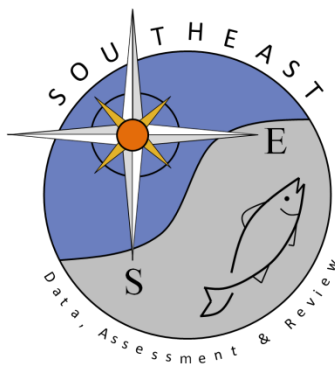# Patterns of Spiny Lobster (*Panulirus argus*) Postlarval Recruitment in the Caribbean: A CRTR Project

MARK J. BUTLER, ANGELA M. MOJICA, ELOY SOSA-CORDERO, MARINES MILLET, PAUL SANCHEZ-NAVARRO, MIGUEL A. MALDONADO, JUAN POSADA, BLADIMIR RODRIGUEZ, CARLOS M. RIVAS, ADRIAN OVIEDO, MARCIO ARRONE, MARTHA PRADA, NICK BACH, NILDA JIMENEZ, MARIA DEL CARMEN GARCIA-RIVAS, KIRAH FORMAN, DONALD C. BEHRINGER, JR., THOMAS MATTHEWS, CLAIRE PARIS, and ROBERT COWEN

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Patterns of Spiny Lobster (*Panulirus argus*) Postlarval Recruitment in the Caribbean: A CRTR Project

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ABSTRACT

As part of the Coral Reef Targeted Research (CRTR) Program, a partnership between the Global Environment Facility and the World Bank, our research team examined the recruitment patterns of Caribbean spiny lobster (*Panulirus argus*) postlarvae among regions in the Caribbean, with a particular focus on Mesoamerica. Our goal was to collect comparable information on postlarval supply among regions and to provide data to test predictions of connectivity generated from a coupled biophysical oceanographic model of lobster larval dispersal. Here we present the results of the postlarval recruitment monitoring program. We monitored the catch of postlarvae on Witham-style collectors at sites in the Caribbean from March 2006 to May 2009, although the duration and frequency of sampling varied among locations. Recruitment varied considerably among months and locations. It peaked in the Western Caribbean in the fall (Oct - Dec), whereas in Florida, Puerto Rico, and Venezuela peaks were in spring (Feb - April) with a smaller peak in the fall. Sites generally fell into two groups with respect to monthly variability in recruitment: low variability sites (e.g., Honduras, southern Mexico, Venezuela) and high variability sites (e.g., Florida, San Andres Islands, Puerto Rico, northern Mexico). Recruitment magnitude varied locally, but generally increased (lowest to highest) from Puerto Rico, San Andres Islands, Honduras, Mexico, Venezuela, to Florida. Recruitment trends mirrored fishery catch in some locations, implying a recruit-to-stock linkage. Recruitment was significantly correlated among several sites, suggesting similarity in their larval sources and oceanographic regimes.

KEY WORDS: Connectivity, recruitment, postlarvae, spiny lobster, *Panulirus argus*

Comparación de los Patrones de Reclutamiento de Larvas de Langosta en el Caribe: Un Proyecto del CRTR

Como parte del Programa de Investigación Enfocada en Arrecifes de Coral (Coral Reef Targeted Research - CRTR Program), una sociedad entre la Fondo Mundial para el Medio Ambiente y el Banco Mundial, el grupo de trabajo de conectividad del CRTR estudio el reclutamiento de peces, corales y langosta en el Caribe occidental. Nuestra equipo de investigación se enfoco particularmente en la langosta espinosa del Caribe (*Panulirus argus*). El objetivo del proyecto fue el de recoger y comparar información acerca del origen y suministro de post-larvas de langosta en el Caribe, proporcionando datos empíricos para poner a prueba las predicciones de conectividad de dispersión de larva de langosta generadas a través de un modelo bio-físico oceanográfico. El Grupo de Conectividad del CRTR también proporció becas para estudiantes de postgrado, talleres para científicos y manejadores de recursos de la región Caribe para discutir la importancia de la conectividad y el reclutamiento de larvas en el manejo de recursos marinos. En este proyecto monitoreamos la retención de post-larvas de langosta utilizando colectores estilo Witham en diferentes localidades del Caribe entre marzo del 2006 y mayo del 2009; sin embargo, la duración y frecuencia del muestreo no fue igual en todas las localidades. El reclutamiento de larvas varió considerablemente entre meses y localidades, mientras que en el Caribe occidental el reclutamiento se aumento durante el otoño (octubre – diciembre), en la Florida, Puerto Rico, y Venezuela el mayor aumento en el reclutamiento fue observado durante la primavera (diciembre - abril) con un pico más pequeño en el otoño. La magnitud del reclutamiento varió localmente, pero aumentó de manera progresiva (orden ascendente) de Puerto Rico, Archipiélago de San Andrés, Honduras, México, Venezuela, a la Florida. Las localidades muestreadas se clasificaron en dos grupos con respecto a la variabilidad mensual de reclutamiento observada, la cual es fuertemente influenciada por patrones oceanográficos: 1) sitios de menor variabilidad de reclutamiento (Honduras, sur de México, Venezuela) y sitios de mayor variabilidad de reclutamiento (Florida, Archipiélago de San Andrés, Puerto Rico, norte de México).

