Spatial and Temporal Patterns of Caribbean spiny lobster, *Panulirus argus*, puerulus Settlement to the Belize Lagoon System

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ABSTRACT

Panulirus argus puerulus settlement to artificial settlement substrates ("witham collectors") was conducted at sites in the Belize lagoon system from August 2003 to April 2006. Sampling sites ranged from just south of Ambergris Caye in the north to St. George's cay in the south. Sampling throughout the lunar cycle indicated that monthly peak settlement periods occurred during the week prior to the new moon. This patterns was most pronounced for transparent postlarvae. Annual peaks in settlement occurred during autumn months, but varied slightly between years. These temporal patterns varied somewhat between sites, primarily due to some sites consistently receiving low numbers of postlarvae and not showing any statistically significant temporal variability. Spatial variability in settlement was fairly consistent, with sites near the north end of Caye Caulker (including the North Caye Caulker, Flats and Calata Sites) having the greatest settlement rates during months when significant differences in settlement rates among sites were detected. Spatial and temporal variability in settlement may be influenced by habitat characteristics and wind-driven transport somewhat, but these factors do not explain much of the observed variability.

KEYWORDS: *Panulirus argus,* postlarval settlement, Belize, puerulus

Patrones espaciales y temporales de la langosta espinosa del Caribe, *Panulirus argus*, establecimiento de puerulus al sistema de la laguna de Belice

El establecimiento de puerulus de *Panulirus argus* a los substratos artificiales del establecimiento ("colectores del witham") fueron conducidos en los sitios en el sistema de la laguna de Belize a partir de agosto de 2003 a abril de 2006. Los sitios del muestreo se extendieron del justo al sur del Cayo Ambergris en el norte hacia cayo St. George en el sur. El muestreo a través del ciclo lunar indicó que los períodos de establecimiento máximos mensuales ocurrieron durante la semana antes de la Luna Nueva. Esto modeló era la más pronunciado para los postlarvae transparentes. Los picos anuales en el establecimiento ocurrieron durante meses del otoño, pero variaron levemente entre los años. Estos patrones temporales variaron algo entre los sitios, sobre todo debido a algunos sitios que recibían constantemente números bajos de postlarvae y que no demostraban ninguna variabilidad temporal estadístico significativa. La variabilidad espacial en el establecimiento era bastante constante, con los sitios cerca del extremo del norte del cayo Caulker (incluyendo cayo norte, Caulker, Flats y los sitios de Calata) teniendo las tazas más grandes de establecimiento durante los meses en que las diferencias significativas en tarifas del establecimiento entre sitios fueron detectadas. La variabilidad espacial y temporal en el establecimiento se puede influenciar algo debido a las características del hábitat y transporte por el viento algo, pero estos factores no explican mucha de la variabilidad observada.

PALABRAS CLAVES: Panulirus argus, establecimeinto artificial, sustrato articificial, Belize

INTRODUCTION

Spatial and temporal variability in the supply of late-stage larvae can have a significant impact on the populations of marine fish and invertebrates (e.g., reviewed in Booth and Brosnan 1995, Doherty 2002). Larval supply can be influenced by a range of environmental factors and physical processes that affect the survival, development and transport of larvae (reviewed in Cowen 2002). Biological processes such as larval behavior influences the distribution of larvae or selection of settlement habitats, and inter-and intraspecific interactions affect growth and survival (reviewed in Cowen 2002, Leis and McCormick 2002, Kingsford et al. 2002). Identifying the patterns of larval settlement, and the processes that shape these patterns is critical for understanding population dynamics of key species and effectively managing their populations.

The Caribbean spiny lobster, *Panulirus argus*, is the most valuable fishery species in the wider Caribbean region. Although commonly found on coral reefs and hard-bottom areas as sub-adults and adults, it has a complex life cycle whereby larvae live in the plankton for an extended period of time (up to 9 months or more), followed by metamorphosis into a puerulus or postlarval stage that transitions lobsters from living in the open ocean as plankton to living as benthic juveniles (Lipcius and Eggleston 2000). Postlarval settlement and subsequent juvenile development occurs off-reef in nearshore shallow water habitats (Lipcius and Eggleston 2000). Although they may use several habitats as juveniles macroalgae, *Laurencia* spp., serves as the primary settlement and juvenile habitat (Marx and Herrnkind 1985).

Previous studies on lobster settlement have suggested that numerous environmental factors may influence settlement spatial or temporal patterns, including small- and meso-scale current patterns (Ryther et al. 1988, Ward 1989, Briones-Fourzan 1994, Lipcius et al. 1997, Quinn and Kojis 1997, Yeung et al. 2001) wind speed and direction (Acosta et al. 1997, Eggleston et al. 1998), and proximity to nursery habitats (Little 1977, Eggleston et al. 1998, Quinn and Kojis 1997). The relative importance of each of these factors may vary between systems, however. For example, wind driven transport can account for up to 50% of the variability in settlement in some systems, but be unimportant in others (Acosta et al. 1997, Eggleston et al. 1998, Yeung et al. 2001).

In this study we identified spatial and temporal settlement patterns of lobster postlarvae settlement in the northern Belize lagoon system between Ambergris Caye and St. George's Caye. Such sampling accurately serves as an indicator of relative supply or flux of postlarvae for a particular point in space and time (Eggleston et al. 1998). Furthermore, we also provide a preliminary examination of the relationship between these patterns with habitat and environmental factors. Specifically, we examined how the timing of lobster settlement varied within and between months and years and whether these patterns were consistent among sites. We also examined how settlement varied among sites across spatial scales of kilometers to tens of kilometers and whether this variability was consistent over time. Finally we examined variability in habitat characteristics and environmental variables such as meteorological conditions to identify processes that may influence observed settlement patterns.

