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Modeling Larval Transport and Settlement of Pink Shrimp in South Florida: Dynamics of Behavior and Tides

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Abstract

The pink shrimp *Farfantepenaeus duorarum*, one of the commercially important Penaeidae, reproduces offshore of the southwest Florida (SWF) shelf. Larvae migrate to nursery grounds in estuarine Florida Bay. Using a numerical approach, we investigated the role of spawning location, larval traits, and physical forces on the transport of pink shrimp larvae. First, the Regional Oceanic Modeling System that is based on tides, air–ocean fluxes, and freshwater flows was used to simulate the SWF shelf oceanography. The model replicates the tides, winds, salinity, currents, and seasonality of the shelf. Secondly, the Regional Oceanic Modeling System was coupled offline with the Connectivity Modeling System, in which virtual larvae were released near the surface from two spawning sites, Dry Tortugas and Marquesas, and tracked until the time for settlement (about 28–30 d). Virtual larvae moved vertically in the water column following ontogenetic behaviors previously observed in the field: diel vertical migration (DVM) and selective tidal stream transport (STST). Lagrangian trajectories indicated that migration paths changed radically between summer and winter during model years (1995–1997). Maximum settlements occurred in summer by larvae crossing the SWF shelf, while the lowest settlement occurred in winter by larvae moving through passes in the Florida Keys. Modeling results demonstrated an effective east-northeast transport across the SWF shelf during summer as a result of the tidal currents, the subtidal currents, and the combined DVM and STST behaviors. The current phase captured during the initial DVM period was critical to determine the direction in which larvae move, favorable (east and northward) or unfavorable (south and westward), before the STST behavior captures the eastward tidal current that brings larvae to the nursery grounds. Unfavorable currents were driven by the summer easterlies and low salinities at the coast. Results indicated that Marquesas is the more effective spawning ground, with 4.5 times more likely settlement of originating larvae compared with Dry Tortugas. Model-estimated seasonal settlement patterns concurred with postlarval influxes previously observed at Florida Bay boundaries.

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Most coastal species of fish and marine invertebrates spawn offshore in shelf waters, and early life stages migrate to coastal estuarine nursery grounds. Coastal oceanographic processes greatly influence transport and settlement of these estuarine-dependent species. The dominant physical mechanisms that may yield successful transport include wind-driven Ekman transport, upwelling fronts, moving frontal systems, counter-currents generated by coastal eddies, coastal boundary layers, and nonlinear internal tides and bores (e.g., Shanks 1995, 2006; Queiroga and Blanton 2004). Larval behavior in the form of diel or tidal ontogenetic vertical migrations is an important mechanism that influences horizontal dispersal (Cowen and Castro 1994; Paris et al. 2002) and enhances local retention in nearshore zones (Paris and Cowen 2004; Paris et al. 2007; Butler et al. 2011) and in upwelling systems (Peterson 1998; Almeida et al. 2006). In this study, we used a modeling approach to determine the effect of physical factors and larval behaviors on the transport and settlement of the important penaeid pink shrimp *Farfantepenaeus duorarum* in southern Florida.

Tropical penaeid shrimps are highly fecund species with short-lived, complex life cycles and highly variable patterns of recruitment. Females usually spawn offshore, and larval stages migrate to estuaries, where juveniles develop and grow before returning to the fishery grounds (e.g., Garcia and Le Reste 1981; Dall et al. 1990). The larvae employ diurnally and tidally modulated behaviors to successfully migrate to the nursery ground. Diel vertical migration (DVM), a widespread behavior in crustacean decapod larvae, has been observed in the early protozoea and mysis stages of several penaeid species (Jones et al. 1970; Rothlisberg 1982; Rothlisberg et al. 1983; Criales et al. 2007). These early larvae, with very limited ability to swim, coordinate their migrations with the day–night cycle, rising in the water column exclusively at night. Later in their development, as they approach the nursery grounds, postlarvae change activity from a diurnal to a tidal rhythm (Rothlisberg et al. 1995, 1996; Criales et al. 2010, 2011). Prompted by environmental cues associated with the tides, postlarvae swim in the water column during the dark flood tide and rest near the bottom during the ebb tide. This general mechanism is known as selective tidal stream transport (STST), and more than one behavior has been associated with it (for review see Shanks 1995; Forward and Tankersley 2001; Queiroga and Blanton 2004).

Pink Shrimp Larval Ecology

The pink shrimp is one of the most economically and ecologically important species in southern Florida and in Campeche Sound, Gulf of Mexico (Sheridan 1996; Ramírez-Rodríguez et al. 2003). This species supports an important year-round fishery on the lower southwest Florida (SWF) shelf between Dry Tortugas and Key West (Klima et al. 1986; Hart 2012). The spawning center and major fishery are located near the Dry Tortugas and Marquesas islands (Cummings 1961; Roberts 1986), and the main nursery grounds are in Florida Bay and other coastal estuaries of the lower southwestern Florida coast (Tabb et al. 1962; Costello and Allen 1966; Browder and Robblee 2009). The Dry Tortugas fishery is directly dependent on young shrimp that migrate from inshore nursery areas onto the offshore fishing grounds (Ehrhardt and Legault 1999; Browder et al. 2002). Larvae develop quickly, passing through several changes in feeding habitats, behavior, and morphologic stages (nauplii, zoeae, myses, postlarvae) and needing only about 30 d to become postlarvae ready to settle (Dobkin 1961; Ewald 1965). Larval development and ocean hydrodynamics must be well synchronized to successfully bring planktonic stages to their coastal nursery grounds. Because Florida Bay interacts with two different continental shelves—i.e., through its western border with the SWF shelf of the Gulf of Mexico and through the eastern and southeastern borders with the Florida Keys coastal zone in the Atlantic Ocean—pink shrimp larvae arriving from Dry Tortugas have alternative routes to recruit to the nursery grounds. The two main hypothesized transport pathways are as follows: (1) larvae may drift south–southeast downstream with the Florida Current front and enter Florida Bay through the tidal inlets of the Lower and Middle Florida Keys (Munro et al. 1968; Criales et al. 2003) and (2) larvae may move east–northeast across the SWF shelf and enter the bay at its northwestern boundary (Jones et al. 1970; Criales et al. 2006).

Simulations of larval transport that include larval behavior have been conducted for penaeid species in the Gulf of Carpentaria, in the Indo-Pacific (Rothlisberg et al. 1995, 1996; Condie et al. 1999), and in the Gulf of California in the eastern Pacific Ocean (Calderon-Aquilera et al. 2003; Marinone et al. 2004). Rothlisberg et al. (1996) and Condie et al. (1999) developed larval behavior models for penaeid species (*Penaeus semisulcatus, P. merguiensis,* and *P. esculentus*) and coupled them to hydrodynamic models from the Gulf of Carpentaria to determine the distribution of effective spawning grounds and the advection of larvae to the nursery grounds. The modeling approach of these two studies was similar in using a transition depth as the point where larvae switch from vertical migration cued by the diel cycle to that cued by the tides. Marinone et al. (2004) studied larval transport from a Lagrangian point of view by including larval behavior as part of the biological component of the model to examine the potential location of spawning grounds for the blue shrimp *Litopenaeus stylirostris* and yellowleg shrimp *Farfantepenaeus californiensis*. In the present study, a biophysical transport model that resolves the ontogenetic behaviors of the pink shrimp larvae was used to determine larval migration of pink shrimp larvae from their spawning grounds to their nursery grounds, the most frequent recruitment pathways, and the larval behaviors and physical forces necessary to successful transport and settlement.

Southwest Florida Shelf Dynamics

The SWF shelf is a wide and shallow shelf with a smoothly varying topography aligned northwest–southeast bounded by Gulf of Mexico waters to the west and Atlantic Ocean waters near the Florida Keys and the Dry Tortugas to the south (Figure 1). Previous studies by Li and Weisberg (1999a, 1999b), Weisberg et al. (2001), Weisberg et al. (2009), and Liu and Weisberg (2012) suggested a dynamically based partition of the shelf that leads to the distinction of outer, middle, and inner shelf regions, plus a nearshore region embedded within the inner shelf. The outer shelf extends an internal Rossby radius of deformation inward from the shelf break, providing a buffer zone between the deep ocean and the shelf and reducing the seasonality of the circulation. The outer shelf circulation is mainly under the influence of the Loop Current and Florida Current (LFC) system and warm core (anticyclonic) and cold core (cyclonic) eddies that propagate southward along the Loop Current front and continue eastward between the shelf and the Florida Straits (Lee et al. 1992; Fratantoni et al. 1998; Le Hénaff et al. 2012).

The inner shelf is the shallow region controlled by friction, where surface and bottom Ekman layers are likely to either interact or be separated from one another by stratification. This region is mainly under the influence of baroclinic, heat-flux-driven and barotropic, wind-and-tide-driven circulations. Using long-term measurements, Liu and Weisberg (2012) found a robust seasonal cycle in velocity that varies across the shelf. The inner shelf circulation is predominantly upwelling favorable from October to April, and the circulation consists of a southward alongshore current on the central and southwestern shelf. From June to September, the circulation is predominantly downwelling favorable and consists of a strong coastal northward alongshore flow on the central shelf. On the southern and southwestern sides of the SWF shelf in summer, the circulation is mostly southward, although the standard deviation of the flow speed and direction is much larger than during other times.

Estuarine-imposed salinity gradients may add an additional baroclinic effect to the nearshore region of the inner shelf that sometimes causes a southward flow in summer. The western Florida coast is under the influence of a significant number of freshwater inputs (Figure 1). They drain freshwater from precipitation (direct or delayed, local or regional) from rivers, streams, lakes, and canals into the near shore, majorly contributing to the estuarine properties of SWF shelf coastal waters. Lee et al. (2002) observed salinity patterns associated with the Shark River Slough low-salinity plume in June 1998. The plume was elongated toward the southeast with little spreading offshore, suggesting advection by a background current. The general movement of the plume was to the southeast through western Florida Bay and middle Florida Keys passages. Extreme discharges or large nutrient inputs have been associated with harmful algal blooms (Zhao et al. 2013) and "black water" events (Hu et al. 2004; Zhao et al. 2013). Zhao et al.

(2013) showed that freshwater coastal plumes tend to move south along the southwestern Florida coast and slowly disperse to the southwest, as well as approaching and moving through the Florida Keys. The complete clearing of low-salinity water from the inner shelf following heavy rainfall events can take several months (Hu et al. 2004; Zhao et al. 2013).

The west Florida shelf (WFS) displays a strong coherent response to synoptic-scale alongshore wind forcing (Li and Weisberg 1999a, 1999b; Weisberg et al. 2000, 2005) that is also observed on the inner SWF shelf (Lee et al. 2002). According to Lee and Smith (2002), synoptic-scale upwelling (downwelling) alongshore winds, together with the coastal constraint, results in barotropic alongshore currents over the shelf aligned with the wind direction at the surface and balanced by set-up (set-down) of the coastal sea level. Using multiyear remotely sensed and sea-level wind measurements, Liu and Weisberg (2012) showed that during the boreal fall, winter, and spring seasons (from October through April), the wind tends to be northeasterly and upwelling favorable. During boreal summer (June through August), the winds tend to be southerly and southeasterly. Monthly mean winds are stronger in winter than in summer on the WFS, including the SWF shelf.

The circulation of the southern portion of the SWF shelf is complex. This area experiences mixed semidiurnal–diurnal tides, whereas tides in the Florida Keys zone are primarily semidiurnal (Wang et al. 1994; Smith 1997, 2000; Wang 1998). Smith (2000) measured the flow exchange between Florida Bay and the SWF shelf and found that the northern two-thirds of the western boundary of the bay is likely a region of inflow, whereas the southern third emerged as a region of weak outflow. According to Smith (2000), westward flow from the southern bay is a logical consequence of the north–south decrease in tidal amplitudes (Smith 1997) and the clockwise rotation of tidal ellipses. The magnitude of flow across the open western boundary related to the oscillatory ebb and flood of the tide can be substantial, even if there is no net volume transport. Moreover, in addition to the tide, larger-scale wind set-up on the inner shelf is likely to drive the net coastal circulation (Wang et al. 1994; Liu and Weisberg 2007).

The southernmost part of the Florida shelf has unique geographic and oceanographic characteristics that present special challenges and opportunities to organisms seeking transport using currents. The presence of the pink shrimp stock and fishery on the SWF shelf provides an especially interesting opportunity to explore the larval behavior and oceanographic and meteorological processes enabling larval migration from spawning to nursery grounds in this complex setting. In the present study, a three dimensional high-resolution, region-wide hydrodynamic model forced by tides and air–ocean fluxes is coupled to a biophysical model that simulates the ontogenetic larval behaviors observed for this species to determine the pink shrimp larval migration pathways from their spawning grounds to their nursery grounds and to explore spatial, seasonal, and interannual contrasts.
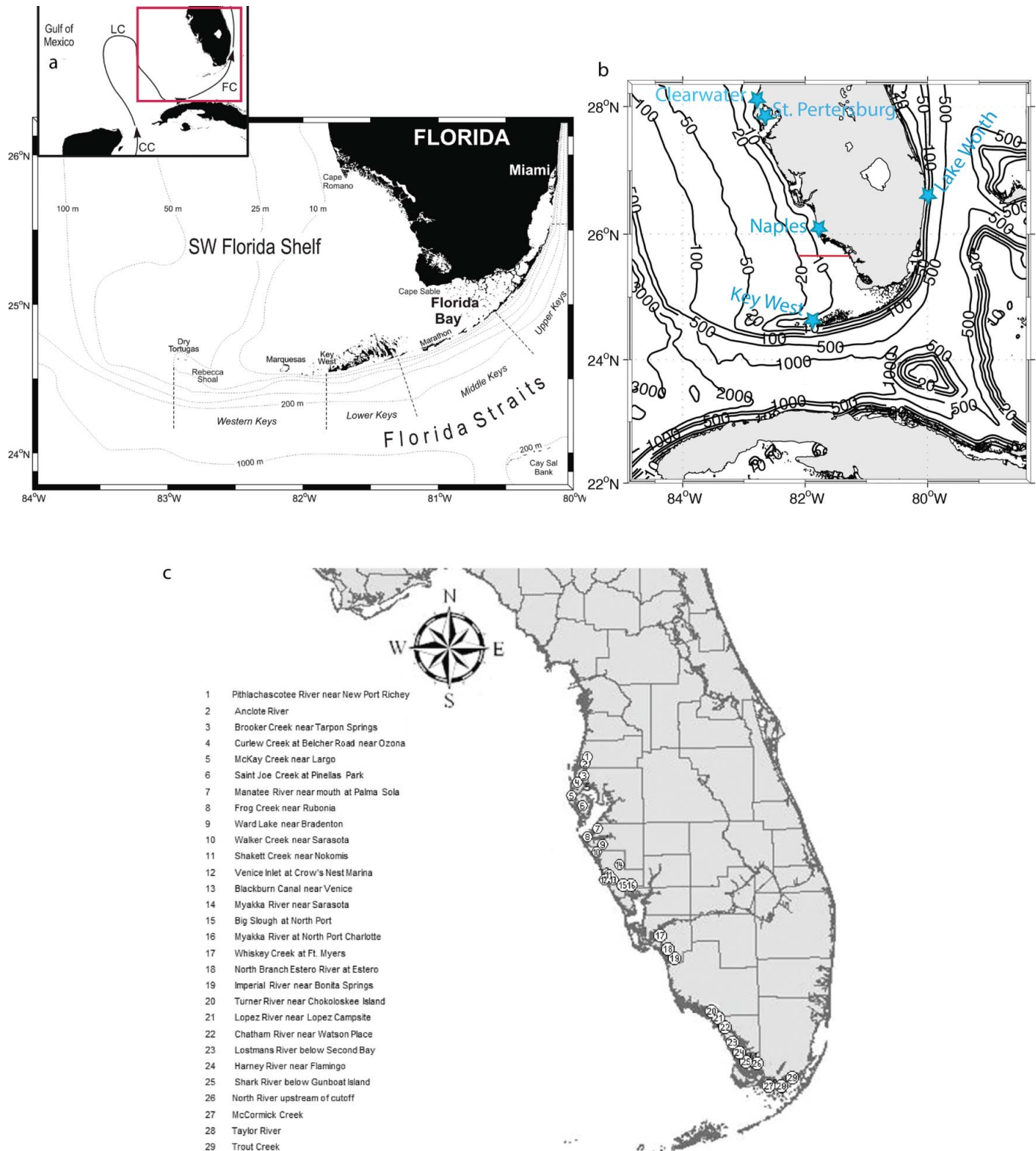
FIGURE 1. Map of **(a)** the southwest Florida shelf study area. The red box on the small map indicates the domain of the Regional Oceanic Modeling System (ROMS) model. Abbreviations are as follows: CC = Caribbean Current, LC = Loop Current, FC = Florida Current, and GS = Gulf Stream. Map showing **(b)** model domain and bathymetry on which blue stars show the location of tidal gauges used for model verification. The horizontal red line at 25.7°N indicates the section used to calculate cross-shore salinity gradient. Map of **(c)** the watersheds and rivers on Florida's west coast that were included in the model. Open circles with numbers denote U.S Geological Survey hydrologic stations, providing flow, temperature, and salinity data.

