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Article

Impact of some environmental factors on the temporal variability of pink and white shrimps postlarvae in Terminos Lagoon, Southern Gulf of Mexico

Impacto de algunos factores ambientales en la variabilidad temporal en la densidad de postlarvas de camarón rosado y blanco en Laguna de Términos, sur del Golfo de México

Mario Alejandro Gómez-Ponce[1], Erik Coria-Monter[2*], César Flores-Coto[2], Julio César Canales-Delgadillo[3], José Gilberto Cardoso-Mohedano[1] and Elizabeth Durán-Campos[4]

[1]Instituto de Ciencias del Mar y Limnología, Estación El Carmen, Universidad Nacional Autónoma de México, Ciudad del Carmen, Campeche, México
[2]Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, CDMX, México
[3]CONAHCYT, Instituto de Ciencias del Mar y Limnología Estación El Carmen, Universidad Nacional Autónoma de México, Ciudad del Carmen, Campeche, México
[4]Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mazatlán, Sinaloa, México
*Corresponding author: coria@cmarl.unam.mx

Resumen.- El camarón rosado *Farfantepenaeus duorarum* y camarón blanco *Litopenaeus setiferus* son especies con un elevado valor tanto ecológico como económico por lo que estudios que analicen su variabilidad temporal a largo plazo y su relación con el ambiente físico resultan necesarios. El objetivo de este estudio fue evaluar el impacto de algunas variables ambientales en la variabilidad temporal de las postlarvas de ambas especies en la Laguna de Términos, sur del Golfo de México, una región reconocida por ser el hábitat de refugio, crecimiento y alimentación de estas especies. Los organismos fueron colectados en tres diferentes profundidades (1,5, 4 y 9 m) con una red múltiple (red trapezoidal, 50 cm de diámetro de boca, 1,5 m de longitud y 505 µm de apertura de malla) en un punto localizado en la conexión entre la laguna y las aguas del Golfo de México a lo largo de cuatro años de muestreos nocturnos, desde mayo de 2010 a septiembre de 2013. En cada muestreo, se registraron datos hidrográficos (*e.g.,* temperatura, salinidad) con ayuda de una sonda multiparamétrica, se adquirieron datos meteorológicos (*e.g.*, precipitación, velocidad del viento) de una estación local, mientras que el patrón de circulación superficial se obtuvo a partir de un modelo numérico. Los resultados señalaron cambios en las variables ambientales, con valores máximos de precipitación (250 mm) en 2010. La temperatura superficial mostró valores de ~30 ºC con ligeras variaciones a lo largo del periodo de estudio. La salinidad presentó valores mínimos (< 30) en las épocas de mayor precipitación, aumentando durante la época seca con valores > 33. En algunas fechas se observaron corrientes intensas (> 0,25 m s^{-1}) en dirección norte a sur que alcanzaron la costa e ingresaron a la laguna. También, se observaron vórtices anticiclónicos (con un diámetro de ~ 30 km) en la región sur del golfo. Se observaron altos valores de densidad de ambas especies, con 33,619 ind 100 m^{-3} para *L. setiferus* y 57,948 ind 100 m^{-3} para *F. duorarum*. Los valores máximos se asociaron a corrientes superficiales que ingresaron a la laguna, lo cual fue confirmado a partir de técnicas estadística multivariada. Los resultados obtenidos contribuyen a la comprensión del papel que juegan las corrientes superficiales y las variables ambientales sobre la densidad de dos especies de alto valor económico y ecológico en la región, lo cual es de relevancia en regiones reconocidas por su alto diversidad biológica.

Palabras clave: *Farfantepenaeus duorarum, Litopenaeus setiferus*, densidad, Laguna de Términos, Golfo de México

Abstract.- The pink shrimp *Farfantepenaeus duorarum* and white shrimp *Litopenaeus setiferus* are species of high ecological and commercial value, therefore, studies that analyze their temporal variability and their relationship with the physical environment in the long term becomes necessary. The aim of this is study was to assess the impact of some environmental factors on the temporal variability of the postlarvae of both species in Terminos Lagoon, Southern Gulf of Mexico, a region recognized for being the refuge, breeding and feeding habitat for these species. Organisms were collected at three different depths (1.5, 4 and 9 m) using a multiple net system (trapezium-type nets, 50 cm of mouth diameter, 1.5 m in length, and mesh size of 505 µm) in a fixed location at the junction between the lagoon and the open waters of the Gulf of Mexico during nocturnal sampling expeditions executed from May 2010 to September 2013. In each sampling expedition, hydrographic data (*e.g.*, temperature, salinity) were recorder using a multiparameter sonde, meteorological data (*e.g.*, precipitation, wind velocity) were acquired from a local meteorological station, while the surface circulation pattern was obtained from a numerical model. The results showed changes in the environmental factors, with highest precipitation (250 mm) in 2010. The surface temperature revealed values of ~30 ºC with slight variations throughout the study period. Salinity showed minimum values (< 30) in the seasons of highest precipitation, increasing during the dry season with values of > 33. Strong currents (> 0.25 m s^{-1}) in a north to south direction that reached the coast and then the interior of the lagoon were observed in specific dates. Mesoscale anticyclonic eddies (with a diameter of ~30 km) were also observed in the southern gulf. High density values of both species were observed, reaching 33,619 ind 100 m^{-3} for *L. setiferus*, and 57,948 ind 100 m^{-3} for *F. duorarum*. Peaks were associated when strong surface currents were observed reaching the interior of the lagoon, which was confirmed from multivariate statistical techniques. The results presented here contribute to the understanding of the role that some environmental factors exert on the density of two species with high, both economic and ecological, value in the Terminos Lagoon, which is of critical relevance in regions recognized for their high biological diversity.

Key words: *Farfantepenaeus duorarum, Litopenaeus setiferus*, density, Terminos Lagoon, Gulf of Mexico

Introduction

Along the coast of the Southeastern United States and Northeastern Mexico, two species of penaeid shrimps are the basis of an economically important fishery, the pink shrimp (*Farfantepenaeus duorarum* Burkenroad, 1939) [also referred to as *Penaeus duorarum*], and the white shrimp (*Litopenaeus setigers*, Linnaeus, 1767) [also referred to as *Penaeus setiferus*]. This fishery produces more than 19,000 metric tons by year, representing a primary source of foreign currency (more than 500 million dollars), and it is a source of employment for thousands of peoples in both countries (Zimmerman *et al.* 2002, Scott-Denton *et al.* 2012).

The pink and white shrimps are present in high densities along the coast of Florida and Mexico (including lagoons and estuaries). Both species are well adapted to environments of low salinity and tolerate relatively low levels of dissolved oxygen (Rosas *et al*. 1999), presenting a lifecycle with a transit from planktonic to benthic life throughout a series of developmental stages including nauplii, protozoea, mysis, and postlarvae, until the currents carry them shoreward (Ditty & Alvarado-Bremer 2011).

During the postlarvae stage, both species benefit from shallow, low salinity semi-enclosed coastal environments where they spend part of this cycle sheltering and feeding because these environments provide abundant organic matter and suitable conditions (*i.e*., temperature) to modulate them growth (Minello & Zimmerman 1991). From an ecological point of view, the postlarvae stage is critical because the density of the organism in this stage controls the recruitment and influences the size population in the adult phase (Underwood & Fairweather 1989).

Several studies have been carried out in order to understand the physical aspects related with the growth and biological performance of the penaeid shrimp populations. To date, water temperature, salinity and dissolved oxygen levels are known to be critical parameters recognized as important in their life cycle and size-dependent (Rosas *et al.* 1999, Pérez-Castañeda & Defeo 2001, Minello 2017).

Additionally, the role that surface currents play in transport (advection) of postlarvae from the open ocean to refuge and nursery areas have now begun to be noticed in the northern Gulf of Mexico. For example, from field data and simulations of transport in the Florida Bay (USA), Criales *et al.* (2006) documented that pink shrimp postlarvae benefit from the surface circulation pattern, traveling with the current and exhibiting a diel behavior travel up to 65 km. Later, Criales *et al*. (2015) demonstrated, using a numerical approach, an effective east-northeast transport across the southwest Florida shelf (USA) during summer as a result of the currents presented in the region which are critical to determine the direction in which postlarvae of pink shrimp move. So, understanding the physical factors that determine the density values of penaeid shrimp populations is imperative.

