



# Connectivity and larval dispersal pathways of *Panulirus argus* in the Gulf of Mexico: A numerical study

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## ABSTRACT

The connectivity among subpopulations of *Panulirus argus* in the Gulf of Mexico is evaluated using a particle-tracking model coupled to a realistic hydrodynamic simulation generated with the Hybrid Coordinate Ocean Model. In 12 potential subpopulations of the Gulf of Mexico, virtual larvae were released daily from March 21 to June 18, 2006–2010. Virtual propagules were tracked for a maximum of 198 days and programmed to undergo vertical migrations and to eventually “die” according to an exponential decay function. The subpopulations that were the most inter-connected and had the highest values of self-settlement were those from the Bay of Campeche (Campeche, Southern Veracruz, Central Veracruz, and Northern Veracruz). This pattern can be explained by the recirculation resulting from the semi-permanent cyclonic gyre in the Bay of Campeche and the back and forth behaviour of the shelf currents at Veracruz. Self-settlement was low at Quintana Roo, Southern Florida, and Northwestern Cuba, because the Loop Current quickly transported the larvae away from those areas. Southern Florida received a considerable number of settlers coming from almost all other subpopulations mainly by means of the Loop Current. Larvae from Yucatan may be transported to subpopulations in the Bay of Campeche by means of both westward Loop Current Eddies and the westward inner-shelf current in the Campeche Bank. The continental shelf of the Bay of Campeche, particularly the islands and cays in the western edge of the Campeche Bank, emerged as both important settlement areas and larval dispersal pathways. A program for the protection of the species in these areas may help increase the population size of *P. argus* in the Gulf of Mexico, potentially favouring local fisheries.

## 1. Introduction

*Panulirus argus* (Latreille, 1804), the Caribbean spiny lobster, is a decapod crustacean distributed in the Wider Caribbean region, from North Carolina to Venezuela (Giraldes and Smyth, 2016). *Panulirus argus* constitutes the most important lobster fishery in the Gulf of Mexico and Caribbean Sea and is a highly demanded product in the international market (Briones-Fourzán and Lozano-Álvarez, 2000; Hunt, 2000; Chávez, 2009). According to Arceo et al. (1997), the average catch from 1982 to 1990 of *P. argus* in the states of Quintana Roo (Mexican Caribbean) and Yucatan (Gulf of Mexico) was approximately 350 and 120 tons of lobster tails, respectively. However, since 1992 the catch in both states has been approximately similar (Briones-

Fourzán and Lozano-Álvarez, 2000; DOF, 2011). A general decline in *P. argus* stocks has been reported both in the Gulf of México (Ehrhardt and Fitchett, 2010; Ríos-Lara et al., 2012) and in the Caribbean Sea (Guzman and Tewfik, 2004; Chávez, 2009), which may be linked to overfishing.

The areas in the Gulf of Mexico where *P. argus* is most abundant, and where the greatest catches occur, are located around the Yucatan Peninsula (Arceo et al., 1997; Ríos-Lara et al., 2013) and Southern Florida (Hunt, 2000). Nevertheless, according to the Ocean Biogeographic Information System (available at <http://iobis.org>, accessed December 2018) and other studies, *P. argus* is also found in Veracruz and Tamaulipas (Briones-Fourzán and Lozano-Álvarez, 2000; Ríos-Lara et al., 2013), Northwestern Cuba (Pintueles-Tamayo et al., 2016), the

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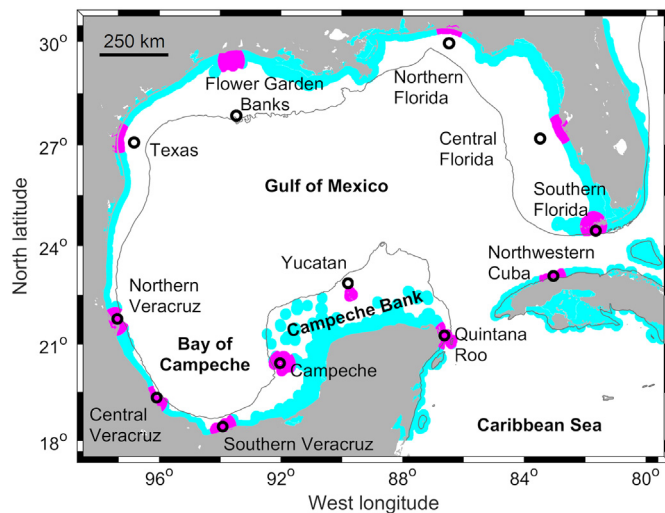
E-mail address: [julioalh@atmosfera.unam.mx](mailto:julioalh@atmosfera.unam.mx) (J.A. Lara-Hernández).

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**Fig. 1.** Release sites (black circles) and settlement sites (magenta sections) of virtual propagules considered in this study. The cyan area is a 20 km thick band from the 5 m isobath that may lead to settlement if reached by post-larvae. The release sites and the settlement sites are different because larval hatching occurs in deeper waters, farther from the coast. The 200 m isobath is shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Flower Garden Banks off the coast of Texas and Louisiana (Wicksten, 2005), and along the west coast of Florida (Hunt, 2000) (Fig. 1). In the northern Gulf of Mexico, records of *P. argus* are relatively rare. However, there exists the possibility of finding considerable numbers of *P. argus* in deeper waters, away from the shore, where commercial fishing is not practiced (Moore, 1962).

The Caribbean spiny lobster develops through benthic stages (juveniles and adults) that inhabit the continental shelf (Butler et al., 2006) and early-life pelagic stages (larvae and post-larvae) that drift in the ocean for months (Goldstein et al., 2008). Because of the long duration of pelagic stages, *P. argus* has dispersal potential throughout the entire Caribbean basin (Naro-Maciel et al., 2011), although biophysical models suggest that most of larval settlement occurs within ~500 km from the spawning site (Butler et al., 2011). Understanding the connectivity, or relationship among subpopulations resulting from dispersal of pelagic stages, can be insightful when planning effective conservation measures for lobsters, such as Marine Protected Areas (Lipcius et al., 2001; Kough et al., 2013; Whomersley et al., 2018). For example, connectivity analysis can be used to identify regions with protection priority, such as those with high potential for larval production and/or settlement (Lipcius et al., 2001; Kough et al., 2013) and those that constitute important connection pathways between subpopulations (Kough et al., 2013; Ortiz-Lozano et al., 2013).

Marine connectivity is determined by several factors such as (1) hydrodynamic regimes: ocean currents and eddies may enable exchange among subpopulations or isolate them (Blanke et al., 2009, 2012; Roughan et al., 2005, 2011); (2) distance between subpopulations: connectivity is usually stronger between closer subpopulations (Wright et al., 2015); (3) pelagic larval durations: connectivity increases as the pelagic larval duration increases (Selkoe and Toonen, 2011); and (4) vertical migrations of larvae: ocean currents change with depth (Paris et al., 2007; Butler et al., 2011). Because direct tracking of thousands of small larvae during extended times and distances is practically impossible, connectivity is usually assessed through indirect techniques such as genetics, observations of settlement (i.e. conversion of a propagule into a benthic stage), and numerical simulations (Kool et al., 2012). Numerical simulations are particularly promising because they allow investigators to model the fate of large numbers of virtual larvae with diverse behaviours and may provide substantial insight into

the design of conservation measures (Jones et al., 2009; Whomersley et al., 2018).

