

# Dispersal modeling of octopoda paralarvae in the Gulf of Mexico

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## Abstract

The dynamics and population structure of octopus species in the Gulf of Mexico (GoM) can be studied by analyzing dispersal paralarvae mechanisms. Accordingly, this study focused on understanding octopus paralarval dispersal using numerical modeling. A Lagrangian approach was implemented using the transport model ICHTHYOP and surface currents from a GoM simulation of the HYbrid Coordinate Ocean Model (HYCOM). We modeled the dispersal of four octopus species from the GoM (*Octopus vulgaris*, *O. insularis*, *Macrotritopus defilippi*, and *Amphioctopus burryi*), considering two regions as the source of larvae in the southern GoM, namely the Yucatan shelf and the Veracruz coastal waters. Additionally, an environmental suitability analysis was incorporated using the maximum entropy (MaxEnt) model to establish potential settlement areas under the influence of the water masses' thermal conditions. The simulation results supported the hypothesis that the abundances recorded in the GoM were influenced by the fertility (egg-laying) of each species, surface water circulation (the Loop Current, eddies, and wind), and sea surface temperature. Greater dispersal was obtained throughout the GoM for Yucatan species *O. vulgaris*, registering the highest settlement rates. In contrast, in Veracruz, *O. insularis* dispersed and settled only in the western portion of the GoM. The relevance of the ecological descriptors proposed to influence the dispersal and abundance of octopods throughout the GoM's coastal waters are discussed.

## KEY WORDS

fertility, Gulf of Mexico, Lagrangian model, larval transport, MaxEnt, octopus, settlement

## 1 | INTRODUCTION

In Mexico, the octopus is one of the five fishery products with the highest economic value, helping render the country the world's third-largest producer (CNP, 2017). An octopus fishery in the Gulf of Mexico (GoM) and Caribbean Sea (annual average of more than 25 thousand tons) is defined by the capture of the Mexican four-eyed octopus (*Octopus maya*) in the Yucatan Shelf and the common and widespread octopus *Octopus vulgaris* (CNP, 2017) recently re-described as *Octopus americanus* in the Campeche bank (Avendaño, Roura et al., 2020) and *Octopus insularis* in the western GoM in Veracruz (Flores-Valle et al., 2018; González-Gómez et al., 2018).

Depending on the species, an octopus' life cycle may or may not have a larval phase (paralarvae), a feature that shapes their potential distribution area (Villanueva et al., 2016). Thus, the lack of a planktonic phase in *O. maya* (Rosas et al., 2014) may restrict its distribution in the Yucatan Peninsula. In contrast, the planktonic phase in *O. insularis* and *O. "vulgaris"* allows these species to undertake horizontal displacements, settling and colonizing distant areas (Villanueva et al., 2016). Adults *O. insularis* have been recorded in GoM and Caribbean Sea coastal waters, the western Atlantic, and oceanic islands in north-eastern Brazil (Flores-Valle et al., 2018; Leite et al., 2009; Lima et al., 2017, 2020). Recent studies indicated that *O. vulgaris* represents a species complex (Jereb et al., 2014), meaning several species are incorrectly assigned under the *O. vulgaris* designation (Amor et al., 2019). For instance, *O. vulgaris* Type I inhabits the GoM and Caribbean Sea (Jereb et al., 2014). In contrast, *O. vulgaris* Type II is associated with South America, although it has been reassigned as *O. americanus* Montfort, 1802 with samples from North America (Avendaño, Roura et al., 2020).

For the GoM and Caribbean, numerous cephalopod species have been reported; however, few octopuses are commercially exploited (Judkins et al., 2010). This may be due to the species' low abundance or small size of adult specimens, making them inadequate for commercial exploitation. For example, *Amphioctopus burryi* and *Macrotritopus defilippi* are octopuses of small to moderate size, between 70 and 90 mm in mantle length (Guerra et al., 2013). Both species have a wide distribution in areas of Europe and America (Guerra et al., 2013; Jereb et al., 2014) and have been recorded in the north and south of the GoM (Forsythe & Hanlon, 1985; González-Gómez et al., 2020; Hanlon & Hixon, 1980; Jereb et al., 2014; Judkins et al., 2017).

In Mexico, pioneer studies related to paralarvae distribution are restricted to the Pacific coast (Aceves-Medina et al., 2017; De Silva-Dávila et al., 2018; Okutani & McGowan, 1969). Despite the economic importance of octopus fisheries in the GoM and Caribbean Sea, few studies of octopus paralarvae exist in Mexico. As far as we know, to date, for the Caribbean Sea and southern GoM, the only studies that have been carried out are those of Castillo-Estrada et al. (2020) and Santana-Cisneros et al. (2021), respectively.

The specific identification of paralarvae represents a critical component to understanding the life cycle of octopuses, providing the systematic and biological information necessary for studies of population dynamics, including their dispersal, distribution,

reproductive season, and spawning areas and the importance of settlement and recruitment of each species (De Silva-Dávila et al., 2013). In the southern GoM, the small size (0.5–2.0 mm ML) of the paralarvae of *O. vulgaris* Type I, *O. americanus*, *M. defilippi*, *A. burryi*, *A. cf. burryi*, *Octopus* sp., *O. insularis*, and *Callistoctopus furvus* obtained by Santana-Cisneros et al. (2021) suggests that the species have hatched in areas near Yucatan and Tamaulipas.

Larval dispersal is arguably the most important but least understood demographic process in the sea due to its assessment difficulty (Swearer et al., 2019). In the southern GoM, it is a poorly studied subject, although some evidence has been obtained for *Panulirus argus* lobster (Briones-Fourzán et al., 2008; Butler et al., 2011; Ehrhardt et al., 2011; Kough et al., 2013), fish larvae (Johnston & Bernard, 2017), corals (Salas-Monreal et al., 2018), and decapods (Sanvicente-Añorve et al., 2018). Dispersal can be understood as the spread of larvae from a population source to a final site (Pineda et al., 2007). Larvae are strongly influenced by advective processes, which induce their transport within the system and shape the environmental conditions they experience (Siegel et al., 2003). Therefore, the assessment of larval dispersal is important when considering the biology of the studied species (Cowen & Sponaugle, 2009; Levin, 2006; Pineda et al., 2007).

Comprehending the dispersal paralarvae mechanisms at play, the environmental and ecological effects that regulate post-larval settlement dynamics, and juvenile recruitment are essential for fisheries management (Ehrhardt et al., 2011). Therefore, larval displacements are often studied to understanding a species' population ecology and benthic community structure. As a result, they generate direct applications for management, conservation, and evolutionary studies (Grimm et al., 2003; Ross, 2016).

Lagrangian particle tracking methods are usually used to simulate particle dispersal in general circulation oceanic models, thereby tracking particles' transport via currents and simultaneously assessing the ocean's hydrodynamic mechanisms (Ross, 2016). Applications of these models have been used to estimate the dispersal of sea turtles (Naro-Maciel et al., 2017), sargassum (Putman et al., 2018), fish larvae (Catalán et al., 2013), corals (Garavelli et al., 2018), and lobsters (Lara-Hernández et al., 2019). To the best of our knowledge, the dispersal pathways of octopus paralarvae have yet to be addressed.

Understanding the pattern of oceanic currents helps to explain larval dynamics. However, the arrival of larvae at a given site does not necessarily imply recruitment success (Kough et al., 2013). Bioinformatic advances that integrate oceanography and biology are tools that researchers can use to address dispersal, recruitment, and connectivity inquiries that were too challenging a decade ago (Kough et al., 2013). The reproductive strategies of each species should be reflected in settlement success, with increased fertility (Kritzer & Sale, 2006) and favorable currents being key elements (Villanueva et al., 2016) that are regulated by the species' adaptation to the environment (Angilletta, 2009).

This study aimed to assess the dispersal and potentially suitable settlement sites of octopus species, namely *A. burryi*, *M. defilippi*, *O.*

*insularis*, and *O. "vulgaris"* which were already recorded by Santana-Cisneros et al. (2021) for the southern GoM using an interdisciplinary approach. In this study, the following hypotheses were tested: (a) dispersal driven by the GoM's oceanic surface currents can explain the distribution of the four species; (b) temperature tolerances influence the species' survival (reflected in their settlement); and (c) the fertility of each species counterbalances the high mortality in plankton. The results provide support to explain why certain species are more abundant within the planktonic and adult size class in the GoM. We expected that eurythermic species and those with higher fertility would have a wide distribution, which could potentially explain their higher abundance in settlement habitats.

## 2 | METHODS

A Lagrangian approach was implemented to simulate octopus paralarval dispersal. We assumed that organisms behave as passive particles advected and diffused from the source regions by the oceanic surface currents. The species and months considered for numerical experiments were previously reported by Santana-Cisneros et al. (2021) for the southern GoM. *A. burryi*, *M. defilippi*, *O. insularis*, and *O. "vulgaris"* were sampled in November 2015; May, June, July, September, October, and December 2016; January, June, September, and November 2017; and July 2018. Those species were chosen because online repositories, such as OBIS and GBIF, have a higher occurrence of these species than the others reported by these authors. Species occurrences are necessary to utilize the ecological niche models presented below.

