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ORIGINAL ARTICLE

Distribution and abundance of zoeae I (Crustacea, Brachyura) on a coral reef in the southwest Gulf of Mexico

Sergio Cházaro-Olvera[1] orcid.org/0000-0002-0667-0043
Ariel Arias-Martínez[1] orcid.org/0000-0003-1392-6219
Rafael Robles[2] orcid.org/0000-0003-0531-5557
Jesús Montoya Mendoza[3] orcid.org/0000-0002-7598-7300

1 Laboratorio de Crustáceos, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México. Tlalnepantla, Estado de México, México.
SCO E-mail: schazaro@gmail.com
AAM E-mail: ariasarielmartinez@hotmail.com

2 Facultad de Ciencias Químico Biológicas, Universidad Autónoma de Campeche. San Francisco de Campeche. Campeche, México.
RR E-mail: roblesrafaelr@gmail.com

3 Instituto Tecnológico de Boca del Río. Boca del Río, Veracruz, México.
JMM E-mail: jeususm_mendoza@yahoo.com.mx

ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub:E5243637-9BFD-4E3B-B49A-C390EB834558

ABSTRACT

In this study we analyze both seasonal and inter-annual variations in the community parameters of Brachyura zoea I in the Parque Nacional Sistema Arrecifal Veracruzano. Planktonic samples from four transects were collected during three weather conditions: cold fronts; rainy and dry conditions in 2011 and 2012; and cold fronts and dry conditions in 2013. We measured temperature, salinity, and dissolved oxygen, *in situ*, to determine whether these parameters could explain the observed variations in the community patterns of brachyuran zoea I. We collected zoeae I of 18 species of brachyurans. The dominant species were *Libinia dubia* H. Milne Edwards, 1834; *Menippe nodifrons* Stimpson, 1859; and *Callinectes sapidus* Rathbun, 1896. The temperature and dissolved oxygen were the highest during the rainy conditions and the salinity during the dry conditions in the southern transects. The highest species richness (14) and diversity (2.97 bits individual^{-1}) were found in central transects during cold front conditions. However, we found the highest species richness and diversity during the dry conditions, in the southern transects. *Libinia dubia* presented the highest density during cold fronts with 1592 ± 127 zoeae 100 m^{-3} in the northern transect, followed by *C. sapidus* in the north-central transect, this was observed for both species in the offshore zone. In conclusion, the parameters of the community of zoea I were influenced by the physical parameters measured in each sampling zone.

KEYWORDS

Brachyura, coral reef, diversity, Gulf of Mexico, zoeae

Corresponding Author
Sergio Cházaro-Olvera
schazaro@gmail.com

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Introduction

True crabs are common inhabitants of coastal waters of the Mexican state of Veracruz, southwest part of the Gulf of Mexico, where around 160 species have been found (Álvarez *et al.*, 1999; 2011), 89 of these species have been registered in the Parque Nacional Sistema Arrecifal Veracruzano (PNSAV) (Hermoso-Salazar and Arvizu-Coyotzi, 2015). The PNSAV is a highly productive ecosystem that was declared as a Marine Protected Area under the category of National Marine Park in 1992 (DOF, 1992; 2012) and as a Biosphere Reserve, within the Man and Biosphere Program, in 2006 (UNESCO, 2006). Furthermore, the park obtained a Ramsar number (1346) in 2004 (FIR, 2004). This reef system is comprised of several single coral reefs and is divided into northern and southern groups by the influence of the fluvial plume of the Jamapa River (Horta-Puga *et al.*, 2016). The importance of PNSAV relies on its great biodiversity, high productivity and the ecosystem services provided. PNSAV provides habitat, spawning and nursery grounds for many species, including many economically important fish species. Additionally, this reef system is the largest in the Gulf of Mexico and probably functions as a bridge for various species of marine invertebrates, including true crabs, to disperse between Caribbean and Florida reefs (Jordan-Dahlgren, 2002).

Having a pelagic larva is an important part of the life history of many benthic invertebrates. Most benthic animals maintain different populations interconnected by having planktonic larvae. The role of larvae in maintaining these connections has been discussed in many studies (Martin *et al.*, 2014) but it is clear that larval dispersal helps to maintain genetic flow among different populations of a species and potentially increases the chances of colonization of new areas. Also, larval dispersal might reduce competition for space, as well as predation rates of juveniles in the adult habitat. One more advantage of larval dispersal is avoidance of physiological stress due to low salinity found in estuarine or coastal parental habitats (Koettker and Freire, 2006).

As with many other benthic species, true crabs (Brachyura) rely on planktonic larvae to disperse. During larval development, most brachyuran species hatch as a zoea and pass through several zoeal stages, which are planktonic, until they reach the megalopa stage that usually is the settlement stage (Pessani *et al.*, 2004; Cházaro-Olvera *et al.*, 2014). Most brachyuran zoea can be found as constituents of meroplankton in coastal zones, such as coral reefs, estuaries and rivers (Gore, 1985; Álvarez *et al.*, 1999). Some zooplankton studies have shown that brachyuran zoea might have a clear association with estuarine inlets and vertical distribution, where first stages of the zoeae can be found in the upper part of the water column, while later larval stages, as well as megalopae, are found in the lower part of the water column (Queiroga, 1996).

Both zoea and megalopa stages have specific characteristics, some being related to feeding habits, behavioral responses to environmental stimuli, and modes of locomotion (McConnaughey, 1974). In particular, the Brachyura zoea I is characterized by sessile eyes, a carapace usually armed with lateral, dorsal or rostral spines, and a pair of antennae and antennules usually with endopod absent or not well-developed; the first two maxillipeds are swimming appendages with bisected exopods and four plumose setae distally, and the telson is attached to the sixth pleonite and presents a furcation on each side, between the furca which usually presents three pairs of setae on the posterior border (Martin *et al.*, 2014).

Global larval ecology studies have been conducted primarily in estuarine and bay areas on commercially important species (Koettker and Freire, 2006). Important contributions about the distribution of larvae in the Atlantic, were made in the 1980s and 1990s, especially about commercially important species such as *Callinectes sapidus* Rathbun, 1896 (Polh *et al.*, 1999). Since 2000, some studies about the distribution of other species have been carried out mainly in Brazil. In Mexico, there has only been one study about the distribution of larvae of *Callinectes* Stimpson, 1860 in an estuary of the Gulf of Mexico (Amador-del Ángel *et al.*, 2004).

In particular, there has been only a few studies performing studies of the zooplankton distributed in the Parque Nacional Sistema Arrecifal Veracruzano (PNSAV) and only for a few taxa, such as appendicularians, chaetognaths, pteropods, copepods and fishes (Flores-Coto, 1965; 1974; Leal-Rodríguez, 1965; Vega-Rodríguez, 1965; Aguayo-Saviñón, 1966;

Campos, 1980; Suárez, 1992; Campos-Hernández and Suárez-Morales, 1994; Ayala-Rodríguez *et al.*, 2016). Okolodkov *et al.* (2011) conducted a study on the biomass of plankton, mentioning that the invertebrates are the most abundant group of the zooplankton in this reef system. Cházaro-Olvera *et al.* (2019) found that 13.77% of the community of zooplankton were decapods, including such commercial species as *Callinectes*, *Menippe* De Haan, 1833, and *Penaeus* Fabricius, 1798. Furthermore, many of these larvae are an important food chain component of fish present in this system (Bedia-Sánchez and Franco-López, 2008). Due to the ecological and economical importance of decapod crustaceans and because of the lack of specific studies on larval assemblages for brachyurans in any of the reef systems in Mexico, our objectives were to analyze the diversity, species richness, distribution and abundance of the community of Brachyura zoea I and to determine whether environmental factors affect these characteristics of the larval community in the PNSAV.

Material and Methods

Study area

The PNSAV is located on the continental shelf off the coast of the Veracruz municipalities of Boca del Río and Alvarado, in the southern Gulf of Mexico (19°00'00" 19°16'00"N, 95°45'00" 96°12'00"W). The park consists of 23 reef banks divided by the mouth of the Jamapa River; 12 reefs are in front of the port of Veracruz (northern group) and 11 more are in front of the Municipality of Antón Lizardo (southern group). In total, they occupy an area of 52,283 hectares. The park presents islands and platform reefs (Granados-Barba *et al.*, 2007; Horta-Puga *et al.*, 2007) (Fig. 1).

