2009-12-12

Assessing the Early Life Stage Processes that Regulate Recruitment in the Brooding Coral, Porites astreoides

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UNIVERSITY OF MIAMI

ASSESSING THE EARLY LIFE STAGE PROCESSES THAT REGULATE RECRUITMENT IN THE BROODING CORAL, *PORITES ASTREOIDES*

By

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A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

December 2009

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
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Assessing the Early Life Stage Processes that Regulate Recruitment in the Brooding Coral, *Porites astreoides* (December 2009)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor John McManus.
No. of pages in text. (192)

Population replenishment through recruitment is an essential process for the long term viability of corals and their associated communities, particularly under increasing stresses that threaten their vitality. Although many researchers have identified specific factors that influence individual processes in the early life cycle of corals, few studies to date have attempted to determine the cumulative success of a cohort's progression through these stages in natural reef settings. Specifically, there is a paucity of knowledge regarding appropriate and realistic techniques to forecast the success of recruitment in natural settings, while taking into account both the individual and environmental factors that regulate these recruitment dynamics at local scales. Because of this need, the overall goals of this dissertation research were to (1) assess key life stage processes leading to recruitment – specifically, settlement and early post-settlement processes – for which previous knowledge was limited or absent; and (2) using this knowledge, develop a local-scale recruitment model that assessed the cumulative success of a cohort's progression through all the early life stages and identified those processes that had a strong relative influence on regulating recruitment dynamics.

Focusing on the common western Atlantic brooding coral, *Porites astreoides*, this dissertation research was divided into three main sections to address the overall objectives: (1) identification and quantification of recruitment patterns in natural reef settings, in order to guide the development and testing of the recruitment model (Chapter 2); (2) assessment of the focal species' behaviors, survivorship rates, and factors affecting those rates during its progression through the primary early life stage processes (i.e., basic habitat preferences during the settlement stage, Chapter 3; early post-settlement survivorship, Chapters 4 and 5); and (3) development of a local recruitment model that accounted for the full complement of early life stage processes in a spatially-explicit simulation framework (Chapter 6).

While unique study-specific insights were gained from each of the individual chapters, a few general insights emerged with respect to the overarching study objectives from this dissertation research. First, larval supply is a key driver for recruitment, where a high degree of larval loss, either through direct larval mortality or export from the reef, occurs prior to settlement on the substrate. Rates of loss were 96-99% in the model analyses, and as such represent the first major population bottleneck for this species and others with similar life histories. Compounding this larval loss is a second population bottleneck during the early post-settlement stage, where mortality was typically greater than 75% within the first week after settlement. Such high rates of loss have important implications for future population dynamics, as relatively minor changes to these rates of loss can have relatively strong influences on future dynamics.

Second, habitat influences on recruitment were found to be relatively minimal when compared to high rates of mortality in both the larval supply and early post-

settlement stages. Although the relative influence of habitat may be strong under unique situations where substantial space preemption limits settlement (e.g., high macroalgal cover, sedimentation, or adult coral cover), these effects may not be reflective of average systems. However, the influence of habitat may still be crucial for ensuring that the few individuals who survive the larval supply and the early post-settlement bottlenecks recruit into the future adult population, and these influences may interact with other density-dependent processes as adult cover increases.

Overall, this research presents valuable and novel insights on a number of the under-studied early life stage processes. By identifying the key processes which regulate recruitment, this work highlights those stages whose responses to environmental change will have strong impacts on recruitment and subsequent population dynamics. In addition to the process-based insights gained on these dynamics, this work provides informative criteria for managers on the stages most responsive to conservation efforts aimed at promoting resilience and recovery.

ACKNOWLEDGEMENTS

Thank you to my wife Cara: you shouldered the brunt of this multiyear adventure, saw me through it all, pushed me along the way when I needed coaxing, and even cheered me through the sewing machine wars in the early days.

An equal thank you to my family, for their continual and whole-hearted support and love throughout all of my education years: without you, I would not have made it half this far.

Thank you to my advisor John: your chance at taking on a bird-guy without an iota of coral reef background, and your enduring support and encouragement provided me the world in which to do this all.

Thank you to my committee members, Drs. Peter Glynn, Don DeAngelis, Su Sponaugle, and Diego Lirman: I could not have asked for a better group by which to focus my often over-extended ideas.

Thank you to my wonderful lab mates, Marilyn, Aletta, Johnathan, Kristine and Dan: your insights and friendship made this all enjoyable and possible.

Thank you to all of the dedicated assistants and graduate volunteers that helped along the way, and everyone else that was kind enough to boat tend or dive: without you this research would still be floating around my imagination.

And finally, but in no ways least, this work was funded by a multitude of sources (in chronological order): NSF Graduate Fellowship, National Center for Coral Reef Research, Project Aware, National Coral Reef Institute, RSMAS Small Boats Fund, International Society for Reef Studies / The Ocean Conservancy Graduate Fellowship, and the Canon National Parks Science Scholars Program.

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CHAPTER 1: INTRODUCTION

Background and Overview of Dissertation

Coral reefs are one of the most diverse ecosystems on the planet (Connell 1978), supporting a host of ecological goods and services to societies worldwide (Moberg and Folke 1999). These goods and services range from direct renewable resources, such as food and medicine, to a wide array of physical services (e.g., shoreline protection), biotic services (e.g., maintenance of resiliency), biogeochemical services (e.g., waste assimilation), and social/cultural services (e.g., recreation, aesthetic values; Moberg and Folke 1999). However, the condition and structure of coral reefs are changing at an alarming rate (Gardner et al. 2003, Wilkinson 2004), resulting from a combination of anthropogenic and climate-related threats (Knowlton 2001, Kleypas et al. 2001, Hughes et al. 2003). Together, these threats will diminish the quantity and quality of goods and services provided by coral reef ecosystems, thereby impacting both the economies and daily livelihoods of reef-dependent people and societies worldwide (Moberg and Folke 1999).

With likely changes to the condition and structure of coral reefs throughout the upcoming decades (Hughes et al. 2003), only successful and sustained recruitment will ensure the long-term viability of these communities and the goods and services they provide. Coral recruitment is the consequence of a progression through multiple life stages, entailing successful gamete production by adult colonies, gamete fertilization, larval dispersal within and among reefs, settlement on the substratum, and subsequent survival, each susceptible to a host of natural and anthropogenic stresses.

The success of this progression at any given reef location is an emergent property resulting from the interactions among physical hydrodynamic forces (Willis and Oliver 1990), species-specific swimming and settlement behaviors (Raimondi and Morse 2000, Stake and Sammarco 2003, Harrington et al. 2004), trophic relationships (Sammarco 1980, Fabricius and Metzner 2004), and habitat quality characteristics (Vermeij 2005), operating across a range of length scales from millimeters to kilometers. Due to the complexity of these interactions, and the logistical difficulties associated with studying microscopic early life stages, identifying the key mechanisms that structure recruitment dynamics for a specific reef location is an arduous task (Vermeij 2005, Baird et al. 2006). Because of these difficulties, recruitment remains one of the most "enigmatic" processes in stony corals (Mumby and Dytham 2006). However, given the current changes to coral reef condition on a global scale (Wilkinson 2004), the urgency to identify these mechanisms cannot be questioned, particularly for conservationists and managers charged with ensuring the continued viability of these ecosystems.

A major factor contributing to the complexity of the recruitment process is the demographically-open nature of most coral populations, where locally-produced propagules are often dispersed from of meters to tens of kilometers among connected sub-populations (Mumby 1999, Wolanski et al. 2004). The degree of connectivity among sub-populations depends on species-specific planktonic durations, behaviors, and the prevailing hydrodynamic regime, which can vary in both space and time. The collection of these connected sub-populations form a metapopulation, an entity of individuals linked through dispersal and interacting on ecological and evolutionary time scales. In broadcast-spawning corals (i.e., those with external fertilization), individuals typically

disperse for a minimum of 3-5 days (Harrison and Wallace 1990, Miller and Mundy 2003), thereby significantly influencing recruitment patterns over broader spatial scales (Hughes et al. 1999). In contrast, brooding corals often disperse shorter distances (Harrison and Wallace 1990), leading to a higher proportion of self-seeding to local reef sites (Underwood et al. 2007). Combined, the degree of among-site dispersal and self-seeding determine the number of larvae supplied to a local reef site for settlement (Cowen et al. 2006).

Once larvae arrive at a site, they encounter a separate host of factors that determine their success of reaching a juvenile stage. Although many researchers have identified specific factors that influence the success of settlement, post-settlement survival, and post-settlement growth (Morse et al. 1996, Babcock and Mundy 1996, Raimondi and Morse 2000, Vermeij et al. 2005; see *Background* sections in Chapters 2-5), few studies to date have attempted to determine the cumulative success of the progression through these stages in natural reef settings. Specifically, there is a paucity of knowledge regarding appropriate and realistic techniques to forecast the success of recruitment in natural settings, while taking into account both the individual and environmental factors that structure these recruitment dynamics at local scales.

Because of this need, the focus of this dissertation research was to (1) assess key life stage processes leading to recruitment – specifically, settlement and early post-settlement processes – for which previous knowledge was limited or absent; and (2) using this knowledge, develop a local-scale recruitment model that assessed the cumulative success of a cohort's progression through all the early life stages and identified those processes that had a strong relative influence on regulating recruitment dynamics. The

approach of this research was to focus on a single species of coral, *Porites astreoides*, and intensively study a number of the key early life stage processes which are less known, in order to develop a local-scale recruitment model capable of simulating the full complement of processes leading to recruitment.

The focal species of this research was *Porites astreoides*, a common brooding coral with relatively high recruitment rates in the wider Caribbean compared to other species in this region (Smith et al. 1997), thereby providing a unique model system to assess the mechanisms structuring recruitment dynamics. Because the difficulty of collecting larvae was a primary constraint for three of the chapters in this research, this species was chosen due to its abundance, ease of collecting high numbers of larvae, and multiple larval release periods throughout the year. *Porites astreoides* occurs as two distinct color morphs, a green and brown morph, which may exist as distinct genetically stable phenotypes (Gleason 1993). Although both morphs can be found at nearly all depths, the green morph dominates in shallow depths, usually ≤2m, while the brown morph dominates in deeper waters (Gleason 1993). Because of the differences among the morphs, this study focused solely on the green morph, which is most abundant in the shallow patch reef environments in Biscayne National Park, FL USA, where this research was conducted. Although this species is not a large framework-building coral, it is one of the most abundant juveniles and adults in the Florida Keys reef tract and Caribbean, and therefore is of ecological interest and importance.

Due to the abundance of data on this species, recent studies have utilized this species as a model system to simulate reef resiliency under variable climate change and herbivory scenarios (Mumby 2006, Mumby et al. 2007a, Hoegh-Guldberg et al. 2007).

In these modeling studies however, the success of recruitment was simulated using a simplified representation of recruitment, and not through a mechanistic representation of the recruitment process that incorporates settlement and early post-settlement processes. This lack of mechanistic detail is partly a result of a general deficiency in understanding of the early life stages for this and many other species, particularly regarding settlement behaviors, early survivorship rates, and early growth rates. Although recruitment success may not be a principal driver of population dynamics in some systems (Mumby et al. 2007b), thereby limiting the need of mechanistic detail in such models, caution should be taken when projecting population dynamics based on parameterized recruitment rates. This is particularly true for situations when the factors under study (e.g., herbivory, climate change) may directly impact the mechanisms structuring recruitment patterns, such as the settlement behaviors and early post-settlement dynamics (e.g., Albright et al. 2008).

Given the need for improved understanding of early life stage dynamics, this dissertation research represents a timely addition to the field by providing detailed information on the key processes structuring recruitment dynamics. The second chapter quantifies natural recruitment patterns on patch reefs within Biscayne National Park, and assesses some of the main factors that drive these patterns, including substrate composition, rugosity, and adult abundances at multiple scales. This chapter provides accompanying data for two of the other chapters in the dissertation, the settlement chapter (Chapter 3) and the modeling chapter (Chapter 6). The third chapter assesses larval settlement behaviors for light intensity, the substrate community, and the orientation of the substrate, and relates these findings to the observed recruitment patterns in the field.

The fourth and fifth chapters describe early post-settlement survivorship rates in natural settings, using two markedly different methods in each chapter. In the forth chapter, survival rates are assessed by transplanting laboratory-settled individuals to the reef, while in the fifth chapter, larvae are settled directly *in situ*, after which their survivorship was monitored. This fifth chapter has important implications for restoration approaches attempting to seed coral larvae onto denuded substrate, and was written with this applied focus. The sixth chapter synthesizes the knowledge gained from these previous chapters through the development of a recruitment simulation model to assess the primary drivers of recruitment (larval supply, settlement, and early post-settlement survivorship). Development of modeling tools for these local-scale life stages is regarded as a key component for the future development of larger scale metapopulation and metacommunity models that account for pre-settlement stages (i.e., gamete/larval production, larval dispersal) and adult stages. And finally, the seventh chapter concludes with a review of the main insights and synthesis from the previous chapters.

CHAPTER 2: PATTERNS OF JUVENILE ABUNDANCES IN RELATIONSHIP TO ADULT COVER, SUBSTRATE, AND RUGOSITY AT MULTIPLE SPATIAL SCALES

Background

To understand the processes that structure juvenile coral patterns in nature, one must first identify the basic patterns that exist across spatiotemporal scales. Coral recruitment has been studied extensively over the past few decades, using a combination of surveys for naturally settled juveniles, typically >2mm in diameter when they can be seen by the naked eye, and those settled on artificial substrate tiles deployed on reefs (see reviews in Harrison and Wallace 1990, Richmond 1997). Many interesting patterns have emerged from these studies, but few have addressed the *within-site* distribution of juveniles on natural substrate (but see Edmunds et al. 2004, Vermeij 2005) in combination with *among-site* distributions. Specifically, more research is needed on the relative contribution of different processes in structuring recruitment dynamics across multiple scales, from micro-habitat settlement and post-settlement dynamics within a site (scales of millimeters to meters) to among-site dispersal patterns (scales of 100s of meters to kilometers). Understanding the processes across these scales that drive juvenile patterns is vital for elucidating the "enigmatic" recruitment process (*sensu* Mumby and Dytham 2006) and developing predictive frameworks for scientific and management applications.

Recently, hierarchical spatial designs to study juvenile coral patterns, which incorporate a within-site component, have led to new insights on the processes structuring these patterns (Hughes et al. 1999, Hughes et al. 2000, Ruiz-Zárate and Arias-González 2004). These studies have found high variability at the smallest spatial scales

(Hughes et al. 1999, Ruiz-Zárate and Arias-González 2004), where differences in the scale of variability among the reproductive modes are common (i.e., brooders versus broadcasters; Hughes et al. 1999). In some cases, large-scale patterns of juveniles (100s of kilometers) are directly attributable to patterns in fecundity of adults at similarly large distance scales (Hughes et al. 2000). Hughes et al. (2000) found that fecundity of adult corals explained 72% of the variability in recruitment among large-scale regions of the GBR for broadcast spawning corals. Because the species they studied spend a few days to a few weeks dispersing in the water column until competent to settle (Harrison and Wallace 1990, Miller and Mundy 2003), the overall reproductive output within a region, assessed as fecundity, drove the total amount of recruitment within a sector. These results demonstrate the interplay between individual reproductive output and the scale of dispersal in driving the availability of larvae to local reef sites (Hughes et al. 2000).

In contrast, the relationship between juvenile and adult abundances in brooding corals is often at smaller spatial scales (Chiappone and Sullivan 1996, Moulding 2007, Underwood et al. 2007), primarily driven by the shorter dispersal distances in this reproductive mode (Harrison and Wallace 1990). Dispersal distances can range from millimeters for species that crawl across the substrate from adult corals (Harrison and Wallace 1990, Vermeij 2005), to 10s of meters at reef site scales (Chiappone and Sullivan 1996, Underwood et al. 2007) and beyond, depending on a specific species' developmental process. For this reproductive group, the abundance of adults at a reef site can be a strong predictor of juvenile abundance at this scale (i.e., stock-recruitment relationship). For example, Chiappone and Sullivan (1996) found strong and highly significant linear stock-recruitment relationships at the site scale for the three brooding

species they studied along multiple sites in the Florida Keys. Because juvenile patterns are driven by processes other than just dispersal, brooding species have proven useful as study models for teasing apart these additional mechanisms (e.g., Vermeij 2005), where minimal dispersal eliminates the overwhelming variability introduced to these patterns at within-site scales. In studying juvenile distributions of *Siderastrea radians*, Vermeij (2005) demonstrated a strong influence by both the adult abundance and the substrate composition in structuring within-site juvenile distributions, signifying that multiple processes operate over these small spatial scales to drive these patterns. Thus, high variability in juvenile distributions are expected at the finest spatial scales due to the highly-heterogeneous nature of reefs, and indeed this is typical when hierarchical sampling designs are utilized (Hughes et al. 1999, Ruiz-Zárate and Arias-González 2004).

The purpose of this chapter was to document patterns of juveniles for a common brooding coral by assessing their size-frequency distributions, orientation, and substrate associations at both quadrat and site-level scales. In addition, a number of factors were statistically tested to determine their influence on juvenile distributions, including adult coral cover, the substrate composition, and rugosity. All juvenile surveys focused on a single brooding species, *Porites astreoides*, as is done throughout the remainder of this dissertation. Because documentation of juvenile patterns was a primary need for two of the other chapters of this dissertation (Chapters 3 and 6), the study presented here had a high importance placed on simple observational documentation of these patterns. As such, discussion on different aspects of the observed patterns is covered both in this chapter's *Discussion* section and in the ensuing chapters where appropriate.

Methods

Juvenile Surveys

Juvenile surveys were performed between June 13th and August 6th in 2008, approximately two months following the peak larval release period for *Porites astreoides*, at 12 shallow patch reef locations, each between 2-5 meters depth, in Biscayne National Park, FL (Table 2.1). Seven of the reef sites were selected randomly from a list of sites used in two previous monitoring studies, where in these previous studies, sites were selected randomly using a habitat-stratification approach. The additional five sites were included in the study to correspond to sites where post-settlement survivorship dynamics were assessed (Chapters 4 and 5) and where recruitment dynamics were simulated (Chapter 6). At each reef site, one or two 30m transect lines were laid along the benthos, each at least 5m apart and parallel if two transects were used. Transects were haphazardly laid starting 5-10 meters from the edge of the reef (to avoid the steeper sides of the patch reef structure) and towards the center of the reef site. While two transects were planned for each site, inclement weather forced a premature departure at a few of the sites, and limited time and resources prevented completion of transects at all sites. However, since the primary objective was to assess a range of habitat types among various sites, effort was placed on sampling more sites than transects within sites. For each transect, fifteen total $0.25m^2$ quadrats were placed every 2m on alternating sides of the transect (*sensu* Miller et al. 2000; Table 2.1). While such a quadrat-placement strategy would lead to bias in the extreme case where a repeating biological pattern is present at the same length scale (i.e., 2m in this case; Fortin and Dale 2005), this approach minimizes potential dependencies among quadrats in close proximity.

Prior to recording the juveniles in each quadrat, a digital photograph of the quadrat area was taken in order to quantify the substrate epibenthic cover. Photographs were later processed using the point count software CPCe v. 3.2 (Koehler and Gill 2006), where the substrate type was quantified for 100 randomly-allocated points per photograph. Using these data, an estimate of percent cover was derived for each substrate type (see *Data Analysis* section below) in each quadrat, including the cover of adult *Porites astreoides* for each quadrat.

After the photograph was taken in the field, loose sediments were removed from the quadrat area by fanning the surface, and the size, orientation (up, up/vertical, vertical, down/vertical, and down), and surrounding substrate directly in contact with an individual were recorded for each observed juvenile (<5cm diameter) of the focal species. Location of recruits was aided through use of the NightSea FL-1 FLASH Light (www.nightsea.com), a powerful fluorescence-excitation light designed for daylight surveys of juvenile corals, which allowed detection of the smallest individuals (<2mm) discernible to the species level (see Figure 2.1 for example of fluorescence response in *Porites astreoides*).

Rugosity Measurements

After the juveniles were recorded, rugosity was measured at each quadrat using both a fine- and coarse-scale measurement. Fine-scale measurements were performed using a chain rugosity measure (McCormick 1994), where a 1-meter long chain was draped across the middle of each recruitment quadrat in a haphazard direction. The straight-line distance that the draped chain traversed across the substrate was recorded

("draped chain length"), and rugosity was calculated as the straight chain length (1m) divided by the draped chain length (<1m). Using this method, a value of 1 reflects a perfectly flat surface, while an increasing value represents increasing topographic complexity.

Coarse-scale rugosity was assessed to simulate rugosity measurements derived from LiDAR (LIght Detection And Ranging) aerial surveys at 1m resolution (e.g., Brock et al. 2004, Brock et al 2006; henceforth referred to as "LiDAR-style rugosity"). The purpose of measuring coarse-scale rugosity in this manner was (1) to test if a relationship between LiDAR-style measurements and juvenile patterns exists; and (2) to test if a relationship exists between LiDAR-style measurements and chain-rugosity measurements, which are the typical rugosity measurements performed for juvenile surveys (e.g., Moulding 2007, Mumby et al. 2007b). Due to the large spatial extent of LiDAR aerial surveys, a relationship between juveniles and LiDAR-style measurements would be valuable for deriving predictions of juveniles at larger spatial scales than can be done by *in situ* observations.

To simulate the LiDAR-derived rugosity measurements, a 2x2m quadrat, delineated to four 1x1m sections, was constructed with four legs of adjustable height in each of the corners (Figure 2.2). A two-way level bar was attached to the middle of the quadrat, and by adjusting the height of each of the four legs, this rugosity quadrat was placed in a level (and thus standardized) orientation over each of the recruitment quadrats. Once level, the height above the substratum was measured from each corner of the 1x1 m sections (9 total measurements), thereby representing a 2x2m grid of 1m resolution height measurements around each focal recruitment quadrat. A coarse-scale

rugosity value was then calculated for each recruitment quadrat using the algorithm presented in Brock et al. (2006). As with the chain rugosity, a value of 1 represents a flat surface, and an increasing value represents higher topographic complexity.

Site-Scale Adult Coral Cover

In order to assess relationships between juvenile and adult abundances at the site scale, each adult *Porites astreoides* (>5cm) was recorded with its size (two maximum perpendicular diameters and height) along each transect and within 0.5m to either side of the 30m long transects. Using these size measurements, the total surface area of adult tissue for each colony was approximated using the Knud Thomsen formula for the surface area of an ellipsoid (Xu et al. 2009):

$$SA = 4\pi \left[\frac{a^p b^p + a^p c^p + b^p c^p}{3}\right]^{1/p} \qquad \text{eq. 1}$$

Here, a and b are the diameters, c is the height, and p is a constant of 1.6075. The total cover of adult colonies per site was then calculated as the total surface area of colonies divided by the total area of reef searched (i.e., for two transects, 60m^2).

Data Analyses

Due to a high proportion of quadrats with no juveniles in the dataset (47%; Figure 2.3), a statistical approach was adopted to deal with zero-skewed data (Fletcher et al. 2005; also known as "delta approach", *sensu* Serafy et al. 2007). This approach consists of two stages: (1) perform a logistic regression on presence/absence data; and (2) for the

presence data only, perform an ordinary regression on the log-transformed density data using a Poisson distribution. An un-biased average density value can additionally be estimated from these tests by combining the two models at average values of the predictor variables. Thus, for the following description of the predictor variables, two separate models were run for each combination of the predictor variables: a presence/absence model, and a density model. All tests were run using the GLIMMIX procedure in SAS (SAS Institute 2006), where transects were nested within sites as random effects to account for lack of independence.

Three categories of predictor variables were assessed for the two models: (1) cover of adults (quadrat scale and site scale); (2) rugosity (chain and LiDAR-style); and (3) substrate (quadrat and site scale; using only crustose corraline algae and macroalgae as predictors, see below). Because significant multicollinearity may exist when attempting to determine the scale at which a predictor variable is important (i.e., same predictor effect is included multiple times in a single model, but measured at different scales), a single model with all of the predictors may be biased, particularly for estimating the regression coefficients in the model (Neter et al. 1996). To reduce the number of predictor variables in the model and thus remove unnecessary collinearity, a backwards-elimination approach was applied, where the variable with the highest p-value (>0.1) was removed from successive model runs, until all predictor variables had a p-value less than 0.1 (Neter et al. 1996). While more advanced model-selection criteria exist that account for multiple aspects of a model's suitability (e.g., Akaike's Information Criterion, AIC), these advanced selection criteria were unreliable for choosing an appropriate best fit model in this situation. This was due to the statistical procedure used

where fit statistics are based on pseudo-likelihoods (pseudo-AIC, pseudo-AICC), which may produce inaccurate comparisons with non-Guassian response variables (here, binary and Poisson; Dale McLerran, SAS-L list-serve online communication). Indeed in this situation, model combinations without significant predictor effects generally produced the best models according to pseudo-AIC and pseudo-AICC, despite the presence of models with multiple significant predictors.

For the substrate predictor category, only the cover of crustose corralline algae (CCA) and macroalgae were included as predictors in the models. This constraint was chosen because difficulties arose in distinguishing bare substrate, sediment-laden substrate, and sediment-laden turf algae in the photographs, where all types frequently appeared as over-exposed white areas depending on the photograph exposure. Because of these difficulties, CCA and macroalgae were chosen due to their ease of identification in the photographs, and because they represent substrate types often considered as crucial for recruitment dynamics (Harrington et al. 2004, Mumby 2006).

As an additional test for a stock-recruitment relationship at the site scale to compare to Chiappone and Sullivan (1996) and Moulding (2007), the average density per site was calculated and assessed as a function of adult coral cover, using both a linear regression and a Ricker stock-recruitment relationship (Ricker 1954) of the form:

$$Density = R1 * Cover * e^{(-R2*Cover)} \qquad \text{eq. 2}$$

Here, R1 and R2 were parameters computed from the NLIN procedure in SAS (SAS Institute 2006).

Results

A total of 434 juveniles of *Porites astreoides* were found in 274 quadrats, leading to a grand average of 6.3 juveniles/m^2. The range in density of juveniles per quadrat was highly variable, with 47% of quadrats having no juveniles, and a maximum juvenile abundance of 19 individuals per single quadrat (density of 76/m^2; Figures 2.3 and 2.4). Although not assessed quantitatively, densities were spatially clumped among sites (Figure 2.4). Specifically, the sites with the highest densities (mid-channel patch reefs) were nearest to each other, while the sites with the lowest densities (inshore patch reefs) were additionally nearest in proximity.

Nearly 50% of the juveniles were less than 1cm diameter, and the proportion of juveniles in each 1cm size-bin decreased linearly with size (Figure 2.5). The highest number of juveniles was found in upwards-facing orientations (45%), followed by vertical (34%), vertical/up (20%), down (<1%), and down/vertical (0%) (Figure 2.6). When comparing the orientation of the juveniles among different size classes, 58% of the smallest individuals (<0.2cm) were found in a vertical orientation, with a linear shift towards upwards-facing orientations for subsequently larger individuals (57% for sizes 4-5cm; Figure 2.6). The substrate types associated with juveniles were variable, with similarly high numbers associated with four major substrate types – bare substrate, crustose corraline algae (CCA), sediment-laden substrate, and turf algae (Figure 2.7). Only a few were found directly in contact with macroalgae (9 individuals; Figure 2.7).

For the presence/absence model of the delta approach, the likelihood of finding a juvenile increased as the cover of adults increased at the quadrat scale. However, the density of juveniles was not related to quadrat-scale adult cover, nor was there a

relationship between juveniles (either presence/absence or density) and the cover of adults at the site scale (Table 2.2). For comparison to other studies that have shown a stock-recruitment relationship between juveniles and adults at the site scale for this species (Chiappone and Sullivan 1996, Moulding 2007), these data were additionally analyzed using site averages (i.e., average site density and adult cover). Here, a linear relationship as in previous studies was not significant ($F<0.0$, $p=0.9985$), but a non-linear Ricker relationship was significant ($F=18.01$, $p=0.0005$; Figure 2.8).

Overall, there was a weak but significant positive correlation between chain rugosity and LiDAR-style rugosity ($r^2=0.078$, $p<0.0001$; Figure 2.9). Despite this correlation, only the chain rugosity was a significant predictor for the likelihood of finding a juvenile in a quadrat, where the likelihood increased as rugosity decreased (Table 2.2). The LiDAR-style rugosity was not significant in either delta approach model, nor was chain rugosity significant in the density model. Finally, the cover of macroalgae in a quadrat had a significant positive effect for the likelihood of finding a juvenile, but the site cover of macroalgae had no effect on the likelihood of finding a juvenile (Table 2.2). As with the other predictors above, this effect was not significant in the density model. CCA was not a significant predictor for either delta approach model at either of the two spatial scales (Table 2.2).

Discussion

Patterns of juveniles assessed at the twelve sites in this study were highly variable among sites, ranging from an average of less than 1 juvenile per m^2 to nearly 20 per m^2. While the low densities are typical from previous studies in this region (Dustan 1977,

Chiappone and Sullivan 1996, Miller et al. 2000, Moulding 2007), the high average densities at a few of the sites are nearly 2 to 3-fold greater than the highest values measured from these other studies (Dustan 1977, Moulding 2007). Notably, the highest densities in this study were spatially-structured, where four of the mid-channel patch reefs near the middle region of Biscayne National Park had the highest measured values, and these rates were particularly high for two of the sites in closest proximity (Figure 2.4).

The discrepancy among this study and others with respect to maximum juvenile density could be due to either differences among census techniques, or may reflect natural variability in recruitment among sites. In this study, fluorescent techniques were used which permitted easier location of the smallest individuals. Although this may have increased the measured rates by some degree, where these techniques have been shown to result in 20-50% higher rates in other studies (Baird et al. 2005), the total percentage of the smallest individuals were still minor, with less than 15% of recruits in the smallest size class (Figure 2.5). The potential does exist that all sizes of individuals were located more readily with the fluorescent light than standard surveys alone, but since this was not tested due to time constraints, this possible methodological enhancement remains unknown. In general, the fluorescent light worked exceptionally well for locating the smallest individuals (<0.2cm), but most of the larger individuals were readily discernable with the naked eye. The increased ability to detect up to 50% more recruits in Baird et al. (2005) could be due to their geographic location in the Indo-Pacific, where higher recruitment rates are typical compared to the Caribbean (Smith 1997), and a higher percentage of the smallest size-classes would be expected. Therefore, it is assumed that

the methods used here did not significantly bias comparisons to other studies by leading to exceptionally higher densities, but instead, the highest density sites assessed here are unique in their high numbers of juveniles compared to other studies.

None of the factors assessed in this study (adult cover, rugosity, or substrate) had an influence on the density of juveniles in a quadrat (i.e., the density model of the delta approach; Tables 2.2, 2.3). However, the nonlinear relationship between the average site density and the site coral cover was highly significant (Figure 2.8), where the density increased with adult cover up to approximately 10% coral cover, but then declined markedly for two of the sites that had exceptionally high cover of *Porites astreoides* (sites M9 and BS; >25% adult cover). In past studies on this species, a strong linear relationship between juveniles and adults was found by both Chiappone and Sullivan (1996) and Moulding (2007) at reef sites along the Florida Keys (Figures 2.10 and 2.11). Chiappone and Sullivan (1996) assessed a stock-recruitment relationship for juveniles <4cm, and found a significant linear correlation with a high correlation coefficient ($p<0.001$, $r^2=0.84$). Moulding (2007) assessed this for the smallest juveniles (<0.5cm), and found a similar positive relationship ($p<0.046$, $r^2=0.45$). Although a nonlinear relationship was found here instead of a linear one, it is important to note that the two highest cover sites in this study were higher in adult cover than any of the sites in either Chiapone and Sullivan (1996) or Moulding (2007). Removing the two high-cover sites as outliers in this study and fitting a linear model produced a significant fit ($p=0.018$) with relatively high r^2 (0.52), consistent with the results in these other studies for all sites but those with exceptionally high adult cover.

Therefore, the discrepancy between this study and others in the stock-recruitment relationship is likely due to inclusion of high-cover sites in this study. The two high cover sites here were markedly higher in their cover values compared to the other sites, where typically only near-shore patch reefs experience cover values in this range (Lirman and Fong 2007). Over half of the sites studied here had adult cover values less than 3%, and all but two of these sites were less than 10% average adult cover. In the case of Chiappone and Sullivan (1996) where a strong linear juvenile-adult correlation was found, their sites were offshore reefs where the highest overall coral cover, for all species combined, was 13%. Similarly, the overall cover for all coral species combined in Moulding (2007) were below 20% for all nine sites in her study. In general, nonlinear relationships between juveniles and adults across the full range of adult cover (up to 100%) are expected due to density dependence, and common stock-recruitment relationships typically represent these relationships as nonlinear with saturating or parabolic relationships (Ricker 1954, Beverton and Holt 1957). In the case of corals and other benthic species, as adult cover increases, the total substrate available for settlement decreases, thus leading to a density dependent effect due to space preemption (Roughgarden and Iwasa 1986, Chesson 1998). Interestingly, Vermeij and Sandin (2008) found a similar nonlinear response, where settlement in another brooding coral, *Siderastrea radians*, increased linearly with adult cover up to 10% cover, but then saturated after this.

If density dependence is present with respect to juvenile and adult densities, this effect could also arise from other factors along with simple space preemption. New evidence is emerging with respect to early post-settlement survivorship dynamics in

relation to distances from adult colonies (Vermeij 2005, Marhaver 2008). In these studies, researchers have shown that survivorship decreases when larvae choose to settle near to adult congeners, suggesting recruitment regulation through a distance-dependent effect (Vermeij 2005). Marhaver (2008) found that this distance-dependent effect is related to microbial activity, which is further supported by Vermeij et al. (2009), where host pathogens or parasites on adults may kill susceptible spat in close proximity. Such an effect would strengthen a nonlinear relationship between juveniles and adults at the site scale, particularly for high-cover sites where the adults are evenly distributed spatially, leading to relatively poor areas for settlement throughout a site. With strong density dependence, carrying capacities arising from these processes may restrict the maximum amount of recruitment possible at a site, despite increases in larval supply. Greater understanding of density-dependent processes and the environmental situations in which they arise would provide valuable insights into the recruitment dynamics of these taxa. However, given the declining nature of many coral populations, density-independent processes may now be most common as the primary drivers of recruitment regulation in these systems.

Although adult cover (quadrat or site scale) did not have an effect on juvenile density in the delta approach analysis, there was a positive linear relationship between the likelihood of finding a juvenile and the adult cover at the quadrat scale. This result suggests that either (1) a percentage of larvae released from an adult are dispersing very short distances (i.e., <1m); (2) larvae are actively choosing to settle in areas already occupied by the adults (e.g., due to preferred habitat near adults); or (3) larvae are settling indiscriminately, but experiencing higher survival in areas already occupied by adults

(e.g., as could arise through favorable environmental conditions where adults are already located). The distance-dependent effects discussed above (Vermeij 2005, Marhaver 2008) suggest that active choice or enhanced survival at settlement locations near adults is unlikely due to increased mortality, although this possibility is untested for this species. Alternatively, larvae of some species, notably *Siderastrea radians,* are known to disperse very short distances from adult colonies upon release (cm-scale), and significant relationships between juveniles and adults have been found for this species at a quadrat scale (Vermeij 2005). Although a proportion of larvae released by *Porites astreoides* do swim upwards upon release (as can be inferred from typical methods used to collect these larvae; Brazeau et al. 1998, Chapters 3-5) and thus disperse greater distances away from adult colonies, a number of individuals swim in random directions upon release to quickly return to the substrate (W. Cooper, personal observation). Such behavior, combined with turbulent water movements which may rapidly transport larvae to the bottom (Koehl et al. 2007), could lead to a proportion of the larvae settling short distances from the natal colony. In addition, larvae of this species can settle and metamorphose within a few hours after release (W. Cooper, personal observation), further strengthening the potential for a juvenile-adult relationship at small spatial scales due to short dispersal distances. Despite this potential, only parent-offspring spatial mapping through direct observation or genetic evidence (e.g., Underwood et al. 2007) can determine if the effect of adult density on quadrat-scale presence/absence is due to short dispersal distances, and not via some other biological mechanism.

Surprisingly, the likelihood of finding a recruit in a quadrat increased as the topographic complexity decreased. This was counter to *a priori* expectations, as a

common notion regarding coral larvae is their general preference for cryptic microhabitats for settlement (e.g., reviewed in Harrison and Wallace 1990; Chapter 3), and specifically, preference for topographically-complex substrates compared to smooth substrates at fine scales (e.g., millimeter scale; Carlton and Sammarco 1987). Despite these common settlement preferences, relationships between rugosity and juveniles at quadrat or site-level scales are less common, and where tested, are typically non-significant (Moulding 2007, Mumby et al. 2007b). It is unknown if the negative relationship found here is due to the preference of larvae to choose or avoid particular areas for settlement based on the rugosity, or to differential post-settlement dynamics due to rugosity (e.g., lower survivorship and/or growth on high rugosity areas). For example, larvae may preferentially settle on cryptic surfaces, and this preference is supported by both the higher abundance of the smallest individuals on vertical surfaces found in this study, and the settlement behaviors presented in Chapter 3. Survivorship and/or growth could theoretically be reduced on these areas, thereby leading to a potential net negative relationship between density and rugosity. However, no evidence exists to support such a post-settlement effect (Edmunds et al. 2004), and on the contrary, cryptic surfaces provided higher survivorship at one patch reef site for this species, and equal survivorship at another reef site (Chapter 4). Therefore, it is unclear what biological mechanism may have led to this negative relationship between juvenile presence and rugosity, and more research on the early post-settlement processes with respect to rugosity is needed to elucidate this relationship. For example, if predation dynamics have a strong effect on early post-settlement mortality, a higher abundance of cryptic predators in

topographically complex habitats could cause high planula mortality, thereby masking the positive relationship due to settlement preferences for complex habitats.

Given the recent availability of high-resolution, remotely-sensed data in coral reef environments (e.g., Brock et al. 2004), the potential for using remotely-sensed data in forecasting large-scale patterns of abundance and community structure now exists (e.g., Kuffner et al. 2007). Of particular interest is the possibility of deriving rugosity measurements from LiDAR data through a simple computation (Brock et al. 2006), thus providing an extraordinary dataset for both within- and among-site comparisons where rugosity is an important feature regulating communities. Therefore, mapping of ecological processes which respond strongly to rugosity could benefit greatly from such extensive, remotely-sensed data (e.g., fish community; Kuffner et al. 2007). The results here suggest that LiDAR-derived rugosity does indeed reflect fine-scale chain measurements of rugosity, although this correlation is weak and variable due to the high heterogeneity of reef systems at fine spatial scales. In this study, LiDAR rugosity was not related to either the likelihood of finding a juvenile or the juvenile density in a quadrat. Although an underlying density-rugosity effect may exist (as shown through the weak chain rugosity relationship), the scale of measurement of the LiDAR rugosity may not be appropriate for relationships to juvenile patterns (e.g., Carlton and Sammarco 1987). If other species are shown to respond to rugosity at scales similar to the LiDAR surveys, these data could prove highly useful. However, at least in the case of *Porites astreoides*, this study suggests these larger-scale data may be of minimal value for predicting juvenile abundances.

