


RESEARCH ARTICLE

Reestablishing larval connectivity in an estuarine landscape: the importance of shoreline and subtidal oysters (*Crassostrea virginica*) in a comprehensive oyster restoration program

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The decline of oyster reefs in estuaries has resulted from a combination of chronic and acute disturbances. The loss has resulted in decreased yield for the oyster fishery as well as a decline in ecological benefits that has led to increased efforts to restore oyster reefs. The need for scientific guidance in accomplishing these restoration goals has become even more pressing in the northcentral Gulf of Mexico in the wake of injury to oyster reefs resulting from the *Deepwater Horizon* oil spill. Restoration of both the shallow, marsh-fringing oyster aggregations and the deeper subtidal oyster reefs is necessary. Historically, fringing oysters have been overlooked in the oyster habitat landscape because of their limited commercial value. Here, we use a biophysical transport model to examine the transport and settlement of oyster larvae in known oyster reefs along the coast of the northcentral Gulf of Mexico. The modeling demonstrated that the majority of oyster larvae settle within the embayment (>98%) or sub-basin (>65%) of their origin. Additionally, the model demonstrated the importance of fringing oysters as a source of larvae to re-seed other fringing oysters along marsh edges as well as subtidal oyster reefs. We conclude that networks of reefs, including both fringing oyster habitat and subtidal oyster reefs within sub-basins, are necessary to provide resilience to the population at the sub-basin level. Finally, we conclude that fringing oyster habitat may serve as an archipelago-like network to enhance larval supply and connectivity for oysters throughout the mesosaline portions of estuaries.

Key words: ADCIRC, biophysical transport models, *Deepwater Horizon* oil spill, Gulf of Mexico, oysters

Implications for Practice

- Restoration of self-sustaining populations of oysters in the Gulf of Mexico must be planned with the realization that restored reefs must be relatively close to existing reefs because successful larval recruitment largely occurs on the scale of kilometers (<20km).
- Proximity to shoreline fringing oysters could be an important source of larval supply for restored reefs because these areas close to the marsh edge are rarely harvested and larvae from these areas seed both subtidal and fringing oyster reefs.
- Because fringing oysters occur as bands along salt marsh, they can serve as an archipelago of reefs throughout estuaries.

Introduction

The continuing decline of the eastern oyster, *Crassostrea virginica*, along the U.S. Atlantic and Gulf of Mexico coasts represents a threat to the ecosystem integrity of estuaries as well as an opportunity for marine scientists to make fundamental contributions to restoration science to reverse this decline. With an estimated decline of 88% of oyster biomass (64% loss of spatial

coverage) from estuaries along the U.S. coasts (zu Ermgassen et al. 2012), the loss of harvest to the fishery has garnered most of the attention of state and federal policy makers and was the historic motivation for intervention (Breitburg et al. 2000).

Author contributions: SPP, HR, JW conceived of and designed the research; SB, JM, DW refined the methods; SB executed the modeling; HR, GF managed the project and provided data analyses; SPP wrote the manuscript; HR, GF edited the manuscript.

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Recognition of the myriad of positive ecosystem services provided by healthy oyster reefs (Coen et al. 2007; Grabowski & Peterson 2007) has led to fundamental policy shifts in oyster reef restoration that have acknowledged the importance of regaining lost ecosystem services, as well as restoring the fishery itself (Blomberg et al. 2018). Through their suspension feeding and creation of organically rich pseudofeces, aggregations of oysters increase benthic-pelagic coupling and thus may decrease phytoplankton standing stock, sequester key nutrients in sediments, and promote denitrification (Kellogg et al. 2014). If harvest of adult oysters is permitted, removal of nitrogen and nutrient sequestration from the system can be even higher (Dalrymple & Carmichael 2015). As a result of their gregarious settlement upon hard structure, generations of oysters create complex three-dimensional habitat that can serve as juvenile nursery habitat for fish and mobile invertebrates and thus increase production of important fisheries species (Lenihan et al. 2001; Peterson et al. 2003; zu Ermgassen et al. 2016). If placed near shorelines, such biogenic habitat can also play a key role in mitigating shoreline erosion (Piazza et al. 2005; Scyphers et al. 2011; Powers et al. 2017b). Although the degree to which such positive ecological effects are realized (or detected) appears very much context specific (Scyphers & Powers 2013; La Peyre et al. 2014; Heck et al. 2017), much of the current impetus for restoration of oyster reefs has shifted from purely oyster harvest to greater inclusion of ecological benefits.

The historic decline of oyster reefs that must be combatted through restoration has resulted from a suite of chronic as well as acute environmental perturbations. Vast quantities of oysters have been removed from estuarine bottoms by fishermen over the last three centuries (Jackson et al. 2001; zu Ermgassen et al. 2012). Because much of the harvest of subtidal oysters used dredges, which were towed by sailing vessels and, later, powered in many areas with hydraulics, both live oysters as well as the underlying shell matrix were removed. Thus, previously complex and tall oyster reefs have been reduced to mounds of scattered shell or unconsolidated sediments (Lenihan & Micheli 2000). Largely in parallel with the reduction of oyster population due to unsustainable harvest, negative consequences of coastal eutrophication developed in estuaries (e.g. hypoxia and toxic phytoplankton blooms) that also continue to pose substantive threats to the health and existence of oyster reefs (Kellogg et al. 2014). Although both overharvesting and the consequences of eutrophication have contributed to the decline of oysters, the interactive effects of loss of vertical structure and exposure to hypoxic bottom waters (Lenihan & Peterson 1998) continue to represent one of the greatest conservation threats and restoration challenges to subtidal oyster reefs (Johnson et al. 2009). Long-term changes in the hydrology of estuaries have also adversely affected the ability of estuarine ecosystems to support oyster reefs (Wilber 1992; Buzan et al. 2009). Elevated salinities as a result of decreased freshwater inflow from upriver damming or from saltwater intrusion as a result of canal construction and ship channel deepening and widening increase the effects of common diseases (e.g. Soniat et al. 2012) and the abundance of oyster predators (e.g. Garton & Stickle 1980;

Kimbrow et al. 2017). Further, increases in salinity because of global sea level rise will continue to pose a challenge for oyster restoration. Finally, hydrologic changes that greatly reduce salinity, such as large-scale river diversions in coastal Louisiana, which are designed to facilitate wetland expansion, also pose a threat to oyster restoration by significantly lowering salinities in some historically productive areas. If the timing and quantity of freshwater inflows are not carefully regulated, large-scale mortality can occur (Grabowski et al. 2017).

