



Spatial and temporal patterns in modeled particle transport to estuarine habitat with comparisons to larval fish settlement patterns

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Abstract

Larval fish settlement in estuarine nursery areas is the end result of numerous biological and physical processes. We used a numerical circulation model coupled to a particle transport model to examine the role that physics play in determining settlement patterns of red drum larvae (*Sciaenops ocellatus*) in nursery habitat along the Texas coast. We examined supply at various spatial scales (supply to inlet, bays, and individual settlement sites). Temporal patterns in larval settlement in Aransas Bay, Texas, are correlated with several indices of modeled particle supply (number of particles inside the bays, integrated particle input to Lydia Ann Channel, and cumulative number of competent particles in Lydia Ann Channel). High abundances of recently settled red drum in Aransas Bay result from a combination of high larval input, limited habitat for settlement, and proximity of habitat to the inlet. In contrast, larval settlement in Corpus Christi and Redfish Bays does not appear to be related to modeled measures of larval supply. Modeled particle supply at the bay-scale suggests that difference in the abundance of recently settled red drum between the bays may be related to larval supply normalized by the amount available settlement habitat within the bay.

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1. Introduction

Larval fish recruitment to estuarine nursery areas results from the interaction of numerous biological and physical processes (Boehlert and Mundy, 1988; Miller, 1988). Much of the previous research has focused on the role of post-settlement losses (e.g., starvation, competition, and predation) in determining recruitment patterns. Some studies have demonstrated that larval fish settlement can also be related to variations of larval supply

associated with physical transport (Jenkins and Black, 1994; Jenkins et al., 1997; Hamer and Jenkins, 1997). Physical transport can enhance larval settlement by increasing either larval supply or the duration of larval retention in suitable settlement habitat. Some studies suggest that larval supply is determined by passive transport (Jenkins et al., 1997, 1999), while others propose that larvae modify their movement through active behavior, such as tidal stream transport (e.g., Weinstein et al., 1980; Rijnsdorp et al., 1985) or active swimming (Leis and Carson-Ewart, 2003). Xie and Eggleston (1999) proposed that stochastic wind forcing could interact with the topography of the coastline and the geographic locations of inlet sources of larvae to produce spatio-temporal variations in larval supply to potential estuarine nursery areas.

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There are few modeling studies examining spatial and temporal transport patterns of fish larvae within bays. Using a passive particle transport model, Jenkins and Black (1994) found that the temporal variability in settlement of the fish King George whiting (*Sillaginodes punctata*) within Port Phillip Bay, Australia, was correlated with particle supply to the bay. Two-thirds of the variability in *S. punctata* recruitment could be explained by passive transport and disturbance by wave action (Jenkins et al., 1997). Jenkins et al. (1999) reproduced spatial patterns in the distribution of *S. punctata* post-larvae and found no improvement in model results when vertical migratory behavior was included. A multiple regression model that included supply of particles and distance from shore explained approximately 70% of the observed spatial patterns.

Brown et al. (2004) demonstrated that variations in wind forcing and coastal sea level produce temporal changes in larval supply to the Aransas Pass inlet, Texas, USA. Variations in forcing may also produce temporal and spatial patterns in larval transport to and retention within estuarine habitat. The influence of winds on circulation patterns is particularly important for shallow bays, such as in the Aransas Pass study area. The effect of temporal and spatial variations in circulation on larval settlement patterns may be accentuated if there is limited

habitat suitable for settlement or if suitable habitat is not uniform in space or quality. In this study, we use the numerical model described in Brown et al. (2004) to examine the role of physical processes in determining settlement patterns of red drum (*Sciaenops ocellatus*) larvae in the Aransas Pass region (Fig. 1). Red drum is an important recreational fishery species in the coastal regions of the Gulf of Mexico (Swingle, 1990). Adults spawn in the nearshore zone outside the coastal bays and estuaries from late August to December, with activity peaking in September or October (Holt et al., 1985; Matlock, 1990). Red drum larvae are typically found within 20 km of the shore, inside the 18-m depth contour (Matlock, 1990).

Larvae too young to be capable of settling even if they encounter suitable settlement habitat are known as precompetent larvae; older larvae capable of settling if they encounter suitable habitat are known as competent larvae. Red drum larvae become competent at an age of about 20 days, when they have an average standard length of 8 mm (Holt et al., 1983; Rooker et al., 1999). Suitable nursery grounds are primarily estuarine seagrass habitat (Holt et al., 1983; Rooker and Holt, 1997; Rooker et al., 1999; Herzka et al., 2002). Only 11% of the bottom in Corpus Christi, Aransas and Redfish bays has seagrass (Pulich et al., 1997). Most (60%) of this seagrass

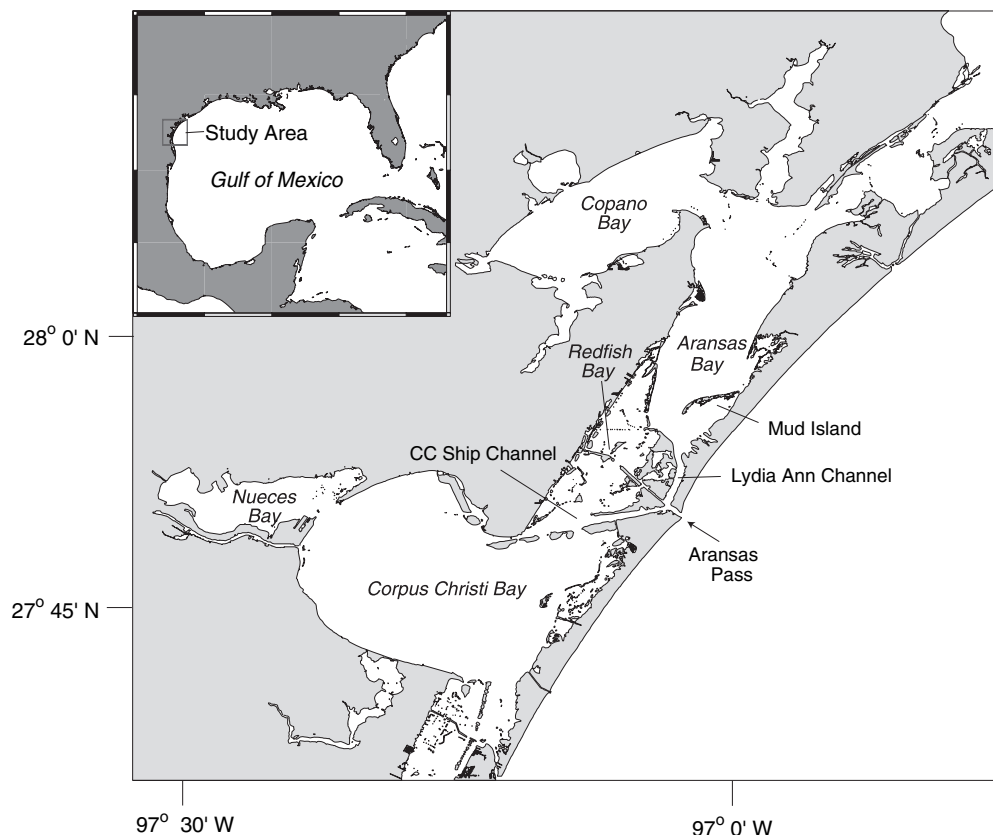


Fig. 1. Location map of Aransas Pass study area.

habitat is in Redfish Bay (Fig. 1). In this paper, we examine transport patterns of passive particles to identify regions where settlement would be facilitated by water movement and retention. We compare modeled transport patterns to observations of settlement. Our goal is to elucidate the relative importance of physical processes on larval settlement patterns.