Several studies have investigated the connectivity of *P. argus* in the Caribbean Sea (e.g. Briones-Fourzán et al., 2008; Butler et al., 2011; Naro-Maciel et al., 2011; Kough et al., 2013; Cruz et al., 2015). In contrast, the connectivity in the Gulf of Mexico has been scarcely addressed (e.g. Yeung and Lee, 2002; Manzanilla-Domínguez and Gasca, 2004). For the subpopulation in Southern Florida, it has been suggested that most of the settlement is due to post-larvae coming from the Caribbean Sea (Yeung and Lee, 2002), although more recent studies suggest that the southwest Florida shelf area plays an important role in the local retention and self-recruitment of larvae originated in the Florida Keys (Segura-García et al., 2019). It has also been suggested that larvae produced in the Yucatan shelf are transported to the Veracruz shelf by anticyclonic eddies (Manzanilla-Domínguez and Gasca, 2004).

Because of the lack of work focused on the connectivity of the Caribbean spiny lobster in the Gulf of Mexico, the objectives of the present study were: (1) to construct connectivity matrices from larval dispersal among 12 potential subpopulations of *P. argus* in the Gulf of Mexico, based on biophysical modelling, (2) to identify subpopulations with high potential as larval exporters, (3) to identify regions with high potential for larval settlement, (4) to analyse the degree of self-settlement in each subpopulation, (5) to identify the main dispersal pathways connecting subpopulations, (6) to analyse interannual variability in the connectivity dynamics, and (7) to provide information useful in the design of conservation measures for *P. argus* in the Gulf of Mexico.

## 2. Pelagic lifecycle of *Panulirus argus*

The pelagic development of *Panulirus argus* comprises 10 larval stages (phyllosoma larvae) and one post-larval stage (puerulus), lasting from five to seven months (Goldstein et al., 2008). Hatching of *P. argus* larvae usually occurs at night, when females travel to deeper waters, up to a depth of ~100 m (Phillips et al., 1980), for larval release (Butler et al., 2006; Ríos-Lara et al., 2013). Larval hatching in the Gulf of Mexico seems to peak during spring, although larval release can occur throughout the year (Davis, 1975; Gregory Jr et al., 1982; Briones-Fourzán et al., 2008). Phyllosoma larvae have negligible horizontal swimming ability. However, they can significantly modify their vertical position through twilight diel vertical migrations (larvae ascend at sunset, make a short-term descent around midnight, ascend again in the latter half of the night, and descend at sunrise) (Ziegler et al., 2010) and ontogenetic vertical migrations (larvae go deeper in the water column as they grow) (Rimmer and Phillips, 1979; Yeung and McGowan, 1991; Yeung and Lee, 2002; Butler et al., 2011). After completing the last larval stage, the larvae metamorphose into non-feeding post-larvae competent for settlement (Goldstein et al., 2008; Espinosa-Magaña et al., 2018). This metamorphosis may be triggered by habitat cues near the shelf break (Phillips and McWilliam, 2009). Post-larvae return closer to the surface and actively swim towards shallow (< 5 m depth) settlement sites (Goldstein and Butler, 2009), which may be distant from the deeper spawning areas (Butler et al., 2006).

## 3. Methods

### 3.1. Study area

The Gulf of Mexico is a multinational basin in the northwest Atlantic Ocean, surrounded by Mexico, the United States of America, and Cuba (Fig. 1). In agreement with previous studies (Hunt, 2000; Wicksten, 2005; Briones-Fourzán et al., 2008; Ríos-Lara et al., 2013; Pintueles-Tamayo et al., 2016) and geo-referenced biogeographic data from the Ocean Biogeographic Information System (available at <http://iobis.org/>, accessed December 2018), 12 potential subpopulations of *Panulirus argus* in the Gulf of Mexico were considered: Quintana Roo, Yucatan, Campeche, Southern Veracruz, Central Veracruz, Northern

Veracruz, Texas, Flower Garden Banks, Northern Florida, Central Florida, Southern Florida, and Northwestern Cuba (Fig. 1). Although the exact location of well consolidated subpopulations of *P. argus* throughout the Gulf of Mexico is not well known, simulating subpopulations in sites with recorded presence of *P. argus* could help to understand the potential of those sites to harbour a well consolidated subpopulation.

Because most of the settlement occurs on substrates shallower than 5 m in depth (Goldstein and Butler, 2009) and post-larvae can track suitable habitats for settlement that are as far as ~20 km away (Goldstein and Butler, 2009; Butler et al., 2011), the region that extends perpendicularly 20 km from the 5 m isobath was considered as the region that may lead to settlement if reached by post-larvae (Fig. 1). Sectors within 100 km of sites with records of *P. argus* and overlapping with the region that can lead to settlement were considered as the potential settlement areas for the connectivity analysis (Fig. 1). Because hatching of larvae occurs in deeper waters that may be distant from settlement sites (Butler et al., 2006), the release sectors of virtual larvae were centred on the 50 m isobath, in areas with records of *P. argus* (Fig. 1).

### 3.1.1. Ocean circulation

The most intense and representative currents of ocean circulation in the Gulf of Mexico are the Loop Current and its related eddies (Fig. 2). The Loop Current goes into the Gulf of Mexico through the Yucatan Strait, turns anticyclonically to the east, and leaves the Gulf through the Florida Strait. Periodically, the Loop Current sheds large anticyclonic eddies that move westward (Oey et al., 2005; Zavala-Hidalgo et al., 2006). The circulation in the Bay of Campeche is characterized by a semi-permanent cyclonic gyre (Fig. 2), which is weaker during summer and stronger during winter (Pérez-Brunius et al., 2013). In the western Gulf of Mexico, a typical western boundary current is found near the shelf break, which is weaker in October and stronger in summer (Sturges, 1993). The circulation over the inner shelf of the Campeche Bank is westward and south-westward during most of the year (Zavala-Hidalgo et al., 2003). Over the continental shelf of Tamaulipas, Veracruz, and Tabasco, low frequency currents are northward during May–August and southward or south-eastward during September–March (Zavala-Hidalgo et al., 2003). Over the inner shelf of Texas and Louisiana, low frequency circulation is westward during September–May and eastward during June–August. Meanwhile, the circulation over the outer shelf is predominantly eastward throughout the year (Nowlin et al., 2005). On the western Florida shelf, currents are mainly southward, except during May–September (Liu and Weisberg, 2012).

### 3.2. Hydrodynamic simulation

The hydrodynamic data come from five years (2006–2010) of a realistic hydrodynamic simulation of the Gulf of Mexico based on the Hybrid Coordinate Ocean Model (HYCOM) and the Navy Coupled Ocean Data Assimilation (NCODA) (available at <https://hycom.org/data/goml0pt04/expt-20pt1>, accessed September 2016). The simulation has a horizontal resolution of  $1/25^\circ$ , 20 vertical layers, and provides daily data. The HYCOM model uses hybrid coordinates, with isopycnal coordinates in open ocean, sigma coordinates in shallow waters, and geopotential coordinates near the surface (Bleck, 2002). The hydrodynamic model assimilates data using the Navy Coupled Ocean Data Assimilation System (Cummings, 2005) and has been validated by Metzger et al. (2010). To identify circulation patterns, a monthly climatology (2006–2010) at surface and 100 m depth was constructed and plotted. Even months are shown in Fig. (2), and odd months can be consulted in Supplemental Fig. (1).

### 3.3. Lagrangian model

A Lagrangian particle-tracking algorithm was programmed in

Matlab® to simulate three-dimensional displacements of *P. argus* larvae. The algorithm is an analogous version of a set of Lagrangian models developed to simulate oil spills (Anguiano-García et al., 2019), but with the ability to reproduce three-dimensional movement and larval swimming behaviour. Virtual larvae were released around 12 central points (Fig. 1), following a normal distribution scheme that uses the central release point as the mean and a radius of 5 km as the standard deviation. In this way, ~68% of larval release occurred over a circular area with a radius of 5 km. Two hundred virtual larvae were released daily at midnight along the 50 m isobath. A sensitivity analysis demonstrated that ~100 particles are sufficient to ensure robustness of connectivity metrics (Monroy et al., 2017). High consistency in connectivity matrices obtained from two runs of the Lagrangian model (using the same circulation data) confirmed that the 200 particles daily released were sufficient for the purposes of this study.

