

Simultaneous estimation of dispersal and survival of the gulf killifish *Fundulus grandis* from a batch-tagging experiment

Olaf P. Jensen^{1,*}, Charles W. Martin², Kiva L. Oken¹, F. Joel Fodrie³, Paola C. López-Duarte⁴, Kenneth W. Able⁵, Brian J. Roberts⁶

¹Department of Marine & Coastal Sciences, Rutgers University, New Brunswick, NJ 08901, USA

²Nature Coast Biological Station, University of Florida, Cedar Key, FL 32625, USA

³Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA

⁴Department of Biology, University of North Carolina at Charlotte, Charlotte, NC 28223, USA

⁵Rutgers University Marine Field Station, Tuckerton, NJ 08087, USA

⁶Louisiana Universities Marine Consortium, Chauvin, LA 70344, USA

ABSTRACT: The gulf killifish *Fundulus grandis* has been widely used as an indicator species for studying impacts of disturbance. However, such use requires an understanding of the spatial and temporal scales over which an individual may have been exposed to a disturbance, i.e. its dispersal range and survival. Here, we present a novel spatial capture-recapture (SCR) model for simultaneous estimation of dispersal and survival from batch-tagging data. The model is applied to simulated data and data from a mark-recapture experiment on gulf killifish in 4 saltmarsh creeks near Cocodrie, Louisiana, USA. The model is relatively robust to misspecification of the functional form of dispersal and outperforms a non-spatial model when dispersal beyond the study area occurs. However, in 2 of the study creeks, the expected decline in recaptures with distance and time from release was not observed. In the other 2 study creeks, model predictions generally matched observations, and the average estimated mortality rate was 3.44 yr⁻¹, equivalent to a maximum age of 1.3 yr. The long-term cumulative 50% dispersal distance averaged 29 m. These results suggest that observed responses of gulf killifish to disturbance generally reflect extremely local conditions (<100 m). Thus, this species can serve as a site-specific indicator of disturbance, though only individuals collected within the same year as the disturbance event are likely to have been directly exposed. Our SCR model is widely applicable to batch-tagging experiments where release and recapture locations are recorded.

KEY WORDS: Site fidelity · Home range · Gulf of Mexico · Deepwater Horizon · Macondo oil spill · Spatial capture-recapture · Fundulidae · Cyprinodontiformes

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Indicator species are commonly used to understand the impacts of a disturbance or contaminant on an ecosystem (Landres et al. 1988, Burger 2006). While there are many criteria that go into selecting indicator species (Siddig et al. 2016), an ideal indicator species must be well matched to the spatial and tempo-

ral scale of the disturbance being studied. For example, a species whose movements encompass a scale of 10s of kilometers cannot be used effectively to study differences between impacted and control sites separated by 10s to 100s of meters. Likewise, individuals of a species with a lifespan of a couple months would not have been directly exposed to a disturbance that occurred years ago. Identifying appropri-

*Corresponding author: olaf.p.jensen@gmail.com

ate indicator species thus requires a detailed understanding of dispersal and survival rates of candidate species. The challenge is that one of our most important tools for estimating these parameters, mark-recapture experiments, frequently confounds these live-history rates.

Killifishes (Fundulidae) are a widely-used indicator species within saltmarsh ecosystems (Couillard & Nellis 1999, Thériault et al. 2007, Nelson et al. 2014). Mummichog *Fundulus heteroclitus* from the east coast of the United States are one of the better-studied marsh fishes and are critical components of these wetland ecosystems due to their high abundance, widespread distribution, and intermediate trophic position in the food web (Kneib 1986, Kneib & Wagner 1994, Able et al. 2007, Burnett et al. 2007, Finley et al. 2009). Moreover, their tolerance to a wide range of environmental conditions (Able & Grothues 2018) makes them attractive for use in laboratory experiments (Boehlert & Mundy 1988, Crego & Peterson 1997). A tagging experiment on this species (Teo & Able 2003a) has demonstrated strong site fidelity but a relatively large home range (15 ha for the 99% minimum convex polygon, equivalent to a circle with radius 219 m). The maximum age of mummichog is estimated at 3 to 4 yr (Fritz & Garside 1975, Kneib & Stiven 1978). Thus, the presence of contaminants in wild-caught mummichog can be assumed to be generally indicative of contaminants in the environment within 15 ha and 3 to 4 yr of the site and time of collection.

Within the northern Gulf of Mexico, the gulf killifish *Fundulus grandis* has been used as an indicator species because of its abundance and importance as a trophic link in estuaries (Fodrie et al. 2014, McCann et al. 2017). As a result, this species has been used to detect impacts of the 2010 Deepwater Horizon oil spill (Whitehead et al. 2012, Able et al. 2015, López-Duarte et al. 2016). Individual gulf killifish exposed to sublethal concentrations of oil have been shown to undergo changes in gill morphology and to express CYP1A, a physiological marker (Whitehead et al. 2012, Dubansky et al. 2013). However, dispersal and natural mortality rates of gulf killifish remain poorly understood. A short-term (1 mo between tagging and the final recapture period) tagging study of gulf killifish in an Alabama salt marsh found little movement among 4 tag and recapture sites separated by 100 to 270 m, with only 3% of recaptured individuals found at a site other than their release location (Nelson et al. 2014). Aging of gulf killifish collected from the St. Marks National Wildlife Refuge, Florida, based on scales resulted in a maximum age of 21.6 mo (Lipcius

& Subrahmanyam 1986). A more recent study that examined otoliths from gulf killifish collected in Louisiana indicated the maximum age could be closer to 27 mo (Vastano et al. 2017). Given the legacy of anthropogenic stressors in this area (e.g. overfishing, habitat modification, and oil spills), it is of paramount importance to gain a more comprehensive understanding of the life history and demographic patterns of key indicator species such as gulf killifish.

Ideally, a tagging study should be able to provide an understanding of both movements and mortality. However, dispersal outside the study area and mortality are generally confounded in most tag-recapture models. That is, when a tagged individual is not recaptured, there are 3 possible explanations that are difficult to distinguish: (1) it was present in the study area but not detected, (2) it left the study area, or (3) it died. A 'robust' version of the Cormack-Jolly-Seber model can accommodate temporary emigration (Pollock et al. 1990) when estimating survival but provides no information about dispersal. In general, models for dispersal have developed independently from those focused on estimating survival (Gilroy et al. 2012). A newer class of spatial capture-recapture (SCR) models provide a suite of methods for separating the 2 processes based on individual recapture histories when the spatial location of tagging and recapture is known (Royle et al. 2013, Ergon & Gardner 2014, Schaub & Royle 2014).