PALABRAS CLAVES: Conectividad, reclutamiento, langosta, *Panulirus argus*

Comparaison de Modeles de Recrutement de Homard Post-Larvaire dans les Caraïbes: Un Projet de CRTR

Dans le cadre du programme Coral Reef Targeted Research (CRTR), une association entre Global Environment Facility et la Banque Mondiale, le Groupe de travail de Connectivité CRTR a étudié le poisson, le corail et le recrutement de homard dans les Caraïbes de l'ouest. Notre équipe de recherche particulière s'est concentrée sur la langouste antillaise (*Panulirus argus*). Notre but était de recueillir des renseignements comparables sur les réserves post-larvaires parmi les régions dans les Caraïbes et fournir des données pour évaluer des prédictions de connectivité produite d'un modèle océanographique biophysique couplé de dispersion de langouste larvaire. Le projet a fourni aussi des bourses aux doctorants antillais et aux ateliers pour les scientifiques et les directeurs de ressource pour discuter le rôle de la connectivité larvaire et du recrutement dans la gestion de ressource. Nous avons surveillé la capture de post-larves sur les collectionneurs de Witham-style sur sites dans les Caraïbes de mars 2006 à mai 2009, bien que la durée et la fréquence d'échantillonnage varient selon les endroits. Le recrutement a varié considérablement selon les mois et les endroits. Il a culminé dans les Caraïbes de l'ouest à l'automne(octobre - décembre), alors qu'en Floride, au Porto Rico et au Venezuela les pics étaient au printemps (décembre - avril) avec un plus petit pic à l'automne. L'ampleur du recrutement a varié localement, mais a généralement augmenté (du plus bas au plus haut) de Porto Rico, Îles de San Andres, Honduras, Mexique, Venezuela, à la Floride. Les endroits entraient généralement dans deux groupes en ce qui concerne la variabilité mensuelle dans le recrutement, qui est fortement sous l'influence de l'océanographie : les sites de basse variabilité de recrutement (par ex, le Honduras, le Mexique du sud, le Venezuela) et les sites de variabilité de recrutement élevée (par ex, la Floride, les Îles de San Andres, Porto Rico, le Mexique du nord).

MOTS CLÉS: Recrutement, homard, *Panulirus argus*, connectivité, CRTR

INTRODUCTION

Connectivity in marine ecosystems generally refers to the exchange of individuals among populations through larval dispersal, an interconnection that influences the dynamics and genetics of those populations, as well as their management. Investigating the scale of marine larval dispersal is critical to understanding connectivity among populations, especially for marine species whose adult movement is limited (Cowen *et al*. 2006). With major declines in fishery stocks and marine biodiversity world-wide, and an increasing demand for ecosystem-based management approaches that rely heavily upon marine protected areas (Worm *et al*. 2006, Guarderas *et al*. 2008, Pauly 2009), the identification of spatial scales of population connectivity is imperative for better resource management (Sale *et al*. 2005).

In the Caribbean, understanding population connectivity of the Caribbean spiny lobster (*Panulirus argus*; Latreille 1804) is perhaps more important and more daunting than for any other species because of its economic significance to the region and its long larval duration, respectively. The Caribbean spiny lobster is the target of the most valuable and widespread fishery in the Caribbean (Bohnsack *et al*. 1994, Harper 1995, Hunt 2000, Chavez 2008). Most stocks, however, are considered fully- or over-exploited (FAO 2006). Like all spiny lobsters (Phillips et al. 2006), *P. argus* has a protracted planktonic larval duration (PLD) that has long been suspected to be 5 - 9 months (Lyons 1980), and recently confirmed to be 5 to 7 months based on laboratory rearing of larvae (Goldstein *et al*. 2008). This is one of the longest PLDs known for a marine animal in the Caribbean. For years, the larval dispersal distance was thought to scale generally with larval PLD (Largier 2003, Siegel *et al*. 2003), the assumption being that the longer that larvae remain in the plankton, the further that ocean currents would transport them away from their natal spawning source. Because *P. argus* possesses an extraordinary long PLD, scientists have long

presumed its pan-Caribbean dispersal (Lyons 1980) and low genetic variation among Caribbean lobster populations supported this hypothesis (Silberman and Walsh 1994, Sibelman *et al*. 1994).

Yet, differences among larval stages in diel and ontogenetic vertical migratory behavior along with complex ocean hydrodynamics moderate the dispersal of marine fish larvae (Paris *et al*. 2007, Sponaugle et al. 2002, Cowen *et al*. 2006), and lobster may be no different. Although lobster larvae appear capable of a high degree of dispersal, the implications of connectivity studies for other species provide reasons to suspect that such dispersal maybe more restricted than previously believed. In lieu of better scientific information on the true connectivity of lobster populations, all Caribbean nations have taken the more conservative and politically tractable approach of managing their respective lobster fisheries by assuming self-recruitment. That is, fishery management is based on the presumption that the adults in an area produce the postlarvae that eventually arrive back to the same area many months later and thus give rise to their fishery stocks. This is almost certainly wrong for most regions. However, there is currently no strong scientific basis for determining how connected each country's lobster stock may be to itself or to other regions. The technological tools needed to address this problem have long eluded us, and solving it would indeed be a break-through for science and lobster management in the Caribbean.

