Chapter 10
Comparing Default Movement Algorithms for Individual Fish Avoidance of Hypoxia in the Gulf of Mexico

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Abstract The northern Gulf of Mexico is the site of one of the largest areas of seasonal, coastal hypoxia (up to 22,000 km^2). Hypoxia can have both direct and indirect effects on fish. Atlantic croaker (*Micropogonias undulatus*) is a good model organism for studying the effects of hypoxia on fish in the Gulf of Mexico because it is a demersal species that lives in the area where hypoxia occurs and has been studied extensively. Virtual croaker movement was examined for three algorithm groups on a two-dimensional grid encompassing the Gulf hypoxia region. The model was run for seven days using four static dissolved oxygen maps reflecting progressively increasing hypoxia severity. Individual fish movement was modeled using a particle-tracking module with outputs from a three-dimensional hydrodynamic-water quality model for the 2002 hypoxia season. The three algorithm groups included the neighborhood search for hypoxia avoidance and the random walk, Cauchy correlated random walk, or kinesis for the default behavior. The results show that the default algorithms have little effect on hypoxia exposure of individual fish, but affect sinuosity (wiggle in fish path). The variables to consider when choosing between the three default algorithms are time step, dispersal, and the effects of stressors other than hypoxia. This study emphasizes the need to acquire suitable data for calibration of fish movement models that are presently not available for the northern Gulf of Mexico.

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10.1 Introduction

The Louisiana–Texas (La-Tex) shelf is the location of one of the largest areas of seasonal, coastal hypoxia (up to 22,000 km^2) (Rabalais et al. 2007). For the Gulf of Mexico (GOM), hypoxia is defined as dissolved oxygen (DO) concentrations less than 2 mg/L (Rabalais et al. 2001). Hypoxia generally occurs from April through October at depths of 5–60 m and can stretch from the Birdfoot delta to the La-Tex border (Turner and Rabalais 1991). Stratification of the water column and surface primary productivity contribute to the formation of hypoxia (Justic et al. 2007). Stratification occurs during the spring and summer on the La-Tex shelf due to the spring floods of the Mississippi and Atchafalaya rivers, regional circulation, and seasonal weather patterns (Rabalais et al. 2001, 2002). Stratification can be broken down by water column mixing caused by cold fronts during late fall to early spring or by tropical cyclone activity during summer and fall. Organic matter that sinks below the pycnocline and decomposes leads to reduced oxygen levels that cannot be replenished quickly due to high stability of the water column (Justic et al. 1996; Rabalais et al. 2002). Primary production is strongly influenced by riverine nutrient loading (Justic et al. 1993).

The areal extent and severity of hypoxia have increased over the past century along with the increase in riverine nutrient concentrations (Turner and Rabalais 1991). The analyses of hypoxia proxies in sediment cores indicate that hypoxia began to appear in the 1900s and started to intensify during the 1940–1950s (Rabalais et al. 2002). Hindcasts from several hypoxia models suggest that widespread hypoxia first developed in the 1970s (Justic et al. 2002; Scavia et al. 2004). Since hypoxia monitoring program carried out by Louisiana Universities Marine Consortium (LUMCON) started in 1985, the extent of hypoxia has remained highly variable. However, a significant increase in hypoxic layer thickness was observed (Obenour et al. 2013).

Hypoxia can have both direct and indirect effects on fish. Hypoxia exposure can lead to increased mortality, decreased fecundity, decreased growth, and changes in movement (Rabalais et al. 2001). Direct mortality can occur if fish are unable to escape from hypoxic water before being asphyxiated. Indirect effects include susceptibility to predation and reduced food availability (Thomas and Rahman 2009). By avoiding hypoxic areas, fish can be more susceptible to predation and experience reduced or suboptimal habitats (Breitburg 2002). Demersal fish are more likely to be affected by a loss of habitat than pelagic fish. Benthic feeding fish can also experience reduced food availability due to changes in numbers and species composition of benthic organisms in response to hypoxia (Rabalais et al. 2002).

Fish commonly avoid hypoxic areas, though thresholds and negative effects are species-dependent. Several species of fish and invertebrates have been shown to avoid hypoxia in the GOM and in Neuse River estuary (Eby and Crowder 2002;

Craig and Bosman 2012). While most fish avoid hypoxia, thresholds can differ among species. Importantly, fish can have different DO thresholds depending on whether the individual is acclimated to hypoxic conditions or not (Brady and Targett 2013). Avoidance can cause movement out of preferred habitats (Eby and Crowder 2002) or a mismatch with prey species with a lower threshold for hypoxia avoidance (Ludsin et al. 2009).

Atlantic croaker (*Micropogonias undulatus*) is a good model organism for studying the effects of hypoxia on fish in the GOM because it is a demersal species that lives in the area where hypoxia occurs and has been studied extensively. Croaker is a dominant member of the fish fauna caught in trawls in a region where hypoxia occurs (Baustian et al. 2009). Hypoxia has been shown to reduce the growth, survival, and fecundity of croaker and other closely related species (Rose et al. 2009). There is a large amount of previous work with croaker, including field data showing the hypoxia effects on reproduction and prey availability, laboratory experiments exposing croaker to hypoxia, and models of hypoxia avoidance and effects of hypoxia on fecundity (Baustian et al. 2009; Creekmore 2011). For example, chronic exposure to hypoxia has been shown to impair oocyte maturation and sperm motility in Atlantic croaker (Thomas and Rahman 2009). This previous work allows for model parameterization and provides some knowledge of how croaker react to hypoxia.

Models of varying levels of complexity have been used to model hypoxia in the GOM, with the more complex models with higher resolution being better suited to representing smaller scale events. Simpler models include modeling the shelf with a river model (Scavia et al. 2003) or modeling the shelf as a two-layered system (Justic et al. 1996). More complex models involve modeling the shelf as a three-dimensional (3-D) system with detailed modeling of the hydrodynamics (e.g., Hetland and DiMarco 2008; Wang and Justic 2009). Two of the 3-D models adapted to model hypoxia in the GOM are ROMS (Regional Ocean Modeling System) coupled to a NPZ model (Fennel et al. 2013) and the coupled FVCOM-WASP (Finite Volume Coastal Ocean Model—Water Quality Analysis Simulation Program) (Justić and Wang 2014). These 3-D models allow for the simulation of the conditions within the hypoxic zone with high spatial and temporal resolutions and are therefore suitable for fish movement modeling. FVCOM is an unstructured grid and open-source ocean circulation model (Chen et al. 2006). WASP is an open-source water quality model with several submodels for processes such as eutrophication (Wool et al. 2006). FVCOM and FVCOM-WASP have been used to model fish movement and hypoxia in the GOM (Justić and Wang 2014; Rose et al. 2014).

Several models have been used to study the effects of hypoxia on fish and fish movement. Models looking at the effects of hypoxia include matrix models, individual-based models (IBM), and models of the internal processes of an individual fish (Rose et al. 2009). IBMs can be used to look at fish movement and hypoxia avoidance (e.g., Creekmore 2011). Even though IBMs typically require more computational power than other model types, they have the advantage of time series (such as for hypoxia exposure) being possible to create for every fish modeled. Having the exposure time series allows for a more realistic look at the direct effects of hypoxia.

There are a number of different approaches to modeling fish and other animal movements. Various representations of random walk, including simple diffusion, have been used to describe and model animal movement (Kareiva and Shigesada 1983; Marsh and Jones 1988). The distance an animal can travel with random movement decreases with the size of the time step (Landau et al. 2013). Avoidance of adverse conditions and attraction to preferred conditions can be modeled using individual movement algorithms or by using a decision-making algorithm. Some movement types include random movement components along with avoidance and attraction components, such as run and tumble (Watkins and Rose 2013) and kinesis (Humston et al. 2004; Watkins and Rose 2013). Run and tumble and kinesis both have the animal only aware of their current environmental conditions and whether those conditions match the preferred conditions. Kinesis does have fish recall their previous heading. Because these movement algorithms have a random movement component, they are still affected by the size of the time step. Other movement algorithms, such as neighborhood search, allow fish to look at the surrounding conditions and move in the direction that is most advantageous (Watkins and Rose 2013; Rose et al. 2014). These types of movements are less affected by time steps, but can allow fish to perceive environmental conditions an unrealistic distance away from their location. Decision-making algorithms, such as those based on game theory, have also been used to allow animals to choose among different movement algorithms depending on the current conditions and memory of past conditions (Goodwin et al. 2006; Rose et al. 2014). Switching among movement types allows for the movement algorithm best suited for a situation to be used, including changing the algorithm with changing conditions.

This paper explores some of the different movement algorithms and how they affect the hypoxia exposure of individual virtual croaker. Fish movement in relation to hypoxia was modeled using a combination of output from the FVCOM-WASP model and a particle-tracking module with different movement algorithms. Three algorithm groups were tested to model fish movement in four different DO scenarios. The default algorithm, i.e., the algorithm used when the fish does not perceive hypoxia, is the main difference among the algorithm groups. The hypothesis tested was that the default algorithms do not affect hypoxia exposure of individual fish if all the fish use the same avoidance algorithm. The results of the paper will give a deeper understanding of how the algorithms tested behave in different situations. A better understanding of the algorithms allows for more effective algorithm selection and ultimately better informed management decisions.

10.2 Methods

Fish movement was examined for three algorithm groups in two dimensions (2-D) for static environmental conditions (maps of bottom DO concentration and temperature). The 2-D model and static conditions were chosen to better examine fish movement for different movement algorithms. Because the model domain is much larger horizontally than vertically (674 km from Galveston to Mobile and 3000 m deep), there is a large difference in the horizontal and vertical size of model elements for any 3-D grid. Moving a particle simultaneously in the horizontal and vertical directions is more complicated than just moving horizontally or vertically. Having the model fish move in only the horizontal direction simplifies the model while allowing for the examination of the properties of different movement algorithms. Also by using static conditions, the behavior of fish using different movement algorithms can be seen more clearly.

10.2.1 FVCOM-WASP

The coupled FVCOM/WASP model (Justić and Wang 2014) was used to model DO concentrations and temperature in the GOM. The FVCOM particle-tracking module was used to model fish movement on the same FVCOM grid. The model domain covers the coastal GOM from Mobile Bay to Galveston Bay and extends offshore up to a depth of about 300m (Wang and Justic 2009). The unstructured nature of the model grid allows for a more accurate depiction of the complex GOM coastline and higher model resolution along the coast. The model has been previously calibrated to accurately represent the circulation and stratification on the La-Tex continental shelf (Wang and Justic 2009).

Fish were modeled using the FVCOM particle-tracking module with output from the FVCOM-WASP. The particle-tracking module interpolated the DO and temperature values to the location of each individual fish using the piecewise linear algorithm employed in the FVCOM. Scenarios were created by taking output from the FVCOM-WASP model for 2002, namely for May 2 (06:00), June 4 (06:00), July 23 (17:00), and September 21 (17:00). These dates and times were chosen because they depict progressively worsening hypoxic conditions in the GOM, here denoted as normoxia (May 2), mild hypoxia (June 4), intermediate hypoxia (September 21), and severe hypoxia (July 23). The May 2 scenario represented conditions before the onset of hypoxia, and the June 4 conditions represented the onset of hypoxia. During late July, the combination of primary production driven by riverine nutrients and strong water column stratification typically results in the maximum extent of hypoxia (Rabalais et al. 2007), which was represented by the July 23 scenario. Water column mixing can cause hypoxia to break up and then reform. The September 21 scenario was representative of such a breakup and reformation of hypoxia in response to Tropical Storm Hanna. All scenarios used the July 23 temperature field so that the only variation between scenarios was due to different DO concentrations. The locations for the values for plotting were listed with longitude/latitude, while the grid locations in the tracking module used Universal Transverse Mercator (UTM) projection.

10.2.2 Movement Algorithms

Movement algorithms were added to the FVCOM particle-tracking module to model fish movement in the model domain based on environmental cues. The FVCOM particle-tracking module is designed to track passive particles that move with the currents calculated by FVCOM. The module was modified as in Rose et al. (2014) to track active particles with movement behaviors such as fish. Movement algorithms were used to calculate x and y velocities.