METHODS

Postlarval settlement into nearshore areas of the Belize lagoon was assessed using modified witham collectors, identical to those used in studies of postlarval lobster settlement in the Bahamas (e.g., Eggleston et al. 1998). Briefly, collectors consisted of six sheets of natural fiber air-conditional filter material, "hog's hair", draped over a PVC frame floating at the surface of the water. Collectors were moored in water ranging in depth from one to three meters at sites ranging from just south of Ambergris Caye in the north to St. Georges Cay in the south (Fig. 1). Sites were selected based on reports from fishermen that early stage benthic juveniles were abundant in the area or *in situ* assessments of settlement habitat suitability, particularly the presence of large clumps of the macroalgae *Laurencia* spp. nearby. Additional site selection criteria included accessibility of the sites and avoidance of areas with high boat traffic or fishing activity that was likely disturb or remove collectors. The latter criteria limited potential sites to those in close proximity to islands, particularly in areas with low population densities.

Prior to deploying collectors at each site, benthic habitats were characterized by conducting *in situ* visual transect surveys to quantify benthic coverage of different habitat categories. During surveys, the substrate type (e.g., mud, sand, rubble, hardbottom pavement) and benthic species (e.g., seagrass species, coral species, macroalgal species or bare substrate) were identified at 25 cm intervals along a 30 m long transect. These data were used to determine the percent coverage of different benthic habitats (e.g. seagrass

Table 1. Timeline of collections conducted at sites throughout the Belize and the total number of months sampled at each site. Sites marked with an asterisk indicate "primary" sites for more than 10 months of sampling was conducted. Statistics are reported for these primary sites in the text, tables and figures.

Site	2003			2004												2005												2006				Total
(from North to South)	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	Months
North Congreho*																																11
South Congreho*																																23
North Caye Caulker*																																28
North Calata*																																15
South Calata																																4
The Flats*																																25
The Split																																5
South Caye Caulker*																																24
Earl Smith's grounds																																5
North Higgs Caye																																4
Manolo's grounds																																2
South Caye Chapel*																																22
South Higgs Caye																																4
Santiago's camp																																5
St. George's Cay																																2

beds, macroalgae, corals) at each site.

Settlement to collectors was monitored monthly from August 2003 through April 2006. At each site, three to four collectors were initially deployed with a minimum spacing of 30 m between collectors. Sites with consistently low lobster postlarval production or frequent collector loss were removed and replaced with new trial sites. The number of collectors at sites that consistently received high levels of postlarval settlement was increased to include up to 15 collectors beginning in November 2004. Table 1 shows site-specific timelines for postlarval lobster collections at each site over the duration of this study. Months for which no data exists include those in which inclement weather prevented access to sites or logistical difficulties (e.g., mechanical problems with boats or lack of fuel) limited sampling. Although collections were made at several sites in the summer of 2005, the number of collectors sampled was low due to frequent hurricane damage. Thus, several sites were eliminated from analyses during this period. Of all sites sampled, seven sites were identified as primary sites based on the consistency of data available from them (Table 1).

Settlement to collectors was monitored three times each month. This regular schedule included collections of lobsters three days before the new moon, on the new moon, and three days after the new moon to coincide with an expected settlement peak during new moon periods (e.g., Eggleston et al. 1998). From April to August 2005, however, this schedule was altered and settlement was monitored at weekly intervals to coincide with the new moon, first quarter moon, full moon and last quarter moon. This was done to test the hypothesis that peak settlement occurs during the new moon period, and assess the effectiveness of our initial sampling design. During inspections of collectors to monitor settlement, all *Panulirus argus* were collected and the abundance of lobsters in different developmental stages recorded. Stages of development included three categories of puerulus (postlarvae) based on the degree to which they were pigmented. Transparent postlarvae (TPL) were newly settled postlarvae. Semi-pigmented postlarvae were those that were opaque and just beginning to be pigmented. Pigmented postlarvae were those in which brown and white pigmentation was well established and were in their final stages of transition prior to molting into the first benthic juvenile stage. All juveniles were also recorded. Based on their size, most juveniles were in their first or second molts following settlement (C.D. personal observation). All lobster postlarvae and juveniles were removed from collectors and brought back to an aquaculture facility on Caye Caulker for further experiments.

Analyses were conducted to determine spatial and temporal patterns in settlement of lobsters. Analyses of settlement rates to collectors were conducted using the number of lobsters at various stages found per collector per

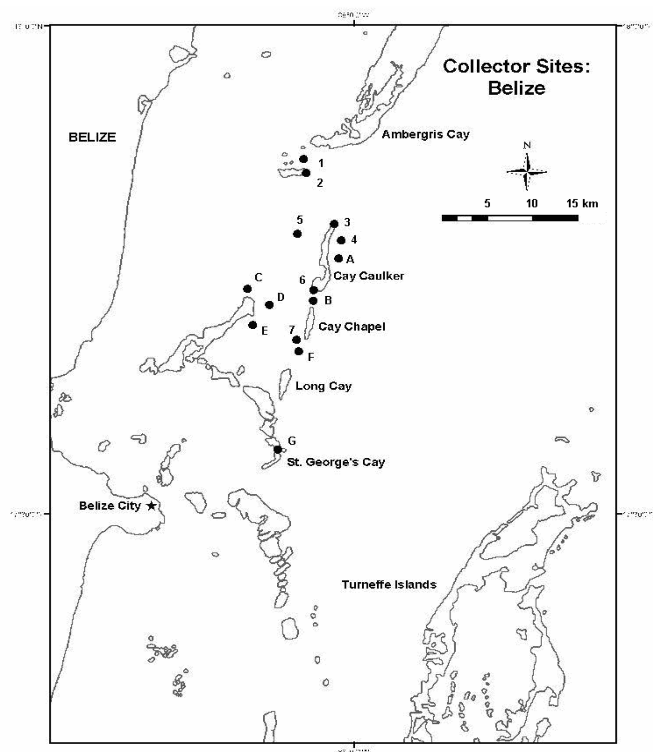

Figure 1. Collector sites in northern Belize. Sites numbered 1-7 include primary sampling sites: (1) North Congreho, (2) South Congreho, (3) North Caye Caulker, (4) North Calata, (5) the Flats, (6) South Caye Caulker, and (7) South Caye Chapel. Sites A-H include all other sites sampled: (A) South Calata, (B) the Split, (C) Earl Smith, (D) North Higgs Caye, (E) Manolo, (F) South Higgs, (G) Santiago, (H) St. George's Caye.

