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Research Article

Postlarval settlement of spiny lobster, *Panulirus argus* (Latreille, 1804) (Decapoda: Palinuridae), at the Caribbean coast of Costa Rica

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ABSTRACT. Lobster fishery (*Panulirus argus*) forms an important part of the fishing activities along the Caribbean coast of Central America. The present study provides information regarding the seasonal abundance and distribution of postlarval *P. argus* in Parque Nacional Cahuita, Costa Rica. During the study period (March 2004-February 2005), a total of 1907 pueruli were obtained from GuSi collectors. Postlarvae were present during all months, with a pronounced peak in January-February 2005 (CPUE of 21.82 and 22.18, pueruli/collector/month, respectively), and minor peaks in May and October 2004. The abundance of postlarval *P. argus* in the study area was comparable to locations which support important lobster fisheries, *e.g.* Mexico. A majority of the postlarvae (1027 ind.) was collected during the first quarter moon, the remaining pueruli (880 ind.) during new moon; these results are in general agreement with similar findings for *P. argus* in the Caribbean area. Based upon our results, we recommend introducing a local or regional monitoring program, studying spiny lobster migration and distribution patterns, and evaluate the introduction of artificial shelters for *P. argus*.

Keywords: *Panulirus argus*, puerulus, recruitment, resource management, Central America, Caribbean.

Asentamiento postlarval en la langosta espinosa, *Panulirus argus* (Latreille, 1804) (Decapoda: Palinuridae) en la costa Caribe de Costa Rica

RESUMEN. Las capturas de langosta (*Panulirus argus*) son de gran importancia en la actividad pesquera a lo largo de las costas del Caribe de Centroamérica. El presente estudio proporciona información relevante de la abundancia temporal y la distribución de postlarvas de *P. argus* en el Parque Nacional Cahuita, Costa Rica. Durante el periodo de estudio (Marzo 2004-Febrero 2005), un total de 1907 puérulos fueron obtenidos del colector GuSi. Las postlarvas fueron colectadas durante todos los meses, con máximos en enero-febrero 2005 (CPUE de 21.82 y 22.18, puérulos/colector/mes, respectivamente), y mínimos en mayo y octubre de 2004. La abundancia de postlarvas de *P. argus* en el estudio es comparada con áreas que soportan importantes pesquerías, p. ej. México. La mayoría de las postlarvas (1027 ind.) fueron colectadas durante el cuarto creciente lunar, los restante puerulos (880 ind.) se obtuvieron en luna nueva. Estos resultados, en general, son consistentes con los encontrados para *P. argus* en el mar Caribe. Basados en estos resultados, se recomienda la introducción de un programa de monitoreo a nivel local o regional, estudiar los patrones de migración y distribución de la langosta espinosa, y evaluar la introducción de refugios artificiales para *P. argus*.

Palabras clave: *Panulirus argus,* puérulo, reclutamiento, manejo de recursos pesqueros, América Central, Caribe.

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INTRODUCTION

Lobsters of the family Palinuridae are commonly known as spiny lobsters or rock lobsters. These decapod crustaceans, which are of great commercial demand on the international market (Phillips *et al.*, 1980), inhabit temperate as well as tropical and subtropical waters (Holthuis, 1991). On a worldwide scale, the Caribbean region, Florida and the Gulf of Mexico are the principal producers of lobster. Among the commercially exploited spiny lobsters, *Panulirus argus* (Latreille, 1804) is economically the most important species (Butler IV, 2001; Cruz, 2002; Seijo, 2007; Chávez, 2009). Major countries harvesting spiny lobster in the region are the Bahamas, Brazil, Cuba, Nicaragua and the United States of America, each with landings above 1,000 ton per year (2000-2007) reported to the FAO (Cochrane & Chakalall, 2001; Muñoz, 2009). However, results of a recent diagnosis (Chávez, 2009) suggest that the *P. argus* fisheries in the Caribbean has been overexploited during most of the years analyzed (1990-2004).