Because spring is the peak hatching period of *P. argus* in the Gulf of Mexico, the release of virtual larvae was performed from March 21 to June 18, 2006–2010. Because of the lack of biological information, the production of virtual larvae was the same for all the subpopulations, which leads to estimates of relative connectivity. Estimates of real absolute connectivity (number of individuals who settle in one site from another) could be obtained by multiplying the estimated relative connectivity based on real larval production. Propagules were tracked for a maximum of 198 days, and settlement could occur at the age of 140 days or more (post-larva competent to settle) (Butler et al., 2011). Consequently, the modelled settlement period occurred from August to December. When virtual post-larvae were located 20 km or less from a potential settlement region (Fig. 1), they were considered as having settled in that region. The presence of post-larvae 20 km or less from a settlement region does not necessarily translate into settlement because settlement also depends on other factors (e.g. predation, larval diseases). However, considering the strong swimming ability of post-larvae, the approach constitutes a reasonable approximation, and it is typically used in similar studies (Butler et al., 2011; Kough et al., 2013).

Displacements of virtual propagules were computed by solving the equations:

$$\Delta x = \Delta t (U + u') \quad (1)$$

$$\Delta y = \Delta t (V + v') \quad (2)$$

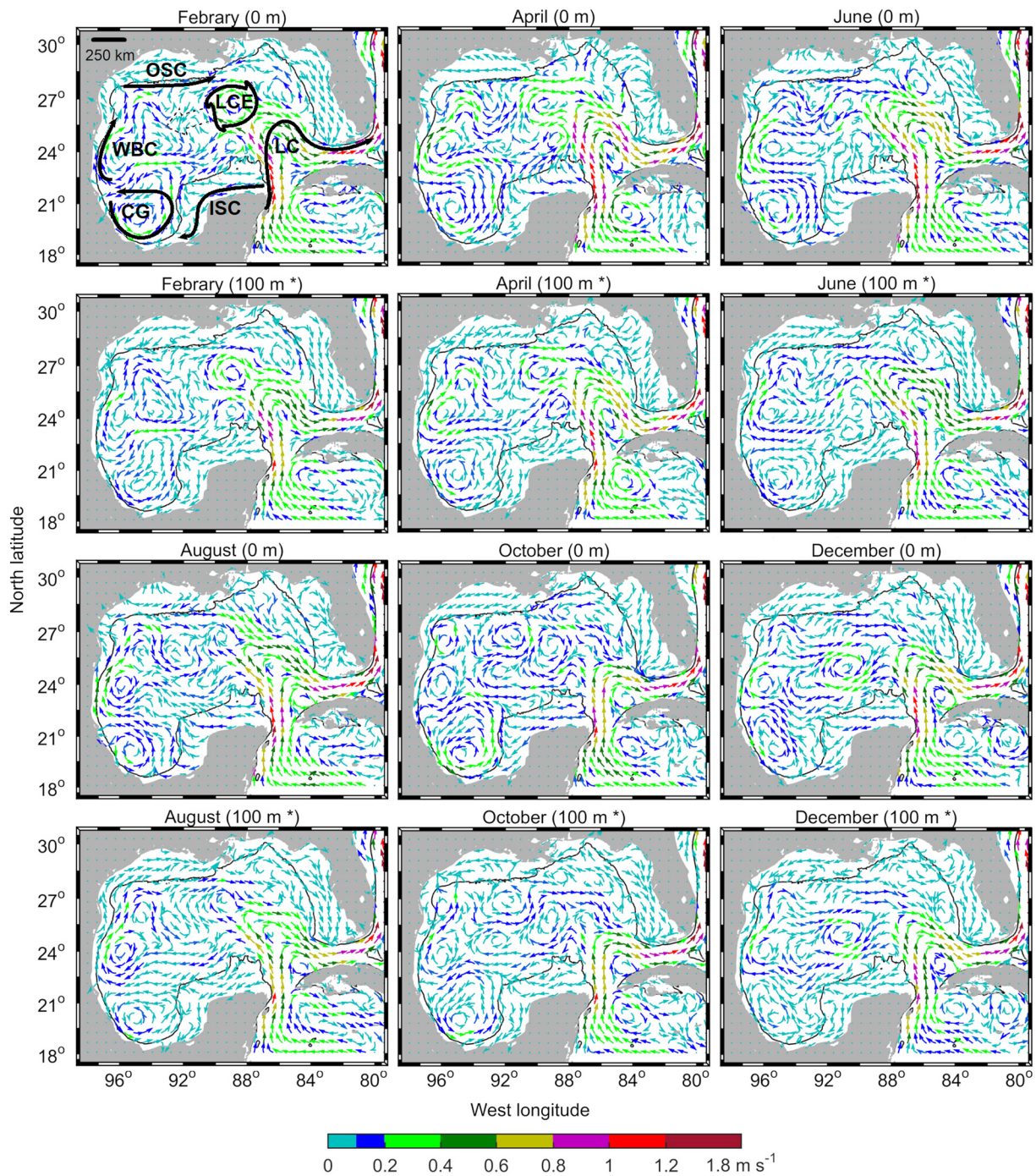
$$\Delta z = \Delta t (W + w_p) \quad (3)$$

where  $U$ ,  $V$  and  $W$  are the advective velocities interpolated from the hydrodynamic velocity fields to the location and time of virtual propagules (trilinear interpolation in space, linear interpolation in time). The equations were integrated with a second order Runge-Kutta algorithm in time and space and a time step ( $\Delta t$ ) of 1350 s. The selected  $\Delta t$  produces instant displacements smaller than the size of the grid cell. This leads to a maximum use of the spatial and temporal resolution of the velocity fields, while reducing numerical errors and maintaining consistency with the Courant-Friedrichs-Lewy criterion of stability (Courant et al., 1967).

The terms  $u'$  and  $v'$  in Eqs. (1) and (2) are random velocities added to model sub grid horizontal turbulent-diffusion, so that  $u' = RU$  and  $v' = RV$ . Factor  $R$  is a random number uniformly distributed between  $-a$  and  $a$  (Döös et al., 2011; Döös et al., 2013). To reproduce the same effect of turbulent-diffusion regardless the selected  $\Delta t$ ,  $a$  is defined as  $a = b/\Delta t^{1/2}$ . Parameter  $b$  was set equal to  $4\Delta t^{1/2} \approx 147$  in order to reproduce a relative dispersion as observed in surface drifters in the Gulf of Mexico (LaCasce and Ohlmann, 2003). This  $b$  value is like that obtained in Döös et al. (2011). Each turbulent-diffusion velocity ( $u'$ ,  $v'$ ) may equally be conceived as a random number from a Gaussian distribution with a mean equal to zero and a standard deviation equal to the advective velocity ( $U$ ,  $V$ ) times  $b/(3\Delta t)^{1/2}$ . See [dataset] Turbulent\_Diffusion.m.

