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Examination of the Allee effect on postlarval recruitment and post settlement survival in the Caribbean spiny lobster *Panulirus argus*

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EXAMINATION OF THE ALLEE EFFECT ON POSTLARVAL RECRUITMENT AND POST-SETTLEMENT SURVIVAL IN THE CARIBBEAN SPINY LOBSTER *Panulirus argus*

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
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Biological Sciences

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by
Adrianna Zito
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Accepted by:
Dr. Michael Childress, Committee Chair
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Dr. David Tonkyn

ABSTRACT

Positive density dependence (the Allee effect) has been reported in a number of species that are attracted to conspecific cues. This effect has been shown to influence the settlement of many species of marine invertebrates. Caribbean spiny lobsters are gregarious den dwellers attracted to conspecific cues. Previous studies have suggested that the benefit of conspecific attraction is a reduced predation risk by decreasing the time to find crevice shelters (the guide effect) or by cooperative group defense once sharing shelters. I tested a third hypothesis that attraction to conspecific cues increases the settlement of lobster postlarvae into the highest quality nursery habitat (settlement cue) in Florida Bay, FL, USA. Y-maze laboratory choice test on postlarval lobsters (N = 67) found a significant preference for odor cues of large juvenile lobsters. To determine if this preference for conspecific odors could influence lobster recruitment, I established sixteen paired field sites (25 m X 25 m) and manipulated the density of large juvenile lobsters by the addition of ten artificial crevice shelter blocks. Treatment sites received unplugged shelter blocks that could house lobsters up to 45 mm CL while control sites received plugged shelter blocks that could house lobsters up to 25 mm CL. Treatment sites attracted and retained large juvenile lobsters (> 25 mm CL) during our six month study and maintained a density five fold higher than the paired control sites. Each month I censused the density of small juvenile lobsters (< 25 mm CL) along with the density of large juvenile lobsters (> 25 mm CL); crab, fish and octopus predators; and percent cover of red macroalgae. The density of small juvenile lobsters was most influenced by large juvenile lobster density. I also seeded (N = 800) and recovered (N = 18) microwire-tagged small juvenile lobsters from both control and treatment sites. I detected a significant correlation in the number of untagged lobsters with large juvenile density, but no correlation in the number of tagged lobsters with large juvenile density. These results suggest that more postlarval lobsters were settling on sites with high juvenile lobster density supporting the predictions of the Settlement Cue hypothesis.

DEDICATION

I would like to dedicate this document to several special people who believed in me and helped shape me into the scientist I've become today. My parents Tony and Betty Zito introduced me to the outdoors and encouraged me to explore my surroundings by asking deductive questions at a very early age. Kathleen Reinsel and James Welch shared with me their enthusiasm for marine invertebrates and marine ecology providing me with unique research opportunities and exceptional guidance during my time as an undergraduate at Wittenberg University. I appreciate their support and that of the countless others who inspired, encouraged, and endured my love of marine biology.

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CHAPTER ONE

REVIEW OF ALLEE EFFECTS

Introduction

In this thesis I examine Allee effects in early ontogeny of the Caribbean spiny lobster, *Panulirus argus*; specifically the positive influence of late benthic juvenile spiny lobster density on the settlement and post-settlement survival of conspecifics. In the first chapter, I review the literature pertaining to density dependence and the Allee effect. I describe the origin of the concept, and its wide application in both animal and plant species. Then I discuss how conspecific attraction is an important component Allee effect and especially how it drives recruitment of several marine organisms. Finally, I discuss how conspecific attraction benefits spiny lobsters in their nursery habitat with examples from the literature. In the second chapter, I describe a manipulative field experiment to test how conspecific attraction may be an important in spiny lobsters during recruitment, habitat transitions, and aggregation in crevice shelters.

What is the Allee effect?

Warder C. Allee was an animal behaviorist interested in the evolution of social behavior in animals. As a researcher in the Ecology group at the University of Chicago, he examined the benefits of animal aggregations to explain the development of sociality and cooperation (Mittman 1988). In 1931 he wrote Animal Aggregations, a review of his own work and the work of others on the factors that influence aggregation in animals from *Paramecium* spp. to *Homo sapiens*. In this work, Allee described mechanisms by which animals form aggregations, including physiological response (innate taxis or tropism), common habitat requirements, and directed motion toward conspecifics. He provided examples of aggregations of marine, aquatic, and terrestrial organisms from studies in the field and the laboratory. He also discussed the diverse benefits enjoyed by animals occurring in groups including resistance to toxins, decreased desiccation, lower oxygen consumption, and increased growth rate. Experiments conducted at the University of Chicago, included a mesocosm study of population growth (reproduction rate) of *Tribolium* beetles at various initial population sizes, respiration studies with *Asterias* sea stars at various densities, and a survival experiment wherein different sized groups of goldfish, *Carassius auratus,* were exposed to an environmental toxin, colloidal silver (Allee 1931). In each of these cases, and countless others cited by Allee (1931), the grouped organisms did better than individuals. Allee noted among other benefits, a positive relationship between population density and per capita growth rate (Allee 1931).

In 1938, Allee published, The Social Life of Animals in which he presented a model relating the rates of biological processes such as reproduction and respiration as a function of density. He used this model to explain consequences of overcrowding (negative density dependence at high population density) and undercrowding (positive density dependence at low population density) and summarized the density dependence of a multitude of biological components affecting a population. Components such as birth rate, sex ratios, reproductive success, and conspecific attraction can contribute to the total population size and growth rate. This book coincided with a change in thinking about populations as cooperative groups instead of individuals who incidentally occur in groups. Allee and his colleagues at the University of Chicago examined the biology of behavior as a selective force and discussed social structure as it influenced population dynamics, and vice versa. Social structure within populations controls many aspects of an organism's ecology, including reproduction, and the acquisition of resources, all of which affect population size and density. It became clear through Allee's study of social structure in fowl, and even in humans, that populations benefit from cooperation between individuals (Allee 1938). He showed that density dependent factors strongly control population size and growth rate (Allee 1938; Stephens and Sutherland 1999). This line of thinking about social structure and its influence on selection helped to form the fields of sociobiology and behavioral ecology; which examine the evolutionary consequences of behavior, and the development of sociality in many animal species (Mittman 1988; Stephens et al.1999).

Defining the Allee effect

Since Allee documented a multitude of positive relationships between population growth rate and a number of biological factors, the concept has become termed the "Allee effect" (Odum and Allee 1954; Mittman 1988). Although there are many current definitions, in general the Allee effect is the tendency of average and/or individual fitness to increase as a factor of population size and/or density. Several recent reviews on the topic have attempted to standardize the definition (Stephens et al. 1999; Courchamp et al.

1999; Petersen and Levitan 2001; Gascoigne and Lipcius 2004a). Many mathematical and conceptual models have been proposed to explain the Allee effect and demonstrate how it may work in natural populations, though definitions remain inconsistent. Here I describe two main types of Allee effects and propose a conceptual model to account for differences in the current use of the term.

In a recent review, Stephens et al. (1999) discussed an important distinction between two types of Allee effects used synonymously in the literature. A component Allee effect is any aspect of fitness that increases as population density increases. Discrete traits such as sperm concentration and conspecific detection are examples of component Allee effects that are positively correlated with population density but may or may not be directly related to fitness of the population (Babcock et al. 1994; Kokko and Sutherland 2001). Demographic Allee effects are net increases in growth rate or fitness of the population based on the sum of all components of fitness (both positive and negative density dependent factors). It is important to make this distinction since demographic Allee effects are more informative than an individual component Allee effect when the goal is predicting population persistence (Stephens et al. 1999). Most Allee effect studies have demonstrated a component Allee effect, that is, negative density dependence of a single factor, and then used these data to declare that the organism is on the brink of extinction (Bessa-Gomes et al 2004; Brassil 2001). While it is alarming to see a strong component Allee effect on a small population, there can be natural counter-component effects that also factor into the overall population dynamics (Babcock et al. 1994; Kindvall et al. 1998; Kuussaarri et al. 1998; Gascoigne and Lipcius 2004a). One cannot infer population decline from a single component Allee effect as detected by most evolutionary and ecological studies (Stephens et al. 1999; Donahue 2006). Here, I have compiled recent studies of proposed Allee effects and classified them as either a component (Table 1.1) or demographic Allee effects (Table 1.2).

Table 1.1: Component Allee effects: single density dependent components of fitness

Citation	Definition	Component	Phase
Allee 1931	Animals benefit from living in groups, there is a positive density dependent effect	Several physiological effects	I, II, III
Lewis and Karieva 1993	Reduced reproductive success at low densities	Reproductive success	I, II
Petersen and Levitan 2001	When populations at low density or size exhibit a positive relationship between per capita population growth rate and population size	Several components as described by Stephens et al 1999	I, II
McCarthy 1997	Negative density dependence (in reproduction when population is below Allee threshold)	Difficulty finding a mate	I
Moller and Legendre 2001	Negative density dependence of reproductive success when population density is low	Female mate choice	I
Kokko and Sutherland 2001	Decrease in individual survival or breeding output at low population sizes	Conspecific attraction	I
Cheptou 2004	Reproduction by out crossing is potentially limited by the density effects on the possibility of pollen transfer	Reproductive success	I
Dennis 1989	A situation at low population densities where the per-individual growth rate is an increasing function of population density	Birth rate	I
Fowler and Ruxton 2002	When an increase in population size yields a decrease in fitness through negative density dependence in an isolated population.	Operational sex ratio	I
Walters and Kitchell 2001	Recruitment declines with stock size (negative density dependence)	Recruitment	I
Veit and Lewis 1996	Disproportionately lowered fecundity below a critical threshold density or abundance	Fecundity	I
Lundquist and Botsford 2004	Below a certain threshold fertilization efficacy declines and so reproduction declines more rapidly than indicated by density	Reproductive success	I

Table 1.1: Component Allee effects (continued)

Citation	Definition	Component	Phase
Stephens et al. 1999	A positive relationship between any component of individual fitness and either number or density of conspecifics	Any single component	II
Stephens and Sutherland 1999	Positive relationship between a component of fitness and either numbers or densities of conspecifics	Conspecific attraction	II
Holt et al. 2004	Increase immigration in location populations by conspecific attraction	Conspecific attraction	II

Table 1.2: Demographic Allee effects - sum of all density dependent components of fitness

Citation	Definition	Phase
Asmussen 1979	Grouped animals show increased efficacy that is sometimes reflected by longer survival or better growth as long as neither too few or too many animals are present	I, II, III
Wang and Kot 2001	An increase in the per capita growth rate at low densities	I, II, III
Etienne et al. 2002	Reduced per capita growth at low densities	I, II, III
Greene and Stamps 2001	When fitness increases as a function of density at low and moderate density and then declines at moderate to high densities	II , III
Fowler and Baker 1991	Animal populations experience a depression of their capacity for increase at very low levels	II, III
Kuussaarri et al. 1998	Decrease in population growth rate at low population densities	I
Fowler and Ruxton 2002	A reduction in fitness due to declining population sizes	I
Courchamp et al. 1999	A scenario in which populations at low numbers are affected by a positive relationship between population growth and density which increases their likelihood for extinction.	I
Tonkyn 1986	An increase in per capita growth rate with population size at low densities	II
Dennis 2002	Any mechanism that causes per capita growth rate to increase as a function of population size	II
Brassil 2001	Increasing per capita growth rate with increasing density	II
Gascoigne and Lipcius 2004b	Any mechanism that causes per capita growth rate to increase as a function of population size	II
Calabrese and Fagan 2004	Any mechanism that causes per capita growth rate to increase as a function of population size	II

Component Allee effects

A common challenge for researchers examining Allee effects in small natural populations is that it is very difficult to obtain data on all positive and negative density dependent factors that contribute to per capita growth rate. Therefore many studies obtain data on one or more components affecting the overall fitness of the population then make assumptions about density's effect on fitness (Table 1.1). From data on key components, especially measures such as reproductive success, these component Allee effects may be used reliably to make recommendations for management of populations (Levitan et al.1992; Stoner and Ray-Culp 2000). Most Allee effects detected in natural populations are, in fact, component Allee effects and therefore researchers should carefully consider their predictive power with respect to population persistence on their own (Bessa-Gomes et al.2004; Gascoigne and Lipcius 2004b).

Component Allee effects have been described as influential in small populations of a multitude of organisms including plants (Groom 1998; Cheptou 2004) and marine animals (Denny and Shibata 1989; Quinn et al. 1993; Myers et al. 1995; Levitan and Young 1995; Stoner and Ray-Culp 2000; Hutchings 2000; Petersen and Levitan 2001; Lundquist and Botsford 2004). Reproduction of broadcast spawners and plants are two prominent systems where examples of component Allee effects have been described to have a major impact on population size (Levitan 1991; Levitan et al. 1992; Babcock et al. 1994; Groom 1998). Several manipulative studies have demonstrated the negative density dependent effects of sperm limitation in broadcast spawners at low densities (Levitan et al. 1992; Babcock et al. 1994; Groom 1998; Cheptou 2004).

Levitan et al. (1992) examined red sea urchin (*Strongylocentrotus franciscanus*) gametes in the field and in the lab to demonstrate that when “females” (eggs in a bag) or “males” (sperm filled syringe), are widely dispersed, or the population is too small, reproductive success decreases. They arranged four grid arrays of “male” and “female.” Sperm were released from syringes at distances of 0.5 m or 2.0 m from the artificial females and reproductive success was quantified. They found that fertilization success was positively correlated with group size and proximity to a “mate.” Similar experiments were conducted with the long spined urchin, *Diadema antillarum*; exploring two density dependent factors, body size and population density, both of which may influence fertilization success (Levitan 1991). They found that body size did not affect fertilization success, whereas, fertilization success significantly increased with increasing population density (Levitan 1991).

Density and group size are even more influential on the reproductive success of plant species (Groom 1998; Cheptou 2004). For example, Groom (1998) manipulated plot density and the degree of isolation in order to determine the reproductive success of *Clarkia cocinna*, an herbaceous plant. Seed sets were compared for focal flowers in plots varying in size from 1-50+ individuals, and analyses were performed on the number of seeds relative to plot size and isolation distance of each patch. She found that as the Allee effect predicts, plants in larger patches received more pollen and produced more seeds than those in smaller isolated patches. She also found that below a threshold initial population size, plants in small patches did not receive any pollen and the population of the patch achieved zero reproductive success.

Cheptou (2004) conducted a theoretical study mathematically modeling the frequency of selfing plants as a result of a selfing Allee effect when the population is demographically stable. If the population is not demographically stable, then the cost of inbreeding depression outweighs the gain of persistence. He concluded that if the population is demographically stable, increasing patch isolation should yield a higher degree of selfing and the population can avoid being driven to extinction.

Though reproductive success is the most frequently measured component of fitness, density dependence of habitat selection mechanisms by gregarious animals can also contribute to Allee effects. Many animals evaluate habitat quality by the presence of conspecifics (Stamps 1988). To model the Allee effect in habitat selection, Greene and Stamps (2001) modified the Fretwell-Lucas (1970) model of ideal free distribution to include conspecific density as an indicator of patch quality. Under this model of positive density dependence, each organism selects a patch of higher quality (higher conspecific density). Positive density dependence in habitat selection will concentrate the animals into a single patch of higher quality. Conspecific attraction at low population numbers, may cause aggregation in poorer habitat (Greene and Stamps 2001; Morris 2002; Greene 2003). In a second example, Morris (2002) examined habitat selection by small mammals and found that animals that rely on conspecific attraction for habitat selection will continue to decline in population size as a result of low population densities and numbers. Since conspecific attraction is most adaptive at moderate densities, this example illustrates a component Allee effect.

It is important to note the limitations of evaluating a species based on component Allee effects. I would caution those scientists that are only able to evaluate one or two components of fitness against using their results to make predictions about population persistence. Often organisms are able to persist and counteract component Allee effects. For instance, to overcome sperm limitation organisms have adapted behaviors such as delaying functional maturity, forming mating aggregations, and performing synchronous mating (Yund 2000; Gascoigne and Lipcius 2004a). Other organisms have overcome isolation by being highly mobile, producing larger flowers, or more concentrated sperm (Babcock et al. 1994; Kindvall et al. 1998). Though it can be difficult to gather data on all components of fitness, and weight each effect, scientists must realize the relationship between the component they measure and overall fitness and interpret the results accordingly.

Demographic Allee effects

Demographic Allee effects are net increases in growth rate or fitness of the population based on the sum of all components of fitness (both positive and negative density dependent factors) (Table 1.2). To understand population trends, especially with respect to the consequences of small, isolated populations, researchers attempt to incorporate all density dependent components of population fitness (Dennis 1989; Kuussaarri et al. 1998; Courchamp et al. 1999; Etienne et al. 2002). By incorporating all positive and negative components of fitness, researchers can identify populations truly at risk for rapid decline and extinction (Etienne et al. 2002; Bessa-Gomes et al. 2004;

Brassil 2001). If one needs all of the pieces to predict the probability of future population persistence, then why not only examine demographic Allee effects? The reality is that it is incredibly difficult to measure all components either positively or negatively affecting fitness in an actual population. As a result, most studies on density dependence of per capita growth rate have been theoretical and based on mathematical models (Stephens et al. 1999).

Exploring demographic Allee effects is important for conservation issues such as the spread of invasive species (Wang and Kot 2001), predicting recovery or extinction in declining populations (Hutchings 2000; Frank and Brickman 2000; Fowler and Ruxton 2002). Brassil (2001) developed a relatively simple model of an Allee effect and used it to predict extinction rates of metapopulations in different patches. He began with the logistic growth equation, and entered terms to modify birth rate, death rate, and migration as density dependent factors, varying Allee strength. He ran computer simulations for a single patch model representing a single isolated population, and one with multiple patches representing metapopulations with migration between patches. An increasing Allee strength led to a decline in mean time to extinction of the population in a single patch model, and with the metapopulation design, the time to extinction was longer (Brassil 2001). Though this and other demographic Allee effect models are informative, they are theoretical and few here been tested with empirical studies in natural populations.

