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Ecology of the Early Life History of the Caribbean Spiny Lobster, *Panulirus argus:* Recruitment, Predation, and Habitat Requirements

Charles A. Acosta
Old Dominion University

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ECOLOGY OF THE EARLY LIFE HISTORY OF THE CARIBBEAN SPINY LOBSTER, *PANULIRUS ARGUS*: RECRUITMENT, PREDATION, AND HABITAT REQUIREMENTS

by

CHARLES A. ACOSTA
B.S. December 1989, University of New Orleans
M.S. May 1992, University of New Orleans

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Approved by:

Mark J. Butler IV (Director)

Cynthia M. Jones (Member)

Anthony J. Provenzano (Member)

ABSTRACT

ECOLOGY AND EARLY LIFE HISTORY OF THE CARIBBEAN SPINY LOBSTER, *PANULIRUS ARGUS*: RECRUITMENT, PREDATION, AND HABITAT REQUIREMENTS.

Charles A. Acosta
Old Dominion University, 1997
Director: Dr. Mark J. Butler IV

Recruitment variability of the early life history stages of marine benthic organisms can have profound consequences on population dynamics. I studied factors affecting recruitment success of postlarvae and early juveniles of the Caribbean spiny lobster. I examined patterns in postlarval supply, investigated wind forcing as a potential transport mechanism for recruiting postlarvae, and quantified predation on postlarvae in south Florida, USA. In an eight-year time series, spiny lobster postlarval supply occurred year-round between the new and first quarter lunar phases. The major annual peak occurred around March corresponding to spawning activity ten months earlier, and a smaller non-seasonal peak occurred with a five-month periodicity. Wind forcing of surface waters was correlated to postlarval supply only during winter months, but this accounted for a small proportion of the total variance. During new moon influx, predation on postlarvae tethered to floating arrays was highest over coral patch reefs and declined along a typical transport path over the coastal lagoon and leeward bay, especially near the surface. In contrast, predation during full moon was similar over reefs and the bay probably due to increased exposure to visual predators, whereas predation during new moon was significantly lower in the bay. In laboratory mesocosms, predation was lower under new moon conditions when prey density was low. These results indicate the adaptive value of recruitment during the darkest lunar phase and use of surface waters for rapid transport pass concentrated predator assemblages near reefs. In benthic habitats, predation was highest in coral crevices than in nearshore seagrass or macroalgae. To compare the role of a possible alternative nursery habitat to that of the south Florida system, I studied the population dynamics of juvenile spiny lobsters in mangrove-associated habitats in Belize. Juveniles use mangrove habitats as nurseries, but usage patterns depend on available shelter and isolation of islands which acts to restrict migration of subadult and juvenile lobsters. Settlement presumably occurs in vegetation, but successful recruitment to benthic populations may depend on the proximity of settlers to crevice shelter associated with mangrove islands or patch reefs. The size of a local spiny lobster population may, thus, be influenced by factors affecting postlarval supply to coastal populations, abundance of predators at areas of concentration which postlarvae must traverse, and the availability of suitable settlement habitat.

This work is dedicated to Alice Mary Scott-Acosta whose small contributions were the most significant.

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CHAPTER I

GENERAL INTRODUCTION

In marine systems, many animal populations are a part of a larger metapopulation in which populations interact solely via the exchange of larvae (Roughgarden et al., 1985; Roughgarden and Iwasa, 1986; Hanski and Gilpin, 1991). Larvae have important functions in dispersal, colonization (Thorson, 1950) and gene flow (Scheltema, 1971), and the process of settlement is often controlled by stringent habitat requirements (Keough and Downes, 1982; Young and Chia, 1982). Thus, larval recruitment can potentially have significant consequences on local population dynamics. Because processes impacting the distribution and abundance of larvae in the open ocean and in coastal settlement habitats are difficult to identify and quantify, those factors which influence variability in larval recruitment and their effects on adult population fluctuations are not well understood.

I use the term “recruitment” in the sense of classic larval ecology theory as the input of new individuals to the benthic population over a period of time (Keough and Downes, 1982; Connell, 1985; Roegner, 1991). This implies that period of time from when larvae (or more often, postlarvae) are in proximity to coastal environments to when they join the benthic population as a juvenile. This is distinguished from “settlement” which is a segment of the recruitment period during which competent larvae search for and metamorphose to the juvenile stage in settlement habitat.

The journal model for this dissertation is Bulletin of Marine Science.

Traditional fisheries-based stock-recruitment models assume that a relationship exists between adult breeding stock and recruitment of larvae back to the adult population (Ricker, 1954; Beverton and Holt, 1957). An alternative to the stock-recruitment models are "supply-side" models that treat larval recruitment to a population as an event that is independent of adult population size and is largely dependent on the probability of successful transport of pelagic larvae to the adult population (Roughgarden et al., 1988; Underwood and Fairweather, 1989; Fogarty et al., 1991). The paucity of data on the interaction between mechanisms which impact larval recruitment has resulted in slow empirical support for either model (Morgan, 1995). Nevertheless, a new paradigm describing the regulation of marine populations and the structure of marine communities has arisen from the recognition that several factors involving the larval phase interact to shape demographic patterns. The temporal and spatial dynamics of a population are associated with the interaction between larval production which is dependent on reproductive cycles (Vance, 1973), favorable transport of pelagic larvae to adult populations (Gaines et al., 1985; McConaugha, 1988; Roughgarden et al., 1991; Phillips et al., 1991), changes in larval mortality (Hjort, 1914; Thorson, 1950; Connell, 1985; Gaines and Roughgarden, 1987), and availability of suitable settlement habitat (Keough and Downes, 1982; Young and Chia, 1982; Caffey, 1985; Raimondi, 1991).

Tropical spiny lobsters (Decapoda; Palinuridae) represent a suitable model for studying recruitment mechanisms that regulate marine benthic populations because the long-lived larval phase is capable of widespread dispersal and may be largely decoupled from a given parent population. For example, the Caribbean spiny lobster *Panulirus argus* has a complex life history with an extensive larval phase lasting up to one year which may link separate coastal populations from Brazil to Florida. Adult *P. argus* mate and spawn on the reef, presumably to expose the eggs to currents which will advect them offshore (Lyons et al., 1981; Gregory et al., 1982). Phyllosome larvae hatch from the eggs within a day of spawning, and the larvae live and feed in the open sea for an estimated four to 11 months (Phillips and Sastry, 1980). The ninth-stage phyllosoma respond to offshore cues yet unknown, which results in the metamorphosis to the puerulus postlarval stage. The puerulus is distinctively different from the leaf-shaped phyllosoma, having a streamlined body that is transparent except for pigmented eyes (Lewis et al., 1952). The postlarva is a non-feeding stage (Wolfe and Felgenhauer, 1991), and it uses energy reserves stored in the hepatopancreas (Takahashi et al., 1994) during its brief existence lasting up to several weeks (Field and Butler, 1994).

Postlarvae recruit to nearshore environments on nightly flood tides during the new moon phase (Witham et al., 1968; Little, 1977), swimming at a rapid pace near the surface (Calinski and Lyons, 1981). In Florida Bay, they prefer to settle in vegetation, especially in clumps of macroalgae, such as *Laurencia* sp. (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986). Following settlement, postlarvae quickly develop pigmentation, molt to the first juvenile stage, and take up a solitary and highly cryptic lifestyle (Butler et al., in press). Juvenile spiny lobsters in nursery habitats undergo an ontogenetic shift in habitat use and behavior, shifting from a solitary existence in vegetation cover to gregariously sheltering in crevices at about 25 mm carapace length (CL) (Childress and Herrnkind, 1994, 1996). Sub-adults greater than size 45 mm CL and age 1.5 yr are more active and can migrate considerable distances during nightly foraging bouts (Kanciruk, 1980). Near the onset of sexual maturity, lobsters begin to migrate to offshore reefs where mating occurs, thus completing the life cycle (Lyons et al., 1981; Gregory et al., 1982; Hunt and Lyons, 1986).

This species is commercially exploited throughout its range, and one possible consequence of heavy fishing is that natural density-dependent pressures on adult populations has declined with a commensurate increase in importance of larval and early juvenile dynamics on the species' demographics. For example, an estimated 90% of all fishery-sized lobsters are taken in Florida each fishing season but the yield has remained relatively stable over the past decade (Hunt, 1994). This suggests that larval input to this system is very high and stable at a level which supports this population size, especially since mortality on young juveniles is believed to be very high, about 99 percent of settlers per month (Forcucci et al., 1994; Butler and Herrnkind, in press). While female spiny lobsters are highly fecund (Gregory et al., 1982; Hunt and Lyons, 1986), it is unlikely that the Florida population is self-supplying, given the magnitude of larval recruitment (Little, 1977; Little and Milano, 1980), genetic homogeneity in populations throughout the Caribbean (Silberman et al., 1994), and local oceanic features (see Lyons, 1980). Larval supply and the factors influencing it are clearly key to understanding recruitment of this species.

Throughout the Caribbean basin, spiny lobsters are confined to shallow coastal shelves, banks and reefs, so the links between populations are the larval and postlarval stages. The factors influencing the supply of larvae to nearshore nurseries and impacting settlement success of new recruits to benthic populations are not fully understood. For this dissertation, I studied several aspects of the ecology and early life history of the Caribbean spiny lobster *Panulirus argus*. In Chapter One, I describe the temporal patterns in postlarval supply to the Florida Keys, USA, over an eight year period and its association with wind forcing that potentially affects the transport of larvae in surface waters. I discuss, in Chapter Two, possible adaptative strategies used by postlarvae which may reduce the impact of predation during the recruitment period in south Florida. I measured predation on postlarvae in the water column and in benthic habitats under several different conditions in the laboratory and field in order to better understand the adaptive value of strategies used by postlarvae to avoid predators. In Chapter Three, I documented the dynamics of juvenile lobsters using mangrove habitat to compare this habitat as an alternative nursery to the macroalgal-dominated hardbottom system of Florida Bay. I describe population structure, habitat use and survival of juveniles in the coastal environment of Belize. Variation in postlarval supply, postlarval mortality due to habitat-specific predation, and characteristics of available habitat may influence changes in local benthic populations.

CHAPTER II

TEMPORAL PATTERNS AND TRANSPORT PROCESSES IN RECRUITMENT OF SPINY LOBSTER, *PANULIRUS ARGUS*, POSTLARVAE TO SOUTH FLORIDA.

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). Due to interactions between these factors, predicting the interannual variability in 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 habitat 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, whereas distinctly 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, 1981; Yeung and McGowan, 1991), along with evidence of genetic homogeneity among Caribbean lobster 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), spring in Jamaica (Young, 1991), and 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).

I analyzed an eight-year time series of *Panulirus argus* postlarval supply to the Florida Keys to discern whether temporal patterns exist. I also investigated 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 in surface waters. I discuss these findings in relation to existing hypotheses on local oceanic circulation and on reproductive dynamics of *P. argus* in the region.

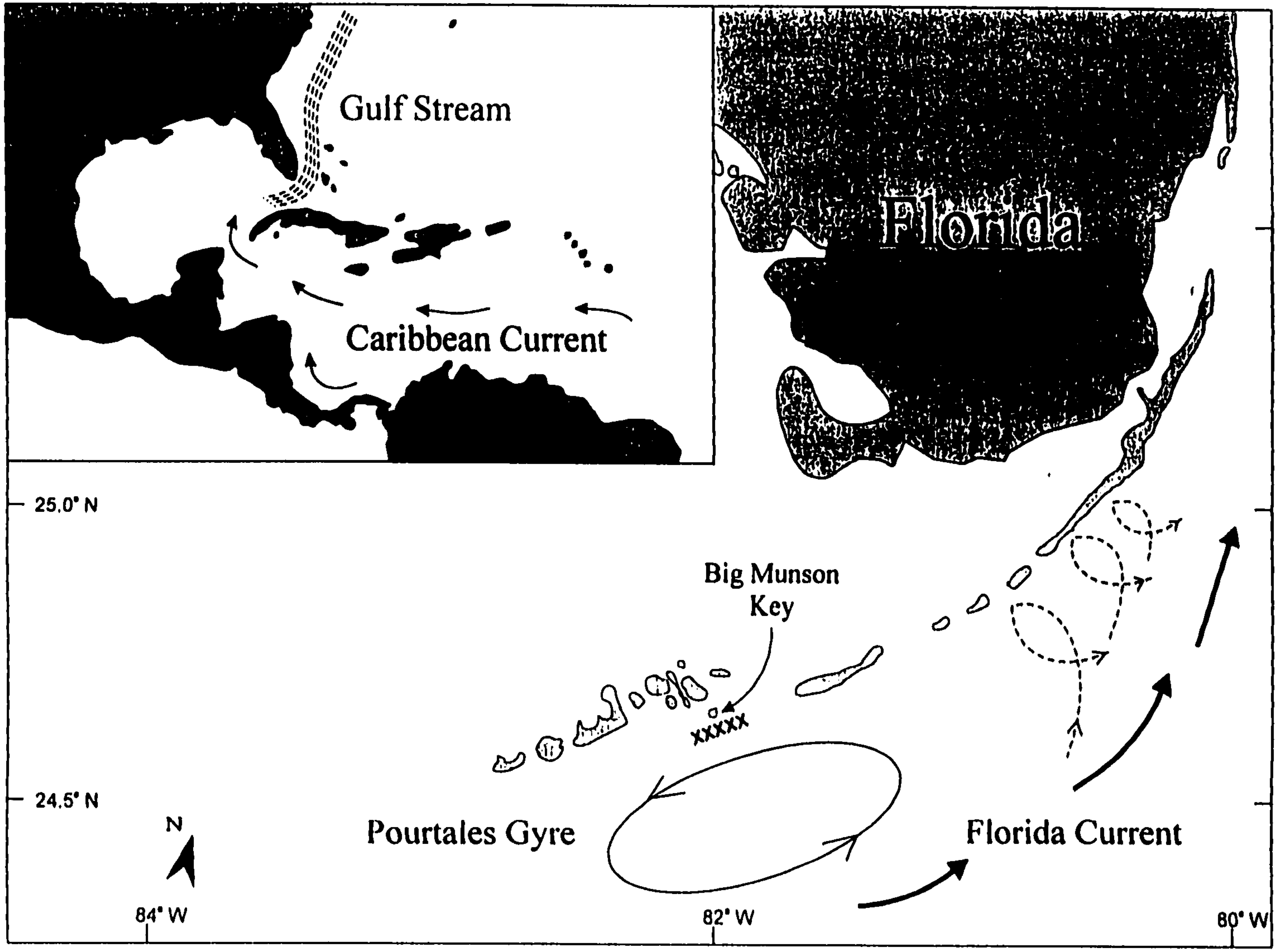
Methods

Temporal patterns

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 on-going 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, USA (Fig. 1). Postlarvae on each collector were counted weekly from 1987 to 1992 and monthly 7 d following new moon from 1992 to 1995. The number of postlarvae/sample was log-transformed to stabilize the variance. I used time series analysis to describe temporal patterns in postlarval influx over the eight year period. Inspection of autocorrelation plots indicated that the data contained autocorrelations that were stationary, i.e. no systematic 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 ±

Fig. 2.1 Map of the Caribbean Sea (inset) showing major currents. Boxed area is expanded to show south Florida region with the Pourtales Gyre and the Florida Current. Postlarval collectors were stationed near Big Munson Key in the lower Florida Keys.


Gulf Stream
Caribbean Current
Florida
25.0° N
24.5° N
Big Munson Key
XXXXX
Pourtales Gyre
Florida Current
N
84° W
82° W
80° W

$2/\sqrt{n}$. I 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, I constructed a bivariate time series using weekly postlarval abundance and a monthly lunar cycle (a 4-point sine curve) and used a 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, I 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 periodicity, 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, I 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 d and 7 d periods prior to the dates of postlarval collection (two separate analyses). I selected a 10 d window of postlarval supply following new moon because the time series analyses on weekly data showed that peak influx occurs during this period (see Results - Temporal Patterns). The 4 d 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 3-4 d and 5-12 d (Pitts, 1994). I removed autocorrelations and periodicities from the postlarval supply 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' (1976) 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, USA). Hourly wind speed and direction measurements were vectorially summed for 24 h periods and averaged for either 4 consecutive days or 7 alternate days prior to date of postlarval collections. These data were inspected for autocorrelations 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.