In coastal environments of the Southern Gulf of Mexico (SGoM), in the Mecoacan Lagoon, the densities and biomass of the pink and white shrimp are derived by salinity, dissolved oxygen, and organic matter variations (Torres *et al.* 2020). In the Carmen-Pajonal-Machona Lagoon, changes in the immigration patterns of the pink and white shrimp's postlarvae were observed in relation to the temperature regime, where the maximum density of both species occurs during the warmest months of the year, from April to November (Flores-Coto *et al.* 2010). In Celestun Lagoon, the population variability of penaeid shrimp (*Farfantepenaeus* spp.) presents a clear seasonal variability in relation with the climatic seasons which in turn generates strong differences in temperature, salinity, and aquatic vegetation, then affecting the spatial patterns of shrimp density (Pérez-Castañeda & Defeo 2001).

Particularly in the Terminos Lagoon, changes in the hydrographic properties of the water column, mainly temperature, and the tides are decisive in the postlarvae immigration of the white shrimp from the open ocean to the interior of the lagoon (Gómez-Ponce *et al.* 2018). Flores-Coto *et al.* (2018) analyzed the immigration density magnitude and entry size of pink and white shrimps postlarvae to the lagoon from samples that covered the annual cycle of 2013; they reported high densities values of both species (> 35,000 ind 100 m^{-3}) with a pattern of immigration linked to climatic variation, particularly with the precipitation.

Although these works have provided very valuable information to understand the variability of pink and white shrimp postlarvae and its possible relationship with the physical environment, there are still some questions about the role that surface currents play over the advection of the postlarvae from open waters of the gulf towards the interior of the lagoon, further considering the dynamic of the SoGM, which is extremely variable; for example, the presence of strong currents and eddies are recurrent features in the region that can play an important role in this advection.

Under this scenario, the aim of this study was to assess the impact of some environmental factors on the temporal variability in the postlarvae density of *Farfantepenaeus duorarum* and *Litopenaeus setiferus* in the Terminos Lagoon. This study primarily focused on analyzing the variability in the density of both species using four years of nocturnal sample data collected from a fixed point located at the connection between the lagoon and the open waters of the Gulf of Mexico.

During the period from May 2010 to September 2013, a total of 31 bimonthly nocturnal sampling voyages were successfully executed in order to collect zooplankton specimens at three different depths, as well as hydrographic data aimed to determine the relationship between the physical factors with the density of the organisms. Additionally, data on the surface currents during each sampling expedition were obtained from numerical modeling in order to analyze the role of the surface circulation pattern over the advection of the postlarvae.

Under the hypothesis that there would be changes in the density of both species due to the variations in the environmental factors, this study intends to increase the knowledge on the ecology of both species in Terminos Lagoon and then be able to propose better management strategies in a region recognized for its high biodiversity and for being an area of refuge, feeding, and growth of different species of flora and fauna.

Materials and methods

Study area

The Terminos Lagoon is considered one of the biggest coastal environments along Mexican territory. It is located at the SGoM, in the western portion of the Yucatan Peninsula, covering a total area of more than 1,500 km^2 (Yáñez-Arancibia & Day 1988) (Fig. 1). The lagoon is separated from the open waters of the Gulf of Mexico by the presence of Del Carmen Island, which in turn presents two inlets, Puerto Real to the east and Del Carmen to the west. The lagoon is a very dynamic environment due to the discharge of fresh water from three large rivers located in their southern portion: Palizada, Chumpan, and Candelaria. It, as well, experiences an inflow of seawater from the gulf through the Puerto Real inlet, while the outflow from the lagoon to the gulf occurs through the Del Carmen inlet (Kjerfve *et al.* 1988, Contreras-Ruiz *et al.* 2014).

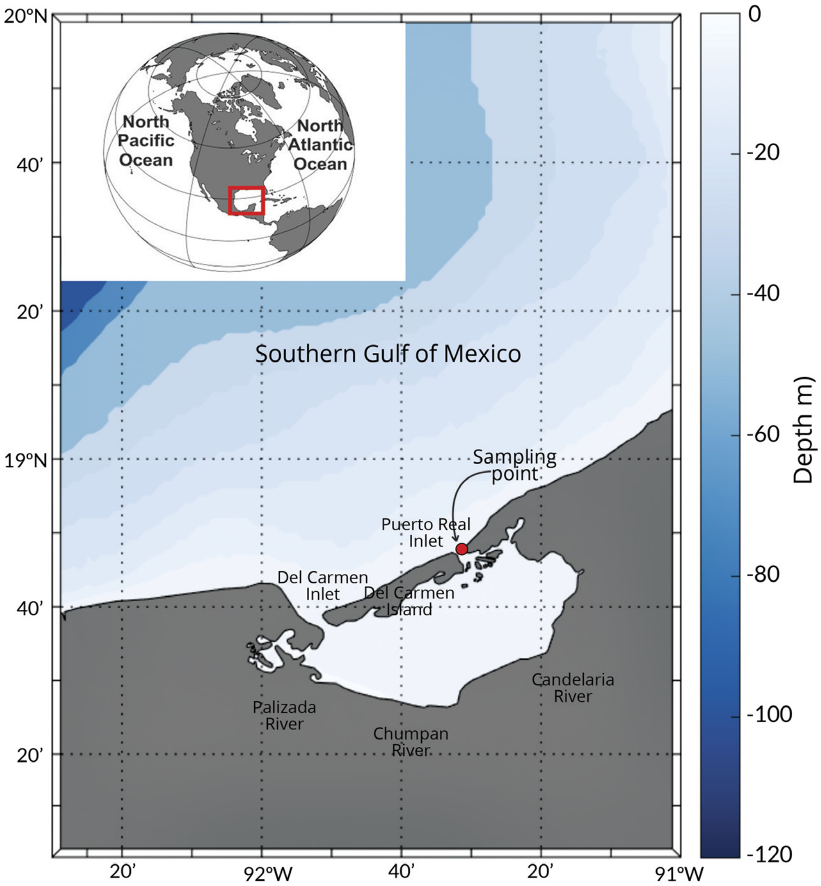

Figure 1. Location of the Terminos Lagoon in the SGoM. The red point represents the fixed location (18°46'12"N, 91°30'0"W) where hydrographic data and zooplankton samples were acquired from May 27th 2010 to September 30th 2013. The bathymetry is shown in meters. The domain shown in the figure (18.1-20ºN, 91-92.5ºW) corresponds from where current data were extracted by the numerical model / Localización de la Laguna de Términos en el sur del Golfo de México. El punto rojo es la posición fija (18°46'12"N, 91°30'0"O) en donde se adquirieron datos hidrográficos y muestras de zooplancton del 27 de mayo de 2010 al 30 de septiembre de 2013. La batimetría se muestra en metros. En el dominio mostrado en la figura (18,1-20ºN, 91-92,5ºO) se extrajeron datos de corrientes a partir de modelación numérica

In climatic terms, three seasons characterize the region including 1) the dry season that takes place from February to May, 2) the wet season from early June to October, and 3) the ‘Nortes’ season that takes place from November to January with persistent and extreme winds (> 80 km h^{-1}) from the north that cross the entire Gulf of Mexico, impacting the region and exerting important changes in the hydrographic properties of the water column (Contreras-Ruiz *et al.* 2014).

In biological terms, the lagoon is a region recognized for its high biological diversity, with abundant mangrove forests, vegetation that serves as a refuge, and feeding areas for several emblematic species, which is why the region, since the 1990s, has been considered by the Mexican authorities as a natural sanctuary with the category of Flora and Fauna Protection Area (Villalobos-Zapata 2015).

