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Assessing the Effects of Physical Barriers and Hypoxia on Red Drum Movement Patterns to Develop More Effective Management Strategies

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Abstract: Human modification of coastal ecosystems often creates barriers to fish movement. Passive acoustic telemetry was used to quantify movement patterns and habitat use of red drums (*Sciaenops ocellatus*) within and around a complex of coastal impoundments, and explored how the presence of artificial structures (i.e., bollards and culverts) and a hypoxia-related mortality event impacted fish movement. Results indicated bollards impede the movement of individuals with head widths greater than the mean distance between bollards (~16.0 cm). Red drum home range area and daily distance traveled were related to water dissolved oxygen concentrations; as oxygen levels decreased, fish habitat use area decreased initially. However, continued exposure to hypoxic conditions increased fish cumulative daily distance traveled. When exposed to anoxic waters, fish daily distance traveled and rate of movement were greatly reduced. These findings suggest prolonged exposure to low dissolved oxygen in combination with artificial structures can reduce movement of red drum, increase risk of mortality, and decrease habitat connectivity. Constructing and maintaining (sediment and biofouling removal) larger culvert openings and/or using wider bollard spacing would improve water circulation in impoundments, increase habitat connectivity, and facilitate movement of large sportfish inhabiting Florida's coastal waters.

Keywords: species management; acoustic telemetry; fish movement; red drum; hypoxia

Key Contribution: This study observes the impacts of artificial structures on fish movement during a hypoxia related fish mortality event. We analyze the changes in movement patterns of red drum as dissolved oxygen levels reduce from normoxic to anoxic.

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1. Introduction

Connectivity is essential to the movement of fish among critical habitats for daily foraging, dispersal, and migration events that connect populations [1–3]. In coastal zones, habitat alterations, such as roads, culverts, and dams, in addition to physical (e.g., temperature) and chemical barriers (e.g., dissolved oxygen and salinity) may impact fish movement [4–6]. As anthropogenic land-use changes threaten to reduce seascape connectivity by altering the distribution and abundance of critically important benthic habitats, such as seagrasses and mangroves, populations may become isolated within smaller habitat patches due to a reduction in the ability of fish to disperse to previously accessible habitats [7]. Furthermore, these habitat alterations and physical and chemical barriers may impede flow, resulting in increased sediment deposition in coastal estuaries, and this reduced hydrologic connectivity may impact the ability of organisms to reach historic spawning sites or prevent dispersal away from an area during disturbances potentially resulting in increased mortality and fish kills [8,9].

In response to adverse environmental conditions, fish may move from preferred habitat, thus influencing their spatial distribution in the environment [10]. However, if anthropogenic barriers prevent the ability of individuals to vacate areas during poor water quality events, fish are often unable to survive, resulting in fish kills [11]. Localized mass die-offs of fish, or fish kills, occur within aquatic environments and can be caused by natural disturbances, such as changes in abiotic conditions, toxic algal blooms, inadequate prey abundance, or disease [9,12]. However, anthropogenic activities (e.g., habitat fragmentation and nutrient runoff) have compounded these effects resulting in an increase in the number of fish kills worldwide [13,14]. While the proximate causes vary, often the ultimate cause of fish kills is the low concentration of dissolved oxygen (DO) in the water often caused by eutrophication from nutrient runoff [15,16]. By convention, hypoxic conditions exist when DO levels fall below 2.0 mg/L, while anoxic conditions occur when DO levels are lower than 0.5 mg/L [17]. Prolonged exposure to hypoxic conditions can cause decreased feeding, locomotion, and growth, and reduce fish survival [10,18]. Studies examining the effects of hypoxia on fish species have found that minimum DO tolerance levels vary among species and across life stages [10,18–21]. Mobile fish species respond to hypoxic conditions by moving to waters with higher DO concentrations, both moving vertically towards surface waters or by traversing outside their normal home range to normoxic water bodies [20,22]. However, the combination of poor water quality and barriers to movement may increase the likelihood of severe mortality events by preventing fish from moving to areas with normoxic water conditions [9].

Coastal impoundments are common physical barriers that alter seascape connectivity and may decrease the ability of fish to move to waters with higher DO concentrations. In the southeastern USA, impoundments are areas of coastal salt marsh or mangrove forest that have been diked to create structures, frequently in an effort to manipulate water levels and control mosquito populations [23]. Impoundments isolate salt marsh and mangrove habitat from estuarine waters and limit estuarine species from accessing these areas as feeding or nursery grounds [24]. Additionally, impoundments can negatively impact coastal habitat by reducing fish species abundance, altering wetland vegetation, increasing algal blooms, and modifying water chemistry [24–29]. Recognition of these deleterious effects has resulted in many coastal impoundments being hydrologically reconnected, thus restoring some natural conditions [6]. However, other impoundments remain connected by relatively small culverts or contain water control structures around the entrances to culverts, limiting hydrologic connectivity [24,30].

Other physical barriers which can compound animal movement and seascape connectivity include barriers, such as weirs, grates, and bollards, which are implemented to block access of larger species in culvert systems. In Florida, bollards are used to prevent the stranding, entrapment, and death of West Indian Manatees (*Trichechus manatus*) in culverts [31–34]. However, it remains unknown how the compounding effects of impoundments, culverts, and bollards, and the onset of hypoxia interact to impact movement and survivorship as individuals attempt to vacate deteriorating habitat.

To address this knowledge gap, the objectives of this study are to quantify the impacts of manatee exclusion bollards and hypoxia on movement patterns of red drums (*Sciaenops ocellatus*) in coastal impoundments. We hypothesized that large fish with head widths greater than the spacing between bollards would not be able to pass from one coastal impoundment into adjacent bodies of water. However, 18 months into this experiment, there was a naturally occurring hypoxic/anoxic event in the focal study area that resulted in a mass fish mortality event. While unintended, this disturbance event provided the unique opportunity to observe and quantify the response of fish movement to hypoxia, and how fish movement changed as water DO concentrations shifted from normoxic to hypoxic to anoxic. The knowledge from both components of this study can be used to guide the development of and evaluate potential management strategies to reduce the effects of hypoxia and improve habitat connectivity in this coastal ecosystem.

2. Materials and Methods

2.1. Study Site

This study concentrated on the inshore waters of central Florida within the Indian River Lagoon (IRL). The IRL spans a dynamic biogeographic transition zone along Florida's east coast, making it one of the most biologically diverse estuaries in the USA [35,36]. Within the lagoon is the Merritt Island National Wildlife Refuge, most of which is land belonging to Kennedy Space Center (KSC) and Cape Canaveral Space Force Station (CCSFS). As a security and public safety measure, KSC and CCSFS have a security zone that has been closed to the public since 1962. This restricted area acts as a de facto protected area benefiting the natural habitat and fish populations [37].

Within CCSFS are two large impoundments created as a byproduct of the dredging involved with the construction of the Integrate-Transfer-Launch (ITL) complex facilities (Figure 1). These facilities were created in 1961 to house and transfer Titan III space craft [38]. The ITL impoundments are the focal study area (Figure 1), and consist of 1300 acres of shallow water habitat, inhabited by high abundances of fishes, namely red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), common snook (*Centropomus undecimalis*), Atlantic tarpon (*Megalops atlanticus*), sheepshead (*Archosargus probatocephalus*), and spotted seatrout (*Cynoscion nebulosus*) [37,39–41]. Historically consisting of large sea grass beds, the ITL impoundments collectively contain more open water than any other impoundment in the IRL (E. Reyier, personal communication). Previous studies suggest that this area was a historic red drum spawning site and essential habitat for red drum within the IRL [42]. The ITL impoundments are completely enclosed by land except for four culverts running under the Titan III Road connecting the southern impoundment to the Banana River (Figure 1). The South Patrol Road crosses and divides the southern and northern impoundments from each other, with another four culverts connecting the two water bodies. In 2016, to comply with Florida Fish and Wildlife Conservation Commission Manatee Sanctuary Act regulations (i.e., to prevent manatee entrapment (Figure 2) [32]. The spacing between bollards in the ITL ranged from 5 cm to 27 cm [43]. While this spacing enables the passage of relatively small fish, where encrusting organisms (i.e., barnacles) grow, reduced gap widths between bollards can prevent the movement and egress of larger individuals [43].

2.2. Model Species

One of the most sought-after recreational fish species in the IRL is the red drum. Red drum are large sciaenids that range along the east coast of the USA from Massachusetts to Florida and throughout the Gulf of Mexico. This species feeds on small crustaceans, such as shrimp, and small schooling fish, such as menhaden (*Brevortia* spp.) and striped mullet (*Mugil cephalus*) [44]. Red drum have been known to live up to 56 years and grow to lengths of 134 cm [45]. Within the IRL, red drum exhibit strong site fidelity, with a portion of fish remaining in the lagoon year-round, foregoing offshore spawning migrations, implying true estuarine reproduction [42,46,47]. This behavior is uncommon in other parts of their range, suggesting future abundance and harvest of red drum in the IRL is partially dependent on continued spawning success in the lagoon.

2.3. Water Quality Characterization

To develop spatial relationships between fish distribution and environmental variables, monthly samples were taken between July 2017 and December 2018 at 44 sites spaced every 400 m throughout the northern and southern ITL impoundments and adjacent Banana River. Abiotic variables of interest included water temperature (°C), depth (m), salinity (ppt), pH, DO (mg/L), and turbidity (FNU). Samples were collected monthly with a YSI ProDSS multi-parameter probe and refractometer. In addition, Onset HOBO continuous temperature loggers were deployed attached to receivers in the northern and southern impoundments, and Banana River. Continuous water quality data, including temperature, salinity, DO, pH, and turbidity, were collected via a continuous YSI multi-parameter probe located in the open estuary under the NASA Causeway, ~1.5 km from the ITL impoundments.

Correlations between data collected at this site and the point samples collected within the ITL were analyzed to estimate environmental conditions between monthly ITL sampling events. One-way ANOVAs and post hoc Tukey HSD tests were used to test for differences in environmental variables per sampling event among the north impoundment, south impoundment, and adjacent Banana River. All statistical analyses were performed using R version 3.5.2 [48].