Three spiny lobster species are known to occur along the Caribbean coast of Costa Rica: *Panulirus argus*, *P. guttatus* and *P. laevicauda* (Vargas & Cortés, 1999; Wehrtmann, 2004). Local fishermen claim that the spiny lobster (*P. argus*) fishery in Costa Rica can be divided into two groups according to the origin of the lobsters: (a) migratory lobsters, and (b) resident lobsters, representing a non-migratory population that can be easily recognized by its different color pattern (Wehrtmann, 2004).

The life cycle of *P. argus* is fairly well known (Booth & Phillips, 1994; Eggleston *et al.*, 1998). Ovigerous females migrate to areas close to the continental shelf, where the phyllosoma-larvae hatch (Cruz, 2002). The planktonic phase lasts between 6-11 months and comprises 11 larval stages (Cruz, 2002). After completing the phyllosoma-phase, larvae metamorphose into a postlarval stage, called puerulus (Lewis *et al.*, 1952), which returns all year-round to coastal areas (Umaña & Chacón, 1994; Briones *et al.*, 1997; Jeffs *et al.*, 2005). Postlarval settlement takes place in shallow, vegetated habitats such as mangrove roots, sea grass beds, and red algae (Witham *et al.*, 1968; Marx & Herrnkind, 1985; Briones & Lozano, 2001). Juveniles are gregarious and change habitats until reaching sexual maturity (Briones *et al.*, 1997; Cruz *et al.*, 2007).

Several studies have demonstrated a close relationship between the magnitude of postlarval settlement and the subsequent abundance of recruits to lobster fisheries (Hancock, 1981; Phillips, 1986; Lozano *et al.*, 1991; Cruz, 1999). Catch predictions based upon recruitment data are valuable information for processes related to regulations of population dynamics and management strategies (Cruz, 1999). Cuba for example established a prediction system based upon data concerning postlarval settlement of *P. argus* (Cruz, 2002).

In Costa Rica, information of recruitment patterns of *P. argus* is almost non-existent (Umaña & Chacón, 1994). During the last years, spiny lobster landings along the Caribbean coast of Costa Rica have diminished substantially (INCOPESCA, 2010), and governmental and non-governmental organizations as well as local fishery communities expressed concern about the sustainability of the *P. argus* population and its fishery. Therefore, the present study provides information concerning the abundance and distribution of postlarval *P. argus* in Parque Nacional Cahuita, Caribbean coast of Costa Rica. The results of this 12 months study are intended to provide basic data for the elaboration of a (regional) management plan for this commercially important resource.

MATERIALS AND METHODS

Study site

Mean air temperatures and precipitation along the Caribbean coast of Costa Rica vary between 25-27^{o}C and 2632-3570 mm, respectively (IMN, 2003). The study was carried out between March 2004 and February 2005 in the Parque Nacional Cahuita (Fig. 1), Limón, Costa Rica, a coastal or marginal coral reef with an external barrier and a shallow reef lagoon (0-3 m) situated between the barrier and the coastline (Cortés, 1981). The reef crest is 4 km long and runs from northeast to southeast (Cortés, 1981). This coastal ecosystem has been recognized for its high species diversity (Rojas *et al.*, 1998); the most characteristic species of hard corals are *Acropora palmata*, *Porites porites*, *Montastraea cavernosa* and *Porites divaricata* (Cortés, 1981). Since the late 1970s, Cortés (1990) observed a poor coral development, increasing areas of dead corals and turbid waters as well as an apparent decrease of fish abundance.

Sampling design

We established six sampling stations (Fig. 1), each one with five collectors parallel to the coastline, totaling 30 collectors. In each station the distance between adjacent collectors was 50 m. The stations were located in the inner part of the coral reef, behind the reef crest, at a depth between 1 and 3 m. The general bottom characteristics of all sampling stations

