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The Colonial Zoanthid Palythoa caribaeorum: Population Dynamics on Southeast Florida Reefs

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THE COLONIAL ZOANTHID *Palythoa caribaeorum*:

POPULATION DYNAMICS ON SOUTHEAST FLORIDA REEFS

BY

JOANNA C. WALCZAK

A PROPOSAL FOR A THESIS IN THE PARTIAL FULFILLMENT OF THE

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ABSTRACT

The colonial zoanthid *Palythoa caribaeorum* (Cnidaria, Zoanthidea)
(Duchassaing and Michelotti 1861) is a major benthic component of most
Caribbean reefs and is an extremely aggressive spatial competitor (Suchanek and
Green 1981). This study looks at annual visits to 16 permanent monitoring sites
over 3 reef designations (Inshore Ridge Complex, Middle Reef, and Outer Reef)
in Broward County, Florida from 2002-2006. The data obtained in this study fills
an informational void regarding the role of zoanthids in the southeast Florida reef
benthic community. The study was conducted in two parts. Part One used digital
imagery analysis to quantify the spatial cover of the *Palythoa* population present
across the study area. The highest percent live cover sites were located in the
Inshore Ridge Complex, suggesting that the more dense *Palythoa* populations are
close to shore. Part Two used digital analysis data to determine if it was possible
to create a size class transition matrix model that could accurately model the
population distribution of such a dynamic organism. To test the accuracy of the
model, the predicted population distribution of the model and the actual observed
distribution from the digital image analysis were analyzed. A Chi-square test
determined that the model successfully predicted size class distribution frequency
of all treatments (All Sites, High Cover Sites, Low Cover Sites, and the 3 reef
tracts) for all years (2002-2006) with the exception of 3 (Low Cover, Middle
Reef, and Outer Reef) of the 6 treatments in 2005. Southeast Florida experienced
extremely severe hurricane seasons in 2004 and 2005, and the data suggests that
the population distribution at the 3 lower cover (farther from shore) sites were
disturbed. Sensitivity and elasticity analyses were run on appropriate results to

examine which size class transitions contribute most to population stability. Although it possesses the ability to outgrow stony corals (and almost all other sessile invertebrates), the current study suggests that the *Palythoa* population in southeast Florida is generally maintaining size rather than over-growing the reef community. With the knowledge gained from this study, we know that it is possible to accurately model the population dynamics present in the southeast Florida *Palythoa* population.

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1.0.   INTRODUCTION

The colonial zoanthid *Palythoa caribaeorum* (Cnidaria, Zoanthidea) (Duchassaing and Michelotti 1861) is a major benthic component of most Caribbean reefs and is an extremely aggressive spatial competitor (Suchanek and Green 1981). *P. caribaeorum* competition strategies and population dynamics have received attention in other locations such as the US Virgin Islands (Suchanek and Green 1981), Panama (Sebens 1982, Fadlallah et al. 1984), Venezuela (Bastidas and Bone 1996), Brazil (Acosta et al. 2001, 2005, Perez et al. 2005), and even the Florida Keys (Mueller 1992; Haywick and Mueller 1997), but only one other study has looked at the *P. caribaeorum* population in Palm Beach, Broward and Miami-Dade counties in southeast Florida. Kemp et al. (2006) compared the thermal bleaching response of *P. caribaeorum* colonies from three discrete regions in south Florida.

This study is focused on one (somewhat atypical) species, and it fills a void of information regarding the role of zoanthids in the benthic community of SE Florida. This study also addresses the data and duration of monitoring needed to accurately model the dynamics of such a key component of the benthic community. Understanding if population changes are constant (or just as importantly, if they are *not* constant) will help to decipher the dynamics present in the *Palythoa* community of southeast Florida. It is necessary to examine community dynamics in order to eventually identify how individual species may be affecting one another. Too often, monitoring programs are content with documenting fluctuations in abundance; it remains unclear whether any of these data are useful for understanding species-specific dynamics. My study should be combined with other local research and knowledge in order to create a comprehensive community

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ecology prediction model. An ecosystem-wide holistic model of the local benthic community could prove to be a very valuable tool for resource managers.

1.1. Study Area: Southeast Florida

North of the Florida Keys reef tract, the southeast Florida reef system extends approximately 170 km from Miami-Dade through Broward, Palm Beach, and Martin Counties (Collier et al. 2007). Collier et al. (2007) estimates that Florida's shallow-water (defined as less than 18 meters (m) or 60 feet (ft) in depth) coral reef habitat spans 30,801 square kilometers (km^2), of which approximately $41 km^2$ is located within the current study area. Particularly in Broward County, the reef tract is composed of three, increasingly deeper, shore-parallel, linear reef terraces, (Inner, Middle, and Outer Reefs) and an Inshore Ridge Complex, located inshore of the Inner reef (Figure 1) (Moyer et al. 2003; Banks et al. 2007; Walker et al. 2007). These high-latitude reef communities are comprised of coral reefs, and colonized hardbottom or pavement, where the biota present generally consists of variable populations of stony corals, ocotocorals, sponges, zoanthids, and macroalgae (Figure 2) (Moyer et al. 2003; Collier et al. 2007).

The southeast Florida reef system is directly offshore a densely populated and urbanized area and is subjected to extensive anthropogenic impacts (Collier et al. 2007), but has no current management plan. Recreational use (e.g. fishing and diving), coastal construction (e.g. beach nourishments, port maintenance and expansion), and land based sources of pollution (e.g. sewer and treated wastewater outfall pipes, and tidal exchanges through inlets), have impacted the reefs. In 2005 alone, 396 million

gallons per day (MGD) of sewer and secondarily treated wastewater from the six active outfall pipes was introduced into the water column near these viable reef communities (Koopman et al. 2006). The three outfall pipes (Boca Raton, Broward/North, and Hollywood) located in (or near to) the study area account for approximately 140 MGD of this nutrient laden wastewater (Figure 3).

Generally, scleractinian (stony) corals receive the most attention in SE Florida reef studies, even though this group contributes less cover (2-3%) than other sessile invertebrates (Gilliam et al. 2005). Functional groups such as sponges, gorgonians, and zoanthids often dominate over stony corals for spatial cover in SE Florida (Goldberg 1973; Jaap 1984; Moyer et al. 2003), yet receive comparatively less attention.
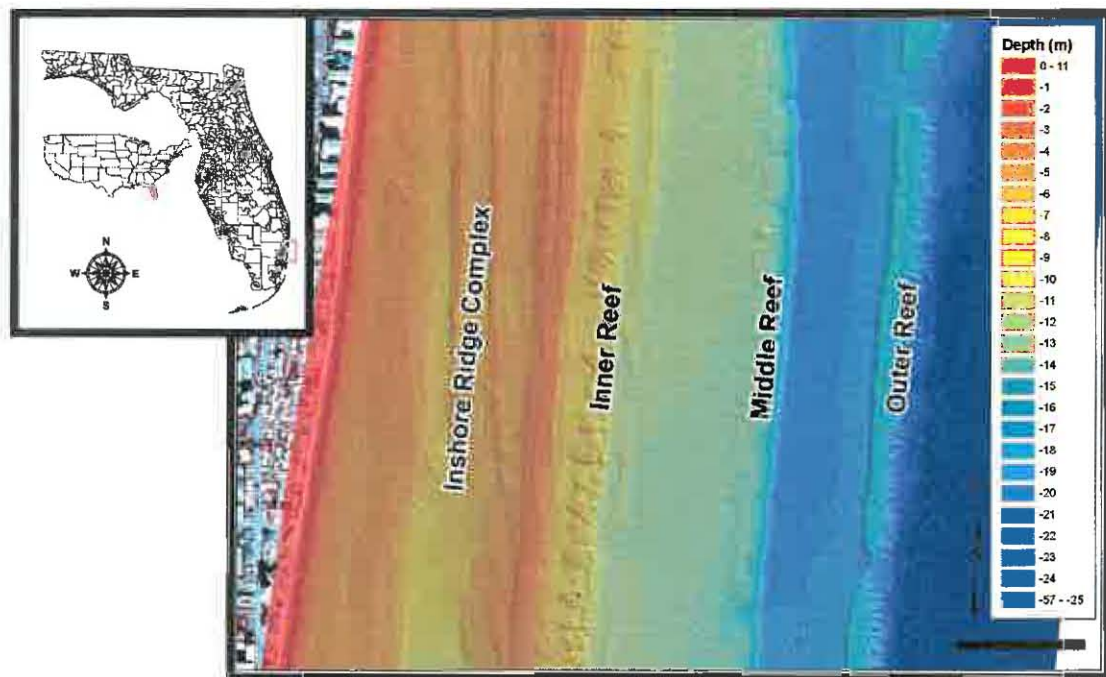
Figure 1: Laser Airborne Depth Sounder (LADS) bathymetry data of Broward County showing the high-latitude reef communities consisting of 3 parallel, linear reef habitats (Inner, Middle, and Outer Reefs). Inshore of the Inner Reef is a series of shallow, nearshore ridges (Inshore Ridge Complex). Note: Depth profile increases with distance offshore.
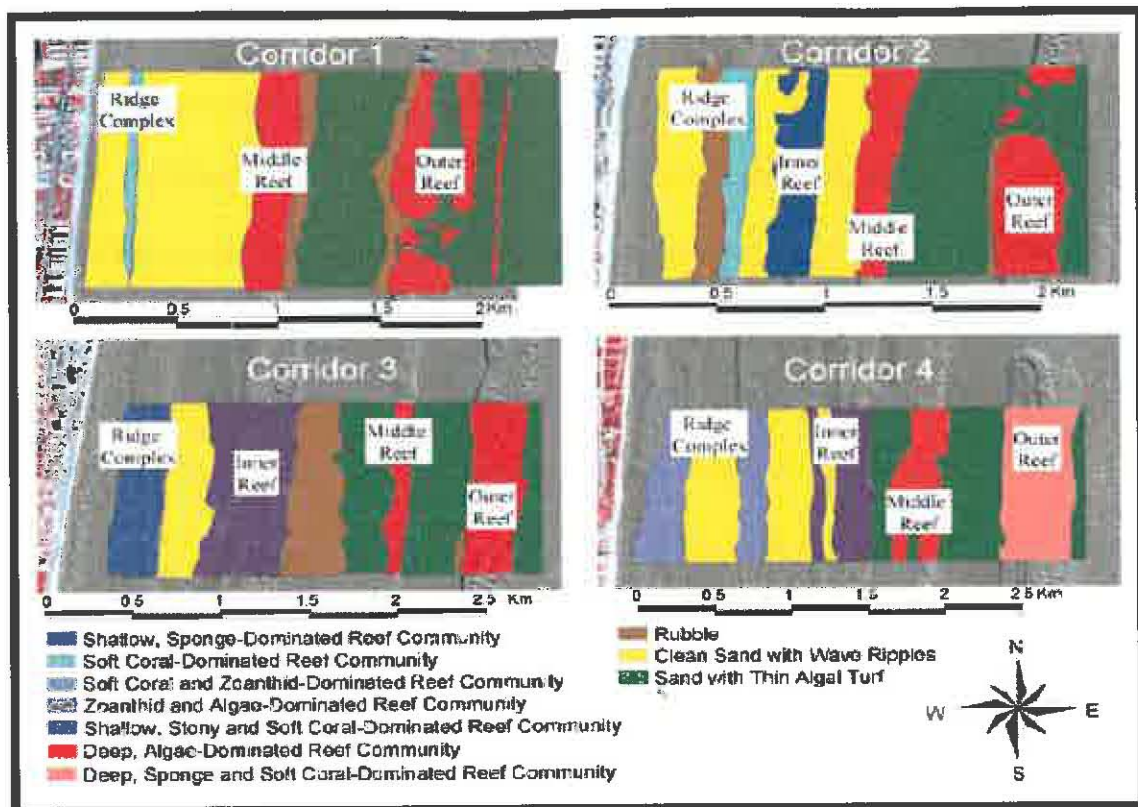
Figure 2: Broward County, FL habitat classifications for four "corridors" identified in the Moyer et al. (2003) study showing the Inner Reef as zoanthid and algae-dominated.

Figure 3: Southeast Florida counties with ocean outfalls (Koopman et al. 2006).

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1.2. Natural History of *Palythoa caribaeorum*

1.2.1. *Taxonomic Description*

Current taxonomic descriptions of the genus *Palythoa* are outdated, and most zoanthid researchers agree that *Palythoa caribaeorum* and *Palythoa mammillosa* are probably the same species (Sebens 1982; Gleibs et al. 1995; Haywick and Mueller 1997). For this study, I consider them to be synonymous (possibly morphotypes) and will therefore refer to them as the more common *Palythoa caribaeorum*.

P. caribaeorum (hereafter referred to as *Palythoa*) colonies are small yellow-brown conjoined polyps that form sheets over the substratum (Sebens 1982; Haywick and Mueller 1997). The polyp diameter (5-10mm) and colony thickness (5-30+mm) are both highly variable (Haywick and Mueller 1997) and according to Sebens (1982) polyp size is generally a colony characteristic and may be related to habitat. *Palythoa* commonly inhabits reefs in the Atlantic and Caribbean seas from central Florida to as far south as São Palo, Brazil (Goreau 1959; Kinzie 1973; Sebens 1977, 1982; Suchanek and Green 1981; Acosta et al. 2001, 2005). Mainly found in shallow reef habitats, *Palythoa* forms distinctive, monospecific mats that often dominate available substrate (Fadlallah et al. 1984; Mueller 1992). Their small polyp size, conjoined polyp colony formation and ability to retain carbonate sediment in their body walls (Figure 4) allows them to survive in high energy areas where strong currents and storm waves frequently disrupt the community (Koehl 1977; Suchanek and Green 1981; Jackson and Hughes 1985; Done 1992; Haywick and Mueller 1997). Their shared column wall morphology and small polyps creates a regular surfaced colony that is capable of minimizing the damaging drag of water flow (Koehl 1977).

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According to Fadlallah et al. (1984) the lack of a hard skeletal structure limits zoanthids to lateral growth over the substrate.
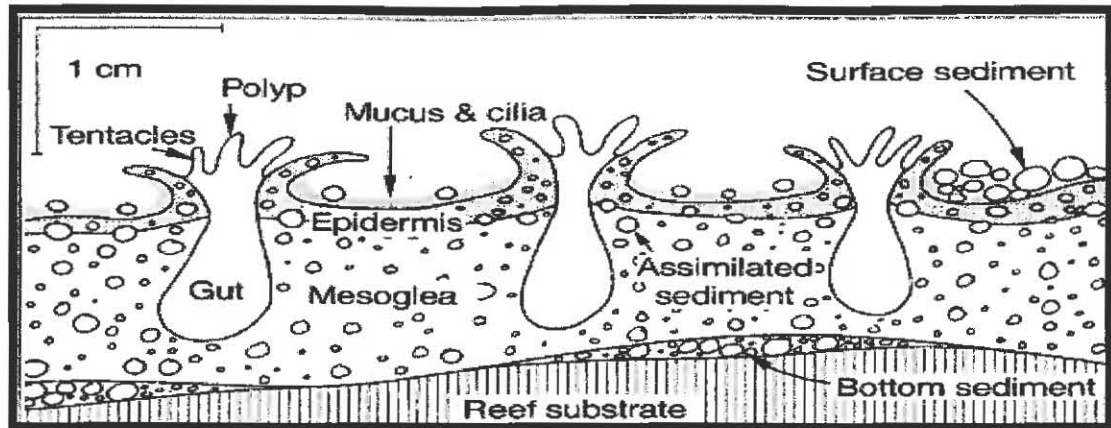
Figure 4: Schematic cross section through *Palythoa* spp. showing conjoined polyps and how they form a sheet over the substratum. Note assimilated sediment throughout the tissue (Haywick and Mueller 1997).

Although zoanthids do not directly contribute to reef formation, *Palythoa* colonies have similar architecture and nutritional resources as scleractinian corals (Sebens 1977; Karlson 1981; Sebens 1982; Suchanek and Green 1981). *Palythoa* colonies rely on both autotrophic and heterotrophic nutrition (Sebens 1977). Sebens (1977) showed that *Palythoa* is diel in nature, and primarily feeds on zooplankton between dusk and dawn while utilizing their zooxanthellae for photosynthesis during the day. *Palythoa* are very sensitive to environmental conditions and are commonly the first to exhibit bleaching, thus they may be useful as a quantitative indicator of bleaching events (Mueller 1992; Kemp et al. 2006).