2. Study area

Aransas Pass is a narrow inlet (400–500 m wide) located along the central Texas coast in the northwestern Gulf of Mexico (Fig. 1). The bathymetry and shoreline configuration of the Aransas Pass region is complex and includes branched channels that connect to multiple bays and the presence of jetties. Water entering the inlet from the Gulf is directed into one of three channels: Corpus Christi (CC) Ship Channel (14 m deep and 120–180 m wide), Aransas Channel (4 m deep and 40 m wide), and Lydia Ann Channel (5–7 m deep and 200–300 m wide near the entrance decreasing to a depth of 4 m and a width of 40 m in Aransas Bay; Fig. 1). Aransas Pass serves as the Gulf connection for six shallow bays, including Corpus Christi, Nueces, Aransas, Redfish, Copano, and St. Charles Bays.

Tides in the Gulf of Mexico are primarily diurnal or mixed diurnal-semidiurnal (Zetler and Hansen, 1970). The amplitudes of the dominant diurnal constituents, K_1 and O_1 , are approximately 15 cm in the Gulf adjacent to Aransas Pass; the amplitudes of the dominant semidiurnal constituents, M_2 and S_2 , are 8 and 2 cm, respectively (Brown et al., 2000). The channels that connect the bays to the coastal ocean filter the tidal motions, preferentially attenuating the semidiurnal constituents (Brown et al., 2000). The study area experiences strong local wind forcing with an average annual wind speed of 6.5 m s^{-1} and a prevailing wind direction from the southeast (Smith, 1979). During the winter months, the prevailing wind patterns are interrupted by strong north winds associated with the passage of cold fronts. The red drum spawning season coincides with this seasonal change in wind patterns. Previous studies have found that subtidal water level variations account for approximately 40% of the total influx of Gulf water through Aransas Pass and approximately 50% of the variations in water level inside the bays (Smith, 1986; Brown et al., 2000).

3. Materials and methods

Circulation patterns were computed using a three-dimensional, free surface, nonlinear finite-element model described by Lynch and Werner (1991) and Lynch et al. (1996). The model configuration was described previously

in Brown et al. (2000, 2004). Since the water-column in the study area is typically well mixed, baroclinic forcing was neglected. Bottom friction was represented using a quadratic slip condition with a uniform drag coefficient of 0.005.

The model domain encompasses Corpus Christi, Nueces, Redfish, and Copano Bays (Fig. 1) and extends 50 km offshore to the 50-m depth contour. The offshore portion of the mesh extends approximately 50 km north of the inlet and about 125 km to the south. The study area is represented in the model with a variable resolution linear triangle, finite-element mesh, which includes 14,534 nodes and 26,721 elements. Nodal spacing varies from about 7 km in the shelf region to about 50 m within the inlet. A model time step of 10 s kept the Courant number ($C_o \equiv u\Delta t/\Delta x$, where u is the fluid velocity, Δt is the model time step, and Δx is the spatial grid scale) less than approximately 0.1. The vertical mesh consists of 11 uniformly spaced nodes under each horizontal grid point.

Simulations were performed for the interval of August 20 to November 11 for 1994 and 1995. Boundary conditions for the shelf boundaries were specified using time-dependent water level data that included tidal and subtidal components. Time-dependent water level forcing was specified using 6-min water level data from Station Bob Hall Pier (27.582°N , 97.217°W) obtained from the Texas Coastal Ocean Observation Network (Michaud et al., 1994). Time-dependent spatially uniform wind stress was applied using hourly wind data from Station 42020 (26.920°N , 96.700°W) of the National Data Buoy Center, National Oceanic and Atmospheric Administration. Station 42020 is located about 100 km south-southeast of the inlet at the 80-m depth contour. The performance of the model at simulating water surface elevation variations and currents was assessed previously in Brown et al. (2000, 2004).

Red drum eggs and larvae are typically found in the inner shelf inside the 20-m depth contour (Matlock, 1990). Recent surveys of red drum larvae in the coastal region adjacent to the Aransas Pass inlet show that red drum larvae are primarily located near the surface (unpublished data, S. Holt). During the 1994 spawning season, red drum eggs were first caught in the inlet on August 24th. To simulate red drum larval transport, passive particles were introduced into the circulation model and tracked throughout the model domain using a fourth-order Runge–Kutta scheme (Blanton, 1995). Passive particles were released in the nearshore region (inside the 20-m depth contour) at a depth of 0.5 m below the surface and held at that depth for the entire simulation. Particles were released beginning on August 22nd and tracked for the duration of the model simulation or until they exited the model domain. A total of 10,560 particles were released in the inner shelf during the interval of August 22 to November 11.

