Dependence of recruitment on parent stock of the spiny lobster, *Panulirus argus*, in Florida

NELSON M. EHRHARDT* AND MARK D. FITCHETT

Marine Biology and Fisheries Division, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

ABSTRACT

Despite management practices to achieve sustainability, commercial landings for Florida spiny lobster (*Panulirus argus*) have experienced a drastic decline (57%) since 2000. This is cause for concern not only for economic reasons, but for issues of sustainability. An annual index of *P. argus* post-larval (puerulus) abundance, estimated with a generalized linear model with significant mean sea-level effects, shows a 36% decrease in annual puerulus supply since 1988. In addition, local Florida spawning stock biomass estimated from an age-structured sequential population analysis decreased 57% since 1988. Puerulus abundance follows a highly correlated ($R = 0.76$) trend with a 12-month delayed spawning stock abundance, which supports the contention that the Florida spawning population is a significant contributing factor to post-larval recruitment in Florida. Residuals about the puerulus on spawning stock abundance function follow closely an interannual North Atlantic Oscillation Index signal. This residual effect is thought of as a secondary regional population effect on Florida puerulus recruitment. The Florida spiny lobster stock is exploited with no fishing mortality controls due to the Pan Caribbean recruitment concept adopted in Florida spiny lobster management. Therefore, the potential of recruitment overfishing exists if fishing mortality controls to protect local spawning stock abundance, such as catch quotas, are not introduced.

Key words: fisheries management, Florida Keys, mean sea level, puerulus, recruitment, spiny lobster

INTRODUCTION

The Caribbean spiny lobster, *Panulirus argus*, is found throughout subtropical areas in the Central Western Atlantic Ocean from Bermuda to Brazil. It is more abundant in the Western Caribbean Sea, including Florida and The Bahamas, and also in Brazil. Widespread distribution of the species is largely attributed to the dispersal of their long-lived pelagic larvae by ocean currents. In Florida, spiny lobster commercial landings have long been identified with recruitment variability (Powers and Bannerot, 1984; Ehrhardt, 2005). Of significant concern to fishers and managers is the conspicuous decrease in landings (57%) observed in the Florida fishery since the early 21st century. Such drastic decreases have occurred in spite of stiff conservation measures historically implemented in the fishery (e.g., 50% trap reduction; 76 mm carapace length to protect immature individuals; 4-month closed season to control mortality during peak spawning).

Significant recruitment variability is common among Palinurids and only a few studies demonstrate the statistical link between oceanic larval abundance and post-larval recruitment with environmental variables (Pringle, 1986; Pearce and Phillips, 1988; Phillips and McWilliam, 1989; Polovina and Mitchum, 1992). These variables affect larval transport and survival of the early life stages in many (but not fully explained) ways. A limited number of statistical models have succeeded in forecasting spiny lobster landings using one or more environmental variables and larval/post-larval abundance indices (Cruz *et al.*, 1993, 1995; Phillips *et al.*, 1994). However, none of the above studies has linked spawning stock abundance and the resulting post-larval abundance; hence, the likely effects of fishery exploitation on recruitment of spiny lobster stocks are not known.

The Florida spiny lobster population is fully functional in that intense seasonal local spawning (Bertelsen, 1999; Bertelsen and Cox, 2001; Bertelsen and Mathews, 2001) generates high larval densities (Bertelsen *et al.*, 2004), and the cycle from post-larval algal stages to mature stock is characterized by well defined and distinct use of juvenile and adult habitats in

addition to seasonal spawning migrations (Marx and Herrnkind, 1985). The *P. argus* planktonic larval span is approximately 6–12 months (Lewis, 1951; Sims and Ingle, 1966; Idyll, 1980; Lyons, 1980; Menzies, 1980; Yeung, 1996; Matsuda *et al.*, 2008) and unfolds while larvae passively migrate through one or more localized ecosystems in the wider Caribbean Sea, which is characterized by strong and persistent ocean currents. Contrasting the biological bases of the Florida population viability is the Pan Caribbean *P. argus* origin postulated by Sims and Ingle (1966) and Lyons (1981), which is supported by results from Caribbean-wide genetic studies (Silberman *et al.*, 1994a,b; Sarver *et al.*, 2000). Using a high-resolution biophysical model for the Caribbean region, Cowen *et al.* (2000, 2003, 2006) reported that typical simulated larval dispersal distances of ecologically relevant magnitudes are on the scale of only 10–100 km for a variety of reef fish species. These findings may imply, therefore, that the much longer-lived *P. argus* phyllosoma larvae released from those reef areas have the potential of developing larval pathways connecting the Western Caribbean spiny lobster populations with that in the Florida Keys. Furthermore, there are significant common signals on the trends and variances associated with spiny lobster production among such distant places as Brazil, Nicaragua-Honduras, and Florida (Ehrhardt, 2005). Such production similarities should exist if there is strong larval connectivity among the spiny lobster populations and/or common atmospheric/ocean processes affecting the sub-regional recruitment processes.

Complex ocean circulation dominates the dynamic physical features that are important to the recruitment of *P. argus* larvae to the Florida Keys. The Caribbean and Yucatan Currents generate seasonal displacements of the Loop Current in the Gulf of Mexico, while the Florida Current (FC) is linked to the Loop Current outflow (Oey *et al.*, 2005) (Fig. 1). Seasonal displacement and intensity of the Loop Current create onshore-offshore meandering of the FC axis over time scales of several days to several weeks (Schmitz and Richardson, 1968; Lee *et al.*, 1985; Molinari *et al.*, 1985; Johns and Schott, 1987). Associated with the meander of the FC is the formation of oceanic recirculation features in the form of cyclonic gyres entering from the Gulf of Mexico and becoming stranded between the cyclonic side of the FC and the Florida Keys (Tortugas and Portales gyres) (Lee and Mayer, 1977). This cyclonic recirculation in combination with onshore surface Ekman drift resulting from prevailing easterly winds induces significant modifications of the onshore transport process off the Florida Keys (Lee *et al.*, 1992, 1994). Therefore, mechanisms of *P. argus* larval retention in this area may be explained by the various temporal and spatial formation of spin-off eddies (Yeung and McGowan, 1991; Yeung, 1996; Limouzy-Paris *et al.*, 1997; Yeung *et al.*, 2001).

Contrary to the Florida Pan Caribbean recruitment paradigm, Menzies and Kerrigan (1980), Menzies (1980) and Yeung (1996) maintain that recruitment to local populations could significantly depend on local counter currents and gyres that entrain, retain, and return locally released larvae. However, the
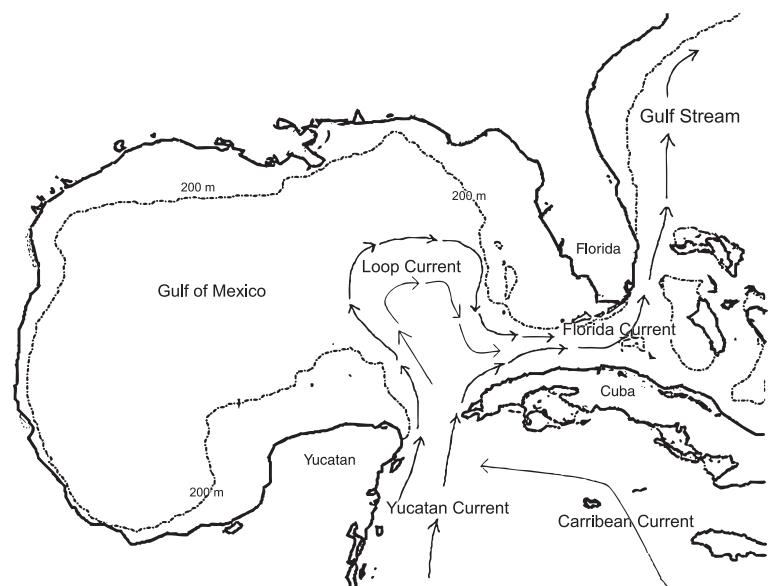

Figure 1. Ocean currents dominating the oceanographic features of the Florida *P. argus* recruitment dynamics.

existing theoretical and empirical Florida *P. argus* fishery management models are based on the Pan Caribbean concept of larval replenishment where fishing mortality is not regulated (e.g., through annual quotas). The models do not provide a comprehensive framework to evaluate the exploitation impacts of complex and apparently local as well as regionally interlinked population dynamics that may be affecting Florida landings. The analyses presented here provide an assessment of the post-larval (puerulus) and local mature stock abundance in an effort to elucidate some of the functional relationships that may exist between local parental stock, post-larval recruitment abundance, Pan Caribbean larval inputs, and future stock recruitment, while considering changes in oceanographic conditions.

