

Simulating larval supply to estuarine nursery areas: how important are physical processes to the supply of larvae to the Aransas Pass Inlet?

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ABSTRACT

Factors controlling the movement of fish larvae from coastal spawning environments to estuarine nursery areas are important to fish recruitment. In this paper, the role of physical processes in larval transport to estuarine nursery areas in the Aransas Pass region, Texas, is examined using a circulation model coupled with a fixed-depth particle transport model. Two phases of transport are examined: transport on the shelf to the tidal inlet and transport through the inlet to estuarine nursery areas. Observed pulsing in the supply of red drum (*Sciaenops ocellatus*) larvae to the tidal inlet is significantly correlated with modeled particle supply. This pulsing is not correlated with a specific physical process, but results from the interaction of several factors affecting water movement, including low-frequency variations in water level and wind forcing. Simulations suggest that the primary spawning region for red drum larvae that utilize nursery habitat in the Aransas Pass region is located north of the inlet. Patterns in the trajectories of particles that successfully enter the inlet reveal that they move alongshelf in the nearshore region and then move into the inlet, rather than moving directly across the shelf to the inlet. The approach path of particles outside the inlet determines the spatial transport patterns for inlets with branched channels and multiple bays. This

study demonstrates that physical processes play an important role in determining larval supply to a tidal inlet.

Key words: larval supply, red drum, *Sciaenops ocellatus*, tidal inlet

INTRODUCTION

The supply of larvae from offshore spawning regions to estuarine nursery areas may be controlled by the circulation through tidal inlets and retention within the estuary (Jenkins and Black, 1994; Jenkins *et al.*, 1997). Episodes of high abundances (pulses) of fish larvae in tidal inlets are common features of estuarine-dependent fish populations (e.g. Boehlert and Mundy, 1987; Hamer and Jenkins, 1997; Hettler *et al.*, 1997). Attempts at correlating these pulses in larval abundance with environmental variables have proven relatively unsuccessful (e.g. Dixon *et al.*, 1999). The temporal and spatial variability of physical processes and larval supply make it difficult to interpret larval abundance data, to discern the dominant processes influencing recruitment, and to infer large-scale recruitment patterns using field observations alone. Combining observations with numerical models of larval transport provides a means of examining the roles of various physical and biological processes influencing recruitment and aids the sampling design for future observations (Colby, 1988; Werner *et al.*, 1997).

Numerical models have provided insight into the mechanisms influencing the transport of fish larvae in shelf and coastal regions (e.g. Hermann *et al.*, 1996; van der Veer *et al.*, 1998; Werner *et al.*, 1999). In recent years, models have been developed to study the transport of fish larvae from shelf regions through inlets to estuarine nursery areas (Jenkins and Black, 1994; Jenkins *et al.*, 1997, 1999; Blanton *et al.*, 1999; Luettich *et al.*, 1999; Xie and Eggleston, 1999; Brown *et al.*, 2000). Smith and Stoner (1993) modeled the transport of larvae through Aransas Pass using predicted inlet current velocities and idealized vertical migration behaviors. Their simulations indicated that

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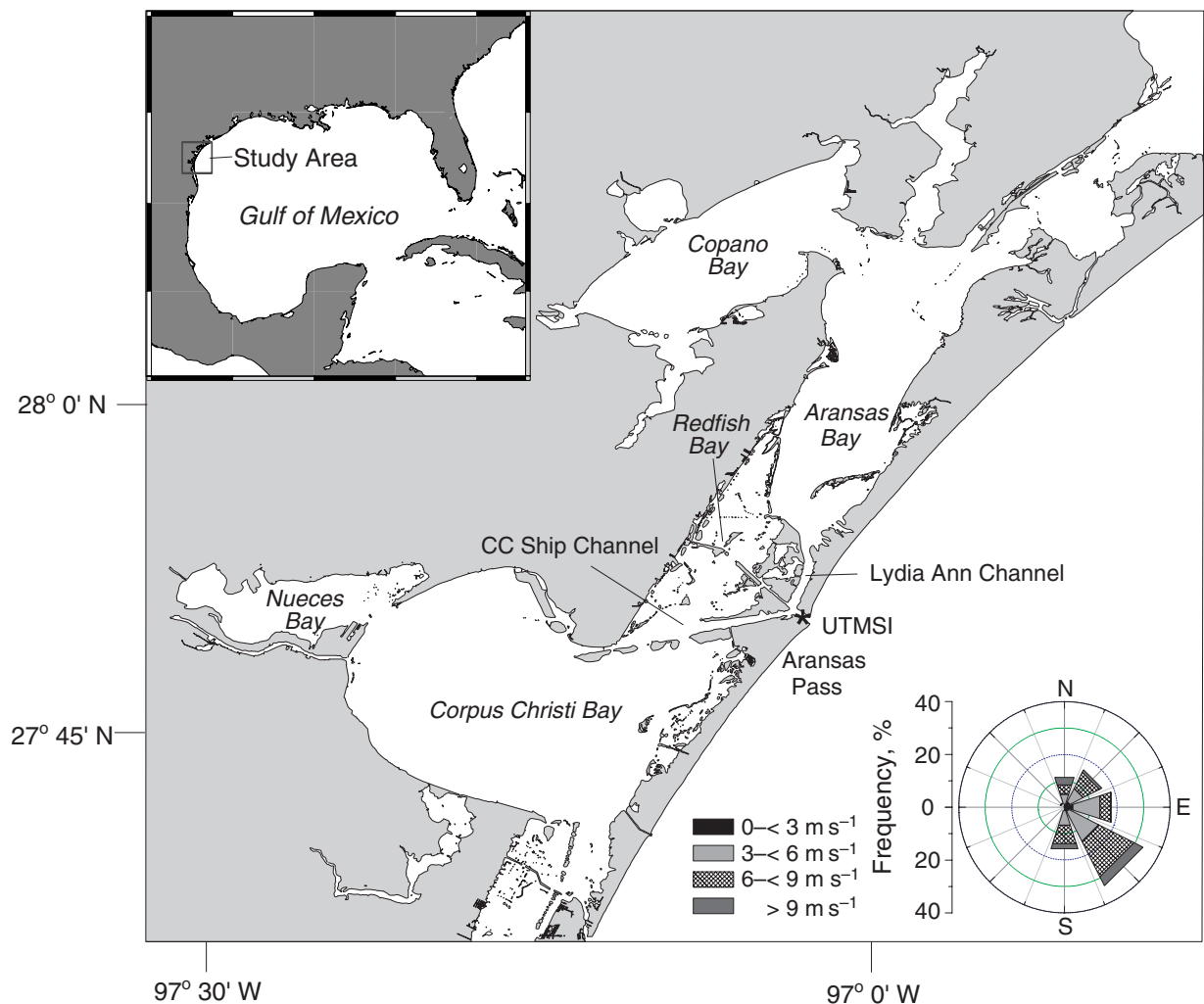
diel vertical migration produced an annual cycle in larval ingress, but non-tidal processes had a much greater effect on larval transport. However, their study did not examine spatial and temporal patterns in transport or focus on a particular species.