In many cases, individual marking is impossible or impractical, and batch marking is employed. Methods for batch marking of fish range from simple fin clips to the use of chemicals or temperature change to mark otoliths (Skalski et al. 2009). Analytical methods for batch-marked capture-recapture experiments are much more limited than those which utilize individual recapture histories. Recently, Viallefont et al. (2012) developed a model for batch-marking experiments that allows for estimation of survival and transition probabilities between discrete states, including developmental stages or capture-recapture sites. This model is a significant advance, but it focuses on improving survival estimates and does not provide a detailed understanding of dispersal in continuous space. Thus, there remains a need for models which can simultaneously estimate dispersal and survival using data from batch-marking experiments.

Here, we develop a simple model for estimating dispersal and survival which we apply to a batch-marking experiment and provide estimates of survival and continuous dispersal rates of tagged gulf killifish at 4 hydrologically separated creeks in southern Louisiana, USA.

2. MATERIALS AND METHODS

2.1. Study sites

The mark-recapture experiment was conducted in 4 tidal salt marsh creeks near the Louisiana Universities Marine Consortium (LUMCON) in Cocodrie, southern Louisiana, USA (Fig. 1). Tidal creeks were chosen as previous research confirmed that gulf killifish *Fundulus grandis* frequently use these habitats (Able et al. 2015), and some site fidelity has been demonstrated in a similar species (*F. heteroclitus*, Able et al. 2012). The 4 selected sites are all separated by >250 m (Creek 1 to Creek 2: 430 m; Creek 1 to Creek 3:

370 m; Creek 1 to Creek 4: 350 m; Creek 2 to Creek 3: 460 m; Creek 2 to Creek 4: 620 m; Creek 3 to Creek 4: 260 m). To investigate potential seasonal differences, tagging was conducted at 2 of the creeks (1 and 2) in October and at the other 2 creeks (3 and 4) in May of the following year. Dominant marsh vegetation in all areas is *Spartina alterniflora*. As in other areas of coastal Louisiana, the tidal amplitude is low (~0.2 to 0.3 m; Turner 2001), and water level is primarily driven by wind and larger-scale meteorological forcing (Rozas 1995). Salinity ranges from 5 to 25 and water temperature from 5 to 25°C throughout the year (LUMCON environmental monitoring station: <http://weatherstations.lumcon.edu>).



Fig. 1. Four tidal creeks used in this study near Louisiana Universities Marine Consortium, Cocodrie, Louisiana, USA. Tagged gulf killifish were released from a central location in the tidal creek (squares) and resampled over time at various distances (circles)

Table 1. Details for tagged gulf killifish and distances for recapture efforts. Number of recapture sites (if >1) given in parentheses. See Fig. 1 for creek locations

Site	Tagging date (mm/dd/yy)	Number tagged	Total length (mm)			Recapture sites (m from release site)
			Mean	Min.	Max.	
Creek 1	10/12/2012	189	60	38	120	0, 5(3), 10(2), 30(2)
Creek 2	10/11/2012	221	59	37	94	0, 5, 10, 15, 30, 60
Creek 3	5/20/2013	89	71	38	131	0, 10(3), 20(3), 30, 40(2), 50, 60, 70
Creek 4	5/21/2013	146	83	41	135	0, 10(2), 20, 30, 40, 50, 60, 80, 90

2.2. Tagging and recapture

Following the methods of Teo & Able (2003a), gulf killifish were collected at each site and tagged using 1.1 mm long × 0.28 mm diameter coded wire tags. Tags were injected into the dorsal musculature of fish using a handheld multishot tag injector, and tag placement was verified using a handheld wand detector (Northwest Marine Technology). Minimal mortality of *F. heteroclitus* has been noted in previous studies using this method (Teo & Able 2003b, Able et al. 2006). For our study, 10 tagged individuals were kept in an aerated 19 l bucket at LUMCON, and no mortality was noted after a 48 h period. All gulf killifish were captured using wire mesh traps (41 cm long, 22 cm wide with 3 mm mesh; Memphis Net and Twine) baited with approximately 5 to 10 pieces of commercially available dog food (Ol' Roy™). For initial collections, trapping was conducted for 1 to 2 d (with trap soak times of 4 to 14 h) until at least 75 fish were captured at each creek. Collected fish were tagged, measured (±1 mm), and kept in an aerated cooler until released at a single release location (denoted Distance 0) at each site (Fig. 1). Release locations were sited far from the creek mouth to limit potential predation mortality of newly released tagged individuals, which was assumed to be higher near the deeper water commonly found at creek mouths. A total of 189, 221, 89, and 146 gulf killifish (average size 68 mm) were successfully tagged in Creeks 1, 2, 3, and 4, respectively (Table 1). This research was conducted under the Rutgers University Institutional Animal Care and Use Committee (IACUC) protocol # 88-042 'Determinants of fish habitat quality in stressed and unstressed estuaries.'

Recaptures were obtained at fixed stations located at set intervals from 5 to 90 m away from the release site, depending on creek morphology

(Table 1). The spacing among adjacent recapture locations was shorter (5 to 10 m) near the release location to maximize expected recaptures from a fixed amount of sampling effort (i.e. number of traps) and wider in Creeks 3 and 4 because these creeks were longer. These recapture sites were sampled successively over time from 1 to 339 d post-release (Table 2). To recapture tagged individuals, 3 traps were placed overnight on the bottom at the edge/marsh interface at each location and checked the next morning such that total fishing effort was consistent among locations within a creek. After recapture, tagged individuals from each location were identified using the aforementioned handheld wand scanner and measured (±1 mm), and all tagged and untagged gulf killifish were counted and recorded. All fish were released at the site of capture to avoid introducing confounding density-dependent factors or altering dispersal patterns. Although coded wire tags can allow for the fate of specific individuals to be tracked via the dissection and examination of tags post capture, retention of recaptured individuals would have resulted in rapid depletion of the tagged population thus limiting the study duration.