Even fewer field studies have endeavored to examine a demographic Allee effect in a natural population. One of these few was a large multi-year study of the endangered

Glanville fritillary butterfly *Melitaea cinxia*, which provides rare data on a demographic Allee effect in the field. Kuussaarri et al. (1998) conducted a large scale study tracking the habitat, reproductive success, and population size of this insect on the Aland Islands of Finland for four years. Since this butterfly is a specialist on two species of plants, and their egg set is conspicuous, it was feasible to study many components of fitness including availability of mates, reproductive effort in the form of larvae, availability of preferred habitat by censusing host plants, emigration rate from a mark recapture effort, and adult population density. This study provides an exceptional example where positive density dependence of emigration rate, and reproductive success, which factored with negative density dependent effects, resulted in positive density dependence of the per capita growth rate. The authors predict that similar efforts examining other insect species could also reap extensive data on the influence of demographic Allee effects.

A conceptual model of Allee Effect definitions

Allee effects can be modeled by altering the logistic growth model (Verhulst 1838) with a constant growth rate (r), and creating instead, a model with a density dependent growth rate. Some Allee models incorporate a threshold value and are unstable (Asmussen 1979; Dennis 1989; Groom 1998; Frank and Brickman 2000; Keitt et al. 2001; Gascoigne and Lipcius 2004a); this consideration demonstrates that if the initial population is above a certain density (N) value, and r is positive the population increases. If, however, the population is below a certain density (N) value, the density dependent r is negative, and the population will decline to extinction (Figure 1.1). The concept of this critical or optimal density will, hereafter be referred to as the “Allee threshold” (Asmussen 1979; Groom 1998; Dennis 1989; Dennis 2002; Fowler and Ruxton 2002). This threshold population size conveys the strength of an Allee effect (Wang and Kot 2001; Greene 2003; Gascoigne and Lipcius 2004a). Determining minimum initial population size is vital for Allee effects models predicting movement of invasive species (Lewis and Karieva 1993; Veit and Lewis 1996; Wang and Kot 2001) and in the conservation of declining or reduced populations (Asmussen 1979; Dennis 1989; Dennis 2002; Stoner and Ray-Culp 2000).

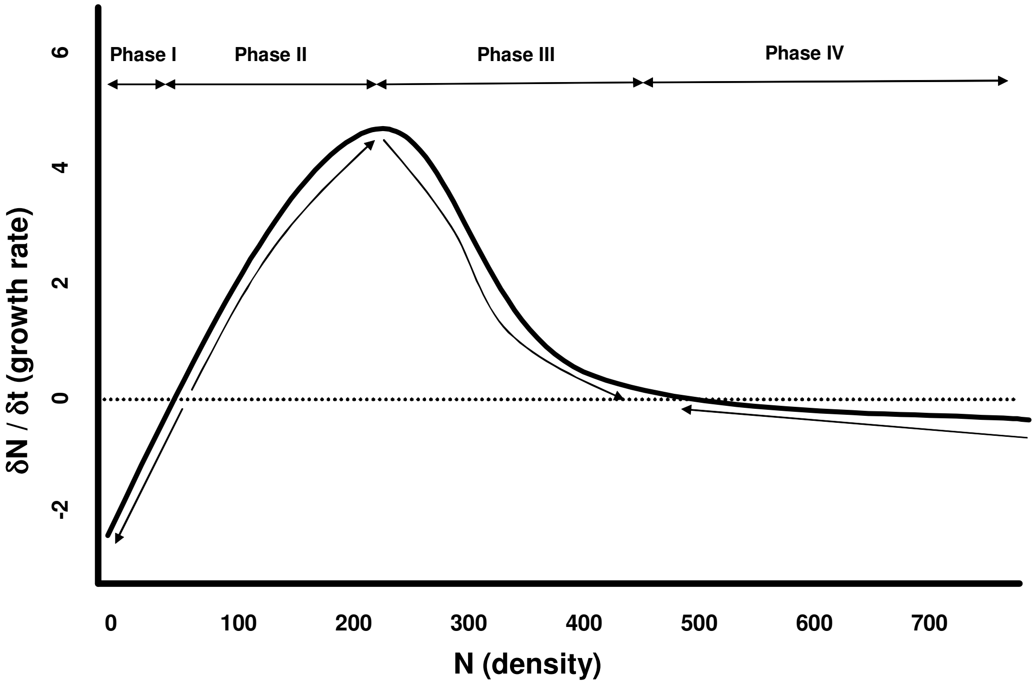

Figure 1.1: **The overall Allee model** with phases I inverse negative density dependence, phase II positive density dependence, phase III negative density dependence when N exceeds K, and phase IV inverse positive density dependence as N returns to K. Arrows indicate direction of population growth rate at the x intercept, an unstable equilibrium related to the Allee threshold and a stable equilibrium state as population approaches K.

Given the models of positive and negative growth rate depending on both carrying capacity K and density (N), I can develop an overall Allee effect model across all population densities and growth rates (Figure 1.1). I have divided the overall Allee effect model (changes in per capita growth rate) to represent four different phases of the Allee effect; inverse negative density dependence (Phase I), positive density dependence (Phase II), negative density dependence when population is approaching the carrying capacity (Phase III), and inverse positive density dependence when the population density falls below the carrying capacity (Phase IV). Thus, the severe confusion between different definitions of the Allee effect is based on how different definitions refer to different sections of this curve, and most do not consider all four phases in their definition of an Allee effect. In Tables 1.1 and 1.2, I have listed, along with the various models reviewed, the phase or phases that each discussion of the Allee effect describes.

Both demographic and component Allee effect models are valuable tools for ecologists, conservationists and population managers as populations worldwide are in decline (Myers et al. 1995; Pauly 1998; Jackson et al. 2001). Demographic Allee models consider all positive and negative density dependent effects and can be used to predict extinction rates, habitat invasions, and the overall trend of population growth (Dennis 1989; Kuussaarri et al.1998; Courchamp et al. 1999; Etienne et al. 2002). Demographic models are seldom used since they are very complex, and it is difficult for researchers to accumulate sufficient data on these parameters in natural populations (Dennis 1989). Most studies of natural populations describe and measure component Allee effects, single density dependent components of fitness (Denny and Shibata 1989; Quinn et al. 1993;

Myers et al. 1995; Levitan and Young 1995; Stoner and Ray-Culp 2000; Hutchings 2000; Petersen and Levitan 2001; Lundquist and Botsford 2004). Component Allee effects are far more prominent in the literature because they are simpler to detect in a population.

Population managers should attempt to gather as much information as possible and consider populations exhibiting Allee effects with special care. It is important to realize at small densities, populations are very unstable; reproduction, predator defense, foraging efficiency, loss of cooperative interaction, and habitat selection may be negatively affected, and that this could cause an ever accelerating decline (Stephens and Sutherland 1999; Courchamp et al. 1999; Gascoigne and Lipcius 2004c). Component Allee effect models can provide useful information to managers though it is important to choose a component that is directly related to population growth rate. A carefully chosen component can be used to examine a population decline, outline the risks of that effect alone, and whether recovery may be possible (Stephens and Sutherland 1999; Courchamp et al. 1999; Petersen and Levitan 2001). As is often the case in natural science, it is important for researchers to acknowledge the limitations of the information they have, and advise managers accordingly.

Do Allee effects influence marine larval recruitment?

Many marine organisms have complex life cycles that involve dispersing larval stages (Caley et al. 1996). In most cases, larvae are released either from eggs or from an adult, and disperse by currents. Larval recruitment refers to the process of arriving at suitable habitat and undergoing metamorphosis to a benthic life stage (Caley et al. 1996;

Schmitt and Holbrook 1996; Zhao and Qian 2002). Settlement processes among marine invertebrates are as diverse as larval forms (Caley et al. 1996). Sessile organisms such as barnacles drop to the bottom, sample the substrate, and then “decide” whether or not to attach based on the presence of settlement cues (Knight-Jones 1953; Crisp and Knight-Jones 1953; Crisp 1967; Shepherd and Brown 1993; Zhao and Qian 2002). Mobile invertebrates such as spiny lobsters undergo a color change, drop to the bottom, and molt into a first stage juvenile (Marx and Herrnkind 1985a; Butler and Herrnkind 2000). Recruitment may be limited by larval supply (Lipcius et al. 1997; Butler et al. 2001) presence or absence of settlement cues (Crisp and Knight-Jones 1953; Crisp 1967; Butler and Herrnkind 1986; Pawlik et al. 1991; Butler and Herrnkind 1991; Jeffs et al. 2005), and/or post settlement survival (Quinn et al. 1993; Walter and Kitchell 2001). Larval settlement strategies vary and are a major component of the organism’s ecology and are therefore important to the study of marine populations. The addition of new individuals is a key component of a population’s sustainability since without successful larval recruitment the population will decline (Caley et al. 1996; Lipcius et al. 1997; Butler et al. 2001).

In some species, selectivity by larvae operates to assure larvae settle in suitable habitat. Larval habitat selection is then critical to population persistence in these species (Crisp 1967; Butler and Herrnkind 1986; Lipcius et al. 1997; Toonen and Pawlik 2001). Habitat selection ability is a major component of individual fitness and, as a result, organisms have developed highly specialized mechanisms for locating suitable settlement habitat (Grosberg 1988; Pawlik et al. 1991; Shepherd and Brown 1993; Toonen and

Pawlik 2001; Zhao and Qian 2002; Jeffs et al. 2005). Settlement cues are suspected to include chemical cues from the environment, mechanical cues, light cues, and even cues from conspecifics (Knight-Jones 1953; Crisp and Knight-Jones 1953; Grosberg 1988; Toonen and Pawlik 2001; Donahue 2006). It is difficult to pinpoint the exact cue in many cases since most larvae are inconspicuous, but laboratory choice experiments and biochemistry assays have been used to gather evidence of direct settlement cues (Crisp 1967; Grosberg 1988; Pawlik et al. 1991; Butler and Herrnkind 1991).

Habitat Selection Models

Habitat selection models are theoretical sets of rules about which habitat an organism or group of organisms will choose relative to the characteristics of the group or the habitat patch. Fretwell and Lucas (1970) first described the ideal free distribution model for habitat selection, suggesting that individuals of a population have the choice of where to settle. Their prediction was that individuals should choose the habitat patch with the greatest resources still remaining. They incorporate negative density dependence of conspecifics into their model, i.e., competition for resources which lowers the quality of each patch as density increases. This model predicts that the first settler will choose the patch of highest quality, as will the second and third etc. until the quantity of resources that make the patch of high quality are no longer greater than the resources available per settler on patches of lower quality. The model also accounts for migration between patches when resources in the higher quality patch fall below that of the lower quality patch. Recent applications have compared actual population densities on different habitat areas and hypothesized reasons for difference between their results and those predicted by the ideal free distribution model (e.g. Morris 2002).

In their dispersal model, Greene and Stamps (2001) also accounted for settlement costs related to conspecific attraction; they used the term “decremental cost” to describe the advantage of conspecific attraction in settlement as population density of a patch increased to carrying capacity. They found that between two patches of unequal quality Allee effects function much like ideal free distribution, with more individuals settling in higher quality habitat. When comparing patches of equal quality, positive density dependence caused a higher concentration of animals at one patch or the other. Greene (2003) also examined persistence of populations under varying Allee effects with density dependent dispersal, and found that populations with strong Allee effects were more likely to persist than those subject to random dispersal.

Conspecific Attraction in Larval Recruitment

One line of thinking in larval ecology is that since the highest mortality of marine invertebrate larvae occurs in the early stages of the life cycle, it may be beneficial to evolve traits that increase survival during that portion of life history (Caley et al. 1996). Aggregation is one such strategy. Historically, studies have tried to demonstrate the importance of conspecific attraction as a mechanism in settlement of intertidal invertebrates such as the eastern oyster *Crassotrea virginica* (Crisp and Knight-Jones 1967) and the barnacle *Balanus balanus* (Crisp 1953). Larvae are more likely to settle on or near conspecifics based on the presence of certain isolated compounds (Grosberg

1988; Pawlik 1991; Zhao and Qian 2002). Study of settlement cues is challenging because it is difficult in situ and in vitro to identify and isolate potential cues. In situ, there are many chemicals, and/or mechanical stimuli that may initiate settlement; in addition, these cues are often species-specific (Pawlik et al 1991).

Pawlik et al. (1991) conducted an experiment with *Phragmatopodium lapidosa californica*, a gregarious tube worm, the worms were placed in a flume in order to evaluate whether flow speed and pattern were driving settlement alone, or if the worms were using conspecific attraction to evaluate habitat. Passive particles were used as a control for worm larvae to indicate the pattern of settlement from hydrodynamic deposition of larvae. These results were compared to settlement assays in which actual worm larvae were allowed to select habitat patches in flow. Sand in which adult conspecifics had lived was used as the treatment substrate, and more larvae settled and metamorphosed there than on the clean sand substrate used as the control.

Grosberg (1988) reviewed allorecognition as a type of conspecific attraction that facilitates grouping of closely related individuals. In sessile, asexually-reproducing invertebrates, closely related organisms exude similar compounds that allow for recognition. Upon tissue contact in sponges, tunicates, and cnidarians, individuals are either recognized or not and as a result they either attach together or have agonistic encounters (reviewed by Grosberg 1988). The mechanism of allorecognition may be a component Allee effect, in a small population, individual fitness may decrease with the ability to form colonies if they are unable to find enough “self-like” individuals.

Conspecifics may benefit larvae during settlement and throughout their recruitment to juvenile and adult stages. Several unique examples of this indirect component Allee effect indicate decline of adult population causing a decline in recruitment when conspecific cues are low or absent. For example, Quinn et al. (1993) found that in the red sea urchin, *Strongylocentrotus franciscanus*, larvae settle in response to adult conspecific density, and they settle onto the adults. In this somewhat extreme case of habitat selection through conspecific attraction, larvae find habitat and live protected between the spines of adults until they are larger. In fishes, Walters and Kitchell (2001) report that decline in adult population size does cause a decline in recruitment to the fishery due to "cultivation effects". Younger age classes of fish benefit from the presence of adult conspecifics, because the adults feed on larval stages of other species, which compete for food in the habitat. Adults enhance the survival of post-settlement fish and increase the density dependence of the population overfishing of the adult fish could lead to extreme population reductions as a result of this Allee effect.

A recent study of porcelain crab settlement found that both conspecific cueing and Allee effect benefits due to reduced predation risk combine to explain conspecific attraction (Donahue 2006). When adults were caged at different densities, the number of new recruits was positively associated with conspecific density. This result was surprising given that previous studies had demonstrated a negative consequence conspecific density on intraspecific resource competition. Donahue (2006) demonstrated that this component Allee effect could be overcome if gregarious settlement was offset by a decrease in predation risk.

Do Allee effects influence spiny lobster recruitment?

Spiny lobsters (Family Palinuridae) are known to be attracted to odors of conspecifics (Atema and Cobb 1980). However, the influence of these odor cues on the settlement of postlarvae has not been previously examined. In this thesis, I will test the hypotheses that conspecific density will increase spiny lobster recruitment by (1) an increase in local settlement of postlarvae due to attraction to conspecific odor, (2) an increase in survival of early benthic juveniles by guiding them to crevice shelters, or (3) an increase in survival of late benthic juveniles by cooperative group defense while sharing crevice shelters.

Spiny lobster life history

Palinurids have a complex life cycle with a long-lived phyllosoma larval stage, and a short-lived puerulus postlarval stage (Booth and Phillips 1994). Gravid adult females release the phyllosome larvae into offshore currents during the period new moon (Ziegler personal communication). The phyllosomes remain in the open ocean for 6-12 months and molt through 10-12 instars (Witham 1964). The final form is the puerulus postlarvae, a non feeding directionally swimming stage which orients toward shore (Phillips and Sastry 1980; Acosta et al. 1997; Manzanilla-Dominguez and Gasca 2004; Jeffs et al. 2005). Once near shore the transparent postlarvae darken in color and settle in vegetated benthic habitat (Butler and Herrnkind 2000).

Habitat selection in spiny lobsters

The pueruli move onshore in large groups but settle individually (Marx and Herrnkind 1985a; Herrnkind and Butler 1994, Acosta et al. 1997). Butler et al. (1997) hypothesized that they do not aggregate as algal phase early benthic juveniles because aggregations of lobsters are far less cryptic than individuals in the vegetated habitat. They found that lobsters tethered in algal habitat in pairs suffered nearly twice as much predation as those tethered alone. Butler and Herrnkind (1991) conducted laboratory preference tests of *Panulirus argus* (Latreille) postlarvae, to six settlement cues including (1) *Laurencia* sp. red macroalgae, (2) macroalgae extract in water, (3) artificial structure similar to algae, (4) artificial structure and algae extract, (5) *Thalassia* sea grass, and (6) blank seawater control. They monitored settlement behavior (pigmentation), and time to the first metamorphosis under these conditions. They found that time to pigmentation was shortest in the presence of red macroalgae, 4.4 days after collection as clear puerulus. Interestingly, the second shortest time to pigmentation was in those animals exposed to artificial algae, suggesting that settlement may be combined effect of tactile and chemical cues (Butler and Herrnkind 1991).

Finding food and avoiding predators are essential for survival of larvae post settlement. When examining preferred habitat of early benthic juveniles, Marx and Herrnkind (1985b) found that algal phase animals were more likely to remain in a clump of *Laurencia* spp. algae if the clump was large and there was abundant food. Algae clumps from which small mollusks had been rinsed were selected less often than clumps with ample food. In a similar study of microhabitat selection, Herrnkind and Butler

(1986) found that early benthic juveniles moved more frequently between clumps when the algal cover was continuous. They also examined predation of algal phase early benthic juvenile lobsters tethered on open sand, in sea grass, and algae, finding the lowest predation rate occurred on algae (Smith and Herrnkind 1992). Mortality is high during larval, postlarval, and algal phases, before they move into crevice shelters, thus it is also important that an area receives adequate larval supply (Smith and Herrnkind 1992, Forcucci et al. 1994).