While the negative effects of chronic stressors have been associated with the historic decline of oysters, acute disturbances (e.g. hurricanes and oil spills) still pose substantive risk to the conservation of existing oyster resources as well as oyster restoration. Recent research has demonstrated that the longevity of oyster shell, the availability of which is necessary to support high settlement of oysters, is limited because of bioerosion and dissolution processes in the environment (Dunn et al. 2014). Consequently, recovery from natural and anthropogenic disturbances may not be achieved if required timescales exceed the lifetime of shell persistence, which is likely to be shortened as the effects of ocean acidification are realized in estuarine systems (Wissihak et al. 2014). Hurricanes have long been recognized as an acute disturbance that negatively affects oyster reefs as a result of physical abrasion, dislodgment, and burial of reefs, and natural recovery from such events normally requires 1–5 years (Livingston et al. 1999; Edmiston et al. 2008). Recently, studies in the aftermath of the *Deepwater Horizon* oil spill have demonstrated that disturbance resulting from oiling and various response activities can have substantial effects on oyster resources. The summer release of large quantities of freshwater from the Mississippi River through two diversion structures (Caernarvon and Davis Pond), a response activity of the State of Louisiana to protect marsh ecosystems from the seaward flow of oil in 2010, resulted in the loss of 2–3 billion market-sized oysters from subtidal areas of Barataria Bay (BB) and Black Bay/Breton Sound estuaries (Grabowski et al. 2017; Powers et al. 2017a). Oysters near the shoreline (fringing oyster reefs) suffered injury from direct oiling as well as response activities associated with oil removal efforts in these nearshore environments. While the magnitude of oyster injury for oysters along the marsh edge was an order of magnitude less than subtidal areas in terms of the number of oysters killed (34 million vs. 2–3 billion market-sized oysters), the loss of fringing oysters from the shoreline resulted in increased marsh erosion and additional loss of spawning stock biomass (Grabowski et al. 2017; Powers et al. 2017a).

Compared to their subtidal counterparts, fringing oysters (oysters within 50 m of vegetated shoreline that occur in depths less than 1 m) have received far less attention from regulatory agencies. Historically, this has reflected the limited commercial value of this portion of the oyster stock in most U.S. States. Except for South Carolina and North Carolina, where harvest of intertidal oysters is a major component of the fishery, and Florida, where modest harvest occurs, fringing oysters are not harvested because of their less desirable shape (elongated without a cup formed in the lower shell), the difficulty in accessing the shallow habitat by boat, and frequent closures by the local public health agencies due to elevated fecal coliform levels.

The limited fisheries value of fringing oysters likely increases their importance from a conservation point of view. The presence of fringing oyster reefs can decrease erosion rates of shorelines (Piazza et al. 2005; Scyphers et al. 2011; Powers et al. 2017b), increase denitrification rates (Onorevole et al. 2018), and provide additional habitat for fisheries species (Gittman et al. 2016). An understanding of these benefits has resulted in increased oyster restoration along vegetated shorelines under living shoreline initiatives (Bilkovic et al. 2016). Because fringing oysters are common along many marshes in the 8–25 psu salinity range, they serve as de facto spawning stock reserves (Yao 2013; Powers et al. 2017b). This reservoir of spawners stretches along the coast and may be critical to maintaining oyster populations in both nearshore and subtidal areas. The importance of this narrow band of oysters along the shoreline as a source of larvae or provision of other ecological benefits requires further study in the light of recent studies documenting the ubiquity of this habitat, with 54% of sites along vegetated shorelines surveyed between Louisiana and the Florida panhandle (Powers et al. 2017b). Spatial coverage of oyster at these sites averaged 12% of bottom habitat.

To evaluate the potential importance of this fringing oyster habitat as a source of larval supply and provide guidance for restoration activities in the northern Gulf of Mexico planned as part of the *Deepwater Horizon* oil spill settlement, we utilized a biophysical transport model in which particles are given the physical and biological properties of simulated oyster larvae and are then subjected to advection in the nearshore environment to assess connectivity between fringing oysters and subtidal oyster reefs. To broaden the applicability of our results, we modeled embayments from Galveston Bay, Texas, to Apalachicola, Florida (Fig. 1) under hydrographic and meteorological conditions in 2012, 2014, and 2015, years that were chosen to represent a range of conditions, including high (2012), low (2015), and

average Mississippi River discharge years (2014) (see discharge data in Turner 2022). Specifically, we estimated the percentage of larvae originating in fringing oyster habitat that settled in subtidal and fringing oyster habitat along vegetated shorelines as well as the settlement location of larvae originating from subtidal areas. We also utilized the results of our modeling effort to identify restoration strategies to increase resiliency (i.e. increase larval supply in an area) or promote connectivity (i.e. transport and successful settlement from one area to another).

Methods

Oyster Larval Transport

We evaluated the spatial and temporal variability in the transport of oyster larvae along the coastline of the northcentral Gulf of Mexico. The study area consisted of habitat polygons, representing nearshore and subtidal oysters, extending from Galveston Bay, Texas, in the west to Apalachicola, Florida, in the east and from the shoreline to the shelf break (120–150 miles from shore). We used the Advanced Circulation (ADCIRC; Luetich Jr et al. 1992) model, a highly parallelizable, unstructured finite element model that solves the shallow water equations, to simulate the depth-averaged currents within the coastal system. These modeled currents were then used to compute the transport of particles that were parametrized to mimic oyster larvae in terms of size and sinking velocity. In this study, ADCIRC employed the SL18TX33 + PRVI + FL mesh, which substantially improves upon the mesh resolution used previously (Powers et al. 2023) (11.7 million nodes vs. 5.0 million) and allowed for greater resolution of the areas close to the shoreline edge that may be inundated irregularly—an area that has been challenging for many hydrodynamic models to resolve.

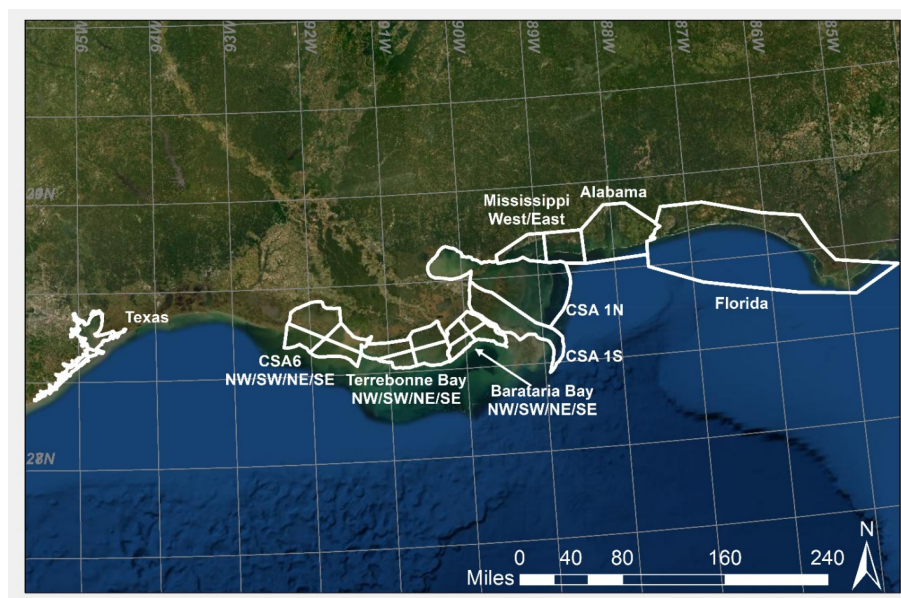


Figure 1. Map of the northern Gulf of Mexico indicating embayments where oyster transport was modeled (CSA = Louisiana Coastal Study Areas).

