

RESEARCH ARTICLE

# Establishing Restoration Strategy of Eastern Oyster via a Coupled Biophysical Transport Model

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## Abstract

For marine fish and invertebrates, larval dispersal plays a critical role in determining connections among source and sink habitats, and the lack of a predictive understanding of larval dispersal is a fundamental obstacle to the development of spatially explicit restoration plans for marine populations. We investigated larval dispersal patterns of eastern oyster in an estuary along the Northern Gulf of Mexico under different simulation scenarios of tidal amplitude and phase, river discharge, wind direction, and larval vertical migration, using a coupled biophysical transport model. We focused on the dispersal of larvae released from the commercially exploited (Cedar Point, CP) and non-exploited (Bon Secour Bay, BSB) oyster populations. We found that high flushing rates through the dominant inlet prevented larval exchange between the commercially exploited and non-exploited populations, resulting in negligible connectivity between them. Variations in

tidal amplitude, river discharge and wind direction played a more important role in the amount of larvae retained in Mobile Bay when they are released from CP than from BSB. Under most of the scenarios, larvae from BSB were retained around the spawning area, while larvae from CP showed a predominant westward flow. Net sinking behavior of late-stage larvae increased larval retention in the bay, but physical transport showed a higher impact in the amount of larvae retained. These findings have enhanced our understanding of larval dispersal of eastern oyster in a wide, shallow estuarine system, and been used to establish spatially explicit strategies for oyster restoration in the Mobile Bay system, Alabama.

**Key words:** *Crassostrea virginica*, larval dispersal, Mobile Bay, Northern Gulf of Mexico, oyster restoration, physical transport, population connectivity, vertical larval migration.

## Introduction

Among the various factors affecting successful recruitment of marine fish and invertebrates, larval dispersal plays a critical role in determining spatial and temporal patterns of abundance that are important components of restoration strategies (Cowen & Sponaugle 2009). The potential for larvae of marine organisms to travel long distances during their planktonic dispersal phase poses a unique challenge for spatially explicit restoration and enhancement efforts because this dispersal often results in a decoupling of local population abundance and recruitment (Pineda et al. 2010). However, if predictable pathways of larval dispersal can be established then this information can be used to determine sustainable local populations by ensuring a supply of recruits. These dispersal pathways can also be used to evaluate connectivity of presumed source populations

of propagule as well as the location of demographic sinks. Equally important, areas of high retention of larvae could provide sustainable populations through self-recruitment. For species whose mobility is restricted at later developmental stages (e.g. plants and sessile invertebrates) establishing predictable larval corridors and patterns of retention could be key to successful restoration (Schulte et al. 2009).

Larval dispersal and retention is determined by both physical transport and biological movement of larvae (Young 1995). Although much controversy exists over the relative importance of biological movement on larval dispersal, the interactions between physical transport and biological movement have been suggested to explain the observed transport and retention of marine invertebrate larvae (Shanks & Brink 2005; Morgan & Fisher 2010). Recognizing the potential importance of both physical transport and biological movement, a coupled biological–physical transport model can be a useful tool to investigate larval dispersal and source–sink metapopulation relationships.

Biogenic reefs formed by the gregarious settlement of oysters have declined over the last decades in many estuarine and coastal ecosystems due to overharvesting, oyster diseases, and deteriorated water quality (Beck et al. 2011). The decline has lowered filtration capacity, degraded water quality, decreased

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stable habitats, and increased coastal vulnerability to extreme events. The Northern Gulf of Mexico provides the highest catches of wild oysters in the world; however, the abundance of native oysters significantly declined and it requires urgent restoration and conservation efforts (Beck et al. 2011).

The Mobile Bay system, Alabama, is a large shallow embayment bisected with a narrow deep ship channel in the Northern Gulf of Mexico (Fig. 1). The system is characterized by micro-tidal range, large river discharge, and exchange with the Gulf of Mexico via relatively narrow passes, all of which are common features of estuaries along the Northern Gulf of Mexico (Schroeder & Wiseman 1999). Oyster populations in the Mobile Bay system have shown distinctive spatial patterns over the past 90 years with much higher production in the southwest part of the study area (May 1971). The Cedar Point Reef complex (CPR) (Fig. 1) has been the single most productive area, contributing over 90% of the oyster harvest in Alabama (May 1971). Oyster harvesting historically had been reported in the east side of the Bay, for example, Fish River Reef (FRR), Bon Secour Reef (BSR), and Shell Bank Reef (SBR) (Fig. 1), but the oyster population is currently too small to support commercial harvest in the area (Stout 1998). The same gradient in oyster spat settlement, decreasing from west to east, has been observed over the past 40 years (Hoese et al. 1972; Kim et al. 2010). These studies have suggested that limited larval supply may be responsible for the poor oyster recruitment in the east side of the Bay. However, larval dispersal and the level of larval connectivity between both oyster populations in close proximity (~30 km apart) are poorly understood. The lack of spatially explicit knowledge of the larval dispersal has been a fundamental obstacle to establishing a comprehensive strategy for oyster restoration in the Mobile Bay system as well as other estuarine systems along the Gulf and U.S. east coast.

We conducted a series of model simulations with different physical transport under various tide, river discharge, and wind conditions to evaluate spatial patterns of larval dispersal and metapopulation connectivity of eastern oysters, *Crassostrea virginica*. We also tested the role of biological movement combined with the different physical transport conditions. Specifically, we addressed the following questions: (1) How do different forcing conditions affect larval dispersal; (2) How does biological movement affect larval dispersal under different forcing conditions; (3) Is there larval connectivity between oyster populations in the west and east sides of Mobile Bay; and (4) How do physical transport and biological movement affect the larval connectivity between oyster populations? We used the model results to evaluate spatially explicit management strategies for oyster restoration.

