Bull Mar Sci. 92(2):207–227. 2016
http://dx.doi.org/10.5343/bms.2015.1015

research paper

Distribution and abundance of *Panulirus* spp. phyllosomas off the Mexican Caribbean coast

Ashanti A Canto-García [1]
Jason S Goldstein [2]
Eloy Sosa-Cordero [1]*
Laura Carrillo [1]

[1] *El Colegio de la Frontera Sur (ECOSUR–Unidad Chetumal), Departamento de Sistemática y Ecología Acuática, Av. Centenario Km 5.5, Chetumal, Quintana Roo, Mexico CP 77014.*

[2] *Department of Biological Sciences and School of Marine Sciences and Ocean Engineering, University of New Hampshire, Durham, New Hampshire 03824.*

* *Corresponding author email: <esosa@ecosur.mx>.*

Date Submitted: 24 March, 2015.
Date Accepted: 7 December, 2015.
Available Online: 15 April, 2016.

ABSTRACT.—We evaluated the abundance and distribution of *Panulirus* spp. phyllosomas collected during two oceanographic cruises in March 2006 and January 2007 along the Mexican Caribbean coast. In total, 1138 phyllosomas were collected in 2006, and 492 were collected in 2007, comprising three families: Palinuridae; Scyllaridae; and Sinaxidae. The most abundant species of *Panulirus* for both cruises was *Panulirus argus* (Latreille, 1804). DNA barcoding methods also confirmed the identity of the phyllosomal stages of *Panulirus guttatus* (Latreille, 1804). The most abundant phyllosomal stages of *P. argus* in both years were early (I–III) and mid stages (IV–VIII) mostly found near Banco Chinchorro. The least abundant late stages (IX–X) were widely dispersed offshore. During both cruises, >70% of phyllosomal abundance was concentrated in the surface layers (0–50 m). Statistical models indicated that depth, along with year, geographical area, and time of day, were important for early- and mid-stage phyllosoma stages. The distribution and densities of phyllosomas off Quintana Roo differed among years and areas, likely due to varying environmental conditions and mediated by physical processes and the seasonality of reproductive activity of the local and regional spawning stock. In addition, early-stage phyllosomas appeared to avoid surface waters during periods of increased moonlight.

Off the coast of Quintana Roo, Mexico (i.e., Mexican Caribbean), the spiny lobster, *Panulirus argus* (Latreille, 1804), is a major fishery resource, both economically and socially (Sosa-Cordero 2003, 2011). Although a decreasing trend in annual landings has been observed since the 1980s, it remains the second largest lobster fishery in the Mesoamerican Reef region after Honduras (Chavez 2009, Sosa-Cordero 2011). In the Gulf of Mexico and Caribbean Sea, three families of lobsters have been described: Palinuridae; Scyllaridae; and Sinaxidae (Manzanilla-Dominguez and Gasca 2004). Within these groups, three species of the genus *Panulirus* are most commonly found: Caribbean spiny lobster, *P. argus*; spotted lobster, *Panulirus guttatus* (Latreille, 1804); and green lobster, *Panulirus laevicauda* (Latreille, 1817) (Padilla-Ramos and Briones-Fourzán 1997).

Like all spiny lobsters, Panuliridae have a long and complex ontogenetic development that includes five distinct phases: egg, planktonic larva (phyllosoma), postlarva (puerulus), juvenile, and adult (Butler and Herrnkind 1997, 2000). The specialized phyllosoma phase has a transparent, flattened, leaf-like shape, and progresses through a series of stages (and numerous instars) that are species-specific (Phillips and Sastry 1980, Phillips and McWilliam 1986). Of the three species, the complete larval development of only *P. argus* has been described via laboratory-based culture by Goldstein et al. (2008). They estimated that the mean pelagic larval duration of *P. argus* is approximately 6.5 mo (range = 4.5–8.0 mo), including 18–21 instars, grouped into 10 distinct stages (Lewis 1951, Goldstein et al. 2008). For *P. guttatus*, only the last few phyllosomal stages have been previously described (Baisre and Alfonso 1994). A recent study characterized the complete development of *P. guttatus* (Goldstein et al. unpubl data) because the early stages (being similar to *P. argus*) are often confused with other species. Likewise, for *P. laevicauda,* only the first three stages and some final stages have been described (Baisre and Ruiz de Quevedo 1982, Abrunhosa et al. 2004). Therefore, one of the goals for the present study was to provide better taxonomic resolution to the abundance and distribution of dominant palinurid phyllosomas in the Mexican Caribbean.

It is well known that phyllosomas express complex behaviors that modulate their distribution in the water column both vertically and horizontally (Minami et al. 2001, Bradford et al. 2005, Ziegler et al. 2010). One such behavior, ontogenetic diurnal vertical migration (ODVM), is a stage-specific trait common in many marine meroplanktonic larvae (Sekiguchi and Inoue 2002, Phillips et al. 2006, Ringelberg 2010). ODVM is strongly linked to a variety of abiotic factors including light intensity, depth, hydrodynamic conditions (e.g., currents, eddies), temperature, and salinity, which influence the vertical distribution of marine larvae including phyllosomas (see Forward 1988, Sponaugle et al. 2002 for reviews). Phyllosomal distribution is determined by their ability to disperse, and is a function of a suite of sensory and behavioral capabilities that enable them to conduct daytime vertical migrations (Minami et al. 2001, Bradford et al. 2005, Butler et al. 2011). For example, late-stages of *P. argus* phyllosomas exhibit negative phototactic behavior and concentrate at greater depths, whereas early-stage phyllosomas tend to show positive phototactic behavior (Ziegler et al. 2010, Butler et al. 2011). Hence, the depth distribution of phyllosomas tends to be, for the most part, a function of their behavioral response to light at each phyllosomal stage (Butler et al. 2011). Lastly, phyllosomas can initiate and display strong vertical movements (and lesser horizontal ones) that allow them to stratify at various depths (Phillips and Sastry 1980, Booth and Phillips 1994, Pineda et al. 2007). Thus, three attributes (limited swimming ability, ODVM, and a protracted larval duration) often result in larval dispersal to wide areas due to advective processes resulting from oceanic currents (Jeffs et al. 2005, Rudorff et al. 2009). As such, another goal of the present study was to quantify the vertical distribution of Palinurid phyllosomas over a spatial scale in selected areas of the Mexican Caribbean.

Although our biological and ecological knowledge for juvenile and adult *P. argus* and *P. guttatus* is well known, studies on phyllosomal distribution and abundance is limited (Alfonso et al. 1999, Yeung and Lee 2002, Manzanilla-Domínguez and Gasca 2004). Furthermore, it is difficult to link phyllosomal abundance to their spatiotemporal distribution in certain geographic areas. This difficulty stems from our limited knowledge of these early stages and physical factors driving their movements coupled

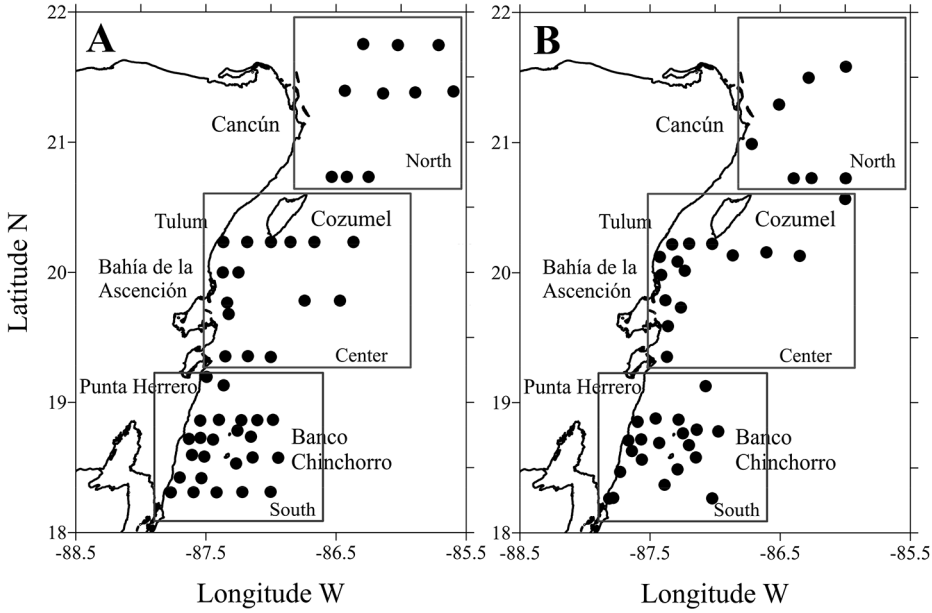

Figure 1. Study area and plankton sampling stations during the NOAA cruises aboard the R/V Gordon Gunter in (A) March 2006 and (B) January 2007.

with a complex and protracted developmental cycle, along with the challenges associated with taxonomic identification. The study of the distribution and abundance of the phyllosomal stages of lobsters in the waters off Quintana Roo serves to expand our ecological knowledge of these species. It also provides potential indicators of the recent reproductive activity of the adult stock and the imminent arrival of recruits (pueruli) according to the presence of early- and late- phyllosomal stages (Fonseca-Larios and Briones-Fourzán 1998, Sosa-Cordero 2003, Briones-Fourzán et al. 2008). The present study seeks to improve understanding of the potential supply, abundance, and recruitment of postlarvae into coastal areas, which may aid in proper management of the lobster resource off the coast of Quintana Roo, and throughout the region.

