**ARTICLE**

**Coastal and Marine Ecology**

# Establishing connectivity patterns of eastern oysters (*Crassostrea virginica*) on regional oceanographic scales

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**Abstract**

Localized depletion of marine and estuarine populations often results from large-scale natural and anthropogenic disturbances (e.g., hurricanes, oil spills) as well as overharvest of fisheries resources. Understanding how such localized depletions may affect populations at larger regional scales requires knowledge of connectivity among local populations within the larger regional landscape or metapopulation. Efforts to restore populations following such decreases require similar knowledge. During the 2010 *Deepwater Horizon* oil spill, dramatic declines of oysters occurred throughout estuaries west and east of the Mississippi River. We examined trajectories of particles, which were parameterized to mimic oyster larvae, using the ADvanced CIRCulation (ADCIRC; https://adcirc.org) model to evaluate potential connectivity within and among embayments from Western Louisiana to Alabama. Patterns of larval settlement, which we defined as the intersection of a larval particle with known or expected oyster habitat at any point 13–21 days post-release, reflected much greater local contributions, with 50%–90% of settled particles originating within the same subdivision of embayments. Exchange among subdivision was much less (0%–40%) and settlement originating from outside the embayment of release was trivial under most scenarios (0%–14%). Connectivity between adjacent basins was greatest for larvae released in the southern portions of the embayment, whereas connectivity among nonadjacent basins was not predicted under the scenarios modeled. Because most local populations are relatively isolated on ecological timescales, areas suffering from extensive local depletion are likely to require extensive time to recover due to the lack of larval subsidy from the overall regional population. Restoration would require building stepping-stone populations or reefs within and among basin to restore a high degree of connectivity.

## INTRODUCTION

Changes in the abundance of marine and estuarine animals are a common effect of large-scale disturbances. Because marine populations are open with respect to dispersal of larvae, changes in species abundance in one area may affect the supply of larvae in adjacent areas. In a fishery context, the consequences of localized depletions on the regional population (metapopulation) are critical to predict future stock status and harvest projections. If localized decreases result from environmental degradation, then both the local and regional effects may be quantified to assess damages and determine recovery times. Similarly, localized increases in population abundance may benefit a wider region through increased supply of larvae into adjacent areas. The benefit of increased export of larvae has been examined for many marine populations within the context of marine protected areas (Gell & Roberts, 2003; Roberts et al., 2001). In several studies of the potential advantages of marine protected areas, biophysical transport models have been utilized to elucidate the potential connection between restored/conserved populations and adjacent and downstream populations (e.g., Kim et al., 2013; Roberts, 1997). Here, we use a similar application of biophysical models to determine the degree of connectivity within and among embayments in the northern Gulf of Mexico. The results of this model helped explain large-scale decreases in the abundance of the eastern oyster (*Crassostrea virginica*) as a result of the *Deepwater Horizon* oil spill and associated oil spill response actions (Grabowski et al., 2017; Powers, Grabowski, et al., 2017), which affected local and distant areas through larval pathways. Such information can also support restoration planning activities that aim to design more resilient oyster ecosystems through interconnected reef systems. More broadly, our analysis addresses a fundamental debate in marine ecology of whether and to what degree marine populations are truly open (Levin, 2006).

Oyster abundance in subtidal areas and nearshore, intertidal areas decreased in response to the *Deepwater Horizon* oil spill and the associated response activities. Abundance of subtidal oysters in two embayments, Barataria Bay (BB; west of the Mississippi River) and Black Bay/Breton Sound (east of the River), experienced dramatic declines (Grabowski et al., 2017; Powers,

Grabowski, et al., 2017). Declines in both embayments were primarily linked to the prolonged summer release of freshwater from the Mississippi River that dramatically lowered estuarine salinity values in vast areas for 16 weeks. The action was taken by the state of Louisiana as part of its oil spill response activities. Powers, Grabowski, et al. (2017) estimated total oyster loss in the two basins from 1.2 to 3.2 billion market-sized (shell height > 75 mm) oysters in 2010. In addition to the loss of subtidal oysters in these two embayments, intertidal oysters (oysters near the vegetated marsh edges) also suffered declines as a result of oiling and shoreline cleanup activities from Terrebonne Bay (TB), LA through Mississippi Sound. For shoreline areas that were heavily oiled following the *Deepwater Horizon* oil spill, oyster habitat was reduced by 77% compared with areas with no detected oiling. For areas that received lighter oiling, oyster habitat was reduced by 33% (Powers, Rouhani, et al., 2017). The loss of oysters from two of the historically productive embayments as well as the affected nearshore areas would be expected to greatly reduce reproductive output in the two embayments.

In order to assess the potential geographic scale of changes in local reproductive capacity (decreases from injury or increases from restoration activities), we examined the connectivity patterns within and among embayments along the northern Gulf of Mexico and between nearshore and subtidal areas using biophysical transport models. Specifically, we examined trajectories of particles, which were parameterized to mimic oyster larvae, using the ADvanced CIRCulation (ADCIRC) model to assess (1) the effective dispersal distance of oyster larvae in our system and (2) the connectivity via dispersed larvae within and among embayments in the northern Gulf of Mexico. More broadly, this paper examines how open marine invertebrate populations are. While larvae can stay in the plankton phase for relatively long periods (3–4 weeks), empirical and modeling evidence suggest that connectivity is on relatively small scales (<10 km).