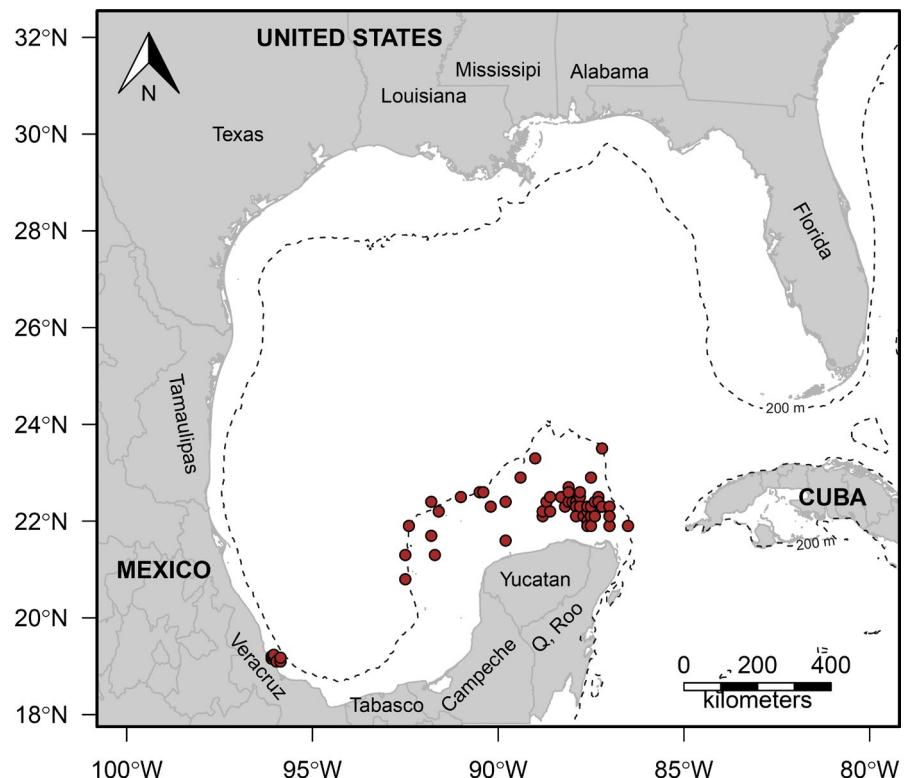
### 2.1 | Source region delimitation

The first requirement to assess paralarval dispersion using the numerical model (ICHTHYOP) was to define the regions of particle release. Two release regions were considered for this study: Yucatan and Veracruz (Figure 1) in the southern GoM. For the Yucatan coastal waters, the sites of occurrence of the *A. burryi*, *M. defilippi*, and *O. "vulgaris"* paralarvae were recorded by Santana-Cisneros et al. (2021). The paralarvae of these species were selected due to their small size and their large abundance in the samples (see Table S1). For *O. insularis*, the Veracruz coastal waters were chosen as release area based on the González-Gómez et al. (2018) report of adult organisms. Per month, a total of 60 release sites were used for *A. burryi*, *M. defilippi*, and *O. "vulgaris"*, whereas eight release sites were used for *O. insularis* (Figure 1).

### 2.2 | Settlement areas delimitation

#### 2.2.1 | Ecological niche model

Due to the absence of information about the octopus species' temperature preferences, an ecological niche model was constructed to determine possible settlement areas. The maximum entropy (MaxEnt) model was employed with this purpose (Phillips et al., 2006). This correlative model requires species occurrence and environmental data (Phillips et al., 2004, 2006; Phillips & Dudík, 2008). Occurrence data were downloaded using the function "occurrence" to access the Ocean Biogeographic Information System



**FIGURE 1** Study area and release regions of octopus paralarvae. Veracruz coast, eastern Campeche Bank (Yucatan coast)

with the packages “robis” (Provoost & Bosch, 2019) and the function “occ\_data” from the package “rgbf” (Chamberlain et al., 2019) to access the Global Biodiversity Information Facility using the R programming language (R Core Team, 2020). Occurrences deemed inaccurate, such as duplicated data, inland records, or environmental outliers, were excluded. Additionally, oversampling zones were reduced by considering only one occurrence per pixel for *A. burryi*, *M. defilippi*, *O. “vulgaris”* and *O. insularis*. Since more data were available for *O. vulgaris*, we used spatial filtering of 50 km using the function “thin” from the package “spThin” (Aiello-Lammens et al., 2015).

For the environmental layer, mean sea surface temperature and bathymetry data were downloaded from “marspec” (<http://www.marspec.org/>; Sbrocco & Barber, 2013) at a resolution of ~5 arc min. The calibration area for the model was defined according to a historical accessibility hypothesis (Barve et al., 2011) using the ecoregions defined by Spalding et al. (2007).

Different combinations of feature (linear, linear-quadratic, and linear-quadratic-product) and regularization multipliers (0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4) were tested. For the calibration of MaxEnt, occurrences were separated into two databases: 75% of the occurrences were used to calibrate different models and 25% to test them (Figure S1). This process was undertaken using the “kuenm” library, which allows robust model calibration processes based on model significance, performance, and simplicity (Cobos et al., 2019).

For the statistical significance test ( $p < .05$ ), we used a partial receiver operating characteristic curve (pROC, Peterson et al., 2008), an analysis derived from the classical ROC, which removes the emphasis on absence data and evaluates models under a predefined acceptable level of omission error ( $E = 5\%$  in this work). The models with statistical significance were subsequently filtered according to an omission rate of 5% ( $OR_5$ ); the  $OR_5$  is a threshold dependent metric, which indicates the proportion of testing data with values lower than a binarization threshold of training data that leave out 5% of the lowest suitability values. Values above 5% could indicate model overfitting (Peterson et al., 2008). Finally, the most parsimonious model was selected from the remaining models using Delta Akaike criterion ( $\Delta AIC_c$ ; Burnham & Anderson, 2002), a metric that reflects the goodness-of-fit and complexity of the model, where models with a value of  $\Delta AIC_c \leq 2$  have substantial support. Therefore, we selected models with the lowest values since they were the most parsimonious ones.

We created binary maps with the best suitability maps (presence-absence) (Figure 2), using the five-percentile training presence method. The value of this threshold omits the 5% of the occurrence records from training data with the lowest values of suitability, similar to  $OR_5$ .

Besides, the average surface temperature (daytime) each year in the GoM was obtained using the remote sensor AQUA-MODIS (<https://oceancolor.gsfc.nasa.gov/I3/>) at a resolution of 4 x 4 km per pixel. The surface temperatures were used to contrast the environmental suitability results (Figure S2).

## 2.3 | Lagrangian transport model

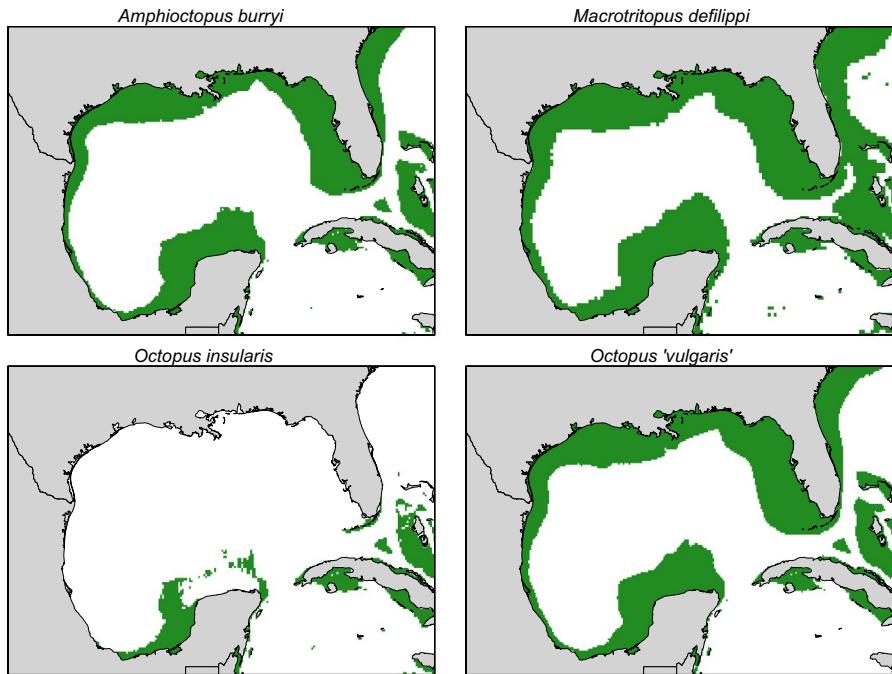
To evaluate particle transport, a numerical model simulating the study area's surface circulation was necessary. Thus, in this study, we used a regional 1/25° (~4.4 km) HYCOM GoM simulation, assimilating data from the Navy Coupled Ocean Data Assimilation (NCODA) system (Cummings & Smedstad, 2013). The NCODA system assimilates available satellite altimeter data, satellite sea surface temperature, *in situ* sea surface temperature, and available *in situ* vertical temperature and salinity profiles from XBTs, Argo floats, and moored buoys, among others. The HYCOM GoM simulations have shown good consistency with observations and accurately reflect eddy characteristics in the GoM (Brokaw et al., 2020; Rosburg & Donohue, 2011; Rosburg et al., 2016). The domain of the model extends from 19 to 32°N and 98 to 76°W in such a way that also includes the Yucatan and Florida currents. That is the area of the GoM where results were interpreted. Given that our analysis period was from November 2015 to July 2018, horizontal surface velocities from Experiment 32.5 (available at <https://www.hycom.org/data/gomlOpt04/expt-32pt5>) were downloaded. The data were tabulated in monthly files with a daily snapshot for temporal resolution to render them compatible with the ICHTHYOP 3.3 model simulations (Lett et al., 2008). Such a resolution allows researchers to represent the realism needed to study marine organism dispersal and is commonly used (Putman et al., 2018).