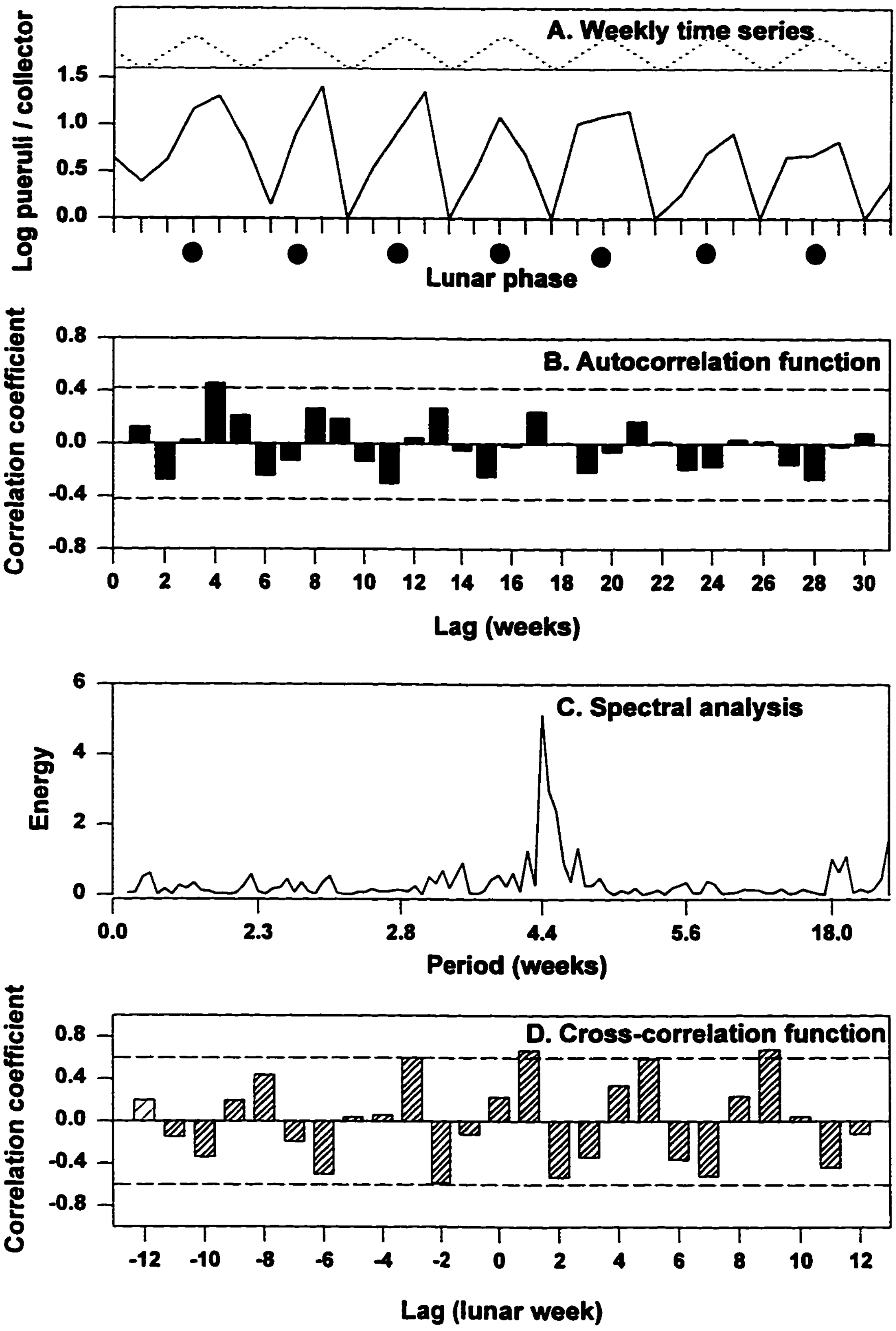
The relationship between centered residuals (i.e., mean removed) of the postlarval time series from the ARIMA model and the decomposed wind data were analyzed using the complex vector-scalar correlation (Kundu, 1976; Johnson & Hester, 1989). This analysis determines the correlation magnitude (R) between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

Results

Temporal patterns

A lunar periodicity in weekly postlarval supply was well defined (Fig. 2A). The autocorrelation function indicates characteristic cycling at two to four week intervals, and a monthly cycle is evident (Fig. 2B). Spectral analysis shows that most energy in the weekly data was concentrated at about 4.5 weeks (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

Fig. 2.2. Time series analysis on supply of spiny lobster postlarvae during the lunar cycle. A. Time series of postlarval supply from June 1987 to June 1992; the dashed line represents the lunar cycle and the dark circles indicate new moon. B. Autocorrelation function with lags in weeks showing significant cycling during the lunar month; dashed lines represent 95% confidence intervals (CI). C. Spectral analysis showing a periodicity of 4.5 weeks; note the non-linear scale on abscissa. D. Cross-correlation analysis on weekly postlarval supply and the lunar cycle showing peak activity at new moon; dashed lines represent 95% CI.


A. Weekly time series
Log pueruli / collector
1.5
1.0
0.5
0.0
Lunar phase
B. Autocorrelation function
Correlation coefficient
0.8
0.4
0.0
-0.4
-0.8
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Lag (weeks)
C. Spectral analysis
Energy
6
4
2
0
0.0
2.3
2.8
4.4
5.6
18.0
Period (weeks)
D. Cross-correlation function
Correlation coefficient
0.8
0.4
0.0
-0.4
-0.8
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
12
Lag (lunar week)

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 patterns exist. 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 the 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 below). 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 (see Fig. 2B), I 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. I then plotted the new correlogram and periodogram. The autocorrelation function shows significant cycling at 5 mo lags which indicates that the secondary peak is real (Fig. 4A), and the new spectral shape shows a dominant periodicity at 5-mo intervals (Fig. 4B).

Fig. 2.3. Time series analysis on annual supply of spiny lobster postlarvae. A. Time series of postlarval supply from June 1987 to June 1995; the dashed lines shows an annual cycle for reference. B. Autocorrelation function with lags in months showing significant annual cycling; dashed lines represent 95% confidence intervals. C. Spectral analysis showing major periodicity at 12 mo and a lesser one at 5 mo; note the non-linear scale on abscissa. D. Cross-correlation analysis on monthly postlarval supply and an annual cycle with peak activity in March; dashed lines represent 95% confidence intervals.

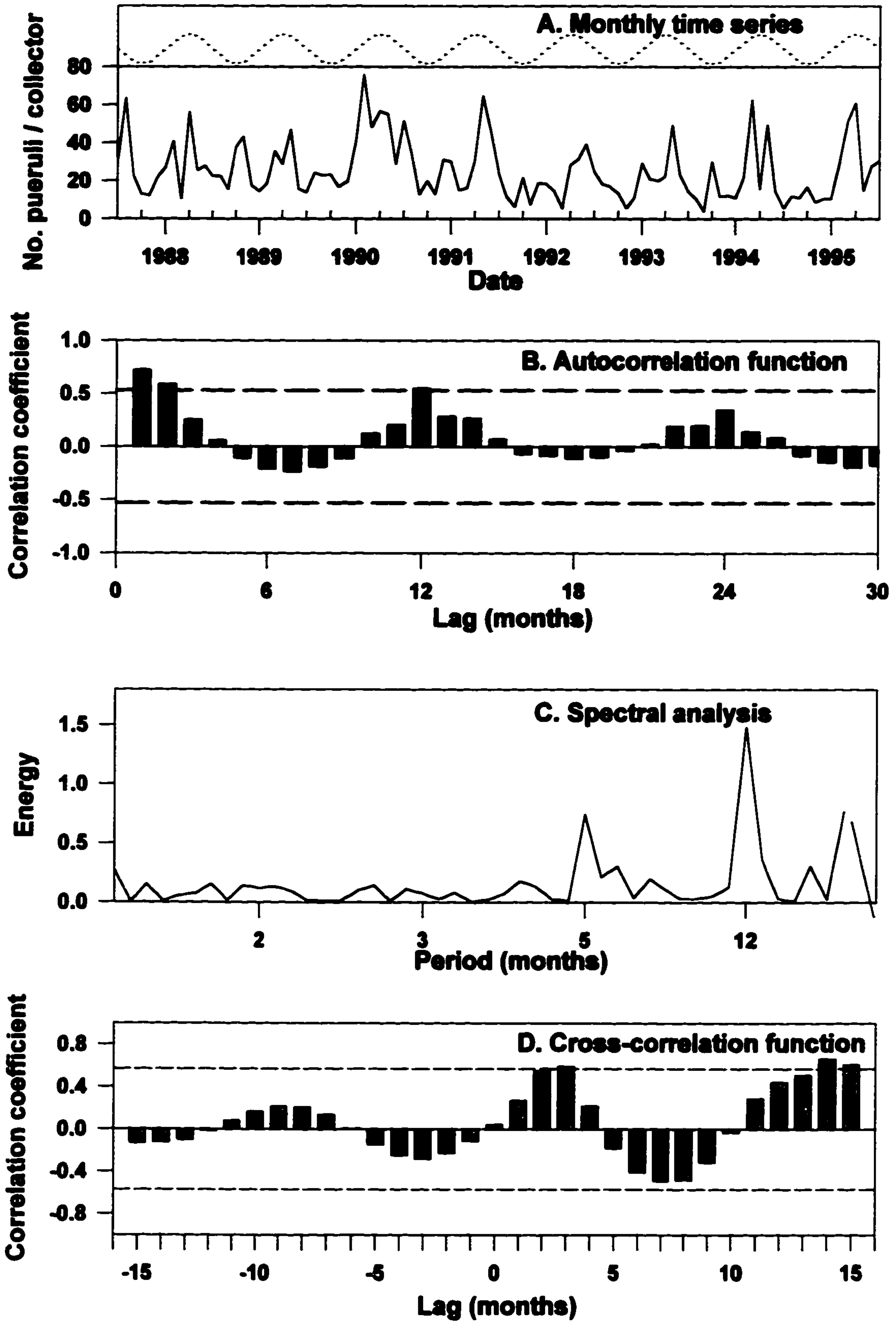
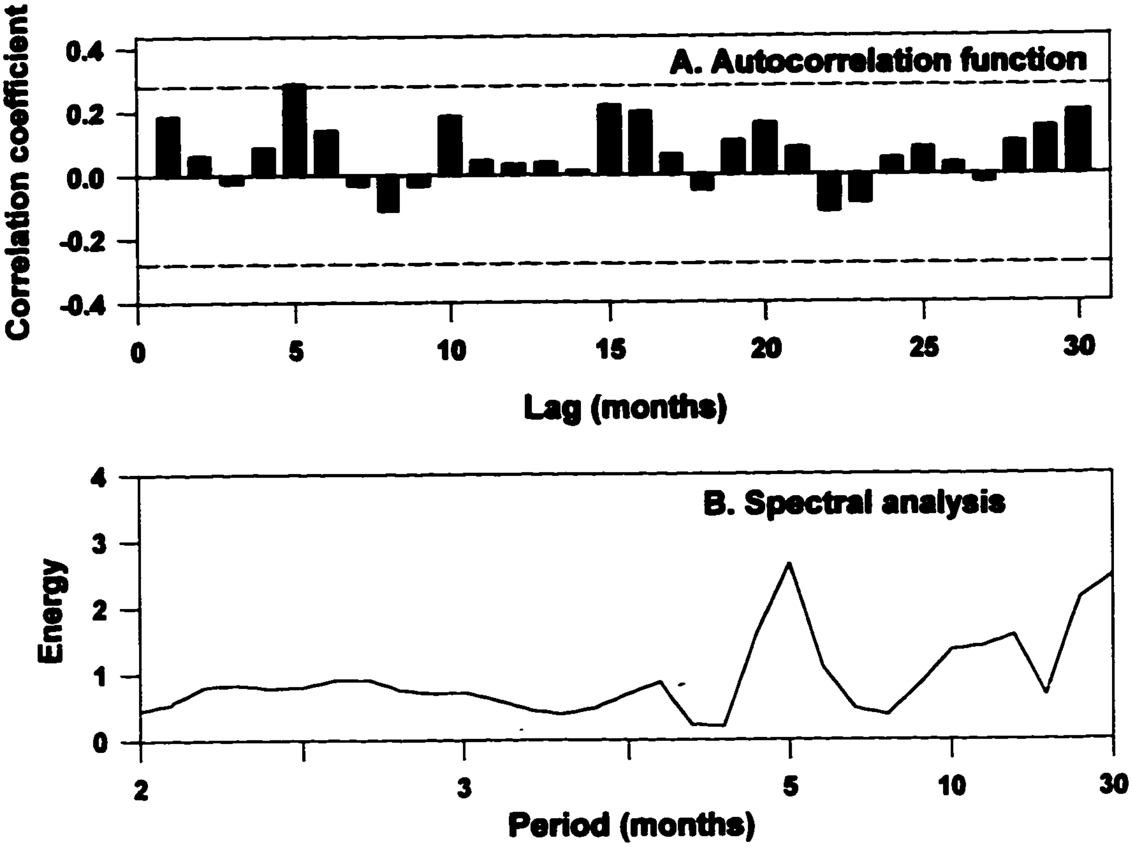

A. Monthly time series
No. puerulli / collector
80
60
40
20
0
1988
1989
1990
1991
1992
1993
1994
1995
Date
B. Autocorrelation function
Correlation coefficient
1.0
0.5
0.0
-0.5
-1.0
0
6
12
18
24
30
Lag (months)
C. Spectral analysis
Energy
1.5
1.0
0.5
0.0
2
3
5
12
Period (months)
D. Cross-correlation function
Correlation coefficient
0.8
0.4
0.0
-0.4
-0.8
-15
-10
-5
0
5
10
15
Lag (months)

Fig. 2.4. Time series analysis on annual postlarval supply to the Florida Keys after the 12-mo periodicity was removed using a Parzen filter. A. Autocorrelation function showing significant cycling activity at 5 mo; dashed lines represent 95% confidence intervals. B. Spectral analysis showing concentration of variance with a 5 mo periodicity.


A. Autocorrelation function
Correlation coefficient
0.4
0.2
0.0
-0.2
-0.4
0
5
10
15
20
25
30
Lag (months)
B. Spectral analysis
Energy
4
3
2
1
0
2
3
5
10
30
Period (months)

Transport due to wind forcing

The ARIMA model fitted to the postlarval data employed a first-order autoregression which accounted for all periodicities (χ^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 winds from the east (φ = 80°). The correlation between postlarval supply and the 4 d wind forcing period was not significant (R = 0.18, P = 0.10).

I 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-April (winter) was stronger than that of the annual time 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 (φ = 39° for 7d ; 57° for 4 d). The May-October ('summer') correlations were not significant.

Discussion

The supply of spiny lobster pueruli to nearshore settlement habitat occurs during the dark moon phase of new moon in several palinurid species (Herrnkind et al., 1994). The analysis on four years of weekly collections of *Panulirus argus* postlarvae in the

Florida Keys confirms that peak supply occurs at intervals of 4.5 weeks, 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 I have confirmed this in field and mesocosm experiments (see Chapter III). However, it is 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, the analysis of monthly postlarval supply over eight years indicates that there is 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-month periodicity in this 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 *P. argus* at the northern limits of their geographic distribution (e.g., Florida) spawn in the spring and early summer (April - 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-June peak in spawning activity in the northern Caribbean, which supports the hypothesis that the planktonic larval phase is 9-10 months 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 - 12 month larval duration (see Lyons, 1980).