2.3. Tag-recapture model

We assumed that the expected number of recaptured individuals at location i at time t , $E(R_{i,t})$, is related to

Table 2. Temporal distribution of sampling at the 4 sites. Numbers indicate days since release (days at sampling separated by commas for sites sampled repeatedly). Months in which no sampling occurred are indicated with a dash.

See Fig. 1 for creek locations

	2012			2013								
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jul	Jul	Aug	Sep
Creek 1	1,2,7	19	58	-	-	152	-	225	-	290	-	338
Creek 2	1,2,8	20	59	-	-	153	-	222	-	291	-	339
Creek 3	-	-	-	-	-	-	-	1	13	44,69	-	117
Creek 4	-	-	-	-	-	-	-	1	12	43,68	-	116

the number of individuals tagged, survival and dispersal processes, and availability to recapture:

$$E(R_{i,t}) = N_0 S^t D_{i,t} \lambda \quad (1)$$

Here, N_0 is the initial number of marked individuals, S is the daily survival rate, $D_{i,t}$ is the relative density of marked individuals at location i and time t (determined by the dispersal model described below), and λ is a scalar representing the availability of marked individuals to the sampling gear. We pooled recaptures across traps within each site-sampling period; modeling each trap separately decreased the estimate of the availability parameter as expected but did not influence estimates related to survival or dispersal. Dispersal is modeled here as a relative frequency ‘distribution of dispersal distances’ (DDD) in continuous space (Paradis et al. 2002, Flostrand et al. 2009) using 3 candidate dispersal models: the half normal, the exponential, and the half Cauchy (Eqs. 2, 3, and 4, respectively),

$$D_{i,t} = \sqrt{\frac{2}{\pi\sigma_t^2}} \exp\left(-\frac{x_i^2}{2\sigma_t^2}\right) \quad (2)$$

$$D_{i,t} = \frac{1}{\sigma_t} \exp\left(-\frac{x_i}{\sigma_t}\right) \quad (3)$$

$$D_{i,t} = \frac{2}{\pi\sigma_t \left[1 + \left(\frac{x_i}{\sigma_t}\right)^2\right]} \quad (4)$$

where $D_{i,t}$ is the relative density of marked individuals at i and time after release t , x_i is the distance between i and the release site, and σ_t is the dispersal parameter at t . Normalizing constants were included so that the 3 distributions had comparable scales. All 3 dispersal models are similar in that they have a single parameter that controls the extent of dispersal. Both the exponential and half Cauchy models have heavier tails than the normal distribution. The Cauchy is a particularly heavy-tailed distribution often used to accommodate the more frequent observation of long-distance dispersals than expected from normal or exponential distributions (Shaw 1995).

In theory, the dispersal distributions should expand over time as individuals move away from the tagging site. If individual movements follow a center-biased random walk (or Ornstein-Uhlenbeck process), the parameter controlling the dispersal distance (e.g. the variance for the half-normal distribution) should approach an asymptote. Therefore, in addition to the simple constant dispersal model, we quantified dynamic dispersal distributions in 3 different ways (hereafter referred to as ‘model structures’): (1) as an

independent dispersal term estimated at each time t , (2) as a random effect where the dispersal term at each time t is a random value drawn from a lognormal hyper-distribution describing average dispersal, and (3) as a 2-parameter asymptotic function of t .

During initial data exploration, we found strong evidence for overdispersion of the recapture counts, i.e. more variability in counts than would be expected from a Poisson distribution. Therefore, we modeled the count data using a negative binomial distribution which estimates an additional variance parameter. This allows the variance of the counts to exceed the Poisson expectation and is often useful in ecological settings with highly variable data (Bolker 2008). The Poisson distribution is a special case of the negative binomial distribution used here.

The model was implemented in R (v3.5.1, R Core Team 2018) using the Template Model Builder package (Kristensen et al. 2016) to perform maximum likelihood estimation. Data were analyzed for each study site separately to allow for comparison. Akaike’s information criterion (AIC) was used to select the most parsimonious model structure and dispersal model.

We tested our estimation model with simulated data for a single hypothetical creek. Simulated data had the same data structure (sampling distances, dates sampled, number of releases) as Creek 2, which has a simple linear morphology with a single channel. We used a daily survival rate of 0.99 (equivalent to a mortality rate of 3.67 yr^{-1} and a maximum age of 1.17 yr), an availability parameter of 2, and an overdispersion parameter of 2, all approximately within the range of the observed data. We allowed the dispersal parameter to increase over time following a Michaelis-Menten-style asymptotic curve: $\sigma_t = 32.5t/(t + 6.35)$, where dispersal reaches 95% of its asymptotic value by Day 121. These parameter values were also approximated from the data. Because the dispersal parameter is not directly comparable among the 3 dispersal models and we wished to investigate the effect of model misspecification, we quantified the distance within which 50% of the DDD falls for the constant dispersal parameter. To achieve comparability among the different dispersal structures (including those with time-varying dispersal parameters), we calculated this statistic for the resampling event 20 d after release. We simulated 500 data sets from each dispersal model and fit all 3 dispersal models to each data set, assuming a constant dispersal parameter, a fixed effect dispersal parameter, a random effect dispersal parameter, a Michaelis-Menten asymptotic dispersal parameter,

and a von Bertalanffy asymptotic dispersal parameter to test the importance of functional form of the asymptote. Note that the von Bertalanffy curve was only fit to the simulated data and not actual data. For comparison, we also fit a non-spatial model to each simulated dataset that ignored dispersal. This made a total of 24 000 fitted models attempted. For each fitted model, we quantified the relative error ($[\text{observed} - \text{true}]/\text{true}$) of both derived quantities related to dispersal (except for the fixed effect model), as well as the maximum age. Maximum age (A_{max}) was calculated from daily survival following Hoenig (1983):

$$A_{\text{max}} = \exp\left(\frac{1.46 - \log M}{1.01}\right) \quad (5)$$

where the mortality rate $M = (-365) \times \log S$, and S is the daily survival rate estimated based on Eq. (1). For each data set, we compared the AIC value for the 3

dispersal models that assumed a Michaelis-Menten asymptote for the dispersal parameter (the true process). This allowed us to test how often the correct dispersal model was selected.