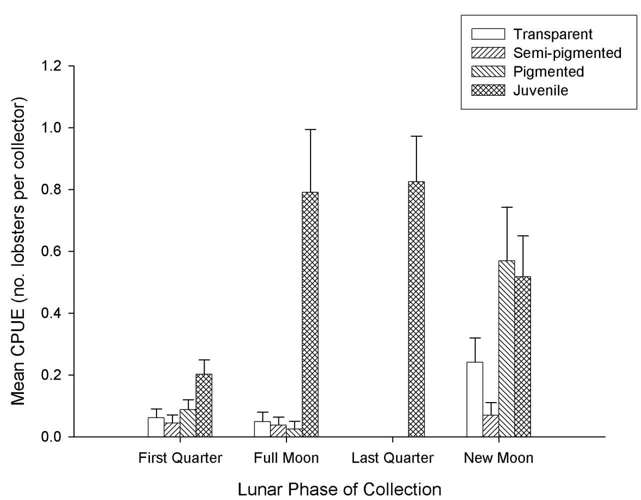

Figure 2. CPUE of lobsters collected throughout the lunar cycle. The lunar phase of the collection date is noted on the bottom axis such that collections on the first quarter included lobsters settling to collectors from the new moon until the first quarter. Error bars represent standard error. See text for details about statistically significant difference between sampling dates for each lobster stage.

sampling period at each site. For sake of clarity in presenting the results, we use the term catch per unit effort (CPUE) for the number of lobsters collected per collector per sampling period. All analyses used ANOVA models treating month, sampling period, or site as factors and Tukey's *post-hoc* tests were used when significant differences were detected to compare individual treatment means. In some cases, interactions between factors were also included in analyses to test specific hypotheses about spatial and temporal variability in observed patterns.

A preliminary analysis of how observed spatial and temporal settlement patterns relate to variability in habitats among sites and weather patterns during sampling period was also conducted. Analysis of spatial patterns included correlating the mean CPUE of sites with the percent cover of nursery habitats at each site. While sampling was not adequate to statistically test hypotheses about the effect of wind speed and direction on CPUE (i.e., the current time series is not long enough to calculate monthly site-specific puerulus anomalies to separate seasonal variability from wind-driven transport, *sensu* Eggleston et al 1998), time series of alongshore and cross shelf components of winds were calculated using data from the international airport in Ladyville, Belize (25-46 km west to southwest of sampling sites on the mainland near Belize City; Fig. 1). Alongshore and cross shelf vectors of winds were calculated from hourly data from 6 p.m. to 6 a.m. This time series allows for visual inspection of the data to assess whether peak collection periods correspond with periods of particularly high or low cross-shelf or alongshore winds, but will not allow for a quantitative assessment of the general role that winds play in influencing settlement patterns.

RESULTS

A total of 1,954 samplings of collectors were made resulting in the capture of over 2,350 total lobsters. Of these lobster, 832 were early benthic juveniles and 1,525 were at the postlarval stage. Postlarvae collected included transparent postlarvae (37%) semi-pigmented postlarvae (18%) and pigmented postlarvae (45%).

The settlement of all post-larval lobsters was influenced by lunar phase ($F_{3,282} = 19.491$; $p<0.001$; Fig. 2), however the affect of lunar phase was not consistent among all sites sites ($F_{18,282} = 1.221$; $p=0.01$). At most sites, new moon collections had significantly higher settlement of postlarval lobsters than all other lunar phases; however, postlarval settlement did not vary significantly among lunar phases at North Congreho, the Flats, South Caye Caulker and South Caye Chapel (Table 2). When only transparent postlarvae were analyzed, settlement varied due to lunar phase ($F_{3,282} = 5.170$; $p = 0.002$; Fig. 2) consistently across all sites, with collections on the new

Table 2. ANOVA comparison of CPUE of lobster stages among lunar phases for primary collection sites. Statistics are only presented for lobster stages in which there was a significant site by lunar phase interaction (see text for transparent and semi-pigmented stages). Collection period for which CPUE was greatest is noted next to p values (Tukey's test). NM indicates collections on the new moon (i.e, lobster settlement over the week prior to the new moon). LQ indicates collections on the last quarter phase of the moon (i.e., lobster settlement during the week following the full moon). Sites for which there were no significant differences (ns) in CPUE between lunar phases for a site is also noted.

Site		Pigmented		All Postlarvae		Juvenile	
(from North to South)	df	F	p	F	p	F	p
North Congreho	3,47	1.613	0.199 ns	2.311	0.088 ns	9	<0.001 LQ
South Congreho	3,65	0.449	0.719 ns	2.75	0.05 NM	5	0.005 LQ
North Caye Caulker	3,32	7.828	<0.001 NM	3.655	0.023 NM	1	0.409 ns
North Calata	3,38	10.93	<0.001 NM	8.125	<0.001 NM	2	0.075 ns
The Flats	3,44	0.492	0.689 ns	1.8	0.161 ns	1	0.275 ns
South Caye Caulker	3,24	0.899	0.456 ns	1.157	0.347 ns	1	0.25 ns
South Caye Chapel	3,32	1.778	0.171 ns	1.778	0.171 ns	2	0.137 ns

Table 3. ANOVA comparisons of CPUE among collection periods during regular collection schedule (3 days prior to new moon, new moon, three days after new moon) for different lobster stages at each primary sampling site. Differences between the three sampling periods are noted next to p values (Tukey's test), with ns indicating no significant difference between sampling periods.

