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Dispersal patterns of shrimp larvae and postlarvae of the genus *Solenocera*

Patrones de dispersión de larvas y postlarvas de camarón del género *Solenocera*

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Resumen.- Se analiza la abundancia y los procesos de dispersión de los primeros estadios larvales y postlarvales de *Solenocera* spp. (Burkenroad, 1939). Los datos obtenidos se basaron en tres campañas oceanográficas realizadas en el sur de la bahía de Campeche, México, durante el verano y otoño de 1993 y primavera de 1994. El verano fue el período de mayor abundancia con una densidad larvaria promedio de protozoeas, mysis y postlarvas correspondientes a 19,8; 22,1 y 1,9 organismos 100 m^{-3}, respectivamente. Las larvas presentaron, en general, un típico patrón diario de migración. Ellas se desplazaron de zonas de mayor profundidad hacia la superficie en la noche, mientras que durante el día éstas tendieron a dirigirse hacia las profundidades. Las protozoeas se distribuyeron con mayor frecuencia en los niveles superficiales mientras que las mysis y postlarvas fueron capturadas en mayor número en los niveles más profundos. En general, las protozoeas y mysis se distribuyeron en profundidades sobre la termoclina, haloclina y picnoclina. La disponibilidad de alimento parece ser el principal factor para determinar la distribución vertical de *Solenocera* spp.

Palabras clave: Crustacea, plancton, distribución, abundancia estacional, migración vertical

Abstract.- The abundance and the dispersal processes during the larval and postlarval stages of *Solenocera* spp. (Burkenroad, 1939) is analyzed. Data were collected in three oceanographic cruises performed in the south of the Campeche Bay, Mexico, during summer and autumn 1993 and spring 1994. Summer was the period with the highest abundance with an average larval density of protozoea, mysis, and postlarvae of 19.8, 22.1, and 1.9 organisms per 100 m^3 respectively. In general, larvae presented a typical daily migration pattern. They moved from deep areas to the surface at night, whereas during the day they tended to move downwards. Protozoeae were most frequently distributed at the surface levels, whereas mysis were rather caught at deeper levels. In general, protozoea and mysis were distributed at depths above the thermocline, halocline and pycnocline. Food availability seems to be the most important factor determining *Solenocera* spp. vertical distribution.

Keywords: Crustacea, plankton, distribution, seasonal abundance, vertical migration

Introduction

The adequate management of a fishery resource requires knowledge on the life cycle of the species; therefore plankton studies provide valuable information on the distribution, abundance, and mortality of the larvae and postlarval stages of the corresponding species. In fact, an adequate fishery management depends on the correct estimation of populations' abundance and knowledge about the recruitment process, as evidenced strongly by the studies on eggs and larvae of fish and crustaceans (Flores Coto *et al*. 1988).

Shrimps, which are one of the most important fishery resource from Mexico, are comprised of species whose commercial value varies according to their size and catch, such as *Litopenaeus setiferus* (Linnaeus, 1767), *Farfantepenaeus aztecus* Ives, 1891, and *Farfantepenaeus duorarum* Burkenroad, 1939, in the Gulf of Mexico. During trawl operations, other small-sized species of lesser value are caught which are not so important in terms of relative abundance. However, these species among which are those of the genus *Solenocera* represent a relevant part of the food web in the marine ecosystem and are a relatively abundant component in the plankton community. In the south of

the Gulf of Mexico, three species of the genus *Solenocera* have been reported (*Solenocera vioscai* Burkenroad, 1934; *Solenocera necopina* Burkenroad, 1939 and *Solenocera atlantidis* Burkenroad, 1939). *Solenocera vioscai* is the most abundant and represents more than 98% of *Solenocera* genus (Vázquez-Bader & Gracia 1994), so it could be expected that a large proportion of the larvae belongs to this species. The goal of this study is to analyze the planktonic dispersal mechanisms of the *Solenocera* genus and to determine the temporal variations in the distribution and abundance during the first life stages of these organisms, associated with local current patterns, temperature, salinity, and photo period.