The mesh resolves the western Atlantic, Gulf of Mexico, and, with increasing resolution, continental shelf, estuaries, and wetlands within those broader areas. Nearshore regions had mesh sizes as fine as 20 m. The primary forcings of circulation in the hindcasts were wind, tides, atmospheric pressure, the Coriolis force, and varying river flow. River inflows were prescribed for the Mississippi River near Baton Rouge, Louisiana, and for the Atchafalaya River near Simmersport, Louisiana, based on the daily discharge data of the Mississippi River at Tabert Landing, Mississippi. Tabert Landing is above the split in the two rivers. Consequently, we use the discharge values of 3/7 of the flow at Tabert Landing in separating the inflows from the Atchafalaya River versus the Mississippi River. Tides were forced on the Atlantic open-ocean boundary (along the 55° W longitude) with nine dominant astronomical tidal constituents: K1 (a lunisolar diurnal constituent that expresses the effect of the moon's declination), O1 (a principal lunar diurnal constituent), M2 (principal lunar semidiurnal constituent that represents the Earth's rotation relative to the moon), S2 (a principal solar semidiurnal constituent that represents the Earth's rotation relative to the sun), N2 (a lunar elliptic semi diurnal constituent), K2 (a lunisolar semi diurnal constituent that modulates the amplitude and frequency of M2 and S2), Q1 (a larger lunar elliptic diurnal constituent that modulates the amplitude and frequency of O1), P1 (a principal solar diurnal constituent) and M4 (shallow water constituent) using data from the TOPEX global tidal model (Egbert et al. 1994). Tidal potential functions for these constituents were also forced within the domain. While the effects of wind-waves were not included in this study, the effect of wind on water movement entered the model through surface stresses. Here, the wind surface stresses were determined by a quadratic air-sea drag law, which was based on the 10-m wind velocities. In this study, we used the CFSv2 winds, which have approximately 22 km spatial resolution and hourly temporal resolution. Finally, the nonlinear advection terms used in this study were critical for generating eddies that are responsible for increased particle transport.

Depth-averaged currents from ADCIRC were recorded in 30-minute intervals (although the ADCIRC time step is significantly smaller), which were then used in transporting oyster larvae (Powers et al. 2023 for additional rationale of the application of ADCIRC to larval recruitment studies). The modeling approach involved seeding the spatial domain repeatedly with larvae over the three study years. Two types of seeded oyster habitat polygons were used: fringing oyster habitat along vegetated shorelines and subtidal. Subtidal polygons were drawn based on oyster habitat maps provided by state biologists (stratum A/A+) as well as their professional advice for unmapped areas (stratum B). Each type (subtidal and fringing) was seeded using the same oyster density weighted by a habitat productivity index, for a total of approximately 1 million larvae in fringing habitats and 11 million larvae in subtidal habitats. The total number of larvae modeled was orders of magnitude less than the number produced in reality; therefore, modeled drifters were considered to represent a proportion of actual larvae and were informative of larval trajectory patterns. Our goal in this analysis was to identify the relative contribution of subtidal

and fringing habitats within individual sub-basin and larger embayment units. It was not to establish a complete matrix of individual sites within sub-basins and embayments where each site during each release could be used to identify specific sources and sinks locations (sensu Pulliam 1988; Peterson et al. 2001). This latter goal would be a daunting and computationally intensive accounting effort on the scale of our study area, but may be appropriate on an individual sub-basin level as a series of discrete studies to guide specific reef restoration. For our modeling study, fringing oyster habitat locations were identified as the area within a 100 m buffer of saline (5–36 psu) vegetated marsh shoreline (50-m buffer placed on both sides of shoreline contour, for a 100-m total buffer width) within the study area. The buffer width was based on a 25-cm elevation shoreline contour. On the land side of the contour, the buffer was clipped to a 50-cm elevation, which was assumed to reasonably capture areas inundated by high tides. Delineating the shoreline is a difficult task in a microtidal, often wind-driven system; elevation heights and shoreline widths were based on observation of field crews in Powers et al. (2017b), who observed where oyster habitat was located relative to the shoreline edge. These observations would be impacted by field conditions (water and wave height) at the time of shoreline surveys and could impact the width of this zone; however, this error is likely small (m's) except during major wind events (>30 kph).

The fringing and subtidal habitat polygons were divided by embayment and sub-basin boundaries shown (Fig. 2). Eight embayments were included in our study areas, stretching a distance of approximately 1000 km along the northern Gulf of Mexico. The furthest west embayment was Galveston Bay, Texas. The four embayments in Louisiana were Coastal Study Areas (CSA) 6 (an area inclusive of Vermilion and Atchafalaya Bays), Terrebonne Bay (TB), BB, CSA 1S (an area inclusive of Black Bay and western Breton Sound), and CSA 1N (inclusive of Lake Borgne, Biloxi Marshes, and eastern Breton Sound). Further east, the embayment included Mississippi Sound (spanning Mississippi and western Alabama), Mobile Bay, Alabama, and the western portion of the Florida panhandle from Pensacola Bay to Apalachicola Bay. Because several embayments in Louisiana and Mississippi Sound had oyster habitat spread throughout the embayments, we further divided these embayments into sub-basins to elucidate larval transport on more local scales (Fig. 2) and provide restoration guidance at a higher spatial resolution. Specifically, CSA 6, BB, and TB were divided into NE, NW, SE, and SW areas. Mississippi Sound was divided into W and E portions.

The two-dimensional, depth-averaged, hydrodynamic particle tracking model used to develop a temporally dependent connectivity matrix assumed vertical mixing was sufficient to use a depth-averaged approach to larval tracking. Kim et al. (2010), in their study of oyster larval transport in Mobile Bay and Mississippi Sound, compared three-dimensional versus depth-averaged two-dimensional approaches in detail and concluded that exclusion of vertical behavior of larval particles and a two-dimensional depth-averaged approach gave results similar to more complex three-dimensional models with vertical swimming behavior of oyster larvae (also see Puckett et al.