To ascertain larval connectivity in the sea, researchers have relied on one of three approaches: investigations of genetic structure and similarities among populations (reviewed by Hedgecock *et al* 2007 and by Weersing and Toonen 2009), mark-recapture based studies of larvae bearing natural geochemical or artificial tags (reviewed by Thorrold *et al*. 2007), and predictions of larval dispersal from coupled physical-biological models (reviewed by Werner *et al*. 2007). Each approach has its advantages and limitations, but for our study of Caribbean spiny lobster

connectivity we chose the latter. Thus far, genetic techniques have failed to identify sufficient genetic substructure among lobster populations in the Caribbean, which is necessary for inferring patterns of connectivity (Silberman and Walsh 1994, Silberman *et al*. 1994). We are also unaware of any geochemical or artificial "tags" that could be used to study larval connectivity in lobsters. However, recent developments in biophysical modeling of connectivity in Caribbean reef fishes (Cowen *et al.* 2000, 2006) are a promising avenue for understanding connectivity that may work for spiny lobster, assuming that knowledge of important larval characteristics (e.g., duration, behavior, mortality) can be obtained to appropriately parameterize the models.

The lobster recruitment project described here is one element of a larger study of lobster connectivity in the Caribbean, and part of the Coral Reef Targeted Research (CRTR) Program, a partnership between the Global Environment Facility and the World Bank. The CRTR program is a worldwide initiative seeking to fill critical gaps in coral reef ecosystems knowledge and to use that information to support management and policy decisions that contribute to the long-term sustainability of coral reefs worldwide. As part of CRTR Connectivity Working Group, the lobster connectivity research team sought to use recent advances in high-resolution oceanographic modeling and larval rearing technologies, coupled with laboratory and field studies of larval and postlarval behavior and patterns of recruitment, to estimate the connectivity of lobster populations in the Caribbean. We focused in particular on the Mesoamerican region targeted by the CRTR program. One goal of the lobster connectivity study was to collect information on postlarval supply throughout the Caribbean to provide empirical data:

  i)   For comparable estimates of recruitment magnitude and temporal patterns among study regions for use by resource managers, and
  ii) To test predictions of connectivity generated from a high resolution bio-physical oceanographic model of lobster larval dispersal.

In this paper, we describe the results of the first objective: comparisons of postlarval spiny lobster patterns of recruitment.

MATERIAL AND METHODS

"Recruitment" of marine species has been variously defined depending on the species and circumstances. In this instance, when we refer to "recruitment" we mean the arrival of planktonic spiny lobster postlarvae to coastal areas from offshore as measured on artificial collecting devices. Our plan for monitoring lobster recruitment was to establish postlarval collectors in Mesoamerica and a few other representative regions of the Caribbean; two sites per region about 10 km apart, with 3 - 5 postlarval collectors per site. We originally established collector sites in 17

regions within nine countries and intended to monitor postlarval recruitment from as early as March 2006 (depending on the initial date each site was established) to May 2009. However, we were unable to maintain that sampling regime and obtained a year or more of simultaneous and comparable data from only six regions (Figure 1).

Figure 1. Map of the Caribbean showing the general location of the regions where time-series data on Caribbean spiny lobster (*P. argus*) postlarval supply were collected (filled circles; USA: Florida Keys; Mexico: Akumal, Cozumel, Xcalak and Banco Chinchorro; Honduras: Cayos Cochinos and Roatan; Colombia: San Andres Islands; Venezuela: Los Roques; and Puerto Rico: Bramadero) and regions where collectors were originally established but later abandoned (open circles).

A variety of postlarval collectors have been developed to estimate the relative recruitment of spiny lobsters worldwide and their general construction and use has been reviewed elsewhere (see Phillips & Booth 1994). At least three types of collectors have seen widespread use in collecting *P. argus* postlarvae in the Caribbean: the Phillips-type collector, the GuSI-type collector, and the Witham-type collector. All are effective at capturing *P. argus* postlarvae, although their rates of capture and relative cost of construction and maintenance vary (e.g., see Phillips *et al.* 2005). The modified Witham-type collector is the only device whose catch has been shown to be correlated with planktonic abundance and with settlement of postlarvae in the region "downstream" of the collector (Herrnkind and Butler 1994). We chose Witham-type collectors for use in this study for this reason and because of their widespread use currently and in previous studies (e.g., Witham *et al.* 1968, Little 1977, Little and Milano 1980, Marx 1986, Bannerot *et al.* 1991, Briones- Fourzan 1994, Forcucci *et al.* 1994, Herrnkind and Butler 1994, Acosta *et al.* 1997, Lipcius *et al.* 1997, Eggleston *et al.* 1998, and others). Our goal was insuring consistency of methods among our study sites and reliable estimates of recruitment, not maximizing catch per se.