Material and methods

The present study was part of the MOPEED project (Monitoring of pre-recruits of estuarine-dependent species, benthic communities, and internal tides in the south of the Gulf of Mexico) from the Instituto de Ciencias del Mar y Limnología, UNAM, and included samples from three oceanographic cruises carried out on board the R/V "Justo Sierra", during three seasons: summer (August 13-22, 1993) and autumn (November 4-14, 1993), and spring (May 22-30, 1994).

The study area is located in the southern portion of the Gulf of Mexico between 18° and 20°N; 91° and 94°W, and comprises parts of the states of Tabasco and Campeche continental shelf (from the Machona Lagoon to the most eastern portion of the Términos Lagoon (Fig. 1).

The sampling grid included four perpendicular transects to the coast located near the main delta systems of the study area, i.e., from the Machona Lagoon in the state of Tabasco to the Términos Lagoon in the state of Campeche, sampling in waters 10 to 200 m depth over the continental shelf (Fig. 1). Zooplankton hauls were performed with opening-closing nets (General Oceanics, model 5100) of 0.75 m opening diameter and 500 μm mesh size provided with torpedo-type digital flow meters to estimate the filtered water volume. Sampling depth varied from 2 to 100 m, with 15 min duration for each cast. The ship towing velocity was 2 to 3 knots during sampling.

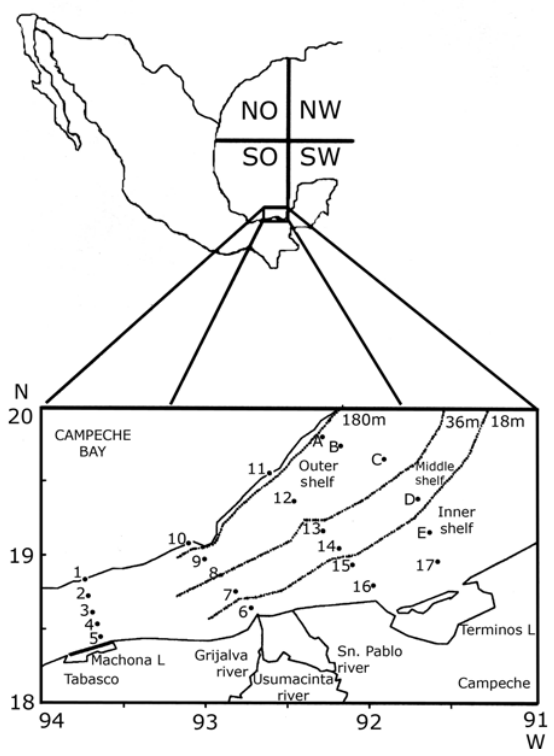

Figure 1

Study area and zooplankton sampling locations in the southwestern Gulf of Mexico

Área de estudio y estaciones de muestreo de zooplancton en el suroeste del Golfo de México

The number of nets (2-5) used in each zooplankton cast varied as a function of the sampling location depths (2, 10, 20, 45 and 100 m) and, in some occasions, this procedure was performed in two stages. Onboard the sample was preserved in 4% formaldehyde neutralized with borated sodium. Once in the laboratory, samples were placed in 70% alcohol. From the total of samples, larvae of the Solenoceridae family were separated and identified according to the keys reported by Cook (1966) and Subrahmanyam (1971).

The zooplankton abundance of each oceanographic cruise was standardized to the number of *Solenocera* spp. larvae 100 m^{-3}, according to the equation of Smith & Richardson (1977).

In order to analyze the vertical migration of the larvae throughout the water column, the day samples were divided in four groups related with the light intensity. It was though considered that dusk and dawn could be critical for vertical migration pattern, so they were included in the analysis in spite of the lesser duration compared to day and night. Light-intensity groups were done according to the seasonal and latitudinal registers of the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/RS): Spring 1994, Day (06:01-18:39 h), Dusk (18:40-19:10 h), Night (19:11-05:29 h) and Dawn (05:30-06:00 h); Summer 1993, Day (06:21-18:33 h), Dusk (18:34-19:14 h), Night (19:15-05:49 h) and Dawn (05:50-06:20 h); Autumn 1993, Day (06:43-17:30 h), Dusk (17:31-18:01 h), Night (18:02-06:11 h) and Dawn (06:12-06:42 h).