The five-month periodicity in postlarval supply remains unexplained. I 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 (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 months and evolves into the Pourtales Gyre which lasts for about 1 to 2 months. 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 month 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, 1981; Yeung and McGowan, 1991) and nearshore waters (Little, 1977; Little and Milano, 1980; Heatwole et al., 1982) as well as direct behavioral observations (Calinski and Lyons, 1983) indicate that pueruli utilize surface waters (0 - 2 m) during inshore migration. Thus, wind movement of surface waters may have a great impact on larval supply to nearshore habitats. 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). I 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 Ekman transport of surface waters. Although there was a significant correlation ($R = 0.32 - 0.34$) between postlarval supply and wind forcing from the northeast ($\varphi = 39° - 57°$) 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 left unexplained.

While larval supply to nearshore environments has been strongly 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. The supply of postlarvae to south Florida is 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. Variation in spawning activity which affect monthly larval abundance and fluctuations in 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 larval recruitment to this region.

CHAPTER III

ADAPTIVE STRATEGIES OF SPINY LOBSTER, *PANULIRUS ARGUS*, POSTLARVAE TO REDUCE PREDATION RISK DURING RECRUITMENT.

Introduction

The role of predation in shaping life history strategies is a central tenet in ecology and evolution. In aquatic systems, predation influences population dynamics (Connell, 1961; Caswell, 1978; Watanabe, 1984; Mattingly and Butler, 1994; Reznick et al., 1996) and community structure (Paine, 1974; Butler, 1989; Navarette, 1996) in direct and indirect ways. Predation has been attributed as being a major cause of recruitment variability in marine populations, especially during influx of pelagic larvae (Shulman, 1985). Most marine organisms have pelagic larval stages which function in dispersal, colonization, and gene flow but which generally experience high mortality (Thorson, 1950). However, the degree to which predation controls the magnitude of larval recruitment to adult populations is still largely unknown (Morgan, 1995). While mechanisms such as unfavorable transport and starvation act on specific stages in the life cycle, predation acts on all stages and may be amplified in larval recruits swimming in the water column and seeking benthic settlement habitat.

In response to predation pressure, aquatic prey have evolved strategies to avoid detection, capture, and contact with predators that involve both morphological and behavioral traits. Crypsis is an important morphological adaptation that serves to reduce detection by predators, and in aquatic systems, this can be accomplished via transparent bodies (e.g., many pelagic larvae and zooplankton) or camouflage coloration (e.g., benthic stages) (see reviews by Sih, 1987 and Morgan, 1995). Diel vertical migrations by zooplankton (Hobson and Chess, 1976; Zaret and Suffern, 1976), horizontal migration by larvae to water masses with low predator density (Bailey and Houde, 1989), and reduced or restricted activity in the presence of predators (Stein and Magnuson, 1976; Mittelbach and Chesson, 1987) are known behavioral mechanisms that also reduce the probability of prey contact with predators.

Quantifying the severity of predation under different field conditions and in different habitats and empirically testing the effectiveness of anti-predator traits under these disparate situations is necessary for understanding the adaptive value of prey behavior or morphology. Yet, few studies have directly quantified the impact of predators on larvae in the field, due to the inherent logistical difficulties in quantifying such events. Lebour (1922, 1923) conducted some of the earliest laboratory experiments on aquatic predator-prey interactions and related her results to natural predator and zooplankton prey interactions. Since then, others have shown that pelagic predators (Huntley and Hobson, 1978; Rumrill et al., 1985; Olson and McPherson, 1987; Young and Chia, 1987) and benthic predators (Cowden et al., 1984; Seben and Koehl, 1984; Young and Chia, 1987) have profound impacts on recruitment of larvae. In many studies, the impact of predation on recruitment variability was inferred from predator stomach contents (e.g., Randall, 1967; Theilacker et al., 1986; Bailey et al., 1993) or changes in the distribution and abundance of predators and potential prey . For example, concentrations of planktivorous fishes at offshore coral reefs (Randall, 1967; Emery, 1973; Hobson and Chess, 1978; Kingsford and MacDiarmid, 1988) and kelp forests (Hobson and Chess, 1976; Gaines and

Roughgarden, 1987) are often negatively associated with the magnitude of larval recruitment to nearshore benthic populations. In only a few cases has predation on marine larvae been carefully studied *in situ*, and in such a manner, that suspected anti-predator adaptations of prey could be directly tested. Direct quantification of predation on ascidian tadpole larvae was accomplished by visual tracking during the larvae's brief pelagic phase from hatching to settlement (Olson and McPherson, 1987).

The postlarvae of tropical spiny lobsters exhibit a suite of behavioral and morphological characteristics, shared with other species with meroplanktonic larvae, and these traits are presumed to have evolved in response to predation by pelagic predators. Palinurid lobsters have a complex life history with a protracted larval phase lasting up to a year; the larvae metamorphose into non-feeding puerulus postlarvae near the continental shelf break (Johnson, 1960; Phillips and Sastry, 1980). Postlarvae of the Caribbean spiny lobster *Panulirus argus* are advected from the Gulf Stream to nearshore habitats in the Florida Keys on rising tides following the new moon phase (Acosta et al., in press). The solitary postlarvae swim in surface waters during influx to coastal settlement habitats, and they display negative phototaxis and become motionless and sink in the presence of strong light (Calinski and Lyons, 1981). During inshore migration, postlarvae must traverse offshore coral patch reefs and other environments to find suitable vegetated habitats nearshore in which to settle. During the pelagic phase, postlarvae are transparent, but they develop cryptic coloration within days of settling in vegetated habitats (Herrnkind and Butler, 1986; Butler and Herrnkind, 1991).

The crucial elements of the postlarval recruitment process, with respect to the evolution of anti-predator traits, are that the postlarvae: 1) are transparent, 2) are solitary,

3) recruit from offshore to the nearshore coastal nursery for only a few days each lunar cycle on rising tides around new moon, 4) use the surface water layer during influx, and 5) develop cryptic coloration shortly after locating suitable settlement habitat. These features of their ecology permit the postlarvae to capitalize on the tidal transport because the strength of tidal currents is maximal during the new and full moon phases. These characteristics may also minimize their risk of mortality by visual pelagic predators because lobster postlarvae are transparent and active only at night during the darkest lunar phase. If predators are concentrated in discrete areas (habitats) along the transport path taken by postlarvae (e.g., offshore kelp forests and reefs; Gaines and Roughgarden, 1987; Kingsford and MacDiarmid, 1988), then rapid transport past these areas also reduces the period of possible encounters with predators. Additionally, postlarval settlers in benthic habitats may reduce detection by predators by developing cryptic coloration soon after settlement. Settlement in habitats where camoflage is maximally effective may indicate the adaptive value of choosing that habitat as a potential nursery.

To understand the role of predation in shaping the behavior of spiny lobster postlarvae during recruitment, I compared predation on postlarvae in the water column and in benthic habitats along a typical transport path, and determined whether predation rates differed between lunar periods (new moon vs. full moon) and with prey density (i.e., predator encounter rates). I measured predation on transparent postlarvae floating at two depths in the water column at night over coral reefs, the coastal lagoon, and in the shallow bay leeward of islands which appears to function as a primary nursery. I also measured predation on transparent and pigmented (settler) postlarvae sheltering in coral reefs, seagrass beds and macroalgal benthic habitats during the day. I hypothesize that: 1) postlarvae swimming in the water column at night experience differential predation over different coastal zones from offshore coral reef to the bay due to differences in resident predator assemblages, 2) postlarvae use surface waters for rapid transport past predator assemblages, 3) shallow macroalgal stands in Florida Bay provide a higher degree of protection from predators than coral reefs, or seagrass and macroalgae in the coastal lagoon, and 4) pigmented settlers experience lower levels of predation in benthic habitats than transparent postlarvae due to cryptic coloration.

To assess the adaptive significance of the new moon timing used by postlarvae during their coastal influx, I measured predation on pelagic postlarvae during new moon and full moon in the field and in laboratory mesocosms. The laboratory studies also permitted me to test the effect of different postlarval densities, thus predator-prey encounter rates, on predation - as might occur if predators are concentrated in certain areas. I hypothesize that: 1) pelagic predators that rely upon vision are less effective during the darkest phase of the moon, and 2) predation rates increase due to a concentration effect of prey. These experiments are designed to determine which traits or strategies are directly responsible for alleviating predation pressures encountered by postlarvae during recruitment.

Methods

Pelagic predation along an offshore-inshore transport path

To measure predation on postlarvae in the water column at night along typical transport paths, I conducted field experiments using spiny lobster postlarvae tethered to floating arrays. Experiments were conducted during the summers of 1994, 1995, and 1996 in the middle Florida Keys over representative coastal zones (Fig. 1). The floating arrays traversed one of three habitat treatments (coral reef, coastal lagoon, and bay), and postlarvae were tethered at each of two depths in the water column (near surface and near bottom). During new moon, floating arrays drifted over: 1) coral patch reefs (depth 3 - 6 m) at East Turtle Shoal (24°43.185N, 80°56.066W) and Tennessee Reef (24°45.353N, 80°46.142W), 2) seagrass and sand bottom in Hawk Channel lagoon (depth 5 - 8 m) (24°44.476N, 80°55.061W and 24°45.251N, 80°46.208W), and 3) seagrass and hardbottom in Florida Bay (depth 2 -3 m) near Long Key bridge (24°47.711N, 80°52.292W) and Channel 5 bridge (24°45.301N, 80°46.191W).

Using 1 m diameter 750 um plankton nets, I first collected transparent postlarvae from the plankton passing through inlets to Florida Bay on new moon flood tides (see Herrnkind and Butler, 1994). Postlarvae were then tethered to a floating array made from 3 m lengths of thin-walled polyvinylchloride (PVC) pipes with several 10 cm diameter styrofoam bouys attached (Fig. 2). Animals were tethered with a 20 cm length of nylon thread secured to the carapace by a small drop of gel cyanoacrylate glue. The thread was attached to a length of 6-lb test, lead-weighted monofilament line tied to the floating array. The thin thread permitted free movement of the tethered postlarva while the weighted monofilament line restricted the animal to a specified depth. Each floating array held 3 tethering lines with postlarvae tethered near the surface treatment (0.5 m depth) and 3 lines with postlarvae tethered near the bottom (3 m depth for reef and lagoon; 1.5 m for bay). Lobsters were tethered at least 0.5 m apart, and none became tangled in any of the experiments. A 2-m length of line with a fluourescent glowstick set in a cylindrical shroud (to minimize light transmission to the water below) and attached to one end of the

Fig. 3.1. Map of the Caribbean region (inset) with the Florida Keys shown expanded. The pelagic and benthic predation experiments were conducted in the middle Keys along postlarval transport paths shown approximated by the arrows. Coastal zones along the paths include reef tracts (stipled), Hawk Channel coastal lagoon, and Florida Bay.

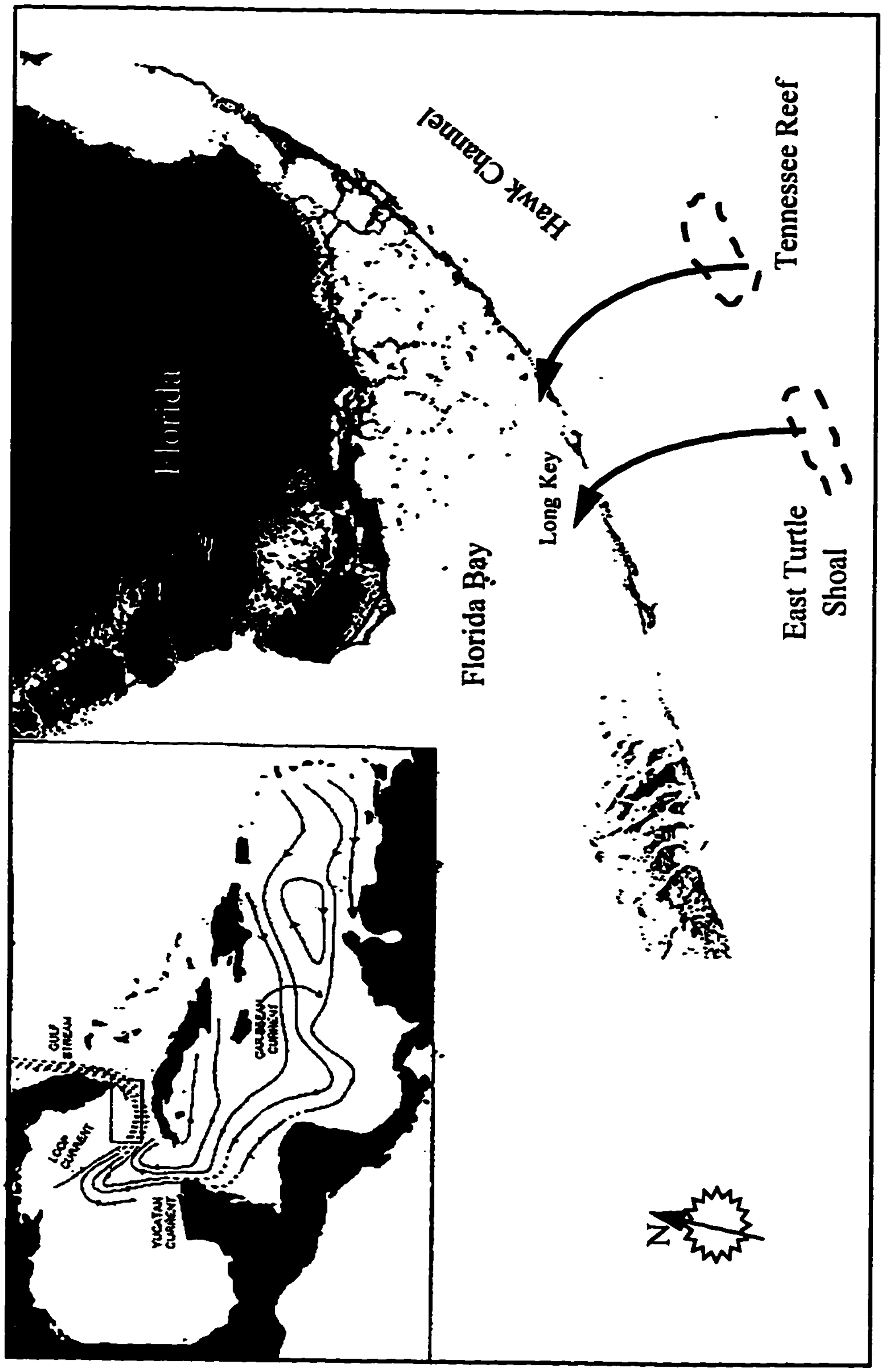
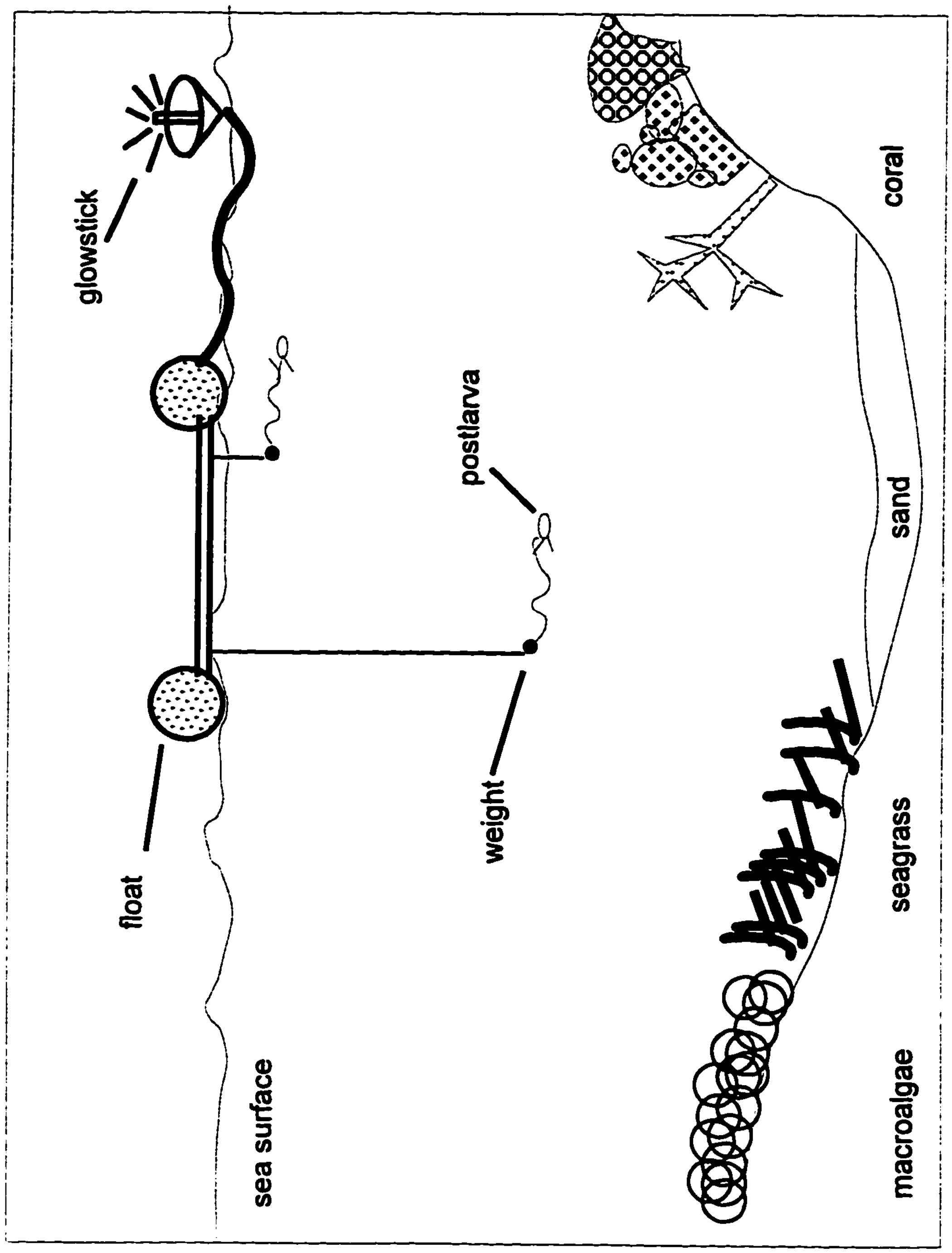