Sampling

A total of 31 nocturnal voyages (from 20:00 h to 05:00 h, see details in Table 1) were executed on a bimonthly basis during the period between May 27th 2010 to September 30th 2013 in a fixed point (18°46’12”N, 91°30’0”W; 14 m of total depth) located at the junction between the lagoon and the open waters of the Gulf of Mexico, in the Puerto Real inlet (red point in Fig. 1). Along Puerto Real inlet, there is a bridge (Unidad bridge) that connects Del Carmen Island with mainland, so one of the bases of the bridge was used as a center of operations to carry out our sampling. This site was selected because it presents the highest inflow of seawater from the gulf to the lagoon, and therefore it is a key site for evaluating the entry of postlarvae into the lagoon. The focus on nocturnal analyses was based on documented evidence that the catch of postlarval shrimp at night is generally more

Table 1. Hydrographic and environmental variables recorded for each sampling expedition in a fixed position (18°46'12"N, 91°30'0"W) located at the junction between Terminos Lagoon and the open Gulf of Mexico / Variables hidrográficas y ambientales registradas en cada expedición de muestreo en un punto fijo (18°46'12"N, 91°30'0"O) localizado en la conexión entre la Laguna de Términos y el Golfo de México

Year	Date	Moon phase	Sampling hour (local time, GMT-6)	Climatic season	PP (mm)	Speed currents (m s^{-1})	Temperature (ºC)	Salinity
2010	May, 28	FM	00:30	Dry	74.5	0.8	31.0	36.0
2010	Jun, 12	NM	01:26	Wet	366.8	0.7	32.0	36.5
2010	Jun, 16	CQ	01:32	Wet	366.8	0.3	30.6	35.3
2010	Jul, 12	NM	01:26	Wet	148	0.7	29.1	30.8
2010	Jul, 25	CQ	01:24	Wet	148	0.8	30.3	27.9
2010	Aug, 09	LQ	00:35	Wet	256	0.7	31.3	26.1
2010	Aug, 19	CQ	23:35	Wet	256	0.9	30.2	27.4
2011	May, 18	LQ	02:20	Dry	5	0.8	29.4	35.7
2011	Jun, 03	CQ	01:11	Wet	220.4	0.6	29.7	38.4
2011	Jun, 16	FM	03:00	Wet	220.4	0.8	30.5	37.8
2011	Jul, 02	CQ	01:45	Wet	46.4	0.8	29.6	34.4
2011	Jul, 16	LQ	03:10	Wet	46.4	0.9	29.7	31.0
2011	Aug, 09	CQ	23:19	Wet	173	0.3	28.2	-
2011	Aug, 22	LQ	21:00	Wet	173	0.9	34.4	31.0
2011	Sep, 06	CQ	00:17	Wet	240.4	0.8	32.7	29.0
2011	Sep, 27	NM	23:20	Wet	240.4	0.7	29.7	28.5
2012	Apr, 12	LQ	03:29	Dry	121.7	0.4	29.8	35.2
2012	Apr, 26	CQ	02:27	Dry	121.7	0.6	29.9	36.2
2012	May, 09	LQ	00:11	Dry	121.7	0.3	28.9	34.6
2012	May, 23	CQ	23:11	Dry	158.6	0.8	31.4	36.0
2012	Jun, 05	LQ	23:03	Wet	158.6	0.3	30.0	33.5
2012	Jun, 20	CQ	23:13	Wet	192.9	0.2	29.8	33.3
2012	Jul, 03	CQ	23:56	Wet	279.8	0.3	30.2	29.0
2013	May, 14	CQ	00:47	Dry	133.5	0.6	30.6	32.7
2013	May, 28	LQ	00:18	Dry	133.5	0.8	30.6	33.0
2013	Jun, 10	CQ	23:45	Wet	133.5	0.3	30.1	31.1
2013	Jun, 24	LQ	23:15	Wet	263.7	0.8	30.1	34.6
2013	Jul, 29	LQ	03:52	Wet	178.4	0.3	31.1	31.6
2013	Aug, 15	CQ	04:47	Wet	178.4	0.3	30.3	30.8
2013	Aug, 29	LQ	05:05	Wet	229.8	0.5	29.7	31.8
2013	Sep, 30	LQ	20:08	Wet	320.3	1.4	29.4	24.3

PP = precipitation, FM= full moon, NM= new moon, CQ= crescent quarter, LQ= last quarter abundant and less variable than during the day (Matthews 2008). This study specifically focused on the dry (May) and the wet season (June to October), which may introduce some bias due to the exclusion of the 'Nortes' season. However, the probability of implementing successful samplings is low at that time of the year where the meteorological conditions are extreme.

As previously mentioned, working on one of the bases of the bridge facilitated the use of a pulley to lower and retrieve the equipment that allowed us to capture zooplankton. The configuration to collect the organisms consisted in a multiple net system (trapezium-type nets, 50 cm of mouth diameter, 1.5 m in length, and mesh size of 505 µm) at three different depths of the water column, the surface (1.5 m), the mid-layer (4 m) and the bottom (9 m) as described in Flores-Coto & Zavala-García (1994). Calibrated mechanical flow meters (General Oceanics) were placed at the mouth of each net in order to calculate the volume of filtered water. Immediately after collection, the organisms were fixed using 4% formaldehyde solution with added sodium borate as a buffer, and then transferred to 70% ethanol solution for final preservation.

The hydrographic properties of the water column (temperature and salinity) during each sampling expedition were monitored with an YSI-30 multiparameter probe previously calibrated by the manufacturer. Additional conditions, such as the moon phase and precipitation were considered in this study, the last obtained from a local weather station (see details in Table 1).

In order to analyze the surface circulation pattern during the time of each sampling expedition, output data at 2 m depth, with a resolution of 1/12º (9 km), were obtained from the Hybrid Coordinate Ocean Model (HYCOM) for the domain between 18.1-20ºN and 91-92.5ºW.

Laboratory analyses

In the laboratory, the postlarvae individuals of *F. duorarum* and *L. setiferus* were picked from the zooplankton samples, counted and identified using a Leica® stereomicroscope and petri glass dish as base, following standard protocols found in Williams (1959), Cook (1966), and Ringo & Zamora (1968). The separation between the species belonging to the genus *Farfantepenaeus* was made following Ditty & Alvarado-Bremer (2011). The percentages of other shrimp species in the samples were very low, with some postlarvae individuals of *Rimapenaeus similis* (0.1%), *Xiphopenaeus kroyeri* (0.4%) and *Farfantepenaeus aztecus* (1.3 %).

Finally, the number of individuals of *F. duorarum* and *L. setiferus* was standardized to density units (ind 100 m^{-3}) using the readings of the flowmeters and standard protocols (Kramer *et al.* 1972).

Data analyses

In order to evaluate the effects of the physical environment and surface currents on the postlarvae density values of both species, a Canonical Correspondence Analysis (CCA) was applied to the data set. Two matrices were constructed, one with the hydrographic data acquired in each sampling (*e.g*., temperature, salinity), the environmental variables (*e.g.*, sampling time, precipitation), and the speed of the surface current. The second matrix was constructed with the density values of postlarvae for each species and each level of sampling. Both matrices were used to construct the CCA ordering diagram.

The CCA is a multivariate statistical technique widely used in aquatic ecology to determine the response of groups of organisms to different physical/environmental variables. Initially proposed by Ter Braak (1986), this technique is based on displaying the unimodal responses between two sets of matrices, with dependent/independent functions, in a low-dimensional space known as an ordination diagram. This diagram was constructed following the standard routines of Canoco V4.5 software (Petr Šmilauer ©2012-2021).

Results

Hydrographic and environmental conditions

The hydrographic and environmental conditions recorded for each sampling expedition are summarized in Table 1.

The mean values of each variable were obtained in order to visualize the variability for each climatic season considered in this study. Within the wet season, the highest precipitation values (250 mm) were observed in 2010, while the minimum values were observed in 2011 which was considered the driest year during this study (Fig. 2a). The water temperature at the surface showed slight variations throughout the study period, revealing values of around 30 ºC (Fig. 2b). As expected, the surface salinity showed changes according to the climatic season with minimum values (< 30) in the season of highest precipitation, while the salinity increased during the dry season with values of > 33 (Fig. 2c).