Conspecific attraction habitat selection in spiny lobsters

Spiny lobsters are attracted to the odor cues of conspecifics and this often leads to den sharing (Herrnkind et al. 1975; Zimmer-Faust et al. 1985). Laboratory studies have shown that adult spiny lobsters orient towards conspecific odor cues regardless of sex (Zimmer-Faust and Spanier 1987). This odor cue facilitates aggregation and is likely to cause den sharing observed in other species of lobsters (*P. ornatus*-Trendall and Bell 1987; *J. edwardsii*-MacDiarmid 1994; *P. argus*-Nevitt et al. 1996).

Attraction to conspecific odors begins shortly after settlement. Early benthic juveniles as small as 12 mm carapace length (CL) are attracted to conspecific odors from late benthic juveniles (> 25 mm CL) although they are not attracted to similar sized conspecifics (Ratchford and Eggleston 1998). These algal phase EBJs (6-15 mm CL) do not alter their activity level or preference for algal clump shelters when in the presence of similar sized conspecifics, but larger post-algal EBJs (15-25 mm CL) increase walking and den sharing in the presence of similar-sized conspecifics (Childress and Herrnkind

1996). Laboratory results corroborate field observations of Marx and Herrnkind (1985a) that algal phase EBJs are usually found by themselves.

An ontogenetic shift in conspecific attraction may influence the ontogenetic shift in habitat since conspecific attraction is first exhibited by EBJs that are large enough to make the transition from macroalgae to crevice shelters beneath corals and sponges. After settlement in macroalgae, lobsters feed and grow for several months until they become too large and too conspicuous to predators (Herrnkind and Butler 1986; Smith and Herrnkind 1992). Once the individual reaches this transitional size, they must move at night to crevice shelters (Childress and Herrnkind 1996). Childress and Herrnkind (2001a) tested ontogenetic shift hypothesis by raising algal phase EBJs in artificial ponds with and without conspecifics. Each pond included artificial algal habitat (hog's hair filter material) and artificial crevice shelters (concrete partition blocks). The size and location of each lobster was noted weekly for eight weeks. The average size at transition to the crevice shelter habitat was 12 mm CL when conspecifics were present and 14 mm CL when conspecifics were absent. This suggests that attraction to conspecific cues might accelerate the transition to crevice shelter habitat (Childress and Herrnkind 2001a).

Palinurid juveniles and adults are gregarious and undergo ontogenetic shifts in habitat beginning with the algal phase and continuing through sexual maturity (Atema and Cobb 1980; Kanciruk 1980; Butler et al. 1997; Ratchford and Eggleston 1998). Several social Palinurid species exhibit den sharing behavior, *Panulirus cygnus*, *Panulirus ornatus,* and *Panulirus argus* (reviewed in Childress and Jury 2006). Juveniles eventually outgrow crevice shelters and must move across the open bottom to offshore mating habitat. Sub-adult lobsters aggregate and form queues to make the journey (Kanciruk 1980; Childress and Jury 2006; Butler and Herrnkind 2006). The formation of a queue is a highly adaptive antipredator behavior; when threatened, the lobsters wind into a rosette shape and face antenna outward to defend the group (Kanciruk 1980; Herrnkind et al. 2001). Lobsters can be very vulnerable to predation during ontogenetic shifts in habitat, and gregariousness has been shown to increase survival (Smith and Herrnkind 1992; Childress and Herrnkind 1994; Childress and Herrnkind 2001b; Yeung and Lee 2002).

Conspecific attraction and Allee effects in spiny lobsters.

For my masters thesis I tested three hypotheses as to the functional significance of conspecific attraction in recruitment of spiny lobsters. Conspecific attraction to LBJs may influence (H_1) settlement of postlarvae (Settlement Cue Hypothesis); (H_2) survival of EBJs through the transition from algae to crevice shelters (Guide Effect hypothesis), and/or (H_3) survival of LBJs inhabiting crevice shelters through cooperative group defense (Group Defense hypothesis). It is possible that conspecific attraction influences lobsters in two or even all three ontogenetic stages. If the benefit of conspecific attraction by one or more early ontogenetic stages serves to increase the density of older juvenile and adult lobsters, this would be evidence of a component Allee effect in *P. argus*. Depending on the actual quality of the habitat with the high conspecific density, the component Allee effect may have either a positive or negative demographic consequence.

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CHAPTER TWO

TESTING THE ALLEE EFFECT RECRUITMENT HYPOTHESIS

Introduction

For many populations growth is density dependent with positive effects at low population densities and negative effects as density approaches carrying capacity (Allee 1931). This "Allee effect", named for W.C. Allee, refers to a density dependent relationship between population size and fitness (Odum and Allee 1954). Historically studies in ecology have focused on negative density dependence, describing how overcrowding and competition for resources can structure populations (Assmussen 1979). Until recently, researchers have failed to consider how positive density dependence or undercrowding may also drive population dynamics (Tonkyn 1986; Dennis 1989; Stephens et al. 1999). This may be particularly important for those species that have specific habitat requirements or a limited ability to locate potential mates (McCarthy 1997; Petersen and Levitan 2001; Bessa-Gomes et al. 2004; Calabrese and Fagan 2004). Study of Allee effects is important for understanding and conserving small isolated populations since positive density dependence may only be realized above some critical minimum density (Courchamp et al. 1999; Levitan et al. 1992). Overfished species such as queen conch, *Strombus gigas*, with a low reproductive rate and limited ability to find potential mates may fall below the critical minimum density to sustain positive population growth (Stoner and Ray-Culp 2000; Gascoigne and Lipcius 2004a).

One Allee effect mechanism that may help populations to obtain a critical minimum density is habitat selection based on the presence of conspecifics (Green and Stamps 2001; Green 2003). For terrestrial species conspecifics attraction and corresponding Allee effect benefits may influence habitat selection (Stamps 1988), reproductive strategy (Etienne et al. 2002; Cheptou 2004), and ability to invade new habitats (Lewis and Karieva 1993; Veit and Lewis 1996; Keitt et al. 2001; Holt et al. 2004). However, habitat selection based solely on the presence of conspecifics can have negative consequences and even reduce population viability (Brassil 2001; Kokko and Sutherland 2001; Dennis 2002).

Conspecific attraction is also an important mechanism operating in settlement of marine invertebrates. Many sessile invertebrates including barnacles, oysters, bryozoans, and tube worms have mobile larvae that use cues emitted by adults to locate suitable settlement habitat (Knight-Jones 1953; Crisp and Knight-Jones 1953; Crisp 1967; Grosberg 1988; Pawlik et al. 1991). The use of such cues in habitat selection tightly links adult populations and settling larvae, creating an Allee effect that can be impact population persistence. A recent study of recruitment in porcelain crabs suggests that conspecific attraction may increase settlement of mobile invertebrates as well (Donahue 2006).

I investigated this hypothesis in the gregarious Caribbean spiny lobster *Panulirus argus* (Latreille). Caribbean spiny lobsters are clawless lobsters of the Family Palinuridae, which are known to be highly gregarious (Childress and Jury 2006). They are attracted to conspecific odors (Ratchford and Eggleston 1998; Nevitt et al. 2000), share crevice shelters (Herrnkind et al. 1975; Childress and Herrnkind 1997) and migrate in coordinated, single-file queues (Herrnkind 1969; Bill and Herrnkind 1976). Previous studies of Caribbean spiny lobster settlement in the Florida Keys nursery have identified red macroalgae as the primary settlement habitat (Marx and Herrnkind 1985a; Herrnkind and Butler 1986). Newly settled early benthic juveniles living in algae are rarely found together (Marx and Herrnkind 1985b) and do not appear to be attracted to similar sized conspecifics (Childress and Herrnkind 1996; Ratchford and Eggleston 1998). As these early benthic juveniles emerge from the algae (postalgal phase) they orient toward conspecifics cues, increase activity and begin sharing crevice shelters under sponges and corals (Childress and Herrnkind 1996; 1997; 2001a).

My study addressed four basic questions **(1)** *Are postlarval lobsters (PL) attracted to odor cues of late benthic juvenile spiny lobsters (LBJs)?* In order for PLs to use conspecific cues in habitat selection, they must be attracted to conspecifics. I used laboratory choice tests to test whether PLs are attracted to LBJs cue animals > 25 mm in carapace length (CL). In the field I used coded microwire tags in a mark recapture study to examine how settlement and post-settlement survival varies with LBJ density. **(2)** *Does the addition of shelter increase LBJ density?* Previous studies have used partition block shelters to artificially enhance crevice shelter abundance in lobster nursery habitat. In my study I used similar artificial shelters but I altered the opening sizes in order to include or exclude late benthic juveniles >25 mm CL to manipulate lobster density on my study sites. **(3)** *Does early benthic juvenile (EBJ) density increase with LBJ density?* I assessed the effect of LBJ density on PLs, $\text{EBJ}_{\text{Algal}}$, and $\text{EBJ}_{\text{Postalgal}}$ by sampling the dependent variable, postalgal EBJ density on sites with varying LBJ density. I chose postalgal phase EBJs as my response variable because they are the first conspicuous juvenile stage and can be sampled easily by systematic search of available crevice shelters. Also EBJs have higher site fidelity than LBJs and therefore one can assume if found on the site, an EBJ has survived on the site since settlement. If EBJ density is positively influenced by LBJ density there is an Allee effect operating through conspecific attraction of PLs and EBJ_{Algal} to larger juveniles. A change in EBJ density will not however indicate the stage(s) at which the Allee effect was beneficial. I used mark recapture techniques to infer how PL settlement and post settlement survival of EBJ_{Algal} differed with LBJ density. **(4)** *What best explains the influence of LBJs on EBJs?* Late benthic juveniles can positively influence three different ontogenetic stages within the nursery habitat in Florida Bay. I tested three Allee effect hypotheses to explain this influence. LBJs can increase settlement of postlarvae by acting as a settlement cue (H_1 Settlement Cue hypothesis). LBJs in crevice shelter can attract EBJs making the transition from algae to crevice shelters guiding them and reducing predation risk (H_2 Guide Effect hypothesis). LBJs in crevice shelters may increase survival of EBJs through cooperative group defense against predators (H_3 Group Defense hypothesis). These hypotheses are not mutually exclusive since ontogenetic stages are not independent; the goal of this study is to provide more detailed information about how conspecific density of juvenile spiny lobsters can affect recruitment in this economically important species.

H_1 Settlement Cue Hypothesis

The Settlement Cue hypothesis predicts that postlarvae are attracted to conspecifics and will preferentially settle in those areas (Figure 2.1). Directly testing the Settlement Cue hypothesis is difficult, since I am not able to measure postlarval settlement in Florida Bay. Studying algal phase juveniles is also a challenge since it is difficult to accurately census newly settled early benthic juveniles dwelling in macroalgae. To estimate levels of natural settlement, I employed a mark recapture method using coded microwire tagged individuals. By seeding a known number of tagged EBJs into algae on study sites each month, I estimated natural recruitment by comparing the density of tagged and untagged postalgal EBJs recovered from each site.

H_2 Guide Effect Hypothesis

Under the Guide Effect hypothesis newly settled EBJs use conspecific attraction to emerge from the algae and move directly into crevice shelters (Figure 2.1). EBJs make this transition presumably when they reach a size at which they are conspicuous to predators. This behavior was first described by Childress and Herrnkind (2001a) who demonstrated that lobsters >17mm CL found a shelter more quickly if it was inhabited by a conspecific juvenile in mesocosm experiments. Childress and Herrnkind (2001b) found that spiny lobsters made the transition from algae to crevice shelters at a slightly smaller size when larger conspecifics were present. Two explanations of this pattern are thatlobsters shift habitat at a smaller size in response to lowered predation risk in the presence of conspecifics, or that conspecific attraction minimizes search time for crevice shelters and increases survival of smaller individuals.

H_3 Group Defense Hypothesis

The Group Defense hypothesis states that LBJs sharing shelters show higher survival through dilution effect and/or the cooperative defense against predators (Figure 2.1). This was the original hypothesis proposed to explain den sharing in spiny lobsters (Butler et al. 1999; Herrnkind et al. 2001). LBJs are nomadic and have been shown to use conspecific attraction to locate suitable shelter which is patchily distributed; large dens often concentrate lobsters into large groups which emit a strong conspecific signal. These groups are better suited to ward off fish predators than lobsters residing in shelters alone. Though EBJs may be too small to effectively defend against a predator on their own, when sharing a shelter with LBJs, they may have increased survival.

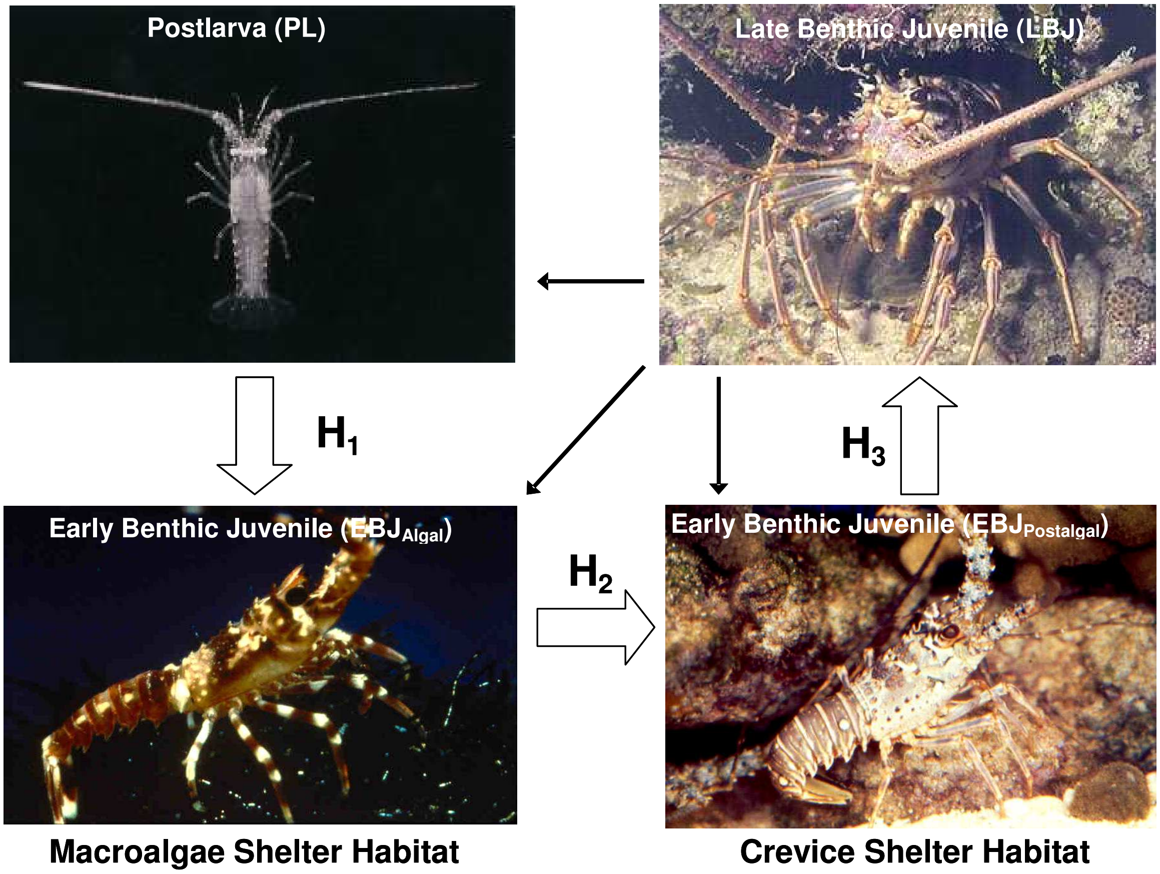

Figure 2.1. The three hypotheses regarding the potential benefit of increased conspecific density. H_1 Settlement Cue Hypothesis LBJ density increases postlarval settlement by signaling the presence of appropriate settlement habitat. **H_2 Guide Effect Hypothesis** LBJ density increases EBJ survival by decreasing search time for crevice shelters once they have left the macroalgae. **H_3 Group Defense Hypothesis** LBJ density increases LBJ survival by cooperative group defense while sharing crevice shelters.

Predictions

My three hypotheses are not mutually exclusive since ontogenetic stages are not independent of one another, nor are they independent of community factors. Study sites were chosen to represent a natural range of lobster habitat in Florida Bay, thus it was expected that locations would differ in postlarval density, algal cover, natural structure, and predator abundance. I considered how community variables could influence EBJ density independently of LBJ density.

Community factors influencing EBJ numbers

Previous studies on juvenile and adult spiny lobsters have examined how spiny lobster populations are affected by the habitat requirements listed above. I also examined these important community factors, attempting to hold them relatively constant to examine the influence of LBJ density.

PL density

Despite the logical relationship between postlarval density and juvenile lobster density, surface collector catches of postlarval *P. argus* are usually unrelated to the local abundance of juvenile spiny lobsters (Herrnkind and Butler 1994). If postlarval density (PL) is an important influence on the number of lobsters on a site, I would expect settlement at each location to correspond to surface collector catches at that location. The highest EBJ density should be found at the location with the highest PL supply, roughly 2-3 months after a peak PL supply month (Table 2.1).

Algal Cover

Studies of settlement microhabitat for postlarval lobsters found that PLs prefer the complex structure and of dense macroalgae, specifically *Laurencia* spp. (Marx and Herrnkind 1985a; Herrnkind and Butler 1986). Thus I expected to find that sites with higher percent cover of red algae would have higher numbers of EBJs. Algal cover may affect the number of postlarvae that settle and the number of algal EBJs that survive predation while in algae to make the transition to crevice shelters (Table 2.1). Algal cover should not influence the abundance of postalgal EBJs surviving in crevice shelters.