We applied a numerical model of coastal currents to investigate the supply and transport of red drum larvae to the Aransas Pass Inlet, Texas. Aransas Pass (Fig. 1) is an important inlet because it serves as the primary connection for numerous Texas bays to the Gulf of Mexico and provides access to these bays for many commercially and recreationally important fishes. The objectives of this paper are to examine the role of advective transport in controlling the variability

in larval supply to the inlet, the source regions for larvae that enter the inlet, and potential pathways for larval transport to estuarine nursery areas.

Red drum (*Sciaenops ocellatus*) is an important recreational fishery in the coastal regions of the Gulf of Mexico (Swingle, 1990). Red drum produce 1-mm-diameter eggs that are buoyant at salinities greater than 25 and sink at lower salinities (Holt *et al.*, 1981, 1985). The density of the eggs and early larvae is dependent upon the development stage, spawning water salinity, and ambient salinity in which the larvae develop (Ponwith and Neill, 1995). Red drum spawn in the evenings in the nearshore in the vicinity of tidal inlets from late August to December, peaking

Figure 1. Location map of study area with wind rose. The wind rose was generated using data for August 17 to November 11, 1994 from Station 42020 (for location see Fig. 2a). The study area was dominated by onshore wind forcing for the majority of the 1994 spawning season. The location of the UTMSI pier where daily larval abundances were measured is indicated by the asterisk (*).



in September or October (Holt *et al.*, 1985; Matlock, 1990). Red drum larvae are typically within 20 km of the shore, inside the 18-m depth contour (Matlock, 1990). The presence of eggs (2–4 h old) in flood waters and their absence in ebb waters indicate that red drum spawn in the Gulf near Aransas Pass (Holt *et al.*, 1989); however, the spatial extent of spawning activity and the degree of alongshore transport of eggs and larvae are unknown.

Owing to the time required for larval development, the timing of larval transport to an estuarine habitat is an important factor in recruitment. If larvae are transported to a suitable settlement habitat but are insufficiently developed (precompetent phase), they will not be able to settle. A significant source of larval mortality may be associated with larvae being transported away from a suitable settlement habitat during this precompetent phase and their inability to reach a suitable habitat when they are competent (Jackson and Strathmann, 1981). Red drum larvae have a precompetent phase of about 20 days, at the end of which they have grown to an average standard length of 8 mm (Holt *et al.*, 1983; Rooker *et al.*, 1999). Competent larvae settle in estuarine nursery grounds, primarily seagrass habitats (Holt *et al.*, 1983; Rooker and Holt, 1997; Rooker *et al.*, 1999; Herzka *et al.*, 2002). In the Aransas Pass region, seagrass beds are primarily located in Redfish Bay, south of Mud Island on the backside of the barrier island, and along the edges of Lydia Ann Channel (Pulich *et al.*, 1997; Fig. 1). Although this study focuses on the transport of red drum larvae, the results may be applicable to other species with similar life histories in this inlet system.

Description of 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 nearest adjacent inlets are Pass Cavallo to the north (approximately 35 km) and Mansfield Pass to the south (approximately 125 km). The natural bathymetry and shoreline configuration of the study area have been modified by the dredging of channels, emplacement of jetties, and creation of islands, all of which influence the circulation in the inlet and bays (Powell *et al.*, 1997). Aransas Pass has jetties that extend about 1 km from the shore to the 9-m depth contour. Water entering the inlet from the Gulf is directed into one of three channels: the Corpus Christi (CC) Ship Channel (14-m deep and 120–180-m wide), the 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, which have a combined surface area of 1100 km² and mean depths of 3.6, 0.7, 2.4, 1.2, 2.2, and 1.0 m, respectively (Ward, 1997).

Tides provide an important driving force for exchange through the inlet. In the Gulf of Mexico, the tides are primarily diurnal or mixed diurnal–semidiurnal (Zetler and Hansen, 1970). The amplitudes of the dominant diurnal constituents, K₁ and O₁, are approximately 15 cm in the Gulf adjacent to Aransas Pass; the amplitudes of the dominant semidiurnal constituents, M₂ and S₂, are 8 and 2 cm, respectively (Zetler and Hansen, 1970; DiMarco and Reid, 1998; Brown *et al.*, 2000). The channels that connect the bays to the coastal ocean filter the tidal motions, preferentially attenuating the semidiurnal constituents (Smith, 1974; Brown *et al.*, 2000). Although the tides in the study area are relatively small, they regularly produce peak current velocities at Aransas Pass of about 1.5 m s⁻¹ (Williams *et al.*, 1991; 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 south-east (Smith, 1979b). During the winter months, the prevailing wind patterns are interrupted by strong north winds associated with the passage of cold fronts. In this study, we examine the transport of fish larvae that spawn during the late summer to fall, a period which coincides with this seasonal change in wind patterns. During the study period, onshore winds dominated (winds from the south, south-east, and east occur approximately 68% of the time) with average wind speed of 5.8 m s⁻¹ (Fig. 1).

Wind forcing provides an important mechanism influencing both exchange between coastal shelves and inland waters, and circulation patterns within bays and on the shelves (Csanady, 1981; Xie and Eggleston, 1999). Subtidal variations in the water level in bays of the Aransas Pass region are related to the wind regime and offshore changes in sea surface height (Smith, 1986). Previous studies have found that subtidal water level variations account for approximately 40% of the total influx of Gulf water into Corpus Christi Bay and approximately 50% of the variations in water level (Smith, 1986; Brown *et al.*, 2000). Along-shelf currents are predominantly wind driven in the nearshore region of the Texas coast (Smith, 1980). Wang (1996) found a high cross-correlation (0.5–0.7) between alongshore wind and alongshore currents in the inner shelf adjacent to Aransas Pass and a relatively short

response time (approximately 5 h) between change in wind forcing and the subsequent response of the current. The low-frequency circulation on the Louisiana-Texas shelf is downcoast (flow with shoreline on the right) except during the months of July and August (Cochrane and Kelly, 1986); however, wind forcing results in low-frequency reversals in alongshore currents occurring over time scales of 1–2 weeks (Smith, 1978).

METHODS

Larval fish sampling

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 (location shown in Fig. 1). 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 -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 m³ 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 unit/volume and the three tows were averaged.