Florida
Hawk Channel
Tennessee Reef
Long Key
East Turtle Shoal
Florida Bay
N
GULF STREAM
LOOP CURRENT
CARIBBEAN CURRENT
YUCATAN CURRENT

Fig. 3.2. The floating tether array for measuring predation on postlarvae over a typical offshore-inshore transport path.


glowstick
float
sea surface
postlarva
weight
coral
sand
seagrass
macroalgae

floating array served as a “beacon” to permit nighttime relocation of the arrays.

The general procedure was to release the floating arrays from a vessel at night at a specified location along the offshore-inshore transport path. After releasing the floating arrays, the vessel was moved approximately 50 m away, and both the floating arrays and vessel drifted along separately in the current. Results of preliminary trials indicated that a 0.5 h period allowed sufficient time for a measureable predation response in a specified habitat. Points of release and retrieval of floating arrays were marked using GPS coordinates, and the transects were checked during subsequent days to ensure that the float traveled over the intended treatment habitats (i.e., reef, coastal lagoon, and bay). During release and retrieval of floats, I worked with hand-held flashlights, having extinguished boat lights to minimize attracting fish predators. Experiments were conducted on relatively calm nights (winds < 10 nm h^{-1}) to minimize accidental killing of lobsters on tethers during vertical displacement by wave action. Once the floating arrays were recovered, I scored each individual postlarvae as being alive or eaten as evidenced by fragment of carapace on the tether. Postlarval lobsters were used only once in experiments.

The possibility of confounding, among-treatment experimental artifacts in the tethering technique has been raised (Peterson and Black, 1994; Aronson and Heck, 1995). I conducted preliminary trials and behavioral observations to look for possible experimental bias. Lobsters on floating arrays did not become entangled and could move freely on the ends of the nylon thread, and there was no evidence that behavior of the tethered animal increases predation rates. I tested for statistical independence among lobsters on a floating array and between arrays graphically by inspecting the spread of residuals of proportional mortality (see Appendix A) and detected no confounding effects. I then inspected the data for homogeneity of replicates from equivalent habitats (coral reefs, coastal lagoon, or bay) in 2 x 2 contingency tables using a G^2 statistic (Zar, 1984). The data from equivalent habitats were homogenous so those data were pooled and then analyzed using a log-linear model for a multidimensional contingency table to model patterns of independence with habitat, depth in water column, and predation outcome as variables (Stokes et al., 1995). If there were no significant interactions between treatments, the model was reduced until differences in predation were detected. I then constructed orthogonal contrasts to detect differences within treatment levels.

Benthic predation along an offshore-inshore transport path

To compare predation on transparent and pigmented postlarvae sheltering in benthic habitats during the day, I conducted dawn-to-dusk tethering experiments in representative habitats along typical transport paths. Experiments were conducted in coral reefs at East Turtle Shoal and Tennessee Reef (depth 3 - 6 m), in seagrass and macroalgal beds (depth 1 - 2 m) in the Hawk Channel lagoon near Long Key (24°45.981N, 80°53.637W) and Conch Key (24°46.782N, 80°53.640W), and in seagrass and macroalgal beds (depth 1 - 2 m) in Florida Bay at Long Key (24°45.978N, 80°57.349W) and Grassy Key (24°44.070N, 80°58.615W). Postlarval lobsters were tethered on 0.5 m lengths of nylon thread secured to the carapace by a drop of gel cyanoacrylate glue, and the thread was tied to a metal spike which was driven into the substrate at least one meter apart along an unmarked transect. I placed animals in the habitat (ensuring that they were hidden in shelters) at dawn and checked for survivors at dusk. Individual lobsters were used only once.

To minimize treatment bias, I again conducted preliminary trials and behavioral observations on tethered lobsters to evaluate the risk of treatment bias (see also Butler et al., in press). Predation on lobsters placed at least one meter apart on the substrate appear to be random and independent events. Behavioral observations revealed that tethered postlarvae hidden in vegetation or coral crevices are quiescent, probably in an attempt to be cryptic as is their normal behavior in these habitats. I tested for statistical independence as stated above. Data were analyzed similar to the procedures listed in Pelagic Predation Along An Offshore-Inshore Transport Path (above). The incidence of predation was found to be homogenous within location and habitats (coral reef, coastal lagoon seagrass, coastal lagoon macroalgae, bay seagrass, and bay macroalgae) and these data were then pooled. A hierarchical log-linear model for a multidimensional contingency table was used with habitat, location, and predation outcome as variables nested within lobster pigment stage (transparent or pigmented).

Effect of prey density and light level on predation

The effect of new moon and full moon light levels on postlarval mortality were tested both in the field and in laboratory mesocosms. Prey density effects were only tested in the mesocosms. For the full moon experiments, I used only the habitat/depth treatment combinations from the new moon studies with the highest and lowest incidence of mortality. That is, I only compared predation during new and full moon for two habitat/depths: reef near the bottom and bay near the surface. Large numbers of postlarvae can only be caught around the new moon period during peak influx. Therefore, to conduct the full moon experiments with transparent postlarvae, I captured postlarvae during the new moon and held them in darkened aquaria in water chilled to 21 °C (which retarded pigmentation) for about 10 days until full moon. Only lobsters that were transparent at full moon were used.

Experiments in laboratory mesocosms permitted measurement of predation on postlarvae under different moonlight levels and prey densities. The mesocosms were 3m-diameter x 1m-deep circular tanks with flow-through seawater dispersed to create a gentle circular flow in the tanks. De Lafontaine and Leggett (1987) found that tank sizes of $3m^3$ and larger are necessary for reducing edge effects and other artifacts in predation experiments on larvae and zooplankton and their predators. A ubiquitous plankton-feeding, crepuscular-nocturnal predatory fish (yellowtail snapper *Ocyurus chrysurus*) was acclimated in each mesocosm at least 12 h prior to start of the experiment. These fish were held in captivity in another tank for at least two weeks and were not fed for 24 h prior to use in experiments. Following the predator acclimation period, lobster postlarvae were introduced to mesocosms at 2200 h each night, and the experiment ended at 2400 h. Preliminary trials revealed that 2 h was adequate to detect predation on postlarvae, if it occurred. At the end of each trial, the fish were captured with a dip net and removed from each tank. The tanks were then drained and all surviving postlarvae were collected and counted; I conducted six replicate no-predator controls to ensure that all lobsters were recaptured by this method. Video observations revealed that postlarvae swam actively when placed in mesocosms under experimental light conditions. Individual postlarvae and fish were used only once.

The experiment was designed as a two-factor (prey density and light level), crossed design with two prey density treatments (low density with 3 postlarvae and high density with 12 postlarvae) and two light level treatments (simulating full moon and new moon). Full moon light levels were simulated with using artificial lighting in the laboratory and new moon was simulated by covering tanks with a tarpaulin. Light level was measured using a hand-held Luna Pro Gossen light meter. The artificial full moon light intensity was 0.30 lx compared to natural full moon intensity of 0.28 lx, and new moon light intensity was 0.02 lx compared to natural new moon light of 0.03 lx at the water surface at East Turtle Shoal reef. I conducted 9 replicates for each density/light level treatment. The appropriate response variable for this study is thus the proportion of mortality of postlarvae/tank (arcsine square root transformed). The assumptions of normality and variance homoscedasticity were met, and a two-factor analysis of variance (ANOVA) was conducted on the results. A Bonferroni multiple comparison procedure was used to test for differences among treatment groups.

Results

Pelagic predation along an offshore-inshore transport path

Estimates of relative predation on spiny lobster postlarvae by pelagic predators over a typical transport path from offshore to nearshore during new moon supported our general hypothesis of differential habitat-specific predation during recruitment. Predation on spiny lobster postlarvae in the water column decreased over the coastal zone transect from the reef to the bay (Fig. 3). Postlarval mortality was significantly higher over the reef than the coastal lagoon or bay, near the surface ($G^2 = 8.98$, $P < 0.01$) and near the bottom ($G^2 = 14.13$, $P < 0.0001$). Total mortality in the coastal lagoon and bay did not differ. Among the depth treatments, mortality was significantly lower near the surface in the bay than at any other depth along the transport path ($G^2 = 14.13$, $P < 0.001$). At least some of the predation in the coastal lagoon was by clupeid fish since I recovered one tethered postlarvae from the mouth of a clupeid ensnared by the operculum on the tether line. These results demonstrate that predation on spiny lobster postlarvae entering the coastal waters of the Florida Keys is higher near the bottom and over coral reefs than in other areas where they are transported.

Benthic predation along an offshore-inshore transport path

I measured relative predation on postlarvae by benthic-feeding predators in representative habitats along a transport path from the reef to the bay during daytime. The location effect on mortality was similar to that seen in the pelagic transects (above). There was no difference between predation in bay and coastal lagoon habitats, but predation was higher on the coral reef for both transparent ($G^2 = 3.97$, $P < 0.05$) and pigmented ($G^2 = 13.28$, $P < 0.001$) postlarvae (Fig. 4). There was no marked difference in predation on transparent and pigmented postlarvae among any single habitat (coral rubble, seagrass, macroalgae), except for a marginally higher mortality of transparent postlarvae in seagrass in the coastal lagoon ($G^2 = 3.57$, $P = 0.05$). These results do not support the hypothesis that rapid pigmentation following settlement confers any advantage for reducing predation on postlarvae in these benthic habitats.

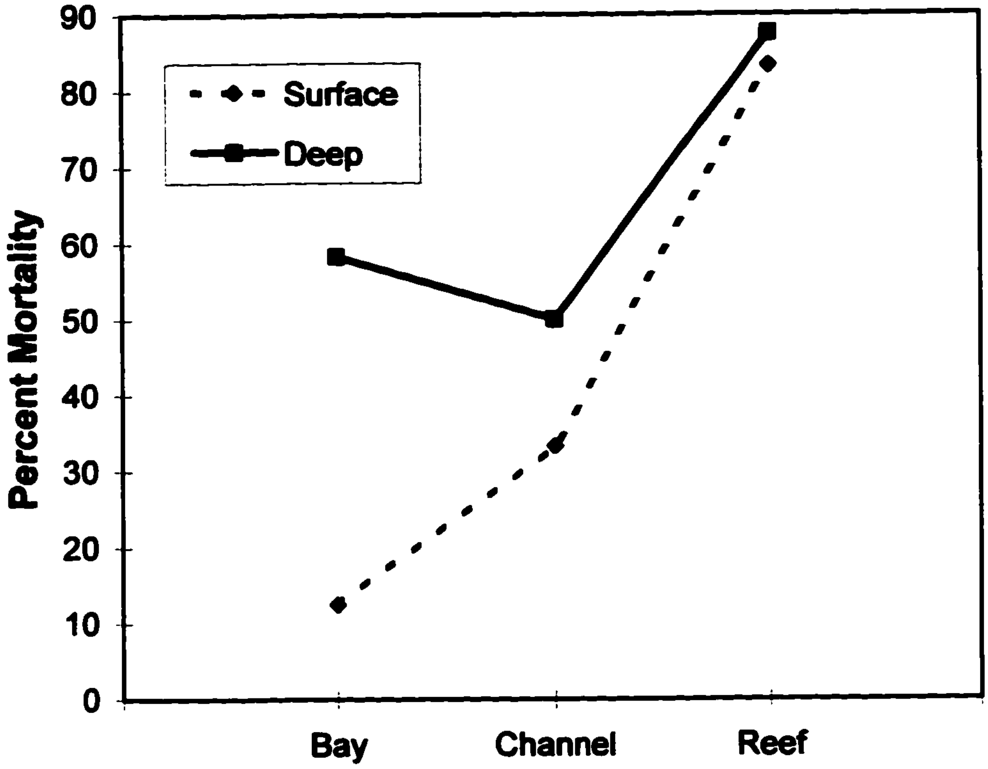


Fig. 3.3. Percent mortality of spiny lobster postlarvae drifting in the water column at night near the surface or near the bottom during new moon over three coastal zones.

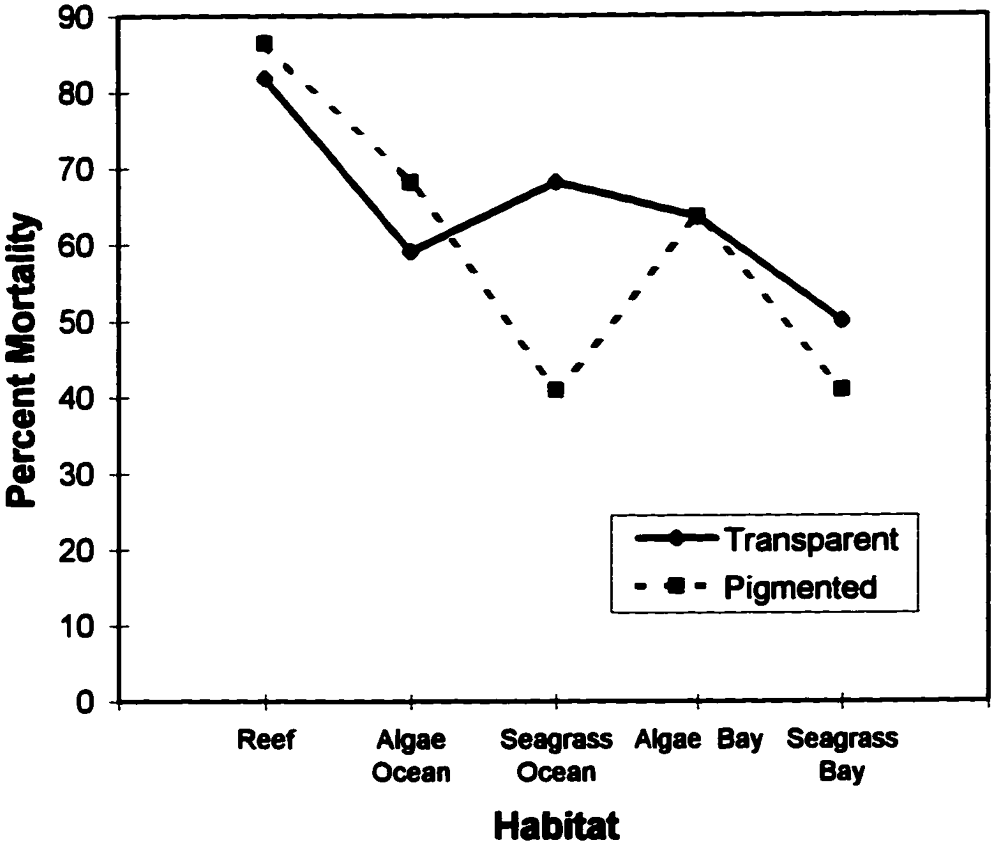


Fig. 3.4. Percent mortality of transparent and pigmented spiny lobster postlarvae tethered on the bottom in benthic habitats along a typical transport path.