Analyses of variance were performed to analyze significant differences among larval densities during the three sampled periods at different depths and day periods.

Results

Solenocera spp. seasonal abundance

During the three oceanographic cruises, a total of 3,102 *Solenocera* specimens were caught, corresponding to three planktonic stages (protozoea, mysis, and postlarvae) (Table 1).

The summer 1993 was the period with the highest abundance: 1689 specimens (771 protozoea, 860 mysis, and 58 postlarvae). During the autumn 1993, the total catch was 1044 specimens (568 protozoea, 465 mysis, and 11 postlarvae), whereas spring 1994 was the period of lowest catches, with 369 specimens (250 protozoea, 86 mysis, and 33 postlarvae).

The analysis of variance among seasons (spring, summer, autumn), period of the day (day, dusk, night, and dawn), and depth of sampling (2, 10, 20, 45, and 100 m) yielded significant differences among larval densities during the three sampled periods at different depths and during the different periods of the day (different depths $F_{(5,15)} = 10.49$; $P = 0.001$; period of the day $F_{(4,12)} = 3.43$, $P = 0.005$; and season, $F_{(3,9)} = 6.44$, $P = 0.003$)

Vertical distribution of *Solenocera* spp.

Spring 1994.- Protozoea larvae were found along the transects located in front of the Machona Lagoon, El Carmen Inlet, and Puerto Real, distributed at all depths sampled. The largest concentrations were found between 2 and 10 m depth, mainly at transect located in front of the Machona Lagoon (61 to 80 larvae 100 m^{-3}) in the state of Tabasco, near the coastline (Fig. 2A). Mysis were found at all transects at depths ranging from 2 to 100 m. The recorded density was similar at the different sampling depths (1 to 20 larvae 100 m^{-3}) (Fig. 2B). The postlarvae distribution was similar to protozoea and mysis stages, and they were also located at depths of 2 to 100 m, with a density of 1 to 20 larvae 100 m^{-3} (Fig. 2C). Nonetheless, postlarvae showed a general distribution pattern with protozoea and mysis near surface and postlarvae in deeper waters.

Summer 1993.- Protozoea larvae were recorded in most of the study area, mainly at transects located off Machona Lagoon and El Carmen inlet. The highest protozoea density was found at depths between 2 and 10 m in front of the El Carmen inlet, with values of 40 and more than 80 larvae 100 m^{-3}. During this season, protozoea larvae were also caught once at depths over 100 m off the Grijalva-Usumacinta River; however, their abundance was low (1-20 100 m^{-3}) (Fig. 3A).

Table 1

Total number of *Solenocera* larvae and postlarvae caught in the different seasons sampled

Número total de larvas y postlarvas de *Solenocera* capturadas en las diferentes temporadas de muestreo

Season	Protozoea	Mysis	Postlarvae	Total
Spring	250	86	33	369
Summer	771	860	58	1689
Autumn	568	465	11	1044
Total	1589	1411	102	3102

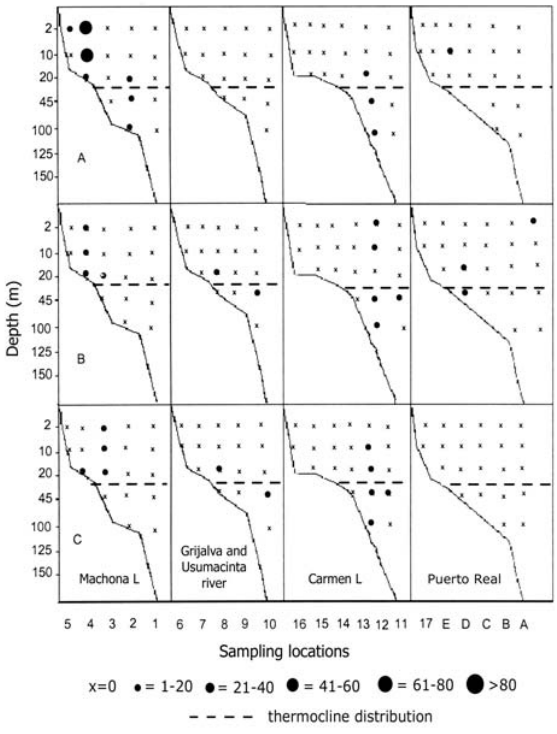

Figure 2

***Solenocera* larval and postlarval abundance (N° 100 m^{-3}) in the different transects and depth levels. Spring 1994. A) protozoea, B) mysis and C) postlarvae**