At each site, collectors were placed in shallow water < 3 m deep over sparsely covered hard-bottom or sandy substrates, and areas were chosen where postlarvae were likely to be concentrated and thus more likely to encounter the collector before entering the nursery proper. Optimal locations included the landward edge of channels leading from offshore to coastal lagoons or the edge of an island closest to the lagoon where postlarvae are concentrated by tidal eddies. Natural settlement habitats (e.g., algal-covered hard-bottom, dense seagrass, reef, mangroves) were intentionally avoided when selecting locations for collectors because collectors placed directly within nursery areas yield unreliable estimates, presumably because collectors are less attractive to postlarvae in such habitats. Witham-type collectors float just below the surface and are easily seen, thus other important criteria we considered for collector site selection were security (to reduce the potential for theft) and navigational hazards. Collectors were permitted to soak for one month prior to the initiation of data collection and the air conditioning filter material used in construction of the collectors was replaced every three months on a rotational basis among collectors. We sampled the collectors once a month seven days following the new moon and recorded the number of transparent and pigmented postlarvae, as well as the number of newly metamorphosed early benthic juvenile lobsters on each collector. These three measures were summed to estimate monthly recruitment per collector per month. Only data from sites providing the longest concurrent data sets were included in this analysis.

RESULTS

Recruitment of *P. argus* postlarvae varied considerably among months at individual locations and among locations each month. In the Western Caribbean (i.e., Mexico, Honduras and Colombia) recruitment generally peaked in the fall (Oct - Dec), whereas in Florida, Puerto Rico, and Venezuela peaks occurred in the winter-spring (Dec - April) with a smaller peak in the fall (Figure 2). Locations fell into two general groups with respect to monthly variability in recruitment, standardized for recruitment magnitude (i.e., comparison of coefficients of variation in monthly recruitment). Sites where recruitment varied little among months (e.g., Honduras, southern Mexico, Venezuela) and sites with high variability in recruitment (e.g., Florida, San Andres Islands, Puerto Rico, northern Mexico; Figure 2). Recruitment of postlarvae was nearly three times as variable among regions in the Caribbean (CV = 81%) as compared to recruitment between sites within a region that were generally < 10 km apart (CV = 32%).

We assessed the concordance in the recruitment of *P. argus* postlarvae (mean number of postlarvae per Witham-type collector per month) among regions in the Caribbean from March 2006 through April 2009 using a Pearson correlation analysis, the results of which are depicted in a correlation matrix (Table 1). Only six of the 36 relationships where correlation analysis was possible (e.g., where n $\geq$ 4) were significant; however, many of the results suffered from low samples sizes (i.e., too few months with overlapping data sets). Significant positive relationships in the temporal pattern of *P. argus* recruitment occurred between and among sites in southern Mexico (i.e., Xcalak and Akumal) and Honduras (i.e., Roatan and Cayos Cochinos). In contrast, recruitment in the San Andres Islands of Colombia (east of Nicaragua) was significantly negatively correlated with those at Cozumel. Recruitment in Florida was the most unique among the sites we studied (i.e., no r-values > 0.50), but this may have been a sampling artifact because the data were more complete for Florida and the correlations between Florida and the other sites thus based on more data.

The overall magnitude of *P. argus* recruitment increased (lowest to highest) from Puerto Rico, San Andres Islands, Honduras, Mexico, Venezuela, to Florida (Figure 3). Recruitment magnitude (mean number of recruits per month) averaged per country was also correlated (r = 0.764; p = 0.065; n = 6) with the average fishery landings of *P. argus* for these countries based on the most recent landings data for 2000 - 2004 (FAO 2006; Figure 4). At one location included in this study, the Florida Keys, a long time-series of postlarval catch and fishery landings exists and are highly correlated. Postlarval recruitment in the Florida Keys over the past 20 years or so explains nearly 70% of the commercial fishery landings (measured as CPUE in kg/trip) 14 months later (r = 0.698, p = 0.006, n = 14; Figure 5).

DISCUSSION

Our goals for this field study-based portion of the CRTR spiny lobster connectivity project were two-fold. First, to determine the spatio-temporal patterns of recruitment among locales in the Caribbean to explore potential similarities that might aid in more regional spiny lobster management. Second, to provide data for validation of biophysical modeling that we are conducting to predict lobster connectivity among regions in the Caribbean (Butler *et al*. In review). The second goal is still in progress; this paper focuses on the first. Although the level of participation from partners in several of our originally established sampling locations was disappointing and greatly diminished the geographic representation and temporal continuity of the data set as originally envisioned, the resultant data still provide the single most widespread and comparable examination of *P. argus* recruitment in the Caribbean.

As is the case for all studies of lobster postlarval recruitment, we too observed considerable variability in the monthly arrival of *P. argus* postlarvae on artificial collectors at each study site. Such temporal variability in recruitment is presumably a result of both biological and physical phenomena. Spatio-temporal variation in

biological events such as spawning (Bertelsen and Matthews 2001), mortality of larvae and postlarvae (Acosta and Butler 1999), and postlarval attraction to local nurseries (Goldstein and Butler 2009) all contribute to monthly fluctuations in recruitment, as does variation in oceanographic circulation in different seasons (Cowen *et*