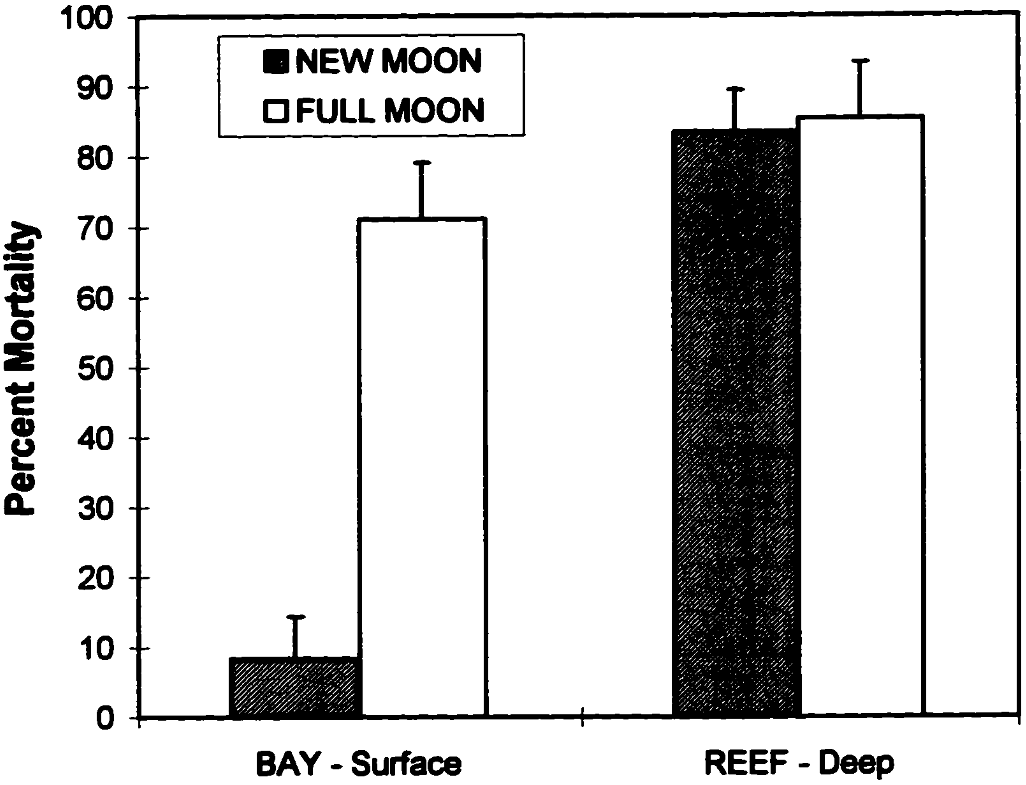


Fig. 3.5. Percent mortality of spiny lobster postlarvae floating at the depth and location of highest (reef near bottom) and lowest (bay near surface) predation during new moon versus that during full moon. Bars are standard errors of floating arrays.

Effect of prey density and light level on predation

In the field, the mortality of postlarvae tethered to floating arrays at the two locations and depths during full moon did not differ (Fig. 5). However, mortality was significantly lower near surface of the bay during new moon than over the reef during both lunar periods ($G^2 = 10.2$, $P = 0.001$). Therefore, the surface waters of the bay appear to be safer for postlarvae than over reef habitats during new moon, but during full moon, postlarvae are equally susceptible to visual predators in all habitats.

In laboratory mesocosms, the fish predator was equally efficient at preying on postlarvae in new moon and full moon light levels when the density of postlarval lobsters was high (Fig. 6). However, when prey density was low, predation was significantly lower in the new moon light treatment than in full moon light or in the high density treatments (Table 1). These results suggest that predator-prey encounters occurred with the high density of prey, regardless of light level. A similar mechanism might be operating on the reef where high predator density and, perhaps, a concentration of prey in a reduced volume of water over the shallow reef, increases predator encounters with postlarval prey.

Discussion

Mortality on larval stages is generally assumed to be catastrophic, unpredictable, and stochastic in time and space. Predation risk is increased during recruitment to benthic populations because larvae and predators are concentrated in coastal environments where larvae (or postlarvae) seek settlement habitats (Morgan, 1992). However, the widespread persistence of species with planktonic larvae suggests that larval stages employ a suite of

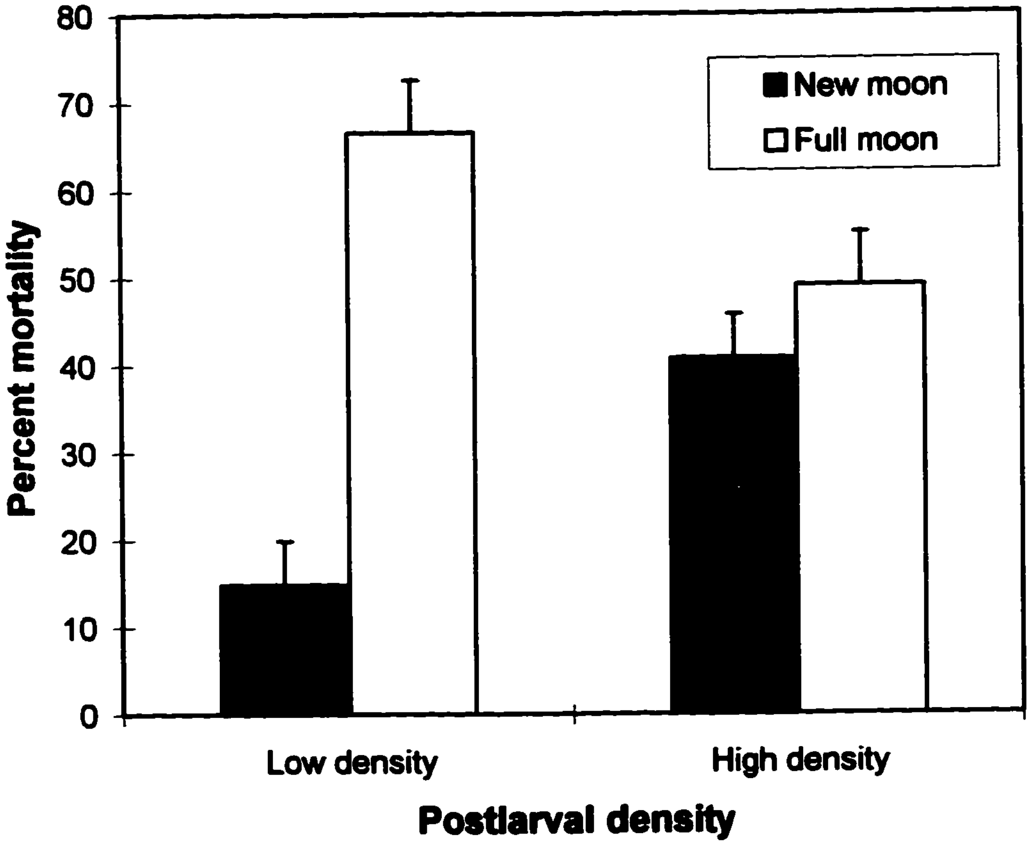


Fig. 3.6. Percent mortality of spiny lobster postlarvae as a function of prey density and light level in laboratory mesocosms. Bars are standard errors of replicates.

Table 3.1 Results of a two-way completely crossed ANOVA on the effect of postlarval density and moonlight level on predation.

Source	Df	MS	F	P
light	1	1.5463	22.9	< 0.0001
density	1	0.072	1.07	0.3094
interaction	1	0.9601	14.22	0.0007
error	32	0.0675		
Total	35	0.1354		

strategies to reduce predation pressure (O'Brien, 1987; Morgan, 1995). Larvae have evolved a number of behavioral, morphological and chemical defensive traits to escape, repel or avoid encounters with predators. The postlarvae of the Caribbean spiny lobster provide strong evidence for this.

Spiny lobster postlarvae experienced the highest level of predation as they crossed the offshore coral reefs where planktivorous fishes are diverse and abundant (e.g., Starck and Davis, 1966; Randall, 1967). Fish and invertebrate larvae form a major part of the diet of these predators (Randall, 1967; Emery, 1973; Goldman and Talbot, 1976; Hobson and Chess, 1976). Although many nocturnal planktivorous fish (e.g., Holocentridae, Priacanthidae, Apogonidae, and Pempheridae) generally feed over reef tracts at night, others (e.g., Clupeidae, Harengulidae and Hemiramphidae) move out over the seagrass beds of the Hawk Channel coastal lagoon to forage at night (Starck and Davis, 1966). Postlarvae may be relatively safer in the shallow waters of Florida Bay because this system does not contain the large schools of nocturnally-foraging planktivores characteristic of the coastal lagoon and reefs (Starck and Davis, 1966). The mortality gradient from coral reef to coastal lagoon and into the bay correspond to the trend in habitat-specific predator assemblages. The higher mortality of spiny lobster postlarvae that I observed over coral reefs than over the other areas may be due to the concentration of both prey and predators in the reduced volume of water over the reefs.

While the difference in predation near the surface and the bottom was not striking over the reef and coastal lagoon, predation was significantly lower in the surface waters of Florida Bay than in all other areas along the transport path. By using surface waters during new moon influx (Acosta et al., in press), postlarvae are quickly transported past reefs and other areas with numerous predators in the strong tidal current of the new moon lunar phase, thus reducing their exposure time. However, this does not explain why spiny lobster postlarvae do not capitalize on the strong full moon rising tides.

Postlarval recruitment during new moon, the darkest lunar phase, appears to be a predator-avoidance strategy to reduce the probability of exposure to visual pelagic predators during influx to nearshore nursery habitats. Predation was similar during new moon and full moon conditions over coral reefs, probably due to the concentration of predators and prey over this area. Predation on postlarvae in the bay increased during full moon probably due to increased exposure of postlarvae to visual pelagic predators. With artificially high densities of prey in laboratory mesocosms, the visual fish predator was equally efficient at killing prey under simulated new and full moon conditions which indicates that predator-prey encounters reached a threshold level. However, at low postlarval densities, predation was markedly reduced under new moon conditions while remaining high under full moon conditions. While these experiments focused on the impact of visual predators, they do not indicate effects other predators using tactile or other prey-detecting mechanisms would have on larval survival.

Predation on postlarvae in benthic habitats had a similar pattern to that in pelagic environments. Postlarvae experienced highest predation in coral reefs while predation was lower in seagrass and macroalgal habitats in both the Hawk Channel coastal lagoon and Florida Bay. The selective agents of predation in these habitats were mainly mobile predators, such as pelagic and demersal fishes and invertebrates. In these experiments, postlarvae were placed in habitat shelters and so predation by sessile invertebrate predators was not a factor. Relative predation on postlarvae was similar in seagrass and macroalgae on both sides of the Florida Keys island chain. While vegetated habitats of Florida Bay function as nurseries as demonstrated by the primary distribution of juvenile spiny lobsters (Herrnkind and Butler, 1986; Forcucci et al., 1994), the paucity of juveniles in vegetated habitats of the coastal lagoon is not explained by predation pressure in this environment. Instead, a combination of other factors, such as tidal flow or chemical cues, may be responsible for the observed benthic distribution of early juveniles in the bay.

Camouflage coloration has been shown to increase prey survival by ensuring crypticity from predators (Sih, 1987; O'Brien, 1987). Transparent and pigmented spiny lobster postlarvae had similar rates of predation in different habitats. Pigmentation of postlarval settlers in benthic habitats did not appear to confer a selective advantage for reducing predation. However, pigmentation has also been attributed as an adaptation to protect organisms against ultraviolet radiation in shallow water habitats (Aboul-Ela, 1958).

The puerulus postlarvae of the spiny lobster is the critical link between the pelagic phyllosome larva and the benthic juvenile lobster. Postlarvae appear to use a combination of adaptive strategies designed to reduce predation pressure during recruitment to nearshore nurseries. Influx in surface waters of strong rising tides during the darkest moon phase appears to be central for decreasing the risk of encountering predators by reducing exposure and visibility. The transparent body and solitary behavior of postlarvae may also act to decrease predation risk in the water column and benthic habitats. The reduced risk of predation in the bay may allow postlarvae more time to choose settlement habitat, and thus, may indirectly influence spatial distribution patterns of juveniles.

CHAPTER IV

THE ROLE OF MANGROVE HABITAT AS A NURSERY FOR JUVENILE SPINY LOBSTER, *PANULIRUS ARGUS*, IN BELIZE.

Introduction

The value of mangrove prop roots as habitat for marine and estuarine fauna is widely recognized (Odum et al., 1982; Robertson and Duke, 1987; Vance et al., 1990; Laegdsgard and Johnson, 1995), but until recently, descriptions of mangrove habitat use by fish and invertebrates have been qualitative and often speculative. Recent quantitative studies have compared the community composition of fish and crustaceans in mangrove habitats to nearby vegetated and non-vegetated habitats in several tropical systems (Thayer et al., 1987; Robertson and Duke, 1987; Chong et al., 1990; Vance et al., 1990; Sheridan, 1992; Laegdsgaard and Johnson, 1995). Mangroves serve as either nurseries for juveniles or as feeding areas for transient fish and crustaceans (Sheridan, 1992; Robertson and Duke, 1990). Several fish species shelter among red mangrove (*Rhizophora mangle*) prop roots in Florida during the day and feed in seagrass meadows at night, similar to the dynamic use of seagrass meadows by some coral reef fish (Thayer et al., 1987). Postlarval penaeid shrimp settle in all types of vegetation in Australia and Malaysia but the juveniles of some species are more abundant near fringing mangroves, indicating that they use this habitat as a nursery (Staples, 1980a, b; Robertson and Duke, 1987; Chong et al., 1990; Vance et al., 1990). However, the degree to which mangrove habitat is used by mobile species varies among systems where shelter characteristics, food organisms, and hydrography are distinctly different. Odum et al. (1982) noted such variation in use of mangrove habitats and described the faunal communities they observed in terms of Lugo and Snedaker's (1974) geological and hydrological classification of mangrove forests. Odum et al. (1982) concluded that the subtidal prop roots of fringing and overwash mangrove forests are important nurseries presumably because they provide juveniles with abundant food and shelter from predators, i.e. the nutrition and refuge hypotheses.