3. RESULTS

3.1. Gulf killifish tagging experiment

Overall, tagged fish exhibited a high degree of site fidelity (Fig. 2). In Creeks 1 and 2, a total of 176 and 208 tagged fish were recaptured from a total of 2494 and 2483 total fish captured in each creek, respectively (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m624p183_supp1.xlsx). In these creeks, recapture was generally highest at the initial release location and decreased with increasing dis-

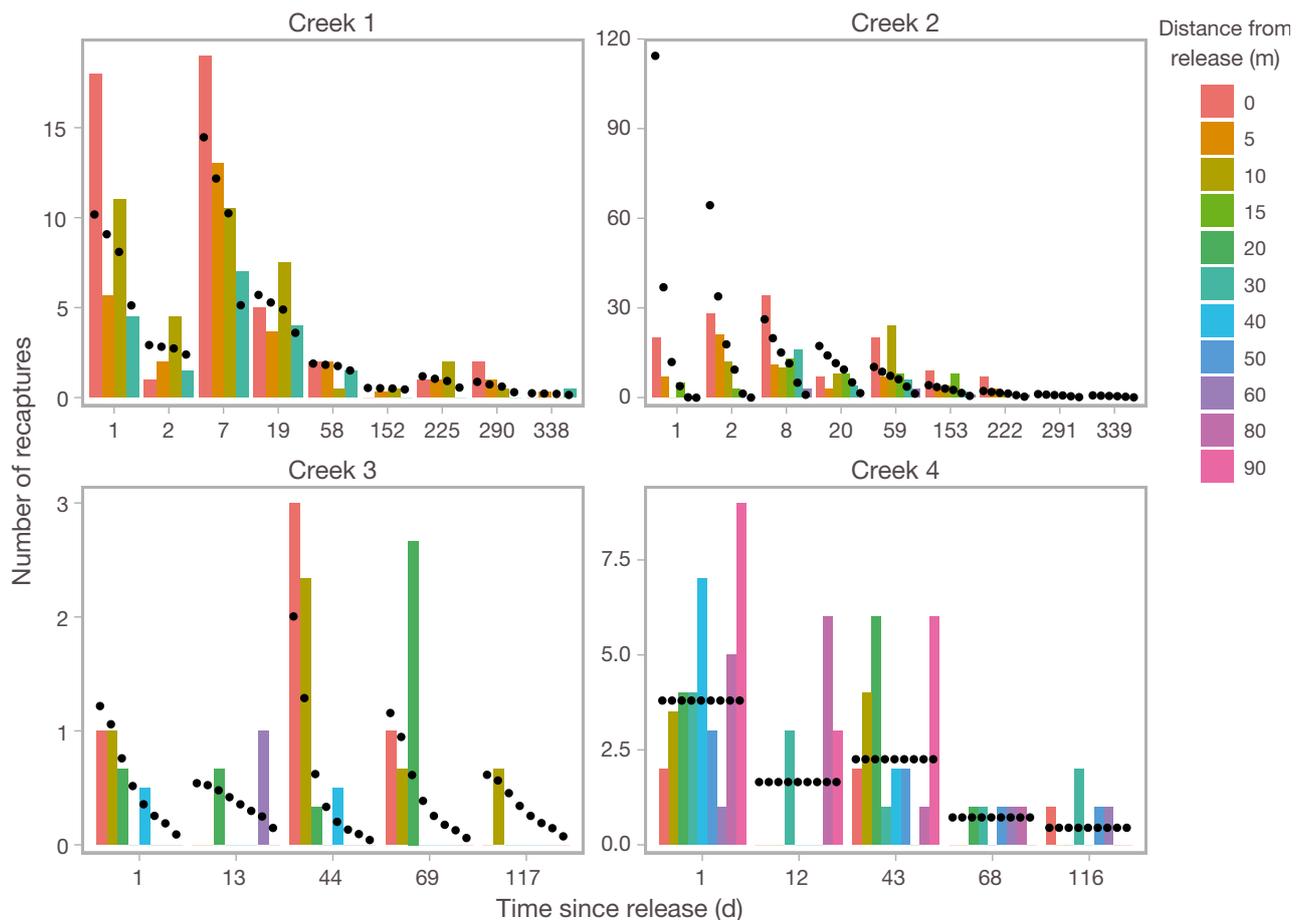


Fig. 2. Observed (bars) and predicted (points) number of recaptures from the model with greatest Akaike information criterion (AIC) support. Note inconsistent scales across panels were used so that trends within creeks with lower recapture rates were visible. In several cases, there were multiple sites within a common distance from the release location. In these cases, bar heights represent averages across sites; however, sites were modeled independently. Because tagging was initiated at different times, the recapture event at Creeks 1/2 on Day 225/222 occurred at approximately the same time as the recapture event on Day 1 at Creeks 3 and 4

tance. In general, this trend weakened over time as fewer recaptures were made. Fewer recaptures of tagged fish were observed in Creeks 3 and 4, however, with 28 recaptures (of 2406 total fish captured) in Creek 3 and 50 tagged fish (of 2314 total fish) recaptured in Creek 4 (Table S1). Over the entire study, we found high initial recapture rates at Creeks 1 and 2 (maximum: 49%). The maximum distance at which a tagged fish was recaptured was 90 m, and the maximum time at large was 338 d after tagging.

3.2. Simulations

Simulation results indicated that survival estimates (and parameters derived from survival, such as instantaneous mortality and maximum age) are robust to misspecifying the form of the dispersal distribution as long as the dispersal parameter is estimated and allowed to vary in time (Fig. 3). Failing to account for dispersal and its changes over time leads to positively biased estimates of mortality (and therefore nega-