Changes in particle position were calculated using the past positions and the velocities, as in Watkins and Rose (2013) and Rose et al. (2014). The formulas used to calculate change in position for all algorithms were as follows:

$$x(t + \Delta t) = x(t) + \mathbf{u}(t) * \Delta t \tag{10.1}$$

$$y(t + \Delta t) = y(t) + \mathbf{v}(t) * \Delta t \tag{10.2}$$

where x and y are fish positions on the x and y axes, u and v are fish velocities, and Δt is the time step for fish movement. Only the positions of fish inside the model domain were updated. For fish outside the model domain, the reflective boundary algorithm was applied as described in Sect. 10.2.2.10. Most of the algorithms, except kinesis, calculated the u and v velocities using the same equations. Velocities for kinesis will be described with the kinesis algorithm (Sect. 10.2.2.5). The velocities of fish in the x and y dimensions were calculated as follows:

$$\mathbf{u}(t) = ss * \cos(\theta(t)) \tag{10.3}$$

$$\mathbf{v}(t) = ss * \sin(\theta(t)) \tag{10.4}$$

where ss is the swimming speed and $\theta(t)$ is the swimming angle relative to due east for that time step. How the speed and angle were calculated depends on the movement algorithms.

Nine algorithms were used to model fish movement (Table 10.1). The top-level algorithm, event-based, is used to choose among the other algorithms. Seven algorithms are categorized into three behaviors for use with the event-based algorithm: default, strategic, and tactical. Default behaviors are used when there is no hypoxia. Three algorithms are classified as default: random walk, Cauchy correlated random walk, and Gaussian kinesis. Strategic behaviors are used after an individual leaves conditions that require immediate reactions, but there is still a memory of those conditions. Two strategic behaviors are used in the model: correlated random walk and logistic kinesis. Tactical behaviors are used when the fish needs to react to conditions immediately. The two tactical behaviors, neighborhood search and sprint, are triggered by encountering hypoxia for neighborhood search or spending too much time in hypoxic conditions for sprint. The ninth algorithm, reflective boundary, is used to address boundary issues with the fish and is not used in the event-based algorithm.

Table 10.1 Algorithm definitions

Algorithm	Definition	Reference	Abbr.	Event-based behavior	DO avoidance
Event-based	Switches between movement algorithms depending on environmental conditions	Watkins and Rose (2013), Rose et al. (2014)	EB	NA	Yes
Random walk	Random angle and swimming speed are selected at each time step from defined probability distributions.	Watkins and Rose (2013)	RW	Default	No
Cauchy correlated random walk	Random walk where the turning angle is taken from a non-uniform distribution (Cauchy) so that some angles are chosen more often	Wu et al. (2000)	CCRW	Default	No
Kinesis-Gaussian	"Random walk approach that continuously adjusts turning angle and swimming speed distributions based on current environmental cues"; uses a Gaussian function	Watkins and Rose (2013)	KG	Default	No
Correlated random walk	Random walk that selects a random speed but uses the previous angle with variation added	Rose et al. (2014)	CRW	Strategic	No
Kinesis-logistic	"Random walk approach that continuously adjusts turning angle and swimming speed distributions based on current environmental cues"; uses a logistic function	Modified from Watkins and Rose (2013)	KL	Strategic	Yes
Neighborhood search	Evaluate growth and mortality cues in neighboring cells, and then to move toward the cell with the highest habitat quality or away from lowest quality	Watkins and Rose (2013)	NS	Tactical	Yes
Sprint	A straight lined movement with higher swimming speeds that is triggered by a counter of consecutive hypoxic time steps		S	Tactical	Yes
Reflective boundary	A NS algorithm used to guide fish back into the model domain after they have jumped out of it; for larger time steps		RB	NA	No

10.2.2.1 Event Based

For this study, an event-based approach was used to model fish decision making. Event-based movement is based on game theory and chooses between different movement algorithms based on utilities, which depend on current and past conditions experienced by the virtual fish (Anderson 2002; Watkins and Rose 2013). Environmental conditions, such as hypoxia, are used to choose between default, strategic, and tactical behaviors. There is only one default behavior used at a time. The default behavior occurs when the main stimulus, here low DO, is not detected. Strategic and tactical behaviors come in pairs for each environmental cue or threshold. A preferred range can be defined using two thresholds, such as for temperature or salinity, resulting in two pairs of strategic and tactical behaviors. Tactical movement occurs when a threshold condition is crossed. Strategic movement occurs when fish are out of conditions that would trigger tactical movement, but a memory term in the equation still has the fish being influenced by the hypoxia exposure. Strategic is an asymmetrical behavior that occurs only after a tactical behavior has been triggered and fish are exiting the hypoxic zone.

The behavior with the highest utility is the one chosen by the event-based algorithm. In a game theory approach, utilities represent how the benefits and costs of a given behavior affect the fitness of the organism (Anderson 2002). Here, hypoxia avoidance success is used as a measure of fitness. The utility values are affected by whether or not events occur. Whether events occur was determined with:

$$e_J(t) = \begin{cases} 0 & val > th \\ 1 & val \leq th \end{cases} \tag{10.5}$$

where $e_J(t)$ is the event value at time t, a Boolean operator of whether the event J is triggered (1) or not triggered (0) at time t. The *val* is the environmental value (e.g., DO) or other value, such as a counter. An example of the threshold, *th*, is 2 mg O_2/L, which denotes the upper DO limit for hypoxia.

The utility of the different behavior options were then calculated for each fish. The behavior with the highest utility is the one chosen by the event-based algorithm. Utility is calculated by:

$$util_{J,K}(t) = utili_{J,K} * prob_{J,K}(t) \tag{10.6}$$

where *util* is the utility for that time step, *utili* is the intrinsic utility, and *prob* is the probability of a triggered event. The integers J and K in Eq. 10.6 indicate behavior groups, where the J value represents a group and the K value indicates whether the behavior is tactical (K = 1) or strategic (K = 2). The probability of an event being triggered was calculated by:

$$prob_{J,K}(t) = (1.0 - mem_{J,K}) * e_J(t) + mem_{J,K} * prob_{J,K}(t - \Delta t) \tag{10.7}$$

where $prob_{J,K}(t)$ is the probability for the behavior J, K at time t, $e_J(t)$ is the event value at time t, $prob_{J,K}(t - \Delta t)$ is the probability calculated last time step, and $mem_{J,K}$ determines what proportion of the event value and past probability make up the current probability. The probability is a running average and allows for the fish to have some memory of past events. The utilities were then compared to a minimum standard value, and the largest value determines which behavior was used. If none of the calculated utilities were larger than the standard minimum, then the default behavior was used (J=0). The event-based behavior was the same as used in Rose et al. (2014). The algorithms used for each event-based behavior are described in Table 10.1.

10.2.2.2 Random Walk

Random walk is a type of movement algorithm where random speeds and angles are chosen without considering environmental conditions. Three random walk algorithms are used in this study, two for default behaviors and one for strategic. The simplest random walk used chooses a random angle and adds variation to a baseline speed for each time step. The speed and angle are calculated using:

$$ss = ss_0 \pm 0.3 * ss_0 * ran \tag{10.8}$$

$$\theta(t) = 2\pi * ran \tag{10.9}$$

where ss_0 is the baseline swimming speed and ran is a uniform random number between 1 and 0. The angle is calculated with relation to a fixed axis, here due east. Equation 10.8 is used to calculate speed for all of the random walk algorithms and is slower than the speed used for the tactical behaviors. So fish slow down when switching from a tactical behavior to one of the random walk algorithms. Random walk has particles/fish move with simple diffusion.

10.2.2.3 Correlated Random Walk

A correlated random walk (CRW) is a random walk with a bias toward one direction (Kareiva and Shigesada 1983). A CRW chooses a random speed and a turning angle. Unlike the simple random walk, a CRW determines the new angle relative to the angle from the previous time step instead of a fixed axis. The variation added to the old angle to get the new angle is called the turning angle. The CRW uses the velocities from the previous time step to calculate the angle:

$$\theta(t) = \mathrm{atan2}(\mathbf{v}(t - \Delta t), \mathbf{u}(t - \Delta t)) + 0.05 * 2\pi * (2 * ran - 1) \tag{10.10}$$

where the first half of the equation, atan2( ), is from the previous time step and the second part is a random component to add variation to the angle. If no random component was added, then when substituted into Eqs. 10.3 and 10.4, θ would produce the fish swimming velocity components u and v of the previous time step. The fish moves in mostly the same direction with some variation when a small random component is added. Speed is calculated with Eq. 10.8. CRW is the algorithm used for the strategic behavior in all runs except those with kinesis. Field data of insect movement have been described using CRW (Kareiva and Shigesada 1983).

10.2.2.4 Cauchy Correlated Random Walk

The Cauchy correlated random walk (CCRW) is a more complicated CRW where the magnitude and direction of the bias can be controlled by choosing the turning angle from a non-uniform, wrapped Cauchy distribution. The CCRW was adapted from Eq. 20 in Wu et al. (2000), which is implemented as the turning angle:

$$\theta(t) = \theta(t - \Delta t) + 2 * \operatorname{atan}\left[\frac{(1-\varepsilon)}{(1+\varepsilon)} * \tan((ran - 0.5) * \pi)\right] + \theta_m \tag{10.11}$$

where ε determines the shape of the wrapped Cauchy distribution, and θ_m determines the center of the distribution. $\theta(t - \Delta t)$ is the previous angle, and the $2 * \operatorname{atan}[\,] + \theta_m$ is the turning angle. Higher values of ε result in more correlation and less randomness to the direction of the fish. By changing θ_m, the fish can be given a bias in whether they turn left or right. The original equation from Wu et al. (2000) was changed by adding the parameter θ_m based on Batschelet (1981) and using the result of the equation as a turning angle instead of the angle of direction. Speed was calculated using Eq. 10.8. Velocities are calculated using Eqs. 10.3 and 10.4.

10.2.2.5 Kinesis

Kinesis compares the ideal condition to the current condition to determine the proportion of random versus previous velocities to use for the new velocities (Humston et al. 2004; Watkins and Rose 2013). Two forms of kinesis were used: Gaussian and logistic. As previously mentioned, kinesis uses a different method from the other algorithms to calculate velocity. Instead of calculating speed and angle at each time step, the velocities for the x and y directions are calculated using a random component and a previous velocity component. The equations are as follows:

$$\mathbf{u}(t) = \mathbf{u}(t - \Delta t) * (h1 * p1) \pm nran * (1 - h2 * p1) \tag{10.12}$$

$$\mathbf{v}(t) = \mathbf{v}(t - \Delta t) * (h1 * p1) \pm nran * (1 - h2 * p1) \tag{10.13}$$

where $p1$, $h1$, and $h2$ are weighting factors. The $p1$ weighting factor is used to determine the proportion of random versus previous velocities in the new velocities and is calculated using the comparison of the ideal and current conditions in a function. The $h1$ and $h2$ weighting factors determine the percentage of the previous velocities and random components, respectively, used in the new velocities. Fish using kinesis slow down in areas where the previous component has more weight than the random component. The previous component is smaller than the actual previous velocity because the $h1$ weighting factor is less than 1. The value $nran$ is a random number from a normal distribution that is screened for extreme values (>|3|). The Kinesis algorithm is based on studies on a variety of organisms including wood lice and protozoa and focuses on a mechanistic approach to animal movement (Fraenkel and Gunn 1961).

10.2.2.6 Gaussian Kinesis

How the $p1$ weighting function is calculated depends on the version of kinesis. The Gaussian kinesis is the form of kinesis used in Watkins and Rose (2013) and Humston et al. (2004). It uses a Gaussian curve in determining the $p1$ weighting factor used in Eqs. 10.12 and 10.13. A Gaussian curve results in fish moving toward the mean of the curve. The $p1$ weighting factor is calculated with:

$$p1 = e^{-0.5*\left(\frac{temp(t)-\mu_{temp}}{\sigma_{temp}}\right)^2} \tag{10.14}$$

where $temp(t)$ is the current temperature, μ_{temp} is the mean of the curve and ideal temperature, and σ_{temp} is the sigma value of the curve. The sensitivity of the algorithm can be altered by changing the curve width with the sigma value. Gaussian kinesis was used as a default behavior in response to temperature.

10.2.2.7 Logistic Kinesis

Logistic kinesis works better than Gaussian kinesis for avoiding poor conditions, as opposed to being attracted to good conditions. Tests were run using Gaussian kinesis to avoid hypoxia, but the algorithm did not perform well. The Gaussian curve represents an ideal condition and progressively worse conditions well, but does not represent good conditions that suddenly become poor conditions at some threshold. A logistic curve better represents the second scenario, so a logistic curve was used instead of a Gaussian curve to calculate the $p1$ weighting function:

$$p1 = \frac{e^{r*do(t)}}{e^{r*do(t)} + b} \tag{10.15}$$

where $do(t)$ is the current DO value, r controls the slope of the curve, and b controls where the curve occurs. The $p1$ value was used to calculate velocities with Eqs. 10.12 and 10.13. The algorithm results in fish moving away from areas with values on the lower part of the curve and then moving mostly randomly in areas where the curve has leveled off. Logistic kinesis is used as a strategic behavior in response to DO.

