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DISTRIBUTION OF HIPPOIDEA (DECAPODA, ANOMURA) LARVAE OFF
VERACRUZ, SOUTHERN GULF OF MEXICO: INFERENCES ABOUT
THEIR MIGRATION ROUTE

BY

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ABSTRACT

The distribution and abundance of hippoid zoeal stages offshore Veracruz, southern Gulf of Mexico, and the migration routes of these larvae in the western Atlantic, were analysed. Samples were collected with a Bongo net and larval dispersal was analysed applying the HYCOM hydrodynamical model; particles (virtual larvae) originating from 35 sites were tracked for 77 days. Larvae of *Albunea paretii* Guérin-Méneville, 1853 were the most abundant, and dispersal simulations indicated that older larvae occurring off Veracruz might originate from Texas. However, a substantial proportion of self-recruitment (7.8%) can occur, mainly due to the seasonal changes in direction of currents over the shelf as well as the high variability in weather conditions. Results also suggest that several generations of *A. paretii* are needed for the species to reach Veracruz from South America. A hypothetical model regarding the migration routes of *A. paretii* larvae in the western Atlantic is proposed.

RESUMEN

Se analizaron la distribución y la abundancia de los estadios zoea de hippoideos en la costa de Veracruz, sur del Golfo de México, y las rutas de migración de estas larvas en el Atlántico occidental. Las muestras se recolectaron con una red Bongo y se analizó la dispersión de larvas aplicando el modelo hidrodinámico HYCOM; las partículas (larvas virtuales) se originaron en 35 sitios y se rastrearon durante 77 días. Las larvas de *Albunea paretii* Guérin-Méneville, 1853

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1 fueron las más abundantes y las simulaciones de dispersión indicaron que las larvas de mayor edad 1
2 registradas en Veracruz podrían originarse en Texas. Sin embargo, una proporción considerable de 2
3 auto-reclutamiento (7.8%) puede suceder debido principalmente a los cambios estacionales en la 3
4 dirección de las corrientes sobre la plataforma y a la alta variabilidad en las condiciones climáticas. 4
5 Los resultados también sugieren que se necesitan varias generaciones de *A. paretii* para que la especie 5
6 llegue a Veracruz desde Sudamérica. Se propone un modelo hipotético de las rutas de migración de 6
7 larvas de *A. paretii* en el Atlántico occidental. 7

8 INTRODUCTION 8

9
10 Hippoidea is a superfamily of decapod crustaceans comprised of three families: 10
11 Albuneidae, Hippidae and Blepharipodidae (Boyko & McLaughlin, 2010). Adults 11
12 are adapted to inhabit sandy beaches and, unlike most other decapods, they have 12
13 lost the ability to effectively walk. Instead, hippoids are able to dig backwards into 13
14 the sand, tail first, until only the antennae and eyes protrude from the surface (Paul, 14
15 1981; Faulkes & Paul, 1997); due to this behaviour, they are called sand crabs or 15
16 mole crabs. Depending on their ecological requirements, sand crab species live 16
17 in different beach environments and display different swimming abilities. Some 17
18 species are subtidal scavengers whose swimming skills are weak; other species 18
19 are intertidal filter feeders who, in order to remove food particles from the water, 19
20 frequently emerge from the sand and swim up and down the beach (Paul, 1981). 20

21 The life cycle of sand crabs includes several planktonic larval stages, followed 21
22 by the metamorphosis of the last zoea larva into a megalopa stage, and the 22
23 settlement of the latter on a beach (Subramoniam & Gunamalai, 2003). The 23
24 number of zoeal stages is different among species, and ranges most frequently 24
25 between three to six stages (Israel et al., 2006; Boyko & McLaughlin, 2010). 25
26 The pelagic larval duration (PLD) among species is also variable. While some 26
27 species spend only two weeks in the plankton (Stuck & Truesdale, 1986), some 27
28 others persist for two or three months (Knight, 1970; Sastre, 1990). The duration 28
29 of the pelagic larval stage affects the overall dispersal potential, the geographical 29
30 distribution, the connectivity among distant populations, as well as the ecological, 30
31 genetic and evolutionary processes of species (Lester et al., 2007; Dawson et al., 31
32 2011; Sanvicente-Añorve et al., 2018). Thus, there is a growing need to understand 32
33 the dispersal pathways, travel time and dispersal distance of larvae in order to better 33
34 understand marine population dynamics. 34