Primary study goals were to determine the abundance and spatial distribution of phyllosomas belonging to the genus *Panulirus* spp. off the coast of Quintana Roo. Phyllosomas were collected during two oceanographic cruises, in March 2006 and January 2007, to examine abundance by developmental stage as well as to determine the influence of five factors: (1) depth; (2) geographical areas; (3) sampling time (day vs night); (4) year or cruise (2006 vs 2007); and (5) moonlight intensity.

Methods

We collected phyllosomas over two oceanographic cruises onboard the R/V Gordon Gunter supported by a collaborative effort by El Colegio de la Frontera Sur (ECOSUR), the National Oceanic and Atmospheric Administration (NOAA), and the University of Miami (UM). Our sampling efforts were conducted in the Mesoamerican Barrier Reef System (MBRS) from 18 March to 1 April, 2006, and from 14 to 30 January, 2007. The surveys included sampling stations from the Yucatán channel to southern Quintana Roo, near the Mexico-Belize border (Fig. 1). Our study

areas were divided into three zones: (1) northern region, Yucatán Channel to Puerto Morelos; (2) central region, from Puerto Morelos to Punta Herrero; and (3) southern region, from Punta Herrero to the Mexico-Belize border (Fig. 1). Biological samples were collected from 56 stations during 2006 and 53 stations in 2007. Plankton tows at each station were conducted using a MOCNESS-1 (Multiple Opening/Closing Net and Environmental Sensing System, diameter = 1 m^2; mesh = 333 μm) net system. A digital flowmeter (General Oceanic model 2030, Miami, Florida, USA) was used to calculate the volume of water sampled for each tow. At selected stations (n = 4, 2007), the net system was reconfigured (diameter = 10 m^2, mesh = 505 μm) to allow the collection of samples in an oblique trawling manner at depths of 0–100 m, as well as four discrete depth intervals: 0–25, 25–50, 50–75, and 75–100 m.

All stations were sampled once during the day (06:00–18:00 hrs) and once at night (18:01–05:59 hrs); the exact time depended on when the research vessel arrived on-site. All phyllosomal samples were fixed and preserved in 70% ethanol onboard the vessel and stored in labeled collection vials. All specimens were brought back to the laboratory and examined under a binocular dissecting microscope (Carl Zeiss SV6). Phyllosomas were visually identified to the lowest taxonomic level possible and assigned to specific developmental stages according to their morphological features using a taxonomic reference library that included: Lewis (1951); Sims (1966); Robertson (1968a,b,c, 1969a,b, 1971, 1972, 1979); Baisre (1969); Baisre and Ruiz de Quevedo (1982); Baisre and Alfonso (1994); and Goldstein et al. (2008). For purposes of statistical analysis, phyllosomas were grouped into (A) total phyllosomas, including all the families of lobsters collected; while the phyllosomas of the genus *Panulirus*, exclusively, were grouped into: (B) early phyllosomas, including the stages I–III; (C) mid-stage phyllosomas (stages IV–VIII); and (D) late-stage phyllosomas (stages IX–X).

Standardized phyllosoma density values were expressed as the number of phyllosomas over each taxonomically-distinct stage(s) per volume filtered for each sampling station or depth stratum. Statistical analyses considered phyllosoma density as the response variable and the independent variables as: (1) depth, as a continuous variable (using the mid-depth values 12.5, 36.5, 62.5, 87.5 m); (2) geographical areas (north, central, and south); (3) time-of-day [day (06:00–18:00 hrs) and night (18:01–05:59 hrs)]; and (4) cruise year (2006 and 2007).

Subsequently, several alternative statistical models were fit to phyllosoma density per station, for total phyllosomas, and selected groupings of *Panulirus* (i.e., early-, mid-, and late-stage phyllosomas). In each case, the patterns of variation with respect to the aforementioned factors (1–4) were examined by fitting a series of ANCOVA models, using the 10-step protocol of Zuur et al. (2009). This statistical method alternates the fitting methods to a generalized least squares (GLS) model and restricted maximum likelihood (REML) method. Both these methods explicitly incorporate variance heterogeneity, without increasing the number of parameters in the model. Thus, instead of assuming a unique and constant variance, the fitting procedure models variance itself. This allowed an "optimal variance structure" algorithm to be chosen using the Akaike information criteria (AIC; Burham and Anderson 2002, Zuur et al. 2007, 2009). AIC scores were used to identify the most appropriate model with the minimum AIC value among a set of alternative models. Final models with the absolute minimum AIC values were considered as having greater support from the data (Burnham and Anderson 2002). However, AIC differences >2 among alternative models are more reliable (Burnham and Anderson 2002). All statistical

analyses were performed with the NLME package featured in the R software bundle (R Core Team 2014).

To examine the effect of moonlight on the vertical distribution of phyllosomas, we analyzed our data from night-only sampled stations separately for each of the two previously defined groups of phyllosomas (early- and mid-stages). Late-stage phyllosomas were excluded from this analysis since there were few observations. Mean depth values (in meters) for stations corresponding to each phyllosomal stage group were selected as the response variable (*Y*). Mean depth, calculated as the weighted mean of depth for each station where each stage group occurred along with the density of the same stage group (number/1000 m^3) was treated as weighted factor. A "moonlight index" (MI) was computed as the product of the fraction of the moon (full = 1, new moon = 0), and moon hours over the horizon (Polovina and Moffit 1995). Moonlight intensity values were queried from the US Naval Observatory (see: http://aa.usno.navy.mil/data/index.php). Nearby Cozumel Island served as a reference location for total moon hours over the horizon and was adjusted to consider only the nighttime hours over the horizon. The lack of cloud cover records during our survey cruises precluded any correction to the values of MI due to this factor. Correlation analyses (Pearson´s correlation index) were used to measure the strength and direction of the linear relationship between MI and the mean depth occupied for each stage group. All calculations were performed in the R software package (R Core Team 2014).

We used DNA barcoding to validate the identification of some of our phyllosomal samples. A subset of 92 specimens collected in 2006 and three adult lobsters of *P. laevicauda* from Bahia de la Ascensión were preserved in 95% ethanol. The amplification of the mitochondrial gene segment COI was processed using two primer sets (Folmer and Folmer_t1). The amplification of PCR (polymerase chain reaction) and purification steps were performed according to the standards of the Barcode of Life protocol (Ivanova et al. 2006, Ivanova and Grainger 2007) at the ECOSUR-Chetumal Barcodes Laboratory (Chetumal, Mexico). Sequencing was conducted at the Canadian Center of DNA Barcoding (CCDB, Guelph, Ontario). For specimens of *P. laevicauda*, we used adult tissue samples as reference material to compare with any presumed phyllosomas.

Results

Abundance and Phyllosomal Stage Composition.—During 2006, we sampled at 56 stations and were able to collect phyllosomas from 49 stations (approximately 88%). Samples were taken from all strata including the oblique haul station. Overall, 1138 phyllosomas were collected belonging to three different families: Palinuridae (88.40%); Sinaxidae (7.47%); and Scyllaridae (4.13%). Six species were identified, with *P. argus* being the most abundant (72.85%), followed by *Palinurellus gundlachi* Von Martens, 1878 (8.49%), *P. guttatus* (5.71%), *Scyllarides aequinoctialis* (Lund, 1793) (1.05%), four phyllosomas of *Justitia longimana* (H. Milne-Edwards, 1837) (0.35%), and one phyllosoma of *Parribacus antarcticus* (Lund, 1793). Some phyllosomas were badly damaged and thus difficult to identify. These could be determined only to the level of genus and included: *Panulirus* (*n* = 152, 9.49%), *Scyllarus* (*n* = 16, 1.41%), *Scyllarides* (*n* = 12, 1.05%), and an unusual specimen which, according to the literature, could be a Scyllarid "Q" phyllosoma (Robertson 1972).

Table 1. Phyllosomal abundance (number) and standardized catch (number/1000 m^3) by stage for *Panulirus argus* and *Panulirus guttatus* in 2006 and 2007 (with oblique haul). Note that no larvae of *Panulirus laevicauda* were found in the samples collected in 2006 and 2007.

	P. argus 2006		*P. guttatus* 2006		*P. argus* 2007		*P. guttatus* 2007	
Stage	Abundance	Catch	Abundance	Catch	Abundance	Catch	Abundance	Catch
I	201	242.5	2	2.6	137	174.6	0	0.0
II	28	35.5	1	1.0	16	26.1	0	0.0
III	99	118.1	21	22.9	26	37.0	0	0.0
IV	256	293.2	17	19.5	98	147.7	0	0.0
V	153	182.8	16	18.0	105	153.3	2	3.5
VI	44	52.8	4	5.0	19	25.8	1	2.0
VII	20	23.1	2	1.6	13	17.5	1	1.0
VIII	16	19.0	0	0.0	10	14.0	0	0.0
IX	8	8.8	1	1.4	3	5.3	0	0.0
X	4	4.5	1	1.3	2	1.8	0	0.0

During 2007, 45 stations were sampled with the Moc-1 (the regular MOCNESS used in 2006) and 492 phyllosomas were collected and identified from three families: Palinuridae (95.12%), Scyllaridae (4.47%), and Sinaxidae (0.41%); an additional 217 phyllosomas were captured with the Moc-10 system. Our analysis considered only data from the Moc-1 (for comparison purposes) and species were identified as follows: *P. argus* (87.20%); *P. guttatus* (0.81%); *S. aequinoctialis* (0.61%); *P. antarcticus* (0.41%); and *P. gundlachi* (0.41%); and two genera were identified: 26 *Panulirus* (7.11%) and 16 *Scyllarus* (3.46%).

