



W&M ScholarWorks

Dissertations, Theses, and Masters Projects

Theses, Dissertations, & Master Projects


1995

Immigration Variability and Post-Settlement Processes of the Spiny Lobster, *Panulirus argus*, in the Exuma Cays, Bahamas

Luis Coba-Cetina

College of William and Mary - Virginia Institute of Marine Science

Follow this and additional works at: <https://scholarworks.wm.edu/etd>

 Part of the [Fresh Water Studies Commons](#), [Marine Biology Commons](#), [Oceanography Commons](#), and the [Zoology Commons](#)

Recommended Citation

Coba-Cetina, Luis, "Immigration Variability and Post-Settlement Processes of the Spiny Lobster, *Panulirus argus*, in the Exuma Cays, Bahamas" (1995). *Dissertations, Theses, and Masters Projects*. Paper 1539617682.

<https://dx.doi.org/doi:10.25773/v5-8r2z-h055>

This Thesis is brought to you for free and open access by the Theses, Dissertations, & Master Projects at W&M ScholarWorks. It has been accepted for inclusion in Dissertations, Theses, and Masters Projects by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

IMMIGRATION VARIABILITY AND POST-SETTLEMENT PROCESSES OF THE
SPINY LOBSTER, *PANULIRUS ARGUS* , IN THE EXUMA CAYS, BAHAMAS.

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

by

Luis Cobá Cetina

1995


APPROVAL SHEET

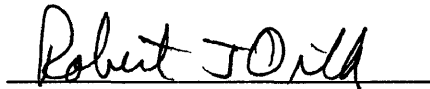
This thesis is submitted in partial fulfillment of
the requirements for the degree of


Master of Arts


Luis Cobá Cetina

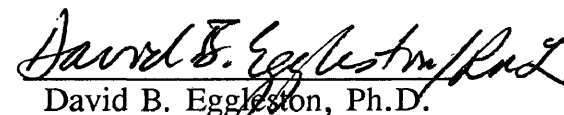
Approved, May 1995


Romuald N. Lipcius, Ph.D.
Committee Chairman/ Advisor


Robert J. Orth, Ph.D.


John Brubaker, Ph.D.


Jacques van Montfrans M.A.


David B. Eggleston, Ph.D.
North Carolina State University

This thesis is dedicated to my parents, my sister and my friends

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	vi
LIST OF TABLES	vii
LIST OF FIGURES	viii
ABSTRACT	x
INTRODUCTION	2
MATERIAL AND METHODS	5
Study site.....	5
Postlarval influx and settlement variability	5
Statistical analysis	
postlarval influx and settlement variability.....	10
Predation on early benthic instars	10
Experimental design and statistical analysis	
early benthic instars	15
Survival of post-algal phase lobsters.....	16
Experimental design and statistical analysis	
post algal phase lobsters.....	17
RESULTS.....	21
Postlarval influx	21
Settlement on artificial substrates.....	21
Survival of early benthic phase lobsters	21
Survival of post-algal phase lobsters.....	31
Predator guilds.....	40

DISCUSSION.....	42
Postlarval settlement and immigration	42
Settlement and planktonic availability.....	43
Survival of algal-phase lobsters	44
Survival of post-algal phase lobsters.....	45
LITERATURE CITED	47
VITA.....	53

ACKNOWLEDGMENTS

My major professor, Rom Lipcius deserves particular and appreciated thanks for his guidance, limitless support and confidence in my academic skills throughout the course of my research. I am grateful to Dr. David Eggleston, who encouraged me to pursue a graduate degree and for his unrestrained confidence in my abilities. I also thank my other Advisory Committee members, Drs. Robert Orth, John Brubaker and Mr. Jacques van Montfrans for being part of my committee and suggestions to improve my work.

This research could not have been successfully completed without the participation of many persons involved in different aspects of my thesis. Special thanks go to David Fuss and Bill Patton for their friendship, patience and more important for the countless hours spent in the field braving mosquitoes and numerous thunderstorms. Many thanks to Rick Rheinhard, Martha Nizinski, Larry Boles, Buck Stockhausen and Jan Cordes who helped either conducting plankton sampling or tethering lobsters. My appreciation goes also to Adele Pile and Lance Garrison for sharing their statistical knowledge.

My sincere recognition goes to Mr. Robert Wicklund and Ms. Gerri Wenz from the Caribbean Marine Research Center for their financial, administrative and logistical support. I am extremely grateful for the sympathy from the members of the Crustacean Ecology Group and the friendship of the CMRC gang: Martha Nizinski, Larry Boles and David Plotner provided me a sincere and truly and inestimable camaraderie. I am also indebted to my international friends at VIMS, Boca (Brazil) and Baek Oon (South Korea) who provided a genuine friendship in good and bad times in a shared foreign land. I also thanks Ms. Sarah Hamrick and Catherine O'Neill for their support and friendship during all these years at VIMS.

I am most thankful for the moral and economic support provided for my parents and sister throughout all these years of academic studies. I am also indebted to Shelly Horvath for her immense patience, encouragement and invaluable affection during my final months at VIMS.

LIST OF TABLES

Table	Page
1. Repeated measures analysis of variance for log (x+1) transformed postlarval densities in October 1992, with time x site and time x day as within-subject effects and day and site as between-subject effects.....	28
2. Mean numbers of potential predators for algal and post-algal phase juvenile lobsters observed during visual belt transects (60m) along experimental plots during crepuscular periods. Piscine guilds are in cm TL, estimated total length. Crustacean sizes are also in cm, CW (carapacewidth).....	43

LIST OF FIGURES

Figure	Page
1. Map of experimental and sampling sites in Barraterre, nearby Lee Stocking Island, Exuma Cays, Bahamas.	8
2. Experimental plot for tethering experiments using early benthic phase lobsters.	16
3. Experimental plot for tethering experiments using two size classes of post-algal phase lobsters, small (25-35 mm CL) and large (35-45 mm CI).	22
4. Mean monthly abundance of lobster pueruli in the plankton at two sites within the nursery grounds of Barraterre. Sampling was conducted three times during flood tide periods of the new moon. Values correspond to mean densities (individuals/1000 m ³) from paired plankton nets. Error bars = standard error.	25
5. Influx variability of lobster pueruli in the plankton at two sites in the nursery grounds of Barraterre during two days of the new moon period in October, 1992. Paired plankton nets were deployed twice during flood tides. Error bars = standard error.	27
6. Monthly settlement of spiny lobster postlarvae at two sites within the nursery grounds of Barraterre in the vicinity of Lee Stocking Island. Settlement	

was quantified using artificial settlement substrates. Sampling was conducted three times during the new moon at three-day intervals..... 30

7. Correlation plot of $\log(x+1)$ transformed data between postlarval densities in the plankton and settlement on artificial settlement substrates. Data correspond to monthly sampling conducted three times during the new moon of nine months at two sites within the nursery grounds of Barraterre..... 32

8. Mean proportional survival of early benthic phase lobsters as a function of lobster density in algal clumps. Horizontal lines connect treatments that were not significantly different. Error bars = standard error..... 35

9. Mean proportional survival of early benthic phase lobsters as a function of algal biomass. Horizontal lines connect treatments that were not significantly different. Error bars = standard error. 37

10. Proportional survival of small post-algal lobsters (25-35 mm CL) as a function of shelter type. Survival of tethered lobsters did not differ across shelter treatments. Experiments were conducted in a mangrove-lined channel within the nursery grounds of Barraterre in October, 1993..... 39

11. Proportional survival of large post-algal lobsters (35-45 mm CL) as a function of shelter type. Survival of tethered lobsters did not differ across shelter treatments. Experiments were conducted in a mangrove-lined channel within the nursery grounds of Barraterre in October, 1993..... 41

ABSTRACT

Postlarvae of the Caribbean spiny lobster, *Panulirus argus*, reinvade and colonize mangrove-fringed nursery habitats of shallow coastal embayments and lagoons. After settlement, early benthic phases and older juvenile lobsters are potentially regulated by an extensive suite of biological and physical factors. Planktonic availability of lobster postlarvae was assessed at two different sites within nursery habitats near Lee Stocking Island, Exuma Cays, Bahamas. Plankton samples were collected during flood cycles of new moon phases in September and October of 1992 and from January-August, 1993. Settlement rates were monitored for one year (September 1992-August 1993) using artificial settlement substrates during new moon periods.

Overall, postlarval recruitment occurred with a major pulse in early fall (October) and a minor pulse in the winter (January). Settlement and planktonic influx were consistent within lunar pulses (1-5 days), but delivery rate of lobster pueruli in the plankton was not uniform during flood cycles. Settlement on collectors varied spatially between sampling stations, even though postlarval supply appeared to be spatially homogeneous on the order of 1-2 kilometers. Postlarval influx and settlement rates were significantly correlated, indicating that settlement of spiny lobster postlarvae is regulated to a large extent by planktonic availability of postlarvae.

By using manipulative experiments, the impingement of predation on survival of the early benthic phase and older juvenile lobsters at different levels of habitat structure (algal biomass and type of shelters) and numbers of conspecifics was examined. Survival of early-benthic-phase lobsters was significantly affected by both algal biomass and density of early-benthic-phase lobsters within a clump. These results suggest that this type of habitat use can result in density-dependent mortality or emigration from algal clumps, producing a sparse distribution in the field.

Survival of two size classes of post-algal phase lobsters (25-35 and 35-45 mm CL) did not differ significantly across shelter types and number of conspecifics (1 or 2). The protection afforded by the different types of refuge was similar and there was no evidence that predation regulated the survival of these larger juveniles across the mangrove channel where experiments were conducted. The higher survival rates obtained in the experiments could be explained by limitations upon the efficiency of the predator assemblages due to extremely high tidal currents.

The collective information indicates that both pre-settlement (e.g., planktonic availability of post larvae) and post-settlement (i.e., predation upon post larvae and early-benthic-phase lobsters) processes determine the distribution and abundance of the Caribbean spiny lobster.

IMMIGRATION VARIABILITY AND POST-SETTLEMENT
PROCESSES OF THE SPINY LOBSTER, *PANULIRUS ARGUS* ,
IN THE EXUMA CAYS, BAHAMAS.

INTRODUCTION

For marine species with long-lived planktonic larvae, recruitment variability is one of the most critical processes regulating population abundance and distribution (Gaines and Roughgarden, 1987; Fogarty et al., 1991; Doherty and Fowler, 1994). Recruitment fluctuations are determined by availability of larval and postlarval stages, settlement rates, post-settlement movements and survival rates, and intra- or inter-specific interactions (Connell, 1985; Caddy, 1986; Scheltema, 1986).