METHODS

Hydrodynamic model description.—The three-dimensional Regional Oceanic Modeling System (ROMS; Shchepetkin and McWilliams 2005) was implemented to simulate the circulation that connects the lower Florida shelf with larger-scale flows of the Gulf of Mexico and the western subtropical North Atlantic, while incorporating detailed coastal dynamics around Florida Bay and the SWF shelf and freshwater discharge from west coast Florida point sources. The model domain is centered on Florida Bay (Figure 1a), encompasses the eastern side of the Loop Current area and the Florida Straits all the way to Cuba to the South and the Great Bahamas Banks to the East (22.000–28.405°N; 84.900–78.317°W; Figure 1b). The horizontal resolution is 2.862 km, the minimum depth is 3 m, and the model depth is discretized over 25 terrain-following *s*-layers. The model was started on January 3, 1994, and run until 2001. The model ocean state variables were relaxed weekly to the high-resolution (1/12°) TOPAZ reanalysis of the North Atlantic for the period 1979 to present (Sakov et al. 2012). Tides were set at the model's boundaries by the TPXO6 global tide model (Egbert and Erofeeva, 2002). Six tidal components, M2 (principal lunar, semi diurnal), S2 (principal solar, semidiurnal), N2 (larger lunar elliptic, semidiurnal), K2 (lunisolar, semidiurnal), K1 (lunisolar, diurnal), and O1 (principal lunar diurnal), were included. The model surface was forced by 3-hourly wind, air temperature, relative humidity, evaporation, and precipitation rates obtained from North American Regional Reanalysis. Wind stress was calculated by the model's air–sea fluxes bulk formulation. Four-hourly net surface shortwave and longwave heat fluxes, as well as the net shortwave radiation, were obtained from the National Center for Environmental Predictions–National Center for Atmospheric Research reanalysis. The model sea surface temperature (SST) and salinity (SSS) were relaxed daily to, respectively, the coarser 4-km-resolution night SST from the National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer Pathfinder SST version 5 and to monthly SSS from the National Center for Environmental Predictions Global Ocean Data Assimilation System.

Rivers were simulated as point sources in the model. Monthly river discharge, temperature, and salinity were calculated from in situ time series for each river listed in Figure 1c. Because of the model's resolution, some rivers were joined together and their respective discharge summed. River data were obtained from the U.S. Geological Survey. Not all rivers had a complete record of input data. The gap was filled by calculating a monthly climatology from the existing records. The model was spun-up for one year (1994) and the frequency of model output was based on the release experiments, which took place in boreal winter (January–March) and in boreal summer (June–September). During the release periods, the output frequency was every 3 h in order to resolve semidiurnal tides, whereas every 8 h the rest of the year. The winter and summer 3-hourly inputs necessary to the larval transport study were produced for only the years 1995–1997.

The connectivity modeling system.—We used the connectivity modeling system (CMS; version 1.0; Paris et al. 2013) to investigate larval migration and the behavior of pink shrimp in south Florida. The CMS is an open access biophysical modeling system developed in a stochastic Lagrangian framework. The CMS consists of a spatially explicit individual-based model composed of different modules that are coupled. Each of these modules can be turned on or off within the configuration files. A Lagrangian stochastic model integrates, along each individual particle path, information derived from the other modules and tracks the trajectories of individual larval attributes (Grimm et al. 2006). In the Lagrangian stochastic model, larvae are moved at each time step ($dt = 7,200$ s in our application) by a fourth-order Runge-Kutta integration of the ordinary differential equation $d\mathbf{X} = \mathbf{u} \cdot dt$, where $d\mathbf{X}$ is the displacement vector and $\mathbf{u}$ the velocity vector (Griffa 1996), that is applied in both time and space (Paris et al. 2013). The latter is based on a time series of three-dimensional velocity fields from the oceanographic module. In addition to advection by ROMS velocities and stochastic diffusion ($K_h = 20$ m^2/s^2), larvae are moved vertically following the ontogenetic vertical migrations prescribed in the biological module and are settled in suitable settlement habitat based on information derived from the seascape module, provided that they arrive when it is their ontogenetically ordained time to settle (also prescribed by the biological module). The CMS allows us to track the source and destination of each larva. The CMS previously was used to investigate the interaction between the life history characteristics and oceanography of coral reef fishes and the spiny lobster in the Gulf of Mexico and the Caribbean Sea (Paris et al. 2005, 2007; Cowen et al. 2006; Butler et al. 2011; Sponaugle et al. 2012; Kough et al. 2013; Holstein et al. 2014). More details on the coupled biophysical algorithms and modeling approach can be found in Paris et al. (2013) (http://code.google.com/p/connectivity-modeling-system/).

The biological module.—The biological module of the CMS accounted for pink shrimp early life history traits, specifically, pelagic larval duration and larval behaviors (ontogenetic vertical migrations consisting of DVM and STST behavior). Other important biological variables such as egg production, larval growth, and larval mortality were excluded from the model in order to isolate the effect of circulation and larval behavior on the spatial trajectories. The pelagic larval duration in the model was set at 30 d based on laboratory studies of the species (Dobkin 1961; Ewald 1965). The five nauplius, three protozoea, and three mysis stages were completed in 15 d, and additional planktonic postlarval stages were completed in another 15 d.

The larval behavior of pink shrimp was parameterized in the model using results derived from repetitive vertically stratified plankton surveys conducted by Jones et al. (1970) and Criales et al. (2007). Larval vertical distribution patterns observed from plankton surveys were used to create the vertical matrix (z, Δt), in which the probability density distributions

in the water column (z) were calculated through time intervals (Δt) for each larval developmental stage (Table 1). Larval stage durations were assigned according to the studies of Dobkin (1961) and Ewald (1965). As Table 1 indicates, pink shrimp larvae perform vertical migrations and the specific behavior changes ontogenetically; protozoeae were found deeper than myses and myses deeper than postlarvae. The relative concentrations of protozoeae in the upper, middle, and bottom layers were consistent with a DVM behavior, whereas that of late myses and postlarvae were consistent with a STST behavior in phase with the flood tide (Criales et al. 2007). The probability vertical matrix was set up for 12-h periods to simulate the DVM behavior. The STST behavior was reproduced in the model by creating a module in which particles move with the current when the sea surface height rises (during flood tide) and stop moving when the sea surface height falls (during ebb tide). The STST behavior was added into the model at day 15, which corresponds to the time reported in the literature (Rothlisberg et al. 1995; Criales et al. 2006).

The benthic habitat module.—The benthic habitat module accounted for pink shrimp spawning ground aggregations and habitats suitable for settlement. The two selected spawning locations were Dry Tortugas and Marquesas. The Dry Tortugas site has been considered the main spawning ground of this species (Roberts 1986) and is located on the outer SWF shelf about 40 km northeast of the Dry Tortugas Islands at a depth of 35 m. The Marquesas site was selected based on the high percentages of early protozoeae collected during the summer months by Jones et al. (1970) and by Criales et al. (2007). The Marquesas site is located about 30 km north of the Marquesas Islands at a depth of 25 m.

The suitable habitats for settlement were represented as polygons of settlement created in ArcMap and coupled to the CMS benthic habitat module as (X, Y, Z), where X and Y were the coordinates of the vertices and Z the polygon number. Thirty-one 10-km × 10-km square polygons were created covering the Florida Bay area and adjacent coastal shelf. A variety of distinct bottom habitats are contained within the area covered by the polygons, including submerged aquatic vegetation (mainly seagrass beds of turtle grass *Thalassia testudinium*, manatee grass *Syringodiun filiforme*, and shoal grass *Halodule wrightii*) and different types of unvegetated bottom (mainly soft and muddy bottom) (Zieman et al. 1989). Pink shrimp postlarvae usually settle in areas covered with dense mixed species of seagrasses (Costello and Allen 1966), therefore the presence of seagrasses may be another factor determining settlement. One major simplification in the settlement module was that particles within the polygon boundaries were considered successful regardless of the type of bottom habitat.

Simulations and analysis of model output.—Ten virtual larvae were released in the surface layer of ROMS daily for 28–31 d, starting at day 1 of each month at midnight, from the two selected spawning sites (Dry Tortugas and Marquesas). Moon phase and stage of the tide were not taken into account at the moment of releasing larvae. Between 280 and 310 virtual larvae were released from each spawning site every month. Virtual larvae were tracked until they settled in the coastal nursery habitats represented by the polygons. Larvae were recorded as "settled" if they arrived within any of the habitat polygons. For each simulation, the CMS model generates two types of files. One output file provides information on the distance traveled, geographic position, and status of each particle. The other file is the connectivity matrix, in which each cell contains the number of larvae from each spawning site settling in each polygon. The monthly percentage of settlement was calculated by dividing the output number of larvae settled at the polygons by the total number of larvae released from each spawning site (i.e., Dry Tortugas and Marquesas).

Simulations conducted during the month of July 1996 were used to explore the contribution of a passive versus active (DVM and the STST behavior) drift on larval dispersal between offshore spawning and onshore nursery grounds. We analyzed three behavior scenarios: (1) passive dispersion or particles purely advected by the current for 30 d, (2) particles drifting with a DVM behavior for 30 d, and (3) particles drifting with a DVM behavior for 30 d plus an additional STST behavior starting at day 15. Another set of simulations was conducted during the summer months of June, July, August, and September 1995–1997 and the winter months of January, February, and March 1995–1997 to determine the effect of seasonality on dispersal and settlement. Simulations were conducted with behavior scenario 3. A two-way ANOVA was carried out on the percentages of settlement to determine the effect of the release location (Dry Tortugas and Marquesas) and the season (summer and winter) on transport and settlement. The percentages were arcsine transformed to resolve the nonnormal distribution of percentages (Zar 2010).

The probabilities of settlement from each spawning location (Dry Tortugas and Marquesas) were examined together with the Lagrangian trajectories to determine the main migration routes that larvae utilize to reach the settlement polygons. Data were separated by season (summer

TABLE 1. Matrix table of the distribution of pink shrimp larvae in the water column used in the biological module of the CMS model, showing the density probabilities (%) of occurrence of the larval stages at each depth and the duration of larval stages (time). The data is from Criales et al. (2007) and is based on vertically stratified plankton sampling.

	Planktonic stages		
Time and depth	Nauplii–protozoea	Mysis	Postlarvae
Time (d)	7	7	15
Depth (m)			
5	0	0	50
15	25	54	25
30	35	26	20
45	40	20	5

versus winter) and by two main migration routes: (1) larvae that arrive at the settlement polygons moving east–northeast across the SWF shelf and (2) larvae that arrive at the polygons moving south–southeast via the Florida Current and Florida Keys inlets and entering through Rebecca Shoal, Marquesas, Key West, and tidal channels of the Upper, Middle, or Lower Florida Keys.

Evaluation of the hydrodynamic model—The hydrodynamic model was evaluated primarily by comparing its representation of the tide to actual observations. The first approach was a statistical comparison of amplitude and periodicity in modeled time series to actual time series of tidal stages at several locations on the Florida coast and in the Florida Keys (Figure 1b). Statistical parameters were the linear correlation coefficient (R), its normalized standard deviation (σ; which indicates agreement in the amplitude of the signal), and the root-mean-square difference (RMSD) between the modeled and corresponding in situ values. The second approach was a graphical comparison of monthly mean modeled flow at seven observation sites on the SWF shelf to observed flow from acoustic Doppler current profiler (ADCP) data at those sites. The third approach was to compare model output fields to the general features of the seasonal circulation pattern and associated patterns of SST observed by Liu and Weisberg (2012). Equations for the statistical parameters are as follows:

For the correlation coefficient, R:

$$R = \frac{\frac{1}{N}\sum_{n=1}^{N}(m_n - \overline{m})(r_n - \overline{r})}{\sigma_m \sigma_r},$$

where N is the number of elements, n is the index, m indicates the model field, r is the reference field, the overbar is the average, and σ is the standard deviation. The correlation coefficient is in the range $(-1, +1)$ and, if the two signals are perfectly in phase, $R = 1$.

For the standard deviation, σ:

$$\sigma* = \frac{\sigma_m}{\sigma_r},$$

where $\sigma = 1$ indicates complete agreement in amplitude of the signal.

For RMSD:

$$\text{RMSD} = \left[\frac{1}{N}\sum_{n=1}^{N}(m_n - r_n)^2\right]^{0.5}.$$

Partitioning components of the current.—Modeled current fields were examined for the effect on larval transport of separated driving currents in order to better understand the main forces affecting variation in larval transport pathways and settlement success between seasons and spawning ground. The main forces driving current patterns in the model were wind, tide, and geostrophic, the latter of which arose mainly from density gradients formed by the combination of temperature and salinity. The wind- and tidal-driven current velocity and direction were obtained by first conducting the simulations with and without each of the two and then subtracting both forced and unforced fields from each other. To understand the effect of the background flow, which only includes the geostrophic and wind-driven current, we calculated what we called the subtidal flow. Because of the critical role of the 12-h DVM period in the shrimp larvae transport, the mean 12-h DVM flow was used to understand its role in the fate of larval transport. Then because of the 15-d time period that characterizes the ontogenetic behavior, the mean, subtidal, wind-driven, tidal, and 12-h DVM flow were averaged biweekly to understand the balance of forces on the fate of larval transport over a 15-d time window. Finally, in order to understand the effect of the wind on the SWF shelf circulation, we projected the wind vectors on the axis of greatest variance as defined by van Aken et al. (2007) in order to capture the direction of most significant influence on the circulation.

RESULTS

Hydrodynamic Model Evaluation

Tides and tidal flow.—The model tides during periods of simulated larval releases were compared with data of the same period from in situ tidal gauges along the southern Florida coast and in the Florida Keys. In Figure 2, the model mean sea levels are overlaid on the ones observed in Lake Worth, Naples, Clearwater, St. Petersburg, and Key West. Beside the relatively coarse resolution of the coastal model, the site specificities of each tidal location shown here are very well reproduced by the model.

Results in Table 2 indicate that the model tide is in phase with the observed tide at all tide gauge locations shown in Figure 1b (i.e., $R \geq 0.75$ at all times and all locations). In Table 2, $\sigma*$ is on average between 1 and 1.5, which indicates that the model tends to overestimate the tidal amplitude and particularly at locations that are in bays (Naples, St. Petersburg) and near a tidal channel (Key West). The RMSD values (also in Table 2) are higher and the R-values are lower in winter than in summer, which may be explained by the stronger winds in winter that yield significant coastal sea level set-up or set-down (Lee et al. 2002; Liu and Weisberg 2012). Smooth bathymetry and coarse resolution are likely to affect the model solution.

