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Research Article

Population dynamics of *Penilia avirostris* and *Pseudevadne tergestina* (Diplostraca) in the Veracruz Reef System National Park, southwest Gulf of Mexico

Sergio Cházaro-Olvera[1], Ignacio Winfield[1]
Manuel Ortiz[1] & Diego Alfonso Torres-Cabrera[1]
[1]Laboratorio de Crustáceos, Facultad de Estudios Superiores Iztacala,
Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México
Corresponding author: Sergio Cházaro-Olvera (schazaro@gmail.com)

ABSTRACT. The present study aimed to evaluate the ecology considering distribution, abundance, population structure, and fecundity of the marine diplostraceans *Penilia avirostris* and *Pseudevadne tergestina* in the Veracruz Reef System National Park, southwest Gulf of Mexico. Surface samples were collected with a 300 μm mesh plankton net at 26 sampling sites in June, August, October (2011), May (2012) and June (2013). Temperature, salinity, and dissolved oxygen were measured *in situ*. The temperature range was 26.53 ± 0.41 and 29.29 ± 0.27°C, salinity between 33.43 ± 0.49 and 35.91 ± 0.09, and dissolved oxygen between 2.92 ± 0.08 and 6.56 ± 0.08 mg L^{-1}. *P. avirostris* and *P. tergestina* presented the highest density, with 2200 ind 100 m^{-3} in June and 5980 ind 100 m^{-3} in October, respectively. Four stages were determined in *P. avirostris*. In *P. tergestina*, there were five instars, with males in August and October. The size of parthenogenic females of *P. avirostris* was 773.4 ± 20.08 μm. In *P. tergestina*, it was 637.6 ± 49.28 μm. The number of embryos in *P. avirostris* was 2 to 7, and in *P. tergestina*, 2 to 8 embryos. The correlations between body length and the number of embryos in both species were statistically significant under the potential model ($r > 0.68$ for both species, $P < 0.001$). The transects with the highest abundance were the northern and the southern zones because they are far from the influence of the Jamapa River. The density of these crustaceans is related to optimal temperature, salinity, and dissolved oxygen values. The low proportions obtained from gamogenic individuals of *P. avirostris* and *P. tergestina* suggest that in tropical and subtropical regions, gamogenesis is not crucial for the life cycle of these organisms.

Keywords: marine zooplankton; crustaceans; diplostraceans; reef system; population structure; fecundity

INTRODUCTION

The superorder Diplostraca Gerstaecker, 1866, plays an important role in the food web of aquatic ecosystems due to its diversity and abundance. It has approximately 620 species (Forró et al. 2008), among which only 10 inhabit marine water (Manrique & Molina 2003). These marine species are grouped within the orders Ctenopoda, with a genus (*Penilia*), and Onychopoda, with four genera (*Evadne*, *Pleopis*, *Podon*, and *Pseudoevadne*) (Onbé 1999).

The ctenopod *Penilia avirostris* Dana, 1849, is widely distributed worldwide in tropical and subtropical marine waters and is seasonally abundant in spring and summer (Johns et al. 2005). This species is the only one considered a true filter feeder among the other species of marine diplostraceans, playing an important role in the dynamics of the trophic webs of plankton (Atienza et al. 2006). The onychopod *Pseudevadne tergestina* Claus, 1877, also has a wide distribution in marine environments worldwide. Both species comprise an important fraction of zooplankton communities, so their density surpasses the aggregates of all the other zooplankton groups (Marazzo & Valentín 2001, Rosenberg & Palma 2003). These species of diplostraceans form an important component of the diets of planktivorous fish and predators of zooplankton, such as chaetognaths and ctenophores (Fofonoff 1994).

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The marine diplostraceans *P. avirostris* and *P. tergestina* are very abundant in the zooplankton community of the Brazilian coast in warm seasons (Miyashita et al. 2010, 2011). In Guanabara Bay and the region to the southeast of the Brazilian coast, both species present the highest densities during the summer (Marazzo & Valentín 2004a). Likewise, these two species of marine diplostraceans have been recorded as common and abundant species in Magdalena Bay, Mexico, surpassing copepods (Hernández-Trujillo et al. 2010). In Veracruz Reef System National Park (VRSNP), Cházaro-Olvera et al. (2019) found that the Diplostraca was the second superorder most abundant zooplanktonic crustacean.

The high food efficiency of *P. avirostris* under oligotrophic conditions (Atienza et al. 2006), the neonates needing a very short period of growth and molting to reach the reproductive stage (Atienza et al. 2008), reduced female size, males appearing in populations, females having less fecundity, and production of resting eggs may explain it's fast blooming and dominance in coastal zooplankton (Marazzo et al. 2004a). Likewise, these factors reinforce the reproductive standard of marine diplostraceans since the first gamogenic species usually present high densities. At the same time, sexual reproduction becomes most intense when the population is about to disappear from a planktonic community (Marazzo et al. 2004a).

There are few studies on the populations of marine diplostraceans, and even fewer in the southwest (SW) of the Gulf of Mexico (GM), despite being an important component of zooplankton due to its high abundance. Thus, the study aimed to evaluate the distribution, abundance, population structure, and fecundity of the marine diplostraceans *P. avirostris* and *P. tergestina* in the VRSNP, SW and GM.

MATERIALS AND METHODS

Study area

The VRSNP is a Marine Protected Natural Area with 28 reef banks that cover 65,516 ha (DOF 2012). The reefs are divided into two groups due to the influence of the Jamapa River. Geographically, it is between 19º02'24"-19º16'00"N and 95º46'19"-96º12'01"W in the southwest Gulf of Mexico (Juárez-Sarvide et al. 1991) (Fig. 1).

The climate in the VRSNP is classified as dry and rainy with cold fronts (Carrillo et al. 2007). The circulation dynamics in the VRSNP are influenced by the winds of the cold fronts, which can produce important mixing processes in the water column. During the diurnal tide, the direction of the tide is modified by the presence of shallow reliefs, reefs, and islands, favoring the formation of cyclonic and anticyclonic gyres (Monreal-Gómez et al. 2004). These factors can modify the distribution and abundance of the zooplanktonic organisms.

Sampling

A total of 26 sampling sites were established in June, August, October (2011), May (2012), and June (2013), positioned on four transects perpendicular to the coast: two towards the north and other two towards the south regarding the mouth of the Jamapa River (Fig. 1). Horizontal hauls at the surface were made on every station using a 1.5 m long WP-2 conical net with a 0.5 m mouth diameter (surface area = 0.196 m^2) and 330 µm mesh opening, on which a flow meter (General Oceanics) was placed 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 km h^{-1} (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.

