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Larvae and macro-crustaceans along the coastline of the Parque Nacional Sistema Arrecifal Veracruzano, SW Gulf of Mexico

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ABSTRACT

We evaluated the composition, distribution, and abundance of the decapod genera at different developmental stages of larvae and adult macro-crustaceans along the coastline of the Parque Nacional Sistema Arrecifal Veracruzano, SW Gulf of Mexico. Collections were made using light traps. Temperature, salinity, oxygen, and pH were measured *in situ*. The samples were fixed with 70 % alcohol, separated, and identified by developmental stage and genus level with specialized literature. The Olmstead-Tukey test, the Shannon-Wiener diversity index, and Pielou equitability test were applied. Canonical correlation and cluster analysis were performed. In total, 20,049 individuals of 56 stage-genera were collected, with *Potimirim* Holthuis, 1954 postlarvae being the most abundant ones. The most abundant taxa were *Potimirim* at Playa Martí, *Macrobrachium* Spence Bate, 1868 at Plaza de la Soberanía, and *Pachygrapsus* Randall, 1840 at Playa Villa del Mar and Playa Tortugas. At Playa Villa del Mar, the highest diversity was found (3.47 bits*individuals^{-1}),

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and this is related to the complexity of the site. In May, the greatest diversity (3.64 bits*individuals^{-1}) was found, related to the time of reproduction of most of the stage-genera. Most stage-genera were classified as rare. Cluster analysis resulted in two groups, one containing taxa found in cold and wet months and the other of taxa found in dry months. Thus, the dynamics of the taxocene structure is determined by the lifecycles of the species, responding to the migration, reproduction, and colonization of each stage-genera.

Keywords

Artificial reefs, community, Crustacea, diversity, dominance

Introduction

The Parque Nacional Sistema Arrecifal Veracruzano (PNSAV) was declared a marine protected Biosphere Reserve, within the UNESCO Man and Biosphere Program (UNESCO, 2006). This system is composed of several coral reefs and is divided into northern and southern groups by the influence of the river plume of the Jamapa River (Horta-Puga *et al.*, 2016). The coral reefs of the PNSAV create conditions for high biodiversity and high productivity, providing habitats as well as spawning and nursery grounds for many species, including commercially important species (Jordán-Dahlgren, 2004). This biodiversity is composed of submerged algal and macrophytic vegetation and aquatic fauna including vertebrates such as mammals and reptiles, as well as species of hemichordates and invertebrates such as sponges, corals, mollusks, polychaetes, and crustaceans (CONABIO, 2021).

Among the crustaceans, the best studied group in the PNSAV are decapod crustaceans, which are represented by 183 species of which 90 are Brachyura, 51 Caridea, and 23 Anomura (Álvarez *et al.*, 1996; Hermoso-Salazar and Arvizu-Coyotzi, 2007). Another group of crustaceans well represented in the PNSAV is the superorder Peracarida (Cházaro-Olvera *et al.*, 2018). Hermoso-Salazar and Arvizu-Coyotzi (2007) listed 68 species of this superorder, of which 63 % are amphipods, 27 % isopods, 9 % tanaidaceans (Winfield and Ortiz, 2011), and 1 % cumaceans (Scheinvar, 2014).

Crustaceans with sizes from 0.5 to 20 mm are called macro-crustaceans (Lalli and Parsons, 1997), with different morphological and physiological adaptations that, as in other crustaceans, have allowed them to colonize microhabitats within coral reefs, soft bottoms, rocky substrates, seagrass beds, algae, coral rubble, sponges (Vonk and Schram, 2007), and man-made structures. These latter structures can function as artificial reefs (ARs) and have been used to increase the number of habitats and, therefore, the number of crustaceans (Delgadillo-Garzón and García, 2009). The stone blocks that are placed along the maritime coastline (breakwaters) have the purpose of reducing the impact of the waves or reducing sand loss from the beaches (Aquantica, 2020). However, the breakwaters also generate new habitats that can be used by different species. In ARs, the process of succession starts with the formation of biofilms composed of free-floating bacteria. Subsequently, these microorganisms produce chemical compounds that determine the differentiation and formation of structures, including the development of a polysaccharide cover. This generates a new substrate interface with new physicochemical properties, where the bacteria associate with diatoms that induce or inhibit the settlement of larvae. These microorganisms are considered pioneer organisms and settle a few hours after immersion. The secondary colonizers are protozoa and macroalgal spores, and the tertiary colonizers comprise macroscopic organisms that settle on these artificial surfaces after 2 or 3 weeks of immersion (Galicia-Nicolás *et al.*, 2018). Macroscopic organisms include mussels, bryozoans, and crustaceans (amphipods, isopods, tanaidaceans, barnacles, and decapods), in different development stages (Winfield *et al.*, 2010).

The studies of macro-crustaceans on hard substrates along the Veracruz coast are few. Only

Hernández *et al.* (2010) and Rocha-Ramírez *et al.* (2016) have carried out research to determine the ecological importance of the species found in these ecosystems, in the south and center areas of the state, respectively. In this context, the aim of this study was to evaluate the composition, distribution, and abundance of larvae and macro-crustaceans found on artificial structures at four sites in the PNSAV.

Materials and Methods

Study area

Initially, the PNSAV was declared a Marine Protected Area (DOF, 1992), then it obtained a Ramsar number (1346) in 2004 (FIR, 2004), and finally, UNESCO Biosphere Reserve status. The PNSAV consists of 28 reef banks that cover 65,516 ha (DOF, 2012). The reefs are separated into two groups due to the influence of the Jamapa River; the northern group is in front of the port of Veracruz, the southern group is in front of the municipality of Antón Lizardo. Some reefs are up to 20 km away from the coastline, whereas others have already been reached by urban growth, such as Hornos reef. Geographically, the PNSAV is located between 19°02'24'' and 19°16'00''N and 95°46'19'' and 96°12'01''W (Juárez-Sarvide *et al.*, 1991) and the climate is classified as dry and rainy, with cold fronts (Carrillo *et al.*, 2007). The winds of these cold fronts can produce important mixing processes of the oceanic water column (Monreal-Gómez *et al.*, 2004). The PNSAV is influenced by the diurnal tide and the direction of the tide is modified by the presence of shallow reliefs, reefs, and islands, favoring the formation of cyclonic and anticyclonic gyres. These gyres generate the reincorporation of organic matter and nutrients into the water column (Salas-Pérez and Granados-Barba, 2008; Salas-Monreal *et al.*, 2009; Chacón-Gómez, 2009; Jasso-Montoya, 2012; Salas-Pérez *et al.*, 2012).