Further model flow evaluation on the shelf and in the vicinity of the spawning grounds is presented in Figure 3. The biweekly mean current halfway through the incoming tide, as it is in the tidal phase ridden by pink shrimp larvae during the
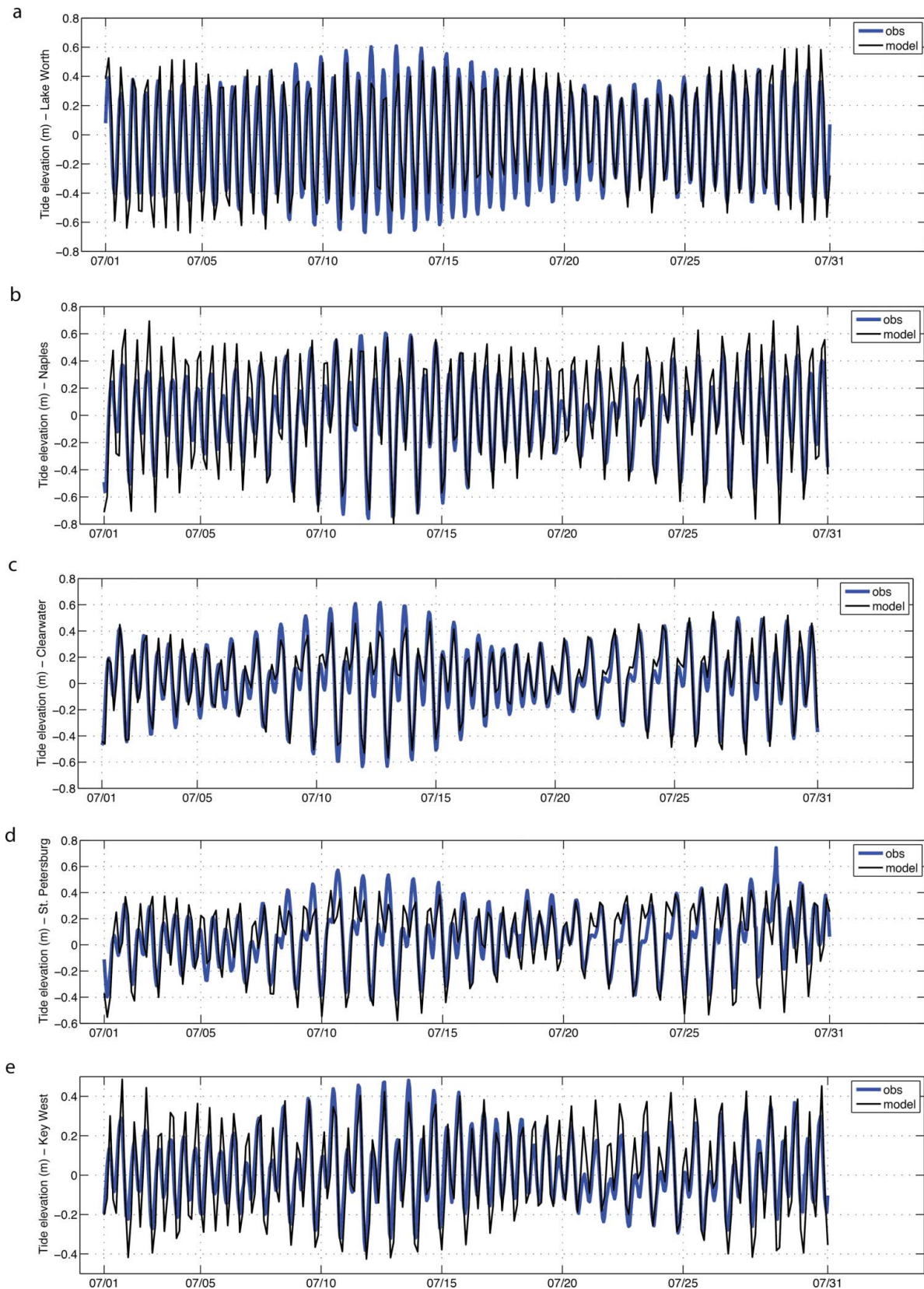
FIGURE 2. Time series of mean sea level in model month July 1995 at the following sites in Florida: **(a)** Lake Worth, **(b)** Naples, **(c)** Clearwater, **(d)** St. Petersburg, and **(e)** Key West. The thick blue line shows the tidal gauge measurements and the thin black line shows the model's water level; obs = observed.

TABLE 2. Pattern statistics of model sea-surface height during months of Lagrangian experiments at tidal gauge locations in Florida. Gauge data were obtained from http://tidesandcurrents.noaa.gov. Abbreviations are as follows: R is the linear correlation coefficient, σ^* the standard deviation ratio, RMSD the root-mean-square difference, S the summer months, and W the winter months.

Statistics	Lake Worth		Naples		Clearwater		St. Petersburg		Key West	
	S	W	S	W	S	W	S	W	S	W
R	0.83	0.77	0.90	0.83	0.93	0.81	0.81	0.77	0.83	0.74
σ^*	1.12	1.05	1.41	1.51	1.04	1.15	1.24	1.32	1.40	1.50
RSMD	0.19	0.22	0.18	0.23	0.09	0.16	0.15	0.18	0.13	0.16

STST transport, is shown. Both the ADCP measurements (Table 3) and the model are interannually consistent in flow amplitude and direction and have limited monthly variability (Figure 3a, b). The model is in agreement with the flow speed and direction at most locations on the shelf, although discrepancies exist at the mouth of Florida Bay.

Mean flow, SST, and SSS.—In order to verify the model mean flow, we calculated the biweekly mean flow both in winter (Figure 4) and in summer (Figure 5) of 1995 and 1997 without de-tiding the flow before averaging. We chose a biweekly average because the larval behavior is divided into two types of behavior: DVM that operates exclusively during the first 2 weeks of development and STST that starts after the first 2 weeks. Therefore, larvae may not face the same mean flow from one fortnight to another.

The modeled circulation in winter (January 1995 and 1997) is characteristic of an upwelling circulation and temperature pattern (Figure 4). Coastal waters on the inner shelf are cooler than offshore. The mean flow is parallel to the coastline, directed mainly southward and intensified at the edge of cool waters. In the Dry Tortugas and Marquesas region, the mean flow is to the southwest. This state of the model is fairly similar to the finding of Liu and Weisberg (2012).

In summer (July 1995 and 1997), the cross-shelf temperature gradient is reversed, as reflected in modeled mean flow (Figure 5). Warmer waters are found inshore and sustain a downwelling circulation pattern, which appears to be unstable. Indeed, the flow is southward on the inner shelf during the first fortnight of July 1995 and turns northward during the second fortnight. Overall, the monthly mean flow has a consistent downwelling circulation pattern (not shown). The mean flow at the spawning grounds is to the northwest. In July 1997, the downwelling circulation only occurs in the second fortnight of July and is very weak. The biweekly mean flow is very weak to the south in coastal waters and to the southwest at the spawning grounds. Overall, the model downwelling regime agrees well with the observations of Liu and Weisberg (2012). As expected, the circulation is in balance with the wind, whose axis of greatest variance is downwelling favorable in July 1997 (Figure 6).

Summer is the rainy season in southern Florida. There is significant variability between years in the input of freshwater into coastal waters as well as shelf waters, as indicated in our analysis of modeled biweekly salinity (Figure 7). The salinity in coastal waters is about 0.75‰ lower on the SWF shelf in July 1997 than in July 1995. The plume of low-salinity water extends further offshore all along the western Florida coast in 1997. Lee et al. (2002) suggested that the freshwater plume is likely to drift southeast along the coast and southwest as it nears the Florida Keys. This motion would oppose the northward coastal current and yield the weaker downwelling circulation in July 1997, even though wind magnitude and direction are similar to July 1995 (Figure 6).

Passive versus active larval transport.—Larvae deployed at the Marquesas and Dry Tortugas spawning stations in July 1996 as passive particles (behavior scenario 1) moved mainly north-northeast along the SWF shelf (Figure 8a, b). From the Dry Tortugas station, some larvae also moved west and entered the LFC system, while the LFC had no effect on larval dispersal from Marquesas. Larvae deployed at Marquesas and Dry Tortugas with a DVM behavior (scenario 2) showed a similar north-northeast drift to those of passive larvae (Figure 8c, d). However, the northern distance traveled with the DVM was greater than that of the passive larvae, suggesting that the DVM behavior may improve the northward drift. The eastward distance traveled was only a few kilometers per larvae. Larvae deployed at the Marquesas and Dry Tortugas sites with DVM and STST behavior (scenario 3) moved mainly east-northeast (Figure 8e, f). The maximum eastward distance traveled was about 200 km, and ~30% and ~63% of the larvae deployed at the Dry Tortugas and Marquesas sites, respectively, reached the settlement polygons located north of Florida Bay. A small number of larvae deployed at Dry Tortugas were caught up in the LFC system and entered the SWF shelf through the Rebecca Shoal Channel, but none of them entered Florida Bay through the Florida Keys. Trajectories of larvae were similar for both spawning grounds, suggesting that tidal currents may be strong
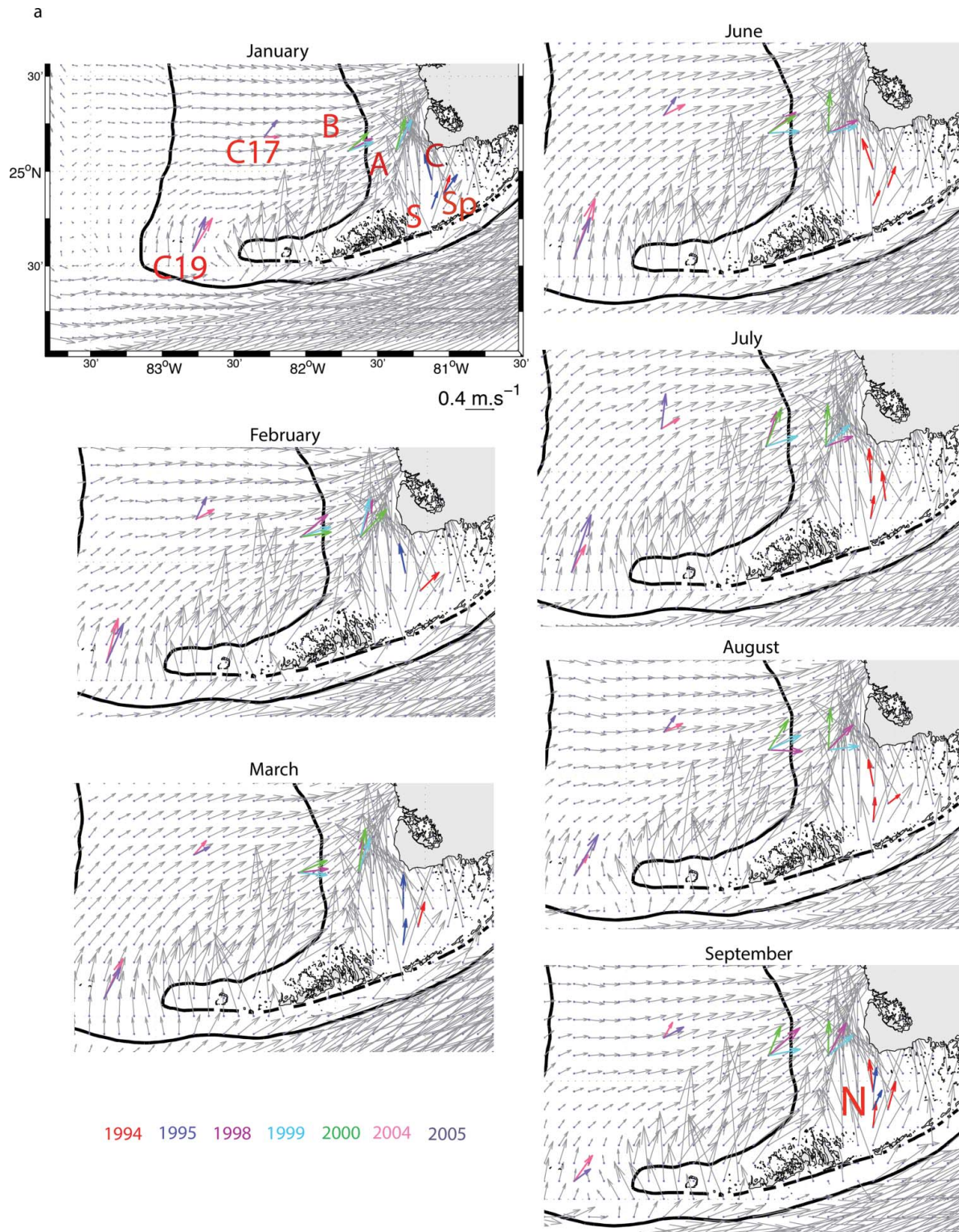
FIGURE 3.   **(a)** In situ current vectors overlaid on model year 1995 current vector maps and **(b)** the model current vectors for 1996 and 1997 at the measurement locations. The vectors shown correspond to the 2-week average of the flow halfway through the incoming tide on the southwest Florida shelf. Each color corresponds to a year. Only months when virtual larvae were released are shown. The names of the moorings listed in Table 3 are shown in red letters on the January and September panels. (*Continued on next page*)
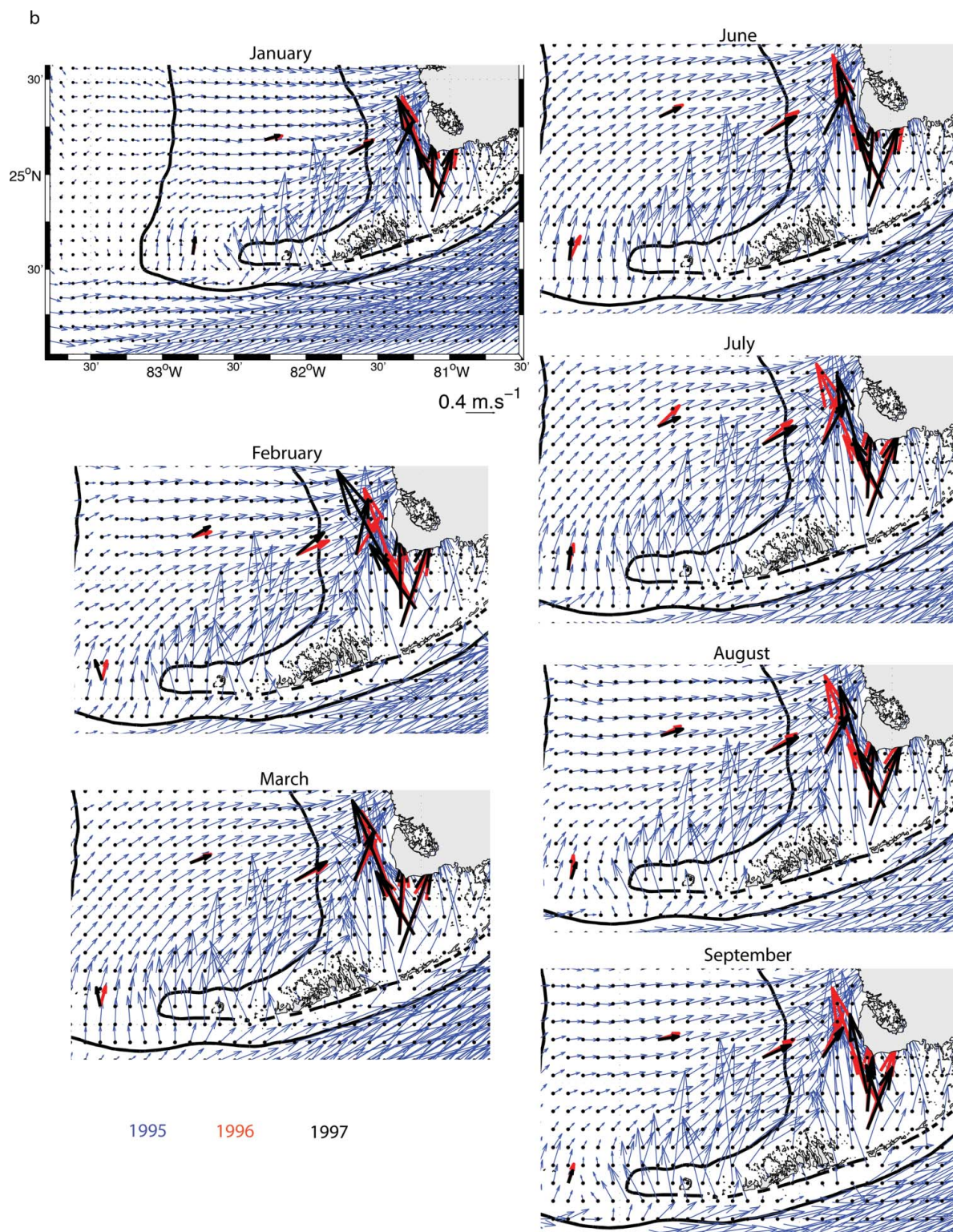
b

FIGURE 3.   Continued.

TABLE 3. Acoustic Doppler current profiler data used for model verification, showing the recorded time period (X indicates data for the whole year). Each location of data collection is shown on Figure 3a. The NOAA South Florida Program (SFP) data are available online at http://www.aoml.noaa.gov/phod/sfp/data/index.php. The Harbor Branch Oceanic Institute (HBOI) Florida Bay (FB) data were made available by N. Smith to the National Oceanographic Data Center (NODC Accession 582, http://www.nodc.noaa.gov/archive/arc0001/0000582/). The University of South Florida (USF) data were kindly made available to us by B. Weisberg and L. Zheng.