The Gulf of Mexico is in a transition area; therefore, seasonal variability is less pronounced in the southern tropical part. For that reason, the climate in the PNSAV cannot be divided seasonally; instead we used dry and rainy seasons and cold fronts (Carrillo *et al.*, 2007). The cold fronts are anticyclonic cold wind currents that enter the Gulf of Mexico from North America, generating strong northern winds and therefore presenting ideal conditions for fetch, causing mature wind waves (Carrillo *et al.*, 2007; Ojeda *et al.*, 2017) that occur from October to March, with occasional precipitation and temperature decrease. The 'dry weather conditions' occur from May to June, with scarce rainfall and higher temperatures. The 'rainy weather conditions' occur from July to September, when temperatures and precipitation increase and winds are weaker (Carrillo *et al.*, 2007; Zavala-Hidalgo *et al.*, 2014). The average annual temperature in the reef zone is 26 °C (Chávez *et al.*, 2007).

Field work

We collected samples during the three seasons to accomplish our objective of analyzing the diversity, species richness, distribution and abundance of the Brachyura zoea I community. Biological material was collected under cold front (Cf), rainy (Rn) and dry (Dr) weather conditions (Wc) in 2011 and 2012 and under Cf and Dr conditions in 2013. Collection in Rn conditions in 2013 was attempted but was not possible due to the weather conditions. A total of 26 sampling stations were established on four perpendicular transects to the coast: two transects to the north (northern, N; north-central Nc) and two transects to the south (south-central, Cs; southern, S) of the mouth of the Jamapa river. Each sampling station had three parallel zones based on its proximity to the coast: foreshore (Fs), nearshore (Ns) and offshore (Offs) (Chowdhury and Behera, 2019) (Fig. 1).

Horizontal hauls at the surface were made on every station using a 1.5 m-long WP2 conical net with a 0.5 m mouth diameter (surface area = 0.196 m^2) and 330 μm mesh opening, on which was placed a flow meter (General Oceanics) to determine the volume of filtered water. The hauls were conducted from a boat with an outboard motor and lasted for 5 min at an average speed of 3 knots (1.543 m s^{-1}), equivalent to an approximate distance of 450 m and water volume of 350 m^3 for each sampling site. Samples were concentrated and fixed in 500 ml flasks with 10 ml of 4% formaldehyde and neutralized with sodium borate. In-situ measurements included salinity, surface temperature of water (°C), and dissolved oxygen (mg l^{-1}) which were measured using a multiparameter water quality portable meter (Hanna HI 9828).

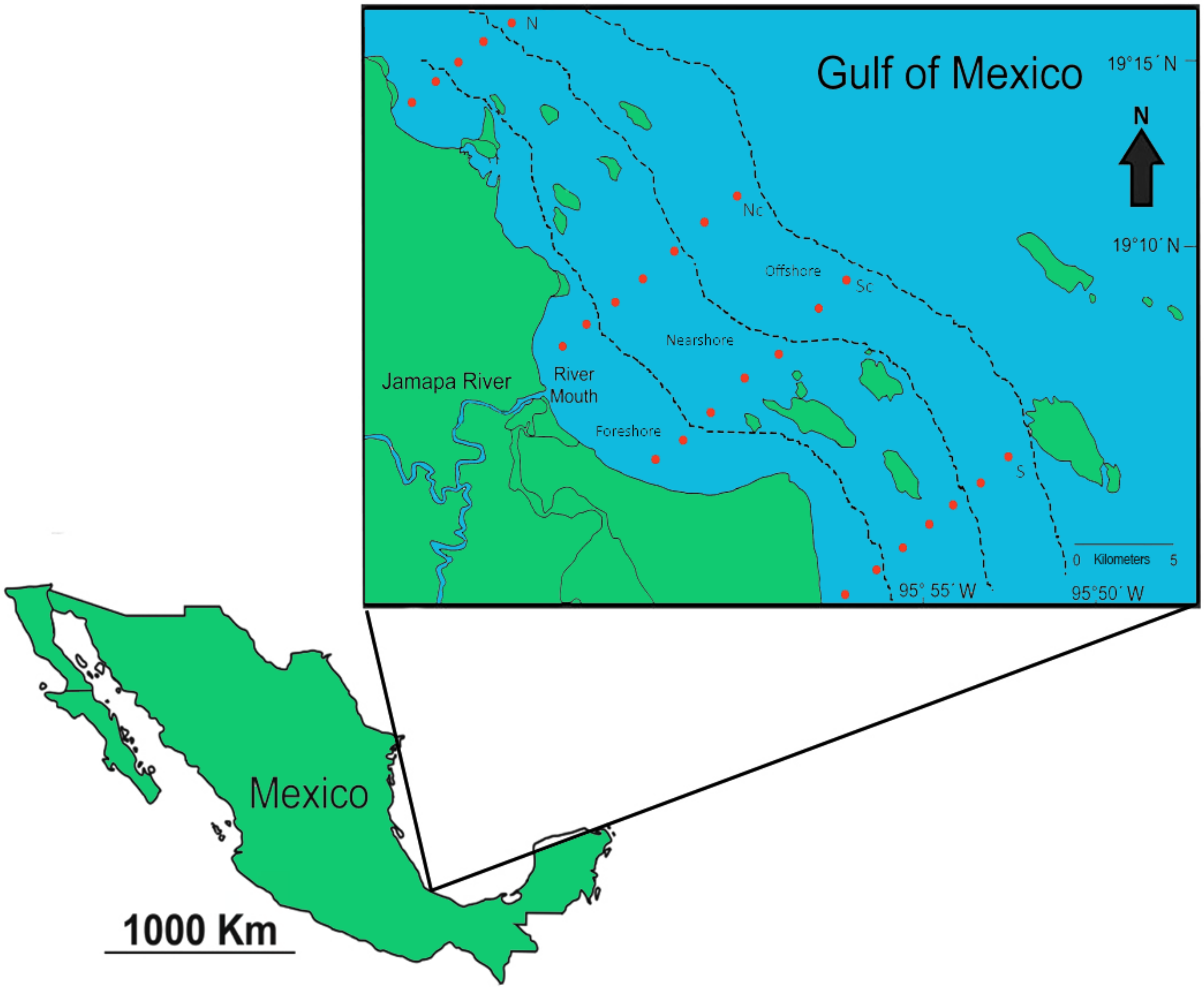

Figure 1. Location of the study area showing transects and sampling stations. N, Northern; Nc, North central; Sc, South Central; S, Southern.

Laboratory work

The biological material was transferred to the Crustacean Laboratory at the Facultad de Estudios Superiores Iztacala of the Universidad Nacional Autónoma de México. Samples were transferred to 70% alcohol 24 h after fixation. We focused our efforts on identifying only brachyuran zoea I because a) we noticed that 98% of our preliminary samples collected were composed of zoeae I; b) our keys of larval identification were biased towards zoeae I; and since we wanted to compare variations in the community of larvae throughout the year in multiple seasons, we needed some degree of consistency. However, we acknowledge that including other larval stages would be a more complete study. For species identification, we used a Motic SMZ-168 stereoscopic microscope and a Leica DM750 microscope with the aid of the most current literature (Boltovskoy, 1999; Pessani *et al.*, 2004; Johnson and Allen, 2012; Koettker *et al.*, 2012; Cházaro-Olvera *et al.*, 2014; Martin *et al.*, 2014). Once we identified our specimens, we corroborated geographic distribution, habitat of adults and bathymetric distribution for each species either with the use of proper literature (Felder and Camp, 2009) or by consulting the World Register of Marine Species (WoRMS, 2020). To obtain the density of zoeae, the total number of individuals per species was counted and standardized to the number of zoea per 100 m^3 (Suárez-Morales and Gasca, 2000).

Statistical analysis

The generalized least squares (GLS) model was used to compare temperature (°C), salinity, and dissolved oxygen (mg L^{-1}) under cold front, rainy and dry weather conditions during three sampling years (2011, 2012 and 2013) (Zuur *et al.*, 2007). GLS was performed using SPSS v25.

To test whether the density of the species changed as a function of weather conditions and sampling zones, a two-way factorial design was performed, with four transects (N, Nc, Sc, S), three years (2011, 2012, 2013) and three weather conditions (Cf, Rn, Dr) as the fixed orthogonal factors. The covariates temperature, salinity and dissolved oxygen were represented using the average value (± standard deviation) of each zone where the samples were taken. This design was applied to analyze the density of zoeae using a permutational multivariate analysis of variance (PERMANOVA) test. The values of environmental parameters were arcsine transformed and normalized. The values of the density of the species were transformed into the fourth root. The resemblance matrix for the density of species was achieved using the Bray-Curtis similarity (Clarke and Gorley, 2015). The analysis was computed with 999 permutations of residuals in a reduced model. Pairwise tests using a t-statistic were used to identify differences between weather conditions. A Bray-Curtis resemblance matrix on the values of the density of zoeae was used to attain the grouping of the weather conditions and transects through a canonical analysis of principal coordinates (CAP). The CAP was also performed to show the relationship with the environmental characteristics, transformed to arcsine and normalized (Paz-Ríos *et al.*, 2020). A similarity percentage (SIMPER) analysis was carried out to determine the set of species characterizing the assemblage of zoeae formed according to the transects and weather conditions using a cumulative contribution of 75% (Clarke, 1993). PERMANOVA and SIMPER were performed as implemented in the PRIMER V7 and PERMANOVA add-ons (Anderson *et al.*, 2008; Clarke and Gorley, 2015).