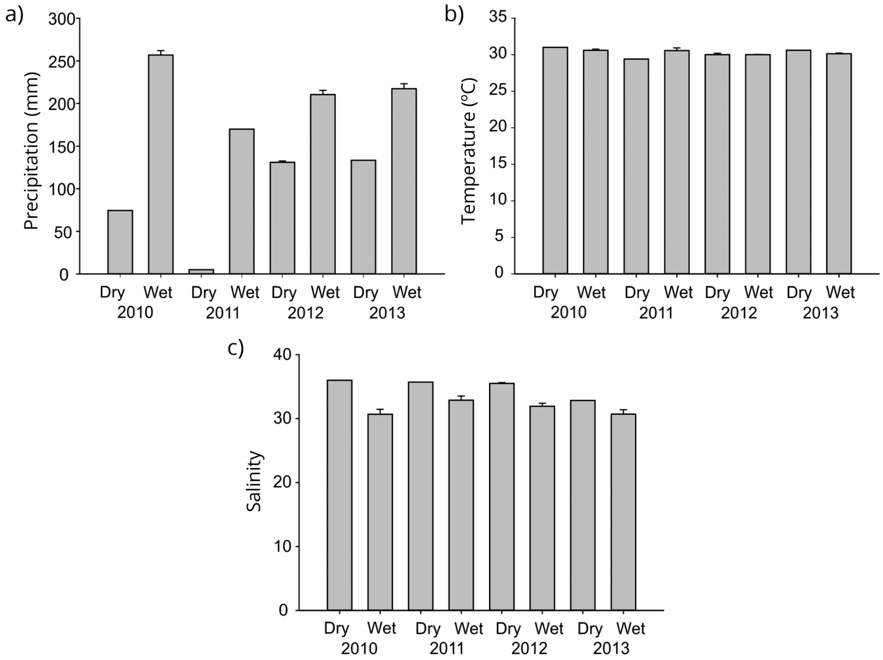

Figure 2. Mean values ± SE by climatic season of a) precipitation (mm), b) water temperature at the surface (ºC), and c) salinity at the surface in a fixed position (18°46'12"N, 91°30'0"W) located at the junction between Terminos Lagoon and the open Gulf of Mexico / Valores promedio ± error estándar para cada época climática de a) precipitación (mm), b) temperatura superficial del agua (ºC), y c) salinidad superficial en un punto fijo (18°46'12"N, 91°30'0"O) localizado en la conexión entre la Laguna de Términos y Golfo de México

The surface circulation for each sampling expedition showed interesting patterns with strong currents (> 0.25 m s^{-1}) in a north-south direction that reached the coast and the interior of the Terminos Lagoon, in particular to the eastern portion. However, it is important to note that the currents that reached the coastline did not always present the same intensity and direction, in some cases intense jets were observed, while in other cases, the currents that reached the coast were weak. Currents in a north-south direction that reached the interior of the lagoon were observed during all the samplings of 2010 (Fig. 3), which was different for 2011 and 2012 (Figs. 4 and 5) when, in some cases, currents were observed in the opposite direction, from the coastal region of the lagoon towards the open gulf. During 2013, the currents observed were similar to those of 2010, in some cases, with high speeds (> 0.25 m s^{-1}) that reached the interior of the lagoon (Fig. 6).

Additionally, mesoscale eddies, particularly anticyclonic, were observed on specific dates, which were associated with strong currents at their periphery. For example, during 2010, anticyclonic eddies with a diameter of ~30 km and speed currents of ~0.25 m s^{-1} at their periphery were observed in the western portion of the domain during the sampling expeditions of May 28, June 28, August 9 and August 19 (Fig. 3). This condition was different for 2011 (Fig. 4), 2012 (Fig. 5), and 2013 (Fig. 6) when the eddies were not of the same intensity. Although they were not as well-defined as in 2010, a weak anticyclonic circulation is suggested, especially in the western portion of the domain.

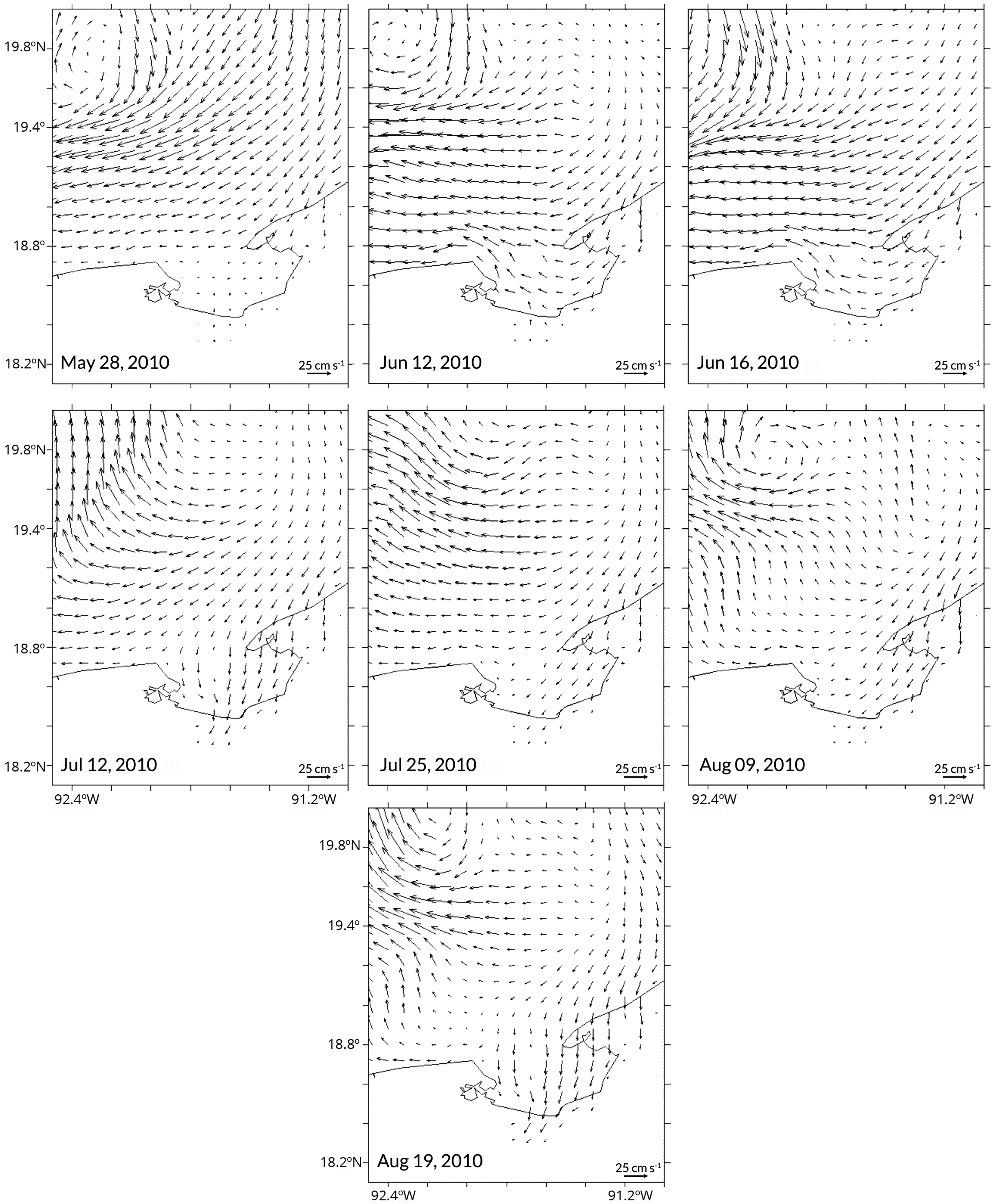

Figure 3. Surface currents (cm s^{-1}, at 2 m depth) obtained during the dates for each sampling expedition of 2010 in the Southern Gulf of Mexico for the domain between 18.1-20ºN and 91-92.5ºW / Corrientes superficiales (cm s^{-1}, a 2 m de profundidad) obtenidas para los días de cada expedición de muestreo del 2010 en el sur del Golfo de México para el dominio 18,1-20ºN and 91-92,5ºO