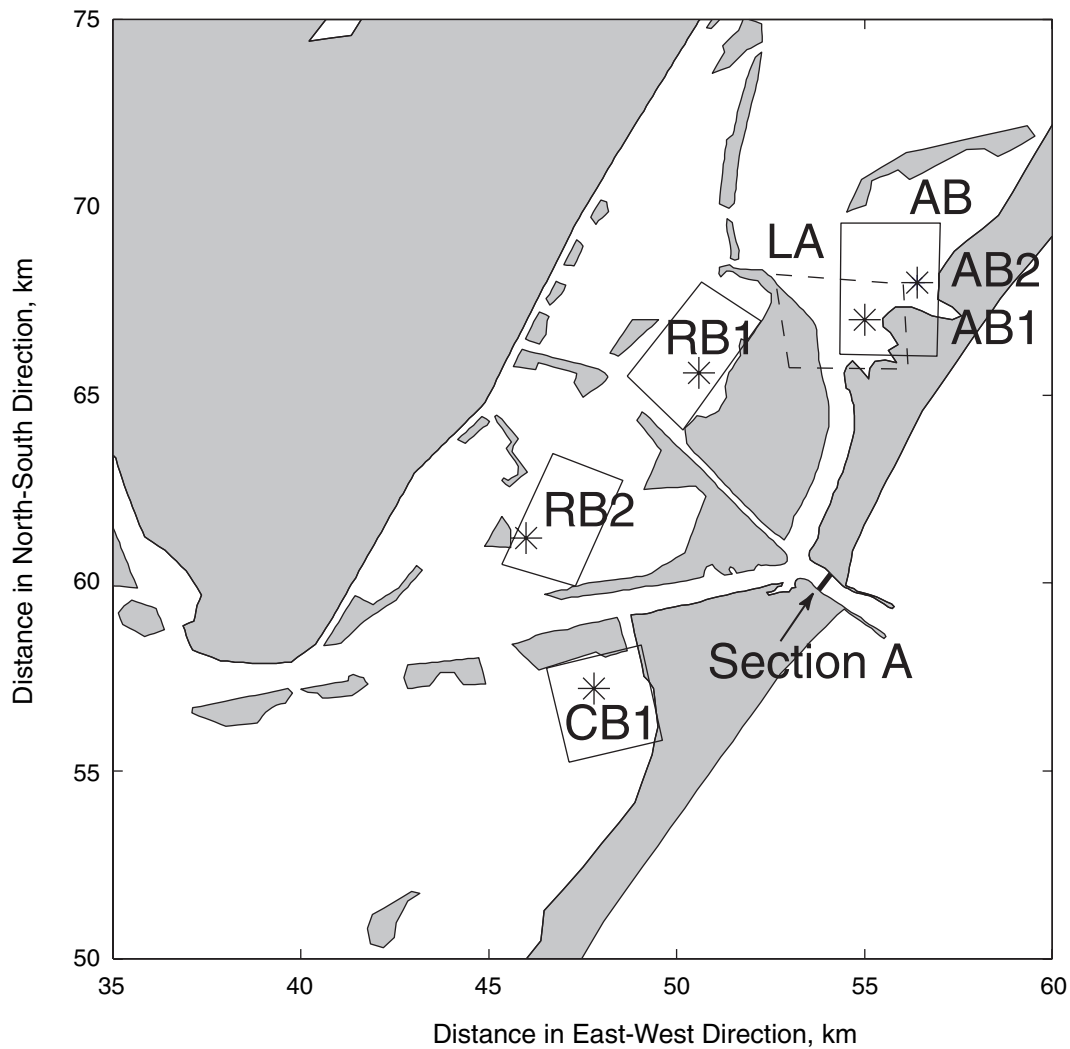


Fig. 2. Map of study area showing location of larval settlement sampling stations (*), regions sampled in the model (polygons), and location of section A used to calculate number of particles in the bay.

The total number of particles in the bays (N_T) is the total number of particles that have entered the inlet (section A in Fig. 2) minus the total number of particles that have exited. Since mortality is high during early life (Houde, 1987), a mortality correction was applied to the number of particles inside the bays (N_T). When each particle was counted, its value, n , was weighted as $n = \exp(-\mu t)$, where t was the age of the particle and μ was the assumed mortality rate, set to 0.1 d^{-1} (Rooker et al., 1999). To examine spatial variations in supply of particles to individual bays, the number of particles in Corpus Christi Bay (N_C), Redfish Bay (N_R), and Aransas Bay (N_A) were counted.

We examined spatial patterns in three measures of particle abundance and supply integrated over time (without mortality corrections): (1) C_T (average concentration of all (pre-competent and competent) particles; (2) C_C (average concentration of competent particles; and (3) I_C (input of competent particles. These

three measures of supply are expressed as number of particles per unit area. C_T is the number of particles (pre- and post-competent) within each spatial element of the model domain summed at each time step and divided by the bottom area of each spatial model element. If a particle remained in an element for multiple time steps it was counted multiple times in this summation. C_C is almost the same as C_T , but without the inclusion of the precompetent particles. For this simulation, a competent particle is defined as a particle between the ages of 14 and 40 days, where the age is the time since the particle was released. Since we only know the approximate age range for competent larvae, we also examined the effect of specifying competent particles as ones between the ages of 20 and 40 days. Because varying the age range did not change the results, we will only discuss results for the 14–40 d competent interval.

We also calculated a flux-based measure of particle supply (I_C) by summing the number of competent

particles that entered a spatial element over the course of the simulation and dividing the result by the element's bottom area. Because each particle is counted only once, I_C is not affected by particles remaining inside elements for multiple time intervals due to slow current velocities.

Bell and Westoby (1986) suggest that larval fish settle in the first seagrass bed they encounter and larval abundances are determined by supply to seagrass beds. To examine this hypothesis, the supply of competent particles to seagrass habitat was determined by recording the location where competent particles first encounter seagrass habitat. To estimate the distribution of seagrass habitat in the model domain, we assumed that all elements that had at least one node with a depth of 1 m or less were seagrass habitat. This depth criterion provided a good approximation of the distribution of the seagrass in the Aransas Pass region, including the seagrass along Lydia Ann channel and in Redfish Bay (Pulich et al., 1997).

3.1. Comparison to observations

Modeled particle supply was compared to observations of the abundance of larval fish entering Aransas Pass and newly settled red drum abundance at five sites in the Aransas Pass region (Fig. 2). The abundance of larval fish entering the Aransas Pass Inlet was measured on each flood tide from August 23 to November 10, 1994 at the University of Texas Marine Science Institute (UTMSI) Pier (located approximately at section A in Fig. 2). The pier extends about 100 m into the channel from the south side. Collections were timed to coincide with predicted maximum current speed using NOAA current tables. Three samples were collected on each flood tide. The first coincided with the maximum flood tide and the others were taken 1 and 2 h after predicted maximum flood tide. Stepped-oblique “tows” from the bottom to the surface were collected with a 1-m, 500 μ m mesh plankton net attached to a mechanical lift system on the pier and fished passively in the current. Sample times were adjusted for current speed such that 300–400 m^3 of water were filtered for each sample. All samples were preserved in 5% formalin and all larvae in the family Sciaenidae were identified to species. Catch data were converted to density (no./ m^3) and the three tows were averaged. The volume of water entering the inlet during a flood tide varies from about 10^5 to $10^8 m^3$ because of the mixed tides in the study area. In a previous paper, we demonstrated that the model reproduces observed total discharge through the inlet (Brown et al., 2000). We calculated the total number of individuals entering the inlet during each flood tide by multiplying the observed red drum larval concentration by the simulated total volume of water entering the inlet during each flood tide as calculated by the model.

Rooker and Holt (1997) sampled newly settled red drum at stations used in the present modeling study approximately weekly (every 5–9 days) using an epibenthic sled. Abundance of recently settled red drum was about 2–3 times higher in *Halodule wrightii* (shoal grass) than *Thalassia testudinum* (turtle grass) habitat (Rooker and Holt, 1997; Rooker et al., 1998b). To avoid differences associated with seagrass species, we compared model results to observed abundances in *H. wrightii* habitat. Hatch dates estimated from otolith-based ages of larvae and juveniles collected during 1994 show that 95% of the larvae that settled hatched between September 2 and October 19 (Rooker and Holt, 1997); therefore, we only included particles released between these dates in particle counts described in this section.

Model results were compared to observations by counting the number of particles in four regions, each 6 km^2 in area, around the field sampling stations (Fig. 2). In this paper, *particles* will refer to model results, while *larvae* will denote observations. Model results for Stations AB1 and AB2 were combined into one box (AB) that included both of these sampling locations because of their proximity. All of the regions had approximately equal non-land areas. Since most of the particles remain inside the channels, a fifth region was added that included the main channel of Lydia Ann (LA, dashed polygon in Fig. 2).

