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Temporal patterns and transport processes in recruitment of spiny lobster (*Panulirus argus*) postlarvae to south Florida

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Abstract We used time-series analysis to identify weekly and annual patterns in the supply of spiny lobster, *Panulirus argus* (Latreille, 1804), postlarvae to the Florida Keys, USA, over an 8 yr period. We also investigated the relationship between postlarval influx and wind forcing as a transport mechanism using the complex vector-scalar correlation analysis. Postlarval supply had a lunar phase periodicity at 4.5 wk intervals, with postlarval abundance peaking between the new moon and first-quarter lunar phases. A distinct annual cycle of postlarval supply with two peak periods was also apparent. Cross-correlation analysis between relative postlarval abundance and a 12 mo cycle showed that the annual peak occurs in spring, centered around March. With the 12 mo periodicity removed, a smaller peak at 5 mo intervals was also well defined. Wind-forcing for 7 d prior to the time of postlarval collection was marginally correlated with postlarval abundance through the entire time-series; the association was strongest during the late fall to early spring months. The analysis indicated that postlarval supply was correlated with winds from the northeast (ca. 45°), which are associated with winter atmospheric fronts. In contrast to results reported for other spiny lobster populations, these patterns suggest that recruitment of lobster postlarvae to south Florida is predictable only at a gross level and is presumably affected by the temporally inconsistent structure of regional oceanic gyres and variability in the timing of lobster spawning in the Caribbean.

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Introduction

Recruitment of marine fish and invertebrate larvae is often highly variable, and identification of patterns requires quantification of biotic and abiotic influences on survival, an understanding of physical transport mechanisms, and long-term settlement data. Many variables may contribute to the temporal and spatial variability in recruitment. Larval behavior, such as vertical migration and response to changes in hydrostatic pressure, may place larvae in proximity to onshore-moving water masses (Sulkin 1984; Cronin and Forward 1986; Shanks 1995). The timing of larval influx to coastal habitats is often associated with lunar and tidal signals (Robertson 1992; DeVries et al. 1994; Thorrold et al. 1994), and settlement patterns can be linked to the movement of the wind-driven surface waters (McConaugha et al. 1984; Farrell et al. 1991; Herrnkind and Butler 1994; Thorrold et al. 1994). Due to interactions between these factors, predicting the interannual variability in the supply of marine larvae to coastal habitats is a difficult process requiring long-term data and an integrated approach to the study of processes affecting recruitment (Underwood and Fairweather 1989).

Palinurid lobsters have a complex life history, with a lengthy larval phase lasting from a few months to nearly two years, and are thus subject to widespread dispersal (Phillips and McWilliam 1986). The puerulus is the transition postlarval stage linking the planktonic phyllosoma larva to the benthic juvenile, and postlarvae settle in shallow nearshore nursery habitats often around the new-moon lunar phase (Little 1977; Herrnkind and Butler 1986; Butler and Herrnkind 1991). The nearshore supply of postlarvae for certain palinurid species has been linked to large-scale oceanic processes. For example, the supply of postlarvae of the Australian spiny lobster *Panulirus cygnus* inshore is greatly reduced when the Leeuwin Current weakens during El Niño years (Pearce and Phillips 1988; Phillips et al. 1991). Transport of pueruli across the Leeuwin Current to nearshore

settlement habitats is also facilitated by onshore-moving storm systems (Caputi and Brown 1993). In the Hawaiian archipelago, sea-level variability associated with the proximity of the Subtropical Counter Current is linked to local current regimes and has been used as an indicator of the magnitude of *P. marginatus* postlarval supply (Polovina and Mitchum 1992).

Spawning of the Caribbean spiny lobster *Panulirus argus* reportedly occurs through most of the year in the Caribbean Sea, whereas seasonal spawning occurs further north in Florida and Bermuda populations (Lyons 1980; Lyons et al. 1981; Gregory et al. 1982; Hunt and Lyons 1986). However, regional patterns in postlarval supply are highly variable and do not necessarily reflect spawning cycles (Herrnkind et al. 1994). Populations in Florida are believed to be sustained by recruitment of postlarvae from Caribbean populations transported via the Caribbean Current to the Straits of Florida (Lyons 1980). Observations of the offshore distribution of phyllosoma larval stages support this hypothesis (Richards and Potthoff 1980; Yeung and McGowan 1991), along with evidence of genetic homogeneity among Caribbean populations (Silberman et al. 1994). Little (1977) suggested that peak puerulus recruitment to south Florida occurs in spring and fall, with occasional summer peaks, which illustrates the high variability in postlarval supply. Ward (1989) suggested that the influx of *P. argus* postlarvae to Bermuda peaks in the summer, and postulated that water temperatures at other times of the year are too low for postlarval survival. Several other studies have attempted to discern patterns in postlarval supply in the Caribbean basin, but clear patterns are difficult to identify because of high variability. Peak postlarval influx has been reported to occur in autumn in Cuba (Cruz et al. 1991) and the Yucatan coast of Mexico (Briones-Fourzan 1994), in spring in Jamaica (Young 1991), and in summer in Antigua (Bannerot et al. 1991). Part of the problem in identifying patterns in postlarval supply may be due to the nature of short time-series, which invariably have autocorrelations and so are not amenable to statistical analyses. Even when variability or noise exists in long-term data, it may be possible to statistically test whether the system oscillates deterministically and if there are significant cyclic patterns underlying the random high-frequency variation (Dowse and Ringo 1989).