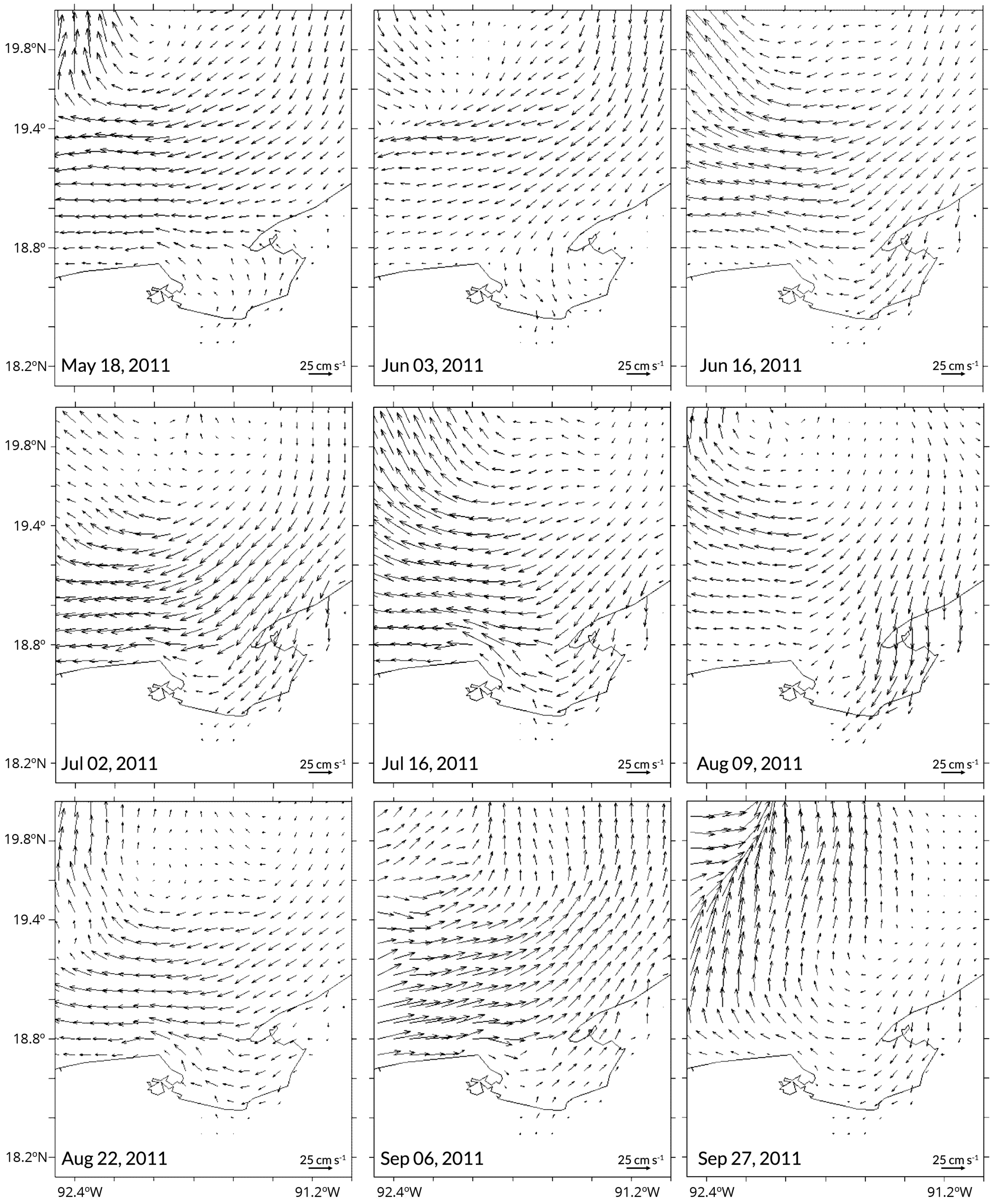

Figure 4. Surface currents (cm s-1, at 2 m depth) obtained during the dates for each sampling expedition of 2011 in the Southern Gulf of Mexico for the domain between 18.1-20ºN and 91-92.5ºW / Corrientes superficiales (cm s-1, a 2 m de profundidad) obtenidas para los días de cada expedición de muestreo del 2011 en el sur del Golfo de México para el dominio 18,1-20ºN and 91-92,5ºO

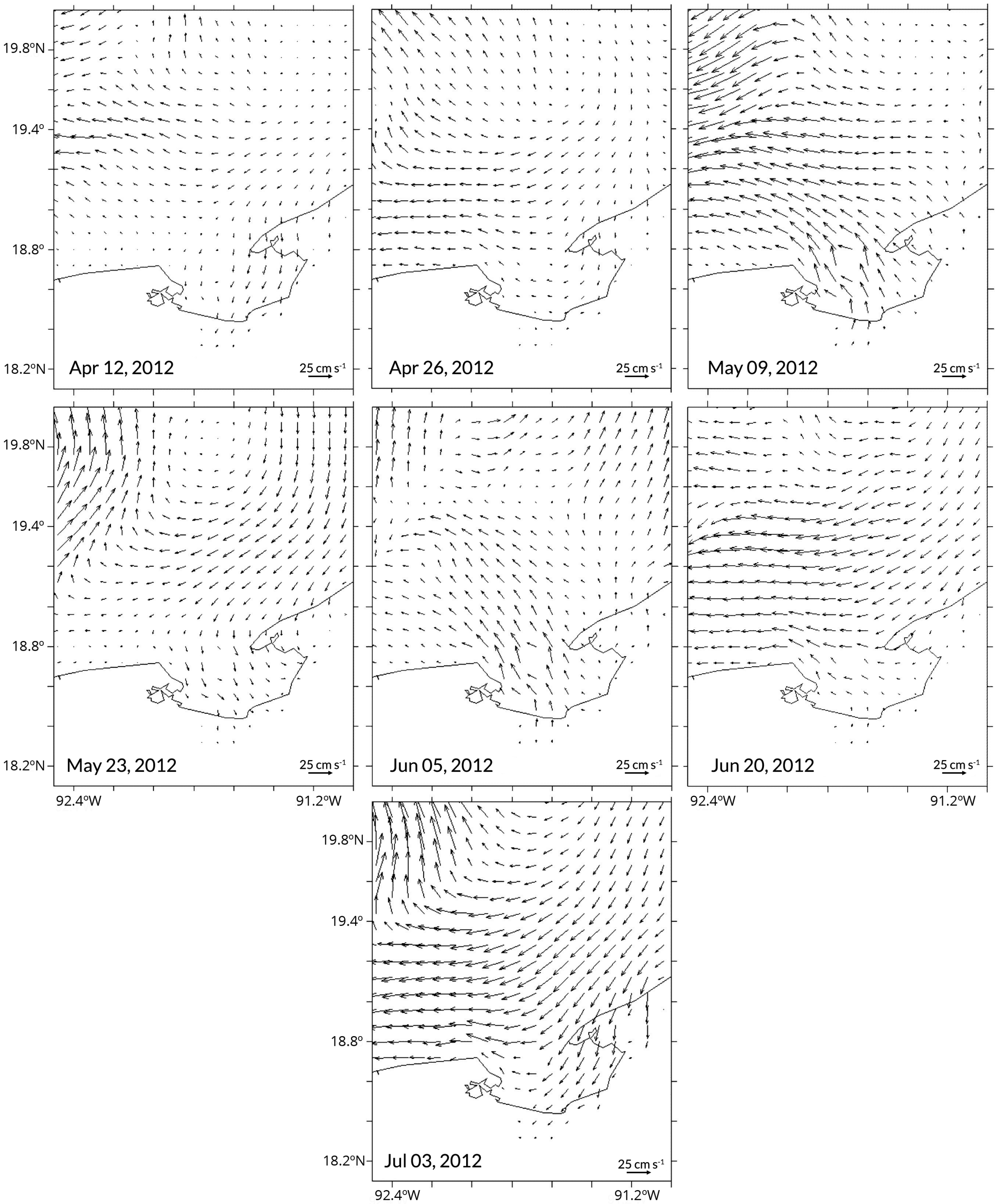

Figure 5. Surface currents (cm s^{-1}, at 2 m depth) obtained during the dates for each sampling expedition of 2012 in the Southern Gulf of Mexico for the domain between 18.1-20ºN and 91-92.5ºW / Corrientes superficiales (cm s^{-1}, a 2 m de profundidad) obtenidas para los días de cada expedición de muestreo del 2012 en el sur del Golfo de México para el dominio 18,1-20ºN and 91-92,5ºO