Field work

We collected samples in the northern part of the PNSAV during May, June, September, and October 2017 and in February and April 2018 at four sites, on the coastline between the rocks of artificial structures, the so-called "breakwaters", to depths between 0.8 to 1 m. These collecting cycles were initiated at 18h00 and stopped at 08h00 on the next day during the new-moon phase. The sites were as follows: Playa Martí (19°10'22.09"N 96°07'4.57"W); Plaza de la Soberanía beach (19°10'31.72"N 96°07'12.57"W); Playa Villa del Mar (19°11'26.9"N 96°07'19.12"W), and Playa Tortugas (19°09'41"N 96°06'01"W) (Fig. 1). The sites were located with a Garmin eTrexHC© satellite geopositioner. Organisms were collected with light traps (sampling unit) made of plastic boxes, with the following dimensions: 0.40 m long, 0.25 m wide, and 0.30 m high; two 4-kg ballasts were placed on top so that the traps were anchored to the bottom of the breakwaters. Four 0.025-m diameter holes were made, one on each side of the trap. At the bottom, a sample receiver was placed, in which a mesh with a 300-µm aperture was placed. Inside the box, separated from the base by 5 cm, a plastic grid with a mesh opening of 0.05 m was installed. A white light lamp of 30 lumens was installed in a sealed plastic container in the upper internal part of the trap (Cházaro-Olvera *et al.*, 2018). After deployment, the contents of the boxes were passed through a sieve with a 300-µm mesh opening. The samples were fixed with 70 % alcohol according to the methodology of Smith and Richardson (1977).

Environmental factors such as temperature (°C), salinity (psu), dissolved oxygen (mgL^{-1}), and pH were measured in situ to a depth of 0.50 m, using a Hanna HI9828® multiparametric equipped with HI769828DO® and HI769828PH® probes.

Laboratory work

The samples were viewed in a stereoscopic microscope and taxonomically separated in the Crustacean Laboratory of the Facultad de Estudios Superiores Iztacala, UNAM. For identification, micro-dissections of diacritical morphological structures were carried out, and the structures were observed under a Motic model SMZ-168 optical microscope.

We refer to "stage-genera" as the combination of the development stages (zoea, megalopa, postlarva, and adult) and the genus. For identification of the stages and genera, specialized literature was used (Holthuis, 1951; 1952; Provenzano, 1959; Barnard, 1969; Gosner, 1971; Chace, 1972; Bousfield, 1973; Gore and Abele, 1973; Barnard and Barnard, 1983;

Menzies and Kruczynski, 1983; Dardeau, 1984; Williams, 1984; Kensley and Schotte, 1989; Martin *et al.*, 2014). To corroborate the presence of any species in the study area, information recorded in Felder and Camp (2009) was used. Abundance was obtained by counting the number of individuals of each stage-genera collected per sampling unit.

Statistical analysis

The Olmstead-Tukey (1947) test was used to classify each stage-genera into one of four established categories (dominant, common, occasional, and rare) according to its abundance (Log n + 1) and frequency of occurrence (%). In the Results section, we provide the names of the dominant stage-genera and then observe whether these genera were present in the sampling sites and months. Shannon-Wiener (H') diversity index values, species richness (S), and Pielou equitability (J') were obtained both temporally and spatially (Magurran, 1988). The diversity values of the sites and months were compared with the values found via the Hutcheson (1970) test. Cluster analysis was performed to determine the patterns of distribution in time and space of macro-crustaceans based on their abundance (Warwick and Clarke, 1991). For the construction of the similarity matrix, the Bray-Curtis index (Clarke and Gorley, 2015) was used; likewise, grouping by the analysis of unweighted arithmetic means (UPGMA) was performed (Crisci and Armengol, 1983). The potential relationship between the abundance matrix of the stage-genera and the averages of the environmental variables of temperature, salinity, dissolved oxygen, and pH was explored by canonical correlation analysis (CCA). We applied Wilks' lambda test (Peres-Neto *et al.*, 2006) with the null hypothesis that the regression coefficients are all zero.

The community parameters were obtained with the PAST software (Harmer *et al.*, 2001). For the cluster analysis and canonical correlation analysis, the XLSTAT program, version 2009 3.02, was used.

Results

Environmental factors

The highest water temperature was observed in June at the Playa Martí station, with 31.53 °C, and the lowest in February at the Playa Villa del Mar station, with 26.46 °C (Tab. 1). The relationship of temperature with sampling sites and months was positive ($r^2 = 0.97$) and statistically significant ($p < 0.001$). Statistically significant differences were found between months ($p < 0.001$) but not between sites ($p = 0.288$). The Tukey test showed that most of the months presented statistically significant differences ($p < 0.05$), except May and June with September and October ($p > 0.05$) (Tab. 2).

Table 1. Values of environmental parameters measured at the four sites during the study period.

Site	Environmental factor	May	Jun	Sep	Oct	Feb	Apr
Playa Villa de Mar	Temperature (°C)	29.15	31.25	30.79	29.21	26.46	30.15
	Salinity (psu)	35.55	34.43	33.61	35.79	35.37	35.05
	Dissolved Oxygen mgL^{-1}	5.58	5.48	3.93	5.32	5.94	5.78
	pH	8.07	7.87	8.16	8.14	8.49	8.01
Plaza de la Soberanía	Temperature (°C)	30.19	31.49	31.39	29.13	27.24	30.02
	Salinity (psu)	35.34	35.44	32.47	35.16	35.16	35.44
	Dissolved Oxygen mgL^{-1}	6.18	5.08	5.7	7.05	6.98	6.98
	pH	8.15	7.85	8.02	8.14	8.69	8.45
Playa Martí	Temperature (°C)	29.43	31.53	31.47	29.43	26.57	29.93
	Salinity (psu)	35.21	35.41	33.73	34.42	35.18	35.11
	Dissolved Oxygen mgL^{-1}	6.15	5.1	5.69	7.9	6.37	6.45
	pH	8.01	7.81	8.03	8.12	8.51	8.11
Playa Tortugas	Temperature (°C)	30.01	30.44	31.23	29.64	26.64	30.21
	Salinity (psu)	34.42	34.52	31.44	31.95	34.2	34.33
	Dissolved Oxygen mgL^{-1}	6.69	6.6	6.05	6.69	6.85	6.29
	pH	8.18	7.8	7.95	8.12	8.59	8.01

Table 2. Results of the relationships of environmental factors with respect to the sites and months with the generalized least squares (GLS) model. Comp, comparison; PM, Playa Martí; PS, Plaza de la Soberanía; PT, Playa Tortugas; PVm, Playa Villa del Mar; r^2, Correlation coefficient.