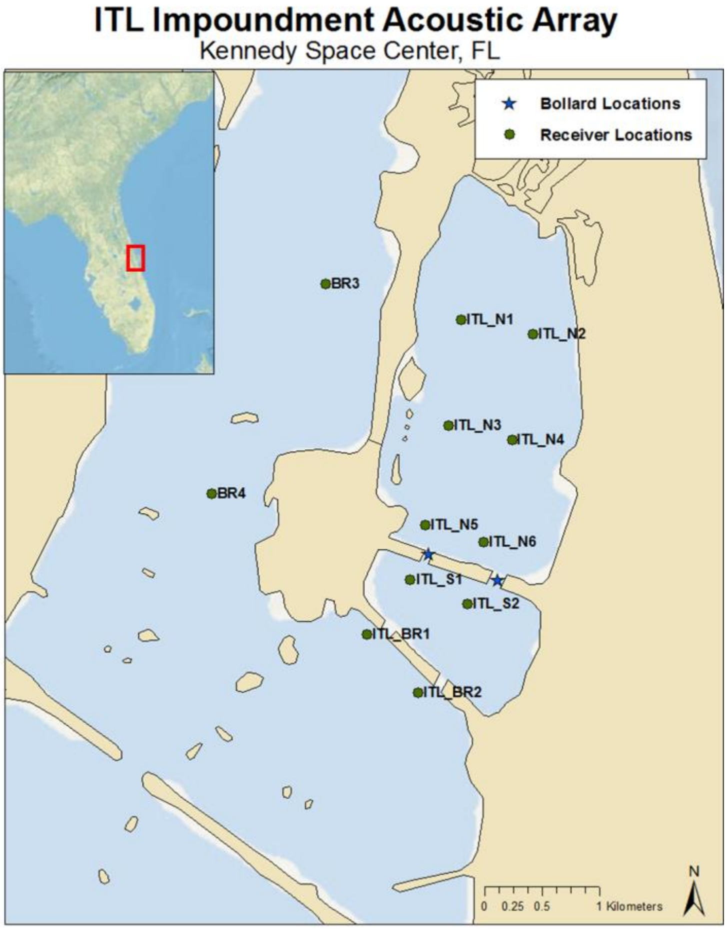

Figure 1. Location of acoustic receivers within the Integrate-Transfer-Launch (ITL) complex and impoundments (north and south) located in the northern Banana River along the central east coast of Florida with the location of acoustic receivers (green dots) and bollards (blue stars). HOBO temperature loggers deployed on ITL_N2, ITL_N5, ITL_S1, and ITL_BR2. Inset map depicts location of the ITL focal study area within Florida (~28°32′ N 80°35′ W), in the southeastern USA.

2.4. *Fish Tagging and Receiver Deployment*

Acoustic telemetry was used to monitor red drum movement patterns within the ITL impoundments between July 2017 and April 2019. From July 2017–October 2017, 30 adult red drum were captured using hook and line. Fish head width, being the broadest part of an individual, was measured using calipers, as it may constrain the ability of an individual to pass through the bollards. Fish were divided into two size classes relative to preliminary measurements of spacing between manatee exclusion bollards and mean head width of individuals captured: 15 large fish with head widths greater than 13 cm, and 15 small fish with head widths less than 13 cm were tagged. A total of 20 fish (10 large and 10 small) were captured from the northern impoundment and 10 (5 large and 5 small) were captured in the southern impoundment. As only adult fish are thought to migrate for spawning, only mature individuals with standard lengths over 35 cm were targeted [49]. Morphometric measurements were recorded, including fish mass (kg), plus standard length (SL), fork length (FL), total length (TL), and head width (HW), in centimeters.

(**a**) (**b**)

Figure 2. Integrate-Transfer-Launch Impoundment culverts (**a**) Manatee exclusion bollards installed around the ITL impoundment culverts.; (**b**) ITL culvert surrounded by bollards which have been fouled by barnacles near the water line.

All 30 fish were tagged with acoustic transmitters (Innovasea V16-4H, 68 mm long × 16 mm diameter, 24 g in air, power output 158 dB) following the methods of Reyier et al. [47]. After capture each fish was transferred to a 100-L tank and anesthetized in a 75 mg/L Tricaine methanesulfonate (MS-222, Western Chemical Inc., Ferndale, Washington, DC, USA) water bath. Fish remained in the water bath solution until stage IV anesthesia was reached (approximately 5–10 min). Once fish were anesthetized, they were transferred to a wooden surgery cradle within a water bath with a small aeration pump to implant the transmitter. An amount of 5 to 7 scales were removed and a 25 mm incision parallel to the ventral midline was made. The V16-4H transmitter was inserted into the peritoneal cavity 2–3 cm anterior to the anus. After the transmitter was inserted the incision was closed with 2–3 absorbable sutures and Vetbond cyanoacrylate tissue adhesive (3M Corporation). Each fish was also tagged externally with a unique dart tag to the left of the dorsal fin. Subsequently fish were transferred to a seawater bath to recover prior to release.

Red drum movement was monitored by an array of 10 submerged Innovasea VR2W receivers placed within and around the ITL impoundments, including 6 in the north impoundment, 2 in the south impoundment, and 2 in the adjacent Banana River (Figure 1). Receiver placement was optimized to detect movement through culverts, and within the impoundments. Initial range testing was used to optimize receiver spacing by placing test tags every 100 m between receivers until tags were not consistently detected and revealed the mean detection distance was approximately 200 m (i.e., the distance at which at least 50% of the possible acoustic transmissions were detected by the receivers) [50,51]. Acoustic receivers were downloaded monthly from August 2017 until April 2019. If fish were to leave the impoundment area, receivers within the FACT Network, a collaborative network of researchers who use and share acoustic telemetry monitoring data, consisting of approximately 885 receivers, including those used in this study, would capture any movement within the broader IRL and/or movement through inlets into adjacent waters [40,41,52].

2.5. Movement Analysis

Acoustic telemetry data were combined with environmental variables and analyzed using the V-Track (recreation of movement patterns), GLATOS (simulation and visualization of acoustic telemetry data), rhr (calculation of kernel density estimates), and adehabitatLT (projection of fish movement trajectory and individual residency times) packages in the statistical program R to recreate movement patterns, estimate centers of activity and assess changes in movement and habitat use [53–56]. False detections were filtered and removed using the White-Mihoff False Filtering Tool [57]. Any fish that was recorded more than 4 consecutive weeks on the same receiver with no movement was presumed to have died or shed its tag in the proximity of the receiver and was not included in analysis.

The small area of this study allowed for almost continuous detection on at least one receiver for all tagged fish throughout the length of the study. Short-term centers of activity (COA) were used to estimate the position of an individual fish (i.e., acoustic transmitter) in reference to two or more receivers for each fish every hour throughout the study [57]. By using the estimated receiver range and the proportion of detections recorded by each receiver, a weighted mean position algorithm (i.e., a transmitter is closest to the receiver with highest proportions of detections) can be used to estimate the location of the transmitter [58]. Movement patterns were analyzed to assess movement rates, distance traveled, and residency times. Daily distance traveled was calculated for each fish for each day it was present within the array by totaling all movement between 60 min COA locations. Prior to analyses, data were assessed for normality, homogeneity of variance, collinearity in variables, independence of variables, and identification of any outliers following Zuur et al. [59].

Kernel density estimates (KDEs) were used to identify core use areas by estimating the use of space by animals as a probability density function [52]. Grid size was set to approximately 100 $\times$ 100 m, and a reference bandwidth method (i.e., an optimum h value assuming normality for large sample sizes) was used for the smoothing parameter (Table A1). Home range areas of individual fish were calculated based on COA estimates using 50% (core use area) and 95% (extent of use) KDEs. Core use area represents the area individual fish are using for more than half of the time they are detected, while extent of use captures a broader area as determined by 95% of the detections of individual fish. KDEs were created for each fish for each month throughout the length of the study.

Generalized linear mixed effect models were used to assess changes in KDE home range area (50% and 95%) and daily distance traveled by fish in response to environmental and temporal changes. KDE home range areas were modeled using a Gamma distribution with a log link. When using acoustic telemetry, no movement may be recorded if a fish is either: not moving, not detected by a receiver, or if the fish is only detected within the range of one receiver. To address this limitation and to remove any technological bias, data were parsed into two classes: movement and no movement. To assess fish movement in response to environmental changes, only the movement class was used in models. Monthly KDE areas (ha) and daily distance traveled (m) were combined with mean monthly and daily environmental conditions recorded by the continuous YSI located under the NASA Causeway. Only days that had environmental data prior to the hypoxia-related fish kill event were used for the development of general movement models unless otherwise stated (i.e., due to instrument downtime/servicing, abiotic data were not available for all days, and fish movement in days following the onset of the hypoxic event were potentially "atypical"). DO concentrations (from the YSI continuous recorder) were categorized into three classes: Anoxic (<0.5 mg/L), Hypoxic (0.5–2 mg/L), and Normoxic (>2 mg/L/l). Explanatory variables included water temperature, salinity, DO concentration, pH, and fish size (i.e., head width), in addition to moon phase, mean wind speed and wind direction data collected at Kennedy Space Center. Individual fish ID was included as a random effect. Corrected Akaike Information Criterion (AICc) was used to assess which models best explained the home range area and daily distance of each fish. Statistical analyses were performed using R version 3.5.2 [48].

2.6. Fish Response to Hypoxia

On 9 August 2018, DO concentrations became hypoxic in the north ITL impoundment. On 10 August 2018, numerous dead small fishes, primarily silver perch (*Bairdiella chrysoura*) were observed in the northern ITL impoundment. The combination of high water temperatures, shallow depth, the presence of brown tide (predominantly *Aureoumbra lagunensis*), and limited water flow contributed to DO concentrations falling below 2 mg/L. DO levels remained low with waters becoming increasingly hypoxic over a period of approximately six days, before ultimately becoming anoxic around 19 August 2018. Anoxic conditions persisted for at least five days until they returned to normoxic levels (Figure 3a). This hypoxia-related event resulted in a large-scale fish kill culminating in the death of thousands of large red drum, black drum, spotted seatrout, and common snook (Figure A1). Another fish kill occurred in September 2018 when waters became hypoxic for an additional five days (Figure 3b).

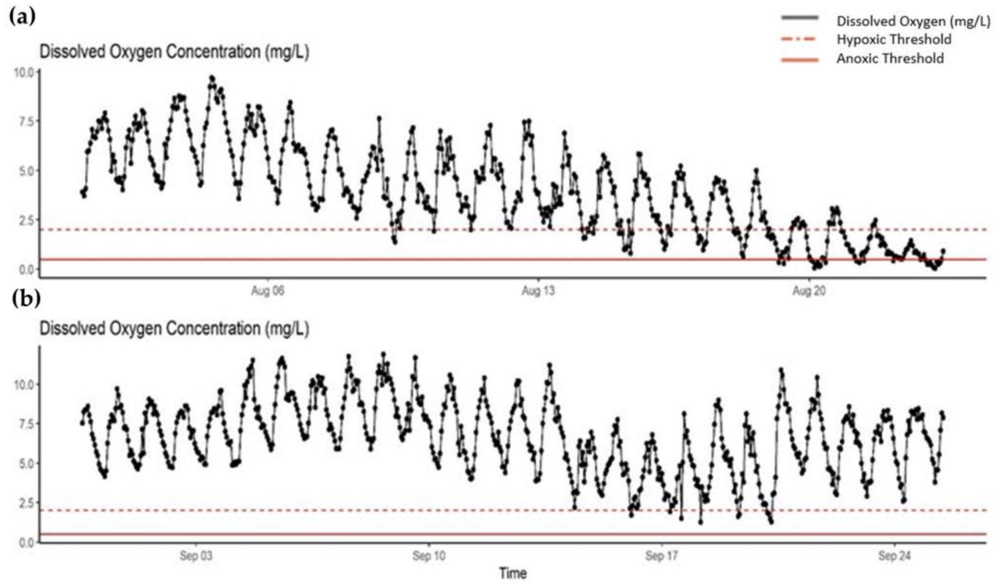

Figure 3. Dissolved oxygen levels collected from underneath the NASA causeway just outside the ITL impoundments reached hypoxic and anoxic levels leading to a localized fish kill in August 2018. (**a**) Dissolved oxygen levels from 1–23 August 2018. (**b**) Dissolved oxygen levels from 30 August to 25 September 2018.

