

# Postlarval settlement of the spiny lobster *Panulirus argus* along the Caribbean coast of Mexico: Patterns, influence of physical factors, and possible sources of origin

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## Abstract

We analyzed and compared 17 yr of monthly settlement indices of postlarvae of the Caribbean spiny lobster, *Panulirus argus*, at two locations on the Mexican Caribbean coast. Along this coast, the shelf is very narrow and the local circulation is driven by waves overtopping subtidal coral reef crests. Settlement occurred year-round, but both locations showed annual rhythmicity, average seasonal maxima during the autumn, and similar interannual variation, reflecting the influence of mesoscale oceanographic processes on settlement. Significant correlations between settlement indices and a number of interrelated physical factors indicate that sea-level variation is the main factor influencing settlement. There was further association between extreme settlement pulses and extreme weather events (tropical storms and hurricanes) during the late summer–autumn. The autumn settlement peak indicates that large hurricane waves enhance the onshore transport of postlarvae that originated during the spring spawning peak. The geographic range of potential sources of larvae that settle along this coast during the periods of March–April and September–October, 5–9 months after hatching (the estimated larval duration for *P. argus*), was investigated by stochastic simulations integrating passive trajectories backward in time using 6 yr of stable outputs from a well-established numerical model for the entire Atlantic Ocean. Trajectories from the model indicate that the local population of *P. argus* depends to a large extent on larval supply from many potential source regions across and outside the Caribbean but that some larvae follow pathways that permit self-recruitment.

Spiny lobsters (Palinuridae) are important fishing resources throughout the tropical and temperate regions of the world, but the Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804), sustains, on average, 50% of the

total world catch of spiny lobsters (Lipcius and Eggleston 2000). The latitudinal range of *P. argus* spans the tropical and subtropical western Atlantic Ocean from North Carolina (U.S.A.) to northeastern Brazil and throughout the West Indies, the Bahamas, and Bermuda. Some genetic differentiation has been found between Brazilian and Caribbean populations, prompting a recommendation for provisional subspecific status (Sarver et al. 1998), but no genetic differentiation has been found among populations across the Greater Caribbean (Silberman et al. 1994; Sarver et al. 1998). These findings support the notion that *P. argus* constitutes a pan-Caribbean metapopulation, with local populations connected via larval dispersal.

Metapopulations consist of a mosaic of local populations distributed among sink and source habitats. In source habitats, self-recruitment is considerable, whereas populations in sink habitats depend to a greater extent on reproductive surpluses from source habitats (Pulliam 1988). Because benthic marine species have pelagic larvae that may be dispersed by currents, there has been a long-standing debate as to whether marine populations are basically open, thereby relying to a large extent on outside sources for larval supply, or basically closed, thereby relying on mechanisms of larval retention near source

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populations (e.g., Strathmann et al. 2002; Cowen et al. 2006). However, in large marine metapopulations, many local populations probably lie somewhere between these two extremes owing to variability in oceanographic processes, larval durations, and benthic habitat quality (Lipcius et al. 1997; Hixon et al. 2002; Johnson 2005). For example, estimated indices of local retention for larvae of reef fishes varied from low to high across the Caribbean depending on large- and mesoscale oceanographic processes (Cowen et al. 2006). Reef fishes, however, have larval durations of 1–2 months, whereas larval durations among species of spiny lobsters are 5–24 months, providing a greater potential for long-distance dispersal. Adaptations of the planktotrophic spiny lobster larva (“phyllosoma”) to a long oceanic life are reflected in its flattened, transparent, leaf-like body (Booth and Phillips 1994).

*P. argus* breeds year-round, but populations from disparate locations across the Caribbean (see Briones et al. 1997) show a main spawning peak during the spring months (March–June) followed by a smaller peak in the autumn (September–October) and a decrease in reproductive activities over the winter months. The larval phase consists of 11 phyllosoma stages (Lewis 1951). Based on the relative frequency of different stages obtained in plankton samples across vast expanses of the western Atlantic at different times of the year, the larval duration of *P. argus* has been estimated to occur between 5 and 9 months prior to metamorphosis into the postlarva (“puerulus”), with possible durations of up to 11 months over the northernmost range of the species (Lewis 1951; Lyons 1980). This variability in larval duration probably reflects individual differences in rate of development and/or a possible delay in metamorphosis as a result of nutritional constraints. Recently, *P. argus* was raised for the first time from egg to juvenile in the laboratory. Metamorphosis into the puerulus phase occurred 140–198 d after hatching (i.e., 4.7–6.6 months), with an average of 174 d (5.8 months) (Goldstein et al. 2006). However, the range in larval duration of palinurids under controlled laboratory conditions is usually shorter than that estimated from the field (Booth and Phillips 1994). Therefore, in the present study, a larval duration of 5–9 months will be considered.

Phyllosomata have little horizontal swimming ability, but their horizontal transport may be modulated by vertical migration (Griffin et al. 2001; Jeffs et al. 2005). Metamorphosis of the final phyllosoma stage into the puerulus, which is a transparent postlarva morphologically similar to the adult, appears to occur in oceanic waters close to shelf breaks and appears to be dictated by the nutritional state of the phyllosoma rather than by environmental cues (McWilliam and Phillips 1997). This may be the case because, unlike phyllosomata, pueruli do not feed but are strong horizontal swimmers. Pueruli swim directionally near the surface across continental shelves toward coastal areas, where they settle in shallow habitats. It has been hypothesized that underwater sound produced by waves breaking on the coast may serve as a directional cue guiding pueruli to coastal areas (Jeffs et al. 2005). Pueruli of *P. argus* swim at velocities up to 10 cm s<sup>-1</sup>, and the

duration of the puerulus phase has been estimated to be 1–2 weeks (Calinsky and Lyons 1983).

Settlement of postlarvae in benthic habitats is an important process in the population dynamics of marine species (Hixon et al. 2002; Sale and Kritzer 2003). For example, in some lobster species, settlement levels have been shown to be related to further recruitment into the fishery (Phillips et al. 2000). However, spiny lobsters show wide spatial and temporal variations in settlement levels, thus necessitating long time series to determine seasonal settlement patterns. Measuring settlement in the natural benthic habitat is extremely difficult owing to the small size, cryptic habits, and wide dispersion of pueruli, but artificial substrates that resemble the natural settlement habitat (“collectors”; Phillips and Booth 1994) provide reasonable indices of settlement strength because they reflect the abundance of pueruli in the nearby water column and the offshore abundance of late-stage phyllosomata (Booth 1994; Herrnkind and Butler 1994; Eggleston et al. 1998). Extensive data on environmental and oceanographic data are also necessary to determine the factors affecting variations in settlement, because oceanographic processes may influence the larval and postlarval phases in different ways. However, physical variables typically explain a relatively low proportion of the settlement variation (e.g., Phillips et al. 1991; Acosta et al. 1997; Eggleston et al. 1998), probably because pueruli do not behave as passive particles. Nevertheless, these correlations provide insight into the forces influencing the influx of pueruli into coastal areas.

The aims of the present paper are (1) to describe and compare the temporal patterns in postlarval settlement of *P. argus* at two locations along the Mexican Caribbean coast using a 17-yr-long time series of monthly settlement indices, (2) to examine the influence of environmental factors on the observed settlement patterns, and (3) to identify the geographical range of potential sources of pueruli settling along this coast. We hypothesized that settlement indices would show similar seasonal patterns and interannual variability in both locations as a result of large-scale oceanographic processes but would show some differences at monthly time scales as a result of the influence of local dynamics. Based on the available knowledge on the relative influence of physical factors on the settlement patterns of palinurid species and on the coastal features of our study area, we also hypothesized that changes in sea level would largely account for variations in settlement. Finally, because of the long larval duration of *P. argus* and the hydrographic regime along the Mexican Caribbean coast, we hypothesized that most pueruli arriving at and settling in to this coast would likely originate from lobster populations elsewhere in the Caribbean rather than from the local population.

## Methods

*Study area*—The Caribbean coast of Mexico is the coast of the state of Quintana Roo, which extends along the eastern margin of the Yucatan Peninsula and is located on the northwestern margin of the Caribbean Sea (Fig. 1).