The composition of collected phyllosomal stages (2006 cruise) of the genus *Panulirus* comprised stages I–X, with the most abundant stages as follows: I (22.37%); IV (30.36%); and V (19.78%); while stages IX (0.90%) and X (0.50%) were the least abundant, with only a total of 0.015 individuals/1000 m^3. The composition of *Panulirus* phyllosomas for the 2007 cruise also included stages I–X. The most abundant were stages I (28%), V (24.5%), and IV (22.8%); the least abundant were stages IX (0.70%) and X (0.47%) (see Table 1). Genetic analyses identified stages I–V) of *P. guttatus* and morphometric measurements were made to further validate these collected specimens (Online Appendix 1).

The overall distribution of phyllosomas showed different patterns for 2006 vs 2007 (Fig. 2). In the 2006 cruise, the greatest total abundance of early- (stages I–III) and mid-stages (IV–VIII) were found in the southern area, near the coast and around Xcalak, a fishing village within a national park, and Banco Chinchorro, a Biosphere Reserve (BR). Late-stage (IX–X) phyllosomas were widely dispersed in offshore waters (Fig. 3). Unlike 2006, the total distribution of early-stage phyllosomas during the 2007 cruise was more widespread, with higher concentrations in the central zone, close to the coasts of the Sian Ka'an Biosphere Reserve (SKBR) and Tulum. There were moderate concentrations of phyllosomas in the south, close to the coast of Xcalak and Banco Chinchorro BR. In particular, we found that mid-stage phyllosomas were highly concentrated in this region. As in the 2006 cruise, late-stage phyllosomas were widely dispersed in 2007 (Fig. 3D). Overall, the total distribution of phyllosomas showed more differences in 2007 compared with 2006 (see Online Appendix 2 for AIC model selection). The highest variation in the composition of *Panulirus* stages was for *P. argus,* the most abundant species with early- and mid-stages in the

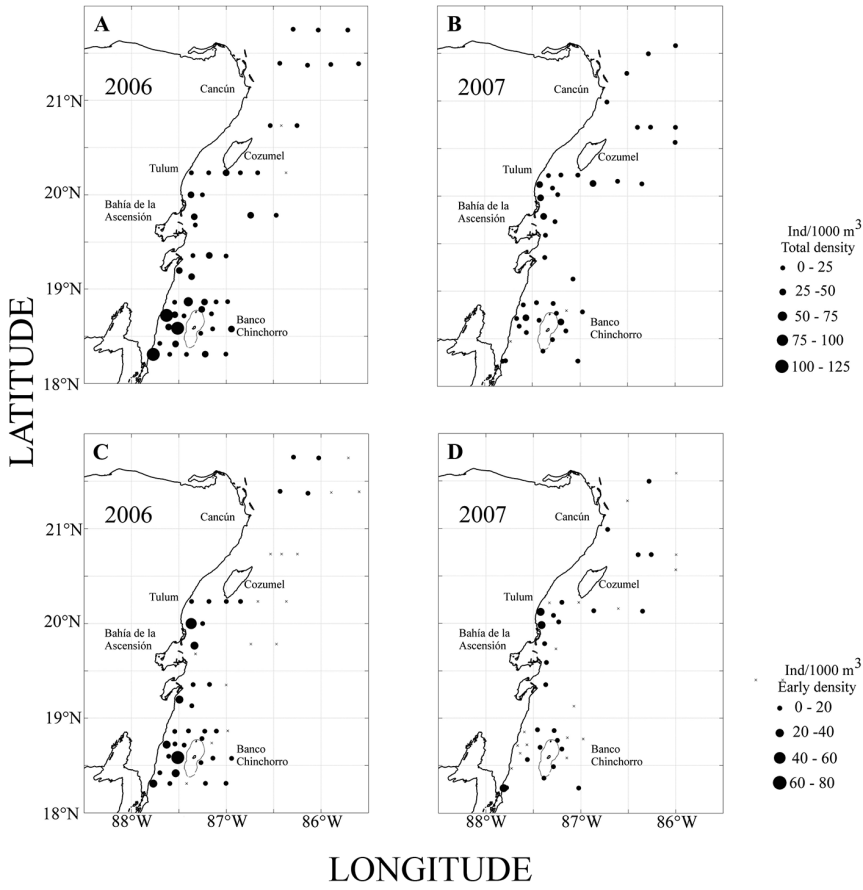

Figure 2. Spatial distribution of density values for phyllosoma. Panels A and B correspond to total phyllosoma density in March 2006 and January 2007. Boxes C and D correspond to densities of early-stage *Panulirus spp.* phyllosomas in March 2006 and January 2007.

southern region. However, it should be noted that in 2006, more phyllosomas were collected than from the cruise conducted in January 2007.

DNA Barcoding.—The use of barcoding techniques to validate spiny lobster species from field-caught phyllosomas was a novel approach used in the present study. Our genetic analysis of 95 samples provided 51 positive sequences for *P. guttatus* and we identified phyllosomal stages (I–V) that were previously undescribed. These data completed the phyllosomal description for *P. guttatus* and further aided in the identification of other phyllosomas from the 2007 cruise samples. We also confirmed 21 positive sequences for *P. argus* and three positive sequences for adult *P. laevicauda* from Bahía de la Ascensión.

Abundance per Stratum and Sampling Time.—In 2006, phyllosoma concentration varied according to the depth and time (day vs night) and there were clear differences among depths. The majority of phyllosomas (75%) were collected from two discrete surface layers: 0–25 and 25–50 m during the day, with a marked decrease

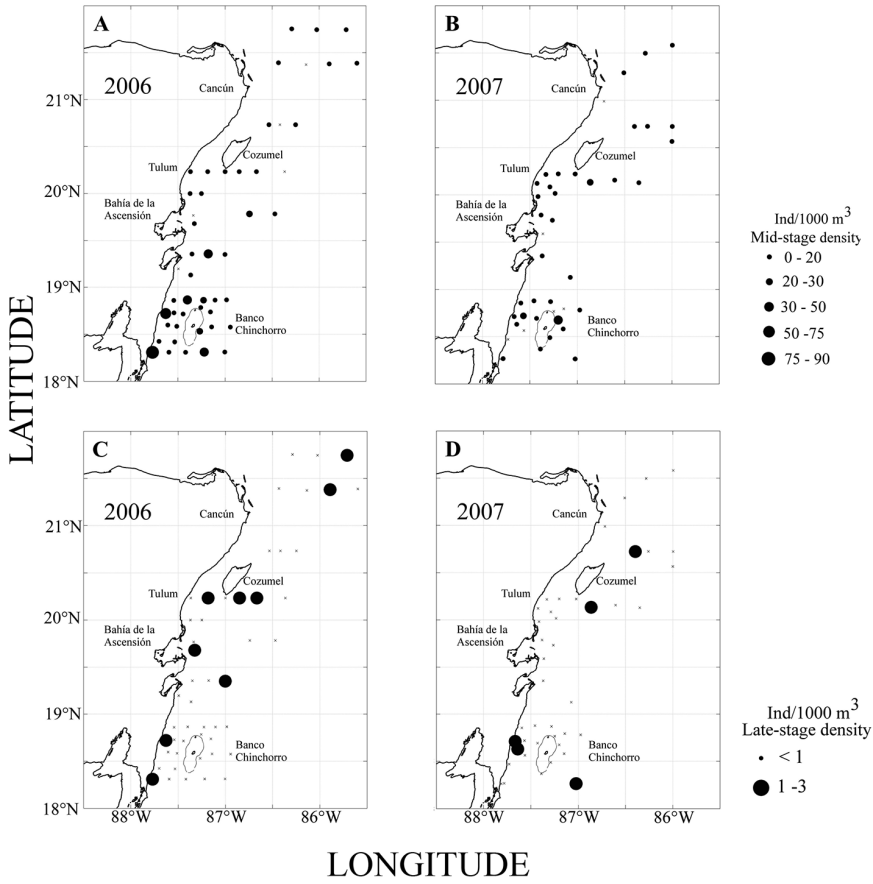

Figure 3. Spatial distribution of density values for phyllosomas. Boxes A and B correspond to densities of mid-stage *Panulirus* phyllosomas in March 2006 and January 2007. Boxes C and D correspond to densities of late-stage *Panulirus* phyllosomas in March 2006 and January 2007. "X" symbols correspond to survey stations that were absent for phyllosomas (larvae).

in abundance below 50 m (Fig. 4A). This trend was reflected in the distribution of phyllosomal groups. Early-stage groups (I–III) were predominately collected in 0–50 m depth strata and the majority (70%) were collected during the day (Fig. 4C). Mid-stage phyllosomas (IV–VIII) were predominately collected in 25–75 m depth strata (Fig. 5A). The majority of mid-stage phyllosomas (79%) were also collected during the day. Even though the majority of late-stage phyllosomas (IX–X) were collected during the day, predominately (90%) were distributed throughout the surface strata to 75 m depth.