35 The coastline of the southern Gulf of Mexico is predominantly composed of 35
36 sand beaches with scattered rocky habitats (Moreno-Casasola, 2004). In spite of 36
37 the ecological importance of sand crabs, studies on hippoids have mostly addressed 37
38 the adult stage (Dexter, 1976; Efford, 1976; Felder et al., 2009; Rocha-Ramírez et 38
39 al., 2016), while the knowledge on larvae still remains limited (Mou-Sue, 1985). 39
40 In this study, we made a first attempt to analyse the distribution and abundance 40

MIGRATION ROUTES OF HIPPOID LARVAE IN WESTERN ATLANTIC

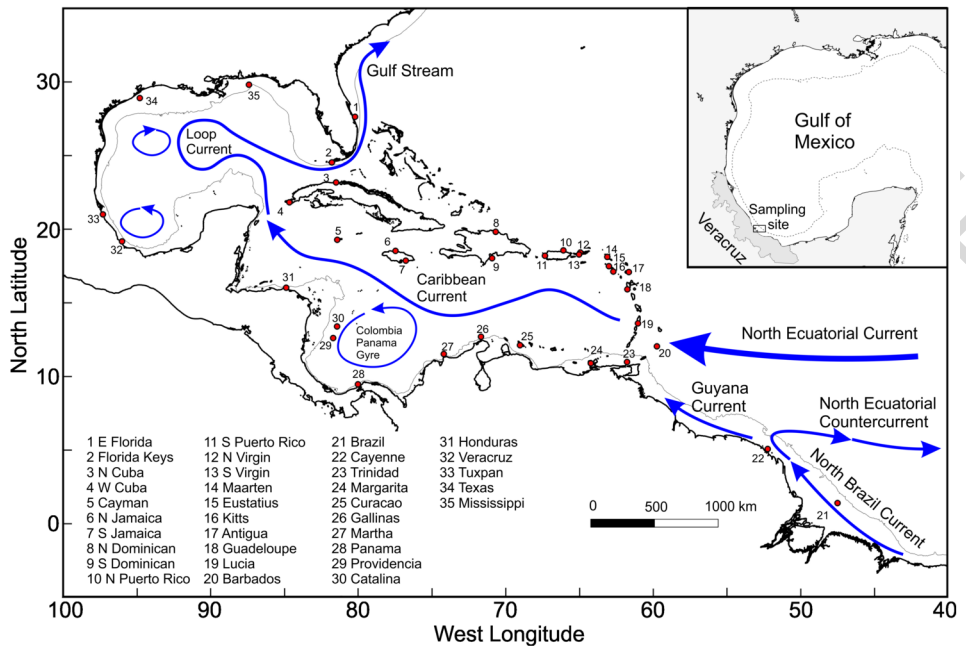


Fig. 1. Zooplankton collection site in the Gulf of Mexico and location of adult populations of *Albunea paretii* Guérin-Méneville, 1853 in the western Atlantic.

of hippoid zoeal stages, offshore of the Mexican state of Veracruz, southern Gulf of Mexico. An additional effort was made to infer the migration routes of larvae throughout the western Atlantic, by means of a hydrodynamic model, and to analyse if the next generation could be recruited to the parental population.

MATERIAL AND METHODS

Collection site and sampling method.— The zooplankton collection site was located in the southern Gulf of Mexico, at 18.8-19.8°N and 95.0-96.3°W, bordered to the west by the shoreline of the state of Veracruz (Mexico) (fig. 1). Zooplankton samples were collected from 29 November to 2 December 2007, over a grid of 21 oceanographic stations covering neritic and oceanic waters, using a Bongo net equipped with 333 and 505 μm mesh size netting and a flowmeter at the mouth of each net. Sampling depth varied from 20 to 200 m, depending on the bathymetry. In the laboratory, all hippoid larvae were removed from the samples and identified using specialized literature (Kurata, 1970; Bullard, 2003; Harvey et al., 2014).