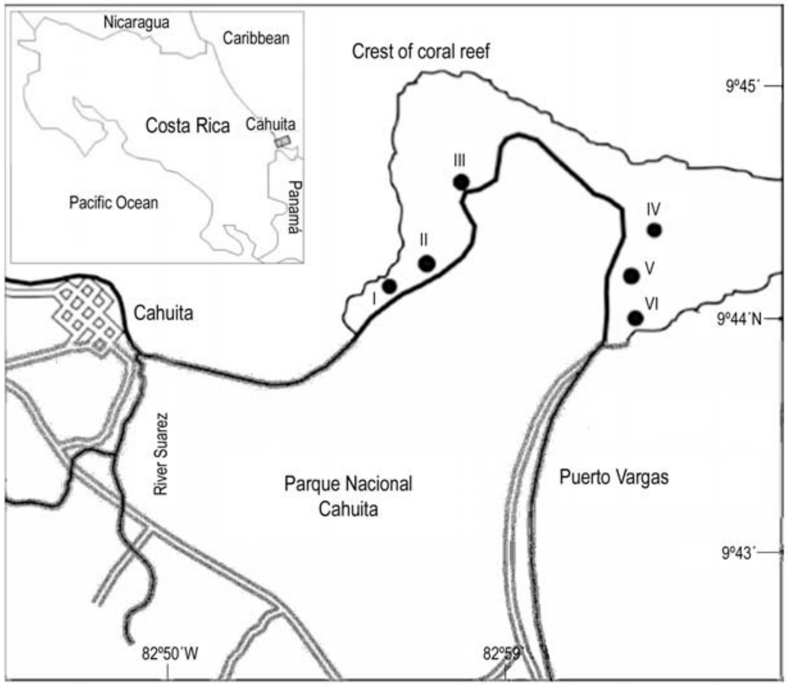

Figure 1. Location of the six sampling stations in Parque Nacional Cahuita, Caribbean coast of Costa Rica.
Figura 1. Ubicación de los seis lugares de muestreo en el Parque Nacional Cahuita, costa Caribe de Costa Rica.

were similar: presence of coral rubble, sea grass *(Thalassia testudinum*), and several species of red algae.

The type of collector ("GuSi") used in the present study is that proposed by Gutiérrez *et al.* (1992), which is based upon the model utilized in Australia (Phillips, 1972). The synthetic fiber strips (flat and 1 cm in width) attached to this type of collector simulate macroalgae, which have been reported as natural settlement habitat for the pueruli of *P. argus* (Marx & Herrnkind, 1985). We choose this type of collector for the following reasons: low costs, easy to handle, and high efficiency to attract postlarval *P. argus* (Gutiérrez *et al.*, 1992; Phillips *et al.*, 2005).

Each station was sampled twice a month, always during the morning between 08.00 and 12.00 h: one day after new moon and first quarter moon, respectively (Phillips, 1972; Phillips & Hall, 1978; Briones & Gutiérrez, 1991; Briones, 1992; Umaña & Chacón, 1994; Cruz, 2002). Each collector was pulled out of the water and carefully shaken over a plastic recipient in the boat. After inspecting for any remaining *P. argus* postlarvae (referring herein to puerulus; no juveniles were collected) on the collector, the content of the plastic recipient was filtered, and postlarvae were separated from the remaining flora and fauna. The spiny lobster postlarvae were preserved in 5% formaldehyde, and subsequently identified according to the morphological characteristics proposed by Briones & McWilliam (1997) to distinguish between *P. argus* and *P. guttatus*, the most common palinurid species reported from Caribbean waters of Costa Rica (Vargas & Cortés, 1999; Wehrtmann, 2004).

Catch per unit effort (CPUE) refers to the total number of *P. argus* postlarvae per station divided by the number of collectors checked at each station during each lunar phase (new moon and first quarter moon). The index of postlarval settlement (IP) was obtained by dividing the total number of postlarvae collected by the total number of collectors checked (Cruz, 1999). Additionally, surface water temperature (YSI-2000), salinity (refractometer), and water visibility (Secchi disk) were recorded during each monthly sampling.

Statistical analyses

We applied a One-Way ANOVA (Sokal & Rohlf, 1973) to determine differences in monthly CPUE during the sampling period. Prior to analysis, the data were transformed to log (x + 1). The effect of the location of each of the six sampling stations upon the settlement of spiny lobster postlarvae was analyzed by means of a One-Way-ANOVA, followed by a Tukey test for unequal sample sizes. Moreover, a correlation analysis (Sokal & Rohlf, 1973) was performed to determine the relations between postlarval abundance and environmental factors.

