Research Article

Evaluation of the entry of white shrimp postlarvae (Decapoda: Penaeidae) to a nursery area in the southern Gulf of Mexico

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ABSTRACT. The immigration of white shrimp *Penaeus setiferus* (Decapoda: Penaeidae) postlarvae (Pls) into the Terminos Lagoon was studied to determine the annual pattern of abundance and its relationship with temperature, salinity, tidal current velocity, and river discharge. Zooplankton samples were simultaneously obtained fortnightly at surface, mid-water, and bottom. The nets used were 50 cm in diameter, 1.5 m in length and 505 μ m mesh size. The results indicated a postlarval seasonal immigration pattern, with the lowest average density values from March to May and October to November, and significantly higher values from June to September; maximum peaks occurred in June and September. High Pls densities were obtained between one and three hours after the tidal inflow started. Temperature and salinity varied little during each sampling period and had no apparent effect on immigration, but did have an effect on the seasonal abundance cycle. The multiple regression models indicated that the tidal current velocity and the temperature explained 86% of the variation in Pls abundance during immigration to the Terminos lagoon. The larval migration varied at different levels, with highest densities occurring at a medium depth of 5 m. The Pls entered an optimal range of tidal current velocity (between 0.6 and 0.9 m³ s⁻¹). The main entry mechanism was through the tide current of the Selective Tide Stream Transport, where the Pls could also select an optimum current velocity, avoiding the strata of higher turbulence that would imply higher energy expenditures.

Keywords: Penaeus setiferus, recruitment, immigration, current velocity, Terminos Lagoon, Mexico.

INTRODUCTION

Penaeid shrimps have a complex life cycle; they use coastal lagoons and estuaries as feeding grounds for postlarvae, juveniles, and sub-adults, which subsequently migrate to the sea to reproduce (Dall *et al.*, 1990; Pérez-Castañeda & Defeo, 2004). Coastal lagoons and estuaries constitute nursery habitats that provide food and refuge against predators and support higher growth rates (Minello & Zimmerman, 1991). In the area of commercial exploitation and management, seasonal yields of species with short life cycles such as penaeid stock depend on the recruitment of the adult population, and the level of recruitment of shrimp populations depends in turn on the reproductive success and survival of postlarvae and juveniles during their

migration and stay in nursery areas (Criales & Mc Gowan, 1994; Noriega & Juárez, 2002; Carbonell *et al.*, 2008; Aschan & Ingvaldsen, 2009).

The processes affecting the dispersal and recruitment of penaeid shrimp postlarvae vary in space and time, and are controlled by a combination of biotic and abiotic factors that include reproductive dynamics and the physiological tolerance of postlarvae, their behavior, and the hydro-meteorological regime (Cowen, 2002; Criales *et al.*, 2006; Ogburn *et al.*, 2013). The recruitment is affected by spawning cycles, ocean circulation patterns, and their seasonal changes. The accumulation of postlarvae at estuarine systems inlets, the interaction between tidal currents, and the behavior of larvae create significant recruitment variability into coastal lagoons (Rothlisberg *et al.*, 2010).

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The southern Gulf of Mexico supports a shrimp fishery based on three species of significant commercial value: brown shrimp Penaeus aztecus (= Farfantepenaeus aztecus) (Ives, 1891), white shrimp Penaeus setiferus (= Litopenaeus setiferus) (Linnaeus, 1767), and pink shrimp *Penaeus duorarum* (= *Farfantepenaeus* duorarum) (Ives, 1891). These species have biological strategies closely linked to the Terminos Lagoon. Their postlarvae and pre-adults use this lagoon as a refuge and feeding area (Gracia & Soto, 1990). The Terminos Lagoon in Campeche, Mexico, functions as a nursery area for white shrimp, and the immigration of planktonic postlarvae takes place through the inlets of Puerto Real and El Carmen, both connecting the lagoon with the Gulf of Mexico (Gierloff-Emdem, 1977; Mancilla-Peraza & Vargas-Flores, 1980). Because white shrimp is the second species of commercial importance in the Campeche Bank, representing approximately 13.5% of the annual production of the shrimp fishery in the area (CONAPESCA, 2012), a better knowledge of the biology and ecology of the postlarval phase, both planktonic and benthic, during the recruitment of white shrimp into coastal lagoons is required.