The term  $w_p$  in Eq. (3) represents the vertical swimming velocity of



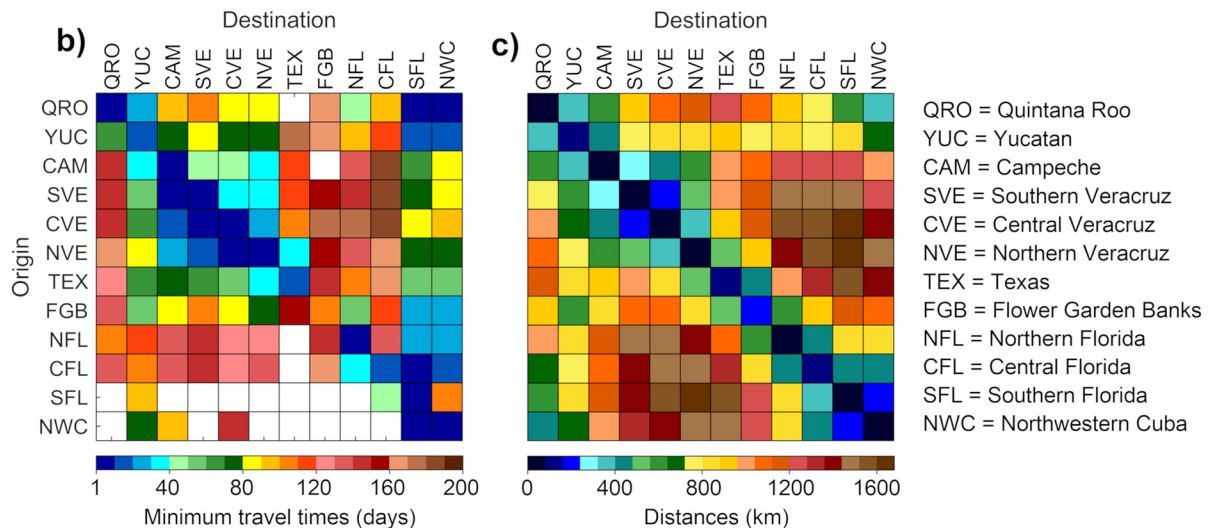
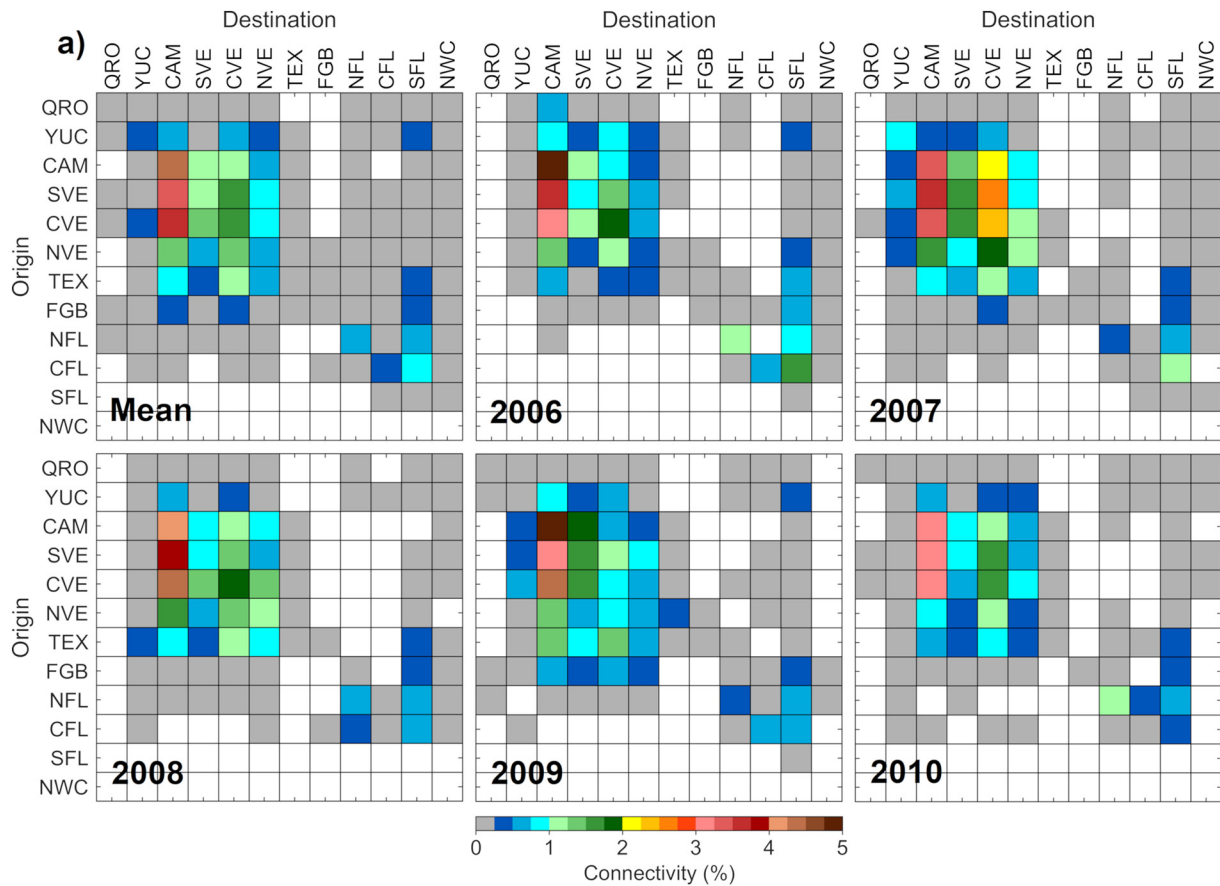


**Fig. 2.** Long-term (2006–2010) monthly mean surface and 100 m depth circulation in the Gulf of Mexico. Only even months are shown. \* The near bottom circulation is shown in the regions where depth is < 100 m. LC = Loop Current; LGE = Loop Current eddy; OSC = Outer shelf current; WBC = Western boundary current; CG = Cyclonic gyre; ISC = Inner shelf current. The 100 m isobath = is shown.

virtual propagules. The magnitude of this velocity was set to  $0.0036 \text{ m s}^{-1}$  for early larvae (< 50 days old),  $0.0045 \text{ m s}^{-1}$  for intermediate larvae (50 – < 100 days old),  $0.0055 \text{ m s}^{-1}$  for late larvae (100 – < 140 days old), and  $0.0195 \text{ m s}^{-1}$  for post-larvae ( $\geq 140$  days old) (Mileikovsky, 1973; Rimmer and Phillips, 1979). As a result of the lack of observations regarding vertical turbulent diffusion in the Gulf of Mexico, the fact that vertical currents are much less intense than horizontal currents, and that the swimming algorithm (explained below) was constructed to reproduce the observed vertical distributions of *P. argus*, no vertical turbulent-diffusion was considered.

Because vertical movement of *Panulirus argus* larvae is an important

aspect to consider in biophysical modelling (Paris et al., 2007; Butler et al., 2011; Kough et al., 2013), virtual propagules were programmed to swim up and down towards probabilistic target depths. The target depths are defined by normally distributed random numbers with a standard deviation of 10 m (Pedersen et al., 2003) and mean values that dynamically change according to the time of the day and the age of the virtual propagules. The scheme was constructed to approximate ontogenetic and twilight diel vertical migrations observed in lobster larvae and post-larvae (Rimmer and Phillips, 1979; Goldstein and Butler, 2009; Ziegler et al., 2010; Butler et al., 2011). The sign of the vertical swimming velocity  $w_p$  in Eq. (3) depends on whether the virtual



**Fig. 3.** a) Annual connectivity during (2006–2010), b) minimum travel times of virtual propagules, and c) distances among 12 subpopulations of *Panulirus argus* in the Gulf of Mexico. White cells correspond to no connectivity or no larval exchange. The distance matrix is not symmetric because the release sites and the settlement sites are not the same.

propagule is above or below the target depth. The maximum depth that virtual propagules could reach was set as 100 m (Butler et al., 2011). The swimming algorithm was verified by plotting the vertical positions of sampled virtual propagules (Supplemental Fig. 2).

Virtual propagules were subjected to mortality according to the following exponential decay equation:

$$S(t) = S_0 \exp(-0.01t) \tag{4}$$

where  $t$  is the time in days,  $S(t)$  is the number of virtual propagules at time  $t$ , and  $S_0$  is the number of virtual propagules at  $t = 0$ . The virtual

propagules removed because of “death” were chosen randomly. Although mortality rates for *P. argus* are unknown, the mortality equation (Eq. 4) is consistent with mortality estimates for fish (Houde, 1989) and with the formulation considered in Kough et al. (2013).