MATERIALS AND METHODS

Puerulus data

To estimate an annual index of abundance for post-larval (puerulus) *P. argus* in the Florida Keys, puerulus catch from an experimental sampling effort with Witham-type puerulus collectors was provided by the Florida Fish and Wildlife Conservation Commission (FWC). Witham Collectors (Witham *et al.*, 1964, 1968; Witham, 1973) consist of a rectangular framework of PVC pipe, with six cross supports from which sheets of 'hogs-hair' air conditioner filter material hang. The hog-hair filters successfully mimic the structure and consistency of the macro-algae *Laurencia*, which is the preferred natural settlement habitat for spiny lobster post larvae. They are suspended below the surface by a series of floats. The collectors were set

in the Lower Florida Keys in several locations; however, the data made available included samples in Long Key (24°79′48.995″N, 80°51′55.000″W) and Big Pine Key (24°41′22.02″N, 81°12′29.484″W). Data from the Big Pine Key (Lower Florida Keys) is the longest uninterrupted (1987–2006, 1376 samples) data set corresponding to collectors set in between sections of the Seven Mile Bridge, one of the largest entrances into Florida Bay from the Atlantic Ocean. On average, there are approximately four collectors employed at any time period at the Big Pine Key site, with no fewer than three collectors employed at a time – with the exception of major hurricane events in September 1992 (Andrew), August 2004 (Charley), and September 2005 (Dennis). Because of its rarely interrupted and long sampling duration, this data set was selected for the analyses of puerulus relative abundance.

Relative indices of puerulus abundance are defined as catch-per-unit-sampling-effort (CPUE) for pueruli caught in collectors soaked for an entire day. During the study period at any given time, an average of three collectors were in place in the Big Pine Key (Seven Mile Bridge) sampling area. Each collector was analyzed as a separate observation for CPUE standardization. Apparent incongruities in sampling soaking times appear from 1987 to 2006 with a 'transitional period' during 1991 and 1992 (Fig. 2). Sampling time was defined by an average 7-day standard soaking time during 1987–93 and then changed for operational reasons to an average 29 days soaking time during 1993–2006. To test for statistical validity of compounding low soak times in 1987–92 to be comparable with the typical 28–30-day sample soaking times in

Figure 2. Soaking times (in days) for Witham collectors by year along the Seven Mile Bridge from 1987 to 2006. Transitional period of highly variable soak times (1991 and 1992) encircled.
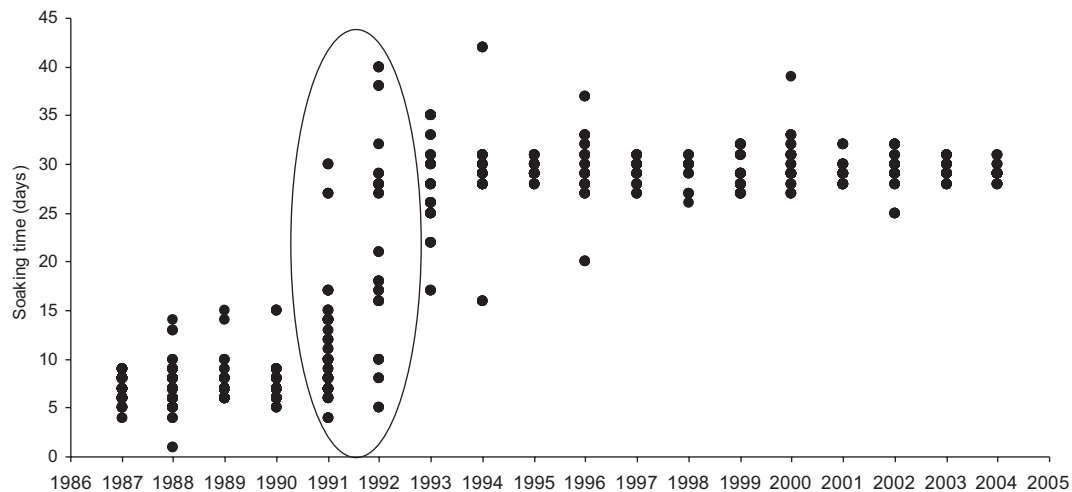
Table 1. ANOVA table of blocking effects of year (1991 versus 1992), season, and soak time on observed daily post-larval collection rates. Years 1991 and 1992 are used because of high variability of short and long soak time durations.

Factor	df	Sum of squares	Mean squares	F tabulated	F value	P > F
Year	1	0.0757	0.0757	4.747225336	0.2711	0.61204
Season	1	2.5881	2.5881	4.747225336	9.2762	0.01017*
Soak	1	0.1843	0.1843	4.747225336	0.6607	0.43215
Residuals	12	3.3481	0.279			

*Statistically beyond 95% confidence interval.

1993–2006, an analysis of variance (ANOVA, R Development Core Team, 2008) was run using the 'transitional' sampling design period in the data base (1991–92) in which observations varied greatly in soaking times. There were 'low' soaking times of 7–17 days (which was the normal range in the years prior to 1991) and 'high' soaking times of 27–32 days (which was a typical soaking time in the years after 1992) in 1991 and 1992. The ANOVA (Table 1) uses factors of year, season, and soaking time ('compounded' versus 'non-compounded') versus a response variable of CPUE and found that only season was a significant factor on CPUE (Table 1). Therefore, the observations for 1987–92 were converged into approximate 28–29-day time periods to be comparable with the average 1993–2006 soak time. This data integration is possible due to the continuous catching process of the collectors and the observation that no saturation of pueruli was ever observed in the collectors (T. Matthews, FWC, personal communication).

Environmental data

Several environmental variables collected on an hourly basis from 1987 to 2006 by the National Buoy Data Center (http://www.ndbc.noaa.gov/) at the Sombrero Key Buoy Station (approximately 1 km from Seven Mile Bridge) were preliminarily assessed against nominal CPUE of puerulus entering southern Florida Bay via Seven Mile Bridge entrance. Mean sea level (MSL) showed the greatest correlated signal relative to the nominal puerulus CPUE. MSL is the direct result of atmospheric pressure change and resulting winds and it is often used as a proxy for wind-driven upwelling in coastal regions when other direct data (e.g., upwelling) are absent or limited (Zelle et al., 2004). Using the wind data collected at the Sombrero Key Buoy Station, we estimated average monthly resulting winds for 1987–2007 as the monthly proportion of winds blowing in a certain direction (N, NE, E, SE, S, SW, W, NW) multiplied by mean monthly intensity (nautical miles per hour) of winds blowing in that particular direction. A net easterly component is the resulting wind of all easterly direc-

tions (NE, E, SE) minus resulting winds of all westerly components (NW, W, SW). The average resulting monthly easterly wind components explain average nominal MSL over most months (Fig. 3), supporting Zelle et al.'s (2004) contention about MSL temporal dynamics.

Given the shallow bathymetry of the puerulus nursery habitat in the Florida Keys, lower MSL could be indicative of a more confined nektonic habitat with an increased probability of higher pueruli density. In contrast, higher MSL may be associated to increased larval dispersal from the recruitment habitat. Therefore, in the absence of other physical variables that could explain cyclonic and wind driven surface currents affecting onshore post-larval recruitment, MSL was used as an explanatory variable that contributes to variance in puerulus catch rates in the analysis of puerulus CPUE data standardization procedures.

Generalized linear models (GLM) are commonly used to standardize CPUE to develop relative indices of abundance for exploited fish stocks (Maunder and Punt, 2004). GLMs are based upon the principle that a response variable (CPUE, $\bar{\mu}$) is dependent on a set of

Figure 3. Seasonal average anomalies of resulting easterly winds and mean sea level off the Florida Keys.
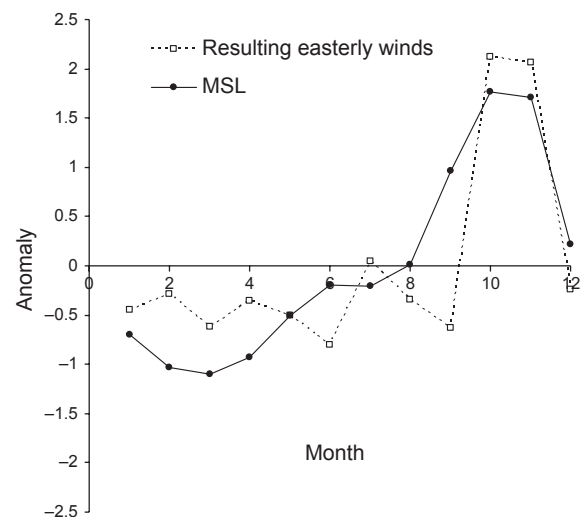
explanatory variables (x_k), which are of interest to explain process-oriented reasoning. The model is generally expressed as:

$$\bar{\mu}(\log_\lambda \text{CPUE}) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k + \varepsilon \tag{1}$$

with β_0 representing the overall mean (intercept) for a given time period, i, in which $\bar{\mu}$ is defined. Each β_i represents the factor at which an explanatory variable, x_i, linearly contributes to the model. GLMs depend on the distribution of CPUE and how some linear combination of a set of explanatory variables (x_i) aid in predicting the expected value of CPUE by reducing extraneous sources of variance. In this study, we use log-transformed CPUE which follow a normal distribution.