Some studies on shrimp larvae in coastal lagoons in the southwestern Gulf of Mexico included analysis of postlarval density in Alvarado Lagoon (Villalobos et al., 1969), and shrimp larvae immigration in Carmen and Machona Lagoons (Flores-Coto et al., 2010). Others studied postlarval immigration of *P. setiferus* and P. duorarum in the Terminos Lagoon and adjacent coastal areas from July 1979 to July 1980 (Gracia & Soto, 1990); this information is currently used for the management of these fisheries in the Gulf of Mexico (GM). However, Cervantes-Hernández & Gracia (2011) warned of inadequate management of the fishery of *P. duorarum* between 1980 and 1989, which was reported to have even lower levels in 1993. The current situation of exploitation of this fishery, however, is unknown, as well as that of the *P. setiferus* fishery.

Considering this situation of uncertainty, it is essential to perform a survey for both shrimp populations to update this information and to continue monitoring the Lagoon Recruitment (RL) and Marine Recruitment (RM) seasons in the southwestern Gulf of Mexico GM to adequately estimate the income pattern of postlarval shrimp to the Terminos Lagoon. Therefore, the purpose of this study was to determine the immigration pattern of postlarvae of *P. setiferus* into the Terminos Lagoon. Moreover, the study aimed to measure the magnitude of the immigration and to identify the main factors involved in these processes to contribute to a more adequate and efficient management of these valuable fisheries in the region.

MATERIALS AND METHODS

Study area

The Terminos lagoon is located in the southwestern Gulf of Mexico, inland of Campeche Bay, between 18°25'-19°00'N and 91°00'-92°20'W. It is a coastal lagoon with an approximate area of 2,500 km². It communicates with the Bay of Campeche through the Carmen and Puerto Real Inlets (Fig. 1), located southwest and northeast of Carmen Island, respectively. The Puerto Real inlet is located at 18°50'N, 92°00'W and has a length of 3.3 km (Jiménez-Salas, 1979; Alarcón-Daows, 1986). The Carmen inlet is in the western portion of the Terminos Lagoon between 18°30'-18°40'N and 92°00'-92°50'W with 4.0 km in length (Álvarez-Guillen et al., 1985). The lagoon is characterized by east to west water net flow, driven by the winds, allowing marine water to penetrate throughout the Puerto Real Inlet and to exit via the Carmen Inlet (Gierloff-Emden, 1977; Mancilla-Peraza & Vargas-Flores, 1980; Graham et al., 1981; Kjerfve et al., 1988).

Field and laboratory work

A special sampling equipment was used with three trapeze-type nets of 50 cm mouth diameter, 1.5 m total length and 505 µm mesh size. This device was placed with ballast at the bottom and secured to a bridge column through parallel cables. With this sampling equipment and the sampling method described by Flores-Coto & Zavala-García (1994), fortnightly white shrimp postlarvae (Pls) entrance within the Terminos Lagoon was monitored during the following dates in the year 2010: March (8 and 23), April (6 and 21), May (4 and 27), June (12 and 26), July (11 and 25), August (9 and 19), September (13 and 30), October (12 and 26), and November (9 and 21). A specific sampling station, located in the Puerto Real Inlet (18°39'17"N, 91°45'31"W) (Fig. 1), was implemented to monitor the presence of Pls. During each sampling, 15 hauls were made, each haul with duration of 15 min, and with a total duration of each sampling of approximately 4 h. The Pls sampling was carried out at the following depth: surface (1 m), mid-water (5 m), and bottom (10 m). Sampled white shrimp Pls were preserved using 4% formalin, neutralized with sodium borate. Once in the laboratory, the Pls were transferred into 70% alcohol and identified to species level according to Subrahmanyam (1971) and Ringo & Zamora (1968).