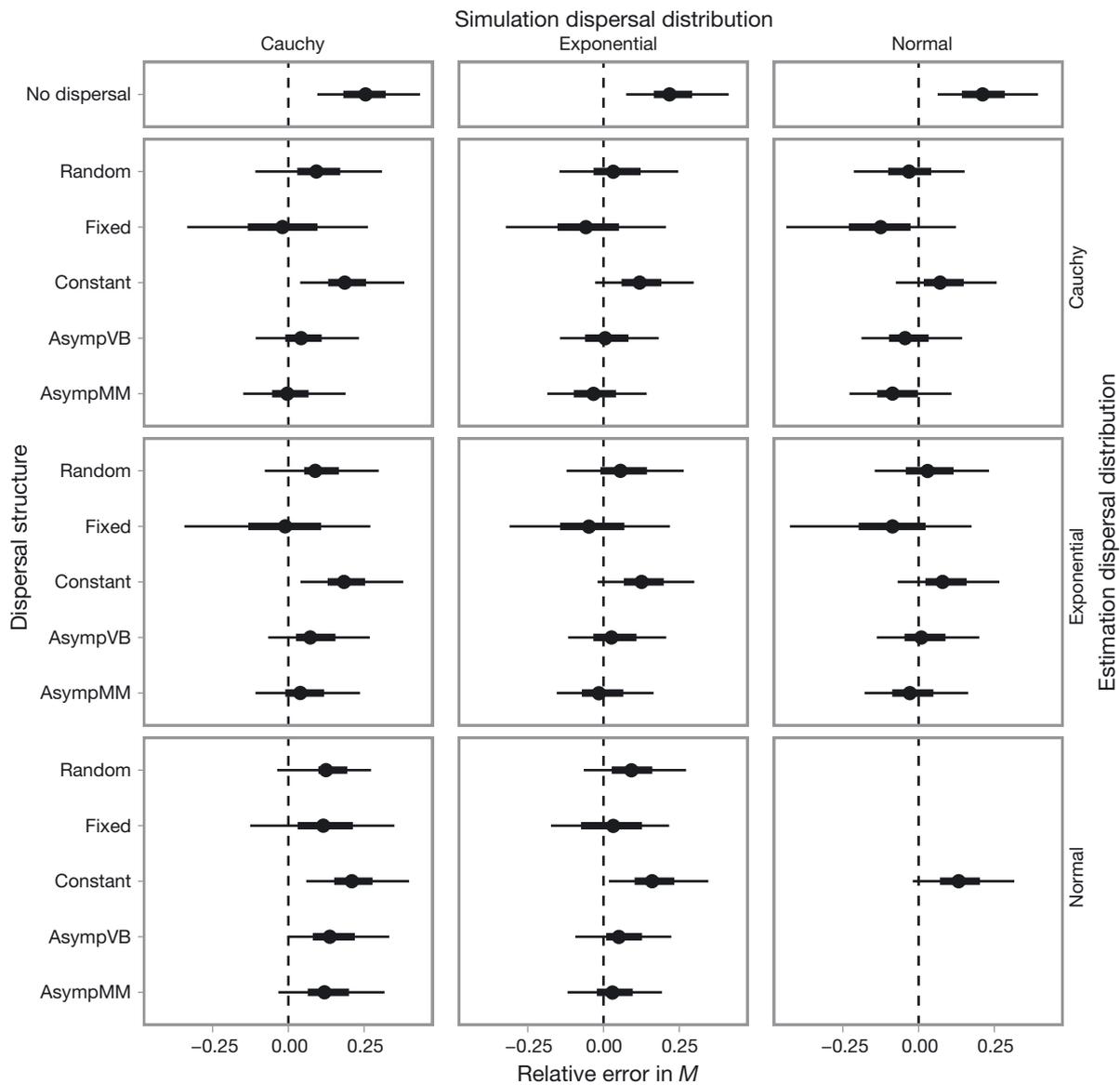


Fig. 3. Simulation results: relative error of estimated annual mortality (M) across different dispersal distributions and structures for estimating the dispersal parameter. The five dispersal structures are random (scale parameter estimated as independent random effect for each sampling occasion), fixed (scale parameter estimated as fixed effect), constant (scale parameter assumed constant across sampling occasions), and AsympVB and AsympMM, which both assume the scale parameter increases in an asymptotic fashion over time, either via a von Bertalanffy (VB) function or a Michaelis-Menten (MM) function. Point is at the median relative error, thick bars represent middle 50% across simulations, thin bars represent middle 90%. Missing scenarios indicate that the model did not converge for any of the 500 simulations

Table 3. Average Akaike information criterion (AIC) \pm 1 SD across simulations. Each row represents a different simulation model; each column is a different estimation model. The correct structure for the dispersal parameter (Michaelis-Menten) was assumed in all cases

	Normal	Exponential	Cauchy	% correct model chosen
Normal	309 \pm 9	300 \pm 10	316 \pm 10	9
Exponential	312 \pm 12	296 \pm 11	304 \pm 11	94.2
Cauchy	313 \pm 13	296 \pm 12	290 \pm 11	84.4

tively biased estimates of maximum age); the estimation model assumes that fish that were not recaptured later in the study died, when they may have instead moved beyond the study area. As expected, dispersal-related quantities were more sensitive to model misspecification than survival-related quantities, though dispersal quantities were generally estimable under the correctly specified model for the Cauchy and exponential dispersal distributions (Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m624p183_supp2.pdf). Overall, precision for the dispersal statistic we examined (distance within which 50% of tagged fish disperse on Day 20) was lower than precision for estimates of mortality.

Among the 4 model structures we tested that do allow the dispersal parameter to change through time, all were reasonably accurate (<22% median relative error in all cases) in estimating the mortality rate (Fig. 3). As expected, the Michaelis-Menten asymptotic model structure (i.e. the true model structure) had the lowest median relative error when averaged across the 9 combinations of simulation and estimation dispersal models (0.00870). The fixed effect model structure that independently estimates the dispersal parameter in each time period performed nearly as well in terms of accuracy (-0.0193), but this heavily parameterized model had poor precision and results were more variable across simulations than those of any other model structure. The incorrect asymptotic model structure (i.e. von Bertalanffy; 0.0440) and the random effect model structure (0.0672) both had a slight positive bias when estimating the mortality rate but similar precision to the true model. No time-varying dispersal models successfully converged when the simulation and estimation dispersal distribution were both normal. Overall, the mortality rate was still overestimated (i.e. positive bias much more common than negative bias) but to a lesser degree than when ignoring dispersal altogether.

When the correct temporal structure for the dispersal term was specified (Michaelis-Menten), AIC model selection was reliably able to select the correct dispersal distribution when data were simulated from the exponential and Cauchy distributions but not the normal distribution (Table 3). However, we note that incorrect specification of the dispersal model did not have a major influence on bias in estimates of mortality (Fig. 3).