Juvenile patterns were only partially related to the substrate composition, where macroalgae was shown to have an effect on the presence/absence of juveniles, while CCA had no effect on either presence/absence or density. Interestingly, this macroalgae effect was positive, where the likelihood of finding a juvenile in a quadrat increased with the cover of macroalgae. As with the rugosity effect, this result was both surprising and contrary to *a priori* expectations, as macroalgae is generally considered to negatively affect recruitment (Hughes 1989, Kuffner et al. 2006, Hughes et al. 2007, Box and Mumby 2007). Many of the studies on the negative impacts of algae have been conducted under experimental conditions, where the macroalgal-juvenile coral interaction is prescribed. What is less well known is the actual occurrence or prevalence of these negative macroalgal-juvenile interactions in natural settings. In this study, only a few of the quadrats had high cover of macroalgae (up to 90%), with less than 20% of quadrats having macroalgal cover greater than 50% (overall average cover of 34% across sites). Therefore, significant macroalgal-free substrate was present in this study, which likely limited the prevalence of negative macroalgal-coral interactions. Because the primary mechanisms of negative macroalgae influences on juveniles are generally considered to be through overgrowth, space preemption, or shading (Hughes 1989, Kuffner et al. 2006, Mumby et al. 2007b), macroalgae may only exert negative effects on juvenile patterns at relatively high cover.

Macroalgae at lower average cover is a natural phenomenon and representative of healthy reefs (Vroom et al. 2006), and in some cases, macroalgae can be beneficial both for the settlement and post-settlement dynamics of corals, although these cases are generally algal species-specific (Maypa and Raymundo 2004). Importantly, recent

evidence suggests that phase shifts to algal-dominated states may be less ubiquitous than commonly assumed (Bruno et al. 2009), and only a small proportion of reefs, mainly in the Caribbean, have algal cover greater than 50% (Bruno et al. 2009). Jamaica is a unique example where a dramatic phase shift did occur (3% to 95% macroalgal cover from 1983-1987; Hughes 1989, 1994), thereby influencing the subsequent perception of coral reef scientists for a decade with respect to the severity of algal phase shifts; however, this example is by no means universal or in the majority (Bruno et al. 2009). Given these recent insights, caution should be exercised when assuming a universal negative effect of macroalgae on recruitment, as these effects may be restricted to a small proportion of cases where algal cover is exceptionally high. Results from this study suggest that macroalgae may be beneficial to juvenile patterns through some unknown mechanism (e.g., metamorphic cue through algal exudates; Maypa and Raymundo 2004), particularly when cover of algae is relatively low.

Figures

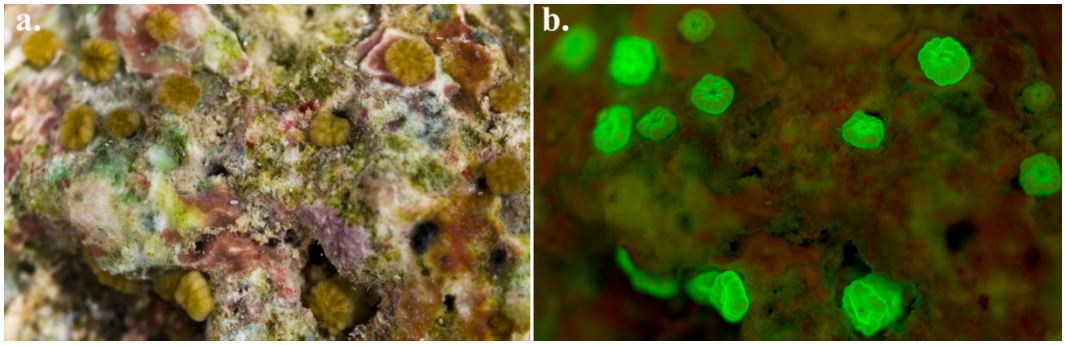

Figure 2.1. Comparison of recently settled *Porites astreoides* spat under (a) white light, and (b) fluorescence-excitation light (here, blue-spectrum wavelength).

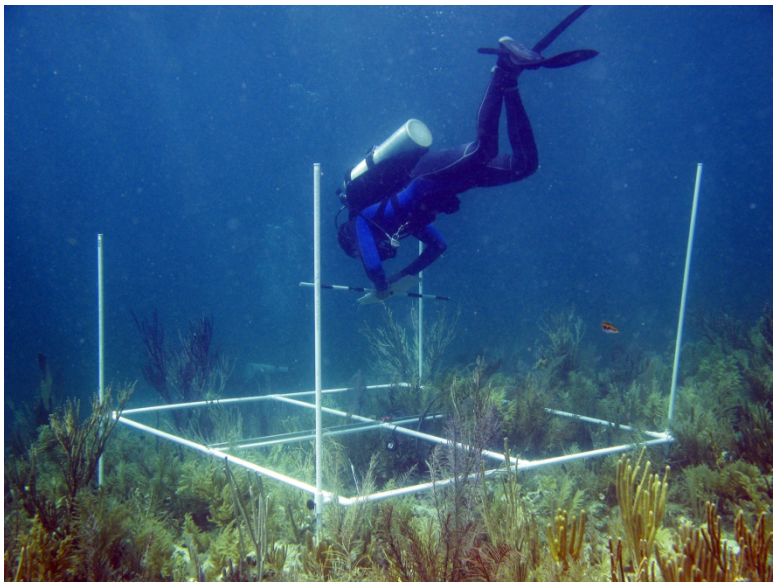

Figure 2.2. Photograph of the 2x2m quadrat used to measure LiDAR-style rugosity at each recruitment quadrat (photograph taken 6.17.09 at site S9).

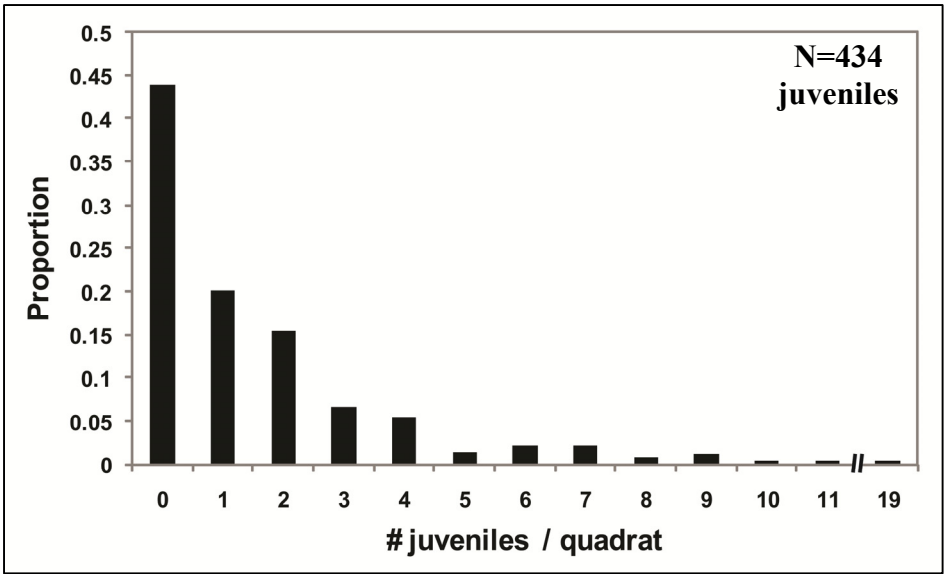

Figure 2.3. Frequency distribution of the number of juveniles per quadrat. Other than 19 individuals per quadrat (shown after break in absicca), there were no quadrats with more than 11 individuals. Due to the high proportion of zero values in the dataset, a delta-approach statistical test was applied to the factor tests (Table 2.2), which accounts for zero-inflated data.

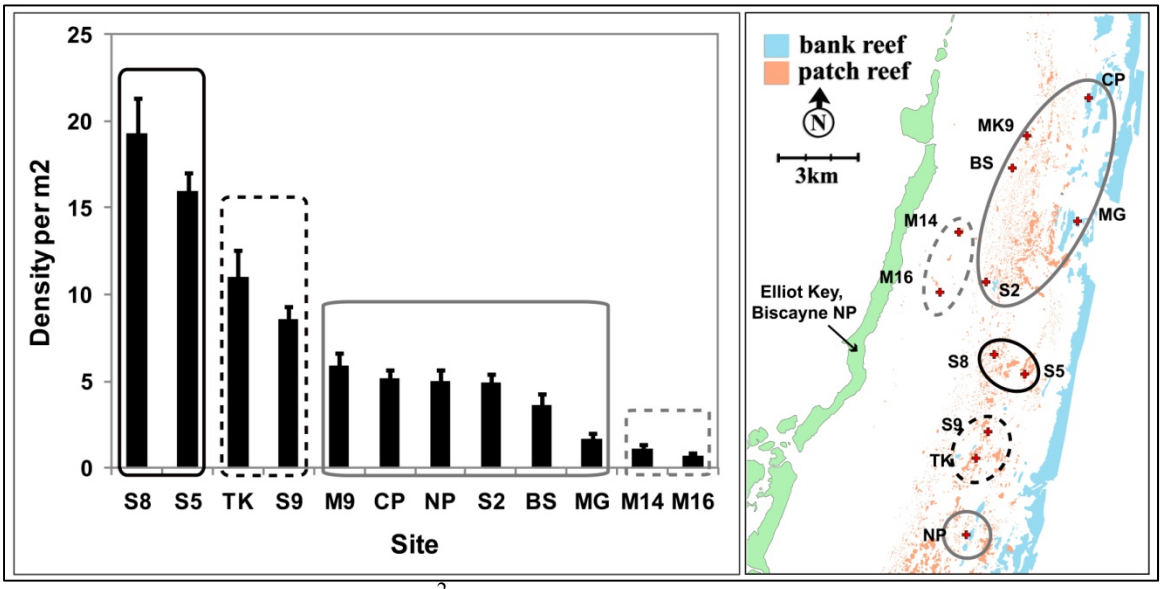

Figure 2.4. Density (±1SE) per m^2 for each site in the study, and a spatial map of these sites ranked by density into groups (represented by the bounding rectangles and circles). See Table 2.1 for coordinates of sites.

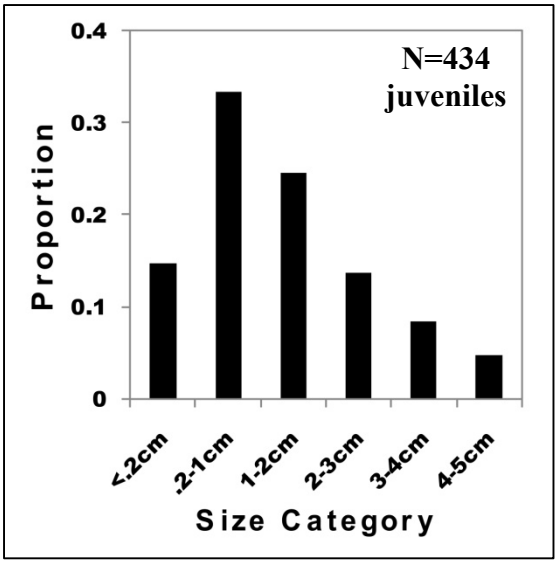

Figure 2.5. Size-frequency distribution of observed juveniles among the six size categories for all sites pooled. Note: the first two bars are within the 0-1cm size bin, but are split into two bars to clarify the proportion of smallest individuals.

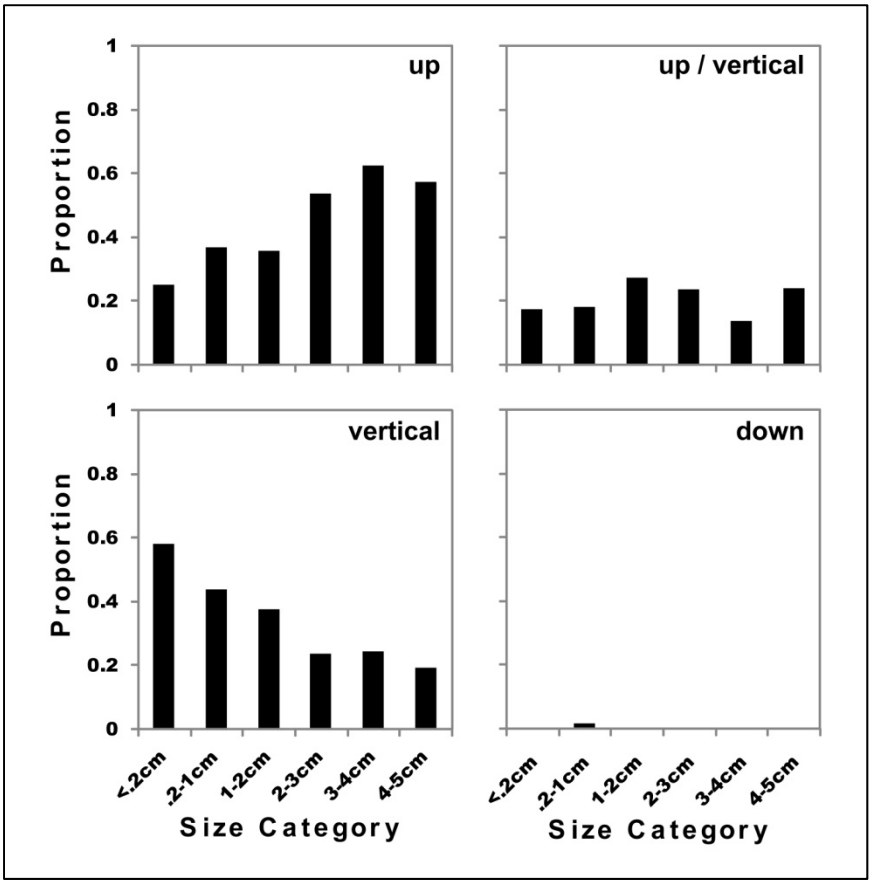

Figure 2.6. Proportion of observed juveniles at each orientation from each size class, for all sites pooled. Note, here proportion at each orientation is calculated relative to the total per size category for all orientations pooled.

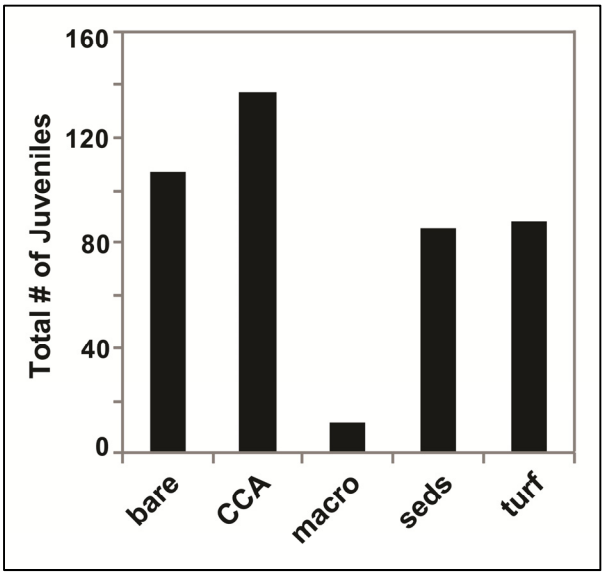

Figure 2.7. Total number of juveniles associated with (i.e., in direct contact with) each of the five major substrate types. Here, bare = bare reef framework, i.e., no living macrobenthic organisms; CCA = crustose coralline algae; macro = macroalgae; seds = sediment-laden substrate; and turf = turf algae.

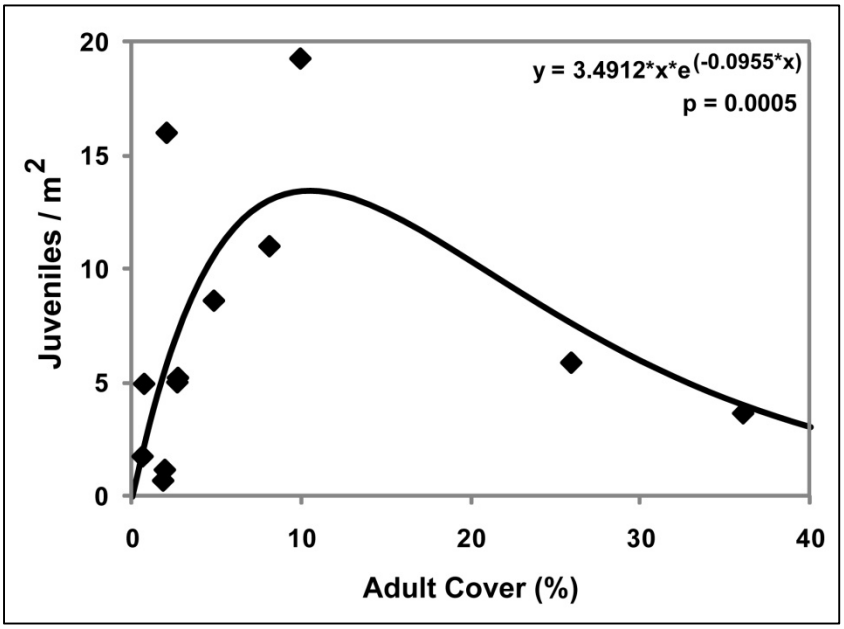

Figure 2.8. Relationship between the density of juveniles (<5cm) and adult coral cover at each of the study sites, with fit to a non-linear Ricker function.

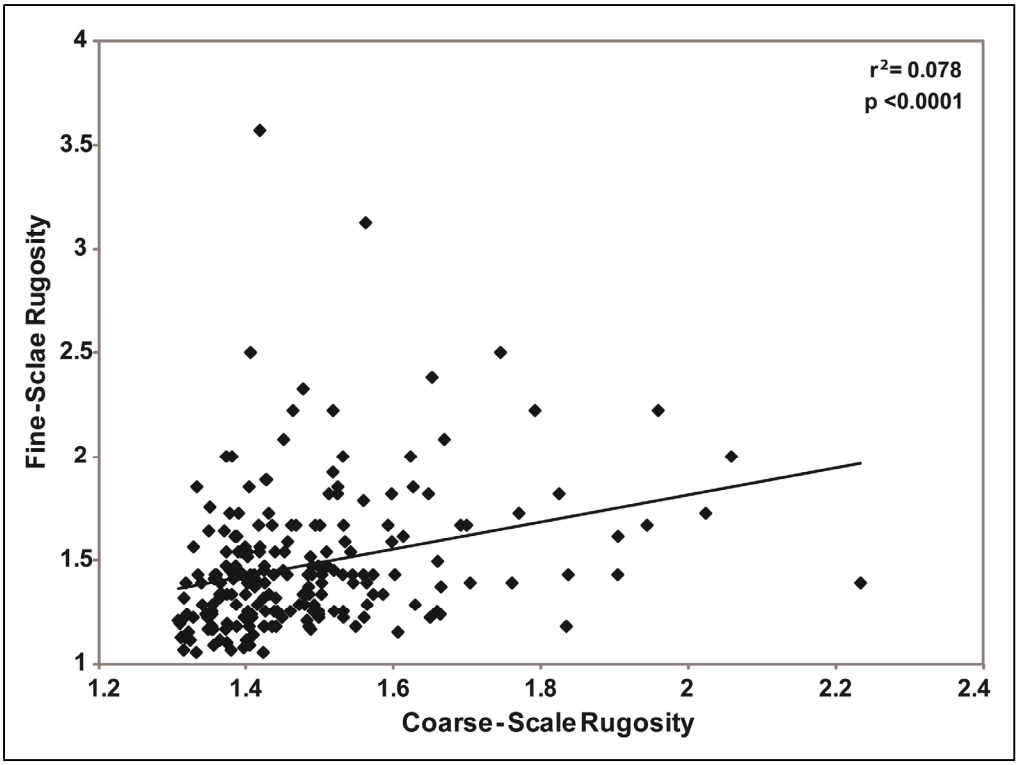

Figure 2.9. Correlation between fine-scale (chain) and coarse-scale (LiDAR-style) rugosity for each quadrat where both rugosity measurements were assessed.

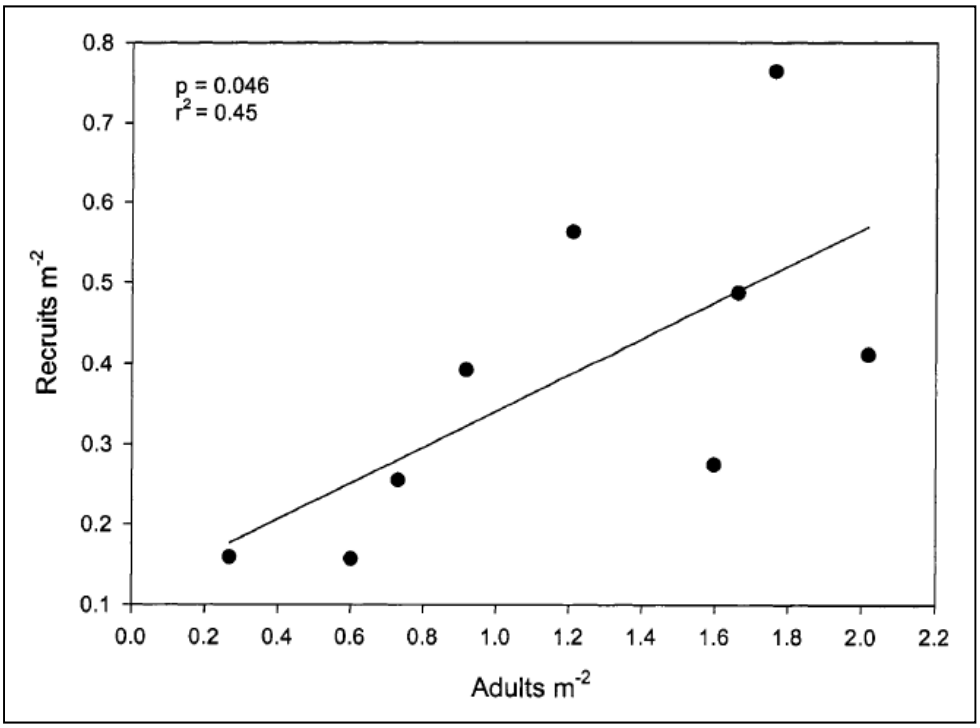

Figure 2.10. Relationship between the density of recruits (<5mm) and adult density in Moulding (2007). Each datum point is one reef. (reproduced with permission)

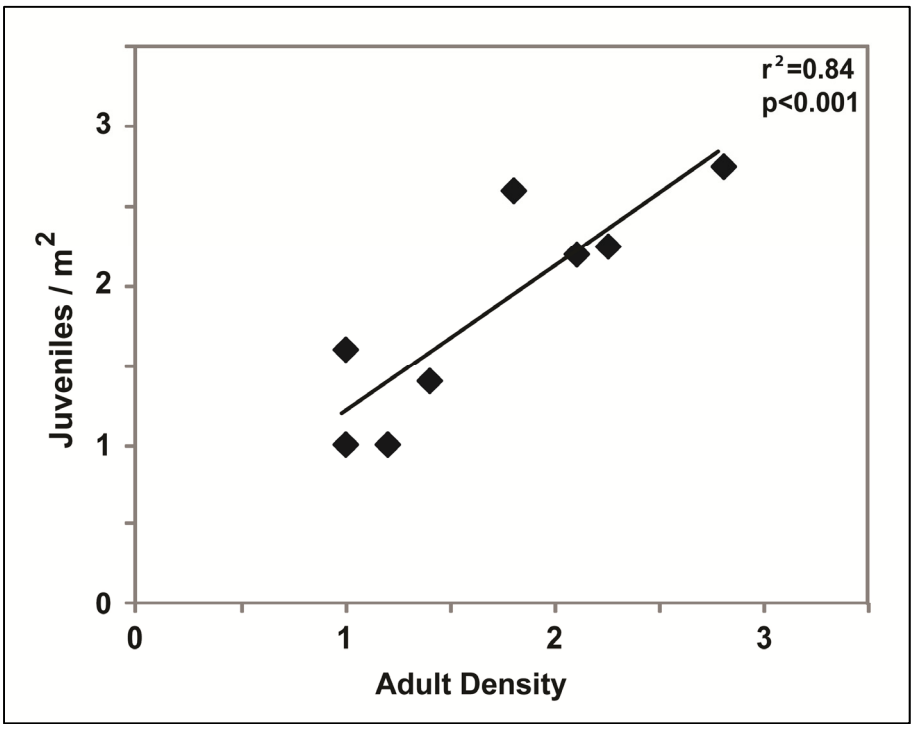

Figure 2.11. Relationship between the density of juveniles (<4cm) and adult density (root-root transformed) of *P. astreoides* in Chiappone and Sullivan (1996). Each datum point is one reef. (figure adapted from their Figure 3)

Tables

Table 2.1. Location, depth, and number of quadrats for recruitment surveys at each of 12 patch reef sites in Biscayne National Park.

Site	Depth(m)	#Quadrats	AdultCover (%)	Latitude (N)	Longitude (W)
S8	3	22	9.9	25.41631	80.14479
S5	3	23	2.0	25.42297	80.15603
TK	4	8	8.1	25.38832	80.16297
S9	4	20	4.8	25.39715	80.15846
M9	2	30	25.9	25.49604	80.14347
CP	4	30	2.7	25.50851	80.12058
NP	4	12	2.7	25.36277	80.16675
S2	3	30	0.7	25.44725	80.15886
BS	3	11	36.0	25.48528	80.14888
MG	5	30	0.6	25.46735	80.12492
M16	3	30	1.8	25.44387	80.17586
M14	3	28	1.9	25.46394	80.16884

Table 2.2. Statistical results from the delta-method approach with all predictor variables in the model.

Test	Factor	Estimate	F-value	p-value
Presence/Absence	Cover-Quad	0.33	4.31	**0.0393**
	Cover-Site	0.00	0.00	0.9918
	Rug-Chain	-1.93	9.87	**0.0020**
	Rug-LiDAR	0.17	0.01	0.9042
	Sub-Quad-CCA	-0.08	1.12	0.2918
	Sub-Quad-Macro	0.03	5.12	**0.0249**
	Sub-Site-CCA	-0.07	0.02	0.9005
	Sub-Site-Macro	0.08	1.64	0.2014
Density	Cover-Quad	0.01	0.63	0.4301
	Cover-Site	0.01	0.53	0.4666
	Rug-Chain	-0.08	0.12	0.7299
	Rug-LiDAR	-0.49	0.79	0.3772
	Sub-Quad-CCA	-0.03	0.39	0.5331
	Sub-Quad-Macro	0.00	0.17	0.6836
	Sub-Site-CCA	-0.02	0.07	0.7894
	Sub-Site-Macro	0.01	0.42	0.5208

Table 2.3. Statistical results from backwards-elimination model selection criteria.

Test	Factor	Estimate	F-value	p-value
Presence/Absence	Cover-Quad	0.26	5.62	**0.0188**
	Rug-Chain	-1.68	9.27	**0.0027**
	Sub-Quad-Macro	0.03	5.27	**0.0228**
Density	**** no predictor variables retained in backwards-selection***			

CHAPTER 3: COMPLEX SETTLEMENT BEHAVIORS IN A BROODING CORAL: LIGHT, SUBSTRATE, AND ORIENTATION PREFERENCES IN RELATIONSHIP TO RECRUITMENT PATTERNS

Background

The settlement stage is a crucial period in the life cycle of benthic marine larvae: whether actively or passively chosen, the microhabitat location where a larva settles will likely influence the future fitness of the individual (Grosberg 1981, Young and Chia 1984). Due to the high spatial heterogeneity in marine environments, active larval behaviors during this stage are often a necessity for individuals to appropriately select their niche before settling to a life of immobility. Behavioral choices prior to and during the settlement stage can have strong controls on recruitment and subsequent population processes, especially in influencing patterns of zonation (Grosberg 1981, Raimondi 1988, 1990). In situations where obligate cues are needed for metamorphosis (Morse et al. 1996), the abundance and distribution of these cues can additionally serve as limiting resources for the successful establishment of individuals and recovery of populations.

For corals, patterns in recruitment can be strongly influenced by settlement behaviors, particularly with respect to zonation, as in other invertebrates (Mundy and Babcock 2000, Raimondi and Morse 2000, Carlon 2002). In both Pacific and Caribbean species, adult depth distributions are often structured by the preferences of larvae to settle within particular microhabitats (Mundy and Babcock 1998, Mundy and Babcock 2000, Raimondi and Morse 2000, Baird et al. 2003), compared to differential survivorship or growth among microhabitats after settlement (Mundy and Babcock 2000, Raimondi and Morse 2000). Given the consequences of settlement behaviors on recruitment success

and future fitness, understanding the cues by which coral larvae select appropriate sites is a vital step for addressing the mechanisms that structure recruitment and recovery dynamics in this ecosystem beset with ongoing degradation (Hughes 1994, Hughes et al. 2007, Mumby and Steneck 2008).

At the time of settlement, larvae may respond to multiple environmental cues to choose their preferred settlement site. Light intensity (Maida et al. 1994, Mundy and Babcock 1998), spectral quality (Mundy and Babcock 1998), substrate orientation (Raimondi and Morse 2000), microtopography (Carleton and Sammarco 1987, Petersen et al. 2005), and substrate composition (Morse et al. 1996, Heyward and Negri 1999, Baird et al. 2003, Baird and Morse 2004, Harrington et al. 2004, Birrell et al. 2005) have all been shown to influence a coral larva's choice for a settlement site. These choices can involve complex behavioral responses to multiple cues, as in the case of *Agaricia humilis*, where larvae respond sequentially to depth (presumably through a pressure or light cue), substrate orientation, and substrate surface chemistry (Raimondi and Morse 2000). Responses to individual cues are often species-specific, and multiple species have been shown to respond differently to a single cue (Mundy and Babcock 1998, Baird and Morse 2004, Szmant and Miller 2006). Therefore, when building a mechanistic understanding of recruitment dynamics for a given species, one must account for the species-specific responses to particular cues and the interactions among cues.

Porites astreoides is a common brooding coral with relatively high recruitment rates in the Caribbean compared to other species in this region (Smith 1997), thereby providing a unique model system to assess the mechanisms structuring recruitment dynamics. This species occurs as two distinct color morphs (green and brown morph)

which may represent genetically stable phenotypes (Gleason 1993). Although both morphs can be found at nearly all depths, the green morph dominates in shallow depths while the brown morph dominates in deeper waters (Gleason 1993). Given the dominance of the green morph in shallow depths where adult cover can reach upwards of 40% in some patch reef environments (Lirman and Fong 2007), previous studies on the establishment of zonation patterns due to settlement behaviors would suggest that larvae of this morph prefer to settle in shallow reef environments. Such a response could arise from cues to the depth-dependent substrate communities (Baird et al. 2003), water column pressure (Stake and Sammarco 2003), or light intensity gradients (Mundy and Babcock 1998).

With the exception of a few studies on specific stressors to early life stage processes in this species (Edmunds et al. 2001, Gleason et al. 2005, Kuffner et al. 2006, Albright et al. 2008), the general larval settlement behaviors of *P. astreoides* with respect to habitat selection remain poorly studied. This lack of information inhibits a fuller understanding of the mechanisms and environmental feedbacks which structure recruitment dynamics in this species. Given the recent use of this species as a model system in a number of high-impact simulation studies (Mumby 2006, Mumby et al. 2007a, Hoegh-Guldberg et al. 2007), lack of information on the settlement process impedes inclusion of mechanistic detail on early life-stage dynamics in these simulation models. This warrants caution in the general applicability of such models, particularly when factors under study (e.g., herbivore-algal dynamics, Mumby 2006; climate change, Hoegh-Guldberg et al. 2007) may directly alter both settlement and post-settlement dynamics (Kuffner et al. 2006, Albright et al. 2008).

Due to the paucity of information on the general settlement behaviors of this species, the goals of this study were to (1) assess the settlement preferences of *P. astreoides* to light intensity, substrate community type, and substrate orientation cues, in an attempt to identify the primary drivers of settlement behavior in this species; and (2) assess the distribution of recruits in natural reef settings to determine if recruit locations (i.e., exposed, vertical, or cryptic microhabitat locations; *sensu* Edmunds et al. 2004) correspond to settlement preferences as determined in the laboratory experiments.

Methods

Larval Collection

Larvae were obtained by collecting and transporting adults of *P. astreoides* from Biscayne National Park to a flow-through seawater system at the University of Miami's RSMAS campus prior to the peak release period in May 2007 and 2008. Twenty adult colonies (>20cm diameter) were collected five days prior to the new moon in each month, when peak release typically occurs around the new moon from April to June (McGuire 1998). Colonies were submerged within a 750L seawater tank, and a cone-shaped larval collection device (adapted from Brazeau et al. 1998; Figure 3.1) was placed over each colony to trap upwards-swimming larvae upon release. Larvae were released from colonies during the night and collected in the morning after sunrise on each day. Once collected, larvae were kept in UV-sterilized, 1μm-filtered seawater at concentrations less than 1 per milliliter until the initiation of the experiment, with daily water changes of approximately 75% of the volume. After the peak release period, adult

colonies were returned to the reef within one week of collection and attached using either hydraulic cement or Z-Spar Splash Zone epoxy.

Settlement Preferences for Substrate, Orientation, and Light

To assess settlement preferences, larvae were given a choice of substrate community type and substrate orientation under different light intensities. To provide a concurrent choice for both the substrate community and orientation, a settlement platform was constructed from a 4.5x4.5x0.5cm PVC block with acrylic legs, designed to elevate the platform 2cm above a ground surface (Figure 3.2). To both the top and bottom side of a platform, three different substrate community types were attached: "cryptic", "exposed", and "rubble" (Figure 3.2). The cryptic and exposed community types were obtained by cutting, via tile saw, 2x2.5cm pieces from the bottom and top side, respectively, of a 40x40x2.5cm limestone plate conditioned on the reef (3m depth) for six months prior to the experiment. The limestone was conditioned for an extended period of time compared to other settlement studies (typically 4-8 weeks; e.g., Mundy and Babcock 1998, Baird et al. 2003) in order to obtain a more established community representative of natural reef substrate. The rubble substrate type was obtained by cutting 2x2.5cm pieces from reef rubble collected at the same reef at 3m depth. Each substrate piece was attached to the platform using hot glue, and was cooled immediately with room-temperature seawater to prevent biofilm scorching on the substrate surface.

Each platform was placed within a 240ml polyethylene container with sterilized and filtered seawater (closed container, no flow), and 100 larvae were added to each individual container during the morning hours approximately 24hrs after first collection.

The total number of larvae per container was based on a preliminary study in April 2007 where 50 larvae per container failed to elicit sufficient settlement numbers per chip (Cooper 2008), and was therefore doubled to 100 larvae per container in May of 2007 and 2008. A total of eight replicate containers were placed under four and five light intensity treatments in 2007 and 2008, respectively, in natural sunlight at the University of Miami's RSMAS campus. Light intensity was controlled by placing varying layers of neutral density shade cloth over the polyethylene containers (0, 1, 2, 4, and 8 layers), where the 1-layer treatment was added in 2008 to discern more resolution in the higher range of light intensities. The containers were kept in an outside flow-through water bath at high flow rates to maintain a constant temperature among light treatments, and temperature measurements made during full sunlight conditions confirmed a standard temperature among treatments within ±0.5°C. Due to potential behavioral responses to UV light (Gleason et al. 2005), a UV-transparent acrylic sheet (UVT Spartech, Clayton, MO; formerly Townsend/Glasflex Plastics) was placed over the water bath to provide a natural light regime and eliminate potential salinity dilution from rainfall during the experiment. Light intensity measurements were made using a LICOR LI-192 Underwater Quantum Sensor at multiple periods during the day (morning through afternoon) over multiple days to quantify the light intensity levels among the treatments at both upwards and downwards facing orientations. Daily water changes were performed using UV-sterilized and filtered (1μm) seawater.

To quantify settlement, each chip on the settlement platform was photographed under a combination of blue wavelength (fluorescence-activating; www.nightsea.com) and white light photography at 1:1 macro using a 12MP digital SLR camera with a

105mm macro lens. The combination fluorescent-white light photographs provided a normal white-light photo with highlighted green fluorescent protein (GFP) excitation of coral tissue, allowing for easy location of settlers (e.g., Figure 3.3). Photographs of each chip were taken daily for four days, providing a record of settlement locations throughout.

Comparison of Light Intensity between the Experiment and Patch Reef Environments

To compare the measured light intensity values from this experiment (i.e., upwards- and downwards-facing orientations in the different light treatments) to expected light intensity values at different orientations in patch reef environments, light intensity was modeled along a depth gradient using the Beer-Lambert Law as:

$$I_{depth} = I_0 e^{-k(depth)} \qquad \text{eq. 1}$$

where I_{depth} is the irradiance at the given depth, I_0 is the surface irradiance, and k is the site-specific light attenuation coefficient. Here, k was estimated as 0.3028m^{-1} by taking the average value of light attenuation measurements from nine reef locations in Biscayne National Park (three each of inshore, mid-channel, and offshore) over a five year period (1995-2001; Florida Keys National Marine Sanctuary's Water Quality Monitoring Program, http://serc.fiu.edu/wqmnetwork/FKNMS-CD/upkeys.htm). Surface irradiance was set to 1800 μmol quanta m^{-2} sec^{-1}, near the average max value of 1776 μmol quanta m^{-2} sec^{-1} as measured for the full light intensity treatment in the experiment. Note that these values represent the total maximum amount of irradiance reaching a given

depth, and therefore reflect the light intensity at a fully-exposed, upwards-facing surface of the benthos. The light intensity on vertical-facing and downwards-facing surfaces on the reef was estimated as 34% and 7% of exposed surfaces, respectively, using data presented in Babcock and Mundy (1996) from *in situ* measurements. The data presented in Babcock and Mundy (1996) correspond well with proportional decreases in light intensity on under-surfaces gathered from the experimental measurements in this study.

Data Analyses

Settlement preference from the experimental study was quantified as the total number of larvae that settled per chip after 96hrs. Count data and light intensity measurements were square-root and log-transformed, respectively, to conform to normality. Preferences to light, substrate, and orientation were tested using a mixed model ANCOVA for 2007 and 2008 separately, where substrate and orientation were treated as fixed categorical variables; light intensity and a (light intensity)^2 term were treated as fixed covariates (squared term included to test for a quadratic response to light); and the settlement platform was treated as a random effect to account for lack of independence among chips on a single platform. Note that an *a priori* quadratic response to light was to be expected, where photo-inhibition is expected at high light levels and under-saturation is expected under low light conditions in corals. In 2007, one replicate platform was removed from the analysis due to an exceptionally high settlement rate above the number of larvae initially added to each container (i.e., >100). While the exact cause is unknown, it was likely due to observer error from a repeated addition of

larvae into a single container at the initiation of the experiment. Removal of this observation did not affect the statistical results in the final analyses.

Results

For both years, the percent of larvae settling on a single platform ranged from 25% to 95%, with a higher average settlement in 2007 versus 2008 (average±1SE: 68.8% ± 2.6 and 57.4% ± 2.1, respectively; $t = 3.39$, $p < 0.001$). Results from both years were statistically similar where larvae demonstrated a strong substrate and light (quadratic) response, but not a response to orientation (Table 3.2; Figure 3.4).

The community composition of the cryptic and rubble substrate communities was qualitatively similar, while the exposed substrate communities were markedly different from the other two community types in both 2007 and 2008 (Figure 3.5). Since the objective of this study was to assess differences in settlement preferences to substrate community types, and not species-specific substrate components, species-level composition per chip was not quantified due to the taxonomic expertise necessary for proper identification of all species. In general however, the cryptic and rubble community types were dominated by a mix of crustose corraline algae species, with a lesser degree of bare substrate, benthic microalgae, bryozoans, and occasional worm tubes. Comparatively, the exposed surfaces were dominated by unidentified biofilm organisms (e.g., microalgae) and bare surfaces, with scattered turf algae and minimal crustose coralline algae.

Larvae actively chose rubble and cryptic community types compared to exposed communities which they tended to avoid (Table 3.2; Figure 3.4). The average number of

settlers per substrate community was 17.1±1.2 (cryp.), 2.8±0.5 (exp.), and 14.5±1.4 (rub.) in 2007; and 20.5±1.3 (cryp.), 2.7±0.4 (exp.), and 5.6±0.7 (rub.) in 2008. The number of settlers per community type was similar for exposed and cryptic substrates in both years, but there was a significant decrease of settlers on the rubble chips in 2008 ($t = 5.8$, $p < 0.0001$).