The potential relationship between the species matrix of the average densities of zoeae and the averages of the temperature, salinity and dissolved oxygen environmental variables was explored using canonical correlation analysis (CCA). We applied the Wilks lambda test (Peres-Neto *et al.*, 2006) with the null hypothesis that the regression coefficients would all be equal to zero. The CCA was performed as implemented in XLstat-2009.

The Olmstead–Tukey test was used to classify each species into one of four categories, (dominant, common, occasional and rare) according to its abundance (log number of zoeae + 1), and frequency of occurrence (%) for each sampled year (Fig. 2) (Olmstead and Tukey, 1947; Sokal and Rohlf, 2012). Dominant species have higher abundance and frequency. Common species have lower densities and higher frequencies than the average. Occasional species have higher densities and lower frequencies than the average. Rare species have both densities and frequencies below average values (Steel and Torrie, 1988). We mentioned in the results the names of the dominant species, with the purpose of observing if these species are maintained over time.

Shannon diversity indices (H) and species richness (S) were obtained both temporally and spatially (Magurran, 1988). Diversity values were compared with the Hutcheson test (1970). All community parameters were obtained with the PAST software (Harmer *et al.*, 2001).

Results

Environmental conditions

Our results show that the highest temperature was recorded during the rainy weather conditions in 2011 with 29.3 ± 0.56 °C on the south central transect, while the lowest temperature was registered in a cold front in 2013 with 23.07 ± 0.56 °C on the northern transect. Temperatures differed depending on weather conditions ($F_{2,27}$ = 42.923, p < 0.001) and year of sampling ($F_{2,27}$ = 16.221, p < 0.001). Such differences were found between the three weather conditions and between the three years (Tukey p < 0.05). The highest salinity was found during dry weather conditions in 2012 with 35.91 ± 0.09 on the southern transect, and the lowest salinity was registered in rainy weather conditions in 2011 with 33.15 ± 0.18 on the south central transect. Salinity differed depending on weather conditions ($F_{2,27}$ = 67.212, p < 0.001) and year of sampling ($F_{2,27}$ = 16.293, p < 0.001). Similar

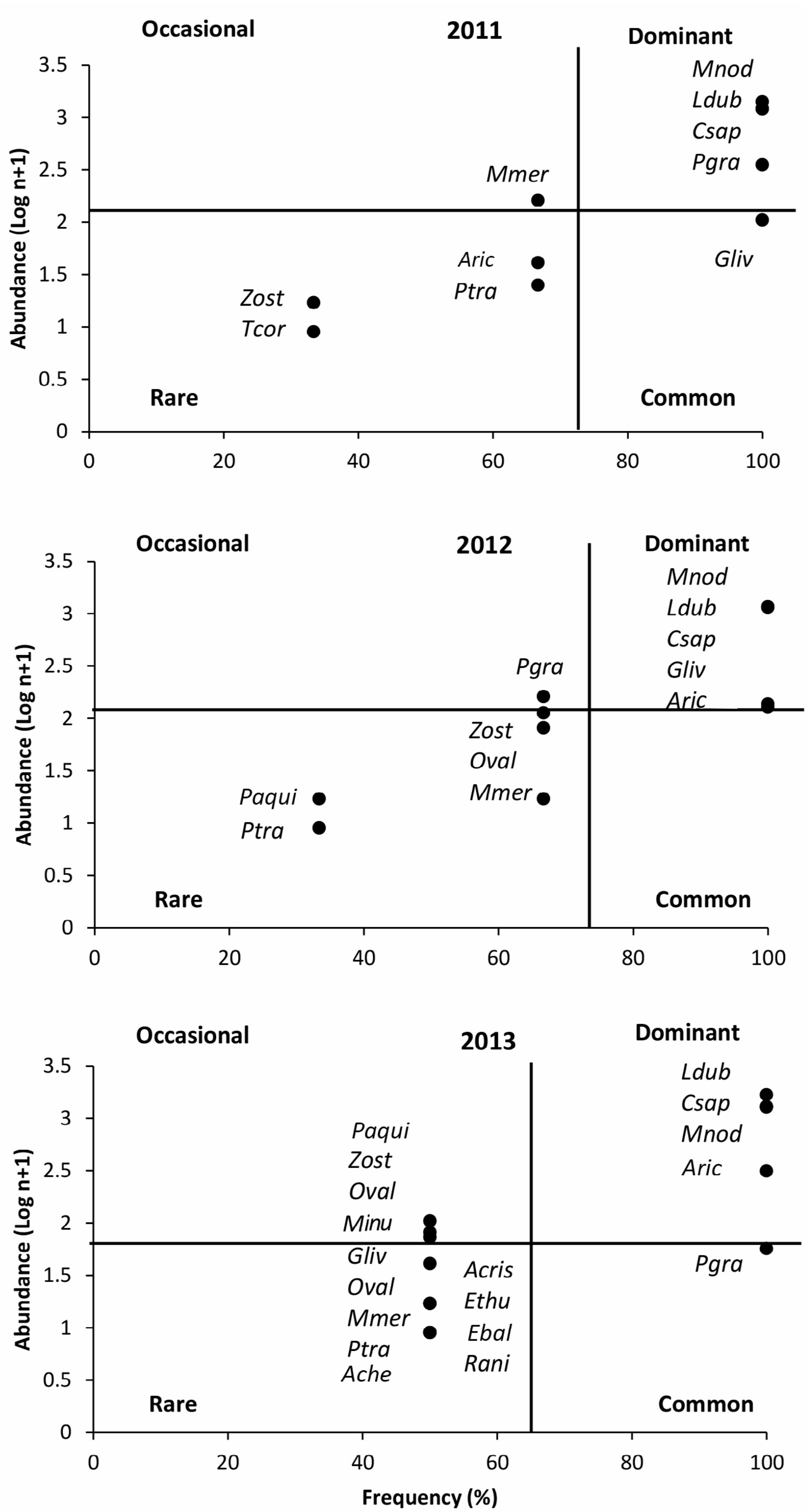

Figure 2. Relation between the frequency of occurrence and density of brachyuran zoea I per year. Species name abbreviations are shown in Table 3.

differences were found between the three weather conditions and years (Tukey $p < 0.05$). The highest dissolved oxygen concentration was found in rainy weather in 2011 on the southern transect with 6.56 ± 0.08 mg L^{-1}, while the lowest dissolved oxygen was registered in dry weather conditions in 2011 with 2.92 ± 0.08 mg L^{-1} on the northern transect. The dissolved oxygen differed depending on weather conditions ($F_{2,27} = 16.821$, $p < 0.001$), being higher during rainy weather conditions than during cold front weather conditions (Tukey $p < 0.05$) (Tabs. 1, 2).

Dominance, distribution and density

We found an average of 1731 ± 1631 Brachyura zoea I larvae per climatic season belonging to 18 species, in 16 genera and 14 families. Over the three years, we found more species during cold front weather conditions (17 spp.), followed by dry and rainy weather conditions (ten and eight spp., respectively) (Tab. 3).

In 2011, four species were dominant (40%): *Menippe nodifrons* Stimpson, 1859, *Libinia dubia* H. Milne Edwards, 1834, *C. sapidus* and *Pachygrapsus gracilis* (de Saussure, 1857); one species (10%) was occasional, four species (40%) were rare and one species (10%) was common. In 2012, five species were dominant (45.45%): *M. nodifrons*, *L. dubia*, *C. sapidus*, *Geograpsus lividus* (H. Milne Edwards, 1837) and *Armases ricordi* (H. Milne Edwards, 1853); one species (9.09%) was occasional, five species (45.45%) were rare and none were common. In 2013, four species were dominant (23.53%): *L. dubia*, *M. nodifrons*, *C. sapidus* and *A. ricordi*; three species (17.64%) were occasional, nine species (52.94%) were rare and one species (5.88%) was common (Fig. 2).

The highest average density, 4768 ± 556 zoeae 100 m^{-3}, was found during cold fronts in 2013, followed by 3568 ± 566 zoeae 100 m^{-3} during dry weather conditions in 2011. *Libinia dubia* was the species with the highest density during cold fronts in 2013, with 1592 ± 127 zoeae 100 m^{-3}, followed by *C. sapidus* (1248 ± 215 zoeae 100 m^{-3}) and *M. nodifrons* (1232 ± 95 zoeae 100 m^{-3}) (Tab. 3).