## METHODS

### Description of model

In the ADCIRC model, the trajectory of an oyster larvae is calculated by integrating Equation (1):

$$\frac{dx(t;x^0)}{dt} = u(x(t;x^0),t), \qquad (1)$$

where $x(t;x^0)$ is the position of the particle at time $t$, given the initial location of the particle $x^0$ at $t = 0$, and $u$ is the velocity of the particle. Larvae are considered to be passive tracers (Kim et al., 2010) fully submerged in the water and driven by the current, unaffected by the wind at the surface. In this study, the current $u$ is obtained from hindcasts of the Gulf of Mexico in 2010 and 2011 using the high-resolution ADCIRC model (Luettich et al., 1992). In addition to understanding the circulation field during the *Deepwater Horizon* oil spill in 2010, these years also represent a range of Mississippi River discharges.

ADCIRC is a highly parallelizable, unstructured finite element model that solves the shallow water equations, which describe the conservation of mass and momentum under the incompressibility, Boussinesq and hydrostatic pressure assumptions. ADCIRC is capable of describing multiscale features, from basin-wide phenomena to intricate small-scale nearshore flows, such as inlets and flows around jetties. In this study, ADCIRC employs the "SL16" mesh, which resolves the western Atlantic, the Gulf of Mexico, and, with increasing resolution, the continental shelf, estuaries, and wetlands. Nearshore regions have mesh sizes of 30 m. Details of the mesh, bathymetry, and bottom friction are described in Dietrich et al. (2010). The primary forcings of circulation in the hindcasts are wind, tides, atmospheric pressure, the Coriolis force, and varying rivers. The effects of wind waves are not included in this study.

In the SL16 model, river inflow conditions are prescribed for the Mississippi River near Baton Rouge, LA, and for the Atchafalaya River near Simmersport, LA, based on the daily discharge data of the Mississippi River at Tabert Landing, MS, from the US Army Corps of Engineers (http://www2.mvn.usace.army.mil/eng/edhd/wcontrol/miss.asp). Note that Tabert Landing is located downstream of the Old River Control Structure. The locations of both river forcing boundaries are downstream of the Old River Control Structure, and therefore we use the discharge values of 3/7 of the flow at Tabert Landing in specifying the inflows for the Atchafalaya River.

Tides are forced on the Atlantic open-ocean boundary (along the 60° W longitude) with eight dominant astronomical tidal constituents, which are the $K_1$, $O_1$, $M_2$, $S_2$, $N_2$, $K_2$, $Q_1$, and $P_1$ constituents using data from the TOPEX global tidal model (Egbert et al., 1994). Tidal potential functions for these constituents are also forced within the domain. Due to the resonant characteristic of the Gulf of Mexico and the Caribbean Sea, a period of model spin-up and simulation are required in order for the initial transients to dissipate and dynamically correct tides to be generated. In this study, the period of the tidal spin-up is 30 days.

The effect of wind on water movement enters the model through surface stresses. Here, the wind surface stresses are determined by a quadratic air-sea drag law, which is based on the 10-m wind velocities. In this study, we use the 10-m North American Mesoscale Forecast System (NAM) wind products (http://nomads.ncdc.noaa.gov/data/namanl/) provided by the National Center for Environmental Prediction. The spatial resolution of this wind product is approximately 12 km and the temporal resolution is 6 h. Note that the wind fields at the time in between two wind snapshots are obtained using linear interpolation.

Depth-averaged currents from ADCIRC are recorded in 30-min intervals (although the ADCIRC time step is significantly smaller), which are then used in tracking oyster larvae. We chose the depth-average model as opposed to a three-dimensional model based on the finding by Kim et al. (2010) that trajectories were not substantively altered by the inclusion of three-dimensional particle behavior. Integration of the Lagrangian transport equation, Equation (1), is performed numerically using a fourth-order Runge–Kutta time stepping scheme with an adaptive time step size to control the integration error. More precisely, the time step is chosen based on the error determined by comparing the position of the particle at time $t + \Delta t$ when integrating with a time step size of $\Delta t$ and $\Delta t/2$. If the error is greater than the given tolerance, the time step is cut in half and reintegrated until the error is less than the tolerance. Note that with sufficiently small error tolerance in the time integration, the resulting time step size will also ensure that the particle will cross only one element at the end of each time marching step. The time marching procedure requires values of the velocity at the particle location. This value is obtained from the linear interpolation in time and space of the nodal data given on the finite element mesh. The particle is not allowed to cross a levee or a land boundary. If a new position of the particle crosses such boundaries, the particle position is instead set to a location on the boundary and subsequently determined by tracking along the edges.

## Oyster larval transport

We evaluated the spatial and temporal variability in the transport of oyster larvae throughout the north-central Gulf of Mexico. The study area, consisting of source and sink polygons, extended from the Texas/Louisiana border (−94.9° W longitude) to the Alabama–Florida border

(−87.4° W longitude) and from the shoreline to the shelf break (190–240 km from shore). The temporal period was specified to capture oysters' main spawning period in this region, which was identified as the time from when the water temperature reached 25°C until the water temperature dropped below 25°C (Kim et al., 2010). In our study, the temporal period ranged from approximately April 28 to November 30 in both 2010 and 2011. During the modeling period of each year, we completed 27 model runs or larval "releases." The start time of each release coincided with every spring and neap tidal cycle, mid-stage between slack and ebb tide (Bernard et al., 2016). Particles were tracked for 21-day oyster larvae drift periods. Results were compiled for two time periods each year: spring (April–June modeling), which reflects the dominant settlement period, and annual (April–November modeling).

