areas and nurs-

ery habitat. The larval and adult behaviors of estuary-dependent fishes serve to place juveniles in areas with higher prey densities, optimal temperatures for growth, and in areas that may be associated with lower predation (Paterson & Whitfield 2000, Manderson et al. 2004). Some of the characteristics that define optimal nursery habitat coincide with those that define susceptibility to eutrophication and hypoxia, such as temperature. Furthermore, species make an active choice to occupy and remain in these potentially low-quality habitats. Therefore, a thorough understanding of the relationship between habitat selection and habitat quality is necessary to diagnose why organisms inhabit sub-optimal habitat and what their behaviorally-mediated realized exposure is to suboptimal conditions.

The most consistent result across all batch releases was the influence of tide on fish movement. Almost all upstream and downstream movements occurred on flood and ebb tides, respectively. Many shallow-water organisms undertake tidally-synchronized horizontal migratory movements to take advantage of prey or refuge opportunities in a heterogeneous environment (Gibson 2003). The current study demonstrates that juvenile weakfish and spot may utilize tidal flow during hypoxia avoidance. If a sharply positive spatial gradient in DO (lower DO in the up-tributary direction) exists, then ebbing tides usually precede low DO coming from hypoxic headwaters. That is, the ebb tide advects less oxygenated water from the headwaters downstream (Tyler et al. 2009). Use of ebb tide to escape low DO under these conditions (with associated reduction in the energetic expenditure necessary) is evident in the escape response of weakfish and spot across all batch releases. More specifically, as the tide ebbs, fish can use tidal flow to remain in water relatively more oxygenated than the water coming from upstream. For instance, the majority of the escape responses exhibited by fish during BR 1 were during an ebbing tide. However, under these conditions, during spatially extensive hypoxia, when the tide turns and begins to flood it is no longer a conveyance to more oxygenated waters, but rather is flowing toward hypoxic waters and as a consequence is a hindrance to escape from hypoxia. This is most evident in the case of the smaller ( $\overline{\text{SL}} = 126 \text{ mm}$ ) spot in BR 1 that reached the mouth of Pepper Creek with the first ebb tide but spent the subsequent flooding tide in hypoxic waters. The 2 larger weakfish ( $\overline{\text{SL}} = 176 \text{ mm}$ ) in this batch release appeared less influenced by the subsequent flood tide, since they reached the mouth of Pepper Creek on the ebbing tide and moved out of the acoustic array into

the open bay on the subsequent flood tide. It is also possible that this was a species-specific difference; however, there is no evidence in the literature for species-specific differences in hypoxia tolerance (Wannamaker & Rice 2000, McNatt & Rice 2004, Shimps et al. 2005, Stierhoff et al. 2009b) and there were not enough coincident releases of spot and weakfish to definitively make this comparison.

Another important observation was that fish did not make upstream and downstream movements during every tidal cycle and would remain at one site over several tidal cycles when DO was  $>2.8 \text{ mg O}_2 \text{ l}^{-1}$  (see Figs. 6 & 7). Ultimately, the smaller spot in BR 1 that became retained in the hypoxic creek during the flood tide may have been exhausted after moving at least 5 km (assuming a completely straight swimming path) in 8 h as DO in the water column decreased. A combination of swimming at speeds above ebbing tidal velocity during the initial avoidance response and swimming against the subsequent flooding tide may have induced exhaustion. Exhaustion was also evident in similar sized weakfish in a mesocosm when the angular correlation between movements declined precipitously below  $1.4 \text{ mg O}_2 \text{ l}^{-1}$  (Brady et al. 2009).

Exhaustion following avoidance of hypoxia has been observed in acoustically tagged spot in the Neuse River, NC, USA (K. Craig pers. comm.). Hypoxia in the Neuse River occurs during periods when wind induced mixing ceases and the bottom of the stratified water column becomes hypoxic. During periods of low wind and spatially extensive hypoxia, spot increase swimming speed (on average 5-fold) and decrease path sinuosity until they reach refuges along shore. Following long 'searches' for normoxic refugia (7 to 24 h), spot have been observed to remain quiescent for 8 to 24 h, presumably to recover. Smaller fish in the current study may have been in the same situation. After moving at speeds of up to  $1\text{--}2 \text{ m s}^{-1}$  ( $8 \text{ to } 16 \text{ BL s}^{-1}$  for a 120 mm fish) during avoidance, the smaller fish remained at the mouth of Pepper Creek and during this recovery period were forced to remain in hypoxia.