Phyllosomal concentrations also differed by depth during the 2007 sampling effort. The highest concentration of phyllosomas (74%) were collected at night from the surface strata (0–50 m) consisting of early- (84%) and mid-stage (70%) larvae. The highest density of phyllosomas (86%) were found late at night (approximately 23:00–03:00), within the 25–50 m depth interval. For early-stage phyllosomas, high concentrations were recorded one night before the new moon. In addition, high

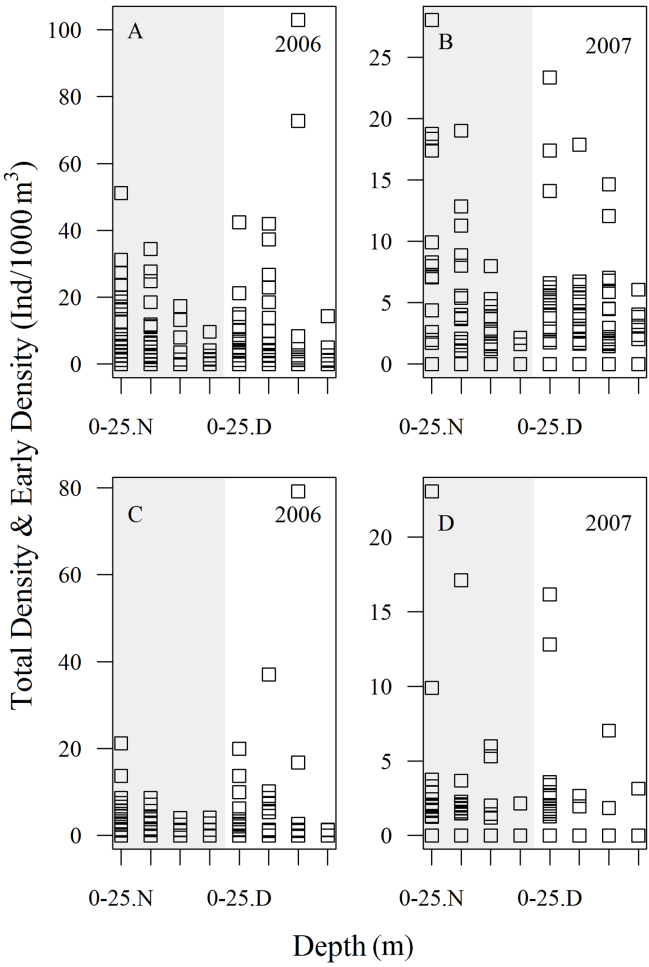

Figure 4. Vertical distribution of phyllosomas by depth stratum and by day (D) vs night (N). Boxes A and B correspond to total phyllosomas in March 2006 and January 2007, respectively. Boxes C and D correspond to early-stage *Panulirus* phyllosomas in March 2006 and January 2007, respectively.

abundances of mid-stage phyllosomas collected before noon were recorded beyond 50 m depth, whereas in the afternoon (approximately 12:00–16:00), they were concentrated above 50 m. Mid-stage phyllosomas showed more variation in terms of their vertical position in the water column (Fig. 6), presumably linked to changes in vertical migration.

Our ANCOVA model (fitted by the GLS algorithm, see Methods section), was chosen to represent the total density of phyllosomas, separated by early-, mid-, and late-stage phyllosomas, with respect to depth (m, continuous variable), and the three discrete factors geographical area, year, and time-of-day (day vs night). The best-fitting models, having the minimum AIC score, for total phyllosomas (AIC = 2162.78), early stage (AIC = 3500.08), and mid stage (AIC = 5748.81, see Online Appendix 2 for more information) had an optimal structure of variance forming part of the random component (Zuur et al. 2009). In all cases, except for the late-stage, the model

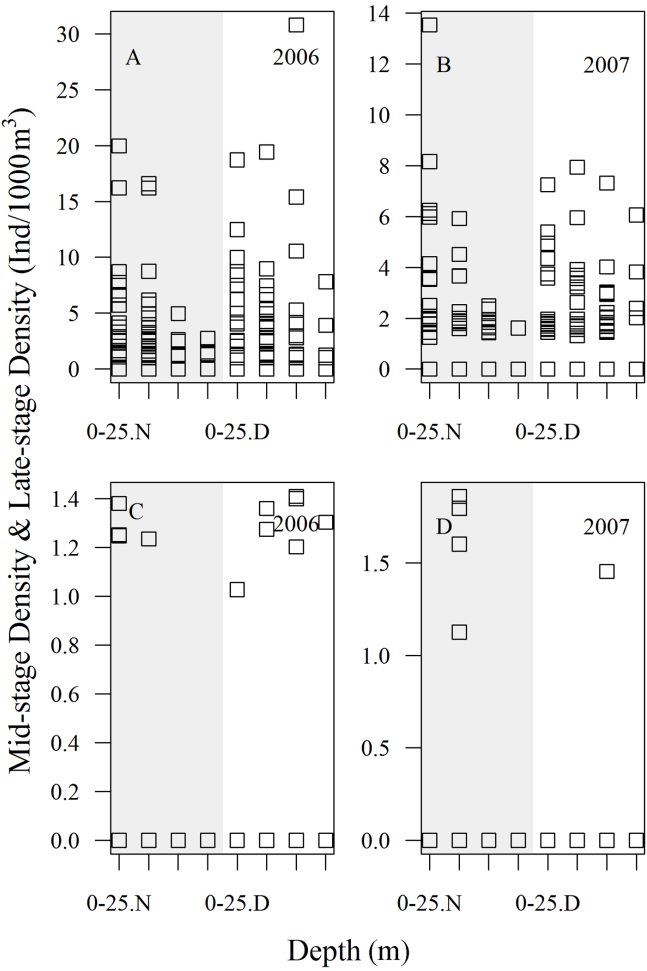

Figure 5. Vertical distribution of phyllosomas by depth stratum and by day (D) vs night (N). Boxes A and B correspond to mid-stage *Panulirus* phyllosomas in March 2006 and January 2007, respectively. Boxes C and D correspond to of late-stage *Panulirus* phyllosomas in March 2006 and January 2007, respectively.

included 12 different variances, one for each combination of depth interval and geographical area. In contrast, for the late-stage, the optimal variance structure incorporated two factors, time-of-day and geographical area.

The most important factors included in our final model for total phyllosomal distribution were depth, geographical area, year, and the interaction depth × area (Table 2). Our model produced three regression lines, a distinct line for each geographical area, which expresses the inverse relationship of the total larvae density with depth and a more widespread horizontal dispersal of phyllosomas in the southern zone (Fig. 6).

In contrast, the final model for early-stage and mid-stage phyllosomas included the time-of-day factor (Table 2) and second order interactions associated with it. Thus, the models for the densities of early-stage and mid-stage phyllosomas each contained 12 distinct slopes with respect to depth, due to the combination of all the factors:

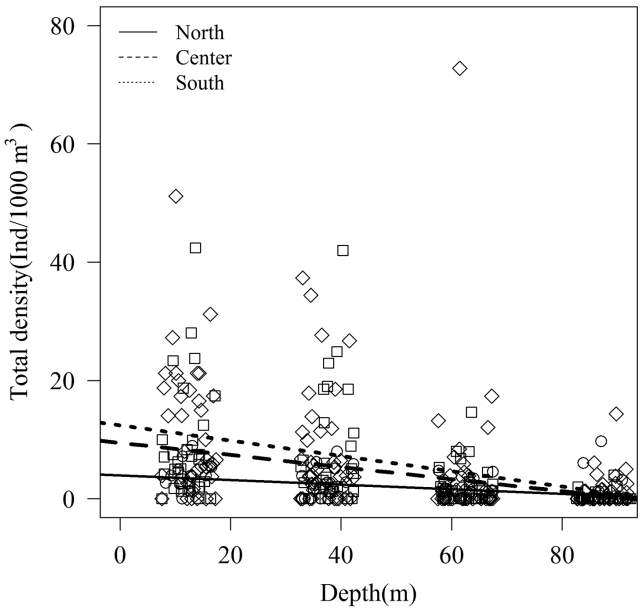

Figure 6. Results of the linear regression model for total phyllosomas for the three zones in different depth strata. Observations of the north (circles), center (squares), and southern zone (diamonds) are included.

time of day, year, and geographical area. On the other hand, our data for late-stage phyllosomas contained a high proportion of zero density records (only 16 of 682 values contained non-zero values). This precluded the application of the statistical tests used on the early- and mid-stage phyllosomas, although some alternatives were attempted. Thus, according to the final model (Online Appendix 2), there was no single factor or variable that explained density variation of late-stage phyllosomas.

Table 2. Variables, factors, and interactions considered in the most appropriate models [based on the minimum Akaike information criterion (AIC) scores] to explain the variation of abundance of distinct groups of phyllosoma larvae. The AIC scores for the final model of each group are included, alternative models for each group and their AIC values are reported in Online Appendix 2. Note that data for late-stage phyllosomas contained a high proportion of zero density records, which precluded application of the modeling approach.