We analyzed an 8 yr time series of *Panulirus argus* postlarval supply to the Florida Keys to discern whether temporal patterns exist. We also inspected the association between the magnitude of postlarval influx, wind speed and wind direction to evaluate whether wind-forcing was a plausible mechanism affecting onshore transport of postlarvae. We discuss our findings in relation to existing hypotheses on local oceanic circulation and on reproductive dynamics of *P. argus* in the region.

Materials and methods

Temporal patterns

The supply of postlarval *Panulirus argus* (Latreille, 1804) was monitored using surface "Hunt" collectors (sensu Phillips and Booth 1994) from March 1987 to August 1995 as part of an ongoing long-term postlarval monitoring program (Florida Marine Research Institute, Florida Department of Environmental Protection). Five collectors were stationed < 1 km offshore of Big Munson Key (25°36′11N; 81°24′10W) in the lower Florida Keys (Fig. 1). Postlarvae on each collector were counted weekly from 1987 to 1992, and monthly 7 d following new moon phases from 1992 to 1995. The number of postlarvae/sample was log-transformed to stabilize the variance. We used time-series analysis to describe temporal patterns in postlarval influx over the 8 yr period. Inspection of autocorrelation plots indicated that the data contained autocorrelations that were stationary, i.e. displayed no sys-

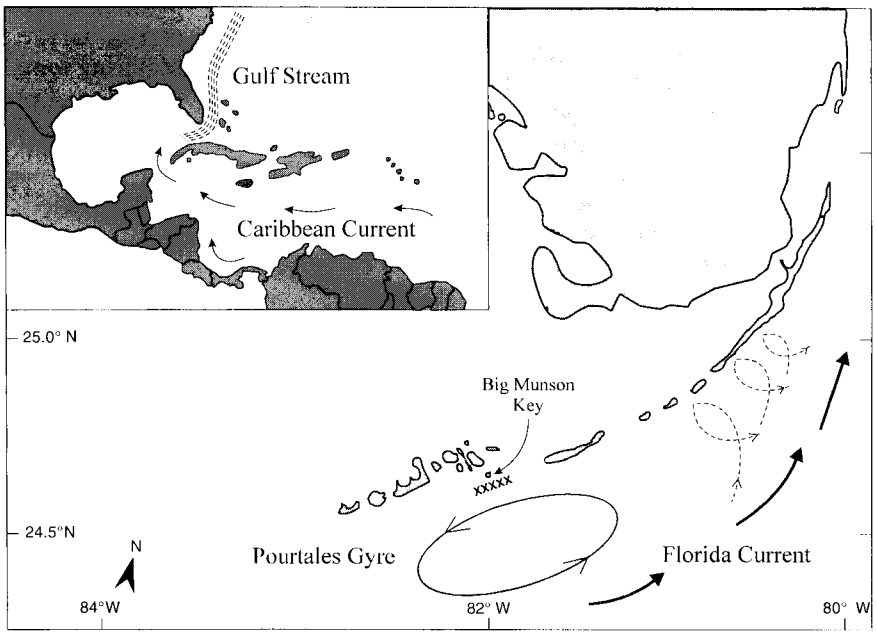

Fig. 1 Oceanic flow in Caribbean region (*inset*) showing Caribbean Current and Gulf Stream; inset area is expanded to show location of postlarval collectors near Florida Keys and flow around south Florida, including Pourtales Gyre (modified from Lee et al. 1994)

tematic fluctuations in mean and variance through the series (Box and Jenkins 1976).