10.2.2.8 Neighborhood Search

Neighborhood search is used in most of the tactical behaviors and is the main algorithm used for hypoxia avoidance. Neighborhood search works by searching the neighboring cells and then moving either away from the lowest quality cell or moving toward the highest quality cell. The quality of the cell can be calculated in different ways (e.g., growth and mortality Watkins and Rose 2013 or salinity Rose et al. 2014). Hypoxia was avoided with a neighborhood search algorithm moving away from the lowest DO value. The neighboring cells are searched for the cell with the lowest DO value and then the swimming speed and angle are calculated with:

$$\theta(t) = \mathrm{atan2}(y(t) - yl(t), x(t) - xl(t)) + 0.15 * 2\pi * (2 * ran - 1) \tag{10.16}$$

$$ss = 2 * ss_0 \pm ss_0 * ran \tag{10.17}$$

where $x(t)$ and $y(t)$ are the current x and y coordinates, $xl(t)$ and $yl(t)$ are the coordinates of the center of the cell with the lowest DO, and ran is a uniform random number. The first part of the equation, atan2( ), calculates the angle, and the second part calculates a random component that adds some variability to the angle. The amount of variation can be increased or decreased by replacing the 0.15 with larger or smaller values, respectively, with a maximum meaningful variation of pi. The swimming speed was faster for avoidance behaviors than for default behaviors because there was more urgency to avoid bad conditions. The variation in swimming speed is similar to Eq. 10.8, but has a higher range of variation. Velocities are calculated using Eqs. 10.3 and 10.4. Hypoxia avoidance with neighborhood search was triggered when the utility is highest for the tactical behavior for low DO avoidance.

10.2.2.9 Sprint

The sprint algorithm was created to deal with the problem of fish moving under neighborhood search getting stuck moving in a narrow region around a local DO maximum. When local maxima with values below 2 mg DO/L occur, fish will get stuck in those cells when using neighborhood search. Adding variability to the neighborhood search angle can keep some fish from getting stuck at local DO maxima, but not all. The sprint algorithm is triggered when a counter of hypoxic steps exceeds a set value. The set value determines the maximum number of time steps the fish can stay in hypoxia before drastic measures need to be used. For this paper, fish start to panic after spending two days in hypoxic conditions. The set value is the number of steps, depending on time step, that occur over two days (200 for 15 min; 25 for 2 h). The sprint is a simple algorithm that calculates the angle and speed with:

$$\theta(t) = \theta(t - \Delta t) \tag{10.18}$$

$$ss = 3 * ss_0 \tag{10.19}$$

The counter is decreased by 1 when the algorithm is triggered and is reset to zero when normoxic conditions are encountered. A decrease of 1 results in the fish sprinting until it exits the hypoxic zone. Changing the amount the counter decreased the affects how long the sprint algorithm is used, but only a decrease of 1 is used in this paper.

10.2.2.10 Reflective Boundary

Neighborhood search is also used in the reflective boundary algorithm. It is not one of the algorithms chosen by the event-based algorithm, but occurs after movement is calculated by the movement algorithms. The reflective boundary algorithm is used with kinesis, which works best at larger time steps (≥1 or 2 h). Particles in the FVCOM-tracking module tend to get stuck on the edges of the model domain at time steps large enough for kinesis to work well. The reflective boundary algorithm uses neighborhood search to calculate the cell with the fewest boundaries and move the fish toward the cell with fewest boundaries. The angle is calculated by:

$$\theta(t) = \mathrm{atan2}(yl(t) - y(t), xl(t) - x(t)) + 0.15 * 2\pi * (2 * ran - 1) \tag{10.20}$$

where the values are the same as Eq. 10.16. The values used are from the location calculated at the last time step and not the new location calculated by the movement algorithms for the current time step. Using the previous values makes sure that the particle is in a cell so neighborhood search will work properly. The only change in the calculation of θ is the order of coordinate values in the atan2 function. Speed is calculated as in Eq. 10.17. The reflective boundary is applied only to particles that have gone outside of the model domain.

10.2.3 Algorithm Groups

Three algorithm groups were used in the model simulations (Table 10.2). Each group had a tactical, strategic, and default behavior and was named after the tactical and default behaviors. Neighborhood search was used for the tactical behavior for all groups. Neighborhood search is an efficient and effective avoidance behavior. CRW

Table 10.2 Algorithm groups: Neighborhood Search (NS), Random Walk (RW), Correlated Random Walk (CRW), Cauchy Correlated Random Walk (CCRW), Kinesis (K), Logistic Kinesis (KL), and Gaussian Kinesis (KG)

Algorithm group	Tactical	Strategic	Default	Panic response (tactical/strategic)	Time step (min)
NS/RW	NS	CRW	RW	Sprint/CRW	15
NS/CCRW	NS	CRW	CCRW	Sprint/CRW	15
NS/K	NS	KL	KG	Sprint/CRW	120

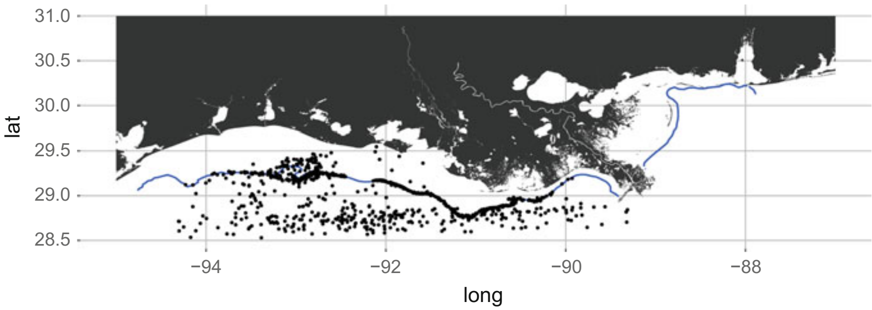

Fig. 10.1 Starting positions for particles/fish in FVCOM-tracking module in the Northern Gulf of Mexico. The *line* is the 26 °C contour

and logistic kinesis were used as the strategic behaviors. Strategic behaviors were matched to the default behaviors, where CRW was used for random walk defaults and logistic kinesis was used for the kinesis default. The default behaviors, RW, CCRW, and Gaussian kinesis (from here on, kinesis refers to Gaussian kinesis), were the major difference between algorithm groups. Each algorithm group also used a subgroup consisting of the sprint algorithm as the tactical behavior and CRW as the strategic behavior.

10.2.4 Model Runs

For simulation set 1, each of the three algorithm combinations (Table 10.2) was run for the four DO scenarios (Sect. 10.2.1). All simulations were for seven days. A time period of seven days was selected because the model fish exposure levels reach steady-state values after about five days. The starting positions of the 913 fish are the result of having fish move with Gaussian kinesis for 124 days (Fig. 10.1). The fish end up mostly gathered around the ideal temperature, which overlaps with the hypoxic zone for the severe hypoxia scenario. The time step used depends on the algorithm group. A 900-s (15 min) time step is used for the algorithm groups with random walk algorithms. A time step of 2 h is used for the kinesis algorithm group. A larger time step is used for kinesis because the algorithm is very inefficient at finding the ideal temperature at smaller time steps. The output time steps were the same as the respective time step for each algorithm group: every 15 min for the random walk groups and every 2 h for kinesis.

For simulation set 2, each of the three algorithm groups with individuals configured to be inefficient at avoidance (poor avoidance) was run on only the severe hypoxia (July 23, 2002) scenario. The effects of poor avoidance are best seen when avoidance is used a lot, so smaller hypoxic areas are less useful. Everything was the same as with the severe hypoxia scenario in set 1 except for the poor avoidance. The ability of the fish to avoid low DO was impaired by changing the 0.15 coefficient in

Eq. 10.16 to 0.5, which added more variation to the movement angle of neighborhood search used for avoidance. The sprint algorithm was also not used for these runs because it is an algorithm with good hypoxia avoidance and allows the fish to easily escape the hypoxic zone after two days. The poor avoidance runs were then compared to the runs for the severe hypoxia scenario from simulation set 1.

10.2.5 Data Analysis and Visualization

10.2.5.1 Statistics

Several statistics are used to compare model runs. The first group of three statistics looks at the conditions experienced by each fish. The first statistic, the percentage of fish in a DO or temperature range, is calculated by first taking the DO or temperature value for each fish at each time step. The number of fish in each range is then divided by the total number of fish to get the percentage. Summary statistics (minimum, mean, and maximum) for DO, the second statistic, are calculated at each time step for all 913 fish. The third statistic, exposure to hypoxia, is calculated by summing the total time spent in hypoxic conditions. For each time step, a value of one is assigned for hypoxic values and zero for non-hypoxic values. The one or zero is then multiplied by the time step, and the resulting values are summed to get the total time exposed to hypoxia. For comparing time spent in hypoxic conditions, multiplying by the time step converts to the unit of time used for the model. Data analysis, manipulation, and plotting were all performed in R (R Core Team 2013). Outliers are as defined by the R plotting method used, generally ggplot2 boxplot.

Three related statistics were used to compare the movement and distribution spread of the fish: sinuosity, net distance, and total distance. The term “distribution spread” refers to how far the fish have spread out from their initial positions. Sinuosity is the amount of wiggle in the path of the fish. It is calculated by dividing the actual path by the shortest, or net, distance between the first and last point for each fish. The actual path, or total distance travelled, is calculated by summing the distances between successive points in the path. Distances between two points use the distance formula.

A categorization test was used to compare hypoxia exposure values. It is not advised to use statistical tests with p-values for interpreting simulation models. In a simulation model, the researcher controls the degrees of freedom, which affects the p-values (White et al. 2014). The algorithm groups are also known to be different, so the questions of “are they different” is not an informative question to ask or answer with statistical tests. Whether the algorithms can be differentiated in a field sample is a more informative question to answer. A categorization test using a linear discriminant analysis (LDA) was used to determine whether the hypoxia exposures for the three algorithm groups could be told apart. The *lda* function in the R package *MASS* was used on training data sets. Each training data set was comprised of 1000 mean exposures for each algorithm group from a sample size ranging from 25 to 900 (by 25). Algorithm groups were only categorized within the same scenario and not among scenarios. The prior for the LDA was 1/3 for each algorithm group training data set, which assumes equal chance of a random sample being in any of the algorithm groups. The LDA was run for each scenario using the training data sets and the miscategorization rate was calculated as 1 minus the average categorization rate. The acceptable rate of miscategorization was 0.05. The normoxia scenario was not included because all the exposure values were zero, which caused *lda* to crash.

10.2.5.2 Growth and Vitality

The effects of hypoxia exposure on growth were calculated for the seven days of the model run and extrapolated to 30 days. The model fish are juveniles between 1 and 2 years of age. Growth was calculated by first calculating the vitality at each time step for growth using the following based on Miller Neilan and Rose (2014):

$$Gvitality = \begin{cases} 1.0 & x \geq Gne \\ 1.0 - Galpha\frac{(x-Gne)^2}{(x-Gne)^2+Gbeta^2} & x < Gne \end{cases} \tag{10.21}$$

where Gne (3.35), $Galpha$ (110.78), and $Gbeta$ (21.06) are constants. Gne is the threshold below which low DO has an effect on the fish, and x is the DO value experienced by the individual fish for that time step. There is also a repair term for growth vitality, $Ggamma$ (0.21), which is the maximum increase in growth vitality per hour. The repair term accounts for a delay in return to normal vitality rates after returning to normoxia. The repair term was applied using:

$$Gvitality_{repair} = \min(Gvitality(t), (Gvitality(t - \Delta t) + Ggamma * \Delta t)) \tag{10.22}$$

where $Gvitality_{repair}$ is the new growth vitality term and Δt is the time step. $Ggamma$ is multiplied by the time step because the data points are either 15 min or 2 h apart while the repair term is hourly. Parameters for growth vitality for Atlantic croaker in the region of the GOM hypoxic zone were provided by Sean Creekmore (personal communication, Louisiana State University).