Currents in the study area.— At tropical latitudes, the surface circulation in the western Atlantic is bound by the equatorial edges of the North and South Atlantic gyres and the westward North and South Equatorial currents, which

1 feed the northward western boundary currents: the North Brazil Current and the 1
2 Gulf Stream (Lumpkin & Garzoli, 2005). After crossing the Equator, the North 2
3 Brazil Current flows along the coast until it retroflects at approximately 7°N 3
4 48°W into the North Equatorial Countercurrent, lasting approximately from June 4
5 to January (Johns et al., 1998; Lumpkin & Garzoli, 2005). At this point, rings 5
6 are shed that propagate northwestwards feeding the Guyana Current (Lumpkin & 6
7 Garzoli, 2005). Both the Guyana and North Equatorial currents feed the Caribbean 7
8 Current, a warm ocean current transporting a large volume of water into the 8
9 Gulf of Mexico through the Caribbean basin. The Caribbean Current's mean 9
10 direction is westwards, but it forms large meanders from the Lesser Antilles 10
11 to the Nicaraguan Rise. The Panamá-Colombia cyclonic gyre characterizes the 11
12 Caribbean Basin (Alvera-Azcárate et al., 2009). As the Caribbean Current passes 12
13 through the Yucatan Channel, water flows into the Gulf of Mexico forming the 13
14 Loop Current, a clockwise current that shows a variable penetration into the 14
15 northern Gulf that sheds large anticyclonic eddies, which travel westwards and 15
16 dissipate near the western continental shelf (Ohlmann & Niiler, 2005; Alvera- 16
17 Azcárate et al., 2009). In the southern Gulf, water circulation in the open sea is 17
18 predominantly cyclonic (Vázquez-de la Cerda et al., 2005; Pérez-Brunius et al., 18
19 2013), whereas over the shelves, circulation is strongly seasonal, mainly driven by 19
20 the wind (Zavala-Hidalgo et al., 2003; Allende-Arandía et al., 2015). 20

21 The hydrodynamic model.— The ocean circulation in the western Atlantic was 21
22 simulated with the Hybrid Coordinate Ocean Model (Atlantic HYCOM). This 22
23 system has a resolution of 1/12 degree (about 7 km at mid-latitudes) and combines 23
24 three types of coordinates by dynamically choosing the optimal distribution of 24
25 ocean parameters: *isopycnal* (density) coordinates, best in deep stratified ocean; *z-* 25
26 *levels* (constant fixed depths) for the mixed layer; and *sigma* (terrain following 26
27 levels) for shallow coastal waters. The reanalysis facility GLBu0.08/expt_19.1 27
28 was used in this study. The data-assimilative system uses surface wind stress, 28
29 air temperature, specific humidity, and short- and longwave radiation (Chassignet 29
30 et al., 2007). To simulate the dispersal pathways of particles (virtual larvae), 30
31 a Lagrangian particle-tracking module was coupled to the Atlantic HYCOM 31
32 circulation model, following the procedure described in Sanvicente-Añorve et al. 32
33 (2018). 33

34 The simulation of larval dispersal routes consisted of the launch of 1000 34
35 particles per day (from 1 July to 30 September 2007) from 35 starting sites, 35
36 i.e., the localities that the adults inhabit (Boyko, 2002; Felder et al., 2009; GBIF 36
37 database) (fig. 1). This means that a total of 92 000 particles were released per 37
38 site. The choice of the length of the period for tracking particles depended on the 38
39 field results. In this study, the most abundant species was *Albunea paretii* Guérin- 39
40 Méneville, 1853, whose PLD is unknown. Thus, we used the data for the closest 40

TABLE I

Absolute numbers of hippoid larvae collected off Veracruz, southern Gulf of Mexico, during November-December 2007

Species	Total	Zoeal stages					
		I	II	III	IV	V	VI
<i>Albunea paretii</i> Guérin-Méneville, 1853	171	67	43	17	13	5	26
<i>Emerita</i> sp.	41	10	2	3	3	3	20
Not determined	2						

related species for which the PLD is known, *Lepidopa myops* Stimpson, 1860 (C. B. Boyko, pers. comm.), which is 77 days (Knight, 1970). Larvae successfully arrived at any site if they were located within a circular area of 20 km radius centred on the site and within a timeframe of 17 days (from the 61st to 77th day of the larval stage). A connectivity matrix, including 35 × 35 sites, was constructed with values of successfully arrived particles, expressed as a percentage (Xue et al., 2008). In this type of matrix, the rows correspond to the starting sites, and the columns to the arrival sites. The diagonal cells correspond to the local retention or self-recruitment of individuals. A site can be recognized as a “source” if emigrants (particles emitted) exceed immigrants (particles received), and as a “sink” in the opposite case.