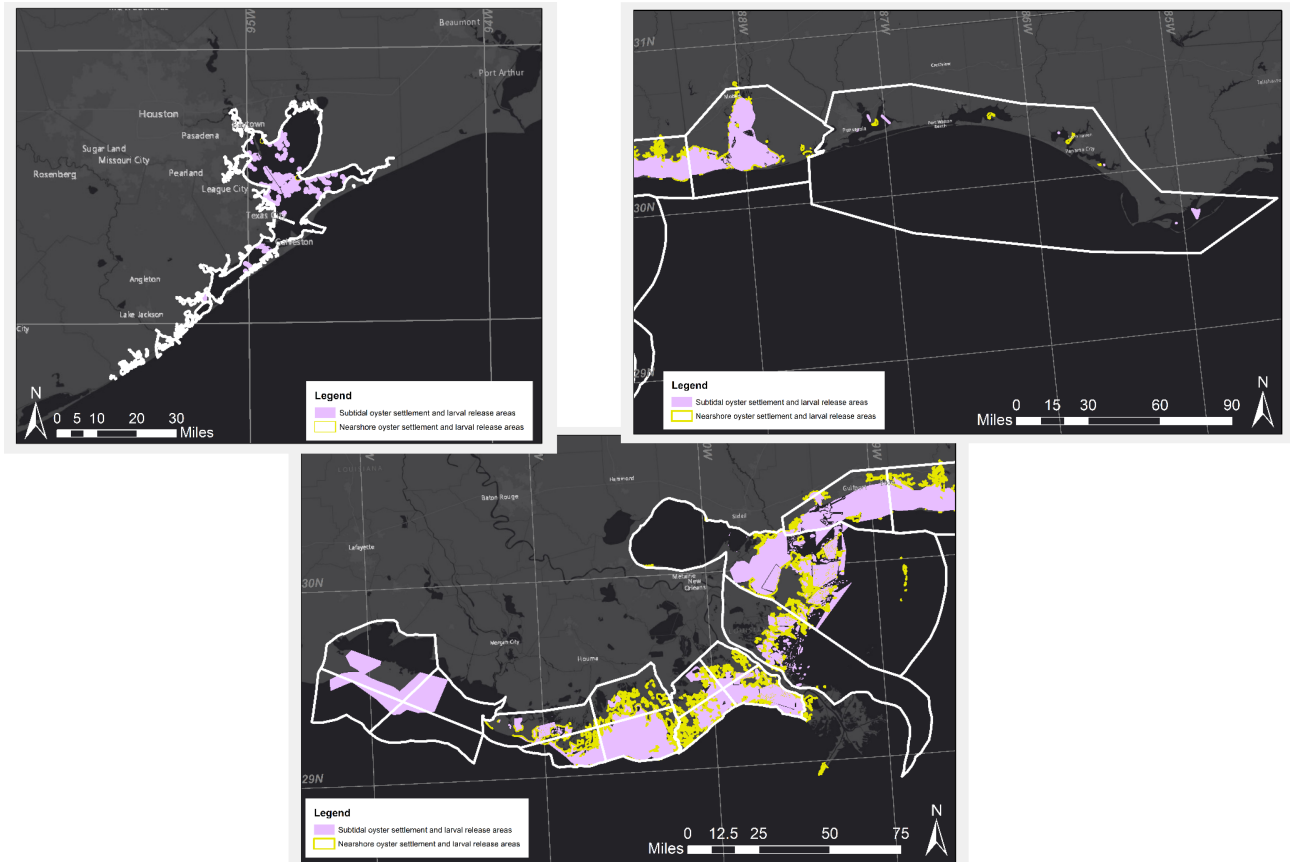


Figure 2. Location of subtidal (pink) and nearshore habitat (yellow) polygons used for release and settlement locations in the biophysical transport model.

2014). We note that North et al. (2008) found that a more complex treatment (three-dimensional with swimming velocity of larval particles) was appropriate in Chesapeake Bay; however, their system was deeper with longer periods of stratification than would be expected in the majority of our study area. The resulting connectivity matrices from our modeling effort quantified the probability that a particle (larva) in a given spatial cell would be advected to any other cell, including coastline locations. Particles were not allowed to cross a levee or a land boundary. If a new position of a particle crossed such boundaries, the particle position was instead set to a location on the boundary and subsequently determined by tracking along the edges. The temporal period was specified to capture oysters' main spawning period in the northcentral Gulf of Mexico, which was identified as the time from when the water temperature reached 25°C and lasted until the water temperature dropped below 25°C (Kim et al. 2010). In our study, the temporal period ranged from approximately 1 April to 24 November in 2012, 2014, and 2015. During the modeling period of each year, we completed 207 particle tracking 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 drift periods. Results were compiled for two time periods each year: spring (April–June modeling) and fall (September–November modeling).

Larval Settlement

As a post-processing step following the completion of each modeled 21-day release, the average settlement probability of larvae in each sub-basin was calculated to characterize larval transport within and among sub-basins and habitat types. "Settlement" was defined as a particle (larva) spatially intersecting an oyster habitat polygon at any point between 13 and 21 days post-release. 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 an oyster reef and successfully settling. Once a larva "settled," its final location was recorded (by embayment, sub-basin, 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 analysis does not account for initial egg size or quality, variation in larval growth, larval performance, planktonic food availability, abundance of predators on larvae, or other factors that may promote or interfere with larval survival and settlement (see Eierman & Hare 2013; Klein et al. 2023, 2024 for evidence of the importance of such processes in determining settlement success). Our modeling efforts assume that during individual 21-day model runs, spatial variability in environmental factors that influence such parameters was random and density independent. Oyster reef in the study

area was not continuous; patchy reefs and hummocks existed in sampled subtidal and fringing oyster habitat areas (Powers et al. 2017b). We created weighted settlement results for each sub-basin by multiplying the raw quantity of larvae that settled in nearshore or subtidal habitat by the estimated percent of oyster habitat cover in that habitat type of the sub-basin (Table 1).

To facilitate presentation of results, we calculated settlement averages for all larvae (fringing habitat and subtidal) for each of the time periods (spring and fall) for each year examined (2012, 2014, and 2015). To examine the question of fringing marsh versus subtidal origin of settlers, we classified all particles within an embayment or sub-basin as originating from a fringing location or a subtidal location and examined the percentages of all larvae settling in the area by origin (fringing versus subtidal). To address the question of whether the release of larvae from fringing areas increases connectivity within and among sub-basins, we determined the average proportion of larvae settling in each sub-basin that originated from that sub-basin or other sub-basin (i.e. the average composition of larvae settling in a sub-basin based on their initial sub-basin locations). This allowed us to summarize larval transport patterns throughout the modeled area as well as identify regions

and habitats (fringing and subtidal) that promote greater larval retention or lead to greater export of larvae and hence enhance connectivity.

Results

Our modeling effort demonstrated little connectivity as distances between oyster habitat increases. Exchange of larval particles was minimal between embayments (0–2%) and remained low even on the scale of sub-basins (<20%) within an embayment. Fringing oyster habitat served as a source of larvae for both subtidal and fringing oyster habitat, whereas subtidal oyster habitat generally seeded another subtidal oyster habitat in a specific sub-basin and not fringing oyster habitat within that same sub-basin.

Connectivity Among Embayments

Despite the highly varied oceanographic and meteorological conditions that occurred during our 3 years of study, few instances of larvae successfully leaving one embayment and entering another were documented (Fig. 3). The effective distance a larval particle would be expected to traverse and find

Table 1. Oyster reef percent cover by habitat polygon. Percent cover values in stratum A/A+ (known and mapped oyster reef) and stratum B (areas exclusive of stratum A/A+ that have the appropriate salinity regime for oyster but do not have mapped resource) polygons were quantified under separate field sampling efforts and together represent oyster reef occurrence in subtidal areas. Fringing oyster habitat along vegetated shorelines (nearshore) was quantified as described in Powers et al. (2017b). AL, Alabama; BB, Barataria Bay; CSA6, Louisiana Coastal Study Area 6; FL, Florida; MS E, Mississippi East; MS W, Mississippi West; TB, Terrebonne Bay; TX, Texas.