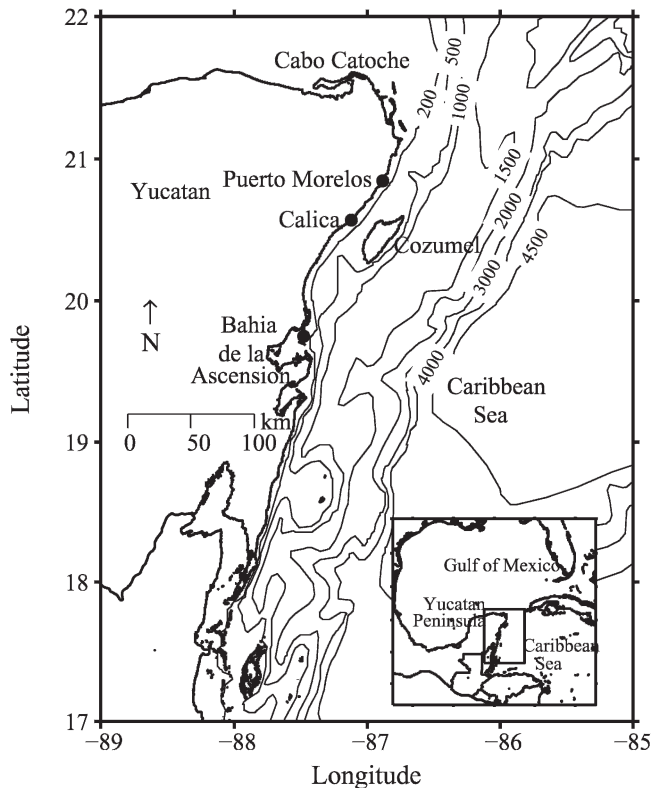


Fig. 1. Location of the Mexican Caribbean coast (coast of the state of Quintana Roo) and of relevant locations along the coast (Puerto Morelos, the Port of Calica, Bahía de la Ascensión).

Therefore, we will refer to this coast as the Quintana Roo coast.

In the northwestern Caribbean Sea, the Cayman current flows from east to west and turns northward when reaching the Quintana Roo coast, around 19°N, giving rise to the Yucatan current. The Cayman current (means speeds of 0.30–0.61 m s<sup>-1</sup>) weakens as it approaches the Quintana Roo coast, but its speeds intensify again as the Yucatan current is formed (Centurioni and Niiler 2003). The Yucatan current accounts for most of the transport from the Caribbean Sea to the Gulf of Mexico (annual average of 25 Sv through the Yucatan strait; Tang et al. 2006) and is one of the strongest and most dynamically active western boundary currents in the world, with an average velocity of 1 m s<sup>-1</sup> and magnitudes of up to 3 m s<sup>-1</sup> prior to its passage through the Yucatan strait. This current variability appears to be strongly influenced by the passage of eddies through the region (Richardson 2005; Cetina et al. 2006). Therefore, currents along the Quintana Roo coast have a predominant northeastward direction (parallel to the coast), are coherent within at least the upper 130 m of the water column, and have a general tendency to increase in velocity as they move northward (Cetina et al. 2006).

The continental shelf along the Quintana Roo coast is very narrow (distance from shoreline < 5 km in general; Fig. 1), ending at approximately 60 m in depth, and includes an important portion of the Mesoamerican Reef that runs approximately parallel to the shoreline. The coral reefs along most of this coast are subtidal, extended

fringing reefs. In this type of Caribbean reef, especially in those that face persistent trade winds (such as along the Quintana Roo coast), waves overtopping the reef crest and the resulting flow from the main driving mechanism for the local circulation (Roberts et al. 1992; Coronado et al. 2007).

Pueruli settlement was measured at two locations along the Quintana Roo coast: Bahía de la Ascensión (19°45'N, 87°30'W), located approximately where the Cayman current impinges the coast and veers north, and Puerto Morelos (20°51'N, 86°55'W), located about 130 km north of Bahía de la Ascensión (Fig. 1), closer to the Yucatan strait. Bahía de la Ascensión is a large (~740-km<sup>2</sup>) and shallow (<6-m-deep) bay bordered by mangroves and swamps. The coral reef tract runs parallel to the mouth of the bay, protecting its inner waters from wave surge. At Puerto Morelos, the coral reef tract lies much closer to the shoreline, leaving a narrow (500–1,500-m-wide), shallow (<5-m-deep) back-reef lagoon between the reef and the coast. Both locations harbor extensive seagrass-macroalgal meadows, which constitute the settlement habitat for pueruli of *P. argus*.

*Pueruli settlement time series*—Pueruli settlement was measured using subsurface “GuSi” collectors that resemble the local marine vegetation (Gutiérrez-Carbonell et al. 1992; Briones-Fourzán 1994). In Bahía de la Ascensión, sampling was conducted from March 1987 to February 2001 and from July 2002 to January 2004, and in Puerto Morelos sampling was conducted from May 1990 to December 2006. During the first 2 yr of study, settlement of pueruli was assessed weekly by counting the postlarvae settled in groups of four to six collectors deployed in nine different sites in Bahía de la Ascensión and in three different sites in Puerto Morelos. From these data, a lunar periodicity was defined, with greater numbers of pueruli settling between the new moon and first-quarter lunar phases (Briones-Fourzán 1994). These data also served to select the most appropriate site in each location to monitor pueruli settlement over the long term. The long-term monitoring site in each location was located approximately 50 m leeward of the coral reef tract and consisted of six collectors situated parallel to the reef tract. The distance between adjacent collectors was approximately 50 m.

From the third year onward, pueruli settlement was assessed monthly, 1–2 d after the first-quarter lunar phase, to obtain a “monthly settlement index” (i.e., the mean number of pueruli collector<sup>-1</sup> month<sup>-1</sup>) in each location. The weekly data obtained during the first 2 yr were pooled to produce monthly indices for the entire series. Occasionally, two lunar monthly intervals occurred within one calendar month. In these cases, we averaged the numbers of postlarvae to give the monthly settlement index (Phillips et al. 1991).

Time-series analyses were used to separately describe the temporal patterns in pueruli settlement in each location across the period of uninterrupted monthly data (14 yr in Bahía de la Ascensión and 17 yr in Puerto Morelos). Prior to analyses, the number of postlarvae from each collector was transformed to log (count + 1) to normalize the data

and stabilize the variance. The series were then smoothed with Tukey's 4253H filter, which has the overall effect of filtering out short-range fluctuations while maintaining the salient characteristics of the original series (Velleman and Hoaglin 1981). Rhythmic cycles in the monthly data were analyzed using the autocorrelation function. Autocorrelation coefficients were plotted against time lags (1 lag = 1 month). Then, to identify dominant periodicities, we used spectral analyses, which partition the variance of the series into its component frequencies (Platt and Denman 1975). The resulting periodogram shows the concentration of variance (i.e., energy) under the curve.

To determine whether temporal settlement patterns were similar in Bahía de la Ascensión and Puerto Morelos, we used a cross-correlation analysis using the data from the 12-yr period of simultaneous data from both locations (May 1990 to February 2001). To check for associations of one series with lags on the other, the analysis was undertaken using the anomalies from the monthly means to remove the annual cycle (Phillips et al. 1991). We then undertook a cross-spectrum analysis of the smoothed series to determine whether both locations showed similar cyclical behavior. In this analysis, the cross amplitude measures the strength of covariance between the respective frequency components in the two series, whereas the squared coherence value is analogous to a squared correlation coefficient (Wei 2006).

To disclose the underlying seasonal pattern in settlement in each location, we averaged the settlement indices for each calendar month across all years (Robertson and Kaufmann 1998). We then subjected these data to a correlation analysis to examine whether both sites showed similar seasonal settlement patterns. Annual settlement indices (data averaged across January–December of each year) were also estimated for both sites, and a correlation analysis was undertaken to assess whether interannual variation in settlement was similar in both locations.

*Relationships between settlement indices and physical factors*—Correlation analyses with environmental (physical) factors were undertaken only for the Puerto Morelos settlement series as a result of its longer length and the availability of local measurements of physical factors simultaneous with at least part of the settlement series. Among the numerous physical factors that have been correlated with settlement indices for different species of spiny lobsters, changes in sea level have been identified as an important factor through their effect on pueruli influx into coastal waters (Phillips et al. 1991; Polovina and Mitchum 1992). However, because the collectors in Puerto Morelos were located inside the back-reef lagoon, it was important to determine first the factors driving the exchange of water between the lagoon and the adjacent ocean. This was recently done by Coronado et al. (2007), who investigated the effect of wind, tides, surface waves, and the Yucatan current variability on this water exchange. The main factor driving the water exchange was the circulation induced by surface waves overtopping the reef and spilling water into the lagoon. This water eventually leaves the lagoon through reef channels. However, the wave

effect is modulated by changes in sea level, since relatively high water enhances the wave action, whereas lower sea-level anomalies, in conjunction with small-amplitude waves, can result in periods of minimal exchange or even of water stagnation in the lagoon. Accordingly, we expected the pueruli time series to show a certain degree of correlation with the monthly sea-level variability in the vicinity of Puerto Morelos.

The longest available time series of sea level simultaneous with the pueruli time series is that from the Port of Calica (Fig. 1), located about 40 km south of Puerto Morelos (Cetina et al. 2006). This series consists of 9 yr (December 1996 to December 2005) of continuous hourly measurements of subsurface pressure and sea surface temperature (SST) that should be quite representative of sea level and SST variability in Puerto Morelos at monthly time scales. However, subsurface pressure needs to be corrected for atmospheric pressure fluctuations in order to reconstruct the true sea surface variability. This was done using National Center for Environmental Prediction (NCEP) Reanalysis of daily atmospheric pressure time series at 20°N, 86°15'W (NOAA-CIRES 2006). In addition, surface wave measurements are available for 2 yr, September 2003 to November 2005, at a site located 500 m from the fore-reef outside the Puerto Morelos lagoon. These wave measurements were taken hourly over a 20-min window (see Coronado et al. [2007] for details).