The highest average density of zoeae I with respect to the proximity to the coast, was found nearshore in 2011 with 3120 ± 545 zoeae 100 m^{-3} followed by offshore in 2013 with 2448 ± 718 zoeae 100 m^{-3}. *Menippe nodifrons* was the species with the highest average density with 1032 ± 142 zoeae 100 m^{-3} in

Table 1. Seasonal temperature (°C), salinity and dissolved oxygen (mgl^{-1}) in three weather conditions and four transects during the years 2011, 2012 and 2013. Northern, N; North central Nc; South central, Sc; Southern, S. (± SD).

Temperature (°C)								
Zone		2011		2012				2103
	Dry	Rainy	Cold fronts	Dry	Rainy	Cold fronts	Dry	Cold fronts
N	27.9 ± 0.52	28.68 ± 0.43	28 ± 0.44	26.82 ± 0.48	29.1 ± 0.45	24.55 ± 0.48	27.76 ± 0.39	23.07 ± 0.53
Nc	27.33 ± 0.40	28.87 ± 0.38	27.69 ± 0.50	27.15 ± 0.18	29.1 ± 0.41	24.06 ± 0.05	27.33 ± 0.36	23.73 ± 0.41
Sc	26.75 ±0.50	29 ± 0.36	27.89 ± 0.39	26.53 ± 0.41	29.2 ± 0.42	24 ± 0.33	27.47 ± 0.08	24.2 ± 0.20
S	27.53 ± 0.35	29.29 ± 0.27	27.67 ± 0.21	27.16 ± 0.13	29.3 ± 0.56	24.4 ± 0.13	27.54 ± 0.10	24.37 ± 0.20
Salinity								
Zone		2011		2012				2103
	Dry	Rainy	Cold fronts	Dry	Rainy	Cold fronts	Dry	Cold fronts
N	35.84 ± 0.05	33.43 ± 0.49	34.92 ± 0.08	35.76 ± 0.11	33.19 ± 0.12	35.68 ± 0.08	35.68 ± 0.13	35.62 ± 0.08
Nc	35.86 ± 0.05	34.31 ± 0.30	35.3 ± 0.15	35.81 ± 0.13	34.15 ± 0.18	35.67 ± 0.04	35.71 ± 0.16	35.31 ± 0.16
Sc	35.73 ± 0.08	34 ± 0.13	35.46 ± 0.14	35.89 ± 0.09	33.15 ± 0.23	35.67 ± 0.08	35.74 ± 0.15	35.3 ± 0.12
S	35.73 ± 0.11	33.99 ± 0.17	35.36 ± 0.13	35.91 ± 0.09	33.18 ± 0.11	35.67 ± 0.08	35.79 ± 0.09	34.93 ± 0.08
Oxygen (mgl^{-1})								
Zone		2011		2012				2103
	Dry	Rainy	Cold fronts	Dry	Rainy	Cold fronts	Dry	Cold fronts
N	2.92 ± 0.08	4.84 ± 0.05	4.16 ± 0.09	3.12 ± 0.08	3.6 ± 0.11	4.52 ± 0.08	2.96 ± 0.05	4.16 ± 0.05
Nc	3.19 ± 0.09	5.74 ± 0.10	4.41 ± 0.09	3.19 ± 0.09	5.8 ± 0.1 1	4.03 ± 0.10	3.21 ± 0.12	4.23 ± 0.11
Sc	3.41 ± 0.12	5.64 ± 0.08	4.59 ± 0.09	3.5 ± 0.40	5.7 ± 0.13	4.33 ± 0.14	3.67 ± 0.14	4.57 ± 0.08
S	3.93 ± 0.08	6.56 ± 0.08	5.53 ± 0.17	3.94 ± 0.05	5.9 ± 0.12	5.67 ± 0.05	3.99 ± 0.09	5.41 ± 0.12

Table 2. The model Generalized Least Squares was applied to compare the temperature (°C), salinity and dissolved oxygen (mgl^{-1}) from zones (Z) of sampling, under weather conditions (Wc) for each sampling year (Y). *, significant differences

Temperature	**SS**	**DF**	**MS**	**F**	***P***
Corrected model	96,349[a]	4	24.087	35.128	<0.001*
Intersection	21472.543	1	21472.543	31314.943	<0.001*
WC	58.864	2	29.432	42.923	<0.001*
Y	22.245	2	11.123	16.221	<0.001*
Residual	18.514	27	0.686		
Total	23787.023	32			
Corrected Total	114.862	31			
a. R^2 = 0.839, p < 0.05					
Salinity	**SS**	**DF**	**MS**	**F**	***P***
Corrected model	15,597[a]	4	3.899	35.119	<0.001*
Intersection	34811.168	1	34811.168	313540.022	<0.001*
WC	14.925	2	7.462	67.212	<0.001*
Y	3.618	2	1.809	16.293	<0.001*
Residual	2.998	27	0.111		
Total	39152.123	32			
Corrected Total	18.594	31			
a. R^2 = 0.839, p < 0.05					
Dissolved oxygen	**SS**	**DF**	**MS**	**F**	***P***
Corrected model	21,181[a]	4	5.295	8.480	<0.001*
Intersection	573.521	1	573.521	918.495	<0.001*
WC	21.094	2	10.547	16.891	<0.001*
Y	1.714	2	0.857	1.373	0.271
Residual	16.859	27	0.624		
Total	616.040	32			
Corrected Total	38.040	31			
a. R^2 = 0.557, p < 0 0.05					

the nearshore zone in 2011, followed by *C. sapidus* with 968 ± 352 zoeae 100 m^{-3} in the offshore zone in 2013 and *L. dubia* with 888 ± 139 zoeae 100 m^{-3} in the offshore zone in 2011 (Tab. 4).

Regarding the zoeal density between the transects, the highest average density was found in the north-central zone in 2013 with 2,272.391 ± 391 zoeae 100 m^{-3}, followed by the south-central zone in 2011 with 1,984 ± 300 zoeae 100 m^{-3}. *Libinia dubia* was the species with the highest average density, with 1,016 ± 102 zoeae 100 m^{-3} in the northern zone in 2013, followed by *C. sapidus* with 944 ± 182 zoeae 100 m^{-3} in the north-central zone, also in 2013 (Tab. 5).

According to the PERMANOVA, the species density changed as a function of weather conditions, year, and transects with temperature, salinity and dissolved oxygen as covariants ($p < 0.05$). The pairwise revealed that differences in the density of the zoeae were found among: a) cold fronts with respect to dry and rainy weather conditions (cold fronts had the highest density); b) the three years of sampling (2013 had the highest density); and c) the north-central zone with respect to the northern zone, and the southern zone with respect to the northern zone (the north central zone had the highest density) ($p < 0.05$) (Tab. 6). With the CAP ordination, too, we observed distinctions between the three weather conditions and the formation of three groups with respect to the transects - one from the northern zone, a second from the southern zone, and both integrated by the south-central and north-central transects (Fig. 3).

According to the analysis of density with SIMPER, the species that defined the 75% cumulative dissimilarity between the transects were: *C. sapidus*, *L. dubia*, *M. nodifrons*, *Ovalipes* sp., *G. lividus*, *M. mercenaria,* and *P. gracilis,* particularly, in the northern zone; *A. ricordi* in the north central zone; *P. gracilis*, *P. aquilonaris* and *Z. ostreus* in the south central zone and

Table 3. List and density species of Brachyura zoea I per weather conditions, sampling year, adult's habitat, bathymetric distribution and spawning zone. Cf, Cold fronts; Dr, Dry; E, estuarine; Fs, foreshore; Inf, infralittoral; Itd, intertidal; M. marine; Ns, nearshore; Offs, offshore; Ra, Rainy; ST, semiterrestrial; Spl, supralittoral; Sym, symbiotic; Year, 2011, 2012 and 2013. Bold, highest density.