Growth is calculated by calculating growth and new weights at each time step. The growth and new weight were calculated for each fish using:

$$Weight(t) = Weight(t - \Delta t) * e^{Gvitality_{repair} * maxGrowthM} \tag{10.23}$$

where $Weight(t)$ is the weight for the current time step, $Weight(t - \Delta t)$ is the weight of the previous time step, and $maxGrowthM$ is the maximum growth under normoxic conditions. The initial weight ($Weight(0)$) and maximum growth rate were calculated using equations from Barger (1985) that determine the length from age and a weight from length. Parameters for the movement and growth equations are in Table 10.3.

Table 10.3 Parameter values for algorithm and weight calculation equations

Parameter	Value	Description
Δt	0.25, 1 h	Time step for particle-tracking module. Value used depends on default algorithm
th	2 mg O_2/L	The threshold for triggering hypoxia avoidance
Utili	2.0, 3.0, 1.0[a]	Intrinsic utility (NS, sprint, default/strategic)
Mem	0.5, 0.9[a]	Memory term (default/strategic, tactical)
Standard minimum	0.175[a]	Value utility must be greater than to affect fish movement
ss_0	0.23148 m/s[a]	Baseline swimming speed
ε	0.9[b]	Determines shape of wrapped Cauchy distribution
θ_m	0[b]	Determines what angle wrapped Cauchy distribution is biased toward
h1, h2	0.7, 0.99[a]	Kinesis weighting factors
μ_{temp}	26 °C[c]	Ideal temperature for croaker
σ_{temp}	2 °C[c]	Sigma value for Gaussian curve
r	3[d]	Controls slope of logistic curve
b	150[d]	Control where logistic curve occurs
Stuck	200, 25[E]	When the counter reaches this number of steps, the fish is considered stuck. Value depends on time step.
Galpha	100.78[f]	Constant
Gbeta	21.06[f]	Constant
Gne	3.35[f]	Threshold for hypoxia affects
Ggamma	0.21[f]	Repair term
Weight(0)	88.72 g[g]	Initial weight calculated for croaker at beginning of second year of life
MaxGrowthM	0.002 g/day[g]	Maximum growth rate in normoxic conditions for croaker from beginning to end of second year of life

[a]Based on Rose et al. (2014)
[b]Determined by testing different values affects on wrapped Cauchy distribution
[c]Based on location of temperature contour where croaker gather in the GOM
[d]Determined by testing different values so that the logistic curve lined up around 2
[e]Number of time steps that make up 2 days
[f]From Sean Creekmore (Personal communication, LSU)
[g]Calculated based on Barger (1985) and Miller Neilan and Rose (2014)

10.2.5.3 Visualization Methods

The map plots were creating using *ggplot2* layers for the coastline, interpolated values, contours, and fish generated in R. For the coastline, a shapefile for the US coast from the USGS (http://coastalmap.marine.usgs.gov/regional/contusa../gomex/gloria/data.html) was cropped down to include the Gulf coast between −95° and −87° longitude and between 27° and 31° latitude. The contour and the interpolated field layers were generated from output from FVCOM-WASP from 2002. DO values for May 2, June 4, July 23, and September 21 were combined with temperature and salinity values for July 23 to create scenarios that vary only by DO values. After converting the final fish locations to latitude and longitude, the locations were added to the plot.

10.3 Results

For simulation set 1 (good avoidance), most fish were able to escape the hypoxic zone within one day and more fish escaped more quickly with the NS/RW algorithm group than with NS/K algorithm group. In the final position maps for the fish (Fig. 10.2), the majority of fish were outside of the hypoxic zone. The fish that were in the hypoxic zone were on the very edge. For mild (d–f) and intermediate (g–i) hypoxia scenarios, it took a day or less for the percentage of fish in conditions <2 mg/L (solid orange line) to approach zero (Fig. 10.3). For the severe hypoxia scenario, it took three days for NS/RW algorithm group (j) and five days for NS/CCRW algorithm group (k) for the percentage of fish in conditions <2 mg/L to approach zero. The percentage of fish in < 2 mg/L for the NS/K algorithm group (l) in the severe hypoxia scenario leveled off at about 5% of fish in conditions < 2 mg/L.

For simulation set 2 (poor avoidance), fish took longer to escape the hypoxic zone compared to simulation set 1 fish and NS/K algorithm group fish had a greater decrease in the percentage of fish within the 1–2 mg/L range than NS/CCRW fish. There were fish in the hypoxic zone for all three algorithm groups for all seven days. All algorithm groups (m–o) had at least 5% of fish below 1 mg/L (teal line) and at least 10% of fish between 1–2 mg/L (solid orange line) during the course of the seven-day simulation (Fig. 10.3). The NS/K algorithm group (o) had the largest decrease in the percentage of fish for the 0–1 mg/L and 1–2 mg/L ranges. The NS/CCRW algorithm group (n) had the smallest decrease in the percentage for these ranges and the percentage of fish in the 1–2 mg/L range stayed constant. The other three ranges (2–3 mg/L, 3–4 mg/L, >4 mg/L) had a general increase in percentage for all three algorithm groups with NS/K algorithm group having the largest change and NS/CCRW algorithm group having the smallest. The >4 mg/L range was an exception, with NS/RW algorithm group having the smallest change in percentage of fish. For NS/CCRW algorithm group, the dispersal of fish was greater than compared to NS/RW algorithm group, resulting in NS/RW algorithm group having a smaller change in percentage for that particular range.

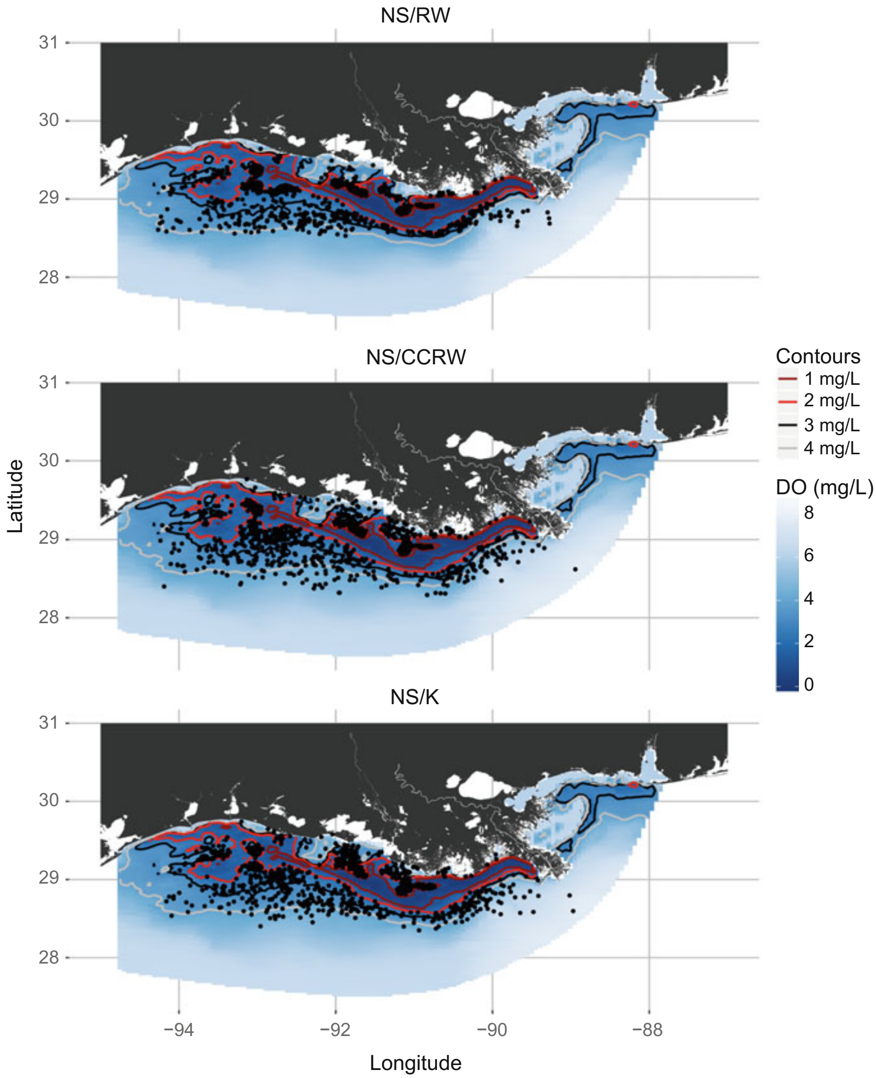

Fig. 10.2 Final fish positions for the severe hypoxia scenario along the Northern Gulf of Mexico. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and Neighborhood Search/Kinesis (NS/K)

The summary statistics of DO for the algorithm groups became less similar as hypoxic area increased, with NS/K algorithm group minimum DO values never rising above 2 mg/L while NS/RW and NS/CCRW algorithm group minimums did. For normoxia (a–c), the mean (black line), minimum (dark gray line), and maximum (light gray line) DO values were about the same for the three algorithm groups

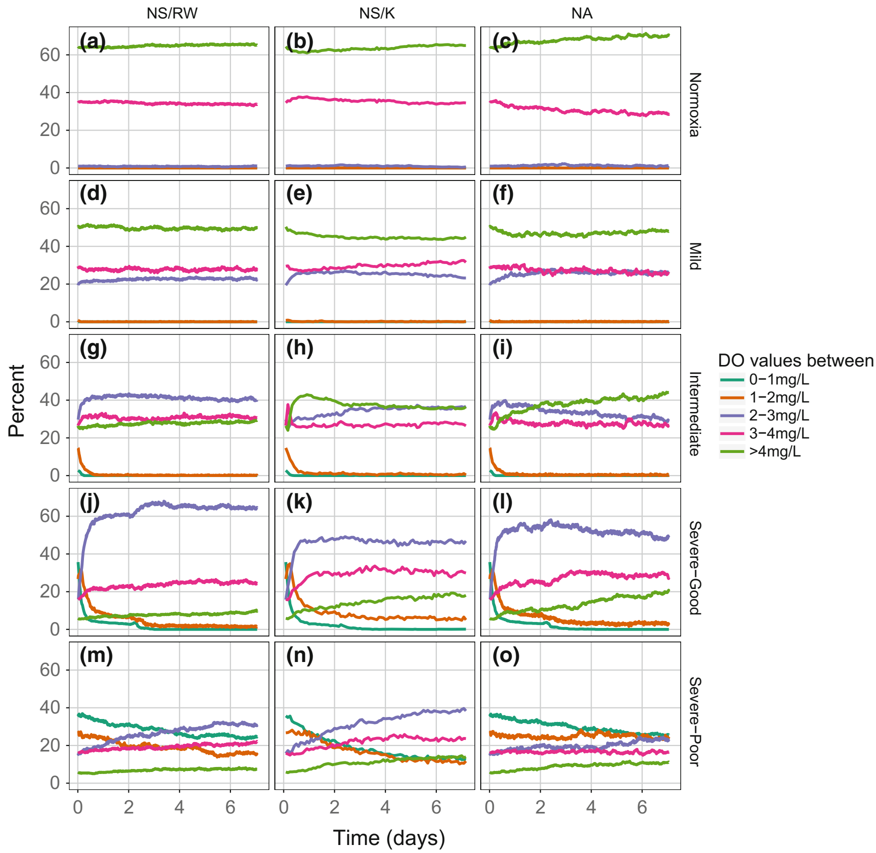

Fig. 10.3 Percentage of fish in five DO ranges (0 to <4 mg/L) over time for each algorithm group/scenario combination. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

(Fig. 10.4). As hypoxic area increased, the mean DO values for the fish decreased, from over 5 mg/L for normoxia to around 3 mg/L in the severe scenario (j–l). The maximum DO values for the fish also decreased with increasing hypoxic area. For NS/RW algorithm group, the maxima tended to stay around the same values for the entire model run, while the maximum values for NS/CCRW algorithm group and NS/K algorithm group tended to increase over time. The minimum values for scenarios with hypoxia tended to increase to 2 mg/L and stay around that value. The minimum values took longer to reach 2 mg/L for the intermediate (g–i) and severe scenarios (j–l), with the longest time of around 5 days for the severe scenario for NS/CCRW algorithm group (k). The intermediate (i) and severe (l) hypoxia scenarios for NS/K algorithm group are the only exceptions to the trend of the minimum