We used the autocorrelation function to determine if there was significant rhythmicity associated with lunar phases in the weekly data (1987 to 1992). The autocorrelation function is estimated from correlation coefficients between pairs of lunar week data-points separated by some lag period, and the results are depicted in a correlogram that plots the autocorrelation coefficients against time lags (Box and Jenkins 1976). Significant departures from a random distribution occur when the lag approximates the period of the cycle at the 95% confidence intervals, calculated as $\pm 2/\sqrt{n}$. We then used spectral analysis to identify dominant periodicities associated with weekly lunar phases. In spectral analysis, the variance is partitioned by Fourier transform into frequency components of harmonics of the data set, and the energy density spectra can be displayed in a periodogram that shows the concentration of energy or variance under the curve (Platt and Denman 1975). To identify peaks in postlarval supply during the lunar month, we constructed a bivariate time-series using weekly postlarval abundance and a monthly lunar cycle (a 4-point sine curve), and we used cross-correlation analysis to identify where peak abundance occurs in the lunar cycle by examining whether the phase relationship is significant at a given time lag.

For the inspection of monthly (seasonal) patterns in postlarval supply, we pooled the weekly data and calculated monthly mean values per collector for all data (1987 to 1995). Rhythmic cycles in the monthly data were analyzed using the autocorrelation function, and dominant periodicities were inspected using spectral analysis as stated above. To identify times during the calendar year when relative postlarval abundance is at its highest and lowest levels, a bivariate time-series was constructed using the monthly postlarval abundance data and an annual cycle (a sine curve with 12-point oscillations). A cross-correlation analysis was then used to determine the phase relationship and to identify any time lags between the series. After inspection and description of these seasonal patterns, the data were filtered using a Parzen filter to remove the annual periodicities and then reinspected for high-frequency periodicities using the autocorrelation function and spectral analysis. All time-series analyses were performed using the computer program MESOSAUR (Kuznetsov and Khalileev 1991).

Transport due to wind-forcing

To examine the association between postlarval supply and onshore transport due to wind-forcing, we used the monthly mean number of postlarvae per collector obtained over 10 d each lunar month (from new moon to 10 d post-new moon), along with wind speed and direction for both 4 and 7 d periods prior to the dates of postlarval collection (two separate analyses). We selected a 10 d window of postlarval influx following new moon because the time-series analyses on weekly data showed that peak influx occurs during this period (see "Results – Transport due to wind-forcing"). The 4 and 7 d wind-forcing windows are based on evidence for coupling of wind and surface currents nearshore in the Florida Keys at frequencies of 3 to 4 d and 5 to 12 d (Pitts 1994). We removed autocorrelations and periodicities from the postlarval influx data by fitting an 'autoregressive integrated moving average' (ARIMA) model to the abundance data, and checked the residuals using a χ^2 test for white noise. ARIMA models may be used to prefilter data using combinations of autoregressive coefficients, degrees of differencing, and moving average terms to account for and remove periodicities (Box and Jenkins 1976). The assumption of independence of residuals was verified using the Box and Jenkins' portmanteau test, and normality was checked using the Kolmogorov–Smirnov D statistic. Hourly wind data for the 8 yr period was obtained from measurements taken at the Key West International Airport (Southeast Regional Climate Center, National Oceanic and Atmospheric Administration, Asheville, North Carolina). Hourly wind speed and direction measurements were vectorially summed for 24 h periods and averaged for either four consecutive days or seven alternate days prior to date of postlarval collections. These data were inspected for autocorrelation and decomposed into north-south (u) and east-west (v) components. Since the assumption of stationarity of the mean and variance was satisfied, no further filtration was necessary.

The relationship between centered residuals (i.e. mean removed) of postlarval time-series from the ARIMA model and the decomposed wind data were analyzed using the complex vector-scalar correlation (Kundu 1976; Johnson and Hester 1989). This analysis determines the correlation magnitude (R) between a scalar variable (postlarval abundance) and its corresponding vector (wind speed and direction), and provides the correlation direction (φ) of the vector when the correlation magnitude is significant. Plots of the postlarval data showed peaks in late winter during which fronts are common. Therefore, we ran separate complex correlation-analyses on data from November to April and from May to October to investigate seasonal associations.

Results

Temporal patterns

A lunar periodicity in the weekly supply of *Panulirus argus* postlarvae was well defined (Fig. 2A). The autocorrelation function indicates characteristic cycling at 2 to 4 wk intervals, and a monthly cycle is evident (Fig. 2B). Spectral analysis shows that most energy in the weekly data was concentrated at ~4.5 wk (Fig. 2C). The cross-correlation function on postlarval supply and a hypothetical lunar cycle identified peak influx between the new moon and first-quarter lunar phases (Fig. 2D). A fourth-order autoregressive model reduced the data to white noise ($\chi^2 = 27.7$; df 21; $P > 0.05$; Durbin–Watson $W = 2.11$), and accounted for 70% of the variance, indicating that no other significant low-frequency pattern exists.