Site		Transparent		Semi-pigmented		Pigmented		All postlarvae		Juvenile	
(from North to South)	df	F	p	F	p	F	p	F	p	F	p
North Congreho	2,133	4.843	0.009 3>2>1	2.643	0.075 ns	1.581	0.21 ns	2.011	0.138 ns	3.648	0.029 2>3;2=1;3=1
South Congreho	2,295	4.139	0.017 3>1,2	1.209	0.3 ns	5.285	0.006 2>1,3	2.683	0.07 ns	4.784	0.009 2,1>3
North Caye Caulker	2,207	2.768	0.065 ns	0.644	0.526 ns	3.056	0.049 1,3>2	0.55	0.578 ns	6.778	0.001 1>2,3
North Calata	2,236	7.293	0.001 1>2,3	1.328	0.267 ns	1.701	0.185 ns	5.553	0.004 1>2,3	3.518	0.031 1>2,3
The Flats	2,196	0.301	0.74 ns	6.874	0.001 3>1,2	4.569	0.012 3>1;2=3;2=1	6.12	0.003 3>2,1	1.149	0.319 ns
South Caye Caulker	2,147	1.207	0.302 ns	1.213	0.3 ns	0.052	0.949 ns	0.008	0.992 ns	1.271	0.284 ns
South Caye Chapel	2,162	1.348	0.263 ns	2.766	0.066 ns	1.473	0.232 ns	1.849	0.161 ns	0.574	0.564 ns

moon being higher than other periods. Collection of semi-pigmented postlarvae did not vary according to lunar phase, but collection of pigmented postlarvae varied according to lunar phase at some sites, but not others ($F_{18,282} = 5.342$; $p<0.001$; Table 2), similar to that of all postlarvae combined. The occurrence of juvenile lobsters on collectors varied by lunar phase at some sites, but not others ($F_{18,282} = 2.057$; $p=0.008$). Juvenile lobster occurrence on collectors was greatest during collections on the last quarter moon at the North and South Congreho sites, but did not vary at any other sites (Table 2).

During targeted sampling of lobsters from collectors during the one week period bracketing the new moon, there were also differences in the number of postlarvae collected among sampling dates ($F_{2,1631} = 3.363$, $p = 0.035$), with collections on the new moon being lower than three days before and three days after the new moon (Table 3, Fig. 3). There was a significant interaction, however, between the effect of sampling period and site on postlarval collections ($F_{46,1587} = 6.664$, $p<0.001$). While most sites did not vary significantly between sampling period, the North Calata site had greatest postlarval lobster collections on the first sampling date (i.e., three days before the new moon) and the Flats site had greatest post-larval collections on the last sampling date (i.e., three days after the new moon) (Table 3). These differences in total postlarval collections appear to be driven by differences in the timing of transparent postlarvae settlement at the North Calata site, and by differences in the timing of later stage postlarvae at the Flats site (Table 3).

Juvenile lobsters collections also varied according to sampling period, and by site ($F_{2,1637} = 7.301$; $p=0.001$) with the first collection period resulting in higher juvenile catches than the second and third sampling period (Fig. 3). Temporal patterns varied among sites ($F_{46,1593} = 2.604$, $p<0.001$), however, with juvenile collections at the North Calata and North Caye Caulker sites being greatest during the first sampling period, and juvenile collections at the two Congreho sites being greatest during the second collection period (Table 3). Collections of juveniles did not differ significantly among sampling periods for other sites.Postlarval settlement to collectors varied between months ($F_{11,1743} = 4.104$, $p<0.001$), with greatest CPUE of lobster occurring in the autumn (September through November) and a smaller peak occurring in the spring (March and April) (Fig. 5). There was some significant annual variability in this monthly pattern ($F_{26,1917} = 10.300$, $p<0.001$). In 2004 postlarval collections peaked in October, but in 2005 the peak occurred in November. There was also a significant interaction between the effect of site and month on postlarval collections ($F_{110,1833} = 7.236$, $p<0.001$, Fig. 5), coupled with the fact that monthly collections were not conducted consistently at all sites, due to different start and end dates for sampling at different sites as well as monthly access to sites being affected by weather to varying degrees.

The CPUE of early stage juvenile lobsters on collectors also varied monthly ($F_{11,1938} = 5.913$, $p<0.001$), but followed a different pattern than postlarvae (Fig 4). Peaks in juvenile occurrence on collectors were in January and October, with smaller peaks occurring in April and August. In general, the occurrence of juveniles was lower than that

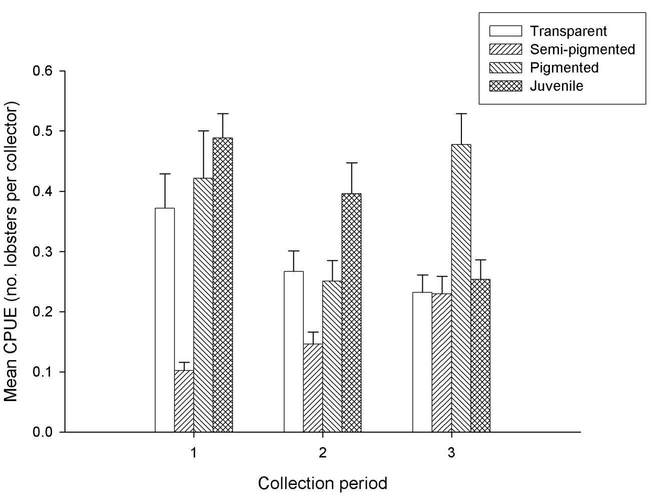

Figure 3. CPUE of lobsters caught during different collection periods of the "regular" collection schedule. Period one corresponded to collections three days prior to the new moon. Period two were collections on the new moon. Period three were collections three days after the new moon. Error bars represent standard error. See text for details about statistically significant difference between sampling dates for each lobster stage.