The measured light intensity in each light and orientation treatment ranged from 2060 to 6 μmol quanta m^{-2} sec^{-1}, with average values between 1776 to 9 μmol quanta m^{-2} sec^{-1} (Figure 3.6). When compared to a corresponding depth in patch reef environments (eq. 1), these light intensity values reflected a depth range of 0 to 17m in fully-exposed upwards-facing surfaces, 0-14m on vertical surfaces, and 0-9m on cryptic surfaces, assuming a 66% and 93% reduction, respectively (Figure 3.6).

Larvae responded to light in a quadratic relationship, suggesting that the highest and lowest light levels were actively avoided. In both years, the highest amount of settlement occurred in the range between 344 - 86 μmol quanta m^{-2} sec^{-1}(Figures 3.4, 3.6). Depending on the choice of orientation in natural reef settings, this light intensity preference could occur at depths between 5-10m on exposed surfaces, 2-6m on vertical surfaces, or 0-1m on cryptic under-surfaces for patch reefs within Biscayne National Park, FL (Figure 3.6). For areas with lower or higher light attenuation (here, the average value was 0.3028), the depth of the preferred light intensity range would be deeper or shallower, respectively. While the settlement orientation did change among light treatments, with more larvae settling on under-surfaces in high light and upper-surfaces in low light (Figure 3.4), this effect was not significantly attributable to orientation when accounting for the response to measured light intensities.

Discussion

Overall, this study demonstrated that larvae of *P. astreoides* have a complex set of larval settlement behaviors, responding to multiple cues concurrently to select appropriate settlement microhabitats, including the substrate community type and the light intensity of the environment. While responses to light and substrate have been shown individually in the past (Maida et al. 1994, Babcock and Mundy 1998, Heyward and Negri 1999, Baird et al. 2003), these results provide evidence for a complex behavioral suite where multiple cues are utilized in tandem for this species. The strength of these effects was highly significant and markedly similar in both years, signifying the importance of both types of cues for settlement dynamics in this species.

Larvae responded strongly to substrate type (Figure 3.4, Table 3.2), preferring to settle on surfaces conditioned in cryptic orientations in shallow waters (3-5m depth) or on rubble pieces, and avoiding surfaces conditioned in exposed orientations. Many species of coral larvae are known to respond strongly to chemical cues from the substrate (Morse et al. 1996, Heyward and Negri 1999), originating from crustose algae (Baird and Morse 2004, Harrington et al. 2004) or bacterial films (Webster et al. 2004). The substrate cue(s) that larvae responded to in this study are unknown, but are likely either (1) positive chemical cues from organisms associated with rubble or cryptic environments, or (2) negative chemical cues associated with the exposed environments. While the magnitude of settlement on exposed and cryptic surfaces was similar between years, settlement on rubble substrate communities decreased in 2008 (Figure 3.4). Although rubble was collected from the same reef in both years, differences in the specific rubble pieces collected, which can vary dramatically in the community composition, may have led to

the discrepancy between years. Conversely, the limestone plates were conditioned at a similar location on the reef in both years, which likely led to similar communities and subsequently similar settlement responses. However, since the substrate community was not quantified among years, it remains unclear if the discrepancy between years in the magnitude of settlement on rubble communities was due to different community compositions. Regardless, the rubble community type was still favored over the exposed communities, supporting the notion that specific chemical cues were likely lacking from exposed surfaces in shallow environments.

The response to light in this study is consistent with results from Mundy and Babcock (1998), where they found an optimal light intensity or spectral quality range in which different species preferred to settle. In addition, *P. astreoides* (brown morph) is known to actively avoid high levels of UVR when searching for an appropriate settlement location (Gleason et al. 2005). Although this study was focused on the green morph of this species, which is more tolerant of high levels of UVR and often distributed in shallower waters (Gleason 1993), avoidance of UVR may explain the preference of under-surfaces in the high light treatments. Given the importance of light intensity to coral fitness, both as a negative influence at high levels (e.g., photoinhibition, UVR damage) and low levels (e.g., limited energy production), the selection of settlement locations in an optimal light intensity range is likely a critical behavioral adaptation.

Along with the direct negative effects of a sub-optimal light environment, light may also be used as a proxy cue for related environmental characteristics which impact fitness (e.g., sediment load, algal competition). Young and Chia (1984) tested this hypothesis explicitly in phototactic larval ascidians, and found that shaded undersurfaces

provided a refuge from multiple mortality factors, including silt, algal overgrowth, and gastropod predation. Similarly, Babcock and Mundy (1996) found initially high mortality on exposed, sedimented surfaces for recently-settled corals preferring low-light cryptic environments, although these surfaces later supported higher survivorship and growth than cryptic surfaces, presumably due to higher light levels. Mundy and Babcock (2000) suggested that choices for microhabitats based on light may be adapted to maximize this early post-settlement survivorship when corals are most susceptible, and corals can later acclimate to various mortality factors (e.g., sedimentation, competitive overgrowth) once they grow into larger size classes and expand into higher-light environments.

In general, light may not be a reliable cue at the time of settlement, particularly if larvae are released early in the night and settle soon after release, as is possible in many brooding species (Harrison and Wallace 1990). In such cases, larvae may choose a settlement location during dark hours which could become a poor environment with respect to light (e.g., through photoinhibition, UVR damage, or under-saturated light levels). Due to the adaptive significance to find a suitable light environment, larvae would need to find an accurate surrogate for positioning themselves in appropriate environments if light is not directly used. These surrogates could include multiple cues – pressure, orientation, and substrate – which combined could lead to predictable gradients for appropriate light environments. For example, a larva could position itself at shallow depths through vertical migration, and choose an orientation or substrate community at those depths to lead to a predictable light environment. These alternatives need not be exclusive, where both light and alternatives could be acted upon when necessary (i.e.,

light or dark conditions). Despite the potential for these alternatives, larvae of *P. astreoides* were shown to directly respond to the light intensity in this study, and to UVR in Gleason et al. (2005), along with other studies on other coral species which have shown light intensity responses (Maida et al. 1994, Mundy and Babcock 1998).

In this study, light responses occurred under natural light conditions, where larvae experienced both day and night conditions over the four day period. Although an extended time frame was used to provide an even ratio of sunlight to dark conditions, the majority of settlement within the four day period occurred within the first 24 hours (87% and 72% in 2007 and 2008, respectively). Because of this rapid settlement, the choice of time for initiation of the experiment (here, morning hours) could have influenced the results, particularly since larvae are often released in a trickle fashion beginning after sunset (personal observations) and can settle within a few hours. In a pre-competency experiment in which larval settlement was assessed at different times after release (4, 8, 16, 36hrs), significant larval settlement occurred within 4 and 8hrs of release (16.7%±0.02 and 24.9%±0.03, respectively; author's unpublished data). Therefore, if the experiment was initiated at the time of larvae release to simulate natural conditions, a portion of the larvae (up to 25%) may have settled prior to their first exposure to a light gradient, leading to a potential over-estimate of a light intensity effect. This would assume an ideal situation where larvae encounter a preferred substrate during dark conditions, thereby representing a maximal 25% proportion of dark-time settlers. While the majority of larvae (>75%) would remain unsettled until sunrise under this scenario, thereby selecting settlement microhabitats based on light intensity, it remains unknown how much of a consequence this issue had on the estimate of a light intensity effect.

The larval preferences shown in this study corresponded favorably to observed juvenile patterns in natural reef settings (Chapter 2). The smallest-sized juveniles (<0.2cm diameter) were found preferentially on vertical surfaces in the shallow depths (2-5 meters) where recruit surveys were conducted (Figure 3.8), which corresponded to the preferred light intensity range in the experimental analyses presented here (Figure 3.6). While the preference for vertical orientations was not assessed in the experimental analyses, the substrate communities often observed on vertical orientations on the reef more closely resemble the experimental cryptic and rubble communities compared to the experimental exposed surfaces (personal observations). The lack of juveniles on cryptic environments in reef settings was possibly due to the low light intensities present in these environments (Figure 3.6), where only reefs at depths of 0-2m would provide the preferred light range in cryptic habitats. For larger recruits found preferentially on exposed surfaces, the observed shift in orientations with increasing size is possibly due to the growth of recruits into upwards-facing orientations as they age.

In this study, the juvenile orientations with respect to light intensity agree well with results from Edmunds et al. (2004), where they found the majority of juveniles on exposed surfaces at depths greater than 14m (presented as multiple species, with a relatively high abundance of *Porites* spp. in their dataset). At these depths and with a light attenuation value measured from the site where their study was conducted (FKNMS WQMP site 164 from 1995-2001; average k=0.1366), the light intensity on exposed and vertical surfaces was estimated (using eq. 1) to be 265 and 90 μmol quanta m^{-2} sec^{-1}, respectively. These values are both within the preferred light intensity range (Figure 3.5), although the vertical surface represents the lower limit of the preferred light range. In

their study, overall recruitment of *Porites* spp. decreased with depth up to 26m. Because they found no differences in survivorship or growth among depths, their results suggest that deeper areas, where light intensity declined below the experimentally-determined preferred range, may have been less preferred for settlement. Results of the juvenile surveys from the present study as well as those of Edmunds et al. (2004) support the hypothesis that larvae of *P. astreoides* choose appropriate settlement locations based partly on light intensity in natural reef settings.

In general, published coral settlement studies in the past have often focused on single-factor cues (i.e., substrate chemical inducers: Heyward and Negri 1999, Baird et al. 2003, Harrington et al. 2004; light: Babcock and Mundy 1996, 1998; pressure: Stake and Sammarco 2003; but see Raimondi and Morse 2000). While insights gained from these studies have been extremely valuable, an understanding of the responses to and interactions among multiple cues provides a more thorough approach for assessing general behavioral theories in corals and other benthic marine species. Combined with previous evidence demonstrating that larvae of *P. astreoides* actively maintain a preferred water depth based on pressure (Stake and Sammarco 2003), results of this study correspond well to the general settlement theory proposed by Raimondi and Morse (2000). These similarities suggest the possibility of a general settlement behavioral theory in corals marked by: depth choice $\rightarrow$ light/orientation choice $\rightarrow$ surface community/chemistry choice. Species-specific preferences to each cue are expected as a result of niche partitioning, but the overall strategy of consecutive cue responses among corals may remain as a general ancestral trait. Chemosensory responses in coral larvae are known to be widespread and of ancestral origin (Morse et al. 1996), and given this,

the existence of additional, widespread settlement behaviors is also likely. The experimental methodology of Raimondi and Morse (2000) provides an exceptional multi-hypothesis framework by which to test this theory against other species to determine any generalizations that may exist. Validation of a general settlement theory amongst multiple coral species would greatly enhance our understanding of this critical life stage of corals by providing a framework in which to mechanistically assess the recruitment process.

Figures

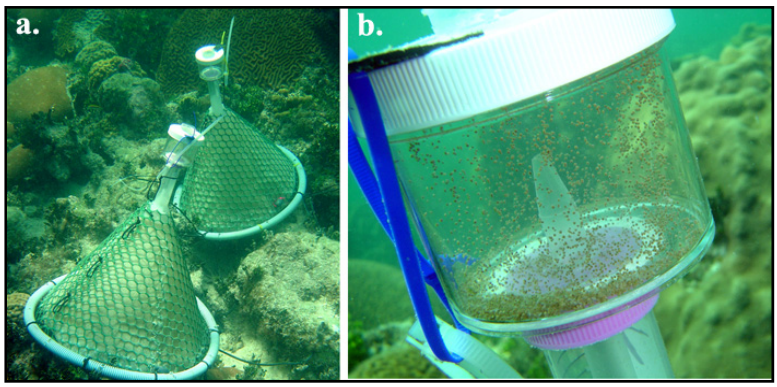

Figure 3.1. (a) Larval trap design (here, shown in field) used for collecting upwards-swimming larvae from adult colonies of *P. astreoides*. (b) Larvae within the larval trap container (each larva roughly 1mm in length).

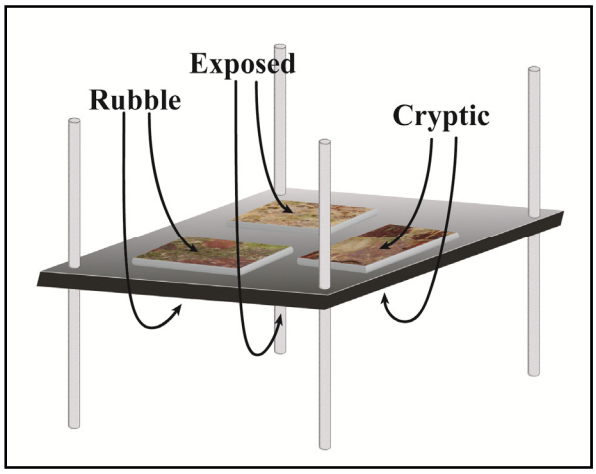

Figure 3.2. Graphic of settlement platform with three substrate community types (rubble, cryptic, exposed) on both upwards- and downwards-facing orientations.

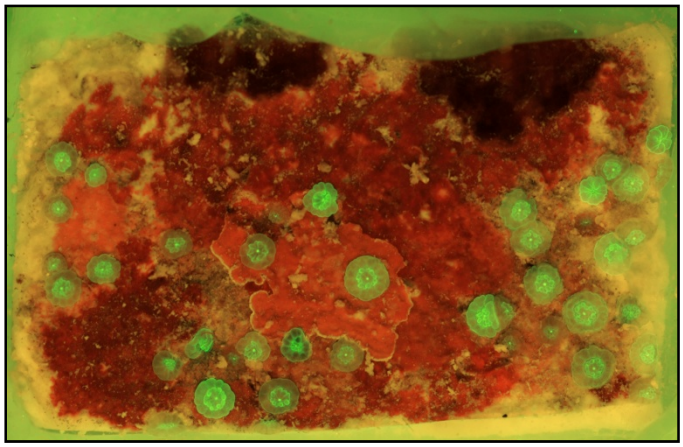

Figure 3.3. Fluorescent-white light photograph of sample substrate chip (here, "rubble" community type).

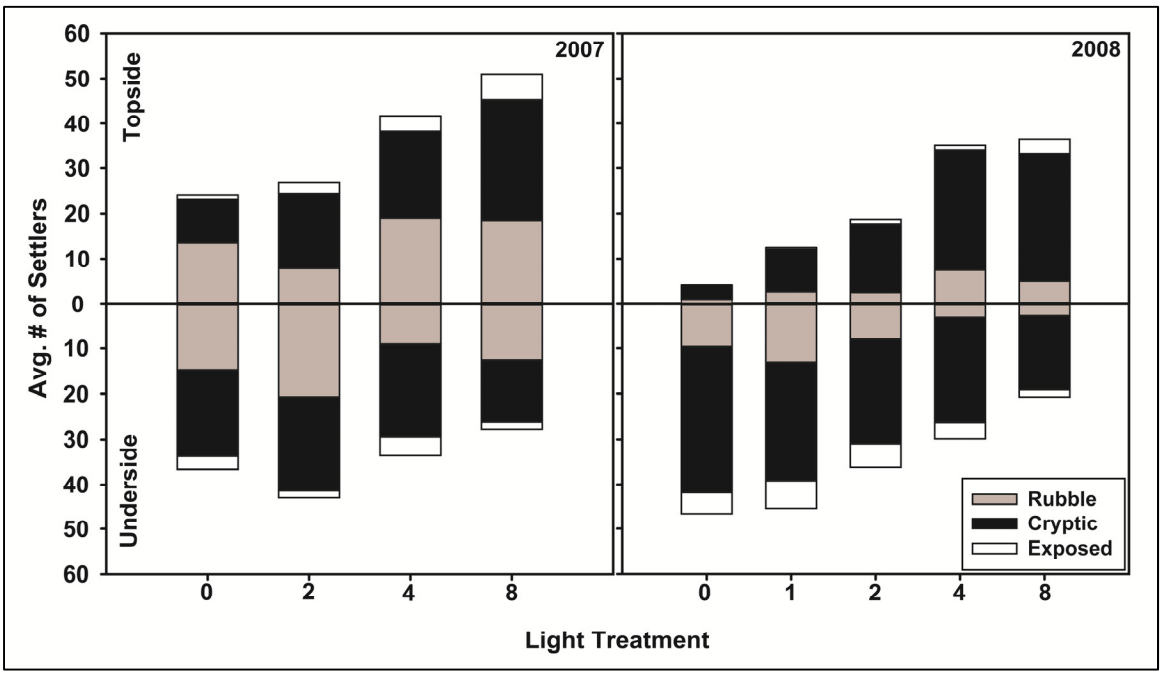

Figure 3.4. Average number of *P. astreoides* settlers per substrate chip on the different substrate community types (rubble, cryptic, exposed; gray, black, and white bars, respectively) on both the topside and underside of settlement platforms (top versus bottom panes) for each light intensity treatment (x-axis) in 2007 and 2008.

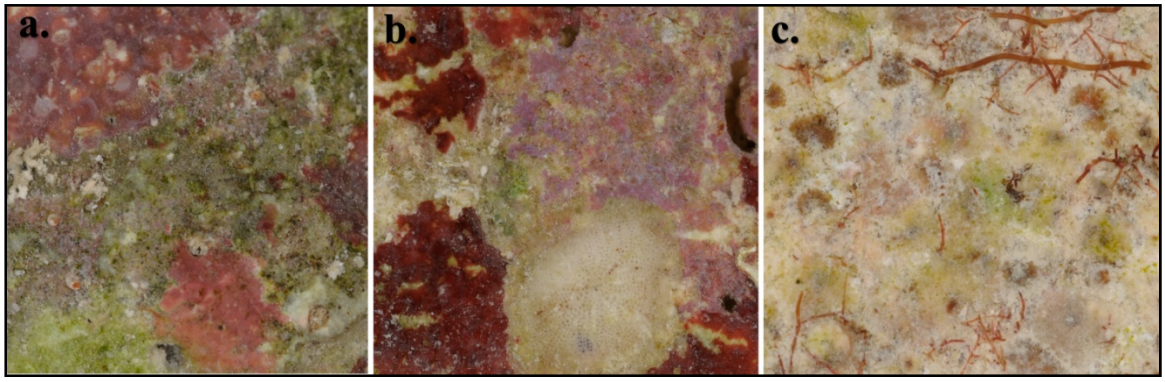

Figure 3.5. Sample photographs of substrate community types for (a) rubble, (b) cryptic, and (c) exposed settlement chips.

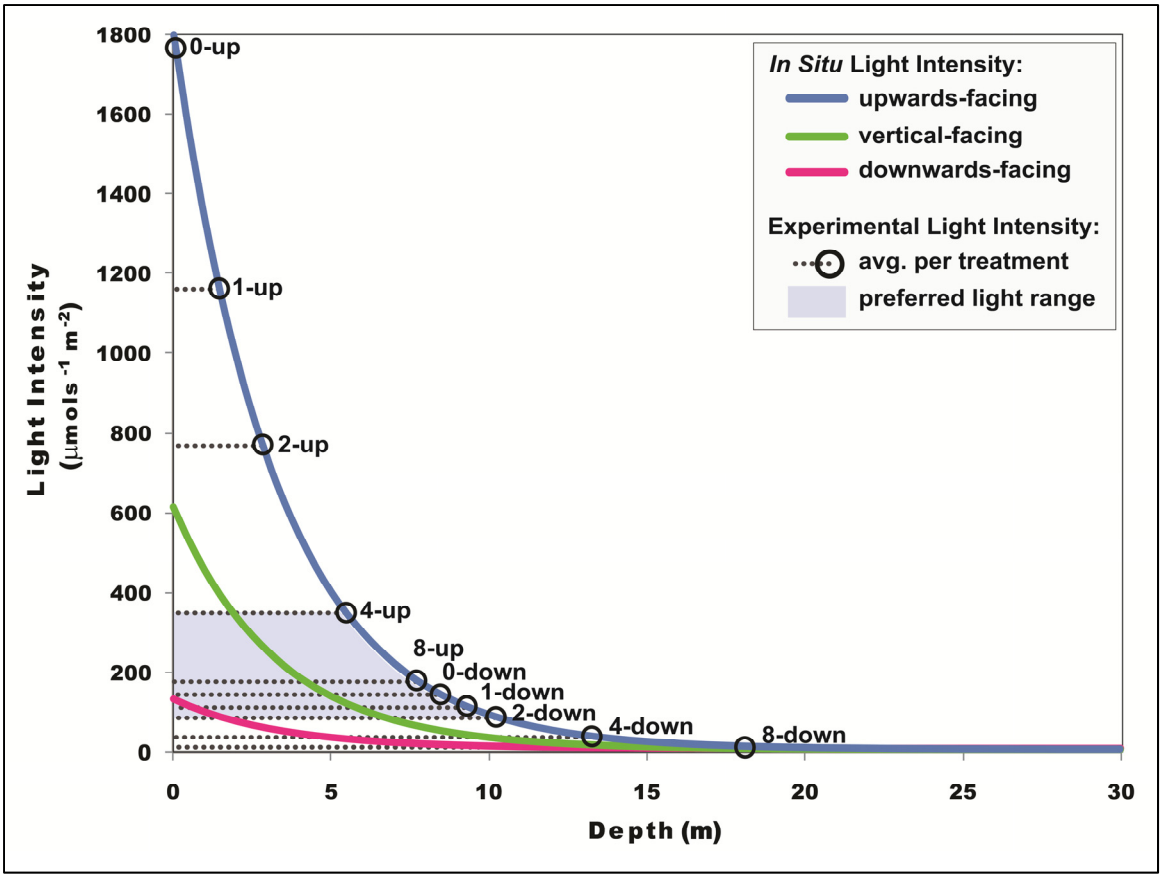

Figure 3.6. Expected settlement orientations across a range of depths based on preferences for light intensity by *P. astreoides*. Here, the area where the orientation-specific light intensity curves (blue, green, and red lines) intersect the preferred light range (solid blue fill) determines the depth at which larvae would prefer that orientation. For example, vertical-facing orientations (green line) are within the preferred light range between 2-6m, while exposed surfaces (blue line) are within the preferred range within 5-10m. The light intensity curves are estimated from the Beer-Lambert Law (see *Methods-Data Analysis* for details). The experimental light values are shown for reference (black dotted lines) with a '*#-orientation*' identifier, where the # refers to the light treatment (0, 1, 2, 4, and 8 shade cloth layers) and the orientation refers to the platform surface (up- versus down-facing).

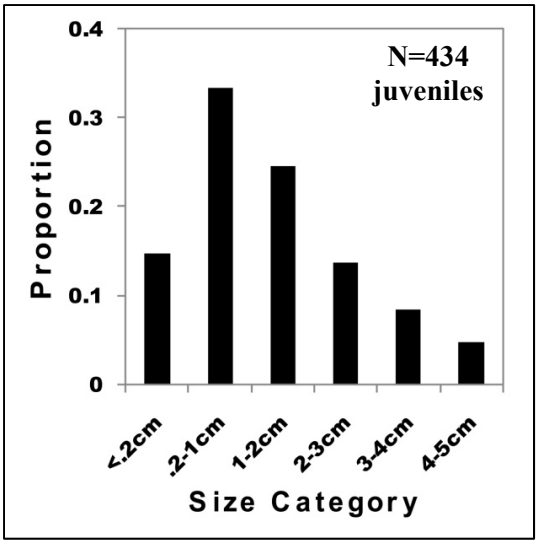

Figure 3.7. Size-frequency distribution of observed recruits among six size categories.

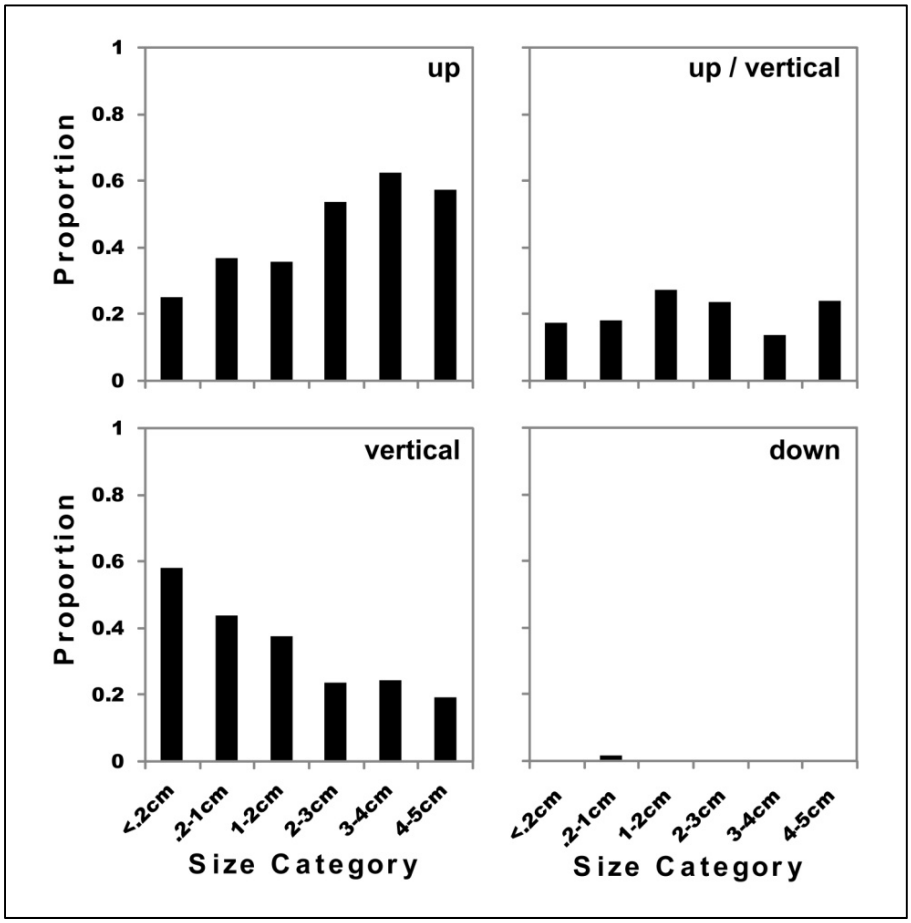

Figure 3.8. Size-frequency distribution of observed recruits for each of four orientations (up, up/vertical, vertical, down). Note, here proportion is calculated relative to the total per size category for all orientations combined to facilitate visual comparisons of size-specific changes among orientations.

Tables

Table 3.1. Location, depth, and number of quadrats for recruitment surveys at each of 12 patch reef sites in Biscayne National Park.

Site	Depth(m)	# quadrats	Latitude	Longitude
S8	3	22	25.41631	-80.14479
S5	3	11	25.42297	-80.15603
TK	4	8	25.38832	-80.16297
S9	4	20	25.39715	-80.15846
M9	2	30	25.49604	-80.14347
CP	4	30	25.50851	-80.12058
NP	4	12	25.36277	-80.16675
S2	3	30	25.44725	-80.15886
BS	3	11	25.48528	-80.14888
MG	5	30	25.46735	-80.12492
M16	3	30	25.44387	-80.17586
M14	3	28	25.46394	-80.16884

Table 3.2. ANCOVA results for the separate settlement analyses in 2007 and 2008.

Year	Factor	df	F value	p value
2007	Substrate	2	72.93	<0.0001
	Orientation	1	1.29	0.2575
	LightIntensity	1	9.46	0.0024
	$LightIntensity^2$	1	11.71	0.0008
	Error	180		
2008	Substrate	2	173.75	<0.0001
	Orientation	1	1.79	0.1822
	LightIntensity	1	72.17	<0.0001
	$LightIntensity^2$	1	80.72	<0.0001
	Error	234		

CHAPTER 4: HABITAT-SPECIFIC AND INDIVIDUAL-LEVEL DRIVERS OF AN EARLY POST-SETTLEMENT SURVIVORSHIP BOTTLENECK IN THE BROODING CORAL, *PORITES ASTREOIDES*

Background

Low rates of early post-settlement survival (EPSS) are often the norm in benthic marine invertebrates and many species of marine fishes, frequently less than 50% after the first few days and less than 1% after the first few months following settlement (reviews in Gosselin and Qian 1997, Almany and Webster 2006). These low rates of survival can serve as population bottlenecks for recruitment (Doherty et al. 2004, Vermeij and Sandin 2008), thereby providing an important regulating force for future population and community dynamics (Gosselin and Qian 1997, Steele and Forrester 2002). Although increasingly more studies are addressing EPSS in corals (Babcock and Mundy 1996, Raimondi and Morse 2000, Harrington et al. 2004, Raymundo and Maypa 2004, Szmant and Miller 2006), many questions remain regarding the processes that drive coral EPSS. This is particularly true for natural reef settings where observational and experimental approaches are logistically challenging due to the microscopic and cryptic nature of recently settled corals (Baird et al. 2005). Because of the importance of the EPSS process for community dynamics, improved understanding of this process in natural reef settings is an essential step for gaining mechanistic insights into recruitment and resilience dynamics of coral communities.

For corals, researchers have typically found low rates of EPSS ranging from zero to a few percent after the first few months following settlement (Babcock and Mundy 1996, Mundy and Babcock 2000, Raymundo and Maypa 2004, Szmant and Miller 2006).

Multiple factors have been shown to influence EPSS, including the substrate composition (Harrington et al. 2004), settlement orientation (Babcock and Mundy 1996, Mundy and Babcock 2000, Szmant and Miller 2006), depth (Raimondi and Morse 2000), and conspecific density (Vermeij and Sandin 2008). Despite this growing body of literature on the factors influencing EPSS, insights into the timing of these mortality factors over the course of days to weeks after settlement have been particularly scarce, as many *in situ* studies monitor survivorship in greater than monthly intervals (e.g., Babcock and Mundy 1996, Raimondi and Morse 2000, Vermeij and Sandin 2008). Given this, higher resolution studies are sorely needed to quantify the timing and magnitude of mortality factors acting in natural reef settings, and to identify potential population bottlenecks acting during the early post-settlement stage. Understanding when bottlenecks ensue is critical, as their occurrence early in the post-settlement stage can influence the sensitivity of future populations to EPSS (Steele and Forrester 2002).

Scientific advancement with respect to coral EPSS in natural settings has been particularly slow due to logistical difficulties in locating and identifying newly-settled individuals, many of which settle in cryptic habitats and are microscopic in size at settlement (Harrison and Wallace 1990). To study EPSS, a number of general approaches have been used: (1) settlement of coral larvae onto experimental structures (often artificial terracotta tiles or quarried limestone plates) within enclosures on the reef (Babcock and Mundy 1996, Babcock and Smith 2000); (2) settlement of larvae onto tiles *ex situ* in laboratory conditions, with later transplantation to the reef (Mundy and Babcock 2000, Raimondi and Morse 2000, Szmant and Miller 2006); (3) indirect EPSS insights from seeding coral larvae directly onto reef substrate for applied restoration

purposes (Raymundo and Maypa 2004; Miller and Szmant 2006, Chapter 5); and (4) observational studies of naturally settled individuals *in situ* (Vermeij 2005, Vermeij and Sandin 2008). While monitoring EPSS of naturally-settled individuals on the reef represents an ideal approach for understanding recruitment dynamics, the current technological ability to assess EPSS through natural surveys is limited, due to the aforementioned logistical challenges. In cases where natural spat are monitored (Vermeij 2005), the number of days or weeks since settlement is currently impossible to determine, thereby precluding the ability to estimate the magnitude of survivorship since settlement. This is especially problematic since low survivorship may be typical within the first few days (Gosselin and Qian 1997). Although experimental approaches forgo this problem by starting with a known number of settlers, they present additional biases when artificial substrates are used (Edmunds et al. 2004), or when the transplantation of initial settlers is prolonged for days to weeks after settlement, thereby underestimating initial mortality.

Because of the global crisis affecting corals and associated reef organisms (Hughes et al. 2007), a fuller understanding of the processes regulating recruitment is critical for the identification of effective management strategies to promote population replenishment and resilience. Specifically, quantification of typical EPSS rates, identification of key mortality factors, and identification of potential population bottlenecks would provide needed insights into the importance of EPSS in structuring future population dynamics. To address these issues, the objectives of this study were to determine the overall magnitude and shape of survivorship during the early post-settlement stage, and to identify some of the primary mechanisms driving EPSS in natural reef settings.

Methods

Larval Collection

Larvae were obtained by collecting and transporting adults of *P. astreoides* from Biscayne National Park to a flow-through seawater system at the University of Miami's RSMAS campus prior to the peak release period in May 2008. Twenty adult colonies (>20cm diameter) were collected five days prior to the new moon in each month, when peak release typically occurs around the new moon from April to June (McGuire 1998). Colonies were submerged within a 750L seawater tank, and a cone-shaped larval collection device (adapted from Brazeau et al. 1998) was placed over each colony to trap upwards-swimming larvae upon release. Larvae were released from colonies during the night and collected in the morning after sunrise on each day. Once collected, larvae were kept in UV-sterilized, 1μm-filtered seawater at concentrations less than 1 per milliliter until the initiation of the experiment, with daily water changes of approximately 75% of the volume. After the peak release period, adult colonies were returned to the reef within one week of collection and attached using either hydraulic cement or Z-Spar Splash Zone epoxy.

Larval Settlement and Translocation

In order to provide a natural settlement substratum, reef rubble pieces were collected from two reef sites in Biscayne National Park, FL USA, where the survivorship studies were conducted (Table 4.1). Rubble pieces were cut into 2x2x0.3cm "chips" using a tile saw, and each chip was randomly allocated to a 20ml container (settlement unit) with 1μm-filtered, UV-sterilized seawater. Twenty-five larvae were added to each

container, and left to settle for 24hrs. All containers were kept indoors under fluorescent lights with approximately 12:12 hours for light:dark. After a majority of individuals had settled within 24hrs, a total of 180 chips were randomly selected to use for the EPSS experiments.

Prior to initiation of the experiment, chips were photographed to map the initial locations, size at settlement, and the substrate on which the larvae settled. Photographs were taken at a single focal length for all chips, using a digital SLR with macro lens and a set of focusing rails. The use of focusing rails was necessary to photograph the individuals at a single focal length, which provided for a standardized size estimate of all photographs by keeping the size of each frame constant. After the chips were photographed, they were attached to a nylon screw using Z-Spar Splash Zone epoxy, and placed in filtered water. Fastening of the nylon screw to the chip provided an attachment point for rapidly removing and reattaching the chips to experimental structures *in situ* (see below).

Once the epoxy was cured (approximately 12hrs), the chips were photographed a second time using a combination of blue wavelength and regular white-light photography, and then transported to each of the two reef sites (Table 4.1). The blue wavelength flash photography was included to capture the fluorescent (GFP) excitation response of corals for easier identification of the coral tissue (Mazel 2005), while the combined white light flash captured the non-fluorescent components of the substrate and accompanying organisms. At each site, a 30m-long transect was randomly laid across the reef structure, and three total chips, randomly pre-assigned, were placed directly under the transect at each meter mark (90 total chips per site), ensuring that the location of chip

attachment was random with respect to the reef habitat. At each meter mark, the three chips were attached to a galvanized wire grid using cord clips (forming a "chip set"), with one chip in each of an upwards-, vertical-, and downwards-facing orientation (see Figure 4.1).

In Situ EPSS Monitoring

EPSS was monitored at nine irregularly-spaced intervals over the course of six months (Table 4.2). Both sites were monitored on the same days, and a higher monitoring frequency was adopted early during the study to ensure an accurate documentation of the shape of the survivorship function during the initial days when mortality was high. Monitoring was done *in situ* using a custom-built photographic dark box into which individual chips were placed and illuminated with a combination of blue wavelength (fluorescence) and standard white light flash (e.g., Figure 4.2). Due to the use of cord clips to attach the nylon screws to the wire grid (Figure 4.1), chips were easily detached from the grid structure, placed into the photographic dark box, and reattached after the photograph was taken. Using this technique, all 90 chips at a site could typically be photographed within a single hour-long dive.

Data Processing

Photographs were assessed to determine the initial spat size, the initial substrate type on which a spat settled, and the survival of each individual spat over the course of the experiment. Only those spat that were fully metamorphosed (flat disk shape with septa ridges evident) were included in the data processing and analyses. Initial settler

size was estimated from the pre-translocation photographs taken at a constant focal length (scale of 4288pixels = 37mm), and was quantified as the longest diameter of each spat, using the freeware ImageJ (http://rsbweb.nih.gov/ij/). The substrate on which each spat settled was determined by assuming the substrate directly surrounding each spat (on mm-scale) was the same as the hidden substrate directly underneath them. Due to lack of expertise in species identification of particular algal groups (crustose coralline, microalgae, and turf), the substrate was recorded at a gross morphological level for the substrates encountered, including: microalgae, solid crustose coralline algae (CCA; i.e., intact structure larger than an individual spat), sparse CCA (i.e., newly-recruited algae, less than a spat's diameter in size), and bare substrate. While other substrate types were present on the chips, these four categories represented the substrates on which larvae predominantly settled.

Data Analyses

Survivorship was assessed as a function of age since settlement, orientation, initial settler size, and settlement substrate, using a logistic-exposure (Shaffer 2004) generalized linear mixed model for each site independently (procedure GLIMMIX, SAS Institute 2006). To deal with irregular monitoring intervals, a custom link function was used (Shaffer 2004):

$$logit(\theta) = Log_e \frac{\theta^{1/t}}{1-\theta^{1/t}} \qquad \text{eq. 1}$$

Here, θ is the probability of survival, and t is the number of days in the monitoring interval for a given observation (i.e., the exposure to mortality risk during that interval). This link function is analogous to the standard logit link with the exception of the exposure parameter t, which serves to standardize survival rates to a daily value (daily survival rate, DSR), thereby facilitating analyses with uneven monitoring intervals (Shaffer 2004). Age was log-transformed (natural log) to improve linearity between age and the linear predictor of the logistic regression. To account for lack of independence among individuals on each chip and each chip set, both the chip and chip set were included as random effects in the mixed model (Millar and Anderson 2004).

For both sites, the logistic-exposure GLMM overestimated mortality for the later time intervals (> 2 weeks). This was primarily due to a sharp transition in the survivorship rates during the first few weeks, and comparatively low sample sizes during the later monitoring periods due to high mortality in the initial weeks. To account for difficulties in fitting a single model that captured the shape of the function during both the initial and later periods, two separate approaches were taken: (1) a weighted GLMM was fit to the data which equalized the contribution of each monitoring interval to overall survivorship; and (2) separate un-weighted analyses were performed for two different periods (first 16 days and remaining six months).

To perform the weighted logistic-exposure GLMM analysis, each observation was weighted (through GLIMMIX's WEIGHT statement) by the quotient of the number of observations in the lowest-sample size monitoring interval (i.e., last interval) over the number of observations in the monitoring interval for a particular observation (weight≤1). This in effect fit a model with similar sample sizes among the different monitoring

intervals, and provided a superior best-fit to the observed data over the full monitoring period compared to an unweighted model (see Results). For the unweighted analyses, a logistic-exposure GLMM was fit separately to the first 16 days and remaining six months, accounting for all predictor variables. While other non-parametric survivorship analyses or "hockey-stick" approaches would forgo the need for a weighted analysis, the logistic-exposure approach was chosen due to its ease in accounting for irregularly-monitored intervals, multiple random factors in a mixed model, and censored data (i.e., not all individuals present each check due to out-of-focus issues, or temporary visual obstructions by macroalgae).