1.2.2. *Reproduction*

Palythoa utilizes both sexual and asexual reproduction (Karlson 1981) in population size maintenance, though asexual reproduction is by far the better

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understood process in zoanthids (Cooke 1976; Karlson 1986a, 1986b; Karlson 1991; Acosta et al. 1998; Acosta and Sammarco 2000a, 2000b; Acosta et al. 2001, 2005; Boscolo and Silveira 2005). Acosta et al. (2001) reports that asexual reproduction in zoanthids is achieved through fission and fragmentation. Fission, defined by Neufeldt (1997) is "a form of asexual reproduction... in which the parent organism divides into two or more appropriately equal parts, each becoming an independent individual" and is primarily endogenous and results in the production of ramets (Acosta et al. 2001). Acosta et al. (2005) examined asexual reproduction by fission in the formation of crevices throughout the *Palythoa* colony. Hughes and Jackson (1985) found that partial colony mortality and fission in clonal organisms may increase the number of colonies as much as or more than sexual reproduction. On the other hand, Hughes (1989) defines fragmentation as "the reproductive process by which a live portion of a colony becomes divided into one or more parts by processes exogenous to the organism", with parts becoming physically separated from the parent colony, and with each having the potential to grow into a complete organism (Highsmith 1982; Acosta et al. 2001). Fragmentation can occur by either biotic factors such as predation, disease, etc. that cause tissue isolation, or by physical factors such as storms, currents or tides (Karlson 1983; Hughes 1989; Acosta et al. 1998; Acosta and Sammarco 2000a, 2000b; Acosta 2001). Acosta (2001) observed a much higher rate of biotic fragmentation in shallow water due to disease, which in itself may be caused by the physical stress factor of increased wave energy. Asexual processes appear to be facilitated by recurrent physical disturbances such as severe

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storms and hurricanes (Highsmith 1981; Tunnicliffe 1981; Karlson 1983), both of which are exceedingly common in southeast Florida.

Sexual reproduction in zoanthids is complicated, and its contribution to population maintenance is not very well understood (Karlson 1981). *Palythoa* colonies contain both male and female polyps, but most colonies are female dominated (Fadlallah et al. 1984; Ryland 1997; Boscolo and Silveira 2005). A small percentage of the individual polyps can also be hermaphroditic (Boscolo and Silveira 2005). Colonies utilize broadcast spawning with external fertilization (a planktonic larval stage) (Babcock and Ryland 1990). Spawning has been correlated with seasonal variations of environmental conditions such as the start of the wet season in Panama (Fadlallah et al. 1984). In Brazil, although egg release was found to be continuous, sperm release was only documented for six months (December to May) (Boscolo and Silveira 2005). Boscolo and Silveira (2005) found that the central regions of the colonies are the most fertile, while the edge regions showed a higher percentage of sterile polyps. These sterile polyps "may be indicative of the importance of asexual division in these colonial organisms" (Fadlallah et al. 1984). As more research concentrates on the population dynamics of zoanthids, sexual reproduction may prove to be an underestimated process in population dynamics.

1.2.3. *Spatial competition*

In shallow reef environments with high recruitment and growth rates of the various colonizers, competition is particularly important (Connell 1983; Schoener 1983). Sessile invertebrates use many different strategies in the competition for

substrate (Jackson 1977). *Palythoa* generally "acquire and dominate space by killing or directly hindering the growth of its competitors both by physical (i.e. growing directly over nearby corals or invertebrates) and chemical means" (Suchanek and Green 1981). When presented with a spatial opportunity, *Palythoa* has a fast initial growth rate (Bastidas and Bone 1996), but once the space is consumed, instead of continuing to grow, the growth rate is suspended (Bastidas and Bone 1996). Members of the genus *Palythoa* contain a very potent neuro-toxin (Palytoxin or PTX) which is speculated to be used as an antifeedant in predatorial defense and possibly as an allomone in spatial competition (Scheuer 1964; Moore and Scheuer 1971; Attaway and Ciereszko 1974; Sebens 1981; Suchanek and Green 1981; Fox 1982; Beress et al. 1983; Gleibs et al. 1995; Haywick and Mueller 1997). Isman (1993) defines an antifeedant as a defense chemical which inhibits feeding, but which is also classified as an allomone. An allomone is a chemical messenger between species that is beneficial to its producer and detrimental to its recipient (Brown et al. 1970).

Although predation is not considered to be an important factor controlling *Palythoa* populations, Attaway and Ciereszko (1974) found that the eggs of Jamaican *Palythoa mammillosa* colonies were highly (PTX) toxic. Also noted is that overall colony toxicity shows seasonal variations (with maximum toxicity reached in the summer months of June, July, and August) as well as habitat variations (Attaway and Ciereszko 1974). The only observed predator is the fireworm, *Hermodice carunculata*, which has been observed feeding on physically injured colonies (Suchanek and Green 1981; Sebens 1981). It has also been observed that *H. carunculata* feeds on certain bands of disease on scleractinian corals (Miller pers.

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comm.), it may prove to be that fireworms are acquiring the PTX (and the coral disease agents) to supplement their own predatorial defense mechanisms, rather than for its nutritional value.

Another form of territorial (as well as predatorial) defense is *Palythoa's* ability to retain sediment in its body walls (Sebens 1981; Suchanek and Green 1981; Fadlallah et al. 1984; Haywick and Mueller 1997). The sediment allows the colonies to survive in very high energy zones by acting as a stabilizer against high wave energy, as well as being highly unappealing to predators (Haywick and Mueller 1997).

Due to its high growth rates (linear growth = 2.5 – 4.0 mm/day) and lack of predators, *Palythoa* is an extremely aggressive competitor for space (Suchanek and Green 1981; Bastidas and Bone 1996; Mueller 1992). With the exceptions of the encrusting gorgonian *Erythropodium caribaeorum* (Karlson 1980; Brazeau and Lasker 1992) and the colonial tunicate *Trididemnum solidum* (Birkeland et al. 1981), *Palythoa* has been shown to be capable of overgrowing most other sessile invertebrates (Karlson 1980; Sebens 1981; Suchanek and Green 1981). *Palythoa's* competitive abilities haven't been studied in southeastern Florida. Future studies will need to take into account that short-term studies lack the ability to identify all factors that might contribute to the patterns observed (Sebens 1981; Bastidas and Bone 1996).

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1.2.4. *Population size regulation*

Fast growing organisms such as zoanthids and sponges can have a competitive edge over stony corals when nutrient supply is high (Buss and Jackson 1981; Goreau 1992; Hallock et al. 1993; McCook 1999; Holmes 2000). Lapointe et al. (2002) believe that *Palythoa* is an indicator of nutrient enrichment, and that reduced stony coral cover is significantly correlated with an increased *Palythoa* population. Costa (2001) also believes that *Palythoa* are the organisms most adapted to take advantage of an increase in nutrient concentrations in coastal areas. The estimated 41km² of shallow reef habitat in Broward County is constantly influenced by coastal run-off, tidal exchanges from Port Everglades and approximately 140 MGD of treated wastewater. With suitable substrate and excessive nutrients available, the question now raised is why isn't *Palythoa* taking over the reefs in southeast Florida since they seem to be in such a prime location for domination? Previous research suggests that *Palythoa* is capable of overgrowing most scleractinian corals, so there must be some unknown limiting factor keeping the population regulated. One possibility is that it is rare for sessile assemblages to be completely hierarchial (Buss and Jackson 1979) due to similar competitive abilities between species (Sousa 1984; Connell and Keough 1985). Sebens (1982) stated that it may be competition with other encrusting organisms or zoanthids that affects *Palythoa*'s distribution. Another possible explanation is that a population equilibrium maximum exists, at which point the population will focus its energy on maintenance, rather than growth (Tanner 1997). Tanner (1997) showed that density has "an obvious negative impact on *Palythoa* colonies..." where the "...main effects of increasing density are an increase in fusion

rates, and a decrease in fission rates". Tanner (1997) also found that large colonies had substantially lower growth rates at the higher densities. Mortality, on the other hand, was unaffected by density, and recruitment was only marginally enhanced at intermediate densities (Tanner 1997). *Palythoa* population size is most likely regulated by fission and/or fusion when density reaches this unknown population equilibrium maximum (Tanner 1997).

1.3. Review of Transition Matrix Models and Their Associated Analyses

1.3.1. *Transition Matrix Models*

The ultimate size of a sessile invertebrate population is determined by its fertility and mortality cycles (Bierzychudek 1982). Once these birth and death patterns have been identified, it is possible to predict changes in population structure through time, and examine the potential effects of those changes on the population (Bierzychudek 1982). Population projection (also known as transition) matrix models are an increasingly valuable tool for the evaluation of size class, age, or stage structured population dynamics (Hughes 1984; Hughes and Connell 1987; van Groenendael et al. 1988; Babcock 1991; Caswell 1997a and 1997b; Bierzychudek 1999). Population growth transition matrix models were first introduced by P.H. Leslie (1945, 1948). The Leslie model uses age-specific fecundity and survival rates to predict the eventual age structure of a population. "These models specify a matrix of transition probabilities between different size classes, age classes, or stages in a population from time t to time t+1" (Bierzychudek 1999). The population (equilibrium) growth rate, lambda (λ), is a function of the entries of the population-

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projection matrix, and can be used to assess the overall health of the population (Horvitz et al. 1997; Caswell 2001; Bierzychudek 1999). According to Bierzychudek (1999), "repeated iterations of a matrix can provide a projection of a population's equilibrium growth rate (under certain assumptions)". Finding the equilibrium growth rate will determine if the population will grow (or shrink) at a constant rate (Hughes 1984). A lambda value greater than 1.0 denotes a population capable of exponential growth, a value equal to one signifies stability, while a lambda between one and zero indicates that the population is in decline to eventual extinction (Hughes 1984). Also, a population with a high growth rate ($\lambda > 1.0$) is expected to exhibit an increased density and may eventually reach a population size at which density becomes a major factor in development (Bierzychudek 1999).

The major assumption of the Leslie model is that the population will grow or decline at a completely constant and linear rate, while preserving a stable age distribution (Hughes 1984). For a size class transition matrix, a population's stable age distribution is defined as the point at which each size class is changing by the factor λ each time period (Bierzychudek 1999). Caswell (1989) makes the point that this kind of model should be considered a projection since stochastic changes in a population's environment make it highly unlikely that the vital rates measured for a population will in fact remain constant over time (Bierzychudek 1999). Keyfitz (1972) states that a projection is what *would* happen to a population if all assumptions and vital rates were constant, instead of forecasting what *will* happen. In 1965, Lefkovitch adapted the standard Leslie matrix model to eliminate any assumptions of relationship between an organism's size and age, thus presenting a model based on

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stages. This was a biologically necessary step since, for most individuals, age is impossible to determine by observation alone, but given a known history of the species, a stage could be more readily identified (Lefkovitch 1965). For example, a human's age could at least be estimated by observing their current stage (e.g. baby, child, teenager, or adult).

Stages can usually be identified in most species, but zoanthids are similar to scleractinian corals in that their growth is not strictly limited to a planar axis and their size does not necessarily reflect their age (Jackson and Hughes 1985). This makes it exceedingly difficult to estimate an individual's age or stage without having observations from the inception of the original parent colony(ies). Even if the parent colonies were known, *Palythoa*'s ability to divide one colony into several "daughter" clone colonies (and fuse back together again) creates huge variations in size between individuals in the same age class (Hughes 1984). These variations can easily lead to an overestimate of survivorship since it is incredibly difficult (if not impossible) to distinguish between a new recruit and a rejuvenating individual (Mertz and Boyce 1956; Hughes and Jackson 1980; Hughes 1984). Therefore, a size-class transition matrix model is the only suitable model for examining *Palythoa* population dynamics.

Additionally, transition matrix models (such as the Lefkovitch model) need to take into account shrinkage, growth, and non-growth. Non-growth represents a stage that does not progress/develop into whichever stage is next, but rather maintains its current size. The Hughes (1984) size-class transition matrix model takes all of these considerations into account but also includes asexual fragmentation and partial mortality. The Hughes model was used as the basis for this study.

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In a size-class transition matrix model, a matrix **M** is constructed of the probabilities (α) of one size class ($_i$), transitioning to another size class ($_j$), which is written as α_{ij} (i.e. if a colony in size class 1 was to transition into size class 7 it would be written as α_{17}). The vector (**v**) represents the number of individual colonies in each size class at time t (Bierzychudek 1982). Thus resulting in a matrix **M**(t) multiplied by the vector (**v**) which provides the "probabilities of transition" between differing size classes at the time interval (t, t+1) (Bierzychudek 1982, 1999). By evaluating the matrix, a population's equilibrium (or stable) growth rate (λ) can (under certain assumptions) be ascertained because, in the terminology of linear algebra, the growth rate (λ) is the dominant eigenvalue of the matrix (Leslie 1945; Caswell 1989; Bierzychudek 1999; Case 2000).

1.3.2. *Sensitivity and Elasticity Analyses*

Critical life history stages can be identified by investigating a transition probabilities matrix with sensitivity and elasticity analyses (Bierzychudek 1999). Sensitivity and elasticity values are a function of the specific entries in the transition matrix (Bierzychudek 1999; Caswell 2000) and can be used to "predict the response of lambda to changes, of any size, in any or all of the parameters" (Caswell 1978, 2001). By identifying the transitions that contribute the most to the dynamics of a population, we know what to focus on for future research.

The sensitivity is the slope of log lambda as a function of α_{ij} and is an integral part of demographic analysis importance using λ as a measure of population growth rate and of fitness (Caswell 1978; Caswell and Trevisan 1994; Caswell 2000; Caswell

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2001; Caswell et al. 2004). Caswell (2001) reports that "elasticity is the slope of log lambda as a function of log α_{ij}". For any single matrix, the elasticities of λ measure the proportional contribution of the matrix entries to population growth and sum to 1 (de Kroon et al. 1986; Caswell 1989; Mesterton-Gibbons 1993; de Matos and Matos 1998; Benton and Grant 1999; Mills et al. 1999; de Kroon et al. 2000; Grant and Benton 2000; Heppell et al. 2000; Ehrlen et al. 2001).

Neither analysis is better suited, less bias, or more accurate than the other, rather, they are different ways of looking at a perturbation of the matrix model. For instance, if a transition probability value were increased from zero to a small positive number the sensitivity indicates what would happen to lambda while the elasticity would indicate what proportion of that change contributes to lambda (see van Groenendael et al. 1994) (Horvitz et al. 1997).

1.4. Study Goals

The current study has two main goals, and was conducted in two parts. The first goal (Part One) is to use digital imagery to quantify the spatial cover of *Palythoa* and provide a general overview of the *Palythoa* population present across the study area. This information fills an informational void regarding the role of zoanthids in the benthic community of SE Florida.

The second goal (Part Two) is use digital analysis data to determine if it is possible to create an accurate size class transition matrix model for *Palythoa*. The model is then tested by comparing the predicted outcomes of the model with observed outcomes from the digital image analysis. Any statistically significant differences

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between the observed and predicted observations are examined and subsequent sensitivity and elasticity analyses were run on the appropriate results. Finally, I assessed the data and duration of monitoring needed for future studies, and explored any limitations of the current study.

2.0. METHODS AND MATERIALS

2.1. Study Sites

Data were collected from 16 permanent reef monitoring sites established for the Broward County Annual Monitoring Project in southeast Florida (Table 1, Figures 1 & 5) (Gilliam et al. 2006, 2007). Each site consists of a belt quadrat transect marked with 21 stainless steel pins fixed in the substrate, one meter apart ($\pm$ 1.0 cm). Transect pins were arranged linearly running generally in a north/south direction. The quadrat in the northeast corner of each transect was assigned quadrat #1 in order to keep the quadrats consistent. Transect analysis at each site is consistent with methodology described by Dodge et al. (1982), with 30m² of bottom being analyzed per transect (0.75m² x 40 quadrats).

Table 1: Coordinates, reef designations, and depths for each of the 16 monitoring sites.