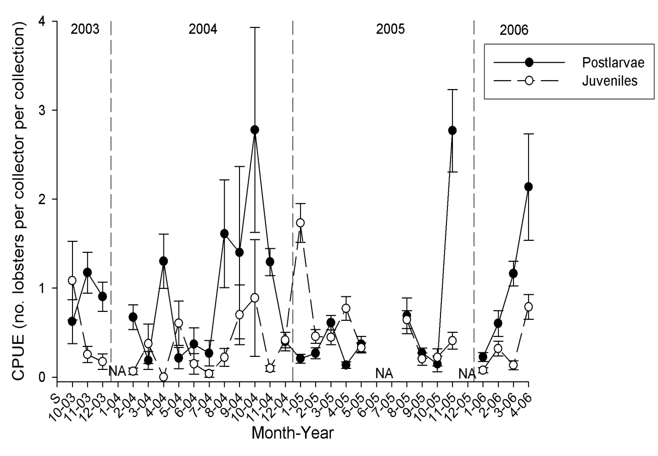

Figure 4. Time series of mean monthly CPUE for postlarval (dark circles, solid line) and juvenile (open circle, dashed line) lobsters. NA indicates no collection data is available for those months. Error bars represent standard error. See text for details about statistically significant difference between sampling dates for each lobster stage.

of postlarvae, with few exceptions. As with postlarvae, the monthly pattern in juvenile abundance was not consistent across all years and sites, with significant interactions between the effects of month and year and month and site (month x year: $F_{26,1923} = 10.215$, $p<0.001$; month x site: $F_{110,\ 1839} = 3.780$, $p<0.001$; Figs. 4 and 5). Peaks averaging more than one juvenile lobster per collector per sampling period only occurred in October 2003 (the first month of sampling) and January 2005 (Fig 5).

Spatial patterns of lobster settlement were analyzed on a month by month basis since not all sites were sampled each month, potentially confounding results. Significant differences in postlarval collections between sites were detected during more than half of the months sampled, usually during months with higher than average total recruitment (Table 4, Fig. 5). Early in our sampling, The Flats and the North Cay Caulker sites were the most productive. Following the introduction of the North Calata site in 2004, however, this new site consistently had the greatest postlarval settlement during months where significant differences among sites were detected (Table 4, Fig. 5). Variability in juvenile collections among sites was less common and showed less consistent patterns (Table 4, Fig 5). When significant differences in CPUE were detected among sites, sites to the north such as North Calata and North Congreho had greatest recruitment.

Habitat characteristics varied considerably among sites, with some sites having up to 28% macroalgae (primarily *Laurencia* spp. *Dictyota* spp.and several species of green algae) and other sites having less than 1% macroalgae (the Flats, South Congreho; Fig. 6). Similarly, seagrass coverage varied among sites with a range of 5% to over 95% (Fig. 6). There were few months in which moderately strong correlations between habitat and CPUE of

Table 4. ANOVA comparison of CPUE of postlarvae and juveniles among sites for each month of sampling. Next to reported p values, statistically significant differences between sites are noted (Tukey's test) or no significant differences (ns) is indicated. Statistical values presented are based on comparisons among all sites sampled during each month. To make data presentation clearer, however, site specific differences are only reported for primary sites, including (1) North Congreho, (2) South Congreho, (3) North Caye Caulker, (4) North Calata, (5) the Flats, (6) South Caye Caulker, and (7) South Caye Chapel. All other sites sampled consistently had CPUE comparable to the lowest grouping of primary sites, with the exception of the South Calata site, which had CPUE similar to the North Calata site whenever it was sampled.

Month & Year	df	All postlarvae F	p		Juveniles F	p	
October-03	4,19	1.596	0.216	ns	2.203	0.107	ns
November-03	7,55	4.228	0.001	5,3>2,6	1.652	0.14	ns
December-03	5,46	3.307	0.012	5>3,2>6	1.273	0.292	ns
February-04	5,40	4.09	0.001	5,3,2>6	0.592	0.706	ns
March-04	5,10	2.179	0.138	ns	2.406	0.111	ns
April-04	5,37	3.666	0.009	3,7>6,2,5	No juveniles sampled		
May-04	4,23	0.679	0.614	ns	1.36	0.278	ns
June-04	4,22	1.412	0.263	ns	0.734	0.579	ns
July-04	4,21	1.106	0.38	ns	0.808	0.534	ns
August-04	4,13	0.681	0.618	ns	1.083	0.405	ns
September-04	1,8	1.465	0.261	ns	1.996	0.195	ns
October-04	2,8	3.056	0.122	ns	1.344	0.329	ns
November-04	7,135	11.47	<0.001	4>1,2,3,5,7; 3>1,2,7	1.422	0.202	ns
December-04	7,112	27.47	<0.001	4>2,3,5,6,7	6.806	<0.001	4>1,2,3,5,6,7
January-05	7,74	1.824	0.095	ns	3.883	0.001	1,2,5>6,7
February-05	7,119	1.343	0.236	ns	1.97	0.065	ns
March-05	7,155	12.1	<0.001	4>1,2,3,5,6,7	2.374	0.025	4>5
April-05	6,133	2.976	0.009	3,4>2,5,7	1.791	0.106	ns
May-05	6,163	2.85	0.011	3,4,6>2,5,7	3.77	0.002	4>1,2,5,6,7
August-05	6,51	2.409	0.04	4>2,6,7	1.292	0.276	ns
September-05	6,89	5.101	<0.001	4>1,2,3,5,6,7	1.688	0.133	ns
October-05	2,24	2.747	0.084	ns	6.182	0.007	1>2
November-05	6,71	13.62	<0.001	4>3>1,2,5,6,7	3.634	0.003	4>1,2,5,6,7
January-06	8,106	1.672	0.114	ns	1.33	0.237	ns
February-06	8,69	2.544	0.017	4>2,3,5,6,7	0.986	0.455	ns
March-06	8,95	6.15	<0.001	4,3>2,5,7	1.329	0.239	ns
April-06	9,71	1.272	0.267	ns	2.565	0.013	4>5

postlarvae existed, however, with stringest correlations occurring during autumn settlement peaks (Table 5). Correlations between juvenile settlement and habitat were generally weak (Table 5).