Results

A total of 2,256 spat on 180 substrate chips were transplanted and monitored at the two sites. All individuals that fused with neighboring spat were removed from the analyses because an initial starting size was impossible to assign (see Figure 4.2 for example of fusion), leaving a remainder of 2,151spat on which analyses were performed. The majority of the spat settled directly onto solid CCA, with increasingly fewer settlers on bare, microalgae, and sparse CCA, respectively (Figure 4.3). The size of settled spat was normally distributed with a mean size of 1.13mm and 1.05mm for sites 1 and 2, respectively (Figure 4.3).

The weighted GLMM analyses provided a superior fit to the overall survivorship of individuals over the course of the experiment. Both the observed and estimated survivorship (Figure 4.4, Table 4.2) were less than 15% after approximately one month, with higher survivorship at site 1 than site 2. The weighted GLMM estimated an ending

survivorship of 5.0% and 2.9% after 183 days for sites 1 and 2, respectively, which corresponded relatively well to the observed end survivorship of 4.7% and 1.2%. When un-weighted analyses were performed on the full experimental period, the GLMM overestimated mortality for the later stages, leading to the comparatively low estimates of 0.0025% and $8x10^{-7}$% end survivorship for sites 1 and 2. Age was the only significant predictor of survivorship in the weighted analyses, where survivorship increased as individuals aged.

In the un-weighted analyses for the initial 16 days of the experiment, survivorship increased significantly with both age and initial settler size for both sites, while the substrate type was a significant predictor for site 1, and the orientation was significant for site 2 (Figure 4.5). For site 1, survivorship was highest on both bare substrate and microalgae, while lowest on solid and sparse CCA. At site 2, survivorship was highest in the downwards-facing orientations, and similarly low for both upwards- and vertical-facing orientations (Figure 4.5). In the un-weighted analyses of the later monitoring intervals, only age was a significant predictor, where survivorship continued to increase as individuals grew older.

Discussion

Overall, the observed survivorship was particularly low within the first few days, where only 43% and 23% of individuals on average survived the first 2 days after transplantation to sites 1 and 2, respectively. These high rates of mortality are similar to results obtained from seeding coral larvae onto the reef *in situ* (Chapter 5), where survivorship averaged 54% and 33% after 2 and 5 days, respectively, at the same site as

in this study (site 1). Combined, these studies demonstrate a significant population bottleneck within the first few days after settlement. Strong population bottlenecks such as found here have been shown for settling fishes (Almany and Webster 2006) and benthic marine invertebrates (Gosselin and Qian 1997, Hunt and Scheibling 1997), but the evidence for an EPSS bottleneck in stony corals has remained limited (but see Raymundo and Maypa 2004, Vermeij and Sandin 2008). Most studies assessing coral EPSS *in situ* have monitored individuals at larger monitoring intervals, typically weeks to months (Babcock and Mundy 1996, Babcock and Smith 2000, Raimondi and Morse 2000, Szmant and Miller 2006), and missed the timing associated with this high initial mortality. An exception is that of Raymundo and Maypa (2004) who studied survivorship of corals they seeded on natural reef substrate, and found high but variable mortality (26-100%) after one week in the central Philippines. This study extends upon their work, and suggests that the majority of this mortality may actually occur within the first few days after settlement.

In this study, the EPSS bottleneck suggests that mortality processes operating within the first few days either gradually become less influential, or differ from processes operating later in life. This was evident from the steadily increasing survivorship with age throughout the full monitoring period, with markedly higher mortality during the initial few days. Mortality functions such as this could arise if predators actively prefer recently-settled spat, or if the spat's susceptibility to predation decreases over time (e.g., through formation of the skeleton). Similarly, choice of a poor settlement location (e.g., with respect to substrate competitors) could additionally produce such a survivorship function, if mortality is enhanced and occurs rapidly on poor settlement microhabitats.

For example, many species of CCA can slough off outer cell layers as an anti-fouling strategy, leading to rapid mortality of spat choosing to settle directly on CCA (Harrington et al. 2004). Conversely, overgrowth of recently-settled spat by neighboring competitors (e.g., CCA, macroalgae, bryozoans) is limited by a competitor's growth rate, often taking weeks after settlement to lead to mortality (author's personal observations). In general, when the exact causes of mortality are unknown, as in this study, knowledge of the timing of mortality is especially useful for developing hypotheses regarding the potential mortality factors.

Along with age, initial larval size was an important factor regulating EPSS for the two weeks after settlement for both sites in this study. Surprisingly, initial larval size was also the only significant predictor of EPSS in a separate laboratory study which compared EPSS among substrate community types, substrate orientations, and light intensities over the course of one month (unpublished data; results from weekly monitoring of the chips in Chapter 3's settlement study over a 2 month period). Although the exact mechanism by which size improved EPSS in this study is unknown, the strength and commonness of this effect, particularly when accounting for other invertebrate groups (Moran and Emlet 2001, Marshall and Keough 2003, Marshall and Keough 2004), suggests larval size is an important determinant of early life-stage success in many benthic organisms.

The positive link between initial size and EPSS is likely related to an individual's condition (Pechenik et al. 1998), where larger individuals, presumably with higher energy reserves, may mediate mortality from extraneous factors over these initial days to weeks. For example, higher individual condition may be an important determinant of growth rate, and if larger individuals grow faster, they can reach a less-susceptible size class

(Raymundo and Maypa 2004, Vermeij and Sandin 2008) sooner than smaller individuals, thereby increasing their EPSS. Although growth-rate enhancement due to larval size could partly explain improved EPSS, other unknown, physiological factors related to larval size or condition may also be driving the EPSS effect. For an example in this situation, individual condition could mediate an individual's tolerance to disease vectors or attack from microbes. While the link between larval size and EPSS has been well documented for other benthic invertebrate groups (Pechenik et al. 1998, Marshall et al. 2003, Marshall and Keough 2008), this is the first evidence, to the author's knowledge, supporting this explicit link in corals.

Importantly, the size of recently-released *P. astreoides* larvae often varies more among colony cohorts than within colony cohorts (author's personal observation). Therefore, the initial size at settlement may be partly related to factors affecting the parental colony prior to larval release. Due to the significance of the settler size-EPSS link found at both sites in this study, this high inter-colony variability can have important implications for EPSS, particularly if larval sizes are influenced by the adult colony's condition (i.e., a carry-over effect; McCormick 2006). If a carry-over effect is present where larval size is mediated by the adult's condition, environmental stresses on adults may be important drivers of EPSS. Although some adult stresses are known to directly impact population replenishment through impacts on adult fecundity (Peters 1978, Tomascik 1987, Harrison and Ward 2001), the factors that influence the size of larvae that a colony produces are currently unknown. Because of the potential implications of this link for EPSS, future research efforts should be conducted to assess how larval sizes are influenced by adult condition or stress.

Interestingly, the microhabitat variables -- substrate and orientation -- had different effects on EPSS among the two sites. At site 1, survivorship differed among the settlement substrates, where survivorship was lower on both solid and sparse CCA than either bare or microalgae substrates. These results support those of Harrington et al. (2004), where the majority of CCA species, with the distinct exception of *Titanoderma prototypum*, were poor settlement sites for coral spat due to anti-settlement defense strategies. As demonstrated in the laboratory study of Harrington et al. (2004), low EPSS can result when CCA slough off outer cell layers as a defensive strategy. This strategy is common for many species of CCA, and may have driven the lower survivorship rates on these substrate types found in this study. However, the relative differences in EPSS between CCA (both solid and sparse) and the other substrate types was minimal (approximately 5-10% after the 16 day period; Figure 4.5), suggesting that the prevalence of sloughing events may be relatively minor compared to other unknown mortality factors driving the EPSS dynamics.

Since the substrate chips at site 2 were from the same collection of chips as on site 1, it is unclear why a similar substrate effect was not detected at the second site. This may have been due to the strong orientation effect swamping any substrate effect, where mortality was nearly 15% higher on upwards- and vertical-facing orientations compared to downwards-facing orientations. Importantly, the rates observed on downwards-facing orientations at site 2 were similar to all orientations at site 1 (Figure 4.5), suggesting that the upwards- and vertical-facing surfaces were poor habitats for EPSS at only site 2. This could have resulted from (1) increased photoinhibition on these surfaces due to a shallower depth at site 2 than site 1 (2m at site 2, versus 4m at site 1); (2) increased

sedimentation rates compared to site 1; or (3) some other environmental difference between the sites. Site 2 was a mid-channel patch reef where both turbidity and sedimentation are typically higher than the offshore environment of site 1 (Boyer and Bricenõ 2006). Given this, differences in light intensity among the two sites was likely minimal, since the attenuation coefficient at mid-channel reefs is higher than offshore reefs (Table 4.1), in effect offsetting any potential increases in light intensity at site 2 due to depth.

While a light effect was likely not driving the enhanced mortality at site 2, differences in sedimentation rates between the sites may partly explain the differences in EPSS. Because of the increased turbidity at site 2, sedimentation is expected to impact upwards- and vertical-facing surfaces more so than downwards-facing surfaces. Babcock and Mundy (1996) came to a similar conclusion where they found decreased EPSS rates on upwards-facing surfaces of settlement tiles, and attributed the effects to enhanced sedimentation impacts on these surfaces. Although sedimentation has not been previously shown to directly affect EPSS through experimentation, indirect evidence supports a sedimentation-EPSS link (Babcock and Mundy 1996), and sedimentation is known to affect other early life stages (fertilization, larval survival, and settlement; Gilmour 1999).

The dissimilar effects of microhabitat factors on EPSS among the two sites may be due to the strength of influence detected by the different mortality factors. Notably, the influence of orientation on EPSS was strong at site 2, while the other factors (initial larval size and substrate, excluding age), were less pronounced or not-significant compared to site 1. Given this, orientation-related mortality factors (e.g., sedimentation)

may have overwhelmed the ability to detect the weaker substrate effect at this site. If this is the case, the influence of substrate may still be present, but only detectable if stronger mortality factors (e.g.,, orientation) are limited.

Because the majority of mortality events occurred at a discrete time and thus were not detected with infrequent photographic monitoring, only a limited number of mortality events could be directly attributed to a specific cause. Attributable events were mainly from competitive interactions, predominately by CCA and polycheate tubes, where the competitor slowly overgrew a settled individual during multiple monitoring periods. In these few cases, the overgrowth event was photographed mid-occurrence, with a living polyp half-covered by a competitor. While the exact causes of mortality were not identified for the vast majority of the spat, it is important to frame the magnitude of mortality found in this study with respect to laboratory-measured rates of EPSS. Specifically, EPSS in semi-controlled conditions (i.e., filtered and sterilized water on natural rubble chips and in natural sunlight conditions) can be high, with upwards of 95% of settled individuals surviving the first month after settlement (authors unpublished data; results from weekly monitoring of the chips in Chapter 3's settlement study over a 2 month period). This suggests that the majority of *in situ* mortality within the first month is related to extraneous environmental factors occurring on the reef (e.g., predation, disease, sedimentation), which may be mediated by individual-level properties (e.g., larval size, settlement choice for preferred microhabitats). This notion is additionally supported by Sammarco and Andrews (1989), where they found that post-settlement mortality of naturally-settled recruits decreased with distance from the reef, suggesting that the primary mortality factors may be localized to reef areas. Given these results, the

question still remains: what is actually killing the majority of recently-settled individuals in natural settings?

One of the great challenges remaining in studying the recruitment process of corals is identifying these specific causes of early post-settlement mortality, which is greatly hindered by the logistical difficulties of studying microscopic and cryptic individuals, and the inability to observe temporally-discrete mortality events as they occur. This study found that differences in habitat-specific factors (substrate and orientation) typically influenced the magnitude of EPSS by 5-15%. Similarly, larval size had a relatively small effect on the magnitude of EPSS on the order of 5-10%. Given these small changes in the magnitude of EPSS by these factors, and the discrepancy of measured rates between the field and laboratory (15% versus 95% survival after one month), it is safe to assume that additional mortality factors, not studied here, are driving the magnitude of EPSS in natural conditions. Predation is typically one of the largest factors leading to early post-settlement mortality in reef fishes, where predators can consume more than 50% of recently-settled fish within a few days after settlement (Almany and Webster 2006). For corals, predation by larger organisms (e.g., fishes) does not appear to have a strong impact on EPSS (Chapter 5), but recent evidence suggests that microbes (Cooper et al. 2007, Vermeij and Sandin 2008, Vermeij et al. 2009) can cause extensive and rapid mortality in recently-settled spat. A significant impact on EPSS by micropredation and/or disease vectors could explain the large discrepancy in EPSS magnitude between field and laboratory studies. This is especially likely since most laboratory studies are conducted with filtered and sterilized seawater, thereby limiting these mortality factors in lab settings where they can be quantified. Quantifying

the magnitude of these impacts *in situ* is logistically challenging at best, given the rapidity of microbe consumption and lack of evidence after an event takes place (Cooper et al. 2007).

Despite these challenges, identifying the specific causes of mortality in natural reef settings is a vital step both for understanding the early life stage dynamics of these populations, and for developing applied management strategies to enhance population replenishment (Chapter 5). Knowledge on the magnitude, timing, and factors affecting EPSS rates is critical for building predictive forecasting frameworks to study population and community dynamics (e.g., Mumby 2006). As Steele and Forrester (2002) discuss, population dynamics are most susceptible to fluctuations in EPSS when high mortality leads to a population bottleneck during the initial post-settlement stage. This study found a significant population bottleneck during the first few days after settlement, and the rates of EPSS during this bottleneck period were related to both habitat-specific factors (substrate and orientation), and individual-level factors (initial settler size). However, other unidentified factors drove the magnitude of mortality, and identifying these factors is crucial for advancing our understanding of EPSS. In this era of increasing stressors on coral reef organisms (Hughes et al. 2007), additional intensification of EPSS bottlenecks due to new stresses may have serious implications for the future replenishment and resilience potential of these populations.

Figures

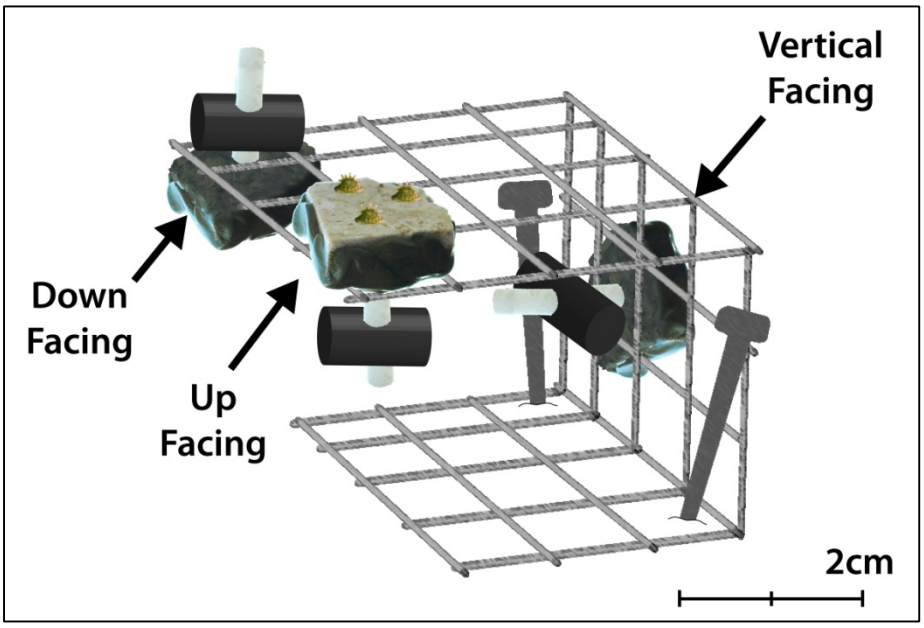

Figure 4.1. Schematic of an *in situ* experimental chip "set" with three settlement chips attached to a galvanized wire grid at three orientations. Chips were epoxied to a nylon screw, and attached to the wire structure using "cord clips", allowing for quick detachment and reattachment for the *in situ* photographic monitoring. Note: spat pictured on the upwards-facing chip are larger than life-size.

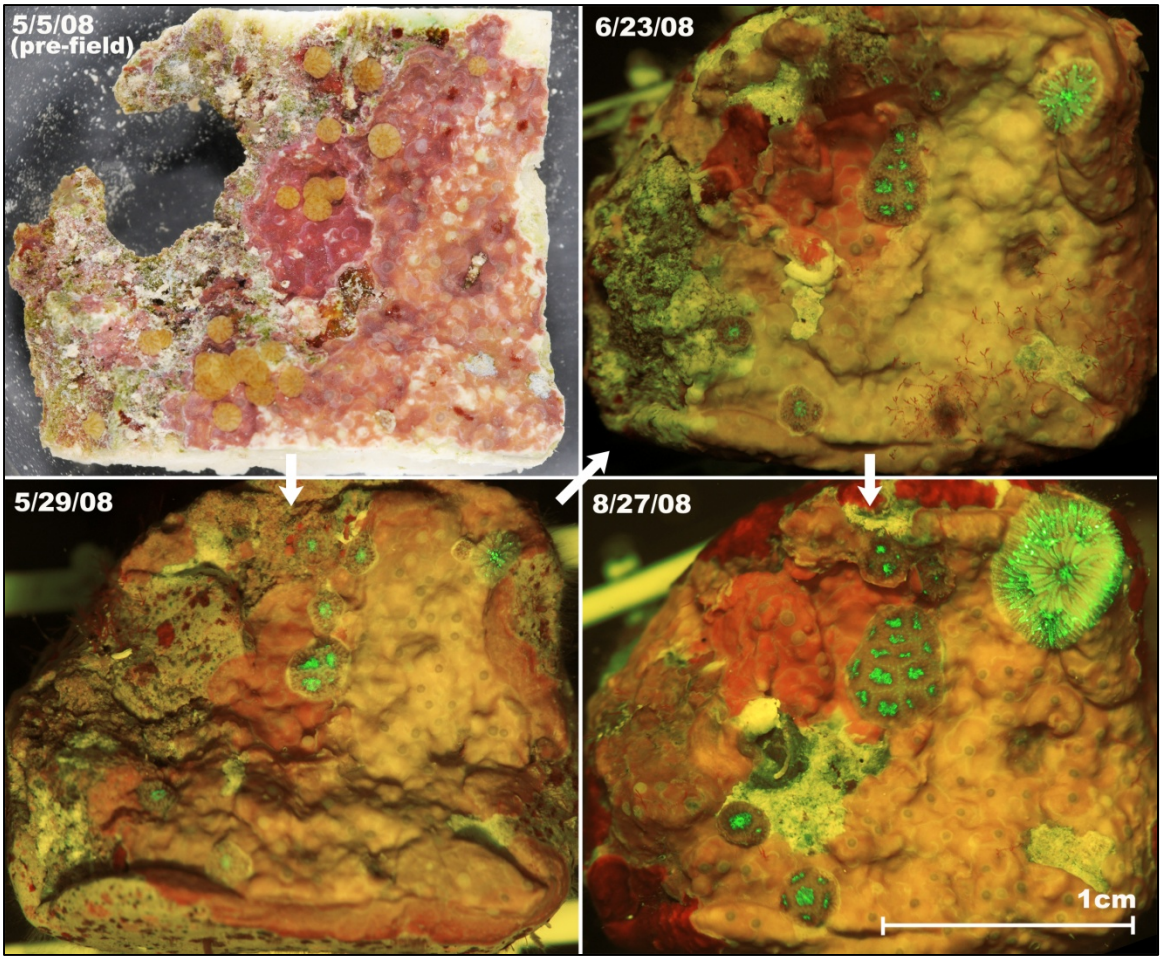

Figure 4.2. An example of the photographic monitoring technique depicting a subset of the picture sequence for a single chip at Site 1. The upper left picture from 5/5/08 was taken using white-light photography prior to placement in the field, while all other photographs were taken *in situ* using the fluorescent/white-light technique. Note: the recruit in the upper right of the *in situ* photographs is an *Agaricia* spp. which recruited to the chip after it was placed in the field on 5/7/08.

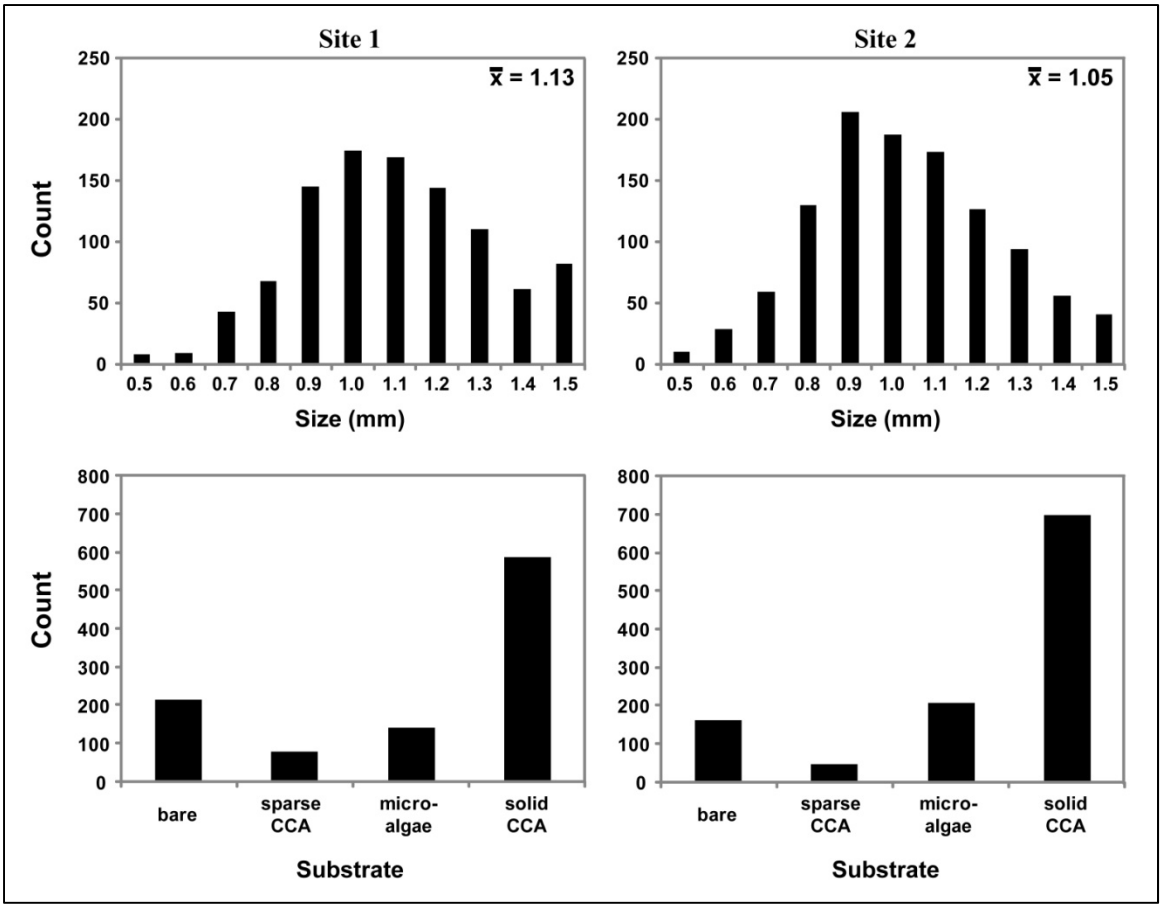

Figure 4.3. Frequency of *Porites astreoides* spat in initial size classes (top row) and settled on each of four substrate classes (bottom row) for site 1 (left column) and site 2 (right column) EPSS experiments.

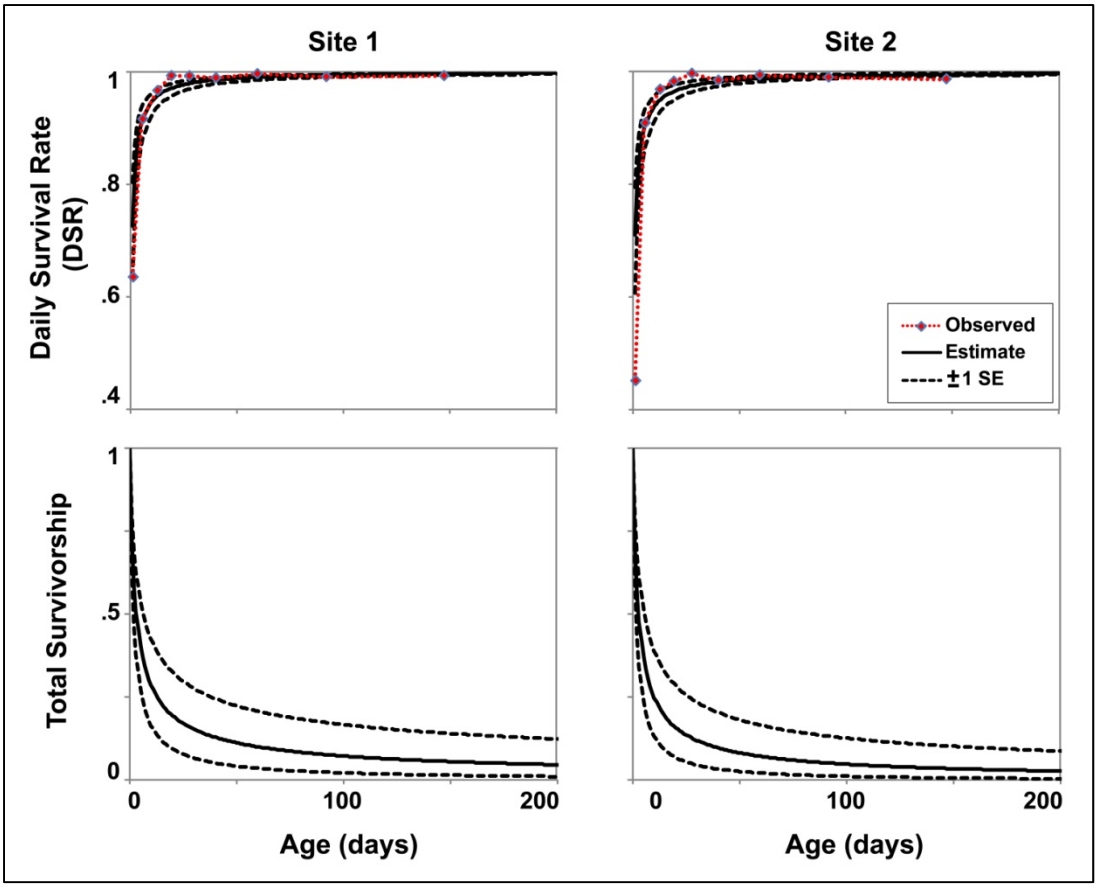

Figure 4.4. Estimated daily survival rates (top row) and corresponding total survivorship (bottom row) for recently settled *Porites astreoides* spat at site 1 (left column) and site 2 (right column). Solid and dotted lines are the estimate and ±1SE, respectively. Estimates produced using a weighted GLMM including all predictor variables at mid-values (initial size = 1.1mm; substrate = microalgae; orientation = downwards- and upwards-facing for site 1 and 2, respectively). Observed DSR denoted by the red dotted line.

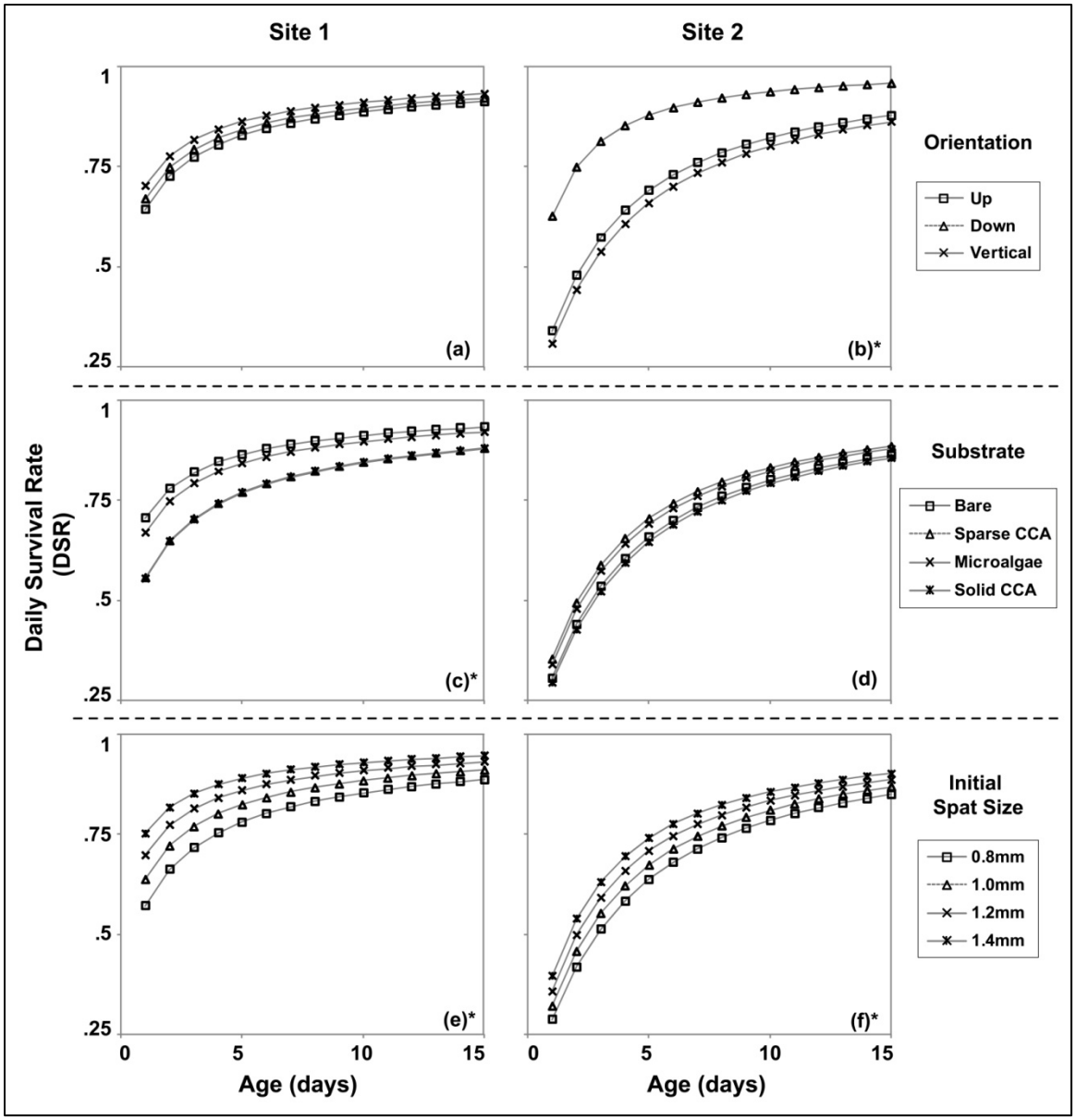

Figure 4.5. Estimated daily survival rates (DSR) for recently settled *Porites astreoides* spat at site 1 (left column) and site 2 (right column) for each predictor variable (top row = orientation; middle row = substrate; bottom row = initial spat size). Estimates produced using an un-weighted GLMM for the first 3 monitoring intervals (0-16 days), at site-specific average or mid-values for remaining predictor variables. Asterisks (*) denote statistically significant effects.

Tables

Table 4.1. Location, depth, habitat type, and average attenuation coefficient, *k*, for the two sites in which survivorship studies were conducted in Biscayne National Park. Attenuation coefficient measurements represent average values from offshore and mid-channel reef sites for Site 1 and Site 2, respectively, from six reef locations in Biscayne National Park over a five year period (1995-2001; Florida Keys National Marine Sanctuary's Water Quality Monitoring Program).

Site	Latitude	Longitude	Depth(m)	*k*
Site 1	25.50851	-80.12058	4	0.206±0.04
Site 2	25.49604	-80.14347	2	0.262±0.03

Table 4.2. Average (±SE) observed interval survival rate (ISR) per chip across all orientations and for each of the three orientations. Daily survival rate calculated as: $DSR = ISR^{1/t}$ where t is the interval length. Chips were translocated to the field on the morning of 5.7.09.

Site	Interval	Interval Days	Total # of Spat	All Orientations		Up-Facing		Vertical-Facing		Down-Facing	
				ISR	DSR	ISR	DSR	ISR	DSR	ISR	DSR
Site 1	1	0-2	1029	0.43±0.04	0.658	0.48±0.07	0.692	0.39±0.07	0.626	0.43±0.06	0.654
	2	2-9	362	0.55±0.05	0.919	0.55±0.09	0.917	0.43±0.09	0.887	0.66±0.07	0.942
	3	9-16	189	0.84±0.04	0.975	0.84±0.08	0.976	0.79±0.10	0.967	0.86±0.06	0.979
	4	16-22	143	0.97±0.01	0.995	0.97±0.03	0.994	0.98±0.01	0.997	0.97±.02	0.995
	5	22-33	135	0.90±0.04	0.991	0.93±0.05	0.994	0.89±0.09	0.989	0.89±0.06	0.989
	6	33-47	123	0.91±0.04	0.993	0.83±0.09	0.987	0.94±0.05	0.996	0.96±0.04	0.997
	7	47-72	109	0.87±0.05	0.995	0.88±0.08	0.995	0.83±0.11	0.993	0.89±0.08	0.995
	8	72-112	100	0.74±0.07	0.992	0.66±0.13	0.990	0.79±0.09	0.994	0.76±0.11	0.993
	9	112-183	68	0.57±0.07	0.992	0.92±0.06	0.999	0.64±0.13	0.994	0.27±0.08	0.981
Site 2	1	0-2	1122	0.23±0.03	0.482	0.17±0.05	0.411	0.13±0.04	0.359	0.39±0.07	0.622
	2	2-9	202	0.58±0.06	0.925	0.39±0.10	0.874	0.81±0.10	0.970	0.58±0.09	0.925
	3	9-16	100	0.85±0.05	0.977	0.81±0.13	0.971	0.80±0.12	0.969	0.91±0.05	0.986
	4	16-22	82	0.93±0.05	0.988	1.00±0.00	1.000	0.89±0.11	0.981	0.92±0.07	0.986
	5	22-33	76	0.98±0.01	0.998	1.00±0.00	1.000	1.00±0.00	1.000	0.96±0.03	0.996
	6	33-47	73	0.86±0.05	0.989	0.86±0.09	0.989	0.88±0.13	0.991	0.85±0.07	0.988
	7	47-72	61	0.84±0.07	0.993	0.71±0.18	0.987	0.86±0.14	0.994	0.89±0.08	0.995
	8	72-112	50	0.68±0.10	0.990	0.17±0.17	0.956	1.00±0.00	1.000	0.75±0.12	0.993
	9	112-183	37	0.38±0.11	0.986	0.40	0.987	0.40±0.24	0.987	0.37±0.14	0.986

Table 4.3. Statistical results for fixed effects of four factors (age, initial size, substrate, and orientation) on early post-settlement survivorship of *Porites astreoides*. *Initial* and *End Periods* refer to the first 16 days and remaining six months, respectively, using an un-weighted GLMM. The *Entire Period* was modeled using a weighted GLMM in order to produce a best-fit estimate over the full study duration.

Site	**Factor**	**Initial Period (*un-weighted*)**		**End Period (*un-weighted*)**		**Entire Period (*weighted*)**	
		F value	**p value**	**F value**	**p value**	**F value**	**p value**
Site 1	log_e(Age)	117.72	<0.0001	5.29	0.0220	164.82	<0.0001
	Initial Size	23.70	<0.0001	0.19	0.6619	2.48	0.1154
	Substrate	4.56	0.0035	0.13	0.9401	0.36	0.7829
	Orientation	0.28	0.7561	0.50	0.6086	0.02	0.9764
Site 2	log_e(Age)	170.66	<0.0001	12.44	0.0005	90.70	<0.0001
	Initial Size	6.06	0.0139	0.21	0.6466	1.20	0.2743
	Substrate	0.55	0.6480	0.72	0.5399	0.37	0.7770
	Orientation	7.57	0.0005	0.08	0.9242	1.16	0.3140

CHAPTER 5: ASSESSING THE EFFICACY OF *IN SITU* CORAL LARVAL SEEDING UNDER HIGH RATES OF EARLY POST-SETTLEMENT MORTALITY

Background

With likely increases in the degradation of coral reefs throughout the upcoming decades (Hoegh-Guldberg et al. 2007, Hughes et al. 2007), only successful and sustained recruitment will ensure the long-term viability of these ecosystems. For degraded reefs with depleted adult stocks, natural recovery may be limited if the supply of larvae from adjacent populations is minimal, particularly for isolated, relatively closed populations experiencing recruitment failure (Hughes et al. 2005). In such cases, active restoration techniques to seed the benthos with new individuals may provide the impetus to replenish the adult stocks, thereby improving the system's own natural potential for regulation and recovery (Edwards and Gomez 2007). Due to the scale of reef degradation globally, a five orders-of-magnitude discrepancy exists between the amount of degraded reef habitat in need of restoration, and the amount that can realistically be restored with current restoration techniques (Edwards 2008). Given this discrepancy, scaling-up techniques are sorely needed, and this necessity presents the next great challenge for the science of reef restoration (Edwards et al. 2008).

In order to effectively scale up current restoration techniques, a primary need is a sustainable source of new individuals for the construction of new source populations. New individuals for restoration can be obtained from multiple sources, including (1) whole colonies or fragments from other reef areas, particularly "corals of opportunity" that would likely die otherwise (Edwards 2008); (2) colonies or fragments from *in situ* or *ex situ* nurseries; or (3) larval collections from planulating or spawning adults (Rinkevich

2005). New and improving techniques are greatly expanding the scale of potential seed stocks, providing 10,000s of new individuals for restoration efforts at relatively low costs (Edwards 2008). Although more research is needed on the efficacy of all techniques for scaling up seed stocks, the use of larvae for seeding denuded substrate is of particular interest due to the relative ease of collecting hundreds of thousands to millions of larvae with minimal negative impacts to the environment, since most of the individuals collected would likely perish otherwise (Richmond 2005).

Collected larvae can be used for restoration approaches by either directly seeding the individuals onto the reef (e.g., Heyward et al. 2002), or settling individuals *ex situ*, rearing the young corals for a period of time, and then transplanting them to the reef (e.g., Raymundo and Maypa 2004). Both approaches have their potential benefits, where *in situ* seeding foregoes the necessity of laboratory rearing, which can become costly and labor intensive depending on the scale of the operation (Raymundo and Maypa 2004). Alternatively, *ex situ* settlement with later transplantation can improve early post-settlement survivorship, which is often extremely low in corals (Raymundo and Maypa 2004, Miller and Szmant 2006) and benthic marine invertebrates in general (Gosselin and Qian 1997).

Several recent studies have demonstrated the potential for seeding coral larvae directly onto the reef (Heyward et al. 2002, Raymundo and Maypa 2004, Miller and Szmant 2006). The most successful seeding study to date has been Heyward et al. (2002), where they artificially increased recruitment rates 100-fold (up to six weeks of age) by seeding millions of larvae collected from spawning slicks onto multiple reef sites of the Great Barrier Reef. Although this procedure provides promise for artificially

enhancing recruitment, the ability to collect similarly large numbers of larval seed stock from spawning slicks in other reef areas is not always possible, and is dependent on spawning predictability, the magnitude of spawning, and weather conditions. In addition, for many reef areas where rehabilitation is needed, low standing adult stocks will decrease the likelihood for the formation of spawning slicks and subsequent collection of large larval stocks. Miller and Szmant (2006) attempted similar larval culturing and seeding approaches to that of Heyward et al. (2002) over multiple years in the Florida Keys, but high mortality rates in the larval cultures inhibited their ability to obtain the high stocking numbers of Heyward et al. (2002). When they were able to successfully seed smaller numbers of competent larvae, they recorded a low recruitment success of 1-2% for *Montastraea faveolata* over 3 months and 3% of *Acropora palmata* over 9 months. Raymundo and Maypa (2004) experienced similar issues with high mortality of seeded individuals, with nearly all recruits dying within six months in multiple seeding attempts.