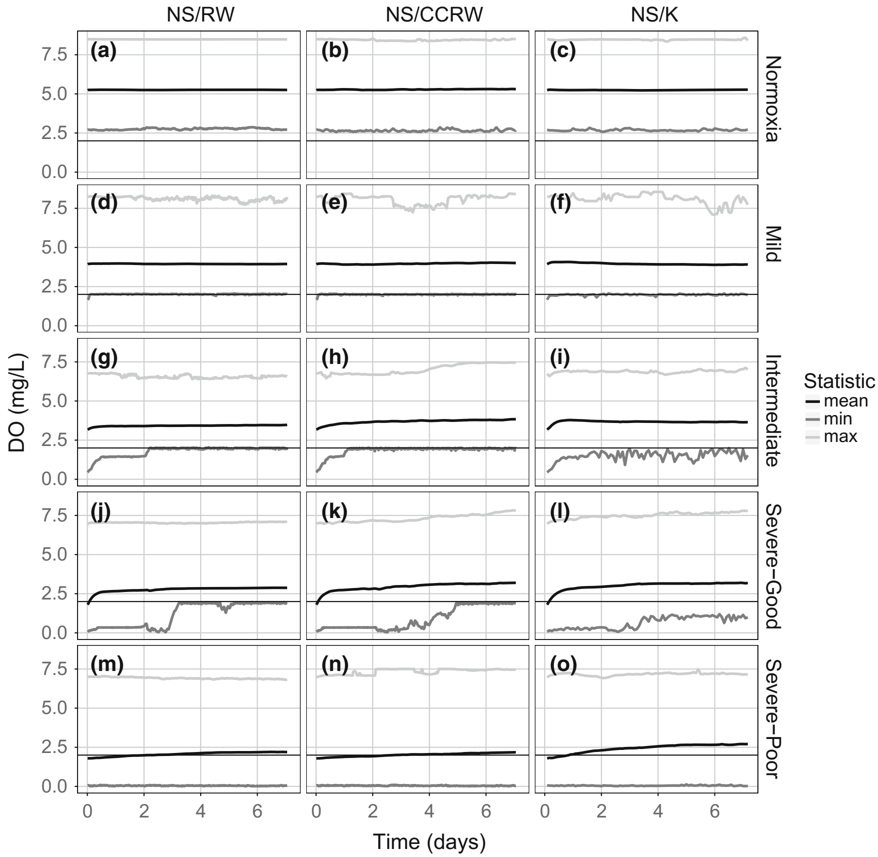

Fig. 10.4 Minimum, mean, and maximum DO values experienced by fish during the seven-day simulation period for each algorithm group/scenario combination. The *thin, black horizontal line* denotes 2 mg/L, so values below the *line* represent hypoxic conditions. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

leveling off at 2 mg/L. Both of these time series had more variation than the corresponding time series for NS/RW algorithm group (g, j) and NS/CCRW algorithm group (h, k). The minimum DO values experienced by fish for the intermediate scenario approach 2 mg/L and for the severe scenario stayed near 1.75 mg/L. Even though the minimum DO values experienced by fish could be below 2 mg/L during the entire simulation period, no fish spent the entire time in the hypoxic zone.

For simulation set 2, there was less variation across time and among the algorithm groups than with simulation set 1, with NS/K having the largest variation. The minimum DO value (dark gray line) for all the fish remained at or near zero for the entire seven days (m–o, Fig. 10.4). There was little variation in the three statistics for all three algorithm groups. The maximum DO value has some variation for NS/CCRW algorithm group (n) and NS/K algorithm group (o), but it was less than 0.5 mg/L. The mean DO values increased very little, less than 0.5 mg/L, over the 7 day period. The NS/K algorithm group had the largest increase in mean DO value, possibly due to the larger time step.

10.3.1 Exposure

Fish exposure to hypoxia increased with hypoxic area, and exposure was not greatly affected by the default algorithm used. As expected, there was no exposure to hypoxia in the normoxia conditions. As the area of hypoxia increased, the number of fish exposed and the exposure time increased (Fig. 10.5). NS/K algorithm group in the severe hypoxia scenario had more fish exposed for over 4 days (l, 47 fish) than did NS/RW algorithm group (j, 6 fish) or NS/CCRW algorithm group (k, 10 fish). For the severe hypoxia scenario, 83% of fish were exposed for less than a day, but there were a number of outliers with longer exposures (about 150 fish for each algorithm group). Two of the NS/K algorithm group outliers had exposures of over six days. The intermediate and severe (good avoidance) scenarios required a sample size of about 375 fish to tell the algorithm groups apart (Fig. 10.6). The mild scenario required a sample size of about 250 fish. Both of these sample sizes are very large for a study recording fish movement and hypoxia exposure. Until fish tracking technology improves, it is unlikely that the movement types described by the algorithm groups could be differentiated in field data.

The instances of longer hypoxia exposure were most likely due to spatial patterns in the hypoxic zone that occurred in the intermediate and severe hypoxia scenarios where fish were surrounded by hypoxic water on at least three sides. In the intermediate and severe hypoxia scenarios, fish tended to congregate in areas of normoxia that were either partially or entirely surrounded by hypoxic water. Fish in these areas were likely to wander back into the hypoxic zone and have higher hypoxia exposure. Because of the larger time step for the NS/K algorithm group, in narrow regions of normoxia, fish could overshoot normoxic areas multiple times and end up with large hypoxia exposures.

When avoidance is poor (simulation set 2), more fish were exposed and the three algorithm groups have similar exposures, though NS/CCRW and NS/RW algorithm groups had more fish at maximum exposure (7 days) than NS/K algorithm group. As expected, the exposures for poor avoidance did not resemble those from good avoidance (simulation set 1, Fig. 10.5). The NS/K algorithm group had fewer fish with about seven days of exposure, which was most likely due to the larger time step. Fish with a seven-day exposure were most likely stuck at local maxima that were still hypoxic and this occurred less with larger time steps. All three algorithm groups had a group of fish with no exposure, which were the fish that started outside the hypoxic area and never entered it. The NS/RW (m) and NS/CCRW (n) algorithm groups resulted in more fish being exposed for the maximum cumulative time

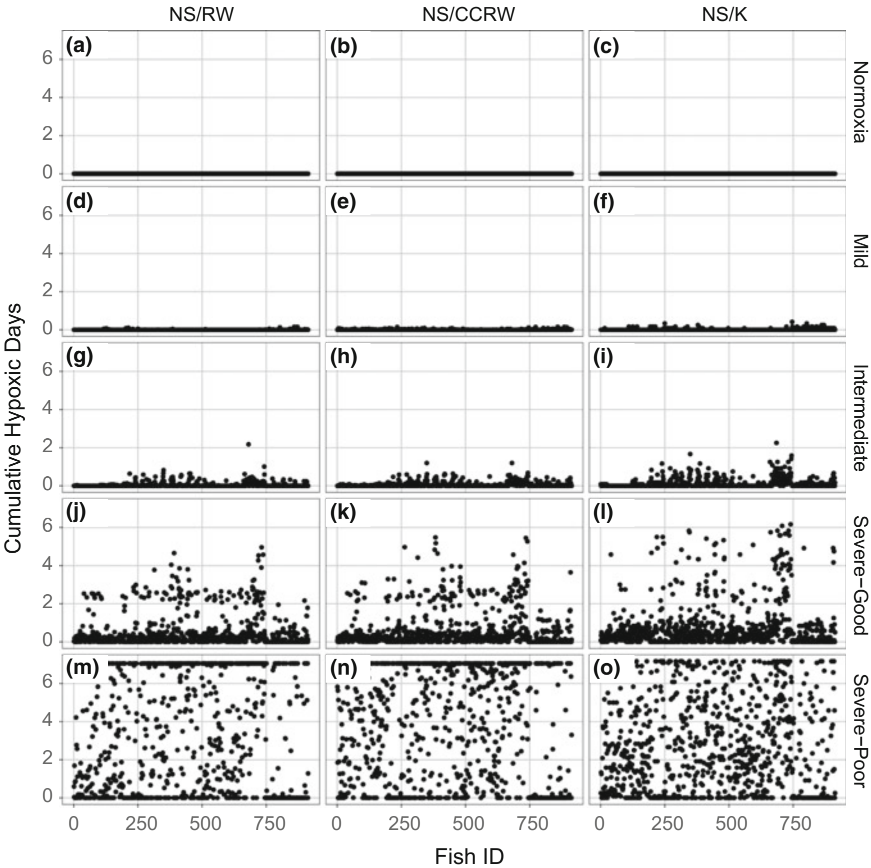

Fig. 10.5 Exposure calculated as the total number of days fish spend in hypoxic conditions plotted for each fish and each algorithm group/scenario combination. The fish are numbered by their model ID number. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

than NS/K algorithm group (o). The NS/CCRW algorithm group had 266 fish at maximum exposure and the NS/RW algorithm group had 273 fish, while the NS/K algorithm group had 45 fish at maximum exposure. The algorithm groups could be differentiated at a sample size of about 250 fish. This sample size was smaller than the sample size for the severe hypoxia scenario with good avoidance.

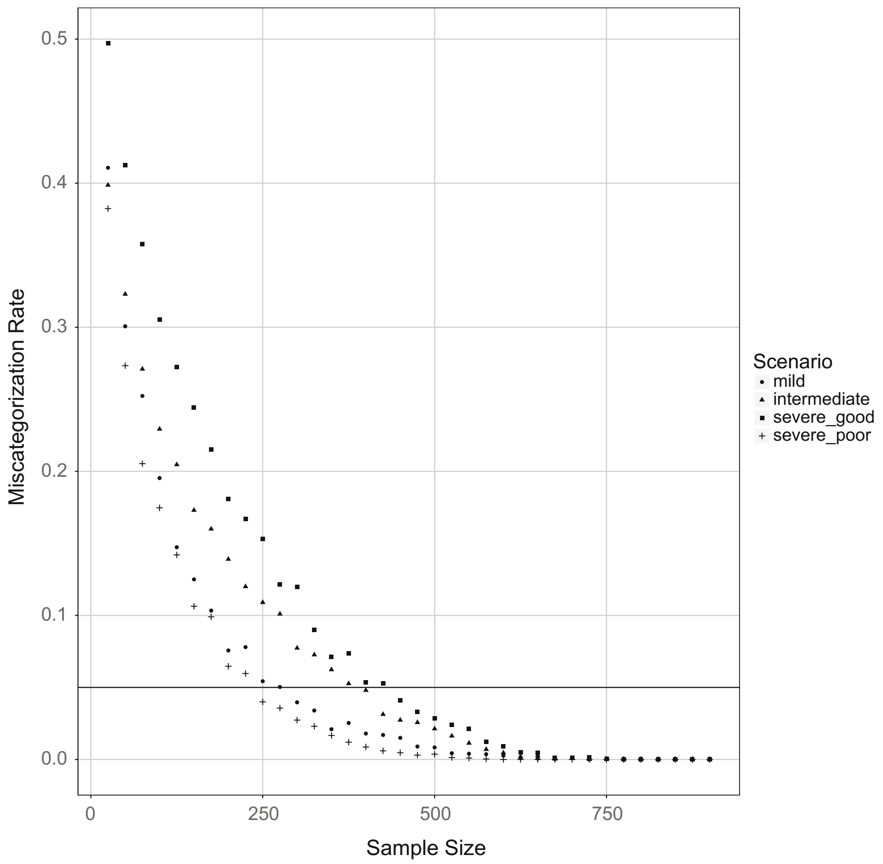

Fig. 10.6 Graph of miscategorization rate of algorithm groups plotted against sample size. The horizontal *black line* is the maximum acceptable miscategorization rate (0.05). The scenarios are mild, intermediate, and severe hypoxia. Severe hypoxia has both good and poor hypoxia avoidance

10.3.2 Distribution Spread

10.3.2.1 Maps

Fish spread further with the NS/CCRW algorithm group than with the NS/RW and NS/K algorithm groups. When looking at the final position maps for normoxia, the three algorithm groups had a different distribution. The NS/RW algorithm group fish (Fig. 10.7) diffused a short distance from the initial positions such that the initial positions are still recognizable. The NS/CCRW algorithm group fish (Fig. 10.7) spread out until the positions looked random, and the initial positions were no longer recognizable. The NS/K algorithm group fish (Fig. 10.7) looked almost exactly like the initial positions because the initial positions are the steady state for kinesis. The