Natural Structure

The availability of natural structure (and crevice shelters) has been shown by a number of studies to influence distribution of EBJ lobsters (Butler and Herrnkind 1997; Herrnkind et al. 1997a; 1997b; Childress and Herrnkind 1997). Size scaling of crevice shelters can increase survival of algal and postalgal EBJs (Eggleston and Lipcius 1992; Smith and Herrnkind 1992; Mintz et al. 1994). I predicted that sites with more natural structures for shelter would have higher numbers of EBJs due to increased survival of EBJ_{Algal} that are able to find shelter and survival of gregarious $EBJ_{Postalgal}$ in shelters (Table 2.1).

Predators

There are many known predators of juvenile spiny lobsters including octopus, swimming crabs, stone crabs, and a variety of benthic feeding fish. Interactions between lobsters and predators are complex because predator species that are den-obligate may also be competing with lobsters for available crevice shelters. Previous studies examining intraspecific interactions involving lobsters have found little evidence of competition or predation influencing lobster populations (Childress and Herrnkind 1997). Since little is known about predation on lobster postlarvae, I cannot make a prediction of how predator density might affect the number of postlarvae arriving on a site. I expect that if predators impact lobster populations, they will have a negative effect on EBJ_{Algal} and $EBJ_{Postalgal}$. EBJ mortality during the transition from macroalgae to crevice shelters and predation on $EBJ_{Postalgal}$ in crevice shelters will result in low EBJ abundance overall (Table 2.1).

Predictions for three hypotheses of conspecific attraction

Settlement Cue

If postlarvae settle in response to a cue from conspecifics, I predicted that sites with higher LBJ density would have higher natural settlement of PLs and ultimately a higher density of untagged postalgal EBJs (EBJ_{Untag}). Since microwire-tagged postlarvae will be placed in equal numbers on all sites independent of LBJ density (artificial settlement), EBJ_{Tag} should not vary with LBJ density. Sites with higher LBJ density should have a lower percentage of tagged EBJs ($EBJ_{\%Tag}$) this is because more untagged postlarvae arrive in response to a conspecific cue than are artificially seeded. Artificial settlement (of tagged PLs) will be diluted by high natural settlement of untagged postlarvae on sites with higher LBJ density. Finally, I predict that if PLs use conspecific attraction, more will choose the LBJ cue over the seawater control in Y-Maze choice test.

Guide Effect

If EBJs are using conspecific attraction to LBJs to locate crevice shelters more quickly (decreasing predation risk), I expected to find more EBJs on sites with higher LBJ density. I predicted that the density of both untagged and tagged EBJs would show this density dependent trend. I also anticipated that EBJs on sites with higher LBJ density would be smaller than those on sites with lower LBJ density.

Group Defense

If LBJs have higher survival from sharing shelters with conspecifics I predict that sites with high and low LBJ densities will be equal in EBJ density, tagged to untagged ratio, and EBJs size. EBJs will have similar survival on treatment and control sites but once they move into crevice shelters shared with LBJs, they will have increased survival. As a result of higher survival when sharing shelters, there will be more EBJs on sites with higher LBJ densities.

Table 2.1. Hypotheses and predictions for field experiment. Plus signs indicate a positive influence of the independent variable on EBJ#, minus signs indicate a negative influence of variable on EBJ # and zeros indicate no influence on EBJ number. Refer to Appendix for abbreviations.

Community variables influencing EBJ #s

Ontogenetic Stage	**PL**	**ALG**	**STRUCT**	**PRED**
PL	+	+	0	0
EBJ_{Algal}	+	+	+	–
$EBJ_{Postalgal}$	+	0	+	–

Predictions for three hypotheses of conspecific attraction

Hypothesis	**PL Choice Test**	**EBJ_{Untag}**	**EBJ_{Tag}**	**% EBJ_{Tag}**
H_1 Settlement	+	+	0	_
H_2 Guide Effect	0	+	+	0
H_3 Group Defense	0	0	0	0

Methods

Laboratory PL choice experiments

Postlarval lobsters (pueruli) were collected monthly (January to June 2006) from eight sets of five Witham (Witham et al. 1964) style surface collectors (Figure 2.2, Table 2.2) (See methods of Acosta et al. 1997). Postlarvae were returned to our dockside laboratory and were housed in 40 liter aquaria. Individuals were tested one at a time in a Y-maze for conspecific attraction. Tests were only conducted on clear pueruli that had not yet begun to pigment. It is at the transition from PL to EBJ_{Algal} that the strongest response to a settlement cue was expected. LBJs of both sexes were randomized as cue animals. This size range of cue animals was similar to the size of crevice-dwelling lobsters present in the field. A cue animal was contained in a compartment at the end of one arm of the flow-through Y-maze (Figure 2.3-location B_1), blocking visual cues, and the other arm's compartment left empty (Figure 2.3-location B_2). The cue animal was randomly assigned to either left or right compartment at the beginning of each trial. A panel of hogshair (Figure 2.3-location C) provided a complex settling substrate at the end of each arm, closest to the cue chamber. The focal animal was released at dusk in the center of the Y–maze (Figure 2.3-location D), allowed to acclimate for five minutes, and checked for position 10-12 hours later.

The proportion of postlarvae (N=68) choosing the odor cue vs. blank cue was compared using binomial probability test. Those individuals that did not choose an arm of the Y-maze (N=41) were excluded from this analysis. I found no significant effect due to side bias (G=0.078, p=0.780) or month (G=5.732, p=0.333).

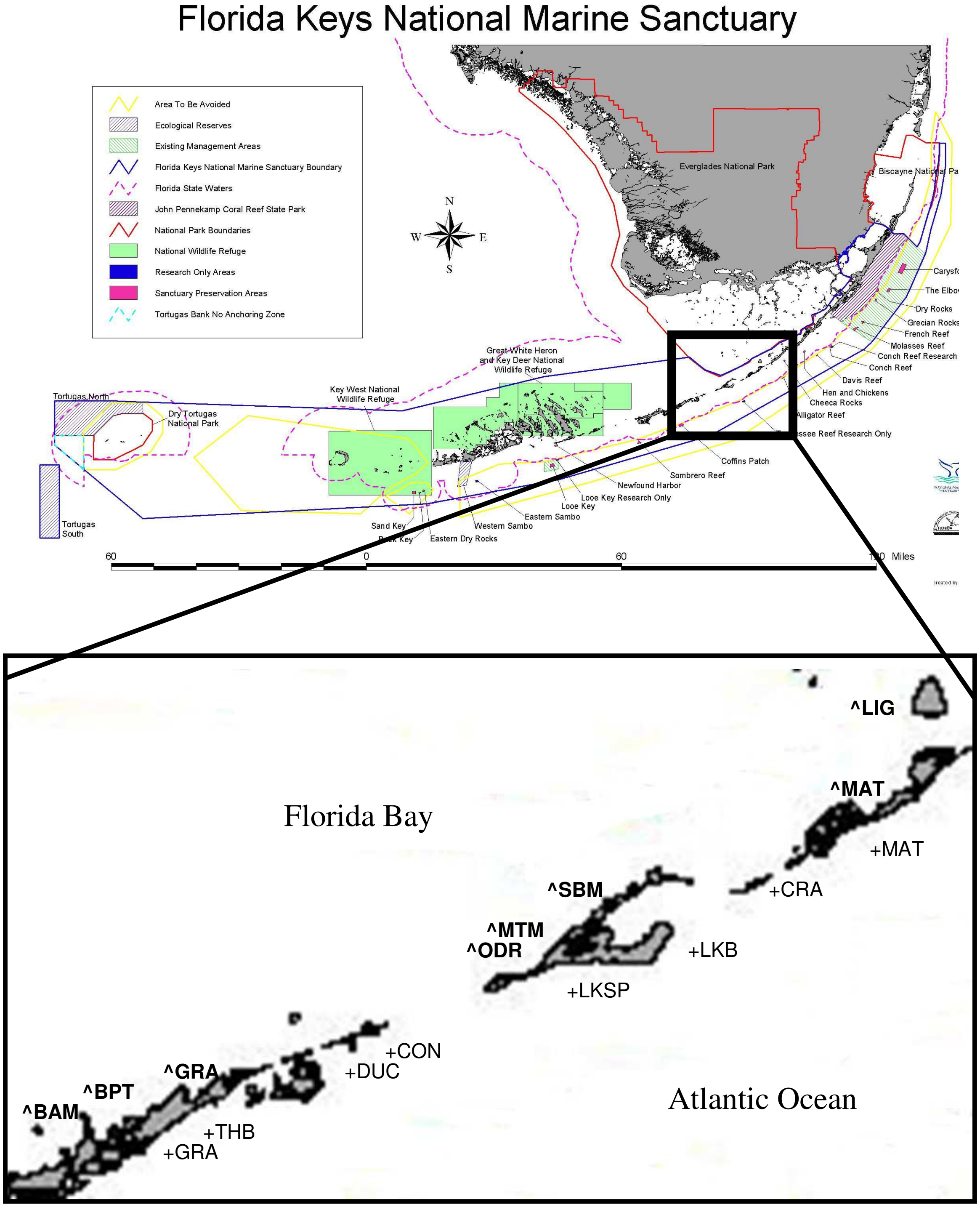

Figure 2.2. Map of census locations and surface collector locations. Census locations in Florida Bay are denoted with the ^ symbol and with bolded text. Surface collectors were placed ocean-side of major cuts and are marked with a plus sign on this map.

Table 2.2. GPS Coordinates of census sites and surface collector arrays listed by location rank from west to east. T/C indicates type of treatment block added.

Abbreviation	Name	Location Rank	T/C	Latitude	Longitude
Surface Collectors					
GRA	Grassy Key	1		N 24° 45.587	W 80° 56.585
THB	Tom's Harbor Bank	2		N 24° 45.668	W 80° 55.800
CON	Conch Key	3		N 24° 46.921	W 80° 53.389
DUC	Duck Key	4		N 24° 46.314	W 80° 54.179
LKP	Long Key Park	5		N 24° 48.269	W 80° 50.243
LKB	Long Key Bight	6		N 24° 48.972	W 80° 47.168
CRA	Craig Key	7		N 24° 49.661	W 80° 45.683
MAT	Matacumbe Key	8		N 24° 51.238	W 80° 43.699
Census Sites					
BAM1	Bamboo Key 1	1	T	N 24° 45.357	W 81° 00.257
BAM2	Bamboo Key 2	1	C	N 24° 45.342	W 81° 00.097
BPT1	Burnt Point Key 1	2	T	N 24° 45.444	W 80° 59.067
BPT2	Burnt Point Key 2	2	C	N 24° 45.305	W 80° 59.031
GRA1	Grassy Point Key 1	3	T	N 24° 46.221	W 80° 57.161
GRA2	Grassy Point Key 2	3	C	N 24° 46.142	W 80° 56.945
ODR1	Outdoor Resorts 1	4	T	N 24° 48.488	W 80° 50.425
ODR2	Outdoor Resorts 2	4	C	N 24° 48.518	W 80° 50.323
MTM1	Mount Trashmore 1	5	C	N 24° 49.075	W 80° 49.602
MTM2	Mount Trashmore 2	5	T	N 24° 49.474	W 80° 49.214
SBM1	SeaBird Marina 1	6	T	N 24° 50.088	W 80° 48.411
SBM2	SeaBird Marina 2	6	C	N 24° 50.116	W 80° 48.341
MAT1	Matacumbe Key 1	7	C	N 24° 51.914	W 80° 43.169
MAT2	Matacumbe Key 2	7	T	N 24° 51.835	W 80° 43.261
LIG1	Lignumvitae Key 1	8	C	N 24° 54.560	W 80° 42.007
LIG2	Lignumvitae Key 2	8	T	N 24° 54.539	W 80° 41.801

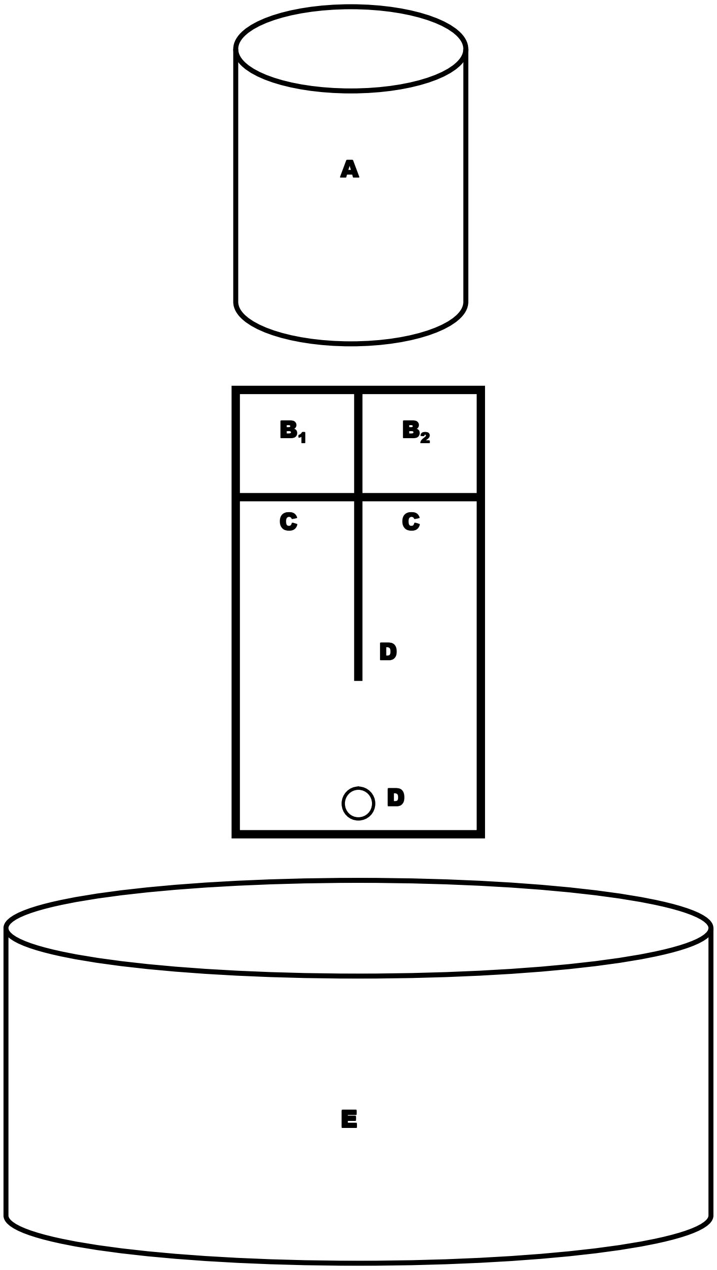

Figure 2.3. Laboratory set up for postlarval choice tests in the flow through Y-maze. Water is pumped into cylindrical gravity filter (A) through a spray bar. Water falls into both end compartments (B) one of which held a cue animal while the other remained empty. Water passes from compartments beneath divider (C) into arms. Dividers are covered with hogshair filter material. Water flows down each arm and out a central drain pipe (D) and into a 150 gallon reservoir (E) from which it is recycled into the cylindrical filter (A). Trials took place overnight, and the puerulus allowed to choose which hogshair panel to settle onto. Trials in which the PL did not move onto either hogshair panel were scored as "no choice".

Site Selection and Mapping

In June 2005 sixteen permanent study sites (25 m X 25 m) were chosen in eight hardbottom areas of Florida Bay (Figure 2.2, Table 2.2). The sites selected were suitable lobster habitat with macroalgae, natural crevice shelters including sponges, seaplumes and/or coral heads, and juvenile spiny lobsters. Eight locations from Lignumvitae to Bamboo Key were chosen for a paired design. Since locations in Florida Bay vary in structure, lobster density, and larval supply they cannot be considered replicates, thus a control (C) and treatment (T) site were randomly assigned at each location (Figure 2.4). Paired sites were spaced a minimum of 500 m from one another so that LBJ and EBJ populations at each site was considered to be independent. Sixteen 25 X 25 m permanent study sites were marked with a block on each corner marked with GPS to ease monthly revisitation. Corner blocks were cement-filled cinderblock with an embedded eyebolt to which a subsurface buoy was attached. After sites were marked, twelve 25 m lead weighted lines were laid over the site to create a 5 X 5 m grid to allow mapping of potential natural crevice shelters. Each 5 X 5 m square was mapped by hand and compiled in Microsoft PowerPoint into a full site map (Figure 2.5). Maps are accurate to 1 m, and were used during census to note exact positions of lobsters, and predators during monthly censuses.