Data source	Abbreviation	1994	1995	1997	1998	1999	2000	2004	2005
Model			X	X	X	X	X		
NOAA SFP southeast A	A			Sep–Dec	X	X	X		
NOAA SFP southwest B	B			Sep–Dec	X	X	X		
HBOI Sprigger	Sp	X	Jan						
HBOI FB mouth south	S	X	Jan–Apr	Aug–Nov					
HBOI FB central	C	X	Jan–Apr						
HBOI FB north	N			Aug–Nov					
USF C17	C17							X	X
USF C19	C19							X	X

enough to facilitate STST transport from as far as the Dry Tortugas site.

Variability in Settlement and its Drivers

Variability in settlement.—Simulated settlement data indicated that there is a high interannual and intermonthly variability in settlement at the coastal nursery habitats (Figure 9), as well as substantial differences in the percent arriving from the two spawning grounds. The highest percentage of settlement occurred during 1996 in almost every month, independent of whether the origin of deployment was from the Dry Tortugas or Marquesas site (Figure 9). July 1996 had the highest settlement rate, and July was the consistently highest settlement month each year. An ANOVA conducted on the percentage of settlements indicated that season (summer versus winter) and location of spawning have a significant effect on the success of larvae settling in the coastal habitats; however, the interaction of these two factors did not have a significant effect (two-way ANOVA for location and season: $P < 0.001$; interaction $P = 0.07$). The larvae released at the Marquesas site during the summer months had the highest larval settlement rate, 15.3 ± 3.1 (mean $\pm$ SD), which constitutes ~81% of the total settlement. Larvae released at the Dry Tortugas site during the summer had a settlement rate of 3.4 ± 3.1. Settlement rates during the winter months were about one-fifth the summer rates. The settlement rate of larvae released at Marquesas during the winter months was 2.4 ± 3.7, while that of larvae released at Dry Tortugas during the winter was 0.9 ± 3.7.

Variability in recruitment pathways.—The probabilities of settlement indicated that larvae recruiting to the settlement habitats might arrive from different routes depending on release location, season of the year, and predominant oceanographic conditions (Figures 10, 11). The examples shown in Figure 10 indicate that larvae released at Dry Tortugas and

Marquesas in the summer months of July 1995 and August 1996 tended to remain on the SWF shelf, moving northeast, and a large percentage of larvae reached the settlement habitats. In three of the four illustrated periods, a part of larvae released at Dry Tortugas were pushed southward and later caught within the LFC system. Especially in July 1995, some of these larvae entered the shelf through the Rebecca Shoal Channel and crossed the tidal channels of the Florida Keys to reach settlement habitat. The rest of the larvae were flushed further north with the LFC. The example from August 1996 indicated different oceanographic conditions at the Dry Tortugas–Marquesas region during the first days of deployment, when larvae were migrating with only a DVM behavior. Some larvae remained in the vicinity of the spawning ground for several days, while some drifted north and others south. After that, during the STST period, some larvae moved eastward across the SWF shelf, but the ones who went south were entrained by the LFC flow and a few entered the shelf through the Rebecca Shoal Channel and the tidal channels of the Florida Keys.

The trajectories from winter showed different patterns from those of summer (Figure 10). In the January and March 1997 examples, none of the larvae released at Marquesas reached the settlement habitats by traveling across the SWF shelf. Those released at the Dry Tortugas in January 1997 drifted westward from the spawning grounds during the DVM period and then were flushed into the LFC system, and only one larva entered the nursery ground area, moving through the Middle Florida Keys. In the March 1997 example, the number of larvae moving with the LFC system was larger and the number of settled larvae was increased in comparison to January 1997.

Probability analysis of the settlement rates at each spawning site indicated that settlement rates and recruitment paths change radically between summer and winter (Figure 11). During summer the majority of larvae recruited to the coastal
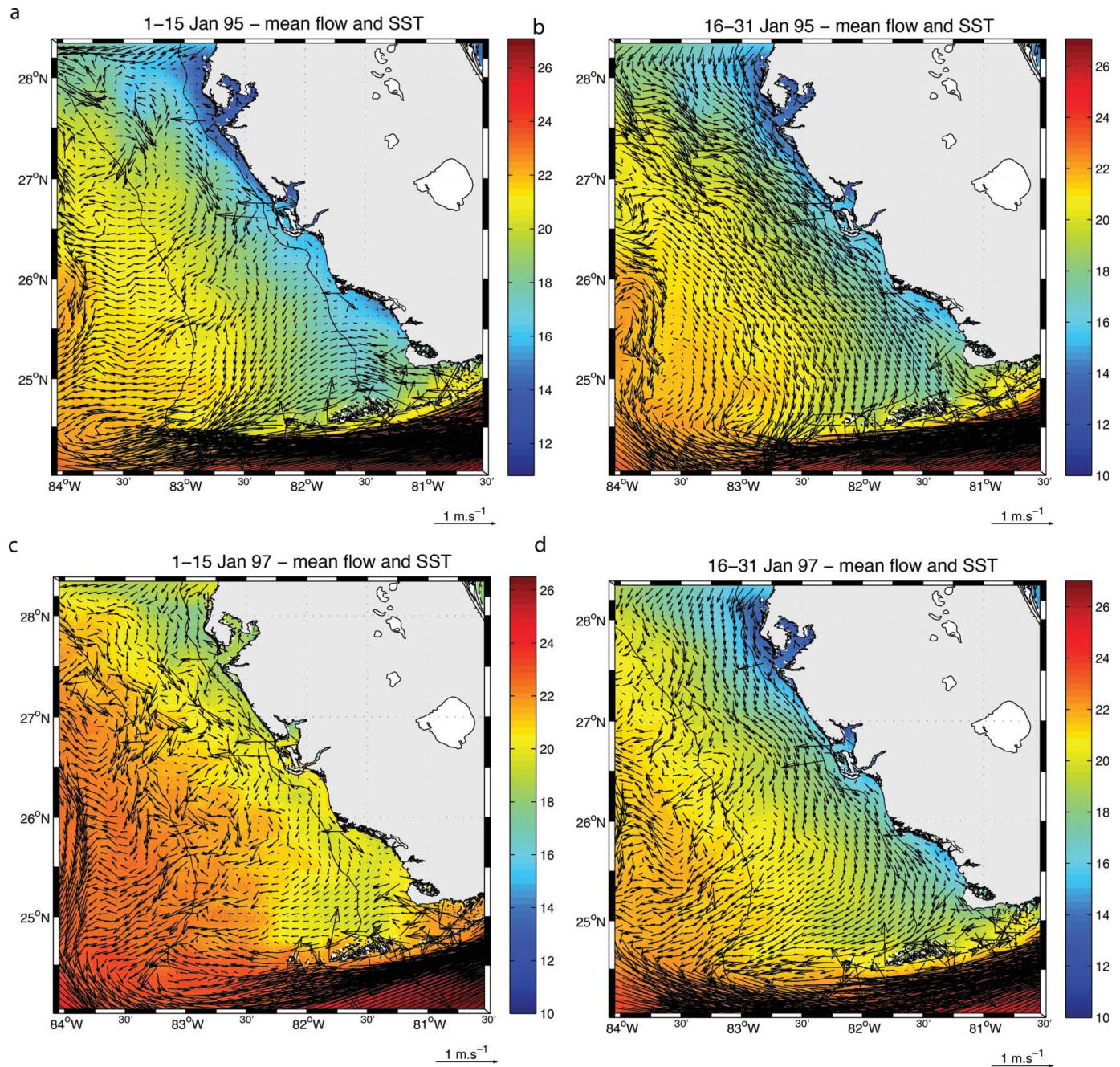
FIGURE 4.   Model sea surface temperature (SST; colored bars in °C) and current vectors during winter 1995 and 1997, showing the **(a)** first and **(b)** second fortnight in January 1995 and the **(c)** first and **(d)** second fortnight in January 1997.

areas moving across the SWF shelf, while recruitment through the Florida Keys was more often in winter months. In summer, about 15% of the larvae originating from Marquesas and 2% of the larvae originating from Dry Tortugas arrived at settlement habitats moving across the shelf, while recruitment through the Florida Keys was 0.1% of larvae originating from Marquesas and 1% of larvae originating from Dry Tortugas. The pattern changed substantially during the winter months. About 1.5% of recruited larvae originating from Dry Tortugas

and 0.9% of larvae originating from Marquesas arrived through the Florida Keys channels during winter months. Recruiting larvae moving across the shelf during winter months made up only 1% of those originating from Marquesas, and there was no recruitment across the shelf from larvae originating from Dry Tortugas during winter months.

Seasonal and interannual variability affecting recruitment.— We previously showed that the seasonal variability on the WFS consists mostly of a current reversal associated with an
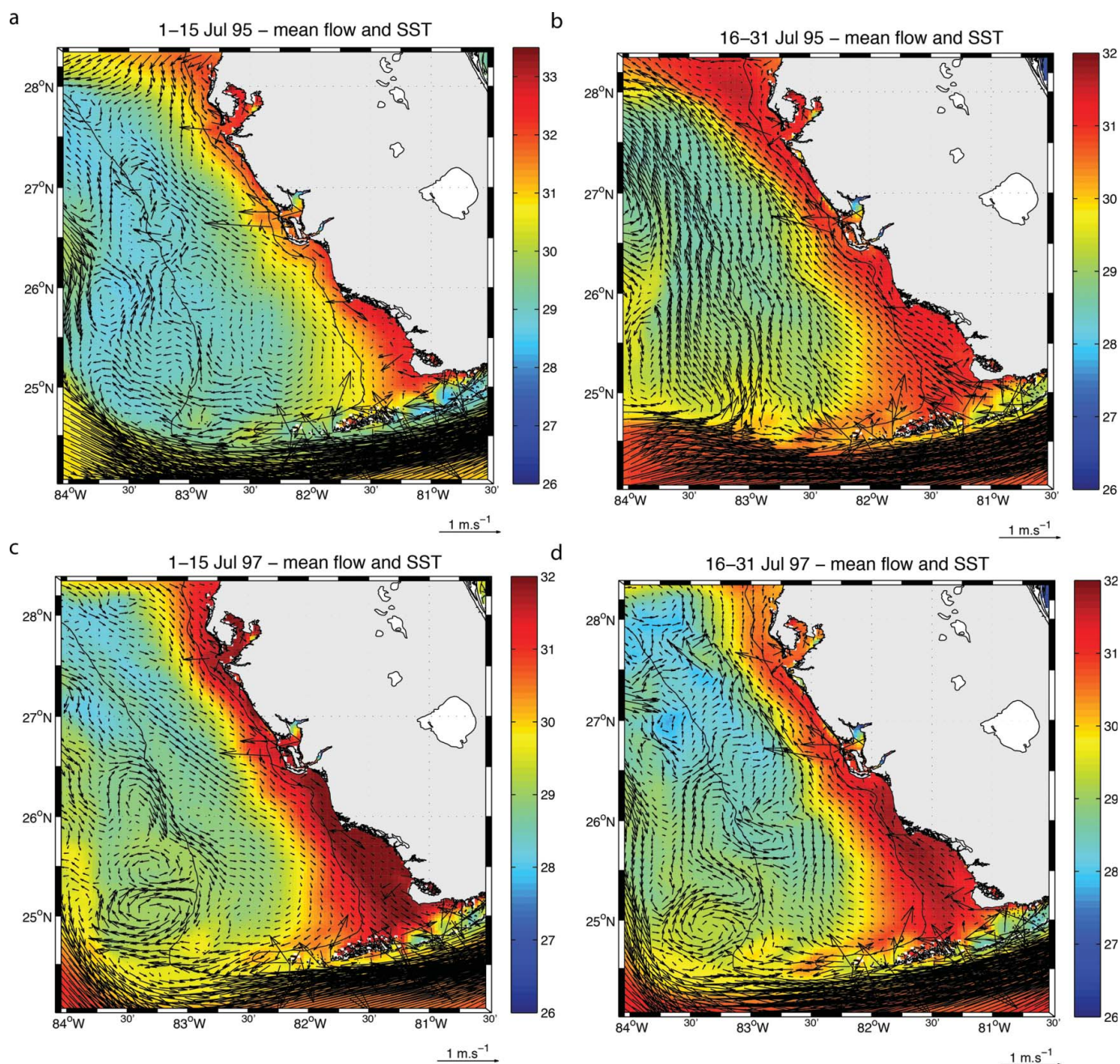
FIGURE 5. Model sea surface temperature (SST; colored bars in °C) and current vectors during summer 1995 and 1997, showing the **(a)** first and **(b)** second fortnight in July 1995 and the **(c)** first and **(d)** second fortnight in July 1997.

upwelling (winter) circulation and a downwelling (summer) circulation. To reach the nursery grounds, larval behavior changes from DVM to STST, and the forces affecting larval transport pathways and recruitment may be different during each of these two behavioral phases.

Diel vertical migration consists of the vertical migration of marine planktonic organisms from deep waters to near surface approximately every 12 h, usually synchronized with the local diurnal cycle occurring at night (e.g., Dall et al. 1990). We,