Environmental factors

In situ measurements included salinity, the surface temperature of water (°C), and dissolved oxygen (mg L^{-1}), which were measured using a multiparameter water quality portable meter (Hanna HI 9828).

Identification and abundance

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. The identification was according to Della Croce's (1974) and Conway's (2012) criteria. The diplostraceans were identified and counted using a Motic SMZ-168 stereoscopic microscope and a Leica DM750 microscope.

Density and spatial distribution

The density was obtained by counting the organisms, and the number of ind 100 m^{-3} of water was standardized. Interpolated distribution maps were prepared using the Surfer program (v.10.1.561, Surface Mapping System, Golden Software, Inc.).

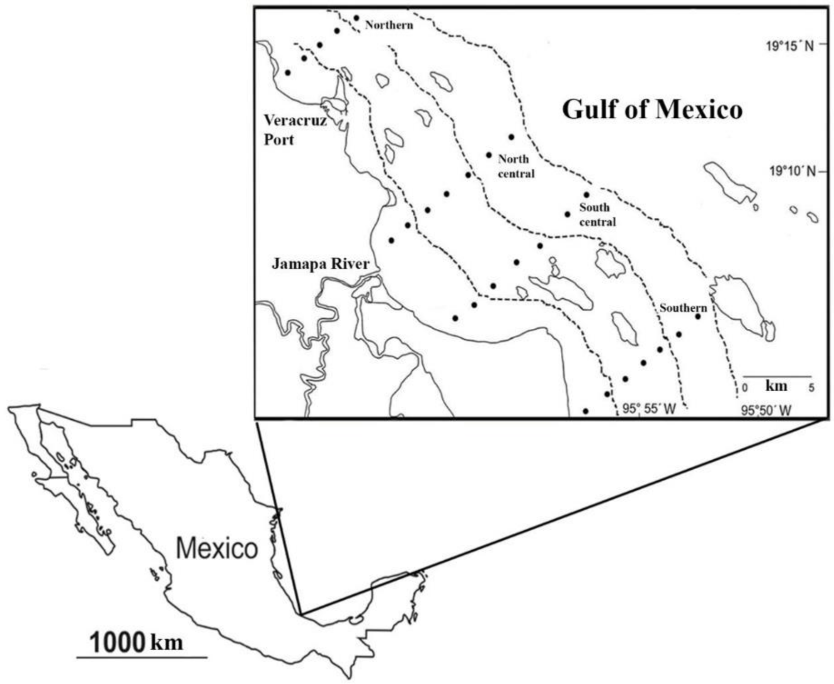

Figure 1. Location of the sampling stations and transects in the Veracruz Reef System National Park study area.

Sizes

The body length (BL) of each organism was measured (in µm). In *P. avirostris*, the BL was considered as the distance between the anterior border of the head and the posterior margin of the dorsal articulation of the carapace. BL for *P. tergestina* was taken from the anterior margin of the head to the dorsal posterior border of the carapace.

Population structure

A total of 100 diplostraceans from each month were randomly selected, measured, and grouped according to the following classes: juvenile (<500 µm for *P. avirostris* and <300 µm for *P. tergestina*), non-reproductive females (lacking embryos), partheno-genetic females (with embryos), gamogenic females (with resistance eggs), and males. The proportion of each group was obtained. The sex of the organisms was determined according to the descriptions of Della Croce (1974) for *P. avirostris* and of Onbé (1978) for *P. tergestina*. Fecundity was obtained by counting the number of embryos per parthenogenic female.

Statistical analyzes

After verifying the normality and homoscedasticity of the data with the Shapiro-Wilk test, a comparison between the values of temperature, salinity, and dissolved oxygen was made between the five sampled months using analyses of variance (ANOVA) and Tukey's *post-hoc* test. Previously, the values of the environmental factors were transformed to arcsine (Cházaro-Olvera et al. 2023). The Mann-Whitney test was applied to compare the average sizes of the reproductive females. The Wilcoxon test was applied to determine the possible differences between the abundances of the two diplostraceans species, considering each sampling month (Sokal & Rohlf 2012).

The relationship between the density of diplostraceans in the transects and the sampling months was analyzed with a generalized linear model (GLM) using the log-linear Poisson distribution for counts ($\log(\mu) = \alpha + \beta x$, where α is the intersection and β is the contribution of the each variable to the model). Each of the parameters was incorporated into the model as a covariate. Subsequently, the significance was obtained for each parameter analyzed ($P < 0.05$) (Zuur et al. 2007).

For fecundity, each female's number of embryos (Ne) and BL were related using a potential model: $Ne = aBL^b$.

For the Wilcoxon analysis, the R Studio program for Windows version 3.5 was used (Systat, 2006). The potential model, GLM, and Mann-Whitney test were performed in SPSS Version 25.

RESULTS

Environmental factors

The temperature presented an average interval between 26.53 ± 0.41°C (May 2012) and 29.29 ± 0.27°C (August 2011), the salinity an average between 33.43 ± 0.49 (August 2011) and 35.91 ± 0.09 (May 2012) and the dissolved oxygen presented an average between 2.92 ± 0.08 mg L^{-1} (June 2011) and 6.56 ± 0.08 mgL^{-1} (August 2011). The three environmental variables presented statistically significant differences among the sampling months and transects according to the ANOVA test ($F_{4,15\ 0.05} = 26.4$, $P < 0.001$; $F_{4,15;\ 0.05} = 42.48$, $P < 0.001$; $F_{4,15;\ 0.05} = 4.36$, $P = 0.016$, respectively). Tukey's test showed statistically significant differences between the three months of 2011 with May 2012 and June 2013 ($P < 0.05$) (Table 1).

The results of the GLM showed that there was a statistically significant relationship between the density of *P. avirostris* and temperature, salinity, and dissolved oxygen ($P < 0.001$); the β values were negative for the three parameters in both species and only positive with the temperature in *P. tergestina* (Table 2), and for *P. tergestina* showed a significant relationship between their density and temperature, salinity, and dissolved oxygen ($P < 0.001$); the β values were negative for salinity and oxygen and positive for temperature (Table 2).