Abundancia de larvas y postlarvas de *Solenocera* (N° 100 m^{-3}) en diferentes niveles de profundidad y transectos. Primavera de 1994. A) protozoea, B) mysis y C) postlarvas

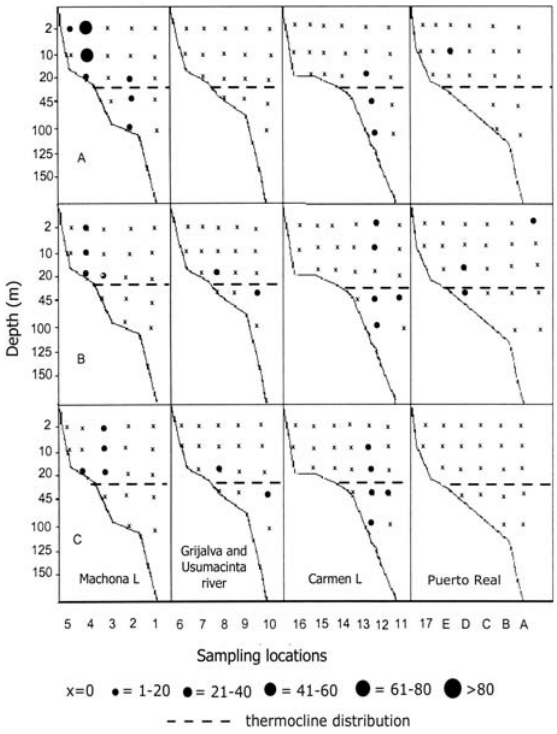

Figure 3

***Solenocera* larval and postlarval abundance (N° 100 m^{-3}) in the different transects and depth levels. Summer 1993. A) protozoea, B) mysis and C) postlarvae**

Abundancia de larvas y postlarvas de *Solenocera* (N° 100 m^{-3}) en diferente niveles de profundidad y transectos. Verano de 1993. A) protozoea, B) mysis y C) postlarvas

The mysis stage depicted a similar distribution pattern that varied from 2 to 100 m, with zones of larger abundance off El Carmen at 10 m depth, recording more than 70 larvae 100 m^{-3} and in front of the Machona Lagoon with 40 to 60 larvae 100 m^{-3} (Fig. 3B). Postlarvae depicted a low density during the summer (1 to 20 larvae 100 m^{-3}), and were distributed from 2 to 100 m depth (Fig. 3C).

Autumn 1993.- Protozoeae were more abundant off the Machona Lagoon and El Carmen. The highest abundances were located between 2 and 45 m depth. A site with more than 80 larvae 100 m^{-3} was recorded at 45 m depth in front of the El Carmen inlet, precisely, and another one of 21 to 40 larvae 100 m^{-3} at 2 m depth in front of the Machona Lagoon (Fig. 4A). The largest mysis abundance was located off the Machona Lagoon at 2 m depth, with values of 61 to 80 larvae 100 m^{-3} and in front of the Términos Lagoon at 20 and 45 m depth with 41 to 60 larvae 100 m^{-3} (Fig. 4B). Postlarvae were only observed off Machona Lagoon and Grijalva Usumacinta River with low abundance (Fig. 4C). In general, protozoea and mysis stages were distributed above the thermocline, halocline, and pycnocline. Only in three stations, during the three analyzed oceanographic cruises, the larvae were found distributed below these regions. However, the abundance in these stations was very low (1 to 20 larvae 100 m^{-3}).