Variable/factor	All stages	Early stage	Mid-stage	Late-stage
Depth	x	x	x	
Night-Day	–	x	x	
Zones	x	x	x	
Year	x	x	x	
Depth*Zone	x	x	x	
Depth*Night-Day	–	–	x	
Night-Day*Year	–	x	–	
Zone*Year	–	–	x	
Depth*Zone*Year	–	x	x	
AIC score	2,162.78	3,500.08	5,748.81	−205.38

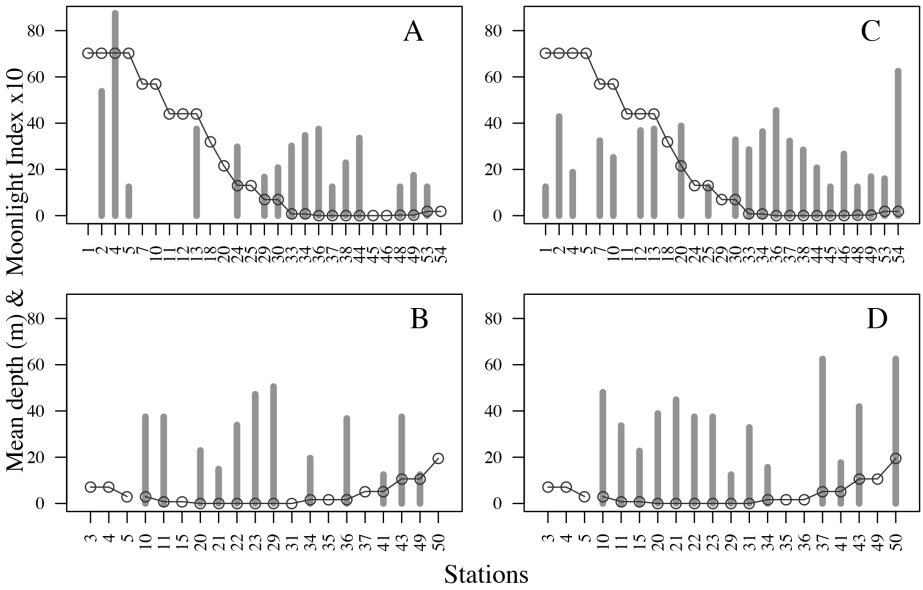

Figure 7. Variation of the mean depth (bars) occupied by stage groups of phyllosoma larvae and the moonlight index (circles and solid lines). The data for each stage category and cruise are shown separately: (A) March 2006, early stages (I–III); (B) January 2007, early stages; (C) March 2006, mid stages (IV–VIII); (D) January 2007, mid stages. Only nighttime stations were considered.

Moonlight Effects on Vertical Distribution of Phyllosomas.—In March 2006, the mean depth for early-stage phyllosomas was calculated for two periods. The first series of MI observations (n = 7) corresponded to a phase of abundant moonlight (mean = 3.9, SD 2.39). During this period, phyllosomas were found in depths ranging from 12.5 to 87.5 m (mean = 36.9, SD 26.32 m, Fig. 6). The remaining observations (n = 9) corresponded to a phase of lower MI values (mean = 0.58, SD 1.94). In this darker period, early stages were found at mean depths ranging from 12.5 to 37.5 m (mean = 23.76, SD 10.41 m; Fig. 7, Table 3). In January 2007, early-stage phyllosomas were found at depths ranging from 16.75 to 37.5 m (mean = 28.0, SD 10.49 m; MI: mean = 3.07, SD 1.76, n =12) and depths ranging from 12.5 to 87.5 m (mean = 29.9, SD 21.37 m; MI: mean = 1.95, SD 3.09; n = 5, Fig. 7).

Table 3. Correlation analysis between the moonlight index and the mean depth where the stage groups of phyllosoma were found in night-time stations of two cruises. Late-stage phyllosomas were excluded from this analysis since there were few observations.

		Pearson's correlation index			Significance test		
Stage group	Cruise date	n	$\hat{\rho}$	95% CI	ts	df	P
Early stages	March 2006	16	0.580	0.11, 0.83	2.64	14	0.019
Early stages	January 2007	12	−0.320	−0.75, 0.32	−1.05	12	0.317
Mid-stages	March 2006	22	0.005	−0.42, 0.42	0.02	20	0.980
Mid-stages	January 2007	14	0.530	−0.01, 0.83	2.15	12	0.053
Early stages	2006 and 2007	28	0.440	0.08, 0.70	2.49	26	0.019
Mid-stages	2006 and 2007	36	−0.045	−0.37, 0.29	−0.27	34	0.790

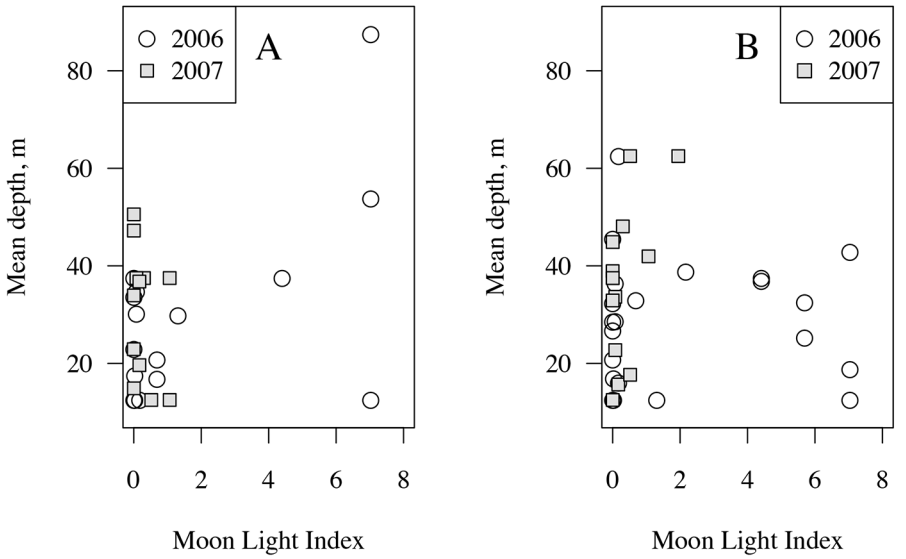

Figure 8. Variation of mean depth occupied by (A) early- (I–III) and (B) mid-stage (IV–VIII) phyllosoma larvae in relation to the moonlight index in two cruises: March 2006 (circles), and January 2007 (squares).

The remaining MI analyses followed a similar pattern. In March 2006, most of the mid-stage phyllosomas were collected during a period with low MI (mean = 1.68, SD 2.52, n = 13) at depths ranging from 12.5 to 62.5 m (mean = 29.8, SD 12.78 m). Mid-stage phyllosomas tended to occupy slightly shallower layers when the moonlight intensity increased (mean = 3.02, SD 2.89, n = 9) over a depth range of 12.5–45.5 m (mean = 26.9, SD 13.68 m; Fig. 7C). However, that pattern was unclear given the few available observations. In January 2007, mid-stage phyllosomas were found at depths ranging from 12.5 to 44.9 m (mean = 30.7, SD 11.15 m; MI: mean = 0.17, SD 0.24; n = 9) and depths ranging from 12.5 to 44.9 m (mean = 46.5, SD 18.48 m; MI: mean = 0.90, SD 0.60; n = 5, Fig. 7). The observed pattern consisted of mid-stage phyllosomas residing in deeper waters as MI increased. Overall, for mid-stage phyllosomas there was no correlation between mean depth and moonlight (Fig. 8, Table 3)

Discussion

We examined variation in density (abundance) and distribution of Palinurid phyllosomas collected over two research cruises in two successive years along the coasts of Quintana Roo and the Yucatán peninsula. Overall, the dominant lobster species in all our samples was *P. argus* (77.2%), a result consistent with previous studies (Olvera and Ordoñez 1988, Manzanilla-Domínguez and Gasca 2004, Manzanilla-Domínguez et al. 2005). The second most abundant species was *P. guttatus* (4.23%), while no phyllosomas of *P. laevicauda* were found despite our genetic analysis (barcoding and using adult tissue as reference material). Also of interest was our ability to provide taxonomic resolution through DNA barcoding in discerning phyllosomas, especially those of *P. argus* from *P. guttatus*. These identifications, coupled with our taxonomic descriptions, serve as a taxonomic reference for future studies.

In both cruises, sampling stations were not evenly distributed as there was a concentration around Banco Chinchorro. This was due, in part, to logistical constraints as the research cruise was engaged in a variety of concurrent research objectives including the collection of fish larvae and associated physical oceanographic data. Despite this potential bias, it is clear that the most productive stations (i.e., high concentrations of phyllosomas) were near the coast of Banco Chinchorro. These findings were reflected in our statistical model results and are also similar to previous reports for phyllosomal distributions along the coast of Quintana Roo (Manzanilla-Domínguez and Gasca 2004, Manzanilla-Domínguez et al. 2005). Furthermore, regarding our sampling efforts over disparate months in 2006 and 2007, our results appear to correspond to two different pulses in the reproductive cycle of Palinurid adults. This pattern is likely related to the annual reproductive activity for lobsters in Quintana Roo, with a major peak in spring-summer from March to July, and a secondary pulse occurring in autumn from October to September (Briones-Fourzán and Gutiérrez-Carbonell 1992, Ramírez-Estévez 1996). These results are also similar to the findings of Alfonso et al. (1991, 1999), who reported higher concentrations of early-stage phyllosomas near the Mexican (Yucatán) coast and decreasing abundances offshore. However, this pattern is not universal. For example, it has been reported that for the Australian rock lobster [*Panulirus cygnus* (George, 1962)], phyllosomal concentrations increased offshore and their vertical distribution was related to varying levels of moonlight (Chittleborough and Thomas 1969, Rimmer 1980). Thus, it is important to evaluate all abiotic factors that may be influential in the spatiotemporal distribution of phyllosomas; laboratory-based studies may be beneficial to deciphering in situ patterns of distribution.