Other physical factors that have been found to influence pueruli settlement to some extent include the southern oscillation index (SOI) (Phillips et al. 1991), wind and wind stress components (Acosta et al. 1997; Eggleston et al. 1998), current variability (Yeung et al. 2001), and rainfall (as an indirect measure of onshore storms; Caputi and Brown 1993). Monthly data on SOI throughout the study period were obtained from NOAA-NCEP (2006). Monthly accumulated rainfall was estimated from daily measurements taken at Puerto Morelos from September 1992 to October 2005. Daily time series of wind and wind stress components (in the oceanographic convention, i.e., with the wind vector pointing toward the direction it is blowing and using trigonometric degrees, measured counterclockwise from the east, which represents 0°) were obtained from the NCEP Reanalysis product at 20°N, 86°15'W (NOAA-CIRES 2006). Wind and wind stress components were calculated along every possible direction between 0° and 360° in 5° increments. Current variability (along main current axis and perpendicular to the main axis) was obtained from Coronado et al. (2007). Monthly averages of all physical factors were cross-correlated with the log-transformed monthly settlement indices over their respective simultaneous measurement periods.

*Geographical range of potential sources of pueruli arriving at the Mexican Caribbean coast*—The geographical range of potential sources of pueruli that reach the Quintana Roo coast were investigated using numerical model simulations. We used the French Océan Parallélisé (OPA) model (OPA 8.1) (Madec et al. 1998) in its CLIPPER configuration with a domain encompassing the entire Atlantic Ocean. The details of the numerics are described in Penduff et al.

(2006). The resolution of the isotropic horizontal grid is  $1/6^\circ$  (approximately 17 km at the latitude of the Yucatan peninsula), and in the vertical there are 42 grid levels, with a resolution decreasing from 12 m at the surface to 200 m below 1,500 m. The specific model run that we used (Reynaud et al. 1998) started from rest and initialized temperature and salinity climatology. It was spun-up for 4 yr (1990–1993) using ERA15 European Centre for Medium-Range Weather Forecasts Re-Analyses (ECMWF)–reanalyzed fluxes and then for 7 yr (1994–2000) using hybrid fluxes combining European Remote Sensing Satellite winds and ECMWF analyzed fluxes. In the present study, we used the last 6 yr of this run (i.e., from the beginning of 1995 to the end of 2000).

Available current fields from the model output are stored in 5-d averages. Between every two consecutive 5-d intervals, the current fields are linearly interpolated to obtain hourly fields, which are used to integrate the trajectories of particles using a second-order integration scheme. This model is well known to reproduce the mesoscale eddy variability (Barnier et al. 2001; Treguier et al. 2003) but it does not resolve small-scale processes. Therefore, we implemented a first-order Markovian scheme (Lumpkin et al. 2002; Mariano et al. 2002) to reproduce the variability at subgrid spatial scales, taking into account the Lagrangian decorrelation time scales ( $\sim 1.5$  d) derived from observed drifter trajectories within the Caribbean (Centurioni and Niiler 2003). Then, to mimic diffusion at suprainertial time scales (of the order of 1 h), a normally distributed random variability with amplitude of  $5 \text{ cm s}^{-1}$  was introduced to the velocity components at every interpolated hourly time step in each trajectory. These stochastic perturbations of the modeled current fields produce different trajectory realizations from the same 6-yr model simulation (see Fig. 2 for an example). Although not independent, these different realizations permit “saturating” the trajectory statistics that are potentially provided by the given current fields from the model.

Rather than integrating the trajectories forward in time starting in a multitude of places distributed randomly across the Caribbean Sea and beyond, a backward time integration starting from locations along the Quintana Roo coast was used. This scheme, which is possible because the current fields are available for the previous 6 yr, is much more efficient for determining the place of origin of trajectories that arrive at a certain location at a specific time (e.g., Incze and Naimie 2000). Accordingly, the specific integration procedure consisted of “releasing” 100 particles evenly distributed along the Quintana Roo coast every 5 d between 01 March and 30 April and also between 01 September and 30 October (i.e., within the two periods of peak reproduction of *P. argus* and also coincident with seasonal peaks in pueruli settlement across the Caribbean; see Discussion) during each of the six available years of model simulations. The current fields used were centered at a depth of 30 m, within the depth of vertical distribution of phyllosomata of *P. argus* ( $< 50$  m; Yeung and McGowan 1991; Alfonso et al. 1995). Each individual trajectory was followed for a 1-yr period or until it either reached a coast or left the integration domain limited by the  $59^\circ\text{W}$  meridian

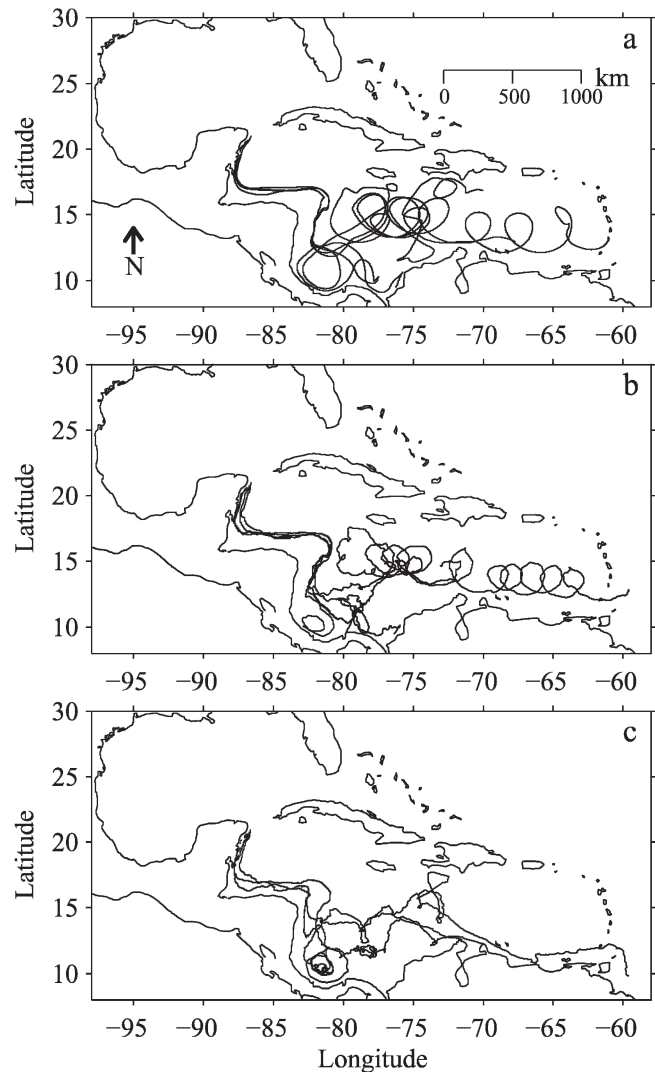


Fig. 2. (a) Example of 10 modeled trajectories without small-scale perturbation during 24 Oct 1998–23 Oct 2000; (b) example of 10 trajectories with small-scale perturbation for the same period as in panel a; (c) another realization of 10 trajectories with small-scale perturbation for the same period as in panels a and b.

and the  $30^\circ\text{N}$  parallel. Once the trajectories had been calculated for all the, say, March–April periods across the 6 yr, the “end positions” (actually the initial positions, since the integration was performed backwards in time) were accumulated in 13 arbitrarily defined geographic boxes throughout the Caribbean Sea and beyond (see Results). For each of the two selected 2-month periods across the 6 yr considered, there were about 6,000 computed trajectories, but the results were based on adding up five stochastic simulations, which potentially analyzed on the order of 30,000 trajectories. However, we only considered the particles originating within each box that took 5–9 months (that is, the range in larval duration) to reach the Quintana Roo coast and estimated the mean ( $\pm$  standard deviation [SD]) of the time in months required for these particles to get from that specific box to the Quintana Roo coast.

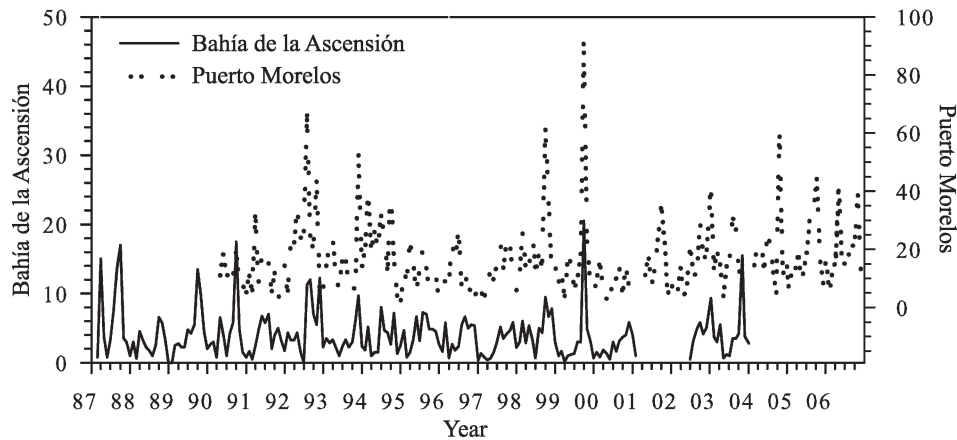


Fig. 3. Time series of monthly settlement indices (mean number of pueruli collector<sup>-1</sup> month<sup>-1</sup>) in Bahía de la Ascensión (March 1987 to February 2001 and July 2002 to January 2004) and in Puerto Morelos (May 1990 to December 2006). Note the different Y-axis for each location.