### 3.4. Connectivity computation

Connectivity was computed as the percentage of virtual larvae released in one site that settled as post-larvae in another site (Xue et al., 2008). One hundred percent (100%) corresponds to 18,000 settlers



because 18,000 propagules were released annually at each subpopulation. Connectivity values were organized in square matrices with mean annual connectivity (2006–2010) and the connectivity for each year. The total percentage of settlers imported by each subpopulation was computed as the sum of values in each column of the connectivity matrix, excluding self-settlement. Similarly, the total percentage of settlers was computed as the sum of the values in each row (Kough et al., 2013). To analyse whether the degree of connectivity between subpopulations is mainly caused by the proximity between subpopulations or by circulation patterns, geographical distances between release sites and settlement sites were computed and organized in a matrix. Minimum times required by propagules to travel from a release site to a settlement site, regardless of settlement and mortality, were also computed and organized in a matrix. Larval dispersal pathways between pairs of release sites and settlement sites were identified by obtaining the trajectories of propagules achieving settlement. Then, using a grid with cells of  $\sim 11 \times 11$  km, the number of positions that fell within each cell was counted; the cell with the highest number of positions was assigned 100%. Finally, dispersal pathways of all post-larvae (propagules  $\geq 140$  days old) were mapped for each month, identifying regions and periods with higher probability of settlement.

#### 4. Results

##### 4.1. Hydrodynamic simulation analysis

The long-term monthly mean circulation (Fig. 2; Supplemental Fig. 1) reproduces the Loop Current and its associated anticyclonic eddies. In the Bay of Campeche, a cyclonic gyre throughout the year is centred at  $\sim 20^\circ$  N,  $95^\circ$  W, being weaker in December. In the western Gulf, a western boundary current with anticyclonic circulation is observed over the slope north of  $\sim 22^\circ$  N. These circulation patterns are detected at the surface and 100 m depth. At the west Florida shelf, the main circulation is southward except during May–April. On the inner Texas-Louisiana shelf, near surface circulation is mainly westward during most of the year, while near bottom circulation is cyclonic with eastward currents on the outer shelf. In the neritic zone of the Tamaulipas-Veracruz shelf, currents are south-eastward during September–February and north-westward during May–August. In the oceanic region, the direction of currents at 100 m depth is similar but not identical to the direction of surface currents. In the neritic region, the direction of bottom and surface currents differs more, mainly over the western Florida shelf and the Texas-Louisiana shelf. The long-term monthly mean current speed was smaller in the neritic zone ( $0.0\text{--}0.2\text{ m s}^{-1}$ ) than in the oceanic region ( $0.0\text{--}1.8\text{ m s}^{-1}$ ). Currents with larger magnitudes ( $1.0\text{--}1.8\text{ m s}^{-1}$ ) occurred in the Loop Current at the Yucatan Strait and south Florida. On average, currents were stronger at the surface ( $0.22\text{ m s}^{-1}$ ) than at 100 m depth ( $0.17\text{ m s}^{-1}$ ).

##### 4.2. Connectivity

According to the mean connectivity analysis (Fig. 3a Mean, Fig. 4), the subpopulations most inter-connected and with the highest values of self-settlement were those in the Bay of Campeche (Campeche, Southern Veracruz, Central Veracruz, and Northern Veracruz). Within the Bay of Campeche, the pairs Campeche–Central Veracruz and Campeche–Southern Veracruz had the strongest connections, followed by Central Veracruz–Southern Veracruz, Northern Veracruz–Central Veracruz, and Northern Veracruz–Campeche. The subpopulations that received the lowest number of settlers from few sites were Quintana Roo (0.02%), Flower Garden Banks (0.03%), Central Florida (0.14%), Texas (0.22%), and Northern Florida (0.35%). Southern Florida and Northwestern Cuba provided few settlers to the other subpopulations ( $< 0.004\%$ ) and had very low self-settlement (0.03% and 0.00%, respectively); however, they received settlers from almost all the other subpopulations. The more inter-connected subpopulations (e.g. Central

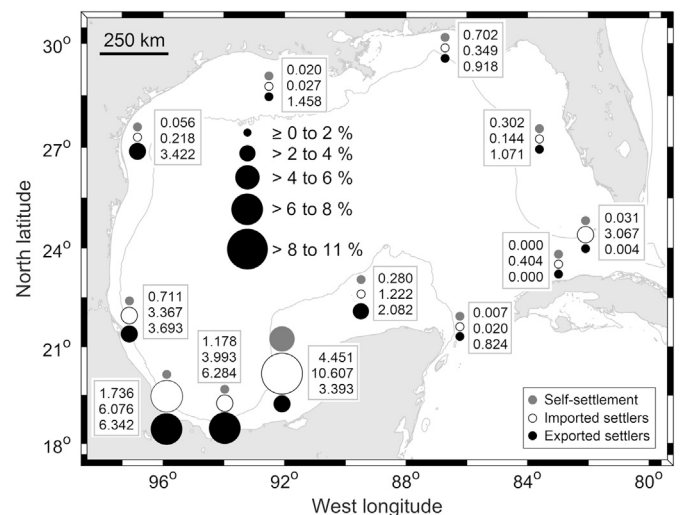


Fig. 4. Self-settlement (top datum, grey dots), imported virtual settlers (middle datum, white dots), and exported virtual settlers (bottom datum, black dots) per subpopulation. Values were derived from the yearly mean connectivity matrix.

Veracruz to Campeche and Southern Veracruz to Campeche) (Fig. 3a Mean) were usually associated with shorter travel times (Fig. 3b) and shorter distances (Fig. 3c). In contrast, some subpopulations closer in distance but associated with longer travel times were less inter-connected (e.g. Southern Florida to Northwestern Cuba). Likewise, some subpopulations farther in distance but associated with shorter travel times had low connectivity (e.g. Flower Garden Banks to Southern Florida, Flower Garden Banks to Northwestern Cuba).

The qualitative pattern described above from the mean connectivity matrix is also observed in the connectivity matrices of individual years (Fig. 3a). However, some differences among years are observed. Overall, the subpopulations in the Gulf of Mexico were somewhat more inter-connected in 2007 (88 connections out of 144) and less inter-connected in 2010 (82 connections out of 144). For instance, the connectivity from Campeche to Central Veracruz was 1.82 times higher in 2007 (2.06%) than in 2010 (1.13%), and the connectivity from Southern Veracruz to Central Veracruz was 1.66 times higher in 2007 (2.73%) than in 2010 (1.64%). On the other hand, the connectivity from Yucatan to Northern Veracruz was highest in 2010 (0.47%) and lowest in 2009 (0.18%), whilst the connectivity from Central Veracruz to Campeche was highest in 2008 (4.47%) and lowest in 2006 (3.20%).

Mean settlement was larger from non-local settlers (imported settlers) than from local settlers (self-settlement), except in Northern Florida and Central Florida (Fig. 4). The ratio of total imported settlers to self-settlement was particularly high in Southern Florida (98.60), Northern Veracruz (4.73), and Yucatan (4.37). The highest value of self-settlement was for Campeche (4.45%), whereas the highest values of imported settlers were for Campeche (10.61%) and Central Veracruz (6.08%). The highest values of exported settlers were for Central Veracruz (6.34%) and Southern Veracruz (6.28%). Northwestern Cuba had the lowest values of both self-settlement and exported settlers (0.00%) (Fig. 4). The qualitative pattern described from the mean settlement and exported settlers is also observed in each individual year; however, some anomalies may be noted (Supplemental Fig. 3). For instance, in Yucatan, self-settlers (0.04%) exceeded imported settlers (0.01%) during 2007. Likewise, in Central Florida imported settlers (0.35%) exceeded self-settlers (0.02%) during 2010. Overall, self-settlement was highest during 2009 (11.24%) and lowest during 2010 (7.17%), whilst imported settlers reached the maximum during 2007 (34.81%) and the minimum during 2010 (23.46%).