3.3. Model application to the gulf killifish mark-recapture experiment

Linearity of the creeks appeared to be an important factor in how well the model fit the data. Creeks 1 and 2 were characterized by a relatively simple linear structure with a single within-channel pathway between the release site and recapture sites. Both observations and model predictions for Creeks 1 and 2 showed a general decline in recaptures with distance from the release site and over time (Fig. 2), as expected. In contrast, Creeks 3 and 4 were surrounded by lower-elevation marsh that was frequently inundated during periods of high water (high tides and/or wind-related high-water events). This resulted in multiple pathways of varying distances by which fish could move from one recapture location to another. In these creeks (3 and 4), we observed little evidence of recapture rates declining with distance from the tagging site, and the recapture rates themselves were also low (Fig. 2). This caused the models to either fail to converge (Creek 3) or to estimate unrealistic results (Creek 4, Table 4). We also cannot discount the possibility that the seasonal timing of tagging resulted in the observed differences between Creeks 1 and 2 (tagged in October) and Creeks 3 and 4 (tagged in May).

Mortality estimates were similar for Creeks 1 and 2 across all 6 models and were equivalent, on average, to a mean (\pm 1 SD) mortality rate of $3.64 \pm 0.78 \text{ yr}^{-1}$ for Creek 1 and $3.25 \pm 0.58 \text{ yr}^{-1}$ for Creek 2. Using Hoenig's (1983) relationship between natural mortality and longevity, these estimates equate to a maximum age of $1.2 \pm 0.25 \text{ yr}$ for Creek 1 and $1.3 \pm 0.23 \text{ yr}$ for Creek 2. Mortality estimates were unreliable for Creeks 3 (unrealistically low) and 4 (unrealistically high; Table 4).

For the well-estimated Creeks 1 and 2, there was support for both the random effect and the asymptotic model structures with greatest support for the random effect in Creek 1 and the asymptotic model (Michaelis-Menten) in Creek 2 (Table 4, Table S2 in Supplement 2). Dispersal occurred quickly in Creek 2,

Table 4. Model estimates of the natural mortality rate (M), maximum age (A_{\max}), distance within which 50% of individuals have dispersed at 20 d or the fourth sampling occasion (for the random dispersal structure), and the dispersal distribution and dispersal structure for the top ranked model for each creek. Uncertainty reported is ± 1 standard deviation. The fourth sampling occasion occurred ~ 3 wk post-release in Creeks 1 and 2 and 10 wk post-release in Creeks 3 and 4

Location	M (yr ⁻¹)	A_{\max} (yr)	Mean dist @ 50% disp.	Dispersal distribution	Dispersal structure
Creek 1	3.6 \pm 0.8	1.2 \pm 0.3	92 \pm 45 m	Exponential	Random
Creek 2	3.3 \pm 0.6	1.3 \pm 0.2	20 \pm 5 m	Exponential	Michaelis-Menten
Creek 3	1.3 \pm 2.1	3.2 \pm 5.1	34 \pm 42 m	Cauchy	Random
Creek 4	6.3 \pm 2.4	0.7 \pm 0.3	712–20 000 km	Equal support	Random

reaching 50% of the asymptotic dispersal distribution in (mean \pm SD) 6.3 \pm 3 d and 95% in 121 \pm 65 d. However, with a coefficient of variation of nearly 50%, there was high uncertainty in the dispersal rate. We also note that the asymptotic model overestimated recaptures for sites near the release location during the first 2 d following release, i.e. it underestimated how quickly tagged individuals dispersed. After 1 wk, fits were more appropriate (Fig. 2). Unlike the simulations, there was very little differentiation in AIC support among the 3 dispersal distributions. Estimates of the distance within which 50% of individuals are found at 20 d post-release ranged from 20 to 92 m for the best supported models in Creeks and 1 and 2.

4. DISCUSSION

Our results generally confirm that the spatial scale of gulf killifish *Fundulus grandis* dispersal and the temporal scale of their lifespan are an appropriate match for the relevant scales in studies that have used them as an indicator species for anthropogenic disturbances such as the 2010 Macondo oil spill. Our model estimates of the average long-term cumulative 50% dispersal distance suggest that half of all tagged individuals can be expected to be found no further than 29 m from the release site. In comparison, oiled and unoiled sites were separated by 50 m to several kilometers in Able et al. (2015) and 10s to 100s of kilometers in Whitehead et al. (2012) and López-Duarte et al. (2016). Our estimated maximum age (1.2 to 1.3 yr) suggests that the adult gulf killifish collected by Whitehead et al. (2012) within the first 4 mo after the spill were likely present in the marsh at the time that oil from the spill first arrived. However, the individuals captured by Able et al. (2015) > 2 yr after the spill were most likely not alive at the time of the spill.

Although there is little quantitative data on gulf killifish dispersal distances, estimates of dispersal

from the application of our spatial mark-recapture model to field data from Creeks 1 and 2 are comparable to another published study on this species and generally within the same range as dispersal distances reported for the congeneric mummichog. The only other quantitative study of gulf killifish dispersal that we are aware of is Nelson et al. (2014), which documented extremely high recapture rates (56%) with 97% of recaptures occurring at the same location. Of the remaining 3% of individuals that were recaptured at a different location, 29 out of 31 (94%) were recaptured 100 m away. However, the time period of the Nelson et al. (2014) study was only ~ 1 mo. Studies of mummichog, the east coast congener, have demonstrated similarly limited dispersal (Crum et al. 2018). For example, young-of-the-year moved 0 to 299 m from their release location (Able et al. 2006). A study of adult mummichog found extremely localized home ranges, with dispersal limited to 36 m (Lotrich 1975). Other studies have found higher, but still relatively localized, home ranges for mummichog, from 6 ha (McMahon et al. 2005, Rudershausen et al. 2014; equivalent to a circle with radius 138 m) to 15 ha (Teo & Able 2003a,b; equivalent to a circle with radius 219 m). The latter study occurred in a restored low elevation marsh that was completely flooded at high tide with no well-defined creeks, similar to our Creeks 3 and 4. This difference may account for the larger home range observed by Teo & Able (2003a,b). Others have found high site fidelity in marshes for other species of *Fundulus*, including spotfin killifish *F. luciae* (Able et al. 2006).