The particle horizontal advection computation was performed off-line the HYCOM GoM domain with the ICHTHYOP model simulations version 3.3 software (Lett et al., 2008). The ICHTHYOP model simulations properly represented some important marine organisms' dispersion patterns in the GoM and Atlantic (Putman & He, 2013). This study's model configuration included a Runge-Kutta fourth-order time-stepping method, a time step of 30 min, and horizontal diffusion along the advection path (Lett et al., 2008). Simulations were carried out for each octopus species. Each simulation was set for a 60 days' forward run period for the planktonic phase (Villanueva & Norman, 2008). Notably, few studies have assessed the settlement step for the species studied here; previous studies have been conducted under controlled laboratory conditions. Therefore, we considered the most extended period of settlement recorded for *O. vulgaris*, as reported by Villanueva and Norman (2008). Additionally, the number of particles released per species was based on the fertility of each species and the number of eggs: 35,000 for *A. burryi* (Guerra et al., 2013), 10,000 for *M. defilippi* (Guerra et al., 2013), 85,000 for *O. insularis* (Lima et al., 2014), and 100,000 for *O. “vulgaris”* (PMPEY, 2009).

## 2.4 | Settlement analysis

In this study, paralarvae settlement success was also estimated considering (1) the Lagrangian transport model obtained for each species and (2) suitable areas where settlement could occur based on the binary maps obtained. In particular, our study considered the

**FIGURE 2** Presence-absence maps obtained from the suitability maps for octopuses of the Gulf of Mexico



**TABLE 1** Combination of features (linear - l, quadratic - q and product - p) and regularization multipliers (RM – 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4) chosen for the suitability maps

Species	Feature class	RM	Training (n)	Test (n)	Joint (n)	pROC ( $p < .05$ )	$OR_5$	$\Delta AICc$	Thresholdvalue
<i>Amphiocetus burryi</i>	lqp	0.5	41	14	55	0	0	0	0.447681
<i>Macrotritopus defilippi</i>	lq	0.5	38	13	51	0	0	0	0.417846
<i>Octopus insularis</i>	l	0.5	37	12	49	0	0.07	0	0.3495
<i>Octopus "vulgaris"</i>	lq	0.5	68	22	90	0	0.04	0	0.134712

Note: The criteria used to choose the best model were the statistical significance ( $p < .05$ ) by the area ratio under the curve of the partial receiver operating characteristic curve (pROC) and the omission rate criteria of 5% ( $OR_5$ ), where values  $>.05$  may indicate an over-fitted model. Lastly,  $\Delta AICc$  was used to assess both the goodness of fit and the complexity of the remaining model; models with a value of  $\Delta \leq 2$  exhibited substantial support, and therefore, we selected those with the lowest values. Additionally, we show the threshold value used to binarize the suitability maps.

binary map obtained from MaxEnt to delimit the settlement areas down to 100 m due to the empirical evidence of settlement occurring at this depth since the depth ranges from 0 to 200 m for *A. burryi*, 6 to 200 m for *M. defilippi*, from 10 to 220 m for *O. "vulgaris"* and from 0 to 30 m for *O. insularis* (Garofalo et al., 2010; Guerra et al., 2013; Lima et al., 2017; Moreno et al., 2014), although the highest abundance of recruits was found at  $<100$  m (Garofalo et al., 2010). Moreover, we considered the literature available to hypothesize the settlement areas.

Given the fertility differences between species, the abundance of settlements according to the dispersal model were standardized through the  $\log(x) + 1$  equation. Nonetheless, even after data were transformed, they did not fulfil the normality and heteroscedasticity assumptions. Thus, non-parametric tests were conducted on transformed data to compare the settlement rate between each species per month. Monthly settlement success between species in the Yucatan was analyzed through the Kruskal-Wallis non-parametric analysis. Where significant differences in the species' settlement were observed, they were designated through Dunn's post-hoc test

using the "ggepubr" library (Kassambara, 2020). For *O. insularis*, the settlement abundance variation analysis per month was presented separately from the other species because it was the only species simulated in Veracruz; therefore, no comparison between months was made.

## 3 | RESULTS

### 3.1 | Ecological niche model and settlement areas in the GoM

The calibration and selection process delivered niche models with good results, except for *O. insularis*, in which the model was slightly overfitted (Table 1). Nevertheless, based on the binary maps (Figure 2) obtained from the suitability maps (Figure 3), all species established permanent populations within the GoM. *A. burryi*, *M. defilippi*, and *O. "vulgaris"* were found to prefer waters at 20–25°C (Figure S3) throughout the GoM.

*Octopus "vulgaris"* showed the best adaptation in the north of the GoM, where water temperatures were lower than the southern GoM. Additionally, in Mexican waters, the most suitable areas for *O. "vulgaris"* were found in the north of the Yucatan Peninsula (Figure 3). Conversely, *O. insularis* proved to be less suited to the GoM because this species' thermal preferences were warm waters, up to 29°C, in Mexico, Cuba, and Florida, United States (Figure 3, Figure S3). According to the response curves, the octopuses were associated with depths <500 m (Figure S4). The settlement areas derived from the binary maps are shown in Figure 2.

### 3.2 | Paralarval dispersal and settlement of octopus species in the GoM

The simulations revealed that the paralarvae's transport paths from the Yucatan shelf (*A. burryi*, *M. defilippi*, and *O. "vulgaris"*) tend to cover the entire GoM (Figure 4), showing a higher dispersal than *O. insularis* from the Veracruz coast (Figure 5). This pattern was associated with the reduced dynamics in the Campeche Sound compared to regions with mesoscale eddies and strong currents from the Yucatan Shelf. The Yucatan shelf dispersal behavior suggests that particles (paralarvae) could be transported through the Florida strait and beyond (September 2016; January, June, September, and November 2017; and July 2018; Figure 4). The *O. insularis* paralarvae simulations in Veracruz showed a tendency to be retained by eddies; however, during June and July 2016, January and June 2017, and July 2018, they exhibited dispersal to non-suitable areas of the United States (Figure 5).

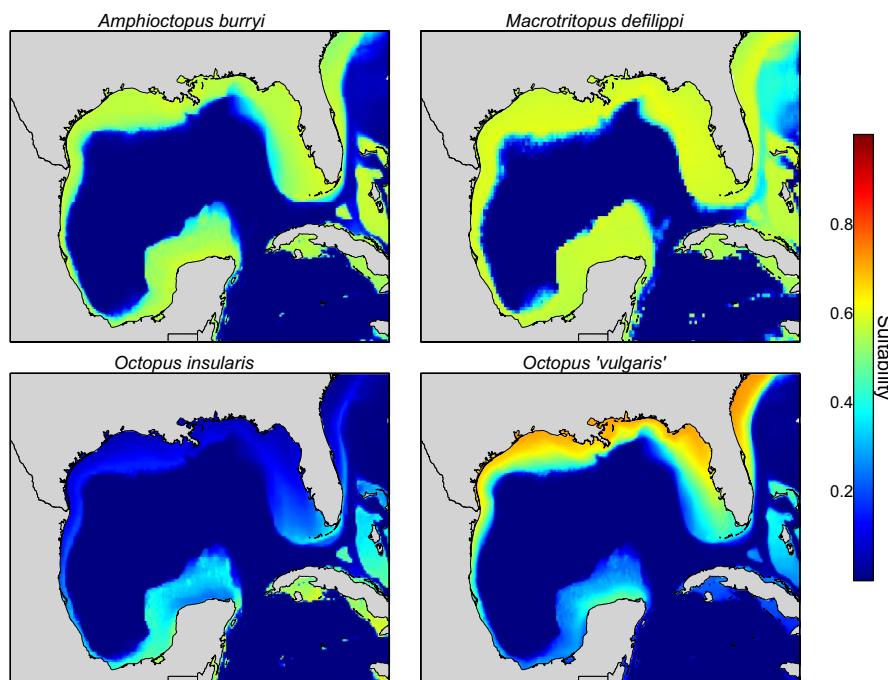
Significant differences in settlement ( $p < .05$ ) took place in almost all the analyzed months, except in November 2015, May, October, and December 2016, and June 2017 (Figure 6). The

highest settlement was recorded for *O. "vulgaris"* followed by *A. burryi* (Figure 6). For *O. insularis*, November 2015 and December 2016 had the greatest settlement success (Figure 7).