Settlement rates are also regulated by local hydrodynamics, environmental conditions, physical and chemical attributes of settlement substrates, mortality rates, larval behavior and nutrition (Lipcius et al., 1990; Raimondi, 1991). After settlement, regulatory processes such as predation, competition, disease and habitat availability can alter patterns defined at settlement. These processes might account for interannual variations in population size and could potentially generate demographic bottlenecks. Therefore, definition of both biological and physical factors regulating recruitment is fundamental for a better understanding of the dynamics of marine populations, particularly that of commercially important species.

The Caribbean spiny lobster, *Panulirus argus* (Crustacea: Decapoda: Palinuridae), is a motile benthic invertebrate characterized by the processes described above. *P. argus* passes through a complex life cycle including: egg, phyllosome larval

stages, puerulus postlarva, juvenile and adult, each of which is characterized by a distinctive habitat use (Phillips et al., 1980). After the larval stages drift 4-8 months in the oceanic plankton, the last phyllosome stage metamorphoses into a transparent, free-swimming and non-feeding puerulus postlarva (Sweat, 1968; Lyons, 1980; Wolfe and Felgenhauer, 1991). Spiny lobster pueruli are advected onshore by oceanic or coastal currents and settle in shallow nursery areas typical of mangrove-fringed coastal embayments (Lewis et al., 1952; Calinski and Lyons, 1983).

Using the intricate habitat structure of red algae (*Laurencia spp.*) as a cue, settlement takes place at approximately 6 mm CL (carapace length, as measured from the base of the rostral horns to the posterior edge of the cephalothorax). After settlement, the young juveniles acquire cryptic pigmentation and occupy clumps of *Laurencia* solitarily until reaching 15-25 mm CL (Andree, 1981; Marx and Herrnkind, 1985 a, 1985b). At this time, they adopt a gregarious behavior as they move out of the algae to seek daytime shelter in physical structures such as solution holes, ledges, sponges, and coral heads (Marx and Herrnkind, 1985a). The young juveniles that dwell in algae and similar habitats are termed early benthic-phase juveniles (Lipcius and Cobb, 1994), and correspond to the early juvenile phase of other lobsters and crabs.

Juvenile lobsters reside in biotic (e.g., loggerhead sponges) or abiotic (e.g., solution holes) structures of nursery habitats such as shallow seagrass beds, and undergo ontogenetic movements as they grow to deeper reef areas where reproduction occurs (Herrnkind, 1980; Lipcius, 1985). Breeding peaks during spring and early summer when

adult females spawn egg masses and release an early phyllosome larval stage which is transported by surface currents into oceanic habitats.

Recruitment of spiny lobster postlarvae to settlement habitats is characterized by a distinctive lunar periodicity, with a peak during the first quarter of the new moon. Settlement is also affected by the availability of adequate substrate, particularly large unsilted clumps of the red alga *Laurencia spp.* (Herrnkind and Butler, 1986). Results of investigations on postlarval recruitment in different regions of the Caribbean reveal interannual variations resulting in geographically-specific patterns (Little, 1977; Lyons et al., 1981; Monterrosa-López, 1986; Farmer et al., 1989; Ward, 1989; Briones-Fourzán, 1994; D. Eggleston and R. Lipcius, unpublished data).

However, attempts to define relationships between the magnitude of recruitment and abundance of juveniles and adults have been unsuccessful, probably due to the scarcity of early benthic instars in the field (1/36 m² in Florida Bay; Marx and Herrnkind, 1985a). This sparse distribution suggests that density-dependent mechanisms may act on these early stages and could indicate a demographic bottleneck (Caddy, 1986).

This research addresses some critical processes influencing recruitment of the Caribbean spiny lobster, *P. argus*, focusing on temporal and spatial variability of settlement and influx of planktonic postlarvae into nursery habitats. I also evaluated the impact of biotic and physical factors such as predation and habitat structure upon spiny lobster survival. In this investigation, "recruitment" is considered as post-settlement individuals surviving arbitrary periods of time to subsequent life stages, and "settlement"

as the influx of postlarvae from the pelagic environment to settlement substrates. In the first part of this study, I investigate the variation in abundance of lobster pueruli in the plankton and settlement of postlarvae in artificial settlement substrates.

The second part of this research examines, through manipulative experiments, the impingement of predation on survival of early benthic phase and older juvenile lobsters at different levels of algal biomass (a component of habitat complexity) and numbers of conspecifics.

MATERIAL AND METHODS

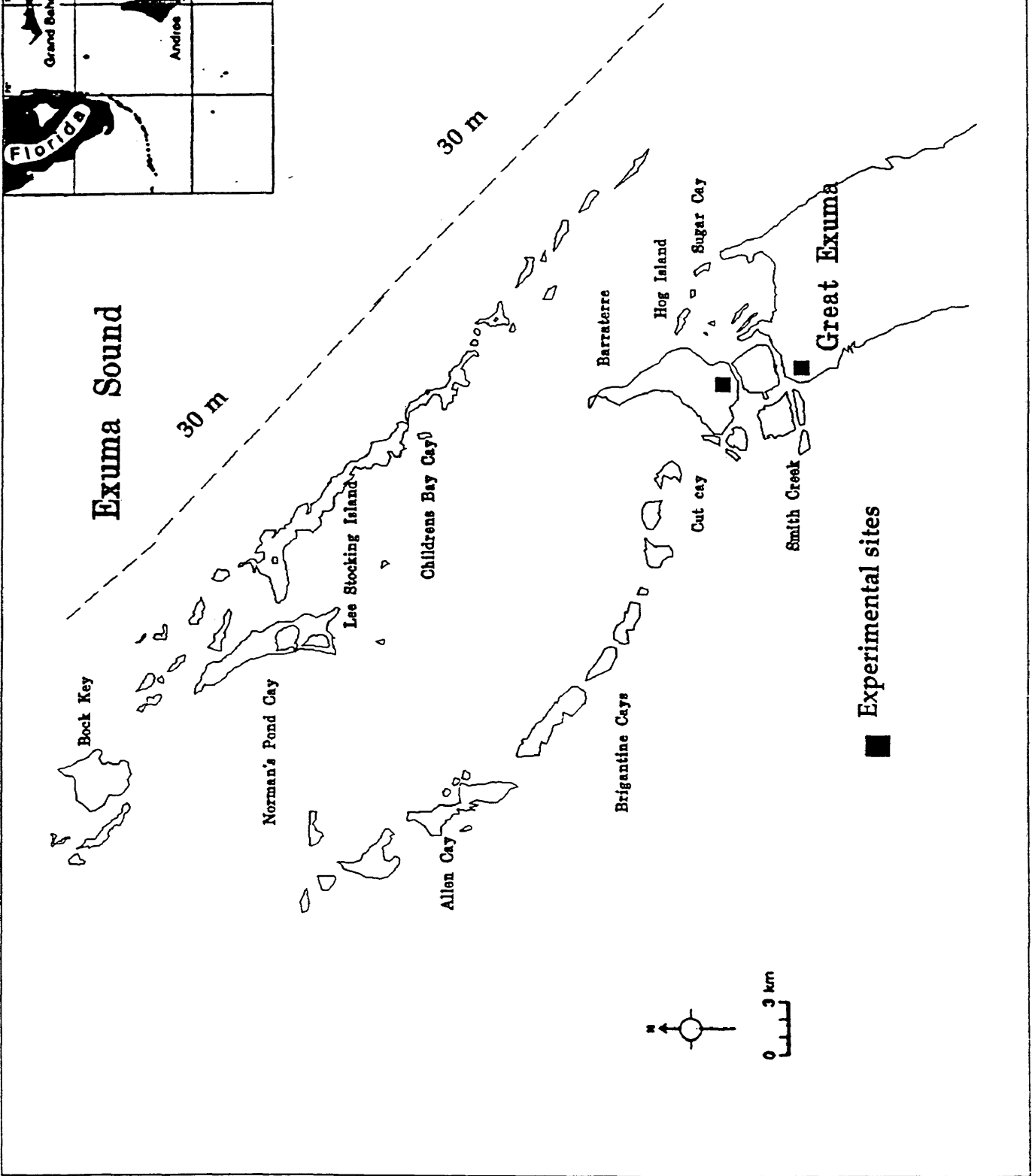
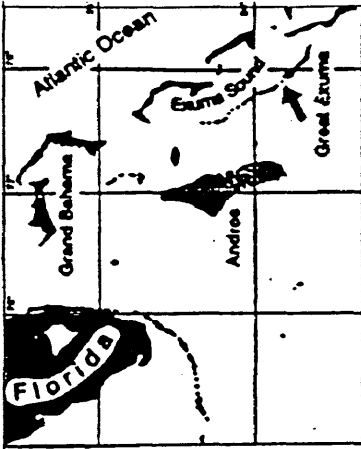
Study site

Experiments were conducted near Lee Stocking Island (23°45' N, 76°10'W) located at the southern Exuma Cays, Bahamas (Fig. 1). The Exuma Cays encompass a chain of islands separating the deep Exuma Sound (2000 m) from the shallow Great Bahama Bank (3-4 m). Numerous tidal cuts separate the islands and allow exchange between the Bank and Exuma Sound. Habitats within the bank consist of a complex system of mangrove-bordered cays and shallow embayments composed of patchily-distributed macroalgal beds (primarily *Batophora spp.* and *Laurencia spp.*), extensive seagrass meadows (*Thalassia testudinum*), and numerous coral formations.

Postlarval influx and settlement variability

Sampling was conducted within nursery grounds of the Barraterre area near Lee Stocking Island. Postlarval influx was quantified during new-moon periods in September and October, 1992 and January through August, 1993. Settlement variability was quantified from September, 1992 through August, 1993. Collections were made on three days of each sampling period at two inter-island channels (located 3 km apart) and influenced by strong tidal flows from the Exuma Sound. Both sites are part of mangrove-fringed channels serving as nursery habitats for postlarvae and young juvenile.

Figure 1. Map of experimental and sampling sites in Barraterre, nearby Lee Stocking Island, Exuma Cays, Bahamas.