The removal of variance due to explanatory variables and their interactions with one another allow the response variable to be considered a more statistically robust index than the variable of the observed (nominal) puerulus CPUE. In this study, we use year and season as fixed class explanatory variables and MSL as a continuous explanatory variable. Seasons take the role of temperature regime changes, whereas *a priori* examinations of puerulus catch rates and MSL showed a negative relationship between these two variables throughout the time series. Years take on the role of interannual recruitment changes. In this study, we use the GLM procedure to determine an annual index of abundance for puerulus recruitment to an important Florida Keys nursery area with the following model:

$$\bar{\mu}(\log \text{CPUE})_{\text{YEAR}} = \beta_0 + \beta_i \chi_{\text{YEAR}} + \beta_j \chi_{\text{SEASON}} + \beta_{i,j} \chi_{\text{MSL}} + \varepsilon \tag{2}$$

with i = year, j = season, and β_i, β_j, and β_{ij} parameters estimated by the GLM procedure and yearly CPUE estimated by the LSMeans procedure in SAS software Version 9.1.2 of the SAS System for Windows (Copyright © 2008 SAS Institute Inc., Cary, NC, USA). The model and corresponding factors were then tested by analysis of variance (ANOVA) for significance. Years were redefined such that July was defined as month 1, and June of the following calendar year was defined as month 12 in order for an annual index to comply with biological processes and capture the seasonal modal behavior of puerulus influx.

Zero-inflated methods are not considered because 1.6% (15/933) of observations used in the GLM analysis are 'zero catch'. This very small fraction is deemed insignificant and is not grounds for pursuing zero-inflated methods, as this small fraction of observations is found entirely in the time periods following peak spawning months and likely represents an absence of post larvae or true zero abundance at that time. Moreover, at no analyzed time period is there more than one observation (of three or more observations) with 'zero catch'.

Fishery data

Spiny lobster abundance at age was independently estimated for male and female spawning stocks aged 3+ and for male and female recruitment at age 1. A tuned age-structured stock assessment algorithm (Ehrhardt, 2007) was implemented using catch-at-age matrices constructed from total (all gear) catch-at-size matrices made available by the FWC. Detailed explanations of this data base are given in SEDAR08 (2005). Transformation of numbers landed at size to numbers at age was accomplished through slicing size frequency data into age frequency using gender-segmented growth equations (Ehrhardt, 2008). The conceptual stock assessment algorithm uses a least squares procedure to minimize the objective function

$$\min \sum_{i=1985}^{2003} \sum_{a_r}^{\max a} (\text{CNA}_{i,a} - q_i \overline{N_{i,a}})^2 \tag{3}$$

with i = season, a = age, r is an index for variable recruitment age, $\text{CNA}_{i,a}$ = observed catch in numbers of lobsters caught per trap-day per trip for ages a_r to maximum age in season i. Seasons run from 1 August 1 to 30 April of the following calendar year. Expected catch in number of lobsters per trap-day per trip is estimated as $q_i = \overline{N_{i.a}}$, where q_i is the catchability coefficient in season i, and $\overline{N_{i.a}}$ is the average abundance of age a estimated by the minimization algorithm in season i, and estimated in the usual manner:

$$\overline{N_{i.a}} = \frac{(1 - e^{-Z_{i.a}})N_{i.a}}{Z_{i,a}} \tag{4}$$

$Z_{i,a}$ is the instantaneous total mortality rate in season i and age a, and $N_{i.a}$ is the abundance of age a at the start of the ith season.

The catchability coefficient (q) was estimated internally by setting the first derivative of the objective function with respect to q equal to zero and solving for q, such that

$$q = \frac{\sum_{i=1985}^{2003} \sum_{a_r}^{\max a} \text{CNA}_{i,a} * \overline{N_{i,a}}}{\sum_{i=1985}^{2003} \sum_{a_r}^{\max a} (\overline{N_{i,a}})^2} \tag{5}$$

The algorithm allows partitioning of the observed data over time (sums over a determined a-range) and ages

Table 2. ANOVA table of yearly, seasonal, and mean sea level effects on GLM estimates of post-larval abundance. The model is defined as: $\bar{\mu}(\log CPUE)_{YEAR} = \beta_0 + \beta_i\chi_{YEAR} + \beta_j\chi_{SEASON} + \beta_{i,j}\chi_{MSL} + \varepsilon$, where i denotes years (1987–2006) and j denotes season (1–4).

Effect	df	Sum of squares	Mean squares	*F* value	*P* > *F*
Year	18	79.380	4.410	8.53	<0.0001*
Season	3	76.081	25.360	49.06	<0.0001*
MSL	1	32.656	32.656	63.17	<0.0001*

*Statistically beyond 95% confidence interval.

(sum over a determined *a*-range) in such a way that it is possible to search for the fit of the objective function that best portrays cohort abundance signals in the catch-at-age matrix and the observed CNA index used in the tuning.

The functional relationship for analyzing female spawning stock abundance and post-larval abundance is one suggested by Cushing (1973) and generalized by Shepherd (1982):

$$R = \lambda PS^{1-\beta} \qquad (6)$$

The parameter λ has the dimensions of puerulus recruit index per unit of parent stock measured in units of female abundance in numbers. The parameter β expresses a particular aspect of the concept of density dependence, namely the degree of compensation involved. Density dependence dominates for all stock sizes in the function expressed by Eqn (6).

RESULTS

ANOVA results for puerulus relative abundance estimation (Table 2) show that each explanatory factor in the selected GLM model significantly reduces the total sum of squares. The annual effect ($\beta_i\chi_{YEAR}$) on CPUE, naturally contributes to a source of variance (6.6%); however, the partitioning of seasonal ($\beta_j\chi_{SEASON}$) and MSL ($\beta_{i,j}\chi_{MSL}$) effects on CPUE contribute to the most amount of variation in the ANOVA (93.4%). Of these two, the variation in nominal CPUE attributed to MSL is more important (52.6%) followed by the seasonal effect (40.8%) that should mostly represent temperature effects. The resulting annual puerulus index should be representative for relative abundance of spiny lobster pueruli entering the Lower Florida Keys via the Seven Mile Bridge entrance.

The estimated standardized annual puerulus relative abundance index shares a similar trend with the nominal CPUE (Fig. 4a), but with consistently lower estimates in the first three seasons for which data were available. Therefore, the decreasing trend in estimated relative puerulus abundance is less conspicuous rela-

Figure 4. Post-larval abundance index estimated from generalized linear model and observed nominal post-larval abundance (a). Average seasonal post-larval abundance index, average seasonal reproductive activity (maturity), and average seasonal Florida Keys mean sea level (b).
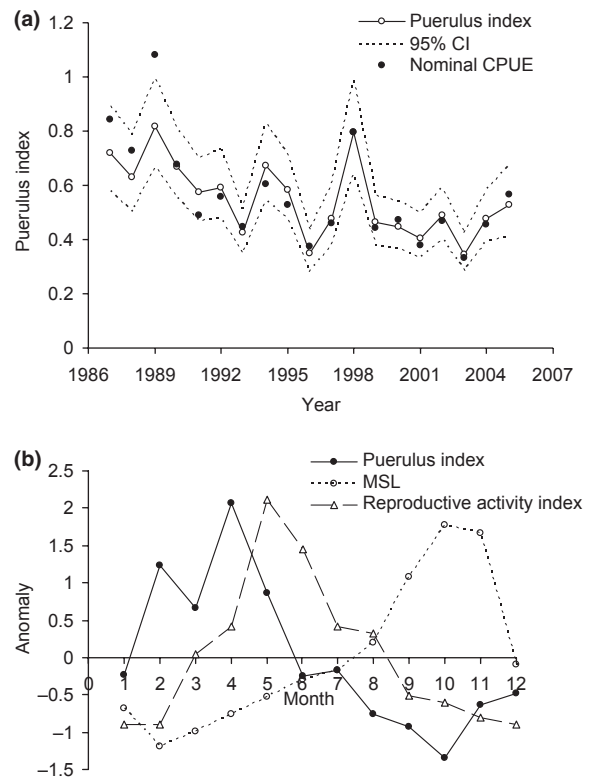
tive to the observed nominal trend. The years with the highest relative post-larval recruitment abundance were 1989 and 1998 and the lowest in 1996 and 2003. Decrease in puerulus relative abundance was about 42% lower in 2003 (a low abundance year) than in 1989 (a high abundance year). The period 2000–2006 shows a more stabilized puerulus abundance relative to the previous seasons, but such stabilization also appears to occur at a much lower level of abundance.