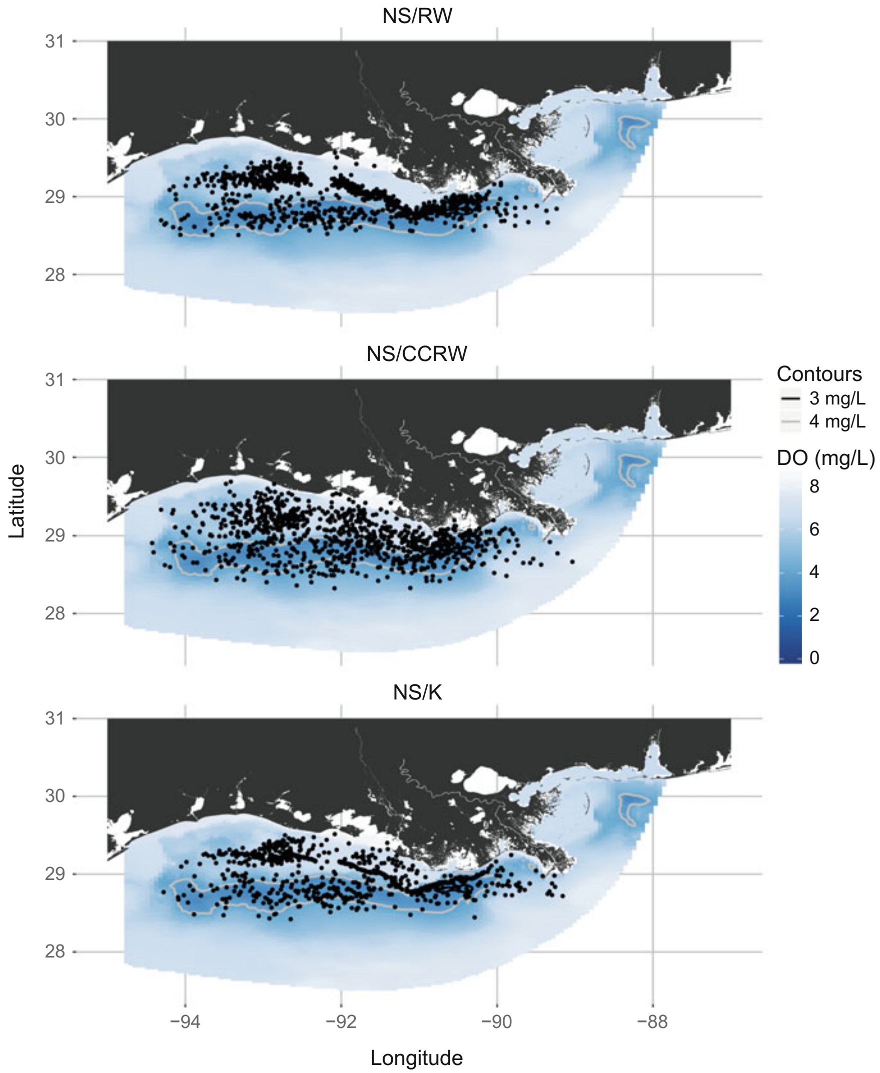

Fig. 10.7 Final fish positions for the normoxic scenario along the Northern Gulf of Mexico. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K)

final position maps for mild and intermediate hypoxia had a similar distribution as the normoxia maps for the respective algorithm.

The final position maps for severe hypoxia (Fig. 10.2) show that for the NS/CCRW algorithm group fish spread more than for the other two algorithms groups and NS/K algorithm group gathered near the optimum temperature when possible. In the area outside of the hypoxic zone, fish were spread out the least with the NS/RW algorithm group and the most with the NS/CCRW algorithm group (Fig. 10.2). Fish gathered closer to the edges of the hypoxic zone with the NS/RW algorithm group and the NS/K algorithm group (Fig. 10.2) than with the NS/CCRW algorithm group. There was an area of normoxic water completely surrounded by hypoxic water (i.e., a normoxic island) for the severe hypoxia scenarios. The spatial distribution of fish within the normoxic island was influenced by the default algorithm. The fish were evenly spread out with the NS/CCRW algorithm group, while they gathered on one side with the NS/RW and NS/K algorithm groups. The fish for the NS/RW algorithm group were largely located on the eastern side of the normoxic island. In contrast, the kinesis fish gathered near the southern side of the normoxic island which was closer to their optimum temperature.

10.3.2.2 Sinuosity, Net Distance, and Total Distance

Sinuosity, net distance, and total distance differed among the algorithm groups with NS/RW having the largest sinuosity while covering the shortest net distance. The NS/RW algorithm group fish generally had larger sinuosities than the NS/CCRW and NS/K algorithm groups (Fig. 10.8). The NS/K algorithm group tended to have a slightly smaller sinuosity than the NS/CCRW algorithm group. Sinuosity was broken into its two components: the net distance from start to end and the total distance of the fish track. For net distance (Fig. 10.9), the NS/RW algorithm group fish tended to cover a smaller net distance than the NS/CCRW and NS/K algorithm groups. The opposite was true for the total distance covered, with the NS/K algorithm group covering a smaller total distance than the other two algorithm groups (Fig. 10.10). NS/CCRW and NS/RW both had similar and relatively small distributions of total distance. The NS/K algorithm group had a larger distribution.

Increasing the area of hypoxia affected sinuosity and its components because NS and sprint algorithms were used more. The sinuosity decreased for the NS/RW algorithm group and increased for the NS/K algorithm group as the area of hypoxia increased (Fig. 10.8). The NS/RW algorithm group sinuosity decreased because the net distance covered by the fish increased. Because fish travel in a mostly straight line using NS and sprint algorithms as opposed to the many turns taken by RW, increasing usage of NS and sprint algorithms increases the net distance. The sinuosity for the NS/K algorithm group increased because the total distance covered increased. The distance travelled for each time step depends on the temperature and the weighting of the random and previous components. The closer to the optimum temperature the fish are, the slower they move. By adding NS and sprint algorithms, which have set distances covered each time step, the total distance covered is increased. NS and especially sprint also contributed to the increase in the number of outliers for net and total distance as the area of hypoxia increased. There was little change for the sinuosity or its components for the NS/CCRW algorithm group as the area of hypoxia increased.

The simulation set 2 fish had larger distribution ranges for sinuosity and total distance than the simulation set 1 fish, but generally followed the same trends as

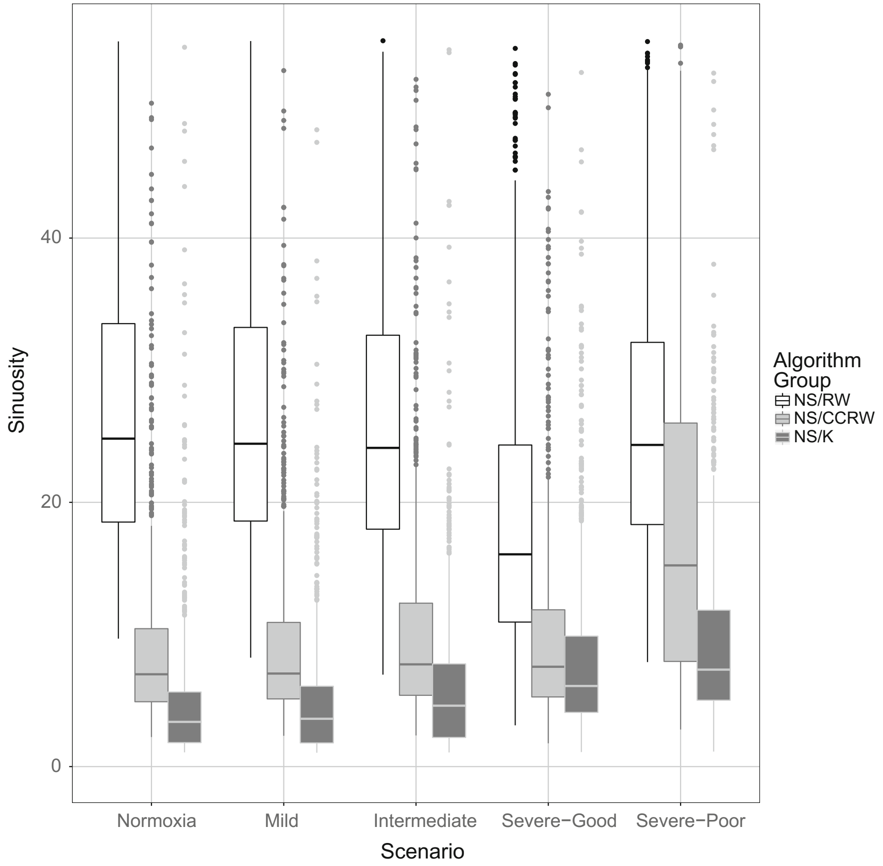

Fig. 10.8 Sinuosity (amount of wiggle) of the fish tracks. *Black dots* denote outliers. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

simulation set 1 fish for the respective algorithm groups. For sinuosity, the NS/RW algorithm group had the highest value and had a median and range similar to the normoxia, mild hypoxia, and intermediate hypoxia scenarios (Fig. 10.8). Because there was no sprint and NS had a large degree of randomness, the sinuosity did not decrease with a larger hypoxic area. For the NS/CCRW algorithm group, sinuosity for poor avoidance was larger than sinuosity for good avoidance. For the NS/K algorithm group, sinuosity was only a little larger, by about one. For net distance, the distribution ranges for poor avoidance were not much greater than those for good avoidance (Fig. 10.9). The poor avoidance distribution ranges were between the sizes of the good avoidance for the severe hypoxia scenario and the other three scenarios. The net distance for the NS/K algorithm group was larger than the net distance for

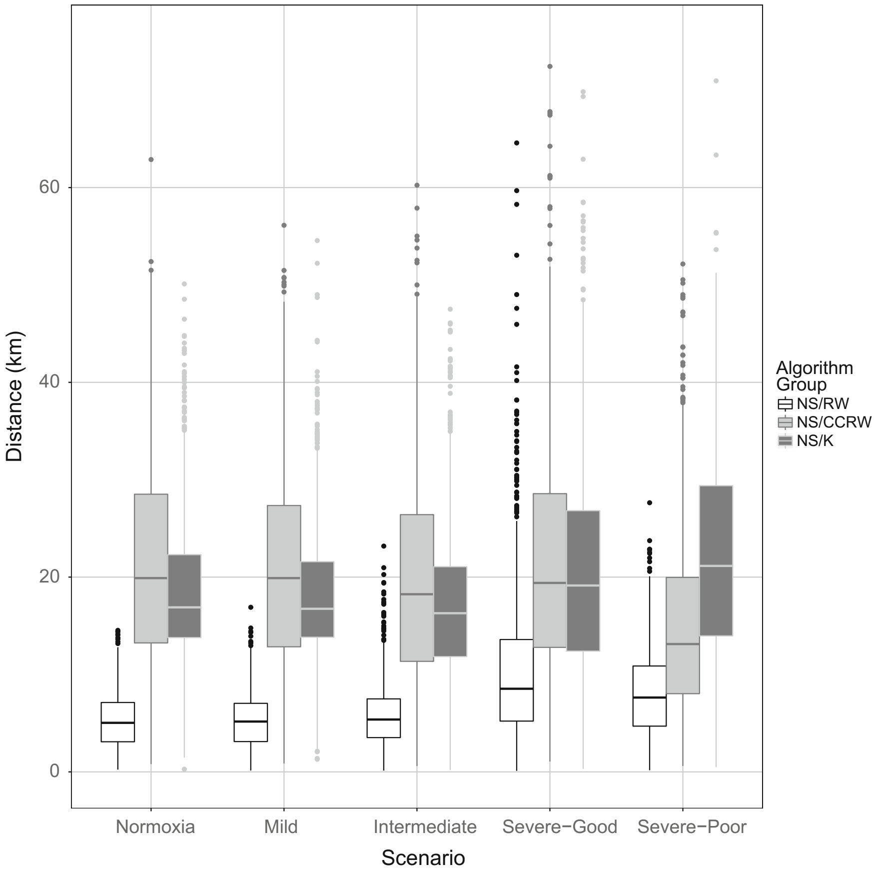

Fig. 10.9 The net, or shortest, distance between the starting and ending positions of the fish. *Black dots* denote outliers. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

the NS/CCRW algorithm group, while for good avoidance they were either similar or the net distance for the NS/CCRW algorithm group was greater. For total distance, the distribution ranges were much larger for the NS/RW and NS/CCRW algorithm groups (Fig. 10.10). For the NS/K algorithm group, the total distance was similar to the values for the normoxia, mild hypoxia, and intermediate hypoxia scenarios. As with good avoidance, for the NS/K algorithm group, the total distance was smaller than the total distance for the other two algorithm groups.