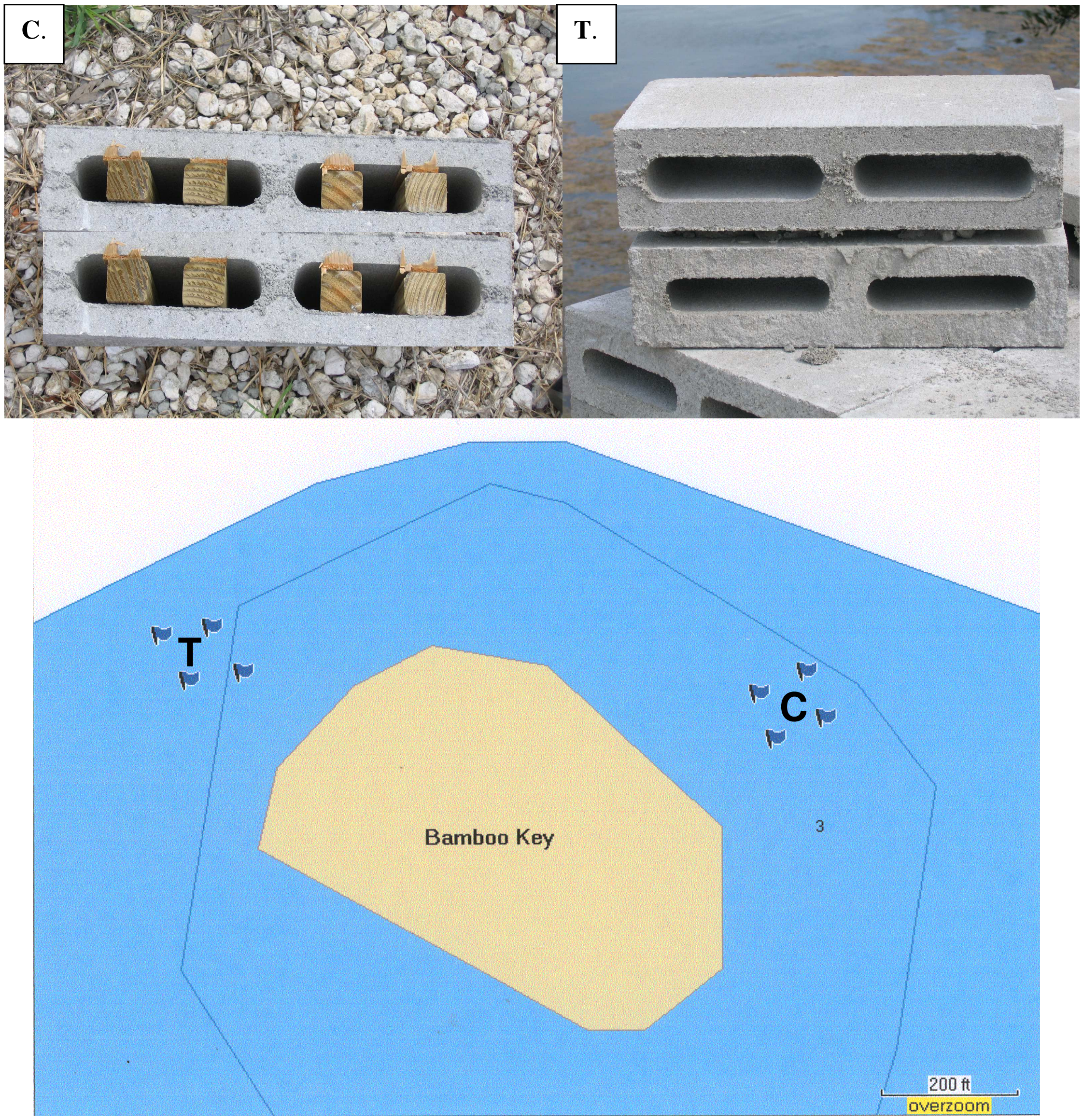

Figure 2.4. Experimental manipulation of paired field sites. Two types of double stacked artificial shelter blocks on a map of one study location - Bamboo Key (BAM). (**C**) Control artificial shelter block, designed to exclude animals exceeding 25 mm CL. **(T)** Treatment artificial shelter block, designed to add shelter for juvenile spiny lobsters < 45 mm CL. Each location has one control site (10 control blocks) and one treatment site (10 treatment blocks). Blue flags represent GPS positions of 4 corners of each 25 X 25 m site. Paired sites were a minimum of 500 m apart.

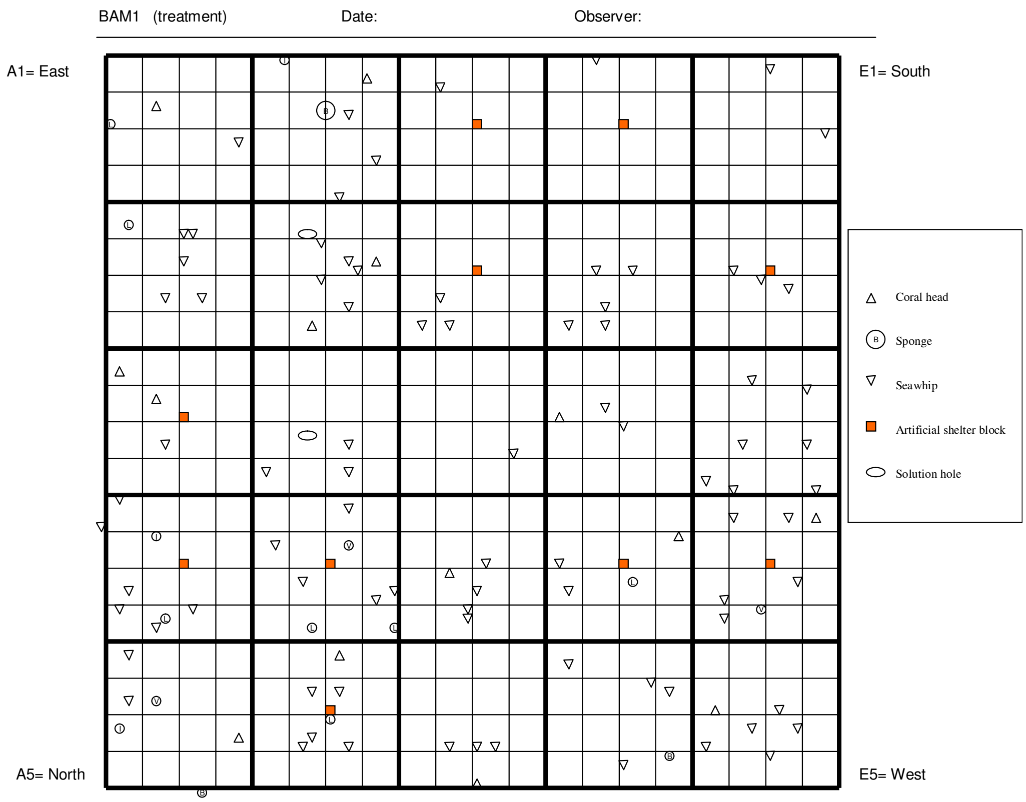

Figure 2.5. **A sample study site map** indicates the type and position of every potential lobster den over 20 mm diameter is represented in symbol on the map. Maps were used during monthly census to assure systematic search of all possible shelters for lobsters, and their predators.

Shelter Manipulation

In August 2005, ten double stacked partition blocks were added to each site. Blocks were randomly assigned to 10 of the 25 subplots (5 m X 5 m) within the site grid, and placed in the center of the square by a snorkeler. Block locations were added to census site maps (Figure 2.5). Treatment sites received double-stacked, two-hole partition blocks (Figure 2.4 - treatment shelter block T) and control sites received double-stacked two-hole partition blocks with two wooden plugs per hole (Figure 2.4-control shelter block C). Treatment blocks provided shelter for juvenile lobsters up to 45 mm CL. Control blocks have much smaller holes due to the wooden plugs and thus could only shelter lobster less than 25 mm CL. Previous studies (Herrnkind et al. 1997a; 1997b) have shown that lobster density increases with the addition of shelter blocks as large juvenile lobsters (> 25 mm CL) will emigrate from nearby natural shelters. Therefore, I expected treatment sites to have an increase in large juvenile lobster density, but control sites would not.

Larval collectors

Witham style surface collectors were deployed to estimate monthly larval supply (PL) to each of the study locations beginning in January of 2006 (Witham et al. 1964). Since larval collectors bayside of the Keys have been unsuccessful in the past, I placed eight sets of five collectors oceanside of each of the major cuts in the island chain closest to our study sites (Figure 2.2, Table 2.2). Collectors were censused twice monthly from January through June of 2006, three and seven days following the new moon. All postlarvae captured on collectors were counted, staged, and taken to the laboratory.

Postlarvae were held in 40 liter aquaria for approximately 2-3 weeks until tagged and seeded on the census sites.

Tagging and Seeding

Postlarvae were maintained in the lab until they were large enough (~ 8-10 mm CL) to tag with binary coded microwire tags (Northwest Marine Technologies, Shaw Island, WA). Before tagging animals each month, before tagging tags were ejected into a bag and labeled for monthly batch reference (see methods of Sharp et al. 2000). All available algal phase EBJs were injected with microwire tags in the first abdominal segment prior to the next monthly census. Equal numbers of microwire tagged EBJ_{Algal} were seeded onto algae on each of the 16 study sites monthly. As part of lobster population censuses from February through July, all juvenile lobsters were collected and scanned for microwire tags using a hand-held CWT detector (NWMT, Shaw Island, WA). Animals that scanned positive for microwire tags were then given a visible implant tag with a unique number code (NWMT, Shaw Island, WA). Those animals found with microwire tags during the final census (July 2006) were sacrificed to identify the month in which they were seeded. The ratio of tagged to untagged individuals was used to estimate natural settlement on sites.

Community Census

From February of 2006 through July of 2006, monthly censuses were conducted on each site. To estimate the proportion of available postlarvae settlement habitat, I conducted two 25 m point-intercept line transects to estimate the percent cover of vegetation each month (Figure 2.6). Vegetation was grouped into three categories; ALRD was all species of the Rhodophyta primarily *Laurencia* spp., ALGR was all species of the Chlorophyta including *Ulva* sp., *Caulerpa* spp., *Halimeda* sp., and SGTH was all the species of sea grasses primarily *Thalassia testudinum*. I found that lobster density was only related to the abundance of red algae and so ALRD was used as an independent variable in my statistical analyses. All percent cover variables were arc-sin square root transformed.

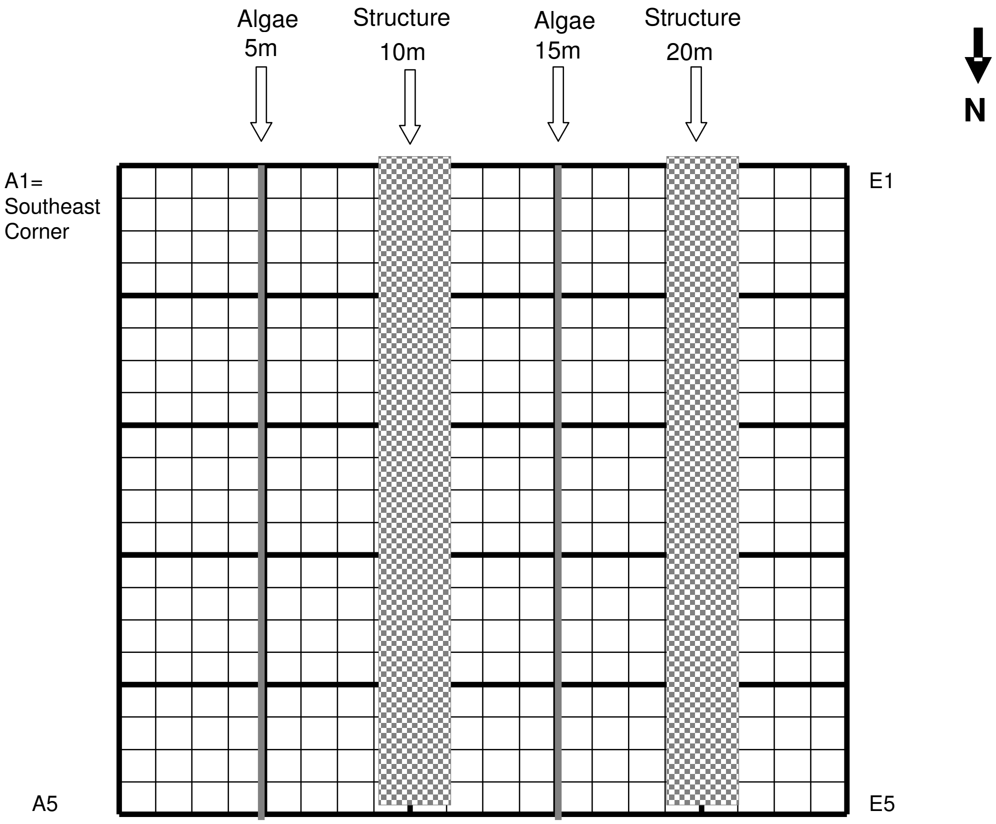

Figure 2.6. Monthly census scheme. Thin gray lines show algal line transects. These are run across the site at 5 and 15 m west of the Southeast buoy (A1). Algal transects are performed monthly and identify patch size and type to evaluate habitat for algal phase animals. The gray hatched bars show two, 2 m X 25 m belt transects for structure at 10 and 20 m west of the A1 buoy. All structures (sessile invertebrates, blocks, solution holes, and other man made shelter) >20 mm diameter are counted to evaluate natural habitat for benthic juvenile lobsters.

To estimate the proportion of natural structures available as shelter for postalgal juvenile lobsters, I conducted two 2 m X 25 m belt transects to estimate natural structure density at the beginning (February) and end of my study (July) (Figure 2.6). Structures were grouped into nine categories; SPL, SPV, SPB, SPO, SWT, SWP, SWO, COR, and SOL according to the methods of Childress and Herrnkind (1997) (see Appendix for structure type descriptions and species identifications). Only structures larger than 20cm diameter were included in the census. Of these nine structures, only five were used as dens by juvenile lobsters; SPL, SPV, SWP, COR and SOL. A sum of all these suitable natural shelters (STRUCT) was used as an independent variable in my statistical analyses.

To estimate the density of potential lobster predators, I conducted a systematic search of the entire study plot (25 m X 25 m) each month. Predators were grouped into seven categories; SPCR, SWCR, STCR, OCTO, TDFS, RAY, SHARK (see Appendix for species identification). The location and type of structure occupied by each predator was noted on a map of the site. A sum of all predator densities (PRED) with the exception of SPCR was used as an independent variable in my statistical analyses. All counts of predators, structure, and lobsters were square root transformed.

Lobster Census

To estimate the density of early benthic juvenile lobsters (EBJ) < 25 mm CL and late benthic juvenile lobsters (LBJ) > 25 mm CL, I conducted a systematic search of the entire study plot (25 m X 25 m) each month. Lobsters were collected by divers on SCUBA using hand nets and sorted into mesh catch bags by structure type. The location and type of structure occupied by each lobster was noted on a map of the site. All lobsters were returned to the boat and were checked for sex (SEX), molt condition (MOLT), carapace length (CL), presence of a coded-wire tag (TAG), injury to antenna (ANT), injury to leg (LEG), and presence of PA-HV1 infection (DIS). Molt condition was assessed to be either pre-molt (Stage D_4), post-molt (Stage A) or intermolt (Stages B-D). Carapace length was measured to the nearest 0.1 mm using calipers. Microwire tag presence was determined by a hand - held tag detector (Northwest Marine Technologies, Shaw Island, WA). Recaptured microwire tagged individuals (EBJ_{Tag}), were injected with a visible alphanumeric tag in their first abdominal segment (NWMT Shaw Island, WA). After measurements were taken, all lobsters were returned to the shelter type from which they were collected. The only exceptions were lobsters with microwire tags found during final census in July, which were sacrificed for recovery of individual tag information.

Lobsters captured in the month of July carrying microwire tags were collected and individually frozen post census. Before dissection in the lab, animals were measured with calipers, and sexed and the site information recorded. Tags were excised from the abdomen of each animal under a dissecting scope. The abdomen was cut into progressively smaller pieces, and each piece was passed over with the detection wand until the tag was located visually and removed. Once tags were located they were cleaned with isopropyl alcohol and placed in a labeled Petri dish on a piece of double sided tape. Each tag bore an individual code in six lines of binary code that yielded an individual value. Reference tags taken prior to tagging each month were also read under a dissecting scope and used to establish the range of values for individuals tagged and seeded in that month. Values for recaptured lobster tags were assigned a month of settlement.

Statistical Analyses

To test the assumption that the paired sites did not differ in their community structure other than the density of late benthic juvenile lobsters, I analyzed the six month average for 50 dependent variables using a one-way analysis of variance with treatment as a fixed main effect. The significance values were adjusted using the sequential Bonferroni method. I expected to find that treatment and control sites would only differ in the number of late benthic juvenile lobsters.

To test the predictions that treatments and control sites should differ in EBJ densities and the ratio of tagged to untagged individuals I conducted a nested analysis of variance using month as a blocking variable. Location was a random factor variable with the fixed factor variable treatment nested within location. The dependent variables were EBJ_{Untag} density, EBJ_{Tag} density, and % EBJ_{Tag}. These dependent variables were square-root transformed to meet the assumption of homogeneity of variances. These transformations were sufficient to meet the assumptions of normality and homogeneity of variances.

To estimate the settlement month for recaptured individuals, I plotted the size and number of months since seeding (month 7 minus seeding month) of EBJ_{tag} individuals sacrificed at the end of the study. I used linear regression to determine the maximum and minimum growth rates assuming that PLs were 7 mm in CL upon settlement. With these growth rates I calculated a size range for each settlement month and used these ranges to assign a size class to each EBJ_{Untag} sampled in the month of July. The size frequency distribution of EBJ_{Untag} on treatment and control sites were compared using a log linear contingency analysis.

I performed a series of multiple regressions to examine the relationship between July EBJ_{tag} values and community and lobsters data from the previous five months. For each month time lag (7 minus month of seeding) I examined the proportion of the variation explained by PL density (PL), red algae cover (ALRD), natural structure (STRUC), predators (PRED), and LBJ abundance. I tested for colinearity and found only two significant correlations between factors out of 60 possible correlations, thus I was able to conduct a multiple regression analysis. I also performed a stepwise multiple regression and found the same significant factors as in the fully fit model. Therefore I present the fully fit model to compare relative strength of each factor across months of time lag.

Results

Are PLs able to detect the odor cues of LBJs?

Of the 68 postlarvae I tested, only 27 PLs made a choice (Figure 2.7). When examining only the trials in which the PL made a choice, 18 chose the conspecific odor and 9 chose the control odor. Results of a binomial probability test indicate that the number that chose the conspecific cue was significantly greater than the number that chose the seawater control ($p=0.035$).

Does shelter addition increase the density of LBJs?

One of the assumptions of the field manipulation was that community factors would differ between locations but be similar within locations (Figure 2.8). One-way ANOVAs were used to examine the difference between paired treatment and control sites for 50 community variables including postlarvae density (PL), percent cover of red algae (ALRD), natural structure density (STRUC), predator density (PRED), late benthic juvenile lobster density (LBJ) and early benthic juvenile lobster density (EBJ). Significance levels for multiple comparisons were adjusted using the sequential Bonferroni method (Table 2.3).