On each sampling date postlarval influx was quantified using plankton nets, and settlement rates were estimated from the numbers of postlarvae and young juveniles settling on artificial settlement substrates. Incoming pueruli were sampled with two plankton nets (2000 μ mesh size) attached to a PVC frame (2 m long x 1 m high), separated 1 m apart, each with a filtering area 50-cm wide extending from the surface to a 1-m depth. Each net array was equipped with three flowmeters (General Oceanics model 2030) to calculate filtered water volume. Two of the flowmeters were suspended from the frame in the opening of each net, and the third one between the two nets. The plankton nets were deployed from two bridges at each site during night flood tides. Each bridge is in the middle of the channel and consists of a cylindrical culvert (2.5-m diameter) connecting both parts of the channel. This configuration minimized the exchange of tidal flow, but created a funneled flux of water through the culverts. Nets were deployed at the leeward side of the bridges as close as possible to the water stream from the pipes to maximize the catch efficiency of the net. Since postlarvae enter settlement habitats at night, collecting periods were adjusted to match the beginning of flood tidal cycles with periods of nightfall. In October 1992, influx variability through time was assessed by deploying each paired net every two hours during flood tide at both sites within one sampling period.

After collection, plankton samples were transferred to plastic buckets, and pueruli then sorted and counted in the lab. Postlarval abundance was standardized as the number of postlarvae per 1000 m³ of water filtered, with a mean density of postlarvae from each

set of paired nets. Water temperature was recorded at the time of collection.

Settlement patterns of spiny lobster and other crustaceans have been successfully monitored using artificial settlement substrates (Witham et al., 1964; Phillips, 1972; Lyons et al., 1981; Monterrosa-López, 1986; Farmer et al., 1989; van Montfrans et al., 1990; Ward, 1990; Bannerott, 1992; Briones-Fourzán, 1994). For the Caribbean spiny lobster, modified versions of the Witham collector (Witham et al., 1964) have been used throughout the Caribbean. Artificial substrates (collectors) were assembled using a rectangular frame of PVC (2-cm diameter) with six cross bars. Substrate material consisted of rectangular sheets (70 cm length x 40 cm width) of air conditioning filter material (i.e., "Hog's Hair") which was folded and tied to each cross bar with plastic cable ties. The resulting settlement substrate had a total of 12 "leaves" with a potential settlement area of 1680 cm². Collectors were suspended at the water surface with two styrofoam buoys tied to the frame, and anchored to a mooring system of two cinder blocks with a marking buoy.

Postlarval settlement was estimated at the nursery grounds around Barraterre, with two sets of four settlement substrates. Artificial substrates were deployed at the windward side of the bridges where plankton samples were taken, lined up in a rectangular array, and separated by 20 m. Hence, collectors were directly exposed to the incoming tidal flow from the Exuma Sound before it passed through the bridges. Collectors were surveyed three times (i.e., every third day) during the new moon period beginning on the first day of the lunar phase. Each collector was retrieved with a nylon

mesh bag (2000 μ), and postlarvae were recovered by two persons searching twice through the "leaves" of the collector. Postlarvae were measured with a caliper (CL in mm) and the stage recorded based upon pigmentation at time of settlement to distinguish between recently settled and early benthic stages with the following code: T=transparent puerlis, O+T= orange and transparent puerlis, both corresponding to recently-settled pueruli, B+W= brown and white, conforming to the first benthic instar phase.

Statistical analysis: postlarval influx and settlement variability

All data were log (x+1) transformed to eliminate homogeneity of variance as recommended by Underwood (1981). Data were plotted and visually inspected to examine conformity to the normal distribution. When sample variances remained heterogeneous the null hypothesis was rejected at a significance level lower than the P-value of the test for homogeneity of variance (Underwood, 1981). In all models, multiple comparison tests were conducted as recommended by Day and Quinn (1989).

Postlarval abundance in the plankton (i.e., densities in individuals/1000m³) and settlement data (mean number individuals/collector/day) were analyzed separately using a two-factor ANOVA model (GLM procedure; SAS Institute, 1985) with month and day as fixed factors and postlarval density as the dependent variable. Settlement on collectors was analyzed with a three- factor ANOVA model with month, day and site as fixed factors and the mean number postlarvae/collector/day as the dependent variable. Correspondence between planktonic influx and settlement was analyzed with a Pearson

correlation analysis.

Influx variability of postlarvae through time was also examined for October 1992 with a repeated-measures ANOVA model testing the null hypothesis of no differences in the number of incoming postlarvae through time, using site and day as between-subjects effects and time as the within subject effect.

Predation on early benthic instars

Postlarval stages of the Caribbean spiny lobster use the intricate structure of benthic macroalgae as a cue for settlement (Marx and Herrnkind, 1985a; 1986). The open lattice-work formed by branches of the red alga *Laurencia* spp. (*L. poteii* and *L. obtusa* : Marx and Herrnkind, 1985a) provides an excellent habitat for newly-settled postlarvae. Algal-phase juveniles make use of both the architecture and heterogeneous mixtures of algal epiphytes, in addition to potential prey, when selecting habitats (Marx and Herrnkind, 1985a; Herrnkind and Butler, 1986; Marx, 1986; Herrnkind et al., 1988). Early benthic instars display a sparse and cryptic distribution (Marx and Herrnkind, 1986a). In the present study area, this apparently sparse distribution was confirmed after unsuccessful attempts at finding early benthic instars in natural substrates (Lipcius, unpublished data), thus precluding attempts to relate natural densities at the time of settlement with planktonic availability. Direct observations of agonistic behavior of conspecifics suggest that algal-phase juveniles might exhibit a cryptic and solitary residency while dwelling in algal clumps (Marx and Herrnkind, 1986). Although

inconclusive, these observations imply that this form of microhabitat use, combined with dispersed larval settlement, predation risk and nomadism, may enhance a scattered distribution of young lobsters (Herrnkind and Butler, 1986).

Also, results from experiments of predation-induced mortality upon different juvenile size classes showed a size-specific response in dissimilar habitats with higher relative mortality for algal-phase lobsters (particularly early benthic instars) compared to older juveniles (Smith and Herrnkind, 1992). This represents a constraint in the number of potential recruits for later life stages, which may produce a demographic bottleneck, determining population distribution and size (Caddy, 1986; Gaines and Roughgarden, 1987; Menge and Sutherland, 1987; Caddy and Stomatopoulos, 1990).

Thus, I used a series of tethering experiments to examine the impact of predation and the effects of algal biomass and number of conspecifics on the survival of recently settled lobsters. Tethering is a valuable technique in assessing relative mortality for crabs (Heck and Thoman, 1981; Wilson et al., 1987; Fernández, 1993; Pile, 1993); mollusks (Marshall, 1992) and early benthic phase lobsters (Herrnkind and Butler, 1986; Smith and Herrnkind, 1992). Although tethering may induce biases by reducing prey ability to escape from predator attacks, it allows the estimation of relative rates of mortality due to predation in the field (Herrnkind and Butler, 1986). Furthermore, this technique is useful for examining the refuge value of habitats since mortality of prey is due to both the effect of habitat structure and to differences in predator guilds (Minello, 1993).

Tethering experiments were conducted in a mangrove-fringed channel around Barraterre. Lobsters used in the experiment were obtained either as first instars or as transparent postlarvae from either artificial settlement substrates or plankton nets. After collection, individuals were kept in aquaria until they reached 6-7 mm CL, corresponding to the first benthic instar. Tethering of algal-phase lobsters has been effectively used in previous experiments in Florida (Herrnkind and Butler, 1986; Smith and Herrnkind, 1992). Responses to the technique were evaluated by observing 10 tethered individuals in an aquarium for 48 hours to assess survivorship and holding capacity of the tether. Postlarvae were tethered by using a 10-cm long, 2-kg-test monofilament line in which one of the ends was glued to the dorsum of the carapace and the other tied to a 30-g flat washer which was then buried in the sand surrounding the clump (Fig. 2).

Three postlarval densities (1, 2 and 8 individuals) and three algal volumes (100, 200 and 800 ml) of the red alga *Laurencia spp.* were used to examine relative survival of postlarvae. Wet algal clumps were measured volumetrically in a 2-L graduated flask. The larger 800-ml clumps were made by the addition of equally measured 100-ml clumps, which were intertwined with a monofilament line using fishing lead sinks to hold them in the sand. Postlarval densities used in each biomass were standardized for a corresponding algal volume. Therefore, combinations of 1, 2 and 8 lobsters were used for 100, 200 and 800 ml clumps, respectively. In this way, a standardized number of lobsters was assigned to each treatment, providing an equally distributed space per individual within a clump, and minimizing encounters between conspecifics.

Figure 2. Experimental plot for tethering experiments using early benthic phase lobsters.



Treatment 1

100 ml wet algal volume x 1 lobster

area = 51.5 cm²



2m



Treatment 2

200 ml wet algal volume x 2 lobsters

area = 81.1 cm²



2m



Treatment 3

800 ml wet algal volume x 8 lobsters

area = 211.1 cm²



2m

Experimental design and statistical analysis: early benthic instars

Tethering trials encompassed 10 replicates per treatment with lobster survival inspected after 24 hours. After that period, any loss was replaced and the remaining lobsters randomly reassigned to treatments (Hurlbert, 1984). Predation events were evidenced by either carapace remnants or conspicuous bite marks at the end of the monofilament line (Herrnkind and Butler, 1986; Eggleston et al., 1990, 1992; Smith and Herrnkind, 1992). Also, to quantify possible piscine predators, crepuscular visual transects were conducted in the experimental area. Belt transects were performed by a diver snorkeling 60 meters along the experimental plot, recording the number and size of any potential predators.

Proportional survival of first-instar lobsters per trial was calculated by dividing the number of lobsters that survived by the number of individuals that did not escape. Data were analyzed with a single-factor ANOVA model with algal volume as the independent variable and proportional survival as a dependent variable.

Survival of post-algal phase lobsters

Post-algal phase juveniles move out from the algae when they reach 15-25 mm CL to occupy solution holes, ledges, coral heads, sponges and other similar structures during daytime, often with other conspecifics (Andree, 1981; Marx and Herrnkind, 1985; Herrnkind and Butler, 1986). This change in habitat and behavior (from solitary to gregarious) represents an ontogenetic shift explained by the apparent requirement for a

suitable habitat where the individual can attain adequate food and refuge from predation.

It has been suggested that, although juvenile lobsters retain a refuge from predation while residing in the algae, they become less effective in their movements and foraging activity (Smith and Herrnkind, 1992). In theory, as juvenile lobsters grow, larger lobsters should experience a lower risk to predation (Smith and Herrnkind, 1992). However, in contrast to the positive size hypothesis suggested by Werner and Gilliam (1984), Lipcius et al., (in press) found an inverted size refuge in seagrass meadows where small lobsters exhibited higher survival rates than larger juveniles.