## Methods

### Biophysical Transport Model

We used a three-dimensional biophysical transport model that was previously developed for coastal Alabama to estimate larval dispersal patterns (Kim et al. 2010). This

model employs the hydrodynamic model in the three-dimensional hydrodynamic-eutrophication model to simulate physical transport. The model application gave a good reproduction of the observed surface elevation, current velocity, and salinity for both total and subtidal components and was able to simulate the features observed to be important for physical transport in the Mobile Bay system (Kim & Park 2012).

We parameterized biological movement of oyster larvae as a function of swimming and sinking velocity estimated as a function of larval size by employing linear regressions (Eqs 2 and 3 in Kim et al. 2010). The present model employs neutrally buoyant net vertical velocity during the early-stage larval period and net sinking velocity with the rate increasing as larvae grow during the late-stage larval period (Fig. 2 in Kim et al. 2010). The model results showed significant correlations with observed larval concentration for an overall average time scale of 1 year ( $R = 0.57-0.62$ ) as well as during spring ( $R = 0.69-0.71$ ) and fall ( $R = 0.62-0.82$ ) (Table 2 in Kim et al. 2010). The correlation decreased during the summer ( $R = 0.37-0.39$ , non-significant).

### Forcing Functions

Hydrodynamic conditions show a great variability in response to tide, river discharge, and wind with their relative impacts varying spatially and temporally, which complicates efforts to define a typical circulation pattern of the study area (Kim & Park 2012). In consequence, it is difficult to assess the effect of each forcing condition on larval dispersal. In this study, therefore, idealized forcing functions were used, which were estimated based on long-term time series data to represent various forcing conditions ranging from typical to extreme in the Mobile Bay system. The forcing variables introduced in the model were tidal amplitude and phase, river discharge, and wind speed and direction.

Tides are predominantly diurnal in the study area. The harmonic constants at the NOAA's Dauphin Island tide station (Fig. 1) show that  $K_1$  and  $O_1$  tides are the two most important components, accounting for 67% of tidal range. A surface elevation by  $K_1$  and  $O_1$  tides shows a tropic-equatorial cycle, with tidal range varying from 0.04 m during equatorial tides to 0.56 m during tropic tides. For all scenario simulations, the surface elevation by  $K_1$  and  $O_1$  tides was used to specify open boundary conditions.

Mobile Bay receives 95% of freshwater input from the Mobile River system (Fig. 1) (Schroeder 1978). Daily river discharge data were obtained from two U.S. Geological Survey gauging stations, Claiborne L&D in Alabama River and Coffeetown L&D in Tombigbee River. We calculated the monthly statistics of daily river discharge for the oyster larval recruitment period in May–October between 1976 and 2006. The 25th, 50th, 75th, and 95th percentiles for this period are 359, 537, 983, and 3,294  $m^3/s$ , respectively. Although daily discharge varies over a wide range between 161 and 8,184  $m^3/s$ , daily discharge between 250 and 450  $m^3/s$  occurs most frequently, accounting for 32% of the data. Six constant discharge conditions of 250, 359, 450, 537, 983, and