Species	Dr 2011	Ra 2011	Cf 2011	Dr 2012	Ra 2012	Cf 2012	Dr 2013	Cf 2013	Adults habitat	Bathymetric distribution	Spawning zone
Achelous sp. De Hann, 1833 (Ache)								16±5	M/Inf	<1-550	Fs-Ns-Offs
Armases ricordi (H. Milne Edwards, 1853) (Aric)	24±8		16±4	40±11	8±4	80±33	40±4	272±19	E-Itd	<1	Fs-Ns
Austinixa cristata (Rathbun, 1900) (Acri)								8±1	M-Inf	0-2	Fs-Ns
Callinectes sapidus Rathbun, 1896 (Csap)	64±11	48±12	1088±232	720±81	40±9	400±61	40±5	**1248±215**	M/E-Inf	0-90	Fs-Ns
Ebalia sp. (Leach, 1817) (Ebal)								8±1	M/Inf	<1-160	Fs-Ns-Offs
Ethusa sp. Roux, 1830 (Ethu)								8±2	M/Inf	3-752	Fs-Ns-Offs
Geograpsus lividus (H. Milne Edwards, 1837) (Gliv)	8±3	24±6	72±39	104±71	8±2	24±6		40±4	M/ST-Itd	<2	Fs
Libinia dubia H. Milne Edwards, 1834 (Ldub)	152±25	32±11	1024±91	880±82	8±3	272±61	80±34	**1592±127**	M-Inf	<1-46	Ns
Menippe mercenaria (Say, 1818) (Mmer)		16±5	144±11	8±2		8±4		16±3	M-Inf	0-51	Fs
Menippe nodifrons Stimpson, 1859 (Mnod)	240±31	248±97	928±175	552±74	24±6	576±63	40±5	**1232±95**	M-Inf	0-3	Ns
Minuca sp. Bott, 1954 (Minu)								72±39	E/ST-Spl	<1	Fs
Ovalipes sp. Rathbun, 1898 (Oval)				8±1		72±27	16±3		M-Inf	<1-31	Ns
Pachygrapsus gracilis (Saussure, 1858) (Pgra)	32±11	40±9	280±8	56±12		104±62	8±2	48±4	M/E-Itd	<1	Fs
Pachygrapsus transversus (Gibbes, 1850) (Ptra)	16±4	8±2		8±3				16±4	M/E-Itd	<1	Fs
Persephona aquilonaris Rathbun, 1933 (Paqui)						16±4		104±2	M-Inf	<4-55	Fs-Ns
Raninoides sp. H. Milne Edwards, 1837 (Rani)								8±2	M-Inf	18-200	Ns-Offs
Troglocarcinus corallicola Verrill, 1908 (Tcor)		8±2							M-Sym	<1-75	Ns
Zaops ostreus (Say, 1817) (Zost)			16±6	104±26		8±1		80±33	M-Sym	<1-3	Ns
Total (±SD)	536±93	424±144	3568±566	2480±363	88±24	1560±322	224±53	4768±556			

Table 4. List and density of species of Brachyura zoea I per sampling zone. Fs, foreshore, Ns, nearshore; Offs, offshore. Bold, highest density.

Species	Fs2011	Ns2011	Offs2011	Fs2012	Ns2012	Offs2012	Fs2013	Ns2013	Offs2013
Achelous sp. De Hann, 1833								16±4	
Armases ricordi (H. Milne Edwards, 1853)	8±2	32±6		8±1	104±14	16±3	144±20	136±23	32±5
Austinixa cristata (Rathbun, 1900)							8±2		
Callinectes sapidus Rathbun, 1896	16±2	552±114	632±278	104±14	352±29	704±121	32±11	288±38	**968±352**
Ebalia sp. (Leach, 1817)								8±2	
Ethusa sp. Roux, 1830									8±3
Geograpsus lividus (H. Milne Edwards, 1837)		88±28	16±4.32	8±2	56±4	72±40	24±6	8±3	8±1
Libinia dubia H. Milne Edwards, 1834	24±6	**888±139**	296±122	496±161	272±4	392±90	616±139	584±189	472±90

Table 4. Cont.

Menippe mercenaria (Say, 1818)		160±38		8±2	8±1			8±1	8±3
Menippe nodifrons Stimpson, 1859	32±11	**1032±142**	352±121	72±15	416±24	664±93	104±26	392±12	776±188
Minuca sp. Bott, 1954							72±40		
Ovalipes sp. Rathbun, 1898				8±3	72±40		8±1		8±3
Pachygrapsus gracilis (Saussure, 1858)		336±69	16±4	16±4	72±11	72±16	8±3	16±4	32±11
Pachygrapsus transversus (Gibbes, 1850)		24±6			8±2		16±4		
Persephona aquilonaris Rathbun, 1933					16±4			40±16	64±34
Raninoides sp. H. Milne Edwards, 1837								8±1	
Troglocarcinus corallicola Verrill, 1908			8±1						
Zaops ostreus (Say, 1817)		8±3	8±2		40±9	72±39		8±3	72±38
Total (±SD)	80±21	**3120±545**	1328±532	720±202	1416±142	1358±402	1032±252	1512±293	**2448±718**

Table 5. List and density of species of Brachyura zoea I per transect. North central zone, Nc; Northern zone, N; South central zone, Sc; Southern zone, S. Bold, highest density.

Species	**Nc2011**	**Sc2011**	**S2011**	**N2012**	**Nc2012**	**Sc2012**	**S2012**	**N2013**	**Nc2013**	**Sc2013**	**S2013**
Armases ricordi (H. Milne Edwards, 1853)	24±6		16±4		8±3	96±13	24±6		104±22	96±22	112±24
Austinixa cristata (Rathbun, 1900)									8±3		
Callinectes sapidus Rathbun, 1896	152±74	664±17	384±150	40±11	704±15	416±88		104±25	**944±182**	104±20	136±27
Ethusa Roux, 1830										8±3	
Geograpsus lividus (H. Milne Edwards, 1837)		24±6	80±32		16±4	96±25	24±6		8±3	16±4	16±4
Ebalia (Leach, 1817)										8±3	
Libinia dubia H. Milne Edwards, 1834	264±85	520±108	424±210	568±38	88±9	408±81	96±18	**1016±102**	408±82	168±32	80±16
Menippe mercenaria (Say, 1818)	64±16	16±4	80±21			8±3	8±3		8±3	8±3	
Menippe nodifrons Stimpson, 1859	128±45	432±91	856±169		88±18	712±78	352±74	112±21	688±75	184±36	288±40
Ovalipes sp. Rathbun, 1898				8±3	64±4	8±3			8±3	8±3	
Pachygrapsus gracilis (Saussure, 1858)		320±71	32±11		16±4	64±16	80±18		16±4	8±3	32±12
Pachygrapsus transversus (Gibbes, 1850)	16±4	8±3					8±3			16±3	
Persephona aquilonaris Rathbun, 1933							16±4		8±3	40±9	56±12
Achelous De Hann, 1833											16±4
Raninoides H. Milne Edwards, 1837								8±3			
Troglocarcinus corallicola Verrill, 1908			8±3								
Minuca Bott, 1954									8±3	64±13	
Zaops ostreus (Say, 1817)			16±4		8±3	88±28	16±4	8±3	64±8	8±3	
Total (±SD)	648±230	**1984±300**	1896±604	616±52	992±60	1896±335	624±136	1284±154	**2272±391**	736±157	736±139

Table 6. Permutational multivariate analysis of variance on the density of the Brachyura zoea I community, based on an orthogonal three-factors model, with environmental parameters as covariates. Pairwise tests between weather conditions (Wc), Years (Y) and Zones (Z) from the standard model of the PERMANOVA. Cold fronts, Cf; Dry, Dr; Transect, Tr; Northern, N; North central, Nc; Rainy, Ra; Southern, S; South central, Sc. *, significant differences $p < 0.05$.

			L-Z					
Source	**df**	**ss**	**MS**	**F**	***p*(perm)**	**Groups**	**t**	***p*(perm)**
Temperature	1	8757.7	8757.7	52.15	0.001*	D-Cf	12.42	0.001*
Wc	2	8433.7	4216.9	25.11	0.001*	R-Cf	8.79	0.001*
Y	2	5150	2575	15.33	0.001*	2011-2012	6.64	0.005*
Tr	3	2206.3	735.42	4.38	0.016*	2011-2013	6.28	0.011*
T*Wc	2	1740.2	870.1	5.18	0.015*	2012-2013	4.89	0.004*
T*Y	2	3420.4	1710.2	10.18	0.002*	S-N	6.13	0.039*
T*Tr	3	1333.9	444.63	2.65	0.080	Nc-N	4.46	0.003*
Residual	10	1679.4	167.94					
Total	25	32722						
Salinity	1	6713.1	6713.1	29.77	0.001*	D-Cf	16.99	0.001*
Wc	2	11550	5775.2	25.60	0.001*	R-Cf	8.22	0.001*
Y	2	3116.6	1558.3	6.91	0.003*	2011-2012	6.43	0.002*
Tr	3	3183	1061	4.70	0.008*	2011-2013	4.46	0.004*
S*Wc	2	2653.8	1326.9	5.88	0.008*	2012-2013	4.03	0.008*
S*Y	2	1767.6	883.81	3.92	0.021*	Sc-N	8.79	0.027*
S*Tr	3	1481.3	493.76	2.19	0.096	Nc-N	6.36	0.003*
Residual	10	2255.8	225.58					
Total	25	32722						
Dissolved oxygen	1	1683.7	1683.7	3.83	0.048*	D-Cf	16.55	0.001*
Wc	2	15482	7741.1	17.62	0.001*	R-Cf	12.57	0.001*
Y	2	3771.1	1885.5	4.29	0.01*	2011-2012	4.93	0.007*
Tr	3	3832.1	1277.4	2.91	0.027*	2011-2013	5.08	0.005*
Do*Wc	2	722.61	361.31	0.82	0.528	2012-2013	5.91	0.001*
T*Y	2	979.04	489.52	1.11	0.352	Nc-N	6.07	0.002*
Do*Tr	3	1858	619.32	1.41	0.233			
Residual	10	4393	439.3					
Total	25	32722						