In this experiment, survival of two size classes of juvenile lobsters (young and older juveniles) was examined as a function of habitat complexity (algal biomass, sponge and bare sand), and number of conspecifics. Considering that for many marine species ontogenetic shifts are regulated by predation risk and refuge usage associated with body size (Werner and Guillian, 1984), I tested the null hypothesis that survival rates of these two size classes of juveniles do not differ by habitat nor by the number of conspecifics.

Size classes were determined after sampling the population structure of juvenile lobsters that reside in algal habitats around Barraterre channels. These were 25-35 mm CL young juveniles and 35-45 mm CL older juveniles. Lobsters used in the experiments were collected from nearby mangrove channels and held in seawater tables. Only intermolt, hard-shelled lobsters that displayed healthy responses (e.g., vigorous tail flipping) were used in the experiments. Lobster survival was tested by tethering juvenile lobsters in four levels of habitat complexity: bare sand, sponge and two algal volumes

(2 and 4-L wet biomass), and using different numbers of conspecifics (1 or 2), with a caged lobster as a control (Fig. 3), resulting in a total of nine lobsters per trial with eight replicates per treatment.

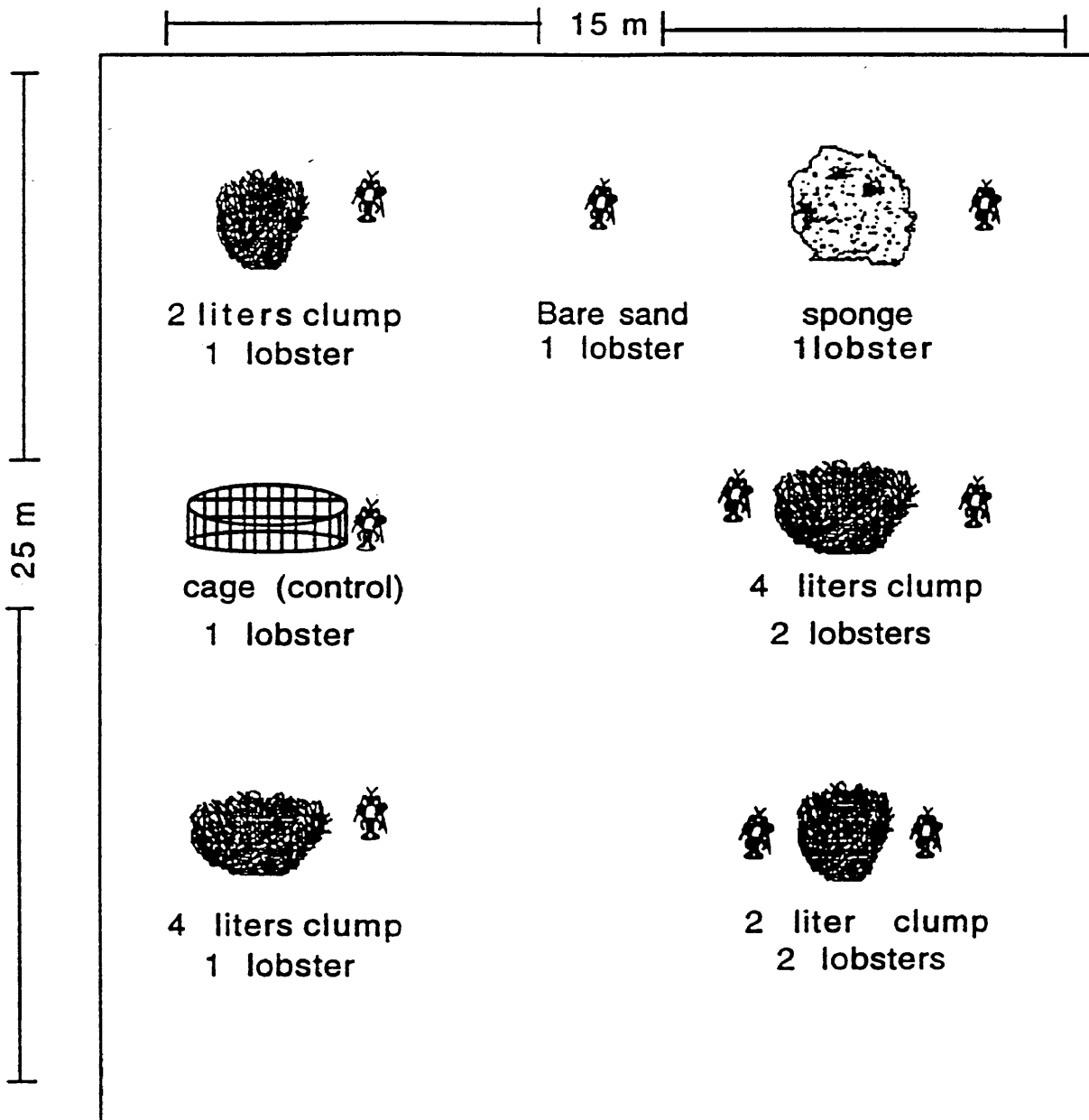
Tethers were made of clear monofilament line (5.5 kg test) and were 35 and 50 cm long respectively, for young and older juveniles. One end of the tether was attached and glued with cyanoacrylate cement to a plastic cable tie and fastened around the lobster carapace between the fourth and fifth walking legs. The cable tie was secured to the lock with a drop of glue and to the dorsal exoskeleton by tying and gluing the other end of the monofilament to a 10-cm galvanized nail. Clumps of red algae (*Laurencia spp.*) were collected from nearby channels; 2 and 4-L wet volume clumps were made by measuring algal volume in a graduated flask. Individual clumps were tied to rebar rods which were then buried in the sand to resemble natural algal clumps. Tethered lobsters were placed near the corresponding treatment and secured to the bottom by hammering the galvanized nail to the substrate.

Experimental design and statistical analysis: post algal phase lobsters

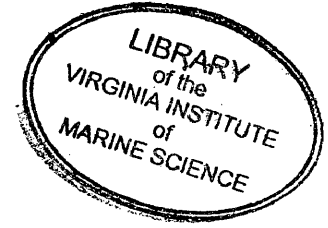
Treatments were randomly allocated, as recommended by Hurlbert (1984), within a rectangular plot measuring 15 m length x 10 m width. In each experimental plot, treatments were separated by 5 meters. Experiments consisted of eight replicates per treatment with a duration of 24 hours per trial. Predation events were corroborated by the presence of carapace remnants that remained glued to the cable tie. For each

experimental plot, frequencies of lobsters that had been killed or survived were recorded and treatments with missing individuals were reassigned new lobsters. Frequencies of mortality for juvenile lobsters were analyzed across treatments for each size class using a log-linear G-test (Sokal and Rohlf, 1981) to examine the hypothesis of no effect of habitat type and number of conspecifics on mortality rates.

Figure 3. Experimental plot for tethering experiments using two size classes of post-algal phase lobsters, small (25-35 mm CL) and large (35-45 mm CL).



RESULTS



Postlarval influx

Mean postlarval densities in the plankton varied from 0.0 to 100.9 individuals/1000 m³. Highest influx of lobster postlarvae occurred in September and October, 1992 and January, 1993 (Fig. 4). Densities of pueruli differed significantly between months (ANOVA, $F=10.58$, $d.f.=8$, $p=0.0001$) but not by days ($p>0.05$). Also, in October 1992, there was a significant difference in the densities of incoming postlarvae through time (Fig. 5, Table 1). None of the remaining effects differed significantly (Table 1).

Settlement on artificial substrates

Abundance of postlarvae on collectors ranged from 0 to 5 (mean number of individuals/collector/day), with peaks of high settlement occurring in September and October, 1992 and January, 1993 (Fig. 6). Settlement of postlarvae differed significantly between months and sites but not between days (ANOVA, $F=4.22$, 17.15 ; $p < 0.05$). Settlement on artificial settlement substrates was significantly and positively correlated with planktonic densities (Fig. 7) (Pearson's $r=0.80$, $P<0.05$).

Figure 4. Mean monthly abundance of lobster pueruli in the plankton at two sites within the nursery grounds of Barraterre. Sampling was conducted three times during flood tide periods of the new moon. Values correspond to mean densities (individuals/1000 m³) from paired plankton nets. Error bars = standard error.

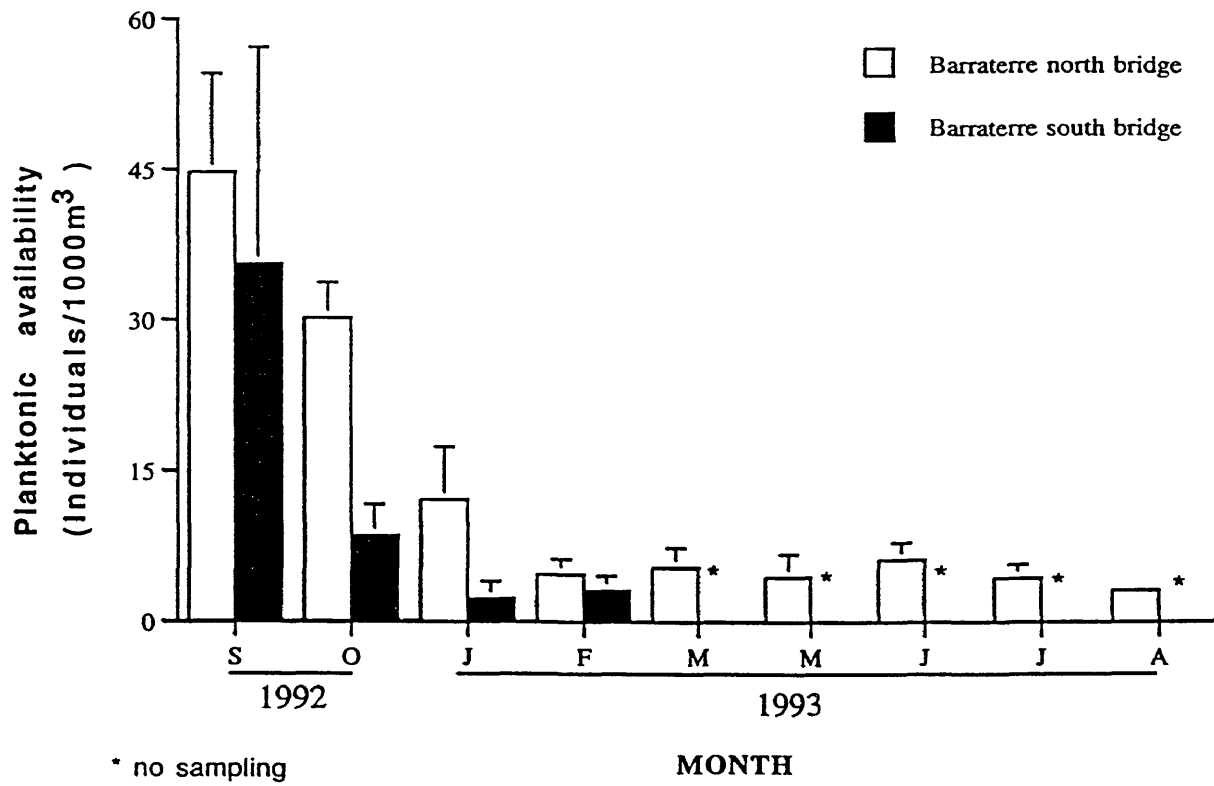


Figure 5. Influx variability of lobster pueruli in the plankton at two sites in the nursery grounds of Barraterre during two days of the new moon period in October, 1992. Paired plankton nets were deployed twice during flood tides. Error bars = standard error.