Wind speed and direction varied throughout the study period. In general, the cross-shelf component of winds was onshore (i.e., winds out of the east were more common than winds out of the west), but the alongshore component varied seasonally, with wind transport being generally stronger and from north to south in the autumn and winter, and somewhat weaker and from the south to north in the late spring and summer months (Fig. 7). While no quantitative analyses were performed to correlate the weather and collection time series, there is no clear relationship between spatial and temporal patterns of lobster collection and wind-driven transport (i.e., peaks in recruitment did not occur during peak wind events from a particular direction).

DISCUSSION

Lobster collections in Belize revealed significant spatial and temporal patterns in settlement to witham collectors. Between month variability in CPUE of postlarvae followed a seasonal pattern with annual peak settlement occurring in the autumn, October or November and a small peak in spring, particularly for the most productive sites. Between site variability in this pattern can be attributed to several sites lacking seasonal peaks due to consistently low CPUE. Monthly peaks in lobster settlement occurred during the third quarter of the lunar cycle at several sites, particularly those that had the highest CPUE. Although sampling on the within this period showed settlement to be highest 3 days prior to the new moon, this may be an artifact of inequality in the number of days that collectors were allowed to go in between collections. Relatively high settlement three days after the new moon during our regular sampling, coupled with highest settlement prior to the new moon during lunar phase sampling suggests that the actual

Table 5. Correlation coefficients for the relationship between between habitat characteristics (percent cover of fleshy macroalgae and seagrass) and lobster CPUE for postlarvae and juveniles during each month of sampling.

Month & Year	All postlarvae		Juveniles	
	Macroalgae	Seagrass	Macroalgae	Seagrass
October-03	-0.411	0.385	-0.324	0.374
November-03	-0.423	0.321	-0.193	0.228
December-03	-0.291	0.075	-0.013	-0.13
February-04	-0.445	0.279	0.059	-0.079
March-04	-0.410	0.234	-0.269	-0.011
April-04	0.420	-0.075	No juveniles sampled	
May-04	0.135	-0.048	0.326	-0.246
June-04	0.205	-0.121	0.312	-0.323
July-04	0.212	-0.137	0.362	-0.358
August-04	0.190	-0.119	-0.054	-0.132
September-04	0.393	-0.393	-0.447	0.447
October-04	-0.553	0.654	-0.283	0.404
November-04	0.440	-0.214	-0.068	0.111
December-04	0.659	-0.336	0.47	-0.238
January-05	-0.021	-0.063	-0.07	-0.065
February-05	0.171	-0.112	-0.016	-0.082
March-05	0.417	-0.247	0.206	-0.076
April-05	0.199	-0.117	0.166	-0.089
May-05	0.107	0.009	0.233	-0.118
August-05	0.393	-0.292	0.241	-0.178
September-05	0.377	-0.237	0.072	0.029
October-05	0.431	-0.432	0.583	-0.583
November-05	0.633	-0.469	0.42	-0.351
January-06	0.215	-0.205	-0.02	0.03
February-06	0.278	-0.266	0.084	-0.079
March-06	0.450	-0.414	-0.019	-0.011
April-06	0.280	-0.26	0.337	-0.303