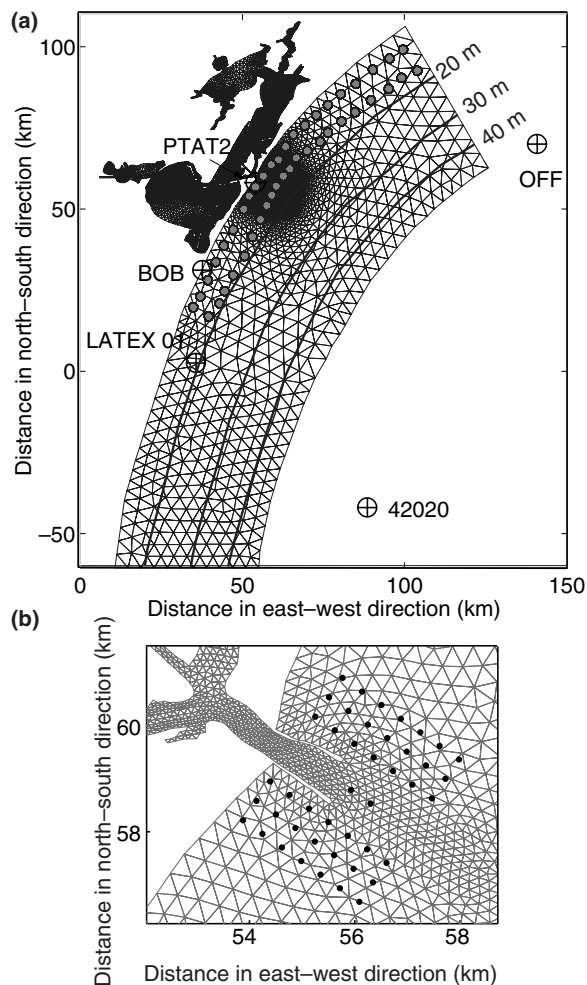
Circulation model

Circulation patterns were computed using a three-dimensional, free surface, non-linear 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). As 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.

Model domain

The model domain encompasses Corpus Christi, Nueces, Redfish, Copano, Mission, and St Charles Bays and extends 50 km offshore to the 50-m depth contour (Figs 1 and 2). The offshore portion of the mesh extends approximately 50 km north of the inlet and about 125 km to the south (Fig. 2a). Due to the pre-

Figure 2. Finite element grid of the study area along the Gulf coast of Texas showing locations of physical observations and where particles were released for (a) nearshore release (gray circles) and (b) inlet release (black circles). Wind stations are located at PTAT2 and 42020, water level stations are located at BOB and OFF, and current observations are located at LATEX 01. The 20-, 30-, and 40-m depth contours are shown on the finite element grid.



dominant downcoast flow (Cochrane and Kelly, 1986), the mesh extended further in the downcoast direction to prolong the length of time particles remain inside the domain before being transported out the southern boundary.

The shoreline configuration of the study area is complex, including numerous islands and intersecting channels. 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. The mesh used in this study was similar to that used in Brown *et al.* (2000) except the coastal

shelf portion was extended approximately 75 km to the south. Nodal spacing varies from about 7 km in the shelf region to about 50 m within the inlet (Fig. 2). The jetties extending from the pass into the Gulf are included in the mesh. 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.

Boundary and initial conditions

Previous studies (Zetler and Hansen, 1970; DiMarco and Reid, 1998; Brown *et al.*, 2000) demonstrated that the amplitude and phase lags of the astronomical tides in north-western Gulf of Mexico are essentially uniform. In addition, comparison of the low-frequency (40-h low-pass filtered) water level variations at a location along the coast and at the 50-m depth contour (Stations BOB and OFF, in Fig. 2a) during the fall to winter of 1993 indicates that the low-frequency water levels co-vary ($r^2 = 0.71$). As the water level fluctuations (both tidal and subtidal) in the coastal portion of the study area are fairly uniform in amplitude and phase, we imposed a spatially uniform surface elevation along the offshore boundary. Time-dependent water level forcing (Fig. 3a) was specified using 6-min water level data from Station BOB for the time period of August 20 to November 11, 1994, obtained from the Texas Coastal Ocean Observation Network (Michaud *et al.*, 1994).

A 'no flow normal to the boundary' condition was applied at the coastlines. Model simulations began with the model domain at rest and water elevation forcing was increased linearly over 3 days. 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 for the time period of August 20 to November 11, 1994 (Fig. 3b). Station 42020 is approximately 100 km south-south-east of the inlet at the 80-m depth contour (Fig. 2a). Wind forcing was started on the third day of the simulation.

Particle transport

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 (S. Holt, unpublished data). During the 1994 spawning season, red drum eggs were first caught in the inlet on August 24. 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). Beginning on August 22, 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.

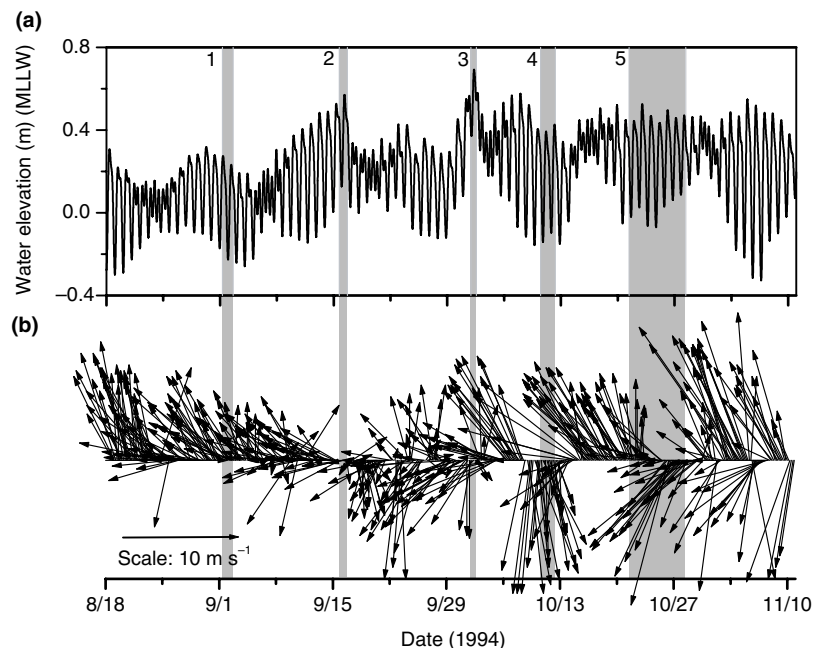


Figure 3. Time-series of (a) water level from BOB and (b) wind velocity from 42020 used to specify boundary conditions and forcing in the model simulations. Locations of BOB and 42020 are shown in Fig. 2. The shading represents periods when there were pulses in larval supply to the inlet.

For all of the simulations, 44 particles were released at each location once per hour at 18:00, 19:00, and 20:00 CDT, resulting in 132 particles released per day. Particles were released around sunset, which is the primary spawning time for red drum in the study area (Holt *et al.*, 1985). To examine the effect of particle release location on the simulation results, particles were released in two configurations: (1) distributed in the nearshore region along the coast and (2) in the vicinity of the inlet (Fig. 2a and b, respectively). The same number of particles was released for each configuration and all other parameters remained constant. Particles were allowed to exit the shelf boundaries. Transport patterns were examined for all particles that entered the inlet and for a subset of competent particles that entered the inlet. Competent particles were defined as particles between the age of 20 and 30 days, where the age of a particle is the length of time since its initial release.