While there was much interannual variability in the annual postlarval time-series, there were several significant features (Fig. 3A). The autocorrelation plot shows sinusoidal cycling with a significant annual rhythmicity (Fig. 3B). Spectral analysis indicates that a significant proportion of the variance is concentrated in this 12 mo periodicity (Fig. 3C). A smaller peak occurs at a 5 mo lag; we later determined that this peak is not a harmonic of the main peak, and is a significant signal in itself (see next paragraph). The cross-correlation analysis on monthly postlarval supply and a hypothetical annual cycle indicates that relative peak postlarval supply occurs at Lag 3 from January, which corresponds to a March peak (Fig. 3D). This is in close agreement to the absolute mean abundance through the 8 yr period which indicates a peak in April (mean ± SE: 43.8 ± 5.4). The period of lowest supply occurs in the summer months.

To further investigate the peak at the 5 mo lag in the annual power spectrum (Fig. 3B), we removed the 12 mo periodicity using a Parzen filter. Although significant at the 95% confidence limits, the variance accounted for by removing annual periodicity was only 24% of the total variance, and therefore a substantial proportion of the annual variation in postlarval influx to the Florida Keys cannot be explained by seasonal patterns. We then plotted the new correlogram and periodogram. The

autocorrelation function shows significant cycling at 5 mo intervals, indicating that the secondary peak is real (Fig. 4A), and the new spectral shape shows a dominant periodicity at 5 mo intervals (Fig. 4B).

Transport due to wind-forcing

The ARIMA model fitted to the postlarval data employed a first-order autoregression which accounted for all periodicities ($\chi^2 = 24.2$; *df* 23; $P > 0.05$). The residuals were stationary and contained no autocorrelations. The association between monthly postlarval supply, wind speed and wind direction through 1987–1995 was analyzed using the complex vector-scalar correlation. The correlation coefficient obtained using the 7 d wind-forcing periods prior to postlarval influx was marginally significant at an α level of 0.05 ($R = 0.23$). The correlation direction for this period corresponded to

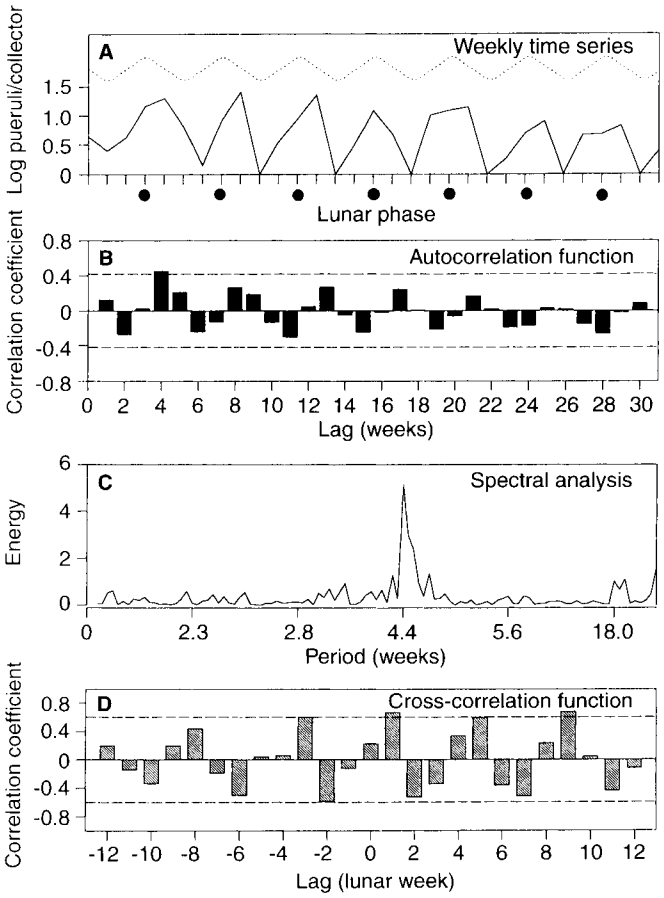

Fig. 2 *Panulirus argus*. Weekly recruitment of postlarvae from March 1987 to January 1992. **A** Time-series of influx over first 30 wk period is shown as example, to emphasize lunar periods (● new moon; *dotted line* lunar cycle); **B** correlogram of postlarval supply with significant cycle of 4 wk; **C** periodogram showing peak periodicity at 4.5 wk-note non-linear scale on abscissa; **D** cross-correlation between weekly postlarval supply and a lunar cycle showing significant association at Lag 1 from new moon (i.e. first-quarter lunar phase) (*Dashed lines* in **B** and **D** represent 95% confidence intervals)