SITE	REEF	DEPTH (ft)	LATITUDE (dd.mmm)	LONGITUDE (dd.mmm)
HH2	Inshore Ridge Complex	19	26 00.694 N	80 06.757 W
JUL6	Inshore Ridge Complex	12	26 04.912 N	80 06.222 W
FTL4	Inshore Ridge Complex	20	26 08.208 N	80 05.844 W
FTL5	Inshore Ridge Complex	25	26 08.985 N	80 05.810 W
FTL1	Inshore Ridge Complex	19	26 09.534 N	80 05.747 W
POMP4	Inshore Ridge Complex	20	26 12.732 N	80 05.201 W
POMP1	Inshore Ridge Complex	20	26 11.435 N	80 05.225 W
JUL1	Middle Reef	40	26 00.301 N	80 05.813 W
POMP2	Middle Reef	48	26 11.328 N	80 04.803 W
HB2	Middle Reef	·35	26 16.535 N	80 04.262 W
DB2	Middle Reef	37	26 18.628 N	80 04.026 W
BOCA1	Middle Reef	30	26 20.803 N	80 03.883 W
POMP6	Middle Reef	52	26 14.566 N	80 04.398 W
JUL8	Outer Reef	50	26 04.995 N	80 05.099 W
POMP3	Outer Reef	51	26 11.214 N	80 04.365 W
HB3	Outer Reef	49	26 16.425 N	80 03.818 W
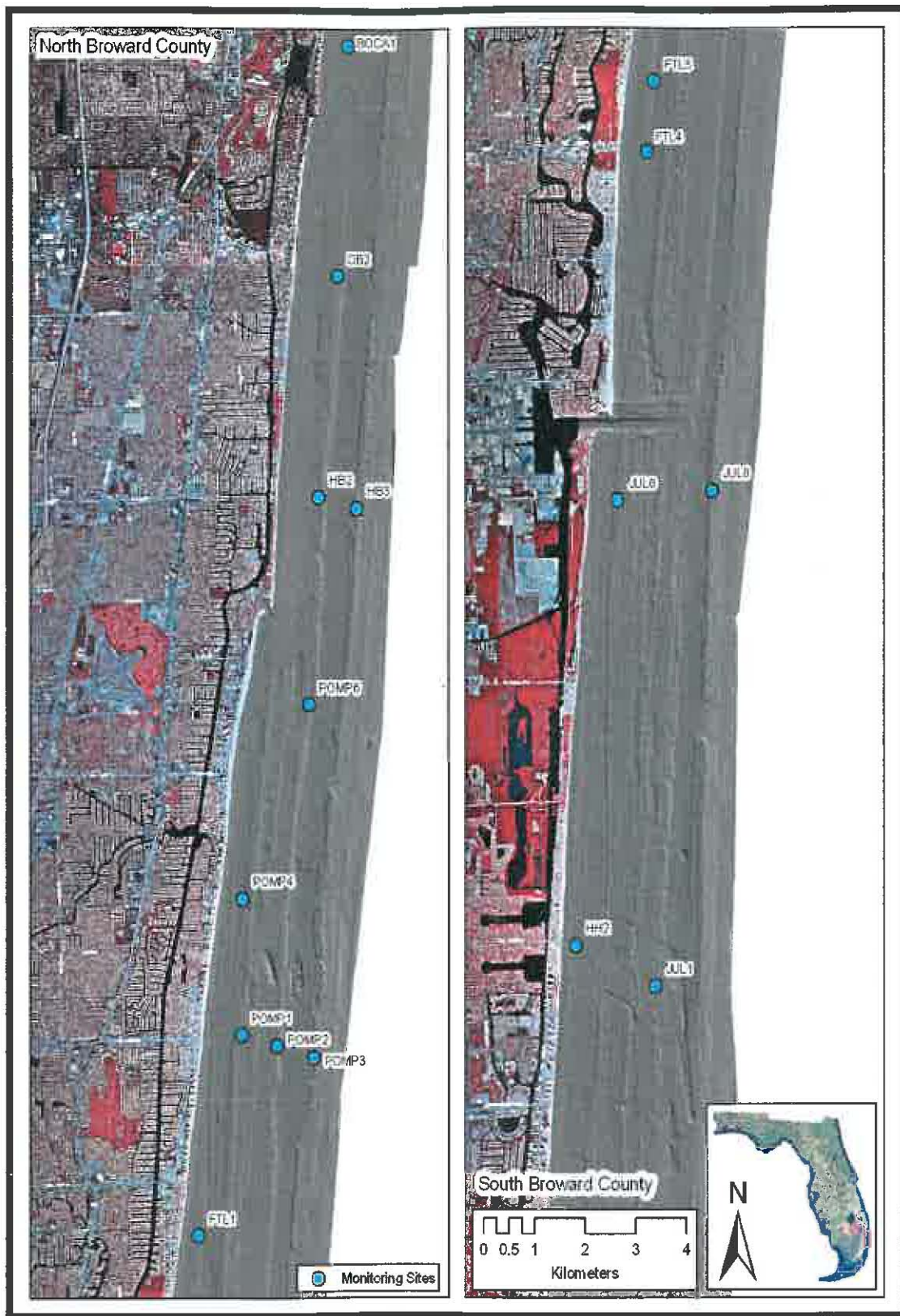
Figure 5: LADS bathymetry data of Broward County, Florida showing the locations of the 16 permanent monitoring sites. Monitoring site locations are shown as labeled dots.

2.2. Data Collection

2.2.1. *Field Techniques*

Using SCUBA, images of each transect quadrat were taken using a digital camera (Olympus 5060 with Ikelite housing) fitted with a wide angle lens (equivalent to a conventional 20mm lens) attached to a 0.75m² quadrat framer (Figure 6). Tags with the site code, quadrat number (1-40) and date were attached to the framer (Figure 7) and included in each image for reference. Two divers were used to control the camera and framer positioning. The dates of the annual visits for 2002-2006 can be found in Table 2.

Figure 6: Diver photographing 0.75m² quadrats along a 30m² transect.
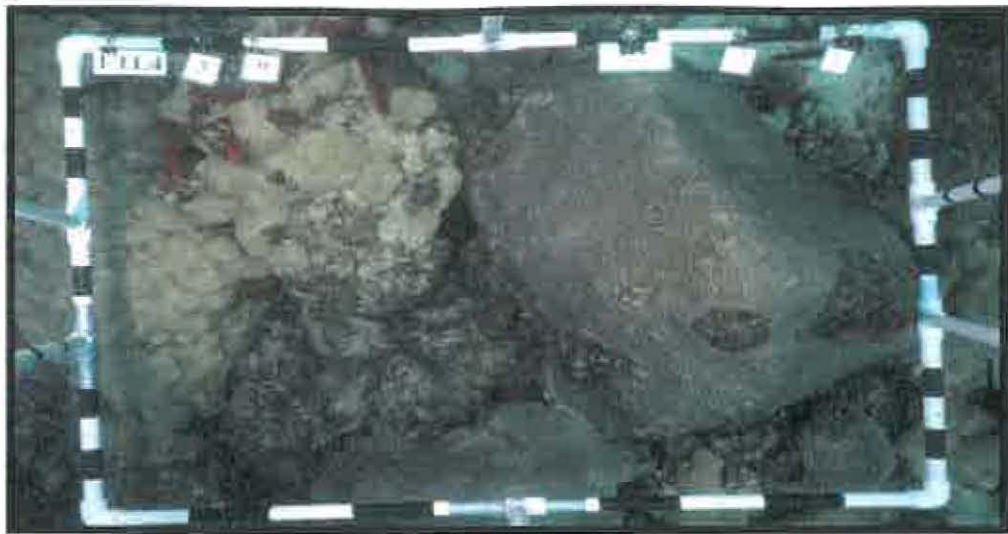
Figure 7: Example of a phototransect quadrat image with *Palythoa* cover. Note site code (FTL4), quadrat number (#39) and date (Sept 21).

Table 2: Dates of the 16 annual site visits (Note: Site FTL5 was added to the project in 2003).

Site	DATE COMPLETED 2002	DATE COMPLETED 2003	DATE COMPLETED 2004	DATE COMPLETED 2005	DATE COMPLETED 2006
HH2	16 Sep 2002	10 Sep 2003	18 Aug 2004	07 Feb 2006	24 Aug 2006
JUL6	23 Oct 2002	13 Oct 2003	14 Oct 2004	09 Dec 2005	24 Aug 2006
FTL4	25 Oct 2002	18 Sep 2003	03 Nov 2004	13 Jan 2006	11 Oct 2006
FTL5	N/A	25 Nov 2003	03 Nov 2004	14 Oct 2005	13 Oct 2006
FTL1	02 Oct 2002	20 Oct 2003	30 Aug 2004	14 Oct 2005	06 Sep 2006
POMP4	09 Oct 2002	20 Oct 2003	19 Aug 2004	20 Dec 2005	11 Oct 2006
POMP1	07 Oct 2002	30 Sep 2003	01 Dec 2004	17 Feb 2006	25 Aug 2006
JUL1	16 Sep 2002	10 Sep 2003	18 Aug 2004	07 Feb 2006	24 Aug 2006
POMP2	09 Oct 2002	01 Oct 2003	19 Aug 2004	09 Dec 2005	11 Oct 2006
HB2	07 Oct 2002	30 Sep 2003	19 Aug 2004	01 Sep 2005	25 Aug 2006
DB2	08 Oct 2002	15 Sep 2003	19 Oct 2004	12 Oct 2005	09 Oct 2006
BOCA1	22 Oct 2002	15 Oct 2003	31 Aug 2004	15 Sep 2005	08 Sep 2006
POMP6	02 Oct 2002	02 Oct 2003	30 Aug 2004	13 Jan 2006	06 Sep 2006
JUL8	16 Sep 2002	10 Sep 2003	18 Aug 2004	07 Feb 2006	24 Aug 2006
POMP3	07 Oct 2002	18 Sep 2003	19 Oct 2004	01 Sep 2005	25 Aug 2006
HB3	08 Oct 2002	15 Sep 2003	26 Oct 2004	12 Oct 2005	09 Oct 2006

2.2.2. *Laboratory Techniques and Photographic Analysis:*

The digital images of each site were analyzed using Coral Point Count with Excel™ extensions (CPCe). Although the monitoring project has 25 sites, 9 of those sites were removed from this study because the sites either did not have *Palythoa* cover for at least one sampling period, or the image sets were incomplete or unsuitable for image analysis. CPCe's scaling calibration (Figure 8) and area trace options (Figure 9) were used to accurately determine the planar area of the *Palythoa* colonies (Kohler and Gill 2006). Care was taken to not include anything outside of the frame, dead spots in the colonies, or any area where another species had overgrown *Palythoa*.
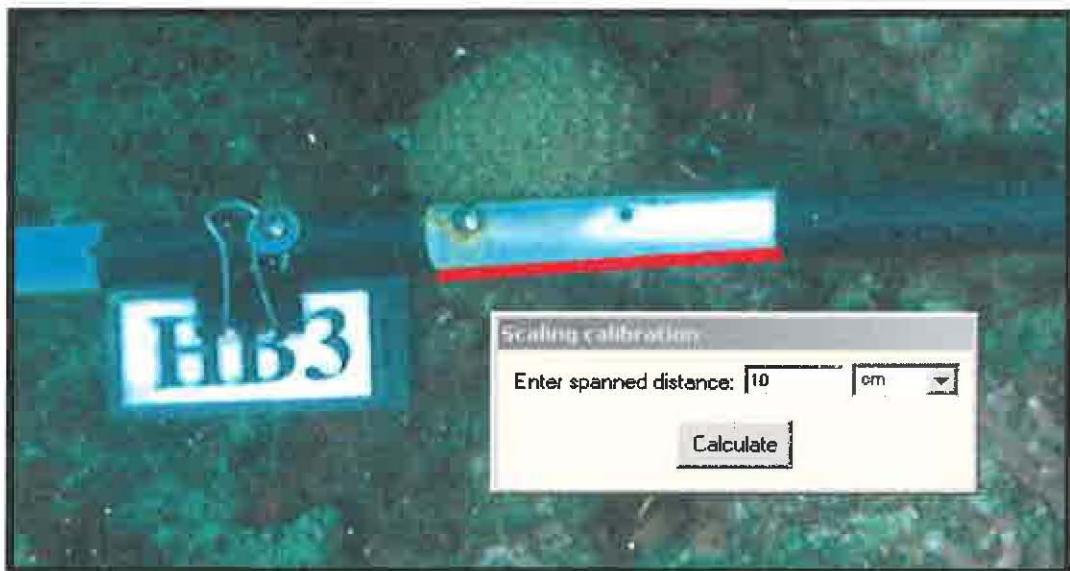
Figure 8: Screenshot of the image scaling and calibration process (Kohler and Gill, 2006)

Figure 9: Screenshot of the CPCe software, showing traced areas and lengths, outlined areas, and movable text boxes. The areas of traced regions can be saved as bitmapped images.

2.2.2.1. Part 1: General *Palythoa* population dynamics

For all 16 sites, the total live *Palythoa* colony area (cm²) of each individual transect quad (1-40) within each site was calculated. Additionally, the total cover area (cm²) and percent live cover were determined for each site. All sites were analyzed in this way for each sampling year (2002-2005) resulting in a mean percent live cover and the yearly change in percent live cover (Figure 10).

The data was then grouped into one of six treatments: All Sites (All), High Cover (HC), Low Cover (LC), Inshore Ridge Complex (IRC), Middle Reef (MR), and Outer Reef (OR) (Note: Although monitoring sites exist on the Inner Reef, they were not included in the present study due to incomplete data). Single factor ANOVA's were run to test for significance within reefs among years and among reefs within years. Parametric ANOVA relies on the assumption of normally

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distributed data and constant variance between groups (sites or years). In order to address these assumptions, *Palythoa* cover data was arcsine transformed prior to statistical analyses.
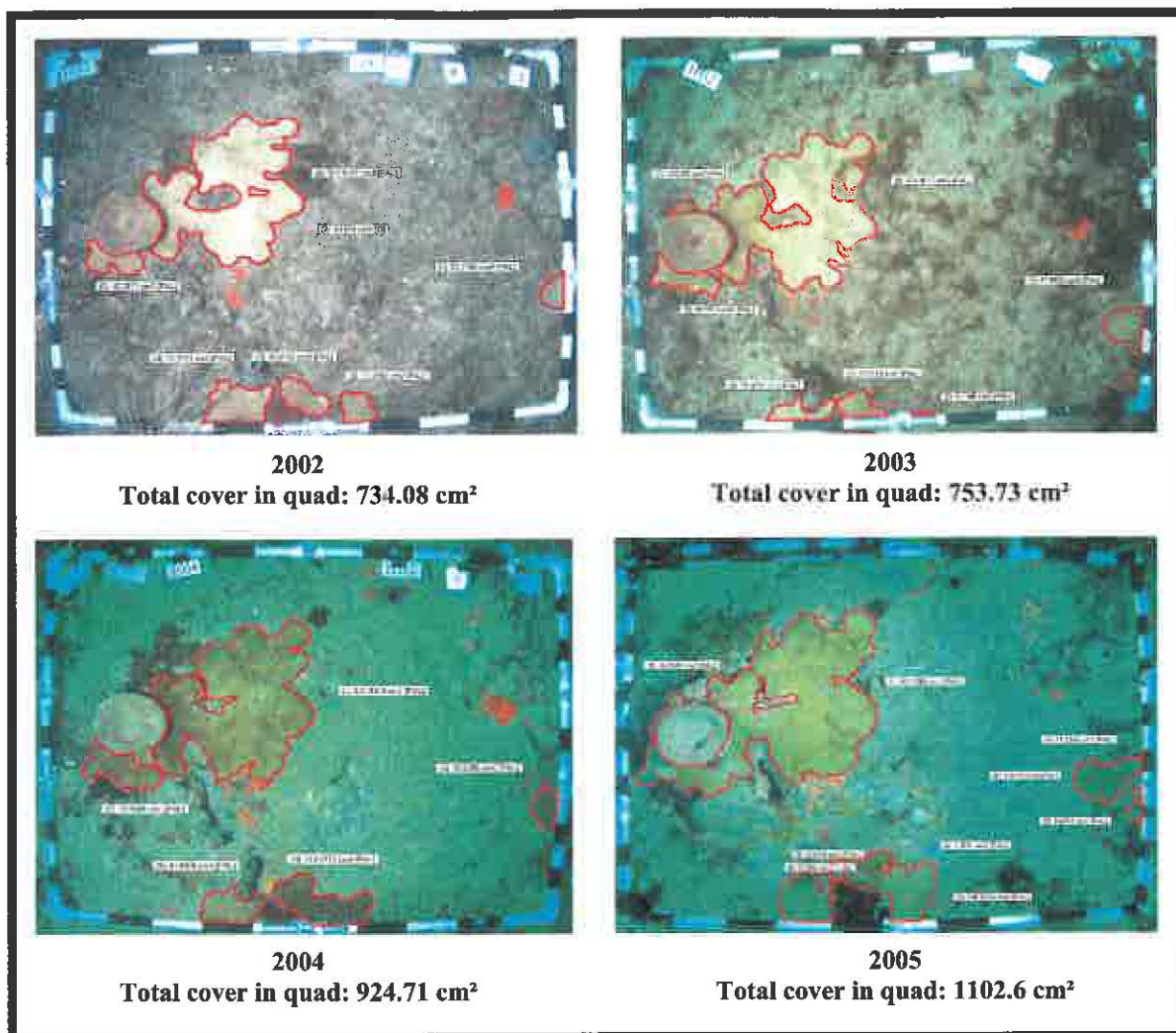
Figure 10: Example images of increase in total *Palythoa* area (cm²) from 2002-2005 at site HB2 Quad #2 using CPCe software. Note: Colonies are outlined in red; individual colony areas (cm²) are listed in white boxes.