For each region, we calculated input of all ($I_{T,n}$) and only competent ($I_{C,n}$) particles during the time interval between sampling trips and the cumulative input of competent particles younger than 40 d ($I_{CN,n}$). The cumulative number of competent particles assumes that any particles that enter the region settle and are therefore included in subsequent sampling dates. Rooker et al. (1999) found evidence of size-based gear avoidance for larvae larger than 25 mm, which correspond to larvae that are about 40 days old. We adjusted the model results to account for this size-based gear avoidance by eliminating particles older than 40 days in $I_{CN,n}$. Therefore, the cumulative number of competent particles can decrease as time elapses if the age of particle exceeds the competent age range (40 days in this case). We also examined the total input over the entire simulation of all ($I_{T,T}$) and competent particles ($I_{C,T}$). To check to see if settlement is related to the number of particles entering the inlet, the particle input to the inlet and Lydia Ann Channel during all of the flood tides between sampling trips ($I_{T,nf}$) was calculated.

Although this paper focuses on results from 1994, we also simulated the 1995 recruitment season by using physical forcing data (water level and wind data) from that year, and releasing particles in the same configuration and at the same rate as used in the 1994 simulations, and compared the resulting indices of particle supply to observed abundance of recently settled red drum in Aransas Bay. Model results were compared to red drum

abundances presented in Rooker et al. (1999), where samples from AB1 and AB2 are pooled.

4. Results

4.1. Supply of larvae to the inlet and number of particles in bays

There were six pulses in larval supply to the tidal inlet during the fall of 1994 that occurred every 10–16 d and typically lasted 1–2 tidal cycles (Fig. 3a). The number of particles inside the bays (N_T) varied over multiple time scales as a result of the interaction of tides, low-frequency coastal sea level variations, and wind forcing (Figs. 3 and 4) with a steady accumulation of particles inside the bays during the simulation. At the end of the simulation, there were about 1040 particles inside the bays; about 80% of them entered the bays over two periods in 1994 (September 7–17 and October 17–27). The first increase in N_T coincided with a gradual rise in the coastal water level that occurred over a 10-day interval (Fig. 3b). Comparison of simulations made with and without wind forcing reveals that the last increase in N_T was associated with wind-driven transport. The largest rise in coastal sea level occurred between September 28 and October 2, but produced only a small increase in N_T . This small increase in N_T could be caused by the rise in water level over a relatively short time period (4 d). Three of the larval

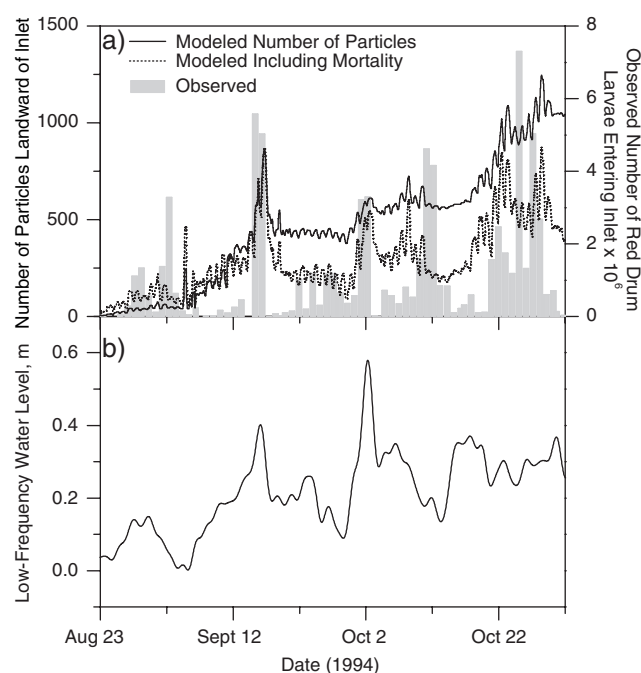


Fig. 3. (a) Comparison of number of particles in bays (N_T) with and without mortality correction and modeled number of particles entering the inlet during each flood tide (gray bars) and (b) low-frequency coastal water level variations. The N_T with the mortality correction is multiplied by a factor of 5.

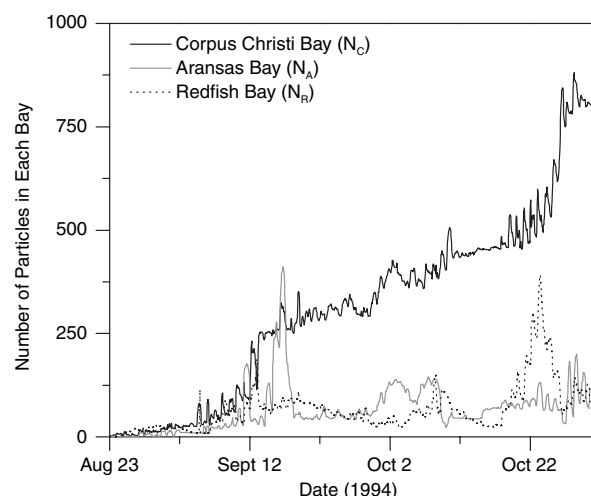


Fig. 4. Number of particles in Corpus Christi (N_C), Aransas (N_A), and Redfish (N_R) bays.

pulses (Fig. 3a) coincided with an increase in N_T . Including mortality-weighting increases the relative magnitude of the change in N_T that occurred between October 2 and October 12, 1994 (Fig. 3a).

Once water enters the Aransas Pass, it is transported into one of three channels (CC Ship, Lydia Ann, and Aransas Channels). The division of flow between the three was approximately 60%, 30% and 10%, respectively, in ratios similar to those of the channel cross sections. The CC Ship Channel supplied particles to Corpus Christi and Redfish Bays, while Lydia Ann and the Aransas Channels supplied Aransas and Redfish Bays, respectively. The number of particles within each bay varied as a result of changes in particle supply, retention within bays, and transport between the bays (Fig. 4). The division of the particles between the bays was neither constant nor proportional to relative flows. The number of particles in Corpus Christi Bay steadily increased throughout the simulation; while the number of particles in Aransas and Redfish Bays had relatively short-lived pulses. During the first large increase in N_T , a large fraction of the particles entered Aransas Bay (N_A); during the remainder of the simulation, most of the particles were in Corpus Christi Bay. The large fraction of particles transported to Aransas Bay during the first number peak resulted from the northern approach path to the inlet of the particles in the Gulf.