Fourteen tagged fish were present in the north ITL impoundment during a hypoxia-related fish kill event in August 2018. Fish movement was monitored pre-hypoxia event, during the event, and after the hypoxia event. Through observations of the acoustic and environmental data available during this study, correlative results on the impacts of hypoxia exposure were made. To assess changes in fish behavior in response to hypoxia, hourly movement data from 10 to 21 August 2018 were combined with hourly environmental data for each fish present within the impoundment during the fish kill. Data were pooled and assessed for four-day DO bins around the fish kill event: Normoxic (10–13 August 2018), Hypoxic (14–17 August 2018), and Anoxic (18–21 August 2018). These periods consisted of three discrete DO levels lasting the majority of each day (i.e., from 10–13 August, DO concentrations remained above 2.0 mg/L for the majority of each day; from 14–17 August, DO concentrations were primarily hypoxic; and from 18–21 August, DO concentrations were primarily anoxic). KDE home range areas, daily distance traveled, and rate of movement were calculated for each fish for each time period. Within the statistical program R, one-way ANOVAs with post hoc Tukey HSD tests were used to test the null hypothesis that there were no significant differences when comparing among these three discrete time-periods [48].

3. Results

3.1. Water Quality Characterization

Water depth throughout the impoundments was relatively uniform (i.e., water depth ranged from 0 m at the impoundment edge to 2.0 m at the deepest location). Generally, the north and south impoundments were shallower, more turbid, and lower in DO than the adjacent Banana River; while the north impoundment had higher salinity than the Banana River and south impoundment (all One-way ANOVA: (F (2,564) > 13.56; $p < 0.0001$; post hoc Tukey HSD $p < 0.05$; Figure A2). There were no notable differences in temperature among the three study regions (please see Mean Temperature, Figure A2).

3.2. Movement Analysis

Mean (±sd) head width and standard length of captured red drum was 13.6 ± 2.9 cm and 77.9 ± 14.6 cm, respectively (Table 1). These fish were tracked throughout the ITL and FACT acoustic arrays for up to 535 days. Mean days at liberty (±sd) were 325 ± 140 days (range: 1–535 days).

Table 1. Measurements of acoustically tagged red drum captured in the ITL impoundments (mean ± sd). Fish were divided into two size classes: Large (>13 cm head width (HW)) and Small (<13 cm HW). Ten Large and ten Small fish were captured in the north impoundment (NI). Five Large and five Small fish were captured in the south impoundment (SI).

	SL (cm)	FL (cm)	TL (cm)	HW (cm)	Mass (kg)	Max SL (cm)	Min SL (cm)	Max HW (cm)	Min HW (cm)
NI Large (n = 10)	91.5 (±6.2)	101.9 (±6.0)	106.6 (±8.5)	16.5 (±1.1)	14.1 (±2.8)	99.0	79.5	17.9	13.9
NI Small (n = 10)	66.3 (±4.1)	75.5 (±4.1)	79.9 (±4.3)	11.3 (±1.0)	5.2 (±1.1)	71.0	58.0	12.7	9.4
SI Large (n = 5)	90.1 (±8.9)	100.1 (±9.9)	104.9 (±10.9)	15.5 (±1.4)	12.6 (±2.8)	99.0	80.0	17.3	13.8
SI Small (n = 5)	61.9 (±5.8)	69.9 (±5.9)	74.0 (±5.4)	10.3 (±1.0)	4.5 (±0.9)	70.0	56.0	11.9	9.2
All Large (n = 15)	91.0 (±6.9)	101.3 (±7.3)	106.0 (±8.9)	16.2 (±1.3)	13.6 (±2.8)	99.0	79.5	17.9	13.8
All Small (n = 15)	64.8 (±4.9)	73.6 (±5.3)	77.9 (±5.3)	10.9 (±1.1)	4.9 (±1.1)	71.0	56.0	12.7	9.2

Individual fish detections were plotted over time with 26 fish actively moving within the array (Figure 4). Four tagged fish in the north impoundment were not detected and were not included in statistical analyses. Results from acoustic telemetry data indicate the majority (92%) of large size class fish (i.e., those with a head width greater than 13 cm) remained within the impoundment in which they were captured. The only large size-class fish to be detected in both the northern and southern impoundments had a head width of 13.8 cm, which is less than the mean spacing between bollards, 16.0 (±3.4) cm. Data indicate small fish (i.e., those with a head width less than 13 cm) were able to pass freely through the bollards and utilized waters in the north and south impoundments and the adjacent Banana River (Figure 4).

Temperature and DO concentration were collinear, and thus no models included both variables (Table A2). DO concentration was identified as the single most important abiotic variable to determine the core use home range size (KDE 50%), while water temperature was the single most important abiotic variable to determine the extent of use home range size (KDE 95%; Table A2). As DO levels increased, fish core use area decreased (Figure A3). As water temperature increased, fish extent of use also increased. Core use area was best described by the interactive model of DO concentration and salinity.

(a) (b)

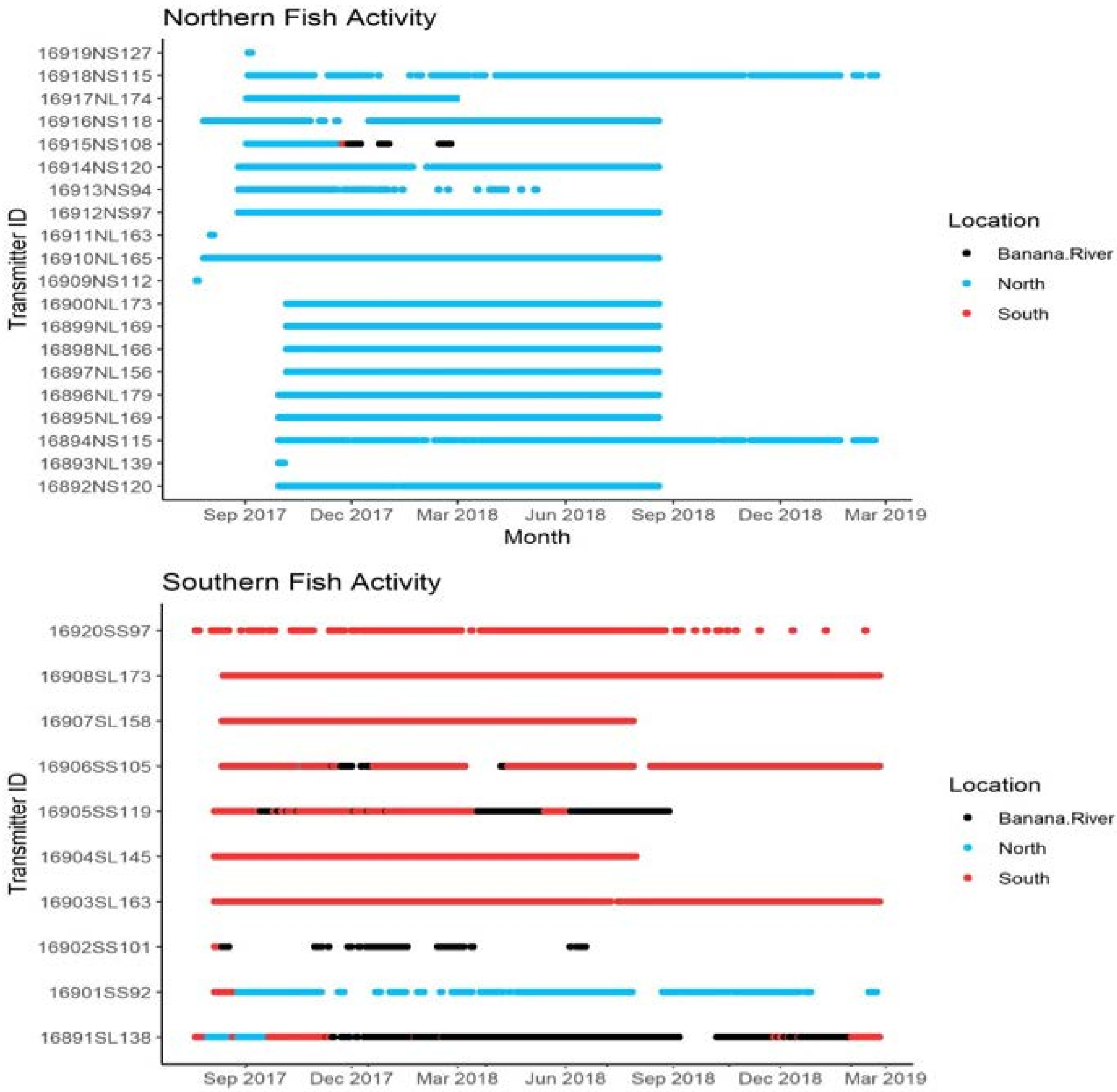

Figure 4. Abacus plot of individual fish captured in ITL impoundments activity over time. Detections in black represent Banana River receivers, blue points represent north impoundment receivers, and red points represent south impoundment receivers. Numbers following transmitter ID represent size class and individual head width measurements (cm); (**a**) Represents fish captured within the northern ITL impoundment. (**b**) Represents fish captured within the southern ITL impoundment.

Extent of use area was best described by the interactive model of water temperature and pH; there were incremental gains in model predictive ability by also including the interactive effect of either water depth, wind speed, or salinity.

The mean (±sd) daily distance traveled by large fish (2913.0 ± 1871.4 m) was greater than distances traveled by small fish (1647.7 ± 1572.0 m). DO concentration class was the most important abiotic variable to explain daily distance traveled by fish within the array. Mean fish daily distance traveled increased from 2745.3 (±1721.3) m in normoxic conditions to 3304.7 (±1154.3) m when dissolved oxygen concentration reached anoxic levels. Daily distance traveled was best described by the interactive model of DO concentration class, temperature, and pH.