2.2.2.2. Part 2: Transition Matrix Model

2.2.2.2.1. *Life Cycle Graph and General Matrix Model*

In order to understand the complex dynamics of *Palythoa*, a life cycle graph was created (Figure 11). "A life-cycle graph describes the transitions an individual can make, during a projection interval, among the *i*-state categories that define its life cycle" (Tuljapurkar and Caswell 1997). Arrow directions represent "the contributions from one stage to another resulting from the movement of individuals from one stage to another (e.g., by growth, or aging) or from production of new individuals (e.g., by birth)" for a determined projection interval (Tuljapurkar and Caswell 1997). The general matrix model entries correlate to the coefficient associated with each of the movements or transitions between stages in the life cycle graph. When looking at a general size-class transition matrix model (Figure 12), "probabilities below the diagonal represent net growth into a larger size class. The diagonal describes the likelihood of an individual remaining in the same size class, either through a slowing down in growth rates, or a balance between growth and shrinkage. Finally, probabilities above the diagonal represent contributions to a smaller size class, i.e., through shrinkage, fragmentation, or sexual reproduction" (Hughes 1984). Following the Hughes (1984) general graph model (Figure 12), I created a life cycle graph for *Palythoa* using a projection interval of one year, and seven separate "nodes" (also known as size classes; see Table 3) (Caswell 1989).
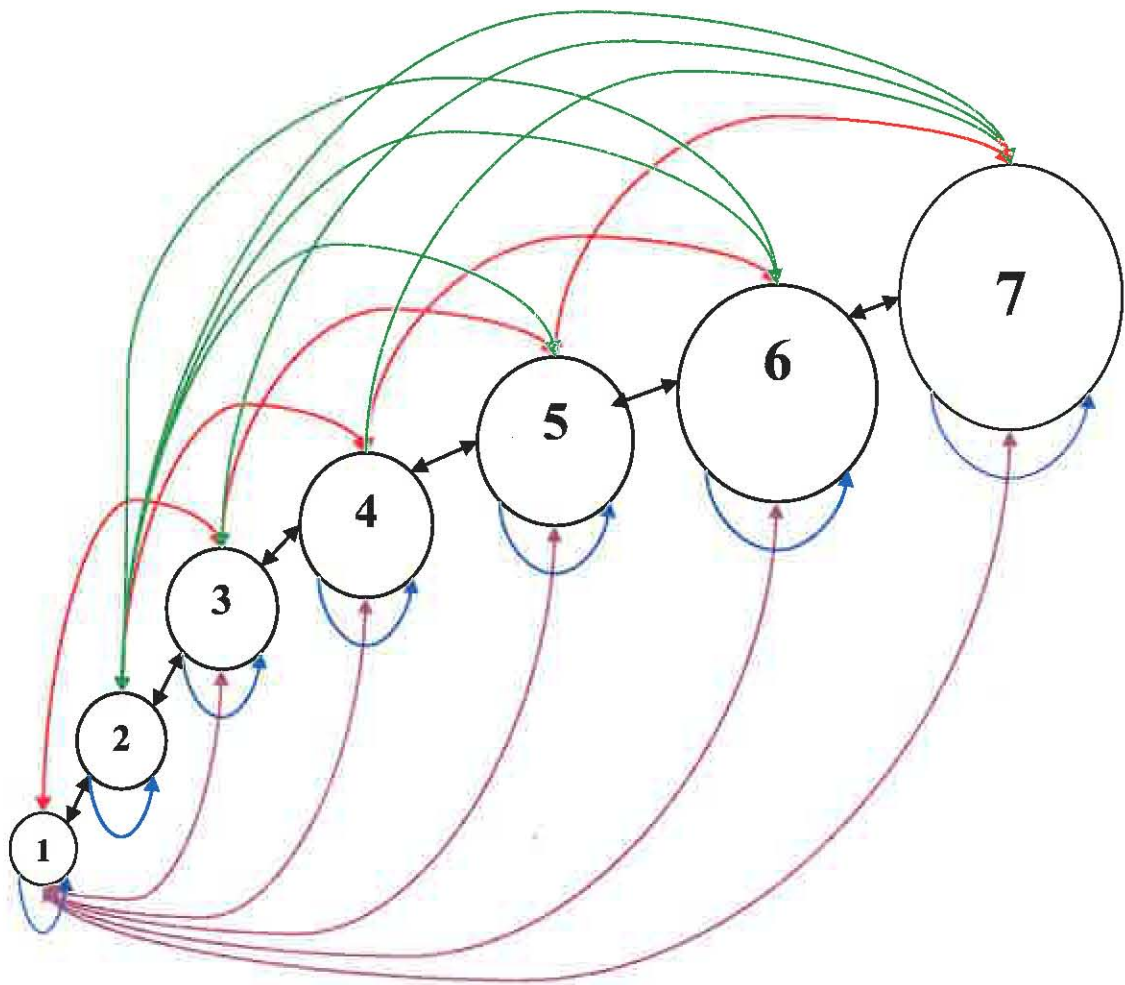
Figure 11: Life cycle graph for *Palythoa caribaeorum*. *Nodes/Size Classes*: n_1 = recruit, n_2 = small juvenile, n_3 = juvenile, n_4 = intermediate, n_5 = small adult, n_6 = adult, and n_7 = super adult. Arrows represent the possibilities of transitions between each size class.

Table 3: Size class designations for the *Palythoa* colonies used to make the transition probability matrices. Size classes were determined by personal observations and the approximate equal distribution over those seven size classes of the 85 colonies selected for the study.

Size Class	Area (cm²)	Description
1	0-10cm²	Recruit
2	11-30cm²	Small Juvenile
3	31-50cm²	Juvenile
4	51-100cm²	Intermediate
5	101-300cm²	Small Adult
6	301-600cm²	Adult
7	601+cm²	Super Adult
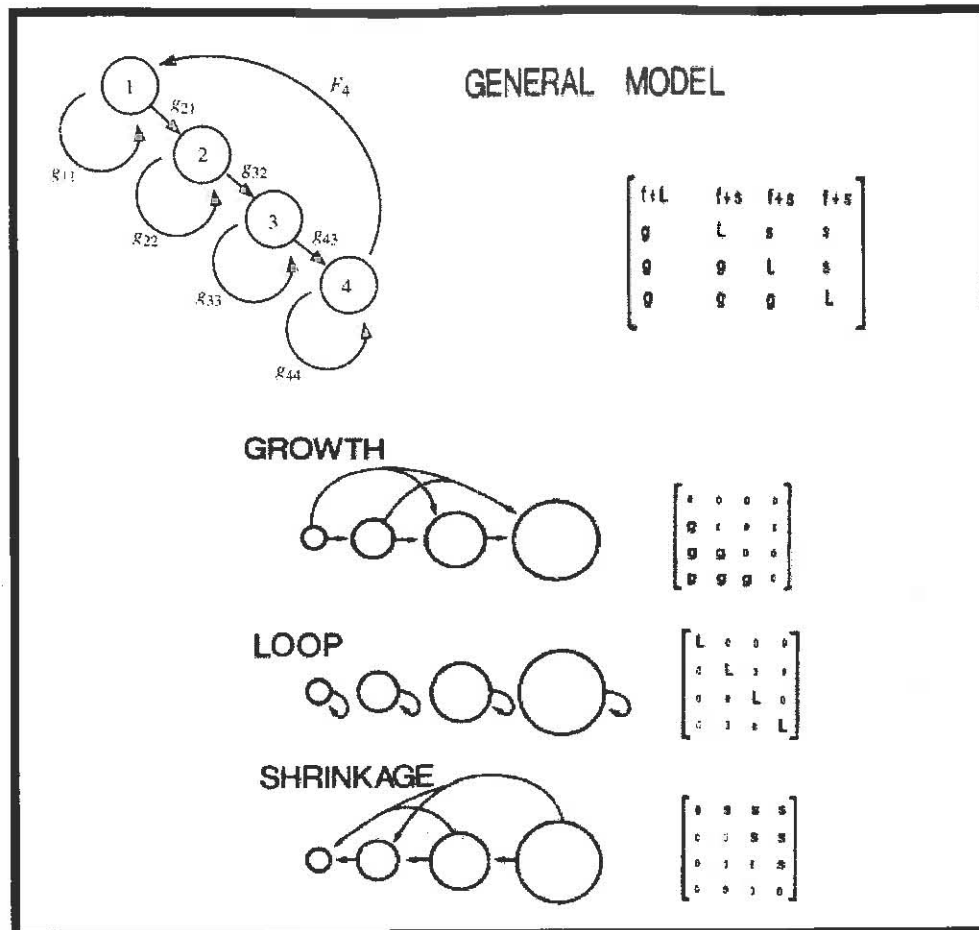
Figure 12: The Hughes (1984) general size class transition probability model showing how transition nodes from the life cycle graph represent transition frequencies values in the matrices.

2.2.2.2.2. *Colony selection and tracing*

Nine sites were selected from the original 16 sites (Part One) based on both their distribution over each of the three reef classifications and the presence of *Palythoa* throughout all sampling periods. Individual colonies were identified from each of those nine sites, and were traced and tracked for all five annual sampling periods (2002-2006). Selection of the colonies included their proximity to the framer center (colonies in the center of the quad were preferred over any that touched the edges, or went outside of the quad), as well as the relief (colonies

that were growing on a flat surface were chosen over any growing on relief or that might be perpendicular to the substrate). If any of the colonies asexually divided, their ramets were also tracked for all five years. Each colony was traced using CPCe to determine their individual area (cm²) values. The colonies were assigned a size class number based on their area (cm²) (Table 3).

2.2.2.2.3. *Size Class Transition Probability Matrix*

The creation of the following matrices and subsequent analyses were done using MATLAB® R2006a. In order to fully understand the demography and dynamics of *Palythoa*, a size class transition model was used. "This approach is appropriate for dealing with zoanthid populations because these tropical cnidarians are long-lived, fission is common, survivorship is size-dependent, and age and size are decoupled as determinants of life history" (Karlson 1988, 1991). A size class transition model makes several important assumptions that have direct bearings on the parameterization of the model:

1) Population density plays no role in the population's growth rate (Bierzychudek 1999).
2) All individuals within the stages are equal; therefore, no information regarding individual colony-fate is entered.
3) Over the modeled time-sequence, the model acts as a single-step Markov chain, which means that outcomes t+1 are always dependent on outcomes at t, independent of t (i.e. the matrix must predict as correctly at step 2 as at step 1000) (Usher 1979). If this isn't the case, a possible biological explanation would be density dependence or altered environment, which leads to different survivabilities in the classes. In such a case, several matrices may be necessary.

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I used the seven "nodes" (or size class designations; Table 3) from the life cycle graph (Figure 11) and followed the Hughes (1984) example to predict the change in the number of individual colonies within a single cohort (i.e. size class). I grouped the highest percent cover (HC) sites (>1%) as well as the low cover (LC) sites (<1%) for each year. I also grouped the sites into their respective reef tracts (Inshore Ridge Complex (IRC), Middle Reef (MR), and Outer Reef (OR)), in order to look at any cross shelf variation. For each treatment (e.g. All, HC, LC, IRC, MR, OR), I found the mean matrix of all years (2002-06).

In a perfect situation with no variability, the vector (v) (number of the colonies in a size class per year) of any given year when multiplied by the mean matrix should result in the following year's vector (vector 2003 * Mean matrix 2002-06 = vector 2004). I then compared the distribution of the observed (from digital image analysis) vs. model predicted vectors for each year using a chi-square test (Zar 1999).

Finally, once the distributions were examined, the dominant eigenvalue was found for the mean matrix of each treatment. Using those values, the sensitivity and elasticity analyses were run in order to identify the elements in the matrix that when changed would influence the model's outcome the most (Tanner et al. 1994). I then addressed any unexplained stochastic variability as well as the assumptions of the model and their biological meaning (Hughes 1984).

SEE APPENDIX FOR:
FLOW CHART OF MAJOR STEPS TO COMPLETE PART ONE AND PART TWO

3.0.   RESULTS

3.1. Part One: General *Palythoa* population dynamics

These results provide a general overview of the extent of the *Palythoa* population on southeast Florida's reefs. Data was collected from 30m² belt transects at 16 sites situated over the three reef classifications off of Broward County, FL for a period of 4 years (2002-2005). Using the information in Table 4, the mean percent live cover was calculated using the total *Palythoa* live cover (cm²) per 30m² transect. Overall mean (±1 SD) *Palythoa* cover for all years was 2.27 ± 0.09%.

Although no significant difference was determined ($p > 0.05$, ANOVA) for the mean percent live cover either within reefs among years or among reefs within years (Figure 13), the Inshore Ridge Complex had two of the three highest percent live cover sites for all years. Those three sites (FTL4, HB2, JUL6) had particularly high mean (±1 SD) covers of 16.1 ± 0.63%, 5.4 ± 0.87% and 4.8 ± 0.38% respectively. The mean percent live cover of those three sites (8.8 ± 5.5%) for 2002 - 2005 is greater than the remaining 13 sites combined (0.8 ± 0.83%). The sites were grouped into High Cover sites (percent live cover >1%) and Low Cover sites (<1%) (Figures 14 & 15) and although it does not lend itself to statistical comparison, the mean percent live covers (+1SD) for both High Cover and Low Cover sites were compared in Figure 16.

Table 4: Digital image analysis results for the 16 monitoring sites (2002-2005), including total area (cm²) of *Palythoa* live cover per quad (1-40), total live cover area (cm²), and percent live cover for the whole transect.

Site (first)

Quad #	Sample Year 2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27		83.99	56.03	72.38
28				
29				
30				
31				
32				
33				
34				
35	310.22	335.03	288.04	350.06
36				
37				
38				
39	114.00	226.98	177.29	237.81
40				
Total Area (cm²)	424.21	645.99	521.36	660.26
Total % Cover	0.14	0.22	0.17	0.22

Site (second)

Quad #	Sample Year 2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1	1278.89	996.23	1365.72	1463.63
2	8.99	117.22	16.14	9.32
3	880.49	838.00	919.46	1072.44
4				
5				
6	1472.37	1359.23	1378.26	2124.60
7	828.94	1159.54	1272.05	1442.52
8				
9				
10				
11				
12	247.03	494.66	380.57	443.93
13	73.80	108.18	42.16	211.36
14	2905.03	3110.03	2914.18	3009.96
15	332.82	280.15	363.34	461.61
16				
17	49.59	36.67	16.23	14.24
18	101.50	95.73	119.82	147.90
19	18.93	14.67	32.59	44.66
20	752.11	708.34	695.42	738.39
21				15.12
22	110.19	127.81	137.44	187.90
23				
24				
25				
26	201.26	171.99	223.25	179.54
27	586.62	743.79	688.88	750.99
28	165.77	291.95	128.60	225.07
29	507.29	627.58	489.07	567.26
30	200.99	247.76	297.02	305.64
31				16.69
32	57.42	199.21	170.22	97.10
33	216.27	258.16	126.32	102.12
34				
35				
36				
37				
38	92.98	97.86	120.51	147.60
39	2039.97	2055.69	2202.86	2079.70
40	14.21	18.03	24.53	26.58
Total Area (cm²)	13143.44	14158.47	14124.64	15885.89
Total % Cover	4.38	4.72	4.71	5.30

Site (third)

Quad #	Sample Year 2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1	555.95	646.26	525.09	409.81
2	950.79	1050.37	1226.00	1038.87
3	2474.58	2753.62	2926.62	2702.79
4	893.50	1363.56	1180.20	1162.52
5	117.89	118.72	186.26	124.61
6	101.52	66.80	94.02	81.58
7	461.75	441.25	492.34	371.84
8	300.36	397.23	359.45	188.18
9	1081.39	1127.44	981.18	797.39
10	1006.90	1288.37	1271.83	1081.41
11	132.92	149.45	236.78	100.17
12	1163.17	1279.89	1240.71	1071.86
13	1641.64	1808.99	1535.89	1415.93
14	2714.62	2577.65	2271.86	2859.11
15	1366.94	764.98	1268.74	1485.08
16			67.10	
17	1141.88	1059.04	1374.39	1257.67
18	917.33	1041.29	1353.53	1186.86
19	3347.79	3336.39	3256.44	3409.41
20	2115.24	2253.01	2867.45	2586.79
21	139.95	239.64	263.62	225.51
22	219.91	235.41	222.98	233.12
23	452.72	529.34	784.83	894.39
24	44.46	28.48	27.45	61.58
25	67.18	132.85	87.74	73.95
26	265.67	228.89	246.95	102.64
27	967.82	1174.62	1427.45	994.49
28	1062.55	1019.01	1033.39	1403.30
29	1806.19	1941.19	2130.40	2123.40
30	18.35	19.08	36.68	4.02
31	1690.32	1584.26	1733.51	1512.51
32	1729.39	1269.21	1393.70	1416.62
33	4409.34	3803.82	4262.09	4323.22
34	898.36	1095.14	1044.52	1129.55
35	1787.37	1530.91	1812.34	1595.99
36	1245.60	1303.49	1422.51	1392.48
37	2750.69	3128.78	2833.16	2845.12
38	1868.71	2026.31	1895.39	87.27
39	1184.59	1439.25	1552.87	1410.47
40	1966.32	2139.03	2084.66	1811.25
Total Area (cm²)	47061.67	48393.00	51012.11	46972.73
Total % Cover	15.69	16.13	17.90	15.66

Site (fourth)

Quad #	Sample Year 2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1	Site	346.36	376.45	391.35
2	not			
3	established	28.46	40.47	156.09
4	until			
5	2003	603.89	776.12	721.35
6				
7		57.52	75.56	78.00
8		80.35	128.90	109.62
9		109.45	86.12	85.27
10		103.74	29.58	31.26
11		92.49	33.58	28.84
12				
13				
14				
15		96.29	91.66	78.18
16		221.58	294.45	240.40
17				
18		30.77	20.20	171.86
19		270.64	322.66	229.05
20				
21				
22				
23				
24				
25				
26				
27		97.74	124.73	163.21
28		22.96		
29				
30				
31			32.71	51.14
32				
33				
34				
35				
36				
37				
38				
39				
40				
Total Area (cm²)	N/A	2190.94	2447.23	2567.28
Total % Cover	N/A	0.73	0.82	0.86

Table 4: Continued.