| Habitat polygon | Percent cover | Habitat polygon | Percent cover |
|--------------------------------|---------------|------------------------------|---------------|
| CSA 6 NW Nearshore | 0.0% | BB NW Subtidal Stratum B | 20.0% |
| CSA 6 NW Subtidal Stratum A/A+ | 0.0% | BB NE Nearshore | 8.3% |
| CSA 6 NW Subtidal Stratum B | 20.4% | BB NE Subtidal Stratum A/A+ | 19.6% |
| CSA 6 SW Nearshore | 0.0% | BB NE Subtidal Stratum B | 25.2% |
| CSA 6 SW Subtidal Stratum A/A+ | 0.0% | BB SE Nearshore | 8.3% |
| CSA 6 SW Subtidal Stratum B | 18.5% | BB SE Subtidal Stratum A/A+ | 19.5% |
| CSA 6 NE Nearshore | 0.0% | BB SE Subtidal Stratum B | 23.8% |
| CSA 6 NE Subtidal Stratum A/A+ | 0.0% | CSA 1S Nearshore | 8.0% |
| CSA 6 NE Subtidal Stratum B | 19.9% | CSA 1S Subtidal Stratum A/A+ | 14.5% |
| CSA 6 SE Nearshore | 0.0% | CSA 1S Subtidal Stratum B | 22.9% |
| CSA 6 SE Subtidal Stratum A/A+ | 0.0% | CSA 1N Nearshore | 8.0% |
| CSA 6 SE Subtidal Stratum B | 18.3% | CSA 1N Subtidal Stratum A/A+ | 13.2% |
| TB NW Nearshore | 8.3% | CSA 1N Subtidal Stratum B | 13.1% |
| TB NW Subtidal Stratum A/A+ | 14.6% | MS W Nearshore | 2.5% |
| TB NW Subtidal Stratum B | 15.2% | MS W Subtidal Stratum A/A+ | 22.3% |
| TB SW Nearshore | 8.3% | MS W Subtidal Stratum B | 12.4% |
| TB SW Subtidal Stratum A/A+ | 0.0% | MS E Nearshore | 2.5% |
| TB SW Subtidal Stratum B | 14.8% | MS E Subtidal Stratum A/A+ | 0.0% |
| TB NE Nearshore | 8.3% | MS E Subtidal Stratum B | 12.5% |
| TB NE Subtidal Stratum A/A+ | 17.8% | AL Nearshore | 2.5% |
| TB NE Subtidal Stratum B | 15.4% | AL Subtidal Stratum A/A+ | 29.8% |
| TB SE Nearshore | 8.3% | AL Subtidal Stratum B | 14.3% |
| TB SE Subtidal Stratum A/A+ | 0.0% | FL Nearshore | 0.0% |
| TB SE Subtidal Stratum B | 14.4% | FL Subtidal Stratum A/A+ | 20.3% |
| BB SW Nearshore | 8.3% | FL Subtidal Stratum B | 1.1% |
| BB SW Subtidal Stratum A/A+ | 17.3% | TX Nearshore | 6.5% |
| BB SW Subtidal Stratum B | 19.0% | TX Subtidal Stratum A/A+ | 0.0% |
| BB NW Nearshore | 8.3% | TX Subtidal Stratum B | 21.0% |
| BB NW Subtidal Stratum A/A+ | 16.7% | | |

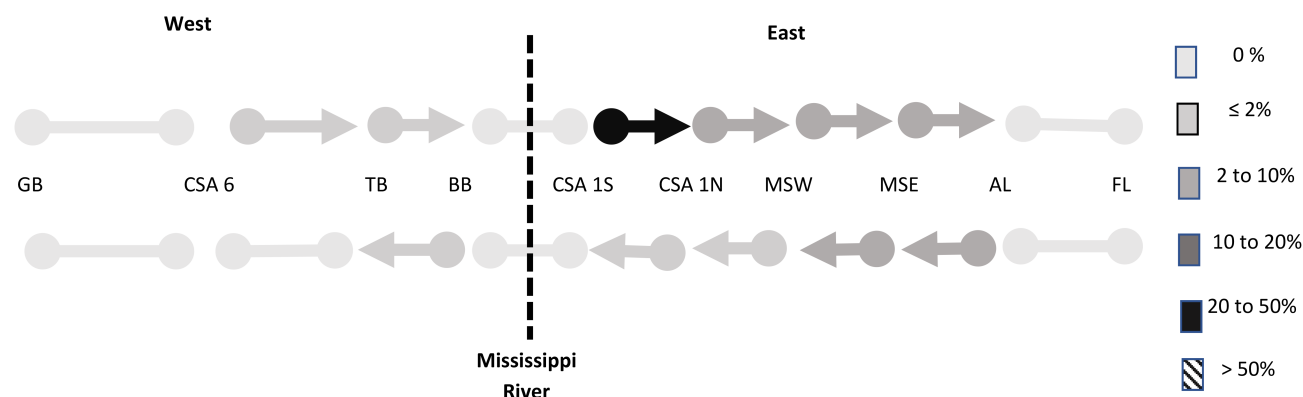


Figure 3. Schematic diagram illustrating connectivity among embayment in the northcentral Gulf of Mexico. Percentages refer to the percent of total particles that mimic oyster larvae released in areas with oyster habitat within the embayment (denoted by a filled circle on the arrow line) that settle on oyster habitat in the adjacent embayment east (upper line) and west (lower line) of the embayment of release. Spacing between embayments is illustrative and not drawn to absolute geographic scale. GB = Galveston Bay, Texas; CSA 6 is located in western Louisiana, TB = Terrebonne Bay, Louisiana; BB = Barataria Bay, Louisiana; CSA 1S and 1N are in eastern Louisiana; MS W and MS E are the Mississippi portion of Mississippi Sound East and West of Gulfport MS; AL refers to the Alabama portion of Mississippi Sound and Mobile Bay, Alabama; Florida represents the region from Pensacola Bay, Florida, to Apalachicola, Florida. Percentages represent the average over all model runs (inclusive of both seasons and all years).

suitable settlement habitat was primarily confined to sub-basin scales, with most larval particles settling less than 25 km from their release point and the majority settling between 5 and 15 km from the release location (Fig. 4). The distance and hence potential connectivity were longer for particles released in subtidal locations than in fringing oyster habitat. Particles released in either habitat type (subtidal or fringing) did not travel far enough to link two adjacent embayments to any great extent. The only areas where connectivity was consistently higher between embayments were on the eastern side of the Mississippi River between embayments with broader borders. Specifically, between CSA 1N and CSA 1S (23% of particles exchanged; Table S1), followed by connectivity between CSA 1N and Mississippi West (MS W). Adjacent embayments with more narrow inlets or large distances between inlets had little connectivity (approximately 0–2%). For example, CSA 6 and TB only had a small proportion of larvae that exited from the southeast sub-basin settle into the southern areas of adjacent sub-basins (<2%). Longer distances between inlets prevented almost all exchange: Galveston Bay showed no connectivity with other basins, and no exchange was seen between Florida and Mobile Bay.

Connectivity Within Embayments

For embayments that were subdivided into sub-basins in our analysis, exchange of particles among sub-basins was modest (3–17%) with sub-basins located in the upper (northern) sub-basins subsidizing sub-basins to the lower (south) (Fig. 5). This connectivity was slightly lower under spring (Table S1) than fall conditions (Table S2). Connectivity between eastern and western areas of Mississippi Sound (Mississippi East [MS E] and MS W) was the highest between any two sub-basins with about 11% of particles released in one area successfully settling in the other. Interestingly, western areas of embayments served as a

source for eastern portions of embayments with minimal east–west successful transport: 11% west to east versus 3% east to west (Fig. 5). Connectivity was much higher for larvae originating in northern sub-basins and settling into southern sub-basins than larvae originating in the southern sub-basins and settling into the northern sub-basins.