3.3. Fish Response to Hypoxia

During the hypoxia-related fish kill, fourteen tagged fish present within the north ITL impoundment were exposed to hypoxic and anoxic conditions for a period of eleven days. Immediately after the fish kill event occurred, 9 acoustic tags were recovered from carcasses along the shoreline using a metal detector. Three additional individuals were presumed to have died due to continuous detections on a single acoustic receiver for four consecutive weeks with no movement; acoustic data indicate two small individuals in the north impoundment survived the hypoxic event (Figure 4).

Fish core use and extent of use areas were greatly reduced when DO levels dropped to anoxic levels (i.e., $\leq$0.5 mg/L; Figure 5). Mean ($\pm$sd) core use area (50% KDE) decreased from 8.2 ($\pm$3.4) ha in normoxic conditions to 4.2 ($\pm$3.2) ha in anoxic conditions (One-way ANOVA: (F (2,39) = 6.80; p = 0.002); post hoc Tukey HSD p = 0.006). Similarly, extent of use area (95% KDE) decreased greatly from 29.1 ($\pm$13.4) ha in normoxic conditions to 1.6 ($\pm$1.6) ha in anoxic conditions (One-way ANOVA: (F (2,39) = 34.41; $p < 0.001$); post hoc Tukey HSD $p < 0.001$).

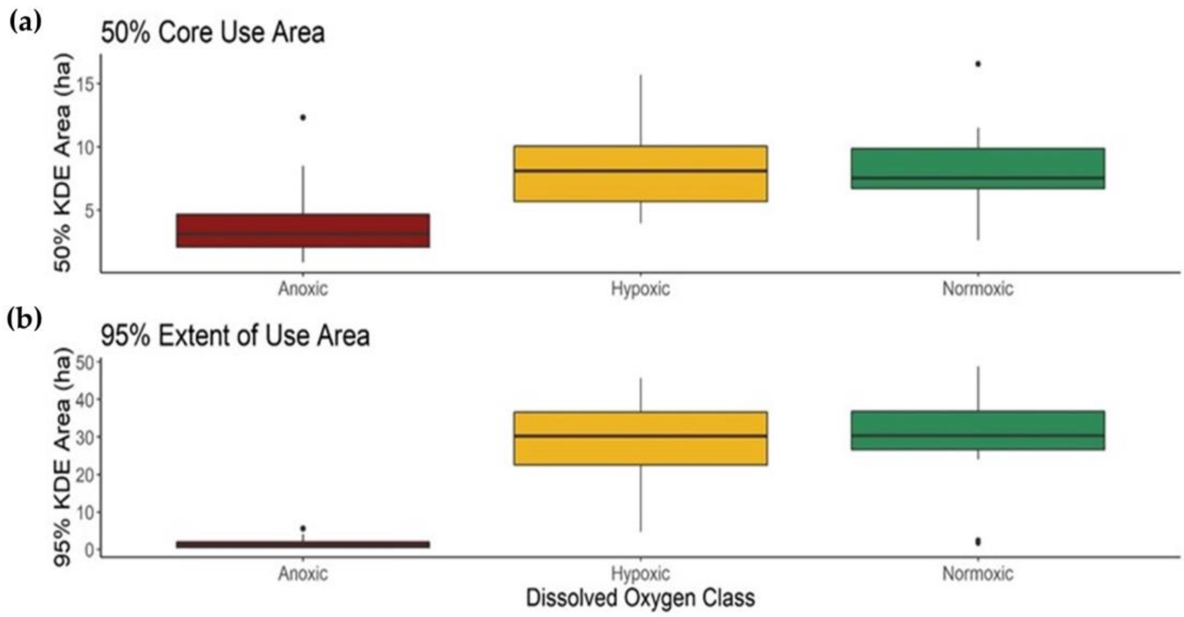

Figure 5. Fish habitat use area was reduced in periods of anoxia; (**a**) Boxplots represent range and median values and quartiles (5th, 25th, 75th, and 95th) of fish core use (50% KDE) area (ha) per dissolved oxygen concentration class. Dots represent outliers. (**b**) Range and median values and quartiles (5th, 25th, 75th, and 95th) for fish extent of use (95% KDE) area (ha) per dissolved oxygen concentration class.

Daily distance traveled was statistically lower in anoxic waters than in hypoxic and normoxic waters (One-way ANOVA: (F (2,1968) = 6.80; $p < 0.001$); post hoc Tukey HSD p = 0.02). Mean ($\pm$sd) fish movement was higher during hypoxic conditions than during anoxic periods (Normoxic: 2572.1 $\pm$ 1105.5 m; hypoxic: 2896.0 $\pm$ 814.4 m; anoxic: 715.0 $\pm$ 395.4 m; Figures 6a and A3). Fish rate of movement also was lower in anoxic waters as compared to hypoxic and normoxic waters (Normoxic: 2.5 ($\pm$1.0) m/s; Hypoxic: 2.5 ($\pm$0.7), Anoxic: 2.1 ($\pm$1.1) m/s; One-way ANOVA: (F (2,1968) = 36.63; $p < 0.001$); post hoc Tukey HSD: 0.003; Figure 6b). Furthermore, across all DO concentrations, there was an inverse relationship between dissolved oxygen concentration and the distance traveled by a fish each day (Figure A3).

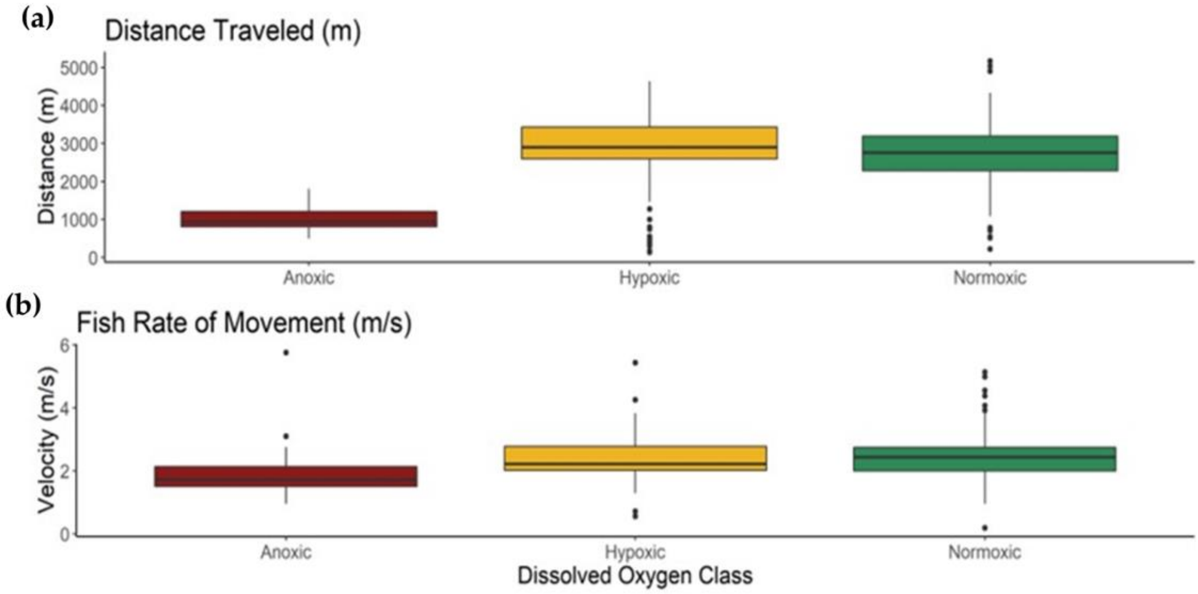

Figure 6. Fish distance traveled (**a**) and rate of movement (**b**) was lower during periods of anoxia; (**a**) Boxplots represent range and median values and quartiles (5th, 25th, 75th, and 95th) for daily distance traveled (m) per dissolved oxygen concentration class. Dots represent outliers. (**b**) Boxplots represent range and median values and quartiles (5th, 25th, 75th, and 95th) for rate of movement (m/s) per dissolved oxygen concentration class.

4. Discussion

4.1. Fish Movement and Habitat Use

The primary objective of this study was to explore how barriers to dispersal, specifically bollards restricting access to culverts, impacted the movement of red drum. Related to this objective, our specific hypothesis was that larger individuals (i.e., those with head widths greater than 13 cm) would not be able to pass through the bollards unimpeded. The results from this study support this hypothesis as only one large individual passed through the bollards into the south impoundment (head width was 13.8 cm, which was less than the mean spacing among bollards). Therefore, bollards do appear to impede the movement of red drum with head widths greater than the mean spacing between bollards, and management actions are required to improve fish passage through culverts in the study region. However, relatively small fish are able to leave the ITL impoundments, with three returning to the study area at a later date. These results support the earlier contention that the ITL impoundments are essential fish habitat and may be a spawning location for these fish [42]. Furthermore, these results support the findings of previous studies that have shown small culverts and water structures reduce fish movement by disrupting seascape connectivity [60,61]. However, the culverts in this study were approximately 2 m wide, which would in theory allow for the passage of the largest fish captured in this study. The addition of bollards around the entrance to the culverts created an additional impediment and a much smaller space for fish passage and may have hindered the ability of larger fish to pass from one impoundment to another. Due to the occurrence of the hypoxia-related fish kill and the reduction in population within the study area, it was not possible to quantify the exact fish size the exclusion bollards impede. Future experimental studies could help to identify the head width or body size of fish negatively impacted by the use of manatee exclusion devices.

Similarly, from a methodological standpoint, there were some constraints that limited the ability to estimate all fish movement. Using the mean weighted approach of estimating center of activity (COA), fish must be detected within range of multiple receivers in order for a meaningful COA to be identified. In the case of fish captured within the south impoundment, all COAs were estimated to be between the two receivers present, unless they were found to be moving between the impoundments or into the adjacent Banana River where they were captured by additional receivers. This caveat limits the KDE estimates and the distance traveled calculations for fish in the south impoundment, and therefore, comparisons between the north impoundment and south impoundment fish were not possible. The array configuration within the north impoundment alleviates this issue as all fish were detected among multiple receivers over the course of this study.

In many estuaries, seagrass serves as settlement and nursery habitat for red drum [62–64]. As much of the IRL has experienced loss of seagrass habitat, the northern ITL impoundment may be one of the few remaining areas with intact seagrass beds [65,66]. Most fish within the north impoundment had high residency along the eastern and southern perimeter of the impoundment, which coincide with areas of higher relative seagrass coverage within the study domain, suggesting red drum utilize seagrass beds as critical fish habitat within the study region [43].