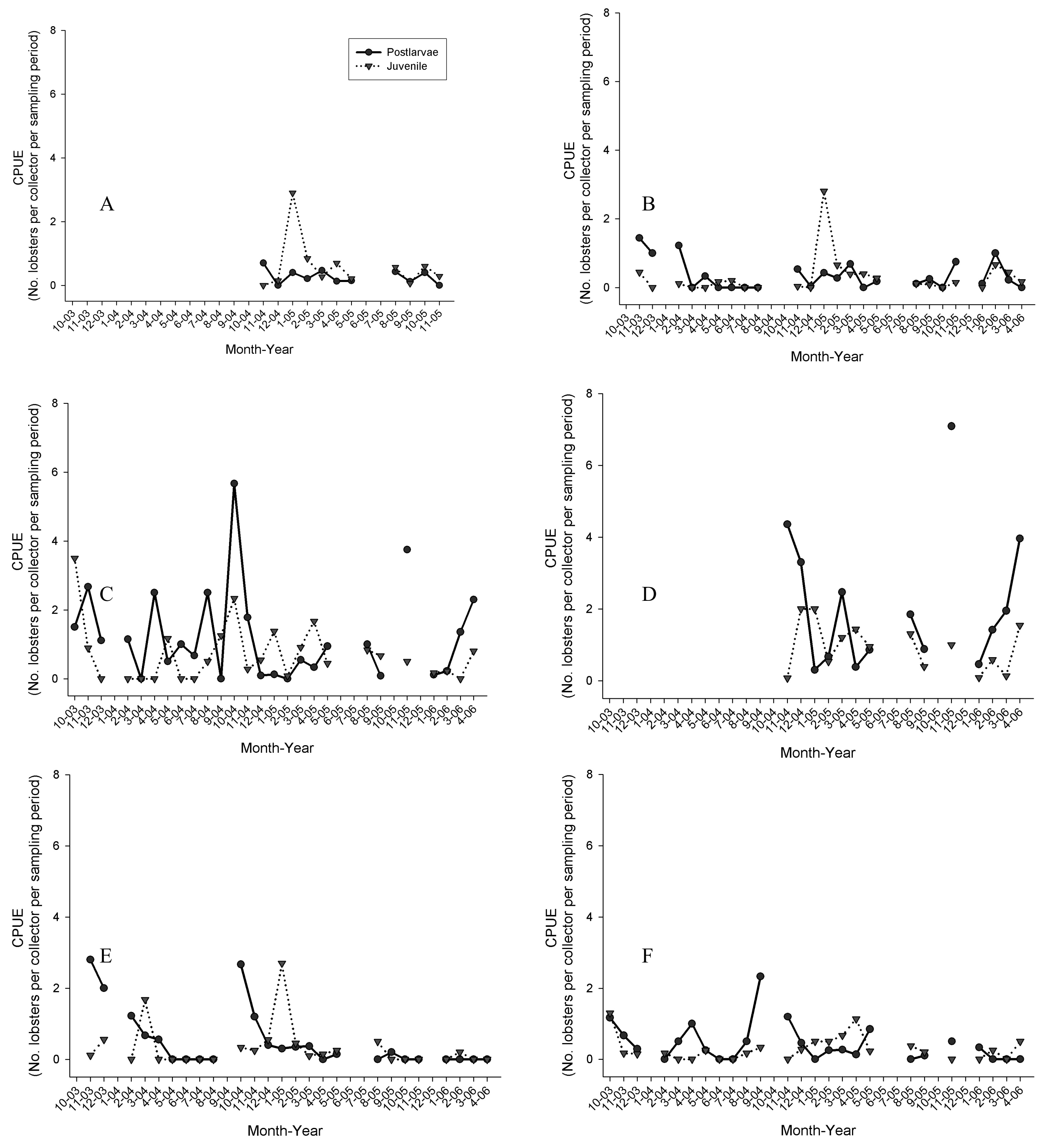

Figure 5. Time series of mean monthly CPUE for postlarval (dark circles, solid line) and juvenile (open circle, dotted line) lobsters from each of the primary sites: (A) North Congreho, (B) South Congreho, (C) North Caye Caulker, (D) North Calata, (E) The Flats, (F) South Caye Caulker, (G) South Caye Chapel. All figures are set to the same scale. For clarity of the figure, error bars are not included. See text and Table 4 for details about statistically significant difference between sampling dates for each lobster stage.

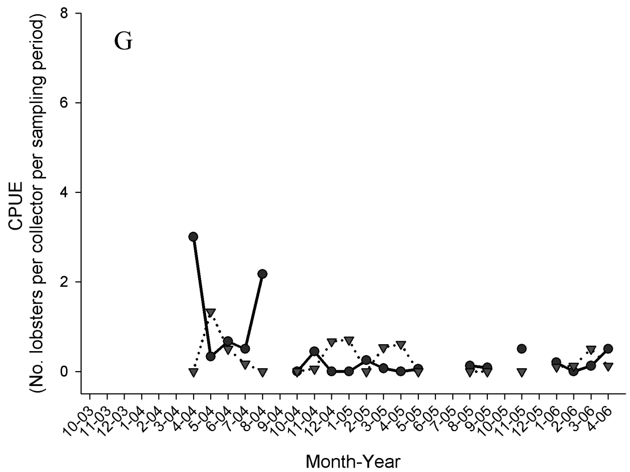

Figure 5. Continued

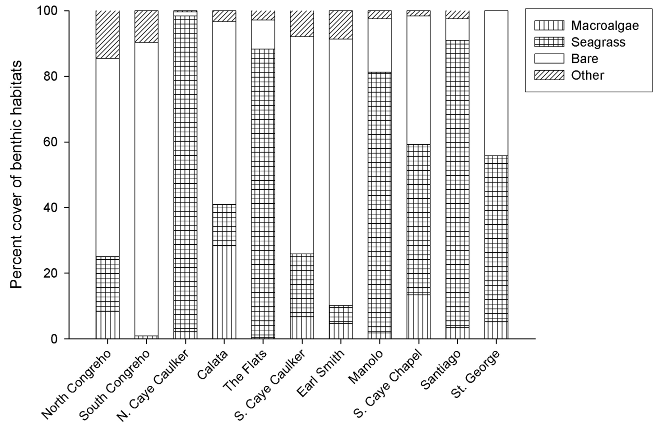

Figure 6. Percent cover of major habitat types at each site in which habitats were surveyed. The Calata site in this figure is representative of both North and South Calata. The macroalgae habitat includes all fleshy macroalgae. Other habitats included corals, sponges and calcareous algae.

timing of the recruitment peak may bracket the new moon by several days. The timing of settlement to correspond to periods around the new moon are likely to be behavioral adaptations that reduce predation rates on postlarvae mak-
timing of the recruitment peak may bracket the new moon by several days. The timing of settlement to correspond to periods around the new moon are likely to be behavioral adaptations that reduce predation rates on postlarvae mak-
ing the transition from oceanic to nearshore environments (Acosta and Butler 1999).

The witham collector sampling used in this and other studies provides an accurate index of postlarval concentration or flux, but may not accurately reflect benthic settlement rates at a particular point in space and time, which may vary due to quantity and quality of available settlement habitats (Eggleston et al. 1998). Other studies have reported greatest influx of postlarvae to coastal areas to be between the third quarter and new moon phases of the lunar cycle (Briones-Fourzán 1993), however, peak settlement to collectors is often reported as being during the first quarter of the lunar phase (i.e., new moon to first quarter moon; Marx 1986, Bannerot et al. 1991). In the Bahamas, for example, Eggleston et al. (1998) found settlement to be greatest during the first (day of the new moon to 4 days after the new moon) and second quarters (i.e., 5-11 days after the new moon) of the lunar cycle. Recruitment peaks during the third quarter and new moon period similar to those reported in this study may exist elsewhere, but the pattern was not detected in these studies due to the temporal resolution of sampling. For example, a study of lobster settlement in Quintana Roo, Mexico with sampling at the end of the first quarter found the vast majority of lobster on collectors to be in early juvenile stages (Briones-Fourzán 1994). Since tranaparent lobster settling onto collectors undergo metamorphosis to the juvenile stage is between 5 and 11 days (Calinsky and Lyons 1983, Butler and Herrnkind 1991, Briones-Fourzán 1993), many of these lobster are likely to have settled shortly prior to the new moon when our peak postlarval settlement occurred or on the day of the new moon.