Fringing Versus Subtidal Release

Larvae originating from fringing marsh habitats settled in both fringing and subtidal oyster habitats. Excluding the four sub-basins of CSA 6 in Louisiana, which had 0% cover of fringing oyster habitat and hence no release of larvae near fringing marsh, 23% of larvae released in the fringing areas settled in fringing areas, with the remaining 77% of larvae settling in subtidal areas (Fig. 6). Variability in fringing habitat settlement was large across embayment and sub-basins examined ranging from 0% in areas that lacked fringing oyster habitat, to 55% settlement along fringing shoreline habitat (Fig. 7). Much of this variability could be explained by the relative quantity of fringing habitat available for settlement. Extensive fringing oyster habitat was present in the northeast, northwest, and southwest regions of BB and in the northeast, southeast, and southwest areas of TB, where settlement from fringing habitat-originating oyster larvae was high. In all areas, the vast majority of oyster larvae originating from fringing oyster habitat was settled in subtidal areas of each sub-basin: greater than 80% of oyster larvae released from the fringing oyster habitat settled in subtidal area. Despite seasonal variability in the meteorological and hydrodynamic environment, patterns of oyster settlement were relatively similar among seasons (Fig. 5) and years (Figs. S1–S6).

The vast majority of oyster larvae release from subtidal oyster areas (stratum A/A+ and stratum B) settled in subtidal areas within all embayments. Overall, 94% of larvae released

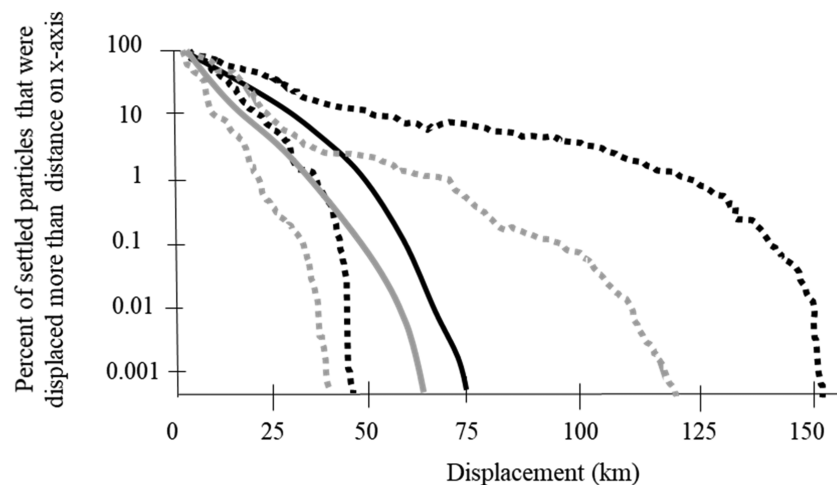


Figure 4. Displacement distance of larval particles released in fringing oyster habitat (gray lines) and subtidal locations (black lines) that would be expected to settle into oyster habitat (subtidal or fringing oyster habitats). Note the log scale on y-axis. Dashed lines to the left present the results of low advective conditions, and dashed lines to the right high advective conditions.

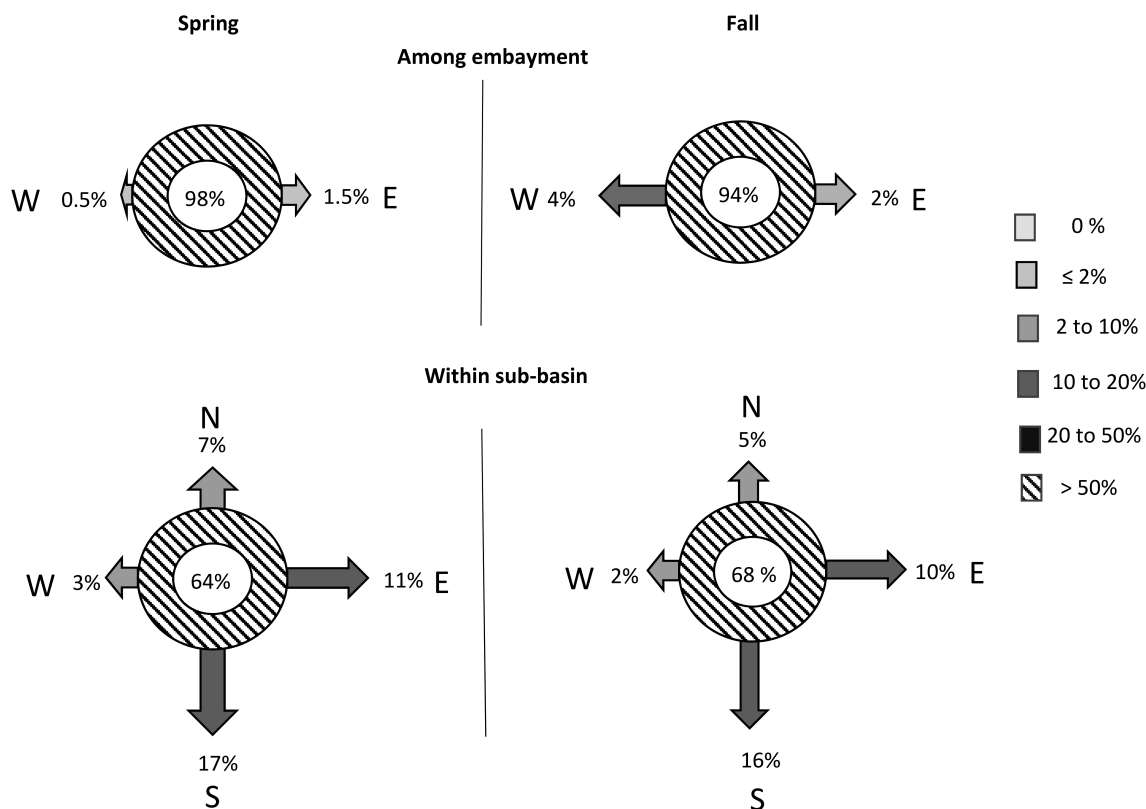


Figure 5. Schematic illustration of average larval particle exchange rates among all embayments and among all sub-basins regardless of embayment. Data used in calculating the averages are presented in Table S1 (spring) and Table S2 (fall).

in subtidal habitats settled in subtidal habitats. This pattern remained relatively constant across sub-basins and seasons (Figs. S1–S6). Even in areas with abundant fringing oyster habitat, subtidal areas received the vast majority of oyster larvae that originated in subtidal areas.