Reproductive activity of *P. argus* in Florida is more conspicuous during March–August (Lyons, 1981; Gregory *et al.*, 1982) with a maximum observed in

May–June (Fig. 4b). The average 1987–2006 monthly post-larval CPUE is conspicuously higher during February–May (Fig. 4b). Furthermore, it was found that the 11-month delayed trends in reproductive activity and average 1987–2006 monthly post-larval CPUE are highly linearly correlated ($R = 0.84$) (Fig. 5). We also plotted (Fig. 4b) the average monthly 1987–2006 MSL and observe that maximum values occur during September–November, which is inversely correlated with seasonal spawning activity but more significantly relative to the average monthly 1987–2006 post-larval CPUE of *P. argus* in Florida.

Analysis of the source of puerulus relative abundance was attempted by assessing the Florida female *P. argus* spawning stock (*PS*) abundance (ages 3+) for the period for which fishery-dependent data were available from the FWC (1985–2003). The assessments generated a significant fit (total sum of squares = 0.513, df 106) of the objective function (Eqn 4) using the observed mature female relative index of abundance (catch in number per trap per trip) as a sequential population analysis tuning index. The resulting trend in female spawning stock abundance indicates that in 2003 it was approximately 36.4% of the maximum spawning stock abundance observed in 1989 (Fig. 6a). The annual apical (age 3) fishing mortality rates (*F*) estimated for the female spawning stock are very high, averaging 0.79 for the period 1985–89, 1.12 for 1990–99 and 1.13 for 2000–2003. These values are two to three times higher than the level of the natural mortality rate (*M*) commonly adopted in stock assessment work for the species (*M* = 0.35) – a condition which may be identified with over-exploitation.

Two very different data bases (puerulus indices and catch at age of mature female stock) generated esti-

Figure 5. Eleven-month lagged regression of average seasonal reproductive activity on average seasonal post larval abundance index.
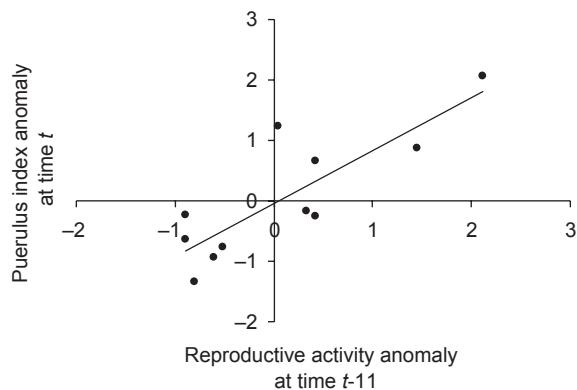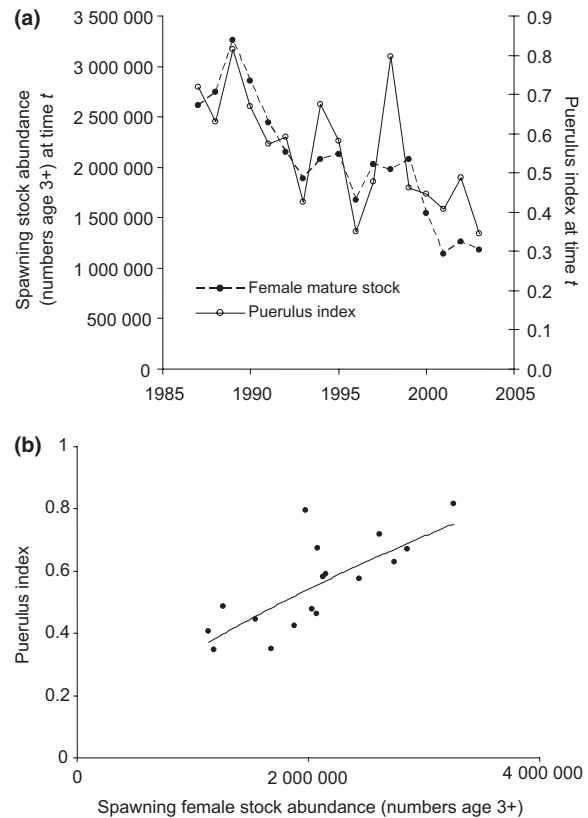

Figure 6. Historic trends of parental stock abundance estimated from sequential population analysis and corresponding post-larval abundance estimated from generalized linear model (a). Functional post-larval recruitment on parental stock (b).

mates of abundance obtained by different assessment algorithms (GLM and sequential population analysis), which follow remarkably similar trends (although with obvious different scales) and approximate variances (Fig. 6a). Furthermore, the decreasing trend in female mature abundance is the consequence of high fishing mortality rates exerted on the stock and the decrease in spawning stock abundance (36.4%) approximates the decrease in puerulus relative abundance (42.4%).

When parental stock abundance (*PS*) estimates are compared with puerulus relative recruitment abundance [*R*(CPUE)] lagged 11 months (Fig. 6b) an unusually well-correlated ($R = 0.766$) post-larval on spawning stock recruitment function is found and expressed as

$$R(\text{CPUE}) = 0.0000312 * PS^{0.6728}$$

Residuals about the spawner-to-puerulus recruitment function were analyzed relative to potential regional physical processes that might suggest Pan Caribbean puerulus recruitment effects on the function. For this

purpose we used the North Atlantic Oscillation (NAO) index (Hurrell, 1995; Hurrell *et al.*, 2003) that is known to affect climate-ocean circulation features in the Caribbean, Gulf of Mexico and the Florida Straits. We found (Fig. 7) that a significant common signal exists between the standardized residuals about the parental stock-puerulus recruitment function and a 1-year delayed NAO anomaly.

Recruitment at age 1 estimated from sequential population analysis does not show dynamic linkages with the post-larval (puerulus) abundance index lagged 1 yr (Fig. 8a). We arrive at this result based on the dissimilarities of the trajectories of recruitment at age 1 as a consequence of post-larval recruitment abundance changes. Additionally, more detailed analyses of these results show that recruitment at age 1 in the last 5 years in the data base (1999–2003) is lower for similar levels of post-larval recruitment abundance in previous years (solid points within circle in Fig. 8a). Recruitment trajectories for 1987–98 and 1999–2003 do not appear linked between these two groups as function of post-larval abundance. These conditions are indicative of a lack of density dependency between post-larval recruitment and recruitment at age 1.

Deviance on the post-larval to age 1 recruitment was further analyzed by estimating a recruitment success index (*RSI*). This index was defined as the ratio of recruitment at age 1 to the puerulus abundance index 1 yr earlier and standardized to the maximum level of age 1 recruitment abundance. Of the several plausible biological and environmental variables that may be the cause of the observed shift in the mortality process