Another possibility is that smaller fish stay at the mouth of Pepper Creek because of potential predation in the open bay. Many studies have demonstrated that predators forage in shoal habitats adjacent to subtidal creeks (Szedlmayer & Able 1993, Rountree & Able 1997, Rypel et al. 2007), and Clark (2001) generally captured adult estuary-dependent fish (e.g. summer flounder, bluefish, and striped bass) in greater abundance at the mouth of the Delaware Coastal Bay tributaries than farther up the tributaries. Szedlmayer & Able (1993) found that tagged

summer flounder (210 to 254 mm SL) released in subtidal creeks in New Jersey, USA preferred to remain at the mouth of those creeks. In the present study, predator avoidance may have had a higher priority than hypoxia avoidance for smaller fish as they approached the open bay. Whether hypoxia exposure was controlled by exhaustion or predation risk, the identification of scenarios wherein fish can be exposed to growth-limiting and even lethally low DO concentrations is important, especially considering that early juvenile spot and weakfish with lower swimming speeds than the late juvenile fish tagged in this study could be caught in spatially extensive hypoxic zones during flood tides.

Support for the exhaustion-induced hypoxic exposure can be found in the Brady et al. (2009) examination of the behavioral responses of weakfish to diel-cycling hypoxia in the laboratory. In that work, saturation-acclimated weakfish were exposed to decreasing DO from  $7.0$  to  $0.4 \text{ mg O}_2 \text{ l}^{-1}$  (at  $\sim 2.5 \text{ mg O}_2 \text{ l}^{-1} \text{ h}^{-1}$ ) and a subsequent increase from  $0.4$  to  $7.0 \text{ mg O}_2 \text{ l}^{-1}$  at the same rate. Even at  $7.0 \text{ mg O}_2 \text{ l}^{-1}$  after the DO recovery phase, saturation-acclimated weakfish only recovered 60% of their original swimming speed (Brady et al. 2009). Several other aspects of the present study correspond with the results of the laboratory investigation. Saturation-acclimated weakfish generally avoided  $2.8 \text{ mg O}_2 \text{ l}^{-1}$  as evidenced by very few estimated locations under these conditions, and increased swimming speed as DO decreased. In the laboratory, saturation-acclimated weakfish increased swimming speed by 46% as DO decreased from  $7.0$  to  $2.8 \text{ mg O}_2 \text{ l}^{-1}$ . The present study shows that this active response occurs in the field as well and may function to allow the best use of hypoxic habitats.

Additional similarity between the laboratory and field studies on juvenile weakfish can be seen in the response of diel-cycling hypoxia acclimated fish to hypoxia. Unlike saturation-acclimated fish, diel-cycling hypoxia acclimated weakfish in the present study did not avoid DO levels from  $1.4$  to  $2.8 \text{ mg O}_2 \text{ l}^{-1}$ , and only increased swimming speed and vacated areas when DO decreased below  $1.4 \text{ mg O}_2 \text{ l}^{-1}$ . Likewise, diel-cycling hypoxia acclimated weakfish in the laboratory were also less responsive to decreasing DO than were saturation-acclimated fish (Brady et al. 2009). The only evidence of an active response in diel-cycling hypoxia acclimated weakfish in the laboratory was an increase in swimming path straightness, a relatively non-strenuous response (Brady et al. 2009). Interestingly, both the laboratory- and field-observed behavioral responses of diel-cycling hypoxia accli-

mated weakfish occurred only when DO was below the lowest acclimation DO level ( $2.0 \text{ mg O}_2 \text{ l}^{-1}$ ). That is, while acclimation tended to mute the escape response, avoidance behavior was still enacted during exposure to DO levels below the lowest levels experienced during the acclimation phase.

Miller (2010) tagged and released summer flounder using the same equipment in the same system (Pepper Creek) and a direct comparison of more active species (i.e. weakfish and spot) with summer flounder ( $N = 17$ ; 197 to 301 mm SL) illustrates some interesting species-specific behavioral dynamics. For instance, instead of generally avoiding  $\text{DO} < 2.8 \text{ mg O}_2 \text{ l}^{-1}$ , summer flounder avoided  $\text{DO} < 4.8 \text{ mg O}_2 \text{ l}^{-1}$  (Miller 2010), a DO level below which summer flounder growth is impaired at temperatures above  $25^\circ\text{C}$  (Stierhoff et al. 2006). Also, summer flounder appear to be more sensitive than weakfish to the rate of DO change. Summer flounder movement and rate of DO change were positively correlated. Weakfish, on the other hand, generally increased movement during low DO ( $< 2.8 \text{ mg O}_2 \text{ l}^{-1}$ ) regardless of the rate of DO change. Being sensitive to the change in DO may be linked to the energetic constraints of weakfish versus summer flounder swimming. Fonds et al. (1992) suggested that flatfish spend relatively less energy in swimming in order to convert more energy into growth than pelagic fish. If so, a relatively increased scope for activity may allow active species to use nursery habitats characterized by dynamic abiotic conditions.