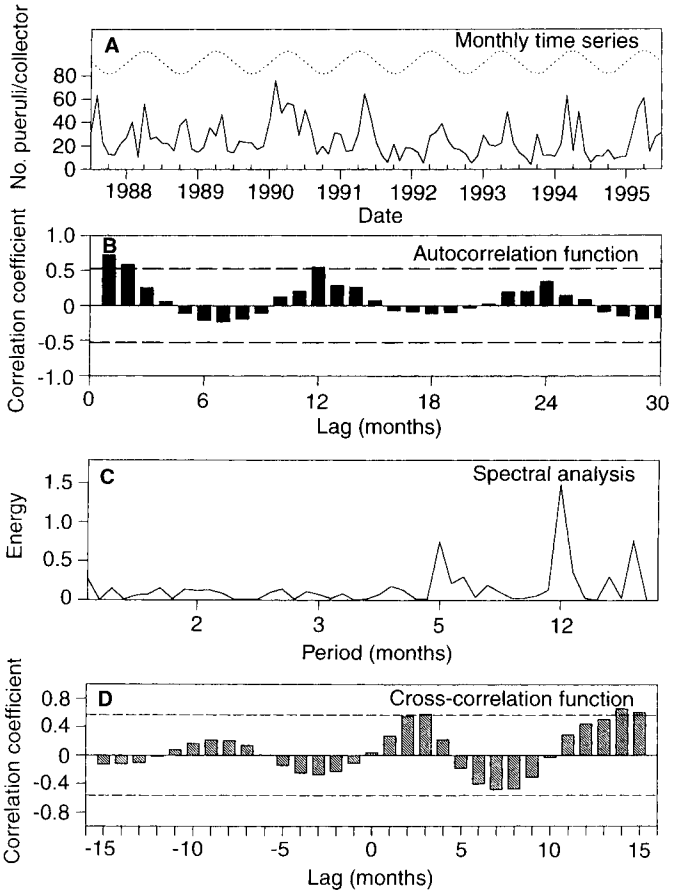

Fig. 3 *Panulirus argus*. Annual recruitment of postlarvae from June 1987 to June 1995. **A** Time-series of influx during new moon (*dotted line* annual cycle); **B** correlogram of postlarval supply with a significant cycle of 12 mo; **C** periodogram showing peak periodicities at 12 and 5 mo lags – note non-linear scale on abscissa; **D** cross-correlation of monthly postlarval supply and an annual cycle showing peak abundance at Lag 3 (March) (*Dashed lines* in **B** and **D** represent 95% confidence intervals)

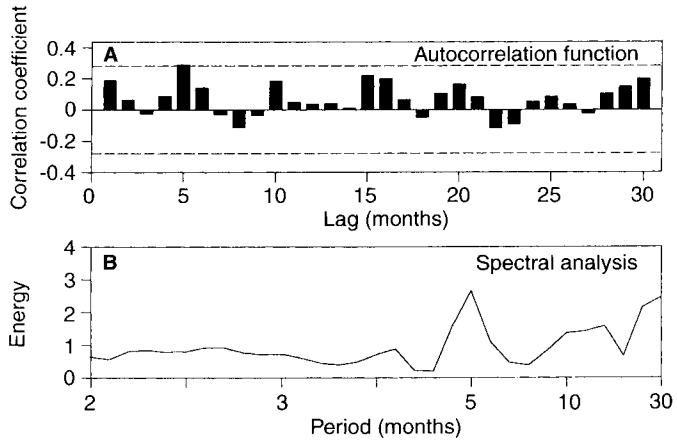

Fig. 4 *Panulirus argus*. High-frequency monthly periodicity in postlarval supply (12 mo cycle removed using Parzen filter). **A** correlogram showing 5 mo rhythmicity (*dashed lines* represent 95% confidence intervals); **B** periodogram showing 5 mo periodicity; note non-linear scale on abscissa

winds from the east ($\varphi = 80°$). The correlation between postlarval supply and the 4 d wind-forcing period was not significant ($R = 0.18$; $P = 0.10$).

We partitioned the data sets and examined the winter and summer periods separately. The association between postlarval supply and wind-forcing for the period from November to April ("winter") was stronger than that of the annual series ($R = 0.32$ for 7 d, 0.34 for 4 d). The correlation direction indicated an association with wind-forcing from the north-east ($\varphi = 39°$ for 7 d, 57° for 4 d). The May to October ("summer") correlations were not significant.