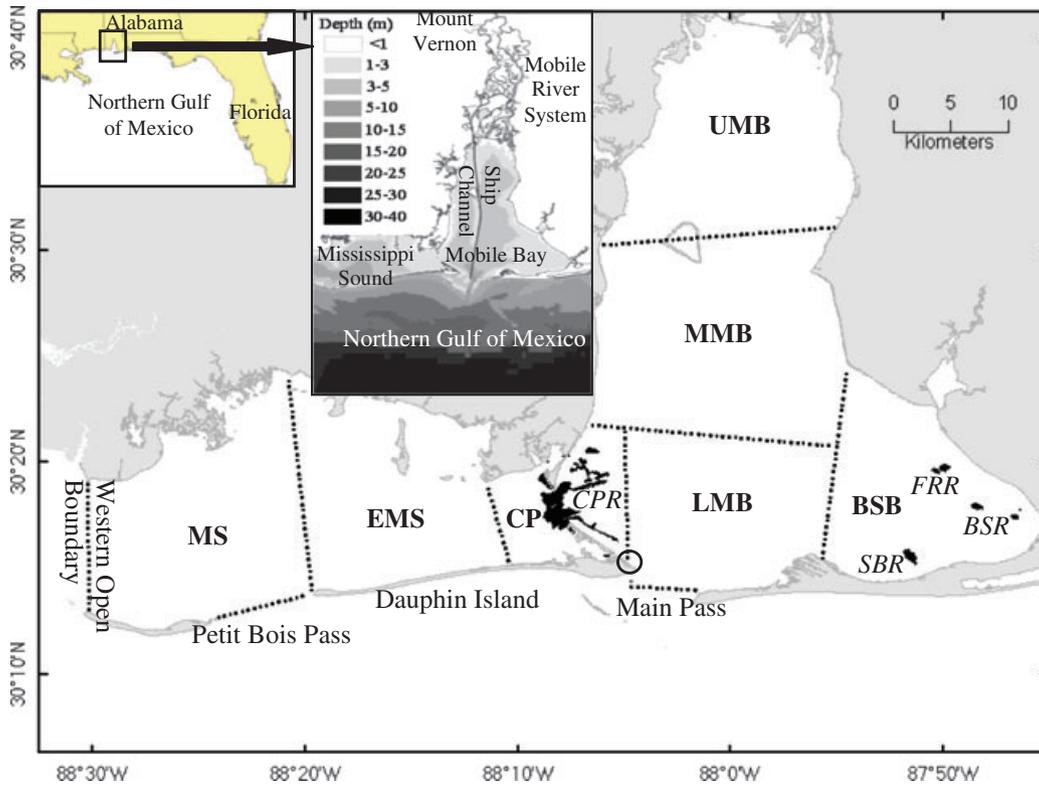


Figure 1. A map of Mobile Bay and eastern Mississippi Sound showing Dauphin Island station (○) for tide and wind observation and existing oyster reefs (filled area) where oyster larvae were released in model simulations, including Cedar Point Reef complex (CPR), Fish River Reef (FRR), Bon Secour Reef (BSR), and Shell Bank Reef (SBR). The dashed lines denote boundaries of seven zones, including Mississippi Sound (MS), eastern Mississippi Sound (EMS), Cedar Point (CP), lower Mobile Bay (LMB), middle Mobile Bay (MMB), upper Mobile Bay (UMB), and Bon Secour Bay (BSB). The insert maps show the modeling domain with depth contours.

3,294 m<sup>3</sup>/s were used for scenario simulations to specify the upriver boundary condition at Mount Vernon (Fig. 1).

The 20-year median wind speed in May–October is 4.3 m/s based on hourly data from 1987 to 2006 at the Dauphin Island station of the National Data Buoy Center (Fig. 1). Southerly winds, including southwest, south, and southeast winds, prevail during May–August, while north and northeast winds dominate during September–October (Fig. 2). The southerly winds account for 56% of spring and summer winds, and the northerly winds for 46% of fall winds. For wind directions, five 11-day periods were selected to represent conditions of dominant southwest (19–30 May 2006), south (10–21 June 2003), southeast (8–19 July 2006), northeast (4–15 September 2005), and north (11–22 October 2005) winds. These five periods were selected such that the dominant wind conditions occurred 45–55% of each period and used for scenario simulations to specify the surface boundary condition.

### Scenario Simulations

Combinations of forcing functions were used for scenario simulations to investigate the variability in larval dispersal according to the representative values of the forcing variables

during the oyster larval recruitment period (Table 1). To facilitate comparison between scenario simulations, typical forcing conditions of the Mobile Bay system were defined as larval release at slack-before-flood (SBF) during an equatorial tide with median river discharge (537 m<sup>3</sup>/s) and wind with median speed (4.3 m/s) and random direction (T1 in Table 1). When the effect of one forcing function on larval transport was examined, the typical conditions were used for the other two forcing functions. The effect of tide on larval dispersal was examined by releasing larvae at different tidal phase, that is, SBF or slack-before-ebb (SBE) during either tropic or equatorial tide, T1–T4. The effect of river discharge was examined for six different discharge conditions, R1–R6. The effect of wind was examined for five dominant wind directions, W1–W5.

Larval period of oysters varied from 10 to 18 days in response to water temperature in the Mobile Bay system (Kim et al. 2010). We chose the most dominant larval period, 10 days, for all scenarios simulations. Over the 10-day larval period, a total of 14 scenario simulations were conducted for various combinations of forcing functions (Table 1). To investigate larval connectivity of oyster populations between the west and east side of Mobile Bay, each of the above 14 scenario simulations was conducted twice for two potential spawning habitats including reefs in CP and BSB (Fig. 1). To

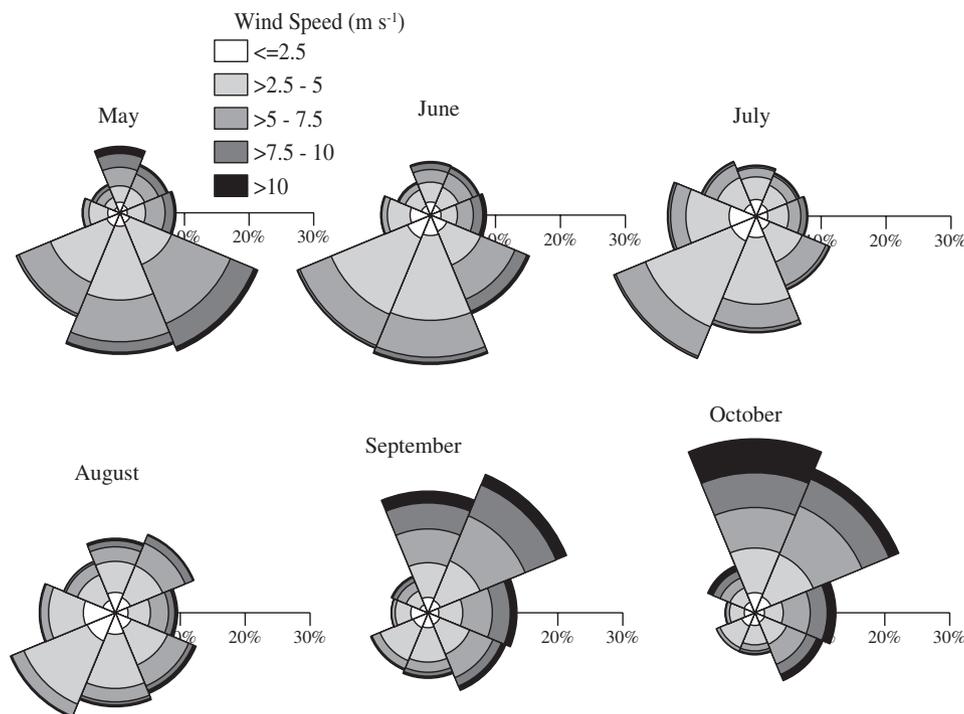


Figure 2. Wind roses showing monthly statistics of hourly data at the Dauphin Island station in 1987–2006 during the oyster larval recruitment period May–October.

Table 1. Design of scenario simulations.