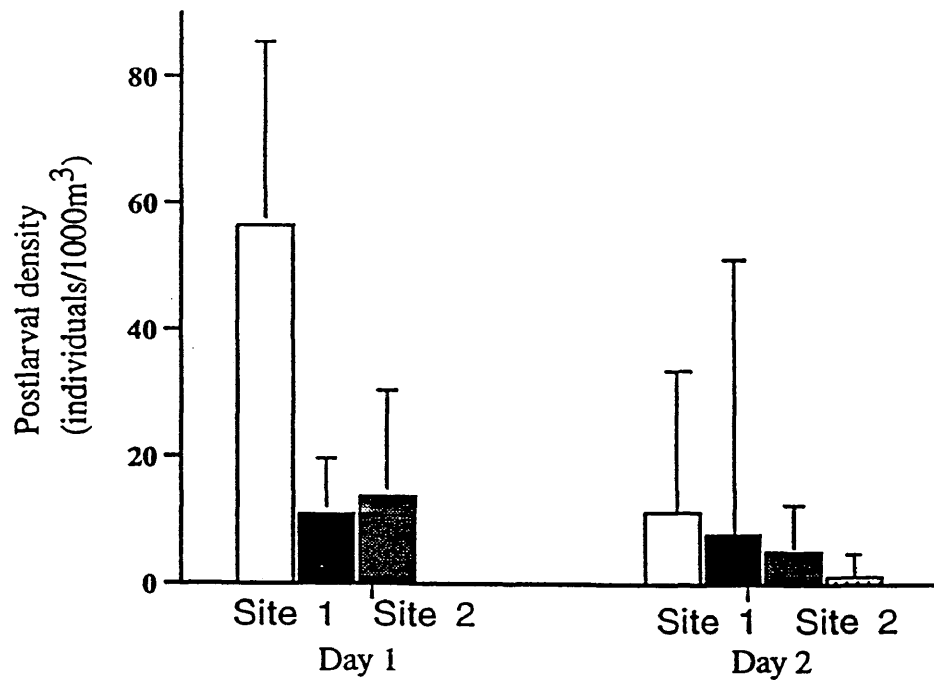


Table 1. Repeated measures analysis of variance for log (x+1) transformed postlarval densities in October 1992, with time x site and time x day as within - subject effects and day and site as between-subject effects.

Within subject effects					
Source	d.f.	SS	Mean Square	F Value	P > F
Time	1	0.79380	0.79380	441.0	.0303*
Time*Day	1	0.08405	0.08045	46.69	.09205
Time*Site	1	0.08405	0.08045	46.69	.09205
Error	1	0.0018	0.0018		

Between subject effects					
Source	d.f.	SS	Mean Square	F	P > F
Day	1	0.2112	0.21125	1.03	0.4951
Site	1	0.73205	0.73205	3.57	.03097
Error	1	0.2048	0.20488		

Figure 6. Monthly settlement of spiny lobster postlarvae at two sites within the nursery grounds of Barraterre in the vicinity of Lee Stocking Island. Settlement was quantified using artificial settlement substrates. Sampling was conducted three times during the new moon at three-day intervals.

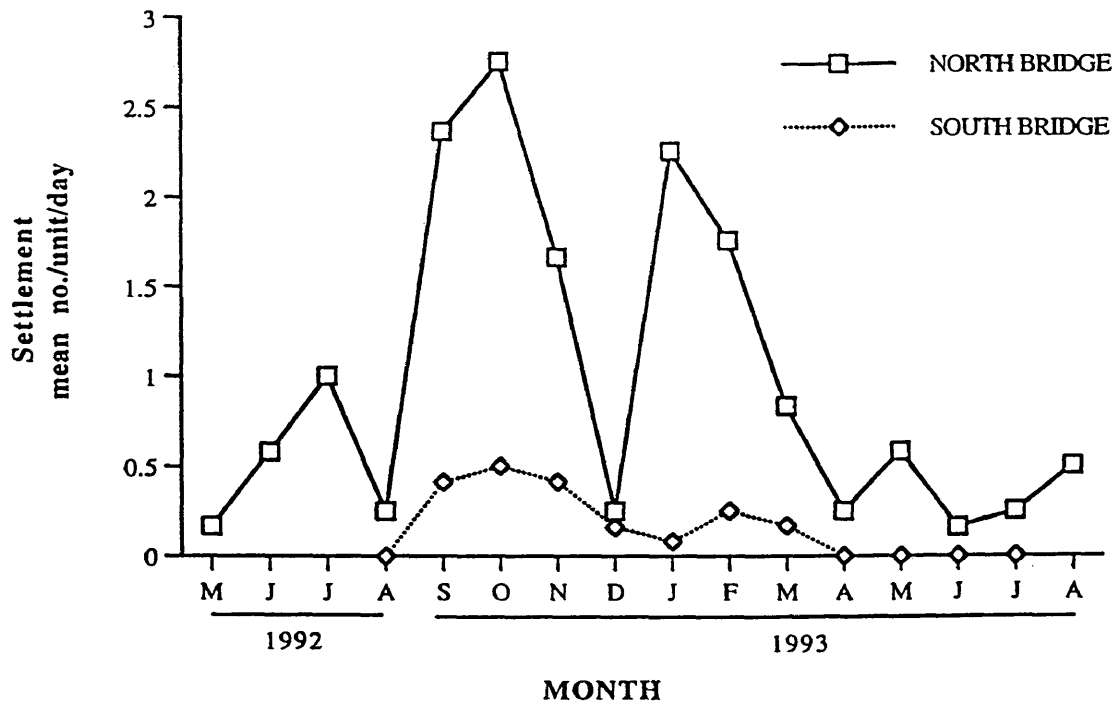
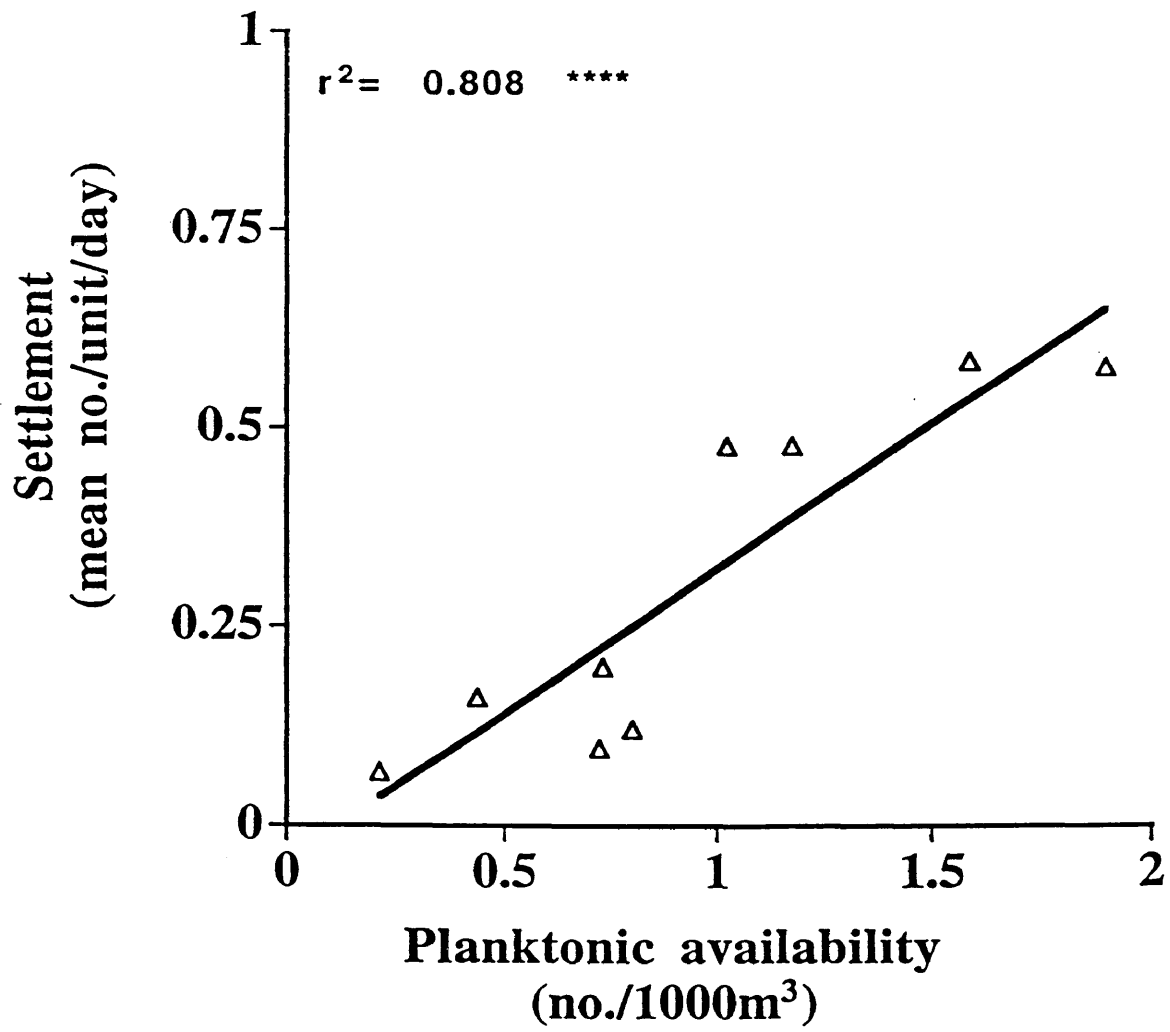


Figure 7. Correlation plot of $\log(x+1)$ transformed data between postlarval densities in the plankton and settlement on artificial settlement substrates. Data correspond to monthly sampling conducted three times during the new moon of nine months at two sites within the nursery grounds of Barraterre



Survival of early benthic phase lobsters

Survival of early benthic phase lobsters differed statistically between treatments (ANOVA, $F=14.72$, d.f.=2, $p=0.0001$). Percent mortality varied from 35% to 100% in large clumps, while for small clumps it varied from 0 to 50%. Postlarval survival differed significantly between high density (8 individuals), large *Laurencia* clumps (800 ml), and that in small and medium size clumps (Fig. 8) (Ryan's Q test, $p < 0.05$).