Discussion

Despite the potential for long-distance transport of larvae as a result of the eastern oyster's approximately 3-week larval period, application of state-of-the-art hydrodynamic transport model using detailed geomorphology and oyster habitat

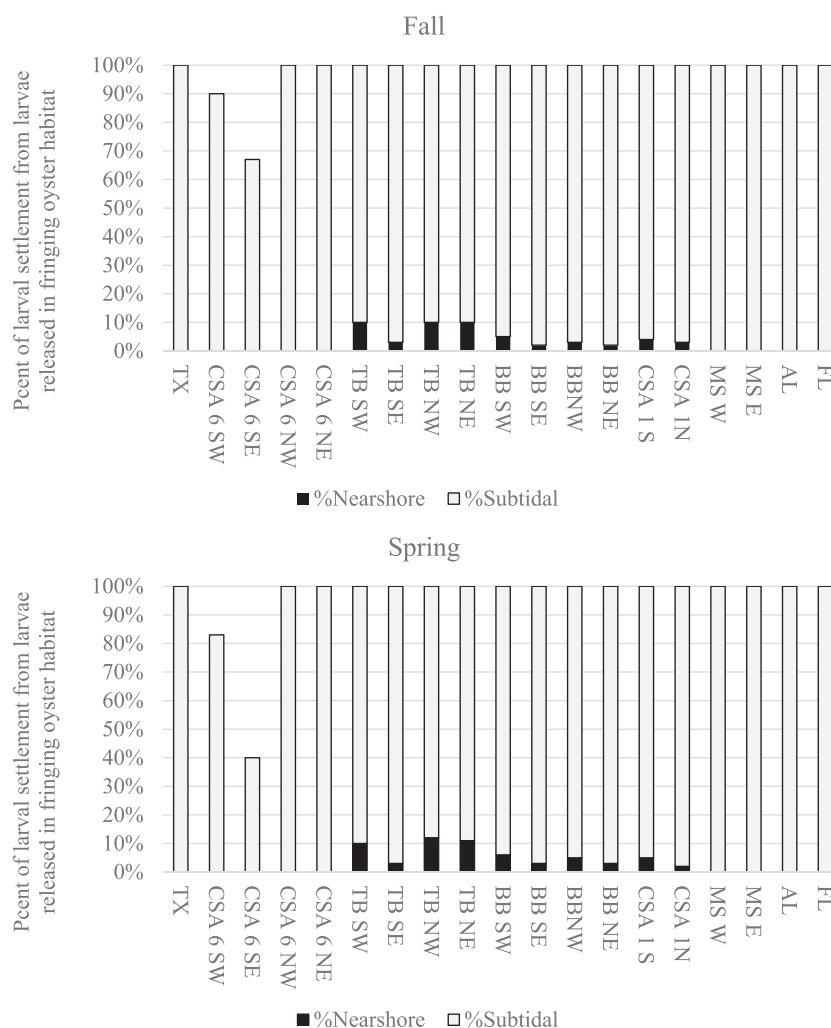


Figure 6. Contributions of oyster larvae released from subtidal habitats to predicted settlement in nearshore and subtidal oyster habitat within subregions of the overall study area in spring (top) and fall (bottom). Note values are averaged from 2012, 2014, and 2015. Average settlement values for CSA 6 SE and SW sum to less than 100% because some model runs resulted in no subtidal larvae settlement (CSA 6 SE—10 of 30 fall model runs and 18 of 30 spring model runs; CSA 6 SW—3 of 30 fall model runs and 4 of 30 spring model runs). Embayments and sub-basins are arranged from west to east. AL, Alabama; BB, Barataria Bay; CSA 6, Louisiana Coastal Study Area 6; FL, Florida (Pensacola Bay to Apalachicola Bay); MS W, Mississippi West; MS E, Mississippi East; TB, Terrebonne Bay; TX, Galveston Bay, Texas.

distribution indicates limited connectivity between embayments along a nearly 1000 km stretch of the northcentral Gulf of Mexico. Even on the finer sub-basin scale within an embayment recruitment of larvae to existing oyster habitat is primarily on a local scale. Within these sub-basins, recruitment of oyster larvae to fringing oyster habitat is almost exclusively from larvae released in the fringing oysters, although the majority of larvae released in the fringing habitat is destined to settle in subtidal oyster reefs. Larvae released in subtidal areas of sub-basins generally seed other subtidal areas and not fringing oyster habitat areas within that sub-basin. Hence, efforts to promote resiliency by ensuring adequate larval settlement to restored oyster reefs should focus on ensuring adequate oyster habitat is restored/conserved within a sub-basin and that greater efforts are focused on fringing oyster habitat,

which can provide larvae to both fringing oyster habitat as well as subtidal habitats.

The limited connectivity among embayments results from the higher residence times of larval particles within embayments and sub-basins, restricted access to neighboring embayments through relatively narrow inlets, and long distances between these inlets. The only real exception to the pattern of very limited connection among embayments was when boundaries between adjacent embayments were larger and less well defined, as was the case between areas in Louisiana east of the Mississippi River and western Mississippi Sound. The pattern of local transport also held at the sub-basin level, where most larvae were predicted to settle in the vicinity of their release location (i.e. the same sub-basin). When larval particles did exit their sub-basin of release and settle into the adjacent sub-basin there was a bias in direction with very low percentages of oyster