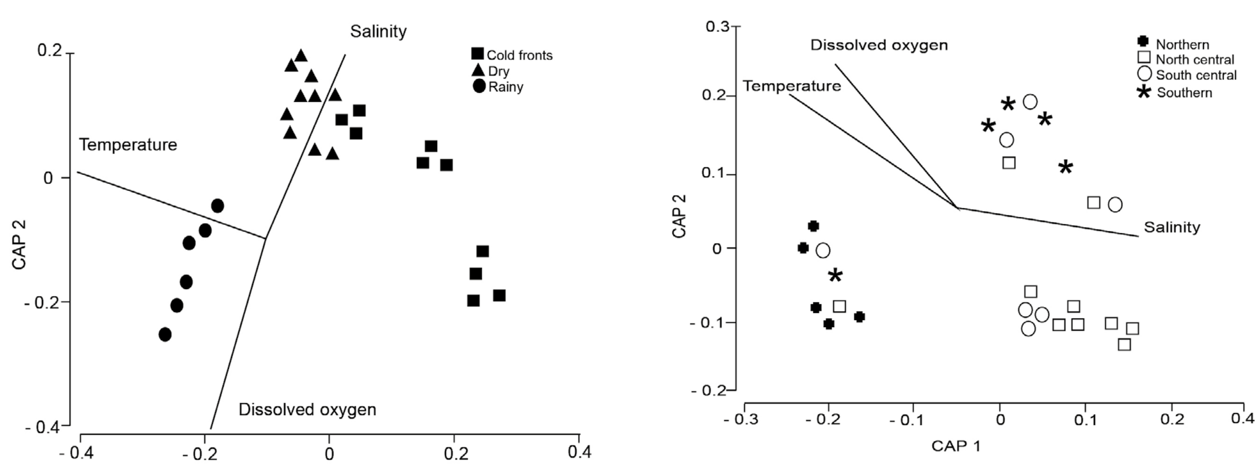

Figure 3. Canonical analysis of principal coordinates (CAP) was used to examine how density of brachyuran zoeae I varied in a multivariate space. Vectors Salinity, Temperature, and Dissolved Oxygen change as a function of weather conditions (a) and sampling zones (b).

P. transversus in the southern zone. The species that defined the 75% cumulative of dissimilarity with the analysis SIMPER considering the weather conditions were: *C. sapidus*, *L. dubia*, *M. nodifrons* and *Ovalipes* sp., particularly, in cold fronts weather; *M. mercenaria*, *P. transversus* and *P. aquilonaris* in rainy weather and *A. ricordi*, *G. lividus* and *P. gracilis* in dry weather. The average dissimilarity between the transects and between weather conditions was 38.95 and 38.86%, respectively.

Using the canonical correlation analysis, we found that the first eigenvalue explained 41.48% of the variance and the second eigenvalue explained 40.47%. The correlation coefficients between the input variables and the canonical variables (Y1) were 0.759 between temperature and F1, and 0.55 between salinity and F2 ($p < 0.05$). From the correlations between the input variables and the canonical variables (Y2), we obtained the structure of four groups. The first group of species with the highest density was present mainly in the north central and south central transects with a temperature of 24.2 ± 0.20 °C, dissolved oxygen of 4.23 ± 0.11 mg L^{-1} and salinity of 35.31 ± 0.16. These species were *Achelous* sp., *A. ricordi*, *Austinixa cristata* (Rathbun, 1900), *C. sapidus*, *Ebalia* sp., *Ethusa* sp., *Minuca* sp., *P. aquilonaris*, and *Raninoides* sp. The second group, which included *T. corallicola* and *Ovalipes* sp., were collected in the southern zone, with a temperature of 29.29 ± 0.27 °C, dissolved oxygen of 6.56 ± 0.08 mg L^{-1} and salinity of 33.99 ± 0.17. The third group, which included *L. dubia*, *M. nodifrons*, and *Z. ostreum*, was collected in all three years, along the four transects of sampling, with a temperature of 23.07 ± 0.53 °C, dissolved oxygen of 2.96 ± 0.05 mg L^{-1} and salinity of 35.89 ± 0.04. The fourth group was formed by *G. lividus*, *M. mercenaria*, *P.gracilis*, and *P. transversus*, and these species were collected mainly in the central transects with intermediate values of temperature 26.53 ± 0.41 °C, dissolved oxygen 5.63 ± 0.08 mg L^{-1} and salinity 34 ± 0.13 (Fig. 4).

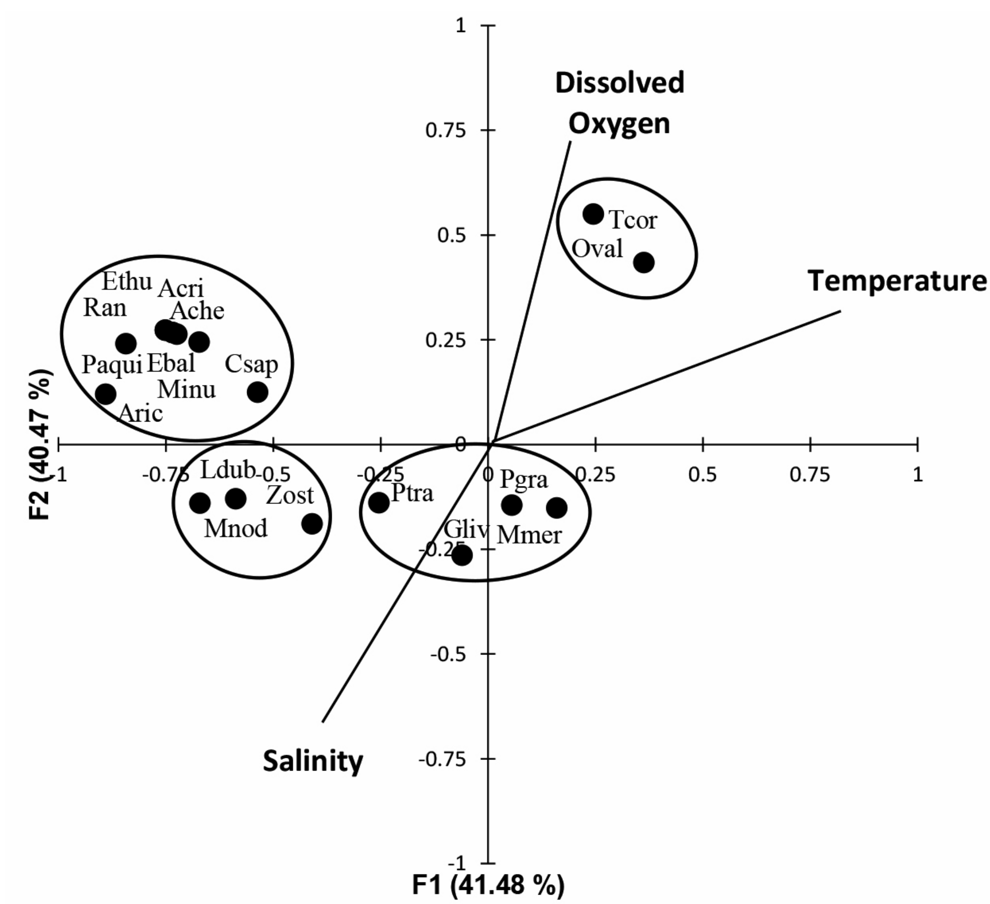

Figure 4. Canonical Correlation Analysis (CCA) between the density of brachyuran zoea I and temperature, salinity and dissolved oxygen ($F = 3.811$, $p < 0.001$). Abbreviation of species names as per Table 3.

Species richness and diversity

In 2011, the species richness was 7 for the dry weather conditions, and 8 for rainy and cold front weather conditions. Diversity was between 2.04 bits individual^{-1} for rainy weather conditions and 2.20 bits individual^{-1} for cold front weather conditions. During 2012, the species richness was 10 for cold front and dry weather conditions, and 5 for rainy conditions with diversity between 1.97 bits individual^{-1} for cold front weather conditions and 2.40 bits individual^{-1} in dry weather conditions. During 2013, the species richness was 16 for cold front weather conditions and 6 for dry weather conditions with diversity at 2.31 bits individual^{-1} for cold fronts and 2.35 bits individual^{-1} for dry weather conditions (Tab. 7).