Temperature			**Months**		**Salinity**			**Months**		**Sites**	
Source	**F**	***p***	**Comp-Tukey**	***p***	**Source**	**F**	***p***	**Comp**	***p***	**Comp-Tukey**	***p***
Corrected model	56.26	<0.001	Apr-Feb	<0.001	Corrected model	7.52	<0.001	Apr-Sep	0.003	PT-PM	0.01
Intersection	173753.05	<0.001	Apr-Jun	0.005	Intersection	69792.91	<0.001	Feb-Sep	0.003	PT-PVm	0.005
Site	1.38	0.288	Apr-Sep	0.008	Site	7.28	0.003	Jun-Sep	0.003	PT-PS	0.011
Month	89.19	<0.001	Feb-Jun	<0.001	Month	7.67	<0.001	May-Sep	0.001		
Error			Feb-May	<0.001	Error			Oct-Sep	0.041		
Total			Feb-Oct	<0.001	Total						
Corrected total			Feb-Sep	<0.001	Corrected total						
a. r^2 = 0.97			Jun-May	<0.001	a. r^2 = 0.80						
			Jun-Oct	<0.001							
			May-Sep	<0.001							
			Oct-Sep	0.004							

Dissolved oxigen			**Months**		**Sites**		**pH**			**Months**	
Source	**F**	***p***	**Comp-Tukey**	***p***	**Comp-Tukey**	***p***	**Source**	**F**	***p***	**Comp-Tukey**	***p***
Corrected model	4.48	0.006	Sep-Oct	0.029	PM-PVm	0.048	Corrected model	15.53	<0.001	Feb-Apr	<0.001
Intersection	2873.28	<0.001			PT-PVm	0.011			<0.001	Feb-Jun	<0.001
Site	5.41	0.010			PS-PVm	0.035	Site	1.81	0.189	Feb-May	<0.001
Month	3.93	0.018					Month	23.76	<0.001	Feb-Oct	<0.001
Error							Error			Feb-Sep	<0.001
Total							Total			Jun-Apr	0.005
Corrected total							Corrected total			Jun-May	0.016
1. r2 = 0.71							a. r2 = 0.89			Jun-Oct	0.007

The highest salinity value was found in October at the Playa Villa del Mar station, with 35.79 psu, and the lowest at the Playa Tortugas station in September, with 31.44 psu (Tab. 1). The relationship of salinity with sampling sites and months was positive ($r^2 = 0.80$) and statistically significant ($p < 0.001$). Statistically significant differences were found between months ($p < 0.001$) and sites ($p = 0.003$). According to the Tukey test, September was the month that presented significant differences with all other sampling months ($p < 0.05$), and Playa Tortugas was statistically significantly different from all other sampling sites ($p < 0.05$) (Tab. 2).

The highest value of dissolved oxygen was found in October at the Playa Martí station, with 7.9 mgL^{-1}, and the lowest one in September at the Playa Villa del Mar station, with 3.93 mgL^{-1} (Tab. 1). The relationship of dissolved oxygen with sampling sites and months was positive ($r^2 = 0.71$) and statistically significant ($p < 0.001$). Statistically significant differences were found among months ($p = 0.018$) and sites ($p = 0.010$). Using the Tukey test, we found that only between September and October, were there statistically significant differences ($p = 0.029$). On the other hand, the highest pH value occurred in February at the Plaza de la Soberanía site, with 8.69 units, and the lowest in June at the Playa Tortugas station, with 7.8 units (Tab. 1). The relationship of pH with sampling sites and months was positive ($r^2 = 0.89$) and statistically significant ($p < 0.001$). Statistically significant differences were found among the sampling months ($p < 0.001$). Based on the Tukey test, there were statistically significant differences between February and the rest of the sampling months, whilst June presented differences with April, May, and October ($p < 0.05$) (Tab. 2).

Total abundance and habitat type

In total, 20,049 organisms were collected, distributed in 56 stage-genera. The most abundant stage-genera were *Potimirim* Holthuis, 1954 postlarvae with 7,278 individuals (36.32 %), followed by *Pachygrapsus* Randall, 1840 megalopae with 3,889 individuals (19.41 %), *Pachygrapsus* zoeae with 2,145 individuals (10.70 %), *Macrobrachium* Spence Bate, 1868 postlarvae with 1,386 (6.92 %), and *Palaemon* Weber, 1795 postlarvae with 1,246 organisms (6.21 %) (Tab. 2). Of the 56 stage-genera, 36 (64.29 %) were marine, 12 were marine-estuarine (21.43 %), 4 were estuarine (7.14 %), 2 were freshwater-marine-estuarine (3.57 %), 1 was freshwater-estuarine (1.79 %), and 1 was freshwater (1.79 %).

Spatial abundance

The highest abundance value was found at Playa Martí with 7,767 individuals (39 %); *Potimirim* postlarvae were the most abundant at this site, with 6,558 individuals (84.43 %), followed by *Palaemon* postlarvae and *Eobrolgus* J.L. Barnard, 1979 adults, each with 406 individuals (5.22 %). In Playa Villa del Mar, 4,788 individuals (24 %) were collected, of which *Pachygrapsus* megalopae were the most abundant with 2,002 individuals (41.9 %). In the Plaza de la Soberanía, 2,891 individuals (14 %) were found, *Macrobrachium* postlarvae being the most abundant with 1,164 individuals (40.26 %), followed by *Pachygrapsus* megalopae with 730 individuals (25.25 %). Finally, at Playa Tortugas, 4,611 individuals (23 %) were collected, of which *Pachygrapsus* megalopae were the most abundant with 2,949 individuals (63.96 %), followed by *Armases* Abele, 1992 megalopae with 441 individuals (9.56 %) (Tab. 4).

Temporal abundance

In May, 665 individuals were collected. The *Cumella* G.O. Sars, 1865 stage-genera was the most abundant one with 127 individuals (19 %), followed by *Penaeus* Fabricius, 1798 postlarvae with 85 (13 %). In June, 4,121 individuals were collected; *Pachygrapsus* zoeae were the most abundant with 1,990 individuals (48 %), followed by *Potimirim* postlarvae with 952 individuals (23 %). In September, 2,793 individuals were obtained; *Macrobrachium* postlarvae were most abundant with 1,267 individuals (46 %), followed by *Pachygrapsus* megalopae with 760 individuals (26 %). In October, 1,447 individuals were found (7 %); *Neopanope* A. Milne-Edwards, 1880 [in A. Milne-Edwards, 1873–1880] megalopae were the most abundant with 435 specimens (30 %), followed by *Armases* megalopae with 332 individuals (23 %). In February, 7,732 individuals were found; *Potimirim* postlarvae were the most abundant with 6,152 individuals, followed by *Palaemon* postlarvae with 688 individuals (8 %). In April, 3,291 specimens were found, of which *Pachygrapsus* megalopae were the most abundant with 2,838 individuals (84 %), followed by *Palaemon* postlarvae with 96 organisms (3 %) (Tab. 3).