The modeling approach involved seeding the spatial domain repeatedly with approximately 10 million numerical drifters (i.e., oyster larvae) with release locations based on spatial oyster habitat polygons, and then running the two-dimensional hydrodynamic particle tracking model forward in time to develop a temporally dependent connectivity matrix using the individual drifter tracks. In shallow waters of the northern Gulf of Mexico, we assumed vertical mixing results in fairly uniform conditions throughout the water column; therefore, based on the result of Kim et al. (2010), we assumed a two-dimensional model reasonably captures the hydrodynamic forcing experienced by passive modeled larvae. The resulting connectivity matrices quantified the probability that a particle (larva) in a given cell (discretized spatial cell) translates to any other cell, including coastline locations.

Two types of seeded oyster habitat polygons were used: nearshore and subtidal. Nearshore habitat locations were identified as the area within a 100-m buffer of saline vegetated marsh shoreline (50-m buffer placed on both sides of shoreline contour, for 100-m total buffer width) within the study area. The buffer width was based on a 25-cm elevation shoreline contour. On the landside of the contour, the buffer was clipped to a 50-cm elevation, which was assumed to reasonably capture areas inundated by high tides. Subtidal habitat polygons represent areas included in oyster resource mapping work performed under *Deepwater Horizon* oil spill natural resource damage assessment work plans and the Louisiana Department of Wildlife and Fisheries (LDWF), for which oyster habitat percent cover estimates are available (Appendix S1: Table S1).

These nearshore and subtidal habitat polygons were divided by the subbasin boundaries shown (Figure 1),

and connectivity matrix results were aggregated to these subbasins. The boundaries of most subbasins were based on Louisiana Coastal Study Areas (CSAs). Several of these CSAs, such as the areas in TB and BB, were further divided in order to elucidate larval transport within the bays, not just among them (Appendix S1: Figures S1 and S2).

A total of 3 million larvae were released in nearshore habitats and 7 million larvae in subtidal habitats. This proportion approximated the amount of living resource in each habitat type. The total number of larvae modeled is orders of magnitude less than the number produced in reality; therefore, modeled drifters are considered to represent a proportion of actual larvae and are informative of larval trajectory patterns.

## Regional larval settlement

As a post-processing step once modeling for each 21-day release was completed, the average settlement probability of larvae in each subbasin was calculated in order to characterize larval transport within and among subbasins and habitat types. "Settlement" was defined as a particle (larva) spatially intersecting a habitat polygon at any point between 13 and 21 days post-release. Habitat polygons were drawn from mapping conducted by the states as well as the professional advice of State biologists. This timing was based on the approximate maturation time of a larva. We assumed that the spatial intersection of a larva with a habitat polygon after this time represents the real-life scenario of a negatively buoyant larva intersecting oyster reef and successfully settling. Once a larva "settled," its final location was recorded (by subbasin and habitat type). Each modeled larva may settle only once; some larvae may not settle at all depending on their trajectory through the study area over time. This settlement analysis does not account for predation, differences in larval viability, or other factors that may promote or interfere with settlement. Oyster reef in the study area was not continuous; patchy reefs and hummocks existed in sampled subtidal and nearshore areas (Powers, Grabowski, et al., 2017). We created weighted settlement results for each subbasin by multiplying the raw quantity of larvae that settle in nearshore or subtidal habitat by the estimated percent of oyster habitat cover in that habitat type of the subbasin (Appendix S1: Table S1).