Discussion

The supply of *Panulirus argus* pueruli to nearshore settlement habitats occurs during the dark moon phase of new moon in several palinurid species (Herrnkind et al. 1994). Our analysis on 4 yr of weekly collections of *P. argus* postlarvae in the Florida Keys confirms that peak supply occurs at intervals of 4.5 wk, between the new-moon and first-quarter lunar phases. Previous reports on shorter time-series of postlarval influx showed similar lunar associations at various locations in south Florida (Witham et al. 1968; Little 1977; Little and Milano 1980; Heatwole et al. 1992) and in the Caribbean (Bannerot et al. 1991; Cruz et al. 1991; Young 1991; Briones-Fourzan 1994). However, Ward (1989) recorded peak settlement of *P. argus* postlarvae from full moon through the new-moon period. The ecological significance of the timing of influx may be linked to the stronger flooding tides that occur during the new-moon phase (Pitts 1994), although this does not explain why postlarvae do not capitalize on the strong full-moon tides. It is generally assumed that mortality attributable to visual predators is lower during the darkest lunar phase, and we have confirmed this in field and mesocosm experiments (Acosta 1997). However, it has yet to be determined whether the paucity of postlarvae nearshore during full moon results from postlarval choice or is a consequence of differential mortality rates during new- and full-moon periods.

Although spiny lobster postlarvae recruit year-round to south Florida, our analysis of monthly postlarval supply over 8 yr indicates an annual periodicity of influx, with a large early spring peak and a smaller non-seasonal peak that occurs at 5 mo intervals. The 12 mo periodicity in our analysis explained 24% of the variance in postlarval supply. Earlier studies in Florida suggested that there may be two or more peak periods of postlarval influx, but their seasonality was not well defined (Little 1977; Little and Milano 1980; Heatwole et al. 1982).

The continuous supply of postlarvae to the Florida Keys and its spring peak are probably a reflection of spawning activity in the Caribbean. Female *Panulirus argus* at the northern limits of their geographic distribution (e.g. Florida) spawn in the spring and early summer (April to July), whereas reproduction reportedly occurs year-round further south in the Caribbean (Lyons 1980; Lyons et al. 1981; Gregory et al. 1982). The year-round postlarval supply in Florida may, therefore, be a consequence of continuous reproductive activity in the Caribbean basin. In addition, variability in phyllosoma larval development would further blur distinction among monthly cohorts. The genetic variability among *P. argus* populations from various regions of the Caribbean and Florida is homogenous enough to indicate that substantial gene flow occurs between these populations (Silberman et al. 1994). The March peak in postlarval supply to the Florida Keys may reflect the May to June peak in spawning activity in the northern Caribbean, which supports the hypothesis that the planktonic larval phase is 9 to 10 mo long. Examination of the relative frequency of the 11 larval stages of *P. argus* obtained from plankton samples taken at different times of the year has yielded estimates of a 3 to 12 mo larval duration (see Lyons 1980).

The significant 5 mo periodicity in postlarval supply remains unexplained. We hypothesize that this high frequency periodicity is related to physical transport processes. Lee et al. (1992) showed that the Pourtales Gyre, which circulates off the middle and lower Florida Keys shelf, is a potential mechanism for larval transport from the Florida Current (see Fig. 1). The Pourtales Gyre is a later stage of the Tortugas Gyre, which originates from meanders of the Caribbean Current as it enters the Straits of Florida (Lee et al. 1994). The Tortugas Gyre is a dominant feature on time scales of 2 to 3 mo, and evolves into the Pourtales Gyre which lasts for about 1 to 2 mo. The cyclonic circulation of the Tortugas–Pourtales Gyre system may remove larvae from the Gulf Stream and transport them onshore via a southwestward flow on the leading side of the gyre (Lee et al. 1992, 1994). While long-term periodic behavior of this system has not been documented, the high-frequency peaks we observed at 5 mo intervals may be associated with onshore transport from the Florida Current by the Tortugas–Pourtales Gyre.