Abundance

The total abundance of diplostraceans collected in the VRSNP from 2011 to 2013 was 88,959 individuals (12,404 of *P. avirostris*; 76,555 of *P. tergestina*). In 2011, *P. avirostris* presented the highest abundance with 8925 individuals, while *P. tergestina* presented the highest abundance, with 53,653 in June 2013 (Figs. 2a-b). When comparing the annual abundances of the two species using the Wilcoxon test, no significant differences were found among the three years ($P > 0.05$) (Table 3).

Density and spatial distribution

In 2011, *P. avirostris* presented the highest density values with 1528, 2200, and 820 ind 100 m^{-3} in June, August, and October, respectively. These densities generally occurred at the stations furthest from the coast in the southern transect (Fig. 3). In the spatial analysis, statistically significant differences were found ($X^2 = 16.21$, $P < 0.05$) between the transect densities; the central-south transect was different from the other three (Dunn's test, $P < 0.05$). In June and October 2011, June 2012, and May 2013, there were no statistically significant differences in density; likewise, there were no statistically significant differences between sampling points or transects.

During 2011, the highest density values for *P. tergestina* were 2380, 4560, and 5980 ind 100 m^{-3} in June, August, and October, respectively. In June, the stations furthest from the southern transect presented the highest densities. In August and October, the highest densities were found in the central-south and northern transects at stations near the coast. In May 2012, the density was 692 ind 100 m^{-3} in the central north transect, while in June 2013, the highest densities were 22,335 and 17,165 ind 100 m^{-3} in the northern and southern transects, respectively, also at stations near the coast (Fig. 4). In June 2011 statistically, significant differences were found between the transects densities ($X^2 = 9.5275$, $P < 0.05$), with the northern and central-south transects differing from the central north and southern transects (Dunn's test, $P < 0.05$). During August, statistically significant differences were found between the transects ($X^2 = 10.256$, $P < 0.05$). On the other hand, the density of *P. tergestina* did not show statistically significant differences between stations or transects between October 2011, June 2012, or May 2013.

Population structure

Four stages were found in the *P. avirostris* population; no males were observed. During June and October 2011, the greatest proportion was parthenogenic females, while in August, the greatest percentage was non-reproductive females. Gamogenic females only represented 1% of the population in June and October 2011. In May 2012, the highest percentage corresponded to non-reproductive females. In June 2013, the highest percentage corresponded to parthenogenic females. Gamogenic females were only found in May 2012 at 3% of the population (Fig. 5a).

In *P. tergestina*, four stages were found. During June and August 2011, May 2012, and June 2013, parthenogenic females represented ~90% of the population. Gamogenic females, males, and juveniles were best represented in June 2013 at ~15%. (Fig. 5b).

Fecundity

P. avirostris presented a minimum of 2 and a maximum of 7 embryos. The size of reproductive females ranged from 600 to 990 µm, with a lower average value in August of 740 ± 8 µm and a higher average of 791 ± 8 µm in October (Table 4). However, no statistically significant differences were found when applying the

Table 1. The average and standard deviation of environmental factors registered in the Veracruz Reef System National Park, 2011-2013. ANOVA F-test and values of significance (*P*) of Tukey's test from comparing the environmental factors between the sampling months. Bold indicates statistically significant difference.

Zone	2011 Jun	2011 August	2011 October	2012 May	2013 Jun
			Temperature (°C)		
Northern	27.90 ± 0.52	28.68 ± 0.43	28.01 ± 0.44	26.82 ± 0.48	27.76 ± 0.39
North-central	27.33 ± 0.40	28.87 ± 0.38	27.69 ± 0.05	27.15 ± 0.18	27.33 ± 0.36
South-central	26.75 ± 0.50	29.01 ± 0.36	27.89 ± 0.39	26.S3 ± 0.41	27.47 ± 0.08
Southern	27.53 ± 0.35	29.29 ± 0.27	27.67 ± 0.21	27.16 ± 0.13	27.54 ± 0.10
			Salinity		
Northern	35.84 ± 0.05	33.43 ± 0.49	34.92 ± 0.08	35.66 ± 0.11	35.18 ± 0.13
North-central	35.86 ± 0.05	34.31 ± 0.30	358.3 ± 0.15	35.81 ± 0.13	34.51 ± 0.16
South-central	35.73 ± 0.08	34.01 ± 0.13	35.46 ± 0.14	35.89 ± 0.09	34.64 ± 0.15
Southern	35.73 ± 0.11	33.99 ± 0.17	35.36 ± 0.13	35.91 ± 0.09	34.79 ± 0.09
			Oxygen (mg L^{-1})		
Northern	2.92 ± 0.08	4.84 ± 0.05	3.16 ± 0.09	3.12 ± 0.08	2.96 ± 0.05
North-central	3.19 ± 0.09	5.74 ± 0.10	3.41 ± 0.09	4.19 ± 0.09	4.21 ± 0.12
South-central	3.41 ± 0.12	5.64 ± 0.08	4.59 ± 0.09	4.50 ± 0.40	4.67 ± 0.14
Southern	3.93 ± 0.08	6.56 ± 0.08	5.53 ± 0.17	4.94 ± 0.05	4.99 ± 0.09
ANOVA					
Environmental variable	F	*P*			
Temperature (°C)	$F_{4,15; 0.05} = 26.40$	< **0.001**			
Salinity	$F_{4,15; 0.05} = 42.48$	< **0.001**			
Dissolved oxygen (mg L^{-1})	$F_{4,15; 0.05} = 4.36$	0.**016**			
Tukey-test					
Comparison	Temperature (°C) (*P*)	Salinity (*P*)	Oxygen (mg L^{-1}) (*P*)		
2011 Jun-2011 August	0.349	0.997	0.335		
2011 Jun-2011 October	0.051	0.995	0.051		
2011 August-2011 October	0.886	0.986	0.345		
2011 Jun-2012 May	**<0.001**	**<0.001**	**<0.001**		
2011 August-2012 May	**<0.001**	**<0.001**	**<0.001**		
2011 October-2013 Jun	**<0.001**	**<0.001**	**<0.001**		
2012 May-2013 Jun	**<0.001**	**<0.001**	**<0.001**		

Mann-Whitney test between the average sizes of reproductive females in different months ($P > 0.05$).

P. tergestina also presented a range without much variation, with a minimum value of 2 and a maximum of 8 embryos. The size of reproductive females ranged from 340 to 930 µm, with a lower average value in June of 602 ± 9 µm and a higher average of 730 ± 8 µm in May (Table 4). However, no statistically significant differences were found when applying the Mann-Whitney test between the average sizes of reproductive females in different months ($P > 0.05$).