4.2. Red Drum Movement in Response to Hypoxia

Fish movement and habitat use area were impacted by both physical constrictions and environmental parameters. With rare exception, large fish captured in the ITL impoundments did not move between the bollards/impoundments, effectively limiting the habitat available to them, and thus, the maximum habitat available for use. Models assessing how environmental changes impact fish habitat use (i.e., 50% and 95% KDE area) and movement (i.e., daily distance traveled) indicate individual fish behavior along with DO concentration and temperature were the primary environmental variables influencing habitat use and fish movement. When DO levels decreased and water temperatures increased, fish KDE home ranges area decreased. This suggests that as fish are exposed to higher temperatures and decreased DO concentrations, their habitat area may be reduced to areas where DO concentrations are greater. However, as hypoxic areas within a water body can act as a chemical barrier to fish movement, this can have a concentrating effect on fish within the ITL as fish are corralled into remaining areas with relatively high DO levels in their efforts to avoid areas with low DO [8,20]. This further reduces habitat availability, while increasing the per unit area respiratory demand for DO by a greater number of fish inhabiting a smaller area as was seen in the reduction in KDE area size as DO decreased.

Short-term exposure to hypoxia (i.e., when DO levels decreased to hypoxic levels, but returned to normoxic conditions within ~12 h) resulted in a rapid increase in fish movement, suggesting fish may be searching for waters with higher concentrations of DO as DO begins to decrease in the water column. Similar increases in movement as waters became hypoxic have been observed in Atlantic Cod (*Gadus morhua*), Atlantic Croaker (*Micropogonias undulatus*), Weakfish (*Cynoscion regalis*), Southern Flounder (*Paralichthys lethostigma*), and other demersal fishes, and have been attributed to an initial avoidance reaction [67–72]. Red drum minimum oxygen tolerance levels are highly correlated with fish mass, with larger fish requiring higher DO levels to maintain standard metabolic function [9], and, on average, red drum survival dramatically decreases in hypoxic waters [73]. Perez-Dominguez et al. [74] found red drum larval survival and growth was lower in relatively warm low DO waters, and individuals actively avoided low DO waters. Results of this study add to these earlier works, suggesting individuals increase rates of movement throughout the available habitat at the onset of hypoxic conditions, to potentially locate waters with higher concentrations of DO.

When fish were exposed to prolonged periods of hypoxia, movement was significantly reduced, especially as waters became anoxic during the August 2018 fish kill event. The combination of decreased habitat use (i.e., KDE size) and reduced movement suggests that decreasing movement and metabolic function as waters remain hypoxic enables fish to reduce oxygen consumption and increase probability of survival [18]. The two red drum that survived the hypoxic event were smaller individuals (67 cm and 69 cm SL, respectively), which may have survived due to lower metabolic demands than larger fish. Of note, a third small individual originally captured in the south impoundment moved into the north impoundment for several months, was not detected on any receiver during the hypoxic event, then "reappeared" within the northern impoundment following the hypoxic event (Figure 4). Given the constraints in the movement and detection data, it is impossible to deduce precisely why these individuals survived, but for the majority of individuals, reduced values in KDE and distance traveled during the anoxic period were precursors to fish mortality events. Movement detected during and after the relatively prolonged anoxic periods were potentially the result of fish drifting along the surface after death until they came to rest on the shoreline or detections may have been caused by transmitters sinking to the bottom between two receivers resulting in apparent detections of movement, before being removed during false detection analyses. Ultimately, we can surmise the prolonged exposure to hypoxic and anoxic concentrations, combined with the inability of fish to move to waters with more oxygen, proved fatal to most red drum included in this study.

4.3. Management Strategies

In this study, bollards were shown to potentially act as a man-made barrier to fish movement, effectively interrupting fish migrations, dispersal, and hindering fish ability to avoid lethal water conditions. The growth of encrusting organisms on the bollards further reduced the spacing between bollards at a relatively rapid pace (i.e., 0.5 ($\pm$0.3) cm per month during summer and 0.1 ($\pm$0.1) cm per month during winter) [43]. Fish with head widths greater than the mean spacing size of fouled bollards did not move through the manatee exclusion devices. This indicates the bollard spacing is not wide enough to allow the passage of large fish through these devices. In the case of the acute hypoxic/anoxic event in August 2018, the bollards may have contributed to the high fish mortality by effectively trapping them within lethal water conditions While it is not possible to verify this due to the unplanned nature of the hypoxic event documented here, if bollards were not present, larger individuals may have been able to pass through the culverts and move into waters with higher dissolved oxygen levels increasing survival probability.

The shallow waters and lack of water flow within the impoundments make this habitat prone to reduced DO levels, especially as water temperatures rise in the summer [75]. Additional hypoxia influenced fish mortality events have occurred at the ITL impoundments in 2020 and 2022 (E. Reyier, personal communication). In response to these additional fish kills, environmental managers at CCSFS have used data from this study to plan and begin implementation of improvements to the ITL impoundments in order to increase hydrologic connectivity, thereby reducing the probability of future hypoxic events occurring. Furthermore, improvements in the routine maintenance of the bollard area have been initiated, including increased frequency in the removal of biofouling organisms and dredging of sediment from the culverts and bollard area. This has restored water flow to the impoundments allowing for an improvement in water quality and maximal spacing between bollards for fish passage.

As the impoundments are currently designed, the only connection to the IRL proper is via culverts on the south side of the south ITL impoundment connecting to the Banana River and onto the IRL. CCSFS is exploring the possibility of installing additional bollard-free culverts on the northern end of the north impoundment, creating an additional egress point that would simultaneously improve water flow and facilitate fish dispersal. Other areas immediately outside of the impoundments are commonly used by protected species, such as manatees and bottlenose dolphins. If the culverts connecting the ITL impoundments to the Banana River were expanded to a size large enough to allow manatee passage, the ability of almost all marine organisms, including protected species, such as green sea turtles, to access this habitat would be unhindered. Alternatively, to reduce the compounding effect of sedimentation near culverts, full removal of the bollards would increase the ecological connectivity and hydrodynamic flow of this area. Previous studies have found management strategies that restore coastal habitat and reconnect impoundments to the broader estuary benefit lower and higher trophic level fishes and macro-invertebrates thereby increasing species abundance and diversity, improving water quality, and restoring pre-impoundment vegetation communities. [6,24,26,30,76,77]. By increasing the number or size of ingress/egress points to the IRL, fish ecological connectivity, access to critical fish habitat, and water hydrodynamics could be improved. If the ITL impoundments were reopened to the lagoon proper through large culverts or creation of small relief bridges it would increase access to what was historically 1300 acres of seagrass habitat and remove barriers to fish or other marine organism connectivity. Ultimately, these management actions could improve the quality of habitat for the fish community within the existing ITL impoundments and decrease the probability of future fish kill events.

5. Conclusions

Acoustic telemetry was used to quantify movement patterns and habitat use of red drum to explore how the presence of culverts and bollards, and a hypoxia-related mortality event impacted fish movement. Artificial structures have a size limiting effect on the ability of relatively large fish to navigate between water bodies, both in normal circumstances and during hypoxic events. Dissolved oxygen concentrations were shown to have large impacts on red drum home range area and daily distance traveled. These findings suggest prolonged exposure to low dissolved oxygen in combination with artificial structures can reduce movement of red drum, increase risk of mortality, and decrease habitat connectivity. In the future, improved maintenance of culvert and bollard areas, including sediment and biofouling removal, expansion of culvert sizing or bollard spacing, and/or the installation of relief bridges or larger box culverts can reduce the likelihood of additional fish mortality events occurring. Together these management strategies may effectively improve water circulation, increase habitat connectivity, and facilitate movement of larger fishes into and out of currently restricted waterbodies, thus moving this recreationally important population of sportfish toward sustainability.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A. Home Range Areas

Table A1. Monthly and total home range areas (50% KDE and 95% KDE) of individual fish were calculated using COA estimates and a reference bandwidth method.

Fish ID	Date	h Value	Points	50% KDE Area (ha)	95% KDE Area (ha)
16891SL138	9/2017	30.67	295	1.36	5.31
16891SL138	10/2017	42.78	1288	3.73	19.59
16891SL138	11/2017	44.44	1166	4.92	18.89
16891SL138	12/2017	32.92	1343	2.15	8.23
16891SL138	1/2018	76.02	340	5.68	7.30
16891SL138	2/2018	33.82	907	1.34	6.44
16891SL138	3/2018	18.58	1071	0.17	1.63
16891SL138	4/2018	35.39	1034	0.57	3.02
16891SL138	5/2018	22.02	775	0.46	2.57
16891SL138	6/2018	106.95	550	5.91	31.57
16891SL138	7/2018	47.61	813	1.90	11.15
16891SL138	8/2018	24.91	1026	1.14	4.79
16891SL138	9/2018	61.00	620	3.40	18.04
16891SL138	Total	58.60	11,384	6.34	35.32
16892NS120	9/2017	67.94	27	5.10	15.00
16892NS120	10/2017	48.15	981	3.93	28.25
16892NS120	11/2017	61.71	768	8.37	35.90
16892NS120	12/2017	59.90	765	7.49	29.97
16892NS120	1/2018	67.45	451	6.68	27.07
16892NS120	2/2018	50.91	582	1.95	15.38
16892NS120	3/2018	4.06	562	0.01	0.04
16892NS120	4/2018	34.39	556	0.84	13.77
16892NS120	5/2018	41.27	907	2.35	16.86
16892NS120	6/2018	47.23	1153	7.38	26.62
16892NS120	7/2018	50.88	1134	8.36	30.50
16892NS120	8/2018	59.78	742	10.86	36.48
16892NS120	Total	37.78	8628	4.93	25.18
16894NS115	9/2017	102.43	21	10.72	24.84
16894NS115	10/2017	79.48	380	6.73	14.75
16894NS115	12/2017	72.12	215	12.04	39.62
16894NS115	1/2018	55.67	187	5.58	28.62
16894NS115	2/2018	51.74	82	2.69	18.52
16894NS115	3/2018	54.49	170	4.32	22.51
16894NS115	4/2018	46.67	286	4.89	22.71
16894NS115	5/2018	77.59	356	11.36	40.36
16894NS115	6/2018	65.60	403	9.35	36.46
16894NS115	7/2018	62.81	521	9.69	34.60
16894NS115	8/2018	78.94	247	10.20	34.26
16894NS115	9/2018	74.97	217	9.25	34.06
16894NS115	10/2018	100.15	90	14.14	44.24
16894NS115	Total	52.97	3244	10.48	34.11
16895NL169	9/2017	78.69	23	5.82	17.18
16895NL169	10/2017	52.68	1248	5.81	30.41
16895NL169	11/2017	56.50	1114	9.53	33.92
16895NL169	12/2017	55.65	1232	10.79	33.29
16895NL169	1/2018	63.51	828	9.94	32.96
16895NL169	2/2018	61.29	981	10.20	34.31
16895NL169	3/2018	61.61	843	9.05	31.92
16895NL169	4/2018	60.19	821	10.67	34.44
16895NL169	5/2018	56.98	930	8.98	33.69
16895NL169	6/2018	44.02	1157	4.56	22.65
16895NL169	7/2018	45.90	1220	6.64	27.08
16895NL169	8/2018	58.27	748	10.26	34.86