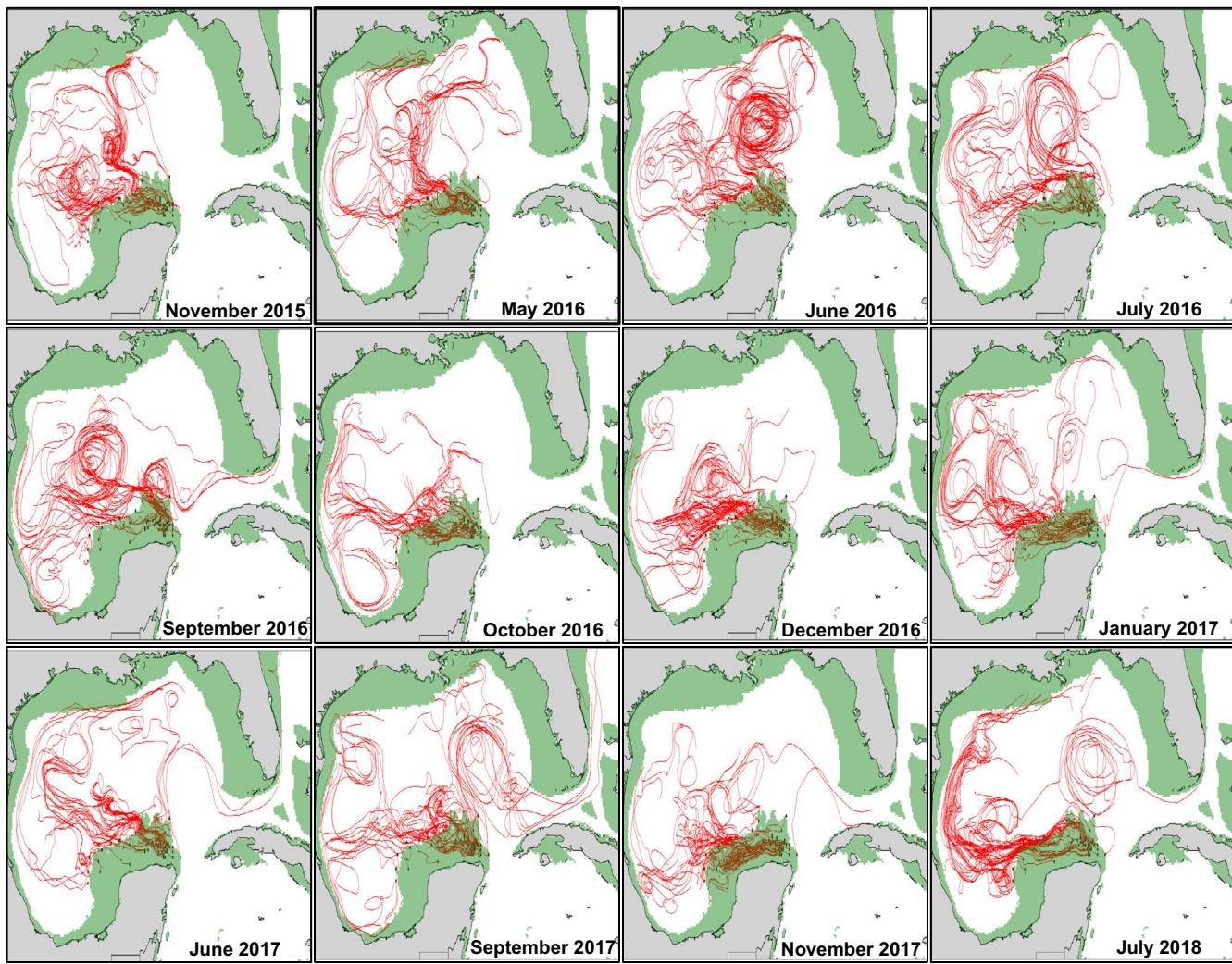
## 4 | DISCUSSION

This study obtained three significant findings for an understanding of paralarval dispersal and settlement in the GoM: (a) paralarvae from the Yucatan shelf can be easily transported to the deeper ocean due to the persistent westward currents here, whereas species dispersal from Veracruz remains (50% of the simulations) trapped due to the Campeche Bay cyclone; (b) *O. "vulgaris"*, *A. burryi*, and *M. defilippi* are better suited to colder temperatures than *O. insularis*. Therefore, octopuses with colder water affinities may present a greater settlement capacity throughout the GoM. (c) species with higher fertility (number of eggs) tend to show greater dominance in settlement simulations.

Our results regarding the suitability of each species allowed us to corroborate differences between the octopus species studied. For three species, a thermal preference close to 20–25°C was reported. The linear relationship between temperature and suitability found for *O. insularis* (Figure S3) could indicate that: (1) this species may prefer higher temperature than other species, and (2) there was a lack of quality in the data (Soberón & Peterson, 2004, 2005) or the volume of data was low (<50 occurrences); thus, the model reliability may be lower than that of the other species (Iturbide et al., 2015). Nevertheless, our results agree with the habitat reported for *O. insularis*, as this species was observed in reef areas (González-Gómez et al., 2018), which are characterized by high temperatures. For example, *O. insularis* preferred temperatures >24°C in Mexico, which coincided with the records of Leite et al. (2008), Leite et al.



**FIGURE 3** Environmental suitability obtained from bathymetry and mean surface temperature via MaxEnt for octopuses of the Gulf of Mexico



**FIGURE 4** Monthly dispersal routes of octopus paralarvae from the Yucatan coast. The green area corresponds to a settlement area based on the binary output of the maximum entropy model

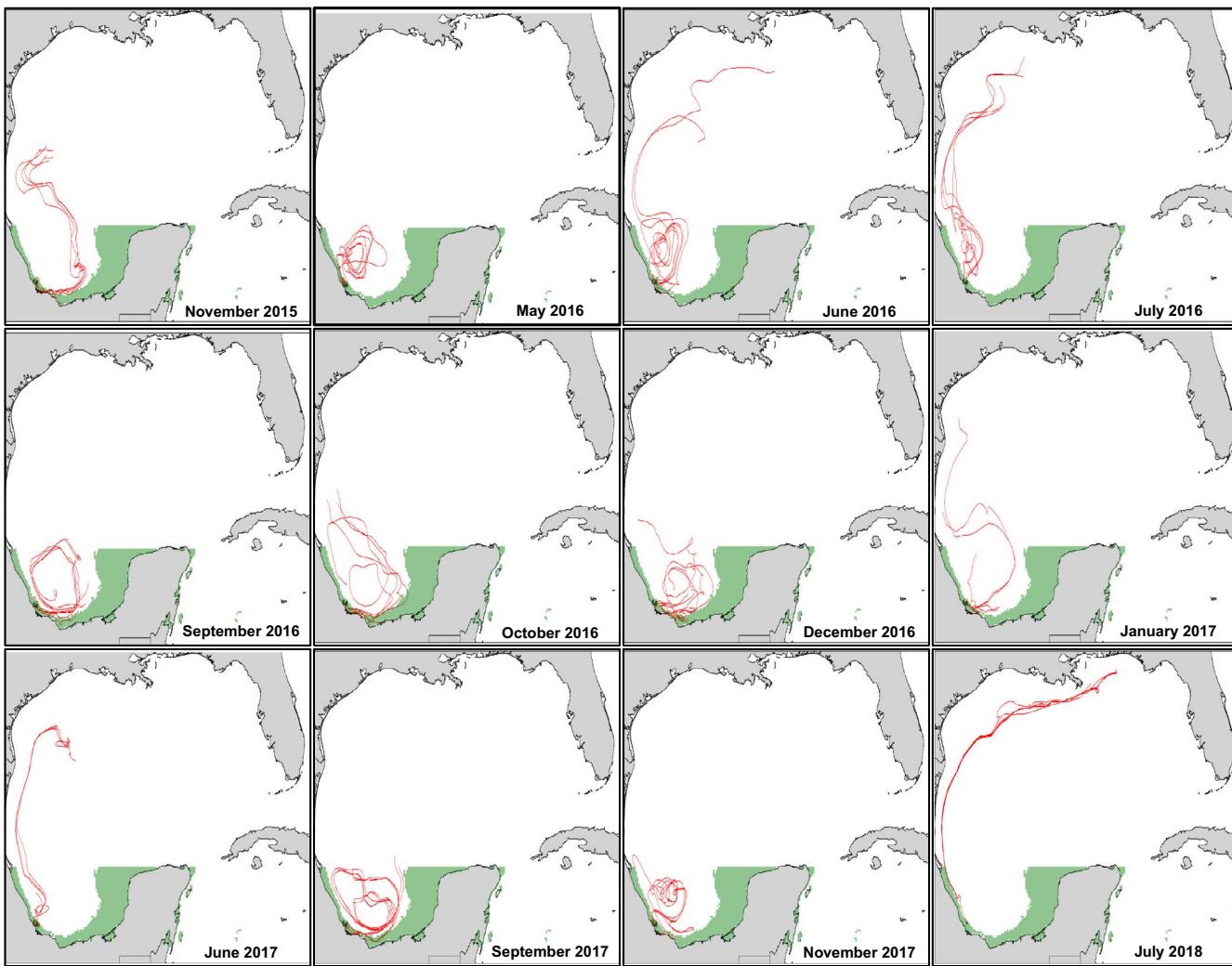
(2009), who noted 24–28°C in Brazil. Additionally, an embryo study of *O. insularis* has shown thermal preferences between 24 and 28°C (Ángeles-González et al., 2020), while a similar model by Lima et al. (2020) established a thermal preference of 26–28°C.

*A. burryi*, *M. defilippi*, and *O. "vulgaris"* shared suitable areas (Figure 2), although the latter had a narrower thermal niche, suggesting a specialization to colder water (Figure 3, Figure S3). Therefore, even though it can establish its populations in the same areas as *A. burryi* and *M. defilippi*, this species has greater suitability for the northern area of the GoM (Figure 3). In our study, the optimal temperatures for *A. burryi* and *M. defilippi* (20–25°C) were consistent with the preferences reported for *A. burryi* by Guerra et al. (2013) in the Canary Islands. Although Guerra et al. (2013) did not directly state thermal preferences for *M. defilippi*, this species may inhabit similar thermal zones to *A. burryi* in this area.

The settlement simulations suggested that the paralarvae's spatial and temporal distributions were strongly influenced by species' fertility and current interactions. In this sense, a higher settlement abundance of *O. "vulgaris"* followed by *A. burryi* and *M. defillipi*, was

obtained in Yucatan throughout most months. This could explain why *A. burryi* and *M. defilippi* have scarce reports and studies in comparison to "*O. vulgaris*". Nevertheless, these species' available records indicate that they share habitats with *O. "vulgaris"* (Díaz et al., 2000; Judkins et al., 2017; Lima et al., 2020). Thus, high fertility and suitable temperatures might explain why *O. "vulgaris"* and *A. burryi* were sampled in almost all oceanographic campaigns in the study by Santana-Cisneros et al. (2021) and why *O. insularis*, another fertile species, was not dominant among the planktonic samples.