Forcing Function	Simulation ID	Larval Release Time	River Discharge <sup>a</sup> (m <sup>3</sup> /s)	Wind	
				Speed <sup>b</sup> (m/s)	Direction <sup>c</sup>
Tide	T1	SBF during equatorial tide	537	4.3	Random
	T2	SBE during equatorial tide			
	T3	SBF during tropic tide			
	T4	SBE during tropic tide			
River	R1	SBF during equatorial tide	250	4.3	Random
	R2		359		
	R3		450		
	R4 <sup>d</sup>		537		
	R5		983		
	R6		3,294		
Wind	W1	SBF during equatorial tide	537	4.3	Southwest
	W2				South
	W3				Southeast
	W4				North
	W5				Northeast

<sup>a</sup> Discharges of 359, 537, 983, and 3,294 m<sup>3</sup>/s are the 25th, 50th, 75th, and 95th percentiles, respectively, in May–October (1976–2006): see the text for 250 and 450 m<sup>3</sup>/s.

<sup>b</sup> Median wind speed of 4.3 m/s (1987–2006).

<sup>c</sup> Dominant wind direction occurring 45–55% of each period: see the text.

<sup>d</sup> Note that simulation R4 is identical to T1.

investigate the effect of biological movement, another set of 14 scenario simulations with the larvae released from CP were conducted with biological movement. The model results with biological movement were compared with those from the corresponding 14 scenario simulations by physical transport only.

For analysis of the model results, Mobile Bay and eastern Mississippi Sound were divided into seven zones: Mississippi

Sound (MS), EMS (Eastern Mississippi Sound), CP, Lower Mobile Bay (LMB), Middle Mobile Bay (MMB), Upper Mobile Bay (UMB), and BSB (Fig. 1). Net larval flux was calculated during the 10-day larval period across the boundaries of the seven zones, and then a tidal, 25-hour, average larval retention was calculated to represent the larvae remained in each zone. Larval flux among zones and retention within

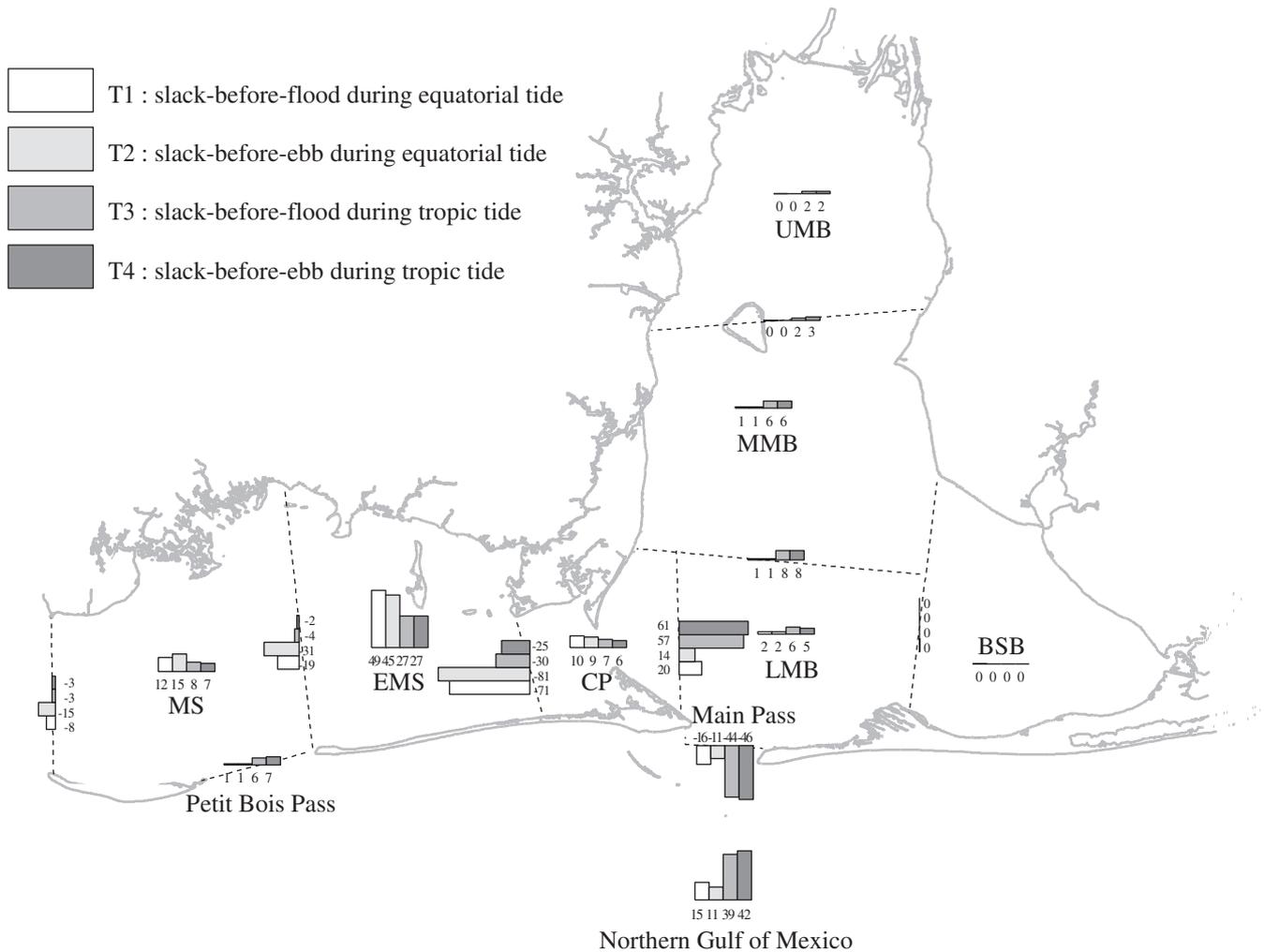


Figure 3. Percent larval retention and flux relative to the initial larvae released from CP for different tide conditions, T1–T4 in Table 1. The bars indicate larval retention in each zone and larval flux across each boundary, with positive values denoting eastward or northward larval flux.

each zone were expressed in percentages relative to an initial amount of larvae released from the spawning zone.