Our estimates of longevity are lower than estimates from aging studies, although the dependence of maximum age on sample size in aging studies makes direct comparison difficult. Maximum age estimates of 1.2 and 1.3 yr (upper 95% CI of 1.7 and 1.8, respectively) were consistent for the 2 creeks (Creeks 1 and 2, respectively) for which the model converged and provided a reasonable fit to the data. These estimates differ from the maximum ages of 1.8 yr from a sample of 12 individuals aged using scales (Lipcius & Sub-

rahmanyam 1986) and 2.3 yr from 77 individuals aged using otoliths (Vastano et al. 2017). The maximum age in a sample from a population increases with the size of that sample (Hoenig 1983) up to some asymptote. Thus, larger samples of aged gulf killifish may result in even higher maximum age.

Our spatial capture-recapture model for batch-marking experiments provided more accurate and precise estimates of survival rate than non-spatial models but struggled more to estimate dispersal-related quantities. When marked individuals disperse away from the tagging site over time (i.e. the dispersal parameter, σ_t , is time-dependent), our model's estimates of survival (and its related quantities) are robust to the selected model parameterization, as long as the structure allows for time-varying dispersal. Estimation of dispersal-related quantities depended more strongly on the selected dispersal model. In the analysis of data from our mark-recapture experiment, estimates of the distance within which 50% of individuals are found differed by ~40% among the 3 dispersal models. Dispersal characteristics defined further out in the tails of the distributions (e.g. the distance within which 90% of individuals are found, not shown) differ even more among the alternative dispersal models, and it is difficult to discern the best dispersal model based solely on AIC support. Therefore, conclusions about maximum dispersal distances are more uncertain than those about average dispersal distances.

The failure of our model to accurately represent the complex patterns observed at Creeks 3 and 4 is most likely a result of interactions between the morphology of these creeks and the seasonal timing of their sampling. The lower elevation of these creeks caused the adjacent marsh surface to be inundated at higher water levels, which commonly occurs during the spring in Barataria Bay (Minello et al. 2012), i.e. near the time when fish were tagged and released in these creeks. Our spatial capture-recapture model cannot easily incorporate dispersal that is sometimes constrained to a channel and at other times unconstrained. However, an additional term to account for variation in recapture efficiency among sampling events could be added without fundamentally changing the model structure. This is a potentially fruitful avenue for further model development in the future.

We recommend use of our spatial capture-recapture model to estimate survival in batch-marking studies where movement away from the tagging site is thought to play a significant role in recapture patterns. In particular, our model can help disentangle movement beyond the study area from mortality.

These 2 explanations for lower tag-recapture rates are confounded in non-spatial capture-recapture models (Schaub and Royle 2014). Individually identifiable markings remain a better way to understand detailed patterns of movement and dispersal, including individual variability and the influence of characteristics such as size or sex on movement patterns. However, batch marking is often the only feasible approach when time and budgets are limited or the size of the organism precludes the use of individually identifiable markings. In such cases, our model represents a significant advance over non-spatial analyses of batch-marking studies.

Data archive: Code and mark-recapture data are available at <http://github.com/okenk/fundulus-dispersal>.

Acknowledgements. This research was made possible by a grant from The Gulf of Mexico Research Initiative to the Coastal Waters Consortium. Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org> (doi: 10.7266/N7J10121). The funders had no role in the design, execution, or analyses of this project. We thank LUMCON for support with logistics and the following individuals for assistance with sampling efforts: R. Blake, C. Filosa, A. Hopple, J. Olin, M. Rich, and A. Riggs. We are grateful for A. Vastano's assistance with manuscript preparation and formatting.

LITERATURE CITED

- Able KW, Grothues TM (2018) Essential fish habitat for nearshore sentinel species of fishes and crabs in heavily urbanized New York Harbor. *Urban Naturalist* 16:1–25
- ✦ Able KW, Hagan SM, Brown SA (2006) Habitat use, movement and growth of young-of-the-year *Fundulus* spp. in southern New Jersey salt marshes: comparisons based on tag/recapture. *J Exp Mar Biol Ecol* 335:177–187
- ✦ Able KW, Balletto JH, Hagan SM, Jivoff PR, Strait K (2007) Linkages between salt marshes and other nekton habitats in Delaware Bay, USA. *Rev Fish Sci* 15:1–61
- ✦ Able KW, Vivian DN, Petruzzelli G, Hagan SM (2012) Connectivity among salt marsh subhabitats: residency and movements of the mummichog (*Fundulus heteroclitus*). *Estuar Coast* 35:743–753
- ✦ Able KW, López-Duarte PC, Fodrie FJ, Jensen OP and others (2015) Fish assemblages in Louisiana salt marshes: effects of the Macondo oil spill. *Estuar Coast* 38:1385–1398
- Boehlert GW, Mundy BC (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. In: Weinstein MP (ed) *Larval fish and shellfish transport through inlets*. American Fisheries Society, Bethesda, MA, p 51–67
- Bolker BM (2008) *Ecological models and data in R*. Princeton University Press, Princeton, NJ
- ✦ Burger J (2006) Bioindicators: types, development, and use in ecological assessment and research. *Environ Bioindic* 1:22–39