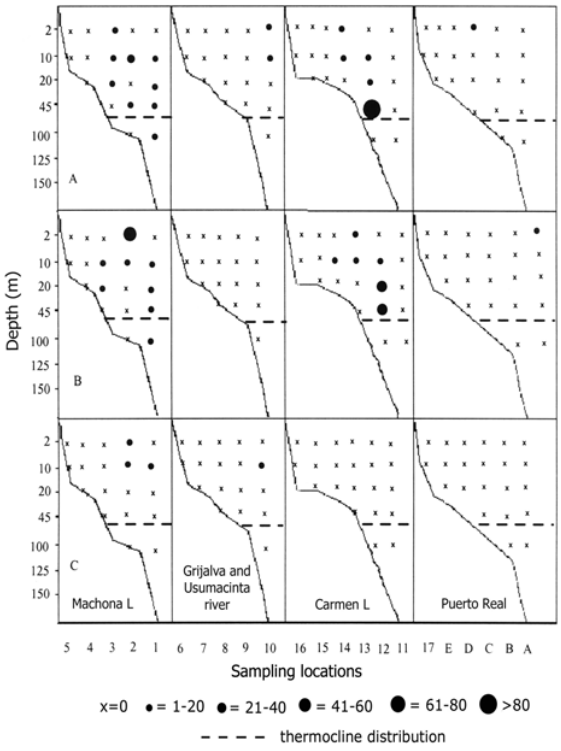

Figure 4

***Solenocera* larval and postlarval abundance (N° 100 m^{-3}) in the different transects and depth levels. Autumn 1993. A) protozoea, B) mysis and C) postlarvae**

Abundancia de larvas y postlarvas de *Solenocera* (N° 100 m^{-3}) en diferente niveles de profundidad y transectos. Otoño de 1993. A) protozoea, B) mysis y C) postlarvas

Postlarvae also seemed to show this behavior but their abundance during the three oceanographic cruises was always very low; thus, they were not representative to conclude something about the vertical distribution of this life stage (Table 2).

During the spring 1994, protozoea were caught only during night, and the greatest abundance was recorded at 10 m depth. Mysis were caught during the day, with the greatest abundance at 20 m, and during the night at 100 m. Postlarvae were collected only during the dark period, with the greatest catching percentage at 100 m depth (Figs. 5A, B and C).

During the summer 1993, protozoea showed a very well defined vertical pattern. In general, they were found at 20 m depth during the day and at 2 m depth during the night, and descended to 10 m at dawn. Mysis depicted a very similar pattern to that of protozoea, whereas postlarvae were mainly found at 20 m depth during the day and at 10 m depth at the dark hours (Fig. 6A, B and C).

Solenocera larval behavior in the autumn was opposed to that observed during the spring and summer. During autumn, larvae did not show a clear vertical migration pattern. The larval distribution in the water column was very irregular during the different periods of the day (Fig. 7A, B and C). Protozoea were collected during this season with the largest abundance at 2 and 45 m depth; at dusk at 45 m, and during the night at 20 m (Fig. 7A). Mysis were most abundant at 2 m during the day, at 20 m at dusk, and between 10 and 20 m depth during the night. Postlarvae presented their highest abundance during the day at 10 m, and during dusk at 20 m depth (Fig. 7B and C).

Table 2

Statistical analysis of *Solenocera* spp. developmental stages density in relation to the distribution of the thermocline

Análisis estadístico de la densidad de los estadios del desarrollo de *Solenocera* spp. en relación con la distribución de la termoclina

Stage	t observed	t from tables	*P* value
Protozoea	2.40	1.89	$0.025 < P < 0.01$
Mysis	1.92	1.86	$0.05 < P < 0.025$
Postlarva	1.54	1.89	$P < 0.05$