We calculated settlement averages for all larvae (nearshore and subtidal) for each of the time periods (spring [April–June modeling] and annual [April–November modeling]). For all larvae, we determined the average proportion of larvae settling in a given subbasin that
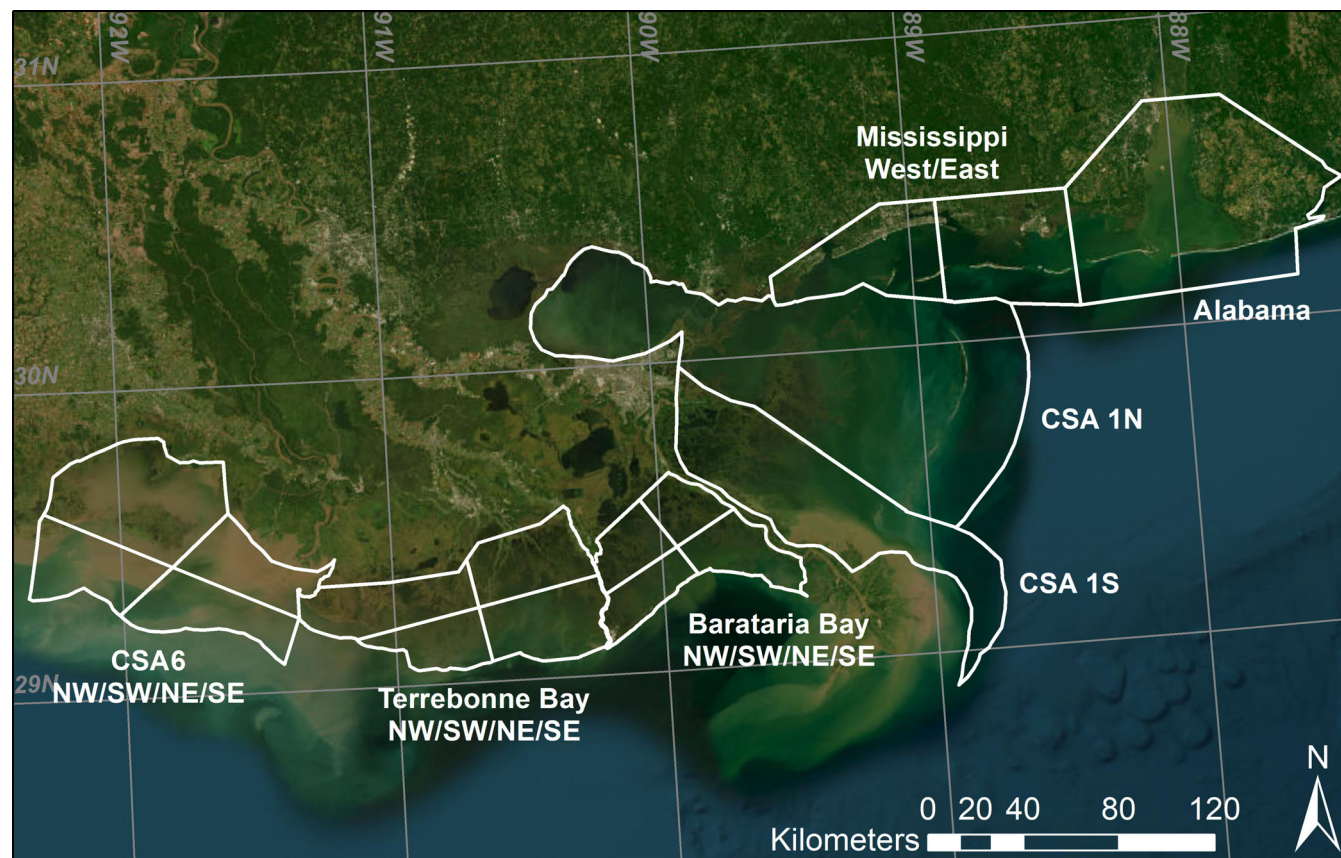
**FIGURE 1**  Subbasin boundaries used in larval settlement analysis of the north-central Gulf of Mexico. CSA, Coastal Study Area.

originated from each other subbasin (i.e., the average composition of larvae settling in a subbasin based on their initial subbasin locations). This allowed us to summarize larval transport patterns throughout the modeled area and identify regions that exchange a greater or lesser proportion of larvae.

To calculate the settlement averages over each time period, we first summarized the number of larvae settling in a given subbasin that originated from each other subbasin for each 21-day tracking period using the connectivity matrix model outputs. We then calculated the percent of larvae settling in a given subbasin that originated from each other subbasin for each 21-day tracking period, as a percentage of the larvae originating in each subbasin. For example, approximately 36,850 of the 60,620 larvae that settled in subbasin CSA 6 NW originated from that same subbasin during the tracking period that began on April 30, 2010. That is to say, approximately 60.8% of larvae that settled in subbasin CSA 6 NW originated from that same subbasin during that period. Once we completed these subbasin-level calculations for all tracking periods, we calculated the mean percent of larvae that settled in each subbasin that originated from each other subbasin.