Given the low survival rates of newly settled corals from the multiple studies where early survivorship was measured (Raymundo and Maypa 2004, Miller and Szmant 2006), high larval stocking densities would be required to make a significant contribution to artificially enhanced recruitment through this direct seeding approach, as in Heyward et al. (2002). As discussed above, this is not always a possibility, and smaller larval stocks collected directly from a few adults may be the norm when attempting to culture spawn. In addition, density-dependent interactions in early post-settlement survivorship (Raimondi and Morse 2000, Vermeij and Sandin 2008) essentially limit the maximum density of individuals that can be seeded in any given seeder apparatus. Therefore, if

direct larval seeding is to be successful compared to other restoration approaches, researchers must identify the conditions under which settlement and post-settlement survival are maximized, and explore potential methods that can enhance the success of reseeding efforts.

To address these issues, the objectives of this study were to (1) assess the potential success of directly seeding larvae on denuded reef substrate as a restoration approach; (2) explore potential strategies to improve direct seeding efforts through caging, choice of substrate community, and the substrate orientation on which to seed; and (3) compare the success of direct seeding to *ex situ* settlement with later transplantation to the reef.

Methods

Larval Collection

Larvae were obtained by collecting and transporting adults of *P. astreoides* from Biscayne National Park to a flow-through seawater system at the University of Miami's RSMAS campus prior to the peak release periods in April and May 2006 and May 2007. Twenty adult colonies (>20cm diameter) were collected five days prior to the new moon in each month, when peak release typically occurs around the new moon from April to June (McGuire 1998). Colonies were submerged within a 750L seawater tank, and a cone-shaped larval collection device (adapted from Brazeau et al. 1998; Figure 5.1) was placed over each colony to trap upwards-swimming larvae upon release. Larvae were released from colonies during the night and collected in the morning after sunrise on each day. Once collected, larvae were kept in UV-sterilized, 1μm-filtered seawater at

concentrations less than 1 per milliliter until the initiation of the experiment, with daily water changes of approximately 75% of the volume. After the peak release period, adult colonies were returned to the reef within one week of collection and attached using either hydraulic cement or Z-Spar Splash Zone epoxy.

Larval Seeding Overview

Once competent to settle, larvae were directly seeded on natural reef substrate using a coral seeder device adapted from Richmond (2005; Figure 5.2), in four separate experiments described below. All seeding experiments were performed at a single reef site (N25.50851, W-80.12058) at 4m depth in Biscayne National Park, FL USA. The seeding device was constructed from a 15cm diameter foam ring "gasket" (3cm wide by 3cm high); a UV transparent acrylic top (UVT Spartech, Clayton, MO; formerly Townsend/Glasflex Plastics) to provide a natural light regime during settlement; 125µm mesh side panels (Sefar Nitex, www.sefar.com); 24oz of lead weight attached to make the device negatively buoyant; and a threaded PVC plug was glued to the mesh to allow the transfer of larvae into the chamber (Figure 5.2a). Seeders were attached with 2½ inch galvanized cut masonry nails to ensure a seal of the foam to the substrate and limit the escape of larvae. Larvae were then injected into each seeder device through the PVC plug using a 10 ounce caulk gun (Figure 5.2b). Approximately 100, 75, and 150 larvae were injected into each seeder during the three experimental study periods (April 2006, May 2006, and May 2007; see below). In 2006, 100 total larvae were planned for each month, but a smaller stock of larvae in May of that year prevented enough for each seeder. In 2007, the total number was increased to 150 to improve the overall settlement

that was found to be low in 2006. Larval numbers were assessed by taking five total 5mL aliquots from the stock container, counting the total density per volume, and allocating the proper volume to each caulk gun for transport to the reef. After the seeding event, the seeders were left attached for 48-72 hours to allow the larvae sufficient time to settle and metamorphose into a flattened and attached coral spat, after which they were removed from the substrate, and all settled larvae were located and mapped. Location and monitoring of recently settled larvae was aided through the use of fluorescence-excitation dive lights (www.nightsea.com), enhancing the detection of species exhibiting a strong fluorescent response (Baird et al. 2005; Figure 5.3). To aid detection, a custom-built dark box was used in combination with the fluorescence-excitation lights to map and monitor individuals during daylight hours. The fate of each settled larvae was monitored at irregularly-spaced intervals over the course of five months. A higher monitoring frequency was adopted early during the separate studies to ensure an accurate documentation of the shape of the survivorship function during the initial days when mortality was high.

Seeding Experiment 1: Effect of Substrate Type and Predator Exclosures

In April and May 2006, 30 total seeders were haphazardly placed along a 30m transect at the reef site. Ten seeders were placed on each of three substrate classes: CCA-dominated, turf-dominated, and a mix of CCA/turf/bare substrate. The substrate classes were subjectively chosen, but quantitative analyses of the substrate community were performed on each location to standardize a substrate effect (see below). In April 2006, 15 additional seeders were intermixed haphazardly along the same transect, five on each

of the three substrate classes, and a cage was placed over each location upon removal of the seeder device. Cages were made from 1cm grid-size galvanized wire to prevent predation of spat by all but the smallest fish or micro-predators. Caging controls were not used in this study due to time restrictions with diving operations and the time-intensive nature of monitoring settled individuals, where 40-50 seeders were the maximum number that could be surveyed in a single day (approximately 1hr per 10 seeders). Although past caging studies of coral reef processes have failed to find caging control effects (e.g., Hughes et al. 2007; authors unpublished data), lack of cage controls in this study prohibited any causative inferences regarding whether a caging effect was due to predation or the cage structure by itself. However, it should be noted that as the purpose of the cage was to test for an improvement on survivorship, the mechanism by which a survivorship increase occurred (e.g., decrease in predation versus effects from the cage structure) was not relevant to the objectives. Cages were left in place for 37 days (first four monitoring intervals). For each of the seeders, a digital photograph was taken of the seeder location prior to attachment of the seeder in order to quantify the percent cover of the substrate types. Photographs were later processed using the point count software CPCe v3.2 (Koehler and Gill 2006).

Seeding Experiment 2: Effect of Substrate Type and Settlement Orientation

In May 2007, the substrate experiment was again repeated as in April and May 2006, with the addition of 20 seeders on vertical surfaces, for a total of 50 total seeders. The additional vertical seeders were placed ten each on a CCA-dominated community and a mixed community on vertical surfaces. Note that a turf-dominated community was

not used due to a general lack of this community type on vertical orientations. After seeders were removed, larvae were mapped as above, and the monitoring sequence initiated. No caging treatment was performed during this experiment as in 2006.

Transplant Experiments

To compare the survival of older recruits to larvae seeded *in situ*, larvae were settled onto substrate chips in the lab in June 2006, reared for four months, and then transplanted to the reef. Larvae were settled by placing 20 larvae each into 15ml containers with small rubble chips, and once the majority of individuals had settled in 1-3 days, the chips were moved to a flow-through flume with filtered seawater. After four months, twelve total chips were attached to a 4x8cm PVC sheet with epoxy, transported to the reef, and attached to the reef with galvanized masonry nails (Figure 5.4). The survivorship of all settled individuals was monitored for approximately one month using fluorescent techniques as described in the seeding studies above.

Data Analyses

Differences in settlement among substrate classes, orientations, and the seeding experiments were tested using single-factor ANOVAs. To compare differences in the substrate composition in the seeding experiments, a permutational multivariate ANOVA with distance matrices was used to test for differences among both the substrate classes (CCA-dominated, turf-dominated, and mixed) and the three seeding experiments (April Substrate, May Substrate, and April Caging), using the *adonis* function in the *vegan* package of the R statistical program.

To assess the influence of substrate type on survivorship, a principal components analysis (PCA) was first performed on the substrate cover data to remove excess covariation among the cover data and standardize the substrate communities among the experiments for comparison. The principal components were then included into the survivorship statistical model as predictor variables (see below). Because turf algae/sediments, CCA, bare substrate, and macroalgae made up the majority of substrate types, the analyses were restricted to these cover types. Due to difficulties in distinguishing sediments from sediment-laden turf algae in the photographs, these two cover types were combined for the analyses.

To assess survivorship as a function of the different predictor variables in each experiment, a logistic-exposure (Shaffer 2004) generalized linear mixed model was fit to the different datasets using the production version of the SAS procedure GLIMMIX (SAS Institute 2006), with the custom link function:

$$g(\theta) = Log_e \frac{\theta^{1/t}}{1-\theta^{1/t}} \qquad \text{eq. 1}$$

Here, *t* is the number of days in the monitoring interval for a given observation, or the exposure to mortality risk during that interval. This link function is analogous to the logit link with the exception of the exposure parameter *t*, which serves to standardize survival rates to a daily value (daily survival rate, DSR), thereby facilitating analyses with uneven monitoring intervals (Shaffer 2004).

The analyses were done separately for each year and each experiment, with the exception of 2007, when high mortality precluded statistical analyses (see Results

below). Survivorship was assessed as a function of substrate, age (considered as the mid-date of the monitoring interval due to the calculation of a daily rate; Shaffer 2004), and caging treatment where appropriate. The substrate effect was assessed by including the two principal component axes explaining the majority of the variability as covariates in the model. For the transplant experiment, only age and experiment type (i.e., transplant vs. seeding) were considered as predictor variables. In all analyses, age was log-transformed (natural log) to improve linearity between age and the linear predictor. To account for psuedoreplication in the form of spatial dependence among individuals in each seeder location or on each chip in the transplant study, the seeder or chip was included as a random effect in the mixed model (Millar and Anderson 2004) for each analysis.

For the caged seeders, two separate analyses were performed: (1) an analysis of survivorship in just the caged seeders with respect to age and substrate (i.e., as above), and (2) a comparison between caged and uncaged seeders, additionally accounting for age and substrate. Here, the uncaged seeders from the first four monitoring intervals of April were used as the comparison, and survivorship was only assessed for a 37 day period when the cages were in place.

In all of the analyses, the logistic-exposure GLMM overestimated mortality for the later time intervals (> 2 weeks). This was primarily due to a sharp transition in the survivorship rates during the first few weeks, and comparatively low samples sizes during the later monitoring periods due to high mortality in the initial weeks. To account for difficulties in fitting a single model, two separate approaches were taken: (1) a weighted GLMM was fit to the data that equalized the contribution of each monitoring

interval to overall survivorship; and (2) separate un-weighted analyses were performed for two different periods (first few monitoring intervals and later monitoring intervals).

To perform the weighted logistic-exposure GLMM analysis, each observation was weighted (through SAS proc GLIMMIX's WEIGHT statement) by the quotient of the number of observations in the lowest sample size monitoring interval (i.e., last interval) over the number of observations in the monitoring interval for a particular observation. This in effect fit a model with similar sample sizes among the different monitoring intervals, and provided a superior best-fit to the observed data over the full monitoring period compared to an unweighted model (see Results).

For the unweighted analyses, a logistic-exposure GLMM was fit to the first few intervals (April caged and uncaged: 0-10 days; May uncaged: 0-8 days; Transplants: 0-15 days), and for the remaining time intervals, accounting for all predictor variables.

Results

The total number of settlers per seeder did not differ among the substrate classes across all seeding experiments ($F=0.42$, $p=0.661$), or the upwards versus vertical orientations in May 2007 ($F=0.15$, $p=0.704$). There was a significant difference in settlement among the four seeding experiments ($F=4.42$, $p=0.006$), with the highest settlement in May 2007 and the lowest in May 2006 (Table 5.1), which corresponded to the total stock of larvae added to each seeder in those months.

In the May 2007 larval seeding experiment, a strong weather event precluded the ability to monitor the settlers for a 17 day period (see Figure 5.5 for average wind speeds). At the end of the 17 day period, all but 1 of 603 mapped settlers had died,

preventing the possibility of statistical analyses on survivorship. Therefore, all statistical results presented below for the seeder survivorship are restricted to 2006.

The three substrate categories on which larvae were seeded in 2006 varied markedly in their community composition ($F=31.5$, $p<0.005$; Figure 5.6, Table 5.1), ranging from nearly 100% cover of turf algae and sediments to 100% cover of crustose corraline algae (CCA). When comparing the April and May communities in 2006, there was generally lower cover of CCA, higher cover of turf/sediments, and higher cover of bare substrate in May than April (Figure 5.7, Table 5.1), although these differences were non-significant ($F=2.69$, $p=0.055$; Figure 5.7).

For assessing the effects of substrate type on survivorship, the first and second axes of the principal components analysis explained 86% and 10% of the variability in the substrate communities, respectively. Here, the first axis corresponded to higher cover of turf algae and sediments, and lower cover of CCA; while the second axis corresponded to higher cover of bare substrate, lower cover of CCA, and lower cover of turf and sediments (Table 5.2). Since the two axes explained 96% of the variability combined, they were both included in the survivorship analyses for the seeding experiments.

The weighted GLMM analyses provided a superior fit to the overall survivorship of individuals over the course of the experiment. Overall, both the observed (Table 5.3) and estimated survivorship (Figure 5.8) were less than 10% after approximately one month in the uncaged seeding experiments, and 15% after one month in the caged seeders of April. The weighted GLMM estimated an ending survivorship of 0.4 and 1.2% after 149 and 120 days for the April and May uncaged seeding experiments, respectively, which corresponded well to the observed end survivorship of 1.0 and 1.1%, respectively.

When un-weighted analyses were performed on the full experimental period, the GLMM overestimated mortality for the later stages, leading to the comparatively low estimates of 0.06 and 0.004% end survivorship, respectively. Age was a significant predictor of survivorship in the weighted analyses, while substrate did not have a significant effect in any of the analyses.

In the un-weighted analyses of the different monitoring periods, the substrate community did not have a marked effect on survivorship, and only the second PCA axis in the May experiment was significant for the initial monitoring period (Figure 5.9; Table 5.4). Here, survivorship was negatively related to the PCA axis 2, suggesting that areas with greater coverage of bare substrate (Table 5.2) had lower survivorship in the May experiment, but only for the first eight days. This trend was similar in the April caged experiment (Figure 5.9) but not significant (Table 5.4). In nearly all of the analyses of the initial monitoring periods, age was a significant predictor of survivorship, while it was not significant in the later monitoring periods. Although the average survivorship of caged seeder locations was roughly 5% greater than uncaged locations, this effect was not statistically significant (Table 5.4).

Finally, the estimated average survivorship of four-month old transplanted individuals was nearly 50% after one month (Figure 5.10), which was significantly greater than the estimated survivorship of the seeded individuals for both the initial and final periods (Figure 5.10, Table 5.4).

Discussion

Overall, survivorship in the seeding experiments was markedly low, with only a few individuals surviving after the three months in which they were first seeded. The majority of individuals (>75%) died within the first week, as is typical for some corals (Raymundo and Maypa 2004, Chapter 4) and for many marine benthic invertebrates (Gosselin and Qian 1997). In general, the seeding enhancement strategies (caging, choice of substrate community, or orientation) did little to improve the survivorship of larvae in the seeding experiments, suggesting that larval seeding as a restoration technique may be an inefficient use of resources, especially given the resource intensive nature of this approach.

If larval seeding is to become a useful restoration approach, either (1) techniques must be developed that enhance survivorship, or (2) large larval stocks must be obtained to settle directly on the reef. Results of this study showed that neither substrate type, orientation, nor caging dramatically improved survivorship rates. In general, young coral spat placed on the reef experienced high mortality rates, while those kept in lab settings usually had comparably low mortality rates (upwards of 95% survival over the first month in the lab; author's unpublished data). This suggests that the main mortality forces at play in natural settings are those not necessarily associated with the substrate type, the orientation, or caging treatments (Chapter 4). Such factors could include micropredators, where recent studies have found mortality of recently-settled spat by both ciliates and microbial associations (Cooper et al. 2007, Vermeij and Sandin 2008). However, identifying the extent of mortality in natural settings by such factors is challenging at best, due to logistical difficulties in monitoring individuals at temporal frequencies

capable of observing rapid mortality events in progress. Overall, lack of understanding regarding the full host of mortality factors for recently settled spat is one of the primary limitations with identifying appropriate methods to enhance survivorship in natural settings for applied restoration goals.

Simply increasing the number of larvae per seeding apparatus, whether it be small seeder devices (e.g., Raymundo and Maypa 2004, this study) or larger tent structures (e.g., Heyward et al. 2002) may prove problematic due to density-dependent mortality at high densities (e.g., Raimondi and Morse 2000, Chapter 2). The combination of high mortality rates and density dependent interactions may thereby limit the ability to improve larval seeding effectiveness by directly increasing the seeding stock. Tenting approaches such as those of Heyward et al. (2002) and Miller and Szmant (2006) may be preferable to small seeding devices, where risks of mortality can be spread over larger reef areas per tent. However, the high mortality rates still require a significant larval stock to ensure some individuals will survive even at low densities, and obtaining large stocks in degraded systems is not always a possibility. In addition, the total numbers of tents that can be seeded during any given restoration attempt is limited, and choice of a poor habitat area may increase the risk of failure when only a few tents are used. While a greater number of small seeders can spread the risk among more habitat areas at a single reef, the small size limits the success per seeder. Thus, there is a trade-off between approaches, where limits to the potential effectiveness are present in both.

During the May 2007 seeding event, all but a single individual on both upwards and vertical facing surfaces died within the 17 period. Since a shorter interval was not monitored during this period due to the weather, it is unclear whether the rate of mortality

was the same among both surfaces or among the substrate types. For instance, vertical surfaces hypothetically could have had a higher survivorship than upper surfaces, but with higher than normal mortality overall leading to complete loss on both surfaces within the 17 day period. Differences in early post-settlement survivorship among settlement orientations have been shown in the past (Babcock and Mundy 1996, Mundy and Babcock 2000), although these differences can be both age-specific (Mundy and Babcock 2000) and site-specific (Chapter 4). Irrespective of any potential differences in mortality among the orientations during this period, the total mortality of individuals on both surfaces suggests that choice of substrate orientation does not lead to substantially elevated survivorship when using larval seeding as a restoration approach, at least in such situations as those studied here.

The exact cause of higher mortality in the 2007 seeding experiment compared to 2006 is unknown, but the corresponding strong weather event (Figure 5.5) suggests a possible physical influence for this mortality in part. Approximately 5-10% of individuals survived after 17 days in the 2006 experiments (Figure 5.8), while only 0.17% survived in 2007. Qualitatively, visibility at this site was the poorest noted in three years on the day the seeder locations were first monitored after the 17 day period (personal observation), which was especially abnormal since visibility is often favorable at this offshore site. Given the poor visibility, sedimentation rates to the substrate were likely enhanced for an extended time during this monitoring interval, potentially resulting in the increased mortality compared to the 2006 experiments. Sedimentation is known to negatively impact multiple early life stages in corals (Gilmour 1999), including the early post-settlement survivorship of corals (Babcock and Smith 2000). While the exact cause

of mortality remains undetermined, this mortality event exemplifies the potential risks and variability associated with attempting larval seeding for restoration purposes.

Overall, the choice of substrate community type had minor effects on survivorship in the 2006 seeding experiments. The single significant effect was for the PCA axis 2 in May 2006, where survivorship was decreased on areas that had a higher cover of bare substrate compared to either CCA or turf algae (Figure 5.9; see factor loading for PCA axis 2 in Table 5.2). Lack of a significant substrate effect in the April experiments could have been partly attributed to the marginally different substrate communities between April and May, where the April seeder locations had less bare substrate than the May experiments (Table 5.2, Figure 5.7). This result in May was counter to *a priori* expectations, because past studies have found reduced survivorship on many species of crustose corraline algae due to sloughing or overgrowth (Harrington et al. 2004, Chapter 4), and by sedimentation associated with turf algae microhabitats (Babcock and Smith 2000). One conceivable explanation could be to due to higher exposure to visually-oriented predators on bare surfaces (e.g., small fish) that are able to locate individuals on these surfaces more easily than in a turf algae matrix or on CCA communities.

While larger recruits with established skeletons may be actively avoided by grazers or predators (Birkeland 1977), recently-settled spat do not have physical defenses against predation, and given their high lipid content, may present a rich food source. It should be noted that larvae were seeded on exposed surfaces with relatively few cracks or holes in the substrate in order to effectively map and monitor the individuals, and create a seal of the seeder to the substrate so that larvae did not escape from seeders. Often spat were found settled at the bases of small rises, suggesting an active choice for complex

microtopography. If the experimental choice of relatively exposed surfaces for seeding influenced survivorship through an increase in predation, the survivorship rates estimated here may be underestimates of typical rates found for naturally settling larvae that have an option to choose more cryptic areas. While this option is possible, separate studies on this species typically fail to find recruits on cryptic surfaces in natural reef settings (e.g., holes, undersurfaces; Edmunds et al. 2004, Chapter 2), and in general, the surfaces seeded in this study are representative of where recruits are found in natural reef settings.

In all the experiments, the age of the settlers significantly impacted survivorship, where survivorship improved with age in a nonlinear, saturating function. The transplant experiment explicitly tested this notion by comparing the survivorship of four-month old individuals to recently settled spat. When comparing the overall survival rates, the recruit transplants had nearly a 50% higher survival rate after 1 month than the younger seeded larvae. This result has an important implication for the use of seeding efforts in general: the longer that newly settled spat can be kept in controlled laboratory conditions until transplanted to the reef, the greater the likelihood that those individuals will survive. Not only can overall survivorship be improved in lab settings, but acute natural disturbances can be avoided (e.g., weather events as in the 2007 experiment, disease outbreaks, bleaching episodes) that may prove especially detrimental to recent settlers. Raymundo and Maypa (2004) came to a similar conclusion with their work on *Pocillopora* in the Pacific, and found that individuals reaching a 10mm size class have a much greater chance of survival than those settled directly on the reef. A key requirement for using transplants of corals settled *ex situ* is maintaining high survivorship in controlled laboratory settings or nurseries until transplantation. Recent studies have

greatly improved upon this by developing techniques to settle individuals in mass cultures within controlled settings, and then retain them in floating cage structures *in situ* until they reach appropriate sizes (Omori 2005, Edwards 2008). These techniques have proven highly effective, providing 10,000s of new individuals at costs less than $1USD per individual (Edwards 2008).

In conclusion, results of this study suggest that the success of *in situ* larval seeding for restoration goals is currently minimal due to high post-settlement mortality, and the lack of known strategies to significantly enhance survivorship *in situ*. However, the ability to enhance survivorship for *in situ* seeding cannot be ruled out, and identifying the primary mortality factors leading to low survivorship within the first 1-2 weeks after settlement will improve the likelihood of discovering appropriate strategies. Techniques to enhance survivorship in this study proved ineffective, and entire cohorts of individuals were susceptible to high mortality. Given the limitations of *in situ* approaches, out-planting of laboratory reared individuals after a few months period provides the most effective utilization of resources for direct restoration actions given our current knowledge of the early life-stage dynamics of corals.

Figures

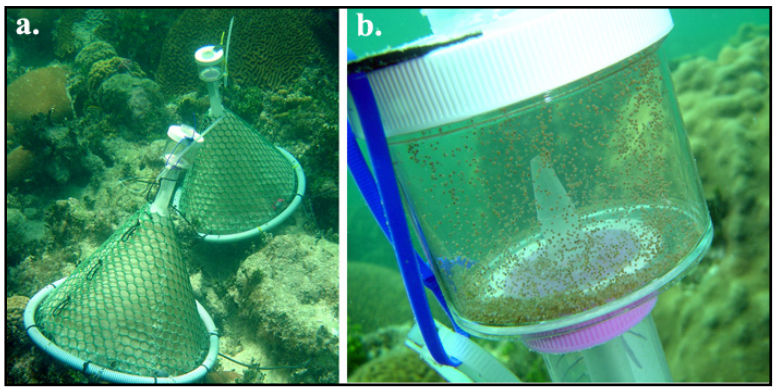

Figure 5.1. (a) Larval trap design (here, shown in field) used for collecting upwards-swimming larvae from adult colonies of *P. astreoides*. (b) Larvae within the larval trap container (roughly 1mm in length).

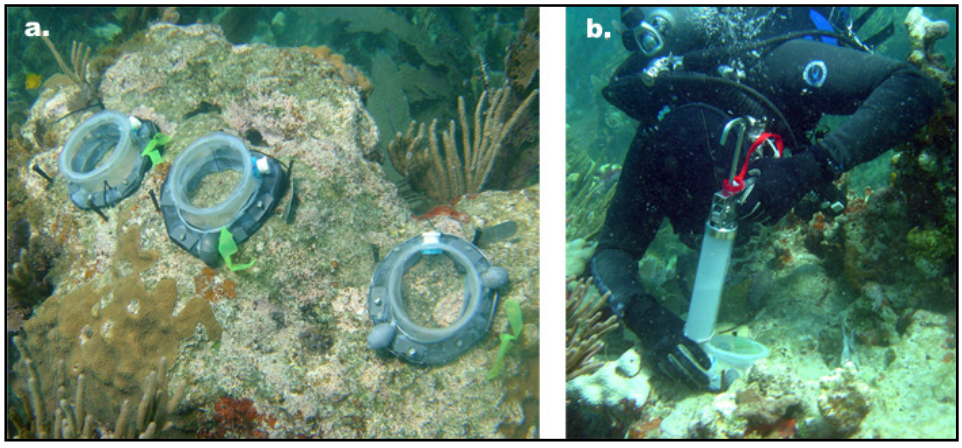

Figure 5.2. (a) Coral seeder device used to settle larvae onto denuded areas of reef substrate. (b) Insertion of larvae into coral seeder device using a 10 ounce caulk gun and cartridge.

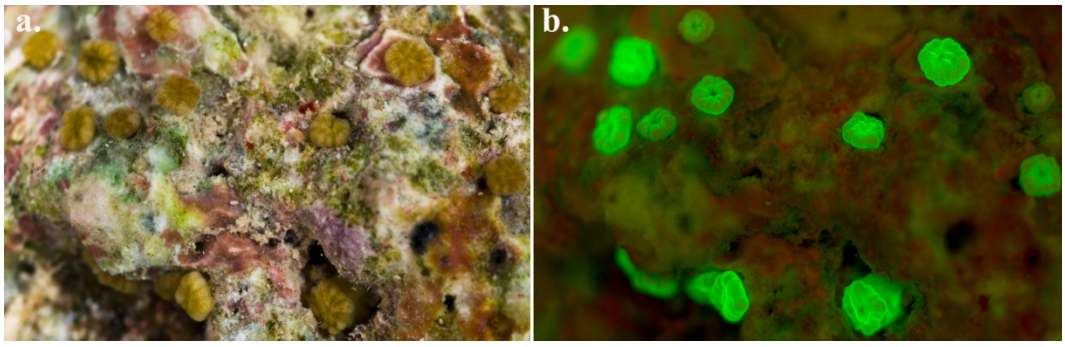

Figure 5.3. Comparison of recently settled *Porites astreoides* spat under (a) white light, and (b) fluorescence-excitation light (here, blue-spectrum wavelength).

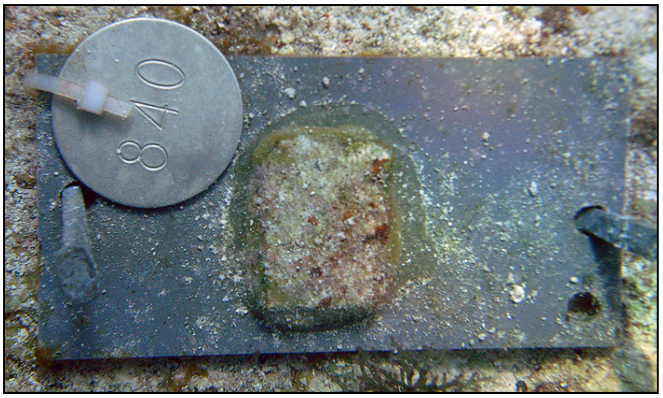

Figure 5.4. Example of substrate chip with recruit transplants attached to the reef as used in the Transplant experiment.

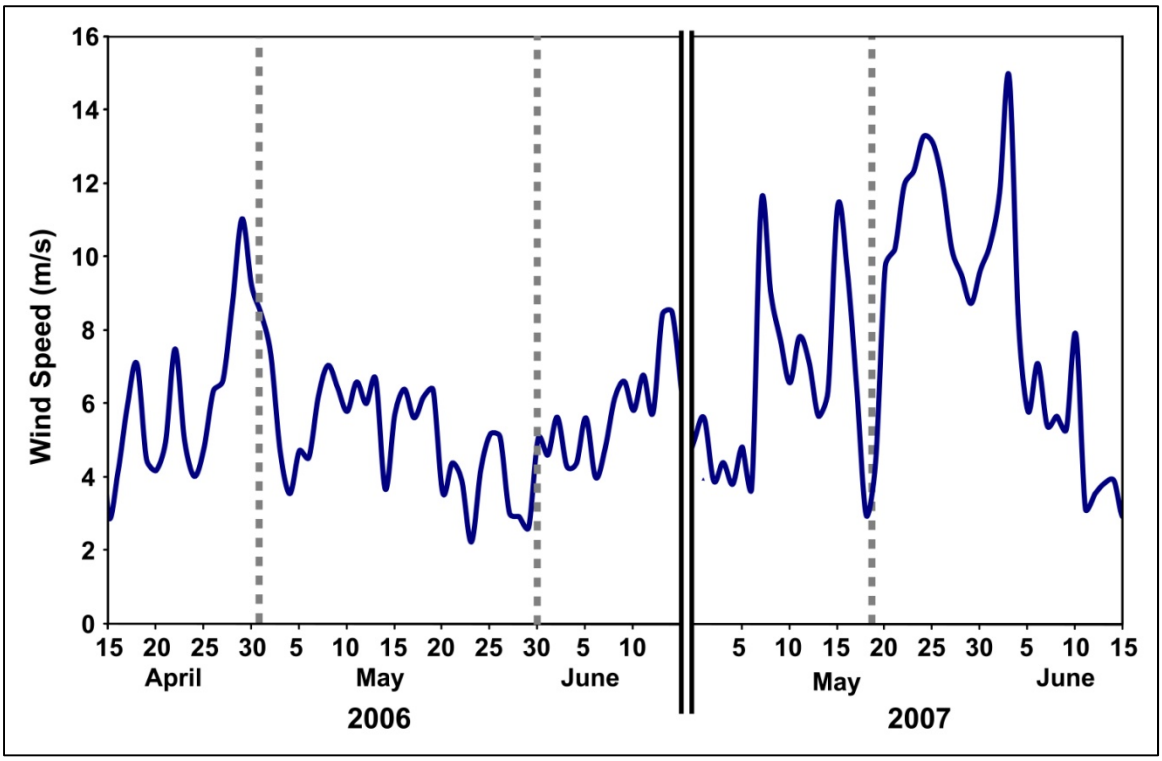

Figure 5.5. Wind speed observations during the larval seeding experiments (data from http://www.ndbc.noaa.gov/ site FWY1, approximately 10km north of the study site). Initiation of the seeding experiments (i.e., day 0 mapping) is denoted by the vertical dotted lines.

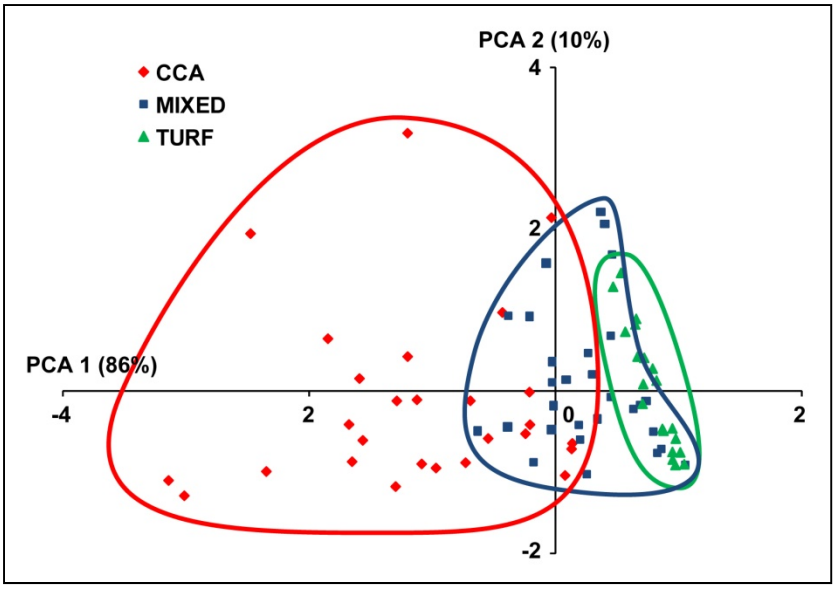

Figure 5.6. Principal components analysis of the substrate communities among the three substrate categories in the direct larval seeding experiments.

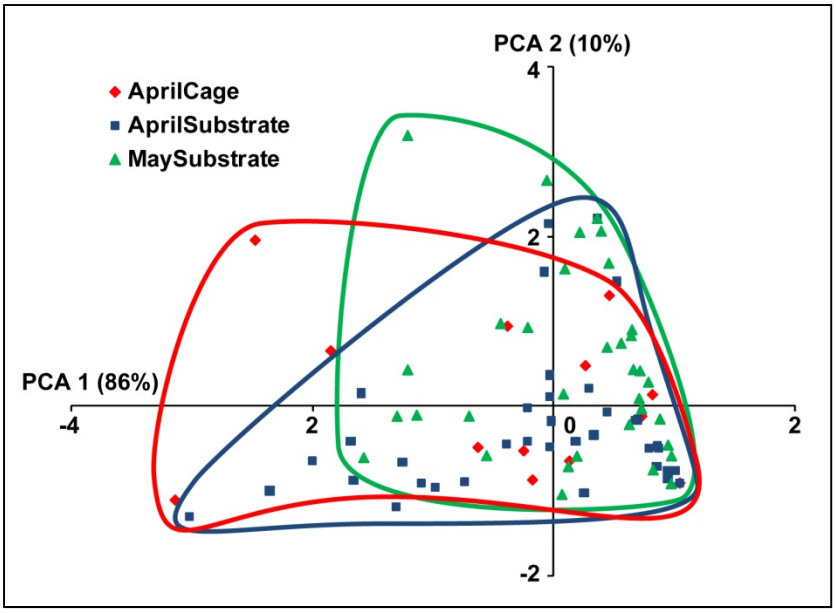

Figure 5.7. Principal components analysis of the substrate communities among the three direct larval seeding experiments in 2006.

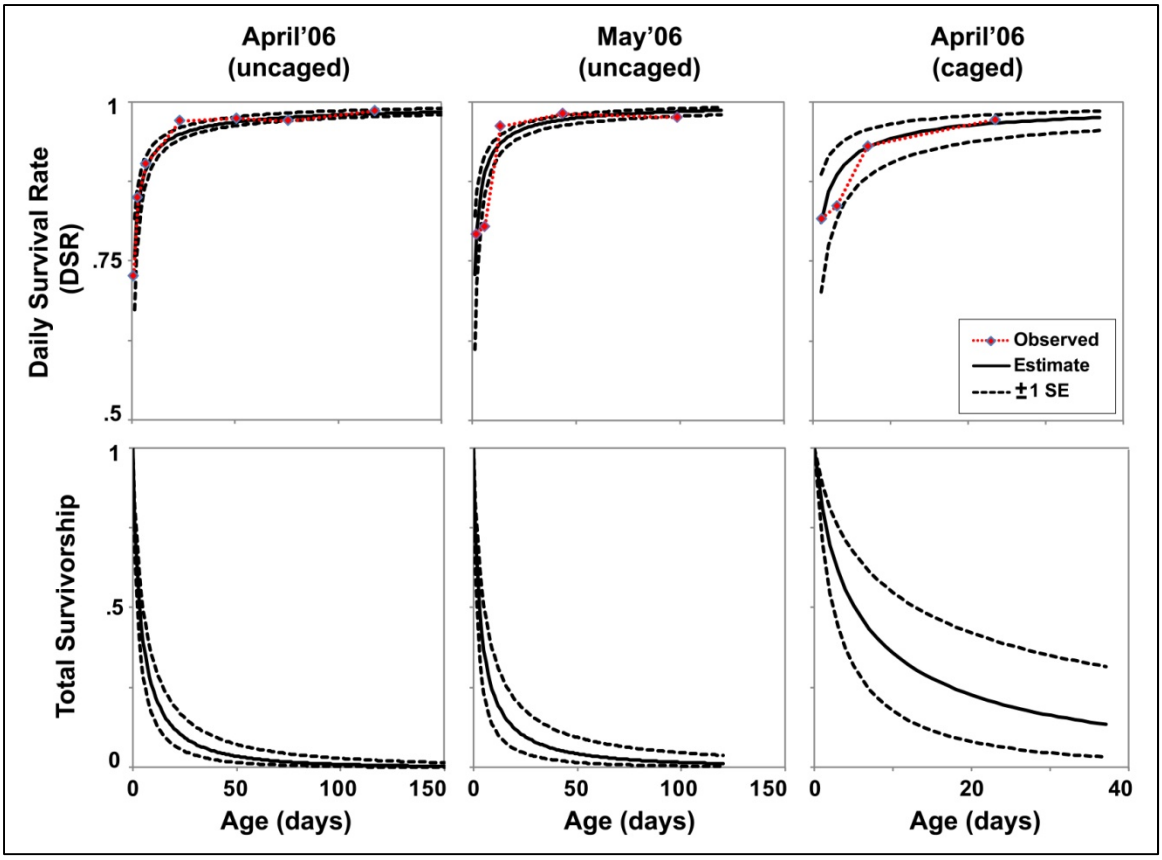

Figure 5.8. Estimated daily survival rates (top row) and corresponding total survivorship (bottom row) for recently settled *P. astreoides* spat in the three seeding experiments (columns). Estimates produced using a weighted GLMM with experiment-specific averages of the substrate principal components axes. Observed DSR denoted by the red dotted line, and calculated as $DSR = ISR^{1/t}$, where t is the interval length, and ISR is the survivorship during the monitoring interval (i.e., Table 5.3).