Figure 7. Anomalies of residuals about the post-larval recruitment on parental stock function and the North Atlantic Oscillation.
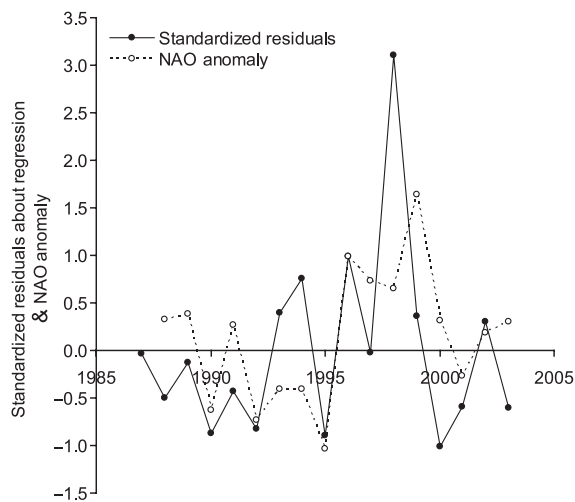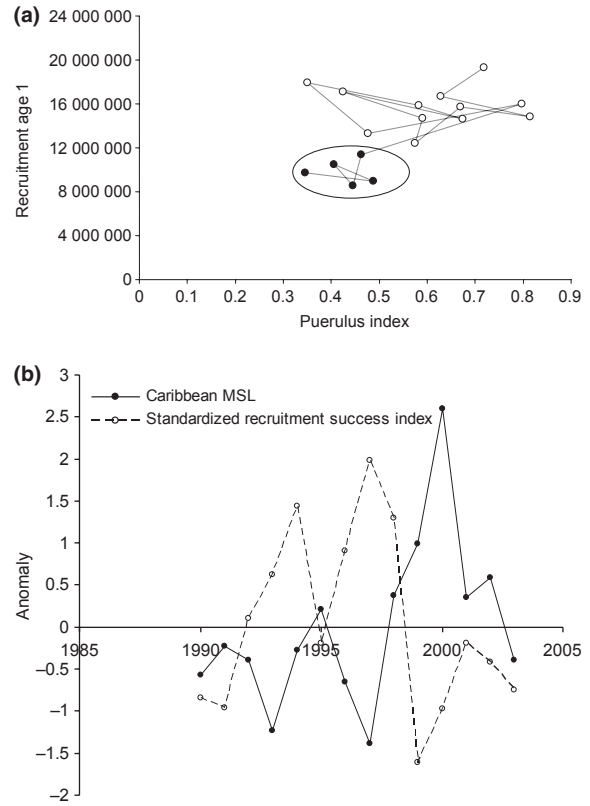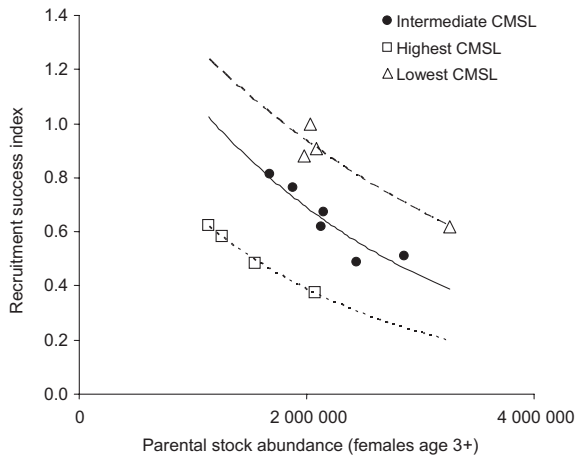
Figure 8. Relationship between post-larval abundance index and resulting immature recruitment at age 1 from sequential population analysis (a). Anomalies of recruitment success and Caribbean mean sea level (b).

observed in Fig. 8a and an influence on the observed variability in annual recruitment success, we found that significant changes in the Caribbean mean sea level (CMSL) occurring during the time of the analysis appear as a negatively correlated signal relative to recruitment success (Fig. 8b). Integration of parent stock, recruitment success and CMSL (Fig. 9) shows that recruitment success carries forward the density-dependent effect of post-larval abundance to local parental stock. CMSL plays a significant role in separating the historic data into three apparent periods from higher CMSL, usually implying lower recruitment success, to lower CMSL, implying higher recruitment success. These RSI are highly correlated functions of the parental stock abundance with separate CMSL effects. The functions are given by

Lowest CMSL $RSI = 1.79115e^{-0.00000032*PS}$
$(R = 0.9589)$

Intermediate CMSL $RSI = 1.7240e^{-0.00000046*PS}$
$(R = 0.9172)$

Highest CMSL $RSI = 1.1405e^{-0.00000054*PS}$
$(R = 0.9979)$

Figure 9. Recruitment success on parental stock abundance stratified by Caribbean mean sea level conditions.

Figure 10. Projection of planktonic larval duration estimated from data in Table 4 in Lewis (1951).


DISCUSSION

Panulirus argus spawn year-round throughout the Caribbean region, with peaks during March–July and September–October (Arce and de León, 2001); however, in Florida a conspicuous maximum reproductive (spawning) activity is observed during March–August, reaching a maximum in May–June (Gregory *et al.*, 1982). The significant presence of early larval stages reported from larval surveys carried out in South Florida during the spring (Lyons, 1981; Yeung, 1996) is the result of intensive spawning activity during this time (Yeung, 1996). Also, the seasonal reproductive activity index anomaly happens on average 1 month ahead relative to the seasonal anomaly of the average 1987–2006 monthly post-larval CPUE estimated by GLM with seasonal data (Fig. 4b), implying that the trend in post-larval recruitment must occur 11 months after the reproductive activity trend for these two trends to match biologically.

Data from Table 4 in Lewis (1951) on the occurrence of different phyllosoma stages found in monthly samples taken at sea have been adapted and presented in Fig. 10. If we assume stage 11 as defined by Lewis (1951) as the terminal stage before metamorphosis to be equivalent to the average last stages defined by Matsuda *et al.* (2008) we obtain a linear model (Fig. 10) which, when extrapolated to the 11th stage, provides an estimated PLD of 11.15 months. As the data on stage 1 correspond to the month of June in Lewis (1951) data, metamorphosis would have to occur approximately 11 months later, or in the month of April. These results coincide not only with the 11 months that we obtained on the lag between peak reproductive activity (spawning) and peak puerulus
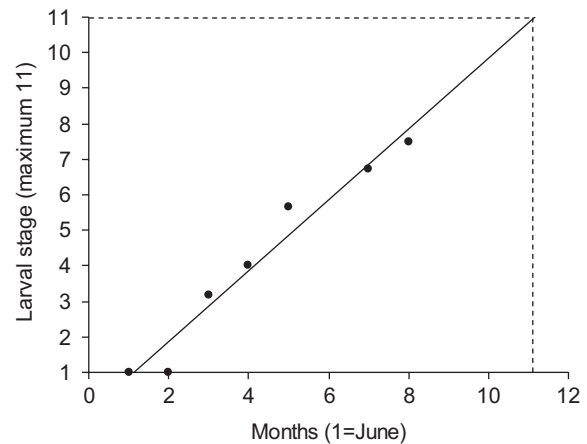
(post-larval) recruitment (Fig. 5), but also coincide with the months of the maximum puerulus recruitment (Fig. 4b).

The fact that the 11-month delayed trends in reproductive activity and average 1987–2006 monthly post-larval CPUE are highly correlated (Fig. 5) provides a statistically credible time link to the growth and recruitment schedule of larval to post-larval *P. argus* in Florida. This approximate 11-month time span falls in the upper end of the 6–12-month *P. argus* planktonic larval span reported by Idyll (1980), Menzies (1980), and Lyons (1980) from seasonal larval size modal progression. In the absence of *P. argus* data from rearing experiments, Yeung (1996) used larval duration obtained for *Panulirus japonicus* reared in the laboratory by Kittaka and Kimura (1988) in water temperatures similar (24–28°C) to those inhabited by *P. argus* in Florida, which resulted in a total larval duration of 11–13 months. Matsuda *et al.* (2008) provide for the first time a description of the morphometric and developmental stages of the *P. argus* larvae from 19 larvae grown under laboratory conditions. The planktonic larval duration obtained in this study varied from 4.7 to 10.4 months, with ranges varying as a function of sample size used in the different experiments. Furthermore, Matsuda and Takenouchi (2006) associated the high survival rate in individual cultures to the use of small glass cups that promoted faster growth of the larvae, most likely due to better feeding conditions. The significant effects of container size on the growth and survival of *P. japonicus* larvae are found in Sekine *et al.* (2000). Data from Matsuda *et al.* (2008) show similar conditions in that when *P. argus* was cultivated in a 40-L container, the PLD was significantly longer and the PLD range

almost five times that of larvae raised in containers of 0.1–0.35 L. Therefore, PLDs obtained under laboratory conditions may not be ecologically applicable to the situation of *P. argus* larvae in the wild. The latter results favor our statistical finding that the average seasonal post-larval recruitment abundance trend estimated from the GLM fitted to the Florida puerulus data matches an 11-month delayed larval abundance trend for *P. argus* in Florida.

The single modal average seasonal distribution of puerulus recruitment abundance estimated for Florida (Fig. 4b) differs from observations in the Caribbean where there is increased post-larval recruitment intensity during May and another peak in October that can last until December in some years (Cruz *et al.*, 2001). Similar data for *P. argus* in Cuba (Arce and de León, 2001) show that the transition from the two seasonal peaks in spawning activity to the corresponding two peaks in seasonal post-larval settlement may take between 7 and 9 months. These recruitment time scales are not only different from our estimates for Florida, but also represent apparently different spawning to age 1-recruitment processes in the Caribbean from those observed in Florida.