The highest diversity was found in the nearshore zone, with 2.56 bits individual^{-1}, species richness of 10 and evenness of 0.77 in 2012 while the lowest diversity was present in the foreshore zone with 1.52 bits individual^{-1}, species richness of 8 and the lowest value of evenness of 0.51 in 2012. When considering distribution with respect to the mouth of the Jamapa river, the highest diversity was found in the south central transect in 2013, with 2.97 bits individual^{-1}, species richness of 14 and evenness of 0.78 and the lowest diversity was located in the northern transect in 2012, with 0.45 bits individual^{-1}, species richness of 3 and evenness of 0.28 (Tab. 7).

When comparing the diversity values, significant differences between dry and cold front weather conditions were found in 2011 ($p = 0.037$) and 2012 ($p < 0.027$). For the different shore zones, most of the comparisons present significant differences ($p < 0.001$). When comparing distribution in the transects, differences between the northern zone and central and southern transects were found in 2012 ($p < 0.001$) but differences between the four transects were found in 2013 ($p < 0.001$) (Tab. 8).

Table 7. Specific richness (Sr), diversity (H) and evenness of Brachyura zoea I community per weather condition (Wc), transects (Tr) and shore zone (Sh-Z). Cold fronts, Cf; Dry, Dr; Foreshore, Fs; North central zone, Nc; Nearshore, Ns; northern zone, N; Offshore, Offs; Rainy, Ra; Southern zone S; South central zone, Sc.

Wc	**Dr2011**	**Ra2011**	**Cf2011**	**Dr2012**	**Ra2012**	**Cf2012**	**Dr2013**	**Cf2013**			
Specific richness	7	8	8	10	5	10	6	16			
Diversity	2.09	2.04	2.2	2.21	1.97	2.4	2.31	2.35			
Equitability	0.74	0.68	0.73	0.67	0.85	0.72	0.89	0.59			
Sh-Z	**Fs2011**	**Ns2011**	**Offs2011**	**Fs2012**	**Ns2012**	**Offs2012**	**Fs2013**	**Ns2013**	**Offs2013**		
Specific richness	4	8	7	8	10	7	10	12	11		
Diversity	1.85	2.32	1.92	1.52	2.56	2.09	1.98	2.28	2.07		
Equitability	0.92	0.77	0.68	0.51	0.77	0.75	0.6	0.642	0.6		
Tr	**Nc2011**	**Sc2011**	**S2011**	**N2012**	**Nc2012**	**Sc2012**	**S2012**	**N2013**	**Nc2013**	**Sc2013**	**S2013**
Specific richness	6	7	9	3	8	9	9	5	12	14	8
Diversity	2.12	2.1	2.1	0.45	1.53	2.36	2.05	0.95	2.06	2.97	2.46
Equitability	0.82	0.75	0.66	0.28	0.51	0.74	0.65	0.41	0.58	0.78	0.82

Table 8. Comparison of the values of diversity Shannon with Hutcheson (1970) test. * significant difference.

Comparison among:		*P*
Weather conditions		
	Dry-Rainy	0.625
2011	Dry-Cold fronts	0.037*
	Cold fronts-Rainy	0.096
	Dry-Rainy	0.027*
2012	Dry-Cold fronts	< 0.001*
	Cold fronts-Rainy	< 0.001*
2013	Dry-Cold fronts	0.402

Table 8. Cont.

Comparison among:		*P*
Parallel distribution		
2011	Foreshore-Nearshore	< 0.001*
	Foreshore-Offshore	0.186
	Nearshore-Offshore	< 0.001*
2012	Foreshore-Nearshore	< 0.001*
	Foreshore-Offshore	< 0.001*
	Nearshore-Offshore	< 0.001*
2013	Foreshore-Nearshore	< 0.001*
	Foreshore-Offshore	0.124
	Nearshore-Offshore	< 0.001*
Latitudinal distribution		
2011	Central North-Central South	0.725
	Central North-Southern	0.737
	Central South-Southern	0.969
2012	Northern-Central North	< 0.001*
	Northern-Central South	< 0.001*
	Northern-Southern	< 0.001*
	Central North-Central South	< 0.001*
	Central North-Southern	0.367
	Central South-Southern	0.003
2013	Northern-Central North	< 0.001*
	Northern-Central South	< 0.001*
	Northern-Southern	< 0.001*
	Central North-Central South	< 0.001*
	Central North-Southern	< 0.001*
	Central South-Southern	< 0.001*

Discussion

We observed that densities of brachyuran zoea I were dependent on changes in temperature, salinity, and dissolved oxygen, which were, in turn, dependent on the weather conditions. Our use of weather conditions, instead of normal seasonal sampling, was thus justified.

We also found that densities of brachyuran zoea I increased with proximity to the estuarine plume of the Jamapa River. Zoeae of some estuarine brachyuran species have been found to progressively decrease as a result of the decreasing estuarine plume at offshore stations; often presenting very low densities (Koettker and Freire, 2006). This is a combination of where the adults are distributed, where the ovigerous females migrate to their respective spawning zone and the vertical migration behavior of larvae, resulting in retention of the zoeae in areas nearest the coast (Sastry, 1983; Anger, 2001; Queiroga and Blanton, 2004).

The changes in environmental factors in the region of the PNSAV during cold front and rainy weather conditions, including tropical storms and hurricanes, cause mixing and incorporate nutrients into the photic zone (Zavala-Hidalgo *et al.*, 2006; 2014). This increase of nutrients can cause a phytoplankton bloom which could promote an increase in zooplankton feeding on this algae (Schwamborn *et al.*, 2001). Winds under cold front weather conditions form currents along the Tamaulipas and Veracruz coasts, which take a southward direction and cause cyclonic currents, while those winds in the states of Campeche Bank and Yucatán form anticyclonic currents. These currents converge at the southern end of the Gulf of Mexico, producing flows perpendicular to the coast, from the neritic-oceanic zone to the oceanic zone (Zavala-Hidalgo *et al.*, 2006). Furthermore, the subtropical water underlying the Campeche Bank favors resuspension of the nutrient-rich sediment in the southern part of the PNSAV. Rodríguez-Gómez *et al.* (2015) found that the highest levels of chlorophyll and, consequently, of gross primary productivity in the PNSAV, begin to appear in September, and last from October until April. Thus, the highest density of zoeae obtained in this study under cold front weather conditions could be related to the increase in dissolved oxygen, due to the increase in chlorophyll, as well as the transport of neritic-oceanic species by surface currents generated by the winds characteristic of this time (Álvarez-Cadena *et al*., 2007).

Our results have shown that the zoeae I community from the PNSAV is structured into four main species assemblages, distributed along a latitudinal gradient. The community responds to the environmental changes from changing weather conditions and, according to the review of literature, to the reproductive zone of the adults.

The species in the first group (*Achelous* sp., *A. ricordi*, *A. cristata*, *C. sapidus*, *Ebalia* sp., *Ethusa* sp., *Minuca* sp., *P. aquilonaris*, and *Raninoides* sp.) were found to exhibit an infralittoral, intertidal and estuarine affinity during cold front weather conditions. Their life cycle includes planktotrophic development, which takes place in lower estuaries or offshore seas (Fransozo and Negreiros-Fransozo, 1986; Alvarez and Ewald, 1990). This group includes semi-terrestrial species that live in the supralittoral fringe up to several hundred meters inland (Diesel and Schuh, 1998), inhabit infralittoral zones among rocks and debris, and burrow in the sediments of beaches, lagoons, estuaries, mouths of rivers, freshwater bottoms, areas near reefs, mangroves, seagrass and algae (Coelho and Ramos, 1972; Franks *et al*., 1972; Williams, 1982; Barnwell and Thurman, 1984; Manning and Felder, 1989; Melo, 1996; Rosenberg, 2001; Hirose, 2009; WoRMS, 2020). Some species are symbionts of ghost shrimp (axiidean crustaceans or ecologically equivalent species) and are found on sandy beaches (Peiró and Mantelatto, 2011). The ovigerous females of this group are found from October to March (Rouse, 1970; Williams, 1984; García-Montes *et al*., 1988; Benneti *et al*., 2007). The ovigerous females migrate to release their larvae in foreshore and nearshore zones (Williams, 1984), consistent with the zoeae found in this study belonging to the same group.