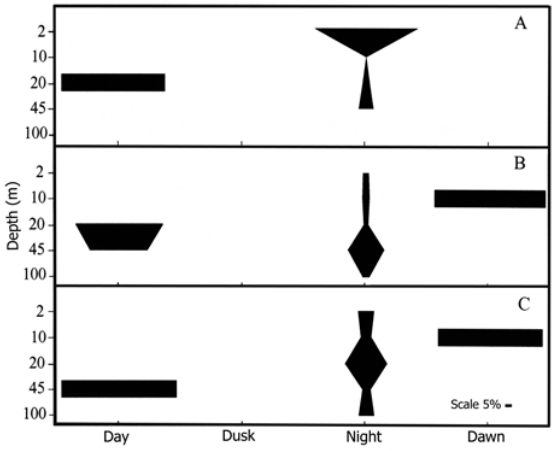

Figure 5

Vertical distribution patterns of *Solenocera* at different light-intensity periods during spring 1994. A) protozoea, B) mysis and C) postlarvae. (scale 5 mm = 5 %)

Patrones de distribución vertical en diferentes periodos de intensidades de luz durante la primavera de 1994. A) protozoea, B) mysis y C) postlarvae. (escala 5 mm = 5 %)

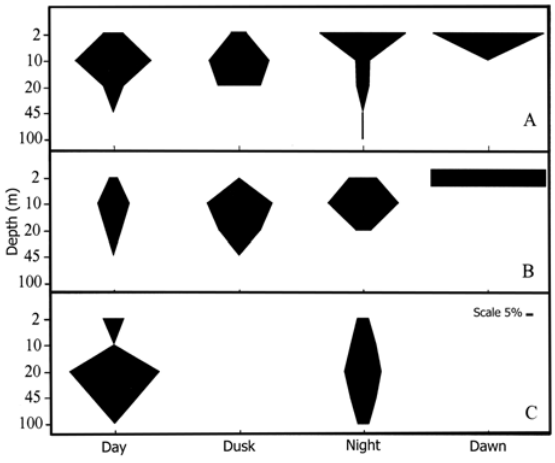

Figure 6

Vertical distribution patterns of *Solenocera* at different light-intensity periods during summer 1993. A) protozoea, B) mysis and C) postlarvae. (scale 5 mm = 5 %)

Patrones de distribución vertical en diferentes periodos de intensidades de luz durante el verano de 1993. A) protozoea, B) mysis y C) postlarvae. (escala 5 mm = 5 %)

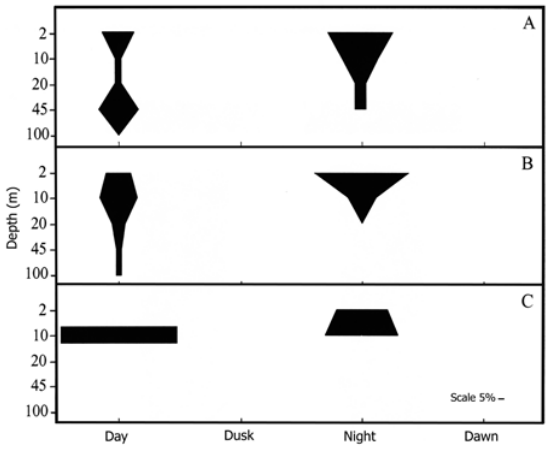

Figure 7

Vertical distribution patterns of *Solenocera* at different light-intensity periods during autumn 1993. A) protozoea, B) mysis and C) postlarvae. (scale 5 mm = 5 %)

Patrones de distribución vertical en diferentes periodos de intensidades de luz durante el otoño de 1993. A) protozoea, B) mysis y C) postlarvae. (escala 5 mm = 5 %)

Discussion

The main concentration of protozoea during the spring was found in front of the Tabasco shelf, near the coast line of the Machona Lagoon between 2 and 10 m depth (Fig. 2A). These larvae probably were hatched from small spawning populations distributed in front of the Machona Lagoon (Vázquez-Bader 1988). On the other hand, mysis and postlarval stages were found distributed with low abundances in a large portion of the area from 2 to 100 m depth. Older larval stages have potential for greater vertical migrations and longer exposure to the currents. Due to the greater movement of these stages as compared to protozoea (Jones *et al.* 1970), they are widespread in the study area. Mysis dispersal could be increased by current advection during vertical migration.