The BL and the number of embryos in both *P. avirostris* and *P. tergestina* in all sampling months are significantly correlated ($P < 0.05$) under the potential model (Figs. 6-7).

DISCUSSION

Abundance

The diplostraceans *P. avirostris* and *P. tergestina* were present in the same collection sites in the VRSNP, and their respective abundances did not differ significantly during the sampling years. This common presence has been found in other studies like those by Onbé (1985), Della Croce & Angelino (1987), Sterza & Fernandes (2006), and Guerrero et al. (2016). In Mexico, the presence of both species has been recorded in the Pacific coasts in Bahía Magdalena Bay and Concepción Bay in Baja California Sur, Mexico (Palomares-García et al. 2002, Hernández-Trujillo et al. 2010), as well as in areas of the GM (Della Croce & Angelino 1987, Lester et al. 2008).

Table 2. Generalized Linear Model. Relationship between the density of diplostraceans with the environmental factors in the Veracruz Reef System National Park, during 2011-2013. Bold indicates statistically significant difference; β signifies the contribution of the variable to the model. *P* in bold, signifies effect of the independent variables statistically significant.

	Parameter	β	X^2 of Wald	*P*
	Intersection	28.624	255.34	< 0.001
	Salinity	-0.591	135.632	< **0.001**
P. avirostris	Intersection	26.796	456.055	< 0.001
	Temperature	-0.685	230.038	< **0.001**
	Intersection	14.099	7428.543	< 0.001
	Dissolved oxygen	-1.224	1496.019	< **0.001**
	Intersection	97.12	1737.99	< 0.001
	Salinity	-2.561	1507.04	< **0.001**
P. tergestina	Intersection	-20.489	158.87	< 0.001
	Temperature	0.978	280.502	< **0.001**
	Intersection	10.795	2340.91	< 0.001
	Dissolved oxygen	-0.782	332.809	< **0.001**

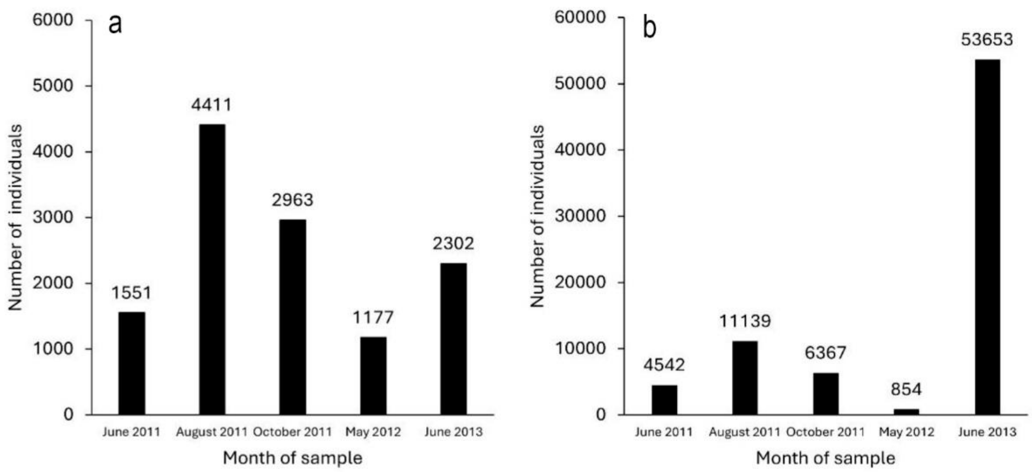

Figure 2. Total abundance of diplostraceans collected in the Veracruz Reef System National Park from 2011-2013. a) *Penilia avirostris*, b) *Pseudoevadne tergestina*.

Table 3. Comparison of the abundance of *P. avirostris* and *P. tergestina* between 2011-2013 using the Wilcoxon-test (W). *P*: significance.

Year	W	*P*
2011	2957	0.72
2012	359	0.63
2013	318	0.69

The coexistence of *P. avirostris* and *P. tergestina* may be related to their different feeding strategies (Marazzo & Valentín 2001). *P. avirostris* belongs to the order Ctenopoda, which is characterized by having a carapace that encloses its six pairs of thoracic limbs, and it should be noted that the gnathobase and endites of the first five pairs of thoracopods present a great density of silks adapted to filter-feeding (Katechakis & Stibor 2004, Sala et al. 2015a). On the other hand, *P. tergestina* belongs to the Onychopoda order. More specifically to the Podonidae family, and in contrast to the order Ctenopoda, the carapace of the family Podonidae is very reduced, forming the incubator chamber, which is why four pairs of thoracopods are exposed, the first three are biramous and long, and the fourth is usually very small. Thus, these appendages make raptorial feeding possible (Sala et al. 2015b).

Regarding the density of *P. avirostris*, some studies have reported abundances in Mexico between 10,000 and 11,000 ind 100 m^{-3} (Hernández-Trujillo et al. 2010 for Baja California Sur, Mexico, and Lester et al. 2008 for the GM), while other authors such as Marazzo & Valentín (2003a) have found densities of 1500-1800