# RESULTS

## ADCIRC model validation

ADCIRC water levels have been extensively validated in numerous studies (Bunya et al., 2010; Dietrich et al., 2010). Throughout these studies, water levels match observations very well at locations all across the Gulf of Mexico. ADCIRC has also previously been used to track oil particles in the Gulf of Mexico (Dietrich et al., 2012). As currents are vital for Lagrangian transport, the computed SL16 currents used here are validated against the time series of observed currents available from different sources. For brevity, only one current station from National Oceanographic and Atmospheric Administration (NOAA) is shown here for a selected time (Figure 2 shows the SL16 currents in blue and the near-surface currents measured at the nearshore NOAA station N-4 at Pascagoula Harbor, LA in red from June 15 to August 15, 2010). This period includes a time frame with fair weather conditions (mid-June) and the passage of Hurricane Alex in the southern Gulf of Mexico (late June to early July of 2010). Comparison between near-surface and depth-averaged currents, like those
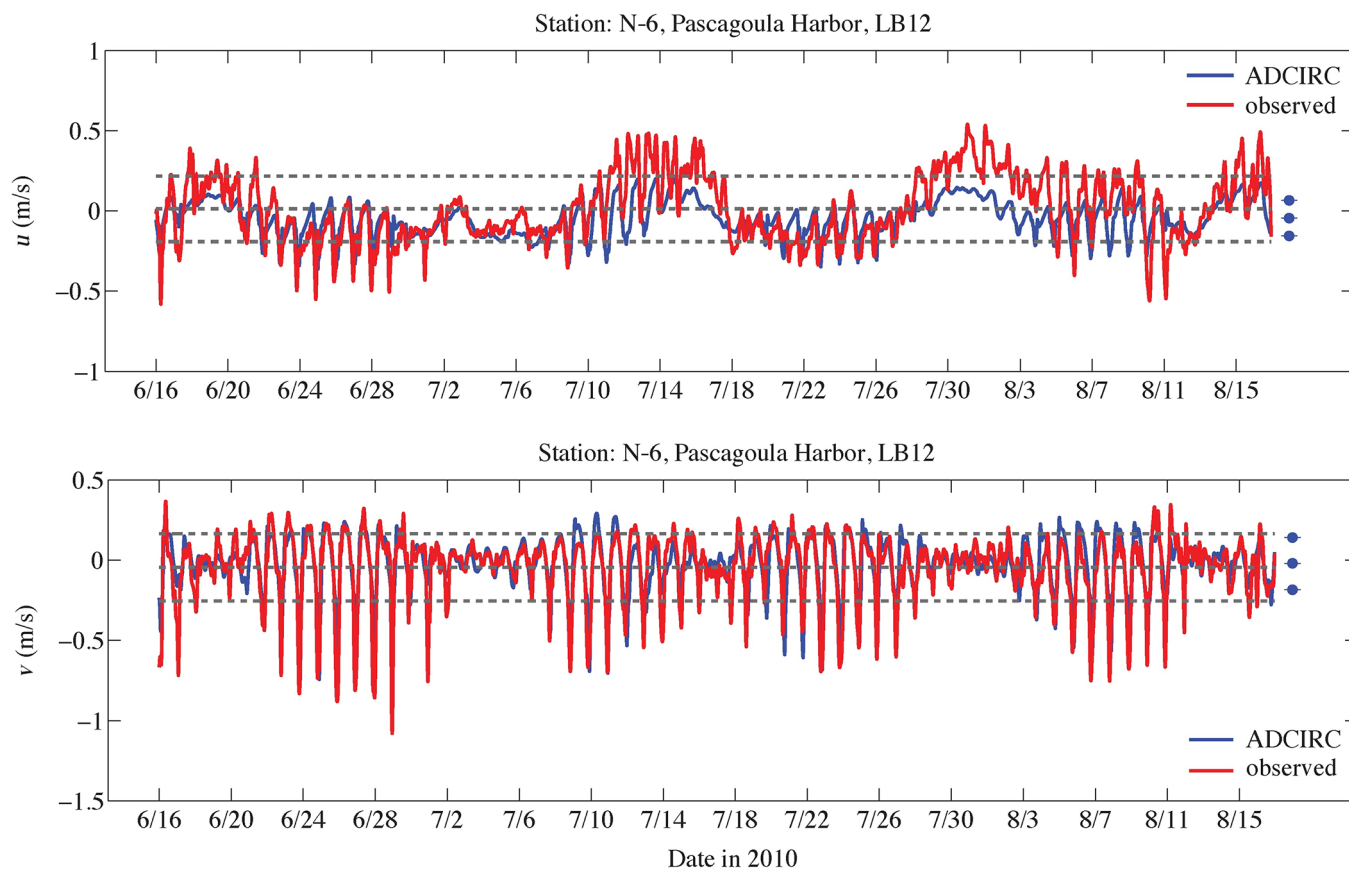
**FIGURE 2**   Time series of the $u$ and $v$ components of the currents at station N-4. Red lines are observed data from NOAA and blue lines are SL16 currents. The arithmetic mean and mean ± SD of the observed data are drawn with the black dotted lines. Blue circles to the right of each plot depict the mean and mean ± SD of the SL16 currents. ADCIRC, ADvanced CIRCulation.

from the ADCIRC model, is reasonable for a well-mixed water column, which can be expected in shallow areas. To reduce the level of high-frequency noise in the observation data, we applied a mild filter, more precisely a finite-impulse-response low-pass filter with a cutoff frequency of a 3-h period, to the time series of the observed currents. The modeled currents match the observed currents relatively well at the station shown as well as for other nearshore stations not shown.

## Dispersal distance

The results of 27 separate larval releases in 2010 and 2011 indicated dispersal of oyster larvae over relatively limited distances. The vast majority of particles that settled, that is, encountered the expected oyster habitat during the last portion of their pelagic period, did so within 50 km of their origin (Figure 3). During low to moderate energy regimes, >95% of the particles settled within a 50-km distance. During the higher energy periods, dispersal distance was higher with >95% of the particles

settling within 100 km. Dispersal distances appeared similar for particles released in subtidal and nearshore locations (Figure 3). Maximum dispersal distances were approximately 170 km, although very few particles (0.001%) would be expected to travel that far.

## Intra- and interbasin connectivity

With a few exceptions (release in CSA 6), those particles that settled did so in the portion of the basin in which they were released. Based on the average of the 27 releases in 2010, 69% of those particles that successfully encountered oyster habitat settled in the basin or subbasin of their release (Table 1). A similar pattern was observed in 2011 with 71% of settled particles predicted to settle within the basin or subbasin of their release (Table 2).