Spatial dominance

The Olmsted-Tukey model showed that 17 types of stage-genera (30.36 %) were dominant: *Alpheus* Fabricius, 1798 postlarvae, *Armases* megalopae, *Belzebub* Vereshchaka, Olesen and Lunina, 2016 adults, *Clibanarius* Dana, 1852 megalopae, *Cumella* adults, *Cyclaspis* Sars, 1865 adults, *Dynaminella* Hansen, 1905 adults, *Eobrolgus* adults, *Exosphaeroma* Stebbing, 1900 adults, *Macrobrachium* postlarvae, *Pachygrapsus* megalopas, *Pachygrapsus* zoeae, *Palaemon* postlarvae, *Panopeus* H. Milne Edwards, 1834 megalopae, *Penaeus* postlarvae, *Potimirim* postlarvae, and *Synalpheus* Spence Bate, 1888 postlarvae. Ten occasional stage-genera (17.86 %), 26 rare (46.43 %), and 3 common ones (5.36 %) were also found (Tab. 3).

Temporal dominance

The Olmsted-Tukey model showed that 17 types of stage-genera (30.36 %) were dominant: *Armases* megalopae, *Callinectes* Stimpsom, 1860 megalopae, *Clibanarius* megalopae, *Cumella* adults, *Cyclaspis* adults, *Dynaminella* adults, *Exosphaeroma* adults, *Macrobrachium* postlarvae, *Neopanope* megalopae, *Pachygrapsus* megalopae, *Pachygrapsus* zoeae, *Palaemon* postlarvae, *Panopeus* megalopae, *Penaeus* postlarvae, and *Synalpheus* postlarvae. Ten were occasional (17.86 %), 26 were rare (46.43 %), and 3 were common (5.36 %) (Tab. 4).

Table 3. Abundance of larvae and macro-crustaceans in four sites on the coastline of the Parque Nacional Sistema Arrecifal Veracruzano. AD, adult; D, dominant; E, estuarine; F, freshwater; Hab, habitat; M, marine; ME, megalopa; O, occasional; O-T, Olmstead-Tukey; PM, Playa Martí; PT, Playa Tortugas; PO, postlarva; Ps, Plaza de la Soberanía; PVm, Playa Villa del Mar; R, rare; Z1, zoea 1.

Stage	Genus	PVm	PS	PM	PT	Total	O-T	Hab
PO	*Alpheus* (Alph)	25	21	23	32	101	D	M
AD	*Ancinus* (Anci)				1	1	R	M
ME	*Armases* (Arm)	9			441	450	D	E, M
AD,	*Belzebub* (Belze)	48	65			113	D	M
AD	*Bemlos* (Bemlos)			11	1	12	R	M
ME	*Callinectes* (Call)	66			94	160	O	M, E
AD	*Cirolana* (Ciro)		2	2	2	6	R	M
ME	*Clibanarius* (Cliba)	35	9	7	29	80	D	M
AD	*Cumella* (Cum)	187		6	1	175	D	M
AD	*Cyclaspis* (Cyc)	176	3	3	13	195	D	M
AD	*Discias* (Dis)	98	32			130	O	M
AD	*Dynamenella* (Dyn)	1	8	81	3	93	D	M
AD	*Eobrolgus* (Eubr)	8	230	406	49	693	D	M
AD	*Eudevenopus* (Eude)	1				1	R	M
ME	*Eurypanopeus* (Eury)	6				6	R	E
AD	*Exospheroma* (Exosph)		28	12	15	55	D	M
AD	*Gamaropsis* (Gamar)			1		1	R	M
AD	*Gnatia* (Gnat)	82				82	O	M
AD	*Hourstonius* (Hour)				1	1	R	M
AD	*Limnoria* (Limn)			1		1	R	M
PO	*Macrobrachium* (Macro)	77	1164	73	72	1386	D	F, E
AD	*Mancocuma* (Manco)	1				1	R	M
AD	*Melita* (Melita)			1		1	R	M
ME	*Mithrax* (Mithrax)	8				8	R	M
ME	*Neopanope* (Neo)	477				477	O	M
D	*Nototropis* (Noto)		1	1		2	R	M, E
AD	*Oxyurostylis* (Oxy)	1				1	R	F, E, M
ME	*Pachygrapsus* (Pachy)	210	730		2949	3889	D	E, M

Stage	Genus	PVm	PS	PM	PT	Total	O-T	Hab
PO	*Palaemon* (Pala)	184	232	406	424	1246	D	F, E, M
ME	*Panopeus* (Pano)	86	7		28	121	D	E, M
AD	*Parhyale* (Parhy)		13	16	1	30	C	M
PO	*Penaeus* (Pen)	176	33	76	56	341	D	E, M
PO	*Periclimenes* (Peri)			25	56	81	O	M
AD	*Photis* (Phot)		9	11	14	34	C	M
ME	*Pinnotheres* (Pinno)	6			23	29	R	M
AD	*Platymerus* (Platy)	4				4	R	M
PO	*Podocerus* (Podo)		1		4	4	R	M
PO	*Potimirim* (Po)	320	188	6558	212	7278	D	F
PO	*Processa* (Proc)			35	10	45	O	M
AD	*Schizotrema* (Schizo)	1				1	R	M
AD	*Armases* (Arma)	46				46	O	E
AD	*Stenothoe* (Stenothoe)	10	6			16	R	M
AD	*Sympodomma* (Sympo)	1				1	R	M
PO	*Synalpheus* (Syn)	74		12	45	131	D	M
ME	*Minuca* (Uca)	17				17	R	E
ME	*Ucides* (Uci)	36				36	R	E
AD	*Vaunthompsonia* (Vaunth)	6			1	7	C	M
Zl	*Acantholobulus* (Zacan)	12				12	R	M
Zl	*Callinectes* (Zcall)	44				44	O	E, M
Zl	*Libinia* (Zlib)	56				56	O	E, M
Zl	*Menippe* (Zmenn)	11				11	R	E, M
Zl	*Pachygrapsus* (Zpach)	2002	109		34	2145	D	E, M
Zl	*Persephona* (Zperse)	13				13	R	M
Zl	*Armases* (ZArm)	24				24	R	E, M
Zl	*Tumidotheres* (Ztumi)	109				109	O	E, M
Zl	*Zaops.* (ZZaops)	34				34	R	E, M

Table 4. Abundance of larvae and macro-crustaceans in six months of sampling on the coastline of the Parque Nacional Sistema Arrecifal Veracruzano. AD, adult; D, dominant; E, estuarine; F, freshwater; Hab, habitat; M, marine; ME, megalopa; O, occasional; O-T, Olmstead-Tukey; PO, postlarva; R, rare; Z1, zoea 1.