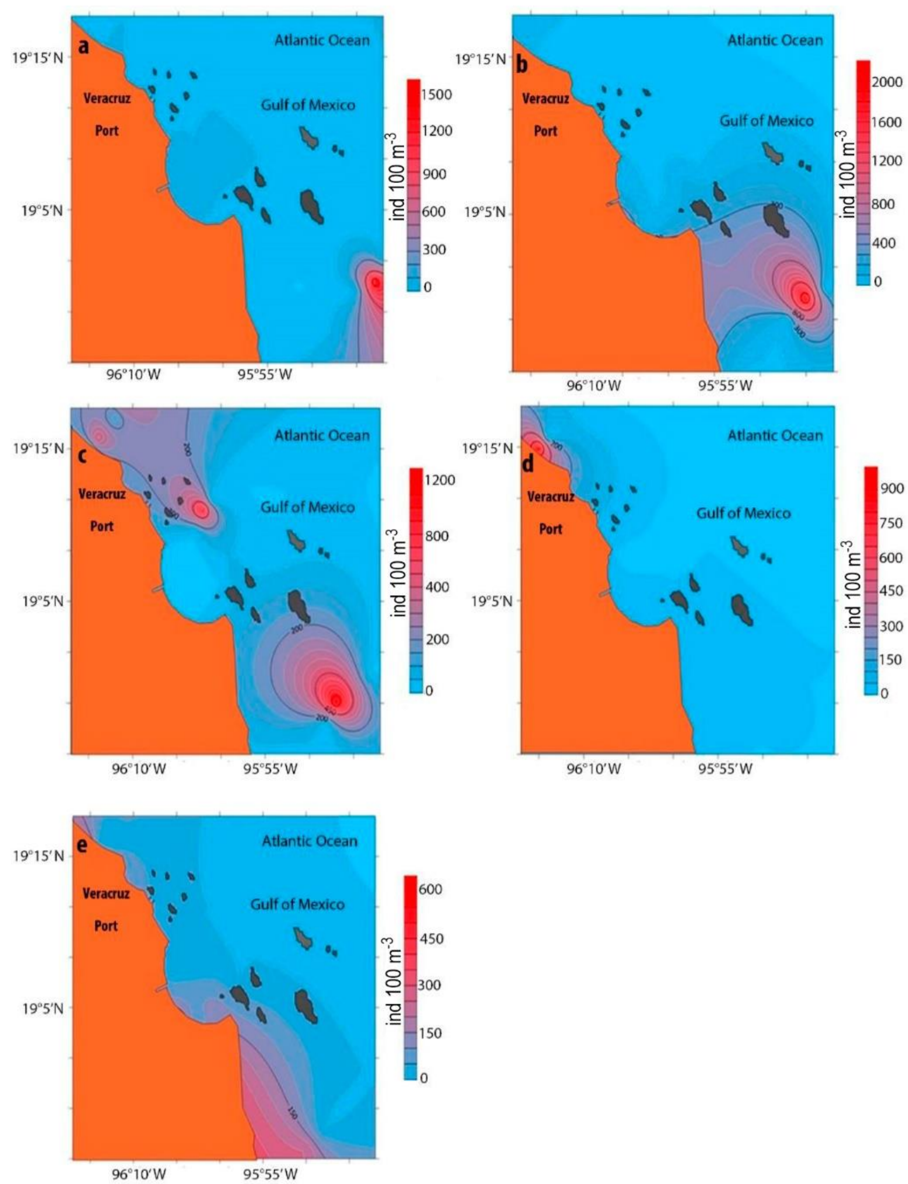

Figure 3. Density and distribution of *Penilia avirostris* collected in the Veracruz Reef System National Park. a) June 2011, b) August 2011, c) October 2011, d) May 2012, e) June 2013.

ind 100 m^{-3} on the coasts of Brazil. The latter is consistent with the results obtained in the present study (Fig. 3).

On the other hand, *P. tergestina* presented lower densities than those found in other studies, which reported 35,000 to 440,000 ind 100 m^{-3} (Marazzo & Valentín 2004a, Miyashita et al. 2011). An important factor to consider is that these studies were carried out at depths of 25-40 m, unlike the present study, which was carried out at the surface of the water column.

In the present study, the density variation of both diplostraceans species was related to the temperature, salinity, and dissolved oxygen. According to the GLM results, the diplostraceans have optimal values where growth and development are adequate. When the values of the environmental factors are highest in these optimals, the density decreases. In this regard, *P. avirostris* is typically found in warm waters, and its optimal conditions are when the water temperature is around 25°C in euryhaline coastal environments (Onbé 1983, Marazzo & Valentín 2000). On the other hand, *P. tergestina* is found on the surface of coastal seas (Marazzo & Valentín 2004a) and is considered an indicator of coastal masses of warm waters (Onbé 1983) at an optimum temperature of 22-24°C (Marazzo & Valentín 2001). In the present study, the recorded

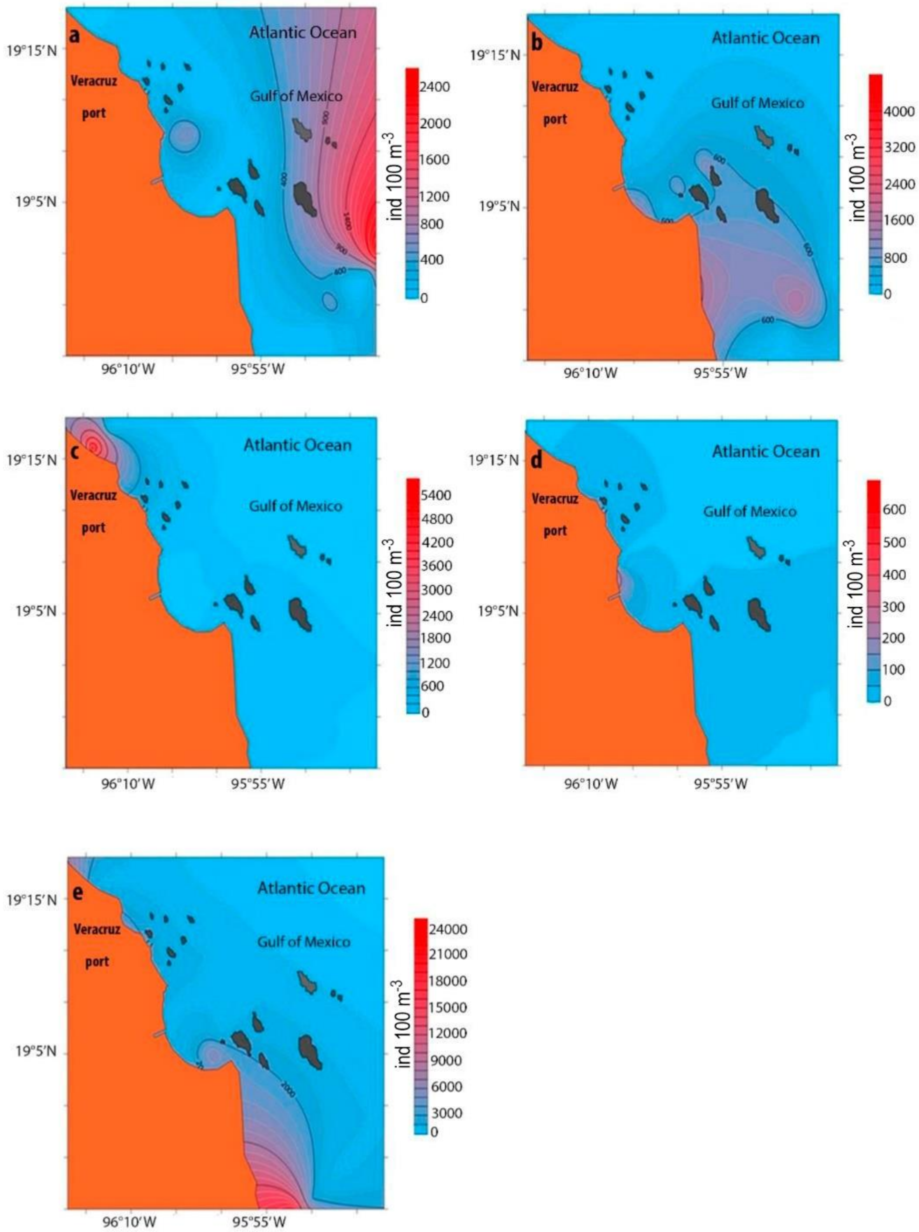

Figure 4. Density and distribution of *Pseudoevadne tergestina* collected in the Veracruz Reef System National Park. a) June 2011, b) August 2011, c) October 2011, d) May 2012, e) June 2013.