Temperature (°C) and salinity were recorded with a thermos salinometer (YSI 30) at each depth level. Monthly river discharge $(m^3 s^{-1})$ data for the year 2010 (Candelaria, Chumpan, and Palizada rivers) were obtai-

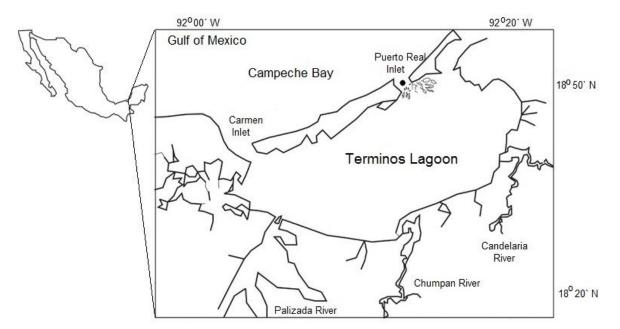


Figure 1. Study area. Terminos Lagoon in the southwestern Gulf of Mexico. Puerto Real Inlet was the sampling point.

ned from the National Water Commission, Campeche (CONAGUA, 2010). Current velocity was measured with a General Oceanic model 2030 flowmeter installed at the mouth of each net. These devices allowed the estimation of the water volume filtered at each sampling depth, and the standardization of the density as the number of Pls per 100 m³ of filtered water (Smith & Richardson, 1977).

Each sampling was conducted during day and night flood tide; it started when the tidal current velocity reached 0.5 m³ s⁻¹ and was finished when the tide velocity decreased again to 0.5 m³ s⁻¹.

Statistical analyses

Estimated abundance of white shrimp Pls was normalized with $\log(x+1)$ to comply with the normality assumption, and the Barttlet Test was used to verify the homogeneity of variances (Zar, 1999). Considering the three depth levels, a factorial ANOVA model and LSD Fisher test (Zar, 1999) were implemented to explain preferential input patterns of white shrimp Pls within the Terminos Lagoon. In addition, at each depth level, the current velocity, water temperature, and salinity were analyzed with a factorial ANOVA, and the existence of significant differences between the different sampled levels was determined. Finally, a multiple regression (forward step-wise) was applied between the PIs densities as the dependent variable, and the temperature, salinity, current speed, and monthly average of the Candelaria, Chumpan, and Palizada rivers discharge as independent variables. All statistic tests were carried out with the Statistica 7 software.

RESULTS

A total of 116,829 postlarvae of white shrimp were obtained from 810 samples taken at three depth levels between March and November 2010.

Postlarvae abundance in the water column

Postlarval entries were recorded at the three depth levels sampled. The abundance showed significant differences between the three depth strata (F = 3.01, $F_{0.05(2,720)} = 14.08$; P < 0.01). The highest Pls abundance was obtained through mid-water (Fig. 2a).

Physical and chemical factors in the water column

Water temperature showed significant differences between depth levels (F = 3.01, $F_{0.05(2.738)} = 4.8 P >$ 0.05); surface and mid-water levels presented the highest temperatures (Fig. 2b). Salinity also showed significant differences between depth levels (F = 3.01, $F_{0.05(2,738)} = 12.5, P < 0.05$). The LSD Fisher test indicated salinity increases from surface to bottom (Fig. 2c). The average current velocity recorded was 0.65 \pm 0.35 m³ s⁻¹ for the surface, 0.77 ± 0.49 m³ s⁻¹ for midwater, and 1.25 ± 0.51 m³ s⁻¹ for the bottom. Strong current flows were always recorded at the bottom (>1 $m^3 s^{-1}$) (Fig. 2d), and were significantly different from those in surface and mid-water (F = 3.01, F_{0.05(2, 738)} = 110.1; P < 0.01) (Fig. 2d). The Pls entered the lagoon more abundantly at a flow velocity between 0.7 and 1.0 $m^3 s^{-1}$.