RESULTS

Postlarval abundance

A total of 1907 spiny lobster postlarvae were collected between March 2004 and February 2005. All specimens belonged to *P. argus*.

Seasonal occurrence

Postlarvae were present on the collectors in all months. Figure 2 shows the mean monthly CPUE (pueruli/collector/month) during the study period. Postlarval settlement was low between March and December 2004, with two minor peaks during this period: May (1.68 CPUE) and October (4.97 CPUE). In contrast, CPUE values in January (21.82) and February 2005 (22.18) were substantially higher than in the other months of the study period. Differences in CPUE between the 12 months were significant (ANOVA; $F = 7.149$; df = 11; $P < 0.05$). The overall mean CPUE during the study period was 5.63 puerulus/collector/month, and the IP was 3.60 puerulus/month.

Most postlarvae were collected during the first quarter moon (n = 1027), and the highest number of postlarvae per individual collector (n = 239) was recorded in January during the first quarter moon (Fig. 3). Although no significant differences were detected when comparing monthly CPUE obtained during the two lunar phases (ANOVA; F = 2.943, df = 1, $P > 0.05$), usually more puerulus were encountered in samples obtained during the first quarter moon than during new moon (exception: February 2005).

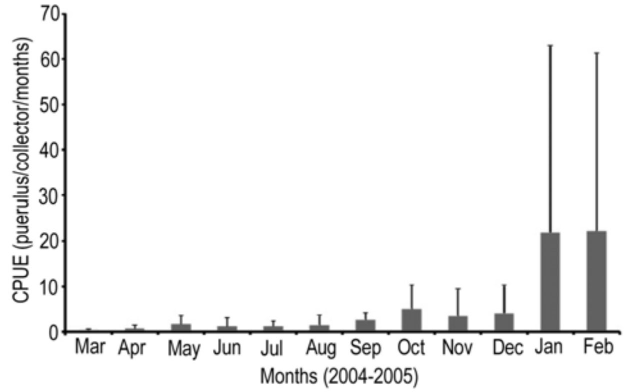

Figure 2. Monthly CPUE of *Panulirus argus* postlarvae in Parque Nacional Cahuita, Caribbean coast of Costa Rica (2004-2005).

Figura 2. Valores mensuales de CPUE de postlarvas de *Panulirus argus* en el Parque Nacional Cahuita, costa Caribe de Costa Rica (2004-2005).

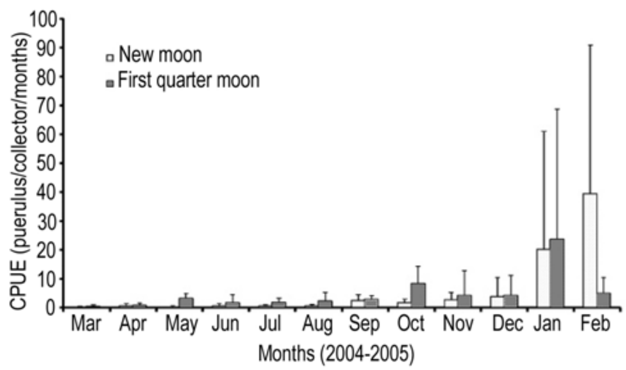

Figure 3. Monthly CPUE of *Panulirus argus* postlarvae during new moon and first quarter moon in Parque Nacional Cahuita, Caribbean coast of Costa Rica.

Figura 3. Valores mensuales de CPUE de postlarvas de *Panulirus argus* durante luna nueva y el cuarto creciente lunar en el Parque Nacional Cahuita, costa Caribe de Costa Rica.

Spatial distribution

Differences in CPUE between the six sampling stations were highly significant (ANOVA; $F = 16{,}747$, d.f. = 5, $P < 0.05$). Results from the Tukey test showed a gradient in CPUE, with the lowest values in stations I, IV, and V, the highest value in station III, and intermediate values in stations VI and II. Therefore, station III presented the highest mean CPUE during the study period (Fig. 4).