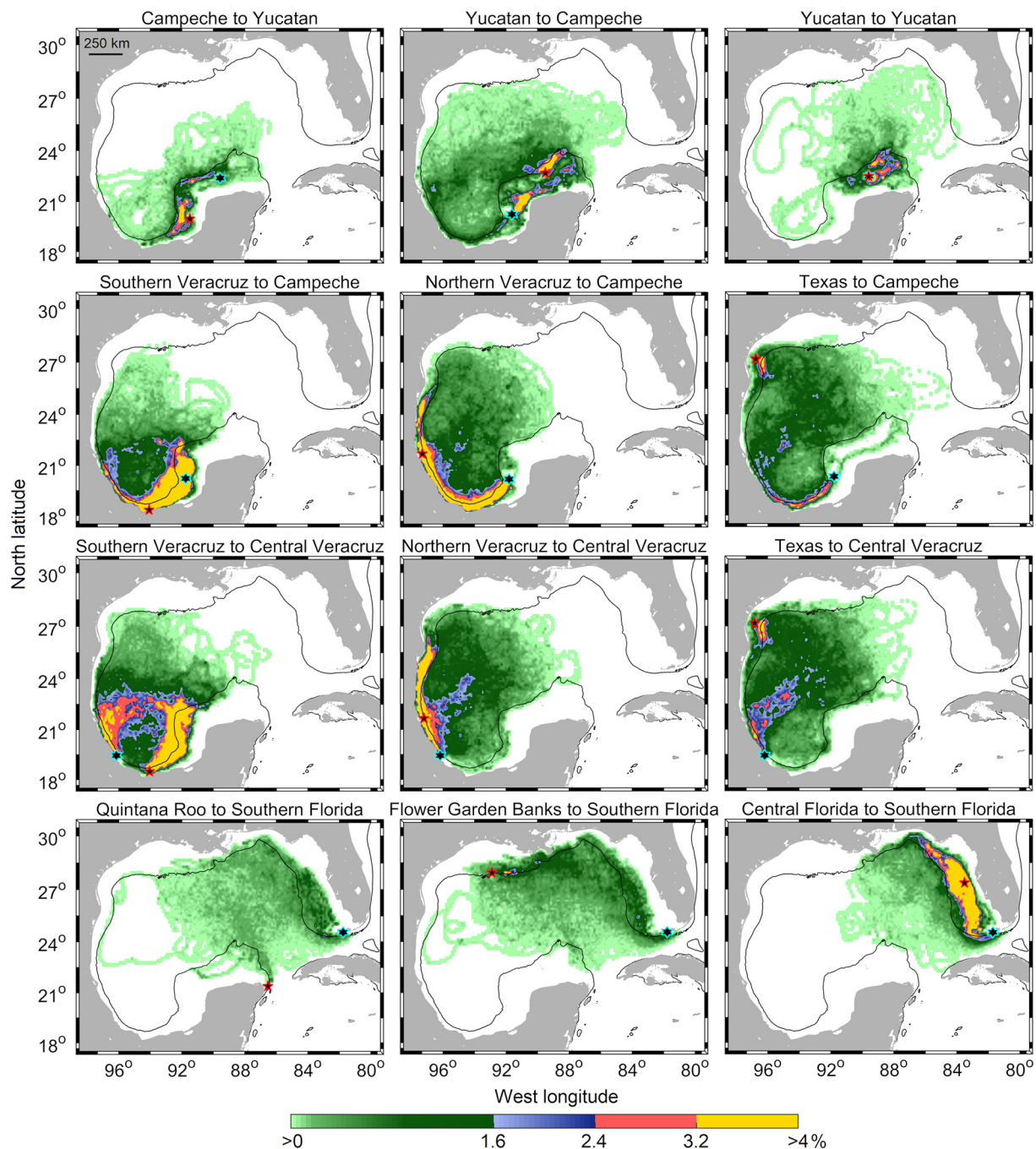


Fig. 5. Dispersal pathways of virtual larvae released from an origin subpopulation that were successfully settled in a destination subpopulation (ensemble of 2006–2010). Only the 12 most representative cases are shown. Virtual larvae were released from March 21 to June 18 (2006–2010) and allowed to settle at ages of 140 d or more. 100% corresponds to the maximum number of positions in an area of ~11 km<sup>2</sup>. The 200 m isobath is shown.

### 4.3. Dispersal pathways

The larval dispersal pathways (Fig. 5) reflected major ocean currents. For example, dispersal pathways from Yucatan to Campeche show that anticyclonic circulation (related to Loop Current eddies) north of the Bay of Campeche may transport larvae released in Yucatan towards the western Gulf of Mexico. Then, the coastal circulation and the cyclonic gyre in the Bay of Campeche may transfer the larvae towards Campeche. As an alternative dispersal pathway, larvae released in Yucatan may also be captured by the inner-shelf current in the Campeche Bank and then transported to the Bay of Campeche, following a shorter path.

Larval dispersal pathways (Fig. 5) from Southern Veracruz to

Campeche and from Southern Veracruz to Central Veracruz highlight retention in the Bay of Campeche caused by the cyclonic gyre in the region. The larval dispersal pathway from Texas to Campeche shows that larvae are initially trapped by an anticyclonic eddy north of the Bay of Campeche. Eventually, larvae are transferred to coastal circulation and to the cyclonic gyre in the Bay of Campeche, forming an inverted S-shaped dispersal pathway. Larval dispersal pathways reaching Southern Florida were strongly dependent on the Loop Current (e.g. Quintana Roo to Southern Florida). Dispersal pathways from Yucatan to Yucatan show that larvae may travel long distances away from the natal subpopulation before returning home for self-settlement. In addition, larval dispersal pathways connecting subpopulations in the Bay of Campeche were strongly dependent on the coastal circulation of