Temporal variation of the abundance of postlarvae

The lowest Pls density values occurred from March to May and at the end of September to November, while

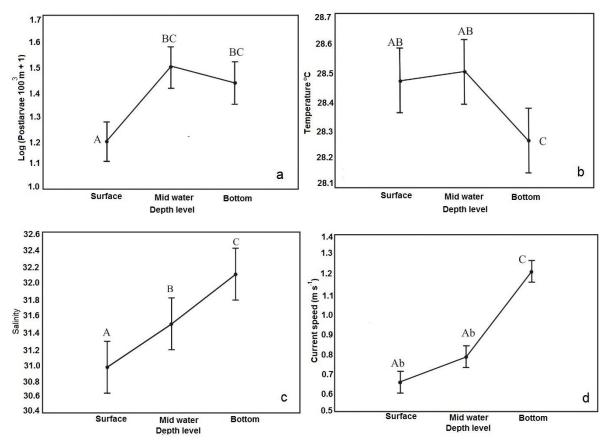


Figure 2. a) Data at three depth strata of postlarval density, b) temperature, c) salinity and d) current velocity in the water column, Terminos Lagoon, southwestern Gulf of Mexico. The results of the *post-hoc* test (LSD Fisher) are also presented. The combined letters represent that there are no significant differences while single letters represent significant differences.

the highest densities were recorded from June to the beginning of September. Two peaks of maximum average abundance were recorded: the first one in June with 740.0 postlarvae 100 m⁻³, and the second in September with 627.3 postlarvae 100 m⁻³ (Fig. 3a). The differences of abundance recorded between samplings were significant (F = 57.009, $F_{0.05(17, 735)} = 57.01$; *P* < 0.01). Post-larval densities were low during the first two casts, followed by a significant increase during the third to fifth casts, followed by a substantial decrease in the subsequent casts. (F = 1.83, $F_{0.05(14, 735)} = 2.03$, *P* < 0.05), (Fig 4).

Temporal variation of the physical and chemical factors

The temperature values recorded varied between 23.3 and 31.5°C. Temperatures higher than 29°C were recorded from May to September. The lowest temperatures (<28°C) occurred from March to April and from October to November. Temperature differences recorded between samplings were significant (F = 1.64, F_{0.05(17, 738)} = 372.3 P < 0.01) (Fig. 3b). Salinity varied significantly (F = 1.64, F_{0.05(17, 738)} = 2.9; P < 0.01)

throughout the year (18.3-36.5; Fig. 3d), with highest values (>36.1) prevailing from March to June, decreasing from July to September, and then increasing again towards the end of the year (Fig. 3c). The current velocity presented significant variations (F = 1.64, $F_{0.05(17, 737)} = 3.1$; P < 0.01) between samplings, with highest values in March, June and October (Fig. 3d).

Multiple regression analysis

The two-step multiple regression (forward step-wise) analysis revealed that the water current speed and temperature explained 86% of the total variation of the recorded postlarvae density ($R^2 = 0.86$, F = 9,08 F_{0.05(2,6)} = 5.76, P > 0.05). (Table 1). According to the model, the current velocity had a significant inverse relationship with the abundance of Pls, while the temperature had a direct non-significant relationship with the postlarvae abundance:

N° postlarvae 100 m⁻³ = 675.97 + $(-0.71 \times X_1)$ + $(0.26 \times X_2)$

where X_1 is current speed (m³ s⁻¹) and X_2 temperature (°C).

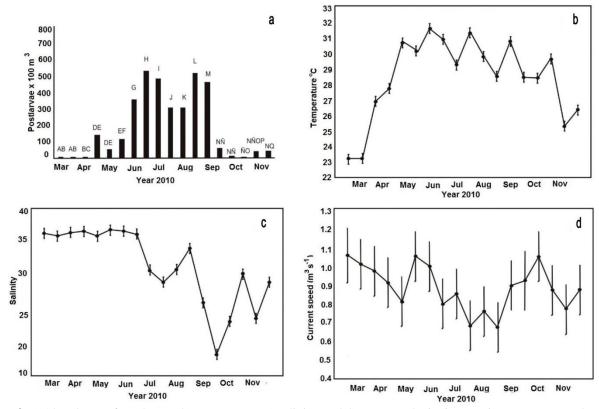


Figure 3. a) Abundance of postlarvae, b) temperature, c) salinity, and d) current velocity in Terminos Lagoon, southwestern Gulf of Mexico.