Environmental factors

Mean surface water temperatures were not statistically significantly different (ANOVA; $F = 33.207$, d.f. =11, $P > 0.05$) during the 12 months sampling period and between the stations. Mean monthly temperatures increased from March onward and peaked in June 2004 (30.6ºC); subsequently, temperatures decreased steadily, reaching the lowest value in February 2005 with 25.8ºC (Table 2). Salinities varied widely and showed no clear pattern (Tab. 2); highest and lowest values were obtained in June 2004 (34.9 psu) and July 2004 (31.3 psu), respectively. Differences of mean salinities were highly significant when comparing the monthly values (ANOVA; $F = 11.054$, d.f. = 11, $P < 0.05$); however, no statistically significant differences were detected between the different sampling stations. Water visibility did not reveal a clear pattern, and differences between months were statistically significant (ANOVA; $F = 12.031$, d.f. = 11, $P < 0.05$). In March and July 2004, the visibility was 100% (down to the bottom); lowest visibility (75%) was in May 2004.

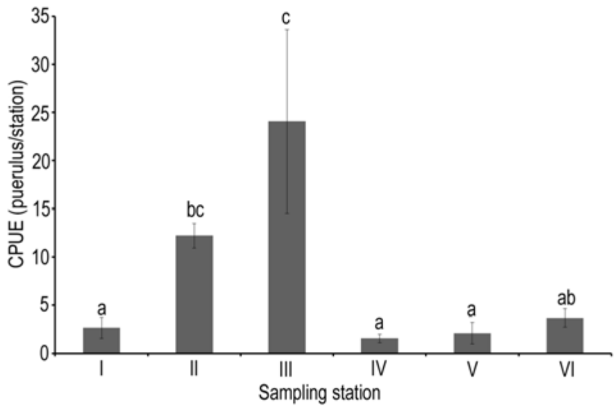

Figure 4. Mean annual CPUE (± standard deviation) of postlarval *Panulirus argus* at the six sampling stations in Parque Nacional Cahuita, Caribbean coast of Costa Rica (2004-2005). Letters above bars denote statistically similar CPUEs (Tukey test for unequal sample sizes).

Figura 4. Promedio anual de CPUE (± desviación estándar) de postlarvas de *Panulirus argus* de las seis puntos de muestreo en el Parque Nacional Cahuita, costa Caribe de Costa Rica (2004-2005). Las letras encima de las columnas indican valores de CPUE estadísticamente similares (test de Tukey para tamaños de muestreas no iguales).

The correlation analyses between these environmental factors and the level of postlarval settlement (during the 12 months study period and the six stations) did not reveal any statistically significant relation.

DISCUSSION

All postlarvae identified in the present study belonged to *Panulirus argus*. This result is consistent with similar observations reported by Briones (1993) from Bahía de la Ascensión, Mexico: during eight years, she collected thousands of puerulus of *P. argus*, and just two of *P. guttatus*. Ecological differences among the representatives of the family Palinuridae reported for the Caribbean of Costa Rica (Vargas & Cortés, 1999) may favor the settlement of postlarval *P. argus* on this type of collector (Colinas & Briones, 1990; Briones, 1995; Briones & McWilliam, 1997).

Highest levels of postlarval settlement of *P. argus* occurred in our study during the first quarter moon, which is in accordance with data obtained from other parts of the Caribbean (Briones & Gutiérrez, 1991; Briones, 1992, 1994; Eggleston *et al.*, 1998). Previous studies have shown that postlarval settlement of *P. argus* takes place principally during the dark phase of the moon; however, it remains unclear which phase (new moon or first quarter moon) is more important for recruitment for the spiny lobster (Little & Milano, 1980; Herrnkind & Butler, 1986; Briones & Gutiérrez, 1991; Briones, 1992, 1993; Cruz, 2002). Darkness will reduce predation risk during settlement of the puerulus-stage, and other factors such as local current patterns may influence whether recruitment is more pronounced during the new moon or first quarter moon phase.