Table A1. *Cont.*

Fish ID	Date	h Value	Points	50% KDE Area (ha)	95% KDE Area (ha)
16895NL169	Total	39.58	11,145	8.82	28.37
16896NL179	9/2017	116.55	12	12.92	14.29
16896NL179	10/2017	52.44	1155	6.03	32.48
16896NL179	11/2017	56.06	1073	10.07	33.57
16896NL179	12/2017	55.67	1155	10.72	34.36
16896NL179	1/2018	65.91	774	11.27	36.98
16896NL179	2/2018	61.48	940	12.27	36.38
16896NL179	3/2018	62.26	1048	11.16	35.55
16896NL179	4/2018	69.65	844	11.43	38.85
16896NL179	5/2018	60.53	983	9.58	33.08
16896NL179	6/2018	55.84	1194	8.56	33.33
16896NL179	7/2018	52.01	1214	8.16	32.35
16896NL179	8/2018	55.46	725	9.63	33.77
16896NL179	Total	40.35	11,117	9.67	29.02
16897NL156	10/2017	62.02	800	7.94	34.78
16897NL156	11/2017	57.24	647	6.99	30.01
16897NL156	12/2017	51.82	516	6.36	24.78
16897NL156	1/2018	70.57	422	9.00	34.89
16897NL156	2/2018	80.79	420	10.12	37.65
16897NL156	3/2018	68.87	432	9.45	34.70
16897NL156	4/2018	66.49	455	8.26	36.37
16897NL156	5/2018	44.97	823	3.46	21.41
16897NL156	6/2018	35.14	1042	2.91	14.17
16897NL156	7/2018	41.41	1002	3.49	20.17
16897NL156	8/2018	60.85	726	10.25	36.19
16897NL156	Total	41.32	7285	5.68	27.66
16898NL166	10/2017	57.67	838	6.97	30.02
16898NL166	11/2017	57.09	664	5.67	25.37
16898NL166	12/2017	54.02	749	4.79	25.36
16898NL166	1/2018	62.42	781	10.23	37.66
16898NL166	2/2018	52.12	741	6.30	27.94
16898NL166	3/2018	53.91	696	6.17	29.36
16898NL166	4/2018	55.32	649	5.82	30.31
16898NL166	5/2018	42.10	1040	4.48	20.87
16898NL166	6/2018	42.07	1131	6.28	23.40
16898NL166	7/2018	41.09	1253	4.84	20.91
16898NL166	8/2018	53.71	788	7.34	28.50
16898NL166	Total	37.11	9330	5.63	25.11
16899NL169	10/2017	58.59	1089	7.00	29.21
16899NL169	11/2017	51.32	1285	5.76	25.50
16899NL169	12/2017	51.21	1427	6.96	27.83
16899NL169	1/2018	60.88	1222	11.76	37.06
16899NL169	2/2018	61.78	1194	9.81	35.43
16899NL169	3/2018	54.16	1259	8.20	31.82
16899NL169	4/2018	54.23	1069	8.41	30.16
16899NL169	5/2018	56.51	1251	8.70	29.72
16899NL169	6/2018	49.25	1293	7.12	28.11
16899NL169	7/2018	46.93	1353	7.17	26.04
16899NL169	8/2018	52.06	783	9.13	30.57
16899NL169	Total	37.78	13,225	8.14	26.12
16900NL173	10/2017	47.23	1143	3.31	19.21
16900NL173	11/2017	60.51	1213	8.43	34.71
16900NL173	12/2017	52.41	1370	5.87	29.14
16900NL173	1/2018	65.54	944	8.13	33.04
16900NL173	2/2018	57.61	1120	6.71	29.20
16900NL173	3/2018	59.27	1115	8.15	32.43
16900NL173	4/2018	61.04	914	9.02	31.48

Table A1. *Cont.*

Fish ID	Date	h Value	Points	50% KDE Area (ha)	95% KDE Area (ha)
16900NL173	5/2018	50.75	1020	5.93	24.82
16900NL173	6/2018	37.43	1248	3.11	13.85
16900NL173	7/2018	38.30	1253	3.83	19.34
16900NL173	8/2018	58.57	780	9.45	34.39
16900NL173	Total	39.64	12,120	6.86	27.52
16901SS92	10/2017	36.58	862	2.31	9.89
16901SS92	11/2017	53.69	136	4.04	17.60
16901SS92	12/2017	36.58	54	2.08	8.06
16901SS92	2/2018	36.21	106	1.13	9.92
16901SS92	4/2018	44.07	75	1.49	8.43
16901SS92	5/2018	76.96	101	7.25	17.93
16901SS92	6/2018	35.36	381	2.13	11.39
16901SS92	7/2018	42.39	848	3.59	19.25
16901SS92	8/2018	47.92	540	4.61	26.42
16901SS92	Total	58.16	3715	8.70	34.58
16902SS101	10/2017	84.07	894	4.36	40.44
16902SS101	Total	84.07	894	4.36	40.44
16903SL163	10/2017	33.15	964	1.81	7.56
16903SL163	11/2017	31.91	1175	1.86	3.79
16903SL163	12/2017	21.75	1291	0.39	2.89
16903SL163	1/2018	15.20	1082	0.10	1.17
16903SL163	2/2018	4.52	902	0.01	0.07
16903SL163	3/2018	16.98	1272	0.16	1.62
16903SL163	4/2018	5.80	906	0.01	0.07
16903SL163	5/2018	7.21	997	0.02	0.14
16903SL163	6/2018	11.13	824	0.06	0.55
16903SL163	7/2018	6.08	586	0.02	0.07
16903SL163	8/2018	25.49	216	0.30	2.65
16903SL163	9/2018	10.52	841	0.05	0.48
16903SL163	10/2018	12.23	1020	0.07	0.82
16903SL163	Total	15.81	12,076	0.17	2.28
16904SL145	10/2017	38.43	878	2.35	3.69
16904SL145	11/2017	32.89	769	0.81	3.38
16904SL145	12/2017	33.92	862	0.90	3.38
16904SL145	2/2018	39.52	819	1.70	3.44
16904SL145	3/2018	38.28	920	1.53	3.60
16904SL145	4/2018	34.33	696	1.14	3.25
16904SL145	5/2018	27.12	1148	0.73	4.47
16904SL145	6/2018	21.83	1209	0.45	3.07
16904SL145	7/2018	26.64	1382	0.92	4.56
16904SL145	8/2018	39.96	810	1.79	3.38
16904SL145	Total	24.55	10,288	0.90	2.70
16905SS119	10/2017	32.35	937	2.02	7.66
16905SS119	11/2017	58.95	1253	6.09	13.41
16905SS119	12/2017	43.03	1017	3.20	12.31
16905SS119	1/2018	38.73	894	2.10	10.19
16905SS119	2/2018	28.84	1032	1.09	6.03
16905SS119	3/2018	22.86	1204	0.83	3.88
16905SS119	4/2018	35.33	916	1.30	8.02
16905SS119	5/2018	19.72	612	0.38	1.94
16905SS119	6/2018	61.36	1216	5.19	11.95
16905SS119	7/2018	48.59	1236	2.27	16.73
16905SS119	8/2018	27.77	1257	1.07	2.28
16905SS119	9/2018	44.29	587	2.15	10.50
16905SS119	Total	38.11	12,161	3.52	16.70
16906SS105	10/2017	29.45	743	1.33	3.11
16906SS105	11/2017	30.02	1079	1.46	3.83
16906SS105	12/2017	27.45	1267	1.40	6.05

Table A1. *Cont.*

Fish ID	Date	h Value	Points	50% KDE Area (ha)	95% KDE Area (ha)
16906SS105	1/2018	96.14	426	11.05	49.08
16906SS105	2/2018	45.29	1027	2.74	16.24
16906SS105	3/2018	27.58	1195	1.22	5.03
16906SS105	4/2018	41.26	535	2.67	3.63
16906SS105	5/2018	64.26	672	5.04	23.31
16906SS105	6/2018	27.95	1202	1.30	5.24
16906SS105	7/2018	37.87	1271	2.59	3.52
16906SS105	8/2018	44.99	691	2.73	3.56
16906SS105	9/2018	20.39	896	0.49	2.22
16906SS105	10/2018	10.06	759	0.05	0.54
16906SS105	Total	29.13	11,763	2.06	8.94
16907SL158	10/2017	35.92	733	1.94	3.71
16907SL158	11/2017	37.14	797	1.90	3.78
16907SL158	12/2017	38.46	1201	2.50	3.43
16907SL158	1/2018	42.23	1029	2.59	3.67
16907SL158	2/2018	40.18	1052	2.71	3.47
16907SL158	3/2018	36.95	1205	2.47	3.50
16907SL158	4/2018	39.50	1060	2.62	3.52
16907SL158	5/2018	31.08	1289	1.70	3.45
16907SL158	6/2018	33.03	1280	2.13	3.75
16907SL158	7/2018	37.53	1372	2.40	3.58
16907SL158	8/2018	43.32	791	2.70	3.34
16907SL158	Total	26.42	11,809	1.75	3.24
16908SL173	10/2017	41.33	563	2.95	9.86
16908SL173	11/2017	34.70	939	1.69	3.44
16908SL173	12/2017	35.37	1166	2.10	3.83
16908SL173	1/2018	42.77	871	2.78	3.46
16908SL173	2/2018	42.72	880	2.76	3.54
16908SL173	3/2018	38.00	1053	2.36	3.79
16908SL173	4/2018	40.23	915	1.81	3.58
16908SL173	5/2018	36.83	1187	2.43	3.75
16908SL173	6/2018	32.84	1278	1.89	3.61
16908SL173	7/2018	39.08	1359	2.58	3.49
16908SL173	8/2018	36.32	1227	1.83	3.46
16908SL173	Total	25.11	13,769	1.42	5.65
16910NL165	8/2017	75.21	817	12.28	23.67
16910NL165	9/2017	60.36	1107	8.54	35.09
16910NL165	10/2017	69.03	1010	10.44	40.07
16910NL165	11/2017	49.17	810	5.21	24.28
16910NL165	12/2017	54.63	828	6.72	29.93
16910NL165	1/2018	70.00	598	10.55	36.01
16910NL165	2/2018	69.93	864	11.17	38.45
16910NL165	3/2018	75.23	922	14.35	26.72
16910NL165	4/2018	55.11	831	5.81	30.53
16910NL165	5/2018	53.46	1012	7.29	31.51
16910NL165	6/2018	65.30	981	11.45	36.38
16910NL165	7/2018	48.59	1249	6.55	26.15
16910NL165	8/2018	56.04	768	9.13	31.97
16910NL165	Total	41.58	11,842	6.97	28.53
16912NS97	8/2017	71.94	144	3.12	23.96
16912NS97	9/2017	66.14	986	7.92	31.78
16912NS97	10/2017	73.02	953	8.02	9.22
16912NS97	11/2017	23.37	814	0.55	4.49
16912NS97	12/2017	24.66	676	0.53	5.23
16912NS97	1/2018	46.17	573	1.35	16.76
16912NS97	2/2018	18.31	632	0.15	0.74
16912NS97	3/2018	34.65	504	0.62	7.79