Overall, there was a greater potential of particle flow and hence higher degree of connectivity among subbasins than among basins. In the far western area of the study, the NE quadrant of CSA 6 received substantial particle from the SW, SE, and NW subbasins (Tables 1 and 2
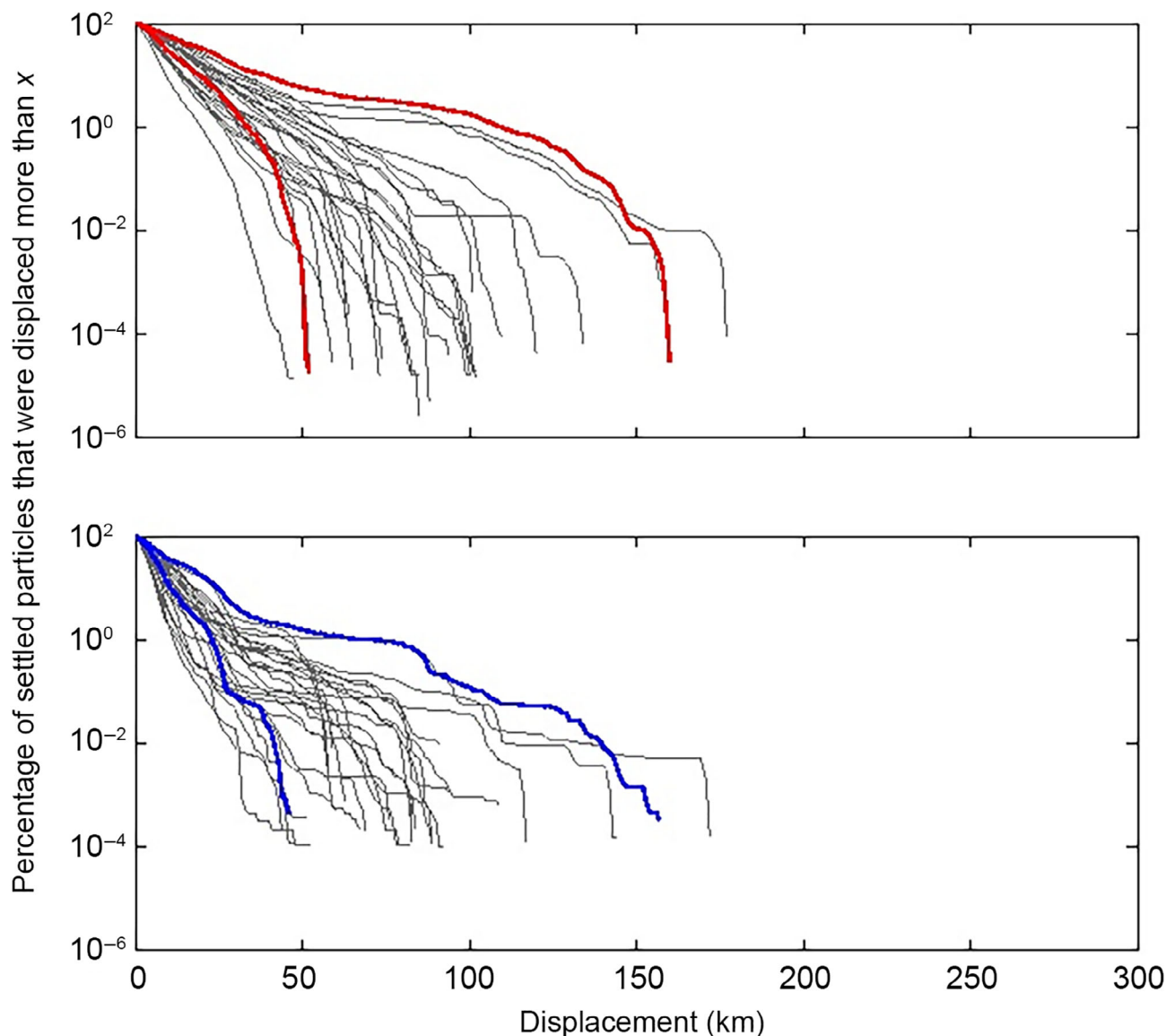
**FIGURE 3**  Displacement distances for settled particles released in subtidal (upper) or nearshore (lower) locations for all 2010 model runs. Gray lines show the results of each of the 27 releases with red- or blue-colored thicker lines highlighting the 6-5 and 6-24 releases, which are the low (left) and high (right) energy releases, respectively.

and Appendix S1: Tables S2 and S3) during 2010 and 2011. Particles released in CSA 6 would be expected to come into contact with oyster habitat in the adjacent embayment to the east (TB). Over the 27 particle releases in 2010, 21% of the particles released in CSA 6 NE would be predicted to seed oyster habitat in TB (7% in TB NW, 11% in TB SW, and 3% in TB SE). Similarly, particles released in CSA 6 SE would be expected to settle in large quantities in TB with 30% of particles released predicted to settle in TB NW (9%), TB SW (12%), and TB SE (9%). In contrast to the relatively high potential for eastward particle movement, little evidence exists that particles would travel westward between the two subbasins (i.e., from TB to CSA 6).