Site 1

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2	70.38	79.88	75.73	80.68
3	780.16	935.87	948.76	936.87
4				
5	5.47			13.05
6	136.24	92.05	69.52	51.59
7				
8				
9	1366.76	1347.86	1290.44	1278.57
10				
11				
12				
13				
14		29.90	3.08	5.62
15				
16				
17				
18	941.33	1028.24	1266.40	1356.27
19				
20	99.72	130.49	126.25	173.70
21			11.65	10.69
22				
23				
24	260.81	302.80	408.49	491.78
25	5.21	17.29	26.90	24.82
26				
27	42.37	67.35	53.25	53.48
28				
29		77.88	75.17	108.90
30				
31				
32				
33	1144.05	1190.14	1318.04	2942.67
34				
35				
36	61.22	54.49	70.30	96.30
37	106.63	87.31	77.34	54.83
38				
39				
40	59.01	117.65	117.93	134.39
Total Area (cm²)	5079.37	5559.19	5939.24	7814.20
Total % Cover	1.69	1.85	1.98	2.60

Site 2

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2	234.97	233.96	214.87	273.88
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27				
28				
29				
30				
31				
32				
33				
34				
35				
36				
37				
38				
39				
40				
Total Area (cm²)	234.97	233.96	214.87	273.88
Total % Cover	0.08	0.08	0.07	0.09

Site 3

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2	10.36	8.62	14.81	15.23
3				
4				
5				
6	36.08	21.50	27.87	23.58
7				
8				
9				
10				
11				
12				
13				
14	22.39			
15	675.10	672.63	816.90	530.49
16	2348.68	2514.59	2857.36	2870.98
17	664.43	851.62	1033.03	920.37
18				
19				
20				
21		141.68	1.42	30.88
22				
23				
24	478.64	672.91	734.47	770.78
25	1295.67	1697.17	1697.68	1359.44
26	454.48	509.91	628.81	500.84
27	194.14	220.65	326.42	178.42
28				
29				
30	1421.54	1150.71		
31	135.27	256.56		
32				
33	80.18	72.69	90.21	74.60
34				
35				
36				
37				
38	227.72	133.96	179.62	194.51
39	126.09	228.75	230.05	159.04
40	296.71	314.43	412.22	401.69
Total Area (cm²)	8467.49	9468.38	9950.87	8028.85
Total % Cover	2.82	3.16	3.32	2.68

Site 4

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2				17.14
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27				
28				
29				
30				
31				
32				
33				
34				
35				
36				
37				
38			13.02	21.26
39				
40				
Total Area (cm²)	0.00	0.00	13.02	38.40
Total % Cover	0.00	0.00	0.00	0.01

Table 4: Continued.

Site 1

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2	303.63	199.80	198.28	321.76
3	19.32	26.36	20.26	21.51
4				
5				
6				
7				
8				
9		22.12	23.51	64.02
10				
11				
12	131.56	116.59	121.75	159.24
13				
14				
15				
16	42.90	38.38	31.81	74.39
17	19.79	29.12	9.92	10.48
18				
19				
20	19.51	45.75	4.81	229.46
21	120.09	187.18	169.00	229.46
22				
23				
24				
25	.			
26	67.76	67.03	72.23	54.55
27	99.64	91.07	122.09	113.03
28	50.50	53.68	24.34	33.41
29				
30	65.18	77.97	36.57	64.14
31				
32				
33				
34				
35	119.90	121.66	93.28	105.59
36				
37				
38				
39				
40				
Total Area (cm²)	1059.73	1076.71	937.85	1481.91
Total % Cover	0.35	0.36	0.03	0.49

Site 2

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1	613.43	495.86	802.21	701.69
2	734.08	753.73	924.71	1102.55
3			8.33	
4	86.64	95.06	97.41	106.57
5	51.17	80.94	99.50	88.54
6	307.60	425.62	620.07	498.52
7	317.08	449.02	350.88	473.56
8	119.49	1012.42	902.48	865.78
9				
10	317.39	439.60	323.97	80.60
11	399.30	461.45	418.25	307.55
12	209.35	180.68	206.39	255.00
13				
14	41.24	51.06	52.79	55.03
15				
16				
17	2221.13	2279.60	2249.51	2177.56
18	596.76	690.91	587.48	599.71
19	28.56	594.87	651.83	471.31
20		644.83	1109.18	1016.18
21		1077.95	696.74	1001.82
22	282.64	276.78	365.91	347.14
23	467.78	500.43	618.71	545.37
24	46.92	48.62	52.52	46.12
25				
26				
27	100.65	51.61	140.62	168.49
28	118.94	124.47	164.12	82.50
29	360.15	342.61	419.42	550.14
30	600.10	578.55	671.47	675.13
31	92.33	47.22	129.32	102.42
32	70.76	88.08	122.21	121.83
33	37.86	53.56	49.40	64.24
34	509.30	422.60	616.03	697.72
35	2028.15	1679.52	2447.11	2876.40
36	383.75	404.15	436.52	406.93
37	325.10	390.94	421.62	330.65
38	802.19	704.88	903.19	653.78
39	211.90	225.53	355.45	340.51
40	85.34	20.17	114.96	178.58
Total Area (cm²)	12564.00	15092.25	18138.76	17989.93
Total % Cover	4.19	5.25	6.49	6.00

Site 3

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2				
3				
4				
5				
6	191.42	258.35	243.18	328.73
7				
8	85.60	77.00	129.41	160.93
9	338.62	414.05	483.62	479.69
10	82.42	141.44	150.94	227.46
11				
12	254.58	191.21	223.12	274.31
13				
14	9.45	25.41	2.62	15.68
15	56.38	7.12	11.04	17.29
16				
17				
18			120.84	146.90
19	112.84	21.30	25.77	6.85
20				
21				
22	165.01	226.10	183.53	194.79
23	50.07	76.55	90.08	119.61
24				
25				
26				
27	82.57	118.01	140.44	148.73
28				
29	127.48			57.63
30	60.55	38.56	62.20	57.67
31	173.68	129.28	37.13	21.80
32	163.76	95.75	55.24	
33	237.08	91.34	112.28	60.31
34	84.07	56.92	32.70	57.93
35	17.76	2.97	9.31	0.88
36				
37				2.31
38				
39				
40				
Total Area (cm²)	2293.35	1971.35	2112.34	2333.48
Total % Cover	0.76	0.66	0.70	0.89

Site 4

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2				
3				
4				
5				
6				
7				
8	25.64	12.62	34.34	68.14
9				
10				
11	27.66	29.83	25.15	41.58
12	294.68	525.19	492.41	550.07
13	124.17	267.38	263.33	203.82
14				
15				
16				
17				
18				
19				
20				
21				
22				
23		72.71	68.93	23.08
24				
25				
26	169.89			
27	208.04			
28	227.01	297.02	260.13	161.19
29		396.04	354.22	376.10
30		498.28	461.82	340.81
31				
32				
33				
34				
35				
36				
37	54.69			
38	78.89			
39				
40				
Total Area (cm²)	1210.66	2699.67	1960.35	1764.89
Total % Cover	0.40	0.70	0.65	0.59

Table 4: Continued.

Site

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27				
28				
29				
30				
31				
32				
33				
34				
35				
36				
37				
38				
39	62.51	116.19	84.74	6.30
40				
Total Area (cm²)	62.51	116.19	84.74	6.30
Total % Cover	0.02	0.04	0.05	0.00

Site

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1				
2				
3				
4				
5				
6	37.17	29.94	47.19	40.39
7				
8				
9				
10				
11				
12				
13				
14	48.45	36.44	54.04	59.78
15	46.13	39.26	43.70	53.53
16				
17				
18	203.24	285.11	251.94	228.04
19				
20				
21				
22				
23	10.76	37.68	29.66	29.68
24				
25				
26				
27				
28				
29				
30				
31				
32				
33				
34				
35				
36	1645.50	1803.58	1910.99	1616.89
37				
38	40.11	17.09	27.19	9.08
39				
40				
Total Area (cm²)	2035.86	2245.10	2354.71	2037.38
Total % Cover	0.68	0.75	0.79	0.68

Site

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1	384.81	464.44	522.67	474.96
2	61.82	63.86	5.70	2.95
3				
4				
5				
6	49.60	44.40	48.67	45.00
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20	532.24	596.83	612.97	718.22
21				
22				
23	104.22	75.90	101.84	104.02
24	85.33	90.65	102.43	115.92
25				
26				
27				
28				
29				
30				
31				
32				
33	49.71	82.23	77.98	116.87
34	78.21			
35				
36				
37				
38				
39				
40	44.03	40.41	52.60	26.19
Total Area (cm²)	2390.92	1455.31	7932.86	1680.13
Total % Cover	3.26	0.49	6.51	6.53

Site

Quad #	2002 Area (cm²)	2003 Area (cm²)	2004 Area (cm²)	2005 Area (cm²)
1	17.78	8.72	26.29	24.63
2	30.08	33.29	38.09	7.79
3	182.76	175.88	184.75	223.27
4	112.15	139.42	71.43	61.34
5	32.02	27.74	40.69	41.60
6	9.36	27.51	16.18	
7				
8	19.18	29.13	32.40	24.38
9	86.02	151.77	151.62	175.71
10	21.85	15.76	43.54	69.94
11	16.66	21.62	28.22	20.13
12	105.01	77.97	92.90	87.69
13	123.43	116.39	139.41	19.47
14				
15	26.95	35.73	34.84	34.34
16				
17				
18	31.79	68.70	86.75	65.76
19	150.06	110.85	79.36	57.04
20	63.65	56.69	90.72	85.21
21				
22	126.99	116.90	126.91	142.05
23	53.16	26.86	66.31	100.84
24	27.62	34.39	59.49	56.80
25				
26	37.87	47.13	94.06	102.92
27				
28	18.29	25.92	26.04	46.38
29				
30	33.21	22.66	34.55	39.54
31	58.33	47.44	93.65	116.15
32	1.94	34.72	27.53	13.14
33	38.45	70.65	75.43	149.37
34			11.00	23.38
35	27.67	41.60	34.50	19.15
36	57.54	36.70	19.47	63.59
37	47.69	86.85	49.56	53.32
38	66.04	3.65	43.23	47.97
39	36.00	36.46	54.10	175.03
40				564.87
Total Area (cm²)	2170.97	2327.48	2591.62	2712.79
Total % Cover	0.72	0.78	0.86	0.98

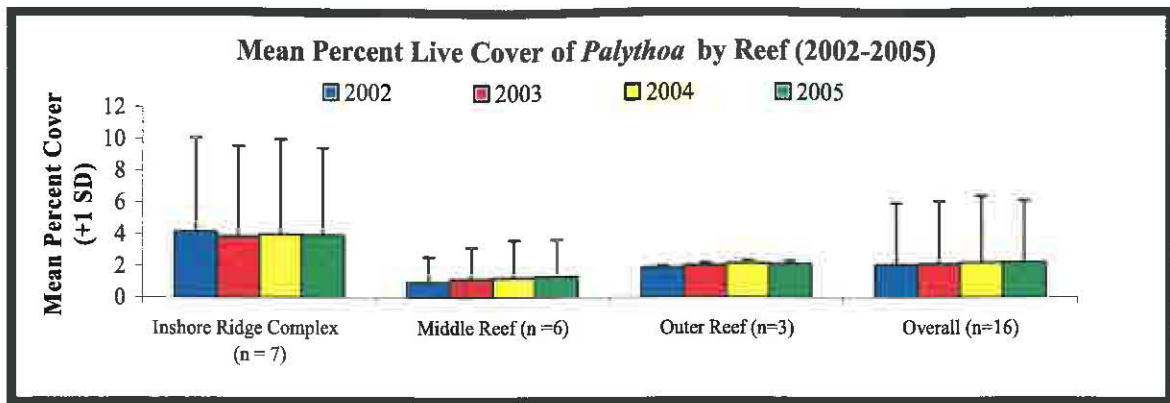Figure 13: Mean percent live cover (untransformed) of *Palythoa* by reef for all 16 sites. Error bars reflect one standard deviation.
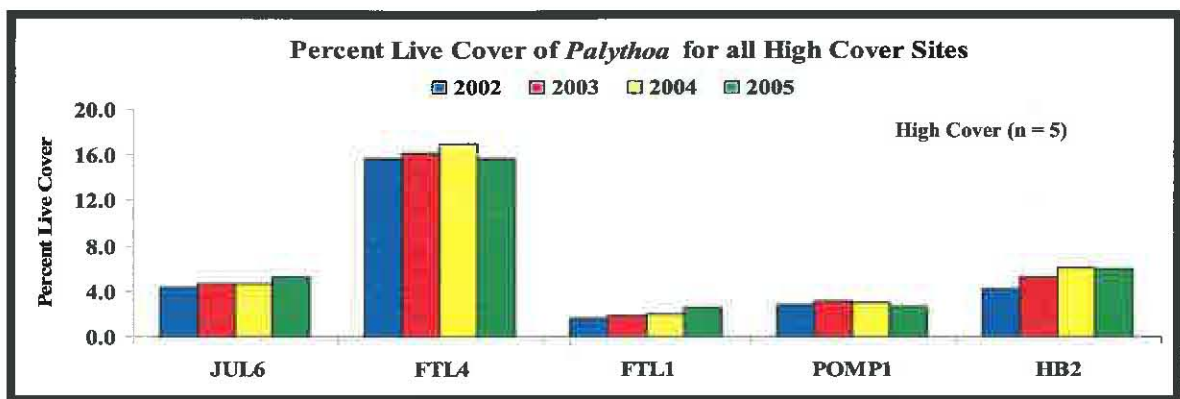
Figure 14: Percent live cover (untransformed) of *Palythoa* by site for all High Cover (>1%) sites for each year (2002-2005).
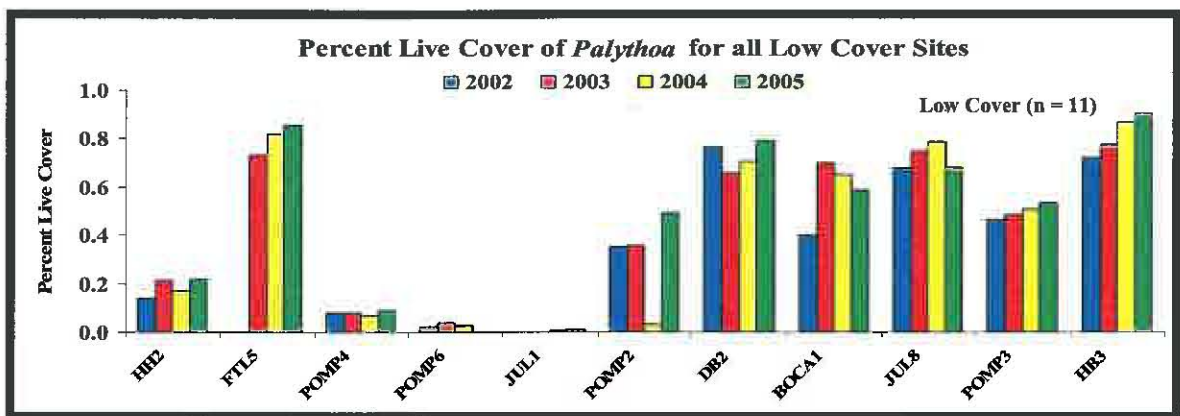
Figure 15: Percent live cover (untransformed) of *Palythoa* by site for all Low Cover (<1%) sites for each year (2002-2005). Note scale change from Figure 14.