## Results

### Larvae Released from CP

When larvae were released from CP, the difference in release time between SBF and SBE caused little change in larval retention and flux (Fig. 3); however, variation existed between tropic and equatorial tides. For larvae released during equatorial tides (T1 and T2), 71–81% of larvae were transported westward away from the spawning zone, and many of them (54–59%) remained in the southwest part of the study area including CP and EMS. When released during tropic tides (T3 and T4), more larvae (57–61%) were transported eastward into LMB and many of them (44–46%) were transported out of the Bay through Main Pass, resulting in retention of fewer larvae (33–34%) in the southwest part. Regardless of tidal conditions,

maximum larval retention occurred in EMS and no larvae were transported into the east side of the Bay (Fig. 3).

Larval flux and retention changed with river discharge (Fig. 4). For dry condition (R1), 32–25% of larvae remained in EMS and CP, with 30% flushed out of the Bay through Main Pass. As river discharge increased, more larvae were transported westward into EMS and fewer larvae lost through Main Pass. For the median discharge condition (R4), 49% of larvae remained in EMS but only 10% in CP. As river discharge further increased beyond the median, westward larval outflux rapidly increased, decreasing larval retention. Under flood discharge condition (R6), 75% of larvae were lost through the western boundary, with only 14% remaining in EMS, 1% in CP, and none in UMB, MMB, LMB, and BSB. Under all discharge conditions, no larvae were transported to the Bay's east side.

Wind condition played an important role in larval transport and retention (Fig. 5). The southwest wind (W1) transported 80% of larvae into LMB and many (52%) were flushed out of

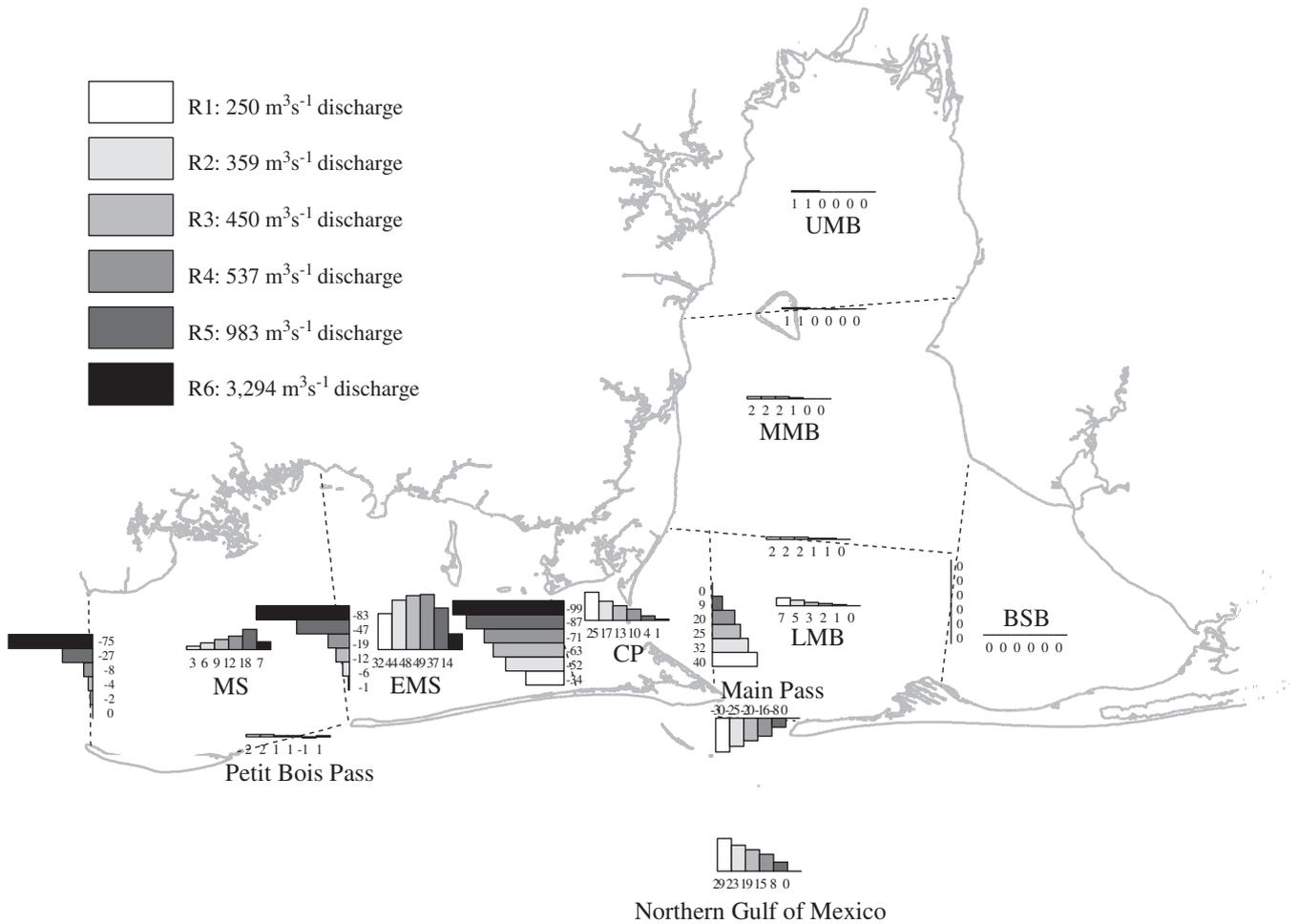


Figure 4. Percent larval retention and flux relative to the initial larvae released from CP for different river discharge conditions, R1–R6 in Table 1. The bars indicate larval retention in each zone and larval flux across each boundary, with positive values denoting eastward or northward larval flux.