Although the effect of moonlight was not the primary goal in our study, we were able to examine its influence on the vertical distribution of phyllosomas. Our analyses of the stations sampled during nighttime contributed preliminary results that we intend to build upon. In contrast, the classic work of Rimmer and Phillips (1979) was able to accurately detect the influence of moonlight on the vertical distribution of phyllosomas. Overall, there was one pattern clearly detected: early-stages of phyllosomas tended to occupy deeper layers at higher moonlight levels. This is consistent with the negative phototactic behavior reported for laboratory-raised *P. argus* phyllosomas that were >3 mo of age (Butler et al. 2011). Our field data in March 2006 corroborates this result; however, this same pattern was not detected in January 2007 when MI was relatively limited (Fig. 7). In the case of mid-stage phyllosomas, there was no clear pattern, although the data collected in January 2007 suggested that mid-stage larvae tend to occupy deeper layers as moonlight intensity increases.

Our findings on the early-stages of phyllosomas of *P. argus* depart from the pattern described for similar stages of *P. cygnus* by Rimmer and Phillips (1979). These authors concluded that early stages (I–III) tend to occur at the surface at night regardless of moonlight intensity. Conversely, we found that early-stages tend to avoid the surface layers when MI values were higher. Our results regarding the mid-stages of phyllosomas were similar, given that Rimmer and Phillips (1979) reported that mid- and late-stages were absent from the surface layers on moonlit nights. For *P. argus*, this behavioral transition to negative phototaxis has been observed in phyllosomas approximatley 100 d after hatching under laboratory conditions (Butler et al. 2011).

Patterns of Distribution with Oceanographic Features.—From our results, the highest densities of phyllosomas were observed in the south zone (Banco Chinchorro) during March 2006, and off the coast of the central zone, in front of the Sian Ka'an BR and south of Cozumel during January 2007. Thus, in general terms, low concentrations of phyllosomas were observed in northern Quintana Roo and a southward gradient of concentration for phyllosomas was recorded. Physical processes, such as transport by currents, together with behavioral-mediated traits in phyllosomas (Pineda et al. 2007, Butler et al. 2011), likely play an important role in the retention and subsequent distribution of phyllosomas in coastal waters off Quintana Roo. The Yucatán current is characterized by a northeastward directional flow that intensifies toward the Yucatán Channel (Sheinbaum et al. 2002, Centurioni and Niiler 2003, Cetina et al. 2006, Carrillo et al. 2015). The Yucatán Current can reach speeds up to 2.0 m s^{-1} near the Yucatán Channel (Sheinbaum et al. 2002, Carrillo et al. 2015), which means that phyllosomas may be carried away and are not likely retained in the northern zone (Briones-Fourzán et al. 2008, Carrillo et al. 2015). This may explain the low density of phyllosomas collected in northern Quintana Roo during both sampling years.

Other studies providing oceanographic data that included the area off Quintana Roo and in the MBRS suggest that, during 2006, the Yucatán Current was generally much weaker and variable in the region located south of Bahia de la Ascensión compared with the northern section (Muhling et al. 2013, Carrillo et al. 2015). It has been suggested that this difference in the transport field had an important influence on retention, thereby concentrating higher densities of larval fishes in the southern MBRS, which includes southern Quintana Roo (Muhling et al. 2013, Carrillo et al. 2015). The same mechanisms may apply to phyllosomal densities. However, there were differences between the March 2006 and January 2007 cruises in phyllosomal distributions. Seasonal and interannual variability in sub-mesoscale features occur along the MBRS (Carrillo et al. 2015), and these likely result in different larval transport and retention outcomes.

Early-stage phyllosomas found in areas adjacent to populations of adult lobsters during their putative reproductive period may be associated with physical retentive processes (e.g., eddy-like features). Banco Chinchorro represents a physical barrier to the northward flow of the currents creating an "island effect" as described by Hamner and Haury (1981) for other regions. Sub-mesoscale eddy-like features (approximately 1–10 km) are associated with the island effect. A satellite-tracked drifter released close to Banco Chinchorro coast was trapped in a sub-mesoscale eddy-like feature of approximately 5 km for about 24 hrs (Carrillo et al. 2015). This suggests that fluctuating eddies around Banco Chinchorro may result in an increased physical retention of propagules, which would explain the higher densities of early- and mid-stage phyllosomas found in this area. Muhling et al. (2013) and Carrillo et al. (2015) reported the presence of a sub-mesoscale cyclonic eddy located south of Cozumel; this cyclonic eddy-like structure generates a coastal countercurrent near Tulum. Both the eddy-like features and the coastal countercurrent may act as a physical structure for larval retention that may have concentrated early- and mid-stage phyllosomas in 2007 in the central zone of Quintana Roo, particularly at stations south of Cozumel Island, close to the coasts of Tulum and Sian Ka'an BR.

Phyllosoma Abundance.—The high abundance of mid-stage phyllosomas in both years may be explained by the reproductive seasonality of lobsters, which occurs on a year-round basis at least for *P. guttatus* and *P. argus* (Padilla-Ramos and Briones-Fourzán 1997) in the Mexican Caribbean. For the congener, *P. laevicauda,* little is known about their reproduction off Mexico, and data for this species continues to remain elusive. However, studies in Puerto Morelos suggest that *P. laevicauda* has a limited breeding season, and only one ovigerous female has been reported to date (Padilla-Ramos and Briones-Fourzán 1997).

In both cruises, there were low abundances and more scattered concentrations of late-stage phyllosomas away from the coast. Moreover, the small number of late-stage phyllosomas precluded a complete analysis. In addition, neither cruise provided a clear idea of whether phyllosomas are carried offshore or if other factors (e.g., food, water quality, depth) influence the arrival of recruits to coastal locales (Goldstein and Butler 2009, Kough et al. 2014). Low numbers of late-stage phyllosomas were expected because, during March, there are typically low influxes of lobster postlarvae (pueruli) along the coast of Quintana Roo (Briones-Fourzán 1994, Briones-Fourzán et al. 2008, Olivares-Escobedo 2011). Arrival of pueruli into more shallow, coastal Quintana Roo waters peaks in the period October to November (Briones-Fourzán et al. 2008, Olivares-Escobedo 2011). Hence, during March 2006 and January 2007, the reduced number of late-stage phyllosomas collected may have been expected.

Because spawning has a relatively similar seasonality in the Caribbean Sea, it is likely that the number of late-stage phyllosomas we caught reflect the secondary peak in reproductive activity in the period September-October (Briones-Fourzán 1994, Briones-Fourzán et al. 2008). However, the likely origin of those phyllosomas was from elsewhere in the Caribbean (Butler et al. 2011, Kough et al. 2013). It has been estimated, through biophysical modeling, that the dispersal trajectory for *P. argus* phyllosomas show two distinct modes: the first at approximately 300 km and the second at approximately 1000 km, from their hypothetical release points (Butler et al. 2011). Thus, it is possible that only some of the phyllosomas we quantified were produced by ovigerous lobsters that hatched in the waters of Quintana Roo. However, further work, including the application of genetic markers, would provide better resolution to the sources and sinks of phyllosomas in these areas (Thorrold et al. 2002).

Highest densities of phyllosomas sampled throughout both cruises were found in the surface layers (0–50 m) both during the day and at night: our final abundance model suggested that time-of-day (day vs night) was not an important factor in density variation. However, it is possible that we had insufficient data to detect the influence of time of day or, perhaps our models lacked statistical power (Sokal and Rohlf 1995). Similarly, Yeung et al. (1993) found no statistical difference in the distribution of phyllosomas between day and night, and these phyllosomas were equally distributed in high concentrations in the surface layers at all times. In contrast to our model for total phyllosomas, the interactions between time-of-day, year, and depth were important in the model describing the distribution of early-stage phyllosomas. This was likely a result of the vertical distribution of early-stage phyllosomas that generally reflected higher densities in the surface layers during day and night. High densities at night have also been reported for early-stage phyllosomas of *P. cygnus* (Rimmer and Phillips 1979). Contrary to phyllosomal distributions near the surface, Alfonso et al. (1995, 1999) found that early phyllosomal stages of *P. argus* displayed negative phototropism hours after hatching, and their concentrations were highest at 50 m

at night. Our results regarding the moonlight effect on vertical distribution of early stage phyllosomas depart from those reported by Rimmer and Phillips (1979), and agree with the findings of Alfonso et al. (1995, 1999).

During the 2007 cruise, the interaction between the factors depth and time-of-day for mid-stage phyllosomas emerged as important. High densities of phyllosomas were distributed in the uppermost layer at night. This was also the case for *P. cygnus* in Australia where phyllosomas began to disperse into depth strata from 6:00AM onward (Rimmer and Phillips 1979). Besides the small number of late-stage phyllosomas collected throughout the depth strata we sampled, it is likely that we did not collect enough phyllosomas to clearly detect these trends and additional sampling efforts would be required to address these patterns. Yeung and McGowan (1991) reported that phyllosomas were distributed in the surface layer (0–50 m) regardless of their stage, as was the case with our results. Butler et al. (2011) found that the last phyllosomal stages (10–15 mm carapace length) of *P. argus* exhibit negative phototaxis and migrate to deeper, darker layers. In Cuban waters, Alfonso et al. (1995, 1999) observed higher concentrations of late-stage phyllosomas in depths of 10–40 m during the night and early morning. Phillips and Pearce (1997) noted that phyllosomas corresponding to mid- and late-stage of *P. cygnus* were distributed from 60 to 140 m during the day. Our data for March 2006 suggest a similar trend as reported by Phillips and Pearce 1997, despite low number of phyllosomas collected. Future sampling targeting late-stage phyllosomas as well as laboratory-based studies along the lines of Butler et al. (2011) are warranted.