The Yucatan paralarvae records were most abundant in the upwelling area (Enriquez et al., 2013). Additionally, the small size of the sampled paralarvae (Santana-Cisneros et al., 2021) suggests that it may be suitable for adult spawning. A relationship between upwelling events and the abundance of octopus larvae has previously been observed in Galician waters in Spain (Otero et al., 2009). The increase in larval abundance and biomass in Galicia was correlated with the simultaneous decrease in water column temperature and the increase in nutrient levels. These conditions occurred during the early stage of the relaxation phase of coastal upwelling events



**FIGURE 5** Monthly dispersal routes of octopus paralarvae from the Veracruz coast. The green area corresponds to a settlement area based on the binary output of the maximum entropy model

when nutrients were being consumed to produce biogenic matter. The characteristics of the upwelling area in our study also raise the possibility that it could be a suitable area for a “larval nursery” and, therefore, associated with larger settlement (Butler et al., 2006). A recent study reported adult presence in these areas (Avendaño, Hernández-Flores et al., 2020).

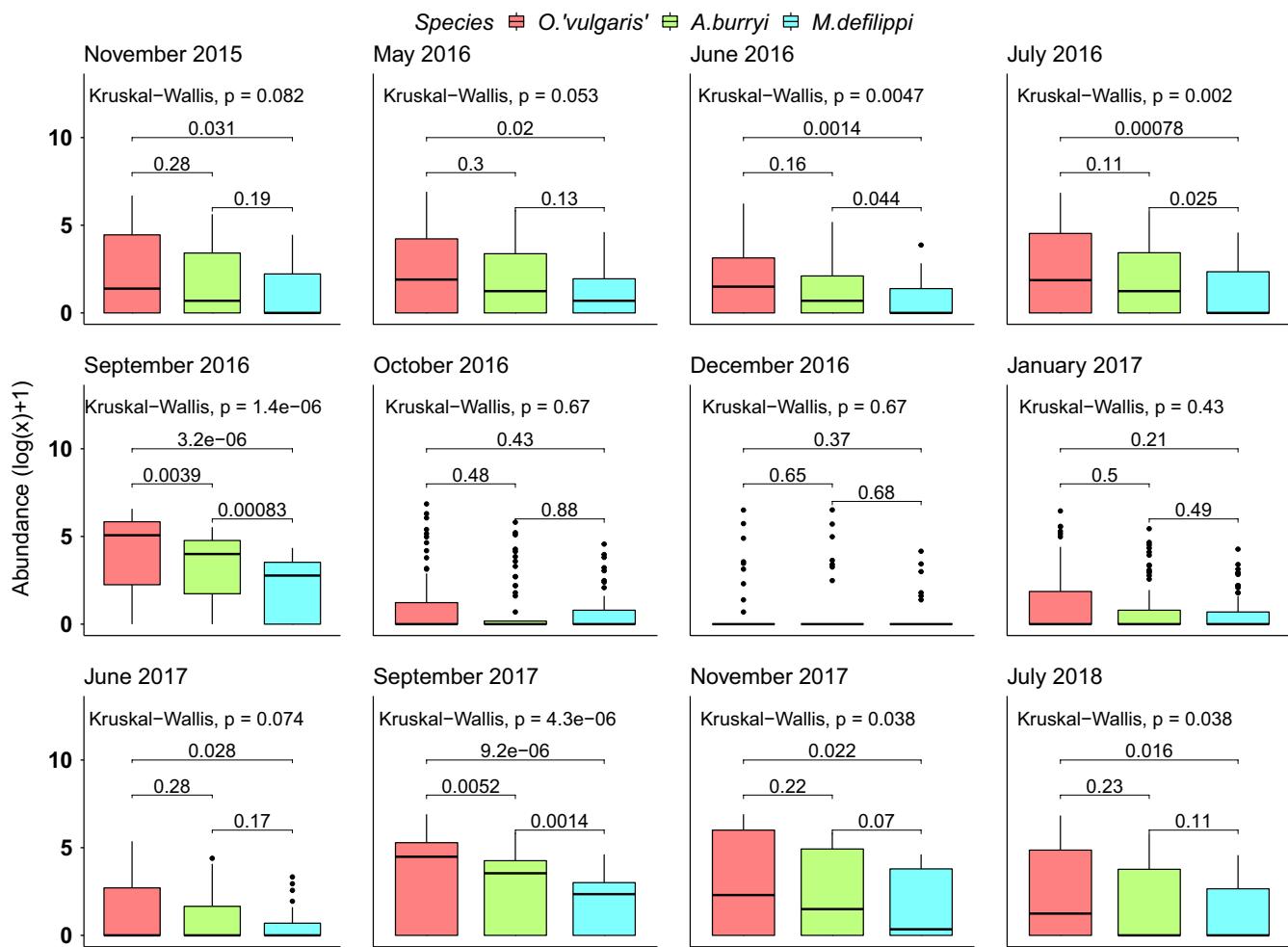
Yucatan's simulated trajectories demonstrate that circulation can easily drive paralarvae beyond the continental shelf, suggesting that larger-sized paralarvae can be pushed further away from it. This pattern encompassing small paralarvae close to the coast and larger sizes in deep waters has been previously reported in Galicia (Rocha et al., 1999). An evaluation of this pattern must consider that larvae transported to areas far from the coast have higher mortality rates due to habitat change (Parrish et al., 1981).

We have also described the months during which paralarvae were transported outside the GoM. These patterns were associated with the presence of the well-developed Loop Current, which emerges from the relative vorticity of the Yucatan Current (Martínez-López & Parés-Sierra, 1998; Reid, 1972) and the convergence of the Florida Current (Judkins

et al., 2010). However, the retention of paralarvae was associated with mesoscale eddies (Butler et al., 2011), a common phenomenon within the general deep-water circulation of the GoM (Stanley, 1995).

The Loop Current was identified in lobster larvae dispersion studies as a transport mechanism that conveys larvae from the Caribbean to the GoM (Briones-Fourzán et al., 2008; Butler et al., 2011; Ehrhardt et al., 2011; Kough et al., 2013). It has also been associated with the higher abundance of cephalopods in Florida (Judkins et al., 2010). Our results agree with these authors, as the Loop Current could transport paralarvae from Yucatan to Florida.

Similarly, studies concerning the dispersal of juvenile sea turtle and lobster larvae have mentioned two contrasting circulation processes along the Florida coast, one associated with the Loop Current, which allows juvenile sea turtles to be transported outside the GoM, while the second supports the retention capacity of juvenile sea turtle and lobster larvae in the GoM by eddies along the western edge of the Loop Current (Lamont et al., 2015; Lara-Hernández et al., 2019). Similarly, our paralarvae show dispersion to the west of the GoM due to wind-driven westward circulation along



**FIGURE 6** Monthly Settlement of octopus paralarvae released from the Yucatan coast

the Yucatan shelf and mesoscale anticyclone advection to the west in deeper waters (Enriquez et al., 2010).

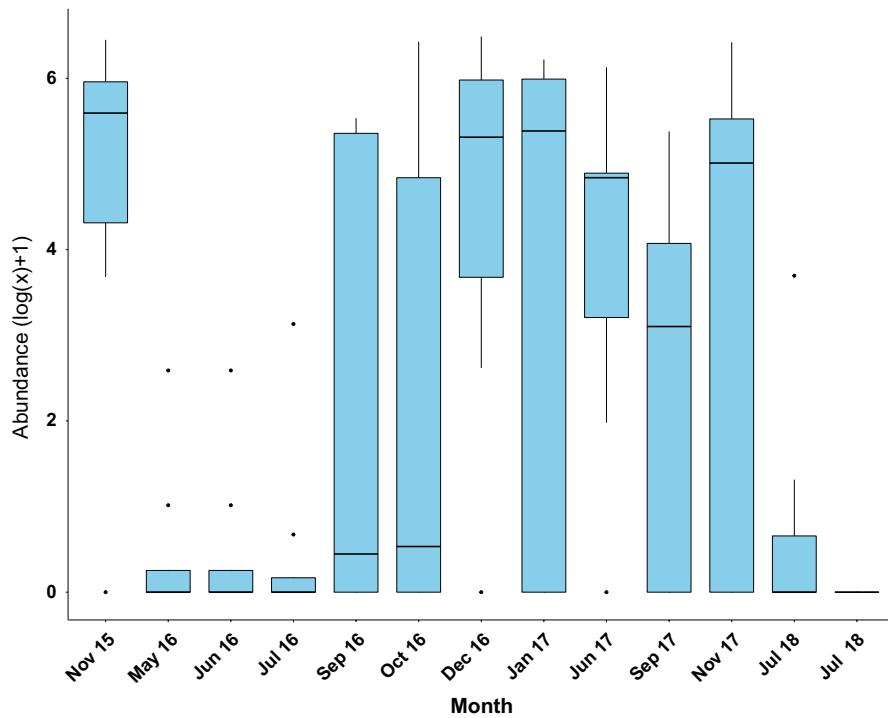
Paralarvae of *O. insularis* tend to remain near Veracruz and neighboring states due to a quasi-permanent cyclonic eddy in that region (Athié et al., 2019; Lara-Hernández et al., 2019). However, there are months during which paralarval transport paths reach the Texas coast and beyond, even though these are areas unsuitable for settlement. Recent studies have shown that the cross-shelf exchange in the western GoM can be substantially influenced by the ubiquitous presence of mesoscale eddies (Guerrero et al., 2020). This pattern has previously been reported by Salas-Monreal et al. (2018), who described a biological corridor for coral larvae from the Flower Garden Reef System (United States) and the Tuxpan-Lobos Reef System (Mexico). They emphasize that coral larvae's greatest connectivity occurs in the south of the GoM between the Tuxpan-Lobos Reef System, the Veracruz Reef System, and the Campeche Reef System. Sanvicente-Añorve et al. (2018) and Lara-Hernández et al. (2019) highlighted the self-recruitment and connectivity of larvae in the Tuxpan-Lobos Reef System and the Veracruz Reef System (west of the GoM). In our study, a lower abundance of *O. insularis* occurred during the spring and summer seasons, given that currents caused

displacement outside the settlement area. These results coincided with Santana-Cisneros et al. (2021) for the Tamaulipas coastal waters, where *O. insularis* paralarva were recorded in June 2017. This finding agrees with Zavala-Hidalgo et al. (2003), who mentioned that the southerly wind aids transportation and circulation from the Mexican shelves to Texas and Louisiana's continental shelf during the spring and summer. During the autumn and winter, the dominant northerly winds cause the opposite effect.