Lee *et al.* (1992) report that mesoscale, cyclonic Dry Tortugas and Portales Gyres occur seasonally off the Lower Florida Keys, constituting a possible mechanism that may retain larvae in the region for up to 8 months. The persistence of higher MSL (Fig. 4b) for up to 6 months with higher values during September–November may be supported by the results of Lee *et al.* (1992) in that MSL may be a potential driving variable, possibly representing several physical features that intervene in the chronological events that could regulate seasonal spawning, such that recruitment from local *P. argus* populations in Florida enhances their own recruitment. Therefore, an 11-month span between reproductive activity and post-larval recruitment could imply that the maximum average 1987–2006 monthly MSL observed in the Florida Keys during September–November (Fig. 4b) is a physical feature notably separating those two events.

One aspect of the results that is of immediate concern from biological and fishery management standpoints is the significant and steady decrease in female spawning abundance that appears to significantly justify the decrease in the post-larval recruitment index (Fig. 6a). Such decline may be the consequence of the high unregulated fishing mortality that characterizes the fishery management regime established for the Florida fishery under the Pan Caribbean recruitment concept. Contrary to the Pan Caribbean paradigm concerning *P. argus* recruitment, we found

dynamically linked trends in spawning parental stock and post-larval recruitment abundance – the first ever indication that the local Florida spawning stock may be significantly important to the replenishment of the local post-larval supply. Therefore, Pan Caribbean larval sources may only be of relative importance to overall recruitment in some seasons.

To emphasize the aforementioned finding, a comparative analysis was carried out relative to the data in Table 3 published by Bertelsen *et al.* (2004) consisting of reproductive population density and resulting population fecundity density of *P. argus* in several marine protected areas (MPA) of different sizes and in different locations in the Florida Keys. This data was used to develop a spawner-recruit function that might exist between the density of spawning stocks in the different MPAs in Florida and their resulting spawning products (the egg densities). The information provided by Bertelsen *et al.* (2004) is indicative of a spawner-to-egg recruitment function for the MPAs, where *P. argus* densities are a function of MPA size, which was found to be one of the driving variables that protect spawning populations in the region. We postulate that the above spawner-to-egg recruitment process should approximate the spawner to post larval process that we found in this study. For comparative purposes, data in Table 3 of Bertelsen *et al.* (2004) are adapted to estimate anomalies (observation minus mean divided standard deviation) to similar anomalies applied to female spawning stock abundance and puerulus recruitment index estimates. The results are presented in Fig. 11. From this figure, it can be concluded that the two regressions are identical and equally highly correlated. This perhaps is the strongest evidence ever found through a comparative analysis of greatly

Figure 11. Anomalies of *P. argus* recruitment (density or index) on parental stock (density or abundance) with data on density adapted from Table 3 of Bertelsen *et al.* (2004) and from this study (index and abundance).
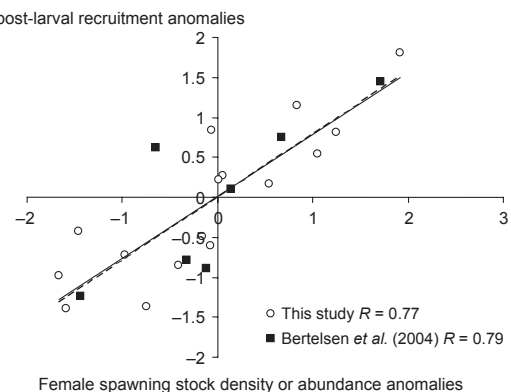
different data bases that a significant amount of the recruitment signal (in the form of either egg density or puerulus index) is explained by the local Florida female population (in the form of either directly observed densities or through a formal sequential population analysis using fishery data). These statistical analyses do not show that the Florida *P. argus* population is completely self recruiting, but that a significant proportion of recruitment, between 0.6231 and 0.7438, is fundamentally explained as a response to the local parental population.

The upstream (extraterritorial) larval recruitment contributions may be represented in Fig. 6b by significant random departures of the puerulus abundance trend relative to the parent stock trend in some years, for example in 1994(+), 1996(−), 1998(+), 2001(+), and 2002(+) (Fig. 6a). Such departures of residuals about the spawner-recruit model in some years (Fig. 6b) may be explained by other physical driving variables modulating regional larval recruitment to Florida (i.e., a Pan Caribbean effect). One such variable that we found correlated to residuals not explained by the spawner-recruit function is the North Atlantic Oscillation (NAO). The NAO is primarily defined as shifts in relative intensity in atmospheric pressure between Iceland and the subtropical Atlantic (Portugal) between 35 and 40°N (Hurrell, 1995; Hurrell *et al.*, 2003). This decadal mode of atmospheric variability influences Atlantic sea-surface temperature, eddy activity, Gulf Stream transport, paths of severe weather systems, and the intensity of easterly trade winds (Hurrell, 1995). The NAO is also significantly correlated with a coupled ocean-atmosphere system centered in the Atlantic – the Atlantic sea-surface temperature dipole (Chang and Li, 1997; Xie and Tanimoto, 1998; Sutton *et al.*, 2001) and in correspondence with the El Niño–Southern Oscillation system in the Pacific Ocean (Janicot, 1997). Therefore, the NAO is one of Earth's climate teleconnections with significant regional influence over the Caribbean Sea, which may have a direct influence on the *P. argus* larval pathways from upstream spawning in the Caribbean Sea to Florida, as well as locally in Florida. The regional NAO signal appears to synchronically influence, through atmospheric–ocean physical features, the unexplained residual recruitment of post-larval *P. argus* to Florida (Fig. 7); however, the synchrony has distinctly different intensity effects on recruitment. Consequently, NAO may not be a statistically significant predictor of upstream and/or local recruitment to Florida, but only expressing a common signal that significantly influences variance observed in the recruitment dynamics of *P. argus* in Florida.

The parental stock density-dependent effects on post-larval recruitment abundance suggested by the statistically significant function in Fig. 6b implies that local population regulation mechanisms are fundamental to the sustainability of the Florida population. However, fluctuations in sub-adult recruitment (age 1) from the algal and post-algal stages do not appear correlated (Fig. 8a) and possibly density-independent mortality mechanisms control survivorship during those stages. The implication is that sub-adult recruitment is not dependent on larval supply. Herrnkind and Butler (1986), Butler and Herrnkind (1992), Butler *et al.* (1997), Eggleston *et al.* (1990), and Mintz *et al.* (1994) demonstrate the importance of nursery habitat characteristics on the recruitment of *P. argus* in Florida. Furthermore, Butler *et al.* (1997) suggest that adult recruitment forecasting from post-larval supply may be hampered in the absence of information on nursery habitat structure. These findings contrast with the Western Australian spiny lobster, *Panulirus cygnus,* adult recruitment dynamics which is highly and sequentially correlated with post-larval abundance supply and physical ocean features driving post-larval recruitment (Chittleborough and Phillips, 1975; Caputi *et al.*, 1995).

The recruitment success index developed in this study follows an unexpectedly negatively correlated signal with Caribbean Sea MSL (Fig. 8a). Such correlation would imply that the mortality process during the algal stages to sub-adult recruitment is controlled by presently unknown environmental effects not explained by nursery habitat structure, but possibly by physical events. Additionally, recruitment success carries forward the population density regulation effect (Fig. 7), which can be distinctly separated by seasons of higher and lower Caribbean Sea MSL. It appears from the results in Fig. 7 that the seasonal environmental effects expressed by Caribbean Sea MSL conditions generate a vertical displacement that is more important than the population regulation effects reflected by the slope of the recruitment success on parental stock abundance. This condition should result in the poor definition of the recruitment trajectories as a function of post-larval abundance in Fig. 8a and generally in any parental stock to recruitment function.

CONCLUSIONS

The importance of wind stress as a retention and dispersion mechanism of larval organisms along the Florida Keys have been explicitly shown by Lee *et al.* (1992, 1994) and Yeung (1996). Additionally, the seasonal formation of gyres and meanders from coastal

currents are also critical retention mechanisms for larval organisms that can be enhanced and disintegrated by wind and resulting wind stress (Bartsch *et al.*, 1989; Lee *et al.*, 1992; Yeung, 1996). Yeung (1996) and Chen (1996) concluded that easterly wind components, notably from the southeast, enhanced the retention and concentration of water masses and larvae into the E–W oriented Lower Florida Keys via Ekman transport and enhance the dispersion in the SW–NE oriented Upper Keys by fueling advection in the Florida Current. These retention mechanisms should frame the statistical models developed in this study, which contributes significant information to the understanding of the recruitment dynamics of *P. argus* in the Florida region. First and foremost, we identify a significant statistical coupling of local Florida spawning stock with local puerulus recruitment abundance. This is contrary to the Pan Caribbean larval replenishment hypothesis that has dominated the spiny lobster management paradigm. Such coupling follows approximate trends and variances that are rarely found in the literature on spiny lobster recruitment dynamics.