The second group comprises the species *T. corallicola* and *Ovalipes* sp., which exhibit an oceanic affinity and were collected during dry and cold front conditions. *Troglocarcinus corallicola* Verrill, 1908 is the most widely distributed of the Atlantic cryptochirids and has been recorded as a symbiont of several species of stony corals, including *Manicina areolata* (Linnaeus, 1758) (Kropp and Manning, 1987). Ovigerous females have been collected year-round from Florida to the Mexican Caribbean (Carricart-Gavinet *et al*., 2004). *Ovalipes* sp. is common on a variety of oceanic bottoms, especially sand (Williams and Wigley, 1977). Ovigerous females have been found from October to February (Dudley and Judy, 1971). These species have a close relationship with other species present in nearshore coral reefs, where they release their larvae.

Species in the third group (*L. dubia*, *M. nodifrons* and *Z. ostreum*) have a marine infralittoral affinity and were collected in rainy weather conditions. The adults can be found on almost all types of benthic habitat in the shallow ocean and are associated with sponges, hydroids, ascidians, barnacles or worm tubes; all common on coral reefs. They can also be found in biogenic substrates such as coral-associated colonies of *Phragmatopoma caudata* Krøyer in Mörch, 1863 and *Schizoporella unicornis* (Johnston, 1847) but also in algal banks of *Sargassum cymosum* Agardh, 1820–1821 (Williams, 1984; Oshiro, 1999; Rodrigues-Alves *et al*., 2013). The ovigerous females can be found from January to September (Williams, 1984; Oliveira *et al*., 2005). In particular, the adults of *Z. ostreus* are found where their hosts live (Cheng, 1973; Kaplan, 1988; Bower *et al*., 1994). The larvae feed on plankton from the open ocean (Sandoz and Hopkins, 1947), explaining their oceanic affinity, while the adults live as parasites in oysters (Stauber, 1945; Cheng, 1973). In this group, adults stay in the nearshore zone and release their larvae close by.

The species in the fourth group (*G. lividus, M. mercenaria, P. gracilis* and *P. transversus*) were mainly collected in cold front weather conditions. The adults live in intertidal areas among rocky pilings, roots of mangroves, and sandy shores at high tide, and are well adapted to salinity ranges near the mouths of estuaries and can survive extreme salinity. The ovigerous females can be found year-round but are more common from February to September (Dudley and Judy, 1971; Rickner, 1977; Williams 1984; Burggren and McMahon, 1988; Cuesta and Schubart, 1999; Poupin *et al.*, 2005; Hartnoll, 2009). The females of these species release their larvae in the swash zone (Williams, 1984).

Our results show that the larval community provides valuable information about the composition, place, and potential spawning season, of the crustacean community. Likewise, the temporal distribution of decapod larvae suggests a larval hatching period for many species with abundance peaks associated with seasonality; all this consistent with Landeira and Soldevilla (2018).

The highest density of Brachyura zoea I found in the PNSAV was consistent with the results attained in estuaries by other authors (Schwamborn *et al.*, 2001; Silva-Falcão *et al.*, 2007), however, it is lower than that reported in bays and lagoons (Costa-Brandão *et al.*, 2011; Fernandes *et al.*, 2002; Silva *et al.*, 2004; Pantaleón-Lópes *et al.*, 2005) (Tab. 9). This can be attributed to the types of sampling used, the geomorphology of the systems, and the reproductive strategies of the adults (Spivak and Cuesta, 2009). On the other hand, we observed that the species with the highest density were *C. sapidus* and *L. dubia*, which have also been subject to most of the academic study. For example, in Ibiraquera Lagoon, Brazil, the larval density of *C. sapidus* (84 larvae 100 m^{-3}) (Costa-Brandão *et al.*, 2011) was found to be higher than that in the mouth of Delaware Bay (55 larvae 100 m^{-3}) (Dittel and Epifanio, 1982). In another study of *C. sapidus* in the estuarine and coastal regions of Patos Lagoon in Southern Brazil, 53.97 zoeae 100 m^{-3} were collected in summer, 13.18 zoeae 100 m^{-3} in autumn and 19.75 zoeae 100 m^{-3} in spring (Ramos-Vieira and Calazans, 2015). The higher density of *Callinectes* and *Libinia* is related to the number of eggs produced. *Callinectes* produces approximately 3.2 million eggs per female in the northern Gulf of Mexico and is influenced by seasonality (highest in Spring) (Graham *et al.*, 2012) while *Libinia* produces approximately 75,000 eggs per female between June and December (Hinsch, 1968; Carmona-Osalde and Rodríguez-Serna, 2012). In the present study we obtained larval density values higher than those reported in the above-mentioned studies and these high densities correspond to cold fronts and dry weather conditions.

The species composition of brachyuran zoea identified in this study was similar to that in other estuarine systems and bays, including of the genus *Menippe* (Schwamborn *et al.*, 1999), species in the families Ocypodidae and Portunidae (Negreiros-Fransozo *et al.*, 2002), and particularly, species of the genus *Callinectes* (Steppe and Epifanio, 2006; Silva-Falcão *et al.*, 2007).

The diversity values obtained in this study were similar to the findings of Magris and Loureiro-Fernandes (2011), who also applied the Shannon-Wiener model to data from a set of decapod larvae in which brachyurans were the dominating fauna within the community, with 69% of the taxa. The authors found a diversity of 0.8 to 2.2 bits individual^{-1} and a species richness of 6 to 16 in the Piraquê-Mirim estuary, and a diversity of 1.2 to 2.5 bits individual^{-1} and a species richness of 7 to 17 in the Piraquê-Açú estuary. The authors concluded that for estuaries located in tropical zones, seasonal variations in larval abundance depend on the dynamics of the temperate waters of the coast, and further that larvae are most abundant in late summer (*i.e.*, the ocypodids are very abundant, so they are important components for pelagic food webs). In another study conducted by Koettker and Lopes (2013) on meroplankton,

Table 9. Density of Brachyura zoea I 100^{-3} in lagoons, bays and estuaries.

Density (zoeae 100m^{-3})	System	Author
3911	Itamaracá estuary, Brazil	Schwamborn *et al.*, 2001
2891	Jaguaribe estuary, Brazil	Silva-Falcão *et al.*, 2007
4768	PNSAV, Mexico	This study
10308	Ibiraquera Lagoon, Brazil	Costa-Brandão *et al.*, 2011
70000	Guanabara Bay, Brazil	Fernandes *et al.*, 2002
253200	Suape Bay, Brazil	Silva *et al.*, 2004
123344	Chacahua-La Pastoría Lagoon, Mexico	Pantaleón-Lópes *et al.*, 2005

brachyuran larvae were analyzed in detail, leading to a list of 61 taxa for the area, 24 of which accounted for half of the total brachyuran larval density. These authors found a diversity of 1.2 to 2.6 bits individual^{-1} at shallow stations with an evenness of 0.7 to 0.9, and 0.7 to 1.9 bits individual^{-1} at deep stations with an evenness of 0.9. Moreover, they mentioned that the analysis of brachyuran larval composition and distribution suggests a negligible influence of estuarine fauna on inner shelf assemblages during winter conditions. It is important to consider that Shannon-Wiener index values lower than 1 are found in places with low environmental stability, values of 1 to 2 are found in places with intermediate stability, and values higher than 3 indicate places with stable environmental conditions (Stub *et al.*, 1970). Therefore, from the data obtained for the community of Brachyura zoea, the PNSAV may be regarded as having intermediate stability (Horta-Puga *et al.*, 2013).

In conclusion, the results obtained in this study are consistent with the other studies, confirming that the abundance and distribution of decapod larvae are influenced by factors such as temperature, salinity, and areas of spawning. In the PNSAV region, environmental parameters are modified by cold fronts and rainy weather conditions, and the estuarine plume of the Jamapa River. Tropical storms and hurricanes cause a mixed layer, reincorporating nutrients into the photic zone, which in turn are used by phytoplankton, which are later consumed by brachyuran zoea. The species with the highest density were *L. dubia*, *C. sapidus* and *M. nodifrons*. Considering environmental factors and reproductive strategies, we observed the separation of three weather conditions, three perpendicular zones (northern, central and southern), and four groups of Brachyura zoea in the PNSAV. The species in the first group move to the marine environment, while some others move from the coast to the infralittoral zone to release their larvae. In the second group, the adults stay in the infralittoral zone and release their larvae there. The species of the third group manifest a close relationship with other species present in coral reefs and release their larvae in such locations. The species of the fourth group live in intertidal areas among rocky pilings and are well adapted to salinity ranges near the mouths of estuaries. This is the first investigation into brachyuran zoea larvae assemblages in Veracruz, Mexico. The obtained diversity values of approximately 2.0 bits individual^{-1} resemble diversity values found in similar studies concerning Brachyura larvae, hence the PNSAV can be deemed as having intermediate stability.

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