values of temperature and salinity are consistent with those mentioned by other authors (Ramírez & Pérez-Seijas 1985, Onbé & Ikeda 1995, Egloff et al. 1997, Marazzo & Valentín 2003a, Wong et al. 2004, 2008, Sterza & Fernandes 2006, Atienza et al. 2008, Miyashita et al. 2009). On the other hand, Álvarez-Tello et al. (2015) reported that both species were collected at concentrations of dissolved oxygen ranging from 2.9 mg L^{-1} during the hot season to 12.4 mg L^{-1} during the coldest season, and these values are consistent with the obtained in the present study (Table 1).

Both species are better represented in the northern and southern areas of the VRSNP, in contrast to the transects of the central zone, which may be due to the constant discharge of the Jamapa River, mainly in the rainy seasons, which modifies the values of the physicochemical variables, mainly salinity (Rodríguez-Gómez et al. 2013). In this regard, it has been observed that *P. avirostris* occurs in places where salinity is high and is absent when it is low (Sterza & Fernandes 2006). Within the VRSNP, there is a phenomenon of great importance that modifies the direction of the currents,

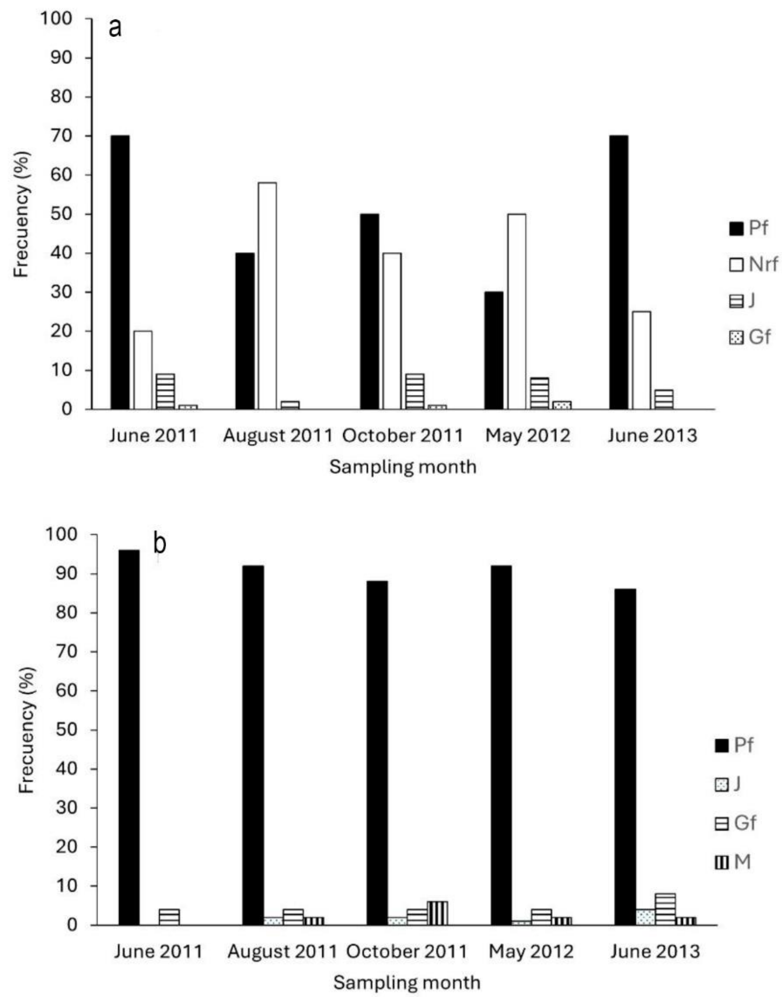

Figure 5. Population structure of a) *Penilia avirostris* and b) *Pseudoevadne tergestina* in the Veracruz Reef System National Park, 2011-2013. Gf: gamogenic females; J: juveniles; M: males; Nrf: non-reproductive females; Pf: parthenogenic females.

temperature, and, consequently, zooplankton distribution: a cyclonic turn that forms just in front of the mouth of the Jamapa River in the transects from the central zone, which generates a lower temperature due to pumping towards the surface of deeper waters, with low temperatures and high nutrient levels (Salas-Monreal et al. 2009). This phenomenon could explain the absence of these diplostraceans in these transects because the decreases in the abundance of *P. tergestina* in temperate regions seem to be associated with changes in the temperature of the water's surface (Ramírez & Perez-Seijas 1985), while in tropical and subtropical regions it is associated with the change in salinity (Marazzo & Valentín 2001).

Population structure

The population structure of *P. avirostris* was mainly represented by parthenogenic females and non-reproductive females comprising about 90% of the collected individuals, consistent with what was reported by Atienza et al. (2008) and Miyashita et al. (2010). Reproductive females only represented around 3%, which is consistent with what was reported by Miyashita et al. (2010).

On the other hand, the population structure of *P. tergestina* was mainly comprised of parthenogenic females, who comprised about 90% of the collected individuals. These values are consistent with those Marazzo & Valentín (2004a) and Miyashita et al. (2011) reported. Gamogenic females represented 3-7%, and similar results were reported by Onbé & Ikeda (1995); however, Onbé (1978) reported proportions of gamogenic females at 20-23%. Marazzo & Valentín (2003b) mention that this proportion can be higher when the population decreases, reaching 70% of the population. Gamogenic individuals comprise a lower

Table 4. Number of embryos in gravid females of diplostraceans collected in the Veracruz Reef System National Park during 2011-2013. SD: standard deviation.