Moving into TB, movement of particles among subbasins was noted in the model runs for 2010 and 2011. A high degree of exchange was noted between the SE and SW portions of TB with 41% of particles released in the SW intersecting oyster habitat in the SE portion of the embayment. The SE portion of TB also received 18% of the particles released from the NE portion of TB. Exchange between TB and BB was very limited with a maximum of 3% of particles released in TB SE encountering oyster habitat in BB (1%–2% in BB SW and 1% in BB SE). Limited western exchange was noted from BB to TB as well. Up to 6% of particles released in BB SW intersected oyster habitat in TB SE during spring 2011 (Appendix S1: Table S3). Connectivity among subbasins

**TABLE 1** Average larval settlement distribution (in percentages) by region (combines nearshore and subtidal larval transport) across annual 2010 model releases, excluding values <0.5%.

| Origin location | CSA 6 NW | CSA 6 SW | CSA 6 NE | CSA 6 SE | TB NW | TB SW | TB NE | TB SE | BB SW | BB NW | BB NE | BB SE | CSA 1S | CSA 1N | MS W | MS E | AL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CSA 6 NW | 75 | 2 | 22 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| CSA 6 SW | 54 | 19 | 26 | 1 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| CSA 6 NE | 10 | ... | 57 | ... | 7 | 11 | ... | 3 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| CSA 6 SE | 9 | 2 | 40 | 1 | 9 | 12 | ... | 9 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB NW | ... | ... | ... | ... | 75 | 22 | ... | 3 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB SW | ... | ... | ... | ... | 4 | 54 | ... | 41 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB NE | ... | ... | ... | ... | ... | ... | 81 | 18 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB SE | ... | ... | ... | ... | ... | 3 | 5 | 90 | 1 | ... | ... | 1 | ... | ... | ... | ... | ... |
| BB SW | ... | ... | ... | ... | ... | ... | ... | 1 | 62 | 8 | 3 | 25 | ... | ... | ... | ... | ... |
| BB NW | ... | ... | ... | ... | ... | ... | ... | ... | 18 | 79 | 1 | 2 | ... | ... | ... | ... | ... |
| BB NE | ... | ... | ... | ... | ... | ... | ... | ... | 3 | 19 | 63 | 15 | ... | ... | ... | ... | ... |
| BB SE | ... | ... | ... | ... | ... | ... | ... | ... | 1 | 2 | 8 | 90 | ... | ... | ... | ... | ... |
| CSA 1S | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 95 | 5 | ... | ... | ... |
| CSA 1N | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 2 | 94 | 4 | ... | ... |
| MS W | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 20 | 68 | 12 | ... |
| MS E | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 8 | 78 | 14 |
| AL | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 3 | 97 |

*Note*: Percentages represent the average percent of settling larvae modeled to recruit to habitat identified in column header from habitat in row header. Location abbreviations are location and cardinal or ordinal directions: AL, Alabama; BB, Barataria Bay; MS, Mississippi; TB, Terrebonne Bay. Average settlement values for Coastal Study Area (CSA) 6 NE and SE sum to less than 100% because some model runs in 2010 resulted in no subtidal larvae settlement here (CSA 6 NE, 3 of 27 model runs; CSA 6 SE, 5 of 27 model runs). Sums of greater than 100% are a function of averaging multiple runs.

in BB was similar to that of TB with modest percentages (1%–19%) of particles successfully exchanged. No successful particle exchange was noted between BB (just west of the Mississippi River) and CSA 1 (1S) (just east of the Mississippi River).

Particle exchange patterns east of the Mississippi River focused on east–west exchange among basins. Again, particles released within a basin showed an extremely high probability of being retained within that basin. For CSA 1S, of the particles that successfully encountered oyster habitat, 93%–97% of those particles were released within CSA 1S. A similar pattern was seen for the adjacent CSA 1N embayment.

# DISCUSSION

A pillar of marine ecology is that populations are open as a result of dispersal of free-swimming larvae. Evidence for the openness of marine invertebrate populations is provided by a host of genetic studies that have shown that in the absence of geological or oceanographic

barriers, populations show little genetic differentiation (see Thongda et al., 2018). While the low level of particle exchange among basins may be sufficient to create a homogenous genetic population, the level of exchange is too low to have any major influence on demographic (recruitment/death rates) dynamics of populations within a basin. In other words, the low level of exchange among basins would not be expected to provide any subsidy of recruits to adjacent basins that would facilitate recovery from a large disturbance. In their seminal review, Caley et al. (1996) concluded that most marine invertebrate populations are in fact demographically open. The consequence of this open nature is that recruitment into an area is uncoupled from local reproductive output, which in turn is a function of adult density. While recognizing that this pattern can be greatly modified by post-settlement mortality (Caley et al., 1996), this view shaped the way marine ecologists viewed marine invertebrate populations for a decade. Over the last decade, empirical and modeling studies have suggested that populations are less open than Caley et al. (1996) suggested. Numerous studies reporting retention of

**TABLE 2** Average larval settlement distribution (in percentages) by region (combines nearshore and subtidal larval transport) across annual 2011 model releases, excluding values <0.5%.

| Origin location | Settlement location | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | CSA 6 NW | CSA 6 SW | CSA 6 NE | CSA 6 SE | TB NW | TB SW | TB NE | TB SE | BB SW | BB NW | BB NE | BB SE | CSA 1S | CSA 1N | MS W | MS E | AL |
| CSA 6 NW | 80 | 4 | 15 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| CSA 6 SW | 51 | 31 | 17 | 2 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| CSA 6 NE | 20 | ... | 54 | ... | 4 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| CSA 6 SE | 16 | 12 | 37 | 2 | 7 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB NW | ... | ... | ... | ... | 88 | 11 | ... | 1 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB SW | ... | ... | ... | ... | 8 | 58 | ... | 34 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB NE | ... | ... | ... | ... | ... | ... | 81 | 19 | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| TB SE | ... | ... | ... | ... | ... | 4 | 5 | 90 | 1 | ... | ... | ... | ... | ... | ... | ... | ... |
| BB SW | ... | ... | ... | ... | ... | ... | ... | 2 | 60 | 13 | 3 | 21 | ... | ... | ... | ... | ... |
| BB NW | ... | ... | ... | ... | ... | ... | ... | ... | 10 | 88 | 1 | 1 | ... | ... | ... | ... | ... |
| BB NE | ... | ... | ... | ... | ... | ... | ... | ... | 2 | 14 | 70 | 13 | ... | ... | ... | ... | ... |
| BB SE | ... | ... | ... | ... | ... | ... | ... | ... | 1 | 1 | 9 | 89 | ... | ... | ... | ... | ... |
| CSA 1S | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 93 | 7 | ... | ... | ... |
| CSA 1N | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 4 | 93 | 3 | ... | ... |
| MS W | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 23 | 69 | 8 | ... |
| MS E | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 2 | 18 | 72 | 9 |
| AL | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 7 | 93 |