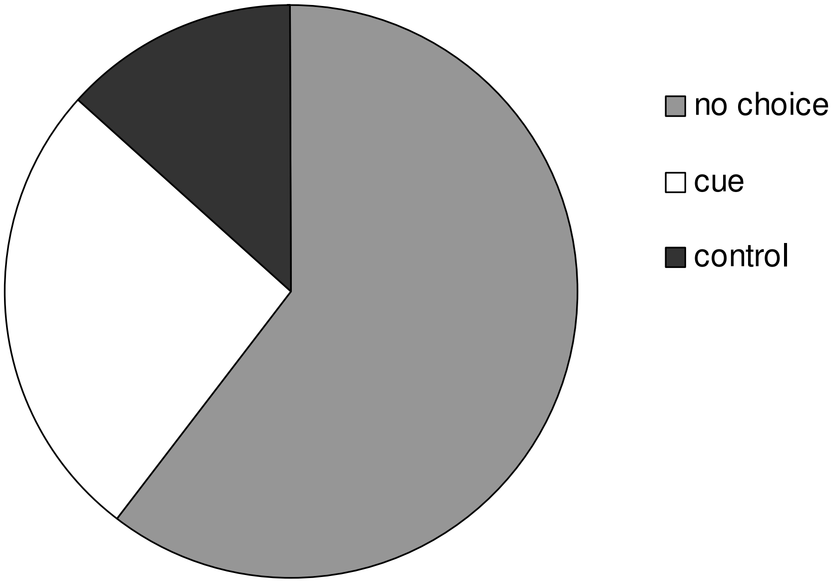

Figure 2.7. Postlarval choice test results. The percent of postlarvae that made a choice in a Y-maze trial and their choices. A binomial probability test indicates a significant difference in the number of postlarvae that chose a conspecific cue over the seawater control (p=0.035).

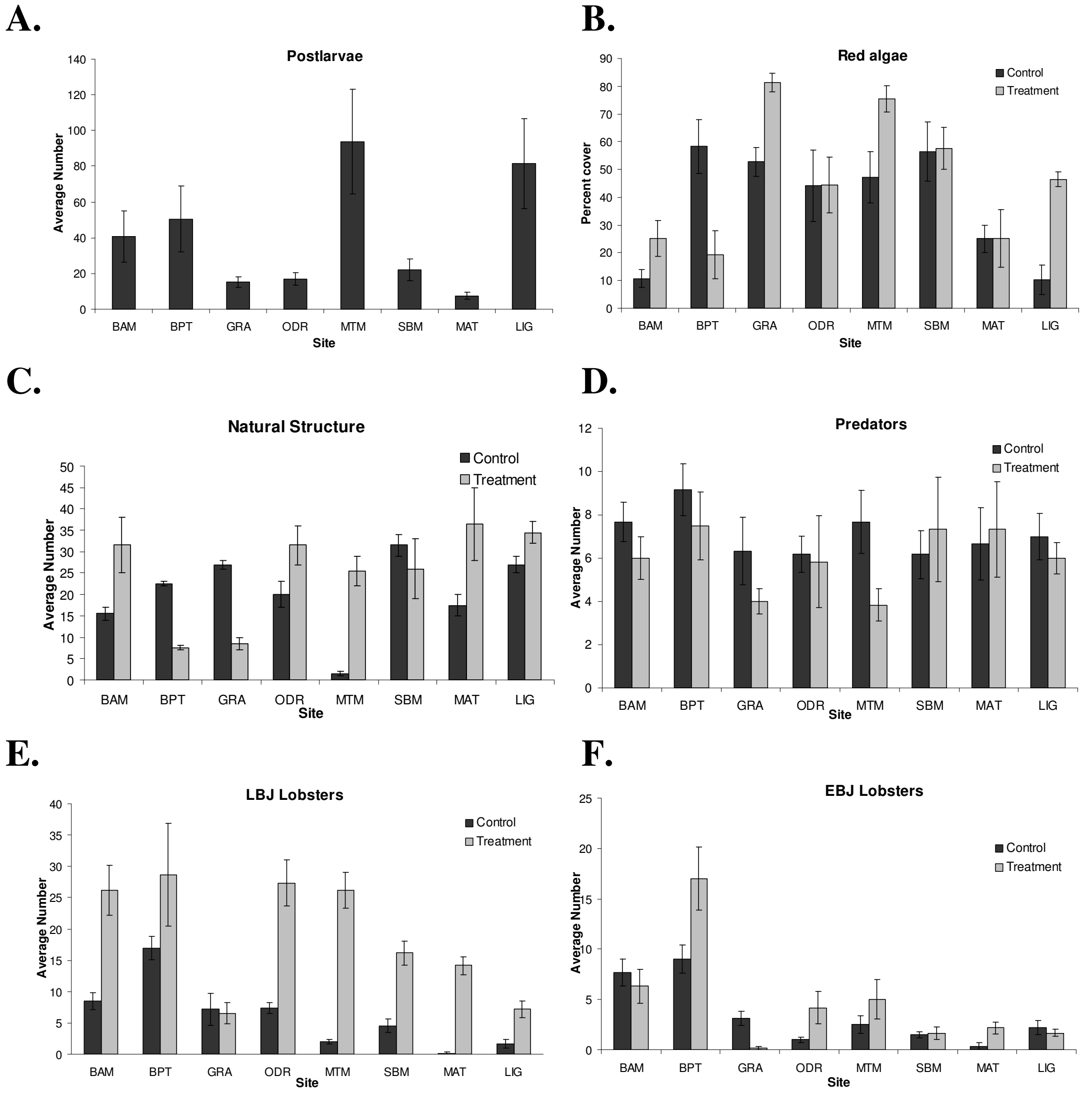

Figure 2.8: **Community variables for treatment and control sites at all eight locations across six monthly censuses**. (A) Postlarval density of the corresponding eight ocean-side surface collector locations. (B) Average percent cover of red algae cover. (C) Average natural structure. (D) Average total predator density. (E) Average LBJ density. (F) Average EBJ density. Error bars indicate standard error.

Table 2.3. Analysis of field manipulation on community covariates using one-way ANOVAs of six month average of control and treatment sites. Refer to Appendix for abbreviations. Inequality symbols specify the direction of relationship between treatment (T) and control (C) sites and α are the adjusted significance level by the sequential Bonferroni method.

Category	**Factor**	**Relationship**	**$F_{1,14}$**	**P**	**α**
LOB	TRAP	T=C	0.609	0.448	
	NAT	T=C	3.376	0.087	
	BLK	T>C	5.643	0.032	0.008
	LOB_{Tag}	T=C	0.048	0.830	
	TOTAL	T>C	6.474	0.023	0.010
EBJ	EBJ#	T=C	0.385	0.545	
	BLK	T=C	2.498	0.136	
	SEX	T=C	0.229	0.640	
	MOLT	T=C	0.068	0.799	
	CL	T=C	1.205	0.291	
	TAG	T=C	0.715	0.412	
	ANT	T=C	0.372	0.552	
	LEG	T=C	0.109	0.746	
	DIS	T=C	0.045	0.835	
LBJ	LBJ#	T>C	11.946	0.004	0.050
	BLK	T=C	0.045	0.835	
	SEX	T=C	0.008	0.931	
	MOLT	T=C	0.962	0.343	
	CL	T>C	8.234	0.012	0.013
	TAG	T=C	1.00	0.334	
	ANT	T=C	1.270	0.279	
	LEG	T=C	0.892	0.361	
	DIS	T=C	0.004	0.951	
ALGAE	ALRD	T=C	0.654	0.432	
	ALGR	T=C	0.006	0.938	
	SGTH	T=C	0.105	0.751	
	TOTAL	T=C	0.955	0.345	
STRUCT	SPL	T=C	1.733	0.209	
	SPV	T=C	0.357	0.559	
	COR	T=C	0.337	0.571	
	SOL	T=C	0.602	0.451	
	TOTAL	T=C	0.020	0.891	
DENS	BLK	T>C	11.184	0.005	0.025
	SPL	T=C	0.019	0.893	
	SPV	T=C	0.477	0.501	
	SPO	T=C	1.445	0.249	
	SWP	T=C	0.050	0.826	
	COR	T=C	1.733	0.209	
	SOL	T=C	0.001	0.972	
	OTH	T=C	0.003	0.956	
	TOTAL	T=C	3.019	0.104	

Table 2.3. Analysis of field manipulation on community covariates (continued)

PRED	SPCR	T=C	2.331	0.149	
	SWCR	T=C	0.003	0.959	
	STCR	T=C	0.073	0.792	
	OCTO	T=C	1.322	0.269	
	'DFS	T<C	9.626	0.008	0.017
	RAY	T=C	0.157	0.698	
	SHARK	T=C	0.055	0.818	
	OTH	T=C	0.259	0.619	
	TOTAL	T=C	0.266	0.614	

As expected the total number of lobsters was higher on treatment than control sites ($F_{1,14} = 6.474$, $p = 0.023$) due to a higher number found in the treatment block shelters ($F_{1,14} = 5,643$, $p=0.032$). These lobsters were LBJs (> 25 mm CL) ($F_{1,14} = 11.946$, $p = 0.004$) with a larger average size ($F_{1,14} = 8.234$, $p = 0.012$). As a result, the number of shelter block dens was higher on treatment than control sites ($F_{1,14} = 11.184$, $p = 0.005$).

All the remaining community measures that have been shown in previous studies to influence the density of EBJs such as percent cover of red algae, predator density and number of crevice shelters were not significantly different between my treatment and control sites. The only exception was that control sites had higher densities of juvenile toadfish ($F_{1,14} = 9.626$, $p = 0.008$). Since these fish are too small to prey on PLs and EBJs, this difference is not likely to have influenced EBJ density. From these results, I can conclude that treatment and control sites differ only in the density of LBJs. Therefore, any significance influence of treatment on EBJ_{tag}, EBJ_{Untag} or $\%EBJ_{tag}$ must be related to LBJ density.

Does EBJ density increase with LBJ density?

Having successfully manipulated LBJ density with treatment block addition, I analyzed the influence of LBJs on EBJs (Figure 2.9). I analyzed three dependent variables EBJ_{Untag} density, EBJ_{tag} density, and $\%EBJ_{Tag}$ using a nestedANOVA with month as a block, location as a random factor, and treatment as a fixed factor nested within location (Table 2.4). Untagged EBJs were more abundant on treatment sites than on control sites ($F_{8,75} = 5.283$, $p<0.001$) but tagged EBJs ($F_{8,30} = 1.303$, $p = 0.279$) and the percentage of EBJs carrying a tag ($F_{8,30} = 1.023$, $p = 0.441$) were not significantly different. Month was significant for EBJ_{tag} ($F_{8,30} = 4.139$, $p = 0.026$) and $\%EBJ_{tag}$ ($F_{8,30} = 5.477$, $p = 0.009$) and location was significant for EBJ_{Untag} ($F_{8,75} = 26.67$, $p < 0.001$) and $\%EBJ_{Tag}$ ($F_{8,30} = 2.824$, $p = 0.022$).

Table 2.4 Analysis of tagged and untagged EBJs in relation to month, location and treatment. Nested-ANOVA table for EBJ_{tag} by month, location and treatment within location. EBJ density was square-root transformed in order to meet the assumption of homogeneity of variances. $\text{EBJ}_{\text{Untag}}$ N=393 EBJ_{Tag} N=18.

$\text{EBJ}_{\text{Untag}}$

Source	**df**	**MS**	**F**	**p**
Month	5	0.339	0.800	0.553
Location	7	10.861	25.677	<0.001
Treatment (Location)	8	2.235	5.283	<0.001
Error	75	0.423		

EBJ_{Tag}

Source	**df**	**MS**	**F**	**p**
Month	2	0.805	4.139	0.026
Location	7	0.329	1.692	0.149
Treatment (Location)	8	0.254	1.303	0.279
Error	30	0.195		

%EBJ_{Tag}

Source	**df**	**MS**	**F**	**p**
Month	2	0.425	5.477	0.009
Location	7	0.219	2.824	0.022
Treatment (Location)	8	0.079	1.023	0.441
Error	30	0.078		

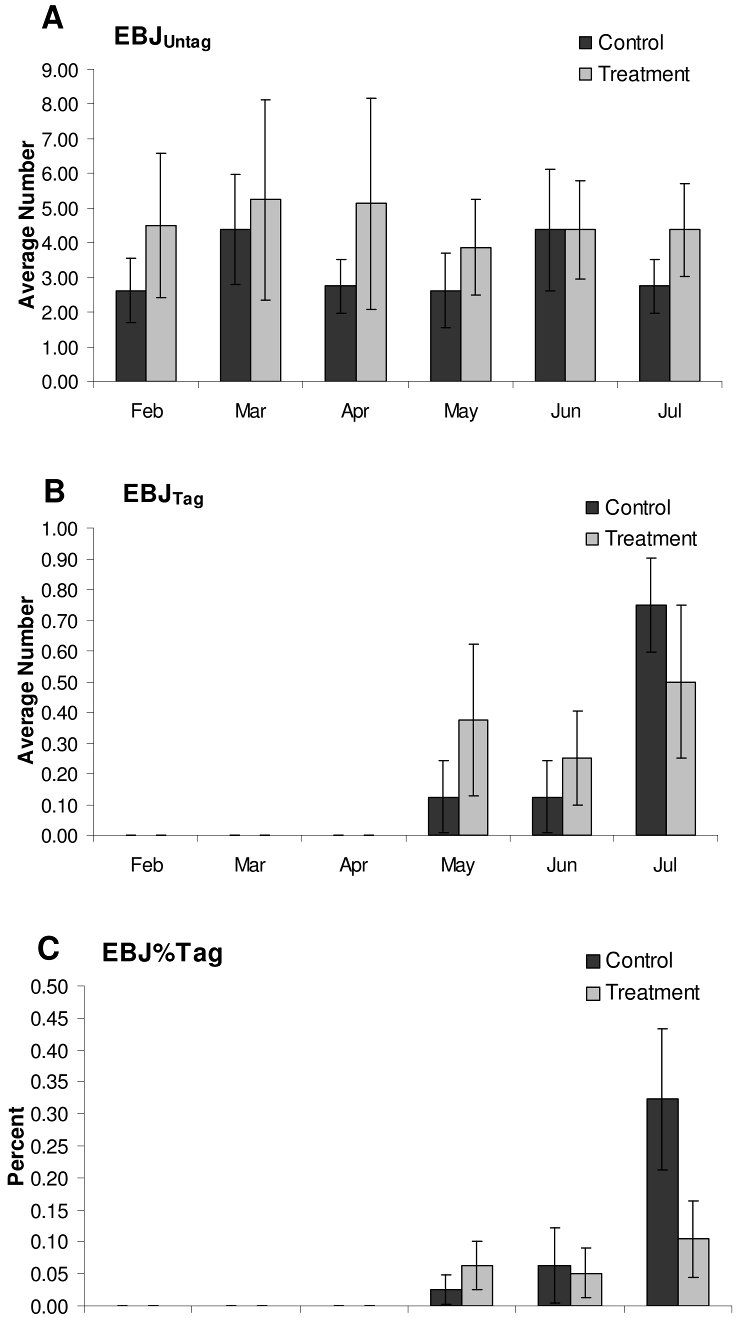

Figure 2.9 Monthly **density of tagged and untagged early benthic juvenile lobsters**. (A) Average density of sampled EBJs not carrying a microwire tag (N=8). (B) Average density of sampled EBJs on study sites carrying a microwire tag (N=8). (C) The average percent of total EBJs censused that were carrying a microwire tag (N=8). Error bars indicate standard error.

From the ten EBJ_{Tag} recaptures in the final month of census July 2006, I was able to calculate maximum growth rate of 4.5 mm CL/month and a minimum growth rate of 3.5 mm CL/month for EBJ_{Untag} settling on our census sites, and estimate time of emergence from the algae. A simple linear regression of growth rate versus months post settlement estimates that EBJs began making the transition from algae to shelter two to three months after settlement (Figure 2.10).

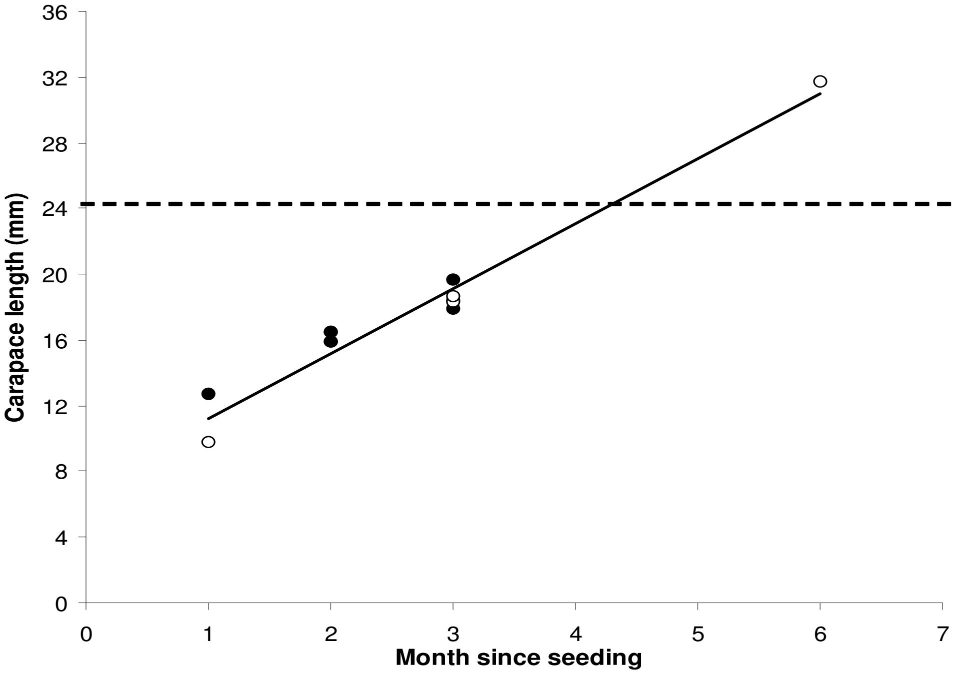

Figure 2.10 Growth of tagged EBJs estimated by size at recapture. Tagged EBJs sacrificed after recapture in July census were assigned to the month of seeding N=10. Month since seeding is seeding month subtracted from month 7 (July). Carapace length was examined to estimate time to transition of EBJs throughout the study period.