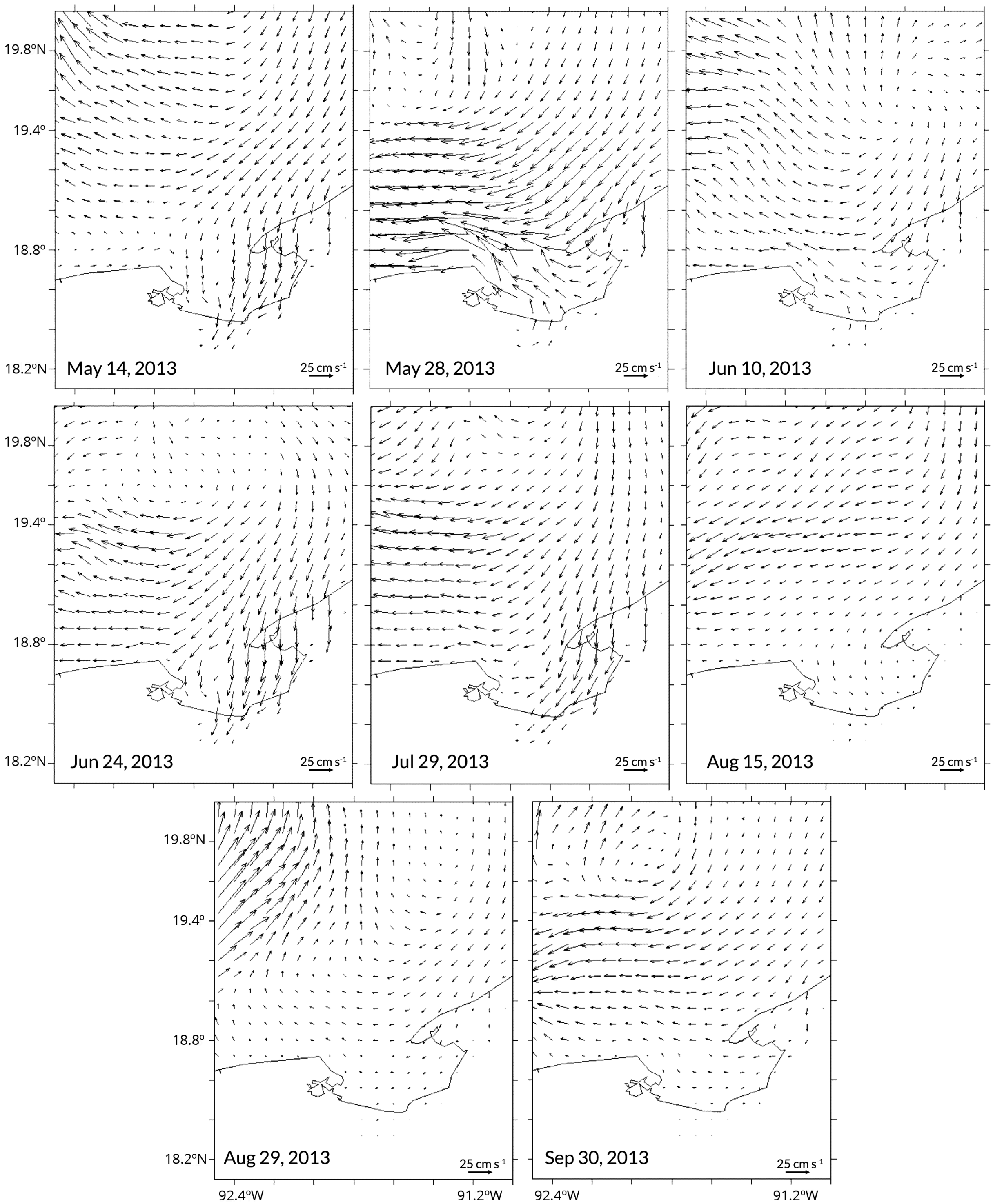

Figure 6. Surface currents (cm s^{-1}, at 2 m depth) obtained during the dates for each sampling expedition of 2013 in the Southern Gulf of Mexico for the domain between 18.1-20ºN and 91-92.5ºW / Corrientes superficiales (cm s^{-1}, a 2 m de profundidad) obtenidas para los días de cada expedición de muestreo del 2013 en el sur del Golfo de México para el dominio 18,1-20ºN and 91-92,5ºO

Density values of *Farfantepenaeus duorarum* and *Litopenaeus setiferus*

The density values obtained for both species at each depth (surface, mid-layer, bottom) and sampling expedition are summarized in Table 2.

The density of both species during the period of this study was observed in high values with an interesting variability according to each depth level, showing marked peaks in specific dates. At the surface, the density values of *L. setiferus* rose into the range from 3 to 11,029 ind 100 m^{-3}, while the density values of *F. duorarum* ranged from 10 to 19,034 ind 100 m^{-3} (Fig. 7A). The mid-layer also showed high density values for both species with *L. setiferus* ranging from 17 to 33,619 ind 100 m^{-3} and *F. duorarum* ranging from 13 to 57,948 ind 100 m^{-3}; the highest density value was observed in August 9th 2011 (Fig. 7B). The density values observed at the bottom showed that *L. setiferus* ranged from 3 to 7,856 ind 100 m^{-3} and *F. duorarum* from 49 to 16,717 ind 100 m^{-3} (Fig. 7C).

In order to better visualize the density values of both species by each climatic season over the four years of this study, mean values were obtained (Fig. 8). The results showed that the maximum density values of both species were observed during the wet season, with the exception of 2012, when the density of both species showed a decrease compared to the other wet season.

Table 2. Density values (ind 100 m^{-3}) of *Litopenaeus setiferus* and *Farfantepenaeus duorarum* were obtained from each sampling expedition at three different depths (surface, mid-layer and bottom) in a fixed position (18°46'12"N, 91°30'0"W) located at the junction between Terminos Lagoon and the open Gulf of Mexico / Densidad (ind 100 m^{-3}) de *Litopenaeus setiferus* and *Farfantepenaeus duorarum* obtenida en cada expedición de muestreo a tres diferentes niveles (superficie, media agua y fondo) en un punto fijo (18°46'12"N, 91°30'0"O) localizado en la conexión entre la Laguna de Términos y Golfo de México

Year	Date	Climatic season	Surface		Mid-layer		Bottom	
			L. setiferus	*F. duorarum*	*L. setiferus*	*F. duorarum*	*L. setiferus*	*F. duorarum*
2010	May, 28	Dry	2388	3133	1556	1301	1222	1091
2010	Jun, 12	Wet	6594	1899	4807	1379	3451	1224
2010	Jun, 16	Wet	9428	4051	8667	2894	5639	1711
2010	Jul, 12	Wet	8189	19034	7648	16054	5772	12336
2010	Jul, 25	Wet	4216	9903	3554	8566	4089	10045
2010	Aug, 09	Wet	5691	2799	9725	9470	3167	1626
2010	Aug, 19	Wet	6921	8711	5735	7508	7531	8535
2011	May, 18	Dry	156	58	167	13	267	148
2011	Jun, 03	Wet	384	31	227	86	308	287
2011	Jun, 16	Wet	11029	7811	8095	2846	3979	1376
2011	Jul, 02	Wet	4479	10769	5038	10583	7688	16717
2011	Jul, 16	Wet	1595	3972	2209	5680	2930	7117
2011	Aug, 09	Wet	2156	4497	33619	57948	1687	3308
2011	Aug, 22	Wet	9242	16278	7048	11610	7856	13250
2011	Sep, 06	Wet	2650	1746	6534	4161	3888	3103
2011	Sep, 27	Wet	484	910	406	773	220	389
2012	Apr, 12	Dry	3	10	17	112	3	90
2012	Apr, 26	Dry	229	822	129	736	423	1412
2012	May, 09	Dry	516	798	1039	624	864	833
2012	May, 23	Dry	33	69	58	71	125	120
2012	Jun, 05	Wet	1234	1792	-	-	391	399
2012	Jun, 20	Wet	3352	1567	1069	366	644	632
2012	Jul, 03	Wet	568	3151	157	842	84	510
2013	May, 14	Dry	235	470	48	136	21	49
2013	May, 28	Dry	3147	3516	3344	4114	1359	2882
2013	Jun, 10	Wet	468	1061	547	890	433	566
2013	Jun, 24	Wet	1178	780	577	938	542	696
2013	Jul, 29	Wet	2729	1280	2220	1466	1478	809
2013	Aug, 15	Wet	4071	1625	2558	1334	1819	512
2013	Aug, 29	Wet	2847	6278	3111	22253	2680	1279
2013	Sep, 30	Wet	355	254	227	678	401	241