4.2. Spatial patterns in transport

The supply of passive particles to estuarine nursery areas depended on the interaction of regional physical forcing, bathymetry, and shoreline configuration. Particles that enter the Aransas Pass inlet could be transported to almost all regions of Corpus Christi, Redfish, and Aransas Bays (Fig. 5). Generally, there were higher

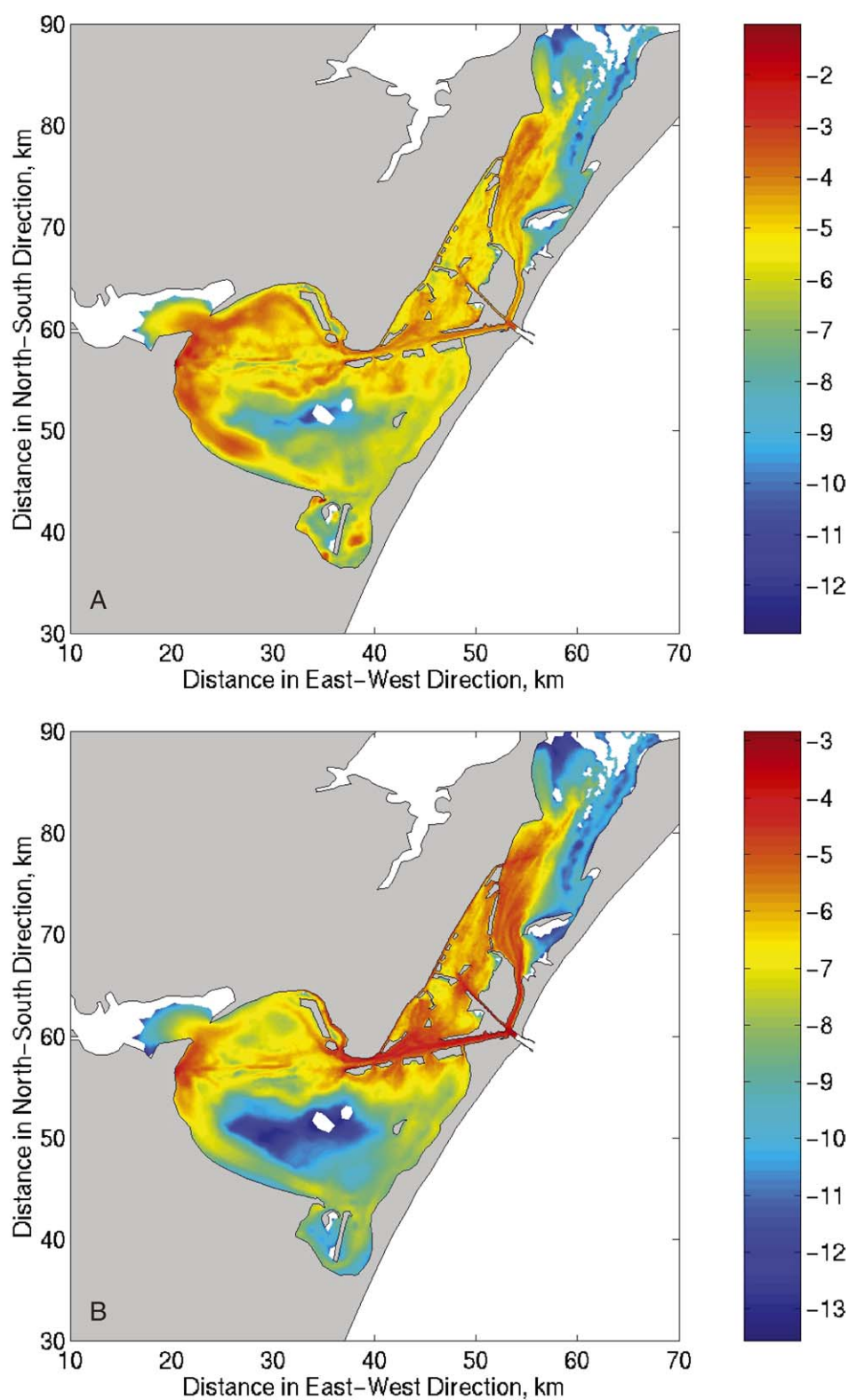


Fig. 5. Average competent particle concentration (C_C , number m^{-2}) for each element landward of the inlet (top panel) and input of competent particles (I_C , number m^{-2}) landward of the inlet. The actual values plotted are natural logarithms of calculated averages; unshaded regions had no particles present.

concentrations of particles (C_T , not presented in this paper) on the western sides of the bays because of surface currents associated with the predominant onshore winds. In Corpus Christi Bay, wind-driven transport caused particles to accumulate in the southern and western regions. In contrast, there were relatively low concentrations in the interior of Corpus Christi Bay and in the northern and eastern portions of Aransas Bay.

The timing of larval transport to nursery habitat is also an important factor in settlement; if a larval fish is transported to settlement habitat, but is not sufficiently developed, it will not be able to settle. The spatial patterns in average particle concentration for all particles (C_T) and competent particles (C_C) were similar, therefore we only present C_C . Competent particles accumulated in the southern and western portions of Corpus Christi Bay (Fig. 5a), as did all (pre-competent and competent) particles. There were relatively few competent particles near the settlement habitat south of Mud Island (sites AB1 and AB2), while concentrations were high in the southern portion of Redfish Bay because of its proximity to the CC ship channel.

During the simulation, 2878 competent particles entered the bays. The input of competent particles shows the importance of the channels to particle supply. The relatively high particle supply to the Lydia Ann Channel region is evident in I_C (Fig. 5b); however, almost no competent particles were transported to the settlement sites in the region (AB1 and AB2). RB1 and CB1 should have relatively low settlement because of the low values of I_C there. The southern site in Redfish Bay (RB2) should have high settlement due to high particle input associated with its close proximity to the CC ship channel. High settlement should occur in the northwestern portion of Redfish Bay, which received particles from the connections with Aransas Bay. Comparison of the concentration of competent particles and the input of competent particles reveals that the high C_C values in the southern and western regions of Corpus Christi Bay resulted from relatively few particles accumulating in this region. The relatively high I_C on the western side of Corpus Christi Bay and the low values in the channel that supply it suggest that the relatively high I_C results from the transport of pre-competent particles that turn competent during their transit.

Approximately 20% of the simulated particles released in the Gulf encounter suitable habitat during their competent phases (Fig. 6). Most of these particles first encounter settlement habitat in Redfish (41%) and Aransas (34%) Bays. About 26% of the particles encounter settlement habitat along the edges of Lydia Ann Channel (including the region south of Mud Island). Along Lydia Ann Channel, the areal abundance of competent particles encountering habitat is high due to high input and limited settlement habitat. In contrast, the particle abundance is much less in Redfish Bay due to

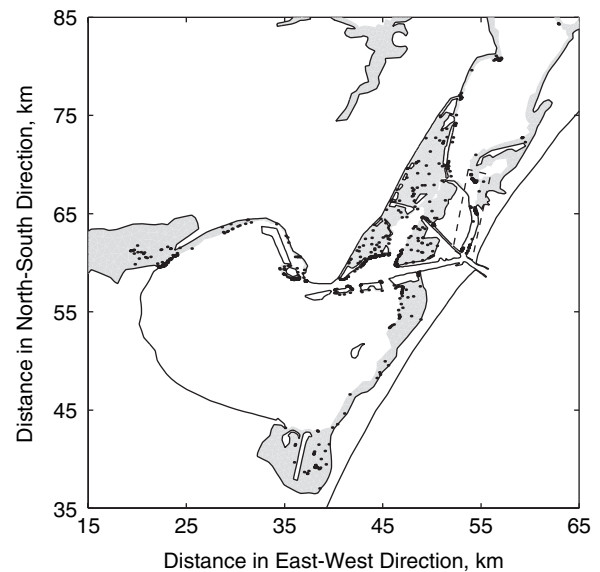


Fig. 6. Locations where competent particles first encounter seagrass habitat. Gray areas indicate regions where seagrasses would be expected based on depth criterion and the dashed box shows particles used to estimate abundance in the vicinity of AB1 and AB2.

limited particle input and extensive habitat. Based on the number of particles encountering habitat in each bay and extent of seagrass habitat (Pulich et al., 1997), modeled average bay abundance is 3.5 times higher in Aransas Bay ($57.8 \text{ particles km}^{-2}$) compared to Redfish Bay ($16.6 \text{ particles km}^{-2}$), which is similar to previously published spatial distributions of newly settled red drum. Rooker and Holt (1997) found that the densities of newly settled red drum was three times higher in Aransas Bay compared to Redfish Bay. Using particles that settle in the dashed box (Fig. 6) and assuming that 50% of the seagrass habitat in Aransas Bay is located in the region along Lydia Ann Channel and south of Mud Island, average abundances are about five times the average abundance in Redfish Bay.