When the growth rate was applied to EBJ_{Untag} captures in July, I found that the size frequency distributions of EBJ_{Untag} did not differ significantly between treatment and control ($G = 2.501$, $p = 0.645$), although there were more EBJs on treatment sites than control sites (Figure 2.11).

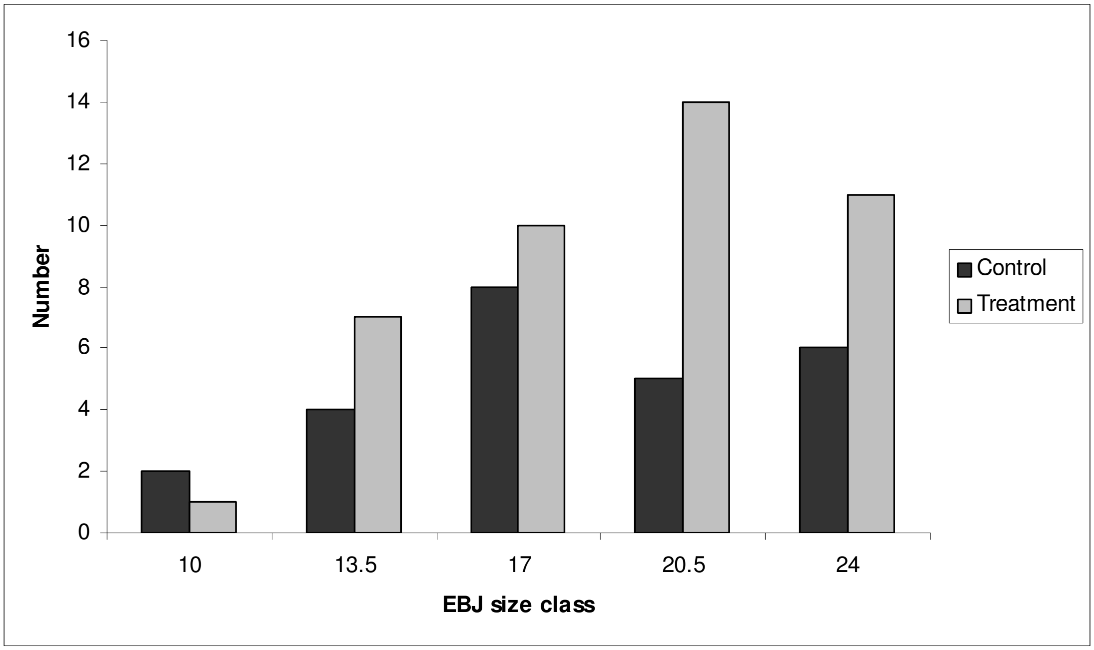

Figure 2.11 Frequency distribution of settlement cohorts of untagged EBJs found on treatment and control sites in the month of July. X axis values are minimum size in mm carapace length for each size class. Size class is presented as a proxy for settlement cohort, smallest size class settling in June and the largest in February. Size classes were generated from growth rate of EBJ_{Tag} calculated by linear regression of EBJ_{Tag} size on settlement month assuming that lobsters settle into the algae at 7 mm CL.

Which Allee effect hypothesis best explains the influence of LBJs on EBJs?

Analyses described in the previous section examined the effect of current conditions (same month) on EBJ tagged and EBJ untagged density. Since possible Allee effects benefits occur for PLs and algal phase EBJs, I also examined the effect of LBJs and community factors in months prior to the July census on EBJ density in July. Results of a fully fit multiple regression models were used to compare relative strength of each factor using community covariates from 0 to 5 months previous (Figure 2.12).

The model for July with zero time lag best explained the variation in July EBJ_{Untag}. Subsequent time lags 1-5 months prior explained over 50% of the variation (lag 1 month $r^2 = 0.614$, lag 2 months $r^2 = 0.551$, lag 3 months $r^2 = 0.641$, lag 4 months $r^2 = 0.577$, lag 5 months $r^2 = 0.545$) (Table 2.5). Percent cover of algae one month earlier, three months earlier, and five months earlier negatively affected EBJ_{Untag} in July (Figure 2.12). The negative effects of algae is most likely a sampling effect, as fewer EBJs were found on sites and in months where percent cover of algae was highest. Postlarval density as estimated from surface collector catch positively affected EBJ_{Untag} in the zero month time lag but was not a significant factor in lagged models. Natural structure was not significant in any of the lag models of EBJ_{Untag}. LBJ density positively influenced July EBJ_{Untag} at time lag zero one month (T = 2.457, p = 0.034), four months (T = 2.306, p = 0.044), and five months prior (T = 0.893, p = 0.053).

LBJ density in each month had a strong positive effect on EBJ_{Untag} density (Figure 2.12). The strongest factor influencing EBJ_{Untag} was the density of LBJs on sites in February, a five month lag (Effect Strength = 0.893). The second most influential month for LBJ density was May (Effect Strength = 0.816) and the third most influential was

March, a four month time lag (Effect Strength = 0.723). The strong influence of LBJ density four and five months earlier suggests that LBJ density influenced the animals captured in July as they were settling as postlarvae. The influence of LBJ density in May also corresponds with EBJ emersion from the algae.

In summary, I found that the effects of community components on EBJ density varied by location as expected but did not explain as much variation as LBJ density (Table 2.6). I found the most support for the Settlement Cue hypothesis which predicts that postlarvae are attracted to LBJs in PL choice tests, postlarval settlement ($\mathrm{EBJ}_{\mathrm{Untag}}$) will increase with LBJ density, and there will be no difference in $\mathrm{EBJ}_{\mathrm{Tag}}$ or $\mathrm{EBJ}_{\%\mathrm{Tag}}$ with LBJ density (Table 2.6). My results also offer some support for the Guide Effect hypothesis which predicts that more there will be more EBJs (untagged and tagged) with an increase in LBJ density. I found that there were more $\mathrm{EBJ}_{\mathrm{Untag}}$ on treatment sites than controls but $\mathrm{EBJ}_{\mathrm{Tag}}$ was equal between treatments. This result indicates that $\mathrm{EBJ}_{\mathrm{Tag}}$ survived the same regardless of LBJ density. The hypothesis with the least support was the Group Defense hypothesis. The hypothesis predicts that EBJs, both tagged and untagged, will have higher survival on treatment sites than control sites due to increased number of LBJs in shelters defending against predators. Since LBJs are nomadic, and I was unable to establish which EBJs were continually sharing shelter with LBJs to compare survival, it is difficult for me to draw any conclusions about this hypothesis. Thus based on my predictions, there is some evidence that LBJs influence postlarvae, algal phase, and postalgal phase lobsters leading to an increase in EBJ density in areas with high LBJ density.

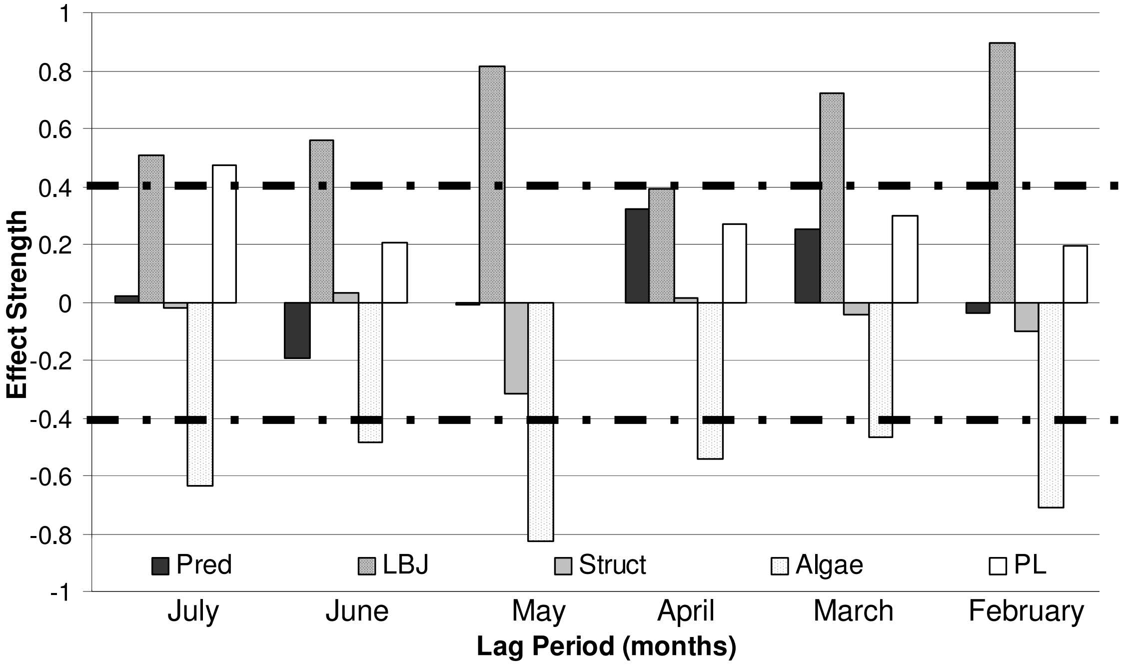

Figure 2.12 Analysis of effect strength of community covariates on EBJ density. Time lag analysis was performed to determine the appropriate time lag for community and lobster independent variables as they explain July density of EBJ_{Untag}. Months indicate census data for 5 months prior to the final census in July. A multiple linear regression model was run to compare relative effects of community and LBJ density within each month. Effect strength represents the standard coefficient of the multiple regression model of EBJ_{Untag} on each community variable. The direction of the bars indicates direction of the effect either positive or negative. Dotted lines at positive and negative 0.4 represent the threshold beyond which there is a significant effect of a specific variable.

Table 2.5 Analysis of field manipulation on community covariates. Multiple regression for time lagged community and lobster values predicting $\text{EBJ}_{\text{Untag}}$ densities in the final month of census. Gray shading indicates statistical significance.

Month Lag	F	p	r^2	Factor	StdCoeff	T	P
0	8.311	0.002	0.806	PL	0.473	2.464	0.033
				ALRD	-0.636	-3.740	0.004
				PRED	0.023	0.145	0.887
				LBJ	0.506	2.457	0.034
				STRUC	-0.022	-0.098	0.924
1	3.175	0.057	0.614	PL	0.203	0.922	0.378
				ALRD	-0.484	-2.305	0.044
				PRED	-0.196	-0.913	0.383
				LBJ	0.560	2.438	0.035
				STRUC	0.030	0.119	0.908
2	2.453	0.106	0.551	PL	0.000	0.001	0.999
				ALRD	-0.828	-2.148	0.057
				PRED	-0.010	-0.035	0.973
				LBJ	0.816	2.210	0.052
				STRUC	-0.318	-0.874	0.403
3	3.566	0.041	0.641	PL	0.269	1.357	0.205
				ALRD	-0.543	-2.527	0.030
				PRED	0.323	1.670	0.126
				LBJ	0.390	1.618	0.137
				STRUC	0.015	0.063	0.951
4	2.725	0.083	0.577	PL	0.296	1.327	0.214
				ALRD	-0469	-1.696	0.121
				PRED	0.252	0.981	0.350
				LBJ	0.723	2.306	0.044
				STRUC	0.041	-0.147	0.886
5	2.393	0.113	0.545	PL	0.192	0.788	0.449
				ALRD	-0.709	-2.149	0.057
				PRED	-0.040	-0.143	0.889
				LBJ	0.893	2.194	0.053
				STRUC	-0.100	-0.359	0.727

Table 2.6 Hypotheses and predictions for field experiment revisited. Results of community factors of influence were analyzed as One-way ANOVAs presented in Table 2.3. Xs represent those results that conflicted with the predictions from Table 2.1, check marks indicate results that support the predictions, and zeros indicate results that failed to be supported but still were not able to be strongly refuted. Refer to Appendix for abbreviations.

Results of community influence on EBJ #s

Hypothesis	**PL**	**ALG**	**STRUCT**	**PRED**
PL	**X**	**X**	**0**	**0**
EBJ_{Algal}	**X**	**X**	**X**	**X**
$EBJ_{Postlalgal}$	**X**	**0**	**X**	**X**

Results for conspecific attraction hypotheses tests

Hypothesis	**PL Choice Test**	**EBJ_{Untag}**	**EBJ_{Tag}**	**% EBJ_{Tag}**
H_1 Settlement	☑	☑	**0**	☑
H_2 Guide Effect	**0**	☑	**X**	**0**
H_3 Group Defense	**0**	**0**	**0**	**0**

Discussion

PLs are attracted to odor cues of LBJs

When I examined the response of PL to late benthic juvenile conspecifics (>25 mm CL) in Y–maze choice test, I found that PLs can detect LBJ conspecifics through odor cues, and that they significantly preferred LBJ odor to a seawater control. This is the first evidence of gregarious behavior by the settlement stage of spiny lobsters and an important prerequisite for the H_1 Settlement Cue hypothesis. Ratchford and Eggleston (1998) tested conspecific attraction in juvenile spiny lobsters at different ontogenetic stages. They discovered that early benthic juvenile lobsters less than 15mm in CL were not attracted to conspecific odors, whereas lobsters greater than 15mm CL were attracted to conspecific odors. Though they tested a broad size range of EBJs and LBJs, they did not examine the response of EBJs less than 10mm CL or postlarvae.

Previous studies on PL settlement have focused on microhabitat requirements of newly settled postlarvae, testing the importance of food and shelter. Early lobster laboratory experiments tested attraction of PLs to different types of vegetative substrate (Herrnkind and Butler 1986; Butler and Herrnkind 1991). Hernnkind and Butler (1986) found that *Laurencia* spp. was preferred by settling postlarvae over *Thalassia testudinum* since it provides complex settlement substrate in which the metamorphosed EBJ_{Algal} remain cryptically hidden until they move into crevice shelters. Additionally, time to pigmentation of postlarvae (prior to metamorphosis to EBJ_{Algal}) was lowest in the presence of *Laurencia* spp. which suggests that it may be triggering settlement (Butler and Herrnkind 1991). When macroalgae percent cover and patch size were measured in the field, they were not correlated with PL settlement or juvenile abundance (Herrnkind and Butler 1994; Butler et al. 1997). Since macroalgal cover is highly ephemeral, it may be inconsistent as a settlement cue in the field, perhaps PLs are more successful in finding suitable habitat when they respond to a combination of cues. My results suggest the presence of late benthic juvenile lobsters along with red macroalgae combine to increase postlarval settlement.

Shelter addition to increase LBJ density

I found more lobsters on treatment sites than control sites. I attribute this to the fact that there were more LBJs on treatment sites than control sites. LBJs were more abundant than EBJs on treatment sites because they were able to use artificial shelter blocks and natural structures whereas on control sites they were limited to use of natural shelters alone. LBJs on treatment sites were also slightly larger than those on control sites. This may be a result of higher retention on sites with abundant shelter.

My study was designed with a community ecology level approach measuring not only the independent variable of interest, LBJ density, but also postlarval density, percent cover or macroalgae, natural structure, and predator density. These community factors have been show in previous lobster studies to influence lobster population dynamics. Marx and Herrnkind (1985a) surveyed many locations in Florida Bay to identify habitat for $\text{EBJ}_{\text{Algal}}$ lobsters and found that sites with dense macroalgae such as Burnt Point (one of my sites) tended to have a larger number of lobsters overall, especially EBJs. Abundance of potential crevice shelters (natural structure) influenced abundance of juvenile lobsters (Eggleston et al. 1990; Herrnkind et al. 1997a).

Other block addition studies found that lobsters readily used artificial concrete block shelters at nearly the same frequency as natural structure (Childress and Herrnkind 1997; Herrnkind et al. 1997b), and that lobsters in block and natural structures had similar mortality due to predation (Childress and Herrnkind 1994). Shelter is important to lobsters and many other benthic marine organisms because it provides protection from predators (Smith and Herrnkind 1992; Mintz et al. 1994). Shelter can significantly enhance survival of lobsters but only if properly scaled to body size (Eggleston et al. 1990; Smith and Herrnkind 1992). The two types of shelter used in the present study were scaled for use by different animals, control blocks were designed to exclude LBJs (>25 mm CL) while providing shelter for EBJs 7-24 mm CL while treatment blocks were designed to shelter animals from 7-45 mm CL.

Shelter manipulations with large commercial casita shelters (Eggleston and Lipcius 1992; Mintz et al. 1994; Sosa-Cordero et al. 1998) or artificial shelter blocks (Butler and Herrnkind 1997; Herrnkind et al. 1997a) have resulted in increase in number of lobsters in an area. Butler and Herrnkind (1997) performed a 12 block addition with shelters similar in size and shape to those used in my study and found that it increased the number of EBJs but did not increase number of LBJs over 35 mm CL. The discrepancy could be attributed to the three hole partition blocks used by Butler and Herrnkind which had smaller openings than the two hole partition blocks I used, thus animals over 35 mm CL were not able to inhabit their blocks. The shelters I built were large enough that animals up to 45 mm CL could use them. Overall, I was able to increase the number of LBJs on treatment sites with a shelter addition while holding all other community covariates constant.

LBJ density increases EBJ density

EBJ density was positively correlated with LBJ density when differences due to month and location were controlled. I found that EBJ density increased with LBJ density, that is to say, more EBJs were found on treatment sites than controls. Average EBJ density was 4-6 individuals per treatment site but only 2-4 individuals per control site. This was not a result of increased shelter for EBJs since EBJs could use both treatment and control blocks.