Stage	Genus	May	Jun	Sep	Oct	Feb	Apr	Total	O-T	Hab
PO	*Alpheus*	55		46				101	O	M
AD	*Ancinus*				1			1	R	M
ME	*Armases*				332	35	76	443	D	E, M
ME	*Belzebub*		71	42				113	O	M
AD	*Bemlos*					12		12	R	M
ME	*Callinectes*		21		63	20	56	160	D	E, M
AD	*Cirolana*			2	2	2		6	C	M
ME	*Clibanarius*	27		2	36	15		80	D	M
AD	*Cumella*	127		10	18	39		194	D	M
AD	*Cyclaspis*	32		31	110	22		195	D	M
AD	*Discias*		44	86				130	O	M
AD	*Dynamenella*			1	12	80		93	D	M
AD	*Eobrolgus*	30		143	205	315		693	D	M
AD	*Eudevenopus*	1						1	R	M
ME	*Eurypanopeus*		6					6	R	E
AD	*Exosphaeroma*	12		5	22	16		55	D	M
AD	*Gamaropsis*					1		1	R	M
AD	*Gnatia*	82						82	O	M
AD	*Hourstonius*				1			1	R	M
AD	*Limnoria*				1			1	R	M
PO	*Macrobrachium*	50		1267	25	12	32	1386	D	F, E
AD	*Mancocuma*					1		1	R	M
AD	*Melita*			1				1	R	M
ME	*Mithrax*				8			8	R	M
ME	*Neopanope*		6		435	36		477	D	M
AD	*Nototropis*			1	1			2	R	M, E
AD	*Oxyurostylis*	1						1	R	D, E, M
ME	*Pachygrapsus*		195	760	96		2838	3889	D	E, M

Stage	Genus	May	Jun	Sep	Oct	Feb	Apr	Total	O-T	Hab
PO	*Palaemon*		297	165		688	96	1246	D	F, E, M
ME	*Panopeus*		32	7	24	58		121	D	E, M
AD	*Parhyale*	1				29		30	R	M
PO	*Penaeus*	85	180	32		18	26	341	D	E, M
PO	*Periclimenes*						81	81	O	M
AD	*Photis*	13		5		16		34	C	M
ME	*Pinnotheres*				18	11		29	R	M
AD	*Platymerus*				3	1		4	R	M
PO	*Podocerus*			1		3		4	R	M
PO	*Potimirim*	56	952	32		6152	86	7278	D	F
PO	*Processa*			45				45	O	M
AD	*Schizotrema*	1						1	R	M
ME	*Armases*					46		46	O	E
AD	*Stenothoe*	1			6	9		16	C	M
AD	*Sympodomma*	1						1	R	M
PO	*Synalpheus*	32	66			33		131	D	M
ME	*Uca*					17		17	R	E
ME	*Ucides*				24	12		36	R	E
AD	*Vaunthompsonia*	4			3			7	R	M
Zl	*Acantholobulus*		12					12	R	M
Zl	*Callinectes*		44					44	O	E, M
Zl	*Libinia*		56					56	O	E, M
Zl	*Menippe*		11					11	R	E, M
Zl	*Pachygrapsus*	12	1990	109		34		2145	D	E, M
Zl	*Persephona*		13					13	R	M
Zl	*Armases*	8	16					24	R	E, M
Zl	*Tumidotheres*	34	75					109	O	E, M
Zl	*Zaops.*		34					34	R	E, M

Spatial diversity

The highest species richness was found in Playa Villa del Mar with 42 species, followed by Playa Tortugas with 28 species. The highest diversity (H') was found in Playa Villa del Mar with 3.47 bits*individuals^{-1}, followed by Plaza de la Soberanía with 2.61 bits*individuals^{-1}. Finally, the highest equitability was observed at Playa Villa del Mar with 0.64, followed by Plaza de la Soberanía with 0.59 (Tab. 5). Based on the results of the Hutchenson test, all diversity index values showed significant differences ($p < 0.05$).

Temporal diversity

The highest species number was found in February, with 28 stage-genera, followed by October, with 24 stage-genera. The highest diversity (H') was found in May, with 3.64 bits*individuals^{-1}, followed by October, with 3.04 bits*individuals^{-1}. Finally, the highest equitability was found in May, with 0.82, followed by October, with 0.66 (Tab. 5). The diversity values showed significant differences ($p < 0.05$), except between June and September ($p = 0.411$).

Cluster analysis

The cluster analysis of the sampling months showed the formation of two groups: the first group was formed by May, September, October, and February and the second group by June and April (Fig. 2A).

Using grouping analysis of the sites, two groups were obtained: the first one contained Playa Villa del Mar and the second one Plaza de la Soberanía, Playa Martí, and Playa Tortugas (Fig. 2B).

Canonical correlation analysis

Based on CCA, we found four eigenvalues, of which each explained 25 % of the variation. The null hypothesis was rejected ($p < 0.001$) based on the Wilks' Lambda test which suggests that the set of environmental variables explains the abundance of stage-genera. The value of the canonical correlations was 1.00 for all factors, and the redundancy coefficients were 0.071, 0.639, 0.123, and 0.167. A pattern of four groups (A–D) was obtained (Fig. 3).

Group A was represented by the stage-genera: *Armases* adults, *Bemlos* Shoemaker, 1925 adults, *Cirolana* Leach, 1818 adults, *Dynamenella* adults, *Eobrolgus* adults, *Exosphaeroma* adults, *Gammaropsis* Lilljeborg, 1855 adults, *Mancocuma* Zimmer, 1943 adults, *Oxyurostylis* Calman, 1912 adults, *Parhyale* Stebbing, 1897 adults, *Palaemon* postlarvae, *Panopeus* megalopae, *Photis* Krøyer, 1842 adults, *Pinnotheres* Bosc, 1801 megalopae, *Platymera* H. Milne Edwards, 1837 adults, *Podocerus* Leach, 1814 adults, *Potimirim* postlarvae, *Stenothoe* Dana, 1852 adults, and *Ucides* Rathbun, 1897 megalopas. This group had a positive relationship with salinity, dissolved oxygen, and pH.

Group B consists of the stage-genera: *Armases* megalopae, *Callinectes* megalopae, *Clibanarius* megalopae, *Cumella* adults, *Cyclaspis* adults, *Hourstonius* Hoover and Bousfield, 2001 adults, *Limnoria* Leach, 1814 adults, *Mithrax* Latreille, 1816 megalopae, *Neopanope* megalopae, and *Synalpheus* postlarvae. This group was close to the origin in the graph, and therefore, the influence of environmental factors was low.