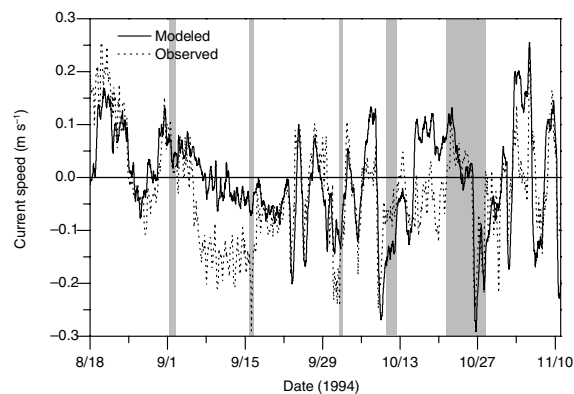
RESULTS

Comparison between modeled and observed shelf currents

The ability of the model to simulate tidal elevations, discharge, and vertical structure of flow inside the inlet and bays was assessed in Brown *et al.* (2000). A comparison of modeled current velocities to observations at Station LATEX 01 allows an assessment of the model performance on the shelf portion of the model domain (data from DiMarco *et al.*, 1997). LATEX 01 is located on the shelf about 60 km south-west of Aransas Pass at a water depth of 14 m with a current meter located 2 m above the bottom (Fig. 2a). During the late summer to fall of 1994, there were low-frequency reversals in the north–south component of the current (Fig. 4). The current at LATEX 01 is predominantly in the north–south direction. On average, the magnitude of the north–south current is approximately five times greater than the east–west component. The model reproduces about 40% of the observed variance in the north–south component of the current ($r = 0.65$, $N = 688$). There is no relationship between the simulated and observed east–west component of the current. Some of the large discrepancies between modeled and observed north–south component of the current, such as between September 7 and 17, are probably related to the imposition of the boundary condition of spatially uniform, offshore water surface elevation.

Prior to September 7, the study area was dominated by winds from the south-east. The south-east winds result in an elevation of the water surface north of the

Figure 4. Comparison of modeled and observed north–south component of current velocity at LATEX 01 (see Fig. 2 for location). Data from DiMarco *et al.* (1997). Positive value indicates that the current is flowing toward the north. The shading represents periods when there were pulses in larval supply to the inlet.



model domain, which was not accounted for in the water surface elevation boundary conditions. During September 7–17, the average wind stress decreased by about 50% compared with that prior to September 7 and the wind was primarily from the east but with substantial diurnal rotation. This change in wind stress resulted in a strong southward-directed return flow along the bottom that was not present in the simulations. After September 17, there were low-frequency reversals in the wind field, which were related to the passage of cold fronts, and the longshore component of the wind dominated.

Observed larval abundances

During the fall of 1994, there were six pulses of larvae inside the inlet (Fig. 5). We define a pulse as a period when the observed larval concentration exceeds the mean concentration by at least 1 standard deviation (using the 1994 spawning season to calculate mean and standard deviation). Pulses were coherent for several sciaenid species with overlapping spawning seasons, including red drum, sand seatrout (*Cynoscion arenarius*), spotted seatrout (*Cynoscion nebulosus*), and Atlantic croaker (*Micropogonias undulatus*) (Fig. 5). Red drum and sand seatrout have similar spawning seasons, whereas spotted seatrout start spawning in early summer and cease spawning by late September and Atlantic croaker spawn from October to March with a peak in November (Reagan, 1985). Observed pulses in larval supply to the inlet occur every 10–16 days. Generally, these pulses last 2 tidal cycles or flood tides. However, during 1994 there was one

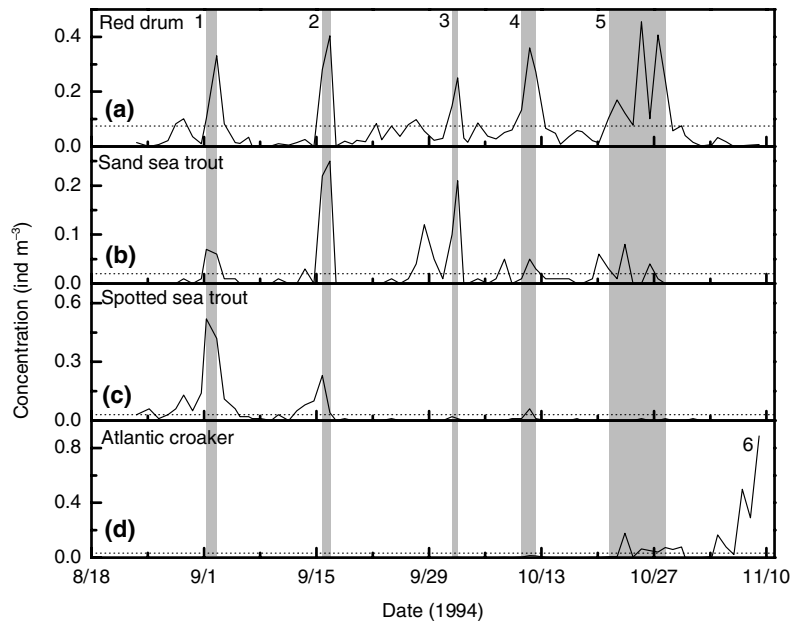


Figure 5. Observed concentration of (a) red drum, (b) sand seatrout, (c) spotted seatrout, and (d) Atlantic croaker entering the Aransas Pass inlet on flood tides during the fall of 1994. The shading represents periods when there were pulses in larval supply to the inlet.

pulse with a duration of approximately 8 tidal cycles (Pulse 5).

These pulses are an important source of larvae to estuarine nursery areas. During the 1994 red drum spawning season, these five pulses (which took place over a 16-day period) accounted for 70% of the larvae entering the inlet; the remaining 30% of larvae entering the inlet were associated with the low background levels that occurred during the remaining 60 days. The last pulse of red drum larvae (Pulse 5) represents 30% of the total larval input.

The coherence of the pulses among multiple species suggests that the pulsing is associated with a physical mechanism. The greater larval concentrations associated with Pulses 2 and 3 coincided with peaks in low-frequency water level variations (Fig. 3a). However, the remaining pulses do not appear to be associated with any particular feature in the water level or wind forcing. There is no significant correlation between larval concentration and environmental variables [low-frequency (40-h low-pass filtered) water level, 24-h average north–south wind speed, 24-h average east–west wind speed, and flood tide discharge].

Comparison between observed larval abundances and simulations

The volume of water entering the inlet during a flood tide varies from about 10^5 to 10^8 m³ 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 enter-

ing 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. To compare the total number of individuals entering the inlet to the model results, the simulated number of particles entering the inlet during each flood tide was counted.

The model reproduces some of the temporal variation in the observed number of red drum larvae entering the inlet (Fig. 6). For the first 70 days of the red drum time series (i.e. during the active spawning season), there is a significant positive correlation between observed number of red drum larvae entering the inlet and the simulated number of particles entering the inlet (Spearman rank order correlation, $n = 70$, $r = 0.376$, $P < 0.001$). The simulation reproduces the occurrence and timing of Pulses 2 and 5, but leads the observations for Pulses 3 and 4 by about 1 and 3 days, respectively. It reproduces the duration of the extended pulse (Pulse 5), which lasts approximately 8 tidal cycles.