We obtained data from all the satellite-tracked drifters released in the North Atlantic between February 1979 and May 2007 (Global Drifter Program Data Assembly Center, National Oceanic and Atmospheric Administration). All drifters that passed offshore the Quintana Roo coast 5–9 months after their release date within the Caribbean Sea or after entering the Caribbean Sea were selected in order to compare their trajectories with the simulated trajectories. However, it is important to clarify that because the model did not incorporate potential effects of biological variables such as larval mortality or behavior across the larval period (i.e., vertical migrations or horizontal swimming capabilities toward the end of the pelagic stage), results from the model should be considered as a “null model” (sensu Siegel et al. 2003) of the potential range of origin of larvae that arrive at the Quintana Roo coast at the appropriate time to settle at peak settlement periods.

## Results

*Patterns of pueruli settlement*—The entire set of time series of monthly pueruli settlement indices for Bahía de la Ascensión and Puerto Morelos are shown in Fig. 3. In both locations, settlement occurred throughout the year, with much variability. In Bahía de la Ascensión, monthly settlement indices ranged from 0 (in January and February 1989 and in July 1992) to 20.5 (in October 1999), and in Puerto Morelos they ranged from 1.5 (in January 1995) to 91 (in October 1999). The mean monthly settlement index in Puerto Morelos (16 pueruli collector<sup>-1</sup>) was four times as high as that in Bahía de la Ascensión (4 postlarvae collector<sup>-1</sup>). Coefficients of variation (CV), derived from the 12-yr period of simultaneous samplings, differed significantly between locations ( $F_{129,129} = 1.371$ ,  $p = 0.037$ ). Puerto Morelos showed a greater CV (0.842) than Bahía de la Ascensión (0.810).

Separate autocorrelation plots for each series show sinusoidal cycling with an annual rhythmicity (Fig. 4a,c). The annual rhythmicity was better defined, with higher autocorrelation coefficients, in Bahía de la Ascensión than

in Puerto Morelos. The spectral analyses show that in each location a significant proportion of the variance was concentrated in a 12-month periodicity (Fig. 4b,d), but these spectral densities were also higher in Bahía de la Ascensión. In the cross-correlation between both series (first Puerto Morelos, lagged by Bahía de la Ascensión), the highest correlation coefficient, 0.516 ( $p < 0.001$ ), occurred at zero lag, followed by a correlation of 0.234 ( $p < 0.05$ ) at lag -1 (Fig. 5a). The cross-spectrum analysis showed the greatest cross amplitude around a 12–13-month periodicity (Fig. 5b), with squared coherency values (analogous to  $r^2$ ) of 0.798 and 0.780, respectively.

In both locations, monthly settlement indices averaged across all years showed peak settlements during the autumn months. In Puerto Morelos, there was a clear peak in October, whereas Bahía de la Ascensión showed a wider time window, from August to November (Fig. 6a). The average monthly settlement indices between both sites were significantly correlated ( $r = 0.740$ ,  $n = 12$ ,  $p = 0.006$ ). Annual settlement indices across the 12 yr of simultaneous data from both locations (Fig. 6b) were also significantly correlated ( $r = 0.630$ ,  $n = 12$ ,  $p = 0.034$ ). The ratio of maximum to minimum annual settlement indices was 3.0 in Bahía de la Ascensión and 2.6 in Puerto Morelos.

*Relationships between pueruli settlement and physical factors*—Cross-correlation functions between monthly averages of physical variables and settlement indices at Puerto Morelos at zero lag and maximum correlation functions with their respective lags are shown in Table 1. Correlations with monthly averages of current components, significant wave heights, SOI, or rainfall were either nonsignificant or not clearly established. Wind (50° trigonometric) and wind stress (65° trigonometric) showed significant correlations at lag -1. Higher correlations occurred with SST (0.455) and atmospheric pressure (-0.301) at lag -1 and with sea level (0.395) at zero lag. Sea level, SST, and atmospheric pressure are interrelated factors (e.g., maximum correlation at lag -1 of sea level, lagged, with SST = 0.598 and with atmospheric pressure of

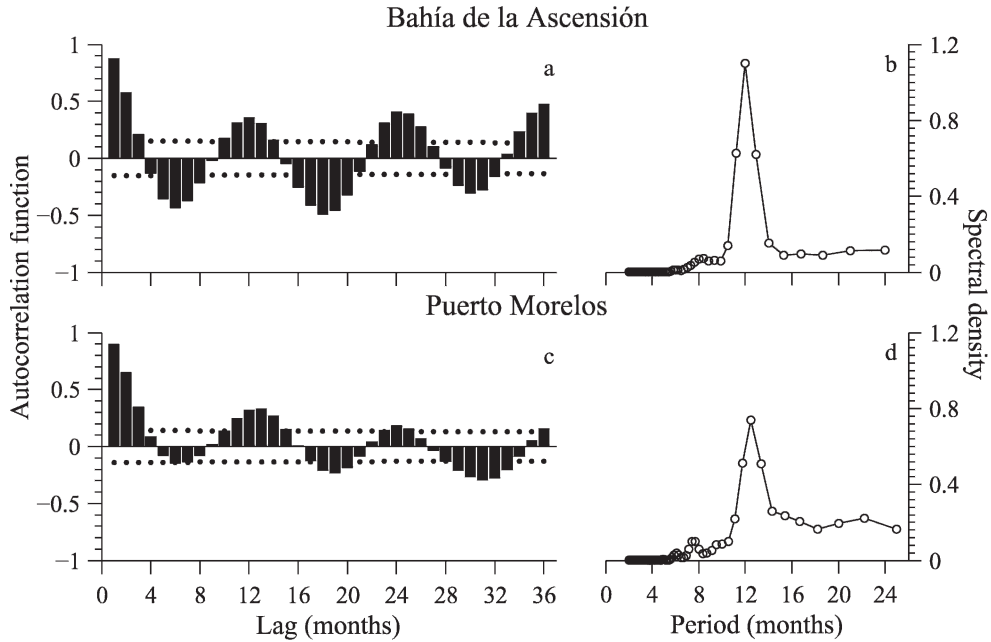


Fig. 4. Autocorrelation plots of smoothed, log-transformed series of monthly settlement indices showing annual rhythmicity in (a) Bahía de la Ascensión and (c) Puerto Morelos; dashed lines are 95% confidence limits. Spectral density for (b) Bahía de la Ascensión and (d) Puerto Morelos, showing peak periodicities at around 12 months.

-0.434). Also, northeasterly winds would tend to pile up water that would flow over the reef crest into the back-reef lagoon and to force the build-up of waves that may further induce inflow by overtopping of the reef crests (Roberts et al. 1992). In conjunction, these results support the notion that sea level is the physical factor most likely influencing settlement indices.

Figure 7 shows the reconstructed series of sea-level anomalies measured at the nearby Port of Calica and the corresponding Puerto Morelos settlement time series. In general, positive sea-level anomalies tended to correspond to relatively high pueruli indices and negative sea-level anomalies to low pueruli indices. Therefore, it would appear that large pueruli influxes into the lagoon occur when there is a large inflow of water from the outside ocean due to large positive sea-surface anomalies accompanied by reasonably significant surface wave height conditions. This,

however, would be true if the availability of pueruli in adjacent oceanic waters was constant and also if the surface wave heights did not vary much, neither of which occurs in reality. The availability of pueruli in adjacent oceanic waters is a complex issue that depends upon many factors (*see Discussion*), whereas the wave regime in front of the lagoon is also quite variable year-round. For example, Fig. 8a shows the data of the two available years (September 2003–November 2005) of monthly average significant wave heights ( $H_S$ ) measured outside the Puerto Morelos reef lagoon and the monthly pueruli indices for the same period, whereas Fig. 8b shows the hourly  $H_S$  data. When averaged across each month, values of  $H_S$  tended to be higher during the winter relative to the rest of the year, reflecting the influence of waves generated by winter cold fronts arriving from the north (Coronado et al. 2007). However, it is during the late summer–autumn months that

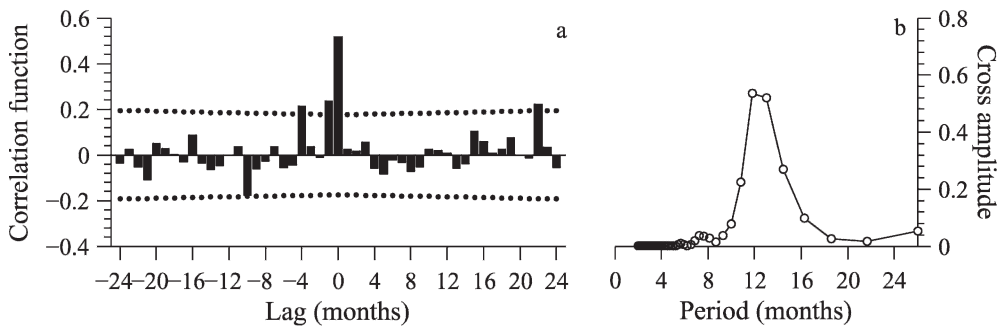


Fig. 5. (a) Cross-correlation between monthly anomalies in settlement indices in Puerto Morelos and Bahía de la Ascensión; dashed lines are 95% confidence limits. (b) Cross amplitude between the frequency components in the two smoothed series, showing the greatest covariance at the 12–13-month periodicities.