Lobster density also had a significant effect on postlarval mortality (ANOVA, $F=13.193$, d.f. =2, $p < 0.0001$). Mortality of early benthic phase lobsters increased as a function of density. Densities with 0.040 indiv./cm² experienced the highest mortality (40%) while solitary lobsters did not experience mortality (Fig. 9).

Survival of post-algal phase lobsters

Survival of small juvenile lobsters (25-35 mm CL) did not differ significantly across shelter types (Fig. 10) (G-test, $\chi^2 = 10.52$, d.f. =6, $p=0.105$). Lobsters allocated in the 4-liter *Laurencia* treatment with one or two lobsters, generally experienced higher predation rates compared to other treatments. The power of the G-test was 0.68. A calculation of sample size indicated a minimum of 180 juvenile lobsters would be required to obtain a conventional power of 0.8. Thus, the observed differences was deemed biologically insignificant.

Large juvenile (35-45 mm CL) did not experience significant differences in survival among treatments (Fig. 11) (G-test, $\chi^2 = 7.67$, $p= 0.264$) . Higher predation

Figure 8. Mean proportional mortality of early benthic phase lobsters as a function of lobster density in algal clumps. Horizontal lines connect treatments that were not significantly different. Error bars = standard error.

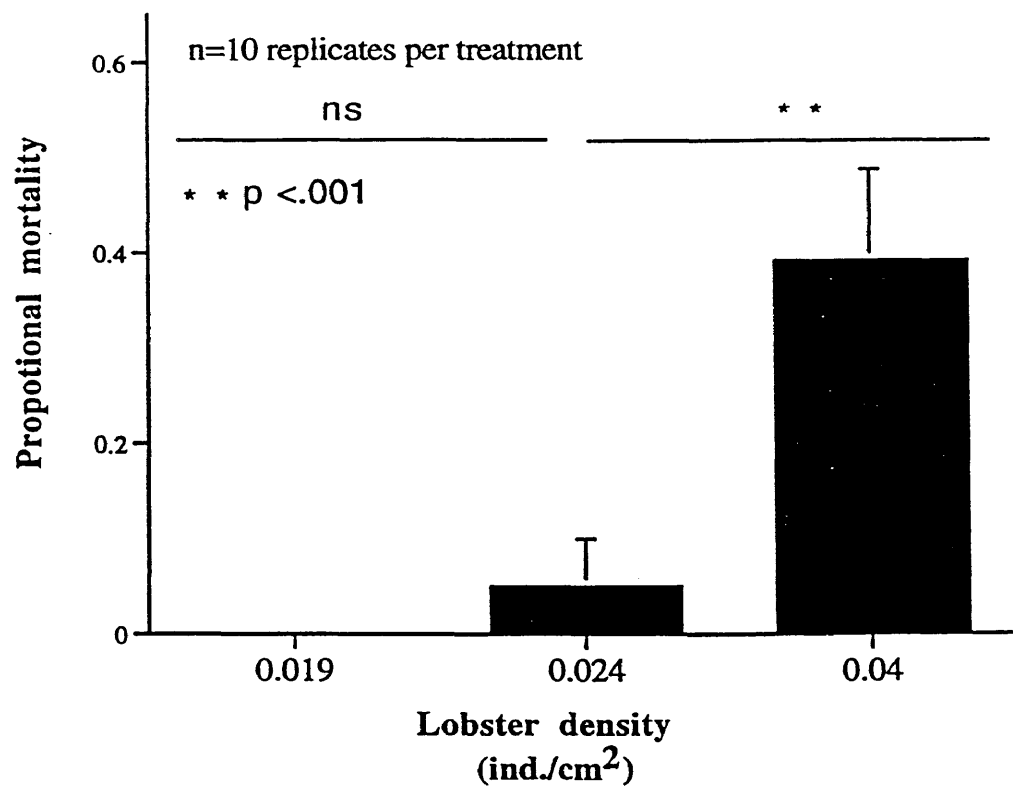


Figure 9. Mean proportional survival of early benthic phase lobsters as a function of algal biomass. Horizontal lines connect treatments that were not significantly different. Error bars = standard error.

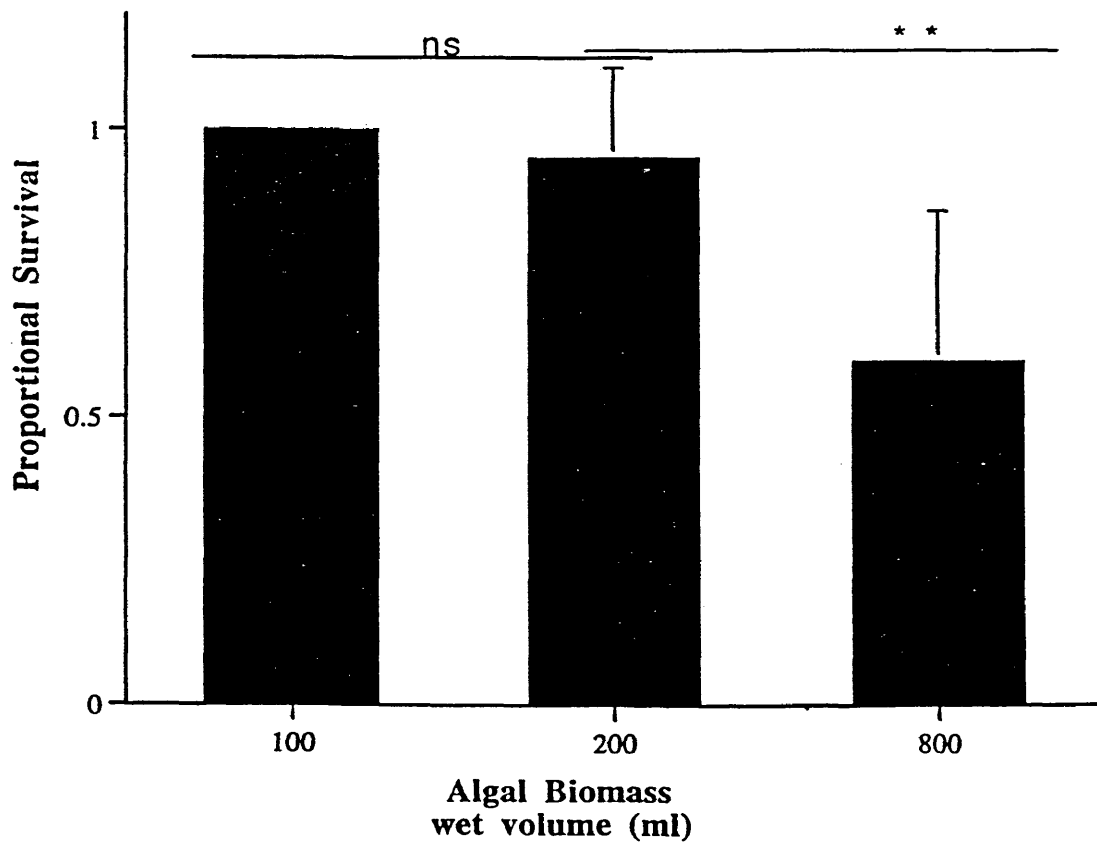
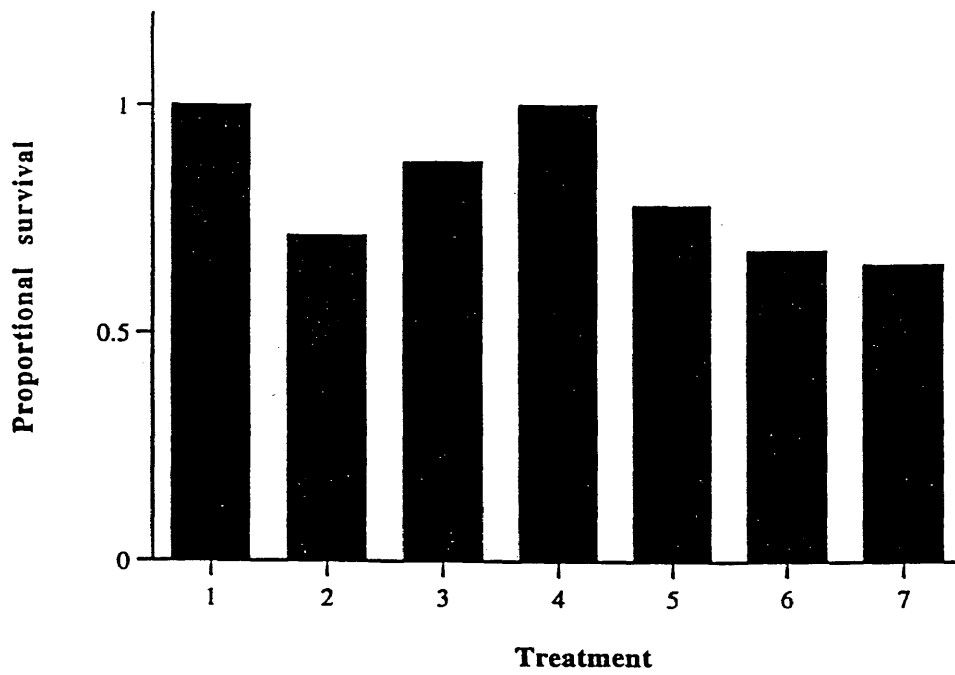