The model predicts a large larval pulse on November 3, but there is only a small increase in the observations on this date. This lack of agreement results from releasing particles into the model after the red drum spawning season had ended. During the 1994 season, spawning of red drum ended on October 18 based on the last date that eggs were caught in the inlet, but particles were released until November 9. For Atlantic Croaker, a species that begins spawning in October, there was a pulse on November 7–9 (Fig. 5d).

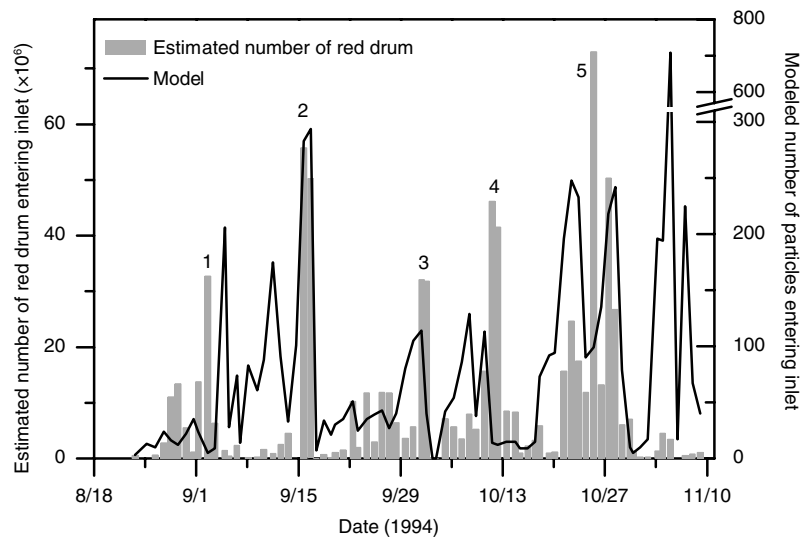


Figure 6. Comparison of modeled and estimated number of red drum larvae entering the Aransas Pass inlet during the fall of 1994. Estimated number of red drum larvae is the product of the observed concentration (Fig. 5a) and volume of water entering the inlet for each flood tide.

The model performs poorly at the beginning of the simulation interval; it does not reproduce the timing of the first observed pulse of red drum larvae and predicts two additional pulses on September 4 and 11, as well as fairly high larval supply between these two dates. One possible explanation for this lack of agreement is that there are fewer particles present in the coastal region early in the simulation because they have not had time to accumulate. Therefore, the results may be sensitive to the time when particles are first released in the model and the number and spatial distribution of particles present.

Sensitivity of model results

As the spatial extent of spawning activity is unknown, simulations were performed with different particle release locations. The simulation with particles released in the vicinity of the inlet (for release locations see Fig. 2) has similar temporal patterns of particle supply to the inlet as does the simulation with particles released along the inner shelf (compare Figs 6 and 7a). However, in the former simulation, more particles enter the inlet because the release locations are closer to the inlet. There is also a shift in the timing of some of the pulses; in the model Pulse 3 occurs on September 29, which is about 2–3 days before the observed pulse. This change in timing suggests that the discrepancy between the model and observations in the timing of Pulse 3 could be associated with the release location of the particles.

In the coastal region, the presence of land influences the wind fields causing substantial spatial differences in wind speed and direction. This effect is particularly important in regions where there is cur-

vature in the shoreline, such as that found in the Aransas Pass study area. To examine the effect of spatial variations in wind forcing, simulations were performed using hourly wind data from Station PTAT2 (location shown in Fig. 2), which is about 0.5 km from the inlet along the coast. The correlation coefficient (r) between the nearshore and offshore wind forcing (PTAT2 and 42020) varied from 0.80 for the north–south component to 0.61 for the east–west component. Although this station is located closer to the inlet than Station 42020, it is more influenced by land effects.

Using data from PTAT2 for wind forcing causes pulsing in the number of particles entering the inlet similar to that using wind data from Station 42020, but with differences in the magnitude and timing of the pulses (Fig. 7b). Using PTAT2 wind forcing, the largest influx of particles occurs between September 11 and 13. There are dramatic shifts in the timing of Pulses 2 and 4, with the simulated pulses occurring approximately 4–5 days prior to the observations. The greater agreement between modeled and observed number of particles entering the inlet using the offshore wind forcing suggests that particle transport in the coastal region is influenced more by offshore rather than nearshore wind patterns. Simulations performed without wind forcing (results not presented) show similar temporal patterns of pulsing with diminished peak abundances.

Source regions

The release locations for particles that successfully entered the inlet (regardless of age) were predominantly located in the vicinity of the inlet, with the two

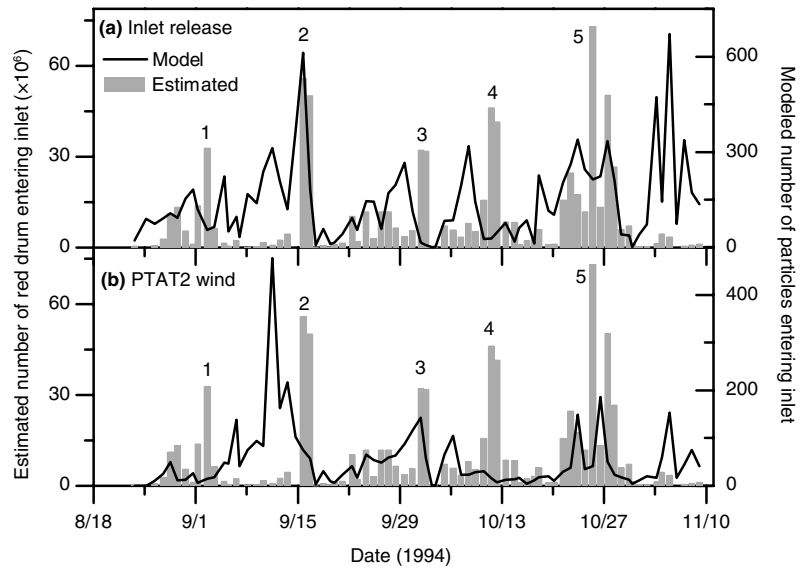


Figure 7. Effect of (a) particle release location and (b) specification of wind forcing on modeled number of particles entering the inlet. The top panel shows simulation results for particles released in the vicinity of the inlet (see Fig. 2b for release locations) and the bottom panel shows model results using PTAT2 wind forcing (see Fig. 2a for location).

most successful release locations being the innermost locations adjacent to the inlet. Approximately 50% more successful particles came from the release locations north of the inlet than south and about 20% more originated at the innermost locations than offshore. The importance of northern particle sources was more pronounced for competent particles that successfully entered the inlet. Successful competent particles originated from all of the 44 release locations, but twice as many came from release locations north of the inlet. The release locations of the successful competent particles were approximately equally divided between the inner and outer release locations.