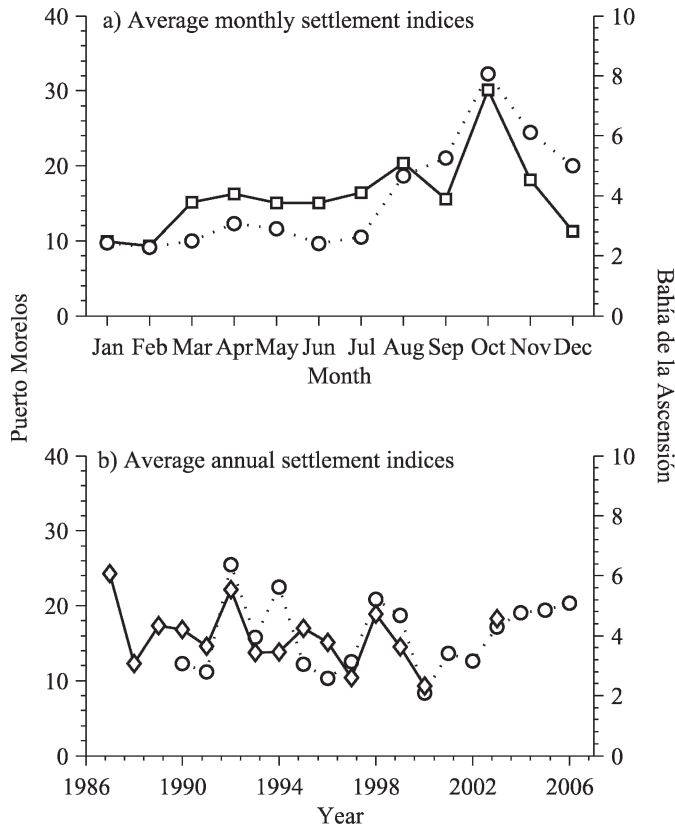


Fig. 6. (a) Average monthly settlement indices (data from each month averaged across 1987–2001 in Bahía de la Ascensión and across 1990–2006 in Puerto Morelos). (b) Average annual settlement indices in each location (data averaged across January–December each year). Note the different Y-axis for each location.

the highest extreme wave events, associated with the passage of tropical storms or hurricanes through the region, are observed. For example, Fig. 8b shows an extreme wave event (with  $H_S$  values up to 5.8 m) that occurred with the passage of hurricane Ivan 250 km off of Puerto Morelos in the middle of September 2004. This extreme wave event was not reflected in the monthly

average wave series, but it may have contributed to the large settlement index obtained on the following collection date (October 2004; Fig. 8a), indicating that sporadic extreme wave events, not necessarily reflected in the monthly wave averages, may enhance the onshore transport of pueruli.

To test this notion, we examined the concurrence of extreme settlement pulses (defined as monthly settlement indices greater than or equal to the mean + 1 SD) and the passage of tropical storms and hurricanes through the region (i.e., the northwestern Caribbean). Data on hurricanes were obtained from the National Hurricane Center (NOAA-NHC 2006). Across the study period, there were 21 extreme settlement pulses in Puerto Morelos ( $\geq 30$  pueruli collector<sup>-1</sup>), 14 (67%) of which were associated with the passage of a tropical storm or hurricane (Fig. 9b). This association with hurricanes also occurred for 17 of 23 (65%) extreme settlement pulses ( $\geq 7$  pueruli collector<sup>-1</sup>) in Bahía de la Ascensión (Fig. 9a). Depending on the time of the hurricane passage relative to the following sampling date, extreme settlement pulses were recorded either on the same month or a full month after the passage of a hurricane. A few extreme settlement pulses were associated with the passage of severe cold fronts. Thus, extreme settlement pulses appear to be related to extreme weather events that generate large surface waves. Although not all extreme settlement pulses were associated with tropical storms, these limited time series indicate that there is about a 65% chance of having a major arrival of pueruli into coastal areas during the passage of a tropical storm or hurricane.

*Geographical range of potential sources of pueruli settling in the Mexican Caribbean coast*—Although the model analyzed 30,000 particles for each of the two selected arrival periods, those that completed their (inverse) trajectories to the Quintana Roo coast within the 5–9-month period (1 month = 30 d) amounted to 5,486 for the 01 March–30 April arrival period (18.3% of 30,000 particles) and to 8,239 for the 01 September–31 October period (27.4% of 30,000 particles). Only these trajectories

Table 1. Cross-correlations at zero lag between monthly averages of physical variables (first) and Puerto Morelos monthly pueruli indices (log-transformed, lagged), and maximum correlations at their corresponding lags.\*

Variable	Length of series (months)	Correlation at zero lag	Maximum correlation (lag)
Atmospheric pressure (Pa)	193	-0.259**	-0.274**(-1)
Wind components (m s <sup>-1</sup> ) (trigonometric degrees)	193	0.109(25°)	0.308**(-1, 50°)
Wind stress components (Pa) (trigonometric degrees)	193	0.114(20°)	0.297**(-1, 65°)
SOI	193	-0.048	-0.211**(-6)
Sea level (cm)	108	0.398***	
SST (°C)	108	0.431***	0.455***(-1)
$H_S$ (m)	25	-0.168	-0.196
Current (m s <sup>-1</sup> ) along principal axis	55	0.024	0.198(-1)
Current (m s <sup>-1</sup> ) perpendicular to principal axis	55	0.065	0.147(+2)
Accumulated rainfall (mm)	154	0.109	0.274**(-23)

\* SOI, southern oscillation index;  $H_S$ , significant wave height; SST, sea surface temperature. Degrees in parentheses following correlation values for wind and wind stress denote direction in trigonometric degrees (i.e., counterclockwise from east, considered as 0°).

\*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

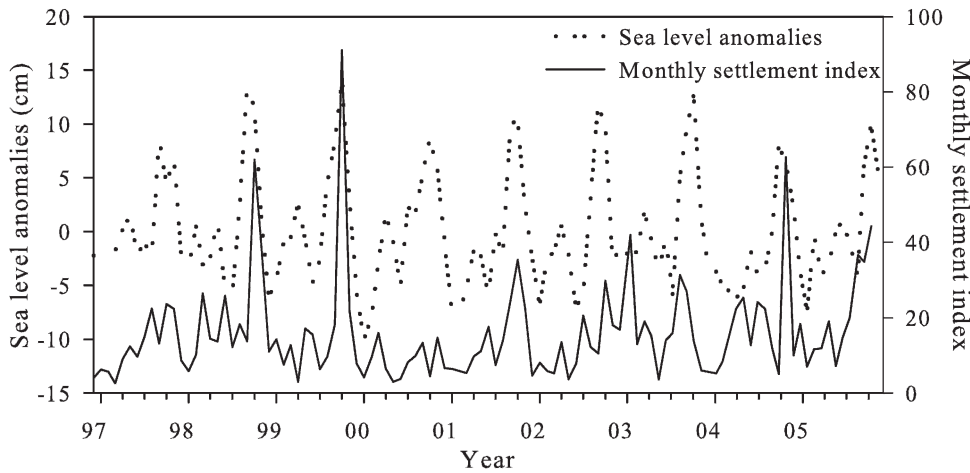


Fig. 7. Time series of mean monthly sea-level anomalies at the Port of Calica and mean monthly settlement indices at Puerto Morelos (December 1996–November 2005).

were used to calculate the percentages of particles originating within each geographic box.

Within the March–April arrival period (Fig. 10a), virtually no particles arrived to the Quintana Roo coast within 5–9 months from boxes 1 (Quintana Roo coast), 13 (Florida), and 8 (central Caribbean), and very few came from boxes 2 (Belize–Nicaragua), 11 (northern Cuba), and 12 (Bahamas–Turks and Caicos). For this arrival period, the most prominent source region for particles arriving to the Quintana Roo coast included boxes 4 (Venezuela) and 3 (Costa Rica–Colombia), followed by boxes 9 (Jamaica) and 6 (Lesser Antilles). Mean ( $\pm$ SD) travel times varied from  $6.0 \pm 0.8$  months for 14 particles originated in box 2 to  $8.1 \pm 0.8$  months for 657 particles from box 6 (Fig. 10b).