RESULTS

In total, 214 hippoid larvae were sorted from the 42 zooplankton samples collected with the Bongo paired nets; the mean hippoid density was 2.81 ind 100 m⁻³. The albuneid *Albunea paretii* accounted for the majority of larvae (171 individuals), followed by the hippid *Emerita* sp. (41 individuals) (table I).

Larvae of *A. paretii* had a wide distribution in the study region, with densities ranging from 0.14 to 16.84 ind 100 m⁻³. Generally, major density values were located near the shore, especially between the Veracruz reef complex and the nearby Alvarado lagoon (fig. 2). Six zoeal stages were recognized, with a decreasing order of abundance from zoea I to zoea V, and increasing again in zoea VI (table I). Larvae of *Emerita* sp. were found at only nine oceanographic stations (fig. 2) with densities ranging from 0.24 to 4.11 ind 100 m⁻³. Six zoeal stages were recognized, of which zoea VI was the most abundant (table I).

The connectivity matrix indicated that the *A. paretii* larvae that arrive in Veracruz after a 77-day journey come mainly from Veracruz itself or from Texas. Subsequently, larvae may arrive in Texas from Mississippi, a location that in turn receives larvae mainly from west Cuba, Catalina, and Honduras (figs. 3-4).

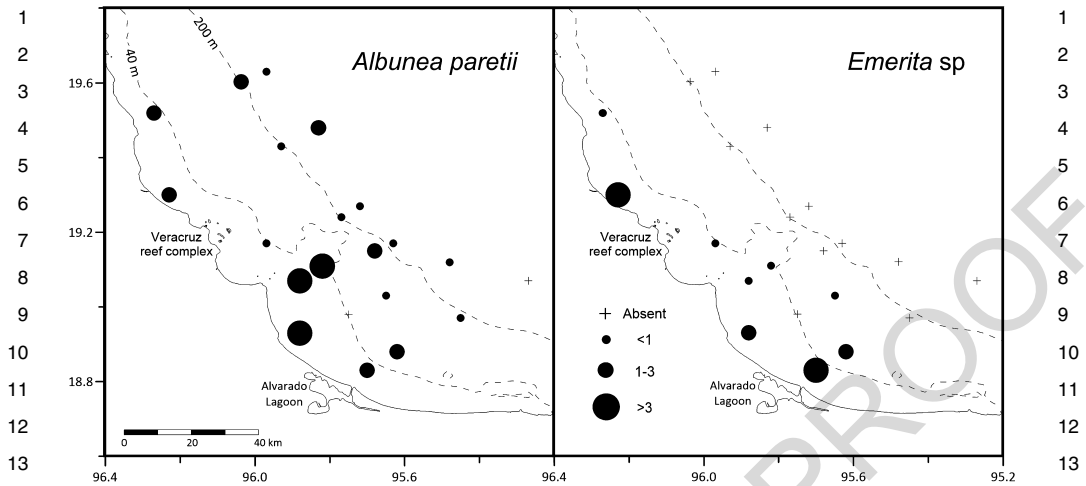


Fig. 2. Distribution and abundance (ind 100 m^{-3}) of larvae of *Albunea paretii* Guérin-Méneville, 1853 and *Emerita* sp. off Veracruz, southern Gulf of Mexico.

Simulations also indicated that the Lesser Antilles (from Saint Maarten to Barbados) emit larvae that travel to the Dominican Republic, Puerto Rico and the Virgin Islands. Localities along the coast of northern South America and Central America (from Margarita Island to Honduras) have a similar relation with local populations of Cuba and Florida; in contrast, the Brazilian population remains isolated (figs. 3, 5).

Considering a reference value above 5% between immigrants and emigrants at each site, some islands of the Lesser Antilles (Kitts, Antigua, Guadeloupe, Lucia, and Barbados) as well as Margarita, Gallinas, and Texas, were important sites of larval emission (sources). On the other hand, some local populations in the Greater (north Cuba, south Jamaica, south Dominican Republic and south Puerto Rico) and the Lesser (north and south Virgin Islands) Antilles, as well as the localities of Martha, Catalina, Tuxpan, Mississippi and east Florida were recognized as sites of high recruitment (sinks). Major self-recruitment values occurred in Panama, Veracruz, Texas and Mississippi (fig. 3).