therefore, examined the potential influence of the direction and magnitude of modeled background flow on the direction and magnitude of the modeled 12-h DVM mean flow and percent of larvae reaching the nursery grounds in the winter and summer months of 1995, 1996, and 1997 (Figure 12). During the winter months of all 3 years, the three flows are toward the same direction (southeast to southwest, i.e., $> 90°$ to $< 270°$), which is away from the coast, resulting in the lowest settlement levels. Transport through Florida Keys channels is the
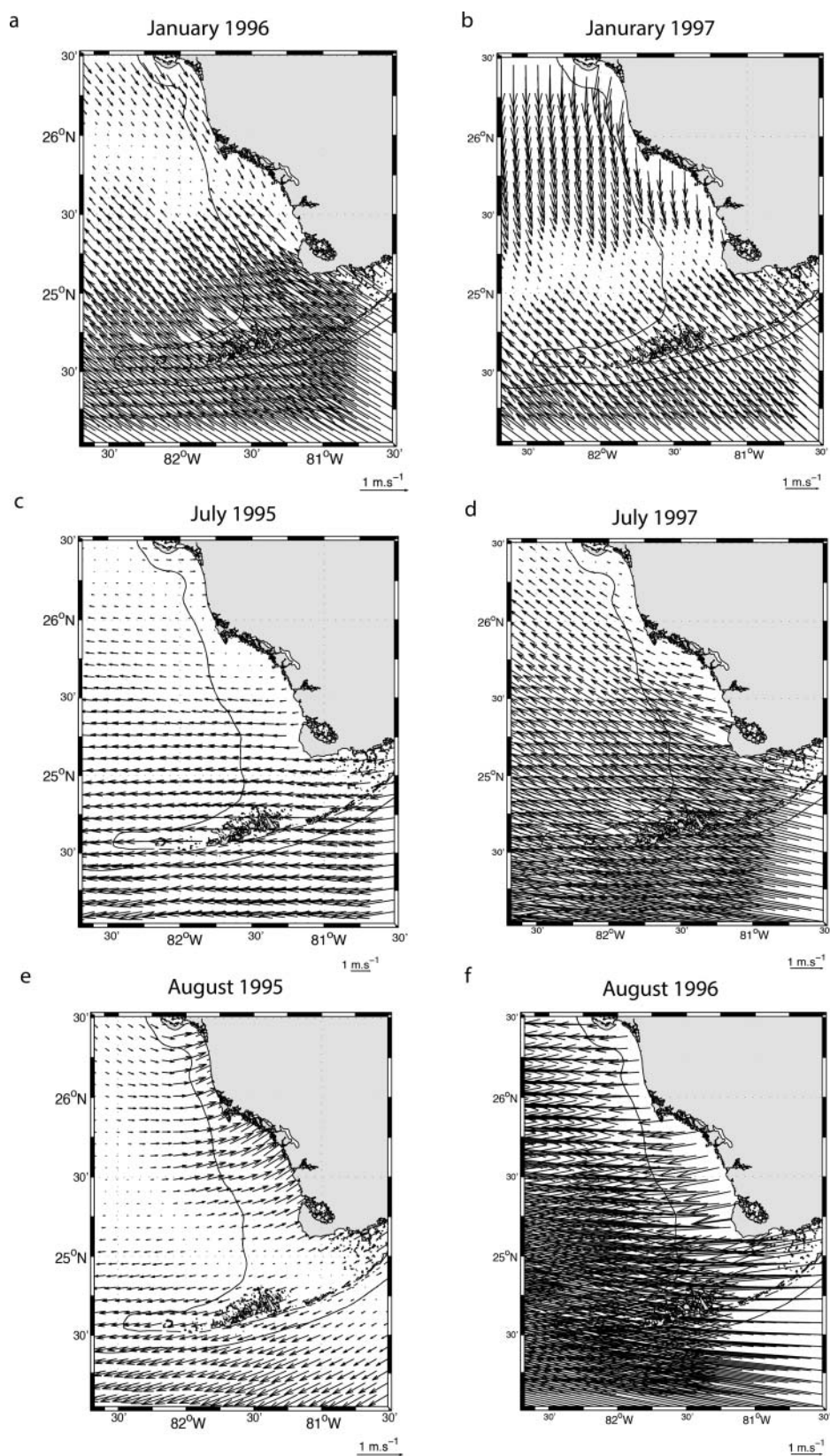
FIGURE 6.   Monthly wind model vectors map along the axis of greater variance for **(a)** January 1996, **(b)** January 1997, **(c)** July 1995, **(d)** July 1997, **(e)** August 1995, and **(f)** August 1996.
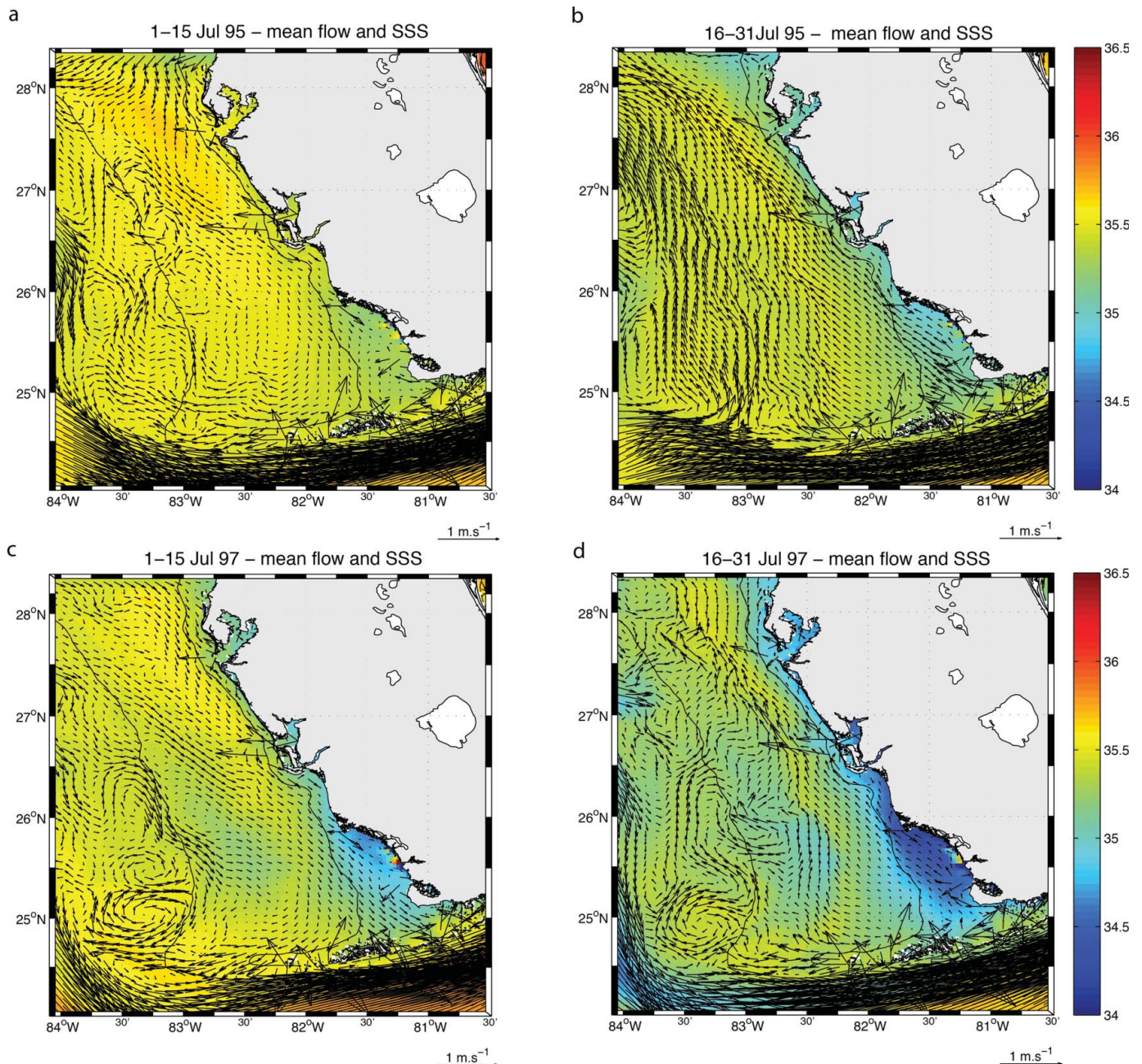
FIGURE 7. Fortnightly model of sea surface salinity (SSS; colored bars in ‰) and current vectors during summer 1995 and 1997, showing the **(a)** first and **(b)** second fortnight in July 1995 and the **(c)** first and **(d)** second fortnight in July 1997.

main pathway for recruiting larvae in the winter months (Figure 11). During the summer months, there is more deviation between the three flows. The highest levels of settlement were obtained in summer months when the 12-h mean DVM flow has an eastward or northward component at both spawning grounds, Dry Tortugas and Marquesas. In June 1996, the 12-h mean DVM flow was to the southwest at Marquesas but to the southeast at Dry Tortugas. The 12-h mean in June 1996 revealed a cyclonic gyre in the vicinity of the spawning

ground, which biased the mean toward the southwest, although particles remained in the vicinity of the spawning location (Figure 13).

Transport during the DVM period will carry larvae a considerable distance from the spawning grounds to their nursery grounds, even when current patterns are not ideal, as in June 1996 (Figure 13a, b). Some of the larvae originating from Dry Tortugas advanced northeast during the DVM period despite the confusion of currents associated with the previously
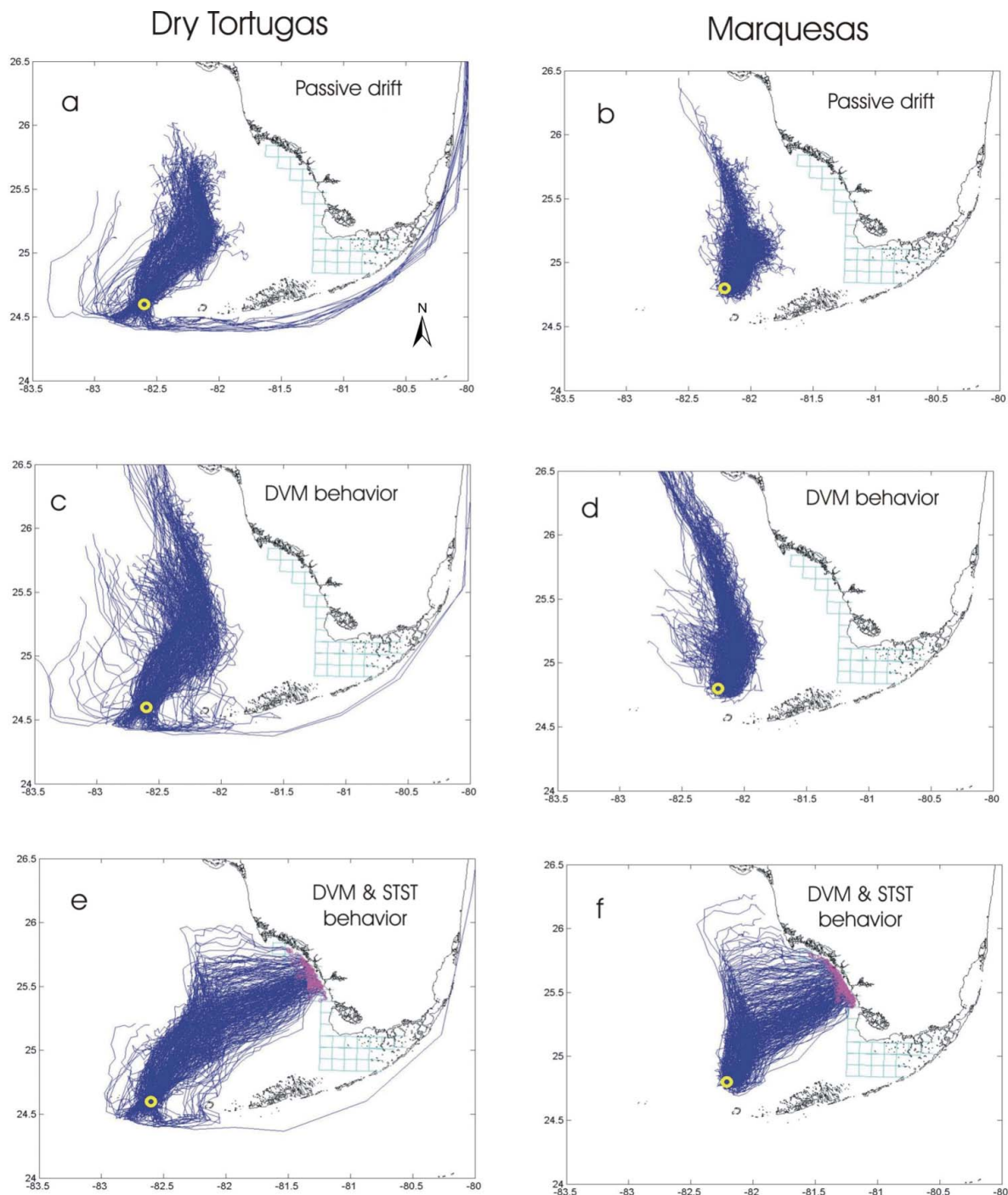
Dry Tortugas

Marquesas

FIGURE 8. Simulated trajectories of pink shrimp larvae under different scenarios of behavior: **(a, b)** passive transport, **(c, d)** active transport with diel vertical migratory (DVM) behavior, and **(e, f)** active transport with DVM and selective tidal stream transport (STST) behavior. Virtual larvae were released daily from July 1–31, 1996, at two spawning locations, Dry Tortugas and Marquesas (yellow circles). Purple dots indicate the larvae that reached the settlement habitats, which are represented by the cyan-colored polygons.

mentioned cyclonic gyre of that period, which is reflected in the fortnightly mean 12-h DVM flow (Figure 13c). The match between trajectories during the DVM period and the 15-day mean of the 12-h mean DVM flow may be inferred by comparing panel c with panels a and b in Figure 13. Nonetheless,

there is a strong seasonal variability in the DVM mean flow, which is mostly westward in winter and northeastward or weak in summer (Figure 12).

Interestingly, the STST movement is always eastward, independent of the time of the year (Figures 3, 13). The tidal
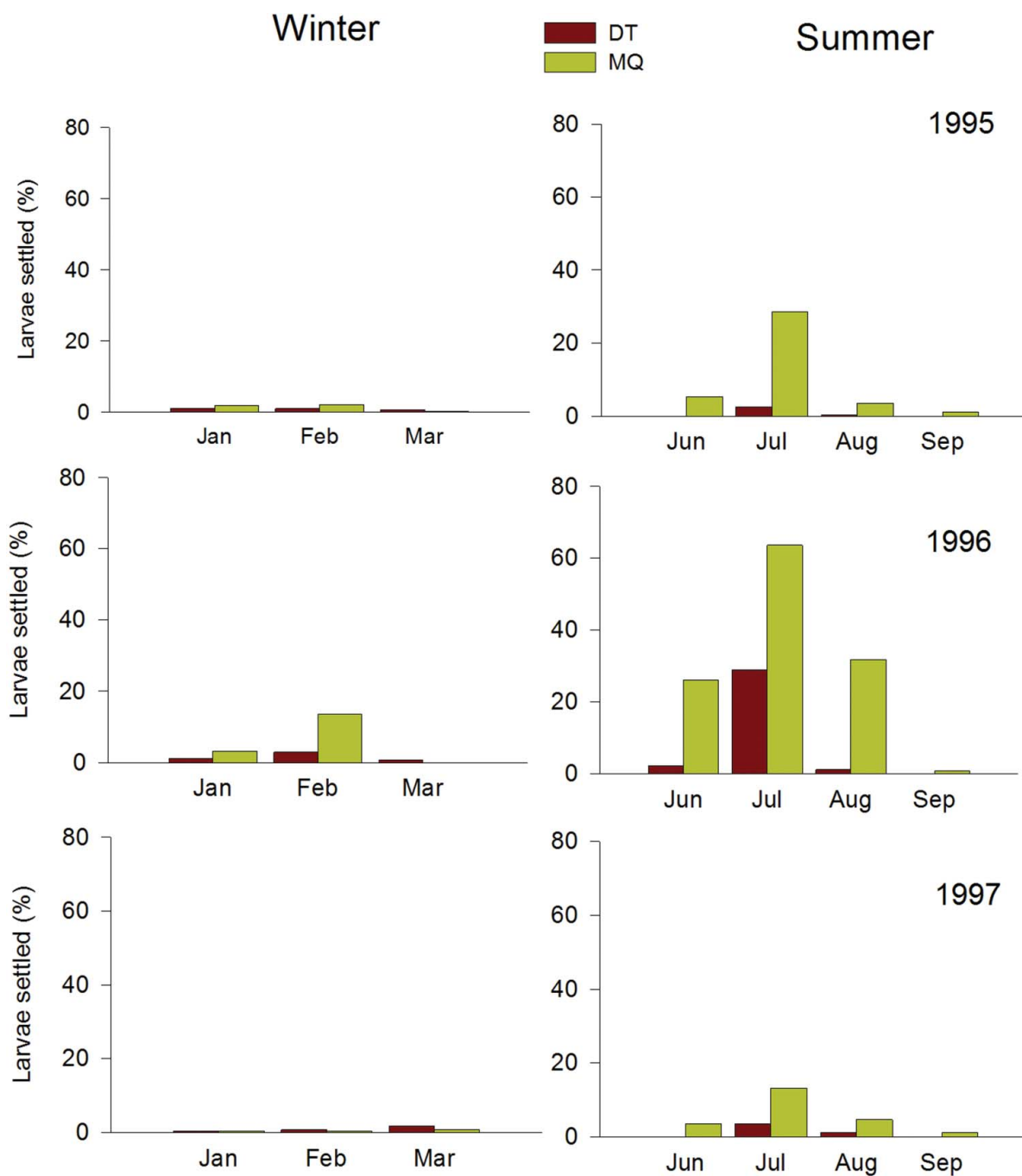
FIGURE 9.   Monthly percentages of simulated pink shrimp larvae released at the Dry Tortugas (DT) and Marquesas (MQ) spawning locations (on the first day of the month at midnight of the indicated date) that settled in the nursery habitat. Virtual larvae were moved with diel vertical migration (DVM) and selective tidal stream transport (STST) behaviors during the summer and winter months of 1995–1997.