The difference in EBJ density between treatment and control sites is perhaps not surprising since spiny lobsters are gregarious throughout their life cycle beginning when they transition from macroalgae to crevice shelters (Marx and Herrnkind 1985a; Childress and Herrnkind 1994; 1996) and are attracted to conspecifics (Ratchford and Eggleston 1998). Childress and Herrnkind (2001b) were the first to show that LBJ odors guide transitional EBJs from their macroalgae shelters into crevice shelters at a smaller size than if they were not exposed to LBJ odors and thus, decreasing predation on transitional lobsters. Censusing EBJs in relation to LBJ density, did not allow us to deduce whether and Allee effect benefit of conspecific attraction first occurs at settlement through habitat selection, or in higher survival of EBJs through transition from algae to crevice shelters, or through increased survival once dwelling in crevice shelters. A mark-recapture study with microwire tagged individuals allowed us to get at that very question by comparing postlarval settlement to post settlement survival.

LBJ density increases PL settlement but not survival or size at transition

To determine which stage(s) benefit from high LBJ density I, artificially seeded microwire tagged postlarvae into macroalgae on treatment and control sites in equal numbers. If natural settlement is unrelated to LBJ density then untagged PLs should also be equal on treatment and control sites. The influence of LBJ density on PL settlement was examined by comparing the number of EBJs tagged and untagged on treatment and control sites. I found that density of $\text{EBJ}_{\text{Untag}}$ was greater on treatment than control sites but EBJ_{tag} remained equal on treatment and control sites. Post-settlement density benefits such as increased survival through habitat transition would be reflected in higher densities of $\text{EBJ}_{\text{Untag}}$ and EBJ_{Tag} on treatment sites than on control sites. Once $\text{EBJ}_{\text{Algal}}$ (microwire tagged, or naturally settling) are in the algae, they should be subject to the same post settlement processes, such as predation. Treatment sites had higher densities of $\text{EBJ}_{\text{Untag}}$ by not of EBJ_{Tag} indicating that LBJ density increases postlarval settlement rather than post-settlement survival.

Butler and Herrnkind (1997) also examined settlement by seeding microwire tagged individuals in a high (N=182) and low densities (N=46). They found that settlement density is a factor in survival and emigration of lobsters on the site. Intuitively, higher densities of settling postlarvae increase the number of EBJs that survive post-settlement mortality and enter crevice shelters. The best- fit multiple regression model of the percent recapture also showed positive influence of macroalgal patch size, study site size, and most pertinent to the present study, total lobster density (Butler and Herrnkind 1997).

I used recaptured EBJ_{Tag} size and month of settlement to calculate growth rate between 3.5 and 4.5 mm CL per month. This growth rate was much higher than the laboratory growth rates of 1.52-1.84 mm CL/month reported by Lellis and Russell (1990). Forcucci et al. (1994) found that lobsters typically grow 1.4-5.0 mm CL per month. Perhaps our values are high because growth is fastest during spring and summer months when there were the highest number of recaptures. It was also possibly due to the rich natural diet available to my study's lobsters in their natural habitat as opposed to a laboratory diet of frozen shrimp or commercial feed.

Using these growth rates, I was able to assign settlement cohorts for EBJs sampled during the July 2006 census. The size frequency distribution of EBJs on treatment and control sites did not differ statistically. EBJs first appeared in crevice shelters (and were censused) after one or two months in the algae, a relatively short period of time, but consistent with the season and rate at which they were growing. EBJs were the same size on treatment and control sites when they emerged from the algae on, thus, sites with a higher LBJ density did not cause EBJs to leave the algae at a smaller size, as predicted by H_2 Guide Effect hypothesis (Childress and Herrnkind 2001b).

Overall, LBJ density influenced EBJ density increasing number of untagged EBJs on treatment sites. Microwire tag recaptures indicate that EBJ density increase is a result of increased settlement of PLs on sites with higher LBJ density. Since EBJ_{Untag} is increased, but EBJ_{Tag} is not, lowered post-settlement mortality is not responsible for increase in EBJ density on sites with higher LBJ density. EBJs do not appear to be emerging from algae at a smaller size on sites with higher LBJ densities nor have higher survival when sharing shelters with LBJs.

LBJ density at time of settlement predicts future EBJ density

The results previously discussed have been the effect of variables measured at the same time as each month's lobster census. The effect of community variables in the current month should best reflect factors influencing postalgal EBJs, but may not correspond as well with factors influencing settling or algal EBJs. The density of $\mathrm{EBJ}_{\mathrm{Untag}}$ on treatment and control sites during each census, was a result of habitat conditions and qualities in months prior to that census. I examined the influence of time lagged community variables on $\mathrm{EBJ}_{\mathrm{Untag}}$ sampled in July 2006 with community variables from the five previous months.

If available PL density influenced $\mathrm{EBJ}_{\mathrm{Untag}}$ there would be a strong effect of PL density during the months of February and March, when the July EBJs would have arrived as postlarvae through the inlets into Florida Bay. I did not see a significant effect of PL density on EBJ density except for time lag zero, PL density for the month of July was correlated with $\mathrm{EBJ}_{\mathrm{Untag}}$ in the month of July. This result was likely a coincidence. Other studies have attempted to use larval collector catches (estimate of PL density) to predict EBJs on a site and have been equally unsuccessful (Marx and Herrnkind 1986a; Forcucci et al. 1994; Herrnkind and Butler 1994). Though there is strong correlation between surface collectors and sampling with plankton nets at the inlets, once PLs enter Florida Bay they disperse patchily and are likely decoupled from supply (Herrnkind and Butler 1994). Patches that often receive PLs simply receive more when supply is higher. The lack or correlation between estimated PL density and EBJ density at a location is due to the inaccuracy of surface collector catches in estimating PL supply to FL Bay. Wind driven currents, shallow banks, and patchy habitat decouple PL supply from PL settlement.

Macroalgal cover can benefit algal and postalgal stage EBJs through provision of complex shelter, or by increasing crypticity of crevice shelters (Butler et al. 1997). A strong positive influence of macroalgae was expected if percent macroalgal cover increase EBJ numbers overall. There was a strong effect of macroalgae in each monthly model but it was negative that is, the higher percent cover of algae, the fewer EBJs I found. This is most likely a sampling effect, because divers were less likely to find smaller lobsters if the site had high macroalgal cover. Algae evidently protects EBJs from divers and likely other visual predators as well, increasing their survival on sites with higher percent cover of macroalgae. This could explain the positive relationship between macroalgal cover and EBJ abundance described by Marx and Herrnkind (1985a) and Butler et al. (1997). Their sampling techniques involved searching algae samples pulled from Florida Bay to locate $\mathrm{EBJ}_{\mathrm{Algal}}$, thus their study was not hindered by algal cover as mine was, they were able to detect a direct positive relationship between the algal cover and $\mathrm{EBJ}_{\mathrm{Algal}}$ density.

Natural structure provides shelter for postalgal EBJs and therefore should be most influential in the months of April May and June and July when EBJs leave the algae and inhabit crevice shelters. I did not find a strong influence of structure on EBJ density in any month. Previous studies have found a positive relationship between natural shelter abundance and juvenile lobster abundance (Eggleston et al. 1990; Butler and Herrnkind 1997; Herrnkind et al. 1997a). These studies examined the influence of structure on EBJ density at locations where shelter was scarce, or in the case of Herrnkind et al. (1997a), a mass sponge die off had dramatically reduced the availability of shelters. My study locations were selected to have a moderate amount of natural structure and were then manipulated to increase shelter, thus I did not see a strong effect of natural structure on lobster density.

Predators may affect EBJs at all stages and thus I expected to see a strong effect in both current and time lagged months. However there was not a strong effect of predators on EBJs in any month, suggesting that predation is not responsible for the variation in EBJs. These results do not necessarily mean that predation does not impact EBJ abundance just that they cannot explain the EBJ density differences between control and treatment sites, thought they do contribute to the variation between locations. Childress and Herrnkind (1997) also found conspecific density rather than predator density was most correlated with lobster den sharing. Most studies of predation have examined the effect of predators on tethered EBJs in algae or in shelters versus in the open rather than looking at overall survival to EBJ stage on sites with low and high predator density (Smith and Herrnkind 1992; Childress and Herrnkind 1994; Butler et al. 1997). Another consideration is that my study recorded mostly benthic and shelter obligate predators which gave a conservative estimate of predator density.

Of all community factors deemed influential by previous community ecology studies of lobsters in nursery habitat, only macroalgae strongly affected the number of EBJ_{Untag} found on my study sites. There was also no correlation between community factors and LBJ density. Time lag analysis of the effect of LBJs on EBJ_{Untag} found a strong positive effect in the current month and the five months previous at the time of postlarval settlement.

Positive density dependence on PL settlement is a component Allee effect

The overall goal of this study was to examine the density dependent effect of LBJs on EBJs within a community context and identify the ontogenetic stage or stages at which this Allee effect occurs. There are three possible component Allee effects resulting in an increased EBJ density on sites with higher LBJ density; increase in settlement (settlement cue), increase in survival of transition from algae to crevice shelters (guide effect), and/or increase in survival once dwelling in crevice shelters (group defense).

The Settlement Cue hypothesis predicts that postlarvae are attracted to odor cues of conspecifics and this attraction results in preferential settlement on sites with higher conspecific density. Three lines of evidence support this hypothesis. First, PLs were attracted to the odors of LBJs. Second, the density of untagged EBJs was higher on control sites than on treatment sites but the density of tagged EBJs was similar on control and treatment sites. Finally, the density of LBJs at the time of PL settlement was highly correlated with the density of EBJs five months later.

The Guide Effect hypothesis predicts that LBJs increase the number of EBJs on a site by increasing survival of EBJ_{Algal} by guiding them into crevice shelters when they emerge from the algae, thus reducing mortality due to predation. Childress and Herrnkind (2001b) predicted that the Guide Effect would lead to a smaller size at transition to crevice shelter. I found no support for this hypothesis. First EBJ size at transition between control and treatment sites did not differ. Second, algae, crevice shelter, and predators densities at the time of transition were not related to the EBJ density differences on control vs treatment sites.

The Group Defense hypothesis predicts that lobsters aggregate in shelters to increase survival through cooperative group defense against predators. Butler and colleagues (1999) found that LBJ (>40 mm CL) New Zealand spiny lobsters *Jasus edwardsii* had higher survival when sharing dens than when alone. I found no support for this hypothesis. First, the density of untagged EBJs was higher on control sites than on treatment sites but the density of tagged EBJs was higher on control sites than on treatment sites. Second, the influence of LBJ density on EBJ density was greater in the months prior to transition than after transition. My results support previous tethering studies that have found that lobsters (LBJs) tethered with conspecifics have similar mortality to those alone in shelter (Childress and Herrnkind 2001a).

Conspecific settlement cues may be an ecological trap

I am not the first researcher to describe positive density dependence in juvenile spiny lobsters, but I am the first to provide evidence that conspecific density can influence postlarval settlement. My discovery of conspecifics as a settlement cue is the most alarming component Allee effect described thus far in *Panulirus argus*. This species of spiny lobster has intense commercial and recreational fisheries in the US and throughout the Caribbean. The fishery in Florida alone has more nearly 1 million traps (Hunt 2000). Fisherman exploit the gregarious behavior of *P. argus* by baiting traps with "shorts" or subadult and juvenile lobsters and using conspecific attraction to draw adult lobsters into traps (Heatwole et al. 1988). If LBJ density is as strong an attractant as my study indicates, concentrations of lobsters in traps may have devastating effects. The practice of removing juvenile lobsters from nursery habitats and artificially concentrating them in traps may significantly alter settlement of postlarvae and survival of EBJs. It is possible that conspecific attraction could become the mechanism of an ecological trap (Schlaepfer et al. 2002) decoupling conspecific density and habitat quality.

Conspecific settlement cues may be a common component Allee Effect

My study on Caribbean spiny lobsters along with recent studies on porcelain crabs (Donahue 2006) and damselfish (Lecchini et al. 2007) suggest that even mobile adults may provide important settlement cues to planktonic larvae. If these cues increase survival or growth by directing larvae to the highest quality settlement habitat they act as important component Allee effects. In gregarious marine crustaceans, and no doubt in many other social organisms, Allee effects structure populations and the overall result is positive density dependence as long as the population exists at low to moderate density. Managers should use this information and conserve and protect not only harvestable adults, but the entire life cycle because density dependence between life stages determines the health of the population overall.

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APPENDIX

Measurement variables abbreviations and the methods of estimation.

Abbreviation	Variable	Sampling method and explanation	Frequency
Dependent Variables			
EBJ	Early Benthic Juvenile	Number of juvenile lobsters <25mm CL on each site by diver collection	Monthly
$\mathrm{EBJ}_{\mathrm{Tag}}$	EBJ tagged	EBJs with coded wire tag	Monthly
$\mathrm{EBJ}_{\mathrm{Untag}}$	EBJ untagged	EBJs without coded wire tag	Monthly
$\mathrm{EBJ}_{\mathrm{Algal}}$	Algal EBJ	Number of juvenile lobsters <12mm CL seeded on sites each month	Monthly
$\mathrm{EBJ}_{\mathrm{Postalgal}}$	Postalgal EBJ	Numbers of juvenile lobsters 12<25mm CL on each site by diver collection	Monthly
$\mathrm{EBJ}_{\mathrm{CL}}$	EBJ size	Average EBJ carapace length	Monthly
$\%\mathrm{EBJ}_{\mathrm{BLK}}$	EBJ shelter	Percent of EBJs found in block dens	Monthly
$\%\mathrm{EBJ}_{\mathrm{Sex}}$	EBJ sex	Percent of males EBJs	Monthly
$\%\mathrm{EBJ}_{\mathrm{Molt}}$	EBJ molt	Percent of intermolt EBJs	Monthly
$\%\mathrm{EBJ}_{\mathrm{Tag}}$	EBJ percent tagged	Percent of EBJs with coded wire tag	Monthly
$\%\mathrm{EBJ}_{\mathrm{Ant}}$	EBJ injured antenna	Percent of EBJs with injured antenna	Monthly
$\%\mathrm{EBJ}_{\mathrm{leg}}$	EBJ injured leg	Percent of EBJs with injured leg	Monthly
$\%\mathrm{EBJ}_{\mathrm{Dis}}$	EBJ disease	Percent of EBJs with viral disease	Monthly
Independent Variables			
C	Control sites	Site with 10 randomly placed control shelter blocks	Fixed factor
T	Treatment sites	Site with 10 randomly placed treatment shelter blocks	Fixed factor
PL	Postlarvae	Total number of postlarval lobsters collected from a set of 5 collectors	Monthly
$\mathrm{Pl}_{\mathrm{at}}$	Tagged postlarvae	Number of first stage early benthic juvenile lobsters with coded microwire tags added to each site	Monthly
LBJ	Late benthic juveniles	Number of juvenile lobsters => 25 mm CL on each site by diver collection	Monthly
$\mathrm{ALG}_{\mathrm{Total}}$	**Algal cover**	**Total percent cover (ALRD + ALGR + SGTH)**	**Monthly**
ALRD	Red macroalgae	Percent cover estimated by two 25 m line intercept transects per site	Monthly
ALGR	Green macroalgae	Percent cover estimated by two 25 m line intercept transects per site	Monthly
SGTH	Turtle seagrass	Percent cover estimated by two 25 m line intercept transects per site	Monthly

STRUCT	**Structures**	**Total number of large SPL, SPV, SOL and COR that could potentially be used as a DEN**	**Annually**
SPL	Loggerhead sponges	Number of *Spheciospongia* sp. sponges in two 2 X 25 m belt transects on each site	Annually
SPV	Vase sponges	Number of *Iricinia* sp. sponges in two 2 X 25 m belt transects on each site	Annually
SPB	Branching sponges	Number of several species of branched sponges in two 2 X 25 m belt transects on each site	Annually
SPO	Other sponges	Number of all other sponges in two 2 X 25 m belt transects on each site	Annually
SWT	Pterogorgia sea whips	Number of *Pterogorgia* sp. sea whips in two 2 X 25 m belt transects on each site	Annually
SWP	Sea plumes	Number of *Pseudopterogorgia* sp. sea plumes in two 2 X 25 m belt transects on each site	Annually
SWO	Other sea whips	Number of all other sea whips in two 2 X 25 m belt transects on each site	Annually
COR	Coral heads	Number of *Solenastrea* sp. Coral heads in two 2 X 25 m belt transects on each site	Annually
SOL	Solution holes	Number of all crevices or holes large enough to shelter a EBJ lobster in two 2 X 25 m belt transects on each site	Annually

DENS	**Dens**	**Total number of structures and blocks inhabited by LOB and PRED**	
BLK	Block shelters	Number of artificial shelter blocks inhabited by LOBs or PRED	Monthly
SPL	Loggerhead sponges	Number of *Spheciospongia* sp. inhabited by LOBs or PRED	Monthly
SPV	Vase sponges	Number of *Iricina* sp. inhabited by LOBs or PRED	Monthly
SWP	Sea plumes	Number of artificial shelter blocks inhabited by LOBs or PRED	Monthly
SWO	Other sea whips	Number of several species of sea whips inhabited by LOBs or PRED	Monthly
COR	Coral Heads	Number of coral heads inhabited by LOBs or PRED	Monthly
SOL	Solution Holes	Number of solution holes inhabited by LOBs or PRED	Monthly
OTH	Other sponges	Number of inhabited by LOBs or PRED	Monthly

PRED	Total Predators	**Total counts of (SWCR + STCR + OCTO + TDFS + RAY + SHARK) on each site**	**Monthly**
SPCR	Spider crabs	Number of majid crabs on each site by diver census	Monthly
SWCR	Swimming crabs	Number of portunid crabs on each site by diver census	Monthly
STCR	Stone crabs	Number of xanthid crabs on each site by diver census	Monthly
OCTO	Octopus	Number of octopus on each site by diver census	Monthly
TDFS	Toadfish	Number of toadfish on each site by diver census	Monthly
RAY	Ray	Number of yellow and southern stingrays on each site by diver census	Monthly
SHARK	Nurse sharks	Number of nurse sharks on each site by diver census	Monthly