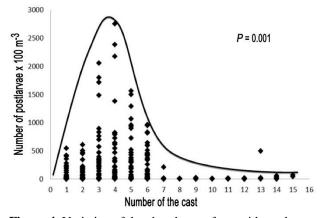


Figure 4. Variation of the abundance of penaeid postlarvae in relation to the casting number, Terminos Lagoon, southwestern Gulf of Mexico.

DISCUSSION

We registered the entrance of *P. setiferus* postlarvae at all three depth levels analyzed, however, the highest abundance entered through mid-water stratum at 5 m depth. During their entrance to coastal lagoons, many fish and invertebrates perform vertical migrations in the water column, which are synchronized with tidal phases to maximize their horizontal transport. This me-

Table 1. Regression summary for dependent variablesassociated with penaeid postlarval density in TerminosLagoon, southwestern Gulf of Mexico. SE: standard error,t: test.

	Beta	SE of beta	t(6)	P-value
Intercept			1.08	0.319
Current velocity	-0.706	0.2359	-2.99	0.024
Temperature	0.258	0.2359	1.09	0.314

chanism has been described as selective tidal stream transport (STST) (Shanks, 1995; Forward *et al.*, 2001; Queiroga *et al.*, 2006). During the STST, organisms perform vertical movements in the water column, remaining in the medium-water and surface strata during tidal flow, and moving towards the bottom during ebb tide (Walker *et al.*, 1978). Some species use both mechanisms at different stages of their life cycle (Criales *et al.*, 2011). Both the mysis and postlarval phases of the pink shrimp *Penaeus duorarum* use tidal flow transport (TFT) during the semidiurnal tide throughout its dispersal in the Florida internal platform (Criales *et al.*, 2007). The vertical migration is a response to environmental factors such as light, pressure, and gravity (Sulkin, 1984); however, salinity,

temperature, and turbulence also affect this migration behavior in the water column (Welch & Forward, 2001). Criales *et al.* (2011) indicated that pink shrimp Pls use TFT to enter into nursing areas in the Florida Bay, and these authors mentioned that Pls ascend in the water column during nocturnal tidal flow and enter the breeding areas.

Physical and chemical factors in the water column Temperature

The temperature varied from 23 to 30°C, and the highest number of Pls entrance was recorded between 28.3 and 28.7°C. Our results agree with those reported by Arenas-Mandieta & Yáñez-Martínez (1981) who mentioned that the highest Pls abundance that entered the Terminos Lagoon in Campeche was registered to 26.8-28.7°C. The results of the present study are also in accordance with those from Alarcón-Daows (1986) who reported for the same location a bimodal behavior of temperature in relation to the abundance of the postlarval entrance. They mentioned that the first peak of Pls abundance occurred between 26 and 27°C and the second at 29°C. On the other hand, Wenner et al. (2005) identified a critical minimum temperature of 27°C for the immigration of *P. setiferus* Pls into coastal lagoons (Ossaba Sound). Other studies did not find a clear relation between water temperature and the entrance of Pls into nursing areas (Pietrafesa & Janowitz, 1988; Gracia & Soto, 1990; Flores-Coto et al., 2010), but high temperatures have been associated mainly with spawning periods (Gracia & Soto, 1990; Flores-Coto et al., 2010).