Recruitment from post-larval to pre-adult stages (age 1) does not show significant linkages, implying a general lack of density-dependent effects in this mortality process. This condition represents the first statistical corroboration of important findings in the scientific literature pertaining to the ecology of the post-larval stages of *P. argus* in Florida (Herrnkind and Butler , 1986; Eggleston *et al.*, 1990; Butler and Herrnkind, 1992; Mintz *et al.*, 1994; Butler *et al.*, 1997) that demonstrate the importance of habitat quality and availability to the early recruitment stages. Recruitment success during the post-larval stages are further affected by mortality sources associated with potential physical features not fully understood at this time, but the results show that these effects are more important than the parental density-dependent effects on recruitment success.

The results show that a plausible reason for the lower landings observed in the fishery after the 2000 fishing season is a significant depletion of the parent stock due to exploitation, as well as a reduced recruitment success from the post-larval settlement to age 1 due to apparent regional physical features impacting nursery habitat. The negatively correlated signals of the Caribbean MSL on recruitment success should prompt new research that may lead to the discovery of the post-larval to recruitment at age 1 variability that ultimately will improve any attempt to forecast landings. The results are also indicative of the need to re-consider the Pan Caribbean recruitment paradigm that dominates the management of the Florida *P. argus* fisheries to include mechanisms that will control fishing mortality and to reduce catch.

ACKNOWLEDGEMENTS

REFERENCES

Arce, A.M. and de León, M.E. (2001) Biology. In: *Report on the FAO/DANIDA/CFRAMP/WECAFC Regional Workshops on the Assessment of the Caribbean Spiny Lobster (Panulirus argus)*. P. Medley & S. Venema (eds). *FAO Fish. Rep.* **619:** 17–25.

Bartsch, J., Brander, K., Heath, M., Richardson, K. and Swendsen, E. (1989) Modeling the advection of herring larvae in the North Sea. *Nature* **340:**632–636.

Bertelsen, R.D. (1999) Spiny lobster spawning potential and population assessment: a monitoring program for the South Florida fishing region: Final Report Third Year: NOAA Techn. Report for NMFS Grant NA57FF0300: pp. 55.

Bertelsen, R.D. and Cox, C. (2001) Sanctuary roles in population and reproductive dynamics of Caribbean spiny lobster. *Spatial Processes and Management of Marine Populations Alaska Sea Grant AK-SE-01-02*. G.H. Kruse, N. Bez & A. Booth *et al.* (eds) Fairbanks, AK, USA: University of Alaska Sea Grant, pp. 591–605.

Bertelsen, R.D. and Mathews, T.R. (2001) Fecundity dynamics of female spiny lobster (*Panulirus argus*) in a south Florida fishery and Dry Totugas National Park lobster sanctuary. *Mar. Freshw. Res.* **52:**1559–1565.

Bertelsen, R.D., Cox, C., Beaver, R. and Hunt, J.H. (2004) A reexamination of monitoring projects of Southern Florida adult Spiny Lobster *Panulirus argus*, 1973–2002: the response of local spiny lobster populations, in size structure, abundance, and fecundity, to different-sized sanctuaries. *Am. Fish. Soc. Symp.* **42:**195–210.

Butler, M.J. IV, and Herrnkind, W.F. (1992) Spiny lobster recruitment in south Florida: quantitative experiments and management implications. *Proc. Gulf Caribb. Fish. Inst.* **41:**508–515.

Butler, M.J. IV, Herrnkind, W.F. and Hunt, J.H. (1997) Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bull. Mar. Sci.* **61:**3–19.

Caputi, N., Chubb, C.F. and Brown, R.S. (1995) Relationships between spawning stock, environment, recruitment, and fishing effort for the western rock lobster, *Panulirus cygnus*, fishery in Western Australia. *Crustaceana* **68:**213–226.

Chang, L.J. and Li, H. (1997) A decadal climate variation in the tropical Atlantic Ocean from thermodynamic air–sea interactions. *Nature*, **385:**516–518.

Chen, P.H. (1996) *Current-Modified Wind-Forced Geostrophic Transport in the Straits of Florida: a Numerical Simulation Study*. PhD Dissertation, Coral Gables, FL, USA: University of Miami, pp. 74.

Chittleborough, R.G. and Phillips, B.F. (1975) Fluctuations of year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). *Aust. J. Mar. Freshwat. Res.* **26:**317–328.

Cowen, R., Lwiza, K.M., Sponaugle, S., Limouzy-Paris, C.B. and Olson, D.B. (2000) Connectivity of marine populations: open or closed? *Science* **287:**857–859.

Cowen, R.K., Paris, C.B., Olson, D.B. and Fortuna, J.L. (2003) The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf Carib. Res. Inst.* **14:**129–137.

Cowen, R.K., Paris, C.B. and Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Science* **311:**522–527.

Cruz, R., Puga, R. and León, M.E. (1993) Fluctuaciones de las capturas de langosta (*Panulirus argus*) en los refugios artificiales. Región del Golfo de Batabanó, Cuba. In: *Memorias del taller Binacional México-Cuba. Lautilización de los refugios artificiales en las pesquerías de langosta: sus implicancias en la dinámica del manejo del recurso*. J.M. González & R. Cruz (eds) Q.R. México: Isla Mujeres. 17–21 Mayo 1993.

Cruz, R., Puga, R. and de León, M.E. (1995) Pronóstico de la captura de la langosta (*Panulirus argus*) por regiones de pesca, Cuba. *Rev. Cub. Inv. Pesq.* **19:**51–58.

Cruz, R., Luckhurst, B. and Muller, R. (2001) Review larval recruitment patterns and variability in spiny lobster (*Panulirus argus*). In: *Report on the FAO/DANIDA/ CFRAMP/WECAFC Regional Workshops on the Assessment of the Caribbean Spiny Lobster (Panulirus argus)*. P. Medley & S. Venema (eds) *FAO Fish. Rep.*, **619:** 25–32.

Cushing, D.H. (1973) The dependence of recruitment on parent stock. *J. Fish. Res. Bd Can.*, **30:**1965–1976.

Eggleston, D.B., Lipcius, R., Coba-Cetina, L. and Millar, D. (1990) Shelter scaling regulates survival of juvenile spiny lobster, *Panulirus argus*. *Mar. Ecol. Prog. Ser.* **62:**79–88.

Ehrhardt, N.M. (2005) Population dynamic characteristics and sustainability mechanisms in key Western Central Atlantic Spiny Lobster, *Panulirus argus*, fisheries. *Bull. Mar. Sci.* **76:**501–525.

Ehrhardt, N.M. (2007) Assessment of seasonal exploitation of the spiny lobster, *Panulirus argus*, in Florida. *Meta Population Stock Assessment Methods Incorporating Climatic and Ecosystem Effects for the Florida Spiny Lobster Fishery*. Final Report to NOAA-MARFIN Grant No.: NA05NMF4331081, Appendix II. pp. 65.

Ehrhardt, N.M. (2008) Estimating growth of the Florida spiny lobster, *Panulirus argus*, from molt frequency and size increment data derived from tag and recapture experiments. *Fish. Res.* **93:**332–337.

Gregory, D.R., Labisky, R.F. and Combs, C.L. (1982) Reproductive dynamics of the spiny lobster *Panulirus argus* in South Florida. *Trans. Am. Fish. Soc.* **111:**575–584.

Herrnkind, W.F. and Butler, M.J. IV (1986) Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. *Mar. Ecol. Prog. Ser.* **34:**23–30.

Hurrell, J.W. (1995) Decadal trends in the North Atlantic oscillation: regional temperature and precipitation. *Science* **269:**676–679.

Hurrell, J.W., Kushnir, Y., Ottersen, G. and Visbeck, M. (2003) An overview of the North Atlantic Oscillation. In: *The North Atlantic Oscillation*. J.W. Hurrell (ed.) Washington, DC, USA: AGU, pp. 1–36.