DISCUSSION

The mean density of hippoid larvae collected in the southern Gulf of Mexico was low ($2.81\text{ ind }100\text{ m}^{-3}$). The low abundance values can be due to the relatively low fecundity of hippoid species. Fecundity studies provide key elements to understanding the population dynamics and evolution of a species (García-Montes et al., 1987; Cobo & Okamori, 2008). Nonetheless, little is known about the

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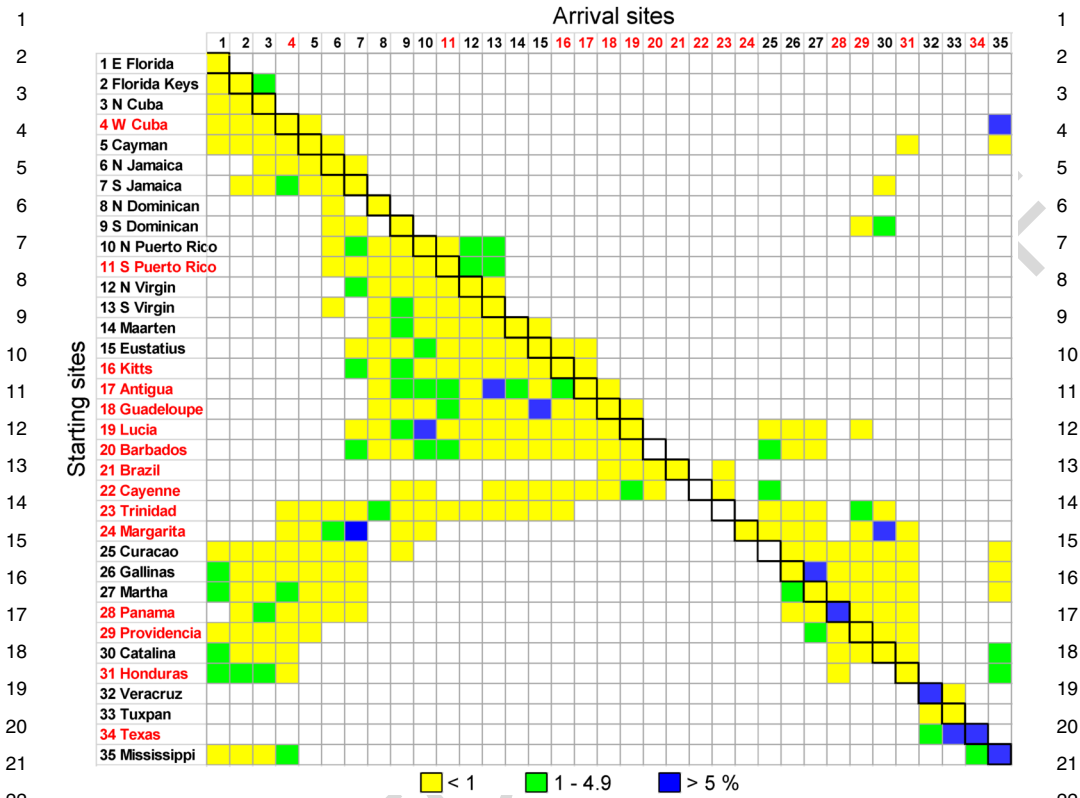


Fig. 3. Connectivity matrix of *Albunea paretii* Guérin-Méneville, 1853 among 35 localities in the western Atlantic. Red, source populations; black, sink populations.

reproductive biology and life histories of most hippoid species (Dugan et al., 1991; Edritanti et al., 2016). In accordance with Cobo & Okamori (2008), the fecundity of crustaceans can vary from less than 5000 to more than 40 000 eggs per female. Several field studies (Dugan et al., 1991; Contreras et al., 2000; Edritanti et al., 2016; Faulkes, 2017) revealed that the fecundity of hippoid species is close to the lowest limit of the range.