Mangrove prop root systems are presumed to be important nurseries for the Caribbean spiny lobster *Panulirus argus*, but little is known about the value of this habitat for postlarval settlers and juvenile lobsters. In Florida, the puerulus postlarvae settle in nearshore vegetated habitats such as macroalgal beds, and perhaps, seagrass (Herrnkind et al., 1994). Juveniles appear to undergo ontogenetic shifts in habitat use and behavior. Young juveniles (1 to 3 months post-settlement) live in vegetation where they are solitary and cryptic, whereas older juveniles dwell gregariously in crevice shelters associated with hardbottom communities (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986; Childress and Herrnkind, 1996). Yet, many regions in the Caribbean do not have extensive hardbottom shelves like those in Florida. Instead, Caribbean coasts typically have extensive seagrass beds with interspersed coral patch reefs and mangrove-fringed shorelines. Mangrove prop roots may be continuously submerged due to the limited tidal range in this region, and so may function as a nursery for lobsters. Due to differences in lobster sizes of those dwelling in mangrove and reef habitats in the U.S. Virgin Islands, Olsen et al. (1975) suggested that mangroves serve as habitat for juveniles.

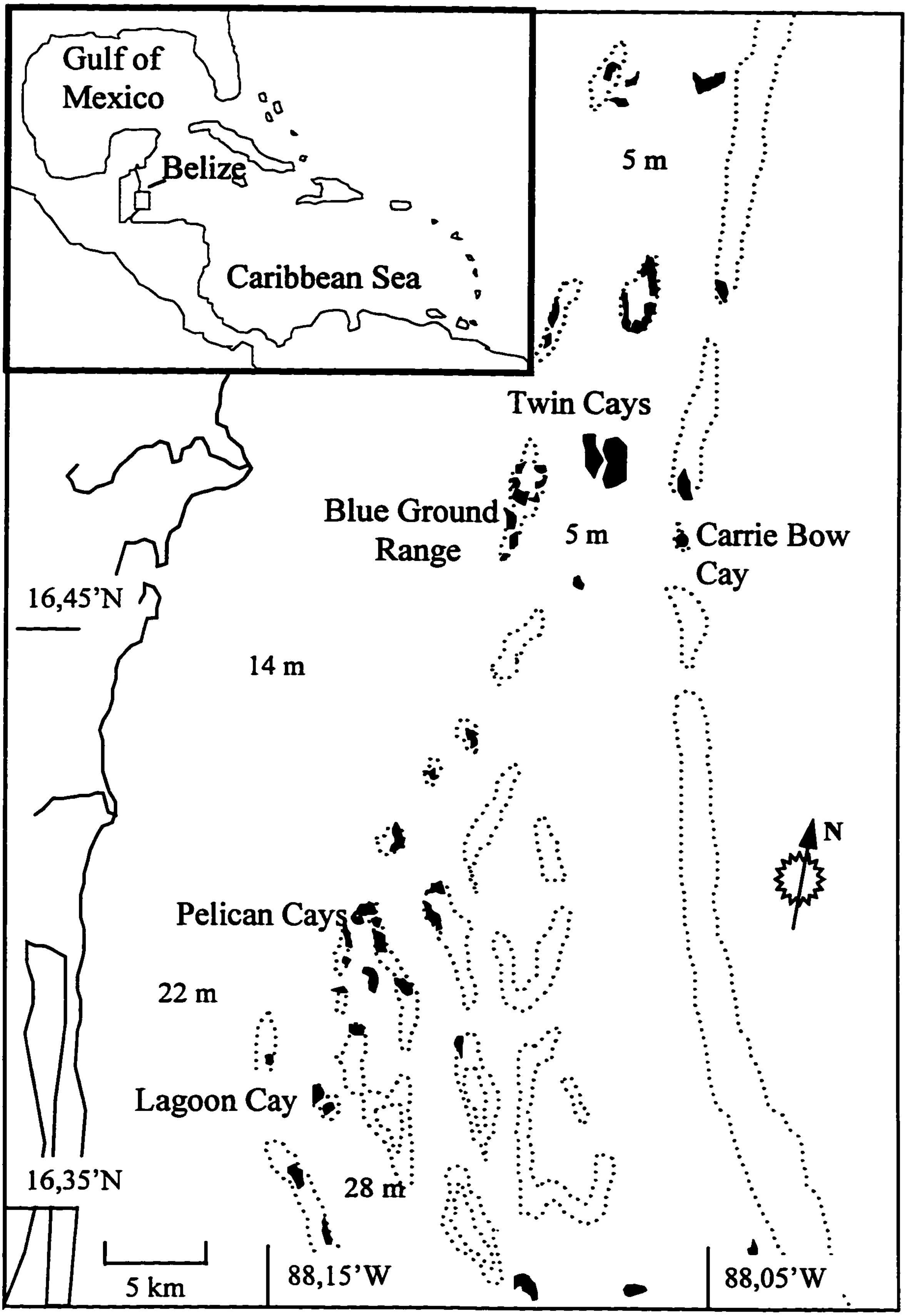
To better understand the role of mangrove habitats in lobster recruitment, I studied the population dynamics of juvenile Caribbean spiny lobsters in Belize around two types of mangrove islands that differ in geomorphology and the density of coral shelters on island margins. I surveyed juvenile spiny lobster populations, quantified their shelter preference, conducted mark-recapture experiments, and measured movement and residence times on sites to test the null hypothesis that use of submerged mangrove habitat by lobsters is not affected by isolation of the island or availability of alternative shelters. To compare habitat-specific survival of different size classes of juveniles in potential nursery habitats, I measured relative habitat-specific predation on lobsters in mangrove prop roots, coral patch reefs, and seagrass. Because predation pressure may influence the ontogenetic shift from vegetation to crevice dwelling, I hypothesized that: 1) survival of newly-settled lobsters is similar in seagrass and mangrove prop roots but lower in crevice shelters on coral patch reefs, and 2) older juveniles survive better in coral crevice shelters than in mangrove prop roots or seagrass.

METHODS

Site description

I studied juvenile lobster dynamics along the fringing mangrove habitat of nine islands off southern Belize in March, August and December 1995 (Fig. 1). The islands lie approximately 5 km leeward of the Belize Barrier Reef, and receive oceanic water from cuts in the main reef. They support both fringing and overwash red mangrove forests (Lugo and Snedaker, 1974) and have a tidal range of 0.3 - 0.7 m. The mangrove trees at the sites have submerged prop root habitat at mean low tide of 0.5 - 1 m deep. Four sites

Figure 4.1. Map of the Caribbean region (inset) and southern Belize, showing the locations of the shallow-water mangrove islands of Blue Ground Range and Twin Cays, and the isolated islands of the Pelican Cays and Lagoon Cay. Stippled areas represent reef tracts and water depths in m are shown.


Gulf of Mexico
Belize
Caribbean Sea
5 m
Twin Cays
Blue Ground Range
5 m
Carrie Bow Cay
16,45'N
14 m
N
Pelican Cays
22 m
Lagoon Cay
16,35'N
28 m
5 km
88,15'W
88,05'W

were typical of shallow-water mangrove islands which are surrounded by seagrass-covered margins 1-2 m deep that gradually increase in depth to about 5 m. One of these sites was located at Twin Cays and three others near islands in the Blue Ground Range (designated Blue 1, Blue 2, Blue 3) (16°48.21N, 88°08.50W). Five other sites were located at the Pelican Cays (Bird Cay, Cat Cay, Fisherman's Cay, Manatee Cay) and at Lagoon Cay (16°40.01N, 88°11.52W). These deep-water mangrove islands constitute a faro, an atoll-like formation surrounded by deep channels and flanked by a shallow shelf 1-2 m deep that drops off abruptly to 25 - 30 m.

Habitat characterization

The widths of all nine island margins range from 3 - 10 m, and the margins contain varying densities of stony corals, gorgonians and sponges that, in addition to mangrove prop roots, may serve as shelter for juvenile lobsters (Forcucci et al., 1994). To quantify differences among islands in habitat structure and density of shelters (dens) along island margins, I measured substratum percent cover and density of alternate shelters along three replicate, randomly-located transects up to 15 m in length (depending on width of island margins) and laid perpendicular to the mangrove line. Percent cover of seagrass *Thalassia testudinum*, macroalgae *Laurencia* sp. and *Dictyota* sp., sand, or a heterogenous mix of corals, sponges, algae, and seagrass were recorded along each transect. The density of various potential shelter for lobsters (e.g., mound corals, fire coral, gorgonians) within 2 m of the transects was also recorded.

A multivariate analysis of variance (MANOVA) was performed to determine if there were differences in habitat structure among islands. I used substratum percent cover and shelter density in the analysis as response variables and Pillai's trace as the MANOVA statistic since it is robust to departures from normality (Scheiner, 1994). The univariate habitat variables were not normally distributed so I used an angular transformation on the percent cover data and a square root transformation on the shelter density data to improve normality. To test for homogeneity of variances and covariance matrices among dependent variables, I conducted correlation analyses on pairs of dependent variables, but no associations were found among island groups. The Ryan-Einot-Gabriel-Welch F (REGWF) test was used to determine which islands differed in habitat structure. All analyses were run using the SAS computer package (SAS Institute 1989).

Habitat utilization

To determine spatial patterns in habitat use, five-day mark-recapture studies were conducted along 100 m of the margins of each of the nine mangrove islands. During each study, lobsters were captured, individually tagged underwater with color-coded antenna tags, measured, sexed and then returned to their original dens which were also marked with unique tags. Following the initial sampling, each island was revisited four times at daily intervals, unmarked lobsters were tagged, and the distance moved by each lobster that was resighted and the type of den it was using were recorded. Population size, loss by mortality/emigration, and immigration per site were estimated from the mark-recapture data using a Jolly-Seber model (Krebs, 1989).

I postulated that movement of lobsters would increase with size, so I initially analyzed mean daily distance moved and mean den residency times using analysis of covariance (ANCOVA) with size of individual lobsters as the covariate. However, size of individuals was not associated with the univariate response variables, therefore a MANOVA was used to test for differences in the individual lobster variables (i.e., lobster size, distance moved, and den residence time) among islands. Roy's Greatest Root was used as the test statistic, and I used a canonical correlation analysis to inspect the relationship among response variables. Because the univariate variables were normally distributed, I used the Box test to check for of equality of variances and covariance matrices. The analysis testing for differences in habitat structure among islands revealed that islands could be placed in two groups: Pelican Cays-type islands (Bird Cay, Cat Cay, Fisherman's Cay, Manatee Cay) and Blue Ground Range-type islands (Blue 1, Blue 2, Blue 3, and Twin Cays) (see Results). I applied a multivariate pairwise orthogonal contrast to these two groups of islands, again using the Greatest Characteristic Root criterion (Harris, 1985). The same analyses was performed separately on the Jolly-Seber population variables (i.e., standing population sizes, loss by mortality/emigration, and immigration), and a similar post-hoc orthogonal contrast was run on the two island groups.

To estimate shelter preference by juvenile lobsters, I used Johnson's rank preference test (Johnson, 1980) and computed the rank order of shelter use by lobsters and shelter density per island to determine if there were differences in shelter preference among island types.

Habitat-specific predation

The relative value of potential nursery habitats in terms of shelter from predation was assessed by tethering two size classes (new settlers 8-15 mm carapace length (CL), and older juveniles 20-45 mm CL) in three habitats: among red mangrove prop roots, in crevices on coral patch reefs, and in seagrass. Lobsters were tethered on a 0.5 m length of 10 kg-test monofilament line secured to the carapace by gel cyanoacrylate glue and placed at random distances at least 1 m apart along unmarked transects. Experiments were conducted for 24 h from dusk to dusk in water depths of about 1 m. Juvenile lobsters tethered among mangrove prop roots or in rock crevices remained quiescent, and those placed at the base of seagrass blades retreated to the ends of their tethers and then also became quiescent. Results were scored as alive or eaten with evidence of predation (fragments of carapace on the tether).

Tethering has been widely applied in predation research despite debate over possible experimental treatment bias (e.g., Peterson and Black, 1994; Aronson and Heck, 1995). My observations of tethered lobsters suggest that tethering artifacts due to behavioral differences among habitat treatments are minimal because tethered lobsters did not behave in a manner that would attract predators. I present results on relative rates of habitat-specific predation among habitats and size classes that I tested. Data were analyzed the data using a log-linear model and the likelihood ratio G^2 test (Stokes et al., 1995). No significant treatment interactions were found so the model was reduced to test for differences in predation by habitat and lobster size class.

RESULTS

Multivariate analyses of island margin habitats show that there are distinct differences in habitat characteristics between the two geomorphologically different island types, i.e. shallow water versus deep water islands. Post-hoc REGWF tests show that the four islands at the Pelican Cays (Bird Cay, Cat Cay, Fisherman's Cay, and Manatee Cay) differed from the four islands at Blue Ground Range (Blue 1, Blue 2, Blue 3, and Twin Cays) and one island at Lagoon Cay by substratum percent cover and alternate shelter density (Table 1). Substratum cover at Blue Ground Range was dominated by seagrass *Thalassia testudinum* (Fig. 2A, 'seagrass'), whereas the substratum at the Pelican Cays consisted of a heterogenous mix of zoanthid and stony corals, gorgonians, sponges, macroalgae and sparse seagrass (Fig. 2A, 'coral mix').

While all types of alternative shelter structure were found on most sites, densities were significantly higher at the Pelican Cays (Fig. 2B). Mound corals such as *Montastrea* and *Diploria* (Fig. 2B, 'mound coral') as well as smaller stony corals such as *Agaricia*, *Acropora* and *Porites* (Fig. 2B, 'other coral'), gorgonians, and sponges were more abundant in the Pelican Cays; the abundance of fire coral *Millepora* was not significantly different between sites. Lagoon Cay is similar in geomorphology to the Pelican Cays in its isolation by deep water, but habitat characteristics were similar to the Blue Ground Range (Fig. 2, Table 1). Due to possible confounding effects and lack of replication for Lagoon Cay, this site was not included in the post-hoc orthogonal contrasts of habitat use by lobsters. Orthogonal contrasts were conducted on lobsters occupying the Pelican Cays (Bird Cay, Fisherman's Cay, Cat Cay, Manatee Cay) versus the Blue Ground Range (Blue 1, Blue 2, Blue 3, Twin Cays).

Spiny lobsters sheltering in mangrove habitat ranged in size from 10 mm to 65 mm CL (mean and SE: 35.15 ± 1.22 mm CL), and the male-to-female ratio was approximately 1:1. Lobsters showed marked preference for stony coral shelters, but their use of mangrove prop roots and undercut peat banks increased when the abundance of

Figure 4.2. Habitat characterization of two types of mangrove islands: shallow-water islands (Blue Ground Range including Twin Cays) and isolated islands (Pelican Cays). This grouping of islands is based on geomorphology and habitat. (A) substratum cover (%); (B) density of alternate shelters. * significant at an α level of 0.05; ns, not significant. Histograms are means and error bars are 1 SE.