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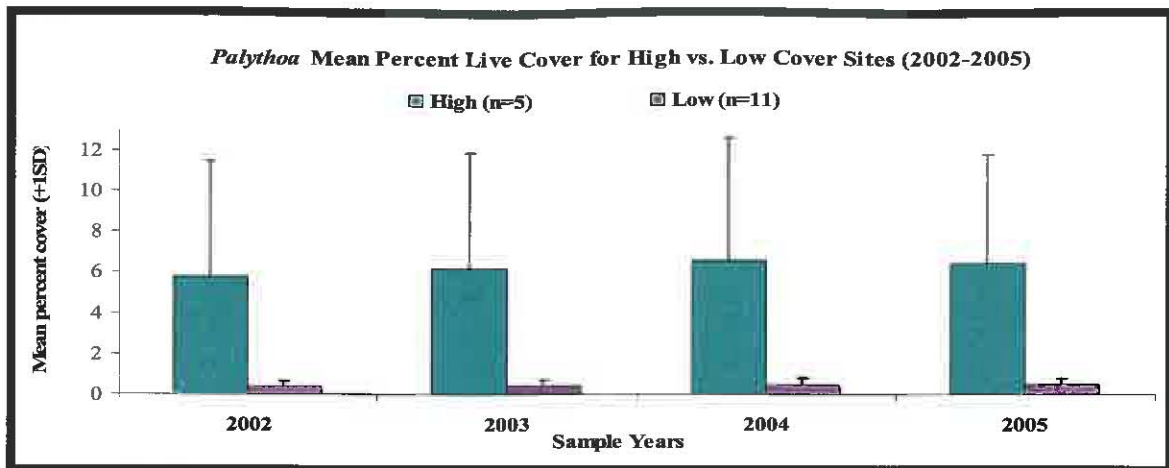
Figure 16: Mean percent live cover (untransformed) of *Palythoa* for High and Low Cover sites. Error bars reflect one standard deviation.

3.2. Part 2: Transition Matrix Model

The second part of the study tracked 85 colonies and their isolates from 9 of the original 16 study sites from 2002-2006 (Table 5). So, as the first step, colony abundance was counted each year respective to the size-class bins that were to be used in the projection matrix (Table 6). When the abundance of each size class was graphed over the entire investigated time-span, an overall trend showed decline in all size classes (Figure 17). This could be seen as an indication of overall population reduction, which made the investigation of the population's λ (overall population growth rate) important. Figures 18 & 19 show the same results broken out into High & Low Cover (Figure 18) and Inshore Ridge Complex, Middle Reef and Outer Reef (Figure 19).

Table 5: High and low percent live cover, and reef designations for the nine Part Two study sites.

High Cover Sites		
Reef	**Site**	**Mean % Cover**
Inshore Ridge Complex	JUL6	4.8 ± 0.38%
Inshore Ridge Complex	FTL4	16.1 ± 0.63%,
Inshore Ridge Complex	FTL1	2.0 ± 0.40%
Middle Reef	HB2	5.4 ± 0.87%
Overall Mean % Cover		7.1 ± 5.57%
Low Cover Sites		
Reef	**Site**	**Mean % Cover**
Middle Reef	POMP2	0.31 ± 0.02%
Middle Reef	DB2	0.73 ± 0.06%
Outer Reef	JUL8	0.72 ± 0.05%
Outer Reef	POMP3	0.50 ± 0.03%
Outer Reef	HB3	0.82 ± 0.08%
Overall Mean % Cover		0.62 ± 0.22%

Table 6: Total number (abundance) of colonies in the 7 assigned size classes in each sampling year (2002-2006) for all 9 sites. The columns refer to size classes described in Table 3.

	1	2	3	4	5	6	7
2002	16	18	14	18	14	8	5
2003	18	15	21	12	17	6	7
2004	19	17	17	14	17	7	10
2005	35	20	11	18	20	6	8
2006	40	26	13	14	18	6	10
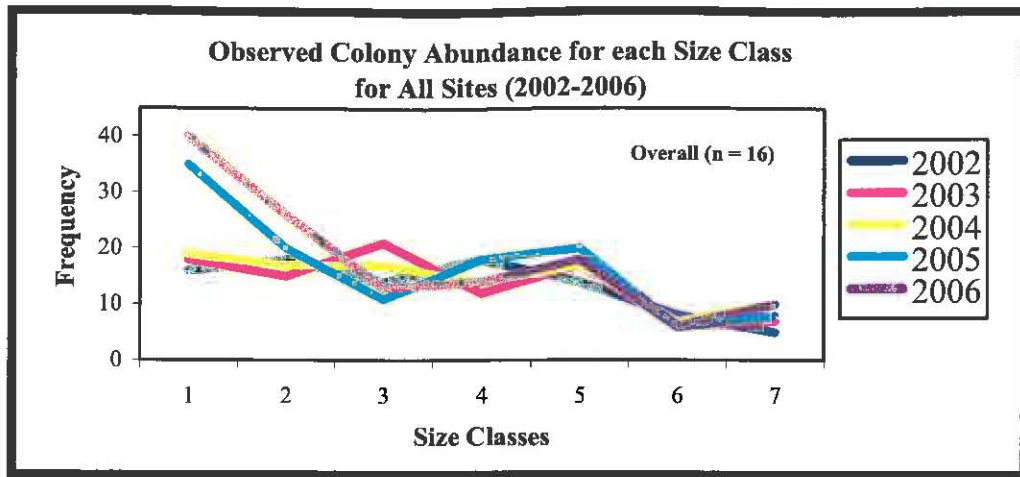
Figure 17: Observed number of individual colonies (abundance) for All sites in the size classes chosen to populate the transition matrix model.
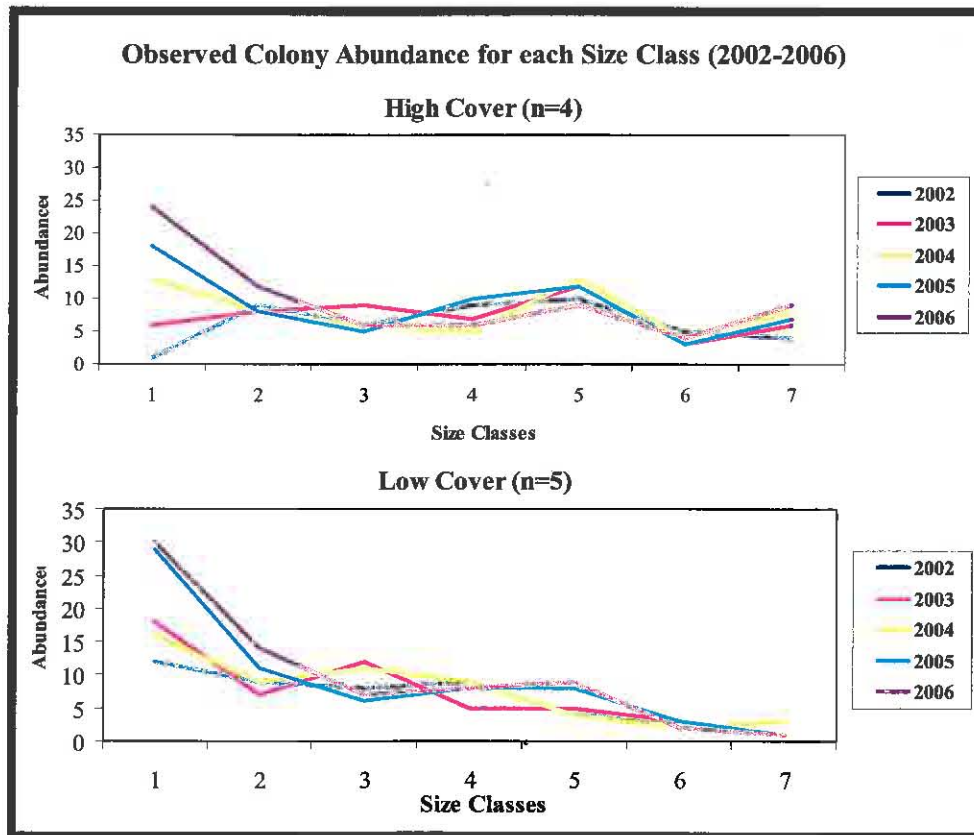
Figure 18: Observed colony abundance in the size classes chosen to populate the transition matrices for High and Low Cover sites.
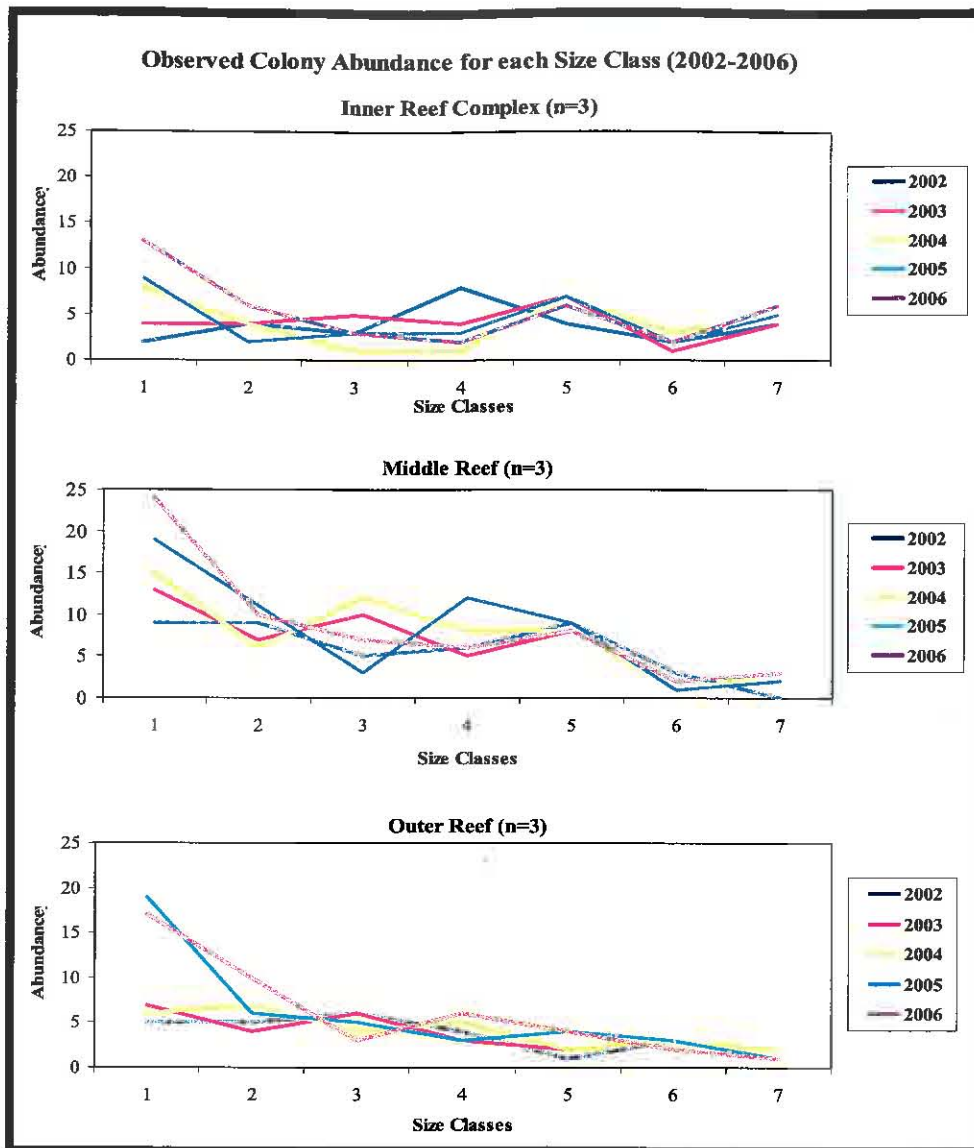
Figure 19: Observed colony abundances in the size classes chosen to populate the transition matrices for the Inshore Ridge Complex, Middle Reef, and Outer Reef.

Bearing the aforementioned model assumption constraints in mind, the transitions among the chosen size classes were evaluated for the eventual parameterization of the matrix model. Table 7 shows the number of colonies within each transition year (e.g. 02-03) and their respective transition frequencies among size classes (i.e. the percentage of how many originally available colonies in size class i changed into size class $i+1$ over a single time interval).

Table 7: The transition year columns (e.g. 02-03, 03-04, etc.) represent the number of colonies present in each size class transition (e.g. α_{11}, α_{21}, etc.) within each transition year while their respective transition frequencies columns represent the percentage of how many originally available colonies in size class i changed into size class $i+1$ over a single time interval (α_{ij}).

Size Class Transitions	02-03	Transition Frequency	03-04	Transition Frequency	04-05	Transition Frequency	05-06	Transition Frequency
α_{11}	10	0.63	20	0.77	24	0.80	41	0.82
α_{12}	3	0.19	5	0.19	2	0.07	9	0.18
α_{13}	3	0.19		0.00		0.00		0.00
α_{14}		0.00	1	0.04	1	0.03		0.00
α_{15}		0.00		0.00	2	0.07		0.00
α_{16}		0.00		0.00		0.00		0.00
α_{17}		0.00		0.00	1	0.03		0.00
SUM	16		26		30		50	
α_{21}	4	0.21	2	0.12	5	0.25	7	0.30
α_{22}	11	0.58	9	0.53	12	0.60	12	0.52
α_{23}	4	0.21	6	0.35	3	0.15	2	0.09
α_{24}		0.00		0.00		0.00	2	0.09
α_{25}		0.00		0.00		0.00		0.00
α_{26}		0.00		0.00		0.00		0.00
α_{27}		0.00		0.00		0.00		0.00
SUM	19		17		20		23	
α_{31}	2	0.13	3	0.14	3	0.18	2	0.18
α_{32}	3	0.19	2	0.10	2	0.12	1	0.09
α_{33}	8	0.50	8	0.38	6	0.35	5	0.45
α_{34}	3	0.19	5	0.24	6	0.35	3	0.27
α_{35}		0.00	2	0.10		0.00		0.00
α_{36}		0.00	1	0.05		0.00		0.00
α_{37}		0.00		0.00		0.00		0.00
SUM	16		21		17		11	
α_{41}	3	0.17	1	0.08	2	0.14	3	0.16
α_{42}		0.00	1	0.08	1	0.07	1	0.05
α_{43}	4	0.22	1	0.08	1	0.07	2	0.11
α_{44}	7	0.39	5	0.38	6	0.43	10	0.53
α_{45}	4	0.22	4	0.31	4	0.29	3	0.16
α_{46}		0.00		0.00		0.00		0.00
α_{47}		0.00	1	0.08		0.00		0.00
SUM	18		13		14		19	
α_{51}		0.00	2	0.12	1	0.06	3	0.15
α_{52}		0.00		0.00	1	0.06		0.00
α_{53}	1	0.07		0.00		0.00	1	0.05
α_{54}	2	0.13	2	0.12	5	0.28		0.00
α_{55}	12	0.80	9	0.53	10	0.56	12	0.60
α_{56}		0.00	4	0.24	1	0.06	3	0.15
α_{57}		0.00		0.00		0.00	1	0.05
SUM	15		17		18		20	
α_{61}	1	0.11	1	0.17		0.00		0.00
α_{62}		0.00		0.00		0.00		0.00
α_{63}		0.00		0.00	1	0.14		0.00
α_{64}		0.00		0.00		0.00		0.00
α_{65}	1	0.11	1	0.17	3	0.43	2	0.33
α_{66}	5	0.56	2	0.33	3	0.43	3	0.50
α_{67}	2	0.22	2	0.33		0.00	1	0.17
SUM	9		6		7		6	
α_{71}		0.00		0.00		0.00		0.00
α_{72}		0.00		0.00		0.00		0.00
α_{73}		0.00		0.00		0.00		0.00
α_{74}		0.00		0.00		0.00		0.00
α_{75}		0.00	1	0.14	1	0.10		0.00
α_{76}		0.00		0.00	2	0.20		0.00
α_{77}	5	1.00	6	0.86	7	0.70	8	1.00
SUM	5		7		10		8	

ALL SITES COLONY SIZE CLASS CHANGE OVER YEARS

From Table 7, four matrices were produced, one for each transition year (2002-3, 2003-4, 2004-5, 2005-6; Table 8). The mean of all transitions over all years of these four matrices was used to build an overall projection matrix (Table 9).