incoming flow is always directed toward the coast on the SWF shelf and toward Florida Bay in the channels through the Florida Keys reef tract. Therefore the recruitment variability of larvae transport across the SWF shelf is mostly dependent upon the fate of larvae during the DVM period, which favors successful recruitment in summer. The lack of

consistency among years in the summer DVM mean flow likely drives the interannual variability of summer recruitment levels. If the mean flow during the DVM period is critical for the fate of pink shrimp larvae, it is important to understand the drivers of the DVM flow, which are described in the following sections.
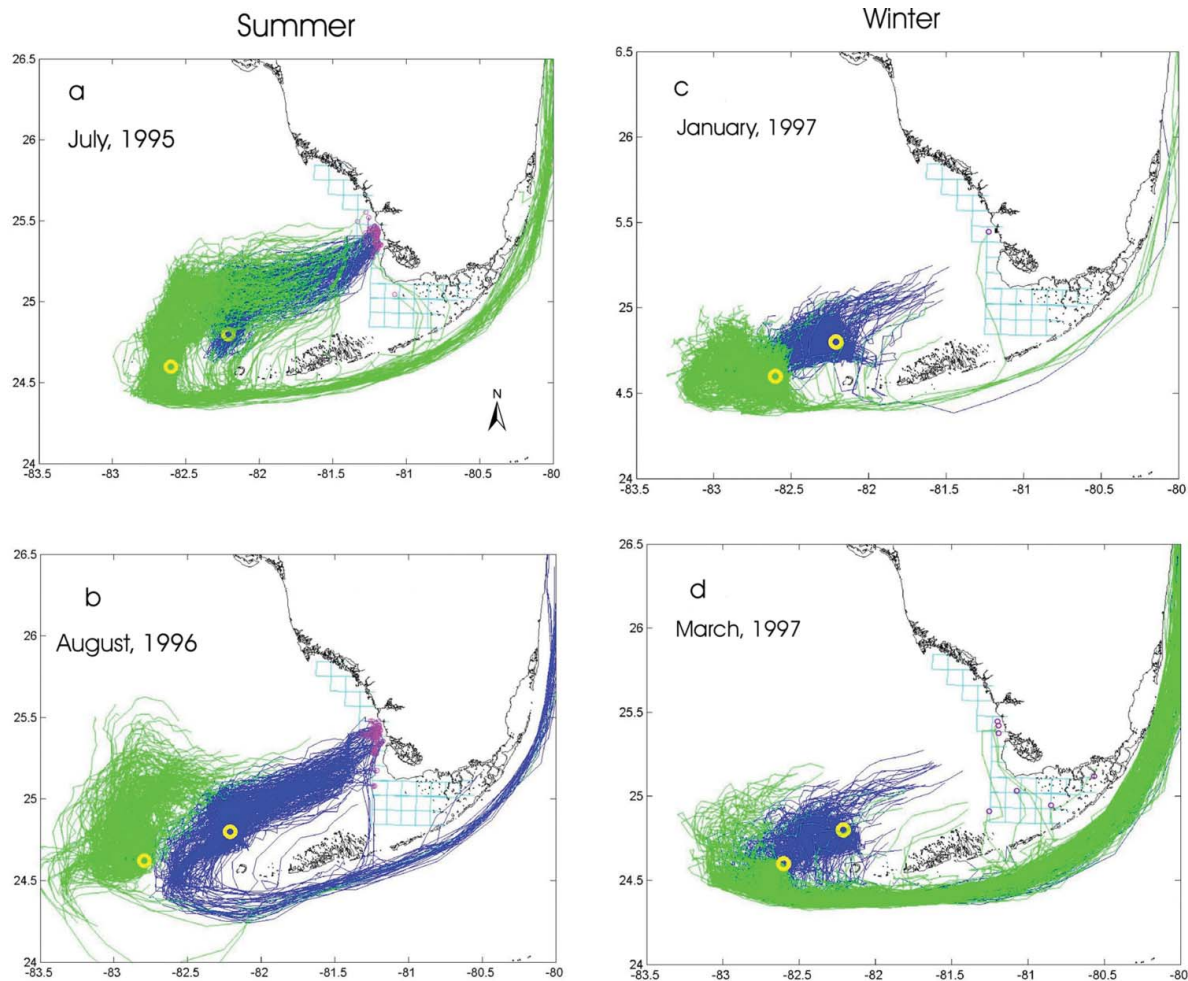
FIGURE 10.   Simulated trajectories of pink shrimp larvae released at the Dry Tortugas and Marquesas spawning sites (yellow circles) and moving with diel vertical migratory behavior and selective tidal stream transport behavior during the summer months of **(a)** July 1995 and **(b)** August 1996 and the winter months of **(c)** January and **(d)** March 1997. The purple dots represent the larvae that settled in the settlement habitats, which are represented by the cyan-colored polygons.

Ekman transport during the DVM window.—As shown by Liu and Weisberg (2012), the WFS exhibits a robust seasonal cycle in velocity, dominantly driven by the wind, but also in temperature and salinity gradients across the shelf. Rather than the arithmetic mean wind direction, we calculated the characteristic mean direction of the wind on the shelf identified by the direction in which the total variance of the velocity component is maximized (van Aken et al. 2007). This direction is the one that has the most influence on the wind-driven circulation. From October to April, the wind is predominantly blowing from the northeast, with a stronger southward component in winter than in fall in the central WFS and a stronger eastward component on the SWF shelf overall. However, year-to-year variability can be significant and wind patterns inconsistent, not only from year to year but spatially within the same timeframe. For example, in January 1996 the monthly wind direction consisted of strong winds from the south-southeast on the SWF shelf and winds from the

northwest on the central WFS (Figure 6a). Similar inconsistencies were also seen in January 1997 (Figure 6b). These wind features could set up opposing circulation cells on the SWF shelf. From June to August, the wind blows from the southeast on the WFS, with a stronger northward component on the central WFS than on the SWF shelf, where it is more west-northwest (Figure 6c, d). Winds during summer are weaker than those of the rest of the year, unless a hurricane is in the vicinity. Again, wind anomalies exist from one year to another and are characterized by opposing wind directions between the central WFS and the SWF shelf, as in August 1995, or by stronger trade winds, as seen on the SWF shelf in August 1996 (Figure 6f).

In order to estimate the wind-driven current on the SWF shelf, we subtracted two simulations that were identical except that one was wind forced. This revealed, for example, that in model month July 1995 the surface flow in the vicinity of the spawning grounds during the 2-week DVM period was
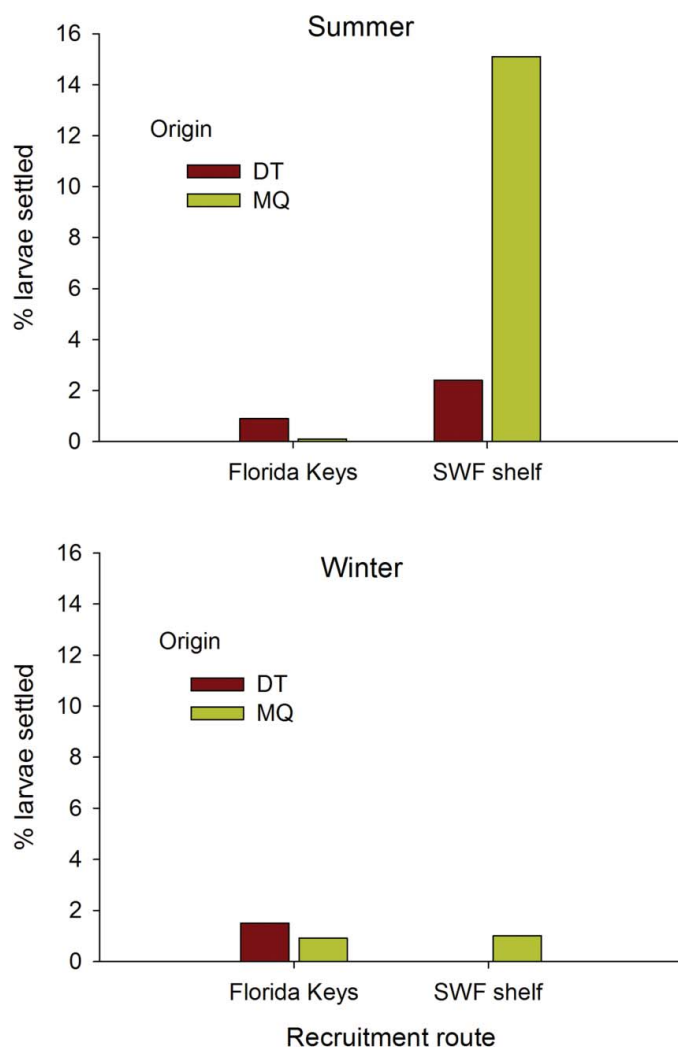
FIGURE 11. Mean percentages of pink shrimp larvae settled within the nursery habitat in summer (upper figure) and winter (lower figure) calculated from the connectivity matrix data based on 3 years of simulations (1995–1997). Larvae originated at the spawning sites of Dry Tortugas (DT) and Marquesas (MQ) and migrated for 30 d with diel vertical migration and selective tidal stream transport behaviors. Settlement percentages were separated into two recruitment routes: larvae that arrived to the settlement habitat moving across the southwest Florida (SWF) shelf and larvae that arrived via the Florida Current across the Florida Keys channels.

westward (i.e., easterlies), the same as the direction of greatest variance in the wind (Figure 14a). This suggests that sustained easterlies are unfavorable to cross-shelf transport.

Tidal-phase-induced variability and DVM mean flow.— Tidal currents are interannually consistent and are always in the same direction at a given stage. An example of tidal-driven flow during the DVM period was obtained for July 1995 by calculating the difference between two simulation fields that are identical except that one was forced by tide (Figure 14b). The fortnightly 12-h DVM tidal current was to the northeast at both spawning grounds when the DVM was initiated at midnight on the first day of release. But the DVM mean flow is

likely to respond to timing in relation to the phase of the tide as shown by the different flow fields obtained for different onsets of the DVM period (Figure 15). Each DVM mean flow shows markedly different circulation patterns over the SWF shelf and, in particular, at the spawning sites. The DVM mean flow can even be in opposite directions, depending on the phase of the tide at the time of the particle's release. This suggests a substantial contribution of the tidal flow to the DVM mean flow.

The sensitivity of the timing of the 12-h mean DVM flow direction to the phase of the tide was tested in order to estimate the optimum release time and tidal cycle that adult shrimp should choose to maximize the eastward flow of their larvae, which would potentially increase their recruitment level. For example, at the Marquesas spawning ground, if the DVM behavior would be started at midnight on July 1, 1995, the mean resultant tidal flow is to the northeast and the incoming flow is synchronized with the nighttime during the 2-week duration of the DVM period (Figure 16a). If the beginning of the 12-h DVM window is shifted forward in time by 6 h, the resultant mean flow is to the southwest (or northwest for a 12-h shift) (Figure 16b, c). Moving the DVM windowing further forward in time, we find that the tidal phase and cycle that leads to the strongest northeastward current is obtained when the 12-h DVM window is started 2 d before the full moon in July 1995. The beginning of the DVM window falls within the incoming tide, which starts at sunset (Figure 16d). The same effect is obtained at the Dry Tortugas spawning ground.

Subtidal flow and coastal salinity influence.—Baroclinicity from freshwater discharge into the nearshore region can locally modify the local advection of riverine water as shown by Lee and Smith (2002), Hu et al. (2004), and Zhao et al. (2013). Although the wind stress was stronger in July 1997 than in July 1995 (Figure 6), the northward flow was much weaker during the second fortnight of July 1997 than in 1995, while the water was fresher at the coast in 1997 than in 1995 (Figure 7b, d). The downwelling-driven northward current can be turned southward by the riverine water in the nearshore region (Lee and Smith, 2002). With increased discharge, the freshwater flow would not only be flushed southward through the Florida Keys channels (Lee and Smith 2002) but also be pushed westward toward the Marquesas and Dry Tortugas sites, as shown by Hu et al. (2004) and Zhao et al. (2013). In order to verify this effect in the model, we calculated the salinity gradient across the SWF shelf and the corresponding monthly subtidal current direction and amplitude for every month of July from 1995 to 2002 (Figure 17). The model shows that large negative salinity gradients, with the lowest salinity inshore and increasing salinity offshore (as in July 1997, 1998, 2001 and 2002), are associated with a southwestward-westward flow at Marquesas and Dry Tortugas, which confirms the westward transport of riverine water north of the Florida Keys. During dry summers, the flow is either
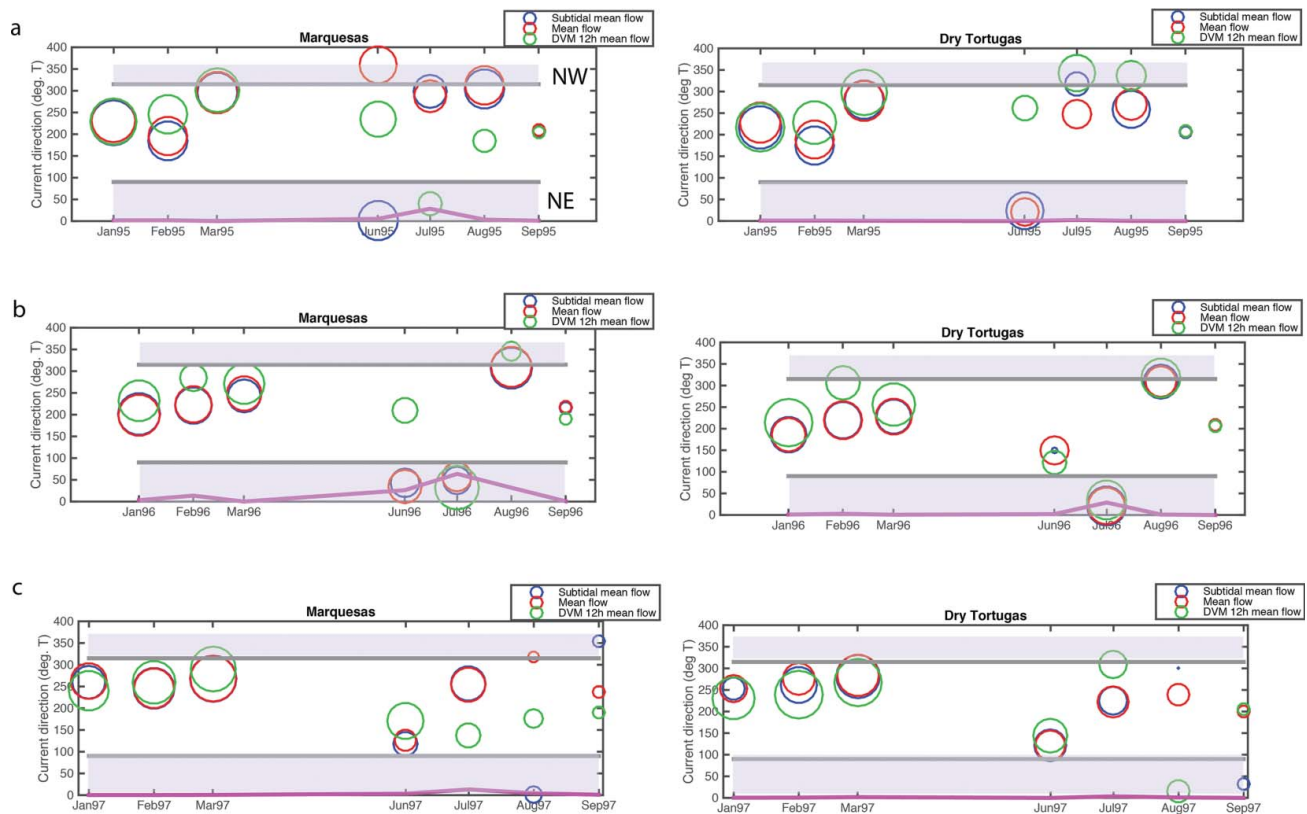
FIGURE 12.   Discrete flow magnitude (circle diameter) and direction (y-axis scale gives compass coordinate, 0° to 360°, of the center of the circle) of the first fort-night subtidal mean flow (blue circles), mean flow (red circles), and 12-h mean diel vertical migration (DVM; green circles) timed with each particle release for **(a)** 1995, **(b)** 1996, and **(c)** 1997 at the Marquesas and Dry Tortugas spawning grounds. The legend circle diameter is equivalent to 5 cm/s. Only the months of pink shrimp transport simulation are shown. Shaded regions indicate a northward component in the flow direction. The thin pink line shows the recruitment percentage on the y-axis, where label 100 on the y-axis corresponds to 100%. Mean flow was calculated in a box around the release location representing the spawning ground.

southward or northward, with an eastward component most of the time. Therefore, independently of the SWF shelf seasonal circulation, the flow at the spawning grounds seems to be under the influence of the freshwater discharge at the coast, which is influenced by both rainfall and water management that controls freshwater inflows to Everglades National Park. Because the influence of tide is removed, the flow direction remains the same if the DVM windowing is applied (i.e., the timing of the 12-h DVM period relative to the tidal phase would not matter), yielding that the subtidal flow during the DVM period would tend to have an eastward component during dry summers.

DISCUSSION

Overall, the ROMS simulations reproduce the dynamics of the WFS as observed by Liu and Weisberg (2012) for both seasons. However, some discrepancies exist in Florida Bay and shallow areas, where the model overestimates velocity magnitudes as shown by Figure 3. Because of resolution-dependent numerical stability constraints, a minimum depth (here 3 m) was set in shallow areas. Therefore, the shallow banks that

slow down the flow at the mouth of Florida Bay are not accounted for in the model, which explains the relatively high velocities of the model in regards to the ones observed, and the water is much deeper in the model throughout the bay. The model accurately simulates the SST and SSS seasonal cycles on the outer and inner shelf. It also roughly simulates the low-salinity patterns as observed by Lee and Smith (2002) in the nearshore region. Salinity values were realistic in a general sense in terms of seasonality, distribution, and magnitude. Values were relatively lower on the inner shelf than off-shelf in the Gulf of Mexico. Salinities are very susceptible to the freshwater input and are highly variable interannually, as shown by the synoptic shipboard survey of NOAA's Atlantic Oceanographic and Meteorological Laboratory South Florida Program (http://www.aoml.noaa.gov/phod/sfp/index.php).