*Note*: Percentages represent the average percent of settling larvae modeled to recruit to habitat identified in column header from habitat in row header. Location abbreviations are location and cardinal or ordinal directions: AL, Alabama; BB, Barataria Bay; MS, Mississippi; TB, Terrebonne Bay. Average settlement values for Coastal Study Area (CSA) 6 NE and SE sum to less than 100% because some model runs in 2011 resulted in no subtidal larvae settlement here (CSA 6 NE, 6 of 28 model runs; CSA 6 SE, 7 of 28 model runs).

larvae near their natal origin have been published, and a new paradigm that reflects more limited connectivity has begun to emerge (see Levin, 2006). Although few studies generally define the spatial scale of terms like "local," "regional," or "open," the degree to which local reproductive output (habitat patches on the scale of 1–100 m) influences local or regional (1–10 km) recruitment dynamics is critical for the application of ecological knowledge to fields like restoration and conservation. The spatial scale of our terms is influenced by our coastal and oyster focus, with local referring to oyster reefs (in meter scale), subregional referring to within embayments (in kilometer scale), regional referring to connections between adjacent embayments (in tens of kilometer), and marine or oceanographic scales reflecting nonadjacent embayments (in hundreds of kilometers).

Despite the solid conceptual basis for concluding that marine invertebrate populations are open, studies over the last few decades have demonstrated that recruitment patterns tend to reflect subregional or regional reproductive output (Atwood & Grizzle, 2020). In one of the first studies to utilize biophysical transport

models to examine marine invertebrate recruitment, Peterson et al. (1996) concluded that bay scallop recruitment could be enhanced by restoring bay scallops (*Argopecten irradians*) within the relatively small (in tens of kilometer long) Bogue Sound, NC. Further, they found little evidence of exchange of larvae among embayments (sounds) along the Outer Banks of North Carolina. DiBacco and Levin (2000) demonstrated via elemental fingerprinting of striped shore crab (*Pachygrapsus crassipes*) zoeae that most of the zoeae reentering San Diego Bay on a flood tide were larvae that originated with that basin. Our estimates of displacement distances also support within-basin dispersal. The majority of particles showed dispersal on a scale of 10–20 km. Such dispersal distances would not be predictive of between-embayment exchange. Although most recruitment in our model is predicted to occur within a few kilometers of the source reef, the chance of self-seeding oyster reefs is much higher than the exchange between adjacent basins. Further evidence of a smaller spatial scale of recruitment can be found in the examination of the connectivity matrix that resulted

from our model runs. The source of recruits for the vast majority of oyster reefs would be predicted to be within subregion of the embayments examined. While our analysis of dispersal distances suggests that local self-recruiting is possible, such "local" recruitment was not resolvable in our modeling framework. Limited regional exchange was predicted in the model. The only exception is particles released in the eastern portion of CSA 6, which were found to seed oyster beds in TB. On marine/oceanographic scales the outflow of the Mississippi River seems to be an effective barrier, which results in limited linkage between Louisiana's two major oyster-producing areas (Barataria Bay vs. Black Bay/Breton Sound).

Injury to subtidal (Grabowski et al., 2017; Powers, Grabowski, et al., 2017) and nearshore (Powers, Rouhani, et al., 2017) oysters was extensive throughout the north-central Gulf of Mexico as a result of the *Deepwater Horizon* oil spill with the most dramatic declines seen in Barataria Bay and Black Bay/Breton Sound. Our analysis strongly suggests that oyster recovery would take several years because larval supply from adjacent embayments will not subsidize the populations and that populations would require active intervention through restoration. In fact, populations of oysters in the region are still viewed as depressed even 10 years after the oil spill (Powers, unpublished data). Our modeling efforts also suggest that oyster restoration approaches need to include reestablishing spawner populations and enhancing connectivity (see Powers & Boyer, 2014) and that these approaches need to be applied on a subregion scale. Small networks of oyster spawning areas that extend from local, within-region scales would enable increased larval supply to oyster reefs as well as enhanced connectivity of subregions within the basin. Biophysical models can be used to guide such activities (Gancel et al., 2021; Kim et al., 2013) by providing areas that are most likely to serve as stepping stones within and between subregions as well as among embayments in the few cases where such connection is possible.

## CONFLICT OF INTEREST
The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT
Data and metadata used to generate tables, figures, plots, and videos/animations (Powers, 2022) are available from Dauphin Island Sea Lab: https://doi.org/10.57778/TCG3-8521.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.