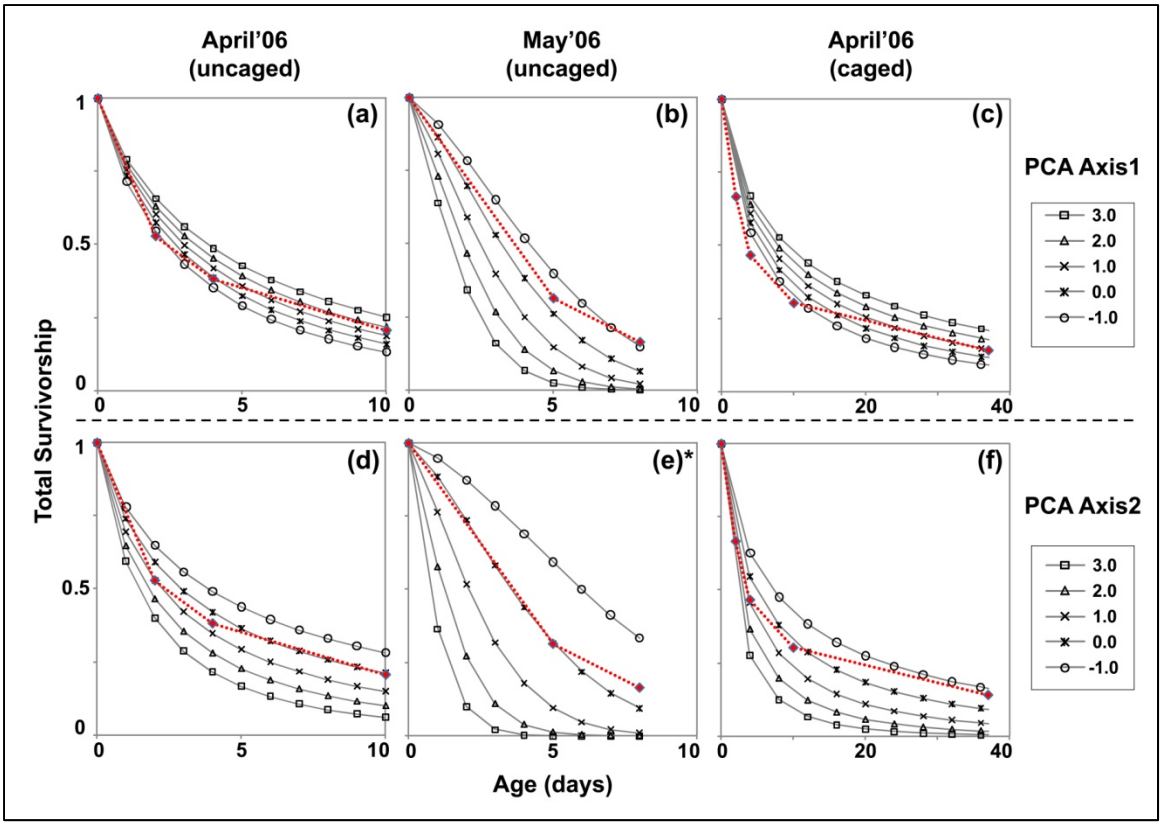

Figure 5.9. Estimated survivorship for recently settled *P. astreoides* spat in the three seeding experiments (columns) for the two substrate PCA axes (rows). Estimates produced using an un-weighted GLMM for the first three monitoring intervals in the un-caged seeding experiments (left and middle columns), and for the full monitoring period for the caged analysis (right column). Total number of observed surviving individuals is denoted by the red dotted line. Asterisks (*) denote statistically significant effects.

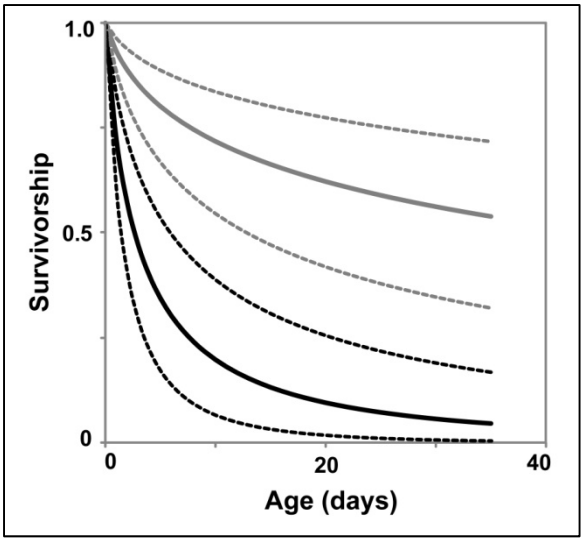

Figure 5.10. Comparison of estimated survivorship functions (±SE) for the seeding experiments (April and May 2006 uncaged experiments combined; black lines) and four-month old transplants (gray lines). Estimates produced using a weighted GLMM.

Tables

Table 5.1. Average (±SE) number of initial settlers and percent cover of substrate types for the three substrate categories on which larvae were seeded.

Experiment	Substrate Category	#Settlers	Substrate Cover (%)			
			CCA	Turf/Seds	Macro	Bare
April'06	CCA	8.9±2.9	51.4±5.5	42.2±5.6	0.9±0.4	2.8±1.3
(uncaged)	Mix	10.1±2.4	11.6±2.0	78.1±2.6	4.0±1.5	3.7±0.7
	Turf	8.8±2.5	0.1±0.1	85.2±9.7	1.9±1.2	2.4±2.1
	Total	***278***				
April'06	CCA	7.0±1.7	31.7±3.4	52.8±5.3	4.5±1.8	8.1±3.1
(caged)	Mix	5.6±2.1	7.4±2.1	77.9±2.9	1.8±0.7	11.4±3.1
	Turf	7.6±2.2	0.3±0.2	88.8±2.0	2.0±0.9	8.7±1.7
	Total	***101***				
May'06	CCA	4.6±1.6	31.7±3.4	52.8±5.3	4.5±1.8	8.1±3.1
(uncaged)	Mix	6.1±2.9	7.4±2.1	77.9±2.9	1.8±0.7	11.4±3.1
	Turf	3.5±1.0	0.3±0.2	88.8±2.0	2.0±0.9	8.7±1.7
	Total	***142***				
May'07	CCA-Up	11.2±2.8	-	-	-	-
	CCA-Vert	12.4±5.7	-	-	-	-
	Mix-Up	12.2±3.0	-	-	-	-
	Mix- Vert	13.8±4.4	-	-	-	-
	Turf-Up	11.9±4.2	-	-	-	-
	Total	***603***				

Table 5.2. Factor loadings and percent of variation explained for each of the four axes (PC1-4) from principal components analysis of seeder substrate communities (April and May 2006 combined).

Factor	PC1	PC2	PC3	PC4
%CCA	-0.66	-0.47	-0.26	+0.86
%Turf/Seds	+0.75	-0.41	-0.18	+0.96
%Macro	-0.05	+0.12	+0.86	+1.00
%Bare	-0.00	+0.77	-0.40	+1.00
Variance	***86%***	***10%***	***4%***	***0%***

Table 5.3. Observed interval survivorship rate (ISR; ±SE) and daily survivorship rates (DSR) per seeder during each monitoring interval and for each experiment. Days represent the time extent of each interval period. DSR was calculated as $DSR = ISR^{1/t}$, where *t* is the interval length.

Experiment	Interval	Days	ISR	DSR
April Uncaged	1	0-2	0.54±0.06	0.73
	2	2-4	0.67±0.06	0.82
	3	4-10	0.42±0.07	0.86
	4	10-37	0.39±0.08	0.97
	5	37-65	0.44±0.12	0.97
	6	65-87	0.51±0.17	0.97
	7	87-149	0.38±0.19	0.98
May Uncaged	1	0-5	0.33±0.09	0.80
	2	5-8	0.47±0.12	0.78
	3	8-20	0.74±0.14	0.97
	4	20-58	0.48±0.16	0.98
	5	58-120	0.30±0.20	0.98
April Caged	1	0-2	0.62±0.13	0.79
	2	2-4	0.75±0.07	0.86
	3	4-10	0.57±0.11	0.91
	4	10-37	0.40±0.11	0.97
Transplants	1	0-2	0.89±0.05	0.94
	2	2-15	0.82v0.06	0.98
	3	15-35	0.68±0.09	0.98

Table 5.4. GLMM test for fixed effects in the direct larval seeding experiments and the seeding versus transplant experiment. For the seeding analyses, the Initial Period refers to days 0-10 and 0-8 for April and May, respectively, and days 0-15 for the transplants study; while the End Period refers to the remaining days. In the April Caged experiment, there was only 1 monitoring interval in the End Period, and therefore no Age predictor effect.

Experiment	**Factor**	**Initial Period (*un-weighted*)**		**End Period (*un-weighted*)**		**Entire Period (*weighted*)**	
		F value	**p value**	**F value**	**p value**	**F value**	**p value**
April Uncaged	Age*(log)*	12.98	0.0004	0.29	0.5928	19.51	<0.0001
	Substrate PC1	0.59	0.4446	0.48	0.4906	0.42	0.5189
	Substrate PC2	0.00	0.9935	0.28	0.6003	0.51	0.4744
May Uncaged	Age*(log)*	4.57	0.0343	0.39	0.5334	16.08	<0.0001
	Substrate PC1	1.14	0.2878	0.52	0.4733	0.00	0.9959
	Substrate PC2	4.88	0.0289	0.27	0.6029	1.30	0.2563
April Caged	Age*(log)*	2.59	0.1101	-	-	18.92	<0.0001
	Substrate PC1	0.00	0.9556	0.16	0.6955	0.10	0.7487
	Substrate PC2	0.03	0.8598	0.75	0.3951	0.53	0.4675
April Uncaged	Age*(log)*	17.05	<0.0001	-	-	96.67	<0.0001
vs. Caged	Cage Effect	3.07	0.0802	0.07	0.7938	2.34	0.1267
	Substrate PC1	0.39	0.5340	0.31	0.5778	0.31	0.5795
	Substrate PC2	0.01	0.9325	0.07	0.7938	0.01	0.9275
Transplants	Age*(log)*	12.44	<0.0004	-	-	76.89	<0.0001
vs. Seeded	Experiment	44.78	<0.0001	4.83	0.0297	34.68	<0.0001

CHAPTER 6: LARVAL SUPPLY AND HIGH EARLY POST-SETTLEMENT MORTALITY DRIVE RECRUITMENT PATTERNS IN A BROODING CORAL

Background

With likely changes to the condition and structure of coral reefs throughout the upcoming decades (Hughes et al. 2003), only successful and sustained recruitment will ensure the long-term viability of these communities and the goods and services they provide. Coral recruitment is the consequence of a progression through multiple life stages, entailing successful gamete production by adult colonies, gamete fertilization, larval dispersal within and among reefs, settlement on the substratum, and subsequent survival, each susceptible to a host of natural and anthropogenic stresses (Harrison and Wallace 1990). Due to the complexity of these interactions, and the logistical difficulties associated with studying microscopic early life stages, identifying the key mechanisms that structure recruitment dynamics for a specific reef location is an arduous task (Vermeij 2005, Baird et al. 2005). Because of these difficulties, recruitment remains one of the most "enigmatic" processes in stony corals (Mumby and Dytham 2006). However, given the current changes to coral reef condition on a global scale (Wilkinson 2004), the urgency to identify these mechanisms cannot be questioned, particularly for conservationists and managers charged with ensuring the continued viability of these ecosystems.

In corals, the early pre- and post-settlement stages are highly sensitive to environmental forcing (Richmond 1994, Gilmour 1999, Ward and Harrison 2000, Edmunds et al. 2001, Kuffner 2001,Gleason et al. 2005, Albright et al. 2008), and due to the presence of population bottlenecks during these stages (Vermeij and Sandin 2008,

Chapters 4 and 5), the early life stage processes may play critical roles in shaping future population dynamics (Gosselin and Qian 1997, Steele and Forrester 2002). Stressors that affect adults (e.g., nutrients, temperature stress, decreases in aragonite saturation) not only directly impact the early life stages (e.g., Ward and Harrison 2000, Edmunds et al. 2001, Albright et al. 2008), but can additionally impact these stages indirectly through feedback loops. As an example, adult coral mortality can result in growth of macroalgae as more space becomes available (McCook et al. 2001), particularly once macroalgal cover reaches a critical mass and exceeds rates at which the existing herbivore guild can suppress it (Williams et al. 2001). This growth of macroaglae can then limit future recruitment through space preemption on settlement dynamics (Hughes 1989, Vermeij 2006), and the subsequently declining populations will further strengthen recruitment failure through decreases in larval supply (Knowlton 2001). Sufficient degradation of the adult stocks, particularly when recovery is impaired by recruitment failure, will eventually lead to Allee effects in many species of coral once population densities are reduced below critical thresholds (Levitan et al. 2004, Levitan and McGovern 2005), thereby reinforcing continued degradation through a feedback mechanism. Understanding these relationships and accounting for them appropriately may be crucial for capturing feedbacks in these dynamics, although limited knowledge for some of these stages has inhibited suitable parameterization and subsequent inclusion (Mumby 1999, Mumby 2006).

Given the complexity of the recruitment process, modeling tools provide a practical and effective means by which to study these dynamics, particularly for key processes where empirical analyses are logistically challenging and uncertainty exists

(Weigand et al. 2003, Weigand et al. 2004, Grimm et al. 2005). Researchers have used models to study coral dynamics for a number of decades (Graus and Macintyre 1976, Maguire and Porter 1977, Karlson and Jackson 1981, Hughes 1984, Bradbury et al. 1990, Johnson and Preece 1992), but model use for these systems has increased substantially during the past decade (e.g., Lirman 2003, Langmead and Sheppard 2004, Wolanski et al. 2004, Sleeman et al. 2005, Mumby 2006, Mumby et al. 2006ab, Mumby et al. 2007a, Hoegh-Guldberg et al. 2007, Wakeford et al. 2008). While a number of these models have explicitly assessed habitat interactions (sedimentation, Wolanski et al. 2004; macroalgae abundance and grazing, Mumby and Dytham 2006, Mumby 2006, Hoegh-Guldberg et al. 2007), explicit incorporation of settlement and early post-settlement survivorship dynamics into these models has been mainly absent, despite the known influence of habitat characteristics on these processes (Babcock and Mundy 1996, Raimondi and Morse 2000, Harrington et al. 2004). Although recruitment may not be a principal driver of population dynamics in some systems (Mumby et al. 2007b), thereby limiting the need of mechanistic detail in such models, high rates of early post-settlement mortality as found in recent studies (Raymundo and Maypa 2004, Miller and Szmant 2006, Chapters 4 and 5) increases the likelihood that these early life stages strongly influence future dynamics (Gosselin and Qian 1997, Steele and Forrester 2002). As such, caution should be taken when projecting population dynamics based on parameterized recruitment rates that forego explicit inclusion of settlement and early post-settlement processes, as parameterized rates may fail to capture important links or feedbacks in the system. This is particularly true for situations where the factors under study (e.g., habitat, herbivory, climate change) may directly impact the early settlement and post-settlement

mechanisms structuring recruitment patterns (e.g., Harrington et al. 2004, Albright et al. 2008).

Given the paucity of understanding on the influences of early life-stage dynamics in structuring recruitment patterns in natural reef settings, there is an urgent need to identify the primary processes and their relative influences in driving recruitment dynamics. Identification of these driving processes will not only provide novel insights into the ecology of these important taxa, but will additionally provide guidelines on the level of detail needed for representing the recruitment process in future population and community models of corals. Therefore, the primary purpose of this study was to assess the relative contribution of multiple early-life stage processes in driving recruitment dynamics, through the development of a simulation model that represented the early life-stage processes mechanistically in a spatially-explicit framework. Specifically, this study assessed the sensitivity of the recruitment process to variability in larval supply to the benthos, settlement behaviors, preferred settlement habitat abundance and distribution, and early post-settlement survival. Due to the complexity of this model, the description below is presented using Grimm et al. (2006)'s ODD approach that provides a standardized description framework for agent-based models.

Methods

Overview

Entities, state variables and scales: The primary entities of the model are (1) individual adult coral colonies from which coral larvae are produced and released; (2) individual coral larvae that disperse from adults and settle on the benthos; (3) settled

individuals that grow into juveniles; and (4) substrate classes that influence where larvae choose to settle and how they survive following the settlement process. Different model processes occur across a range of spatial scales, from millimeters to meters over which larvae search for suitable settlement habitats, and from meters to a kilometer over which larvae disperse from adult colonies. The temporal scale was adaptive depending on the process, with a total temporal extent of 10 years for the simulation.

The focal species of this study, *Porites astreoides*, was chosen due to the availability of data on different aspects of its life cycle (e.g., reproduction and fecundity, McGuire 1997, Moulding 2007; settlement and early post-settlement dynamics, Chapters 3-5), knowledge of recruitment patterns (Chiappone and Sullivan 1996, Moulding 2007, Chapter 2), and its reproductive strategy as a brooding coral. In addition, the commonness and relatively high recruitment rates of this species compared to other Caribbean corals (Chiappone and Sullivan 1996, Smith 1997, Miller et al. 2000, Moulding 2007) made it possible to locate an adequate number of natural recruits during recruitment surveys to calibrate the model predictions. Although the typical dispersal distances by this species are unknown, other brooding species are known to have short dispersal distances (e.g., Vermeij 2005, Underwood et al. 2007), and strong stock-recruitment relationships exist for this species (Chiappone and Sullivan 1996, Moulding 2007; see Chapter 2), which could be produced by mainly localized dispersal on the reef-site scale (e.g., 10-100m). By assuming that dispersal is mainly local for this species, dispersal could be modeled mechanistically using a simplified approach in which larvae were transported variable distances from adults within a local site and from surrounding reef sites in close proximity, thereby excluding the need of sophisticated hydrodynamic

models. Lastly, this species was a useful study species because it has been the focus of other recent modeling studies (Mumby 2006, Mumby et al. 2007a, Hoegh-Guldberg et al. 2007), thereby providing a unique comparison to these studies.

Four sites were chosen on which to calibrate and validate the simulation runs (Table 6.1). These sites represented two inshore and two offshore patch reef locations, and were chosen because of the general differences in the substrate composition among the sites (Table 6.2) and the availability of data from these sites in which to parameterize the model processes. In addition, previous monitoring research on early post-settlement survivorship was available for these sites (Porter and Cooper 2008), and the formulation of survivorship used in this study was representative of survivorship measured at these sites. Although these focal sites were relatively low in juvenile densities compared to other sites in similar surveys (Chapter 2), they are representative of juvenile densities typical of Florida reefs in general (Chiappone and Sullivan 1996, Miller et al. 2000, Moulding 2007).

Process overview and scheduling: The general structure and flow of the recruitment simulation model (Figure 6.1) was to (1) develop a simulated "landscape" that represented a 32x32meter area of the benthos at a mm-scale pixel resolution, using habitat classes that integrated both biological and physical characteristics; (2) distribute adult corals across the landscape based on measured patterns in their spatial distribution; (3) release realistic numbers of larvae from adults based on available fecundity data and variable rates of larval mortality, (4) simulate dispersal using multiple dispersal distances (i.e., near dispersal within meters of the adult, uniform dispersal up to 1km from the adult, and variants in between); (5) allow larvae to choose appropriate settlement sites

based on their habitat preferences and the spatial distribution of the habitat classes; (6) simulate mortality of the recently-settled spat based on measured survival rates and based on their local habitat; (7) represent growth of larvae using measured rates from the field; (8) after the simulation run time (10 years), quantify the simulated juvenile patterns (i.e., density, density variability, size-frequency distribution, and settlement habitat associations) of those juveniles less than 5cm in diameter; and (9) directly compare the simulated patterns to measured patterns in the field using a model goodness-of-fit calculation (termed model *fitness*). Once an appropriate model was calibrated and optimized to the observed recruitment patterns, elasticity analyses were performed to directly assess which processes had a relatively strong influence in structuring recruitment dynamics.

Since recruitment patterns on a reef are the accumulation of multiple years of life and death processes, model simulations were run for 10 virtual years in order to establish a multi-year representation of the juvenile population (i.e., individuals <5cm diameter). Model processes occurred at one-month time intervals (planulation, post-settlement survivorship), with the exception of the larval dispersal and settlement phases, which were simulated without a time constraint by allowing larvae to disperse, search, and select a settlement site directly following release from adults during the same time step. Simulations at each of the reef sites were performed independently since no interactions occurred among sites.

Design concepts

Interactions and emergence: The primary recruitment patterns assessed in the model – density, density variability, size-frequency distributions, and habitat associations – were not forced by the model design, but emerged from the interactions among larval supply, larval behaviors, spatial heterogeneity, and differential mortality risks. The representation of the model entities (adult and substrate composition and distribution) and processes (larval settlement, post-settlement survival) were based on empirical measurements and knowledge, thus providing structural realism in the model in which the patterns could emerge as in natural systems (DeAngelis and Mooij 2005, Grimm and Railsback 2005).

Sensing: Individual larvae could sense the substrate on which they were in contact (e.g., Harrison and Wallace 1990, Morse et al. 1996, Harrington et al. 2004), but not the surrounding matrix; therefore, they moved in a random direction across the benthos and not in a choice-based direction. The decision to represent movement in this fashion was due to lack of knowledge on directed movement in corals (e.g., through following a chemosensory gradient; Koehl et al. 2007), although this is plausible.

Stochasticity: Stochasticity was included in the model for fecundity, dispersal, survival rates, and growth rates, where values were drawn from different distributions based on measured rates in the reef (see *Submodel* sections below for specification). Stochasticity was not included for either the habitat (e.g., grazing, Mumby 2006; competitive interactions, Wakeford et al. 2008), or for larger-scale processes (e.g., coral diseases, bleaching events, hurricanes), in order to retain simplicity in this model formulation. Importantly, this model assumed a static habitat representation, because

appropriate parameterization of habitat dynamics at the mm-scale of larval selection behaviors is challenging, and would require significant computing resources to develop and run suitable submodels (e.g., through competitive networks as in Wakeford et al. 2008). Instead, this study focused specifically on how larvae interact spatially with the substrate only during the settlement process (allowing for a static representation), and represented habitat interactions implicitly through variability in post-settlement survivorship rates (see *Calibration* section).

Observation: At the end of the 10 year simulation period, recruit patterns were recorded in the model using the same sampling techniques as in standard recruitment surveys (i.e., two 30m long transects, 15 0.25m^2 quadrats per transect; see Chapter 2). For each virtual quadrat, the density of juveniles, size-frequency of juveniles, and habitat classes on which individuals settled were recorded and output as a data file from the model. Since some of the sites had low densities, and therefore relatively random size-frequency and settlement habitat associations at low numbers, the size-frequency and habitat on which individuals settled for the total population of a site was additionally recorded for model calibration and testing purposes (see *Calibration* section below).

Details

Input: Prior to initialization, the following sources of input were read directly from data files and stored in computer memory to improve efficiency during run-time (see Figure 6.1): (1) relevant site characteristic data (site specific values for adult cover, adult size-frequency distributions, substrate cover; Table 6.2); (2) survival rates for each survivorship function during each month (Table 6.3); (3) raster habitat maps for each

simulation site (see *Initialization* section), and (4) connectivity matrices for each dispersal function (see *Submodel - larval dispersal* section).

Initialization: At the initiation of a simulation for each site, virtual adults were distributed onto the landscape to simulate realistic levels of coral cover, size-frequency distributions (five total size classes: 10-20, 20-30, 30-40, 40-50, 50-60cm diameter), and adult spatial aggregation. Coral cover and size-frequency distributions were set to site-specific levels, while adult spatial aggregation was set to a global value for all sites due to lack of site-specific information (Table 6.2). To distribute adult individuals, first the total number of individuals in each size class was computed that mimicked the measured rates of coral cover and size-frequency distribution for a given site (Table 6.2), and these were stored as a list of individuals for the site. Next, a location on the landscape for each individual in the list was assigned using an approach similar to Lundquist and Botsford (2004), where three total parameters determined the spatial aggregation of adults: α_{adult}, β_{adult}, and β_{adult} standard deviation (β_{adult}SD). For this approach, a fraction of the total individuals (α_{adult}, or the *seed* individuals) were first distributed across the virtual landscape to a random location. Second, the remaining individuals were randomly assigned to a seed individual, and distributed a random distance and direction from their respective seed individual, where the distance was uniformly drawn from zero to a max distance. Here, the max distance was randomly drawn from a normal distribution with a mean of β_{adult} and standard deviation of β_{adult}SD (note: Lundquist and Botsford did not use a β_{adult}SD parameter, but this was included here to provide added variability and ensure all locations within a reef were available for placement of an adult, versus strict circular zones surrounding a seed in which individuals could be placed). Once a specific

location was chosen for an individual of a specific size, the location was first checked to guarantee it was free of other adults, where overlap was not permitted for adult colonies. If the location was already occupied, alternate locations were randomly checked until an empty location was found.

To determine the appropriate values for α_{adult}, β_{adult}, and $\beta_{adult}SD$ at each of the four sites, a set of separate simulations were run that compared simulated aggregation patterns to measured aggregation patterns of *P. astreoides* obtained from 2-dimensional video mosaics (nearest-neighbor index of 0.62-0.599; courtesy of Brooke Gintert, University of Miami). For this, adults were distributed for each site as described above using a total of 192 parameter combinations of α_{adult}, β_{adult}, and $\beta_{adult}SD$, and using site-specific values for coral cover and size-frequency distributions. For each simulation with a unique parameter combination, a nearest-neighbor index was calculated for all adults in the virtual landscape as:

$$NNIndex = \frac{MeanNND_{aggregated}}{MeanNND_{random}} \qquad \text{eq. 1}$$

Here, $MeanNND_{aggregated}$ is the mean nearest neighbor distance for an aggregated population ($\alpha_{adult} < 1$), and $MeanNND_{random}$ is a mean nearest neighbor distance when the population is randomly distributed ($\alpha_{adult} = 1$). $NNIndex$ values < 1 reflect more aggregated populations, while values >1 reflect more uniformly distributed populations. The parameter combinations within the measured range (0.62-0.599) were then selected as appropriate combinations, and the combination with the highest α_{adult} was subjectively

selected as the best-fit set, because a higher α_{adult} value minimized computer runtime based on the model formulation.

Because the 32x32m core area represented a section within a larger patch reef area from which larvae may disperse, an overlapping non-core area of 1008x1008m was additionally simulated surrounding each of the four focal sites (i.e., the core area was the center 32x32m within the 1008x1008m total extent; all four simulation sites were greater than 2km apart so no overlap existed between non-core areas). The non-core area was only used to simulate dispersal of larvae from the non-core area to within the core-area, and not for any other model processes (i.e., no settlement or post-settlement processes were assessed outside the core 32x32m area). For the non-core area, a geo-referenced benthic habitat map of reef and non-reef locations (FWRI 2001), rasterized to 8x8m cell sizes, was used to represent suitable adult habitat. Note, for the 32x32m core area, the simulation location was strategically chosen to be fully reef area (no areas of non-suitable adult habitat), and these core areas were additionally at the same locations as where the real recruitment surveys were conducted (Chapter 2). To distribute adults onto the non-core area, the adult cover and size-frequency distribution was assumed to be the same as the core area, but the adults were randomly located onto reef area within the 8x8m cells, versus distributing them using the spatial aggregation approach. This choice was made because the non-core area was assessed at this grosser resolution (8x8m grid cells) within which the spatial aggregation would be present. A size of 8x8m was chosen for the grid cells to improve computer efficiency during the dispersal stage, discussed below in the *Submodel - larval dispersal* section.

Submodel - larval release: After adult corals were distributed onto the landscape, the simulation began in monthly time steps corresponding to the Julian calendar month. During the active planulation months (April, May and June; McGuire 1997, Moulding 2007), simulated larvae were released from adults in realistic numbers, using fecundity data from Moulding (2007). Here, fecundity included the likelihood of a given adult planulating during a given month (value drawn from normal distribution), and the total number of larvae per area of tissue when adults did planulate (drawn from normal distribution; see Table 6.2 for parameter values). The amount of tissue surface area for each adult was computed by (1) randomly assigning a diameter within the size class of each individual; (2) using this diameter, computing two surface area values for the individual coral, assuming a flat circular shape and a hemispherical shape (i.e., the extremes in possible colony shape); and (3) randomly choosing a surface area value between these two shape extremes using a uniform distribution. Surface area calculations were done using this approach because *P. astreoides* colonies can vary between flat to hemispherical in their shape. To account for possible lack of reproductive activity at tissue margins, the amount of fecund tissue was set to 70%. Determination of this value was made by comparing the median adult size and number of larvae released from real colonies in laboratory settings (Figure 6.2) to the estimated release of larvae assuming the average fecundity parameters of Moulding (2007). Five alternative fecund tissue values were compared (90, 80, 70, 60, and 50% fecund tissue), where 70% was found to produce the best fit average value to the real data.

Each adult was set to an invariant size throughout the 10 year period, thereby assuming that the adult population was stable without any major disturbances during this

period, and all growth was equally offset by mortality processes with respect to the net amount of available tissue. Larval mortality was additionally represented during this step to simulate all mortality processes from larval release to settlement. This was done by indiscriminately reducing the total number of larvae released per colony by a larval mortality rate. Because rates of natural larvae mortality are unknown for this species, this parameter value was varied and calibrated during the testing phase (see below).

Submodel - larval dispersal: Once larvae were released from adults in the core area, they were dispersed away from adults using a beta distribution at four parameter combinations to represent dispersal. Since actual dispersal distances are unknown for this species, a range of potential distances were chosen based loosely on other brooding species (e.g., Vermeij 2005, Underwood et al. 2007). Dispersal occurred in a random direction (uniform from 0-360˚), and the distance of dispersal was randomly determined from a beta distribution with four sets of parameter values (α_{disp}=1.1; β_{disp}=100, 35, 10, 2; scaled to 0-1km max dispersal; Figure 6.3, Table 6.4). Here, a beta distribution with α_{disp}>1 was used so that individuals were dispersed a minimal distance away from adults. All larvae that dispersed outside of the 32x32m core area were removed from the simulation.

To represent dispersal of larvae originating from adults in the non-core area, a probabilistic connectivity matrix approach was used. This was done because nearly an order of magnitude more adults resided in the non-core area, and initial model runs where dispersal was represented mechanistically for each larva originating in both the core and non-core area, as above, were slower than feasible for assessing the modeling objectives. To create connectivity matrices (one for each of the four mechanistic beta distributions),

a separate simulation was conducted where the 1008x1008m non-core area was divided into 8x8m cells, and 10 million larvae were released from each cell in the non-core area at a randomly chosen location (to 1m resolution) within the 8x8m cell. Dispersal was simulated from that location in a random direction and variable distance (as above, using the four beta distribution parameter combinations), and the total proportion of larvae arriving at each of the 8x8m core-area cells from each of the non-core area cells was recorded. Using these proportions, a probability of dispersal was computed for each core/non-core cell combination and stored as the connectivity matrix for each of the four parameter combinations. During the recruitment model simulation, these connectivity probabilities were then used to determine the total number of larvae arriving to the core area from each planulating adult in the non-core area. The total number of larvae produced per each colony in the non-core area was first computed; second, the simulation iterated through each adult in the non-core area, for each of the 16 8x8m cells in the core area separately; and third, for each adult, the probability of dispersal from that adult's location in the non-core area to the specific core area cell was multiplied by the total number of larvae produced by that adult to obtain the total number of larvae dispersing to the core-area cell. Because probabilities were low and would often result in numbers of dispersing larvae <1 for a single cell-to-cell connection, the total number of larvae arriving to each of the core-area cells were first summed amongst all adults in the non-core area as a decimal value, and then truncated to an integer value before proceeding with the settlement stage. Each larvae arriving to the core area was assigned a random starting location within the 8x8m cell of the core area.

Submodel - larval settlement: After dispersal, larvae searched the virtual landscape for preferential micro-habitats on which to settle. Movement of larvae was represented at a 1x1mm cell resolution and was done randomly to one of the 8 surrounding cells, using a toroidal landscape at the boundaries of the 32x32m area. Rather than representing specific substrate types to choose from (e.g., bare, crustose corraline algae, turf algae, etc.), the habitat choices were simplified to classes that had site-specific values of abundance and spatial distribution. Three total habitat classes were used: *preferred* substrate (i.e., cryptic surfaces, including bare and crustose-corraline algae substrate types), *tolerable* substrate (i.e., exposed surfaces, including turf-algae, sediment-laden substrate), and *avoided* substrates (i.e., all additional substrate types, including coral, macroalgae, gorgonians, sponges, etc). These habitat classes were chosen because clear settlement preferences by *P. astreoides* are exhibited for these classes (Chapter 3). As a larva moved across the landscape, it would choose to either settle or continue moving based on a settlement preference assigned to each substrate type (Table 6.2; derived from Chapter 3 and calculated as the average proportion of individuals that settled on each of the substrate categories). Here, the probability of settlement was equal to the settlement preference. To ensure that individuals did not search the substrate indefinitely, a subjective settlement mortality parameter was set to 0.01, where a larva had a 1% chance of dying each time it moved across the virtual landscape.

To improve computational memory requirements from representing 32000x32000 habitat cells at 1x1mm resolution during the settlement phase, a cell's habitat type was probabilistically assigned "on-the-fly" as larvae moved across the landscape. In order to

accurately portray realistic values of spatial aggregation in the substrate using an on-the-fly approach, a probabilistic approach was devised where, assuming larvae move to a new cell each step, they are more likely to encounter the same habitat class than a new habitat class when spatial aggregation is present. To accomplish this, an autocorrelation metric, *Corr*, was devised, where:

$$Prob_1 = Corr \qquad \text{eq. 2}$$

$$Prob_{2,3} = (1 - Corr) * \frac{Cover_{2,3}}{Cover_1 + Cover_2 + Cover_3} \qquad \text{eq. 3}$$

Here, $Prob_1$ refers to the probability of the next habitat class being the same as the current habitat, while $Prob_{2,3}$ refers to the probability of the next habitat being either of the two different habitat types. $Cover_i$ refers to the measured site cover of the habitat classes from field surveys (see Table 6.2 for parameter values). As *Corr* approaches 1, the spatial aggregation increases and the next habitat type will have a higher probability of being the same. With a high number of total habitat cells in a landscape (as here with 32000x32000), the resultant landscape cover of each habitat class is similar in both randomly-assigned landscapes and landscapes with high values of *Corr*.

A unique value of *Corr* was set for each site in the simulation based on measured substrate patterns in the field. The field substrate patterns were determined by draping two 10m long chain transects over the substrate at each of the four focal sites, and the substrate type was recorded at 10cm intervals along the length of each chain. Preferred

substrate was recorded as all corraline algae and bare surfaces (including microalgae encrusted); tolerable substrate was recorded as all turf algae and sediment-laden substrate; and avoided were all other substrates. The total cover of a habitat class was calculated from these data as the total number of point intercepts for a habitat class divided by the total number of points per site. To quantify the spatial aggregation of habitat classes, the three habitat classes were dummy-coded to an integer value, and a spatial aggregation coefficient for the observed data was calculated using the 1-dimensional spatial correlation approach presented in Denny et al (2004). To find an optimal value of *Corr* for each site, separate simulations were run where habitat classes were distributed using equations 2 and 3 across a range *Corr* values, and the resulting spatial correlation was calculated as above for the observed data, and compared directly to the observed spatial correlation. For this, a genetic algorithm optimization procedure was employed (programmed with the Java Genetic Algorithm Package, JGAP: http://jgap.sourceforge.net/), where an optimal *Corr* value that simulated the observed spatial correlation was determined.

Submodel - post-settlement growth and mortality: Once a larva settled, it underwent growth and mortality at monthly time steps for the remaining months of the ten-year period. The initial larvae size at settlement was first assigned randomly using a normal distribution based on measured sizes from Chapter 4, and monthly growth rates were assigned randomly using a normal distribution from juvenile growth data in Moulding (2007). Here, the mean growth rate was kept constant throughout the recruit's virtual life because Moulding (2007) found no differences in growth rates based on size for this species. Monthly survival rates were assigned based on survivorship data from

Chapters 4 and 5 (ages 1-12 months) and Moulding (2007) (ages 12+ months). To obtain a best-fit estimate of survivorship at monthly intervals from this combined dataset, a nonlinear function was fit to the mean daily survival rate (DSR) per chip as a function of age for the combined data (Chapters 4 and 5, and Moulding 2007). Since the Moulding (2007) data were presented in terms of survivorship as a function of size, the age at which an average larva would grow into a size class based on the average growth rate was computed, and this survivorship as a function of age was combined with the Chapters 4 and 5 data as the independent predictor. The nonlinear function was of the form:

$$DSR = \frac{V_{max} * Age^{c}}{K_m + Age^{c}} \qquad \text{eq. 4}$$

Here, V_{max} was set to 0.999 (i.e., DSR approaches 0.999 as an individual ages), and K_m and c were estimated using the SAS NLIN procedure (SAS Institute 2006). Two separate survivorship functions were fit to the data in order to test the influence of the shape of the survivorship function on recruitment rates (Figure 6.4): (1) a standard Michaelis–Menten saturation function where c=1 (hereafter termed MM Function), and (2) a modified Hill equation where c was estimated through the nonlinear procedure (hereafter termed Hill Function). For the Hill Function, only the Chapter 4 data were utilized, because theyprovided a markedly different shape than the MM Function (see Figure 6.4; specifically, higher initial mortality within the first two weeks), versus when the Chapter 4 and 5 data were combined to fit the Hill Function.

The DSR rates from the two survivorship functions were then used to calculate a mean monthly survival rate (MSR) for each month that was the probability of survival to

the next month (Table 6.3, Figure 6.5). Using these mean MSR rates, $\overline{MSR}$, the actual survival rate, MSR, that individual *i* experienced during the first month was calculated as:

$$MSR_{i,1} = N(\overline{MSR}_1, MSR_{SD}) + MSR_{Offset} \quad \text{eq. 5}$$

Here, $N(\overline{MSR}_1, MSR_{SD})$ is a value drawn from a normal distribution with a mean monthly survival rate for month 1 (Table 6.3) and a standard deviation set to a constant 0.03 for all months (based on data from Chapters 4 and 5, and Moulding 2007). MSR_{Offset} is a global survival offset parameter between -0.04 and 0.04 (i.e., up to 4% offset), used to vary the overall survivorship rates during model calibration and testing among runs (Tables 6.5 and 6.6). To calculate the survivorship rate in subsequent months, first the deviation, MSR_{dev}, between the calculated 1st month survivorship, $MSR_{i,1}$, and the mean survivorship, $\overline{MSR}_1$, was computed:

$$MSR_{dev} = MSR_{i,1} - \overline{MSR}_1 \quad \text{eq. 6}$$

This deviation represents the total deviation accounting for both stochasticity due to natural survival variability and the survival offset parameter. This value was then used to calculate the survivorship in subsequent months, *j*, as:

$$MSR_{i,j} = \overline{MSR}_j + MSR_{dev} * p_{dev} \quad \text{eq. 7}$$

Here, i is an individual, j refers to the month, and p_{dev}, termed the proportional deviation factor (Table 6.3), was a decreasing multiplicative adjustment for the survival deviation (i.e., p_{dev} approaches 0 as $\overline{MSR}$ approaches 1). The p_{dev}values were calculated empirically through trial and error, and were added to ensure that the net deviation decreased with age so that survival rates were constrained to less than 1 as individuals aged, while allowing for a smooth survival function when offsets were used. As a calculation example, a -0.04 survival offset with the Hill function at the mean survival rate (i.e., $S_{SD}$of 0), would produce the following monthly survival rates: month1 of 0.04 (from $\overline{MSR}_1$ of 0.08); month2 of 0.729; month3 of 0.840, etc. (see Table 6.3 for mean survival values and proportional deviation factor to follow calculation example). By using an offset parameter in this capacity, the overall survivorship function could be smoothly increased or decreased to account for variability during the model calibration, while still retaining the functional shape. If a survival offset was not used, the survivorship rates were computed as in equations 5-7 but with MSR_{Offset}= 0. For a single model run, the shape of the survivorship function (MM versus Hill Function) was kept constant for all larvae, but was varied for separate model runs in the Calibration procedures (see *Calibration* section below).

Model Calibration

To calibrate parameters in the model with high uncertainty, two techniques were performed: (1) a parameter sweep to assess the full range of the model and determine the best parameter combinations at a few discrete values, and (2) an optimization procedure using a genetic algorithm approach to find optimal values for selected parameters. In

both cases, a single model *fitness* value was used to test the goodness-of-fit of the simulation to observed patterns in the field (see below for description of fitness calculations). For the parameter sweep, a parameter set was assessed at a few discrete values for each parameter in the set, and every possible parameter combination was run as a separate simulation (Table 6.5). To determine the best parameter combinations from the sweep, four replicate sweeps were performed for each simulation site at each parameter combination, and the top 10 parameter combinations with the highest model fitnesses were used to obtain an average best-fit value for each of the parameters. Only four replicate simulations were run because of extensive computer run times at all parameter combinations, and because lack of large-scale stochasticity (e.g., reef-wide disturbances) limited variability among replicate runs.