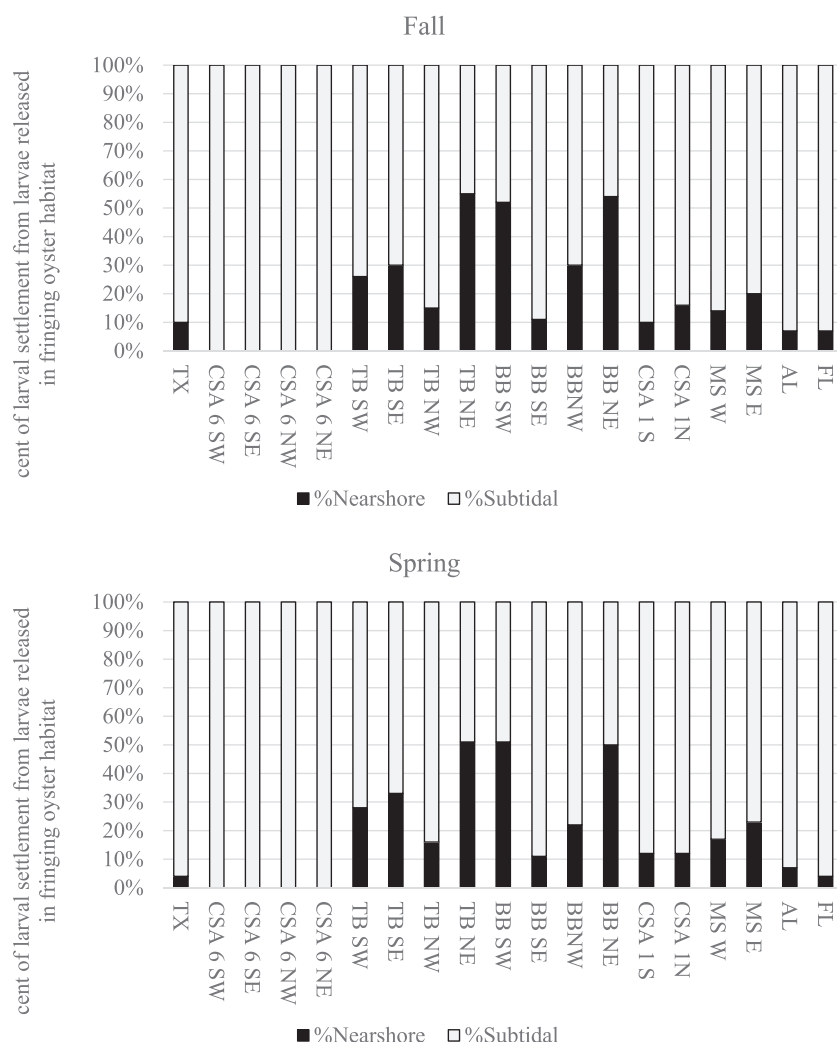


Figure 7. Contributions of oyster larvae released from nearshore habitats to predicted settlement in nearshore and subtidal oysters within subregions of the overall study area in spring (top) and fall (bottom). Note values are averaged from 2012, 2014, and 2015. Embayments and sub-basins are arranged from west to east. AL = Alabama; BB = Barataria Bay; CSA 6 = Louisiana Coastal Study Area 6; FL = Florida (Pensacola Bay to Apalachicola Bay); MS E = Mississippi East; MS W = Mississippi West; TB = Terrebonne Bay; TX, Galveston Bay, Texas.

larvae from the northern areas of embayments settling in the southern areas and even fewer from southern areas settling in northern areas. While very low exchange rates among embayments may be sufficient to provide a high degree of genetic homogeneity (Thongda et al. 2018), our limited embayment connectivity supports the conclusion that oyster populations in estuaries are demographically independent. The limited exchange of larvae at the sub-basin level is similar to the results of Gancel et al. (2021) in their study of Mobile Bay and eastern Mississippi Sound that also concluded that larval settlement was likely a function of self-recruitment or limited connectivity over relatively short distances.

Our modeling efforts also demonstrate that restoration/conservation of fringing oyster habitat can be a powerful tool in increasing recruitment at the sub-basin level and may increase connectivity among sub-basins. Restoring oysters along vegetated shoreline creates spawning areas that can serve as a source

of larvae for subtidal areas as well as other fringing marsh habitats. Because average displacement distances were kilometers less for larvae released in fringing oyster habitat, the effect of these spawning areas would be greater on a more localized area. If expanded through restoration activities, these fringing oyster habitats can increase resilience at sub-basin scales. Further, oysters along vegetated shoreline habitat are generally not harvested in our study area because of the difficulty for fishermen to access these areas, which are very shallow. Consequently, restoration in these areas likely result in a longer-term benefit than subtidal areas that are open to higher rates of exploitation.

Our analysis also demonstrates the relatively low supply of oyster larvae that successfully re-seed fringing oyster habitat, which indicates that oyster population occurring along these vegetated shorelines are less resilient to disturbance. Consequently, fringing oyster habitat requires additional protection as well as targeted restoration if this habitat is injured.

Extensive injury was demonstrated as a result of the *Deepwater Horizon* oil spill and associated response activities (Powers et al. 2017b). Oysters along fringing shoreline may also be more sensitive to the impacts of hurricane landfall because damage from large wave action may be greater in the shallow edge communities than the deeper subtidal reefs. Our modeling demonstrated that the main source of larvae to re-seed fringing oyster habitat comes from other fringing oyster habitat, with very few oyster larvae released from subtidal areas expected to settle in fringing areas. Because of the lower areal coverage of fringing oyster habitat compared to subtidal oyster habitat and the lower probability of oyster larvae released in subtidal areas seeding fringing oyster habitat, fringing marsh area has a lower supply of oyster larvae than its subtidal counterpart. Hence, while conservation and restoration in fringing oyster habitat can greatly assist restoration practitioners in restoring subtidal oyster reefs, restoration of fringing oyster reef is a critical element in ensuring the persistence of fringing oyster habitat.

Given the relatively short distances the majority of oyster larvae are expected to travel, restoration plans should account for the fact that creation of successful, self-sustaining oyster populations will require neighboring oyster habitat on the scale of 5–10 km. Strategies that rely on a few large reef projects may succeed in producing a large pool of larvae; however, this large pool may not seed oyster reefs over a broad area. In the same vein, local restoration efforts should not assume subsidy of oyster larvae from long distances. Locating restored oyster reefs near existing sources of oyster larvae (on the scale of km to no more than 10 km) should be a major consideration when siting a restoration project. This will likely require a longer-term strategy of establishing stepping stones over time: multiple restoration activities within a radius of several kilometers, followed by locating subsequent reefs further out as those previously restored reefs build oyster density. Such strategies would eventually result in highly connected archipelagos of reefs. Fringing oyster habitat along salt marshes could provide this archipelago-like benefit by extending on both sides of an estuary a band of oysters that can serve as a source of oyster larvae. With protection, this band could persist for years, serving as a de facto spawning reserve while also providing valuable shoreline protection (Piazza et al. 2005; Scyphers et al. 2011) and enhancing juvenile fish habitat (Grabowski et al. 2005; Scyphers et al. 2011). Restoring such archipelagos of subtidal reefs through sequential restoration projects or by restoring fringing oyster habitat throughout a sub-basin is the most promising way to ensure larval supply is enhanced.

More broadly, our results demonstrate the use of biophysical models in developing larger-scale marine restoration programs (Haase et al. 2012; Kim et al. 2013). Understanding the scale at which restoration practitioners can depend on natural settlement of organisms is a critical element in developing successful restoration plans for self-sustaining populations (Atwood & Grizzle 2020). When areas are spread too far from existing sources of recruits, supplements with hatchery-derived organisms or relay of existing adults must be considered (Powers & Boyer 2014). Further defining the scale at which connectivity

occurs is important in marine communities because the assumption of entirely open, demographically interconnected populations is not always applicable (Levin 2006). In light of our results that larval supply is primarily from local scale sources, future restoration planning should consider conducting biophysical models on the sub-basin or embayment scale that can utilize finer scale resolution data on oyster density, habitat size, mortality, and reproductive output to determine which areas serve as net demographic sources and which areas are sinks and develop shell budgets (Powell et al. 2006).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Average larval settlement distribution by region (combines fringing oyster habitat and subtidal larval transport) across spring model releases for all years, excluding values <0.5%.

Table S2. Average larval settlement distribution by region (combines fringing oyster habitat and subtidal larval transport) across fall model releases for all years, excluding values <0.5%.

Figure S1. Percentage of larvae released in nearshore (fringing) oyster habitat that settled in nearshore or subtidal habitats within embayments or sub-basin examined under conditions in 2012.

Figure S2. Percentage of larvae released in nearshore oyster habitat that settled in nearshore or subtidal habitats within the embayments or sub-basin examined under conditions in 2014.

Figure S3. Percentage of larvae released in nearshore oyster habitat that settled in nearshore or subtidal habitats within embayments or sub-basin examined under conditions in 2015.

Figure S4. Percentage of larvae released in subtidal oyster habitat that settled in nearshore or subtidal habitats within embayments or sub-basins examined under conditions in 2012.

Figure S5. Percentage of larvae released in subtidal oyster habitat that settled in nearshore or subtidal habitats within embayments or sub-basins examined under conditions in 2014.

Figure S6. Percentage of larvae released in subtidal oyster habitat that settled in nearshore or subtidal habitats within embayments or sub-basins examined under conditions in 2015.

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