Release locations for the individual particles that make up Pulses 2 and 5, whose timing the model successfully reproduced, were from north of the inlet, but the source region did not extend to the northern boundary of the model domain. For Pulses 3 and 4, where the modeled pulses led the observations and underestimated the magnitude of the pulse, the release locations are north of the inlet with a large fraction of the particles originating at the northernmost release locations. The particle source regions suggest that the discrepancy between the model and observations in the timing and magnitude of Pulses 3 and 4 may result from the source of larvae for these pulses being beyond the northern boundary of the model domain. A more northern source region could delay the timing of Pulses 3 and 4, decreasing the difference between observed and simulated timing. This is consistent with a sensitivity test performed releasing particles near the inlet, which results in a larger discrepancy in the timing between the model and observations.

During the interval of September 4–11 when the model predicts more particles entering the inlet than were observed, all of the simulated particles that entered the inlet originated from the south. An additional simulation with particles released only north of the inlet reduced the number of particles entering the inlet during that period and increased the number of particles entering during Pulses 3 and 4, but it did not improve the timing of the modeled pulses. The correlation between the modeled particle supply and observed red drum abundance improved for the sources located only north of the inlet (Spearman rank order correlation, $N = 70$, $r = 0.482$, $P < 0.0001$). These results suggest that during 1994, larvae that entered Aransas Pass originated primarily from spawning areas located to the north of the inlet.

Fraction of particles that enter the inlet

During the 2.5-month simulation period, 10 560 particles were released and tracked in the model. Approximately 45% of the particles entered the inlet at some time during the simulation, but only about 8% of all particles released entered the inlet during the competent stage (20–30 days old). To estimate larval losses associated with their not being near suitable habitat at a time when they can settle, we counted the number of particles entering the inlet that are competent to settle as a function of the length of the precompetent period. This number decreases as the length of the precompetent period increases (Fig. 8). By fitting an exponential decay function to the portion of the curve corresponding to a precompetent period of 18–36 days (see inset of Fig. 8), we estimated these advective losses for red drum

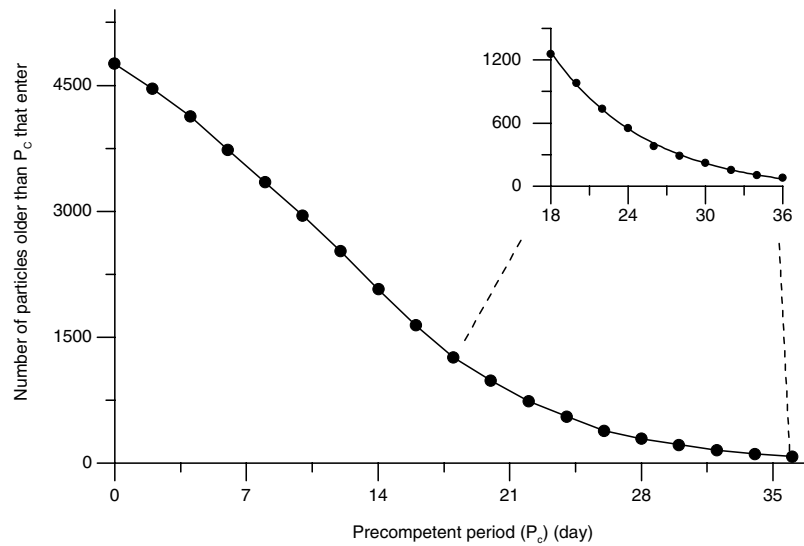


Figure 8. Number of competent particles entering the inlet as a function of duration of precompetent period. Competent particles (P_c) are defined as particles between the age of 20 and 30 days, where the age of a particle is the length of time since its initial release. Inset shows exponential decay fit to model results for precompetent period of red drum.

to be approximately 0.13 day^{-1} . A similar advective loss (0.12 day^{-1}) was estimated for the simulation releasing particles north of the inlet.

Trajectories of settlement-age particles that enter the inlet

Transport of surface particles is strongly influenced by local wind forcing. The trajectories of settlement-age particles that enter the inlet have several characteristic patterns in their transport on the inner shelf (Fig. 9). Transport is predominantly longshore and in the downcoast direction, but there are frequent reversals. Some particles pass the inlet and are transported back to Aransas Pass by the current reversals (Fig. 9b). There is also a net onshore transport of surface particles due to the onshore wind forcing. Settlement-age particles move to the nearshore region by the onshore wind and move toward the inlet by the currents associated with the alongshore winds. The dominant offshore transport mechanism is associated with the ebb tidal jet of the inlet (Fig. 9a).

Division of particles between channels

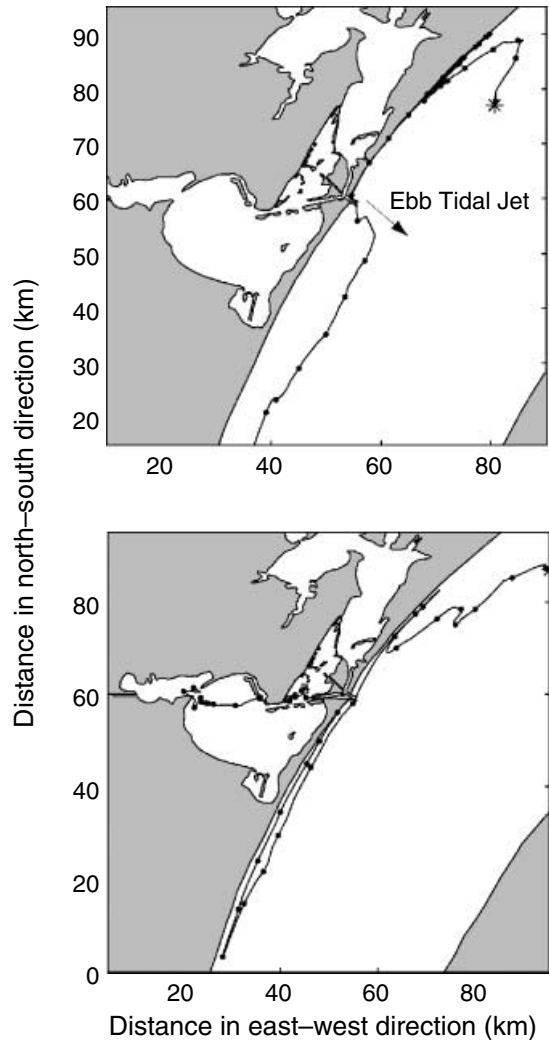
Examination of all of the particles that enter the inlet at any age reveals that about 60% travel down CC Ship Channel, 30% down Lydia Ann and the remaining 10% travel down the Aransas Channel, which is similar to the distribution of flow in the channels (Brown *et al.*, 2000). However, competent particles that enter the inlet have a slightly different transport pattern. From August 22 to November 1, 50% travel down the CC Ship Channel, 43% travel down Lydia and the remaining 7% enter the Aransas Channel. For certain pulses there are more dramatic differences in the distribution of the particles between

the channels from that expected based on division of flow; for example, Pulse 2 had approximately 80% of the particles travel toward Aransas Bay via Lydia Ann and only 16% enter the CC Ship Channel. During this same interval, the division of the flow between the channels (CC Ship, Lydia Ann, Aransas) remained 60, 30, and 10%. The difference between the division of flow and particles is associated with the approach path of the particles outside the inlet. The majority of the particles entering the inlet during Pulse 2 approached the inlet from the north.