Many studies have demonstrated that fish have a distinct diel-periodicity in their movement patterns (Rountree & Able 1993, Holland et al. 1996, Rountree & Able 1997, Cartamil et al. 2003). In the present study, fish were more likely to move at night during BRs 1 and 2, but more likely to move during the day in BRs 3, 4, and 6. Severely hypoxic conditions ( $< 1.4 \text{ mg O}_2 \text{ l}^{-1}$ ) during BRs 1 and 2 caused fish to move downstream on either the first or second night post-release; whereas DO conditions during the other batch releases were generally less severe ( $> 1.4 \text{ mg O}_2 \text{ l}^{-1}$ ). Weakfish are visual predators and generally forage during the day (Chao & Musick 1977, Greccay & Targett 1996). Results of the present study suggest that weakfish are preferentially active during the day but may be forced to move during particularly severe nighttime decreases in DO.

Downstream movements far outnumbered upstream movements across all batch releases. In the case of spatially extensive hypoxia, the increased number of downstream movements facilitated escape (e.g. BRs 1 and 2). However, fish also made more downstream movements during batch releases

characterized by less hypoxia. Many fish species display a positive size–depth relationship (Macpherson & Duarte 1991, Kneib 2000), and juvenile weakfish prefer deeper habitat as they grow (Derickson & Price 1973, Casey & Doctor 2003). The depth difference between upper Pepper Creek and Indian River Bay is only  $\sim 1 \text{ m}$ . However, larger weakfish ( $> 150 \text{ mm}$ ) may benefit from following the depth gradient down estuary closer to the open coast for migration to overwintering grounds.

Hypoxia is likely not the only factor influencing emigration from estuarine tributary habitats. Weakfish released on August 28, 2006 before a storm event (BRs 4 and 5) began leaving the creek almost immediately after release. Creek residency for these individuals was less than half the time of fish released after the storm was over on September 4, 2006 (BR 6, Table 1). Sackett et al. (2007) reported that storm-related emigration of tagged summer flounder (289 to 535 mm SL) from the Mullica River, NJ, USA occurred more than 3 times faster than non-storm related emigration. Emigration to deeper water may be episodically impacted by storm events in addition to low DO and high temperature.

Weakfish and spot clearly avoided  $\text{DO} < 1.4 \text{ mg O}_2 \text{ l}^{-1}$ . Indeed, there were very few instances when either species was exposed to  $\text{DO} < 2.8 \text{ mg O}_2 \text{ l}^{-1}$ . Only during spatially extensive hypoxic events when the tide was flooding were fish exposed to  $\text{DO} < 2.8 \text{ mg O}_2 \text{ l}^{-1}$ . In the laboratory, neither species experiences a growth detriment until DO declines to  $1.5 \text{ mg O}_2 \text{ l}^{-1}$  (McNatt & Rice 2004, Stierhoff et al. 2009b). The lower lethal DO limit is unknown for weakfish, but the lethal concentration,  $\text{LC}_{50}$ , for spot ranges from  $0.70 \text{ mg O}_2 \text{ l}^{-1}$  (Burton et al. 1980) to  $1.1 \text{ mg O}_2 \text{ l}^{-1}$  (Shimps et al. 2005). Consequently, the relatively long (hours) exposure to  $\text{DO} < 1.4 \text{ mg O}_2 \text{ l}^{-1}$  in smaller spot during BR 1 could have been lethal, although in this particular case the fish subsequently moved so some short-term respite from lethal conditions must have been available. Tyler et al. (2009) found that DO in the water column was generally homogeneous in Pepper Creek except in the early morning when DO at the surface increased somewhat faster than bottom water DO. Therefore, any surface DO refuge available for fishes not capable of aquatic surface respiration is infrequently available, thereby increasing the importance of longitudinal movement in hypoxia avoidance. As effective as avoidance is in ameliorating exposure to low DO, Stierhoff et al. (2009a) observed correlations between *in situ* growth and low DO in Pepper Creek for weakfish and summer flounder. However, it should

be noted that the weakfish and summer flounder captured in Stierhoff et al. (2009a) were significantly smaller (54 to 85 mm SL for weakfish and 43 to 104 mm SL for summer flounder) than the weakfish tagged in the present study and the summer flounder tagged by Miller (2010). Smaller individuals (<100 mm) with lower swimming speeds would not have the same ability to regulate position longitudinally in the creek as larger individuals which could either lead to more hypoxia exposure or decreased foraging area.