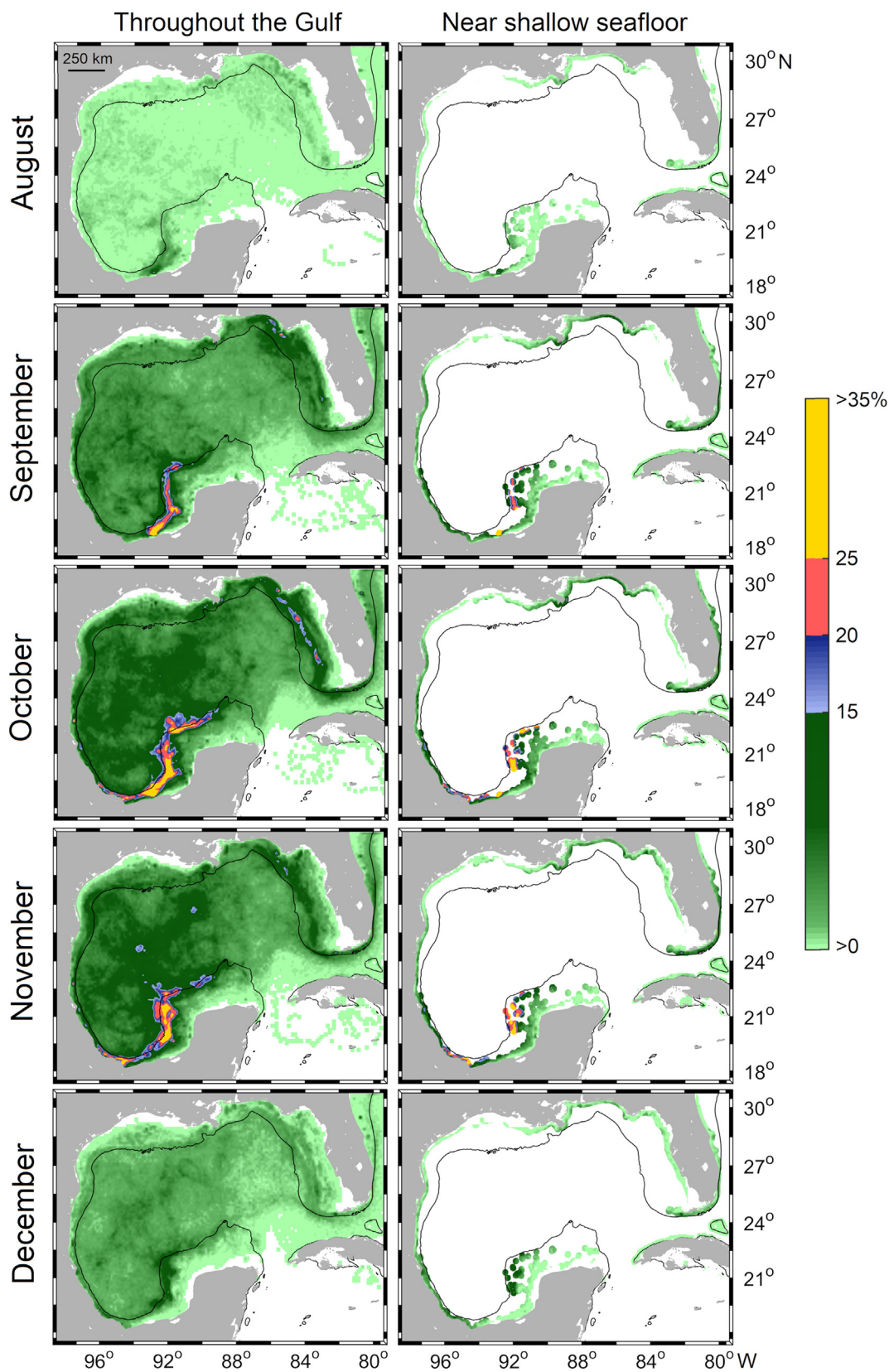


Fig. 6. Monthly dispersal pathways of all the virtual post-larvae (competent for settlement). The settlement period was from August 20 to December 31 (ensemble of 2006–2010). 100% corresponds to the maximum number of positions in an area of  $\sim 11 \text{ km}^2$ . The 200 m isobath is shown.



the southwestern Gulf of Mexico. Although some deformation may be observed, such as elongation, compression, or more meandering, the dispersal pathways display practically the same pattern year after year (Supplemental Figs. 4–8).

Finally, post-larval dispersal pathways for each month (Fig. 6) show that, although most of the Gulf of Mexico may be occupied by post-larvae, the occurrence of post-larvae is larger on continental shelves and along shelf-breaks. In particular, the western edge of the Campeche Bank comprised the shallow region most populated by virtual post-larvae throughout the whole settlement season (from August 20 to December 31). During October–November, virtual post-larvae were also particularly abundant over the shallow and narrow continental shelf of Veracruz. Likewise, a relatively high occurrence of post-larvae is observed along the outer shelf of western Florida during this season. These patterns were consistently observed during the 5 years (Supplemental Figs. 9–13). In 2008, an important accumulation of post-larvae was observed in oceanic waters, centred about 93°W, 24°N (Supplemental Fig. 11).

## 5. Discussion

A particle-tracking model coupled to a realistic hydrodynamic simulation was used to fill information gaps on connectivity dynamics of *Panulirus argus* in the Gulf of Mexico, a region poorly studied in this regard. The main findings suggest that the Bay of Campeche may contain the sub-populations with the highest inter-connectivity and settlement throughout the Gulf. Moreover, it was found that these subpopulations could have some degree of independence from larval supply of subpopulations in other regions of the Gulf and Caribbean Sea. The estimated connectivity patterns remained rather constant during the studied years, although lower levels of connectivity were observed in 2010. This reduced connectivity could be related to changes in ocean circulation caused by atypical atmospheric perturbations over the Gulf during that year (Section 5.1). The larval dispersal pathways connecting subpopulations confirmed well-known hydrodynamic patterns (e.g. Loop Current) while revealing less conspicuous patterns (e.g. an inverted S-shaped current connecting Texas with Campeche). Regions with the highest post-larval abundances were found on the continental shelves and along the edge of continental shelves, particularly in the Bay of Campeche (from Veracruz to Campeche). Because neritic waters in the Bay of Campeche constitute both frequent larval dispersal pathways and regions for post-larval aggregations (high settlement), they are likely to play an important role in population dynamics of *P. argus*. Detailed discussion is provided in the next sections.

### 5.1. Connectivity

The high inter-connectivity and settlement in subpopulations in the Bay of Campeche seems to be a consequence of the joint effect of: (a) the long pelagic larval duration (Goldstein et al., 2008), (b) the recirculation caused by the cyclonic gyre in the Bay of Campeche (Pérez-Brunius et al., 2013), and (c) a back and forth behaviour of currents in the Veracruz shelf (Allende-Arandía et al., 2016). Self-settlement was low at Quintana Roo, Southern Florida and Northwestern Cuba because the Loop Current quickly transported the larvae far away. Southern Florida received a considerable number of settlers coming from almost all the other subpopulations mainly by means of the Loop Current. This result supports the idea that an important proportion of settlement in Southern Florida is maintained by foreign post-larvae (Yeung and Lee, 2002; Ehrhardt and Fitchett, 2010; Segura-García et al., 2019).

Southern Florida and Northwestern Cuba provided almost no settlers to the other subpopulations because their larval production quickly left the Gulf of Mexico through the Florida Strait. In Flower Garden Banks, Central Florida, Texas, and Northern Florida, settlement was low because the shelf currents in these regions were not favourable

for inshore transport during the settlement period (August–December). Quintana Roo received the fewest settlers from the Gulf of Mexico because the Loop Current usually drove away the larvae that approached the Mexican Caribbean. This is consistent with previous modelling efforts suggesting that most settlers in Quintana Roo come from the southern and eastern Caribbean Sea, by means of the Caribbean Current (Briones-Fourzán et al., 2008; Kough et al., 2013).

The existence of connectivity between the farthest subpopulations (Northern Veracruz to Southern Florida) (Fig. 3) supports the idea that larval dispersal of *P. argus* may occur throughout the Gulf of Mexico, preventing genetic differentiation among subpopulations (Naro-Maciel et al., 2011; Segura-García et al., 2019). As noticed from the connectivity matrices (Fig. 3a) and the minimum travel times matrix (Fig. 3b), there were cases (e.g. Southern Florida to Yucatan) when larvae reached a subpopulation but not during the competency period (when larvae are ready for settlement). This implies that the competency period, in addition to the pelagic larval duration, is a factor driving connectivity. Similarly, if propagules had not been “killed” by the mortality function, they might have settled in some subpopulation (e.g. Central Florida to Southern Veracruz); that is, mortality also affects connectivity (Paris et al., 2007).