Table 8: Transition frequency matrices of All sites for each transition year.

2002-2003						
	1	2	3	4	5	6	7
1	0.63	0.19	0.19	0.00	0.00	0.00	0.00
2	0.21	0.58	0.21	0.00	0.00	0.00	0.00
3	0.13	0.19	0.50	0.19	0.00	0.00	0.00
4	0.17	0.00	0.22	0.39	0.22	0.00	0.00
5	0.00	0.00	0.07	0.13	0.80	0.00	0.00
6	0.11	0.00	0.00	0.00	0.11	0.56	0.22
7	0.00	0.00	0.00	0.00	0.00	0.00	1.00
2003-2004						
	1	2	3	4	5	6	7
1	0.77	0.19	0.00	0.04	0.00	0.00	0.00
2	0.12	0.53	0.35	0.00	0.00	0.00	0.00
3	0.14	0.10	0.38	0.24	0.10	0.05	0.00
4	0.08	0.08	0.08	0.38	0.31	0.00	0.08
5	0.12	0.00	0.00	0.12	0.53	0.24	0.00
6	0.17	0.00	0.00	0.00	0.17	0.33	0.33
7	0.00	0.00	0.00	0.00	0.14	0.00	0.86
2004-2005						
	1	2	3	4	5	6	7
1	0.80	0.07	0.00	0.03	0.07	0.00	0.03
2	0.25	0.60	0.15	0.00	0.00	0.00	0.00
3	0.18	0.12	0.35	0.35	0.00	0.00	0.00
4	0.14	0.07	0.07	0.43	0.29	0.00	0.00
5	0.06	0.06	0.00	0.28	0.56	0.06	0.00
6	0.00	0.00	0.14	0.00	0.43	0.43	0.00
7	0.00	0.00	0.00	0.00	0.10	0.20	0.70
2005-2006						
	1	2	3	4	5	6	7
1	0.82	0.18	0.00	0.00	0.00	0.00	0.00
2	0.30	0.52	0.09	0.09	0.00	0.00	0.00
3	0.18	0.09	0.45	0.27	0.00	0.00	0.00
4	0.16	0.05	0.11	0.53	0.16	0.00	0.00
5	0.15	0.00	0.05	0.00	0.60	0.15	0.05
6	0.00	0.00	0.00	0.00	0.33	0.50	0.17
7	0.00	0.00	0.00	0.00	0.00	0.00	1.00

Table 9: Mean transition frequencies for All sites (2002-2006).

Mean (2002-2006)							
	1	2	3	4	5	6	7
1	0.76	0.16	0.05	0.02	0.02	0.00	0.01
2	0.22	0.56	0.20	0.02	0.00	0.00	0.00
3	0.16	0.13	0.42	0.26	0.03	0.01	0.00
4	0.14	0.05	0.12	0.43	0.25	0.00	0.02
5	0.08	0.02	0.03	0.13	0.62	0.11	0.01
6	0.07	0.00	0.04	0.00	0.26	0.46	0.18
7	0.00	0.00	0.00	0.00	0.06	0.05	0.89

Using Matlab®, the dominant eigenvalue (λ) was obtained from the mean (2002-2006) matrix (e.g. Table 9) for all treatments (All, HC, LC, IRC, MR, OR) (Table 10). Since all treatments resulted in a lambda value equal to or near 1.00, this would suggest that the *Palythoa* population in southeast Florida is stable (neither growing nor shrinking) (Figure 17).

Table 10: Dominant eigenvalues (lambda values) for the mean transition matrices of all treatments.

Lambda Values for Mean Matrices	
Treatment	λ
All Sites	1.00
High Cover	1.00
Low Cover	0.99
Inshore Ridge Complex	1.00
Middle Reef	0.99
Outer Reef	1.00

Since a base assumption of stage-based models is that a single matrix can predict population growth at any arbitrary time-step, I used this matrix to test whether it could indeed correctly predict the population vectors of the known (observed) following years (population vectors in Table 6) (Figures 20-25). A standard chi-square test was run for each treatment (e.g. All, HC, LC, IRC, MR, OR) each year to determine if there were any significant differences between the distribution of the observed (from digital analysis) and predicted (from the model) results. The results and any significant differences are found in Table 11. Any significant differences were examined in order to determine any factors that may have impacted the results.
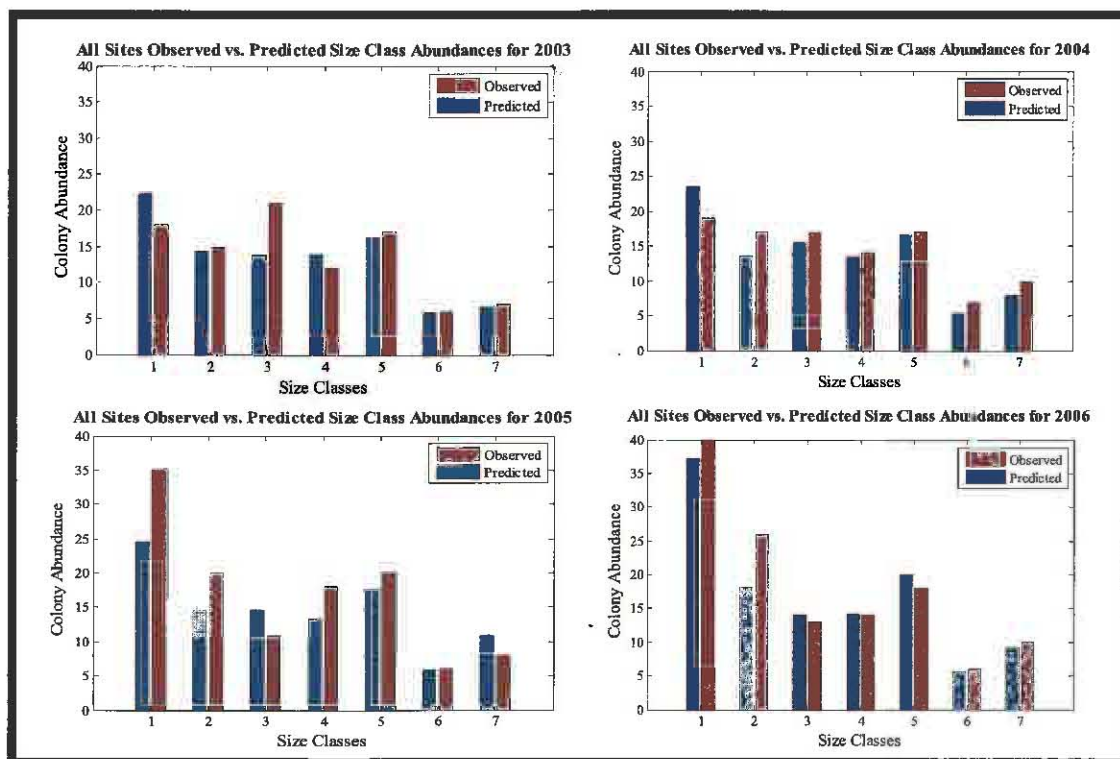

Figure 20: Observed vs. predicted colony abundance in each size class per year for All sites.
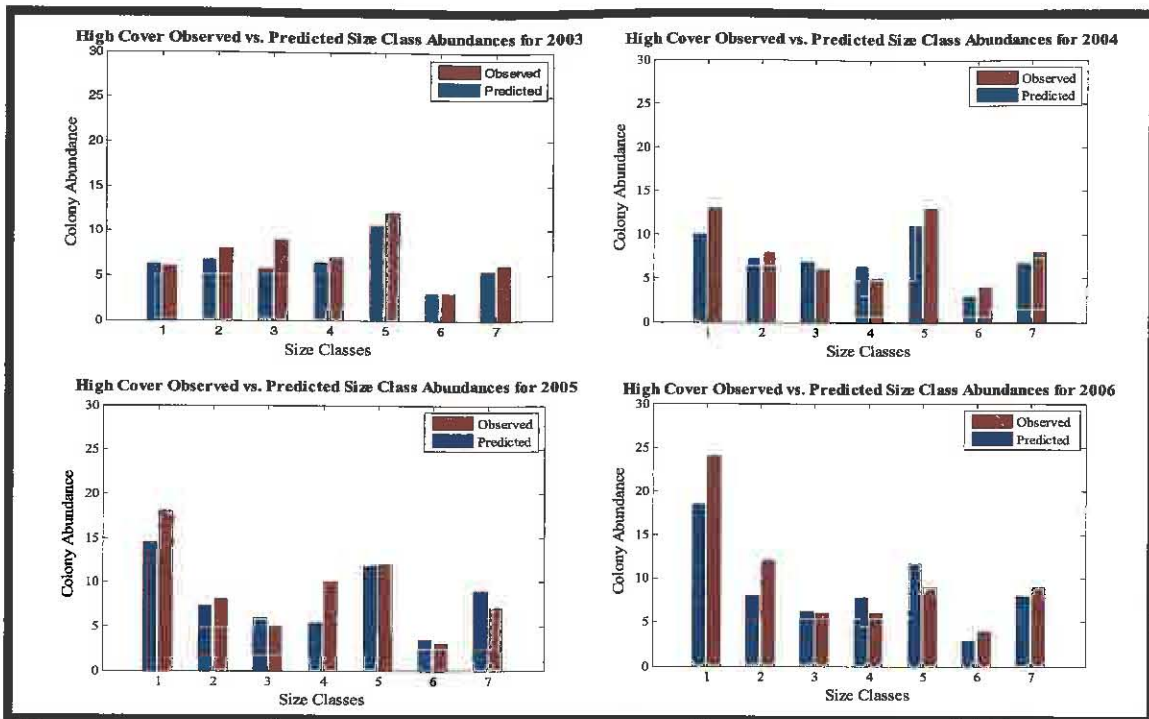
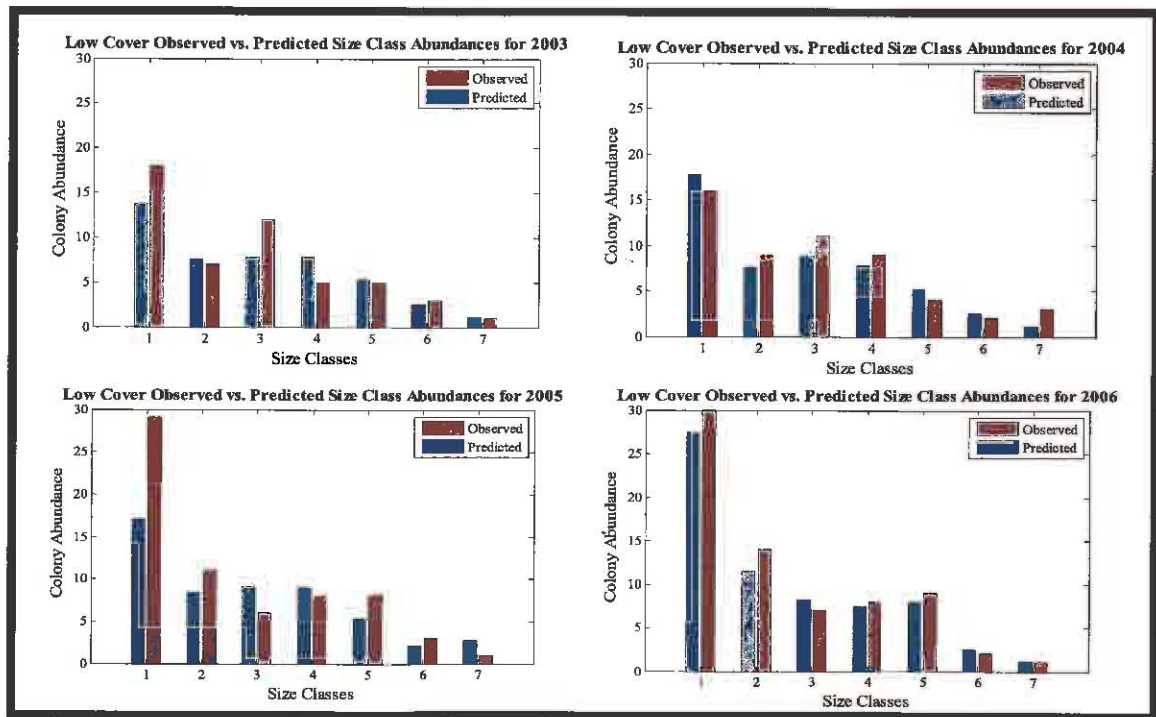Figure 21: Observed vs. predicted colony abundance in each size class per year for the High Cover sites.

Figure 22: Observed vs. predicted colony abundance in each size class per year for Low Cover sites.
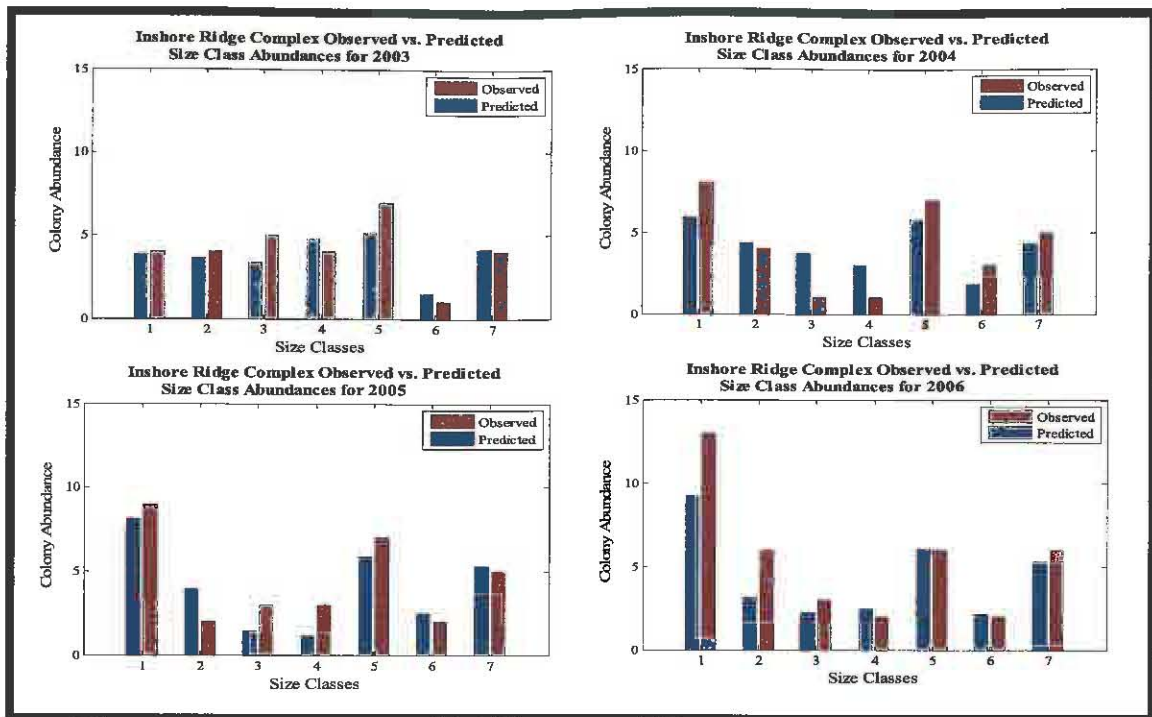
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Figure 23: Observed vs. predicted colony abundance in each size class per year for Inshore Ridge Complex sites.
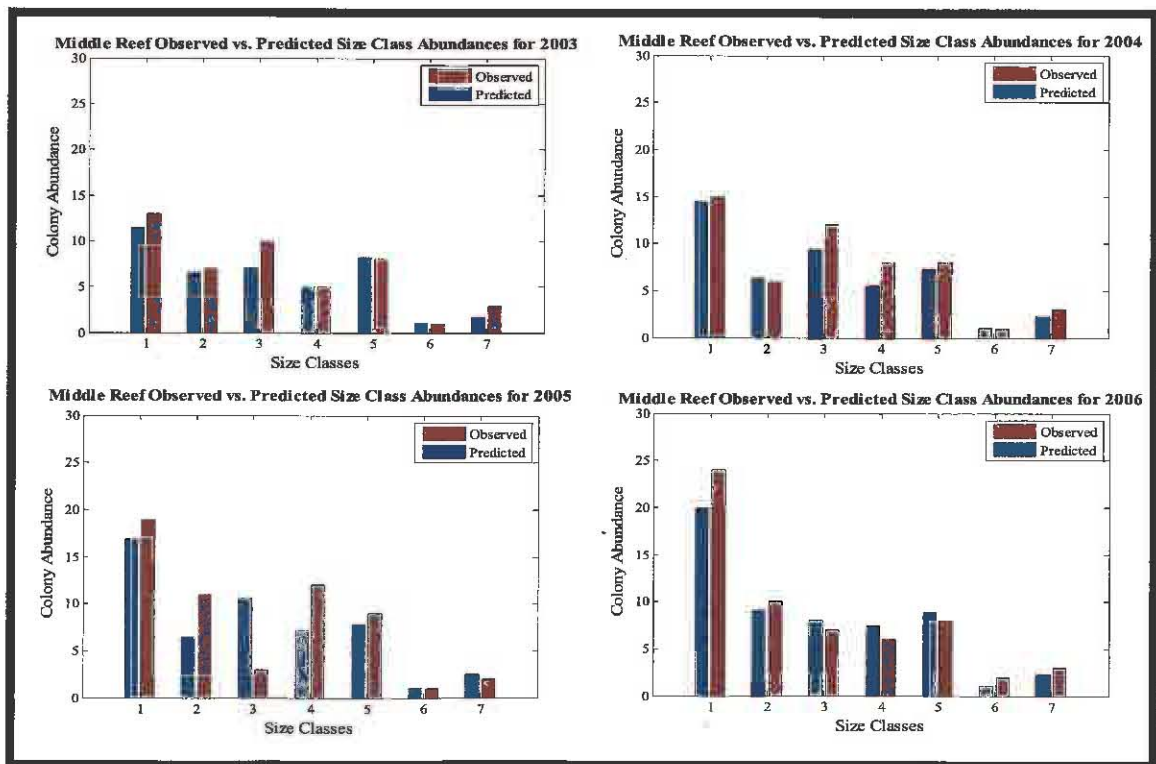