al. 2003, Briones *et al*. 2008) and at different scales (Paris *et al*. 2007) that affects the dispersal of larvae and postlarvae. Our attention here is not on those short-term fluctuations in recruitment or what processes create them, but instead on regional similarities in those patterns.
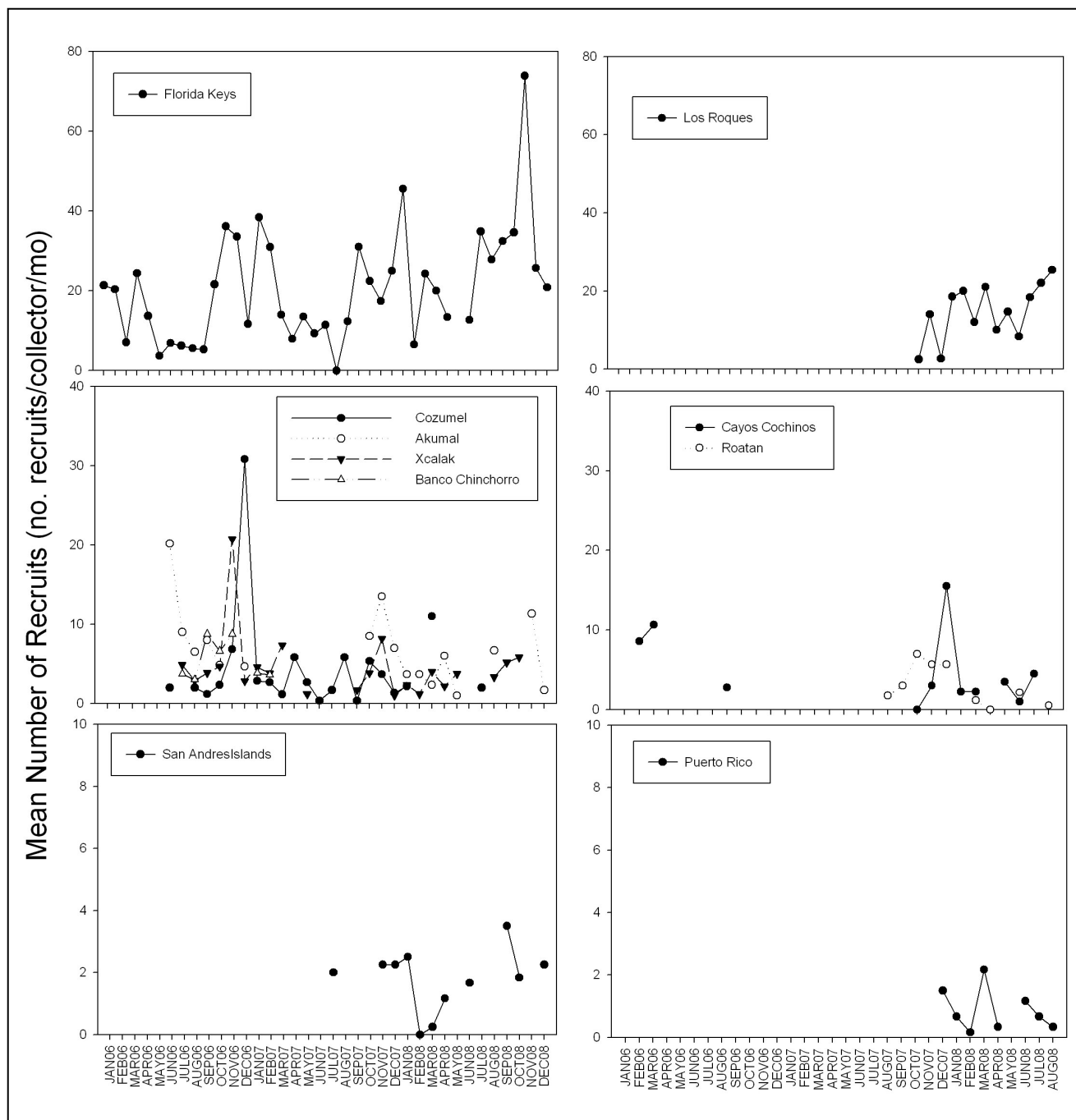