The dispersal and settlement tendencies established in this study support the fertility and environmental suitability hypothesis and agree with the abundances recorded by Santana-Cisneros et al. (2021). Our study's results indicate that species' fertility is a relevant factor in explaining their abundance. A species' capacity to adapt to different habitats represents a possible factor behind some species dominance.

#### 4.1 | Weaknesses and recommendations

Recruitment success requires a successful settlement and settlers' survival to a specific size when they reach a reproductive population



**FIGURE 7** Monthly settlement of *Octopus insularis* paralarvae released from the Veracruz coast

(Pineda et al., 2007). However, factors not considered in this study may influence larval recruitment success. For instance, food availability is a fundamental factor for larval survival (Eckman, 1996; Nixon & Mangold, 1996; Pineda et al., 2007) since starvation and predation are the main factors of larval mortality (Bailey & Houde, 1989; Hunter, 1976; Nixon & Mangold, 1996). Nevertheless, this remains a great challenge to be incorporated into larval simulation. Moreover, we did not evaluate paralarvae survivability due to the environment during the dispersal process; instead, the temperature was only considered during the settlement process. However, adults and juveniles of *A. burryi*, *M. defilippi*, and *O. "vulgaris"* have been recorded in the northern areas of the GoM, with the first two species being mainly associated with sandy and muddy areas (Guerra et al., 2013), while *O. "vulgaris"* is typically an intertidal to shallow subtidal species that inhabits the continental shelf on rocky, sandy, or muddy substrates (Jereb et al., 2014). In contrast, *O. insularis* species prefer dens under rocks in soft bottoms and horizontal crevices (Lima et al., 2017) and are commonly found in coral areas of the GoM (González-Gómez et al., 2018). Unfortunately, no information of settlement success of this species exists for the region; however, for the population of *O. "vulgaris"* sensu stricto in Europe, the settlement success for muddy areas is lower than rocky bottoms (Moreno et al., 2014). The characterization of settlement success from field observations needs to be integrated into the models to develop more realistic simulations since the optimal ocean floor type is needed for survival (Nixon & Mangold, 1996; Pineda, 2000) and, therefore, larval recruitment.

Additionally, vertical migration processes are related to larval retention capacity in coastal waters (Cowen, 2002; Villanueva & Norman, 2008). However, there are still no PL studies that evaluate those processes in the GoM. Given that this was the first study

to assess paralarval dispersal in the GoM, knowledge gaps such as those mentioned above were not considered. Further studies could include this information, but first studies analyzing these factors are needed.

## 5 | CONCLUSION

Our results provide insights into understanding the population dynamics of the octopus species within the GoM. Differences were identified in the transport analysis carried out along the Yucatan coast relative to Veracruz's coastal waters, justifying the greater dispersal of the species observed in the Yucatan and enabling comprehension of the distribution of four octopus species within the GoM. The temperature tolerances and fertility of each species strengthened the analysis and explained the observed settlement differences. This study confirmed that the thermal environmental suitability of *O. insularis* in the GoM is more limited than the other species, particularly compared to *O. "vulgaris"* because both species are similar in fertility and commercial harvesting potential. In contrast, the fertility of *A. burryi* and *M. defilippi* justify the scarce reports in the GoM. Further studies, including vertical migration and ocean floor type, are suggested to corroborate this study's results.

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## CONFLICT OF INTEREST

The authors report no potential conflict of interest.

## AUTHOR CONTRIBUTIONS

MLSC, IVA, PLA, AFG, and IMT conceived and designed the study. MLSC, LEAG, and MCL conducted the simulations and analysis. UOL and all co-authors critically revised and contributed to the final manuscript. All authors agreed for the work to be published.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from corresponding author upon reasonable request.

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## REFERENCES

- Aceves Medina, G., De Silva-Davila, R., Cruz Estudillo, I., Durazo, R., & Avendano Ibarra, R. (2017). Influence of the oceanographic dynamic in size distribution of cephalopod paralarvae in the southern Mexican Pacific Ocean (rainy seasons 2007 and 2008). *Latin American Journal of Aquatic Research*, 45, 356–369. <https://doi.org/10.3856/vol45-issue2-fulltext-11>
- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545. <https://doi.org/10.1111/ecog.01132>
- Amor, M. D., Doyle, S. R., Norman, M. D., Roura, A., Hall, N. E., Robinson, A. J., & Strugnell, J. M. (2019). Genome-wide sequencing uncovers cryptic diversity and mito-nuclear discordance in the *Octopus vulgaris* species complex. *bioRxiv*, 573493. <https://doi.org/10.1101/573493>
- Ángeles-González, L. E., Lima, F. D., Caamal-Monsreal, C., Díaz, F., & Rosas, C. (2020). Exploring the effects of warming seas by using the optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico. *Journal of Thermal Biology*, 94, 102753. <https://doi.org/10.1016/j.jtherbio.2020.102753>
- Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. USA: Oxford University Press.
- Athié, G., Salas-Monreal, D., & Marín-Hernández, M. (2019). Circulación sobre la Plataforma de Veracruz Asociada al Giro de Campeche y su Efecto en los Sistemas Arrecifales. Estudios Científicos en el Corredor Arrecifal del Suroeste del Golfo de México, 37 pp.
- Avendaño, O., Hernández-Flores, A., Velázquez-Abunader, I., Fernández-Jardón, C., Cuevas-Jimenez, A., & Guerra, Á. (2020). Potential biomass and distribution of octopus in the eastern part of the Potential biomass and distribution of octopus in the eastern part of the Campeche Bank (Yucatán , Mexico). *Scientia Marina*, 84(2), 133–142. <https://doi.org/10.3989/scimar.05007.01>
- Avendaño, O., Roura, Á., Cedillo-Robles, C. E., González, Á. F., Rodríguez-Canul, R., Velázquez-Abunader, I., & Guerra, Á. (2020). *Octopus americanus*: a cryptic species of the *O. vulgaris* species complex redescribed from the Caribbean. *Aquatic Ecology*, 54(4), 909–925. <https://doi.org/10.1007/s10452-020-09778-6>
- Bailey, K. M., & Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25, 1–83. [https://doi.org/10.1016/S0065-2881\(08\)60187-X](https://doi.org/10.1016/S0065-2881(08)60187-X)
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., Soberón, J., & Villalobos, F. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, 222, 1810–1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>
- Briones-Fourzán, P., Candela, J., & Lozano-Álvarez, E. (2008). Postlarval settlement of the spiny lobster *Panulirus argus* along the Caribbean coast of Mexico: patterns, influence of physical factors, and possible sources of origin. *Limnology and Oceanography*, 53, 970–985. <https://doi.org/10.4319/lo.2008.53.3.0970>
- Brokaw, R. J., Subrahmanyam, B., Trott, C. B., & Chaigneau, A. (2020). Eddy Surface Characteristics and Vertical Structure in the Gulf of Mexico from Satellite Observations and Model Simulations. *Journal of Geophysical Research: Oceans*, 125(2), e2019JC015538. <https://doi.org/10.1029/2019JC015538>
- Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. *Ecological Modelling*, 172, 488. <https://doi.org/10.1016/j.ecolmodel.2003.11.004>
- Butler, M. J. IV, Paris, C. B., Goldstein, J. S., Matsuda, H., & Cowen, R. K. (2011). Behavior constrains the dispersal of long-lived spiny lobster larvae. *Marine Ecology Progress Series*, 422, 223–237. <https://doi.org/10.3354/meps08878>
- Butler, M. J., Steneck, R. S., & Herrnkind, W. F. (2006). *Juvenile and adult ecology. Lobsters: biology and management* (pp. 263–309). Blackwell Scientific Press.
- Castillo-Estrada, G., De Silva-Dávila, R., Carrillo, L., Vásquez-Yeomans, L., Silva-Segundo, C. A., Avilés-Díaz, L., & Markaida, U. (2020). Horizontal and vertical distribution of cephalopod paralarvae in the Mesoamerican Barrier Reef System. *Journal of the Marine Biological Association of the United Kingdom*, 100(6), 927–937. <https://doi.org/10.1017/S0025315420000648>
- Catalán, I. A., Macías, D., Solé, J., Ospina-Álvarez, A., & Ruiz, J. (2013). Stay off the motorway: resolving the pre-recruitment life history dynamics of the European anchovy in the SW Mediterranean through a spatially-explicit individual-based model (SEIBM). *Progress in Oceanography*, 111, 140–153. <https://doi.org/10.1016/j.pocean.2013.02.001>
- Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., & Ram, K. (2019). rgbf: Interface to the Global ‘Biodiversity’ Information Facility ‘API’. *R package version 0.9. 8*. <https://cran.r-project.org/web/packages/rgbf/index.html>
- CNP (2017). Carta Nacional Pesquera. Instituto Nacional de Pesca y Acuacultura de Mexico (INAPESCA).
- Cobos, M. E., Peterson, A. T., Barve, N., & Osorio-Olvera, L. (2019). kuenm: an R package for detailed development of ecological niche models using Maxent. *PeerJ*, 7, e6281. <https://doi.org/10.7717/peerj.6281>
- Cowen, R. K. (2002). Oceanographic Influences on Larval Dispersal and Retention and Their Consequences for Population Connectivity. *Sale PF Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, 149–170. San Diego: Academic Press.
- Cowen, R. K., & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*, 1(1), 443–466. <https://doi.org/10.1146/annurev.marine.010908.163757>
- Cummings, J. A., & Smedstad, O. M. (2013). Variational data assimilation for the global ocean. In Park S & Xu (Eds.), *L Data Assimilation for Atmospheric, Oceanic and Hydrologic Applications* (pp. Vol II, 303–343). Berlin, Heidelberg: Springer. [https://doi.org/10.1007/978-3-642-35088-7\\_13](https://doi.org/10.1007/978-3-642-35088-7_13)