For the September–October arrival period (Fig. 11a), no particles arrived to Quintana Roo within 5–9 months from boxes 13 and 8, and very few particles came from boxes 1 (Quintana Roo), 2, 11, and 12. As was the case with the March–April data, the most prominent source region included boxes 4 and 3, but this time followed by boxes 5 (outside the Caribbean), 6 (Lesser Antilles), and 10 (southern Cuba). Within this arrival period, mean ( $\pm$ SD) travel times of particles (Fig. 11b) varied from  $5.6 \pm 0.7$  months for four particles originating in box 2 to, interestingly,  $8.1 \pm 1.2$  months for two particles originating in Quintana Roo (box 1).

When comparing Figs. 10b and 11b, it is interesting to note a seasonal variability in the travel times of trajectories originating within each box. Particles originating in most boxes tended to present faster trajectories for the September–October arrivals relative to the March–April arrivals. This seasonality in the Caribbean circulation is not an artifact of the model but rather an actual phenomenon verifiable through other independent observations, such as the seasonal cycle in the kinetic energy in surface currents deduced from altimetry observations within the Caribbean Sea (CNES 2007).

Results from the model for both arrival periods indicate that the potential exists for larvae of *P. argus* originating almost anywhere across the greater Caribbean (except

Florida) to pass close to the Quintana Roo coast at the appropriate time to metamorphose and settle. However, a rigorous statistical comparison with trajectories followed by real drifters was not possible. Out of 2,646 drifters released in the North Atlantic between February 1979 and May 2007, 643 passed through or were released in the Caribbean Sea, but only 52 passed offshore the Quintana Roo coast, and only 14 did so 5–9 months after entering the Caribbean or after their date of release (Fig. 12). Five of these 14 drifters traveled from the Lesser Antilles arc (our box 6), three from box 4, two each from boxes 3 and 7, one from box 12, and one (drifter No. 59861) actually

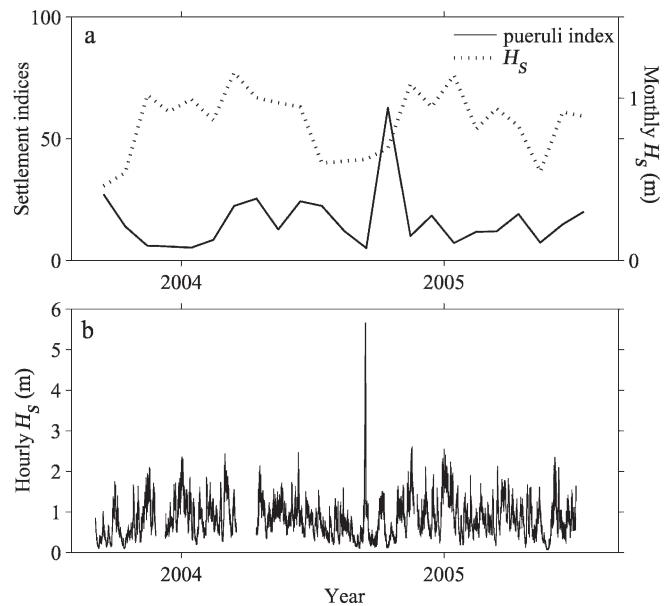


Fig. 8. (a) Monthly settlement indices at Puerto Morelos and monthly average significant surface wave height ( $H_s$ , m) measured outside the reef lagoon from September 2003 to November 2005. (b) Hourly measurements of significant wave height, showing an extreme wave event during the passage of Hurricane Ivan on 14 September 2004. The yearly ticks correspond to the beginning of each year.

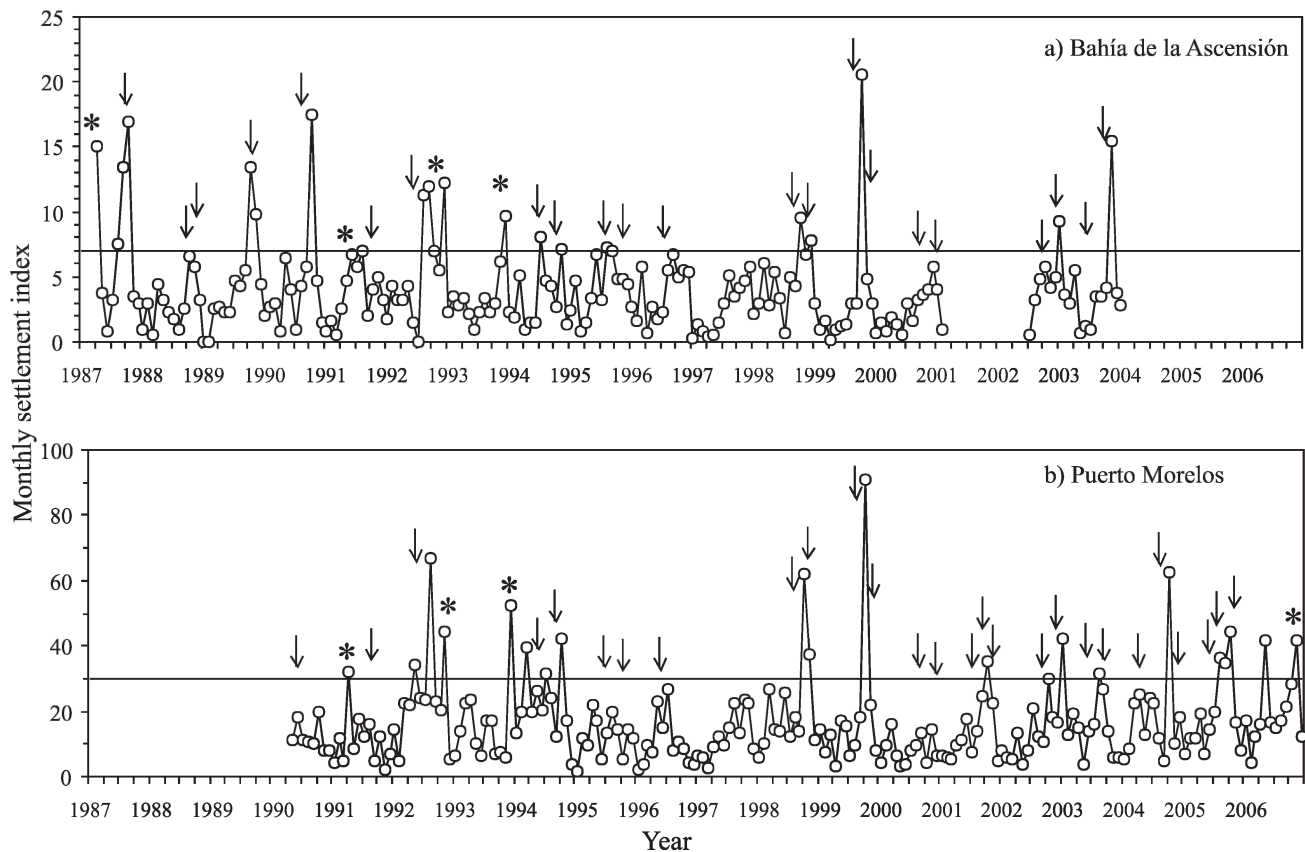


Fig. 9. Occurrence of tropical storms and hurricanes (arrows) through the western Caribbean region and their relationship to extreme settlement pulses (defined as the mean pueruli index  $+1$  SD] and denoted by horizontal line) in (a) Bahía de la Ascensión and (b) Puerto Morelos. Asterisks denote extreme settlement pulses associated with strong winter cold fronts.

returned to Quintana Roo. This drifter was released about 30 km southwest of Cozumel Island. It went first into the Gulf of Mexico, then returned into the Caribbean bordering the western point of Cuba and remained for a time looping in a cyclonic–anticyclonic eddy field southwest of Cuba. The drifter then passed again close to Cozumel Island 8 months after its release date. Thus, the travel time of this drifter was similar to the travel times of the two particles that returned to Quintana Roo in our model run (7.2 and 8.9 months).

## Discussion

Our results show that postlarvae of *P. argus* settle along the Quintana Roo coast year-round and that despite the greater level of settlement in Puerto Morelos relative to Bahía de la Ascensión, settlement patterns were similar in both locations, with average seasonal maxima during the autumn. Coherence in temporal settlement patterns of spiny lobster postlarvae across nearby locations is common, indicating that factors that drive postlarval settlement operate over wide expanses of coast (Phillips et al. 1991; Booth 1994; Eggleston et al. 1998). However, the cross-spectrum result indicates that the two settlement time series are decoupled during some years. Also, the annual cycle was better defined at Bahía de la Ascensión than at Puerto

Morelos, reflecting the higher settlement variability at Puerto Morelos. These results may reflect the further influence of local dynamics on settlement patterns. Bahía de la Ascensión lies in the area impinged by the Cayman current, where the current is wider but less intense and the effect of eddies in its intensity is also less pronounced, whereas Puerto Morelos lies closer to the Yucatan strait, where the current is narrower but its intensity is greater and is more strongly modulated by the passage of eddies (Centurioni and Niiler 2003; Cetina et al. 2006).