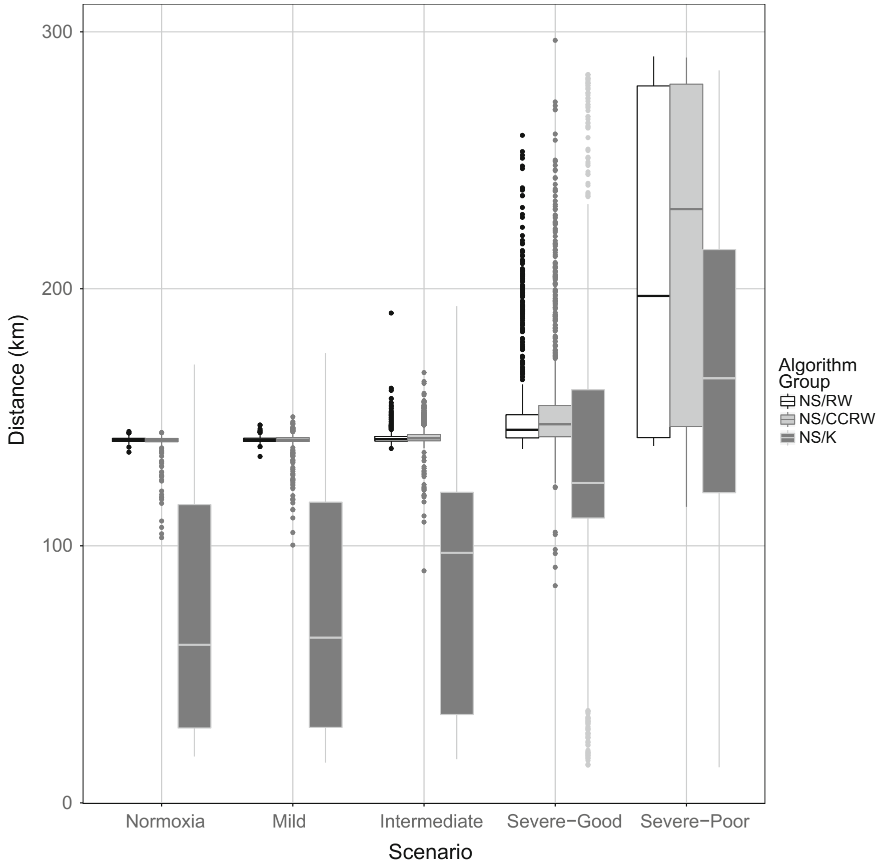

Fig. 10.10 Total distance covered by the fish. *Black dots* denote outliers. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

10.3.3 Temperature

The temperatures experienced by the fish depended on the default algorithm used, with a greater percentage of fish near the optimum temperature for NS/K algorithm group, except for the severe hypoxia scenario. The percentage of fish in the 25–27 °C range (solid purple line), which brackets the optimum temperature of 26 °C, decreased over the course of the seven days for NS/RW and NS/CCRW algorithm groups (Fig. 10.11). The 25–27 °C range was added to see how the percentage of fish around the optimum temperature changes. The percentage of fish in the 25–27 °C range for the NS/RW algorithm group decreased less than for the NS/CCRW algorithm group because the NS/RW algorithm group fish do not travel as far. For

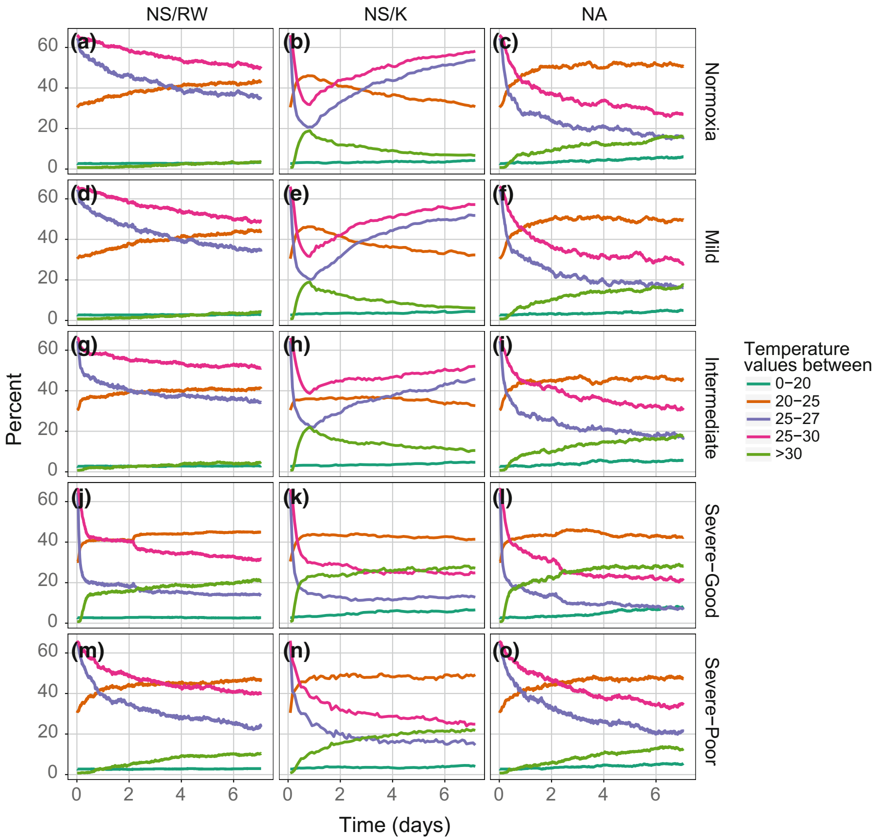

Fig. 10.11 Percentage of fish in temperature ranges over time for each algorithm group/scenario combination. The optimum temperature is 26 °C. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

the NS/K algorithm group, the percentage of fish in the 25–27 °C range increased for the normoxia (a–c), mild hypoxia (d–f), and intermediate hypoxia (g–i) scenarios. For the severe hypoxia scenario (j–l), the percentages for all three algorithm groups looked similar. For example, while the 25–27 °C range was over 50% by the end of the run for the less severe hypoxic scenarios, the percentage was less than 20 for the severe hypoxia scenario. The hypoxic zone overlaps with the 26 °C contour, so the NS/K algorithm group fish were not able to congregate near the contour line. The percentage of fish in the >30 °C range (dotted dark gray line) tended to increase for NS/CCRW algorithm group but not for the other algorithm groups, most likely because the NS/CCRW algorithm group fish spread out the most.

For simulation set 2, the percentage of fish in different temperature ranges was similar to the severe hypoxia scenario for simulation set 1. For all three algorithm groups (m–o), the percentage of fish in the 25–27 °C range decreased over the seven days (Fig. 10.11). The major difference between the poor and good avoidance for severe hypoxia scenarios was that there was a smaller percentage of fish in the >30 °C range for the poor avoidance (m–o) than for the good avoidance (j–l). This was probably due to the fact that many fish never left the hypoxic zone and did not have the chance to disperse away from it. The NS/K algorithm group (o) had the highest percentage of fish in the >30 °C range, but the percentage of fish was still lower than in case of good avoidance (l).

10.3.4 Growth and Vitality

There were only small difference in weights (<1 g) or growth (<0.05 g/day) due to default algorithm or scenario (Fig. 10.12). There was a small difference between different scenarios, but even the severe scenario (j–l) had less than 1 g difference in weight due to low DO exposure for most of the fish. The growth rates differed by less than 0.05 g/day among scenarios and algorithm groups. When extrapolated out to 30 days, the weights between algorithm groups covered the same numerical range. About 83% of fish were exposed for less than a day, which is probably why the effects on growth were so small.

The final weights for the poor avoidance set covered a similar range of values for all algorithm groups within that set and also a larger range compared to the good avoidance set. The poor avoidance runs had similar distributions of final weights with slight differences. The range for poor avoidance weights ranged from 90 g for the fish least affected by hypoxia to just below 87 g for the fish most affected (Fig. 10.12). For good avoidance, only less than 20 fish had weights below 89.5 g.

10.4 Discussion

10.4.1 Avoidance and Default Behaviors

The model results suggest that avoidance and default behaviors can be separated and evaluated independently. For example, avoidance can be modeled without having to consider the default algorithm because it did not affect the hypoxia exposure. The default behavior can be chosen based on its characteristics without considering any interaction between the avoidance and default behaviors. Importantly, the avoidance and default algorithms could be validated and calibrated separately. There is not a large amount of field data for validating and calibrating fish tracks from IBMs, so being able to use data even if all the environmental conditions used in a model are not recorded in the field data is essential.

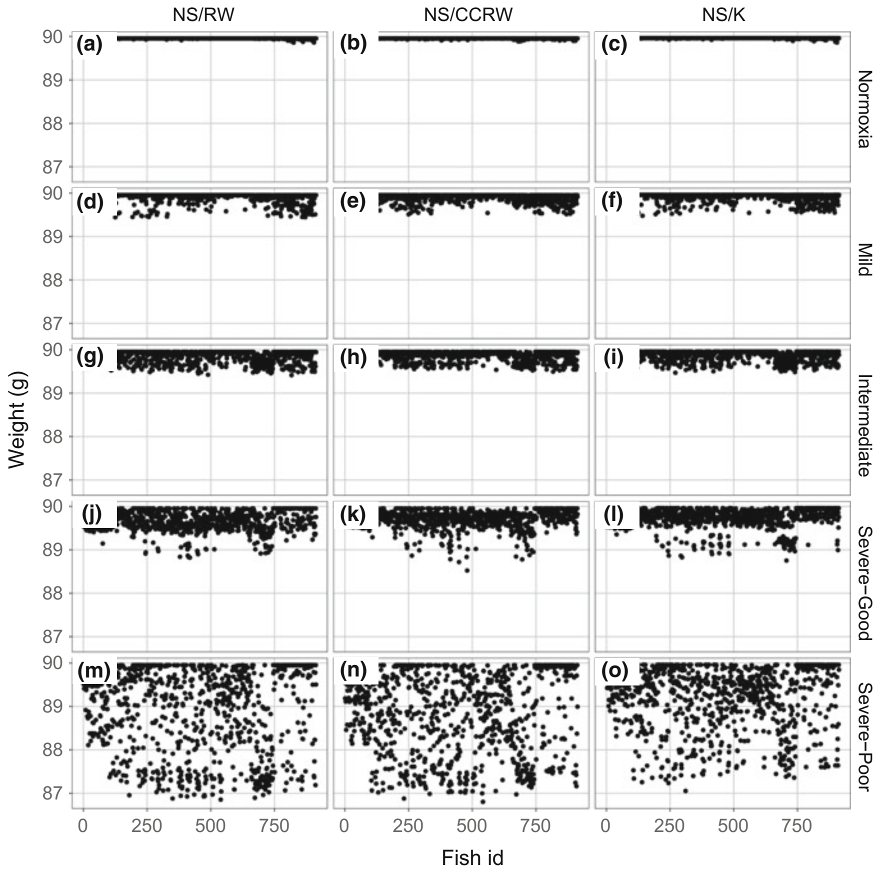

Fig. 10.12 Final weights plotted for each fish by model id number. Algorithm groups are neighborhood search/random walk (NS/RW), neighborhood search/Cauchy correlated random walk (NS/CCRW), and neighborhood search/kinesis (NS/K). The scenarios are normoxia, mild hypoxia, intermediate hypoxia, and severe hypoxia (with good and poor hypoxia avoidance)

10.4.2 Exposure

The default algorithms were found not to affect hypoxia exposure for the model fish, but the tactical behavior did affect exposure. It makes sense that the tactical behavior should have an important effect on hypoxia exposure because the tactical behavior was responsible for having the fish avoid conditions such as hypoxia. What differences there were between the default algorithms were shown when the effectiveness of the tactical behavior was changed from good to poor avoidance (Fig. 10.5). Poor avoidance magnified the differences between the default algorithms. The difference between good and poor avoidance can also be seen in the smaller sample size required to differentiate between the algorithm groups (Fig. 10.6). The difference was most likely due to the different time steps used for the random walk algorithm groups and the kinesis algorithm group. The time step used was chosen because of the characteristics of the default algorithm, but the exposure differences mostly occurred because of that time step's effect on the tactical behavior. So even when there was a difference in exposure between algorithm groups, it was generally due to the tactical behavior and not the default behavior.