- De Silva-Dávila, R., Avedaño-Ibarra, R., & Franco-Gordo, M. (2013). Calamares y pulpos de la costa sur de Jalisco y Colima. In Franco-Gordo M.A. (Ed.), *Inventario De Biodiversidad De La Costa Sur De Jalisco Y Colima*, 43–56. Autlán de Navarro: Universidad de Guadalajara.
- De Silva-Dávila, R. D., Avendaño-Ibarra, R., Young, R. E., Hochberg, F. G., & Hernández-Rivas, M. E. (2018). First record and description of *Planctoteuthis* (Cephalopoda: Chiroteuthidae) paralarvae in the Gulf of California, Mexico. *Latin American Journal of Aquatic Research*, 46(2), 280–288. <https://doi.org/10.3856/vol46-issue2-fulltext-4>
- Díaz, J. M., Ardila, N., & García, A. (2000). Calamares y Pulplos (Mollusca: Cephalopoda) del MarCaribe Colombiano. *Biota Colombiana*, 1(2), 195–201.
- Eckman, J. E. (1996). Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *Journal of Experimental Marine Biology and Ecology*, 200(1–2), 207–237.
- Ehrhardt, N., Puga, R., & Butler, M. J. IV (2011). Implications of the ecosystem approach to fisheries management in large ecosystems. The case of the Caribbean spiny lobster. In *Towards marine ecosystem-based management in the Wider Caribbean* (pp. 157–175).
- Enriquez, C., Mariño-Tapia, I. J., & Herrera-Silveira, J. A. (2010). Dispersion in the Yucatan coastal zone: Implications for red tide events. *Continental Shelf Research*, 30(2), 127–137.
- Enriquez, C., Mariño-Tapia, I., Jeronimo, G., & Capurro-Filograsso, L. (2013). Thermohaline processes in a tropical coastal zone. *Continental Shelf Research*, 69, 101–109. <https://doi.org/10.1016/j.cs.2013.08.018>
- Flores-Valle, A., Pliego-Cárdenas, R., Jiménez-Badillo, M. D. L., Arredondo-Figueroa, J. L., & Barriga-Sosa, I. D. L. Á. (2018). First record of *Octopus insularis* Leite and Haimovici, 2008 in the octopus fishery of a marine protected area in the Gulf of Mexico. *Journal of Shellfish Research*, 37(1), 221–227. <https://doi.org/10.2983/035.037.0120>
- Forsythe, J. W., & Hanlon, R. T. (1985). Aspects of egg-development, post-hatching behavior, growth and reproductive biology of *Octopus burryi* Voss, 1950 (Mollusca: Cephalopoda), & (Eds.), *Vie Milieu* (pp. 35, 273–282).
- Garavelli, L., Studivan, M. S., Voss, J. D., Kuba, A., Figueiredo, J., & Chérubin, L. M. (2018). Assessment of mesophotic coral ecosystem connectivity for proposed expansion of a marine sanctuary in the northwest Gulf of Mexico: larval dynamics. *Frontiers in Marine Science*, 5, 174. <https://doi.org/10.3389/fmars.2018.00174>
- Garofalo, G., Ceriola, L., Gristina, M., Fiorentino, F., & Pace, R. (2010). Nurseries, spawning grounds and recruitment of *Octopus vulgaris* in the Strait of Sicily, central Mediterranean Sea. *ICES Journal of Marine Science*, 67(7), 1363–1371.
- González-Gómez, R., de los Barriga-Sosa, I., Pliego-Cárdenas, R., Jiménez-Badillo, L., Markaida, U., Meiners-Mandujano, C., & Morillo-Velarde, P. S. (2018). An integrative taxonomic approach reveals *Octopus insularis* as the dominant species in the Veracruz Reef System (southwestern Gulf of Mexico). *PeerJ*, 6, e6015. <https://doi.org/10.7717/peerj.6015>
- González-Gómez, R., Meiners-Mandujano, C., Morillo-Velarde, P. S., Jiménez-Badillo, L., & Markaida, U. (2020). Reproductive dynamics and population structure of *Octopus insularis* from the Veracruz Reef System marine protected area. Mexico. *Fisheries Research*, 221, 105385. <https://doi.org/10.1016/j.fishres.2019.105385>
- Grimm, V., Reise, K., & Strasser, M. (2003). Marine metapopulations: a useful concept? *Helgoland Marine Research*, 56(4), 222. <https://doi.org/10.1007/s10152-002-0121-3>
- Guerra, Á., Caro, M., Sealey, M., & Lozano-Soldevilla, F. (2013). Two new records of octopods in Canary Islands: *Amphioctopus burryi* (Voss, 1950) and *Macrotritopus defilippi* (Vérany, 1851) [Cephalopoda: Octopodidae]. *Sociedad Española de Malacología*, 31, 19–26.
- Guerrero, L., Sheinbaum, J., Mariño-Tapia, I., González-Rejón, J. J., & Pérez-Brunius, P. (2020). Influence of mesoscale eddies on cross-shelf exchange in the western Gulf of Mexico. *Continental Shelf Research*, 209, 104243. <https://doi.org/10.1016/j.csr.2020.104243>
- Hanlon, R. T., & Hixon, R. F. (1980). Body patterning and field observations of *Octopus burryi* Voss, 1950. *Bulletin of Marine Science*, 30(4), 749–755.
- Hunter, J. R. (1976). *Report of a colloquium on larval fish mortality studies and their relation to fishery research*. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Iturbide, M., Bedia, J., Herrera, S., del Hierro, O., Pinto, M., & Gutiérrez, J. M. (2015). A framework for species distribution modelling with improved pseudo-absence generation. *Ecological Modelling*, 312, 166–174. <https://doi.org/10.1016/j.ecolmodel.2015.05.018>
- Jereb, P., Roper, C. F., Norman, M., & Finn, J. (2014). *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date, Volume 3(4): Octopods and Vampire Squids*. FAO Species Catalogue for Fishery Purposes. ISSN 1020-8682.
- Johnston, M. W., & Bernard, A. M. (2017). A bank divided: quantifying a spatial and temporal connectivity break between the Campeche Bank and the northeastern Gulf of Mexico. *Marine Biology*, 164(1), 12.
- Judkins, H., Vecchione, M., Cook, A., & Sutton, T. (2017). Diversity of midwater cephalopods in the northern Gulf of Mexico: comparison of two collecting methods. *Marine Biodiversity*, 47(3), 647–657. <https://doi.org/10.1007/s12526-016-0597-8>
- Judkins, H. L., Vecchione, M., Roper, C. F., & Torres, J. (2010). Cephalopod species richness in the wider Caribbean region. *ICES Journal of Marine Science*, 67(7), 1392–1400. <https://doi.org/10.1093/icesjms/fsq092>
- Kassambara, A. (2020). *ggpubr: "ggplot2" Based Publication Ready Plots*. <https://CRAN.R-project.org/package=ggpubr>
- Kough, A. S., Paris, C. B., & Butler, M. J. IV (2013). Larval connectivity and the international management of fisheries. *PLoS One*, 8(6), <https://doi.org/10.1371/journal.pone.0064970>
- Kritzer, J. P., & Sale, P. F. (2006). *The metapopulation ecology of coral reef fishes, marine metapopulations*. Elsevier Inc.
- Lamont, M. M., Putman, N. F., Fujisaki, I., & Hart, K. (2015). Spatial requirements of different life-stages of the loggerhead turtle (*Caretta caretta*) from a distinct population segment in the northern gulf of Mexico. *Herpetological Conservation and Biology*, 10, 26–43.
- Lara-Hernández, J. A., Zavala-Hidalgo, J., Sanvicente-Añorve, L., & Briones-Fourzán, P. (2019). Connectivity and larval dispersal pathways of *Panulirus argus* in the Gulf of Mexico: A numerical study. *Journal of Sea Research*, 155, 101814. <https://doi.org/10.1016/j.seares.2019.101814>
- Leite, T. S., Haimovici, M., Mather, J., & Oliveira, J. L. (2009). Habitat, distribution, and abundance of the commercial octopus (*Octopus insularis*) in a tropical oceanic island, Brazil: Information for management of an artisanal fishery inside a marine protected area. *Fisheries Research*, 98(1–3), 85–91. <https://doi.org/10.1016/j.fishres.2009.04.001>
- Leite, T. S., Haimovici, M., Molina, W., & Warnke, K. (2008). Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. *Journal of Molluscan Studies*, 74(1), 63–74. <https://doi.org/10.1093/mollus/eym050>
- Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., & Blanke, B. (2008). A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling & Software*, 23(9), 1210–1214.
- Levin, L. A. (2006). Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology*, 46(3), 282–297.
- Lima, F. D., Ángeles-González, L. E., Leite, T. S., & Lima, S. M. (2020). Global climate changes over time shape the environmental niche distribution of *Octopus insularis* in the Atlantic Ocean. *Marine Ecology Progress Series*, 652, 111–121.
- Lima, F. D., Berbel-Filho, W. M., Leite, T. S., Rosas, C., & Lima, S. M. (2017). Occurrence of *Octopus insularis* Leite and Haimovici, 2008 in the