The earlier occurrence of peak settlement in Belize suggests that the timing of settlement in there is more closely timed to peak larval influx than reported in other studies. The timing of settlement may be influenced by the proximity of collection sites to offshore sources of postlarvae. Our findings that transparent postlarvae, the earliest developmental stage sampled, were captured with the greatest CPUE on the first day of sampling (3 days prior to the new moon) at the Calata site, closest to the reef and offshore areas, but later stage larvae were captured later in the sampling period with the greatest CPUE at the Flats site, which was farthest from the reef, suggest that the timing of settlement is influenced by the distance that postlarvae travel to settlement habitats. Similar collections skewed towards later stage postlarvae at sites farther from the open ocean have been detected in other studies (e.g., Monterrosa 1991, Heatwole et al. 1991, Cruz et al. 1991, Briones-Fourzán 1994).

Findings of the greatest juveniles collections being on the first collection period, three days prior to the new moon, suggests either that postlarvae continue to settle throughout the month (albeit at low CPUE based on our sampling throughout the lunar cycle), or secondary dispersal whereby juvenile lobsters move onto collectors after settlement. Secondary dispersal via juvenile movement or advection by currents may be an important means of expanding nursery habitats away from areas in close proximity to the source of larvae (Etherington and Eggleston 2003). In the Belize lagoon system, such secondary disper-

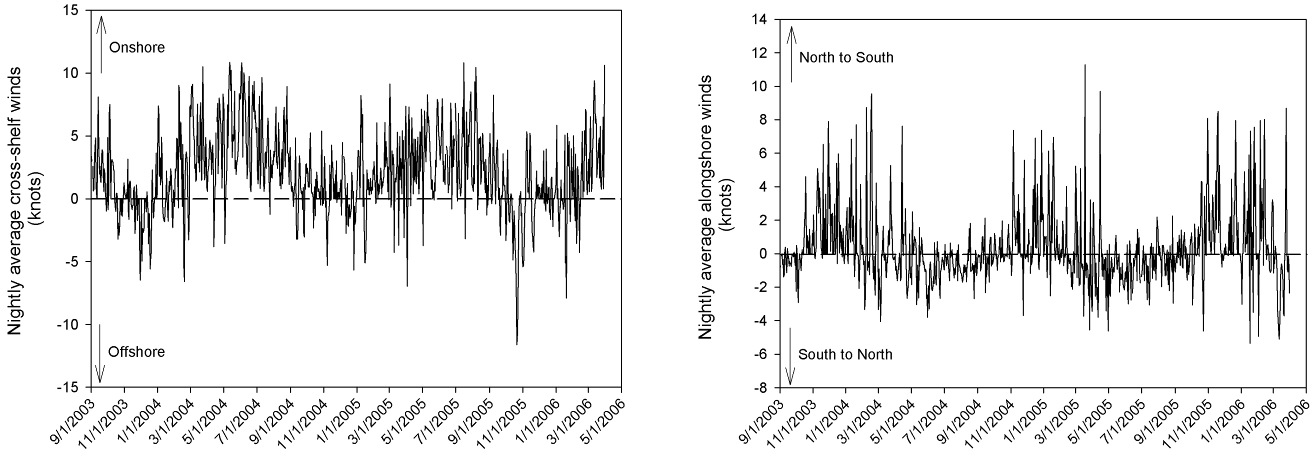

Figure 7. Alongshore (A) and cross-shelf (B) nightly winds recorded from the International airport in Ladyville, Belize (near Belize City) throughout the study period.

sal may be an important mechanism by which juvenile lobsters reach sites that have suitable nursery habitats, but low postlarval supply, such as the two sites at Congreho.

In the present study, the sampling time series was not sufficient to examine cross correlations between environmental variables and settlement variability after controlling for seasonal variability. The fact that peak settlement events did not consistently occur during periods of strong cross-shelf or alongshore winds, suggests that wind-driven transport may not have a strong influence on lobster settlement in this system. Nevertheless, these factors may play some role in the observed spatial and temporal patterns. For example, observed variability in the timing of these peaks from year to year may be due to the influence of variable wind-driven transport or other environmental factors (e.g., Eggleston et al. 1997). In our study, strong winds blowing offshore during the October 2005 sampling period may have suppressed CPUE compared to October 2004, when moderate onshore winds may have contributed to the annual settlement peak. Similarly, the sites with the greatest settlement, particularly during peak settlement events (i.e., Calata and North Caye Caulker) were southwest and closest in proximity to a large cut in the barrier reef (Fig 1). Winds during these peak settlement times were frequently moderate and usually out of the northeast, potentially contributing to settlement at these sites as opposed to those farther from cuts (e.g., the Flats) or northwest of major cuts (e.g., Congreho, South Caye Caulker, South Caye Chapel).

Other characteristics of sites may have also contributed to spatial variability in postlarval settlement. Settlement may have been low at some sites due to high siltation of collectors. Settlement of lobster to clumps of *Laurencia* spp. has been demonstrated to be lower to silted algae than clean algae (Herrnkind et al. 1988). Thus, collectors that were heavily silted at sites like St. George's Caye and Exis Caye (F.S. personal observation) may have been avoided by settling lobsters.

Although collection sites were selected based on criteria including the presence of important settlement and juvenile habitats, there was some variability in the amount of these habitats at each site. Spatial patterns in settlement do not appear to be correlated with habitat characteristics of sites (i.e., settlement is not highest at sites with the most macroalgal settlement habitat), however, the site receiving the greatest settlement, North Calata, had the most fleshy macroalgae habitat, which included *Laurencia* spp. but was mostly green algae. The fact that habitat does not appear to be a strong predictor of settlement may be due to the scale at which sampling was conducted. Since high quality macroalgal settlement habitat, primarily clumps of macroalgae dominated by *Laurencia* spp. is patchily distributed, limited transect sampling conducted in this study may not provide an accurate assessment of the amount of this habitat available to lobsters. Similarly, it is not known how lobsters sample and select settlement habitats. For example, lobsters use chemical odors from habitats to cue onshore migrations. Thus, they may not be able to detect small scale variability in the amount of settlement habitat, but may be able to sample the amount of settlement habitat in a larger area based on the concentrations of chemicals in the water.

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