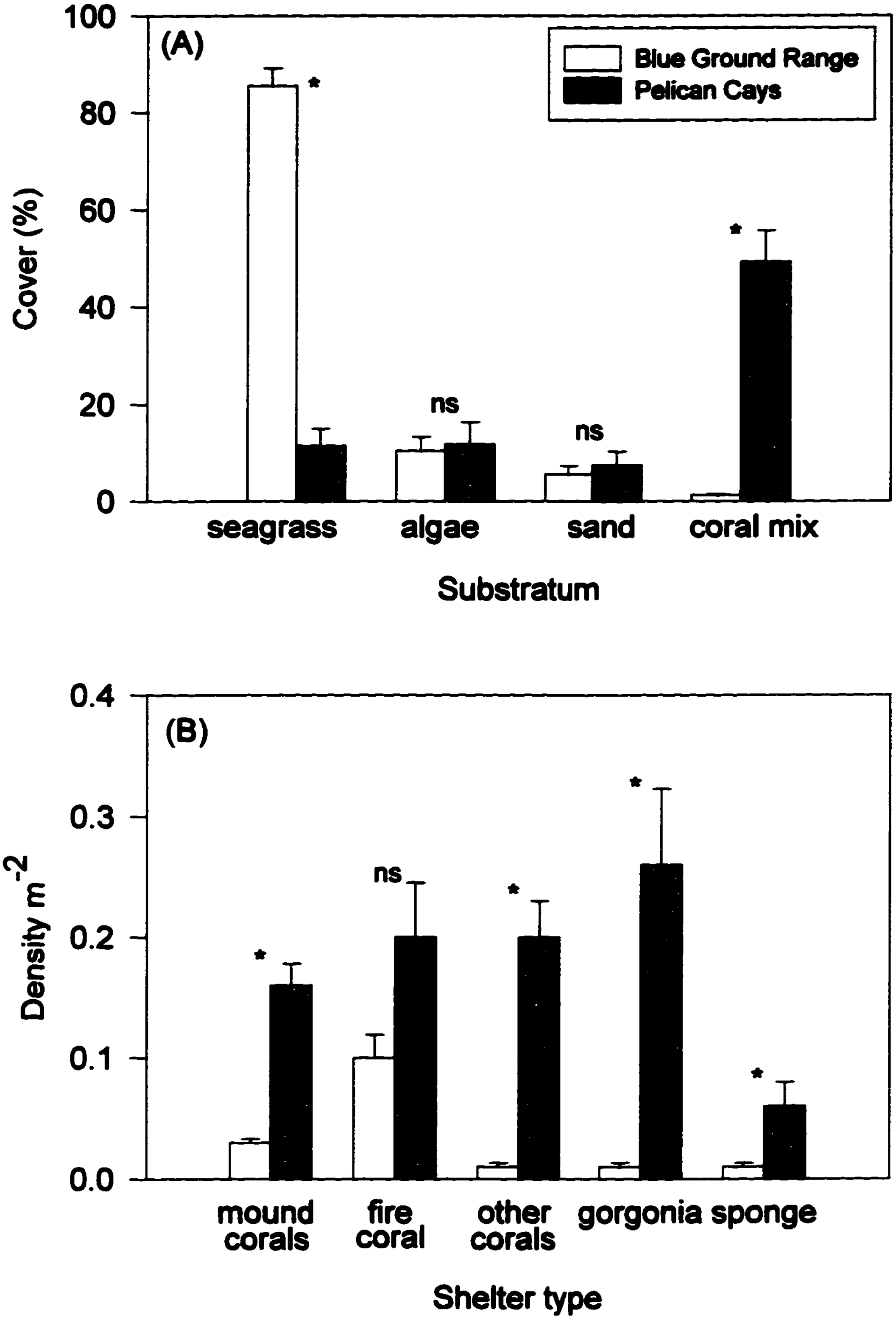

(A)
Blue Ground Range
Pelican Cays
Cover (%)
100
80
60
40
20
0
*
ns
ns
*
seagrass
algae
sand
coral mix
Substratum
(B)
Density m^{-2}
0.4
0.3
0.2
0.1
0.0
*
ns
*
*
*
mound corals
fire coral
other corals
gorgonia
sponge
Shelter type

Table 4.1 Results of a MANOVA testing whether: A.substratum percent cover or B. density of alternate shelters differ among islands. Results are shown for the MANOVA using Pillai's trace for significance tests, the standardized coefficients for the first two canonical variates from a canonical analysis, and results of post-hoc REGWF tests for determining significant differences among island groups; island groups sharing a line do not differ significantly for that dependent variable.

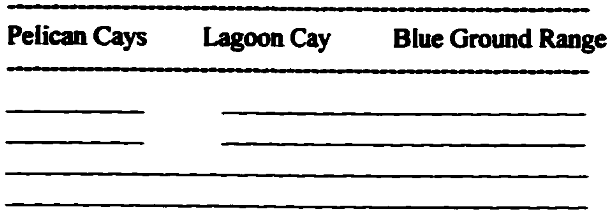
A. MANOVA on Substrate Percent Cover.

Source	Pillai's trace	F	Num DF	Den DF	Pr>F
Island	2.2723	2.9	32	72	0.0001

Standardized canonical coefficients

Percent cover	can1	can2
seagrass	1.6824	1.0229
coral mix	-1.6107	0.6752
macroalgae	-0.4249	1.5001
sand	-0.2877	-0.0419

REGWF tests



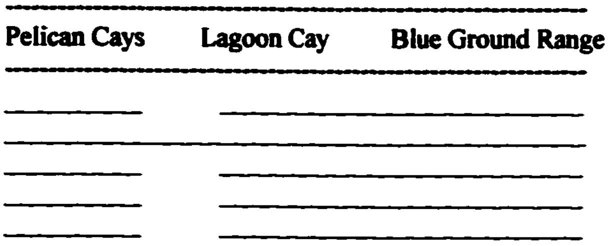
B. MANOVA on Shelter Density.

Source	Pillai's trace	F	Num DF	Den DF	Pr>F
Island	2.4832	1.6	48	108	0.02

Standardized canonical coefficients

Shelter density	can1	can2
mound coral	1.2375	2.0558
fire coral	0.4542	-0.6511
other coral	1.5135	-0.9777
gorgonians	0.9836	-0.5245
sponges	1.0040	-0.0740

REGWF tests



alternate shelters decreased on the island margins, i.e. at Blue Ground Range and Lagoon Cay (Johnson's rank preference test: $F = 65.4$, dF 1 11, $P < 0.001$).

During the 5 d censuses of the 100 m transects on the nine mangrove islands, 112 lobsters were captured (Table 2A). The individual lobster variables of lobster size, den residence time, and distance moved differed significantly among island types, as indicated by the MANOVA results (Table 2B). However, the orthogonal contrast between the Pelican Cays and Blue Ground Range was not significant, suggesting that the single Lagoon Cay site had the greatest effect on the MANOVA response variables. The canonical analysis revealed that individual lobster size and distance moved were associated and were inversely related to den residence time. The first canonical variate indicates that residency accounted for most of the differences among island types (canonical $r^2 = 0.22$ or 51% of the explainable variation). Den residence time was greatest on Lagoon Cay where most lobsters, regardless of size, remained on the site. Individual size, den residence time and distance moved within sites were similar at the Pelican Cays and Blue Ground Range despite differences in habitat structure.

Multivariate analysis also indicated that island types differed significantly with respect to population size, loss by mortality/emigration, and immigration (Table 2C). In this case, the orthogonal contrast revealed a significant difference between the Pelican Cays and Blue Ground Range; the latter had larger populations and greater immigration rates. Canonical analysis indicated that population size and immigration were positively correlated and were inversely related to mortality/emigration, with changes in population size accounting for most of the variation (canonical $r^2 = 0.87$ or 68 % of the explainable

Table 4.2. A. Mean ± SE and MANOVA testing whether: B. individual lobster variables or C. population parameters differ among islands. Results are shown for the MANOVA using Roy's greatest root for significance tests, orthogonal contrasts for island groups (Pelican Cays (PC) and Blue Ground Range (BG)), and the standardized coefficients for the first two canonical variates from a canonical correlation analysis.

A. Mean (± SE)

Island	Ind. size	Residence	Movement	Pop. size	Loss	Immigration
Twin	36.0 (2.5)	2.0 (0.46)	15.4 (8.4)	13.5 (1.0)	0.8 (0.14)	1.43 (0.0)
BG 1	40.4 (5.8)	2.08 (0.42)	24.5 (5.7)	14.8 (8.2)	0.58 (0.4)	2.2 (0.3)
BG 2	30.0 (2.1)	3.6 (0.36)	18.4 (7.9)	15.3 (2.1)	0.92 (0.2)	1.7 (0.8)
BG 3	39.3 (4.2)	2.1 (0.71)	20.8 (6.2)	15.4 (1.9)	0.89 (0.11)	3.9 (0.0)
Bird	40.9 (5.2)	2.75 (0.62)	16.6 (12.2)	4.3 (1.0)	0.87 (0.07)	0.55 (0.7)
Fisherman	43.8 (5.9)	2.2 (0.32)	15.7 (10.7)	4.7 (1.2)	0.83 (0.12)	1.63 (0.1)
Cat	36.4 (4.0)	3.0 (0.63)	16.9 (12.2)	4.8 (0.7)	1.0 (0.0)	0.7 (0.0)
Manatee	27.6 (2.1)	2.58 (0.42)	18.2 (11.1)	6.2 (1.7)	0.77 (0.51)	1.1 (0.3)
Lagoon	38.1 (2.8)	4.38 (0.42)	5.4 (1.4)	11.9 (1.3)	0.95 (0.05)	1.9 (0.2)

B. MANOVA results for Individual Variables.

Source	Roy's Greatest Root	F	Num DF	Den DF	Pr>F
Island	0.2863	3.61	8	101	0.001
Contrast: BG vs. PC	0.0389	1.28	3	99	ns

Standardized canonical coefficients for Individual Parameters

Parameter	can 1	can 2
Individual size	-0.6104	0.7690
Residence time	0.9181	0.4525
Movement rate	-0.0838	-0.6757

C. MANOVA results for Population Parameters.

Source	Roy's Greatest Root	F	Num DF	Den DF	Pr>F
Island	7.0781	15.93	8	18	0.0001
Contrast: BG vs. PC	3.8608	20.59	3	16	0.0001

Standardized canonical coefficients for Population Parameters.

Parameter	can1	can2
Population size	2.0854	1.3910
Immigration	0.8952	-1.4933
Mortality/Emigration	-1.1142	-0.1357

variation). This suggests that the Blue Ground Range have larger populations of lobsters due to immigration, perhaps from the surrounding seagrass meadows or nearby islands. Fewer lobsters immigrated into the more isolated Pelican Cays where deep water may serve as a barrier to migration for juveniles.

Small juveniles (8 - 15 mm CL) had significantly higher survival in mangrove prop root habitat than in seagrass or coral shelter on patch reefs ($G = 29.6$, df 2, $P < 0.0001$; Fig. 3). Larger juveniles (20 - 45 mm CL) had similar survival in mangroves and coral crevices ($G = 1.81$, df 2, $P > 0.05$) which were both higher than in seagrass. Predation on small juveniles was higher than on larger lobsters in all habitats.

DISCUSSION

Geomorphology and habitat structure along island margins differ remarkably among mangrove islands in Belize. The Blue Ground Range and Twin Cays are typical of shallow-water fringing mangrove islands, having gently sloping margins with a seagrass substratum and with low densities of corals and other shelter for juvenile spiny lobsters. The Pelican Cays, however, have high densities of alternate shelters on their margins, are flanked by steep rubble slopes, and are isolated from each other by deep channels. Species diversity on these islands appears to be unusually high (e.g., ascidians; Goodbody, 1995). Lagoon Cay possessed characteristics of both island groups, being isolated by deep water proximity to oceanic water and are relatively silt-free, representing adequate habitat for juvenile lobsters which have a low tolerance for silty environments (Herrnkind et al., 1988). The spiny lobsters preferred the crevice shelter of stony corals,

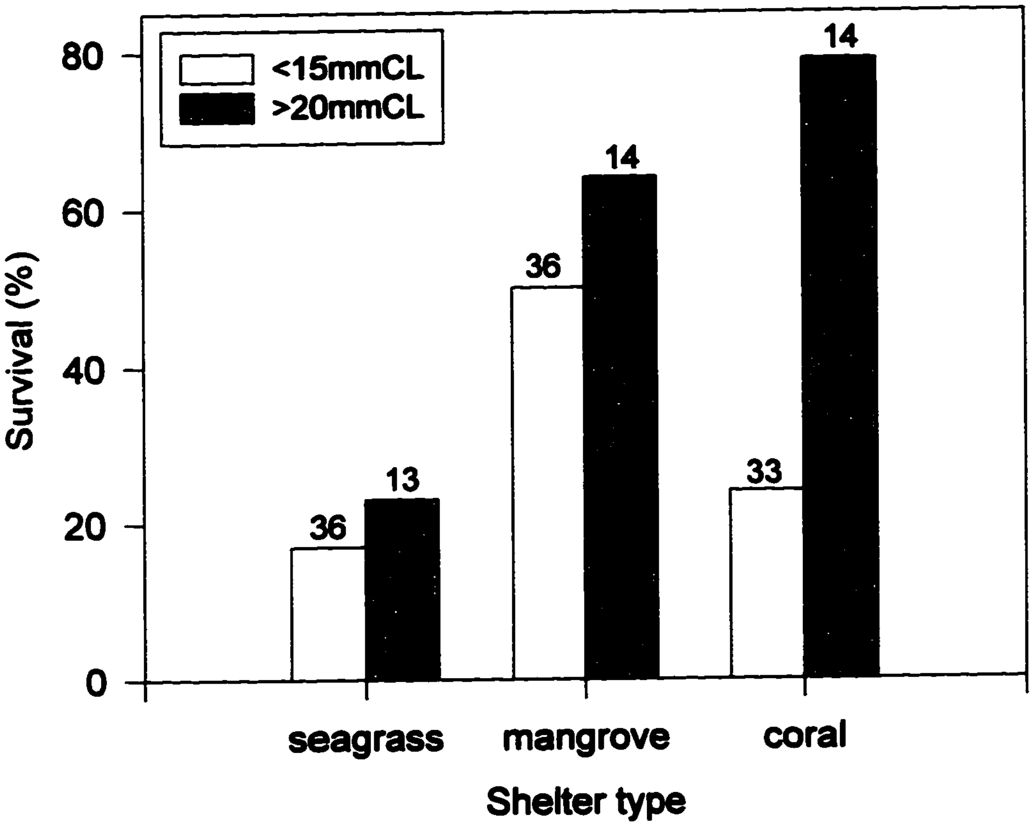


Fig. 4.3. Survival of two size classes of spiny lobster tethered in three shelter types. The number of lobsters tethered in each habitat is shown above each histogram.

but their use of mangrove prop roots or undercut peat banks increased wherever coral cover was sparse on island margins.

The size and sex ratios of juvenile lobsters found on the two types of islands were similar, but lobster abundances were different. The shallow-water islands of the Blue Ground Range had higher densities of juveniles which appears to be a consequence of higher rates of migration among islands. At Lagoon Cay however, all lobsters moved little, which extended their mean residence time per den. The isolation of this island and the low density of alternative shelter structures may explain this pattern of habitat use, but this type of site was unreplicated in this study. Since movement on to and out of the isolated islands at the Pelican Cays as well as Lagoon Cay was minimal, I suspect that population sizes there may reflect actual levels of postlarval recruitment and survival in the absence of migration of juveniles among islands.

Loss by mortality/emigration was not different among islands, and the Jolly-Seber mark-recapture method does not discriminate between these two sources of loss. However, measurement of predation on lobsters tethered in different shelter types gives us a relative estimate of shelter effects on mortality for different size classes. Small juveniles (recent settlers) had highest survival in mangrove prop root habitat, whereas larger juveniles survived equally well in mangrove prop roots and coral patch reefs but had low survival in seagrass. Although my field surveys indicate that large juvenile lobsters preferred to shelter under corals and other crevice shelters along island margins, they readily fled to the fringing mangrove prop roots to escape capture. Thus, their proximity to this additional shelter may decrease successful predatory attacks. Mangrove prop root habitat may be especially important for sheltering small juveniles in regions where other densely vegetated habitats for settlers may be scarce.