- Tropical Northwestern Atlantic and implications of species mis-identification to octopus fisheries management. *Marine Biodiversity*, 47(3), 723–734. <https://doi.org/10.1007/s12526-017-0638-y>
- Lima, F. D., Leite, T. S., Haimovici, M., & Oliveira, J. E. L. (2014). Gonadal development and reproductive strategies of the tropical octopus (*Octopus insularis*) in northeast Brazil. *Hydrobiologia*, 725(1), 7–21. <https://doi.org/10.1007/s10750-013-1718-z>
- Martínez-López, B., & Parés-Sierra, A. (1998). Circulación del Golfo de México inducida por mareas, viento y la corriente de Yucatán. *Ciencias Marinas*, 24(1), 65–93.
- Moreno, A., Lourenço, S., Pereira, J., Gaspar, M. B., Cabral, H. N., Pierce, G. J., & Santos, A. M. P. (2014). Essential habitats for pre-recruit *Octopus vulgaris* along the Portuguese coast. *Fisheries Research*, 152, 74–85.
- Naro-Maciel, E., Hart, K. M., Cruciat, R., & Putman, N. F. (2017). DNA and dispersal models highlight constrained connectivity in a migratory marine megavertebrate. *Ecography*, 40(5), 586–597. <https://doi.org/10.1111/ecog.02056>
- Nixon, M., & Mangold, K. (1996). The early life of *Octopus vulgaris* (Cephalopoda: Octopodidae) in the plankton and at settlement: a change in lifestyle. *Journal of Zoology*, 239(2), 301–327.
- Okutani, T., & McGowan, J. A. (1969). Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California Current, April 1954–March, 1957. *Bulletin of the Scripps Institution of Oceanography*, 14, 1–89.
- Otero, J., Álvarez-Salgado, X. A., González, Á. F., Gilcoto, M., & Guerra, Á. (2009). High-frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf. *Marine Ecology Progress Series*, 386, 123–132. <https://doi.org/10.3354/meps08041>
- Parrish, R. H., Nelson, C. S., & Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography*, 1(2), 175–203.
- Peterson, A. T., Pápeš, M., & Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, 213(1), 63–72. <https://doi.org/10.1016/j.ecolmodel.2007.11.008>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3–4), 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31(2), 161–175. <https://doi.org/10.1111/j.2007.0906-7590.05203.x>
- Phillips, S. J., Dudík, M., & Schapire, R. E. (2004). A maximum entropy approach to species distribution modeling. *Proceedings, Twenty-First International Conference on Machine Learning, ICML 2004; Banff, Alta; Canada; 4 July 2004 through 8 July 2004*, 655–662. New York: ACM Press.
- Pineda, J. (2000). Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanography of the Eastern Pacific*, 1(2000), 84–105.
- Pineda, J., Hare, J. A., & Sponaugle, J. A. (2007). Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography*, 20(3), 22–39.
- PMPEY (2009). *Programa Maestro de Pulpo en el Estado de Yucatán*. Comisión Nacional de Acuacultura y Pesca (CONAPESCA).
- Provost, P., & Bosch, S. (2019). *robis: Ocean Biogeographic Information System (OBIS)*. R package version 2.1.8. [https://cran.r-project.org/web/packages/robis/index.html?fbclid=IwAR1RcNSQROKLU MF57COo19eJtbJq1tLaaEqkP3sbwxkk7hFXe3nFDpD\\_nZY](https://cran.r-project.org/web/packages/robis/index.html?fbclid=IwAR1RcNSQROKLU MF57COo19eJtbJq1tLaaEqkP3sbwxkk7hFXe3nFDpD_nZY)
- Putman, N. F., Goni, G. J., Gramer, L. J., Hu, C., Johns, E. M., Trinanes, J., & Wang, M. (2018). Simulating transport pathways of pelagic Sargassum from the Equatorial Atlantic into the Caribbean Sea. *Progress in Oceanography*, 165, 205–214. <https://doi.org/10.1016/j.pocean.2018.06.009>
- Putman, N. F., & He, R. (2013). Tracking the long-distance dispersal of marine organisms: sensitivity to ocean model resolution. *Journal of the Royal Society Interface*, 10(81), 20120979. <https://doi.org/10.1098/rsif.2012.0979>
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reid, R. O. (1972). A simple dynamic model of the Loop Current. *Contributions on the Physical Oceanography of the Gulf of Mexico*, 2, 157–159.
- Rocha, F., Guerra, Á., Prego, R., & Piatkowski, U. (1999). Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). *Journal of Plankton Research*, 21(1), 21–33. <https://doi.org/10.1093/plankt/21.1.21>
- Rosas, C., Gallardo, P., Mascaró, M., Caamal-Monsreal, C., & Pascual, C. (2014). *Octopus maya*. Cephalopod Culture, 2, 383–396. [https://doi.org/10.1007/978-94-017-8648-5\\_20](https://doi.org/10.1007/978-94-017-8648-5_20)
- Rosburg, K., & Donohue, K. (2011). *A Performance Evaluation of the HYCOM Gulf of Mexico Model*. SURFO Technical Report No. 11-01, 55.
- Rosburg, K. C., Donohue, K. A., & Chassignet, E. P. (2016). Three-dimensional model-observation comparison in the Loop Current region. *Dynamics of Atmospheres and Oceans*, 76, 283–305.
- Ross, R. E. (2016). *Investigating the role of larval dispersal models in the development of an 'ecologically coherent' network of deep sea marine protected areas*. Doctoral Dissertation. University of Plymouth.
- Salas-Monreal, D., Marin-Hernandez, M., de Jesus Salas-Perez, J., Salas-de-Leon, D. A., Monreal-Gomez, M. A., & Perez-España, H. (2018). Coral reef connectivity within the Western Gulf of Mexico. *Journal of Marine Systems*, 179, 88–99.
- Santana-Cisneros, M. L., Rodríguez-Canul, R., Zamora-Briseño, J. A., Améndola-Pimenta, M., De Silva-Dávila, R., Ordóñez-López, U., Velázquez-Abunader, I., & Ardisson, P.-L. (2021). Morphological and molecular identification of Octopoda (Mollusca: Cephalopoda) paralarvae from the southern Gulf of Mexico. *Bulletin of Marine Science*, 97(2), 281–304. <https://doi.org/10.5343/bms.2020.0027>
- Sanvicente-Añorve, L., Zavala-Hidalgo, J., Allende-Arandía, E., & Hermoso-Salazar, M. (2018). Larval dispersal in three coral reef decapod species: Influence of larval duration on the metapopulation structure. *PLoS One*, 13(3), e0193457. <https://doi.org/10.1371/journal.pone.0193457>
- Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: Ocean climate layers for marine spatial ecology. *Ecology*, 94, 979. <https://doi.org/10.1890/12-1358.1>
- Siegel, D. A., Kinlan, B. P., Gaylord, B., & Gaines, S. D. (2003). Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, 260, 83–96. <https://doi.org/10.3354/meps260083>
- Soberón, J., & Peterson, T. (2004). Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359(1444), 689–698.
- Soberón, J., & Peterson, T. A. (2005). Interpretation of models of fundamental ecological niches and 'species' distributional areas. *Biodiversity Informatics*, 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C., & Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57, 573. <https://doi.org/10.1641/B570707>
- Stanley, S. (1995). *A Global Representative System of Marine Protected Areas. Volume 2, Marine Region 7: Wider Caribbean* (pp. 15–42). Great Barrier Reef Marine Park Authority, The World Bank, The World Conservation Union (IUCN).
- Swearer, S. E., Tremblay, E. A., & Shima, J. S. (2019). A review of biophysical models of marine larval dispersal. In S. J. Hawkins A. L. Allcock A. E. Bates L. B. Firth I. P. Smith S. E. Swearer & P. A. Todd (Eds.),

- Oceanography and marine biology: An annual review*. Boca Raton, Florida, USA: CRC Press.
- Villanueva, R., & Norman, M. D. (2008). Biology of the planktonic stages of benthic octopuses. *Oceanography and Marine Biology*, 45, 105–202.
- Villanueva, R., Nozais, C., & Boletzky, S. V. (1995). The planktonic life of octopuses. *Nature*, 377(6545), 107. <https://doi.org/10.1038/377107a0>
- Villanueva, R., Vidal, E. A., Fernandez-Alvarez, F. A., & Nabhitabhata, J. (2016). Early mode of life and hatchling size in cephalopod molluscs: influence on the species distributional ranges. *PLoS One*, 11, e0165334. <https://doi.org/10.1371/journal.pone.0165334>
- Zavala-Hidalgo, J., Morey, S. L., & O'Brien, J. J. (2003). Seasonal circulation on the western shelf of the Gulf of Mexico using a high-resolution numerical model. *Journal of Geophysical Research: Oceans*, 108, 1–19. <https://doi.org/10.1029/2003JC001879>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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