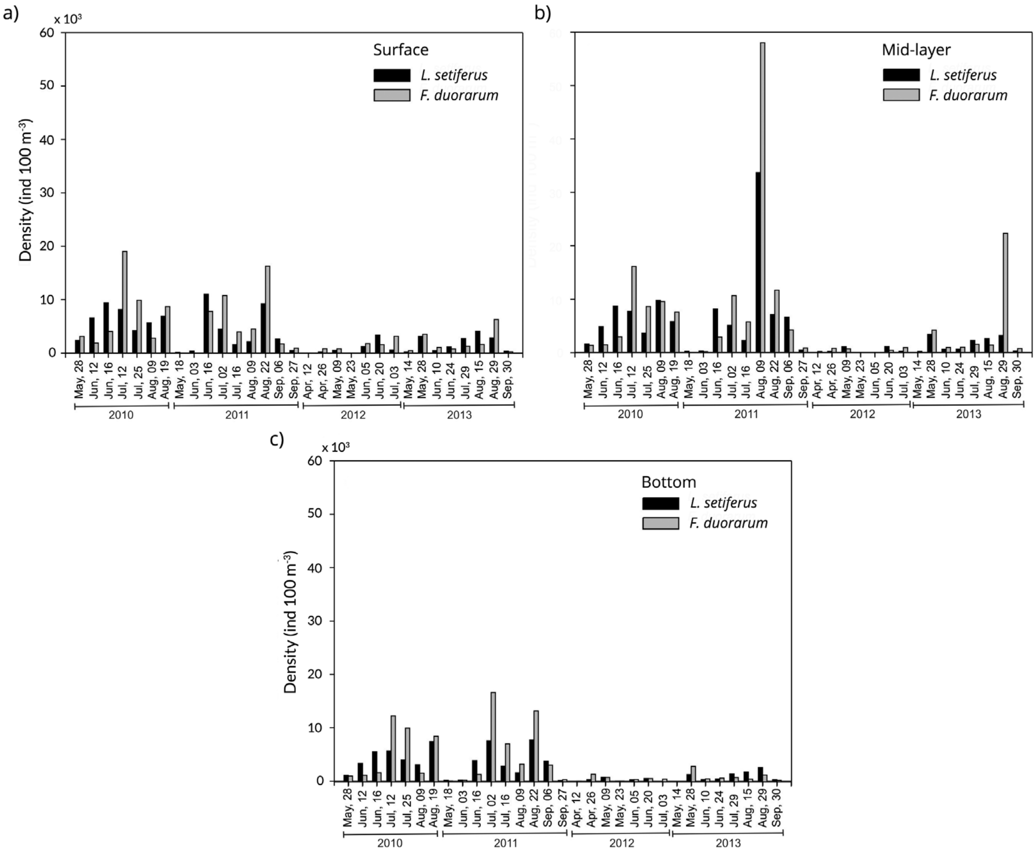

Figure 7. Density values (ind 100 m^{-3}) of *Litopenaeus setiferus* and *Farfantepenaeus duorarum* obtained at each sampling expedition at three different depths: a) surface, b) mid-layer, and c) bottom in a fixed position (18°46'12"N, 91°30'0"W) located at the junction between Terminos Lagoon and the open Gulf of Mexico / Densidad (ind 100 m^{-3}) de *Litopenaeus setiferus* y *Farfantepenaeus duorarum* obtenida de cada expedición de muestreo en tres diferentes profundidades: a) superficie, b) capa media y c) fondo en un punto fijo (18°46'12"N, 91°30'0"O) localizado en la conexión entre la Laguna de Términos y Golfo de México

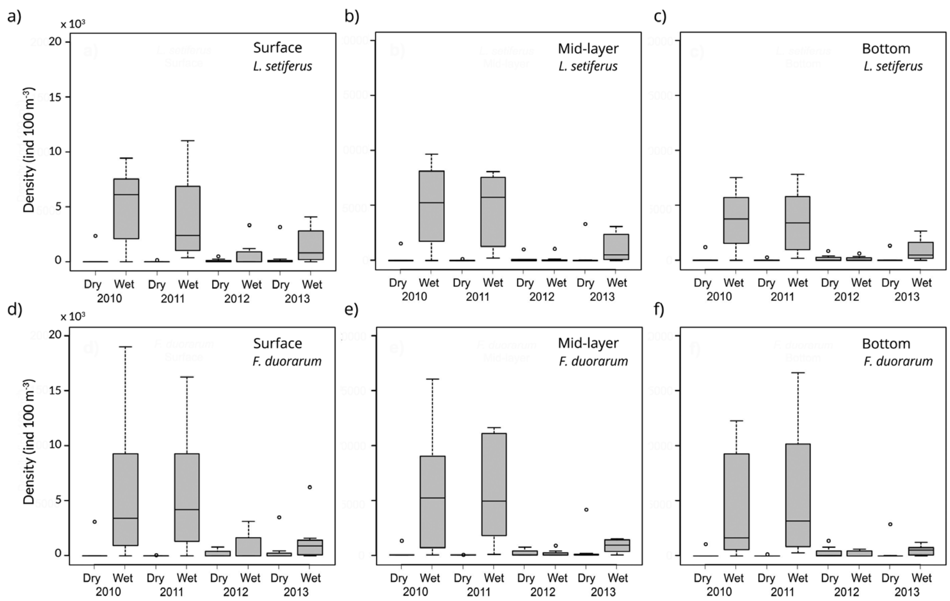

Figure 8. Mean density values (ind 100 m^{-3}) for each climatic season and depth level for: *Litopenaeus setiferus* at the surface (a), mid-layer (b), and bottom (c); *Farfantepenaeus duorarum* at the surface (d), mid-layer (e), and bottom (f); in a fixed position (18°46'12"N, 91°30'0"W) located at the junction between Terminos Lagoon and the open Gulf of Mexico / Valores de densidad promedio (ind 100 m^{-3}) para cada época climática y profundidad de muestreo para: *Litopenaeus setiferus* en superficie (a), capa media (b) y fondo (c); *Farfantepenaeus duorarum* en superficie (d), capa media (e), y fondo (f); en un punto fijo (18°46'12"N, 91°30'0"O) localizado en la conexión entre la Laguna de Términos y Golfo de México

The CCA ordering diagram generated from environmental data set and densities of both species for each sampling depth showed that 80% of the variance was explained by the first two axes. Interestingly, the species in this study showed dependence with environmental variables according to the depth level at which they were sampled. For example, the density of *L. setiferus* both at the surface and the bottom showed a dependence with the temperature values, while the density of *F. duorarum* in the bottom showed a dependence with the speed of the currents. Salinity apparently also influenced the density of *L. setiferus* at the bottom, while precipitation showed a relationship with the density of *L. setiferus* at the surface (Fig. 9).

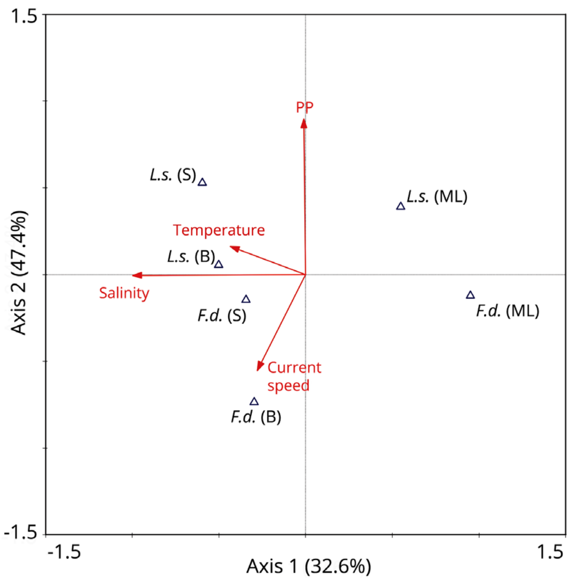

Figure 9. CCA biplot with the density of *Litopenaeus setiferus* (*L.s.*) and *Farfantepenaeus duorarum* (*F.d.*) for each depth in relation to the environmental variables were recorded. (S)= surface, (ML)= mid-layer, (B)= bottom, PP= precipitation / Diagrama CCA que muestra la densidad de *Litopenaeus setiferus* (*L.s.*) y *Farfantepenaeus duorarum* (*F.d.*) para cada profundidad en relación con las variables ambientales registradas. (S)= superficie, (ML)= capa media, (B)= fondo, PP= precipitación

Discussion

The use of a long-term monitoring allowed us to identify a marked seasonal variability in the density values of the pink and white shrimp postlarvae at the junction between Terminos Lagoon and the open Gulf of Mexico in relation to changes in some environmental variables, agreeing with previous reports in coastal environments inside the Gulf of Mexico, including Mecoacan (Torres *et al.* 2020), Carmen-Pajonal-Machona (Flores-Coto *et al.* 2010) and Celestun (Pérez-Castañeda & Defeo 2001). All of these works showed a clear dependence between the density of shrimps and the environmental factors (mainly temperature, salinity and dissolved oxygen); however, they did not consider hydrodynamic aspects, particularly the role played by surface currents in the advection of organisms.