The collectors of station III consistently harbored the highest numbers of postlarval *P. argus*, followed by station II (Fig. 4). These results suggest that this area presents the main entrance of postlarvae into the reef lagoon of the Parque Nacional Cahuita. However, the geographic coverage of our study area was limited; therefore, other zones in the reef system might be at least equally important for spiny lobster settlement as our stations II and III, but at the moment no data are available to corroborate this speculation. Based on our data set, stations III and II can be recommended as locations to initiate a long-term monitoring program of spiny lobster settlement in the Parque Nacional Cahuita. According to Briones & Gutiérrez (1992), such a program should have a small but sufficient number of representative sampling stations to reduce the variability of the estimations and to increase the possibility to detect significant differences in settlement rates of spiny lobster (Phillips & Hall, 1978).

Postlarval recruitment of *P. argus* was continuous during the sampling period, with small peaks in May and October 2004, and much higher peaks in January and February 2005 (Fig. 2). Arce & De León (2001) reviewed the recruitment patterns of *P. argus* in different areas of the Caribbean, and the observed peaks in May and October in our study coincide with the pattern described by these authors. Likewise, Eggleston *et al.* (1998) analyzed the spatio-temporal variation in Caribbean spiny lobster recruitment in the Bahamas and the results of this study revealed well-pronounced settlement peaks in October. The conspicuous increase of the number of collected postlarvae in January and February 2005 (Fig. 2) has not been described previously as a general temporal recruitment pattern for the Caribbean spiny lobster. However, Afonso & Gruber (2007) found in the Bahamas peak abundances in September, November, and also in February; but on the other hand, pueruli settlement was virtually absent in January and February in one study location, and recruits were completely absent in March in all study sites. The reasons for the observed peaks in January and February in the present study remain unclear, but they may be related to oceanographic events occurring far away from the study area. For example, several authors have shown that storms can affect the levels of postlarval settlement (Little & Milano, 1980; Phillips

& Booth, 1994). Moreover, Briones *et al.* (2008) indicated that sea level variations are the main factor influencing settlement of the spiny lobster along the Caribbean coast of Mexico; these authors also detected an association between extreme settlement pulses and extreme weather events like tropical storms and hurricanes during the late summer-autumn. Thus, the substantial variability in monthly pueruli recruitment of *P. argus* into the coastal zones throughout the Caribbean and Florida, as shown in this and other studies, might be related to both large-scale and local hydrographic and meteorological features (Briones, 1994; Acosta *et al.*, 1997; Eggleston *et al.*, 1998; Briones *et al.*, 2008). Future studies need to substantiate this hypothesis and to disclose the underlying factors.

The CPUE-values obtained in the present study are higher than those reported by Umaña & Chacón (1994) from Refugio de Vida Silvestre Gandoca-Manzanillo, Caribbean coast of Costa Rica, located a few kilometers south of our sampling area (Table 1). These authors used a modified Witham collector (Witham *et al.*, 1968). In terms of CPUE, the GuSi collector seems to be more efficient than the Witham collector (Briones & Gutiérrez, 1991; Phillips *et al.*, 2005), which might explain the differences between the CPUE-values reported for Parque Nacional Cahuita (present study) and the Refugio de Vida Silvestre Gandoca-Manzanillo (Umaña & Chacón, 1994).

The high levels of postlarval settlement (IP) in Parque Nacional Cahuita may indicate an interesting potential for the lobster fishery along the southern Caribbean coast of Costa Rica. Table 1 shows that the IP-values of the present study are higher than those reported for Mexico (same methods) and U.S.A. (different methods). These two countries export on average around 475 ton of lobster tails per year; in contrast, the average annual lobster catch per year (1997-2004) of the Caribbean of Costa Rica was just 109 ton (INCOPESCA, 2010). Other factors, such as smaller fishing effort and fishing areas, might be contributing to the lower production in Costa Rica. It is speculated that the discrepancy between a high IP-value and low levels of *P. argus* fishery in Caribbean Costa Rica might be related to the lack of sufficient and adequate natural refuges for subsequent ontogenetic phases of lobsters. Similar to our study, Briones & Lozano (2001) found high IP-values in areas along the Caribbean coast of Mexico where adult lobsters were scarce. We suggest performing ecological studies on subsequent local benthic phases to clarify the mismatch between IP-values and lobster landings.