Albunea paretii was the most abundant hippoid species in plankton samples collected off Veracruz (fig. 2; table I). This species is distributed in the western Atlantic, from Bermuda and Florida, throughout the Gulf of Mexico, the Caribbean and Central America, up to northern Brazil (Boyko, 2002; Felder et al., 2009). There is no information about the reproductive cycle of the species in the southern Gulf of Mexico, but records of zoea I in the study area may indicate that *A. paretii* is able to reproduce in autumn. At the same time, the presence of older zoeal stages off Veracruz suggests that individuals are close to being recruited and becoming part of the adult population. In some hippoid species, a delay in metamorphosis of

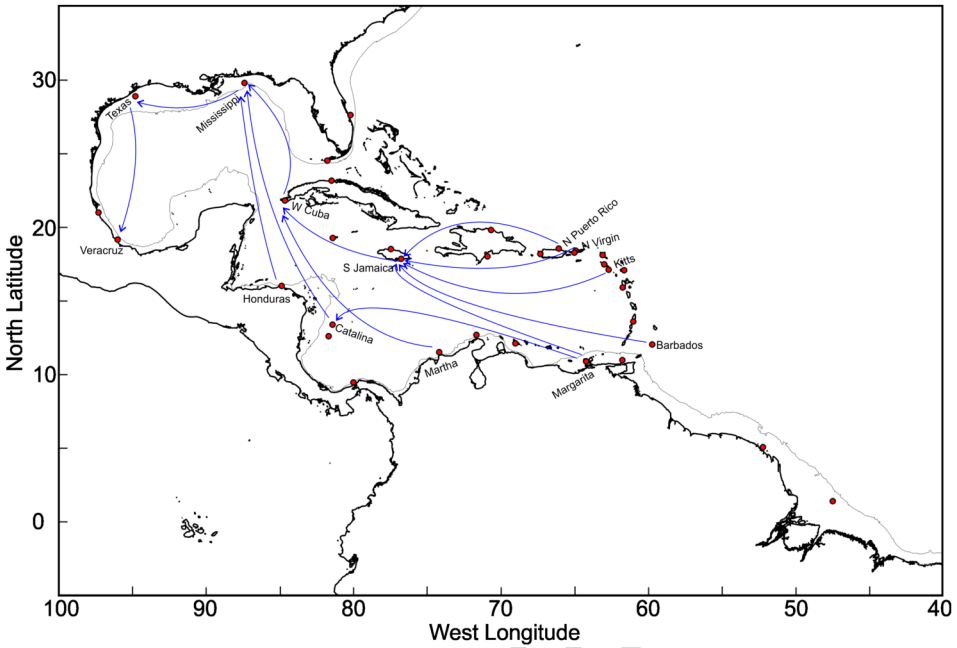


Fig. 4. Hypothetical migration route of *Albunea paretii* Guérin-Méneville, 1853 larvae, from South America to Veracruz (Mexico), as deduced from Lagrangian simulations.

the megalopa stage to the first juvenile stage, while searching for suitable habitat conditions, may occur (Boyko & McLaughlin, 2010).

Simulations of dispersal pathways of particles (larvae) released in summer 2007 indicated that older *A. paretii* larvae recorded off Veracruz might originate from Tuxpan or from Texas, although a considerable proportion (7.8%) of self-recruitment may occur (fig. 3); simulations also suggest that larvae arriving in Texas come from Mississippi. Based on the model results, a hypothetical migration route of larvae, from South and Central America to Veracruz, can be inferred (fig. 4). For example, larvae starting in Margarita may arrive in south Jamaica, continue to west Cuba, Mississippi, Texas and, finally, Veracruz. This long route suggests that a single generation in the *A. paretii* population is not enough to reach the coasts of Veracruz state from South America.

The *A. paretii* population of Veracruz showed a high self-recruitment value (fig. 3). The seasonal changes in the currents' direction over the shelf and the high frequency of the variability in weather conditions could be the main cause of self-recruitment in this local population (Sanvicente-Añorve et al., 2014). Larvae can be trapped in the coastal currents for several weeks, moving back and forth, and be recruited to the adult population when they are physiologically and morphologically ready.