Larval dispersal and survival depend on multiple factors including spawning seasonality, pelagic larval duration, availability of prey, and predation pressure (Pineda et al. 2007). Along with light intensity, physical processes (e.g., transport and turbulence), vertical migration, and changes in behavior during ontogenetic development influence larval transport (Sponaugle et al. 2002, Phillips et al. 2006). It is not yet possible to accurately predict which forces determine the spatiotemporal patterns of phyllosomal concentrations off Quintana Roo. Further studies are needed, at both local and regional scales, focusing on phyllosomal behavior, vertical distribution, and diel behavior. Ultimately, we suggest that the interaction of the seasonality of reproductive activity (spawning), along with oceanographic features (currents), and behavioral responses (ODVM) of phyllosomas may produce a dynamic output that favors a higher potential for larval retention off the central and southern coasts of the Mexican Caribbean.

Acknowledgments

We gratefully acknowledge the National Oceanic and Atmospheric Administration (NOAA) and the officers and crew of the R/V Gordon Gunter for their assistance over the course of the research cruises. We also thank the University of Miami- ECOSUR Joint Project 517/04 led by J Lamkin and staff at the ECOSUR-Zooplankton and Oceanography Laboratory for help processing our samples. Instituto Nacional de Pesca (INAPESCA) was the official participant in the cruises. We thank L Vásquez-Yeomans for providing data, and A Ramírez-González and S Morales-Gutiérrez for sorting samples, as well as to D Acevedo and J Cohúo. Our gratitude to A Martínez-Arce for the DNA extraction. The comments of R Kliber and two anonymous reviewers improved this work. We wish to also thank R Kibler for her editorial comments and suggestions to this manuscript. Partial support for this project was provided by a Mexican scholarship from Consejo Nacional de Ciencia y Tecnología (No. 490217) to ACG.

Literature Cited

Abrunhosa FA, Abrunhosa JP, Costa RM. 2004. The early larval stages of phyllosomas of the spiny lobsters *Panulirus echinatus* Smith, 1869 and *Panulirus laevicauda* (Latreille, 1804) (Decapoda: Palinuridae). Nauplius. 12:21–29.

Alfonso I, Frías MP, Baisre BJ, Campos A. 1991. Distribución y abundancia de larvas de la langosta *Panulirus argus* en aguas alrededor de Cuba. Rev Inv Mar. 2(1–3):3–19.

Alfonso I, Frías MP, Baisre BJ, Hernández B. 1995. Distribución vertical de filosomas de *Panulirus argus* y su relación con algunos factores hidroclimáticos al sur del Golfo de Batabanó, Cuba. Rev Cuba Investig Pesq. 3–9.

Alfonso I, Frías MP, Baisre BJ. 1999. Distribución y abundancia y migración vertical de la fase larval de la langosta comercial *Panulirus argus* en aguas cubanas. Rev Invest Mar. 20:1–3.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference. A practical information-theoretic approach. 2nd ed. New York: Springer.

Baisre JA. 1969. A Note on the phyllosoma of *Justitia longimanus* (H. Milne Edwards) (Decapoda, Palinuridea). Crustaceana. 16:182–184. http://dx.doi.org/10.1163/156854069X00439

Baisre JA, Ruiz de Quevedo ME. 1982. Two phyllosome larvae of *Panulirus laevicauda* (Latreille, 1817) (Decapoda, Palinuridae) from the Caribbean Sea with a discussion about larval groups within the genus. Crustaceana. 43:147–153. http://dx.doi.org/10.1163/156854082X00470

Baisre JA, Alfonso I. 1994. Later stage larvae of *Panulirus gutattus* (Latreille, 1804) (Decapoda, Palinuridae) with notes on the identification of phyllosomata of *Panulirus* in the Caribbean Sea. Crustaceana. 66:32–44. http://dx.doi.org/10.1163/156854094X00134

Booth JD, Phillips BF. 1994. Early life history of spiny lobster. Crustaceana. 66:271–294. http://dx.doi.org/10.1163/156854094X00035

Briones-Fourzán P, Gutiérrez-Carbonell D. 1992. Postlarval recruitment of the spiny lobster, *Panulirus argus* (Latreille 1804), in Bahía de la Ascensión, Q.R. Proc Gulf Caribb Fish Inst. 41:492–507.

Bradford RW, Bruce BD, Chiswell SM, Booth JD, Jeffs A. 2005. Vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island, New Zealand. N Z J Mar Freshw Res. 39:593–604. http://dx.doi.org/10.1080/00288330.2005.9517338

Briones-Fourzán P. 1994. Variability in postlarval recruitment of the spiny lobster *Panulirus argus* (Latreille, 1804) to the Mexican Caribbean coast. Crustaceana. 66:326–340. http://dx.doi.org/10.1163/156854094X00062

Briones-Fourzán P, Candela J, Lozano-Álvarez E. 2008. Postlarval settlement of the spiny lobster *Panulirus argu*s along the Caribbean coast of Mexico: patterns, influence of physical factors, and possible sources of origin. Limnol Oceanogr. 53:970–985. http://dx.doi.org/10.4319/lo.2008.53.3.0970

Butler MJ IV, Herrnkind WF. 1997. A test of recruitment limitation and the potential for artificial enhancement of spiny lobster populations in Florida. Can J Fish Aquat Sci. 54:452–463. http://dx.doi.org/10.1139/f96-281

Butler MJ, Herrnkind WF. 2000. Puerulus and juvenile ecology. *In*: Phillips BF, Kittaka J, editors. Spiny lobsters: fisheries and culture. Blackwell Science Ltd. p. 276–301. http://dx.doi.org/10.1002/9780470698808.ch15

Butler MJ IV, Paris CB, Goldstein JS, Matsuda H, Cowen RK. 2011. Behavior constrains the dispersal of long-lived spiny lobster larvae. Mar Ecol Prog Ser. 422:223–237. http://dx.doi.org/10.3354/meps08878

Carrillo L, Johns E, Smith R, Lamkin J, Largier JL. 2015. Pathways and upper hydrography in the Mesoamerican Barrier Reef System: Part 1 Circulation. Cont Shelf Res. 109:164–176. http://dx.doi.org/10.1016/j.csr.2015.09.014

Centurioni RL, Niiler PP. 2003. On the surface currents of the Caribbean Sea. Geophys Res Lett. 30:10–13. http://dx.doi.org/10.1029/2002GL016231

Cetina P, Candela J, Sheinbaum J, Ochoa J, Badan A. 2006. Circulation along the Mexican Caribbean coast. J Geophys Res. 111:1–19. http://dx.doi.org/10.1029/2005jc003056

Chavez EA. 2009. Potential production of the Caribbean spiny lobster (Decapoda, Palinura) fisheries. Crustaceana. 82:1393–1412. http://dx.doi.org/10.1163/001121609X12481627024373

Chittleborough RG, Thomas LR. 1969. Larval ecology of the western australian marine crayfish, with notes upon other panulirid larvae from the eastern indian ocean. Aust J Mar Freshwater Res. 20:199–223. http://dx.doi.org/10.1071/MF9690199

Fonseca-Larios ME, Briones-Fourzán P. 1998. Fecundity of the spiny lobster *Panulirus argus* (Latreille, 1804) in the Caribbean coast of Mexico. Bull Mar Sci. 63:21–32.

Forward RB. 1988. Diel vertical migration: zooplankton photobiology and behaviour. Oceanogr Mar Biol Annu Rev. 26:361–393.

Goldstein JS, Butler MJ IV. 2009. Behavioral enhancement of onshore transport by postlarval Caribbean spiny lobster (*Panulirus argus*). Limnol Oceanogr. 54(5):1669–1678. http://dx.doi.org/10.4319/lo.2009.54.5.1669

Goldstein JS, Matsuda H, Takenouchi T, Butler MJ IV. 2008. The complete development of larval Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) in Culture. J Crustac Biol. 28:306–327. http://dx.doi.org/10.1163/20021975-99990376

Hamner WM, Haury IR. 1981. Effects of island mass: water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. Limnol Oceanogr. 26:1084–1102. http://dx.doi.org/10.4319/lo.1981.26.6.1084

Ivanova NV, deWaard JR, Hebert PDN. 2006. An inexpensive, automation-friendly protocol for recovering high-quality DNA. Mol Ecol Notes. 6:998–1002. http://dx.doi.org/10.1111/j.1471-8286.2006.01428.x

Ivanova NV, Grainger CM. 2007. CCDB protocols, sequencing. [Accessed 24 October, 2014]. Available from: http://www.dnabarcoding.ca/CCDB_DOCS/CCDB_Amplification.pdf

Jeffs AG, Montgomery JC, Tindle CT. 2005. How do spiny lobster post-larvae find the coast? New Zeal J Mar Fresh. 39:605–617. http://dx.doi.org/10.1080/00288330.2005.9517339

Kough AS, Paris CB, Staaterman E. 2014. In situ swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae. Mar Ecol Prog Ser. 504:207–219. http://dx.doi.org/10.3354/meps10748

Kough AS, Paris CB, Butler MJ. 2013. Larval connectivity and the international management of fisheries. PLoS ONE. 8(6):e64970. http://dx.doi.org/10.1371/journal.pone.0064970

Lewis JB. 1951. The phyllosoma larvae of the spiny lobster *Panulirus argus*. Bull Mar Sci Gulf Caribb. 1:89–103.

