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

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.

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 (McConaughy 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 Munny Key (25°36′11″N; 81°24′10″W) 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-

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*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)
consecutive days or seven alternate days prior to date of postlarval influx into Florida (Box and Jenkins 1976). 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

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 (\( \phi \)) 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 \( \approx 4.5 \) 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 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 \( \pm SE; 43.8 \pm 5.4 \)). 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.
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 $\alpha$ level of 0.05 ($R = 0.23$). The correlation direction for this period corresponded to
winds from the east ($\varphi = 80^\circ$). 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 ($\varphi = 39^\circ$ for 7 d, $57^\circ$ 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 Panulirus 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 Panulirus 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. 1992).

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 Panulirus 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 Panulirus 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 Tortugas 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 Tortugas 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 Tortugas 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...
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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