MIGRATION ROUTES OF HIPPOID LARVAE IN WESTERN ATLANTIC

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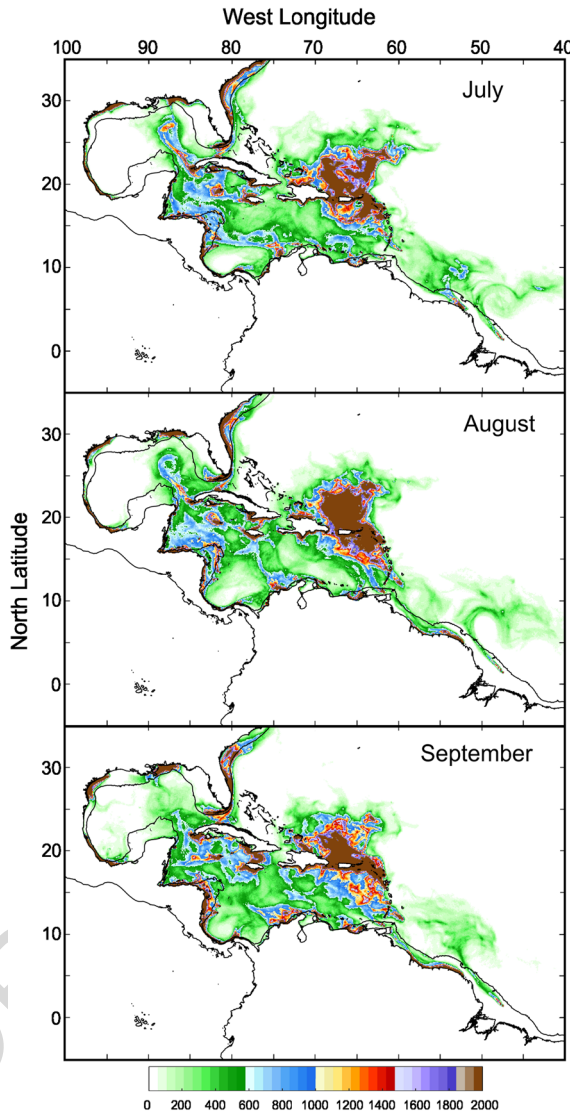


Fig. 5. Simulation of larval dispersal of *Albunea paretii* Guérin-Ménéville, 1853 in the western Atlantic considering three hatching months. Colours indicate a relative scale regarding the number of particles per unit area.

Patterns of larval dispersal (fig. 5) indicated that connectivity among distant populations is fundamental for the survival of some local populations. Puckett & Eggleston (2016) highlighted the role of connectivity in the persistence-through-time of sink populations. This could be the case for north Cuba, south Jamaica, south Dominican Republic, south Puerto Rico, Martha, Catalina, Tuxpan, Mississippi and east Florida, sites recognized as sinks. Of particular interest for the

1 Veracruz population is the maintenance of south Jamaica. This site receives a large 1
2 quantity of larvae from the Lesser Antilles, and after a generation, is able to emit 2
3 larvae into west Cuba, that then follow the migration route here proposed after 3
4 several generations (fig. 4). 4

5 Larvae of *Emerita* sp. were the second most abundant hippoid species in the 5
6 study area (fig. 2; table I). The Gulf of Mexico is the only site where distribution of 6
7 two *Emerita* species overlap: *Emerita talpoida* (Say, 1817) and *Emerita benedicti* 7
8 Schmitt, 1935 (cf. Efford, 1976). Field studies registered the presence of adults 8
9 of either *E. talpoida* or *E. benedicti* on the beaches of the southern Gulf, without 9
10 them being found sharing the same habitat (Dexter, 1976; Pacheco-Ríos, 2010; 10
11 Rocha-Ramírez et al., 2016). Perhaps the grain size of the beaches is determinant 11
12 on their micro-distribution. We can not assign a species to the *Emerita* larvae here 12
13 encountered, but the presence of the zoea VI stage suggests that the recruitment to 13
14 the adult population could take place soon. 14

15 In summary, the results of this study indicate that the persistence of the *A. paretii* 15
16 population of Veracruz is mainly due to the high self-recruitment values, as well 16
17 as to the influx of immigrants coming from Central and South America during 17
18 several generations. The seasonal changes in the currents' directions over the shelf 18
19 and local meteorological phenomena could play a fundamental role in the high 19
20 self-recruitment of such a population. Almost all the local populations of *A. paretii* 20
21 in the western Atlantic exhibit a high degree of connectedness, except for that in 21
22 Brazil, which remains isolated. 22
23

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34

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