4.3. Comparison to observations

4.3.1. Spatial patterns

Mean observed abundances of recently settled red drum are about three to five times higher in Aransas Bay (AB1 and AB2) than in Redfish and Corpus Christi bays (RB1, RB2, and CB1) (Rooker and Holt, 1997). Comparison of the total particle input ($I_{T,T}$) to each of the regions located at the settlement sites (Table 1) shows that approximately 20–30% more particles are transported to the Aransas Bay sites (AB) than the sites in Corpus Christi Bay and the northern part of Redfish Bay (CB1 and RB1). Highest particle input is in Lydia Ann Channel (LA) and RB2. The input of competent particles ($I_{C,T}$) is lowest in the Aransas Bay region because of limited mixing of

Table 1

Total input of pre- and post-competent particles ($I_{T,T}$) and competent particles ($I_{C,T}$) for 1994

Box location	$I_{T,T}$	$I_{C,T}$
AB	404	106
CB1	306	151
LA	742	304
RB1	343	226
RB2	686	384

particles out of the channel. Highest $I_{C,T}$ values are in the LA and RB2 regions.

In addition to variations in supply of particles, the amount of time particles spend in the regions varies spatially. The average time particles remain in the vicinity of AB1 and AB2 is only about 6–7 h. The average time particles remain in the boxes at RB1, RB2, and CB1 range from about 12 to 17 h.

4.3.2. Temporal patterns

Model results suggest that variability in larval settlement in Aransas Bay (AB1 and AB2) is associated with physical transport (Figs. 7 and 8). There is a significant correlation between observed abundances of newly settled red drum and three modeled measures of larval supply (Table 2): input of particles ($I_{T,nf}$) to Lydia Ann Channel ($r=0.80-0.83$, $p=0.01-0.2$), number of particles in all bays (N_T) ($r=0.72-0.86$, $p<0.03$) and cumulative number of competent particles ($I_{CN,n}$) entering Lydia Ann Channel ($r=0.76-0.91$, $p\leq 0.01$). Integrated supply of particles to the inlet and Lydia Ann Channel was high on September 22, 1994, at a time preceding the appearance of red drum larvae at the settlement sites. After removing this data point from the time series, we calculated a significant correlation between

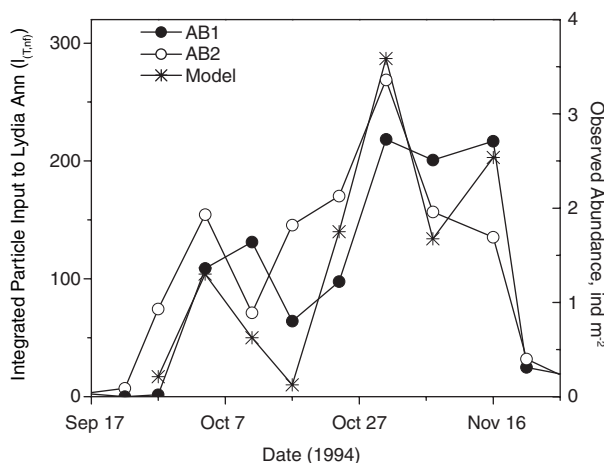


Fig. 7. Comparison of observed abundance of recently settled red drum at AB1 and AB2 and integrated particle input to Lydia Ann Channel ($I_{T,nf}$) during 1994.

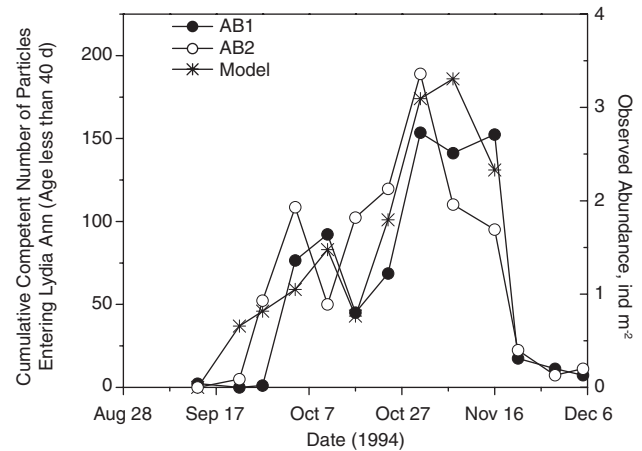


Fig. 8. Comparison of observed abundance of recently settled red drum at AB1 and AB2 and modeled cumulative number of competent particles ($I_{CN,n}$) entering Lydia Ann Channel during 1994.

modeled supply and observed settlement. During the two intervals in 1994 when there were increases in abundance of recently settled red drum, there were also increases in number of particles in the bays (N_T) (Fig. 3). During 1994, there is not a significant correlation between observed abundances and any modeled measures of particle supply for sites in Redfish (RB1 and RB2) and Corpus Christi (CB1) Bays.

During 1995, there was only one pulse in recently settled red drum in Aransas Bay during the first 2 weeks of October. There is a significant correlation ($r=0.872$, $p<10^{-5}$) between observed abundance and cumulative number of competent particles entering Lydia Ann Channel (Fig. 9); however, there is not a significant correlation between observed abundance and number of particles in the bays and input of particles to Lydia Ann Channel. Fewer competent particles entered Lydia Ann Channel in 1995 than in 1994 (peak values of 56 versus 186 in number of cumulative competent particles).

Table 2

Correlation between observed abundance of recently settled red drum at two locations in Aransas Bay (AB1 and AB2) during 1994 and modeled measures of particle supply using Pearson product moment correlation

Modeled Supply	r		Probability		n
	AB1	AB2	AB1	AB2	
<i>Integrated particle input ($I_{T,nf}$)</i>					
Lydia Ann Channel	0.829	0.798	0.011	0.018	8 ^a
<i>Number of particles inside</i>					
All bays (N_T)	0.716	0.857	0.030	0.003	9
Cumulative number of competent particles ($I_{CN,n}$) in Lydia Ann	0.755	0.910	0.012	<0.001	9

^a Excluded first data point in integrated supply.