Manzanilla-Dominguez H, Gasca R. 2004. Distribution and abundance of phyllosoma larvae (Decapoda, Palinuridae) in the southern Gulf of Mexico and the western Caribbean Sea. Crustaceana. 77:75–93. http://dx.doi.org/10.1163/156854004323037900

Manzanilla-Domínguez H, Gasca R, Suárez-Morales E. 2005. Notes on the distribution of phyllosoma larvae in an Oceanic Atoll-like Reef System in the western Caribbean. Crustaceana. 78:505–512. http://dx.doi.org/10.1163/1568540054473567

Minami H, Inoue N, Sekiguchi H. 2001. Vertical distributions of phyllosoma larvae of Palinurid and Scyllarid lobsters in the western North Pacific. J Oceanogr. 57:743–748. http://dx.doi.org/10.1023/A:1021244711315

Muhling BA, Smith RH, Vásquez-Yeomans L, Lamkin JT, Johns EM, Carrillo L, Sosa-Cordero E, Malca E. 2013. Larval fish assemblages and mesoscale oceanographic structure along the Mesoamerican Barrier Reef System. Fish Oceanogr. 22:409–428. http://dx.doi.org/10.1111/fog.12031

Olivares-Escobedo JC. 2011. Ingreso mensual de poslarvas de langosta *Panulirus argus* en el Parque Nacional Arrecifes de Xcalak: variación estacional y comparación de dos tipos de colector. Thesis Degree. Instituto Tecnológico de Chetumal. Quintana Roo. 67 p.

Olvera LMR, Ordoñez AL. 1988. Distribución y abundancia relativa y desarrollo larvario de langostas *Panulirus argus* y *Scyllarus americanus* en la Z.E.E. del Golfo de México y Mar Caribe. Cienc Pesq Int Nal la Pesca Sria Pesca. 6:7–31.

Padilla-Ramos S, Briones-Fourzán P. 1997. Características biológicas de las langostas (*Panulirus* spp) provenientes de las capturas en Puerto Morelos, Quintana Roo, México. Cienc Mar. 23:175–193.

Phillips BF, Sastry AN. 1980. Larval Ecology. *In*: Cobb JS, Phillips BF, editors. The biology and management of lobster. Vol. 2. New York: Academic Press. p. 11–57. http://dx.doi.org/10.1016/B978-0-08-091734-4.50008-1

Phillips BF, McWilliam PS. 1986. The pelagic phase of spiny lobster development. Can J Fish Aquat Sci. 43:2153–2163. http://dx.doi.org/10.1139/f86-264

Phillips BF, Pearce AF. 1997. Spiny lobster recruitment off Western Australia. Bull Mar Sci. 61:21–41.

Phillips BF, Booth JD, Cobb JS, Jeffs AG, Mcwilliam P. 2006. Larval and postlarval ecology. *In*: Phillips BF, editor. Lobsters: biology, management, aquaculture and fisheries. Blackwell Publishing Ltd. p. 231–262. http://dx.doi.org/10.1002/9780470995969.ch7

Pineda J, Hare J, Sponaugle S. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography. 20:22–39. http://dx.doi.org/10.5670/oceanog.2007.27

Polovina JJ, Moffit RB. 1995. Spatial and temporal distribution of the Phyllosoma larvae of the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Bull Mar Sci. 56:406–417.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org

Ramírez-Estévez A. 1996. Reproducción de la langosta espinosa *Panulirus argus* (Latreille, 1804) en la costa Noreste de Quintana Roo. México. Masters thesis. Facultad de Ciencias Universidad Nacional Autónoma de México. México, DF. 85 p.

Rimmer DW, Phillips F. 1979. Diurnal migration andvertical distribution of phyllosoma larvae of the western rock lobster *Panulirus cygnus.* Mar Biol. 54:109–124. http://dx.doi.org/10.1007/BF00386590

Rimmer DW. 1980. Spatial and temporal distribution of early-stage phyllosoma of western rock lobster, *Panulirus cygnus.* Aust J Mar Freshwater Res. 31(4):485–497. http://dx.doi.org/10.1071/MF9800485

Ringelberg J. 2010. Diel vertical migration of zooplankton inlakes and oceans. Causal explanations and adaptive significance. Springer Netherlands. 356 p. http://dx.doi.org/10.1007/978-90-481-3093-1

Robertson PB. 1968a. The complete larval development of the sand lobster, *Scyllarus americanu*s (Smith) (Decapoda, Scyllaridae) in the laboratory, with notes on larvae from the plankton. Bull Mar Sci. 18:294–342.

Robertson PB. 1968b. The larval development of some western Atlantic lobsters of the family Scyllaridae. PhD Dissertation. University of Miami. Coral Gables. 1027 p.

Robertson PB. 1968c. A giant scyllarid phyllosoma larva from the Caribbean Sea, with notes on smaller specimens (Palinuridea). Crustac Suppl. 83–97.

Robertson PB. 1969a. Biological investigations of the deep sea. No. 48. Phyllosoma larvae of a scyllarid lobster, *Arctides guineensis*, from the western Atlantic. Mar Biol. 4:143–151. http://dx.doi.org/10.1007/BF00347040

Robertson PB. 1969b. Phyllosoma larvae of a palinurid lobster, *Justitia longimana* (H. Milne Edwards), from the western Atlantic. Bull Mar Sci. 19:922–944.

Robertson PB. 1971. Biological results of the university of Miami deep-sea expeditions. 84. The larvae and postlarva of the Scyllarid lobster *Scyllarus depressus* (Smith). Bull Mar Sci. 21:841–865.

Robertson PB. 1972. A unique scyllarid phyllosoma larva from the Straits of Florida (Decapoda, Palinuridea). Crustaceana. 22:309–312. http://dx.doi.org/10.1163/156854072X00606

Robertson PB. 1979. Larval development of the scyllarid lobster *Scyllarus planorbis* Holthuis reared in the laboratory. Bull Mar Sci. 29:320–328.

Rudorff CAG, Lorenzzetti JA, Gherardi DFM, Lins-Oliveira JE. 2009. Modeling spiny lobster larval dispersion in the tropical Atlantic. Fish Res. 96:206–215. http://dx.doi.org/10.1016/j.fishres.2008.11.005

Sekiguchi H, Inoue N. 2002. Recent advances in larval recruitment processes of scyllarid and palinurid lobsters in Japanese waters. J Oceanogr. 58:747–757. http://dx.doi.org/10.1023/A:1022806726150

Sheinbaum J, Candela J, Badan A, Ochoa J. 2002. Flow structure and transport in the Yucatán Channel. Geophys Res Lett. 29(3):1–4. http://dx.doi.org/10.1029/2001GL013990

Sims WH Jr. 1966. Notes on the occurrence of prenaupliosoma larvae of spiny lobster in the plankton. Bull Mar Sci. 15:223–227.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W.H. Freeman, New York.

Sosa-Cordero E. 2003. Trends and dynamics of the spiny lobster, *Panulirus argus*, resource in Banco Chinchorro, México. Bull Mar Sci. 73:203–217.

Sosa-Cordero E. 2011. La langosta, pesquería emblemátia de Quintana Roo. *In*: Pozo C, Canto A, Calmé S, editors. Riqueza Biológica de Quintana Roo. Un análisis para su conservación. ECOSUR, CONABIO, Gobierno del Estado de Quintana Roo y PPD. México, D.F. p. 183–189.

Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, et al. 2002. Predicting self-recruitment in marine population: biophysical correlates and mechanisms. Bull Mar Sci. 70:341–375.

Thorrold SR, Jones GP, Hellberg ME, Burton RS, Swear SE, Neigel JE. 2002. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bull Mar Sci. 70:291–308.

Yeung C, McGowan MF. 1991. Differences in inshore-offshore and vertical distribution of phyllosoma larvae of *Panulirus, Scyllarus* and *Scyllarides* in the Florida Keys in May-Jun,1989. Bull Mar Sci. 49:699–714.

Yeung C, Couillard JT, McGowan MF. 1993. The relationship between the vertical distribution of spiny lobster phyllosoma larvae (Crustacea: Palinuridae) and isolume depths generated by a computer model. Rev Biol Trop. Suplemento. 41:63–67.

Yeung C, Lee TN. 2002. Larval transport and retention of the spiny lobster, *Panulirus argus*, in the coastal zone of the Florida Keys, USA. Fish Oceanogr. 11:286–309. http://dx.doi.org/10.1046/j.1365-2419.2002.00209.x

Ziegler TA, Cohen JH, Forward RB. 2010. Proximate control of diel vertical migration in phyllosoma larvae of the Caribbean spiny lobster *Panulirus argus.* Biol Bull. 219:207–219.

Zuur AE, Ieno EN, Smith G. 2007. Analyzing ecological data. New York: Springer Verlag. 680 p. http://dx.doi.org/10.1007/978-0-387-45972-1

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Springer. 574 p. http://dx.doi.org/10.1007/978-0-387-87458-6