Across the study period, the temperature and visibility data did not show significant variations, whereas salinity varied considerably. However, we found no relationship between the monthly recruitment index and these local environmental factors. Overall, the temperature and salinity values recorded during our study (Table 2) can be considered as suitable for a nursery habitat of *P. argus* (Field & Butler, 1994). Similarly to the *P. argus* recruitment patterns reported from the Florida Keys, (Acosta *et al.*, 1997), we assume that environmental factors, especially the wind forcing and the current regime might be important in influencing the recruitment patterns of *P. argus* in the study area. This assumption is consistent with the results of Eggleston *et al.* (1998): they found a significant relationship between along-shore wind speed and postlarval anomaly at their three study sites; however, roughly half of the variation was unexplained by wind speed and direction alone. More studies are needed to clarify the relation between small/medium-scale coastal wind forcing and circulation (current velocities and direction) and temporal recruitment patterns of *P. argus*.

Table 1. *Panulirus argus*: comparison of the index of postlarval settlement (IP) obtained in the Parque Nacional Cahuita, Caribbean coast of Costa Rica, with other studies carried out in the region.

Tabla 1. *Panulirus argus*: comparación del índice de asentamiento postlarval (IP) obtenido en el Parque Nacional Cahuita, costa Caribe de Costa Rica, con otros estudios realizados en la region.

Country	IP	Type of Collector	Reference
Cuba	13.39-29.71	Phillips (modified)	Cruz *et al.* (1991)
Costa Rica (Caribbean)	3.60	GuSi	Present study
Costa Rica (Caribbean)	0.47	Witham (modified)	Umaña & Chacón (1994)
Jamaica	2.95	Witham (modified)	Young (1991)
U.S.A. (Virgin Islands)	1.09	Witham (modified)	Kojis *et al.* (2003)
México (Bahía de la Ascensión)	1.07	GuSi	Briones & Gutiérrez (1991)

Table 2. Average monthly temperatures and salinity values at Parque Nacional Cahuita, Caribbean coast of Costa Rica.

Tabla 2. Promedio de las temperaturas mensuales y de salinidad en el Parque Nacional Cahuita, costa Caribe de Costa Rica.

	Temperature (ºC)	Salinity
March 2004	28.1	33.5
April 2004	28.7	34.6
May 2004	28.8	32.1
June 2004	28.8	34.9
July 2004	28.9	31.3
August 2004	30.6	34.3
September 2004	29.8	34.8
October 2004	29.5	33.5
November 2004	27.6	33.9
December 2004	27.0	32.5
January 2005	27.2	32.7
February 2005	25.8	34.7

CONCLUSIONS

Our data demonstrate the importance of the Parque Nacional Cahuita coral reef for postlarval settlement of *P. argus*. Recruitment occurred during the entire year, with peaks during new moon and first quarter moon. Interestingly, settlement levels of postlarval *P. argus* in the study area were comparable to locations which support important lobster fisheries, *e.g.* Mexico. The factors responsible for the spatial distribution of the postlarval settlement in our study area remain to be studied.

The use of pueruli collectors has been suggested as an efficient technique to assess management strategies (*e.g.* Quinn & Kojis, 1997; Eggleston *et al.*, 1998). Thus, and to facilitate an adequate management of the spiny lobster resource in Costa Rica (and neighboring countries), we suggest (a) initiating a long-term program to monitor postlarval settlement in Parque Nacional Cahuita and adjacent areas, ideally as part of a Central American monitoring program, with the participation of local communities, research groups, and governmental as well as non-governmental agencies; (b) studying migrations and distribution patterns of different life stages of *P. argus* through capture-recapture studies, (c) evaluating the economic, social and ecological viability of introducing artificial shelters (so-called "casitas"); the introduction of "casitas" in Cuba and Mexico (Arce *et al.*, 1997; Briones & Lozano, 2001; Briones *et al.*, 2007; Cruz *et al.*, 2007) was highly successful, and both local fishery communities and marine environment benefited from this management measure. Moreover, and according to Afonso & Gruber (2007), the prevalence of appropriate habitat for juvenile lobsters with adequate shelter next to algal-stage habitats should enhence their survival, therefore improving recruitment to the adult population and consequent harvestable stock-size.

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