DISCUSSION

Catches of red drum larvae entering the Aransas Pass inlet on flood tides during the 1994 spawning season were characterized by low concentrations on most days and high concentrations on just a few days. Similar patterns of immigration of larvae through inlets have been observed in other locations (e.g. Boehlert and Mundy, 1987; Hamer and Jenkins, 1997; Hettler *et al.*, 1997). In the Aransas Pass region, these high-concentration pulses occurred approximately every 10–14 days and are an important source of potential immigration to the nursery sites. Although these pulses are not linearly correlated with low-frequency water level variations or wind components, results of model simulations that integrate the physical transport over space and time suggest that these environmental variables are significant factors in the occurrence of pulses. Similarly, Hettler *et al.* (1997) proposed that unknown factors operating over larger scales are more important than locally measured environmental variables in determining pulses in supply of larval fish to

Figure 9. Trajectories of two particles in the coastal region that were released on (a) August 23 and (b) September 30. Trajectories (lines) are based on position at 6-h intervals and are marked (•) at 24-h intervals, and release locations (*) are shown.



Beaufort Inlet. The agreement between our model results and observed larval concentrations is surprisingly good, especially considering the simplifying assumptions of the model (e.g. simple boundary conditions and spatially uniform wind forcing for the physical model, continual particle introduction, and lack of mortality and behavior).

Previous studies have attempted to identify the dominant factors influencing larval transport using regression techniques. Often the relationship between larval supply and environmental variables is weak or absent. The lack of correlation is often attributed to the presence of unknown variables that are not included in the analysis, limitations in estimating

larval abundances, or stochastic effects. Our results are similar to those of Jenkins and Black (1994), who found pulses in larval fish settlement could not be correlated with a single oceanographic event but rather resulted from the interaction of several factors. Particle transport depends upon the time-history of events, rather than the presence or absence of a single event or the strength of such an event. The limitations of regression techniques are illustrated by applying this technique to our model results. Temporal patterns in simulated particle supply are not influenced by factors such as sampling limitations, behavior, or mortality. In addition, simulated particle supply is deterministic and does not incorporate stochastic effects. There is not a significant correlation between modeled particle supply and the forcing variables of the model (coastal water level variations and wind forcing). Even in this simplified simulated system, the non-linear transport dynamics hinder the identification of factors controlling transport. To understand recruitment dynamics, we need to develop models that incorporate these non-linear variations in transport.

Dixon *et al.* (1999) applied both linear and non-linear time series analysis to relate the fluctuations in larval supply of a reef fish to physical variables. Non-linear analysis provided a significant improvement in prediction of larval supply over linear analysis techniques, suggesting that larval supply is a non-linear process. Dixon *et al.* (1999) attributed the episodic nature of larval supply to amplification of stochastic physical forcing by biological processes. In contrast, our results suggest that the pulsing of larval supply is a non-linear process resulting from the non-linear dynamics of currents and does not require non-linear biological responses. However, non-linear biological responses might further amplify the non-linear effects as proposed by Dixon *et al.* (1999).

Temporal variations in red drum larval supply to the Aransas Pass Inlet during the 1994 spawning season were related to advective transport. Simulations suggest that the primary source region for all larvae that entered the inlet during 1994 was north of the inlet. This northern source is particularly important for supply of settlement-age larvae as a result of the predominant downcoast flow during the spawning season. The transport of settlement-age larvae is determined by the average coastal currents during the 20-day precompetent period. Although there were reversals in the instantaneous current direction associated with changes in alongshore wind forcing, the 20-day running average of the current was downcoast after August 31 during the 1994 spawning season. The 20-day running averages of the

current at LATEX 01 ranged from 3 to 7 cm s⁻¹ (with a mean value of 5 cm s⁻¹). Settlement-age larvae that enter Aransas Pass could originate as far as 120 km upcoast of the inlet if they moved at 7 cm s⁻¹ for 20 days. This current speed may be an underestimate as LATEX 01 measurements are near the bottom of the water column; however, model simulations also suggest that the maximum 20-day average downcoast flow at the surface is about 7 cm s⁻¹. This simple calculation of the extent of the source region for Aransas Pass is consistent with simulation results that the larval source extended beyond the northern model domain boundary (65 km upcoast of the inlet). To improve model results, the model should be extended to include a larger portion of the Texas shelf.

Extending the model domain would also allow us to examine the role of physical processes in determining large-scale patterns of recruitment in estuarine-dependent species in the Gulf of Mexico and the degree of mixing of larvae between adjacent inlet-bay systems in the coastal region. Along the Texas coast the distance between adjacent inlets is about 50–100 km. Scharf (2000) examined interannual variation in abundance of juvenile red drum at nine estuaries along the Texas coast during a 20-yr period and found that temporal variations in age-0 red drum abundances are positively correlated among estuaries. Scharf (2000) proposed that physical transport might be responsible for these large-scale patterns in distribution of juvenile red drum.

Failure of larvae to settle successfully can result from mortality associated with predation or starvation or from transport away from favorable habitat. Larvae that remain in unfavorable habitat will eventually perish due to predation or starvation. For larvae that spend most of their time on the shelf waiting to be transported through a tidal inlet to estuarine nursery areas, transport away from favorable habitat may represent an important presettlement loss of larvae. Such transport is particularly important for estuarine-dependent larvae if the spacing between adjacent inlets is large compared with the distances that larvae travel during their precompetent phase. If a competent larva fails to enter the first inlet it encounters, it probably will not survive the transit to the next inlet.

There have been few estimates of mortality for red drum larvae. Comyns *et al.* (1991) estimated the mortality for red drum larvae on the Louisiana-Mississippi-Alabama shelf to be about 0.52 day⁻¹. This mortality estimate includes losses due to advection. Rooker *et al.* (1999) estimated mortality rates for post-settlement red drum larvae in the Aransas Estuary to

be about 0.13–0.14 day⁻¹. From the present study, advective losses associated with larvae not being in the vicinity of an inlet when they are sufficiently developed to be able to settle (competent) are estimated to be about 0.13 day⁻¹. Thus, advective transport may represent an important presettlement loss for red drum larvae, which has the same magnitude as other losses such as predation and starvation.

The estimate of advective losses is dependent upon the size of the model domain in the alongshore direction. Advective losses may be overestimated if a large number of precompetent particles exit the model boundaries. If the domain was larger, these particles might have reached an inlet during the remainder of their precompetent interval. Almost 80% of the particles exiting the model boundaries are older than 2 weeks and 84% exit the southern boundary. Due to the predominant downcoast currents, very few of the particles that exited the southern boundary would be transported back to Aransas Pass in time to settle; however, some of the particles might have arrived at Mansfield Pass, which is about 25 km south of the model domain, in time to settle.