Salinity

In the present study, the entrance of P. setiferus postlarvae was more abundant at salinities between 31 and 33. Arenas-Mandieta & Yáñez-Martínez (1981) showed that postlarval immigration to the Terminos Lagoon through the mouth of Puerto Real took place within a wide range of salinity (18-38). Subsequently, Alarcón-Daows (1986) reported, for the same location, three salinity intervals where the maximum abundance of P. setiferus Pls obtained: 24-25, 32-33 and 31-35. Gracia & Soto (1990), also for the Terminos Lagoon, reported a salinity interval of 22-34 where they recorded the highest abundance. Penaeid shrimps are euryhaline organisms, which have the ability to survive in different salinities, but this ability changes with ontogenetic development (Chong-Robles et al., 2014). Results of experimental studies revealed that the early stages of the penaeid Pls are more related to salinities very similar to the sea, while more advanced Pls are associated with lower salinities (Mair, 1980; Chong-Robles et al., 2014). The more advanced Pls become

benthic postlarvae and develop into juveniles, which must adapt to a highly variable environment in relation to salinity in order to survive (Mair *et al.*, 1982). On the other hand, our multiple regression analysis did not show any significant relation between salinity and the entrance of *P. setiferus* Pls to the Lagoon, which coincides with the results of other studies (Mair, 1980; Mair *et al.*, 1982; Zimmerman *et al.*, 1990). Likewise, it has been observed that changes in salinity during tides are detected by Pls as a cue to enter the nursing areas (Boehlert & Mundy, 1988; Pietrafesa & Janowitz, 1988).

Current speed

Many mechanisms have been described for the transport of larvae and postlarvae of penaeid shrimp from spawning areas in the continental shelf to their entry into the nursing areas (Criales *et al.*, 2007). The most important mechanisms are those associated with the wind through Ekman transport, upwelling, countercurrents generated by cyclonic and anticyclonic turns, and internal tidal currents (Shanks, 1995, 2006; Pineda, 1999; Epifanio & Gravine, 2001). Tidal current tides associated with vertical migration behavior are a mechanism used to maximize horizontal dispersal of the organisms, using the current velocity differences generated in the different strata of the water column. This mechanism is known as selective tidal stream transport (STST) (Forward et al., 2003; Queiroga & Blanton, 2005). Organisms using tidal stream to enter nursing areas are referred to tidal flow transport (TFT) (Morgan et al., 1996; Queiroga & Blanton, 2005), and when they use ebb tide currents to enter the marine area or to leave the nursing area, we refer to an ebb tide transport (ETT) (López-Duarte & Tankersley, 2007; Ogburn et al., 2007). Penaeid shrimp use during their life both mechanisms (Criales et al., 2011) when they enter coastal lagoons in the postlarval stage. Subsequently and in their juvenile stage, they use the ETT to leave the nursing or recruitment areas. Criales et al. (2006, 2011) indicated a higher abundance of penaeid shrimp Pls distributed in the water column associated with the nocturnal phase of the tide flow. The significant differences in abundance found in our results indicated a higher entrance of Pls at 5 m depth during their entry to the lagoon; this suggests that P. setiferus Pls use TFT to maximize their horizontal transport and to ensure their arrival to settlement areas. Maximum abundances corresponded to the nocturnal sampling hours, a situation that also favors a lower depredation rate (Christy & Morgan, 1998), and therefore a higher settlement rate. Alarcón-Daowz (1986) reported a direct relation of tidal flow current velocity with the abundance of white shrimp Pls in the Terminos Lagoon. On the other hand, Poli (1983) and

Flores-Coto *et al.* (2010) did not find a significant relationship between the current velocity and the abundance of Pls during their entrance to nursing areas. We found higher Pls abundance in a current velocity range varying from 0.6 to 0.9 m³ s⁻¹, which suggests that Pls can select the most suitable current velocity conditions for their entrance, thus avoiding strong currents where there could be higher turbulence and therefore higher energy expenditure, which can be used during the settlement process (Forward *et al.*, 2001).