	P. avirostris			
	Embryo number range	Average embryo number (± SD)	Female size range (µm)	Average size of females µm (± SD)
June 2011	2-6	3.85 ± 1.05	660 to 950	792 ± 7
August 2011	3-5	3.70 ± 0.78	620 to 870	740 ± 8
October 2011	2-6	3.32 ± 0.86	630 to 990	791 ± 8
May 2012	2-5	3.34 ± 0.84	620 to 920	774 ± 8
June 2013	2-7	4.25 ± 1.43	600 to 920	763 ± 7
	P. tergestina			
	Embryo number range	Average embryo number (± SD)	Female size range (µm)	Average size of females µm (± SD)
June 2011	2-7	3.95 ± 1.33	360 to 770	602 ± 9
August 2011	2-6	4.16 ± 1.15	360 to 800	634 ± 9
October 2011	2-6	4.07 ± 1.19	340 to 830	627 ± 9
May 2012	3-8	5.05 ± 1.16	560 to 930	730 ± 8
June 2013	2-7	4.23 ± 0.89	360 to 830	603 ± 9

	P. avirostris			
	Embryo number range	Average embryo number (± SD)	Female size range (µm)	Average size of females µm (± SD)
June 2011	2-6	3.85 ± 1.05	660 to 950	792 ± 7
August 2011	3-5	3.70 ± 0.78	620 to 870	740 ± 8
October 2011	2-6	3.32 ± 0.86	630 to 990	791 ± 8
May 2012	2-5	3.34 ± 0.84	620 to 920	774 ± 8
June 2013	2-7	4.25 ± 1.43	600 to 920	763 ± 7
	P. tergestina			
	Embryo number range	Average embryo number (± SD)	Female size range (µm)	Average size of females µm (± SD)
June 2011	2-7	3.95 ± 1.33	360 to 770	602 ± 9
August 2011	2-6	4.16 ± 1.15	360 to 800	634 ± 9
October 2011	2-6	4.07 ± 1.19	340 to 830	627 ± 9
May 2012	3-8	5.05 ± 1.16	560 to 930	730 ± 8
June 2013	2-7	4.23 ± 0.89	360 to 830	603 ± 9

percentage of the population structure on marine coasts, where environmental conditions tend to be more stable (Hairston & Cáceres 1996).

Fecundity

The average clutch size observed for *P. avirostris* in the VRSNP was like those obtained in other studies carried out in the Gulf of Mexico, off the coasts of Brazil, and China, with values between 3-4 embryos (Della Croce & Angelino 1987, Mullin & Onbé 1992, Tang et al. 1995, Marazzo & Valentín 2004a, Atienza et al. 2008, Miyashita et al. 2010). On the other hand, the clutch size range is like that reported by Della Croce & Angelino (1987), Mullin & Onbé (1992), Marazzo & Valentín (2003a), and Atienza et al. (2008). However, it is lower than what was reported by Della Croce (1966), Tang et al. (1995), and Marazzo & Valentín (2004b).

The average clutch size for *P. tergestina* is similar to that reported in other studies in the Gulf of Mexico and off the coast of Brazil, where there are three to four embryos (Mullin & Onbé 1992). However, it is lower than those reported in the Caribbean Sea, West Florida, and off the coasts of Brazil with 5-8 embryos (Della Croce & Angelino 1987, Bryan 1974, Marazzo & Valentín 2004a,b). For the clutch size range, values like those obtained in other studies in the GM were obtained (Della Croce & Angelino 1987, Mullin & Onbé 1992). However, a wider range of 1-14 embryos were found in the Chesapeake Bay and off the coasts of Brazil (Bryan 1974, Marazzo & Valentín 2001, 2004a,b).

The analysis of the relationship between BL and clutch size was direct and fitted to the potential model in *P. avirostris*, which is consistent with what was reported by Della Croce (1966), Della Croce & Venugopal (1973), and Atienza et al. (2008).