The hypoxia conditions and "local" conditions had a greater effect on hypoxia exposure than the default algorithm. There was an obvious increase in exposure with increased hypoxic area. More fish were exposed in larger areas and took longer to escape the hypoxic area. There was also the increased chance of fish getting stuck and having to rely on the sprint algorithm to escape the hypoxic zone. The different scenarios also had different smaller scale or "local" features that affected hypoxia exposure. The severe scenario in particular had several features such as the normoxic island and the normoxic sliver that affected exposure. In particular, the normoxic sliver, i.e., the thin area of normoxia surrounded by hypoxia on three sides in the severe scenario, was a relatively small area for fish to inhabit. Because all the default algorithms diffuse to some extent, the fish in a small normoxic area tended to spread out into the hypoxic area. Most of these fish then used the tactical behavior and returned to the normoxic sliver. Thin hypoxic areas such as the normoxic sliver feature led to increased hypoxia exposure. Fish are known to gather at the shoal that corresponds to the normoxic sliver (Craig 2012), so whether real fish continually wander back into the hypoxic area or stay on the shoal without getting exposed would be an interesting question to explore. It would help with making the model better reflect reality and increase knowledge of the behavior of the fish.

10.4.3 Algorithm Comparison

The choice of the default algorithm did not make a significant difference in the hypoxia exposure of the fish or changes in growth due to hypoxia exposure for static conditions, so other characteristics of the algorithm must be considered when choosing which algorithm to use. As shown in the results, the temperatures experienced by the fish and the distance covered by the fish were different among the default algorithms. The time step that the algorithm can be used for is also important to consider.

The main way that the default algorithms differed was sinuosity and temperature sensitivity. There were only small differences in exposure between the default algorithms, whether avoidance was good or bad. The area covered by the fish was the major difference among the algorithms (Fig. 10.8). Fish using the RW algorithm moved only a short distance in very convoluted paths while fish using the CCRW algorithm spread out the furthest. Fish using the kinesis algorithm tended to gather along the 26 °C contour where possible, so these fish travelled farther than the RW using fish but did not spread out like the CCRW using fish. Kinesis was the only algorithm that took temperature into account and so was the only algorithm that affected temperature-related movement in the non-severe hypoxia scenarios (Fig. 10.11). The RW algorithm had more fish near the optimum temperature than the CCRW algorithm, but this was due to the RW fish not diffusing far from the starting positions along the 26 °C contour.

The time step used can limit what algorithms are effective. Kinesis is not very effective at time steps smaller than an hour on large grid cells because the fish are unable to find the preferred temperature. The CCRW and RW algorithms work at smaller time steps. While the RW algorithm works at smaller time steps, fish clearly move a shorter distance using that algorithm than with kinesis or CCRW as shown in the results. For greater diffusion, a large time step would need to be used with RW. Because CCRW is a more directional algorithm, a larger distance is covered when using that algorithm even at smaller time steps.

Selection of an appropriate time step depends on the system and the organism. Generally, a larger time step is used for slow moving particles and for large areas while a smaller time step would be used for faster moving particles and small areas. Physical variables are typically evaluated on the time frame of seconds, even for large areas. For example, the FVCOM-WASP model calculates physical and environmental data at time steps of 5 s for grid cells that can be 10 km in size (Justić and Wang 2014). For fish, the time step often depends on the grid size used. Time steps and grid sizes that have been used to model fish movement include 1-km cells with a time step of 1 hr (Creekmore 2011), 20–500 m cells with a 9-s time step (Rose et al. 2014), and <1 m with a 2-s time step (Goodwin et al. 2006). Field data could be used to determine whether croaker movement in response to hypoxia in the GOM can be modeled in sufficient detail with a 2-h time step.

The distance covered by the model fish depends on the default algorithm and the time step used. The area that a random walk algorithm can cover is limited by the time step. The average radial distance from the starting to ending point for a random walk is $\sqrt{N}$, where N is the number of steps (Landau et al. 2013). For a fixed time period, the number of steps is inversely proportional to the time step. So the number of steps is greater for the 900 s time step than for the 2-h time step. This is why for RW the fish do not travel very far and why kinesis does not work well at the shorter time step. Kinesis is the combination of the previous direction and a random walk, so the radial distance covered by kinesis is affected by the time step. The fish using kinesis do not cover a large enough area with a 900-s time step to find the preferred temperature. The CCRW algorithm is not a uniform random walk because of the use of the Cauchy distribution when choosing angles. CCRW is the only default algorithm where fish cover a large distance at the smaller time step, with the distance at 900 s for CCRW being comparable to the distance covered using kinesis for a 2-h time step. If smaller time steps are a better fit for croaker movement, the CCRW movement algorithm would be the preferred default algorithm among those compared in this paper.

In systems where multiple environmental conditions affect fish movement and distribution, being able to model fish responses to multiple conditions or stressors is useful. It is more realistic for fish to be affected by multiple stressors or conditions. Temperature and distance from shore affect the distribution of croaker in the GOM

(Craig 2012). In tidal systems, salinity and tides are important environmental conditions that can affect fish movement in conjunction with hypoxia (Brady and Targett 2013). Multiple conditions or stressors can be modeled using an event-based algorithm to choose between different algorithms depending on the condition or stressor. Event-based algorithm is useful for conditions or stressors that have clear cut offs or thresholds where the fish is either affected or not affected. For conditions or stressors that are always present and have no clear cut off or threshold, it is more useful to use a default algorithm that moves fish based on the condition or stressor. The ability to take environmental conditions, such as temperature, into account is a strength of kinesis as a default algorithm.

Determining the most appropriate default algorithm for a particular model and organism requires weighing the advantages and disadvantages of the different algorithms. For GOM croaker, more information is needed to determine which of the algorithms covered in this paper is most appropriate. Looking for additional algorithms to use as the default is also worth considering. The CCRW algorithm was adapted to work with the FVCOM particle-tracking module as an alternative to kinesis and RW. CCRW works at smaller time steps while covering a larger distance than RW. This is useful in situations where diffusion-type movement is required, but the grid cells are too large and the time step is too small for RW to sufficiently diffuse from the starting position.

10.4.4 Real Versus Model

The lack of appropriate data makes it difficult to calibrate or validate IBMs for hypoxia avoidance in the GOM. Most available data for fish locations in the GOM are from trawls or other group sampling methods that only show where fish are at one point in time. Such data sets can be compared to the general locations of fish in the model. Fish have been shown to concentrate on a shoal (Craig 2012) that corresponds to the normoxic sliver where fish gather in the severe hypoxic scenario. But for comparing fish tracks and hypoxia exposure, data sets need to have detailed information on fish movement over time and not just general locations or locations for one time step. Fish can be tracked using acoustic tags, but this does not guarantee that the horizontal movement is recorded with enough detail.

Existing data sets are either in areas that are difficult to compare to the GOM or are not detailed enough. A data set for croaker in the GOM was part of a study looking at the vertical movement of croaker in response to hypoxia. Because horizontal movement was not part of the study, it was not recorded in detail. The horizontal locations of the fish can be reconstructed after the fact from the strength of the acoustic tag signals (Grothues et al. 2013), but the resulting data have confidence intervals too large to be used to compare to the model. Two data sets that are detailed either temporally (Pepper Creek, DE, Brady and Targett 2013) or spatially (Neuse River, NC, Kevin Craig personal communication) are from shallow tidal areas with diurnal DO changes. The area, depth, and DO cycle are very different between the tidal areas and the GOM. Pepper Creek is a narrow tidal creek where the fish movement was recorded as one dimensional (Brady and Targett 2013). Neuse River is larger than Pepper Creek, but still much smaller than the GOM. Fish tracks were recorded in two dimensions at Neuse River. The tides also have a greater effect on the tidal areas, which are located on the Atlantic coast, as compared to the GOM shelf where the tides are weak. All of these differences make it difficult to compare fish behavior in the tidal areas to fish behavior in the GOM.

Despite the differences in the areas, there are still some ways that the field data can be used. The most important information that can be taken from the three existing field data sets is that fish avoid hypoxia and can survive brief exposures to hypoxic water (Brady and Targett 2013). The DO values experienced by the GOM croaker were interpolated from CTD casts near the fish location. None of the croaker were found in hypoxic conditions. This suggests that the fish were able to successfully avoid hypoxia, keeping in mind the stress due to tagging that may have affected behavior and that hypoxia was weak where the fish were tracked (Thomas Grothues personal communication). The Pepper Creek and Neuse River had fish that were exposed to hypoxia and then moved out of the hypoxic area and continued to move, indicating the exposure was sublethal. The fact that non-fatal exposure occurs means that direct effects other than mortality and indirect effects are possible. As previously mentioned, sublethal effects of low DO exposure have been found in croaker (Thomas and Rahman 2009). Even when field data cannot be directly compared to the model output, the field data can demonstrate that the processes described in the model exist in the field.

10.4.5 Impacts

The work in this paper is important because it builds on what has been done with movement algorithms and the models used. Similar movement algorithms have been used with different grids (Creekmore 2011), for different locations with different stressors (Rose et al. 2014), or in abstracted grids (Watkins and Rose 2013). This paper represents the first attempt to use the movement algorithms with a grid based on a snapshot of the FVCOM-WASP output. The CCRW algorithm was also added to the list of algorithms used before with the FVCOM-tracking module with the FVCOM-WASP output. The CCRW algorithm adds another option to the default algorithms that is not as limited by time step. There was also an increased understanding of how different algorithms behave as default algorithms in an event-based setup compared to each other. A better understanding of how algorithms behave allows for choosing the more appropriate algorithm for a given model and scenario.

Modeling movement helps to study the impacts of environmental conditions and stressors on organisms such as fish, especially when field data are hard to obtain. As mentioned in Sect. 10.4.4, there is limited field data for the interactions of croaker and the GOM hypoxic zone. There is particularly limited data for movement of individual croaker relative to the hypoxic zone. A model helps to look at the impacts of the hypoxic zone using what information there is on croaker and hypoxia. The use of a model does not negate the need for field data, but it can help to fill in gaps where field data are hard to obtain or absent.

Appropriate models can be used to help inform management decisions. Choosing the appropriate model and movement algorithms requires knowledge of the system, possible models, and possible movement algorithms. Increasing knowledge of the behaviors of different movement algorithms helps with the decision of choosing the appropriate model. Field data and a validated model can be used for management decisions. An example is a fish movement model used to model fish movement around various objects near a hydroelectric dam (Goodwin et al. 2006). If the necessary field data were collected for calibration and validation, the model in this paper could be used to inform decisions that involve the GOM hypoxic zone and fisheries.

10.5 Conclusion

This paper tested the hypothesis that the default algorithm does not affect the hypoxia exposure for model fish. The results of running three algorithm groups for four scenarios based on output from the FVCOM-WASP hydrodynamic-water quality model suggest that the default algorithm does not affect hypoxia exposure in static conditions. While exposure is not affected by the default algorithm, sinuosity and its components, total and net distance, are affected by the default algorithm used. For static conditions, the factors that should be considered when choosing a default algorithm are dispersion, time step, and environmental conditions other than DO.

For the results and conclusions of this paper to be applied to dynamic conditions or 3-D conditions and not just static 2-D conditions, the algorithms must be tested for dynamic conditions and 3-D conditions. The algorithms were tested for static 2-D conditions, which do not reflect reality very well. Consequently, the results of the paper increase the knowledge of how these algorithms perform; the results may not apply to dynamic or 3-D conditions. To better reflect reality and be more useful for management purposes, the properties of the algorithms need to be compared in dynamic conditions and in 3-D.

Validated models can help inform management decisions when field data is difficult or impossible to obtain. Models are particularly useful in situations where field data are difficult to obtain (e.g., exposure time series for large numbers of fish) or impossible to obtain (e.g., effects of future climate change). Managers can use results from a range of model scenarios to decide between different management actions. To ensure the model scenarios reflect reality as closely as possible, it is important to understand the model and to have field data for calibration and validation. By testing how the model reacts under different conditions helps the modeler to better understand the behavior of the model. Investigating how the default algorithms affect exposure helps to better understand the model for hypoxia avoidance for fish. Appropriate field data allow for calibration and validation, which help insure the model is close enough to reality. There is a need for appropriate field data for the model described in this paper. Obtaining detailed movement tracks and hypoxia time series for relatively small fish such as croaker is difficult, but worth doing to improve the model and its usefulness. Developing methods for obtaining movement and hypoxia exposure time series for croaker is also important because it establishes methods for successfully obtaining the data which could be applied to economically important species such as red snapper or shrimp.

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