- Burnett KG, Bain LJ, Baldwin WS, Callard GV and others (2007) *Fundulus* as the premier teleost model in environmental biology: opportunities for new insights using genomics. *Comp Biochem Physiol Part D Genomics Proteomics* 2:257–286
- Couillard CM, Nellis P (1999) Organochlorine contaminants in mummichog (*Fundulus heteroclitus*) living downstream from a bleached-kraft pulp mill in the Miramichi Estuary, New Brunswick, Canada. *Environ Toxicol Chem* 18:2545–2556
- Crego GJ, Peterson MS (1997) Salinity tolerance of four ecologically distinct species of *Fundulus* (Pisces: Fundulidae) from the northern Gulf of Mexico. *Gulf Mex Sci* 1: 45–49
- Crum KP, Balouskus RG, Targett TE (2018) Growth and movements of mummichogs (*Fundulus heteroclitus*) along armored and vegetated estuarine shorelines. *Estuar Coast* 41:131–143
- Dubansky B, Whitehead A, Miller JT, Rice CD, Galvez F (2013) Multitissue molecular, genomic, and developmental effects of the Deepwater Horizon oil spill on resident Gulf killifish (*Fundulus grandis*). *Environ Sci Technol* 47: 5074–5082
- Ergon T, Gardner B (2014) Separating mortality and emigration: modelling space use, dispersal and survival with robust design spatial capture–recapture data. *Methods Ecol Evol* 5:1327–1336
- Finley MA, Courtenay SC, Teather KL, van den Heuvel MR (2009) Assessment of northern mummichog (*Fundulus heteroclitus macrolepidotus*) as an estuarine pollution monitoring species. *Water Qual Res J Canada* 44: 323–332
- Flostrand LA, Schweigert JF, Daniel KS, Cleary JS (2009) Measuring and modelling Pacific herring spawning-site fidelity and dispersal using tag-recovery dispersal curves. *ICES J Mar Sci* 66:1754–1761
- Fodrie FJ, Able KW, Galvez F, Heck KL Jr and others (2014) Integrating organismal and population responses of estuarine fishes in Macondo spill research. *Bioscience* 64: 778–788
- Fritz ES, Garside ET (1975) Comparison of age composition, growth, and fecundity between two populations each of *Fundulus heteroclitus* and *F. diaphanous* (Pisces: Cyprinodontidae). *Can J Zool* 53:361–369
- Gilroy JJ, Virzi T, Boulton RL, Lockwood JL (2012) A new approach to the ‘apparent survival’ problem: estimating true survival rates from mark–recapture studies. *Ecology* 93:1509–1516
- Hoening JM (1983) Empirical use of longevity data to estimate mortality rates. *Fish Bull (Wash D C)* 82: 898–903
- Kneib RT (1986) The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *Am Zool* 26:259–269
- Kneib RT, Stiven AE (1978) Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. *J Exp Mar Biol Ecol* 31:121–140
- Kneib RT, Wagner SL (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Mar Ecol Prog Ser* 106:227–238
- Kristensen K, Nielsen A, Berg CW, Skaug H, Bell BM (2016) TMB: automatic differentiation and Laplace approximation. *J Stat Softw* 70:1–21
- Landres PB, Verner J, Thomas JW (1988) Ecological uses of vertebrate indicator species: a critique. *Conserv Biol* 2: 316–328
- Lipcius RN, Subrahmanyam CB (1986) Temporal factors influencing killifish abundance and recruitment in Gulf of Mexico salt marshes. *Estuar Coast Shelf Sci* 22: 101–114
- López-Duarte PC, Fodrie FJ, Jensen OP, Whitehead A, Galvez F, Dubansky B, Able KW (2016) Is exposure to Macondo oil reflected in the otolith chemistry of marsh-resident fish? *PLOS ONE* 11:e0162699
- Lotrich VA (1975) Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. *Ecology* 56:191–198
- McCann MJ, Able KW, Christian RR, Fodrie FJ and others (2017) Key taxa in food web responses to stressors: the Deepwater Horizon oil spill. *Front Ecol Environ* 15: 142–149
- McMahan KW, Johnson BJ, Ambrose WG Jr (2005) Diet and movement of the Killifish, *Fundulus heteroclitus*, in a Maine salt marsh assessed using gut contents and stable isotope analyses. *Estuaries* 28:966–973
- Minello TJ, Rozas LP, Baker R (2012) Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. *Estuar Coast* 35:501–514
- Nelson TR, Sutton D, DeVries DR (2014) Summer movements of the Gulf Killifish (*Fundulus grandis*) in a northern Gulf of Mexico salt marsh. *Estuar Coast* 37: 1295–1300
- Paradis E, Baillie SR, Sutherland WJ (2002) Modeling large-scale dispersal distances. *Ecol Modell* 151:279–292
- Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture–recapture experiments. *Wildl Monogr* 1:3–97
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Royle JA, Chandler RB, Sollmann R, Gardner B (2013) Spatial capture–recapture. Academic Press, Cambridge, MA
- Rozas LP (1995) Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18: 579–590
- Rudershausen PJ, Buckel JA, Dubreuil T, O’Donnell MJ, Hightower JE, Poland SJ, Letcher BH (2014) Estimating movement and survival rates of a small saltwater fish using autonomous antenna receiver arrays and passive integrated transponder tags. *Mar Ecol Prog Ser* 499: 177–192
- Schaub M, Royle JA (2014) Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods Ecol Evol* 5:1316–1326
- Shaw MW (1995) Simulation of population expansion and spatial pattern when individual dispersal distributions do not decline exponentially with distance. *Proc R Soc B* 259:243–248
- Siddig AA, Ellison AM, Ochs A, Villar-Leeman C, Lau MK (2016) How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in *Ecological Indicators*. *Ecol Indic* 60: 223–230
- Skalski JR, Buchanan RA, Griswold J (2009) Review of marking methods and release–recapture designs for estimating the survival of very small fish: examples from the assessment of salmonid fry survival. *Rev Fish Sci* 17: 391–401
- Teo SLH, Able KW (2003a) Growth and production of mummichogs (*Fundulus heteroclitus*) in a restored marsh. *Estuaries* 26:51–63

- ✦ Teo SLH, Able KW (2003b) Habitat use and movement of the mummichog (*Fundulus heteroclitus*) in a restored salt marsh. *Estuaries* 26:720–730
- ✦ Thériault MH, Courtenay SC, Munkittrick KR, Chiasson AG (2007) The effect of seafood processing plant effluent on sentinel fish species in coastal waters of the Southern Gulf of St. Lawrence, New Brunswick. *Water Qual Res J Canada* 42:172–183
- ✦ Turner RE (2001) Of manatees, mangroves, and the Mississippi River: Is there an estuarine signature for the Gulf of Mexico? *Estuaries* 24:139–150
- ✦ Vastano AR, Able KW, Jensen OP, López-Duarte PC, Martin CW, Roberts BJ (2017) Age validation and seasonal growth patterns of a subtropical marsh fish: the Gulf Killifish, *Fundulus grandis*. *Environ Biol Fishes* 100: 1315–1327
- ✦ Viallefont A, Besbeas P, Morgan BJ, McCrea RS (2012) Estimating survival and transition probabilities from aggregate sightings of animals. *J Ornithol* 152: 381–391
- ✦ Whitehead A, Dubansky B, Bodinier C, Garcia TI and others (2012) Genomic and physiological footprint of the Deep-water Horizon oil spill on resident marsh fishes. *Proc Natl Acad Sci USA* 109:20298–20302

*Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA*

*Submitted: October 22, 2018; Accepted: June 24, 2019
Proofs received from author(s): July 31, 2019*