the Bay through Main Pass. The south wind (W2), however, facilitated larval retention in the southwest part of the study area, remaining 27–44% of larvae. The southeast wind (W3) pushed most larvae (95%) further westward of CP, resulting in maximum retention of 57% in EMS. Under the northerly wind conditions (W4 and W5), 57–81% of larvae were transported out of the study area, resulting in low larval retention in the southwest part. As in the case of tide and river discharge, negligible numbers of larvae were transported into the east side of Mobile Bay under any wind conditions.

Total outflux/loss of larvae through Main Pass, Petit Bois Pass, and the western open boundary is compared between physical transport only versus inclusion of biological movement of larvae when released from CP. The loss of early-stage larvae showed great variability in response to forcing conditions, losing 2–75% of initial larvae (Fig. 6a). The larval loss during the late-stage larval period, with or without biological movement, varied not as much as that during the early-stage larval period (Fig. 6b). Under different wind conditions, for example, 2–75% of larvae were flushed out of the Mobile Bay system during the early stage, while 3–33% were flushed

out during the late-stage larval period. For all forcing conditions, the net sinking late-stage larval behavior decreased the larval loss by 2–13%, resulting in increased larval retention (Fig. 6b).

**Larvae Released from BSB**

Larvae released from BSB showed little change in larval flux and retention for different tide conditions. Most larvae (68–86%) were remained in the spawning zone (BSB). Different from larvae released from CP, the tropic and equatorial tides did not influence much larval retention in the bay. Increases in river discharge from R1 to R6 enhanced flushing of larvae through Main Pass from 12 to 27%, but most larvae were still retained near the spawning zone. Under southwest (W1), south (W2), and north (W4) wind conditions, more than 80% of larvae remained in the spawning zone. Under the easterly wind conditions (W3 and W5), 44–63% of larvae were remained in the spawning zone and 37–57% were transported westward into LMB, with much of them (24–42%) flushed out of the Bay through Main Pass. Negligible larvae