Biophysical simulations indicated that a successful settlement of pink shrimp larvae would require not only the appropriate circulation conditions for transport but also the right combination of DVM and tidal rhythm activity (STST) behavior. Larvae deployed at the Dry Tortugas and Marquesas spawning grounds as passive particles or with only a DVM behavior cannot reach the coastal nursery grounds in 30 d, the
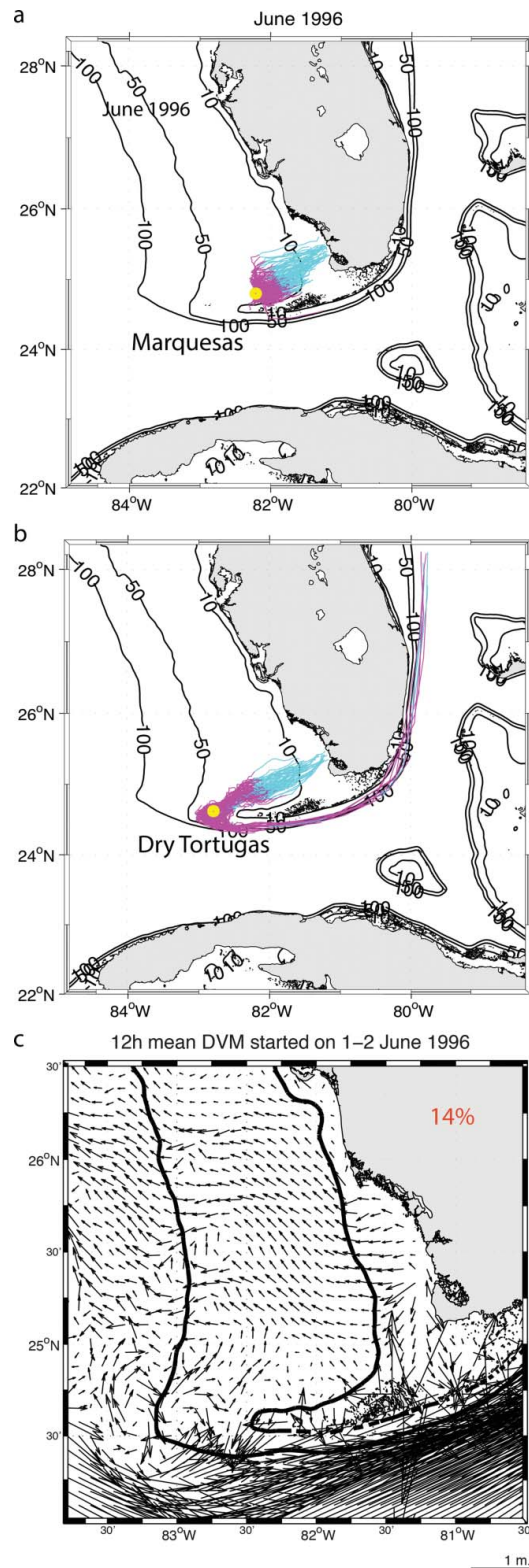
FIGURE 13. Particle trajectories, including diel vertical migration (DVM; magenta) and selective tidal stream transport (cyan), from their release locations in June 1996 at **(a)** Marquesas and **(b)** Dry Tortugas and **(c)** the corresponding 15-d mean of 12-h DVM mean flow started on June 1, 1996. The total recruitment percentage is indicated in red.
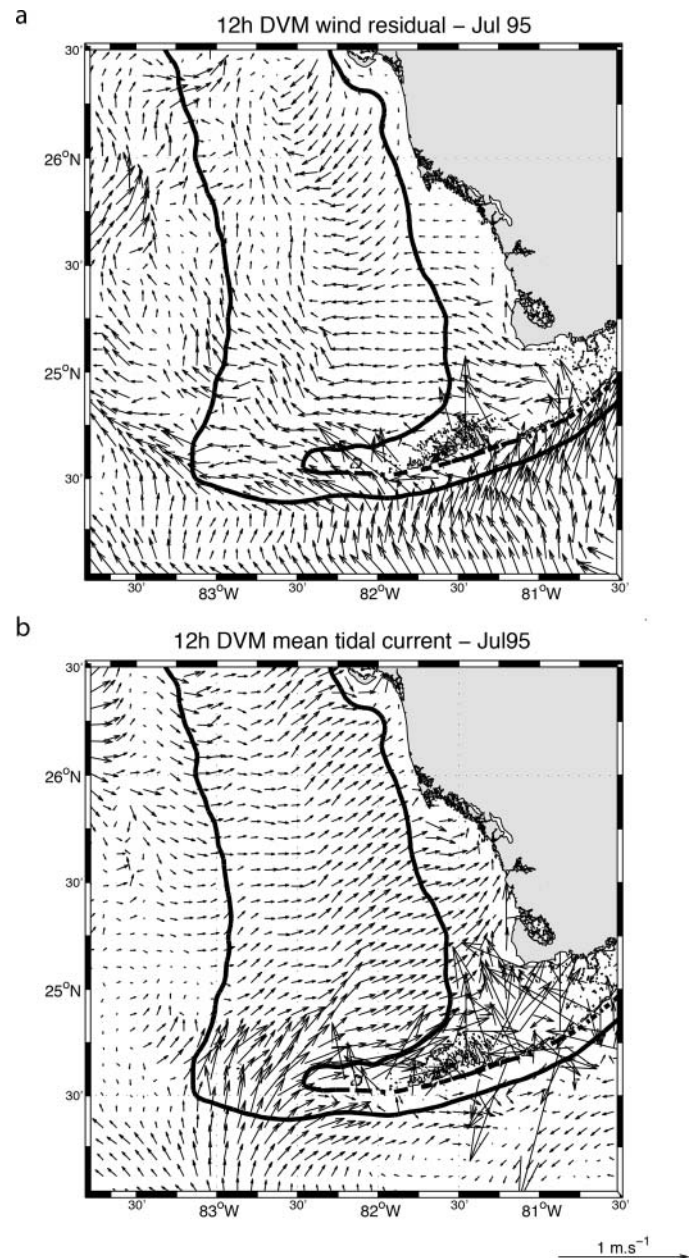

FIGURE 14. **(a)** First fortnightly 12-h diel vertical migration (DVM) mean wind-driven surface current in July1995 and **(b)** the first fortnightly 12-h DVM mean tidal surface current for a DVM initiated at midnight of the first day of particle release in July 1995.

estimated period of larval transport (Figure 8). By adding an STST behavior at day 15 of migration, ∼15% of the larvae released at Marquesas and 2% of the larvae released at Dry Tortugas reached the nursery grounds, moving north-northeast across the SWF shelf during summer. The maximum eastward distance traveled by larvae with DVM and STST behavior depends on the strength of the circulation, the season of the year, the release location, and the stage of the tidal current at the time of initiating the larval DVM period.
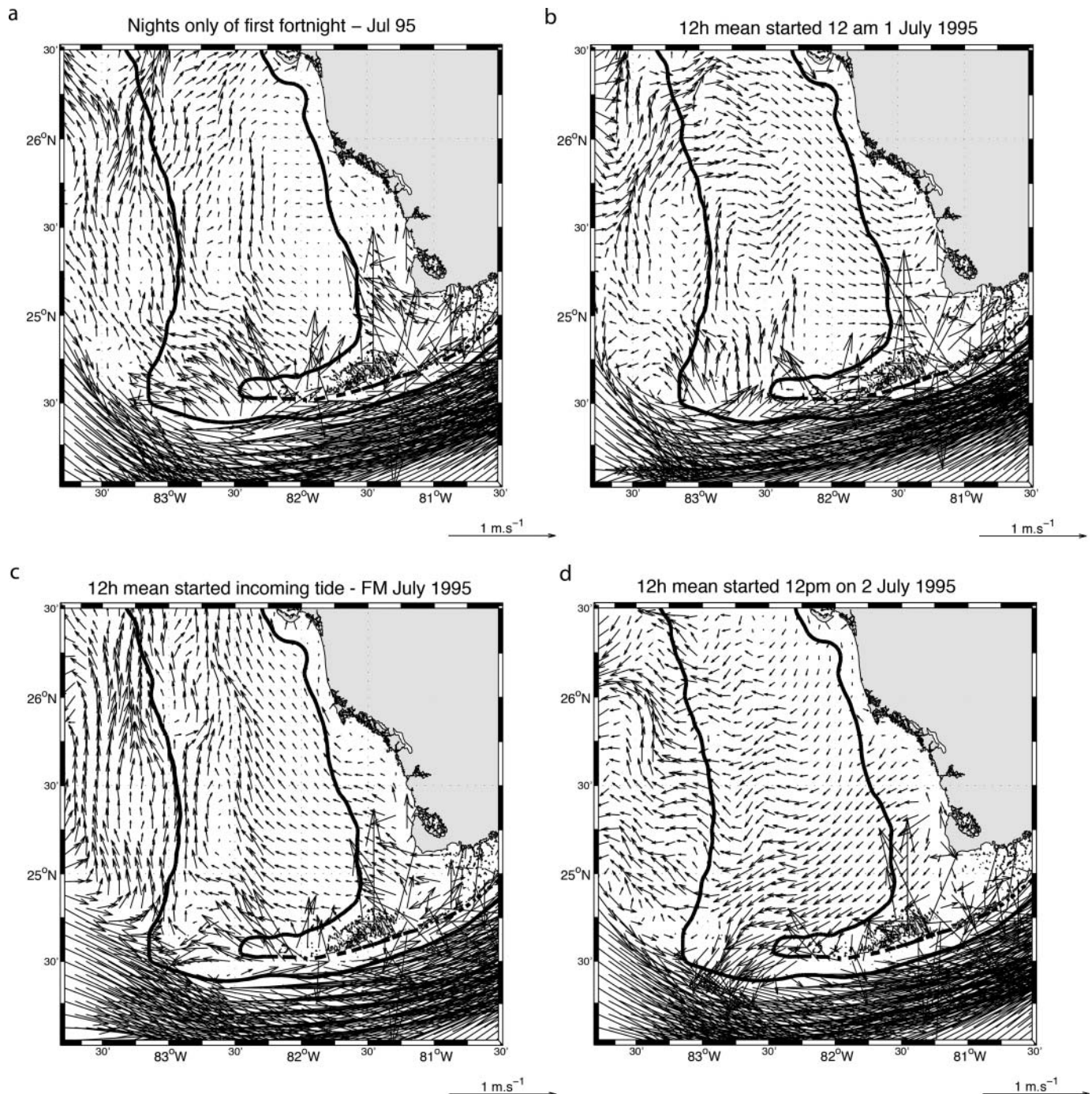
FIGURE 15.   Fortnightly 12-h mean diel vertical migration (DVM) current vector field **(a)** based on model nights from only the first fortnight of July 1995, **(b)** started at midnight on July 1, 1995, **(c)** started with the incoming tide on the full moon of July 1995, and **(d)** started at noon on July 2, 1995.

Biophysical simulations revealed substantially different seasonal patterns in larval migration and in settlement. These different migration patterns were in accordance with the general circulation patterns described for the region, partly dependent on synoptic-scale winds, coupled with a strong seasonality of the subtidal flow and strong tidal currents (e.g., Weisberg et al. 1996; Smith 2000; Lee et al. 2002). The transport of passive particles or particles with a DVM behavior from the spawning grounds to the coastal nursery grounds appeared to be controlled by a combination of four factors: (1) the subtidal flow, namely the geostrophic flow, which is in general very weak in summer and southward in the vicinity of the spawning grounds; (2) the coastal freshwater-driven density current, mostly controlled by watershed discharge
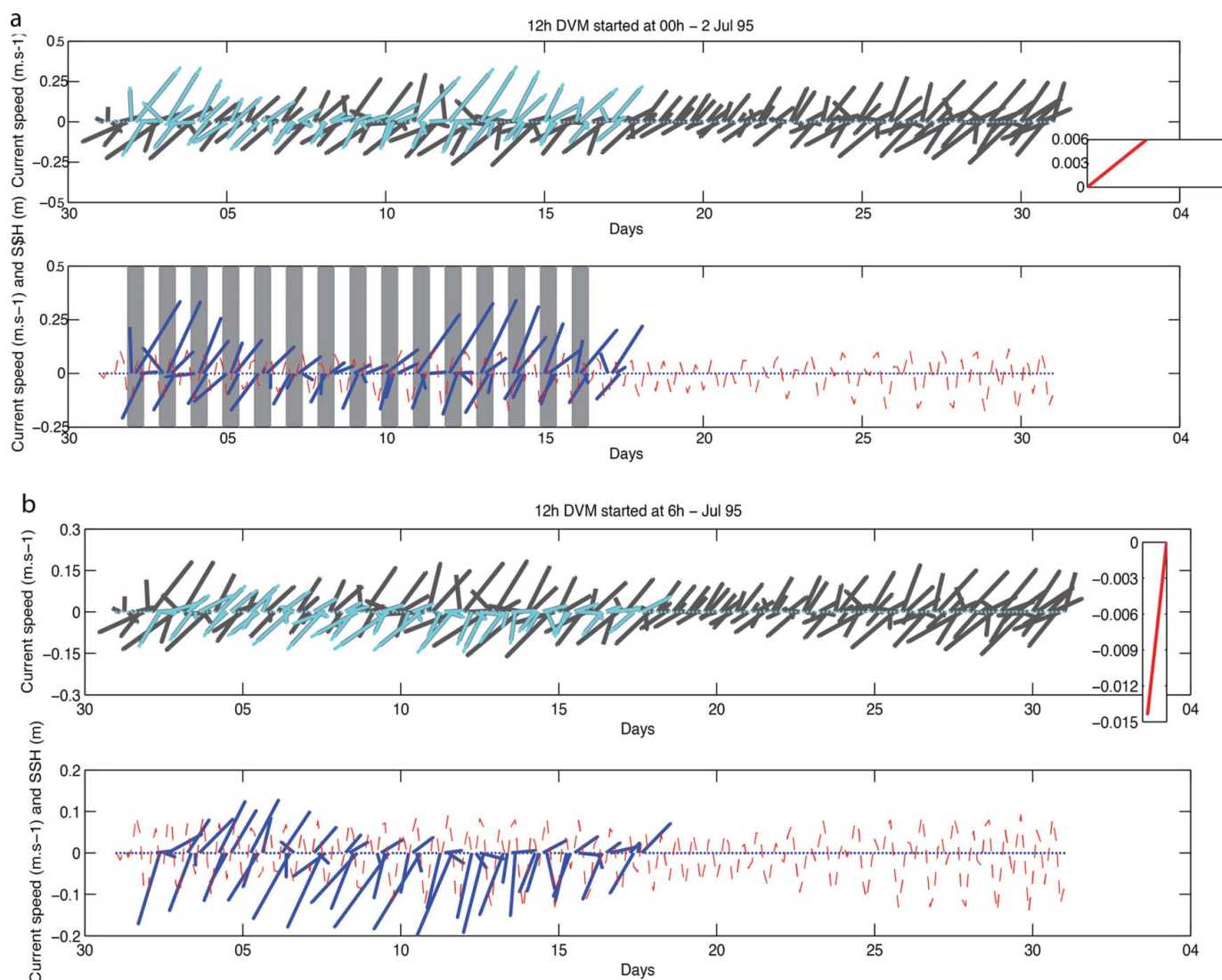
FIGURE 16. Current stick diagram at Marquesas spawning ground for the month of July 1995 (black sticks), showing **(a)** the 12-h DVM started at 0000 hours on July 2, **(b)** the DVM started at 0600 hours on July 2, **(c)** the DVM started at 1200 hours on July 2, and **(d)** the DVM started on July 10, 2 d before the full moon, at 1800 hours. The cyan-colored sticks in each of the upper diagrams show the current vectors selected by the 12-h DVM. The red stick in the small box shows the corresponding mean current direction. In each of the lower diagrams, the sticks selected by the 12-h DVM are overlaid with the mean sea level (red dashed line). The shaded gray bars show the nights. (*Extended on next page*)