In marine animals, passive transport distances tend to increase exponentially with larval duration (Shanks et al. 2003; Siegel et al. 2003). For example, successful passive transport of reef fish larvae between Cape Hatteras (U.S.A.) and Bermuda, although sporadic, would occur more frequently for a species with a larval duration of 55 d relative to other species with larval durations of 22–32 d (Schultz and Cowen 1994). As a result of their much longer larval duration and their lesser horizontal swimming abilities, compared to reef fish larvae, phyllosomata of *P. argus* have a greater potential for horizontal passive transport. This potential is exemplified by the sporadic records of adults of *P. argus* off the Atlantic coast of Africa (Freitas and Castro 2005). But despite this potential for long-distance transport, the Caribbean metapopulation of *P. argus* would not be able to persist in the absence of

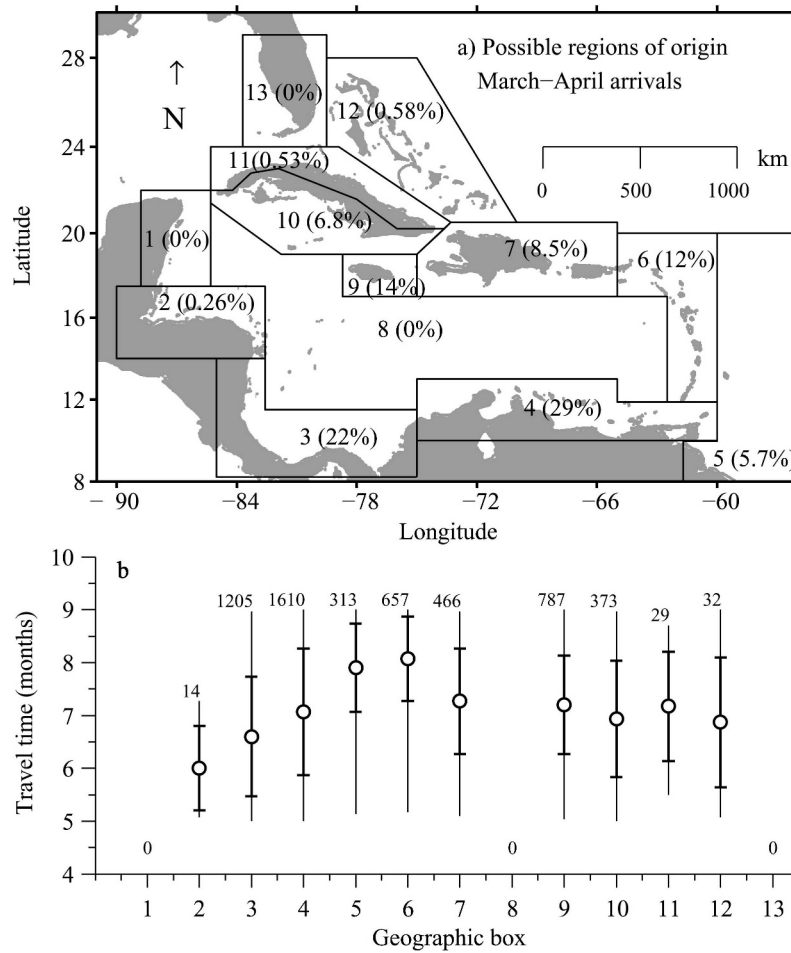


Fig. 10. Results of the backward integration of modeled trajectories of particles “released” along the Quintana Roo coast between 01 March and 30 April of 6 yr (1995–2000). (a) The 13 arbitrarily defined geographic boxes (first number in box) and the percentage of particles (in brackets) originating in each of these boxes that would arrive to the Quintana Roo coast (box 1) within 5–9 months (estimated larval duration). Total number of trajectories is 5,486. (b) Travel times of trajectories originating in each geographic box (open circle: mean; vertical line: range; horizontal lines:  $\pm 1$  SD; numbers above lines are the numbers of particles originating in each box).

mechanisms of larval retention near at least some source populations or of larval connectivity pathways that permit self-recruitment (i.e., feedback from some local population to itself; Armsworth 2002). Retention of phyllosomata probably occurs in regions with persisting recirculation features, such as southwest Cuba (Yeung and McGowan 1991; Alfonso et al. 1995; Cruz 1999), where cyclonic eddies lasting up to 10.5 months have been revealed by satellite-tracked drifters (Richardson 2005); the Exuma Sound in the Bahamas (Lipcius et al. 1997); the Campeche Bank in the Gulf of Mexico (Manzanilla-Domínguez and Gasca 2004); and the Panama–Colombia gyre, where drifters have persisted up to 13 months (Centurioni and Niiler 2003; Richardson 2005). Also, importantly, advection may be further modulated by vertical migrations, which tend to increase in depth range with phyllosoma stage, as shown for some lobster species in which larval vertical migrations span 150 m or more (e.g., *Jasus edwardsii*, Booth 1994; *Panulirus cygnus*, Griffin et al. 2001). Although phylloso-

mata of *P. argus* seldom occur in waters deeper than 50 m and cooler than 24°C (Yeung and McGowan 1991; Alfonso et al. 1995), their advection may certainly be modulated in regions in which vertically stratified flows occur within this shallow depth range (e.g., Yeung and Lee 2002; Paris and Cowen 2004). However, because maximum flows of the main Caribbean currents occur within this depth range (Schultz and Cowen 1994; Cetina et al. 2006; Tang et al. 2006), phyllosomata that are entrained into these currents may be considerably advected.

Extended retention of pelagic larvae in swift western boundary currents, such as the Yucatan current or the Gulf current, would appear unlikely. For example, Cowen et al. (2006) estimated that, even accounting for larval behavior, self-recruitment of reef fishes (larval duration of 30 d) to the Mexican Caribbean coast would amount to a mere 9%, compared to self-recruitments of up to 57% along the Caribbean coast of Colombia. Similarly, Yeung and Lee (2002) concluded that most pueruli of *P. argus* settling in

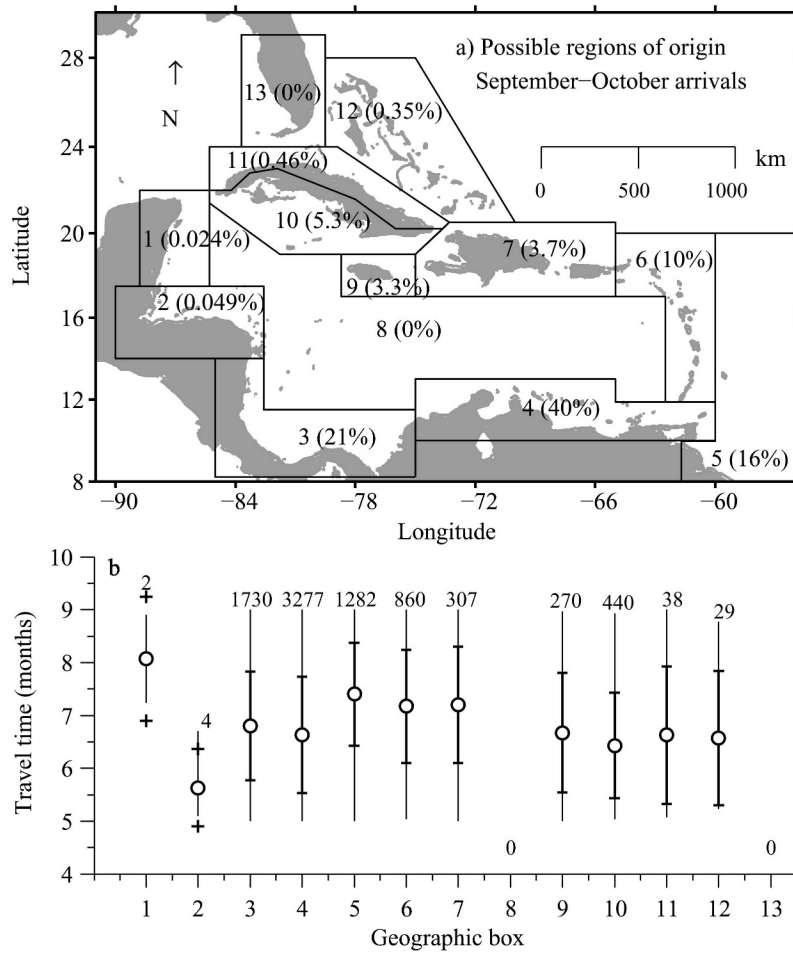


Fig. 11. Results of the backward integration of modeled trajectories of particles “released” along the Quintana Roo coast between 01 September and 30 October of 6 yr (1995–2000). (a) The 13 arbitrarily defined geographic boxes (first number in box) and the percentage of particles (in brackets) originating in each of these boxes that would arrive to the Quintana Roo coast (box 1) within 5–9 months (estimated larval duration). Total number of trajectories is 8,239. (b) Travel times of trajectories originating in each geographic box (open circle: mean; vertical line: range; horizontal lines:  $\pm 1$  SD; numbers above lines are the numbers of particles originating in each box).

the Florida Keys probably originate from upstream sources in the Caribbean, despite the local occurrence of mesoscale eddies that would retard larval advection. However, even though extended retention of phyllosomata would appear unlikely along the swift Yucatan current, which is coherent within at least the upper 130 m of the water column (Cetina et al. 2006), one real drifter and two particles in our model run returned to the Quintana Roo coast within a period consistent with the larval duration of *P. argus*. Thus, even though our null model was based on passive horizontal transport centered at 30 m in depth, it shows that there are pathways that may allow some self-recruitment from the *P. argus* population in Quintana Roo to itself. This null model, however, should be considered as a “working hypothesis” that needs to be verified by future investigations that incorporate potential effects of vertical migrations and mortality across the larval period.