Another physical agent that may influence the magnitude of the monthly "pulse" of postlarvae arriving inshore is wind-forcing. Plankton tows taken in offshore (Richards and Potthoff 1980; Yeung and McGowan 1991) and nearshore (Little 1977; Little and Milano 1980; Heatwole et al. 1992) waters, as well as direct behavioral observations (Calinski and Lyons 1983), indicate that pueruli utilize surface waters (0 to 2 m) during inshore migration. Thus, wind movement of surface waters is likely to have a great impact on postlarval supply to the nearshore nursery. Strong atmospheric fronts and their associated winds are most common from late fall through early spring, when postlarval supply is maximum in the lower Florida Keys, and nearshore flow during this period is typically alongshore toward the southwest (Pitts 1994). We therefore suspected that the strongest association between postlarval supply and wind-forcing would be

during this period when wind velocity was greatest and from a direction which would facilitate onshore movement of surface waters. Although we found a significant correlation (R = 0.32 to 0.34) between postlarval supply and wind-forcing from the northeast (39 to 57°) during the winter, wind forcing accounted for only 6% of the variance in monthly postlarval supply to the lower Florida Keys. With the additional 24% of the variance explained by seasonal patterns in postlarval supply, 70% of the variance is still left unexplained.

While larval supply to nearshore environments have been linked to wind-forcing in several studies (Johnson et al. 1984; Taggart and Leggett 1987; Farrell et al. 1991; Thorrold et al. 1994), the explanation is not nearly so simple here. Patterns in the supply of spiny lobster postlarvae to south Florida are weakly associated with wind-forcing, and only with winter winds from the northeast which promote the onshore movement of surface waters from the Florida Current. Spatial and temporal variation in spawning activity in the Caribbean affecting monthly larval abundance and fluctuations in the development of large-scale gyres which periodically move onshore may interact with seasonal wind-forcing to determine the nearshore supply of postlarvae. Identification of periodic behavior associated with Gulf Stream gyres may improve our understanding of spiny lobster postlarval recruitment to south Florida.

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References

Acosta CA (1997) Ecology and early life history of the caribbean spiny lobster, *Panulirus argus*: recruitment, predation, and habitat requirements. Ph.D. dissertation. Old Dominion University, Norfolk, Virginia

Bannerot SP, Ryther JH, Clark M (1991) Large scale assessment of recruitment of postlarval spiny lobsters, *Panulirus argus*, to Antigua, West Indies. Proc Gulf Caribb Fish Inst 41: 471–486

Box GEP, Jenkins GM (1976) Time series analysis: forecasting and control. Holden Day, Oakland, California, USA

Briones-Fourzan P (1994) Variability in postlarval recruitment of the spiny lobster *Panulirus argus* (Latreille, 1804) to the Mexican Caribbean coast. Crustaceana 66: 326–340

Butler MJ IV, Herrnkind WF (1991) Effect of benthic microhabitat cues on the metamorphosis of pueruli of the spiny lobster *Panulirus argus*. J Crustacean Biol 11: 23–28

Calinski MD, Lyons WG (1983) Swimming behavior of the puerulus of the spiny lobster *Panulirus argus* (Latreille, 1804) (Crustacea: Palinuridae). J Crustacean Biol 3: 329–335

Caputi N, Brown RS (1993) The effect of environment on puerulus settlement of the western rock lobster (*Panulirus cygnus*) in Western Australia. Fish Oceanogr 2: 1–10

Cronin TW, Forward RB (1986) Vertical migration cycles of crab larvae and their role in larval dispersal. Bull mar Sci 39: 192–201

Cruz R, de Leon ME, Diaz E, Brito R, Puga R (1991) Recrutamiento de puerulos de langosta (*Panulirus argus*) a la platforma cubana. Revta Investnes mar, Cuba 12: 66–75

DeVries MC, Tankersley RA, Forward RB Jr, Kirby-Smith WW, Luettich RA Jr (1994) Abundance of estuarine crab larvae is associated with tidal hydrologic variables. Mar Biol 118: 403–413

Dowse HB, Ringo JM (1989) The search for hidden periodicities in biological time series revisited. J theor Biol 139: 487–515

Farrell TM, Bracher D, Roughgarden J (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. Limnol Oceanogr 36: 279–288

Gregory DR, Labisky RF, Combs CL (1982) Reproductive dynamics of the spiny lobster *Panulirus argus* in south Florida. Trans Am Fish Soc 111: 575–584

Heatwole DW, Hunt JH, Blonder BI (1992) Offshore recruitment of postlarval spiny lobster, *Panulirus argus*, at Looe Key reef, Florida. Proc Gulf Caribb Fish Inst 40: 429–433

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

Herrnkind WF, Butler MJ IV (1994) Settlement of spiny lobster, *Panulirus argus* (Latreille, 1804), in Florida: pattern without predictability? Crustaceana 67: 46–64