(Hu et al. 2004; Zhao et al. 2013); (3) the Ekman transport, which is on average northwestward (Liu and Weisberg 2012); and (4) the tidal current, which is highly consistent. If both the wind-driven and the geostrophic current are weaker than the tidal current, the 12-h DVM mean flow can be northeastward, which increases the chances of larvae reaching the western Florida coast by crossing the SWF shelf. The strength of the geostrophic flow is partly controlled by the salinity at the coast, and it can overcome the tidal flow, as happened in July 1997. The subtidal flow points to the southwest as shown in Figure 7c, and the 12-h mean DVM flow is directed to the northwest at Dry Tortugas and to the south at Marquesas (Figure 12), which suggests that the geostrophic current was

against the northeastward tidal current at both Dry Tortugas and Marquesas. In July 1995, the relatively low freshwater discharge in inshore waters (Figure 7a) yielded a geostrophic flow directed to the northwest at Dry Tortugas and Marquesas (Figure 12). Combined with the selected tidal flow, the resulting 12-h DVM current was to the northeast at Marquesas and to the northwest at Dry Tortugas, yielding a much higher recruitment percentage in July 1995 than in July 1997 (Figure 9). In July 1996, the subtidal flow and the selected tidal flow were in the same direction and contributed to a strong northeastward 12-h mean DVM flow (Figure 12), yielding the largest recruitment percentage among the 3 years we simulated. This analysis shows that the current balance
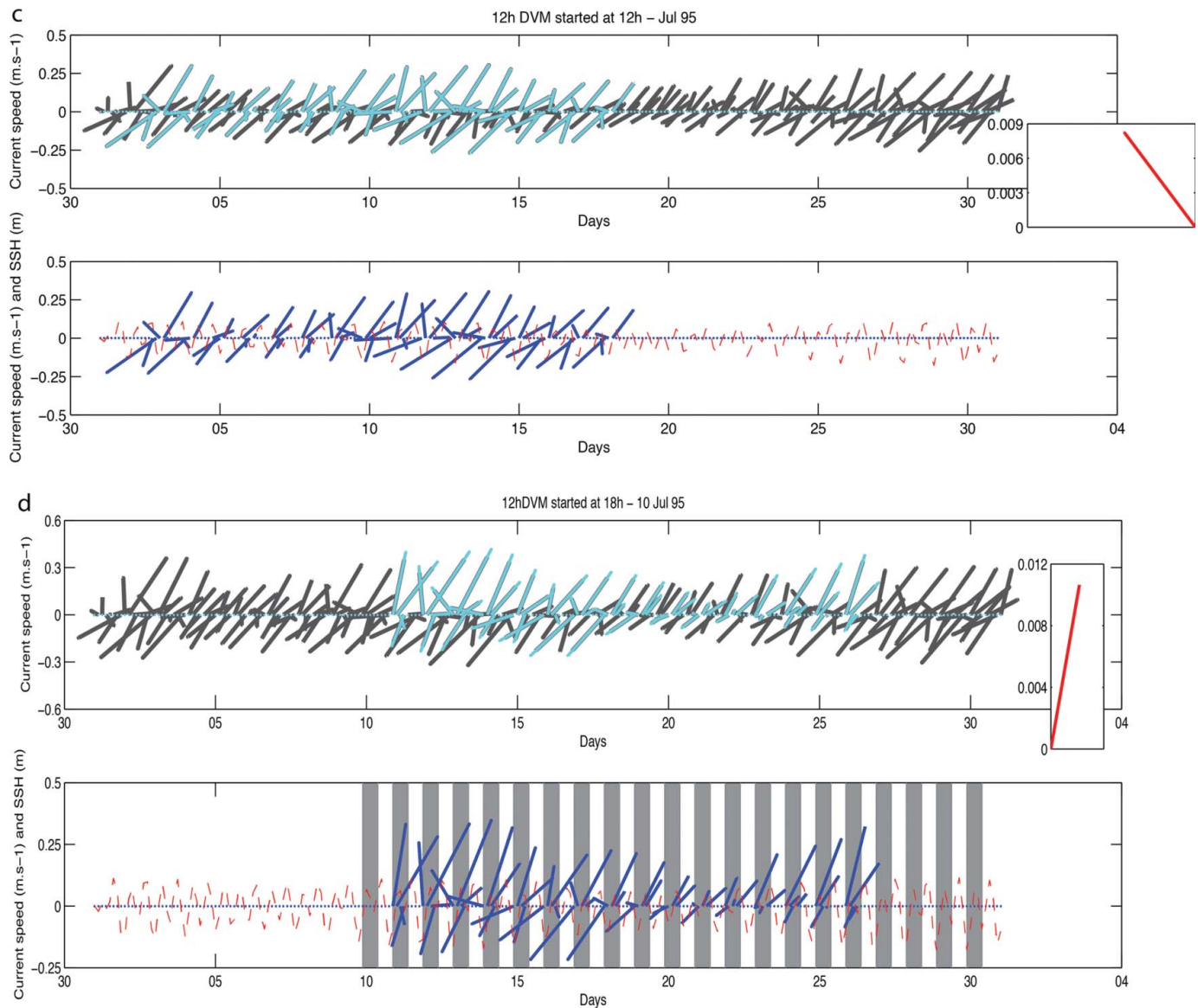
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FIGURE 16.   Extended.

captured during the DVM period is critical to determine the direction in which larvae initially move, whether it is favorable (east or northward) or unfavorable (south or westward) to larval transport toward the nursery grounds.

The migration pattern changed radically during the winter months. Larvae moving with DVM and STST behavior during winter advanced only a short distance east-northeast across the SWF shelf because the DVM flow was westward (Figures 10 and 12). Some of the larvae originating at Dry Tortugas may move to the northwest, others may be caught by the LFC and associated gyre circulation, such as cyclonic eddies that originate westward of the Dry Tortugas and move downstream along the edge of the shelf (Fratantoni et al. 1998; Yeung et al. 2001; Yeung and Lee 2002). The different oceanographic conditions observed between summer and winter produce different migration routes that larvae use to reach the settlement grounds. During summer, most larvae released at Marquesas and at Dry Tortugas that recruited to settlement habitat arrived there by moving across the SWF shelf. During winter the settlement rates were about 5 times lower than during summer, and most larvae arrived at the settlement grounds via the Florida Current through the Florida Keys channels. This seasonal pattern in transport and settlement observed in our simulations agrees with previous field observations on postlarval influxes of pink shrimp into Florida Bay (Criales et al. 2006). The influx of postlarvae entering Florida Bay through its northwestern border, having crossed the SWF shelf, was about seven times greater than the influx through the channel of the
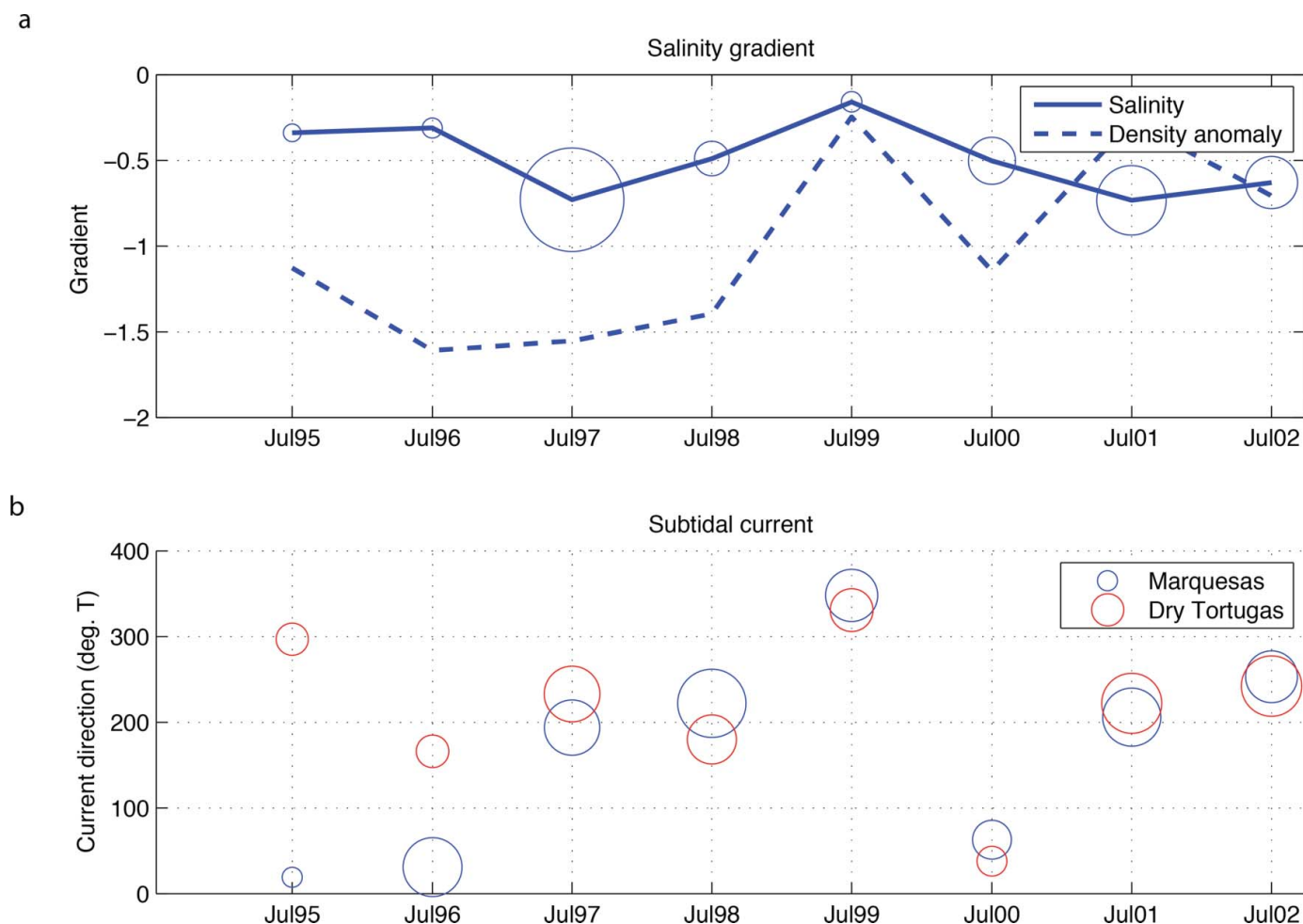
a

b

FIGURE 17.   Graphs of salinity and subtidal flow, showing an **(a)** 8-year time series of model monthly salinity gradient (solid line) and density anomaly (dashed line) in July along a zonal section at 25.7°N (shown in Figure 1b). Circles show the gradient concavity, which indicates the width of the gradient. Also shown is **(b)** subtidal monthly mean flow direction (*y*-axis coordinate of the center of the circle) and magnitude (circle diameter) at the Marquesas and the Dry Tortugas sites.

Middle Florida Keys. Furthermore, the peaks of abundance at the northwestern Florida Bay border were centered in summer for four consecutive years, whereas the influx of postlarvae through the Middle Florida Keys channels exhibited a highly variable seasonal pattern from year to year.

The highest settlement rates of pink shrimp larvae were observed in summer. Besides the favorable balance of the forcing on currents previously described, these settlements may have been enhanced by a horizontal displacement caused by the interaction between the periods of the DVM and the tidal constituents (e.g., Hill 1991a, 1991b; Smith and Stoner 1993; Power 1997; Criales et al. 2005). Organisms that use tidal currents with a DVM behavior for onshore transport may take advantage of an annual tidal cycle to improve their chances of reaching coastal nursery habitats. However, there are significant geographic variations in the seasonal diel transport. Using a simple Lagrangian model for the SWF shelf, Criales et al. (2005) estimated that particles moving at night with a STST behavior could enhance their eastward-traveled distance by up to 65 km due to the

superposition of the phase of the tidal constituents (solar semidiurnal S_2 and diurnal K_1) with the 12-h DVM period during long summer days. We found in the DVM onset sensitivity analysis that in July the strongest northeastward tidal current was synchronized with a 12-h DVM windowing starting with the incoming tide at night. The strongest northeastward tidal current at Dry Tortugas and Marquesas spawning grounds was obtained when the DVM started on July 10, 1995, 2 d before the full moon (Figure 16d). Pink shrimp females spawn all year round, but the highest frequency of ripe females (Cummings 1961) and the highest concentrations of larvae (Munro et al. 1968; Jones et al. 1970) occur in summer. The fact that the highest settlement rates in our simulation also occurred during summer may suggest that the reproductive cycle of this species in southern Florida is synchronized with the summer months when the oceanographic conditions (currents, tidal currents, tidal phase, and wind) are the most favorable for the DVM and the STST behavior.

The main nursery grounds of pink shrimp are located on the seagrass banks of western Florida Bay (Costello and Allen

1966), but other coastal estuaries of the lower southwestern Florida coast, such as Lostman's River, Oyster Bay, Ponce de Leon Bay, and Whitewater Bay, are also nursery grounds (Browder and Robblee 2009). Our model results indicated that, during summer, the vast majority of pink shrimp postlarvae settled at a location between the mouth of Lostman's River and Ponce de Leon Bay, north of Florida Bay (Figures 8, 10). Some of these postlarvae may actually settle in these small bays, but the great majority of them must move south along the coast from this location to reach Florida Bay. The connection between Florida Bay and interior bays was closed with the construction of the man-made Buttonwood Canal in Everglades National Park in 1982. Trajectories from surface drifters deployed at Shark River by Lee et al. (2002) during summer showed a northwestward displacement along the coast; however, Lee et al. (2002) also noted that salinity patterns associated with the Shark River low-salinity plume are generally oriented toward the southeast, with little spreading offshore of the river mouth. As previously shown, freshwater from the rivers that constitute the nursery grounds sustain a southward flow along the coast. Postlarvae arriving at the coast north of Florida Bay could use this southeastward flow to reach the seagrass banks inside of Florida Bay.

The number of ripe females reported from pink shrimp fishery data suggested that the main spawning ground of the species in southern Florida is located northeast of the Dry Tortugas (Cummings 1961; Roberts 1986). Based on the number of early planktonic stages (protozoeal stages), a location northward of Marquesas has also been suggested as spawning grounds (Jones et al. 1970; Criales et al. 2007). Our model results support Marquesas as the most effective spawning ground for pink shrimp, since larvae released at Marquesas were 4.5 times more likely to recruit to settlement habitats than larvae released at Dry Tortugas. Factors in the model that may have contributed to making Marquesas the more favorable spawning ground are as follows: (1) the distance to the nursery grounds, which is about half of that from Dry Tortugas, and (2) the circulation around Dry Tortugas, which is more variable than at Marquesas and larvae could be caught by the LFC and associated gyres, which usually hug the shelf edge southwest of the Dry Tortugas, and travel downstream with the Florida Current (Lee et al. 2002). Results of simulations conducted for other penaeid species have reached similar conclusions to ours. The estimated distance between effective spawning and nursery grounds for penaeid species in the Gulf of Carpentaria and the Gulf of California was closer to shore than the original estimates (Condie et al. 1999; Marinone et al. 2004), suggesting that the contributions of nearshore spawning grounds should not be underestimated.

In summary, results of the biophysical model clearly demonstrated the seasonality in larval settlement and in the migration routes to reach the nursery grounds. An effective transport mechanism promoting travel east-northeast across the SWF shelf occurs during summer as the result of tidal currents, favorable wind, geostrophic flow and a combined DVM and STST behavior. The current phase captured during the DVM period appeared to be critical at selecting how far from the nursery ground larvae will be moved before the STST behavior enables the larvae to capture the eastward phase of the tide, which will move them to the nursery grounds. Interannual variability of the DVM was shown to be driven by the wind and the salinity at the nursery grounds, which is driven by rainfall and freshwater discharge. Therefore, salinity may be an important environmental factor controlling pink shrimp recruitment. Results suggest that adult pink shrimp may select spawning locations where one of the flow drivers is always favorable to their transport across the SWF shelf toward their nursery grounds, as tide is at the shrimp spawning grounds. The migration pattern changed in winter months when the alongshore winds reversed direction and the resultant flow component at the spawning grounds was westward. A few larvae that originated at Dry Tortugas and Marquesas reached the nursery grounds via the Florida Current and Florida Keys channels, but none of the larvae that originated at Dry Tortugas arrived at the nursery grounds via the SWF shelf. The Marquesas ground may be a more effective spawning ground than the Dry Tortugas ground, since larvae released at Marquesas were 4.5 times more likely to recruit to settlement habitats than larvae released at Dry Tortugas. These results will enable more effective management of this important fishery species.

An obvious next step of the study should include in the model other important nonlinear biological processes such as egg production, larval growth, and mortality to improve predictions of spawning ground locations and spatial distributions of settlement. New modeling should also determine the behavior and timing necessary to allow some of the postlarval pink shrimp that reach the southwestern Florida coast to finish the journey to Florida Bay. This model should also cover the flow of larvae among subpopulations of pink shrimp in Florida such as those in Biscayne Bay, Sanibel, and St. Augustine.

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