Table A1. *Cont.*

Fish ID	Date	h Value	Points	50% KDE Area (ha)	95% KDE Area (ha)
16912NS97	4/2018	42.63	491	1.38	14.86
16912NS97	5/2018	46.09	685	2.85	17.34
16912NS97	6/2018	36.95	668	1.90	12.52
16912NS97	7/2018	33.53	1068	1.90	15.23
16912NS97	8/2018	54.38	698	5.77	29.77
16912NS97	Total	36.79	8895	2.14	21.34
16913NS94	8/2017	26.17	219	0.96	3.13
16913NS94	9/2017	79.74	425	9.75	39.29
16913NS94	10/2017	73.30	710	6.29	30.39
16913NS94	11/2017	85.02	187	3.09	7.22
16913NS94	12/2017	89.04	202	9.93	39.17
16913NS94	Total	64.41	1833	6.88	34.40
16914NS120	8/2017	35.42	215	1.59	6.52
16914NS120	9/2017	42.75	1063	3.09	14.61
16914NS120	10/2017	21.90	1297	0.49	3.40
16914NS120	11/2017	19.45	1297	0.44	2.52
16914NS120	12/2017	35.39	978	1.42	12.29
16914NS120	1/2018	64.00	256	6.25	30.61
16914NS120	2/2018	40.65	456	2.95	15.82
16914NS120	3/2018	43.66	1052	2.51	18.23
16914NS120	4/2018	41.01	1026	1.50	12.29
16914NS120	5/2018	61.18	462	4.10	18.90
16914NS120	6/2018	72.03	321	7.03	27.53
16914NS120	7/2018	61.87	360	4.89	22.83
16914NS120	8/2018	73.19	485	9.88	37.51
16914NS120	Total	30.36	9268	1.45	12.19
16915NS108	9/2017	44.87	1051	3.78	13.58
16915NS108	10/2017	52.49	1140	5.26	23.14
16915NS108	11/2017	156.66	725	21.35	132.50
16915NS108	12/2017	89.62	611	4.27	32.27
16915NS108	1/2018	16.37	33	0.24	0.72
16915NS108	2/2018	70.28	207	2.14	10.28
16915NS108	Total	220.61	3767	45.93	236.45
16916NS118	7/2017	50.42	126	4.46	14.96
16916NS118	8/2017	34.66	1275	2.31	13.35
16916NS118	9/2017	40.17	1240	3.33	14.62
16916NS118	10/2017	62.48	660	7.76	29.34
16916NS118	11/2017	56.63	64	4.32	18.20
16916NS118	12/2017	56.87	252	7.19	29.38
16916NS118	1/2018	56.38	436	8.84	28.21
16916NS118	2/2018	38.15	672	3.67	16.43
16916NS118	3/2018	46.58	416	4.28	23.06
16916NS118	4/2018	43.79	580	4.03	19.62
16916NS118	5/2018	44.03	540	3.23	17.42
16916NS118	6/2018	43.77	613	3.21	17.42
16916NS118	7/2018	37.59	939	3.25	14.89
16916NS118	8/2018	59.27	790	9.20	33.85
16916NS118	Total	32.10	8603	3.62	19.82
16917NL174	9/2017	44.73	613	3.05	19.15
16917NL174	10/2017	56.51	522	3.48	15.76
16917NL174	11/2017	45.92	403	2.11	12.10
16917NL174	12/2017	20.44	508	0.20	1.65
16917NL174	1/2018	48.46	376	1.45	11.52
16917NL174	2/2018	44.94	741	3.03	6.50
16917NL174	3/2018	29.34	534	0.44	4.37
16917NL174	Total	35.36	9878	1.60	9.24
16918NS115	9/2017	46.62	749	4.19	23.04
16918NS115	10/2017	50.21	500	3.47	18.79

Table A1. *Cont.*

Fish ID	Date	h Value	Points	50% KDE Area (ha)	95% KDE Area (ha)
16918NS115	11/2017	49.60	105	2.68	12.02
16918NS115	12/2017	39.66	52	1.34	8.61
16918NS115	1/2018	61.30	37	3.14	18.42
16918NS115	2/2018	32.84	247	1.06	9.26
16918NS115	3/2018	66.85	66	4.02	21.11
16918NS115	4/2018	58.11	156	5.32	26.21
16918NS115	5/2018	78.54	319	10.61	40.90
16918NS115	6/2018	64.81	387	9.12	36.24
16918NS115	7/2018	61.78	528	9.44	33.68
16918NS115	8/2018	81.74	237	10.74	36.28
16918NS115	9/2018	76.69	190	9.66	33.02
16918NS115	10/2018	94.66	107	12.33	42.17
16918NS115	Total	45.97	3680	7.18	29.14
16920SS97	9/2017	31.01	77	0.45	3.06
16920SS97	10/2017	55.82	106	1.46	1.55
16920SS97	1/2018	8.41	399	0.03	0.27
16920SS97	2/2018	24.71	652	0.31	3.46
16920SS97	5/2018	23.84	522	0.44	2.86
16920SS97	6/2018	23.16	781	0.30	2.93
16920SS97	7/2018	21.75	585	0.21	2.34
16920SS97	8/2018	7.71	311	0.03	0.16
16920SS97	Total	22.23	4068	0.27	3.11

Appendix B. Observations of August 2018 Fish Kill Event

Figure A1. Tens of thousands of fish died during a major localized fish kill occurring in the ITL impoundments on 19 August 2018. Photo credit: B. Ahr, E. Reyier, and S. Baker.

Appendix C. Mean Abiotic Variables

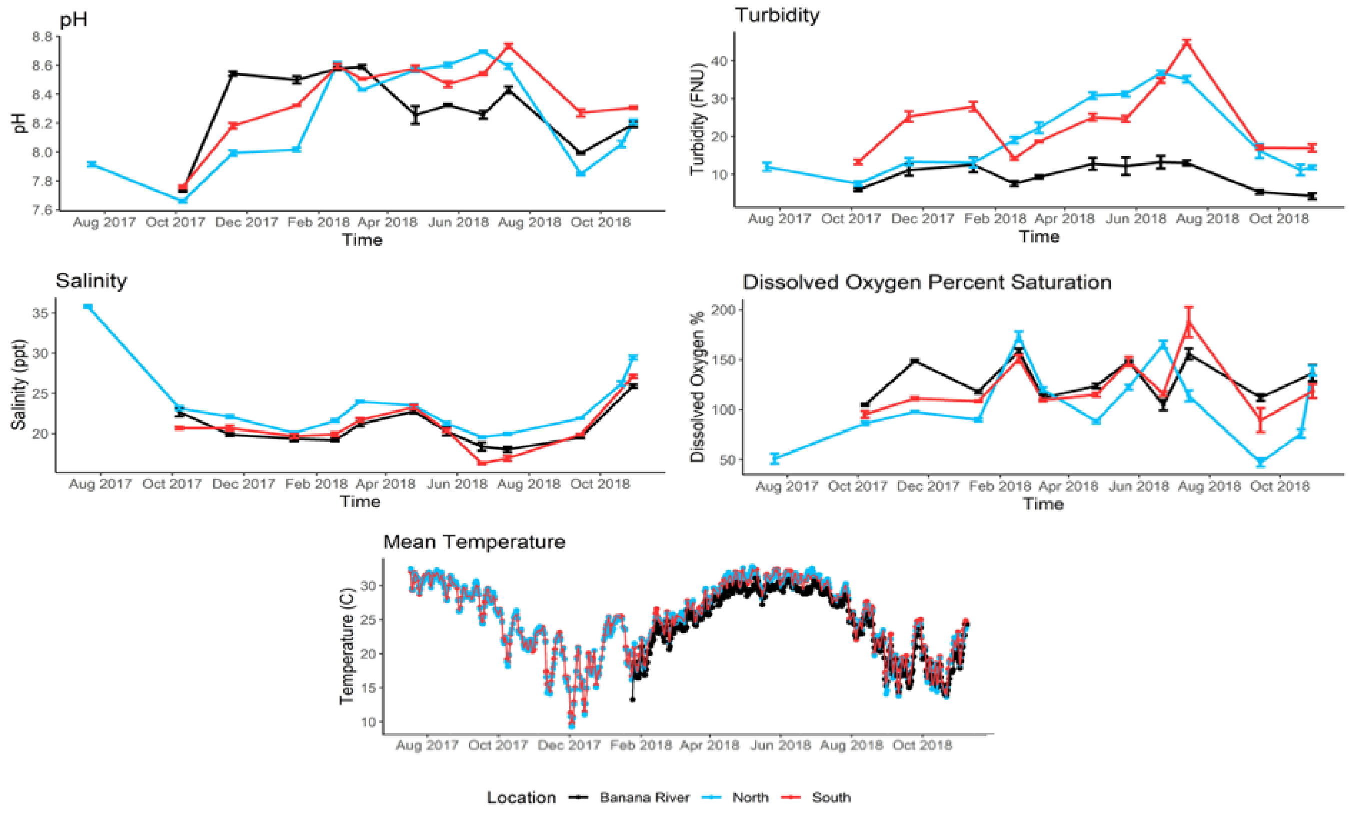

Figure A2. Mean abiotic variable values (±sd) sampled monthly throughout ITL impoundments and adjacent Banana River. Blue lines represent the northern impoundment, red line the smaller southern impoundment, and black the adjacent Banana River.

Appendix D. Statistical Models

Table A2. Generalized linear mixed effect models used to explain KDE home range areas and daily distance traveled.