Table 5. Community factors of larvae and macro-crustaceans during six months of sampling along the coastline of the Parque Nacional Sistema Arrecifal Veracruzano.

Community factor (Sample localities)	Playa Villa del Mar	Plaza Soberanía	Playa Martí	Playa Tortugas		
Species richness	42	21	22	28		
Abundance	4788	2891	7767	4611		
Diversity	3.47	2.61	1.04	2.12		
Equitability	0.64	0.59	0.23	0.44		
Community factor (Months)	**May**	**Jun**	**Sep**	**Oct**	**Feb**	**Apr**
Species richness	22	20	22	24	28	8
Abundance	665	4121	2793	1447	7732	3291
Diversity	3.64	2.48	2.45	3.04	1.35	0.95
Equitability	0.82	0.57	0.55	0.66	0.28	0.32

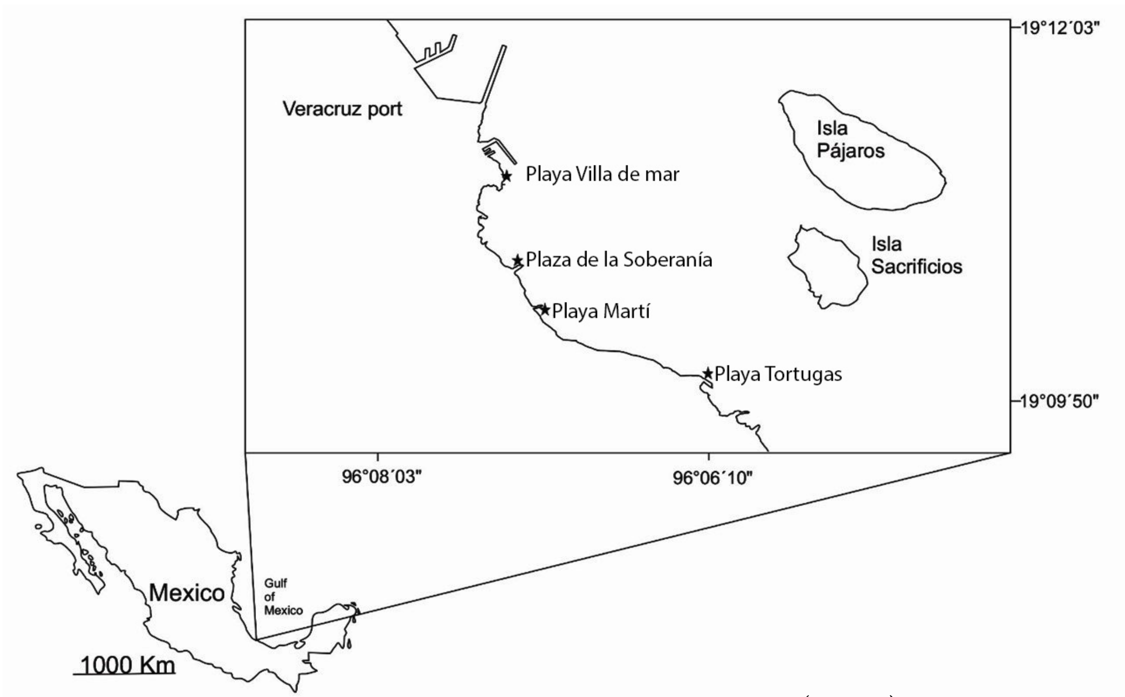

Figure 1. Location of the study area. Parque Nacional Sistema Arrecifal Veracruzano (PNSAV), SW Gulf of Mexico.

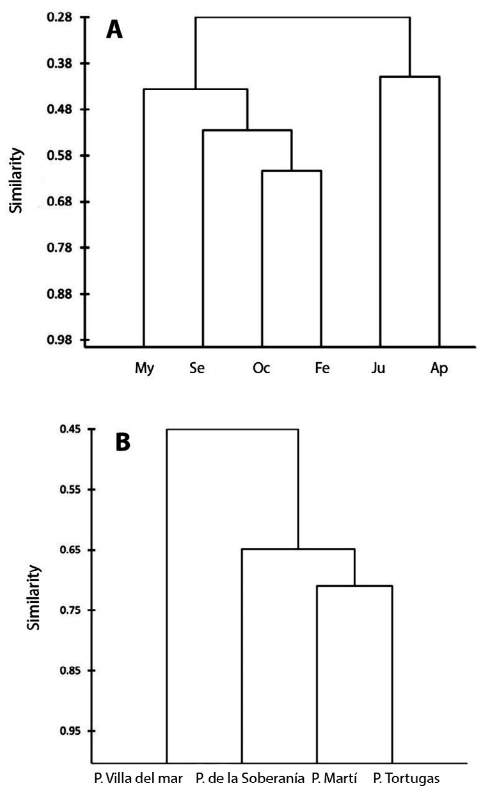

Figure 2. Cluster analysis. **A**, Grouping analysis of the sampling months; **B**, Grouping analysis of the sites from Parque Nacional Sistema Arrecifal Veracruzano (PNSAV), SW from Gulf of Mexico.

Group C was formed by the stage-genera: *Alpheus* postlarvae, *Discias* Rathbun, 1902 adults, *Melita* Leach, 1814 adults, *Nototropis* Costa, 1853 adults, *Pachygrapsus* megalopae, *Periclimenes* O.G. Costa, 1844 postlarvae, and *Processa* Leach 1815 [in Leach, 1815-1875] postlarvae. Its group was positively related with temperature and inversely related with salinity, dissolved oxygen, and pH.

Group D was composed of the stage-genera: *Acantholobulus* Felder and Martin, 2003 zoeae, *Armases* zoeae, *Belzebub* adults, *Callinectes* zoeae, *Eurypanopeus* A. Milne-Edwards, 1880 [in A. Milne-Edwards, 1873-1880] zoeae, *Eudevenopus* Thomas and Barnard, 1983 adults, *Libinia* Leach, 1815 zoeae, *Macrobrachium* postlarvae, *Menippe* De Haan, 1833 [in De Haan, 1833-1850] zoeae, *Penaeus* postlarvae, *Persephona* Leach, 1817 zoeae, *Schizotrema* Calman, 1911 adults, *Sympodomma* Stebbing, 1912 adults, *Tumidotheres* E. Campos, 1989 zoeae, *Vaunthompsonia* Bate, 1858 adults, and *Zaops* Rathbun, 1900 zoeae. Its group showed a positive relationship with temperature and a slightly positive relationship with pH, salinity, and dissolved oxygen.