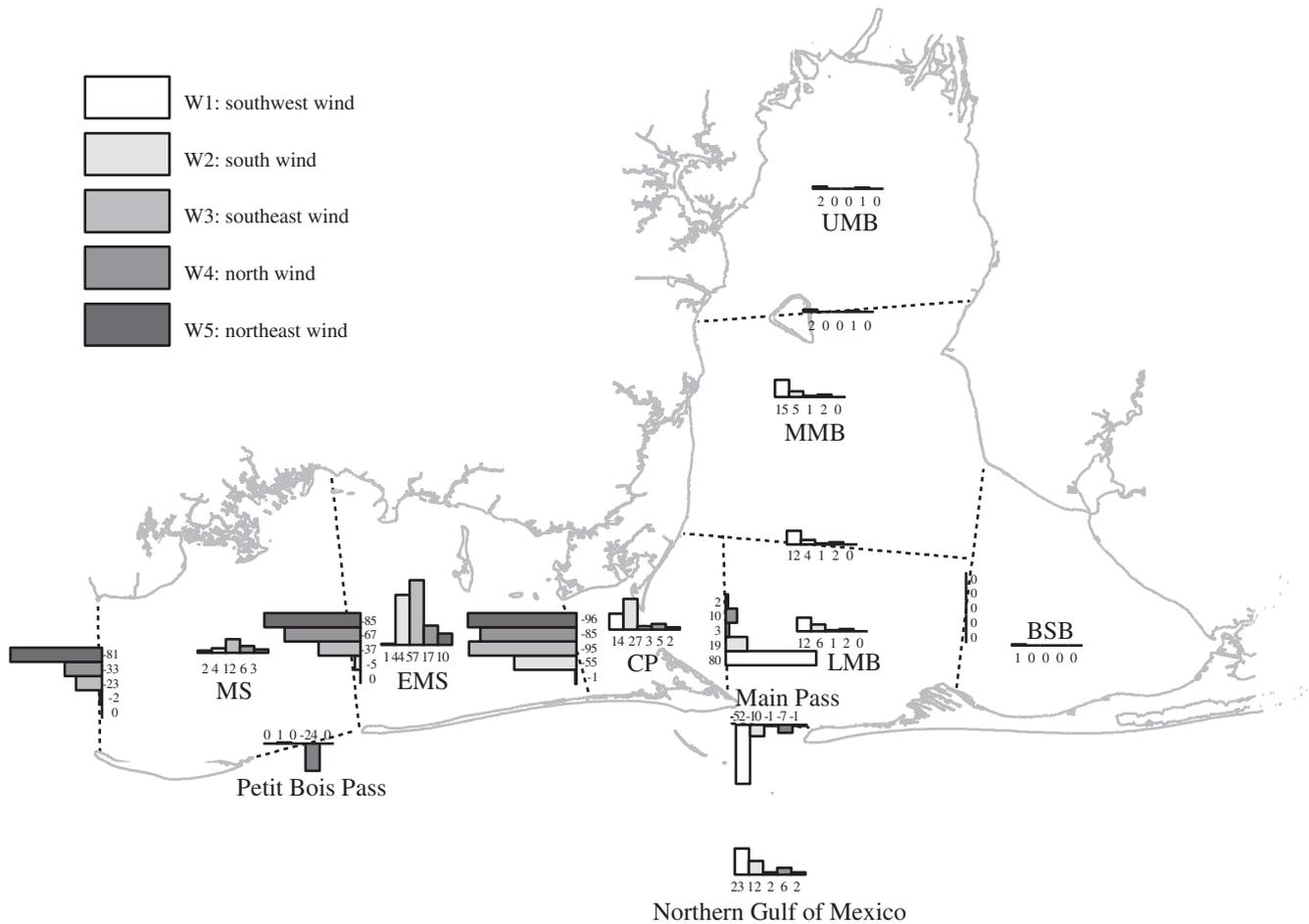


Figure 5. Percent larval retention and flux relative to the initial larvae released from CP for different wind conditions, W1–W5 in Table 1. The bars indicate larval retention in each zone and larval flux across each boundary, with positive values denoting eastward or northward larval flux.

reached the west side of the Bay regardless of forcing conditions.

**Discussion**

In most estuarine systems, more than 85% of oyster reef habitat has been lost and restoration of this critical habitat has proven to be a challenge (Beck et al. 2011); however, Mobile Bay and the eastern Mississippi Sound is one of few bays where reefs are in good condition and provides a real opportunity to achieve both goals for conservation and sustainable fisheries. Oyster reef restoration requires the addition of substrate suitable for oyster settlement; however, the addition of substrate alone is not sufficient to ensure success (Powers et al. 2009). Site-selection is a key determinant of success, largely because of spatial heterogeneity in larval recruitment. The majority of oyster reef creation is performed under the narrow goal of fisheries enhancement (Coen & Luckenbach 2000) and focuses on adding substrate to existing productive areas. Few resources are devoted to restoration in areas that historically supported oyster reefs but no longer support densities of oysters high

enough for harvest. Broader goals now motivate many oyster reef restoration activities (e.g. water quality, fish habitat, shoreline stabilization) (Coen et al. 2007) and have increased the areas targeted for oyster reef restoration. Our model provides a spatially explicit resource to evaluate oyster reef restoration strategies that include restoration in areas of historic abundance, which no longer supports high densities of oysters, as well as current areas of high productivity.

In the Mobile Bay system, CP contains the most productive oyster reefs, accounting for over 90% of the oyster harvest in Alabama, thus supplying the majority of larvae in the Mobile Bay system. Our results showed a predominant westward larval transport from CP. On average 63% of larvae released in CP were transported to the west, resulting in a maximum retention in EMS. Only negligible numbers of larvae were transported into the east side of the Bay and the result is a gradient in larval supply decreasing from west to east for all ranges of forcing conditions. Variations in forcing conditions, therefore, seem to exert minor influences on the west-east gradient in larval supply in the Mobile Bay system. The persistent decreasing gradient from west to east in larval supply could be responsible for the corresponding gradient in

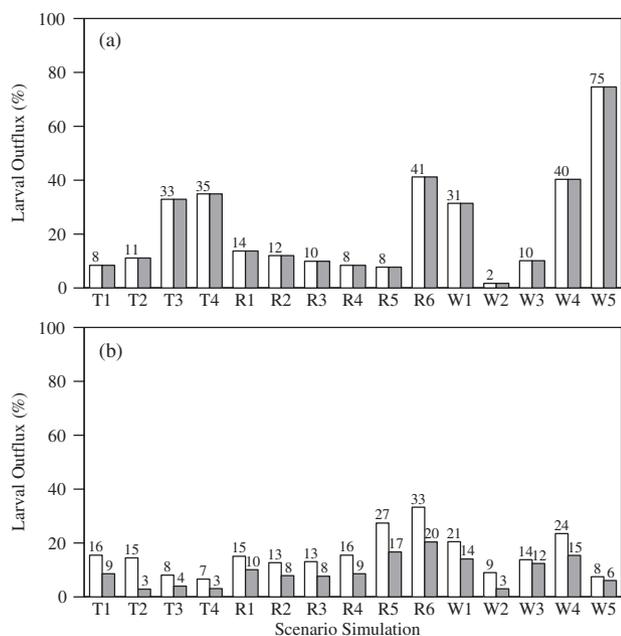


Figure 6. Total outflux/loss of larvae through Main Pass, Petit Bois Pass, and the western open boundary for (a) neutrally buoyant early-stage larvae and (b) net sinking late-stage larvae under different forcing conditions, comparing physical transport only (empty bar) and inclusion of biological movement of larvae (filled bar). Note that biological movement does not affect neutrally buoyant early-stage larvae in (a).

oyster spat settlement and adult oysters that has been observed over the past 40 and 90 years, respectively (May 1971; Hoese et al. 1972; Kim et al. 2010). Nonetheless, forcing conditions highly determined the amount of larvae retained in the west side of the bay.

Tidal amplitude did influence the transport and retention of larvae released from CP. The larger tidal excursion during tropic tides enhanced larval dispersion, with more larvae transported into LMB and EMS under both releasing-time scenarios for flood and ebb tides. Much of the larvae reaching LMB were flushed out of the Bay through Main Pass and considered as net larval loss for simplification of the model interpretation. Consequently, fewer larvae were retained in the southwest part of the study area when they were released during tropic tides.

Seasonal variations in river discharge affected westward transport of larvae released from CP. Relatively high river discharge prevailing in spring facilitated westward transport of larvae into eastern Mississippi Sound. Low discharge common in summer and fall favored larval retention in the southwest part of the study area. A flooding event larger than 95th percentile can occur at any time during the recruitment period of oyster larvae, and can greatly reduce larval retention, particularly in CP where the most productive oyster reefs exist.