Chlorophyll *a* (chl *a*) data, collected by Delaware's Department of Natural Resources and Environmental Control (R. Tyler pers. comm.) and by the University of Delaware's Citizen Monitoring Program ([www.citizen-monitoring.udel.edu](http://www.citizen-monitoring.udel.edu)), indicate the Delaware Coastal Bays were much less productive in 2006 than in 2005. Average chl *a* in Indian River during 2006 were 63% lower than the concentrations measured in 2005. Consequently, the maximum DO concentration observed during the week following BR 4 (2006) was only 8 mg O<sub>2</sub> l<sup>-1</sup>; whereas the maximum DO concentration over the course of the week following BR 3 (2005) was 24 mg O<sub>2</sub> l<sup>-1</sup>. Finally, productivity differences between these years also manifested itself in the number of fish kills during the 2 yr: none in 2006 versus 7 in 2005 (Shirey 2005–2007).

Differences in movement patterns between 2005 and 2006 suggest that hypoxia avoidance may be modulated by productivity. Since diel-cycling hypoxia is the result of eutrophication, areas with large daily DO ranges are extremely productive. Fish behavior in hypoxic zones balances the risks and consequences of hypoxia exposure with potential advantages of high productivity. Craig et al. (2010) found that cownose rays *Rhinoptera bonasus* track highly productive surface waters and hypoxic bottom waters possibly to take advantage of additional feeding opportunities. Weakfish released in 2005 under conditions of high productivity and spatially extensive hypoxia left Pepper Creek on the first or second day post-release, but other fish released in 2005, when the DO range was still quite large but hypoxia was contained in the headwaters, remained in the creek for at least 5 d. In contrast, fish released in 2006, when chl *a* measurements indicate that the Delaware Coastal Bay tributaries were less than half as productive as the previous year, only remained in the creek for an average of 2 d (Table 1). A prerequisite for taking advantage of highly productive areas is a sensitive hypoxia detection and avoidance system that appears to be in place for weakfish as long as hypoxia is not spatially extensive.

In addition to productivity, hypoxic habitats may also represent areas where prey is more available. Craig & Crowder (2005) found that Atlantic croaker *Micropogonias undulatus*, another sciaenid with an overlapping diet of benthic invertebrates (Skilleter & Peterson 1994, Lankford & Targett 1997, Eby et al. 2005, Powers et al. 2005), crowded into the edge of the hypoxic zone in the Gulf of Mexico. In fact, the abundance of Atlantic croaker decreased exponentially with distance from the hypoxic edge and they speculated that high densities at the edge were due to high prey availability. Evidence for increased prey availability in the most heavily hypoxia-impacted area (upper) of Pepper Creek has been reported by Tuzzolino (2008), who found that juvenile weakfish stomach fullness was higher in the upper creek (denoted PC2 in the present study, ~1 km from the head of tide) than at middle and lower sites (~2 and 5 km from the head of tide, respectively). In addition, weakfish stomachs contained more polychaetes at the upper site and more mysids at the lower site (Tuzzolino 2008). Polychaetes are likely to become more available under hypoxic conditions as they move to the sediment surface (Tuzzolino 2008). However, if periods of hypoxia become prolonged, benthic invertebrate abundance can become severely reduced (Powers et al. 2005). Generally, tagged fish in Pepper Creek moved only enough to remain on the edge of hypoxia (>2.8 mg O<sub>2</sub> l<sup>-1</sup>) as it developed through the night as long as hypoxia was not spatially extensive, suggesting that secondary/primary productivity benefits outweighed risks of hypoxia exposure.

In conclusion, juvenile weakfish and spot avoided severe hypoxia (<2.0 mg O<sub>2</sub> l<sup>-1</sup>) by increasing swimming speed and using tidal flow to facilitate escape. There was evidence that tidal flow may also act as a deterrent to escape if flooding tides occur during spatially extensive hypoxia due to the additional energetic expenditure of swimming against tidal flow. Hypoxia-acclimation (5 d exposure to DO cycling between 2.0 and 11.0 mg O<sub>2</sub> l<sup>-1</sup>) appeared to reduce the avoidance threshold from 2.8 mg O<sub>2</sub> l<sup>-1</sup> to 1.4 mg O<sub>2</sub> l<sup>-1</sup> for weakfish. Fish in estuarine tributaries may balance the benefits of highly productive nursery areas with the risks of low DO. Measuring DO and fish movement at fine temporal (~15 min) and spatial (~0.5 km) scales is perhaps the only method that can aid modeling efforts to scale hypoxia exposure effects up to population level. Toward that end, more work on the role of predation and opportunistic feeding for fishes navigating hypoxic zones is needed to further understand and model the indirect effects of hypoxia in estuarine nursery areas.

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