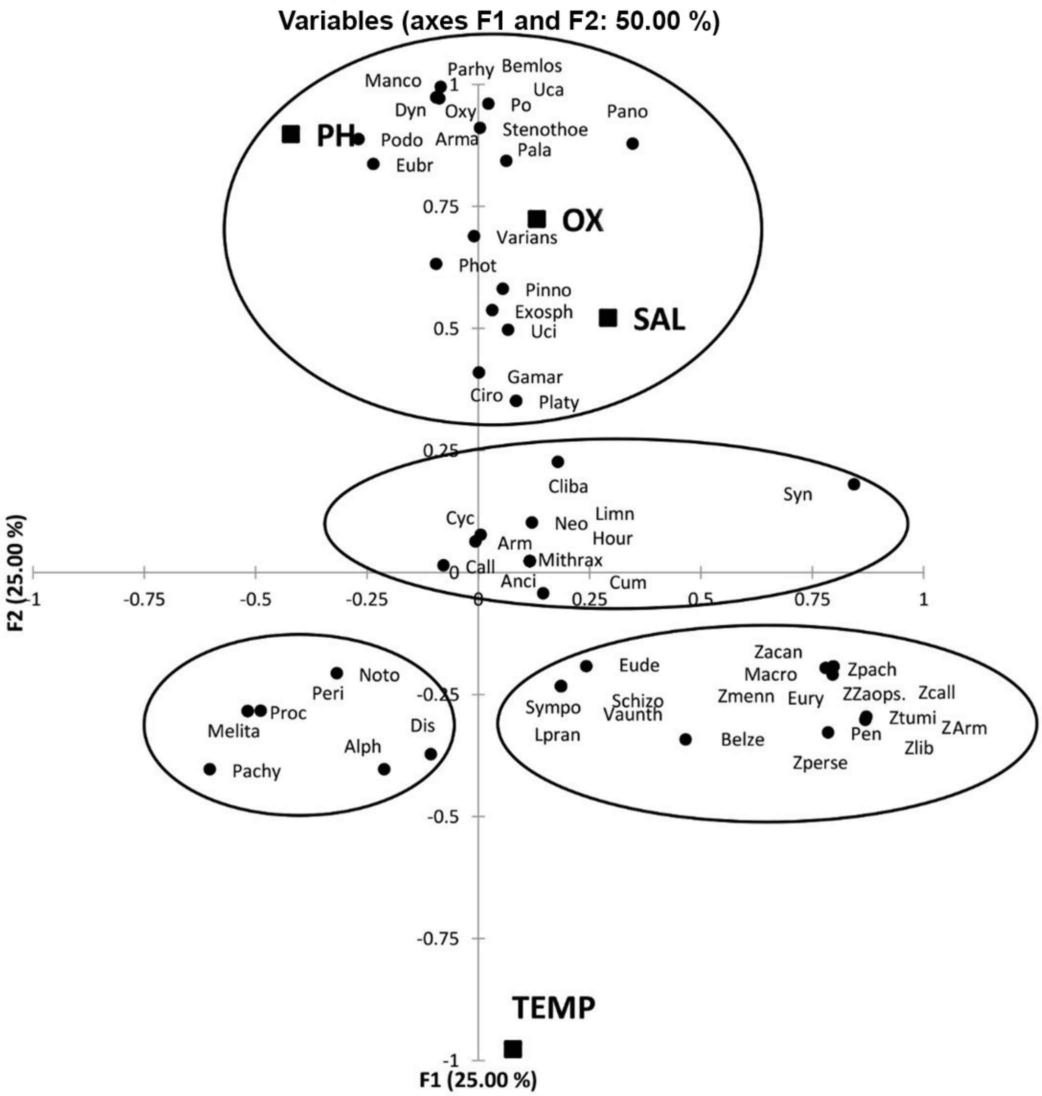

Figure 3. Canonical correlation analysis. Relationship between the abundance matrix of the stage-genera and the averages of the environmental variables. Stage-genera name abbreviations are shown in Tab. 3.

Discussion

In the PNSAV, during July to March, tropical storms and hurricanes occur in association with cold fronts and rains, deepening the mixing layer and incorporating nutrients into the photic zone (Zavala-Hidalgo *et al.*, 2006; 2014). The transport of food influences the conformation of the structure of the stage-genera in the northern part of the PNSAV.

Of the 56 stage-genera found in this study, 15 have been mentioned by Hermoso-Salazar and Arvizu-Coyotzin (2007), highlighting *Alpheus* and *Synalpheus*, with more than 10 species each, corresponding to what is found in the marine environment. Likewise, Winfield *et al*. (2010) mention five stage-genera that were also found in the present study (*Periclimenes*, *Photis*, *Podocerus*, *Stenothoe*, and *Synalpheus*). The marine influence towards the coast is dominant, and therefore, 68.86 % of the stage-genera found in the present study belong to the marine environment, whereas the remaining ones migrate during their lifecycles (Álvarez *et al*., 1996, Cházaro-Olvera *et al*., 2007). In this regard, there are two fundamental types of migration. The first is where marine organisms reproduce on the continental shelf, and their larval, post-larval, and juvenile stages are recruited into estuaries, finding protection and food in preparation for their later return to the continental shelf as pre-adults (Williams, 1984). The genera *Callinectes* and *Penaeus* exhibit this type of migration. The second migration type is carried out by organisms that, during their adult stage, are freshwater organisms and inhabit rivers but in their larval stages, they are transported to coastal lagoons or estuaries, where the environmental conditions allow them to complete their larval and post-larval development (Camacho *et al*., 1997). Thus, due to these different migratory behaviors and transport by the currents, we found *Callinectes*, *Macrobrachium*, *Menippe*, *Pachygrapsus*, *Palaemon*, *Panopeus*, *Penaeus*, *Potimirim*, *Tumidotheres*, and *Zaops* in more than one of the three environments (marine, estuarine, and/or freshwater).

As mentioned above, the highest abundance occurred in February. In this regard, Suárez-Caballero (2018) also found the highest abundance values of crustaceans in February on the rocky beach of Balzapote, Veracruz.

Considering the total number of individuals in the whole study, the four stage-genera with the highest abundances were *Macrobrachium* post-larvae, *Pachygrapsus* megalopae, *Palaemon* post-larvae, and *Potimirim* post-larvae. All of them migrate during their lifecycles from freshwater into the estuary and as observed here, are then transported to the marine environment. In this regard, Miranda-Vidal *et al*. (2016) found that the most abundant species in the lower basin of the Papaloapan River, Veracruz, was the Mexican *Potimirim mexicana* (de Saussure, 1857), a species with high tolerance to environmental variation and a wide distribution on the coastal plain of the Gulf of Mexico. These environmental variations occur on the coastline of the port of Veracruz as it is directly influenced by the Jamapa River. On the other hand, the prawn *Macrobrachium* sp. can also tolerate high environmental variation, which allows it to be distributed in tropical and subtropical climates from sea level to an elevation of 1,000 m in various substrates such as submerged aquatic vegetation, sunken tree trunks, among the roots of riparian vegetation, under rocks, and in river rapids (Álvarez *et al*., 2005). Due to this high tolerance to environmental variation, *Macrobrachium* can be classified as eurytopic (Calvo, 2009), which allows it to distribute widely in different environments during its lifecycle.