Idyll, C.P. (1980) Summary and importance of the GCFI sessions on spiny lobster. *Proc. Gulf Caribb. Fish. Inst.* **33:**322–335.

Janicot, S. (1997) ENSO impact on atmospheric circulation and convection over the tropical Atlantic and West Africa. *Ann. Geophys.* **15:**471–475.

Johns, W.E. and Schott, F. (1987) Meandering and transport variations of the Florida Current. *J. Phys. Oceanogr.* **17:**1128–1147.

Kittaka, J. and Kimura, K. (1988) Culture of the Japanese spiny lobster *Panulirus japonicus* from egg to juvenile stage. *Nippon Suisan Gakkai Shi* **55:**963–970.

Lee, T.N. and Mayer, D.A. (1977) Low-frequency variability and spin-off eddies along the shelf of Southeast Florida. *J. Mar. Res.* **35:**193–220.

Lee, T.N., Schott, F. and Zantopp, R. (1985) Florida Current: low-frequency variability of the Florida Current as observed with moored current meter stations during April 1982–June 1983. *Science* **227:**298–301.

Lee, T.N., Rooth, C., Williams, E., McGowan, M.F., Szmant, A.F. and Clarke, M.E. (1992) Influence of Florida Current, gyres, and wind driven circulation transport of larvae and recruitment in the Florida Keys coral reefs. *Cont. Shelf Res.* **12:**971–1002.

Lee, T.M., Clarke, M.E., Williams, M., Szmant, A.F. and Berger, T. (1994) Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bull. Mar. Sci.* **54:**621–646.

Lewis, J.B. (1951) The phyllosoma larvae of the spiny lobster, *Panulirus argus*. *Bull. Mar. Sci.* **1:**89–103.

Limouzy-Paris, C.B., Graber, H.C., Jones, D.L., Röpke, A. and Richards, W.J. (1997) Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. *Bull. Mar. Sci.* **60:**966–983.

Lyons, W.G. (1980) The post-larval stage of scyllaridean lobsters. *Fisheries* **5:**47–49.

Lyons, W.G. (1981) Possible sources of Florida's spiny lobster population. *Proc. Gulf Caribb. Fish. Inst.* **33:**253–266.

Marx, J.M. and Herrnkind, W.F. (1985) Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for juvenile spiny lobsters, *Panulirus argus*. *Bull. Mar. Sci.* **36:**423–431.

Matsuda, H. and Takenouchi, T. (2006) Larval molting and growth of the Japanese spiny lobster *Panulirus japonicus* under laboratory conditions. *Fish. Sci.* **72:**767–773.

Matsuda, H., Goldstein, J.S., Takenouchi, T. and Butler, M.J. IV (2008) A description of the complete development of larval Caribbean spiny lobster *Panulirus argus* (LATREILLE, 1804) in culture. *J. Crust. Biol.* **28:**306–327.

Maunder, M.N. and Punt, A.E. (2004) Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* **70:**141–159.

Menzies, R.A. (1980) Biochemical population genetics and the spiny lobster larval recruitment problem: an update. *Proc. Gulf Caribb. Fish. Res. Inst.* **33:**230–243.

Menzies, R.A. and Kerrigan, J.M. (1980) The larval recruitment problem of the spiny lobster. *Fisheries* **5:**42–46.

Mintz, J.D., Lipcius, R.N., Eggleston, D.B. and Seebo, M.S. (1994) Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecific abundance. *Mar. Ecol. Prog. Ser.* **112:**255–266.

Molinari, R.L., Wilson, W.D. and Leaman, K. (1985) Volume and heat transports of the Florida Current: April 1982 through August 1983. *Science* **227:**295–297.

Oey, L.-Y., Ezer, T. and Lee, H.-C. (2005) Loop current, rings and related circulation in the Gulf of Mexico: a review of numerical models and future challenges. In: *Circulation in the Gulf of Mexico: Observations and Models. Vol. 161.* W. Sturges & A. Lugo-Fernandez (eds) Washington, DC, USA: American Geophysical Union, pp. 31–56.

Pearce, A.F. and Phillips, B.F. (1988) ENSO events, the Leeuwin Current, and larval recruitment of the western rock lobster. *J. Cons. int. Explor. Mer.* **45:**13–21.

Phillips, B.F. and McWilliam, P.S. (1989) Phyllosoma larvae and the ocean currents off the Hawaiian Islands. *Pac. Sci.* **43:**352–361.

Phillips, B.F., Pearce, A.F. and Guzman, S.A. (1994) Spiny lobster catches and the ocean environment. In: *Spiny Lobster Management, Chapter 16.* P.S. Phillips, J.S. Cobb & J. Kittaka (eds) Oxford: Fishing News Books, pp. 420–446.

Polovina, J.J. and Mitchum, G.T. (1992) Variability in spiny lobster *Panulirus marginatus* recruitment and sea level in the Northwestern Hawaiian Islands. *Fish. Bull. U.S.* **90:**483–493.

Powers, J.E. and Bannerot, S.P. (1984) *Assessment of spiny lobster resources of the Gulf of Mexico and southeastern United States.* Miami, Florida: National Marine Fisheries Service, Southeast Fisheries Center, pp. 25.

Pringle, J.D. (1986) California spiny lobster (*Panulirus interruptus*) larval retention and recruitment: a review and synthesis. *Can. J. Fish. Aquat. Sci.* **43:**2142–2152.

R Development Core Team (2008) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Sarver, S.J., Freshwater, D.W. and Walsh, P.J. (2000) The occurrence of the Brazilian sub-species of the spiny lobster (*Panulirus argus westonii*) in Florida waters. *Fish. Bull. U.S.* **98:**870–873.

Schmitz, W.J. Jr and Richardson, W.S. (1968) On the transport of the Florida Current. *Deep-Sea Res.* **15:**679–693.

SEDAR08 (2005) Assessment of spiny lobster, *Panulirus argus*, in the Southeast United States. *Stock Assessment Report prepared by the SEDAR 08 U.S. Stock Assessment Panel. 29 April 2005.* pp. 96.

Sekine, S., Shima, Y., Fushimi, H. and Nonaka, M. (2000) Larval period and molting in the Japanese spiny lobster *Panulirus japonicus* under laboratory conditions. *Fish. Sci.* **66:**19–24.

Shepherd, J.G. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *J. Cons. Int. Explor. Mer.* **40:**67–75.

Silberman, J.D., Sarver, S.K. and Walsh, P.J. (1994a) Mitochondrial DNA variation and population structure in the spiny lobster, *Panulirus argus*. *Mar. Biol.* **120:**601–608.

Silberman, J.D., Sarver, S.K. and Walsh, P.J. (1994b) Mitochondrial DNA variation in seasonal cohorts of spiny lobster (*Panulirus argus*) post-larvae. *Mol. Mar. Biol. Biotechnol.* **3:**165–170.

Sims, H.W. Jr and Ingle, R.M. (1966) Caribbean recruitment of Florida's spiny lobster populations. *Q. J. Florida Acad. Sci.* **29:**207–243.

Sutton, R.T., Norton, W.W. and Jewson, S.P. (2001) The North Atlantic Oscillation: what role for the ocean? *Atm. Sci. Lett.* **1:**89–100.

Witham, R. (1973) Preliminary thermal studies on young *Panulirus argus*. *Florida Scientist* **36:**154–158.

Witham, R., Ingle, R.M. and Joyce, E.A. Jr (1964) Notes on postlarvae of *Panulirus argus*. *Q. J. Florida Acad. Sci.* **27:**289–297.

Witham, R., Ingle, R.M. and Joyce, E.A. Jr (1968) Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. *Florida Board. Cons. Mar. Res. Lab. Tech Ser. No.* **53:**31.

Xie, S.-P. and Tanimoto, Y. (1998) A Pan-Atlantic decadal climate oscillation. *Geophys. Res. Lett.* **25:**2185–2188.

Yeung, C. (1996) *Transport and Retention of Lobster Phyllosoma Larvae in the Florida Keys.* PhD dissertation, Coral Gables, FL, USA: University of Miami, pp. 217.

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

Yeung, C., Jones, D.L., Criales, M.M., Jackson, T.L. and Richards, W.J. (2001) Influence of coastal eddies and counter-currents on the influx of spiny lobster, *Panulirus argus*, post-larvae into Florida Bay. *Mar. Freshw. Res.* **52:**1217–1232.

Zelle, H., Appeldoorn, G., Burgers, G. and van Oldenborgh, G.J. (2004) On the relationship between sea surface temperature and thermocline depth in the eastern equatorial Pacific. *J. Phys. Oceanogr.* **34:**643–655.