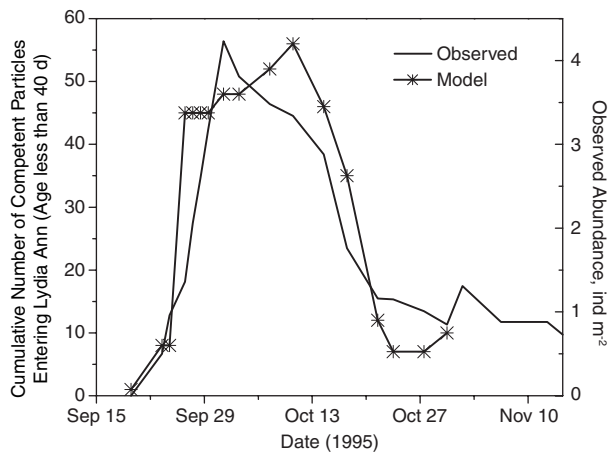


Fig. 9. Comparison of observed abundance of recently settled red drum in Aransas Bay and modeled cumulative number of competent particles ($I_{CN,n}$) entering Lydia Ann Channel during 1995.

5. Discussion

The rate of larval settlement in an estuarine nursery area is determined by the interaction of numerous biological and physical processes that occur between egg release and arrival at the nursery. Currents can affect settlement patterns by influencing the larval supply and retention in suitable habitat. If recruitment is supply-limited, increases in larval supply to settlement habitat should enhance settlement. Because many larval fish have limited swimming abilities and slow response times, they require time upon encountering favorable habitat to react and settle if they are to be successful. Retention of a larval fish in a region with suitable habitat may result in higher probability of settlement. To examine the role of physical transport in larval supply, we examined supply at various spatial scales (e.g., supply to inlet, bays, and individual settlement sites).

The patterns in modeled particle supply depend upon the measure of supply used. The measures, in turn, depend on the amount of detail that is needed to capture the important features of the larval availability, including distinguishing competent particles, accounting for particle mortality, and accounting for larval loss as water passed over previous habitat. Average particle concentration could be an adequate measure if larval settlement depends solely on overlying larval concentration and there are no significant losses during a water parcels passage over previous habitats. For regions where suitable settlement habitat is limited and larval settlement rate is rapid, particle input may be a better measure of supply.

Field observations have shown that the highest abundances of recently settled red drum and other sciaenids are found in Aransas Bay (Rooker and Holt, 1997; Rooker et al., 1998b). Simulations suggest that the high abundance of recently settled red drum within nursery areas in Aransas Bay result from a combination

of high particle input (i.e., high larval supply), limited habitat for settlement, and close proximity of this habitat to the inlet. Limited habitat tends to concentrate larval settlement, resulting in high observed areal abundances in the suitable habitat. Simulations suggest that larvae that settle in Aransas Bay are those that enter the inlet while competent and settle in the first seagrass habitat that they encounter.

The number of particles inside the bays serviced by Aransas Pass varies with changes in coastal sea level and winds. Unfortunately, there is not a simple relationship between number of particles inside the bays and physical processes, as there is no simple relationship to inlet particle supply (Brown et al., 2004). Particles accumulate inside the bay primarily as a result of non-tidal processes, with about 16% of all the particles released and 36% of those that do enter the inlet present inside the bays at the end of the simulation. Model simulations that include only tidal forcing have lower retention with <5% of the particles that enter the inlet present after 6 days (Brown et al., 2000). During the late summer to early fall, the study area is dominated by wind forcing from the south east (Brown et al., 2000). Model simulations with tidal forcing and steady wind forcing from the southeast and east (wind speed of 5 m s^{-1}) increases the amount of particles retained landward of the inlet after 6 days to 53% and 46%, respectively, with most of the particles being retained in Redfish Bay (unpublished results). The addition of the wind stress results in the particles being transport further into the bay, so that they are not flushed out of the bay on the subsequent ebb tide. Including wind forcing and subtidal variations in water level results in a substantial increase in the number of particles inside the bays (as compared to only tidal forcing). Although larval behavior is frequently invoked to explain larval accumulations inside bays, our results show that physical processes can produce substantial retention of particles in the absence of behavior.

The division of particles between the different bays of the Aransas Pass region varies as a result of the interaction of physical processes with bathymetry and of how the particles in the Gulf approach the inlet. Aransas and Redfish Bays have short-lived pulses in the number of particles inside the bays; while Corpus Christi Bay accumulates particles throughout the simulation. Most of the previous studies of larval transport for estuarine-dependent species focus on transport on the shelf but neglect the bays or they focus on movement only from the inlet to the bays, but few studies include both components of larval transport. Our results (this paper and Brown et al., 2000) show that it is important to link both phases of transport. Differences in how or when a larva approaches the inlet can have dramatic effects on distributions within the bays.

Our results show that variations in red drum larval settlement in Aransas Bay are associated with number of

particles within the bay, which is determined by supply of particles and their retention inside the bays. Particle retention within bays is often estimated using residence time. For species that spawn and settle inside bays, the larval supply is related to residence time. As an example, Gaines and Bertness (1992) found that almost 80% of the interannual variance in settlement of the barnacle *Semibalanus balanoides* in Narragansett Bay, Rhode Island is explained by bay residence time. For species that spawn offshore and enter the estuaries as juveniles, this concept needs to be extended to include temporal variations in larval supply to the inlet. Particle supply and retention depends upon the interaction of physical processes with local bathymetry. Wind forcing can produce large variations in flushing rates (especially for shallow bays) occurring on time scales of days to weeks (Geyer, 1997; Goodrich, 1988). In addition, there may be large variations in flushing associated with location (e.g., Brooks et al., 1999), which could result in spatial variations in settlement.

Our model simulations suggest that the variability in abundance of recently settled red drum in Aransas Bay (AB1 and AB2) is related to changes in larval supply associated with physical transport. During 1994 there were five pulses in supply of red drum larvae to the inlet, but only two of these pulses resulted in an increase in settlement of red drum larvae in Aransas Bay. Settlement of red drum larvae in Aransas Bay is not correlated with the observed concentrations of larvae in the tidal inlet during the flood tide prior to the sampling at the settlement site, but is correlated with integrated measures of supply. Gaines and Bertness (1993) proposed that the study of long distance larval dispersal must be sampled using integrative techniques. A similar principle applies to comparing observed settlement data to supply from model results, for which it is necessary to integrate over relevant temporal scales. In addition, stronger correlations were found between model results and observed settlement patterns than observed concentrations of larvae in the inlet (Brown et al., 2004), suggesting that integrative measures of larval abundance may help us to elucidate the connection between physical processes and larval recruitment.

Observed settlement patterns in Aransas Bay during 1994 are correlated with modeled input of particles to the Lydia Ann Channel ($I_{T,n}$), cumulative number of competent larvae entering Lydia Ann Channel ($I_{CN,n}$), and the number of particles within all bays (N_T); however, during 1995 observed patterns are only correlated with cumulative number of competent larvae entering Lydia Ann Channel ($I_{CN,n}$). This suggests that temporal variations in settlement in Aransas Bay are determined by physical processes that vary the supply of competent particles to Lydia Ann Channel. Physical processes not only influence the supply of particles to a tidal inlet, but also the age-structure of particles entering the inlet. The

particle transport model reproduces variations in larval settlement in Aransas Bay, but not the interannual difference in the abundance of recently settled red drum. During 1995, the peak cumulative number of competent particles ($I_{CN,n}$) entering Lydia Ann Channel is about one-third the value in 1994; however, the peak observed abundances in larval settlement is similar during these 2 years. This might result from interannual differences in egg production or pre-settlement mortality that we have not incorporated in our models. Unfortunately, data are not available on variability in egg production or pre-settlement mortality in this region. Data such as these would be useful to separate the importance of physical versus biological factors in determining interannual variations in settlement and to incorporate in future larval supply modeling studies.