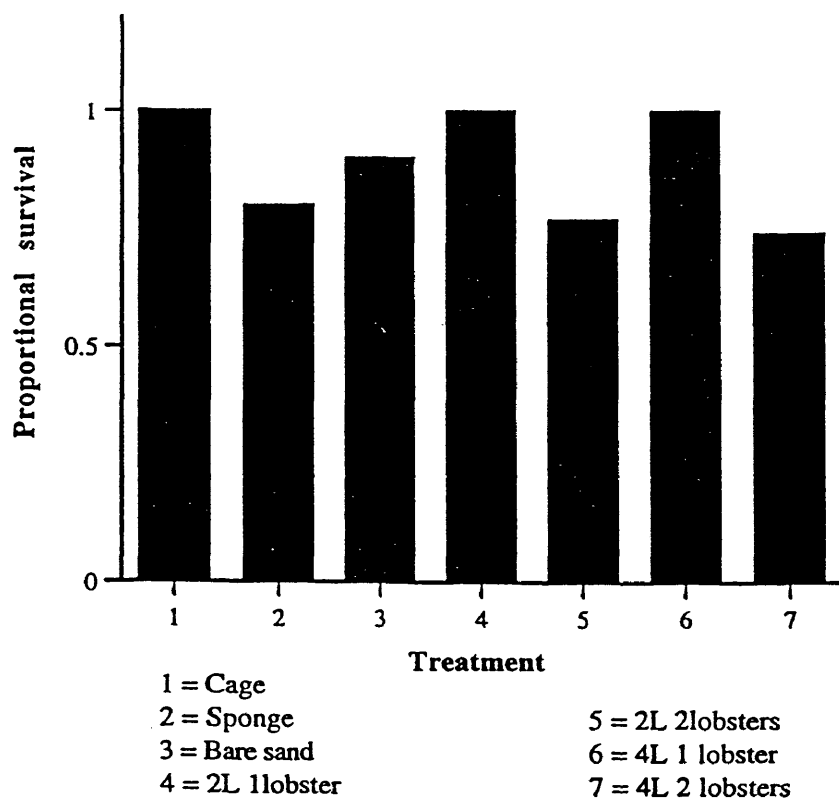
Figure 10. Proportional survival of small post-algal lobsters (25-35 mm CL) as a function of shelter type. Survival of tethered lobsters did not differ across shelter treatments. Experiments were conducted in a mangrove-lined channel within the nursery grounds of Barraterre in October, 1993.



1 = Cage
2 = Sponge
3 = Bare sand
4 = 2L 1lobster

5 = 2L 2lobsters
6 = 4L 1 lobster
7 = 4L 2 lobsters

Figure 11. Proportional survival of large post-algal lobsters (35-45 mm CL) as a function of shelter type. Survival of tethered lobsters did not differ across shelter treatments. Experiments were conducted in a mangrove-lined channel within the nursery grounds of Barraterre in October, 1993.



occurred in the treatments of individual lobsters tethered to 4 liter clumps of *Laurencia*. Power for this experiment was 0.4. A minimum sample size of 244 lobsters was required to obtain a conventional power of 0.8. Hence, the differences were again deemed biologically insignificant.

Predator guilds

Visual transects across the experimental site revealed that potential predators of both early benthic phase and post-algal phase juveniles were abundant (Table 2). Juveniles of the Nassau grouper (*Epinephelus striatus*) were the most abundant, followed by mojarras (*Gerres spp.*), grunts (*Haemulon spp.*) and snappers (*Lutjanus spp.*). Large juvenile Nassau grouper (15-25 cm TL) were often found cohabiting with post-algal juvenile lobsters or with conspecifics inside solution holes.

Potential predators of algal-phase lobsters, such as juvenile Nassau groupers (8-10 cm TL) were found concealed within large clumps of *Laurencia* growing on *Porites. spp* corals. This size class of Nassau grouper was also often sharing shelter with transitional algal-phase lobsters (18-25 mm CL). Other potential predators of algal phase lobsters included schools of mojarras (*Gerres spp.*), which approached algal clumps with tethered lobsters, bar jacks (*Caranx ruber*) and jolthead porgys (*Calamus bajonado*). Large snappers were also observed foraging close to mangroves roots near the experimental plots.

Table 2. Mean numbers of potential predators for algal and post-algal phase juvenile lobsters observed during visual belt transects (60 m) along experimental plots during crepuscular periods. Piscine guilds sizes are in cm TL, estimated total length. Crustaceans size are also in cm, CW (carapace width).

Potential Predators	No.	mean size (cm)
Teleost		
<i>Gerres cinereus</i>	20	10.6 TL
<i>Caranx ruber</i>	6	17.7 TL
<i>Calanus bajonado</i>	10	18.6 TL
<i>Lutjanus griseus*</i>	25	20.7 TL
<i>Lutjanus apodus</i>	20	15.0 TL
<i>Epinephelus striatus</i>	14	13.7 TL
<i>Haemulon sciurus*</i>	20	16.8 TL
<i>Red hind</i>	8	15.5 TL
<i>Ocyurus chrysurus</i>	10	8.5 TL
Crustaceans		
<i>Portunus spp.</i>	5	7.5 CW
<i>Menippe mercenaria</i>	4	8.0 CW

DISCUSSION

Postlarval settlement and immigration

There is an extensive suite of potential mechanisms responsible for fluctuations in recruitment of marine populations over broad spatial and temporal scales (Doherty, 1983; Victor, 1983, 1994; Sale et al., 1984; Carr, 1991; Levin, 1991; Doherty and Fowler, 1994).

In this study, the patterns of planktonic influx and settlement on artificial settlement substrates by spiny lobster postlarvae in nursery habitats were seasonal and periodic about the new moon. The major seasonal peaks differed from those occurring during spring and summer in Florida (Calinski and Lyons, 1983) and the Mexican Caribbean (Briones-Fourzán, 1994). Postlarval recruitment near Lee Stocking Island occurred with a major pulse in early fall (October) and a minor pulse in winter (January). Although this investigation was conducted over only one year, the results are corroborated by a 4-year study of settlement in the same area (D. Eggleston and R. Lipcius, unpublished).

Temporal variability in recruitment is related to various processes; the time scales at which this variability occurs can be on the order of days, months or longer (Olmi, 1992). Throughout this investigation, settlement and planktonic influx appeared to be

consistent within lunar pulses (1-5 days), as no differences were detected among sampling dates through the sampling periods. However, delivery rate of lobster pueruli in the plankton was not uniform during flood tide. Measurements of puerulus influx conducted during a major pulse (October 1992) revealed that higher densities occurred during the first hours of flood, which could be due to differences in flow rates during flood in combination with lunar effects. In addition, lobster postlarvae might alter their behavior during early flood to optimize the reinvasion into nursery areas. For example, Olmi (1992) suggests that blue crab megalopae reside on the bottom during ebb tide and return to the water column to swim with flood currents into estuarine habitats. Although the water circulation through the tidal channels of the Exuma Cays presents complex interactions of net flow between the Exuma Sound and Great Bahama Bank, the instantaneous flow is governed by tidal oscillations (Pitts and Smith, 1994). These small-scale processes of short duration, comprising periods of flood and ebb, could have effected the immigration patterns of lobster postlarvae. For instance, tidal creeks with large areas of fringing mangroves frequently present ebb-flood tide asymmetry, where peak ebb tidal currents are often 20-50% higher than peak flood currents (Wolanski et al., 1980). This kind of asymmetry presents a time lag between ebb and flood tides such that when the tidal prism reaches the head of the creek, ebb is already taking place at the mouth, thus creating a slope steep enough to intensify ebb currents. By ingressing at higher densities during the early phase of flood, lobster pueruli might avoid being exported out of the nursery habitats due to the tidal asymmetry .

Settlement and planktonic availability

Settlement is a critical process in the life cycle of many marine species as it represents a transitional shift in habitat, and is usually accompanied by behavioral and physiological changes (e.g., substrate selection and metamorphosis). In this study, settlement on collectors varied spatially between sampling stations even though postlarval supply in the plankton appeared to be spatially homogeneous within the nursery grounds on the order of 1-2 kilometers. Spatial differences in settlement rates could be explained by the interactive mechanisms of water movement and settling rates of the postlarvae, which includes an array of environmental and behavioral processes (Jackson, 1986). Ontogenetic changes in postlarval behavior that enhance searching and sampling of the proper substratum, in combination with chemical cues and the presence or lack of preferred settlement substrates are significant determinants of settlement (Scheltema, 1974; Chia, 1978; Young and Chia, 1982; Sulkin, 1984).

The strong correlation between postlarval influx and settlement rates substantiates the use of artificial settlement substrates for the assessment of delivery of lobster pueruli. Moreover, it indicates that settlement of spiny lobster postlarvae is determined to a large extent by the planktonic availability of postlarvae. However, these estimates which reflect the number of potential recruits to the natural substrate must be regarded as specific to this particular habitat. Future research should focus on determining the degree of association between postlarval availability and natural settlement rates.

Survival of algal-phase lobsters

High survival of individuals residing at low densities in small clumps suggests that solitary residency in algal clumps might be optimal as a refuge from predation. Postlarvae settling at high densities in areas characterized by low densities of suitable habitat could suffer higher mortalities or have to emigrate to more suitable habitats. In many species, the spatial aggregation of individuals can strongly alter susceptibility to predation (Godfray, 1986; Auerbach and Simberloff, 1989; Faeth, 1990; Moller 1991).

Results of recent laboratory experiments have shown that algal-phase lobsters do not exhibit behavioral differences while residing solitarily or in the presence of conspecifics (Childress and Herrnkind, 1994), and that reduced food as a result of crowding can increase predation risk as lobsters search for food in alternative algal patches. Typically, algal-phase lobsters leave algal clumps once food has been depleted (Marx and Herrnkind, 1985b; Herrnkind and Butler, 1986). Results from this experiment suggest that this form of habitat utilization can result in density dependent mortality. Highest survival will likely occur when algal-phase juveniles are distributed sparsely.

Survival of post-algal phase lobsters

Throughout their benthic existence, the abundance and distribution of particular size classes of spiny lobsters are regulated by the availability of size-specific shelters (Eggleston et al., 1990; Lipcius et al., in press). Moreover, mortality rates of post-algal

juvenile lobsters are regulated by the number of conspecifics within a shelter, physical attributes of a refuge and the presence of predator guilds (Eggleston et al., 1990; Eggleston and Lipcius, 1992; Childress and Herrnkind, 1994).

In this study, the survival of two size classes of post-algal phase lobsters did not differ significantly among different types of shelters and the number of conspecifics. Overall, the protection provided by the different shelter types was similar and there was no evidence that predation significantly regulated the survival of these larger juveniles across the mangrove channel where the experiments were conducted.