Temporal variation of postlarval abundance

The continuous migration of planktonic Pls in the area suggests a prolonged and constant reproductive activity for P. setiferus, which has been reported for other tropical penaeid shrimp (García & Le Reste, 1986). Dall et al. (1990) and Velázquez & Gracia (2001) mentioned that the white shrimp spawns continuously throughout the year with different peaks of reproductive activity. Arenas-Mendieta & Yáñez-Martínez (1981) reported a constant entry of shrimp Pls into the Terminos Lagoon through the mouth of Puerto Real, with maximum abundance peaks from June to September, which roughly coincides with our results. Alarcón-Daowz (1986) documented a constant entry of white shrimp Pls into the Terminos Lagoon from November 1982 to October 1983, with highest abundance peaks from August to October. Gracia & Soto (1990) mentioned a continuous entry of white shrimp Pls with higher abundance peaks in July and November. Such seasonal variability of abundance peaks may be associated with the fact that a female can spawn several times during one year (García & Le Reste, 1981; Velázquez & Gracia, 2001).

The highest abundance peaks recorded in our study were associated with periods of higher reproductive activity in the area (Gracia & Soto, 1990). Regis (1996), based on a study of gonadal maturity of P. setiferus in Campeche, showed that there were two peaks of higher reproductive activity for this species: the first during April to May and the second in August, moreover a proportion of immature individuals were present from October to February, when the water temperatures were low. In addition, periods of maximum migration of Pls to the Terminos Lagoon were related to the rainy season and with an increase in primary production and planktonic biomass along the continental shelf (Flores-Coto et al., 1988). This food availability favors the survival of the shrimp larvae, and, along with the high number of eggs produced by a single female and the year-round reproduction of the species, increase the possibility of the larvae to reach the estuaries (Gracia & Soto, 1990).

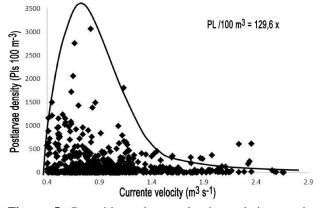


Figure 5. Penaeid postlarvae density, relative to the current speed in Terminos Lagoon.

We collected a total of 119,829 Pls and our maximum peak was 2,755 Pls 100 m⁻³. These values are substantially higher than those reported for the same area by Arenas-Mendieta & Yáñez-Martínez (1981) (n = 4,740 and maxima abundance of 44.76 Pls 100 m^3), Alarcón-Daowz (1986) (n = 1.977 and maxima abundance 60 Pls 100 m⁻³) and Gracia & Soto (1990) (n = 4,743 and maxima abundance 45 Pls 100 m⁻³). These discrepancies are possibly due to the different methodologies employed: however, the methodology employed (Flores-Coto & Zavala-García, 1994) in our study seems to be the most efficient for the collection of shrimp Pls. Flores-Coto et al. (2010) used the same methodology in Carmen and Machona lagoons, recording high densities of P. setiferus, with maximum density values in individual samples of 1,788.4 Pls 100 m⁻³ (Fig. 5).

The immigration pattern described here consists of two sequences: the first involves a low-density phase, a subsequent second phase of high Pls abundance, followed by a progressive abundance decrease (Fig. 4). During the first sequence, Pls tend to accumulate at the inlet and enter the lagoon when the current speed increases. Thereafter, when the tidal inflow increases its intensity, most of the Pls have entered during the first hours. Similarly, Rothlisberg et al. (1995) recorded the highest postlarval immigration peaks two hours after the beginning of the flow tide. In Australia, high densities of Pls entered the estuary during the first half of the high tide current (Young & Carpenter, 1977). Similar results were obtained from the inlet of Carmen and Machona lagoons in Tabasco, where a rapid increase in postlarval abundance occurred during the first hours of the flow tide, followed by a gradual decrease in density (Flores-Coto et al., 2010).

The variation of postlarval abundance entering the lagoon through the mouth of Puerto Real is independent of saline and thermal factors, and the main entry mechanism is through the tide current of the selective tide stream transport.

The Pls can select an optimal entry velocity, avoiding levels with a higher turbulence, which would require higher energy expenditure. The remaining energy sources will be used when they settle into the benthos and when they perform their transformation from the planktonic to the benthic phase.

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