Simulated measures of particle supply are not correlated with larval settlement in Redfish or Corpus Christi Bays. There are several possible reasons for the model working in some areas of the Aransas Pass region and not others, such as errors in the hydrodynamic and particle transport model, the proximity of settlement sites to the source of larvae, spatial and temporal variations in spawning intensity, variations in pre- and post-settlement mortality rates, and larval behavior. The settlement sites where the model reproduces temporal patterns in larval settlement are located closest to the Gulf, while the sites where the model performs the poorest are located further from the inlet in regions with indirect connection with the Gulf. In another modeling study, Jenkins and Black (1994) found that larval fish settlement in Swan Bay was correlated with modeled measures of particle supply to Port Phillip Bay, Australia, but was not correlated to modeled measures of particle supply to Swan Bay, a small embayment adjacent to the entrance of Port Phillip Bay. Jenkins and Black (1994) attributed this difference in model performance to their model not adequately representing the configuration of the small Swan Bay and the fact that their settlement data were based on examination of otolith microstructure which they proposed changes when the larvae enter Port Phillip Bay, rather than when they arrive at settlement sites in Swan Bay. In a later study, Jenkins et al. (1997) found that a particle transport model explained larval settlement at a site closest to the entrance of the bay and at another site an intermediate distance into the bay; however, at the site furthest into the bay the particle transport model did not explain patterns in recruitment. The authors attributed the differences in performance of the model to larval behavior becoming more important at interior locations or inadequacies in the two-dimensional hydrodynamic model in the interior portions of the bay. The causes of spatial variation in the performance of the model in our study might be associated the same causes presented in the Australia modeling studies. Unfortunately, we do

not have adequate data to determine the causes of the error. The similarity between our results suggests that studies examining spatial variations in larval behavior (specifically behavior near entrances versus interior locations) and confirmation of the hydrodynamic and particle transport model in shallow, interior regions are important future research directions.

Redfish Bay contains the most extensive seagrass habitat in the Aransas Pass region; however, larval supply to Redfish Bay is low because of its small direct connection with the inlet (i.e., Aransas Channel) and its limited connections with adjacent bays. Many particles enter Redfish Bay from the north or south instead of through the Aransas Channel. During the simulation, 1465 competent particles entered Redfish Bay, but only about one-third of them entered via the Aransas Channel. About one-half of the competent particles inside the bays enter Redfish Bay at sometime during their competent period. In addition, model simulations including tidal forcing and steady southeast wind forcing (the dominant wind direction) show that there is an accumulation of particles inside Redfish Bay (unpublished model results). Model simulations suggest that Redfish Bay might be an important settlement region for red drum larvae because it has longer retention in suitable habitat for those larvae that do arrive. On average, competent particles spend about 56 h in Redfish Bay, which may provide larvae with time to settle and possibly move to alternate settlement habitat depending on factors such as food availability and predation pressure.

The spatial variation in the amount of time passive particles remain in the vicinity of settlement sites may influence larval behavior. Passive particles remain in the vicinity of AB1 and AB2 for 6–7 h. A larva that settles successfully in these relatively high-current flow regions must be able to respond relatively rapidly to remain in this settlement habitat. The average time particles remain in the boxes at RB1, RB2, and CB1 is about double that at AB1 and AB2, suggesting that rapid larval response might not be as important in these regions.

The lack of a correlation between modeled particle supply and observed abundances of recently settled red drum in Redfish Bay might be associated with larval behavior while being transported, such as vertical migration or active habitat selection. During transit to sites in Redfish Bay (especially particles traveling to RB1), larvae pass over seagrass habitat in which they may choose to settle. In contrast, at the Aransas Bay sites there is limited habitat for settlement and the region is closer to the inlet so that there is a higher probability that any contact with settlement habitat is the first one. The currents near Lydia Ann Channel are higher and the larvae are probably at a greater risk of being swept away during an ebb tide if they leave the seagrass beds. Under such conditions, larvae might be more likely to remain in

the first seagrass bed that they encounter. This behavior is consistent with observations of red drum abundance at AB1 and AB2, which show elevated abundances for about 2–3 weeks after an initial increase in settlement. The settlement sites in Redfish Bay do not show similar temporal patterns in observed abundance.

Our simulations suggest that the southern portion of Redfish Bay (RB2) should have high settlement due to high particle input associated with its proximity to the CC ship channel; however, there are low observed abundances in this region. The relatively low observed abundances at RB2 may result from elevated post-settlement losses associated with biological or physical factors or errors in the particle transport model. Previous larval studies in Australia have demonstrated that other physical factors, such as disturbance by wave action (Jenkins et al., 1997; Moran et al., 2004), can influence larval fish settlement. Moran et al. (2004) found that recently settled fish larvae may be resuspended from seagrass beds during high wave action and experience secondary planktonic dispersal. As a result of the predominant wind direction and the location of the settlement sites, there is higher wave action at the RB2 site than at the Aransas Bay sites (observations of S. Holt), which might result in higher post-settlement losses.

Although observed abundances in Redfish Bay are about one-third of those in Aransas Bay, the suitable habitat is more extensive in Redfish Bay. Based on the product of observed mean abundance and area of settlement habitat, approximately 30% more larvae settle in Redfish Bay than in Aransas Bay. We suggest that it is important to have more extensive spatial sampling of larval settlement in Redfish Bay to see if this is so. Because of the episodic supply of larvae and patchiness, better estimates of mean abundance of newly settled larvae require more extensive sampling within the bay. In addition, examining supply to Redfish Bay as a whole may establish the role of physical transport in settlement. Studying supply at the bay scale might improve the correlation between observed abundance and modeled supply by reducing the impacts of habitat selection and post-settlement movement within the bay.

Particles are transported to and accumulate along the southern boundary of Corpus Christi Bay. Corpus Christi Bay is primarily sandy bottom (except along the backside of the barrier island) and not suitable for red drum settlement. Rooker et al. (1998a) found that predation rates were 3–4 times higher in unvegetated habitats than seagrass habitat. Larvae that accumulate in the southern portion of Corpus Christi Bay may not survive due to greater predation mortality.

There is considerable variation in larval fish settlement in estuarine nursery areas, both in space and in time. Because of the complex interaction of physical and biological factors that influence settlement, it is difficult to interpret observations of larval abundance without

accounting for their effects. This study suggests that numerical models may be useful to interpret patterns in larval data. Through the comparison of modeled transport patterns and spatial and temporal larval settlement patterns, we have suggested several areas for future research that we believe would help further our understanding of the factors that influence larval settlement in this region.

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