Protozoeae were distributed throughout the water column with a general tendency to find the highest concentrations near surface levels. Early larvae were also found near the bottom where they hatched from demersal eggs and then had a vertical migration. The larger abundance of protozoea and mysis in front of

Términos Lagoon during summer and autumn agrees with the idea of a circular larval movement pattern for retention and recruitment to adult *Solenocera* population proposed by Gómez-Ponce & Gracia (2003). The largest proportion of females in this area had been recorded during summer (Vázquez-Bader & Gracia 1994, Gómez-Ponce & Gracia 2003), which coincides with high abundance of first larval stages of *Solenocera*. On the other hand, during summer, an increase in phytoplankton abundance occurs (up to 6.3 millions of cells L^{-1} (Licea & Luna 1999). The vertical variation of phytoplankton abundance showed high values between the surface and 20 m depth (Licea & Luna 1999), and consequently, an increase in zooplankton biomass in this depth was also found (Flores-Coto *et al*. 1988, 1993). This is associated with the large amount of organic matter supplied by the river plumes as a consequence of the high pluvial rates observed during rainy season (Shirasago 1991). Larger available food could enhance larval survival probabilities and favor recruitment success from larval/postlarval stage to the adult phase. Greater primary productivity may favor a peak of *Solenocera* reproductive activity during the summer-autumn rainy season. Widespread distribution of postlarvae during summer indicates that recruitment process to the adult population occurs mainly at mid outer shelf in front El Carmen during this season. During the winter, movements of postlarval populations to greater depths have been frequently observed associated with the recruitment process to the adult population, which is largely distributed between 50 and 100 m depths (Vázquez-Bader 1988). Gómez-Ponce & Gracia (2003) suggest that this recruitment can be part of the main reproductive period that could extend over various months like in other tropical peneids (Gracia *et al*. 1997, Sandoval Quintero & Gracia 1998).

Solenocera larvae depicted the typical day vertical migration pattern that varied with the season of the year and the larval stage. It was possible to observe a migrating behavior during the spring and summer seasons in which larvae tended to concentrate at deeper sites during the light-hours, whereas during the dark-hours, larvae moved towards the surface; similar results were reported by Ringelberg (1995). These results agree with those found by Jones *et al.* (1970), Rothlisberg (1982) and Rothlisberg *et al*. (1983), who stated that the largest proportion of larval stages of organisms from the Penaeidae family distribute themselves towards the surface during the night and close to the bottom during the day; since younger larvae tend to distribute in the surface water layers and the older ones in the deeper strata. During the autumn 1993 (November), larvae did not present a clearly defined vertical migration pattern as they distributed indistinctly at different depths, independently from the light period. Temple & Fisher (1965), in a study near Galveston, Texas, observed a similar behavior in peneids. In that study, they mentioned that given the environmental conditions affected by strong wind season (called "Nortes"), the mixing zone becomes deeper and consequently the thermocline is displaced to greater depths, or is not formed at all, resulting in the absence of a defined vertical migration pattern.

It has been observed that often the vertical movements of larvae start before light intensity changes. In other cases, the reference factor could be temperature, thus the migration pattern is not observed if temperature is uniformly distributed through the mixed water column (Sastry 1983a, 1983b). In this sense, the thermocline seems to mark a division or physical barrier, as suggested by the results from the Student's t test applied to the spring season in this study (Table 2). The thermocline could be a barrier for the younger *Solenocera* stages (protozoea and mysis), a phenomenon that has also been proposed by Criales & Lee (1995) and Lougee *et al.* (2002). However food availability in the upper layers could be a more determinant factor for *Solenocera* larvae distribution at these layers.

Vertical migration could be modified by the horizontal current movements of the water layers through the water column, i.e., the up and down migrations of the *Solenocera* larvae allow them to be transported to potential habitats for their dispersal and colonization. Migration has also been interpreted as a defense mechanism against visual predators; in the sense that during the daylight hours these organisms can be easy preys for predators: larvae move to deeper sites to avoid this predation pressure (Gault 1953, Zaret & Suffern 1976, Rothlisberg 1982, Rothlisberg *et al.* 1983, Hessen & Rukke 2000, Bo-ping & Straskraba 2001, Eiane & Parisi 2001). In this case most of the *Solenocera* larvae seem to remain in the 20 m upper layer during mysis and protozoea stages where food availability could play a more determinant role.

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