Wind condition, along with shoreline configuration of the eastern Mississippi Sound, played an important role in the retention of larvae released from CP. Southerly winds prevailing in spring and summer pushed larvae toward the northern shore of EMS and CP, a shallow (<1 m) and well-protected

region, facilitating larval retention. Northerly winds prevailing in fall pushed larvae into a relatively deeper southern part of EMS and CP and facilitated larval outflux through the western open boundary and Petit Bois Pass. In spring, both wind and river conditions favored larval supply to EMS and the consequent larval concentration was significantly correlated with spat settlement ( $R = 0.69$ ) (Table 2 in Kim et al. 2010). These results suggest that the maximum spring peak in oyster spat settlement in EMS was likely due to the high larval supply driven by seasonal river and wind conditions.

Larval dispersal was predominantly westward when larvae were released from CP independently of the forcing conditions, but outflux/loss of early-stage larvae was sensitive to forcing conditions. The inclusion of sinking behavior in later stages of larval development reduced the outflux in every scenario. Nevertheless, according to our model, physical forcing showed a greater influence on loss of larvae than the behavioral component. This result agrees with a previous larval transport modeling experiment performed in the same area (Kim et al. 2010).

With regard to the larval supply to BSB, our results showed no larval interchange with the CP population, but most of the larvae released in this area were retained close to the parental habitat independently of the tides, seasonal variation in river discharge and non-easterly wind conditions. Easterly winds, however, could effectively transport larvae into LMB and most of them were flushed out of the Bay through Main Pass. The modeled residual current and salinity distribution showed that freshwater discharges favored transport to the western side of Mobile Bay as they approach the mouth of the bay, in agreement with Schroeder (1978). This may explain why larvae released from BSB were much less sensitive to the variation in river discharge than those from CP.

Variations in environmental and biological conditions may result in dramatic changes in larval dispersal of oysters within a small spatial and short time scale (Kennedy 1996). However, we employed rather simplified biological conditions, with the assumptions of a single spawning event for each scenario, a constant linear growth rate and larval period, simple biological behavior, and no mortality of oyster larvae. Such simplifications may be responsible for the model results being less dynamic than the data (Kim et al. 2010). Despite these potential limitations, we demonstrated that the scenario-driven modeling applications gave a good overall description of larval dispersal in the Mobile Bay system. The model reproduced average patterns of both larval concentration ( $R = 0.57$ – $0.62$ ) and oyster spat settlement ( $R = 0.40$ – $0.47$ ) (Table 2 in Kim et al. 2010).

Our scenario-driven study using a biophysical transport model can be used to establish spatially explicit restoration strategies for eastern oysters. The present model results show that high flushing rate through Main Pass prevented larval exchange between the west and east side of the Bay resulting in negligible connectivity between the commercially exploited and none-exploited oyster populations. These findings indicate that two oyster populations separated by only 30 km are

isolated from each other, and might also need different restoration strategies. In contrast to the relatively simple restoration techniques that can be utilized in eastern Mississippi Sound, low spawning stock biomass and limited connectivity in BSB makes this environment substantially more challenging and likely costly to restore oyster reefs. BSB provides a well-protected environment for retention of locally spawned larvae, which suggests that increases in local population abundance may result in increases in local recruitment of the unproductive oyster population. Thus, planting oysters and creating spawning sanctuaries may be a good strategy to augment low levels of natural larval supply to the east side of the Bay. Because of the high fecundity of oysters, it is also possible that other factors affecting larval survival, settlement or post-settlement mortality were determining the size of the adult population. For example, high mortality caused by summertime anoxic events and siltation negatively affected oyster survivorship in BSB (Saoud et al. 2000); however, both factors could be mitigated by creating reefs with high vertical relief (Gregalis et al. 2008; Schulte et al. 2009).

Oyster reef restorations near our identified areas of high oyster recruitment may be relatively simple and require addition of suitable substrate. The most productive oyster reef complex (CPR) supplies maximum larvae into the southwest part of the study area including CP and EMS. Such high larval supply, however, did not produce successful recruitment of oysters in EMS because of a lack of suitable settlement surface (May & Bland 1969, Powers, unpublished data) and addition of hard substrate could enhance settlement in this area (Gregalis et al. 2008). Because of relatively high salinity in the area, however, oysters are more susceptible to oyster drills and diseases (May & Bland 1969) and an effort to reduce post-settlement mortality should be considered.

The lack of spatially explicit knowledge of larval dispersal and source-sink metapopulation relationships has been a fundamental obstacle to establish restoration strategies for exploited marine populations in many estuarine systems (Cowen & Sponaugle 2009). The present study clearly shows that a scenario-driven approach using a biophysical transport model can provide essential information on larval dispersal and help decision-makers/stakeholders establish spatially explicit restoration strategies. Although this study was designed specifically for *Crassostrea virginica* in the Mobile Bay system, the approach is applicable to many other marine invertebrates and fish with planktonic larval stages in various estuarine ecosystems. Especially, the findings in this study can be directly applicable to the other estuarine systems in the northern Gulf of Mexico, which share many common attributes.

#### Implications for Practice

- Spatially explicit models of larval transport can guide restoration plans.
- Strategies that sequentially “step-out” restoration from areas of current high oyster abundance over time is likely

a cost-effective strategy to restore oyster reefs throughout an entire estuarine system.

- Biophysical models might help to identify connected and isolated populations, and also local limiting factors to develop adequate restoration projects.
- Increasing habitat availability in the predominant direction of larval dispersal might be an effective strategy.
- In isolated populations, larval supply might be the limiting factor even when physical transport conditions enhance larval retention, because of the small size of the adult population (BSB). Planting oysters and creating spawning sanctuaries may be a good recovery strategy for this situation.

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