The Gulf of Mexico is one of the most dynamic marginal seas in the world, due to the incursion of the Loop current, an intense jet of warm and hyaline water that enters the gulf from the Caribbean Sea throughout the Yucatan channel in the east portion of the Yucatan Peninsula (Athié *et al.* 2015). The current that is directed towards the interior of this system induces the formation of mesoscale eddies that move to the west, supplying bio-essential elements to the primary producers (Durán-Campos *et al.* 2017), which, in turn, exerts an important influence on the secondary producers. These eddies reach the southern portion of the gulf, in the Bay of Campeche, where they exert a marked influence on the circulation of the region.

Over the last decade, intense research has been done in this region in order to determine the main physical processes that govern these circulations with much focus on the wind and topography (Díaz-Flores *et al*. 2017). This circulation affects planktonic organisms and is known to exert a notable influence on the supply of nutrients to the euphotic zone, which impacts the phytoplankton (Durán-Campos *et al.* 2017) and zooplankton populations.

The output data of the numerical model used in this study reproduced well the conditions of the surface circulation into the SoGM, showing the presence of mesoscale eddies (mainly anticyclonic) and strong currents associated with it which reached the coastline and the interior of the lagoon, which could explain the density values of both species. For example, the maximum peaks in the density of both species observed on June 12th 2010, August 9th 2011, and August 22nd 2011 coincided with a time when strong currents were observed that reached the interior of the lagoon (Figs. 3b and 4f-g). Additionally, the anticyclonic eddies observed could explain the retention of larvae and their subsequent advection from the portion of the Yucatan Peninsula towards the lagoon. These particular mechanisms have been recently named as eddy trapping and stirring, which refers to the retention and transport of planktonic organisms and their grazers through different ocean regions (Della-Penna & Gaube 2019).

To date, it is known that during the planktonic stage the postlarvae mainly depend on the currents to move between environments and ensure their entry to the nursery areas. In this sense, it has been noted that the coastal currents directly affect the distribution of the organisms, approaching them from ocean regions towards the coast where they accumulate and then be transported to the interior of the lagoons and estuaries (Gómez-Ponce *et al*. 2018). Other works in which similar transport and retention mechanism have been reported in the Gulf of Mexico including the pink shrimp and the spine lobster. For example, Criales & Lee (1995) documented that postlarvae of the pink shrimp at the Dry Tortugas and Lower Florida Keys (USA) are subject to the hydrodynamic of the region, where the presence of an eddy combined with wind driven transport on the southeast Florida shelf is the most reasonable recruitment pathway for pink shrimp to the nursery grounds of Florida Bay. Later, Criales *et al*. (2003) reported a clear seasonal variability of the pink shrimp postlarvae in the region that connect the Atlantic Ocean with Florida Bay (USA), strong related with the presence of a cyclonic eddy that induce a coastal countercurrent flow that favors onshore larval transport. A similar mechanism has been reported for the postlarvae of the spiny lobster (*Panulirus argus*) in Florida Bay, where the presence of a mesoscale cyclonic eddy facilitates onshore larval transport over a scale of several tens of kilometers (Yeung *et al.* 2001).

The high-density values observed for both species, particularly at the surface and the mid-layer, considering that during the entry of the postlarvae to the interior of lagoons, the organisms realize vertical migrations, which in turn are synchronized with currents, then maximize them transport and then ensure the entry into the lagoon. This particular mechanism has been described as selective tidal transport (Shanks 1995, Forward *et al*. 2001, Queiroga *et al*. 2006), and has been reported for different species, including the American eel (McCleave & Kleckner 1982), the red drum (Holt *et al.* 1989), and the rock eye salmon (Levy & Cadenhead 1995), among others.

Vertical migration is a pivotal mechanism as a response to environmental factors such as light and pressure (Sulkin 1984). However, salinity, turbulence, and temperature also affect not only the migration behavior along the water column (Welch & Forward 2001) but also the growth, survival and biomass productivity of postlarvae of penaeid shrimps (Zink *et al*. 2013). In this study, the maximum density values of both species were related to temperatures within the range between 28.3 ºC and 28.7 ºC, which coincides with previous reports in the Terminos lagoon. For example, Arenas-Mendieta & Yáñez-Martínez (1981) showed that maximum density values of shrimp postlarvae in the lagoon occurred when temperature rose at the range of 26.8 ºC to 28.7 ºC. Alarcón-Daows (1986) also noticed a bimodal temperature distribution in relation to the density of post larvae, with the first peak between 26-27 ºC and a second peak at 29 ºC. In other domains, such as the Ossabaw Sound System Lagoon (Atlantic coast of USA), Wenner *et al.* (2005) reported that a key factor determining the transport of *L. setiferus* postlarvae to the interior of that system is the temperature, with a critical minimum value of 27 ºC. High temperature values (> 27 ºC) have also been associated with spawning periods (Flores-Coto *et al.* 2010).

As mentioned above, the highest density values of the postlarvae for both species were observed in relation to the wet season, as well. Despite the fact that the white and pink shrimp reproduction remains constant throughout the year, there have been reported peaks in their activity. Based on a study of gonadal maturity, Regis (1996) observed that the reproduction of *L. setiferus* occurs in two peaks, one in April-May, and other in August, which corresponds to the wet season. The last could explain the high-density values of both species observed during the wet seasons, which can also be explained due to the fact that during the rainy season there is an increase in the contribution of organic matter from the rivers to the interior of the lagoon, which ensures the availability of food and favors the survival of the postlarvae.

In conclusion, to date it is relatively well known that the environmental variables exert a notable influence on the seasonal and interannual variability of all species that inhabit coastal and oceanic environments. In the case of the pink and white shrimps, it is known that temperature and salinity represent one of the most important variables; also, it is known that surface currents can transport organisms from oceanic areas to the interior of coastal lagoons (and *vice versa*) particularly those organisms in larval stages. For the coastal environments of the SGoM, in particular the Terminos Lagoon, one of the largest coastal waterbodies in the Mexican territory, information on the role played by some environmental variables and the surface circulation pattern in the variability of pink and white shrimp postlarvae it is still scarce. The results presented in our study suggested that there is a clear dependence between the density values of both species postlarvae with the environmental factors and the surface circulation patterns because of the advection of the organisms between the open waters of the Gulf of Mexico towards the interior of the lagoon. Currently, there is a need to continue generating knowledge about the dynamics in the SGoM and the role that the hydrographic parameters and the surface currents exert on the organisms.

The results presented in this study contribute to the goal of furthering our knowledge on the ecology of the pink and white shrimps and highlight: 1) the need to implement long-term monitoring programs covering different climatic seasons in order to identify possible seasonal and interannual changes in the population density of both species, and 2) the need to develop multidisciplinary research that uses different methodological approaches in order to achieve a better interpretation of ecological behavior in systems recognized for being highly dynamic, such as the Terminos Lagoon. These would benefit from the implementation of better management strategies for the rational use of marine resources and achieve food security from a sustainable point of view and contribute to local economies. Besides, the increasing deterioration of coastal environments due to anthropogenic impact raises the need to establish baseline conditions, which become essential in any marine ecosystem.

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