Figure 2. Time-series of Caribbean spiny lobster postlarval recruitment (mean number of recruits per collector per month) at study sites reporting at least months of data from March 2006 through April 2009.
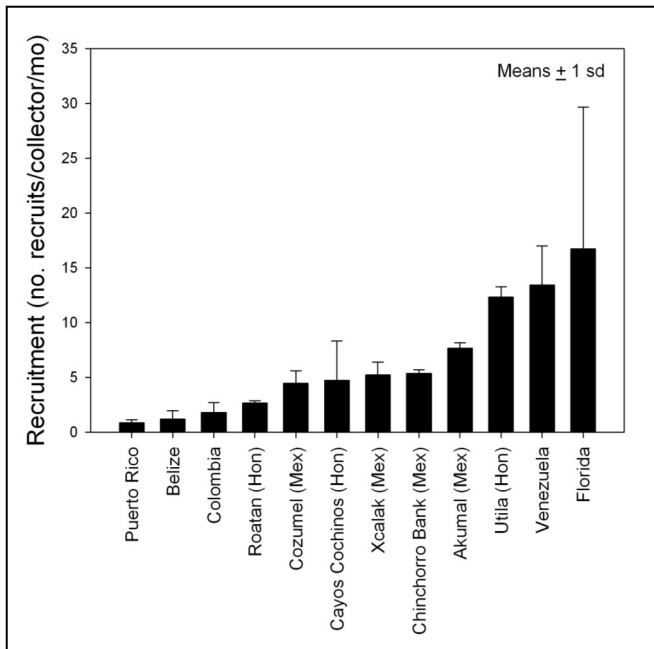
Figure 3. Mean recruitment (mean number of recruits per collector per month) (± 1 SD) of postlarval Caribbean spiny lobster at study sites reporting at least 6 months of data from March 2006 through April 2009. Note the difference in scale on the y-axis for the different plots.
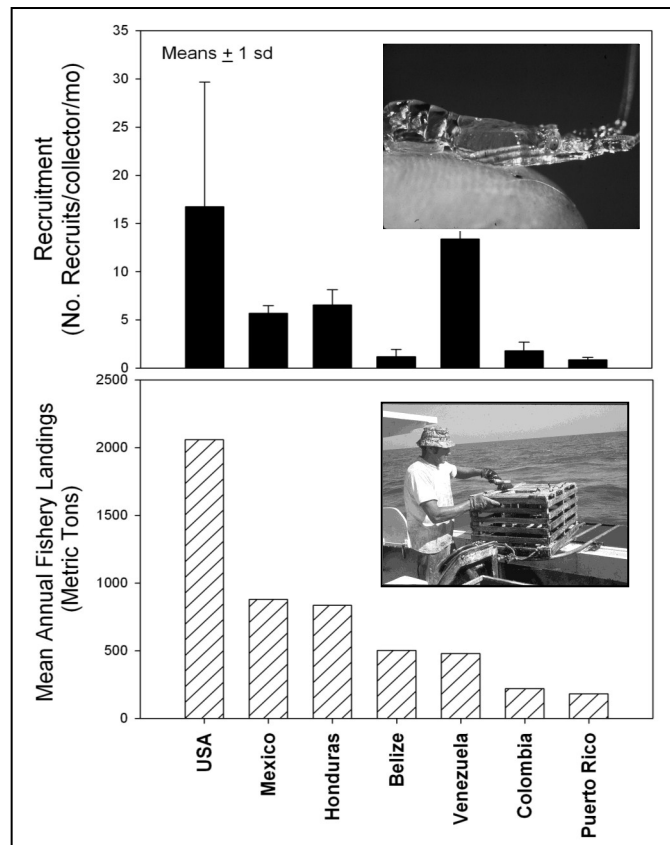
Figure 4. **(**Top) Mean recruitment (mean number of re-cruits per collector per month) (± 1 SD) of Caribbean spiny lobster postlarvae summarized per country reporting at least 6 months of data from March 2006 through April 2009. Inset photo: postlarval *P. argus* (photo credit: William Herrn-kind). (Bottom) Mean annual *Panulirus argus* fishery land-ings (metric tons) by region from 2000 through 2004 (FAO, 2006). Inset photo: commercial fisherman with trap in Flori-da (photo credit: John Hunt).
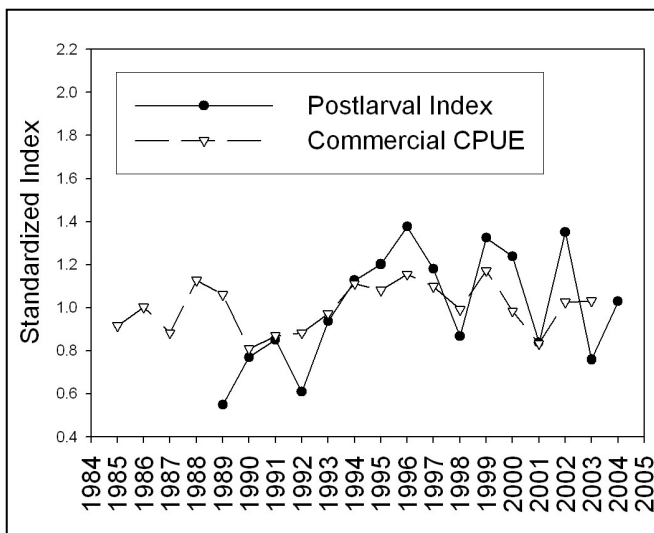
Figure 5, Time-series showing the Caribbean spiny lobster postlarval index with a 14 month time lag (black line) rela-tive to five indices of adult lobster abundance (panels). Index values were standardized to their means to permit easier visualization.

The seasonal patterns in recruitment that we observed differed among regions in the Caribbean, but were generally consistent with previous observations (Little 1977, Little and Milano 1980, Marx 1986, Bannerot *et al*. 1991, Acosta *et al*. 1997, Eggleston *et al*. 1998, Cruz *et al*. 2001, Briones-Fourzan 1994, Kojis *et al*. 2003, Gordon and Vasquez 2005, Briones-Fourzan *et al*. 2008). In brief, recruitment peaks in the fall in the Western Caribbean (i.e., Mexico, Honduras and Colombia) and in the spring (Feb - April) in most of the rest of the Caribbean (e.g., Antigua, Cuba, Florida, Puerto Rico, Virgin Islands, Venezuela) where a smaller fall peak sometimes occurred. These patterns do not correspond in a straightforward way with spawning. In much of the Caribbean, *P. argus* spawns throughout the year, although its magnitude is greatest in the late spring and early summer in many areas, the extreme being in Florida where spawning occurs only in late spring to early summer (Bertelson and Matthews 2001). Recent success at rearing *P. argus* in the laboratory through all of its larval stages indicates that its pelagic

larval duration is about six months long, but varies between 4.5 and 7.5 months (Goldstein *et al.* 2008), which is similar to the hypothesized PLD based on examination of field data (Lyons 1980). A spring peak in spawning would logically correspond with a fall peak in recruitment, which applies to the results for some sites but not all. Delayed larval metamorphosis and mixing of larval sources may explain the disconnect between spawning schedules and recruitment in many regions of the Caribbean. Postlarvae are indeed capable of delaying metamorphosis by a few days if appropriate nursery habitat is not encountered (Goldstein and Butler 2009), but we as yet do not know if larvae are capable of doing this.