Because only a few values for each parameter were used in the sweep to limit extensive computer run times, an optimization procedure was then performed after the parameter sweep to find optimal values for a few selected parameters with high uncertainty, including the larval mortality and the survivorship offsets for both tolerable and preferred substrate types. The optimization procedure was not used for the survivorship function, because the Hill function was chosen in all situations as the highest fitness value in the sweep. Likewise, the settle mortality values with the highest fitness were similar among runs and were set to a constant value of 0.01 for the optimization procedure. Although some variability existed in the best-fit dispersal distance from the parameter sweep, attempts to find an optimal value using the genetic algorithm approach proved unsuccessful, and subsequent elasticity analyses (see *Results* below) found a limited effect of the dispersal distance parameter choice on recruitment patterns.

Therefore, the dispersal distance was kept constant at α_{disp}=1.1 and β_{disp}=10 for the optimization procedure of the remaining parameters, which represented the median value from the highest fitness averages of the sweep across sites. To conduct the optimization procedure, the Java Genetic Algorithm Package (JGAP) was used at default settings to select the optimal value from a range of plausible values (Table 6.5).

A single model fitness value was used to quantitatively compare simulated and observed recruitment patterns in both the sweep and optimization. This value was computed as a weighted average from individual goodness-of-fit values for each of the six patterns used in this study, which included (1) quadrat density; (2) quadrat density standard deviation; (3) size frequency skewness; (4) size frequency kurtosis; (5) proportion settled on preferred habitat; and (6) proportion settled on tolerable habitat. The individual pattern fitness values were computed as (adapted from Marzluff et al. 2009):

$$PatternFitness_i = 1 - \frac{\left[\frac{Simulated_i - Measured_i}{Measured_i}\right]}{c} \qquad \text{eq. 8}$$

Here, $PatternFitness_i$ is the goodness-of-fit value for pattern *i*; $Simulated_i$ and $Measured_i$ refer to simulated and measured patterns, respectively; and *c* was a constant added for patterns with low measured values (i.e., close to zero) in order to minimize large differences between simulated and measured values (*sensu* Marzluff et al. 2009). For the size-frequency and habitat association patterns, a low abundance of juveniles in the simulated quadrats led to apparent randomness because too few individuals were present to allow patterns to emerge. This randomness was common to both the simulated

and measured data, thereby providing poor patterns for which to calibrate the model when using the quadrat data alone. To account for this, these patterns were assumed to be site invariant (i.e., set to a global value across all sites), and the combined recruitment data from all 12 sites (Table 6.1) was treated as the true *Measured* averages for these patterns. In these cases (size-frequency and settlement habitat patterns), the fitness values were computed as:

$$PatternFitness_i = 1 - \frac{\left[\frac{Simulated_i' - Measured_{\overline{x}}}{Measured_{\overline{x}}}\right]}{c} \qquad \text{eq. 9}$$

Here, $Measured_{\overline{x}}$ is the mean measured value from all 12 sites, and $Simulated_i'$ is the site's entire population of juveniles (i.e., not from just virtual quadrat surveys as in $Simulated_i$, but summed across the entire 32x32m site).

Using the $PatternFitness_i$ values from equations 8 and 9, the weighted average fitness value, $TotalFitness$, was calculated as:

$$TotalFitness = \frac{\sum_{i=0}^{n}(w_i * PatternFitness_i)}{\sum_{i=0}^{n} w_i} \qquad \text{eq. 10}$$

Here, n is the total number of patterns, and w_i is a weight given to each pattern. Since the density and densitySD patterns were directly comparable between simulated and measured quadrats, they were given higher weights (1 and 0.5, respectively), while all other patterns were given lower weights (0.25). Therefore, density was the main driver of the $TotalFitness$ value, while the other patterns were influential to lesser degrees.

Model Elasticity Analyses

To address the study goals and determine the processes that had a strong relative contribution to recruitment dynamics, elasticity analyses were performed for each of the key parameters in the model, including: (1) larval mortality; (2) substrate-specific post-settlement survival (preferred and tolerable); (3) dispersal distance; (4) survival functional shape (MM and Hill); (5) adult cover; (6) substrate cover (preferred and tolerable); and (7) substrate preference (preferred and tolerable). Analyses were done for each individual model fitness value (i.e., $PatternFitness_i$) and for the overall fitness ($TotalFitness$), thereby providing insights into the influence of each model parameter on each of the recruitment patterns.

Elasticity analyses were performed by assessing the proportional changes in the model fitness of a particular pattern in response to proportional changes in the parameter's values (Benton and Grant 1999). By using this approach versus a standard sensitivity analysis, the relative contribution of different parameters could be assessed for a single pattern, because the use of proportional changes in effect standardizes the elasticity measure across parameters with different units of measure (Benton and Grant 1999). For the parameters represented as continuous variables (all but dispersal distance and survival function type), the proportional changes in the parameter values were made for every 5% from 0% (i.e., optimal) to 95%. Here, the single exception was the substrate cover parameter, where incremental changes were made from 0 to 75%, in order to avoid percent cover values that summed to greater than 100%. For the categorical parameters (dispersal distance and survivorship function), a similar approach was taken, where the proportional changes in the fitness values were assessed for the non-optimal

categorical values. Using these adjusted parameter values, 100 replicate simulations were run for each incremental change or non-optimal categorical value, and the resultant fitness values for each of the seven patterns were recorded. The proportional change in each fitness value was then computed relative to a global optimal model fitness value for each site. The global optimal model fitness values were determined as the average of 100 replicate simulations at the optimal parameter values for each site. A linear regression was then fit to these data for each parameter to assess the change in the parameter value (x-axis) on the relative change in the model fitness value (y-axis). Here, the slope of the regression reflected the elasticity, or the unit change in the model fitness value with each % change (or categorical change) in the parameter value. By comparing the model elasticity for each parameter, this approach provided a standardized means by which to assess and quantitatively compare the effect of key life-stage processes on recruitment.

Model Execution

All components of the model were programmed in the Java programming language (6.0), and simulation runs were performed on the University of Miami's High Performance Computing Center (http://www.ccs.miami.edu/) using concurrent programming techniques for executing batch simulations.

Results

Calibration

The two calibration approaches (parameter sweep and optimization) produced similar best-fit values for the parameters with high uncertainty (larval mortality and survivorship offsets on different substrate types; Tables 6.5 and 6.6). Larval survival rates were found to be extremely low, ranging from 1-7% in the parameter sweep (Table 6.5), and 0.7-3.7% in the optimization (Table 6.6). The survivorship offsets were more similar among the calibration approaches than the larval survival parameter, and all offsets were positive except for preferred substrate types at site MG, and cryptic substrate types at site M16.

Both the survivorship functional shape and settle mortality parameters were similar across sites during the parameter sweep, and for the case of the survivorship function, not a single run using the MM function was included in the ten highest model fitness runs for each site. Therefore, both parameters were removed from the genetic algorithm optimization, and were instead set to constant values (0.01 for settle mortality, and Hill function for survivorship shape; Table 6.5). Based on the parameter sweep, the dispersal distance categories that produced the best model fitness were variable both within and among sites, ranging from some sites where the average optimal values was small (i.e., shorter dispersal; site CP, 0.6±0.5) compared to other sites (sites MG and MK16, 2.5±1.0 and 2.5±0.7, respectively; Table 6.5). Note, the averages of the dispersal distance represent averages from categorical values (0-3), which correspond to the four parameter combinations for dispersal distances. When an attempt was made to optimize the dispersal distance category, the optimization procedure did not converge to an

optimal category, mainly due to a weak overall elasticity of the model to dispersal distance (see sections below; Figures 6.6-6.12). Therefore, a constant parameter combination (α_{disp}=1.1,β_{disp}=10) was subjectively chosen as the median value among the four reef sites, and this value was then used as the optimal value in the elasticity analysis.

Elasticity Analysis

Overall, there was a marked difference among which parameters influenced the different model patterns (Figures 6.6-6.12). The parameters related to the number of individuals (larval mortality, adult cover, and to a lesser extent, dispersal distance and the substrate survival offsets) strongly influenced the density pattern (Figures 6.6 and 6.13). This was especially true for larval mortality and adult cover, which directly determined the total number of larvae available for settlement. The dispersal distance also had an influence on density, but this was only pronounced for the longest dispersal distances in which a higher proportion of individuals were transported off of the reef (Figure 6.13g depicts this non-linear decrease in off-site transport at the highest dispersal distance category). Despite the potential for more individuals from surrounding reefs to be transported into the core-area at these higher dispersal distances, this did not offset the net off-site transport. Finally, density increased linearly with the survival substrate offsets, but to a lesser degree than with larval survival or adult cover.

The only parameter that had a strong influence on the size frequency distribution, both the skewness and kurtosis, was the shape of the survivorship function (Figures 6.7 and 6.8). Since the net survivorship rates among the two functional shapes were similar (i.e., similar numbers surviving after a few months period), the functional shape mainly

influenced the proportional dominance of the smallest size classes in the model. With the Hill function, a higher number of the recent settlers were removed from the model, leading to a higher relative proportion of older size classes that more closely simulated the observed patterns.

For the remaining patterns (density variation, and the two substrate associations), the parameters did not have a strong influence on these patterns relative to the other patterns discussed above (elasticity values < 0.3, versus values around 1 for density and size frequency distributions; Figures 6.6-6.12). The density variation pattern was most strongly influenced by the survival functional shape and the dispersal distance, and to a lesser extent by the factors affecting the total numbers of individuals (Figure 6.9). The substrate cover parameters had the strongest relative influence on the habitat association patterns, while the settlement preference and substrate survival offsets had less of an influence on these associations (Figure 6.10 and 6.11).

When the relative contributions of the parameters to the overall model fitness were assessed (i.e., using a weighted average of all patterns), larval mortality and adult cover had the strongest influence on the overall model fitness (Figure 6.12). This is mainly a result of the weighted formulation for the overall model fitness, as the density pattern was given the highest weight due to its consideration as the strongest pattern among the group. As such, the parameters that had the strongest influence on density (e.g., Figure 6.6) had the strongest influence on the overall model fitness. The shape of the survival function also had a strong effect on the overall model fitness (Figure 6.12), due to the overwhelming effect this parameter had on the size frequency distribution (Figures 6.7 and 6.8).

Discussion

While the recruitment patterns were influenced by multiple early life-stage processes, only a few of the processes had a relatively strong influence on recruitment – namely larval survival, adult cover, and the shape of the early post-settlement survivorship function. This was evident from comparing the elasticity values from the averaged model fitness analysis (Figure 6.12), where even an un-weighted comparison across patterns would have produced similar results due to the overwhelming strength of these three processes. The density pattern, arguably the principal indicator used when assessing recruitment in general, was almost exclusively driven by those processes related to larval supply – the larval survival and adult cover. This finding strongly supports other research efforts that have found strong linear stock-recruitment relationships for this species at the site scale (Chiappone and Sullivan 1996, Moulding 2007, Chapter 2), suggesting that supply determines the overall mean recruitment, while other local processes (e.g., those influenced by habitat) determine the variability around this mean. Even for non-brooding species where stock-recruitment relationships are not evident at the site scale (e.g., Chiappone and Sullivan 1996), recruitment is still strongly influenced by the processes related to larval supply, just at larger spatial scales (e.g., fecundity; Hughes et al. 2000). These results are consistent with supply-side ecology in general (Gaines and Roughgarden 1985, Young 1987, Underwood and Fairweather 1989, Hughes et al. 2000), and underscore the need to account for those processes structuring larval supply – specifically, adult fecundity, fertilization success, larval survival and dispersal – when assessing the primary drivers of recruitment dynamics.

Importantly, this modeling effort focused on four simulation sites with low coral cover of the focal species *P. astreoides* (<3%), which represent normal coral cover values for the majority of the sites assessed in the recruitment surveys (Chapter 2). Because higher cover sites were not included, this study simulated the dynamics of these systems only during the linear portion of the stock-recruitment relationship found for this species, which occurs up to approximately 10% cover for this species (Chapter 2). Therefore, this study's results on the primary processes driving recruitment should only be considered as appropriate for reef sites where these linear stock-recruitment relationships hold. Above this linear portion of the stock-recruitment relationship, density-dependent factors likely have a greater relative influence on recruitment dynamics and future population abundances (Schmitt et al. 1999). For instance, suitable habitat may become more limiting at high coral cover values, leading to a stronger relative influence of settlement dynamics in response to the habitat distribution. Future simulations that incorporate high-cover sites would be necessary to determine changes to the primary processes regulating recruitment under density-dependent scenarios.

One of the strongest factors influencing juvenile density was the level of larval mortality needed to simulate the observed patterns, which was between 96-99% from larval release to settlement. This mortality rate was unknown to begin, and the magnitude of this mortality was only identified through the inverse modeling approaches used here. A strength of this model compared to other coral models (e.g., Mumby 2006, Wakeford et al. 2008) was the representation of realistic rates of fecundity and post-settlement survivorship, which, along with the larval mortality, simulated the major production and loss rates leading to recruitment. Despite trade-offs being made to allow

for this high-resolution of representation in the early life stage dynamics (i.e., full population dynamics were not assessed here as in other models), this study's approach provided a means for larval "accounting" and subsequent identification of this missing larval loss in driving recruitment dynamics.

While these larval mortality rates seem exceptionally high, they are not surprising given the potential for intense predation on plankton by filter-feeding organisms on the reef (Glynn 1973, Fabricious and Metzner 2004). For example, Fabricious and Metzner (2004) found that mortality of free-swimming coral larvae ranged from 7-86% per hour in a recirculating system with a diverse community of filter feeding reef species, and in an extreme situation, one species of zooanthid could ingest upwards of 98% of larvae over a two-hour period. In addition, another recent study on coral larval mortality found high rates of initial mortality in free-swimming larvae even under controlled conditions (i.e., no apparent predators), due to some unknown mechanism possibly related to larval energetics (Graham et al. 2008). High rates of predation are considered normal during the planktonic to benthic transition of reef fish (Doherty et al. 2004), and similar rates of loss are likely natural in most species with planktonic larvae as they return to the benthos for settlement. Combined, these natural mortality processes – both intense predation and a larva's energetic condition – could produce the estimated high rates of larval mortality found in this study.

The high rates of larval mortality found here may also be partly attributable to how larval dispersal was represented in this study. In particular, as the dispersal distance increased, more larvae were lost from a reef site, and this effect intensified in a non-linear fashion as the dispersal distance increased (see Figure 6.13g, particularly for site CP).

Since actual dispersal distances are unknown for this species, a range of potential distances were chosen for use in this study based loosely on other brooding species (e.g., Vermeij 2005, Underwood et al. 2007). However, these chosen values may have been skewed to shorter distances than what the focal species of this study actually experiences. If longer dispersal distances are typical, more larvae would be exported from a reef site, leading to a lower estimated larval mortality rate than the 96-99% found here. Because of this uncertainty, future work on identifying the dispersal distances of this species will be invaluable for developing and refining similar predictive models on these recruitment dynamics and determining realistic levels of these mortality processes.

Along with potential biases in the typical distances of dispersal used here, this model also used a highly simplified representation of the dispersal mechanism, namely that dispersal was in a random direction from adults (thereby ignoring hydrodynamic influences), and the distances followed a beta distribution. This representation was chosen because larvae are assumed to move at least a minimal distance from adults (hence beta distribution with $\alpha_{disp} > 1$), and that direction would be random over short distances within a reef site due to high reef heterogeneity and resulting turbulent water movement. While this is plausible, limited data are available for how coral larvae actually disperse from adults, particularly over small spatial scales (e.g., meters scale) that are typically not represented in predictive hydrodynamic models (Werner et al. 2007). Recent insights by Underwood et al. (2007) found that a high proportion of individuals settled within 20m of their parental colony, but how they were transported across these distances is difficult to ascertain. For example, some amount of upwards swimming from the adult colony would likely be necessary to transport the individuals up

to 10s of meters away, and intraspecific variability in these swimming behaviors may explain the infrequent transport of individuals over kilometers by the species studied in Underwood et al. (2007). Understanding how these larval swimming behaviors interact with the local hydrodynamics is a crucial step for identifying the mechanisms leading to such patterns (e.g., Cowen et al. 2006). Once these behaviors are identified for the species of interest, coupled biophysical dispersal models can then be used to accurately model dispersal mechanistically while accounting for realistic variability in hydrodynamic forcing (Werner et al. 2007). In the case of *P. astreoides*, a proportion of larvae swim upwards upon release (as can be inferred from typical methods used to collect these larvae; Brazeau et al. 1998, Chapters 3-5) and are thus likely transported a minimum of meters to tens of meters away from adult colonies. However, a number of individuals swim in random directions upon release to quickly return to the substrate (author's personal observation), and these behaviors, combined with turbulent water movements that may rapidly transport larvae to the bottom (Koehl et al. 2007), could lead to a proportion of the larvae settling short distances from the natal colony. Because these insights are currently limited and mainly observational, more work is needed to quantify the timing of larval behaviors of this and related species – both swimming behaviors along with pre-competency periods – in order to construct coupled biophysical dispersal models for an accurate portrayal of this process. Detailed parent-offspring genetic mapping, as recently done by Underwood et al. (2007), provides a promising future research approach for gaining valuable insights into these dispersal dynamics.

Although the larval supply process had the largest impact on juvenile densities in this study, the shape of the survivorship function almost exclusively influenced the size-

frequency distributions. Specifically, when mortality was high during the initial time periods (Hill equation), the model provided a better representation of the observed size-frequency distributions. While other forces not addressed in this study could additionally influence size-frequency distributions, such as pulses of arriving larvae (e.g., Doherty et al. 2004) or differential growth rates among size classes or cohorts, the strong influence by the functional shape of early post-settlement survivorship as found here suggests this process is a key driver for these distributions in natural reef settings. It is important to note that the shape of the survivorship function can be variable over time, as found in Chapter 5 where abnormally high mortality likely resulted from unfavorable weather conditions during one of three experimental trials. Such variability is likely common in many situations where differential mortality results from acute or chronic disturbances, and may explain variability in juvenile size-frequency distributions common to some reef sites (Miller et al. 2000, Moulding 2007).

The two shapes of the survivorship function used in this study were based on actual data, where the MM function was estimated from two data sources (Chapters 4 and 5), and the Hill function was estimated from one of these sources (Chapter 4). The strong influence of this functional shape on the size-frequency pattern has important implications for how early post-settlement survivorship is estimated from empirical studies. In particular, the overall shape was relatively similar among the two estimates (Figures 6.4 and 6.5), and was mainly a difference in the choice of the non-linear function used. It should be noted that both estimates were highly significant in their fit to the data, thereby strengthening the importance placed on accurate estimation of early post-settlement survival. Therefore, when choosing a survivorship function to use in similar

recruitment models, particular attention should be placed upon the techniques used to estimate survivorship, as seemingly minor differences in decisions may have strong influences on the simulated size-frequency distribution.

Both the density variation and the habitat association patterns assessed in this study were less sensitive to the model processes than either the density or size-frequency distributions. In the case of the density variation (i.e., variability in the quadrat density within a site), all parameters had estimated elasticity values of less than 0.06, which was over 16-fold less than the maximum elasticity values from the density and size-frequency distribution patterns (all >0.88). This pattern was originally included with the purpose of calibrating the dispersal process, mainly for the potential of relatively short dispersal distances that could lead to increased variation in density among quadrats. For example, with dispersal over centimeter to meter scales, the variation in quadrat density should be more variable when adults are non-uniform in their distribution. If adults were distributed uniformly across the simulated landscape, variation in density would be low, but increasing spatial aggregation with short dispersal distances would lead to higher density variability. Despite this potential to tune the dispersal distance parameter based on density variability, this pattern proved ineffective, especially compared to other patterns in this study.

Elasticity values from the habitat associations were higher than the density variability, but still less than 0.25 maximum. For the habitat associations, the cover of the substrate types had the highest influence on the habitat associations, with preferred substrate being more important than tolerable substrate. This result is a consequence of how larvae choose to settle, where the likelihood of settling on a preferred substrate was

greater than tolerable substrates. However, if there was a low cover of the preferred substrate (in some sites, as low as 9% cover) and those substrates were additionally spatially aggregated, the likelihood of some larvae finding a preferred substrate before compromising for a tolerable substrate could be low. As such, the ability of larvae to actually find a preferred substrate type was a primary constraint in determining the overall distribution of juveniles on the two different habitat types. Although this result demonstrates the important interplay of interactions between larval settlement behaviors, substrate cover, and the spatial distribution of substrate types, the overall influence of these habitat-related processes (e.g., habitat cover, survivorship among habitat types, and settlement preferences) on recruitment dynamics was still minimal when compared to other mortality processes acting earlier in the life cycle.

That being noted, the role of habitat and the processes related to it may be vital for determining subsequent patterns of recruitment after the majority of mortality has ensued, but in relative terms, this influence is minimal. Exceptions to this weak influence could occur when high macroalgal, sediment, or adult cover prevent successful settlement through space preemption. For example, high macroalgal cover occurred in Jamaica after the loss of *Diadema* and multiple hurricanes led to a marked phase shift in the system (Hughes 1994), and recruitment significantly declined as space was preempted by macroalgae (Hughes 1989). Subsequent reductions in the abnormally high coverage of macroalgae once *Diadema* partially returned led to noticeable increases in recruitment (Carpenter and Edmunds 2006), thereby signifying the strong influence of habitat-related processes on recruitment success in some systems. Despite this, the occurrence of similarly high macroalgal cover may be limited in general, as recent evidence from meta-

analyses from both the Indo-Pacific and Caribbean show that ubiquitously high rates of macroalgal cover are not as common as typically assumed (Bruno et al. 2009). Also, the flexibility of many species to settle on multiple substrate types (Heyward and Negri 1999, Webster et al. 2004, Chapter 2) signifies that settlement is possible as long as space preemption is not abnormally high.

Overall, identification of the primarily processes structuring recruitment in this study, particularly the larval mortality rate that was unknown to begin, was only possible through inverse-modeling techniques (e.g., Wiegand et al. 2003, Wiegand et al. 2004, Grimm et al. 2005). Using these techniques, it was possible to filter inappropriate values for relatively unknown parameters through the calibration procedure, and choose values that reproduced the model patterns appropriately. The strength of these approaches lies in using multiple patterns (Grimm and Railsback 2005), particularly when several parameters have high uncertainty and different patterns are needed to calibrate them independently. The choice of patterns is critical, and under ideal situations, the modeler should have an exclusive pattern for each unknown process (i.e., a pattern that is mainly influenced by only a single unknown parameter). This approach of choosing multiple patterns to tune process parameters independently is of great value for testing and calibrating similar models, and efforts should be made to utilize as many patterns as appropriate when constructing pattern-oriented models (Grimm and Railsback 2005), since the ability to reproduce multiple patterns lends support to the realism of the model (Grimm and Railsback 2005, Grimm et al. 2005).

Conclusions

By assessing the early-life stage processes leading to recruitment in a mechanistic framework, this study provided a number of novel insights into the factors driving recruitment dynamics for the focal species, *Porites astreoides*. First, this study found a high degree of larval loss, either through direct larval mortality or export from the reef, that occurs prior to settlement on the substrate. Rates of larval mortality approached 99% under plausible dispersal scenarios, and represent a major bottleneck for this species and others with similar life histories. Such a high rate of loss has important implications for future population dynamics (Steele and Forrester 2002), as relatively minor changes to the rates of this loss can have relatively strong influences on future dynamics, compared to variability in later life stages. Since neither larval mortality rates nor typical dispersal distances of this species are known, the degree to which this loss is attributable to larval mortality or off-site dispersal remains unclear. However, a substantial percentage of this loss is likely due to direct larval mortality, because of the intense predation typical on reefs (e.g., Fabricious and Metzner 2004) and emerging research on high larval mortality rates (Graham et al. 2008). Despite the representation of dispersal from adjacent reef areas, the magnitude of on-site transport was minimal, and did not offset the net loss of larvae from the core reef area. Future research on the mechanisms of pre-settlement mortality and biophysical dispersal will shed valuable insights into the magnitude and prevalence of this first major population bottleneck during these early life stages.

Second, the shape of the survivorship function had an overwhelming influence on the size-frequency distribution of juveniles in the system. This occurred despite a relatively small difference between the two shapes of the survivorship function used.

While other processes not studied here may additionally contribute to size-frequency distributions, this finding has an important implication with respect to the representation of survivorship in future recruitment models, particularly if size-frequency distributions are used as patterns to calibrate model processes. If survivorship is represented parametrically as here (versus mechanistically, which is unrealistic until the major drivers of survivorship dynamics are identified; see Chapter 4), care must be taken in how survivorship is estimated, and due to the strong sensitivity to this process, a range of plausible functions should be used for calibration and testing purposes.

Finally, the influence of habitat on recruitment dynamics was found to be minimal when compared to other processes that led to population bottlenecks earlier in the life cycle. Given the purpose of this study – to assess the relative influence of these different processes by standardizing their contribution to recruitment patterns – this result is not surprising due to the high cohort mortality (>99%) prior to when habitat effects typically occur during the life cycle. While habitat could exert a stronger influence on recruitment dynamics when suitable settlement habitat is limited (e.g., under high sediment or macroalgal cover in degraded systems, and as adult cover increases), settlement failure may be generally restricted to these situations, as larvae are mobile and can search for scarce microhabitats on which to settle. This is not to say these situations do not exist (e.g., as in Jamaica, Hughes 1994; or high sediment load areas, Wolanski et al. 2002), but they may not represent the norm in most systems, at least in the case of macroalgal preemption (Bruno et al. 2009). In addition, habitat interactions may be crucial for ensuring that the few individuals who do survive the larval supply and the early post-settlement bottlenecks recruit into the future adult population, and therefore direct

analogies between *relative* influences and *biologically-meaningful* influences should be avoided. Importantly, this study only assessed sites with low average coral cover, and this focus limited the potential for density-dependent effects to arise. Future studies on sites with higher coral cover would be valuable for validating this model under different conditions, and determining whether habitat influences become more important as the levels of larval supply increase and approach carrying capacities in the system (e.g., Schmitt et al. 1999, Shima and Osenberg 2003).

Given these results, a number of important implications emerge for future modeling efforts on coral population and community dynamics. First, high priority should be placed on improving realistic representations of larval supply into these models, as this process has an overwhelmingly strong influence on recruitment, as shown here for a brooding coral and shown previously for broadcast spawners (Hughes et al. 2000). Biophysical dispersal modeling has been a highly active field of development (Cowen et al. 2007), and improvements in computing resources and techniques are constantly advancing the resolution of these models (Werner et al. 2007). However, dispersal is only a part of this larval supply process, and equal effort must focus on improving and incorporating estimates of larval production, particularly for fertilization success in broadcast spawning coral species. The fertilization process, in combination with fecundity, may be a key driver of recruitment rates across broad spatial extents (Hughes et al. 2000), and despite this influence, this process has not been represented dynamically in any coral population or community models to the authors knowledge. Equally important is improving estimates of larval mortality, both during the planktonic dispersal phase and once they return to the reef. While larval supply may set the mean

recruitment rates, at least for linear stock-recruitment relationships, the representation of habitat may be important for modeling the variability around the mean recruitment levels set by supply. When suitable settlement space becomes limited (e.g., high macroalgal, sediment, or adult cover), habitat may be a primary factor regulating recruitment, and development of dynamic habitat sub-models at the appropriate spatial scales of interaction (e.g., mm-scales for larval settlement) may be necessary to capture the dynamics of the system. Combined, these improvements will greatly enhance realism in coral models, and may be vital for identifying important feedback mechanisms that drive the future trajectory of the populations and communities.

Figures

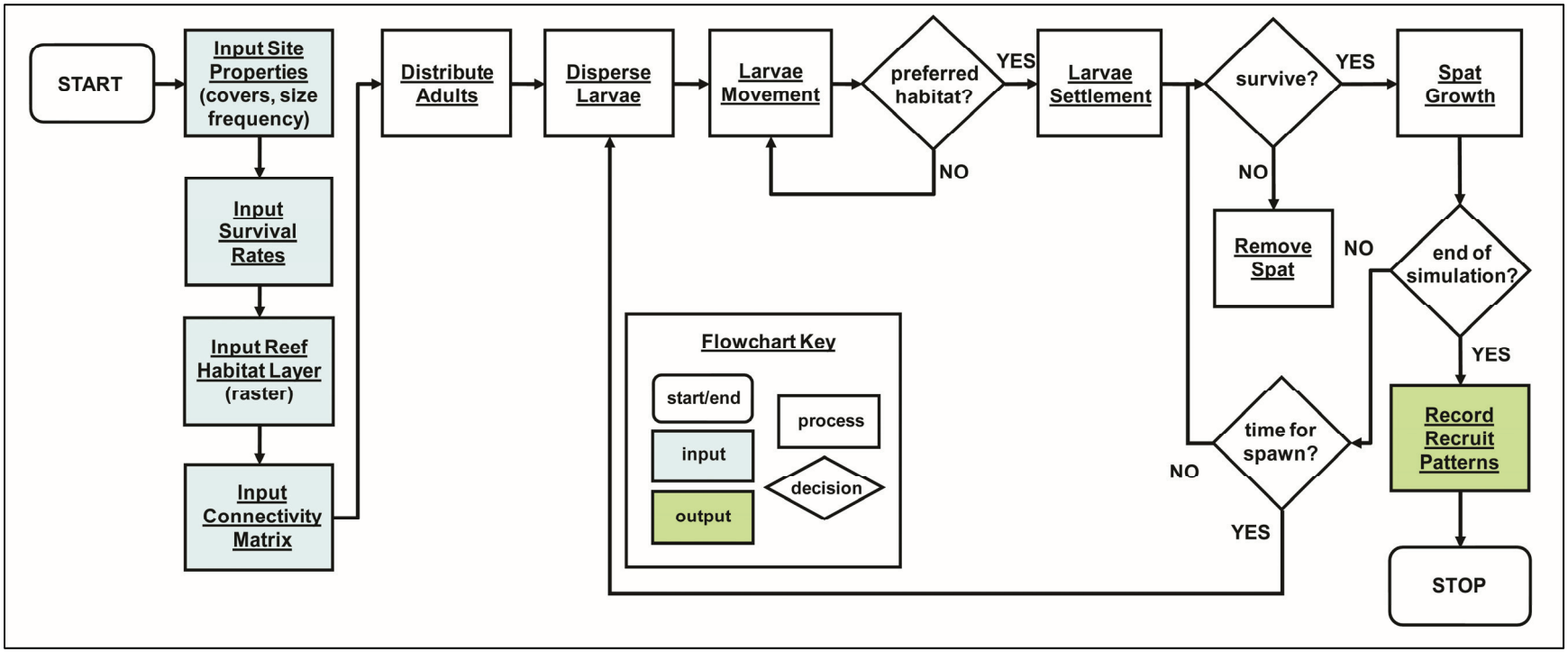

Figure 6.1. Flowchart depicting the steps in the model, done separately for each focal simulation site (i.e., no interactions among sites). Note: each model step refers to an individual's step, and each model step will be iterated through all individuals before proceeding to the next model step.

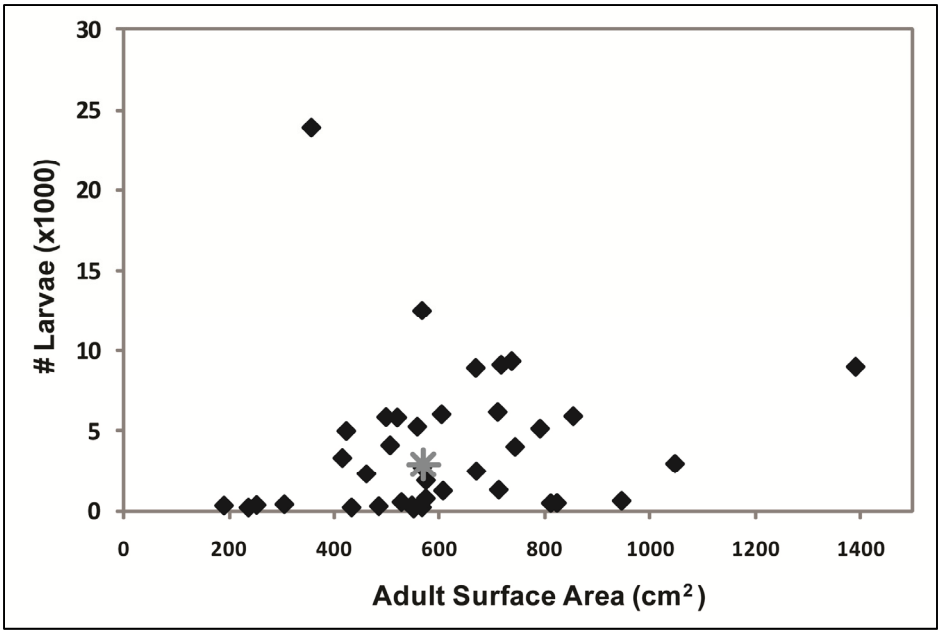

Figure 6.2. Measured fecundity of adult *P. astreoides* from larval collections (using methods from Chapters 3-5), where larvae were counted by hand as the total number of larvae an adult colony released over the peak week of larval release. Red diamond denotes the median size and median number of larvae.

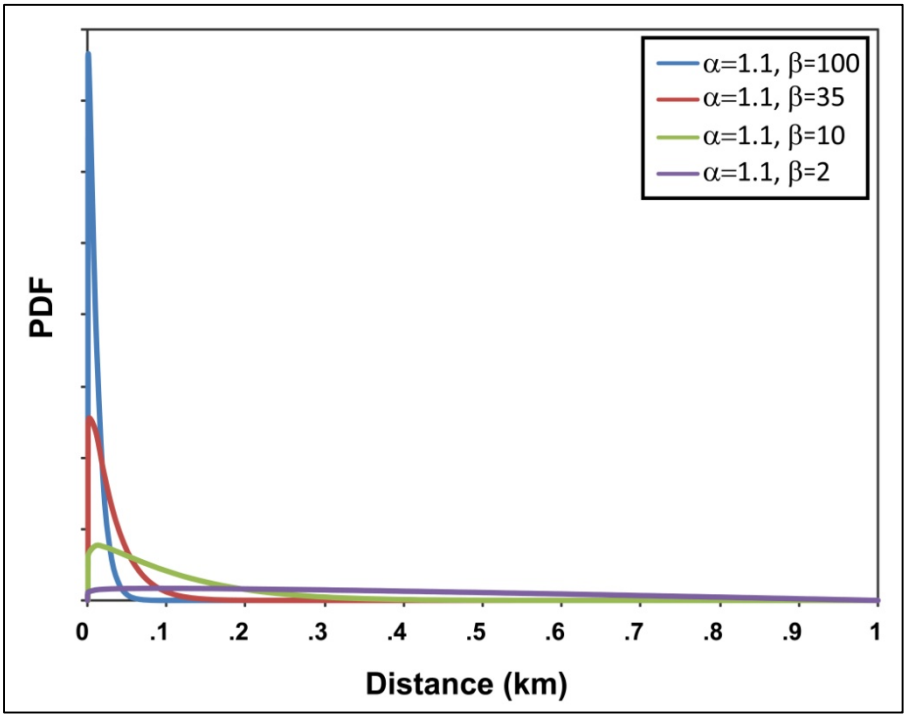

Figure 6.3. The four Beta distribution dispersal functions, with parameter values in caption, used to model the dispersal distance of larvae away from adult colonies, where maximum dispersal was set to 1km.

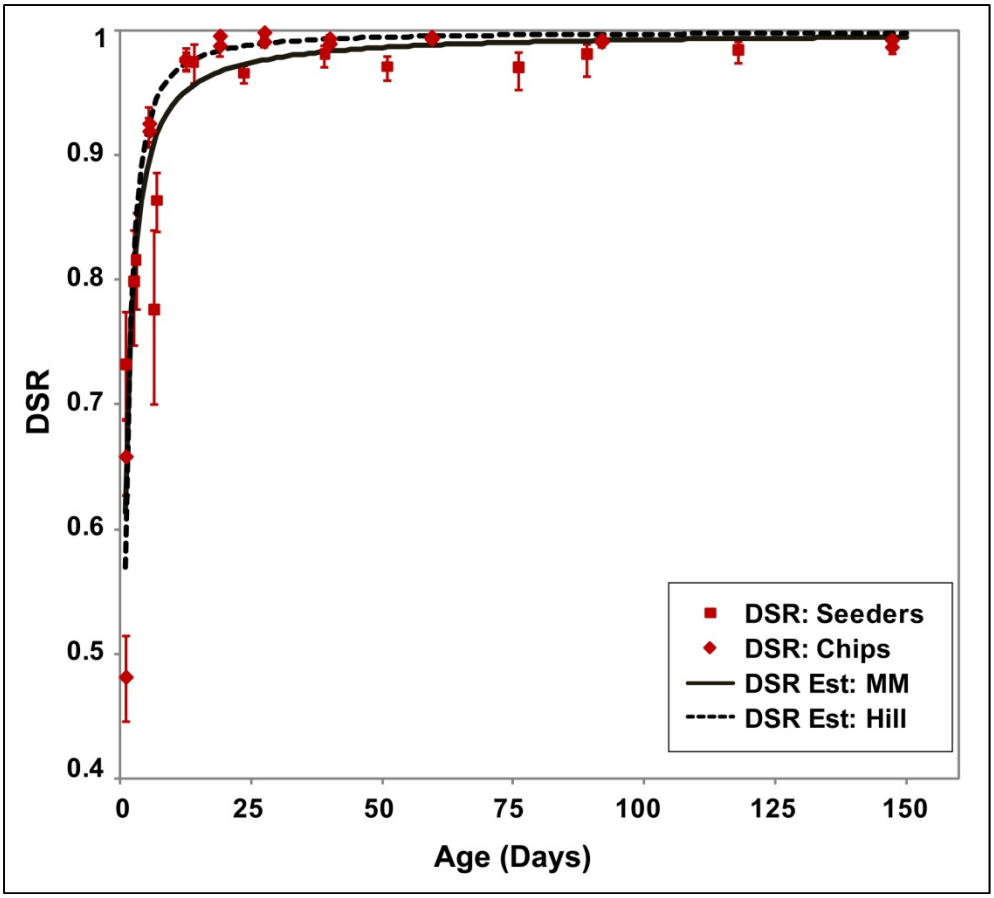

Figure 6.4. Observed and estimated daily survival rates (DSR), used to calculate the monthly survival rates (MSR; Figure 8) for the two different survival functions used in the simulation (MM and Hill, solid and dotted lines, respectively). Observed DSR denoted as squares (Chapter 5 seeding study) and triangles (Chapter 4 survival study), and presented as site averages ±SE per monitoring interval.