	KDE 50% Home Range		
	One Environmental Variable		
Model	**Model Variables**	**AIC Score**	**Weight**
50M1	DO Concentration + (1 ǀ FishID)	649.8	0.550
50M2	Temperature + (1 ǀ FishID)	652.2	0.167
50M3	Salinity + (1 ǀ FishID)	653.1	0.107
50M4	Wind Speed + (1 ǀ FishID)	655.1	0.040
50M5	pH + (1 ǀ FishID)	655.2	0.037
50M6	Depth + (1 ǀ FishID)	655.2	0.037
50M7	Head Width + (1 ǀ FishID)	655.5	0.032
50M8	(1 ǀ FishID)	655.5	0.031
	Two Environmental Variables		
50M9	DO Concentration × Salinity + (1 ǀ FishID)	647.2	0.205
50M10	DO Concentration × Wind Speed + (1 ǀ FishID)	647.7	0.161
50M11	DO Concentration × pH + (1 ǀ FishID)	648.1	0.131
50M12	DO Concentration + pH + (1 ǀ FishID)	648.1	0.130
50M13	DO Concentration × Depth + (1 ǀ FishID)	648.2	0.130

Table A2. *Cont.*

Model	Model Variables	AIC Score	Weight
	KDE 50% Home Range		
	One Environmental Variable		
Model	**Model Variables**	**AIC Score**	**Weight**
50M14	DO Concentration + Salinity + (1 | FishID)	649.4	0.070
50M15	DO Concentration + Head Width + (1 | FishID)	649.7	0.059
50M16	DO Concentration + Wind Speed + (1 | FishID)	649.8	0.058
50M17	DO Concentration + Depth + (1 | FishID)	649.8	0.057
	Three Environmental Variables		
50M18	DO Concentration × Salinity × Wind Speed + (1 | FishID)	647.0	0.15
50M19	DO Concentration × Salinity × pH + (1 | FishID)	647.0	0.15
50M20	DO Concentration × Salinity × Depth + (1 | FishID)	647.0	0.15
50M21	DO Concentration × Salinity + Head Width + (1 | FishID)	647.2	0.14
50M22	DO Concentration × Salinity + Depth + (1 | FishID)	647.2	0.14
50M23	DO Concentration × Salinity + Wind Speed + (1 | FishID)	647.2	0.14
50M24	DO Concentration × Salinity + pH + (1 | FishID)	647.2	0.14
	All Environmental Variables		
50M25	DO Concentration + Salinity + pH + Depth + Standard Length + (1 | FishID)	647.8	1.0
50M26	DO Concentration + Salinity + pH + Depth + Standard Length	731.7	<0.001
	KDE 95% Home Range		
	One Environmental Variable		
Model	Model Variables	AIC Score	Weight
95M1	Temperature + (1 | FishID)	1024.1	0.398
95M2	Salinity + (1 | FishID)	1025.1	0.236
95M3	DO Concentration + (1 | FishID)	1025.8	0.165
95M4	pH + (1 | FishID)	1027.8	0.062
95M5	Head Width + (1 | FishID)	1028.8	0.038
95M6	Wind Speed + (1 | FishID)	1028.9	0.035
95M7	Depth + (1 | FishID)	1029.0	0.035
95M8	(1 | FishID)	1029.2	0.031
	Two Environmental Variables		
95M9	Temperature × pH + (1 | FishID)	1023.7	0.14
95M10	Temperature + pH + (1 | FishID)	1023.8	0.13
95M11	Temperature × Depth + (1 | FishID)	1023.9	0.13
95M12	Temperature × Salinity + (1 | FishID)	1023.9	0.12
95M13	Temperature + Salinity + (1 | FishID)	1023.9	0.12
95M14	Temperature × Wind Speed + (1 | FishID)	1024.0	0.12
95M15	Temperature + Wind Speed + (1 | FishID)	1024.0	0.12
95M16	Temperature + Depth + (1 | FishID)	1024.1	0.11
	Three Environmental Variables		
95M17	Temperature × pH × Depth + (1 | FishID)	1021.7	0.220
95M18	Temperature × pH × Wind Speed + (1 | FishID)	1021.7	0.220
95M19	Temperature × pH × Salinity + (1 | FishID)	1021.7	0.220
95M20	Temperature × pH + Head Width + (1 | FishID)	1023.2	0.102
95M21	Temperature × pH + Wind Speed + (1 | FishID)	1023.7	0.081
95M22	Temperature × pH + Depth + (1 | FishID)	1023.7	0.080
95M23	Temperature × pH + Salinity + (1 | FishID)	1023.7	0.078
95M24			
	All Environmental Variables		
95M25	DO Concentration + Salinity + pH + Depth + Standard Length + (1 | FishID)	1023.3	1.0
95M26	DO Concentration + Salinity + pH + Depth + Standard Length	1123.7	<0.001

Table A2. *Cont.*

Model	**KDE 50% Home Range One Environmental Variable Model Variables**	**AIC Score**	**Weight**
	Daily Distance Traveled One Environmental Variable		
Model	Model Variables	AIC Score	Weight
ATM1	DO Class + (1 ∣ FishID)	19,828.7	1.0
ATM2	Temperature + (1 ∣ FishID)	19,847.8	<0.001
ATM3	Salinity + (1 ∣ FishID)	19,912.1	<0.001
ATM4	DO Concentration + (1 ∣ FishID)	19,932.3	<0.001
ATM5	Wind Speed + (1 ∣ FishID)	20,020.4	<0.001
ATM6	Moon Phase + (1 ∣ FishID)	20,063.4	<0.001
ATM7	Depth + (1 ∣ FishID)	20,063.9	<0.001
ATM8	Head Width + (1 ∣ FishID)	20,066.3	<0.001
ATM9	(1 ∣ FishID)	20,083.0	<0.001
ATM10	pH + (1 ∣ FishID)	20,083.4	<0.001
	Two Environmental Variables		
ATM9	DO Class × Temperature + (1 ∣ FishID)	19,616.3	1.0
ATM10	DO Class + Temperature + (1 ∣ FishID)	19,707.3	<0.001
ATM11	DO Class × Wind Speed + (1 ∣ FishID)	19,710.6	<0.001
ATM12	DO Class × pH + (1 ∣ FishID)	19,729.7	<0.001
ATM13	DO Class × Salinity + (1 ∣ FishID)	19,730.1	<0.001
ATM14	DO Class + Salinity + (1 ∣ FishID)	19,748.3	<0.001
ATM15	DO Class + Wind Speed + (1 ∣ FishID)	19,771.3	<0.001
ATM16	DO Class × Depth + (1 ∣ FishID)	19,779.8	<0.001
ATM17	DO Class + pH + (1 ∣ FishID)	19,808.5	<0.001
ATM18	DO Class + Head Width + (1 ∣ FishID)	19,810.9	<0.001
ATM19	DO Class + Moon Phase + (1 ∣ FishID)	19,818.8	<0.001
ATM20	DO Class + Depth + (1 ∣ FishID)	19,823.2	<0.001
	Three Environmental Variables		
ATM21	DO Class × Temperature × pH + (1 ∣ FishID)	19,475.0	0.95
ATM22	DO Class × Temperature × Wind Speed + (1 ∣ FishID)	19,480.9	0.05
ATM23	DO Class × Temperature × Depth + (1 ∣ FishID)	19,505.3	<0.001
ATM24	DO Class × Temperature × Salinity + (1 ∣ FishID)	19,511.6	<0.001
ATM25	DO Class × Temperature + Wind Speed + (1 ∣ FishID)	19,546.5	<0.001
ATM26	DO Class × Temperature + pH + (1 ∣ FishID)	19,547.0	<0.001
ATM27	DO Class × Temperature + Moon Phase + (1 ∣ FishID)	19,596.8	<0.001
ATM28	DO Class × Temperature + Head Width + (1 ∣ FishID)	19,598.0	<0.001
ATM29	DO Class × Temperature + Depth + (1 ∣ FishID)	19,610.9	<0.001
ATM30	DO Class × Temperature + Salinity + (1 ∣ FishID)	19,616.3	<0.001
	All Environmental Variables		
ATM31	Temperature + DO Class + Salinity + pH + Standard Length + Wind Speed + Moon Phase + (1 ∣ FishID)	19,511.1	1.0
ATM32	Temperature + DO Class + Salinity + pH + Standard Length + Wind Speed + Moon Phase	20,106.6	<0.001

Appendix E. Daily Distance Traveled as a Function of Dissolved Oxygen Concentration

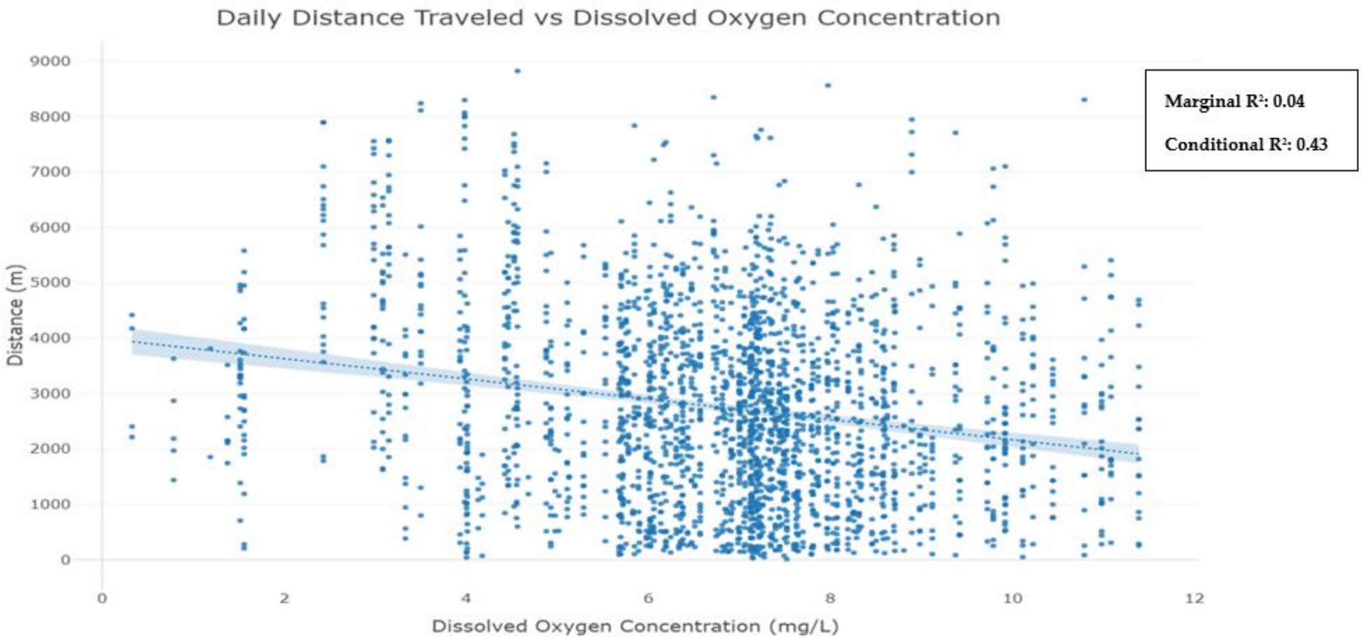

Figure A3. Linear model of daily distance traveled as a function of dissolved oxygen concentration.

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