With respect to monthly variability in recruitment, our sites generally fell into two groups: low variability sites (e.g., Honduras, southern Mexico, Venezuela) and high variability sites (e.g., Florida, San Andres Islands, Puerto Rico, northern Mexico). We hypothesize that these differences, if indeed representative of the true condition given the limited sample sizes in some sites, may also represent the influence of different oceanographic regimes. Regions experiencing a more consistent supply of larvae

(i.e., low variability sites) may perhaps be those more directly connected to one or a few source regions rather than many, as might be the case for sites whose recruitment is tied together within an oceanic gyre. Our sites within the Bay of Honduras, which is subject to a persistent cyclonic gyre, may be just such an example. In contrast, other sites experience high variability in recruitment and these tend to occur in areas dominated by strong boundary currents (e.g., Florida Keys, Mexican Caribbean coast) that are strongly influenced by sea level anomalies and hurricanes (Briones-Fourzan *et al.* 2008).

Recruitment was also significantly correlated among several of our study sites, which again suggests similarities in stock source and oceanographic regimes. The concordance in recruitment patterns among certain regions in the Caribbean, particularly in Mesoamerica where this study focused, match expectations based on examination of oceanographic current patterns and recent results of biophysical modeling of lobster connectivity in the Caribbean (Butler *et al.* In review). The gyre that dominates the oceanography of the southern Bay of Honduras provides a compelling example of the importance of

Table 1. Correlation matrix comparing the relationships among regions in the Caribbean in the recruitment of *P. argus* postlarvae (mean number of postlarvae per Witham-type collector per month) among sampling dates from March 2006 through April 2009. Sampling locations are given at the top and left of the matrix (Florida = FL; Akumal, Mexico = Akumal; Cozumel, Mexico = Cozumel; Xcalak, Mexico = Xcalak; Chinchorro Bank, Mexico = Chinchorro; Cayo Cochinos, Honduras = Cochinos; Bramadero, Puerto Rico = PR; Los Roques, Venezuela = VE; San Andres Island, Columbia = CO; Roatan, Honduras = Roatan). The Pearson correlation coefficient, the significance of the correlation (shown as a P-value), and sample size (n) are given within each cell of the table. Sample size varied among correlations due to differences in sampling dates among recruitment monitoring stations during the study period. The lower left portion of the matrix is redundant so is blacked out. Photo inset is of a Witham-type collector, the type used in this study (photo credit: John Hunt).

Correlations

		FL	Akumal	Cozumle	Xcalak	Chinchorro	Cochinos	PR	VE	COL	Roatan
FL	Pearson Correlation	1	-.267	.404	.020	-.052	-.289	.119	-.058	-.110	-.498
	Sig. (2-tailed)		.300	.069	.931	.911	.389	.778	.858	.763	.173
	N	17	21	21	7	11	8	12	10	9	
Akumal	Pearson Correlation		1	-.303	.580*	-.096	.668	-.317	-.239	.353	.892*
	Sig. (2-tailed)			.394	.030	.904	.070	.541	.698	.438	.042
	N		10	14	4	8	6	5	7	5	
Cozumle	Pearson Correlation			1	.035	.323	.151	.797	.ᵃ	-.948*	-.020
	Sig. (2-tailed)				.900	.532	.747	.203	.	.014	.970
	N			15	6	7	4	1	5	6	
Xcalak	Pearson Correlation				1	.585	.937**	.360	.634	.358	.467
	Sig. (2-tailed)					.167	.000	.483	.251	.383	.351
	N				7	9	6	5	8	6	
Chinchorro	Pearson Correlation					1	.ᵃ	.ᵃ	.ᵃ	.ᵃ	.ᵃ
	Sig. (2-tailed)						.	.	.	.	.
	N					1	0	0	0	0	
Cochinos	Pearson Correlation						1	.904	1.000**	.279	.241
	Sig. (2-tailed)							.096	.	.650	.697
	N						4	2	5	5	
PR	Pearson Correlation							1	-.382	.021	-.123
	Sig. (2-tailed)								.618	.968	.877
	N							4	6	4	
VE	Pearson Correlation								1	.383	-1.000**
	Sig. (2-tailed)									.525	.
	N								5	2	
COL	Pearson Correlation									1	.496
	Sig. (2-tailed)										.317
	N									6	
Roatan	Pearson Correlation										1
	Sig. (2-tailed)										
	N										