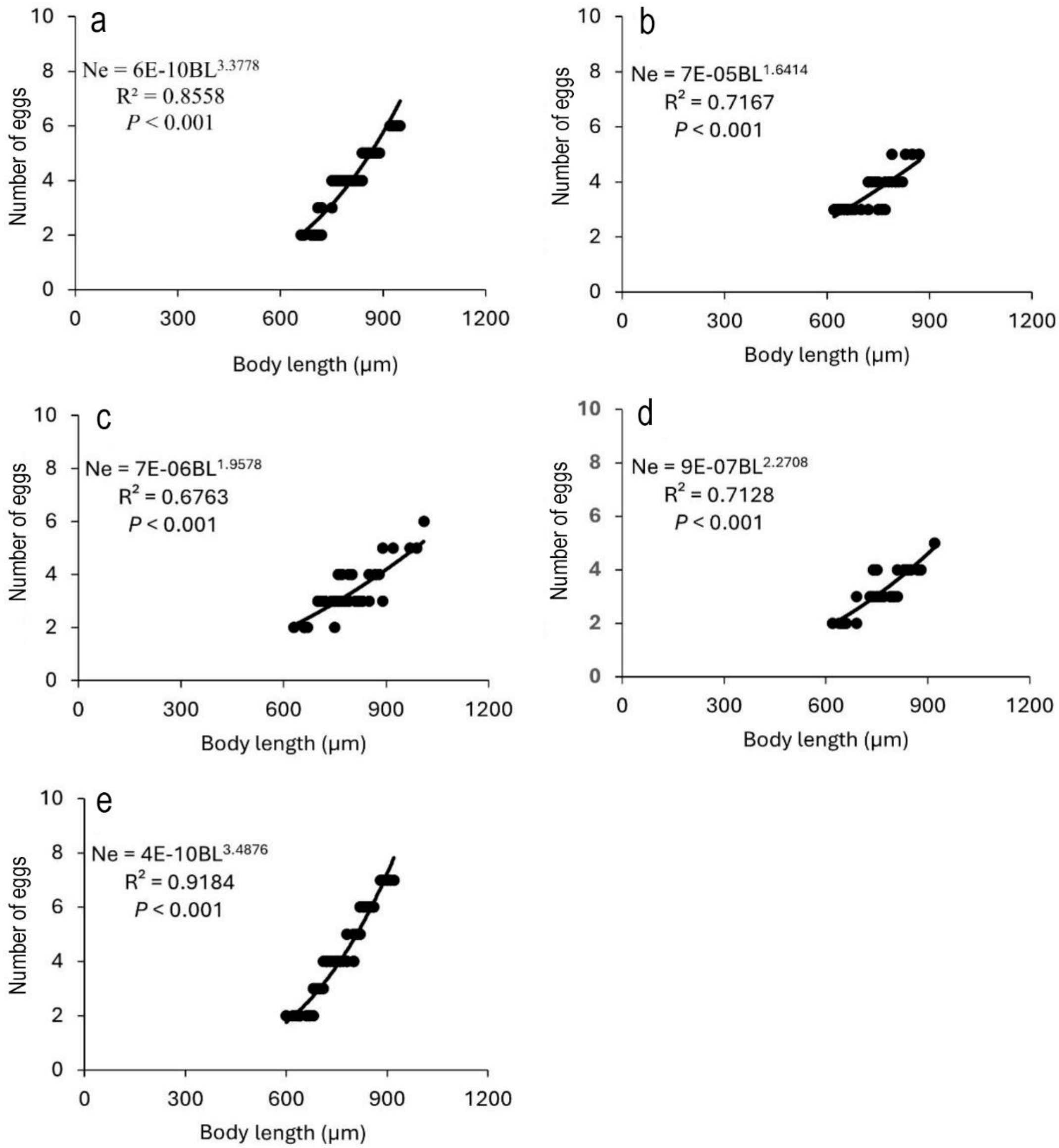

Figure 6. Relationship between the body length (BL) of the gravid females *Penilia avirostris* and the number of embryos (Ne) collected in the Veracruz Reef System National Park. a) June 2011, b) August 2011, c) October 2011, d) May 2012, e) June 2013.

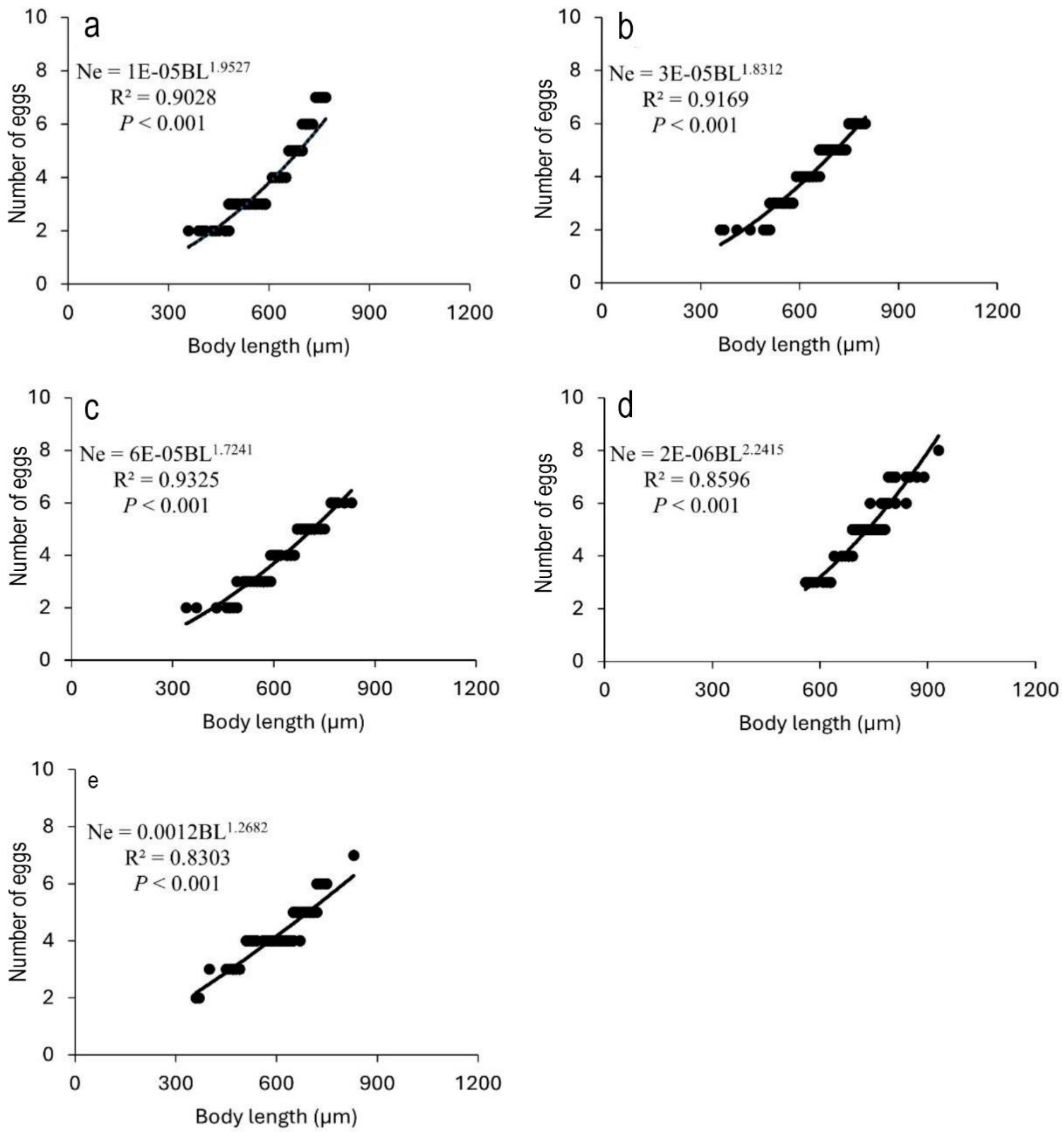

Figure 7. Relationship between the body length (BL) of the gravid females *Pseudoevadne tergestina* and the number of embryos (Ne) collected in the Veracruz Reef System National Park. a) June 2011, b) August 2011, c) October 2011, d) May 2012, e) June 2013.

Regarding *P. tergestina*, Miyashita et al. (2011) also found a high correlation between clutch length and size in this species and other podonids. Marazzo & Valentín (2004b) described a similar pattern.

CONCLUSIONS

In conclusion, the north and south zones were the transects with the highest abundance. In contrast, those that obtained the lowest abundances were the south-central and north-central zones, attributed to the plume of influence of the Jamapa River. The density of diplostraceans was related to temperature, salinity, and dissolved oxygen. The low proportions of gamogenic individuals of *P. avirostris* and *P. tergestina* obtained suggest that in tropical and subtropical regions, gamogenesis is not crucial for the life cycle of these organisms (Miyashita et al. 2010). It can be established that the change in the reproductive mode of diplostraceans reflects the changes or stability of external environmental conditions. Two of the most related factors are temperature and population density (Berg 1931, Egloff et al. 1997).

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