Postlarval *Panulirus argus* arriving from the oceanic plankton appear to preferentially settle in macroalgae in south Florida where there are extensive areas of macroalgae-dominated hardbottom meadows (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986; Herrnkind et al., 1994). After a few months, the juvenile lobsters take up residence under large sponges and in solution holes in hardbottom areas that serve as the primary nursery habitat in this region (Herrnkind et al., 1994; Forcucci et al., 1994; Butler and Herrnkind, in press). This type of habitat is rare in Belize and most other regions of the Caribbean. In the Caribbean basin, the fringing mangroves with associated margins of seagrass, macroalgae, and coral crevice shelters function as nursery habitat for juvenile spiny lobsters. Nearshore coral patch reefs can also shelter large juveniles, but smaller lobsters experience high mortality in these habitats. While postlarvae may primarily settle in vegetated habitats, survival of larger juveniles may depend on their proximity to fringing mangroves and adjacent coral crevice shelters. The relative role of mangrove prop root habitat as a nursery for Caribbean spiny lobsters probably depends on habitat quality, areal extent of submerged mangrove prop roots, and proximity of mangrove habitat to oceanic currents that supply lobster postlarvae. Mangrove prop roots not only provide food and shelter for a host of fish and benthic invertebrates but also function in stabilizing sediments and reducing siltation (Odum et al., 1982). Therefore, the quality and availability, and thus, the protection of fringing mangrove forests may be essential for maintaining lobster populations in Caribbean regions because destruction of mangroves will decrease nursery habitat area and may increase siltation in nearby habitats.

CHAPTER V

SYNOPSIS

Caribbean spiny lobster populations are linked by the planktonic larval phase, and the processes affecting the recruitment success of the postlarvae are likely to have profound consequences on the dynamics of local benthic populations. My studies show that recruitment of postlarvae to benthic populations is governed by the interaction of several factors, namely: 1) the supply of postlarvae from the open sea and the conditions that affect transport of postlarvae to coastal areas, 2) the probability of postlarval mortality, especially in coastal environments where predators may be concentrated, and 3) the availability of suitable settlement habitat.

My analyses of an eight-year time series of postlarval supply to the lower Florida Keys showed that recruitment occurs in distinct lunar, annual and non-seasonal cycles (Chapter II). Larval recruitment associated with the new moon lunar phase was confirmed for *Panulirus argus* postlarvae (Witham et al., 1968; Little, 1977; Herrnkind and Butler, 1994) and is common to many marine species (Robertson, 1992; Thorrold et al., 1994). This lunar periodicity may be the result of metamorphosis to the postlarval stage near the continental shelf break induced by longer periods of moonless nights or differential predation rates in nearshore environments with lowest predation during the darkest lunar phase of new moon. Because postlarvae have a strong aversion to light, it may be that predation pressure is indirectly responsible for the evolution of recruitment during new moon.

The annual cycle of postlarval recruitment with an early spring peak provides some support for cyclical spawning and a larval duration of nine months, but this does not explain the year-round influx of postlarvae to the Florida Keys. While spawning occurs from April to June in Florida (Lyons et al., 1982; Gregory et al., 1982), it is possible that Caribbean populations spawn during most of the year (Lyons, 1980; Cruz et al., 1991). A plausible scenario is that the Caribbean spawn supplies south Florida with postlarvae all year long while the early spring peak in postlarval supply is due to the additional input of postlarvae spawned in or near Florida and retained in oceanic gyres long enough to recruit back to the Florida population. Regional differences in the spiny lobster reproductive cycle must be examined before the dynamics of the Caribbean metapopulation is understood.

A complicating factor is the variability in the physical oceanographic features that transport postlarvae from the Florida Current to nearshore environments of the Florida Keys. Wind forcing is a potential transport mechanism that is best developed during winter months when the annual peak is prominent, but it accounted for only a minor proportion of the variance in postlarval supply to the Florida Keys. Wind forcing could not account for the lessor peak in postlarval supply that cycles at five-month intervals. Large-scale, long-lived gyres in the Florida Current have been described and represent a possible mechanism for these non-seasonal peaks in supply of postlarvae to the Florida Keys (Lee et al., 1992, 1994). But until the periodic behavior of these oceanic systems are better known, I cannot infer a cause-and-effect relationship.

Because larvae may have evolved a variety of adaptive strategies to reduce predation, predators play a key, albeit indirect, role in influencing their recruitment dynamics (Chapter III). Habitat-specific predation on spiny lobster postlarvae along typical transport pathways correspond with patterns in the subsequent distribution of juvenile lobsters (Herrnkind and Butler, 1994; Forcucci et al., 1994). Mortality on pelagic and benthic postlarvae was highest in offshore coral reefs where juvenile *P. argus* are rarely found, and predation was lower in vegetated habitats of Florida Bay where juveniles are most abundant. Differences in mortality due to predation may, thus, account for local spatial variability in recruitment. This variability may be explained by differences in resident predator assemblages along the coastal zones that postlarvae must traverse to find suitable settlement habitat. Many species of planktivorous fishes are concentrated at offshore reefs whereas fewer fish species feed in the water column over the seagrass beds of Hawk Channel lagoon and fewer still are resident in Florida Bay (Starck and Davis, 1966). In addition to local recruitment variablity, predation may account for regional differences in postlarval abundance. I conducted the predation studies near low-relief patch reefs of limited area and recorded relatively high rates of predation. These results would lead one to expect that predation will be even higher in other regions where more well-developed reefs support larger predator assemblages.

Beyond the effect of predation on postlarvae, the recruitment process is also influenced by habitat factors, such as habitat area and suitability, and chemical and physical cues that induce settlement. Settlement cues have not been identified for spiny lobster postlarvae. However, density-dependent regulation of larger juvenile lobsters has been noted in nurseries with limited crevice shelters (Forcucci et al., 1994; Butler and Herrnkind, in press). This may not affect postlarval settlers which are generally not abundant enough to saturate settlement habitat due to high predation rates and stochastic supply processes. However, the availability of suitable settlement habitat, such as macroalgae and seagrass, will affect population size. If vegetation cover is drastically reduced by environmental disturbances, postlarval recruitment may show a corresponding decline (Butler et al., 1995).

Florida Bay is an expansive area of shallow vegetated habitats and hardbottom communities with numerous crevice shelters, such as sponges and solution holes. It is a productive nursery, supporting a large population of lobsters with a correspondingly large fishery (Hunt, 1994; Butler and Herrnkind, in press). By comparison, the coastal environment of Belize in the Caribbean is distinctively different, having an extensive barrier reef system with numerous mangrove islands and coral patch reefs separated by seagrass beds. The juvenile spiny lobsters in Belize use shelters associated with subtidal mangrove root systems and coral patch reefs. Even if postlarvae settle in the extensive seagrass meadows present in the Belize back reef lagoon, the ultimate population size of lobsters may depend on the proximity of settlers to crevice shelters near mangrove islands and patch reefs and the areal extent of those habitats. The degree of isolation of these habitats by deep water and the concentration of key habitats in a limited area may have important effects on local population dynamics. These factors will regulate the distribution of the population by concentrating juvenile and subadult lobsters in these productive habitats because lobsters of these sizes have limited migration capabilities (Chapter IV).

Natural factors affecting the settler-recruit stages of marine benthic species have important consequences in regulating population dynamics (Gaines and Lafferty, 1995). Additionally, human exploitation of these populations can have disruptive effects on local and regional scales. Furthermore, marine species with metapopulation dynamics cannot be treated as a single, homogenous population or stock for exploitation because each local population may be impacted by different processes. Much is known about the ecology of *P. argus* in Florida which is at the northern limit of the species' range. Whether the same dynamics are operational on southern Caribbean populations remains to be seen.

There are, however, several factors which will have pervasive effects on all populations in the region. First, reduction in reproductive stocks via overfishing will have regional effects on larval supply. It is possible that overfishing of mature adults and poaching of juveniles in areas like Belize, Jamaica and the Mosquito Bank of Nicaragua will eventually result in fewer larval recruits to other populations (e.g., Florida and Cuba). Second, drastic changes in local oceanic regimes may affect larval transport to coastal populations. A predicted consequence of global climate change is that oceanic flow regimes in some coastal regions will change, and this will have immediate consequences for the balance in pelagic communities (Cushing, 1982; Glantz, 1992). If gyres spinning off the Florida Current are mainly responsible for transport of larvae to nearshore environments in Florida, then any disruption of this mechanism will have far-reaching consequences for larval recruitment. Third, spiny lobsters use a heterogenous mix of habitats to complete the ontogenetic phases of its complex life cycle. If critical habitats are not identified and preserved, the probability of local extinction will increase, driven by the additional pressures of exploitation. In this regard, it is prudent to adopt a regional strategy to understanding the ecology and managing the exploitation of key species like the Caribbean spiny lobster.

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Appendix A

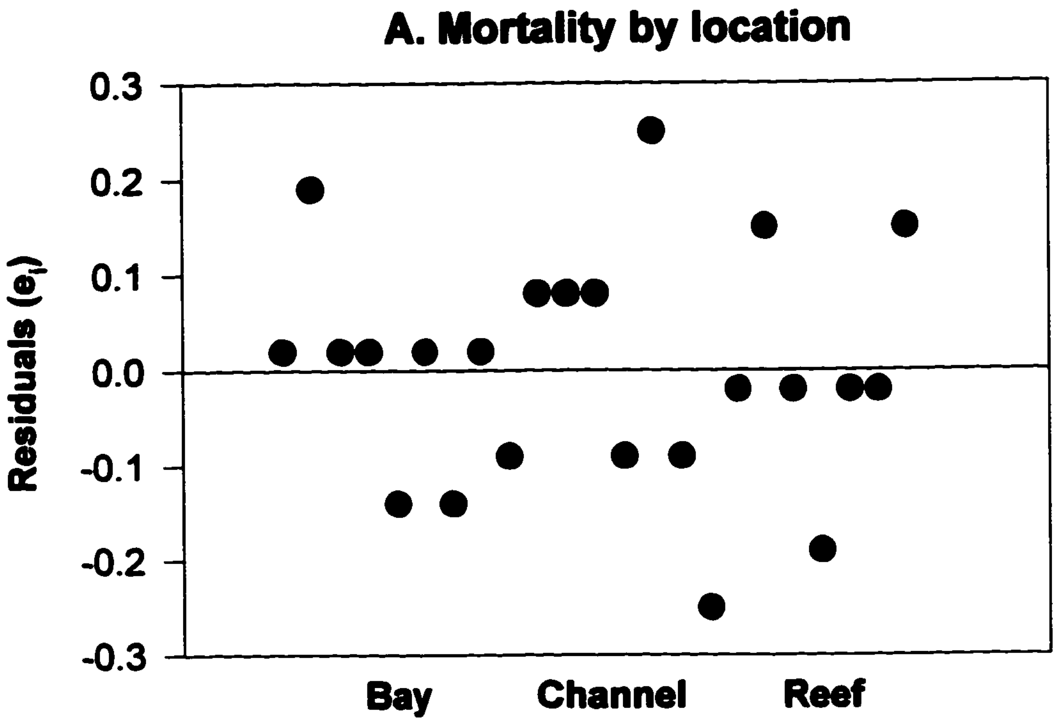
Independence of Replicates in Tethering Experiments

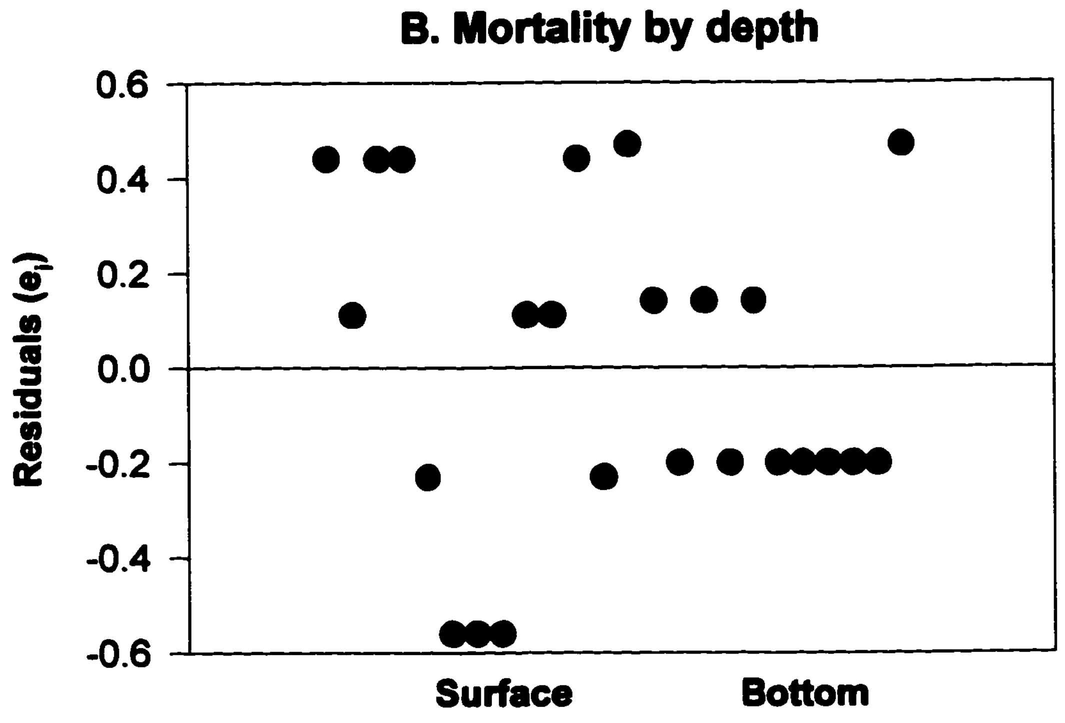
Actual predation on marine prey is difficult to quantify. Such measurements may be direct, as in video observations of predation events, or indirect, as in estimating the densities of prey and their predators. One of the most widely used techniques to obtain relative rates of predation is by tethering the prey under some experimental condition. In tethering experiments, the prey is tethered for some period of time in some habitat in which predation pressure specific to that habitat is to be estimated. Use of this technique has yielded valuable data but has been criticized as having several possible confounding factors which are generally not controlled in experiments. Such factors include attraction of predators by struggling prey or the test organism becoming entangled in the tether line increasing its exposure.

In tethering experiments to estimate relative rates of predation (see Chapter III), I took several measures to reduce enhancement of experimental artifacts. In experiments in which lobsters were tethered in different benthic habitats, individuals were tethered greater that 1 m apart on either side of unmarked transects. Another study (Butler and Herrnkind, in press), showed that predation on benthic prey in the same coastal environment occurred randomly when tethered prey were at least 1 m apart but predation on tethered prey less than 0.75 m apart was systematic. A distance greater than 1 m is apparently adequate to prevent a benthic-feeding predator from forming an efficient search image. Additionally, observations on lobsters tethered in benthic habitats show that they behave quiescently in an attempt to be cryptic in a given habitat.

In the pelagic tethering experiments, six postlarval lobsters were tethered at two depths (near surface and near bottom) to a 3 m floating array. This particular design was adopted after preliminary trials showed that tethered lobsters did not become entangled for the duration of the experiment. To test for independence of predation on tethered postlarvae on floating arrays, I plotted the residuals of percent mortality by location and depth treatments (Fig. 1), and inspected the spread for clumped or other patterns which may indicated confounding effects. The residuals of mortality on floating arrays appear to have a random spread. For the near bottom treatments, the actual depth along the floating transect was determined using a depth sounder to ensure that postlarval mortality did not increase due to contact with the bottom substrate. These results, along with preliminary trials and behavioral observations, indicate that the experiments were free from serious confounding artifacts and provide a reliable estimate of relative rates of habitat-specific predation.

Fig. 5.1. Residual error among replicates of floating arrays in tethering experiments. Residuals of the proportion of mortality on A. floating arrays among locations and B. floating arrays by depth.


A. Mortality by location
Residuals (e$_i$)
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
Bay
Channel
Reef


B. Mortality by depth
Residuals (e$_i$)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
Surface
Bottom

VITA

Charles Anthony Acosta was born on June 13, 1962 in Belize City, Belize in the western Caribbean. After serving for four years in the U. S. Army, he entered the University of New Orleans where he received the Bachelor of Science degree in Biological Sciences and Science Education in December 1988. He went on to receive the Master of Science degree in Marine Science from the University of New Orleans in May 1991. He has published several peer-reviewed articles from his MS thesis and this Ph.D dissertation in international scientific journals. During his graduate tenure, he was awarded several competetive research grants and assistantships.

Address: Glover's Reef Marine Research Center
P. O. Box 2310
Belize City
Belize