advective and retentive oceanography features in influencing recruitment. The presence of persistent retentive features such as large gyres may not only influence recruitment magnitude, but also the variation in recruitment. Recruitment magnitude, its variability, and what these measures imply with respect to larval connectivity among adult populations is relevant to management of lobsters in the region, and thus the socio-economic well being of fishers. For example, Marine Stewardship Council decisions on fishery certifications - such as those now underway for portions of the Mexican Caribbean coast - is based not only on local management practices, but also on whether management in an area can sustain fisheries, which is dubious if most larvae are from exogenous sources. Determination of the sources of larvae for a particular region is an obvious solution, but many of the techniques used to empirically study larval dispersal in other marine species are not applicable to spiny lobsters. Lobsters have no calcified internal structures (e.g., otoliths in fish), so the use of geochemical markers for assessing connectivity is not possible (see Thorrold *et al.* 2007). To date, genetic studies of lobster connectivity have not been particularly successful given high genetic variability and poor subpopulation genetic structure (Silberman *et al.* 1994, Sarver *et al.* 2000). So researchers have instead relied on oceanographic simulation modeling to examine larval dispersal in spiny lobsters, including studies of *P. argus* in the Bahamas (Stockhausen and Lipicius 2001, Lipcius *et al.* 2001), Mexico (Briones-Fourzan *et al.* 2008), and the south Atlantic (Rudorff *et al.* 2008). However, the results of these models are not likely to be reliable because none developed so far for *P. argus* have included the details of larval biology. This is a crucial distinction because an overwhelming number of studies on other taxa have shown that dispersal of passive planktonic particles is remarkably different than that for larvae with behavior (see Sponaugle *et al.* 2002, Pineda *et al.* 2007, Paris *et al.* 2007 for reviews).

Although postlarval recruitment magnitude varied locally at our study sites, it generally increased (lowest to highest) from Puerto Rico, San Andres Islands, Honduras, Mexico, Venezuela, to Florida. Those trends in magnitude generally mirror fishery catch in those locations, with the obvious exception of Venezuela (Figure 4). This implies a recruit-to-stock linkage, although not necessarily the reverse given the dispersal capabilities of lobster larvae. The possible relationship between postlarval recruitment and fishery landings in the countries studied here highlights the importance of understanding recruitment and connectivity for fishery management. For example, long-term monitoring of *P. argus* postlarval supply has been successful in Cuba, Florida, and Mexico where data has been collected for a few decades (Acosta *et al.* 1997, Cruz *et al.* 2001, Briones-Fourzan *et al.* 2008). The goal of those monitoring studies is an attempt to mimic the success in Western Australia where fishery catch is accurately

predicted from postlarval supply on artificial collectors and used in management of fishing effort on adult stocks. The same degree of success in predicting lobster stocks from postlarval recruitment has not been fully achieved in the Caribbean (Butler and Herrnkind 1997, Lipcius *et al.* 1997, Cruz *et al.* 2001) where adult stock structure is more fragmented and currents that transport larvae are more complex than off the coast of Western Australia. Although significant correlations between postlarval recruitment and fishery stocks are known at some Caribbean locations (e.g., Cuba and Florida), those relationships are insufficiently accurate for prediction of fishery catch for management purposes. Nevertheless, lobster recruitment monitoring data have proven useful for other purposes such as stock assessment (Muller *et al.* 1997), the examination of potential linkages between recruitment and meterological or oceanographic phenomena (Acosta *et al.* 1997, Eggleston *et al.* 1998, Briones-Fourzan *et al.* 2008), and for experimental or stock enhancement purposes (Marx 1986, Bannerott *et al.* 1991, Field and Butler 1994, Herrnkind and Butler 1994, Butler and Herrnkind 1997, Lipcius *et al.* 1997, and others).

Although measurement of postlarval abundance (i.e., recruitment magnitude as defined here) is of obvious relevancy to the maintenance of adult lobster stocks, it is not the sole determinant. The availability of nursery habitat can be important locally in regulating *P. argus* post-settlement survival (Butler and Herrnkind 1997), as it is more generally for other reef taxa (Steneck *et al.* 2008), and limitations in nursery habitat quality can create demographic bottlenecks that decouple the relationship between postlarval supply and adult stocks. Statistical relationships between postlarval recruitment and fishery landings obtained through monitoring are no substitute for knowledge of the ecological processes that link life stages. Indeed, an over-reliance on monitoring and fishery-dependent assessments and models alone can lead to undesirable surprises. Recently, troubling signs have emerged in the predicted future fishery for *P. cygnus* in Western Australia, arguably one the best managed fisheries in the world and the first to receive the sustainability certification of the Marine Stewardship Council. Measures of postlarval recruitment have plummeted the past few years and foretell a significant downturn in the fishery despite little evidence of a spawning stock decline (pers. comm.; S. DeLestang, Western Australia Fisheries Management Agency). The situation points to changes in oceanic conditions that may influence the survival or dispersion of planktonic larvae, and there is now a scramble better understand those processes.

In the Caribbean, the science needed to understand spiny lobster recruitment processes and connectivity also continues, but it is largely uncoordinated among countries and uneven in its geographic distribution due to regional variation in financial support and scientific capacity. Fishery regulations in the Caribbean are a hodge-podge,

although efforts to better coordinate them are underway in various forums and workshops. Still, enforcement is universally weak and current regulations insufficient to curtail the rapid decline in Caribbean lobster stocks so evident in recent years (FAO 2006). If adult stocks throughout the Caribbean are indeed largely a reflection of postlarval recruitment, as evidence (including that shown here) indicates, then a determined Caribbean-wide effort to increase spawning stocks is the only management option available to enhance larval recruitment and avoid a collapse of the fishery. Combined with protection of critical coastal nursery habitats for lobster, building lobster spawning stocks should be a Caribbean-wide priority for management.

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