Tropical species that settle year-round may show considerable interannual seasonal variation in settlement.

The wider this variation is, the greater the number of years of monthly data that are required to disclose the underlying seasonal patterns (Robertson and Kaufmann 1998). For example, short time series of *P. argus* pueruli settlement (usually 1–2 yr long) obtained at different times on disparate locations across the Caribbean region (see Briones-Fourzán 1994) have shown settlement peaks in different seasons. In contrast, monthly settlement indices averaged across our 14- and 17-yr-long time series showed settlement peaks during the autumn. Autumn settlement peaks were also disclosed when averaging monthly pueruli indices across 6 yr in the Bahamas (Eggleston et al. 1998) and across 8 yr in Cuba (Cruz 1999). Cruz (1999) contended that this autumn settlement peak is mainly driven by settlement of pueruli cohorts originated during the spring spawning peak of *P. argus*.

Year-round settlement of pueruli of *P. argus* probably reflects the year-round adult spawning activities and the variation in larval durations. It may also reflect that once

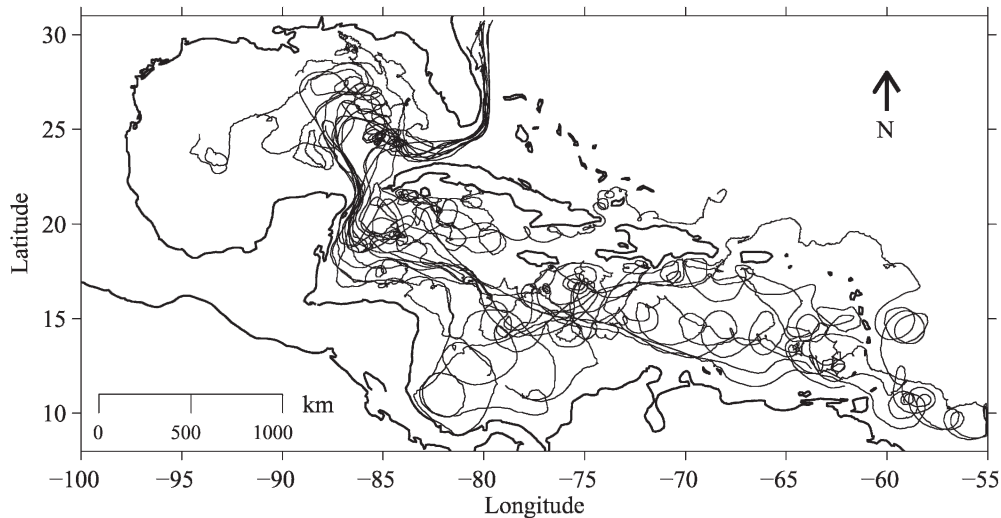


Fig. 12. Trajectories of 14 satellite-tracked drifters that passed close to the Quintana Roo coast ( $86.5^{\circ}\text{W}$ ) within 5–9 months after entering the Caribbean or after their date of release within the Caribbean.

metamorphosis takes place, pueruli will tend to swim toward the coast regardless of the prevailing conditions. If metamorphosis occurs in shelf-break areas, and assuming calm conditions and no currents, it would take a puerulus swimming at a constant speed of  $5\text{ cm s}^{-1}$  about 17 h to cross the narrow Quintana Roo shelf (an average distance of 3 km from the shoreline). This amount of time, however, could vary widely depending on many factors. Moreover, settlement variation likely results from a combination of physical and biological factors, because physical factors typically explain a relatively low portion of this variation. In the Bahamas, for example, wind speed and direction explained about 50% of the variation in pueruli indices (Eggleston et al. 1998). In one study conducted in the Florida Keys, onshore wind stress in conjunction with seasonal patterns in monthly pueruli supply explained about 30% of the variation in the pueruli indices (Acosta et al. 1997), whereas in another study, counter-current flow explained 50% of the variance in pueruli influx into coastal areas, while almost no variance was explained by onshore wind stress (Yeung et al. 2001). In our study, monthly pueruli indices showed significant correlations with several physical factors. Each of these factors would separately explain a low proportion of settlement variation (8–21%), but their interrelationship indicates that sea level would be the factor more directly influencing pueruli settlement. In addition, the association between 65% of extreme settlement pulses and the passage of tropical storms and hurricanes underlines the potential joint modulating effect of wave height and sea level on pueruli influx into coastal waters.

Tropical storms and hurricanes represent the most extreme meteorological systems in the tropical regions. These systems generate storm surges and extreme waves over a long fetch, with the dominant waves being remotely generated swell (Young 2006). In areas with narrow shelves, such as the Quintana Roo coast, storm surges may be relatively low, but hurricane waves reach consid-

erable heights, and the breaking of these large waves over the subtidal coral reefs may greatly increase the influx of nearby oceanic waters into back-reef lagoons and shallow bays. This action may also enhance the onshore transport of pueruli already swimming in those waters toward the coast. That many extreme settlement pulses were associated with tropical storms and hurricanes, whereas only a few were associated with strong winter cold fronts, further indicates that the availability of pueruli in nearby oceanic waters is greater during the late summer–autumn period (5–8 months after the main spring spawning peak across the Caribbean) than during the winter, supporting the contention of Cruz (1999) that the spring spawning peak of *P. argus* is an important biological factor underlying the interannual autumn settlement peak.

It may be argued, however, that larvae produced by a peak spawning event could potentially follow multiple dispersal pathways (as indicated by our modeled trajectories), which in conjunction with high and variable levels of larval mortality could result in settlement patterns largely independent of patterns at the time of spawning (Sale and Kritzer 2003). Indeed, we did not record large settlement pulses during the autumn of every year or with the passage of every tropical storm, but the extreme settlement pulses associated with hurricane systems greatly influenced the interannual autumn settlement peak. Therefore, settlement patterns reflect a complex interplay between biological factors (e.g., variability in the timing and level of larval production among Caribbean lobster populations and in the larval durations and mortality levels) and physical processes, but our findings indicate that large hurricane waves are an important factor aiding in the onshore transport of pueruli originated during the spring spawning peak. Pursuing this issue is important, because variation in settlement may be reflected in subsequent variation in local population size (Phillips et al. 2000; Armsworth 2002; Hixon et al. 2002).

Life history traits of a species, which result from complex evolution driven by numerous selective pressures, tend to match the problems posed by its natural habitat. Because population persistence requires larval connectivity pathways conducive to self-recruitment, it has been hypothesized (1) that long larval periods did not evolve to ensure dispersal but rather evolved as an incidental byproduct of the ontogenetic migration from and then back to the parental habitat (Strathmann et al. 2002) and (2) that some life history traits evolved to exploit hydrographic regimes that improve the odds of larvae returning to settle in or close to the parental population (Shanks and Eckert 2005). However, physical processes have the potential to influence multiple biological processes, such as the strategy and timing of adult reproduction, larval transport, and the timing of settlement (Cowen 2002), and selection favors some level of dispersal in spatially varying environments (McPeck and Holt 1992). Thus, a benthic species may persist in those locations subjected to physical features that successfully retain larvae, but also in locations in which physical processes aid in the transport of larvae to suitable habitats at the appropriate time to settle (Cowen 2002). In Quintana Roo, extreme settlement pulses of *P. argus*, which greatly influenced the interannual seasonal pattern, were associated with the passage of tropical storms and hurricanes. Storms have also been shown to influence onshore transport and alongshore distribution of fish larvae (Shenker et al. 1993), crab larvae (Etherington and Eggleston 2000), and larvae of *P. cygnus* (Caputi and Brown 1993). Because tropical storms and hurricanes are common events in the tropical western Atlantic and typically affect large areas or entire regions, they may represent a spatial environmental autocorrelation with important implications for the source-sink dynamics of metapopulations (Etherington and Eggleston 2000; Schiegg 2003).

Long larval phases are a trait shared by all palinurid lobsters, but if extreme settlement pulses were found to be associated with hurricanes in other Caribbean regions, this could indicate that the reproductive strategy of *P. argus* may have evolved in concert with the hurricane season to maximize onshore transport of its largest postlarval cohorts (i.e., those originated during the spring spawning peak). Testing this hypothesis would require long and simultaneous time series of pueruli settlement in several locations across the Caribbean to examine whether extreme settlement pulses follow the passage of tropical storms and hurricanes through different regions.

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