According to Reséndez and Kobelkowsky (1991), Álvarez *et al*. (1996), Sánchez *et al*. (1996), Raz-Guzmán and Sánchez (1996), Barba (1999), and Corona *et al*. (2000), there are two types of estuarine crustaceans: those found in estuaries, preferably as adults (which are diverse and include shrimp of the genus *Palaemon* and *Periclimenes* as well as crabs such as genus *Pachygrapsus*), and those found only as larval stages (prawns of the genus *Macrobrachium* and shrimp of the genus *Penaeus*). This information agrees with the data obtained in the present study, since *Macrobrachium*, *Pachygrapsus*, and *Palaemon* were well represented throughout the sampling period.

The species of genus *Pachygrapsus* are estuarine and are adapted to salinity ranges near the mouths of estuaries, surviving from freshwater up to 35 psu and they can be found on various substrates such as rubble, algae, rocks, and mangrove roots, on riverbanks, and on the coastline (Poupin *et al*., 2005).

In general, the genus *Palaemon* is found in marine, freshwater, and brackish environments, with high abundance and frequency values. It is a eurytopic genus (Calvo, 2009) and can survive in a wide range of salinities (Cházaro-Olvera, 2009). In fresh or hypersaline water systems (0 to 55 psu), *Palaemon pugio* (Holthuis, 1949) (Kirby and Knowlton, 1976; Morgan, 1980) has been found in high abundance at temperatures of 5 to 38 °C (Wood, 1967; Christmas and Langley, 1973). The temperature and salinity values recorded in this work allowed us to frequently locate this stage-genera, given its high tolerance.

According to Williams (1984), the reproductive season of many species of decapods found in this study occurs in the months of May to July, with water temperatures above 31 °C, and this coincides with the rainy season.

Thus, it is suggested that the increase in temperature and the appearance of rainy climatic conditions influences the reproductive cycles of freshwater, estuarine, and marine crustaceans (Odinetz-Collart, 1991; Da Silva-Castiglioni *et al*., 2007).

The highest abundance value was found for Playa Martí for *Potimirim* (84.43 %). According to various authors, in rainy weather conditions, temperature stimulates the reproduction of crustaceans in areas where these parameters are influenced by river current patterns (Abele and Blum, 1977; Martínez-Mayén and Román-Contreras, 2000; 2003). These authors carried out studies with the family Atyidae and observed that the most important reproductive peaks occur in rainy weather conditions when the water temperature increases, and higher amounts of nutrients are available as a result of strong river flow towards these areas. Consequently, the abundance of phytoplankton increases, facilitating the development of different decapod larvae. On the other hand, in some places, the substrate provides shelter and food to the organisms, facilitating, for example, the development of different decapod larvae (Abele, 1974; Brusca, 1980; Ruesink, 2007; Álvarez and Villalobos, 2015). Therefore, in some habitats population densities are high, whereas in other places, the force of the waves reduces the possibility of settling on a habitable substrate, and not all genera can reach high population densities.

The values of diversity and species richness (1.04 and 3.47 bits*individuals^{-1}, with 21 to 42 stage-genera) found in the present study are higher than those obtained by other authors. For example, Miranda-Vidal *et al.* (2016) found Shannon-Wiener diversity values in Sontecomapan between 0.5 to 1.08 bits*individuals^{-1}, with 16 stage-genera, in a study carried out in the lower basin of the Papaloapan River, Veracruz. Rocha-Ramírez *et al.* (2016) recorded values of 1.10 to 1.96 bits*individuals^{-1}, with nine stage-genera, in a study of macro-crustaceans on a sandy beach in the north-central region of Veracruz. This difference can mostly be explained by the number of stage-genera found in each study, which modifies the diversity value.

Stage-genera classified as rare represent more than 45 % of the total diversity. Similarly, other studies have mentioned that rare species make up about 50 % of the total collections (Escobar-Briones, 1984; Román-Contreras, 1986; 1988; Barba, 1992; Raz-Guzmán *et al.*, 1992; Raz-Guzmán and Sánchez, 1996; Villalobos, 2000; Hernández, 2002; Hernández *et al.*, 2010; Monroy-Velázquez, 2017; Suárez-Caballero, 2018). These authors attribute the high proportion of rare taxa to the high heterogeneity of habitats, which allows for the temporary establishment of these genera. In addition, some of these taxa are susceptible to changing dynamics of the environment. During cold conditions, for example, disturbances occur, such that strong winds and currents can remove some genera, leaving spaces available to start recolonization (Hernández *et al.*, 2010).

The cluster analysis produced two groups of which the first group had the highest values of species richness, diversity, and abundance of *Potimirim* postlarvae and *Macrobrachium* postlarvae and adults of *Cumella*, *Cyclaspis*, and *Eobrolgus* (May, September, October, and February). The second group consisted of the months with the lowest species richness and diversity values (June and April), where the megalopae of *Pachygrapsus* and postlarvae of *Penaeus* showed the highest abundances.

The ACC indicated that the genera in group A require marine conditions for their larval and post-larval development, and therefore, the relationship with salinity and oxygen was very positive. The genera in Group B are extremely tolerant to changes in environmental factors (Williams, 1984), whereas the genera in Group C are purely marine and only slightly tolerant to variation in salinity and oxygen. Group D contains Brachyura zoeae genera and holoplanktonic organisms and they are positively correlated with the higher water surface temperature (Cházaro-Olvera *et al.*, 2017). The presence of the first larval stages was also related to the reproductive season of many of the present stage-genera.

In conclusion, *Potimirim* post-larvae were the most abundant decapods of the entire sample, and they were most abundant at Playa Martí, whereas *Macrobrachium* post-larvae were dominant at Plaza de la Soberanía and *Pachygrapsus* megalopae dominated at both Playa Villa del Mar and Playa Tortugas. At Playa Villa del Mar, the highest values of specific richness, diversity, and equitability were found, related to the greater diversity of the habitats. In February, the highest values of specific richness and abundance were recorded, whereas in May, we found the highest value of diversity, related to the reproductive period of many of the stage-genera collected in the present study. The greatest abundance of stage-genera was also recorded during the cold season, including a greater number of rare stage-genera, which suggests that the coastline could have a high degree of perturbation.

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