Eggleston et al. (1998) reported low inter-annual variability in settlement of *P. argus* in the central Bahamas, with differences among sites being relatively stable over time (i.e. some regions always showed more settlement than others). Similarly, in the present study, the main patterns of connectivity were consistent through time, although some differences were observed, mainly in 2010. In this year, more tropical cyclones (atmospheric low-pressure systems) crossed the Gulf of Mexico, moving from the Caribbean Sea through the Yucatan Peninsula and then across the western Gulf of Mexico. This cyclonic wind patterns induced cyclonic ocean circulation, mainly on the shelves, modifying the biological connectivity. This was observed from a careful qualitative analysis of the oceanic and atmospheric patterns through a HYCOM reanalysis and from Atmospheric 10-m winds generated in our research group (available at <http://grupo-ioa.atmosfera.unam.mx/pronosticos>, accessed September 2019). A detailed and quantitative study of the interannual variability of the circulation in the Gulf of Mexico goes beyond this study. To better characterize the inter-annual variability of connectivity dynamics of *P. argus* in the Gulf of Mexico, future research considering a greater number of years should be conducted.

### 5.2. Dispersal pathways

The larval dispersal pathways from Yucatan to Campeche (Fig. 5) confirm the idea of Manzanilla-Domínguez and Gasca (2004) that larvae of *P. argus* released in Yucatan may be transported to Veracruz by anticyclonic eddies moving westward, and then carried to the western Campeche Bank by shelf currents and the cyclonic gyre in the Bay of Campeche. However, larvae released in Yucatan may also be incorporated into the Bay of Campeche by the westward inner-shelf current of the Campeche Bank (Fig. 5). A considerable number of larvae released in Yucatan was also transported to Southern Florida by the Loop Current, as suggested by Yeung and Lee (2002).

In general, the western edge of the Campeche Bank (up to ~25° N) was the region with larger fluxes of successfully settled virtual larvae (Fig. 5). Similarly, other studies have shown that this region functions as an ecological corridor that connects coral reefs in the southwest Gulf of Mexico (Sanvicente-Añorve et al., 2014; Ortiz-Lozano et al., 2013). Moreover, post-larval dispersal pathways (Fig. 6) show that the western edge of the Campeche Bank is the region most populated by virtual post-larvae. Consistently, Manzanilla-Domínguez and Gasca (2004) found high concentrations of late-stage larvae of *P. argus* in plankton samples taken in this region. Thus, the continental shelf of Veracruz and the western edge of the Campeche Bank resulted very important not only as larval dispersal pathways but also as post-larval settlement areas. In October and November of 2008, a considerable accumulation

of virtual post-larvae occurred in oceanic waters, north of the Bay of Campeche. The spatiotemporal identification of post-larval patches is useful for delimiting oceanic regions and times where the species may be more sensitive to ocean pollution (e.g. oil spills). Whether post-larvae in these areas under different levels of pollution could survive long enough to settle remains to be determined.

Although settlement of *P. argus* can occur throughout the year (Little 1977; Marx 1986), the settlement season reproduced in the present study (summer and fall) is consistent with observed settlement peaks in the Caribbean Sea (Briones-Fourzán et al., 2008; Kough et al., 2013), Southern Florida (Little 1977; Marx 1986) and central Bahamas (Eggleston et al., 1998). The settlement season reproduced in this study is a result of the selected spawning season (spring) and the selected post-larval competency periods (140–198 d). Future research could be conducted to characterize the connectivity of *P. argus* in the Gulf of Mexico resulting from spawning during off-peak seasons.

### 5.3. Larvae from the Caribbean Sea

The Caribbean Sea is considered an important source of *Panulirus argus* larvae for the Mexican Caribbean (Briones-Fourzán et al., 2008; Kough et al., 2013) and Southern Florida (Yeung and Lee, 2002; Butler et al., 2011). However, it is unclear if Caribbean larvae are equally important for northernmost and westernmost subpopulations in the Gulf of Mexico. To further examine this issue, virtual larvae were released from Chinchorro Bank and Grand Cayman Island (Supplemental Fig. 14). Most of the larvae released from Chinchorro Bank were entrained in the Loop Current and transported to Southern Florida and Northwestern Cuba for potential settlement. This finding is consistent with previous studies showing that Lagrangian particles in the eastern half of the Gulf of Mexico are highly connected with the Northwestern Caribbean Sea but relatively isolated from the western half of the Gulf of Mexico (Miron et al., 2017, 2019). In contrast, most of the virtual larvae released from Grand Cayman Island remained within the Northwestern Caribbean Sea, and only a small fraction was trapped by the Loop Current in the eastern Gulf of Mexico. This is also consistent with the idea of a Lagrangian province in the Cuban Caribbean that isolates Lagrangian particles from the Gulf of Mexico, particularly from the western half of the Gulf (Miron et al., 2017). It seems that the Loop Current functions as a hydrodynamic barrier limiting Caribbean larval supply to subpopulations in the western half of the Gulf of Mexico.

The contribution of Caribbean larvae to settlement in Yucatan could still be important if larval production were higher in the Caribbean Sea than in the Gulf of Mexico. However, the mean connectivity analysis for Yucatan indicates that self-settlement (0.28%) can be four times higher than settlement of post-larvae originated in Quintana Roo (0.07%), on the border between the Mexican Caribbean and the Gulf of Mexico. Even if the larval production of Quintana Roo were three times higher than that of Yucatan, self-settlers in Yucatan would still be ~1.33 times more abundant than settlers originated from Quintana Roo. In addition, Yucatan received a considerable proportion of settlers from Campeche (0.24%), Southern Veracruz (0.25%), and Central Veracruz (0.28%). Therefore, settlement of post-larvae in Yucatan could be more dependent on larvae from the Gulf of Mexico, particularly from subpopulations in the Bay of Campeche, than on larvae from the Caribbean Sea. Limited biological connectivity between the Mexican Caribbean and Yucatan has also been reported for the Queen conch, *Lobatus gigas* (previously *Strombus gigas*) (Paris et al., 2009).

### 5.4. Marine protected areas

Studies have demonstrated that the establishment of Marine Protected Areas, selected regions with restrictions for fishing, tourism, and other industrial activities, allow the preservation of *P. argus* stocks while adding to and maintaining fishing yields (Kojis et al., 2003; Cox and Hunt, 2005; Ley-Cooper et al., 2014). According to scientific

guidelines for designing Marine Protected Areas (Brock et al., 2012), it is a priority to protect habitats with crucial functions driving ecosystem processes. The continental shelf in the Bay of Campeche, particularly the western edge of the Campeche Bank, was identified as a key region providing two important ecological functions for *P. argus*: 1) larval pathways connecting subpopulations and 2) areas with high probability of settlement. The western edge of the Campeche Bank has many shoals and submerged reefs, as well as emergent reef structures (Jordán-Dahlgren and Rodríguez-Martínez, 2003), which could provide important habitats for *P. argus* (Butler et al., 2006). Because habitats are more likely to maintain their ecological roles if they are less exposed to anthropogenic disturbances. Setting spatial restrictions by means of Marine Protected Areas in the continental shelf of the Bay of Campeche should be highly beneficial for the sub-population network of *P. argus* in the Gulf of Mexico.

Protection of Yucatan and Quintana Roo would also be important under the concept of helping to maintaining post-larval supply to Southern Florida (an important fishing region of *P. argus*; Hunt, 2000), which has shown some degree of dependence on distant stocks (Ehrhardt and Fitchett, 2010). Likewise, maintaining healthy environmental conditions (e.g. low levels of marine pollution) in southern Florida will be necessary for post-larvae to successfully settle and develop subsequent benthonic stages. Protecting the larval sink is probably as important as protecting the larval source. The northernmost Gulf of Mexico was not hydrodynamically favoured with larval or post-larval supply. Thus, although *P. argus* may be present in the northernmost Gulf of Mexico, the existence of a large subpopulation not yet discovered in little-explored regions of the northernmost Gulf (Moore, 1962) seems unlikely. As far as *P. argus* is concerned, establishing Marine Protected Areas in northern regions would not entail as many benefits as protecting southwest areas of the Gulf (i.e. Bay of Campeche, Yucatan and Quintana Roo).

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### Declaration of Competing Interest

None.

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### Appendix A. Supplementary data

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