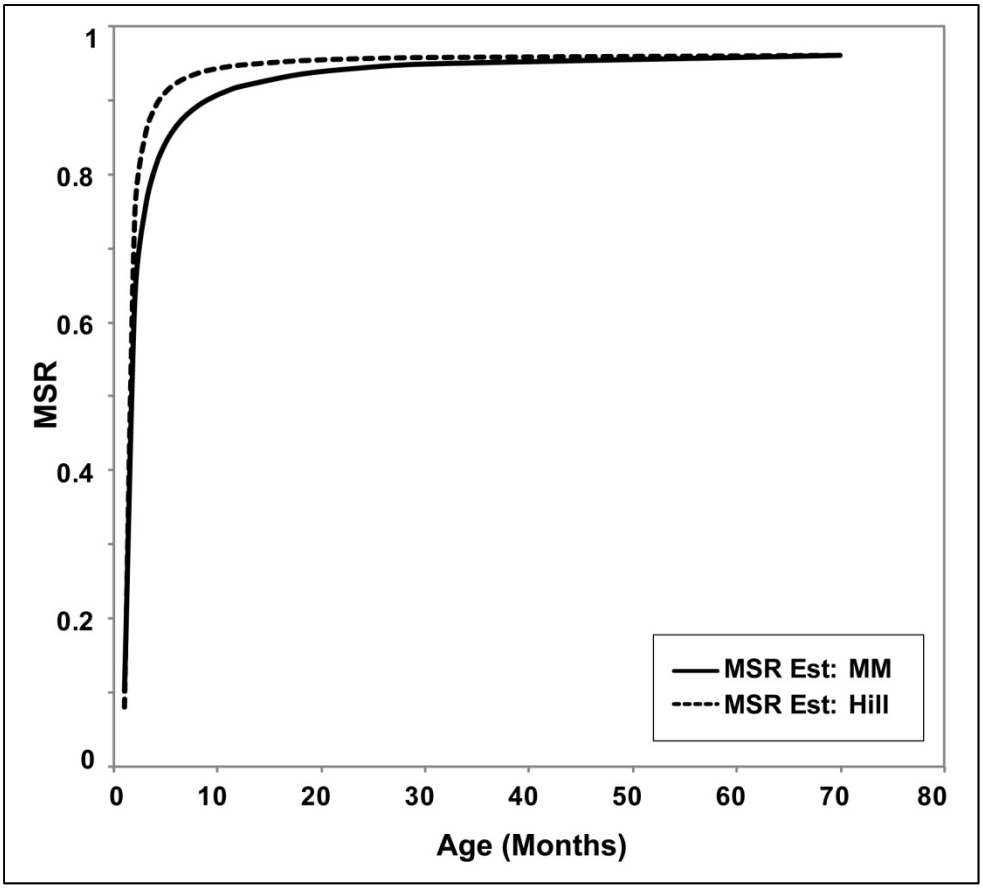

Figure 6.5. Mean monthly survival rates ($\overline{MSR}$) for the two different survival functions used in the simulation (MM and Hill, solid and dotted lines, respectively).

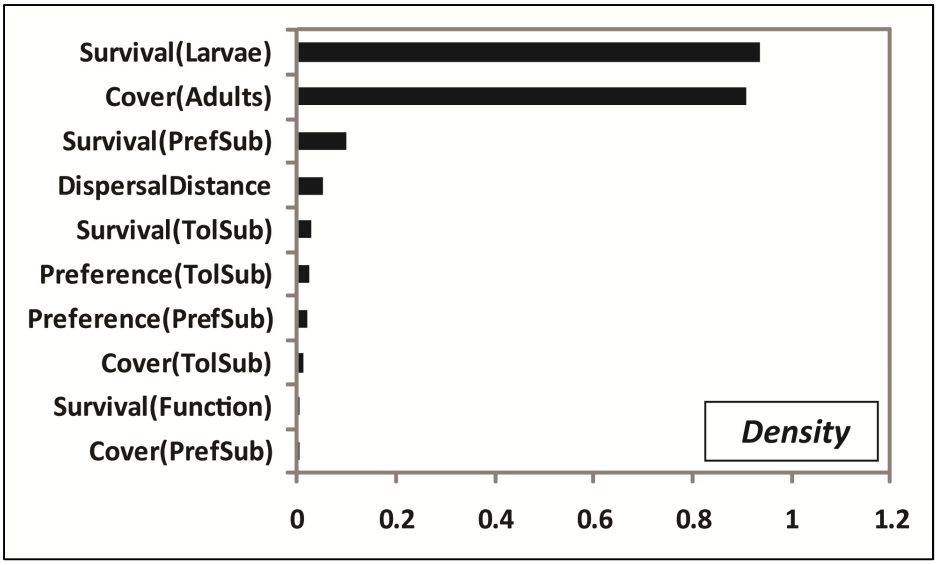

Figure 6.6. Elasticity values for each of the selected parameters on the model fitness for the density pattern. Here, the parameter values are averaged over the four simulation sites, and a higher elasticity value represents a greater relative contribution of that process to the model pattern.

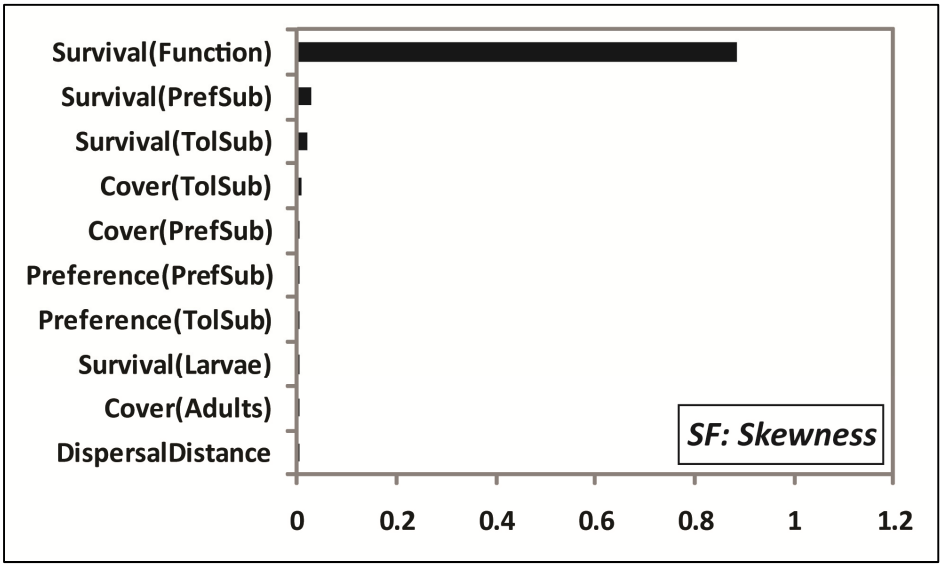

Figure 6.7. Elasticity values for each of the selected parameters on the model fitness for the size frequency skewness pattern.

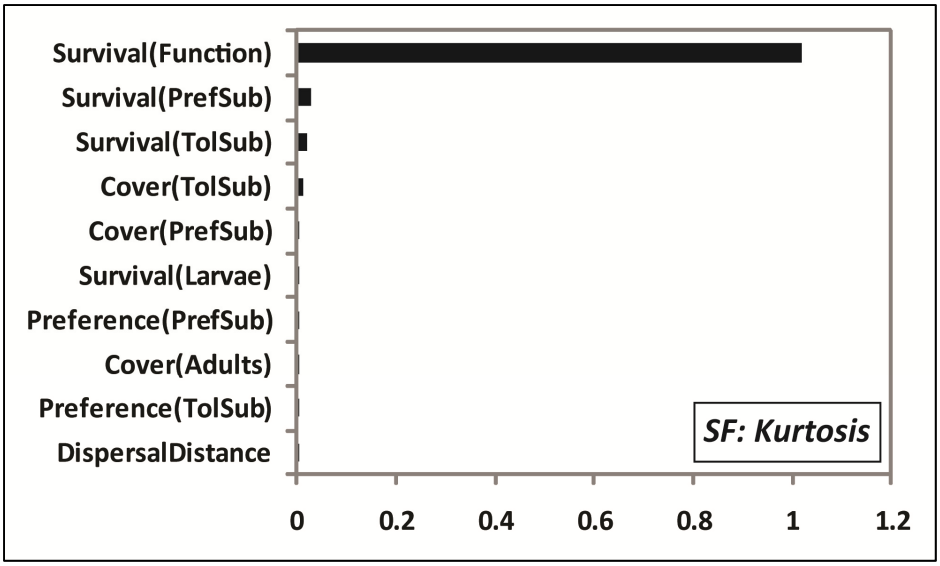

Figure 6.8. Elasticity values for each of the selected parameters on the model fitness for the size frequency kurtosis pattern.

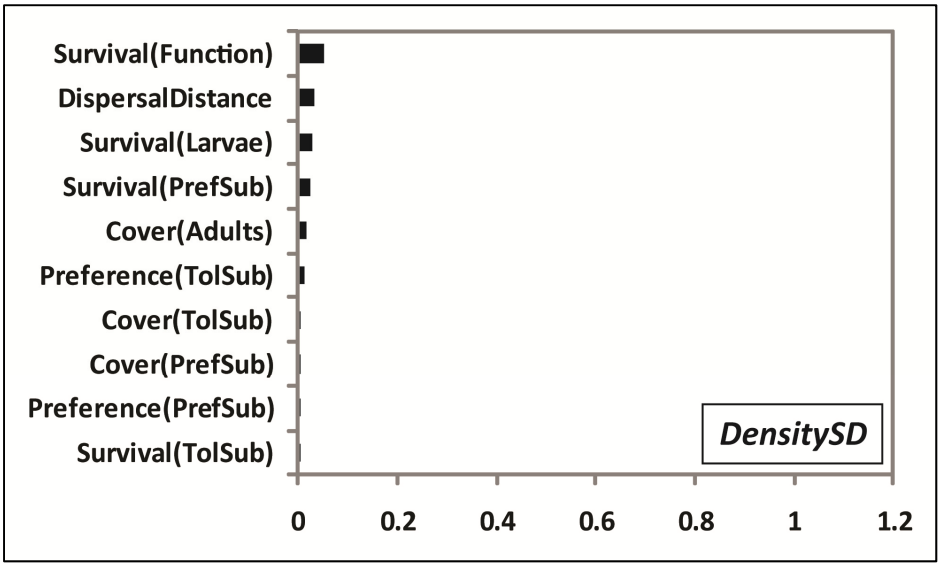

Figure 6.9. Elasticity values for each of the selected parameters on the model fitness for the density standard deviation pattern.

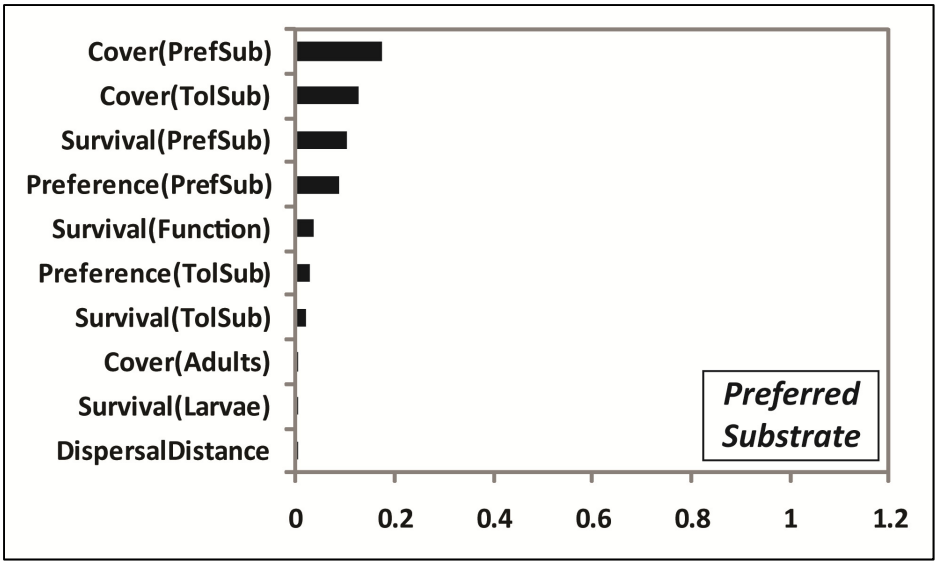

Figure 6.10. Elasticity values for each of the selected parameters on the model fitness for the proportion settled on preferred substrate pattern.

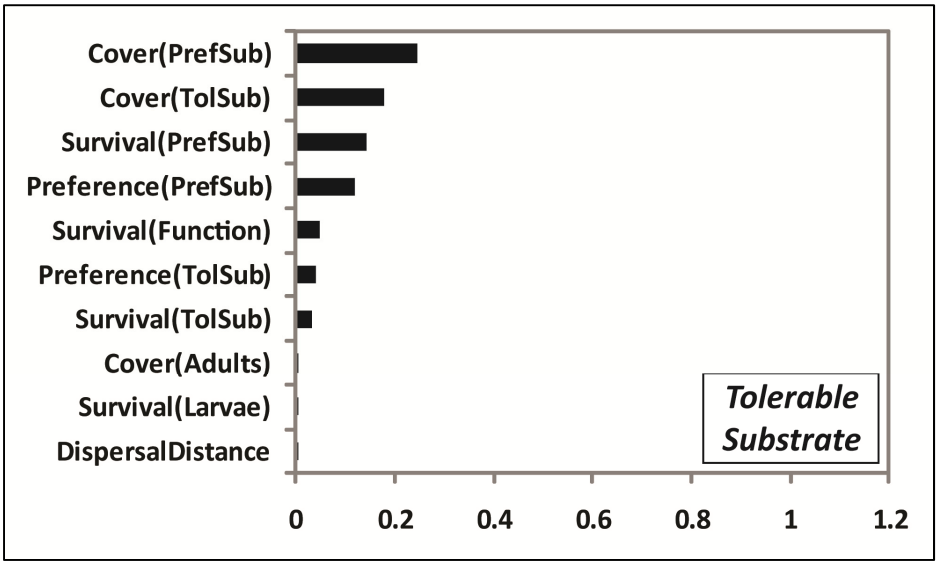

Figure 6.11. Elasticity values for each of the selected parameters on the model fitness for the proportion settled on tolerable substrate pattern.

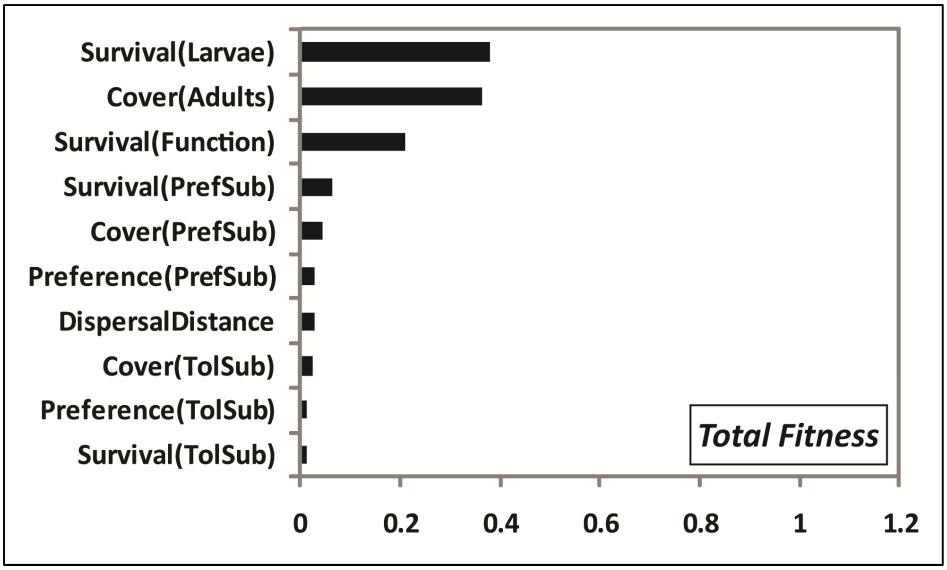

Figure 6.12. Elasticity values for each of the selected parameters on the weighted-average model fitness.

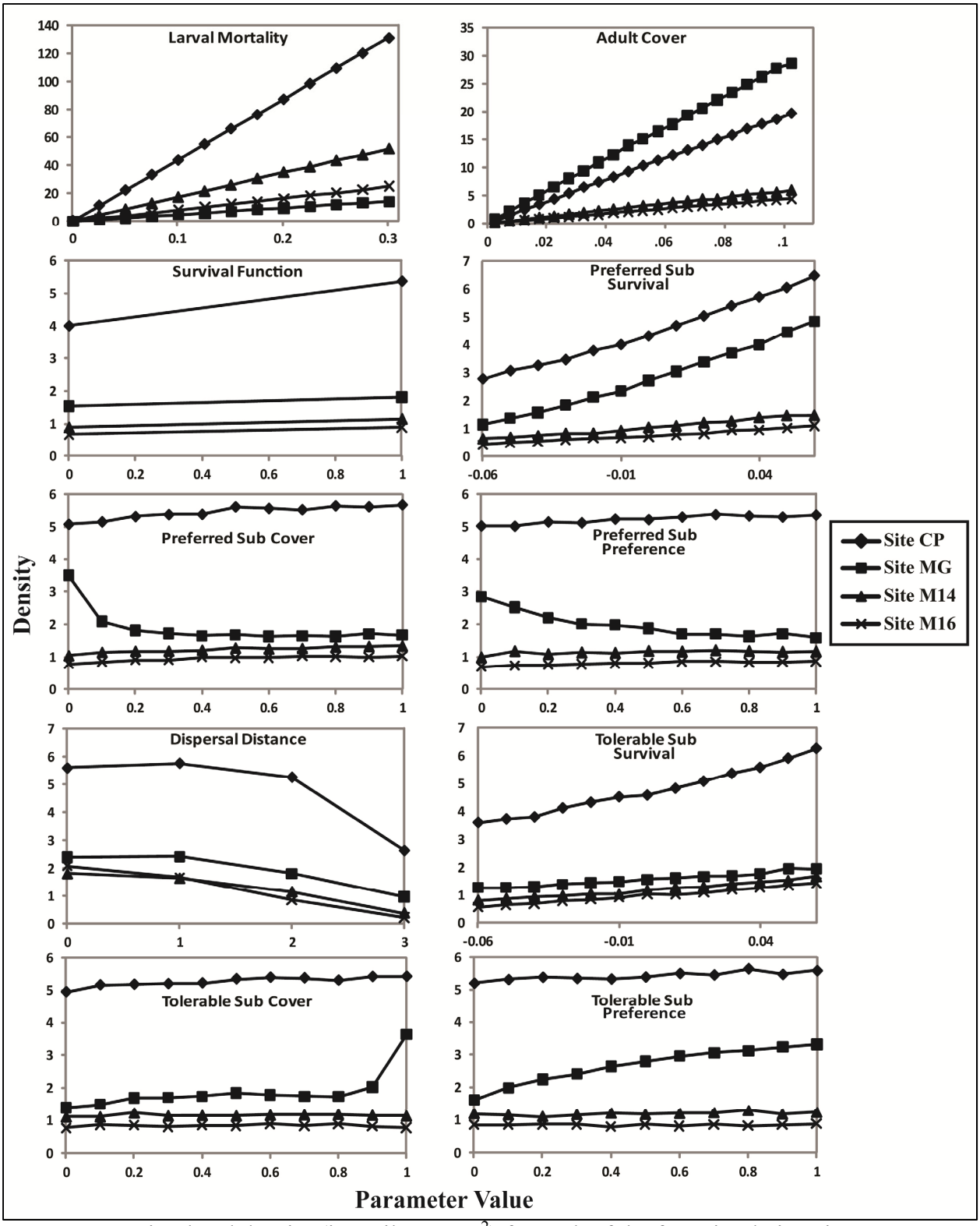

Figure 6.13. Simulated density (juveniles per m^2) for each of the four simulation sites (chart series) across a range of parameter values for focal parameters assessed in the elasticity analyses (Figures 9-15).

Tables

Table 6.1. Location, depth, and number of recruit survey quadrats for both the focal simulation sites and the recruit survey sites (see Chapter 2 for more details).

Site	Depth(m)	# quadrats	Latitude	Longitude
CP (focal)	4	30	25.50851	-80.12058
MG (focal)	5	30	25.46735	-80.12492
M16 (focal)	3	30	25.44387	-80.17586
M14 (focal)	3	28	25.46394	-80.16884
S8	3	22	25.41631	-80.14479
S5	3	11	25.42297	-80.15603
TK	4	8	25.38832	-80.16297
S9	4	20	25.39715	-80.15846
M9	2	30	25.49604	-80.14347
NP	4	12	25.36277	-80.16675
S2	3	30	25.44725	-80.15886
BS	3	11	25.48528	-80.14888

Table 6.2. Parameter values used in the simulations for each of the focal sites.

Parameter	Site			
	CP	**MG**	**M14**	**M16**
Adult Cover	2.7	0.6	1.9	1.8
Adult Spatial				
α_{adult}	0.5	0.7	0.5	0.5
β_{adult}	5	10	10	10
$\beta_{adultSD}$	5	1	3	3
Adult Size Freq.†				
skewness	1.26	2.93	0.96	0.45
kurtosis	1.93	8.83	-0.67	-0.18
Adult Fecundity				
April likelihood		.69±.31		
May likelihood		.83±.24		
June likelihood		.61±.29		
larvae/cm^2		.08±.09		
prop. fecund tissue		0.70		
Prop. Reef Habitat	0.34	0.39	0.05	0.03
Substrate Spatial	0.79	0.13	0.87	0.85
Substrate Cover				
preferred	0.18	0.24	0.17	0.09
tolerable	0.39	0.42	0.36	0.45
Settle Preference				
preferred		0.569		
tolerable		0.056		
Survival SD		0.03		
Dispersal Distance		** see Table 5*		
Larval Mortality		** see Table 5*		
Survival Rates		** see Tables 3 and 5*		
Settle Mortality		** see Table 5*		

† Site-specific values of adult size frequency were represented as proportions per size class in the model, and not as skewness and kurtosis values. The skewness and kurtosis are presented here for brevity.

Table 6.3. Mean monthly survival rates for both survival functions used in the model (Michalis-Menten and Hill), with the monthly proportional adjustment factors used to calculate a monthly offset for the calibration and testing procedures (see *Submodel – Early-post settlement growth and mortality* for description of calculations).

Age (months)	Survival Rates ($\overline{MSR}$)		Proportional Adjustment (p_{dev})
	MM	HILL	
0-1	0.101713	0.08	1
1-2	0.633982	0.75	0.513345
2-3	0.754939	0.854186	0.347544
3-4	0.811592	0.892972	0.263523
4-5	0.84459	0.912647	0.212614
5-6	0.866215	0.924328	0.17841
6-7	0.88149	0.93197	0.153821
7-8	0.892856	0.937312	0.135278
8-9	0.901644	0.94123	0.120787
9-10	0.908642	0.944211	0.109144
10-11	0.914348	0.946546	0.099582
11-12	0.919088	0.948418	0.091586
12-18	0.936363	0.954664	0.062005
18-24	0.944939	0.957384	0.047015
24-30	0.950065	0.958866	0.037932
30+	0.96173	0.961729	0.016789

Table 6.4. Dispersal distance statistics, based on a beta distribution (scaled from 0-1000 meters) with a total of 1,000,000 random draws of virtual larvae.

Dispersal Category	Parameters		Distance (m)		
	α_{disp}	β_{disp}	min	median	max
0	1.1	100	<0.0001	7.9	141.9
1	1.1	35	0.0002	22.3	413.1
2	1.1	10	0.0006	75.5	817.8
3	1.1	2	0.001	320.6	999.2

Table 6.5. Parameter values used in the parameter sweep calibration approach, and the resultant average best-fit values (mean±1SD). Here, the best-fit value was the average of the parameter values from the ten simulation runs with the highest model fitness.

Parameter	Values	Best-fit Value ($\bar{x} \pm SD$)			
		CP	MG	M14	M16
Dispersal distanceǂ	0,1,2,3	0.6±0.5	2.5±1.0	1.6±0.8	2.5±0.7
Survival function†	0,1	1±0	1±0	1±0	1±0
Larval survival	.01,.05,.1,.33,.66	0.01±0	0.03±0.02	0.01±0	0.02±0.03
Survival rate offset‡					
preferred	-.04,-.02,0,.02,.04	0.036±0.01	-0.030±0.01	0.008±0.03	0.012±0.03
tolerable	-.04,-.02,0,.02,.04	0.024±0.02	0.036±0.01	0.008±0.02	-0.016±0.02
Settle mortality	0, .01, .02	0.009±0.01	0.015±0.01	0.011±0.01	0.013±0.01

ǂ Values from 0 to 3 represent beta distribution dispersal distances from nearest to farthest (Table 4).

† The survival functions were MM and Hill for 0 and 1, respectively.

‡ The survival offset parameter served to increase or decrease the survivorship function depending on the value. See Table 3 and Methods text for description of how these offset parameters were used.

Table 6.6. The range of values used in the optimization procedure and the resultant optimal values for the select parameters used. Note, dispersal distance, survival function, and settle mortality were set to constant values for this optimization (see *Calibration* section for justification).

Parameter	Value Range	Best-fit Value			
		CP	MG	M14	M16
Dispersal distance	2	--	--	--	--
Survival function	1	--	--	--	--
Larval survival	{.001, 0.3}	0.012	0.037	0.007	0.010
Survival rate offset					
preferred	{-.04, .04}	0.029	-0.034	0.017	0.016
tolerable	{-.04, .04}	0.027	0.035	0.000	-0.019
Settle mortality	.01	--	--	--	--

CHAPTER 7: CONCLUSIONS AND IMPLICATIONS

Overview

As stated in the introduction, the overall goals of this dissertation research were to (1) assess key life stage processes leading to recruitment – specifically, settlement and early post-settlement processes – for which previous knowledge was limited or absent; and (2) using this knowledge, develop a local-scale recruitment model that assessed the cumulative success of a cohort's progression through these life stages and identified those processes that had a strong relative influence on recruitment dynamics. Although the second objective was the sole focus of Chapter 6, and as such, syntheses among the chapters are provided therein, an explicit discussion regarding relationships among the chapters is lacking. Therefore, this final chapter focuses specifically on summarizing the major conclusions and implications drawn from each individual chapter, and where appropriate, discusses cumulative insights drawn from multiple chapters.

Chapter-Specific Conclusions

Chapter Two

This chapter assessed juvenile patterns of *Porites astreoides* across twelve patch reef sites in Biscayne National Park, FL USA, and related these patterns to adult abundances, rugosity measurements, and substrate composition at different spatial scales. Major conclusions from this chapter include:

(1) Adult cover is an important factor structuring recruitment and subsequent juvenile densities, both at small spatial scales for this species (i.e., quadrat scale of

meters), and at larger site scales. A significant site-scale stock-recruitment relationship was found for this species based on the nonlinear Ricker function (Ricker 1954), where juvenile densities peaked around 10% adult cover. This result supports Vermeij and Sandin (2008) where they found a saturating stock-recruitment relationship above approximately 10% coral cover, suggesting density-dependent processes may become important above this magnitude of adult coral cover. This research also supports other studies where linear stock-recruitment relationships were shown for the focal species at relatively low adult coral cover (Chiappone and Sullivan 1996, Moudling 2007). This was the case in the modeling analyses of Chapter 6, where coral cover was less than 3% for each of the focal simulation sites, and as such, there was a strong linear relationship between juvenile densities and coral cover. Because nonlinear relationships could arise from both adult space pre-emption and additional density-dependent processes (e.g., space pre-emption by intolerable substrate; distance-dependent microbial mortality, Vermeij 2005, Marhaver 2008), future modeling efforts should include density-dependent processes explicitly along with high coral cover sites in order to assess changes to the relative influence of various processes when density-dependence is present.

(2) The positive influence of macroalgae on the presence of juveniles underscores the potential importance of nonlinear relationships between macroalgal cover and coral recruitment. In this study, macroalgal cover was not exceptionally high, where the average cover was 34%. Therefore, negative coral-algae interactions or significant space pre-emption by macroalgae was possible, but likely limited in prevalence. Combined with recent evidence that macroaglae dominance is not as

widespread as commonly assumed (Bruno et al. 2009), this study suggests that macroalgae may only be a key driver of recruitment failure in unique systems with high macroagal cover, and not in average systems where cover is typically less than 25% (Bruno et al. 2009). The modeling analysis from Chapter 6 corroborates this result, where the cover of avoided substrate types (which included macroalgae) did not have a strong influence on recruitment, particularly when compared to larval supply. Inclusion of direct post-settlement mortality factors (e.g., competitive interactions, predation events, sediment smothering) through a dynamic habitat model would greatly improve the ability of this model to assess all potential macroalgal interactions with recruitment, but is currently difficult to do because of the general lack of knowledge on the primary factors driving early post-settlement mortality in natural reef settings (Chapters 4 and 5).

Chapter Three

This chapter assessed the key settlement preferences of *Porites astreoides* with respect to the substrate community, light intensity, and substrate orientation. Major conclusions from this chapter include:

(1) The substrate community is the major factor by which larvae of this species select appropriate settlement sites, choosing to preferentially settle on surfaces from cryptic environments on the reef (i.e., those surfaces dominated by crustose corraline algae). These results support those from Chapter 2, where the highest number of juveniles on the reef were found associated with crustose corraline algae, followed by bare surfaces, turf algae, and sediment-laden substrate. Although the settlement

preferences measured here were strong, the influence of these preferences had a relatively small effect on overall recruitment dynamics when assessed in Chapter 6. As stated previously, this was due to the overwhelming influence of high larval loss and high mortality during the first week after settlement. Despite the relative lack of influence when compared to these other processes, settlement behaviors may still be crucial for ensuring that the few individuals that do survive the larval supply and the early post-settlement bottlenecks recruit into the future adult population, particularly when preferred settlement space is limited.

(2) Larvae of *Porites astreoides* have a preferred light intensity range in which they settle, and they adjust their orientation of settlement to remain within this range. Plasticity in orientation selection based on light intensity is known for multiple species of coral, both from experimental laboratory observations (e.g., Babcock and Mundy 1996) and field observations (e.g. Birkeland et al. 1981). Because of this plasticity and the habitat heterogeneity on the reef, larvae can remain within their preferred light intensity range across a broad depth distribution. In the case of *Porites astreoides*, larvae could locate a preferred light intensity from depths between 0m and 10m in moderately turbid environments, and substantially deeper in low-turbidity areas where light penetration is increased. Even outside this preferred depth range, larvae have the potential to survive, but growth may be compromised due to lower light assimilation. Results from this chapter support the observed distribution of individuals from Chapter 2, where the smallest juveniles were found preferentially on vertical orientations at shallow depths within their preferred light range.

(3) Larvae of *Porites astreoides* have a complex set of settlement behaviors,

responding to multiple cues concurrently to select appropriate settlement microhabitats. Similarities between this study and Raimondi and Morse (2000) suggest the possibility of a general, hierarchical behavioral theory for coral settlement, marked by: depth choice → light/orientation choice → surface community/chemistry choice. Species-specific preferences to each cue are expected as a result of niche partitioning, but the overall strategy of consecutive cue responses among corals may remain as a general ancestral trait. The experimental methodology of Raimondi and Morse (2000) provides an exceptional multi-hypothesis framework by which to test this theory against other species to determine any generalizations that may exist. Validation of a general settlement theory amongst multiple coral species would greatly enhance our theoretical understanding of this critical life stage.

Chapter Four

This chapter assessed the early post-settlement survivorship of *Porites astreoides* in natural reef settings, and tested a number of potential factors that influenced survivorship, including the substrate orientation, the substrate type, and the initial size of a spat at settlement. Major conclusions from this chapter include:

(1) Recently-settled spat experience a major population bottleneck within the first few days after settlement, with measured survivorship rates of 23% and 43% after two days at two separate sites. This result has important implications for coral populations, as higher rates of initial post-settlement mortality have a stronger relative influence on the future population dynamics (Steele and Forrester 2002). Importantly, the factors under study – substrate orientation, substrate type, and initial spat size – had relatively minor

influences on the overall magnitude of early post-settlement survivorship, although all of these factors were significant in at least one of the two reef sites. Instead, it remains unclear which mortality factors in nature are causing these exceptionally high rates of early post-settlement mortality. These high rates are typical of many benthic invertebrates and reef fish, and are often attributed to high predation during this stage for a range of taxa (Gosselin and Qian 1997, Almany and Webster 2006). If predation is driving these high rates, it is likely due to small predators, since caging studies in Chapter 5 with 1x1cm grid cages found only slightly reduced rates of mortality. New evidence suggests that micropredators (e.g., microbes, ciliates) may be driving some early post-settlement mortality (Vermeij 2005, Cooper et al. 2007, Marhaver 2008), but the extent to which these micropredators are responsible for the magnitude of mortality is unknown. Identifying the specific mortality factors responsible for these high rates is vital for advancing this field, and such insights are a necessary prerequisite for building mechanistic detail of the early post-settlement process into future recruitment models. Development of novel techniques will be necessary to identify these factors, since microscopic sizes and the rapidity of mortality events (Cooper et al. 2007) limit the ability to detect these events and their causes in natural reef settings.

(2) The initial size of spat at settlement was an important factor affecting early post-settlement survival at both sites. Although the exact mechanism by which increasing size improved survivorship is unknown, the strength and commonness of this effect, particularly when accounting for other invertebrate groups (Moran and Emlet 2001, Marshall and Keough 2003, Marshall and Keough 2004), suggests larval size is an important determinant of early life-stage success in many benthic organisms. This effect

is presumably due to enhanced energetic reserves in larger individuals, permitting them more flexibility in tolerating and surviving a harsh new environment once they settle. Interestingly, personal observations noted that larval sizes were typically less variable within a colony than among colonies, where some adults produced a cohort of very large and active larvae, while other adult colonies produced markedly smaller individuals as a whole. The fluorescent response of larvae was also noticed to vary in a similar fashion, where a batch of larvae from a single colony typically had a singular brightness in their fluorescent response. If variability in larval sizes among adults is a consequence of the maternal condition (e.g., a healthy adult produces big larvae, leading to carry-over effects, McCormick 2006), factors that stress adults could also indirectly stress their future young, thereby magnifying the net effect of a particular stressor on population dynamics.

Chapter Five

This study assessed the early post-settlement survivorship resulting from seeding larvae directly onto denuded areas of the reef, and explored potential mechanisms by which to enhance survivorship for restoration purposes. Major conclusions from this chapter include:

(1) As in Chapter 4, early post-settlement survivorship was low, and techniques to enhance survivorship (choice of substrate, orientation, or caging) were largely ineffective and had a minimal influence on the magnitude of mortality. This directly corroborates the results of Chapter 4, and underscores the lack of knowledge, and need for more research, on the major mortality factors that drive the magnitude of

early post-settlement survivorship. Importantly, until these mortality factors are resolved, the efficacy of larval seeding as a restoration approach is limited, because lack of knowledge on the major mortality factors impedes development of suitable techniques to enhance survivorship.

(2) Because of the high effort and low return for larval seeding as a restoration approach, restoration efforts should focus on *in situ* settlement and rearing, with *ex situ* transplantation of older individuals to the reef. Because individuals can be kept in controlled conditions with high survivorship while they are most susceptible to mortality (nearly 95% survivorship up to one month in controlled laboratory settings), the early post-settlement survivorship bottleneck can be circumvented, and transplantation of older individuals to the reef can greatly improve their chances of survival. Recent studies have developed enhanced techniques to settle individuals in mass cultures within controlled settings, and then retain them in floating cage structures *in situ* with high survivorship until they reach appropriate sizes for use in restoration (Omori 2005, Edwards 2008). These techniques have proven highly effective, providing 10,000s of new individuals at costs less than $1USD per individual (Edwards 2008), and further advancement of these techniques may provide a substantial source of new individuals for restoration purposes.

Chapter Six

This study assessed the primary drivers of recruitment dynamics by accounting for the full complement of early life stage processes in a spatially-explicit simulation model. Major conclusions from this chapter include:

(1) The loss of larvae from the system prior to settlement on the substrate is particularly high, and can result from either direct larval mortality or export from the reef. Rates of loss approached 99%, and as such represent a major bottleneck for this species and others with similar life histories. Such a high rate of loss has important implications for future population dynamics, as relatively minor changes to the rates of this loss can have relatively strong influences on future dynamics, compared to variability in later life stages. Future research on empirically quantifying pre-settlement mortality and typical dispersal distances will shed valuable insights into the mechanisms and prevalence of this first major population bottleneck during the early life cycle.

(2) The shape of the survivorship function had an overwhelming influence on the size-frequency distribution of juveniles in the system. This occurred despite a relatively small difference between the two shapes of the survivorship function used. While other processes not studied here may additionally contribute to size-frequency distributions, this finding has an important implication with respect to the representation of survivorship in future recruitment models, particularly if size-frequency distributions are used as patterns to calibrate model processes. If survivorship is represented parametrically as here, care must be taken in how survivorship is estimated, and due to the strong sensitivity to this process, a range of plausible functions should be used for calibration and testing purposes.

(3) The influence of habitat on recruitment dynamics was found to be minimal when compared to other processes that led to population bottlenecks earlier in the life cycle. Given the purpose of Chapter 6 – to assess the relative influence of these

different processes by standardizing their contribution to recruitment patterns – this result is not surprising due to the high cohort mortality (>99%) prior to when habitat effects typically occur during the life cycle. As stated above, habitat interactions may be crucial for ensuring that the few individuals that do survive the larval supply and the early post-settlement bottlenecks recruit into the future adult population, and these effects may become more pronounced as suitable habitat becomes limited.

Overarching Synthesis and Implications

In addition to the insights and implications gained from the individual chapters, a few overarching topics emerged as key insights into the understanding and future study of recruitment dynamics. First, as discussed above in the conclusions from multiple chapters, habitat influences on recruitment success were found to be comparatively weak in this dissertation research, since greater than 99% mortality occurs before individuals typically experience habitat effects on post-settlement processes. In addition, habitat effects on settlement may be minimal in average situations, because larvae are motile and can find suitable settlement sites except in unique conditions where space preemption is substantial (e.g., as in Hughes 1989, where algal cover increased from 3% to 95% from 1983-1987). This is not to say these situations do not exist, but they may not represent the norm in most systems of current day (Bruno et al. 2009). As such, simplified models (e.g., Ricker stock-recruitment model) that represent only larval supply processes and avoid computationally-expensive, high-resolution habitat models may be adequate for simulating average recruitment rates for many reef site locations, if the modeling objectives are solely focused on forecasting average recruitment rates.

Second, larval supply is a key driver for recruitment both in broadcast spawning corals (e.g., Hughes et al. 2000), and in brooding corals as found here for *Porites astreoides*. Advancing our understanding of the processes affecting supply is vital (i.e., fecundity, fertilization success, larval mortality, and dispersal), as relatively small changes to rates of supply can have large influences on future dynamics. Of particular importance are fertilization success and larval mortality, since these rates are extremely challenging to ascertain empirically in natural reef settings (e.g., see Levitan et al. 2004 for example on estimating natural fertilization rates). While simple stock-recruitment models (e.g., Ricker 1954, Beverton and Holt 1957) may be suitable for brooding coral species that have short dispersal distances and relatively stable fecundities, complex models incorporating details on fecundity, fertilization, and dispersal mechanisms may be necessary for most broadcast-spawning species (Hughes et al. 2000).

Third, by identifying the key processes that regulate recruitment, this work highlights those stages whose response to environmental change will have exceptionally strong impacts on recruitment and subsequent population dynamics. From a management perspective, knowledge of these relative influences can be vital when faced with decisions on how best to manage the environment given limited resources. For example, if two manageable environmental stressors (coastal run-off and overfishing) each influenced a different early life stage (planktonic larval mortality and post-settlement survivorship, respectively), managers could make an informed decision on which stressor to treat first based on which management option would have a stronger net benefit for recruitment and subsequent population recovery. Here, treating coastal run-off may be most beneficial since larval mortality has the strongest relative influence on recruitment,

and improving these survivorship rates would have a stronger net benefit on future recruitment than improving survivorship in later life stages. However, such choices need to be made with the specifics of the system in mind, as the relative influences of the processes are dependent on the characteristics of the location (e.g., levels of adult cover).

Finally, pattern-oriented and inverse modeling techniques (Wiegand et al. 2003, Grimm et al. 2005) provide a powerful approach for advancing the study of recruitment dynamics. Especially for aspects of the life stage processes that are currently unknown or difficult to assess (e.g., fertilization, larval mortality, post-settlement mortality factors), inverse modeling approaches can identify appropriate parameter estimates if suitable patterns are used to calibrate these unknown processes (Wiegand et al. 2003, Wiegand et al. 2004). The need for multiple patterns by which to calibrate these parameters (Grimm and Railsback 2005) underscores the importance of monitoring programs and natural history observations that focus on simple documentation of patterns in nature. While the modeling techniques presented in this dissertation are an initial start to exploring the cumulative progression of a cohort through these early life stages, it is hoped that these ideas and techniques can serve as a stepping stone for future studies to further our grasp of this enigmatic process.

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