Successful competent particles that enter the inlet have consistent patterns in their trajectories in the nearshore region outside the inlet. Although the dominant mode in larval transport is in the longshore direction, the cross-shelf component is important in transporting larvae toward the coast. Our simulations show that particles that enter the inlet are first transported toward the coast, then they move alongshelf in the nearshore region (inshore of the 10-m depth contour) to the inlet, rather than moving directly across the shelf to the inlet.

The simulated onshore transport of surface water is consistent with current measurements at several locations inside the 33-m depth contour offshore of the Aransas Pass inlet (Smith, 1978, 1979a, 1980). These studies found substantial onshore transport throughout the water column during the transition from summer to winter conditions (June–January). The onshore transport is also evident in the high recovery rate (and trajectories) of drift bottles released inshore of the 15-m depth contour in the study area (Watson and Behrens, 1970). A surprising result of the simulation was the large percentage (45%) of released particles that enter the inlet at some time during the simulation. The onshore wind-driven transport could be an efficient mechanism for transporting passive surface particles to the inlet-bay system, especially for marine organisms that spawn inshore and have estuarine nursery areas. The primary offshore transport

mechanism for surface particles is the ebb tidal jet associated with the inlet (Brown *et al.*, 2000).

There are several caveats about these simulated nearshore trajectories. Near land boundaries, there may be large discrepancies between simulated and observed flow fields associated with the specification of boundary conditions. In addition, the circulation model used in this study does not include currents due to surface waves, which would be important in the nearshore region.

One of the primary questions resulting from this study is: are there red drum larvae in the nearshore region? There are few published studies discussing red drum larvae distribution in the nearshore region. Simmons and Breuer (1962) found large numbers of 12–15-mm-long sciaenid larvae in the surfzone along the Texas coast; however, they found few red drum larvae. Ruple (1984) sampled larval fishes in the inner and outer surf zone regions (depths of 0.5 and 4–7 m, respectively) in the northern Gulf of Mexico, finding larval fish concentrations as high as 10 larvae m^{-3} in the surf zone, with higher concentrations in the outer surf zone region. They did find red drum larvae in the surf zone with higher concentrations at the inner stations. Results of our study suggest that the surf zone may be an important habitat for larval fishes due to its potential as a transport pathway and we need more information of the distribution of larval fish in this region.

In addition to horizontal distributions, the vertical distribution of fish larvae can also influence transport patterns. Near bottom current measurements at LATEX 01 indicate that during the fall of 1994 there was net offshore transport at depth. For larvae that occupy the bottom of the water column or vertically migrate, the patterns discussed in this paper may not be valid. Hare *et al.* (1999) found a secondary effect of vertical distribution on larval transport. Variations in vertical distribution influenced the magnitude of particle supply but did not affect the timing of ingress.

Although our results need to be verified (e.g. by sampling for larvae in the surf zone, vertical distribution of larvae, current measurements, and examining the trajectories of drifters in the nearshore region), other studies support our results that the nearshore region may be an important pathway for transport of larvae to estuarine nursery areas. Churchill *et al.* (1999) deployed drogues outside Beaufort Inlet, North Carolina, and found that the drogues that entered the inlet originated in a narrow nearshore region within 2 km from the coast (inshore of the 10–15 m depth contour). In addition, numerical simulations of particle transport at Beaufort and North Edisto inlets suggest that principal pathways that particles follow into the inlet are via alongshore transport in the nearshore region (Blanton *et al.*, 1999;

Luetlich *et al.*, 1999). Blanton *et al.* (1999) speculated that the presence of jetties associated with tidal inlets could block these nearshore pathways for larvae, potentially influencing recruitment to estuarine nursery areas. However, our study reveals that the nearshore pathways remain an effective transport route even in the presence of jetties.

Hettler and Hare (1998) sampled the nearshore region adjacent to Beaufort Inlet for seven species of ocean-spawned, estuarine-dependent fish larvae. They found the concentration of fish larvae decreased with distance offshore for all species except for *Brevoortia tyrannus* (Atlantic menhaden). In addition, Hettler and Hare (1998) and Powles (1981) found evidence of accumulation of estuarine-dependent larvae in the nearshore region with larger (presumably older) larvae found onshore. Harris and Cyrus (1996) found that the surf zone adjacent to St Lucia Estuary in South Africa functions as a transit route and nursery habitat for estuary and non-estuary-associated fish species. These studies and our results show a consistent pattern that the nearshore region accumulates larvae and serves as an important path to the estuaries.

Brown *et al.* (2000) found that there are spatially distinct source regions of flood water for each of the channels. The spatially distinct sources for branched channels are particularly important for larval transport to settlement habitat if there are spatial differences in distribution or quality of nursery habitat within the bays. In the Aransas Pass region, red drum settlement habitat is primarily located along the edges of Lydia Ann and within Redfish Bay. The majority of flow is transported toward Corpus Christi Bay via the CC Ship Channel (60%) with the remaining flow transported toward Aransas Bay (30%) and Redfish Bay (10%); however, high larval abundances are found in Aransas Bay. In the present study, model simulations show that a slightly larger percentage of competent particles travel down Lydia Ann and the Aransas Channel (50%) compared with that expected based on division of flow (40%); however, during certain intervals, such as Pulse 2, there is an even more dramatic difference with 80% of the particles traveling down Lydia Ann and only 18% entering the CC Ship Channel. This difference is associated with the approach path of the particles outside the inlet, which is supported by other studies (e.g. Churchill *et al.*, 1999). The spatially distinct sources for each channel combined with the predominant downcoast flow may result in a greater fraction of larvae being transported to Lydia Ann Channel than the amount expected based on division of flow. Simulations suggest that larval abundance at one location in the inlet may not

be representative of supply to individual channels. Larval surveys show that sometimes larvae are uniformly distributed inside the inlet, while at other times there are cross-channel differences in abundance (S. Holt, unpublished data). We propose that these cross-channel variations in abundance are associated with the approach path of the larvae outside the inlet.

Simulations suggest that larval transport is an important factor influencing supply of larvae to nursery areas; however, other years should be examined to determine whether the patterns elucidated in this paper are valid for other environmental and biological conditions. This paper addresses only barotropic transport. During high freshwater inflow conditions, baroclinic effects may become important in this region. Biological factors may also influence larval supply to the inlet, such as the spawning intensity, predation, and starvation.

Our results, combined with previous studies (observational and modeling), suggest that the transport patterns discussed in this paper may be a common feature for larval transport at other inlets. Physical processes and variations in physical transport may be important factors determining intra- and inter-annual variability in recruitment for many estuarine-dependent fishes along the Gulf of Mexico coast.

Numerical models are useful tools for examining the effect of changes in transport on larval recruitment. Models allow us to integrate complex, non-linear processes occurring at multiple temporal and spatial scales over time scales that are relevant to organisms. Such models allow us to quantify the effect of modifications to the systems, such as dredging of channels. They also may allow us to predict future changes to recruitment. Global warming and climate changes are expected to alter wind patterns. Because of the strong linkage between larval transport and wind forcing, changes in larval supply to estuarine nursery areas may be expected. Models provide a means to examine these relationships.

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