The relative significance of the interaction of physical and biological factors acting in a mangrove system can be influence changes in physical attributes and types of predators in the system (Wilson, 1987). The higher survival rates obtained in these experiments could be explained by limitations upon the efficiency of the predator assemblages. This could be due to the combined effect of spatial configuration and hydrodynamics of this particular habitat. For organisms living in highly dynamic habitats, such as the mangrove channel, additional elements such as tides can alter feeding behavior by limiting foraging time (Kaiser, 1991).

Tidal cuts and mangrove channels in the Exuma Cays are characterized by extremely high currents that can reach velocities of up to 100 cm/s (Pitts and Smith, 1994), which reduces the foraging efficiency of piscine guilds. During the experiment, I observed that potential piscine predators (e.g., grunts, snappers), when able to approach the experimental treatments, encountered difficulties remaining at a specific site due to

the currents. Given such conditions, piscine predators could only forage efficiently during slack tides, which because of the tidal asymmetry, were of extremely short duration. Thus, lobster survival was not only affected by the configuration and spatial arrangement of a particular habitat, but also by hydrodynamic features of a particular location. The diversity of these habitat characteristics need to be considered collectively when dealing with the controlling factors of survival of juvenile spiny lobsters.

LITERATURE CITED

- Andree, S. (1981) Locomotory activity patterns and food items of benthic postlarval spiny lobsters, *Panulirus argus*. M. Sc. Thesis. Florida State University, Tallahassee, Florida, USA.
- Auerbach, M. and D. Simberloff (1989) Oviposition site preference and larval mortality in a leaf mining moth. *Ecol. Entomol.* 14: 131-140.
- Bannerot S. P; J. H. Ryther and M. Clark. (1992) Large-scale assessment of recruitment of postlarval spiny lobsters, *Panulirus argus*, to Antigua, West Indies. *Proc. Gulf. Carib. Fish. Inst.* 41: 471-486.
- Briones-Fourzán P. (1994) Variability in post-larval recruitment of the spiny lobster, *Panulirus argus* (Latreille, 1804) to the Mexican Caribbean coast. *Crustaceana* Vol. 66. 326-341.
- Calinski, M. D. and W. G. Lyons. 1983. Swimming behavior of the puerulus of the spiny lobster *Panulirus argus* (Latreille, 1804) (Crustacea: Palinuridae). *J. Crust. Biol.* 3:329-335.
- Caddy, J. F. (1986) Modeling stock recruitment processes in Crustacea: some practical and theoretical perspectives. *Can. J. Fish. Aquat. Sci.* 43: 2330-2344.
- Caddy, J. F. and Stomatopoulos, C. (1990) Mapping growth and mortality rates of crevice dwelling organisms onto a perforated surface: the relevance of 'cover' to the carrying capacity of natural and artificial habitats. *Est. Coast. Shelf Sci.*, 31, 87-

106.

- Chia, F. S. (1978) Perspectives: settlement and metamorphosis of marine invertebrate larvae. In: Chia, F. S. Rice, M. E (eds.) Settlement and metamorphosis of marine invertebrate larval. Elsevier, New York, pp. 283-285.
- Day, R. W. and G. P. Quinn. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59:443-463.
- Doherty P. and A. Fowler (1994) Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. *Bull. Mar. Sci.* Vol. 54, No. 1, 1994.
- Eggleston, D. B., R. N. Lipcius, and D. Miller. (1992) Artificial shelters and the survival of juvenile Caribbean spiny lobster: spatial, habitat and lobster size effects. *U. S. Fishery Bulletin.* 90: 691-702
- Faeth S. H. (1990) Aggregation of leafminer, *Cameraria spp.* Nov. (Davis): consequences and causes. *J. Anim. Ecol.* 59:569-586
- Fernández, M. O. Iribarne, and D. Armstrong, (1993) Habitat selection by young of the year Dungeness crab and predation risk in inter-tidal habitats. *Mar. Ecol. Prog. Ser.* 92: 171-177.
- Godfray H. J. (1986) Clutch size in a leaf-mining fly (*Pegomyza nigrotarsis*: Anthomyriidae). *Ecol Entomol.* 11: 75-81
- Green, R. 1979 (1979) Sampling design and statistical methods for environmental biologists. Wiley & Sons, N.Y.

- Herrnkind, W. F. (1980) Spiny lobsters: patterns of movement. *In: The Biology and Management of Lobsters*. Vol. I (Ed. by J. S. Cobb and B.F. Phillips), pp. 349-407. Academic Press, New York, USA.
- Herrnkind, W. F. and M. J. Butler (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobster, *Panulirus argus*.. *Mar. Ecol. Prog. Ser.* 34:23-30.
- Herrnkind, W. F., M. J. Butler, and R. A. Tankersley. (1988) The effects of siltation on recruitment of spiny lobsters, *Panulirus argus*. *U.S. Fishery Bulletin* 86:331-338.
- Herrnkind, W. F. and R. N. Lipcius. (1989) Habitat use and population biology of Bahamian spiny lobster. *Gulf and Caribbean Fish. Inst. Proc.* 39: 265-278.
- Hurlbert, S. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- Kaiser, M. J. and R. N. Hughes (1993) Factors affecting the behavioral mechanisms of diet selection in fishes. *Mar. Behav. Physiol.* vol. 23, (1-4): 105-118.
- Lipcius, R. N., E. J. Olmi, III and J. van Montfrans. (1990) Planktonic availability, molt stage and settlement of blue crab postlarvae. *Mar. Ecol. Prog. Ser.* 58:235-242.
- Lipcius, R. N. (1985) Size-dependent reproduction and molting in spiny lobsters and other long-lived decapods. In *Crustacean issues*, Vol. 3 (edited by A. M. Wenner), pp. 129-48. Balkema Press, Rotterdam.
- Lyons, W. G. D. G. Barber, S. M. Foster, F. S. Kennedy, Jr. and G. R. Milano. (1981) The spiny lobster, *Panulirus argus*., in the middle and upper Florida Keys:

Population structure, seasonal dynamics, and reproduction. Fla. Mar. Res. Publ. No. 38, 38 pp.

Marshall, L. S. Jr. (1992) Survival of juvenile queen conch, *Strombus gigas*, in natural habitats: impact of prey, predator and habitat features. Ph. D. dissertation, The College of William and Mary, School of Marine Science, Gloucester Point, Virginia USA.

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

Marx, J. M. and W. F. Herrnkind. (1985b) Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*. :food and shelter. J. Crust. Biol. 5: 650-657.

Marx, J. M. (1986) Settlement of spiny lobster, *Panulirus argus*, pueruli in South Florida: An evaluation from two perspectives. Can. J. Fish. Aquat. Sci. 43: 2221-2227.

Menge, B. A., and J. P. Sutherland. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist. 130:730-757.

Minello T. J. (1993). Chronographic tethering for measuring prey survival time and testing predation pressure in aquatic habitats. Mar. Ecol. Prog. Ser. Vol. 101:99-104.

Moller A. P. (1991) Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. Ecology 72: 1336-1349.

- Monterrosa-López, O. (1986) Post-larval recruitment of the Spiny lobster, *Panulirus argus* (Latreille), in Southwestern Puerto Rico including observations of substrate selection in aquaria. Master Thesis. University of Puerto Rico. 44 pp.
- Olmi, E. J. (1992) Immigration of blue crab (*Callinectes sapidus*) megalopae in the York River, Va : Patterns and Processes. Ph. D. Dissertation, The College of William and Mary, School of Marine Science, Gloucester Point, Virginia USA.
- Pile A. J. (1993) Effects of habitat and size-specific predation on the ontogenetic shift in habitat use by newly settled blue crabs. Master of Arts thesis. The College of William and Mary, School of Marine Science, Gloucester Point, Virginia USA. 84 pp.
- Pitts, P. A. and N. P. Smith (1994) Annotated Summary of Current Meter Data from the Vicinity of Lee Stocking Island, Exuma Cays, Bahamas. Caribbean Marine Research Center Technical Report Series No. 94-4
- Phillips, B. F., G. Morgan and C. Austin. (1980). Synopsis of biological data on the western rock lobster *Panulirus cygnus* (George, 1962). FAO Fish Synop. No. 128
- Raimondi P. T. (1991). Settlement behavior of *Chthamalus anisopoma* larvae largely determines the adult distribution. *Oecologia*, 85:349-360.
- Scott P. Bannerot, J. H. Ryther and M. Clark (1992) Large scale assessment of recruitment of postlarval spiny lobsters, *Panulirus argus*, to Antigua, West Indies. *Proc. Gulf. Carib. Fish. Inst.* 471-486
- Scheltema, R. S. (1974). Biological interactions determining larval settlement of marine

- invertebrates. *Thalassia Jugosl.* 10: 263-296.
- Smith , K. W. and W. F. Herrnkind (1992) Predation on early juvenile lobsters, *Panulirus argus* : influence of size an shelter. *J. Exp. Mar. Biol. Ecol.* 157: 3-18.
- Sokal, R. R., Rohlf, F. J. (1981) *Biometry*, 2nd edn. W. H. Freeman, San Francisco.
- Underwood, A. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 19:513-605.
- Ward , J. A. (1990). Patterns of settlement of spiny lobster (*Panulirus argus*) post-larvae at Bermuda. *Gulf and Caribbean Fish. Inst. Proc.* 39: 255-264.
- Werner, E. E and J. F. Gilliam. (1984). The ontogenetic niche and species interactions in size structured populations. *Ann. Rev. Ecol. Syst.* 15: 393-425.
- Wilson, K. A. (1987) Ecology of mangrove crabs: predation, physical factors and refuges. *Bull. Mar. Sci.* 1989. vol. 44(1): 263-273
- Wolfe , S. H. and B. E. Felgenhauer. (1991) Mouthpart and foregut ontogeny in larval, post-larval and juvenile spiny lobster *Panulirus argus* Latreille (Decapoda, Palinuridae). *Zool. Scripta* 20: 57-75
- Wolanski, E., Jones, M., and Bunt, J. S., 1980. Hydrodynamics of a tidal creek-mangrove swamp system. *Australian Journal of Marine and freshwater Research* 31: 431-450.
- Wolanski, E., Mazda Y., Ridd P., 1992. Mangrove Hydrodynamics. In: A. I. Robertson and D. M. Alongi (Eds.). *Tropical mangrove ecosystems*. pp. 43-62. American Geophysical Union.

VITA

LUIS COBÁ-CETINA

Born in Mexico City, Mexico 20 June 1963. Graduated from the High School of the University of Yucatan in 1981. Earned B.S. in Marine Science from the University of Colima in 1987. Entered master's program at College of William and Mary, School of Marine Science in 1991.