Herrnkind WF, Jernakoff P, Butler MJ IV (1994) Puerulus and post-puerulus ecology. In: Phillips BF, Cobb JS and Kittaka J (eds) Spiny lobster management. Blackwell, Oxford, pp 213–227

Hunt JH, Lyons WG (1986) Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys. Can J Fish aquat Sciences 43: 2243–2247

Johnson DR, Hester BS (1989) Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. Estuar, estl Shelf Sci 28: 459–472

Johnson DR, Hester BS, McConaugha JR (1984) Studies of a wind mechanism influencing recruitment of blue crabs in the Middle Atlantic Bight. Contin Shelf Res 3: 425–437

Kundu PK (1976) Ekman veering observed near the ocean bottom. J phys Oceanogr 6: 238–242

Kuznetsov S, Khalileev A (1991) Mesosaur: a companion to SYSTAT. JV Dialogue and SYSTAT, Inc, Evanston, Illinois, USA

Lee TN, Clarke ME, Williams E, Szmant AF, Berger T (1994) Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull mar Sci 54: 621–646

Lee TN, Rooth C, Williams E, McGowan M, Szmant AF, Clarke ME (1992) Influence of the Florida Current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. Contin Shelf Res 12: 971–1002

Little EJ (1977) Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the south Florida coast. Fla mar Res Publs 29: 1–35

Little EJ, Milano GR (1980) Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Fla mar Res Publs 37: 1–16

Lyons WG (1980) Possible sources of Florida's spiny lobster population. Proc Gulf Caribb Fish Inst 33: 253–266

Lyons WG, Barber DG, Foster SM, Kennedy FS, Milano GR (1981) The spiny lobster, *Panulirus argus*, in the Middle and Upper Florida Keys: population structure, seasonal dynamics, and reproduction. Fla mar Res Publs 38: 1–38

McConaugha JR, Provenzano AJ, Johnson DF, Clark J, Sadler P (1981) Offshore displacement and reinvasion of *Callinectes sapidus* larvae in Chesapeake Bay. Estuaries 4: 277–278

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

Phillips BF, Booth JD (1994) Design, use, and effectiveness of collectors for catching the puerulus stage of spiny lobsters. Rev Fish Sci 2: 255–289

Phillips BF, Pearce AF, Litchfield RT (1991) The Leeuwin Current and larval recruitment to the rock (spiny) lobster fishery off Western Australia. J Proc R Soc West Aust 74: 93–100

Phillips BF, McWilliam PS (1986) The pelagic phase of spiny lobster development. Can J Fish aquat Sciences 43: 2153–2163

Pitts PA (1994) An investigation of near-bottom flow patterns along and across Hawk Channel, Florida Keys. Bull mar Sci 54: 610–620

Platt T, Denman KL (1975) Spectral analysis in ecology. A Rev Ecol Syst 6: 189–210

Polovina JJ, Mitchum GT (1992) Variability in spiny lobster *Panulirus marginatus* recruitment and sea level in the northwestern Hawaiian Islands. Fish Bull US 90: 483–493

Richards WJ, Potthoff T (1980) Distribution and seasonal occurrence of larval pelagic stages of spiny lobsters (Palinuridae, Panulirus) in the western tropical Atlantic. Proc Gulf Caribb Fish Inst 33: 244–252

Robertson DR (1992) Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panamá. Mar Biol 114: 527 537

Shanks AL (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward LR (ed) Ecology of marine invertebrate larvae. CRC Press, New York, pp 323–368

Silberman JD, Sarver SK, Walsh PJ (1994) Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus*. Mar Biol 120: 601–608

Sulkin SD (1984) The behavioral basis of depth regulation in larvae of brachyuran crabs. Mar Ecol Prog Ser 15: 181–205

Taggart CT, Leggett WC (1987) Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time-series analysis of physical–biological data. Can J Fish aquat Science 44: 438–451

Thorrold SR, Shenker JM, Maddox ED, Mojica R, Wishinski E (1994) Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. Mar Biol 118: 567–578

Underwood AJ, Fairweather PG (1989) Supply side ecology and benthic marine assemblages. Trends Ecol Evolut 4: 16–19

Ward J (1989) Patterns of settlement of spiny lobster (*Panulirus argus*) postlarvae at Bermuda. Proc Gulf Caribb Fish Inst 39: 255–264

Witham RR, Ingle RM, Joyce EA (1968) Physiological and ecological studies on *Panulirus argus* from the St. Lucie estuary. Tech Ser Fla St Bd Conserv 53: 1–31

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

Young GR (1991) A preliminary study of spiny lobster postlarval settlement in a Jamaican south coast bay. Revta Investnes mar, Cuba 12: 83–88