Figure 24: Observed vs. predicted colony abundance in each size class per year for Middle Reef sites.
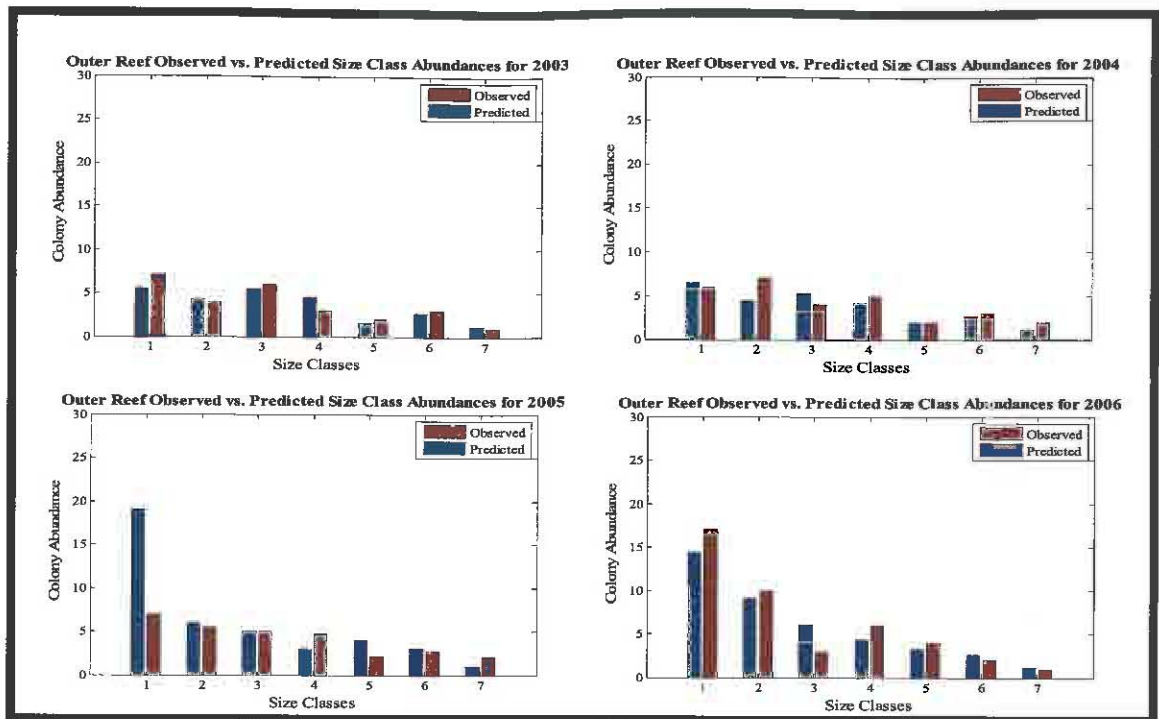
Figure 25: Observed vs. predicted colony abundance in each size class per year for Outer Reef sites.

Table 11: Chi-square comparison of observed vs. predicted model results for All, High Cover, Low Cover, Inshore Ridge Complex, Middle Reef, and Outer Reef sites (2003-2006). For DF= 6, a χ^2 = 12.592, therefore any p-value >12.592 represents a significant difference in distribution (value denoted with an asterisk).

Chi-Square Results	
DF=6	P-value
All Sites	
2003	4.647
2004	3.124
2005	10.004
2006	4.181
High Cover	
2003	2.100
2004	2.192
2005	6.897
2006	5.708
Low Cover	
2003	0.736
2004	5.450
2005	14.340*
2006	1.878
Inshore Ridge Complex	
2003	1.750
2004	5.167
2005	9.292
2006	5.478
Middle Reef	
2003	2.149
2004	2.381
2005	13.917*
2006	2.790
Outer Reef	
2003	1.154
2004	2.686
2005	23.293*
2006	2.967

When originally creating my model I chose not to include any density variables. Since the results of the chi square test showed that only the lower cover sites had significant differences from the model, I presumed that it implied that the high cover sites were density-dependent, and so therefore were not affected by the same environmental variations as the lower cover sites. Thus, since the density-dependent high cover sites violate the assumptions of my model, if I were to run the final sensitivity and elasticity analyses the results may not be accurate. So, in order to determine which size class transitions contribute the most to the dynamics of the population, the sensitivity and elasticity analyses were run only on the mean matrices of the treatments that had significant difference between the distribution of the observed and predicted vectors (LC, MR, OR) (Figures 26-37). Figures 26-37 are graphical representations of the resulting matrices and should be read accordingly. For example, Figures 26 and 27 represent the same data set (i.e. the results of the sensitivity analysis for the mean low cover matrix) and in both figures, the top left corner (in Figure 26- dark blue, and Figure 27- lime green) represents the transition from size class 1 to size class 1 or α_{11}. The major difference is that Figure 27 is the scalar view (i.e. the log) of Figure 26. This was done in order to give a different view of the results and their significance. Any similarities or differences in the results of the analyses between treatments were examined and are explained in the discussion.
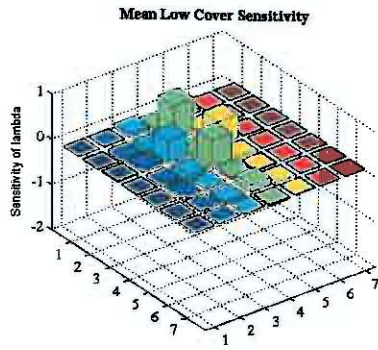
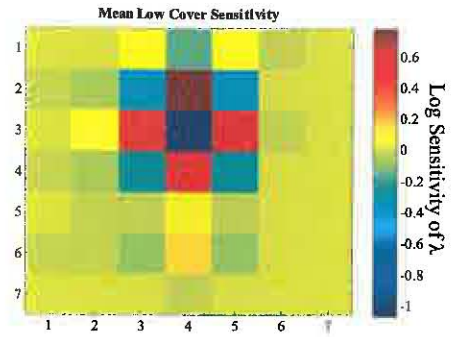Figure 26: Eigenvalue sensitivity analysis of the mean Low Cover matrix.

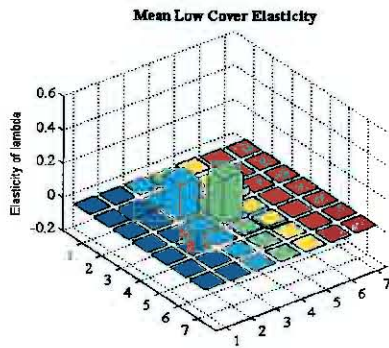Figure 27: Eigenvalue sensitivity analysis of the mean Low Cover matrix-scalar view.

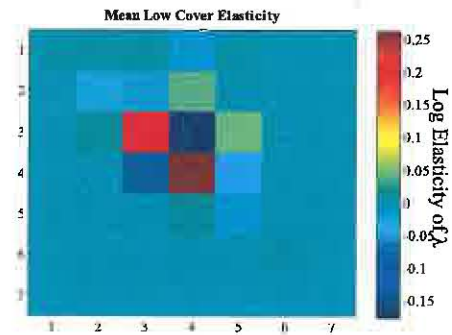Figure 28: Eigenvalue elasticity analysis of the mean Low Cover matrix.

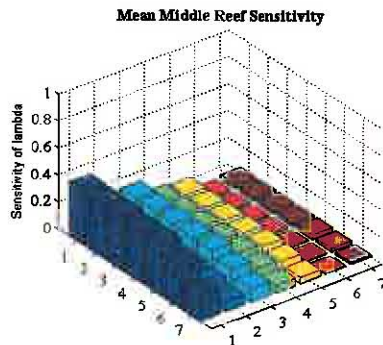Figure 29: Eigenvalue elasticity analysis of the mean Low Cover matrix- scalar view.

Figure 30: Eigenvalue sensitivity analysis of the mean Middle Reef matrix.

Figure 31: Eigenvalue sensitivity analysis of the mean Middle Reef matrix-scalar view.

Figure 32: Eigenvalue elasticity analysis of the mean Middle Reef matrix.

Figure 33: Eigenvalue elasticity analysis of the mean Middle Reef matrix- scalar view.

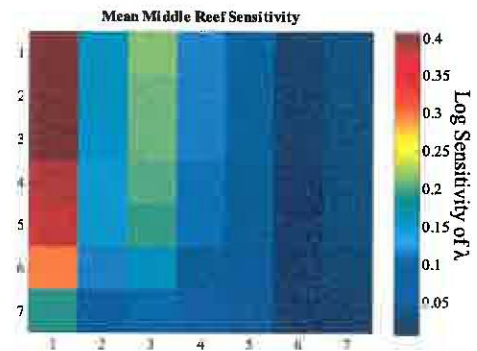Figure 34: Eigenvalue sensitivity analysis of the mean Outer Reef matrix.

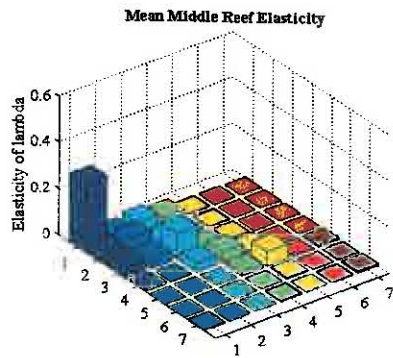Figure 35: Eigenvalue sensitivity analysis of the mean Outer Reef matrix- scalar view.

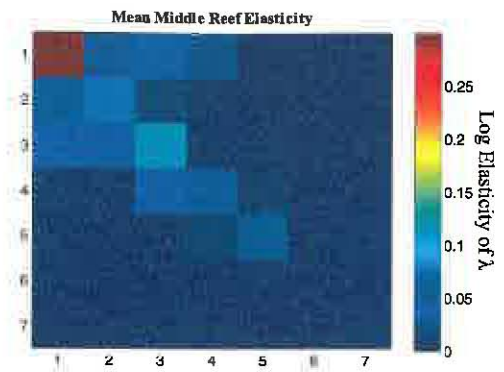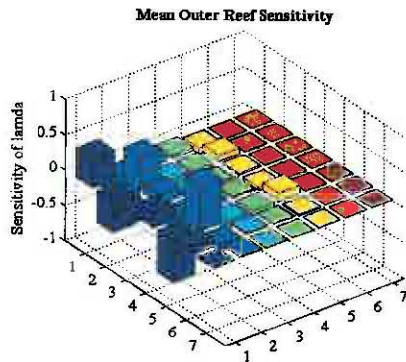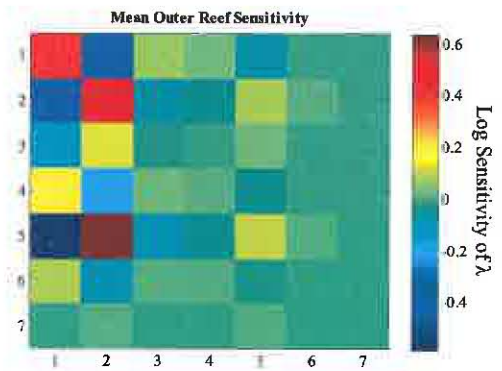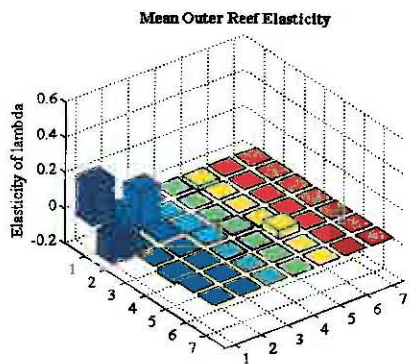Figure 36: Eigenvalue elasticity analysis of the mean Outer Reef matrix.
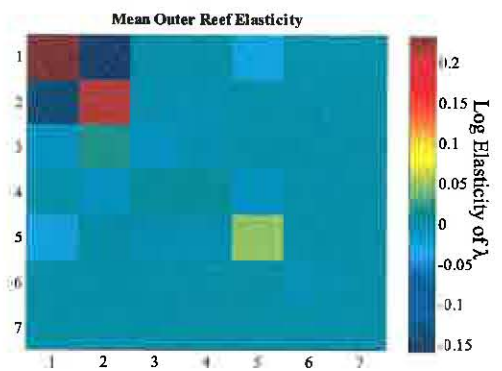

Figure 37: Eigenvalue elasticity analysis of the mean Outer Reef matrix- scalar view.

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4.0. DISCUSSION

The zoanthid *Palythoa caribaeorum* population dynamics have been analyzed to assess the current community in the southeast Florida reef system. In order for this project to be valuable to local resource managers, temporal and spatial changes in *Palythoa* were examined. This study was conducted in two parts.

4.1. Part One: General *Palythoa* population dynamics

The goal of Part One was to use digital imagery analysis to quantify the spatial cover of *Palythoa* and provide a general overview of the *Palythoa* population present across the study area (2002-2005). These results fill a void of information regarding the distribution of zoanthids in southeast Florida.

The results of the Moyer et al. (2003) paper (Figure 2) suggest the Inner Reef is zoanthid and algae-dominated. The study attempted to classify a large area, and I believe it may have led to an over simplification of the community present on the Inner Reef. The results of this study show that although no Inner Reef sites were included in this study, there is no indication of zoanthid domination on southeast Florida reefs. Interestingly, the Inshore Ridge Complex had 2 of the 3 highest *Palythoa* cover sites for all four sampling periods (2002-05) (Figure 13). Those three sites (FTL4, HB2, JUL6) had particularly high average individual covers, but the current study design does not allow for any hypotheses as to why these are the most populated sites.

By using digital image analysis, I determined that there was no significant change in *Palythoa* percent live cover from 2002-2005. This is of importance because

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although *Palythoa* has been reported as an aggressive spatial competitor, the results show that the population is actually maintaining size in southeast Florida.

A common perception in southeast Florida is that *Palythoa* may have a negative effect on stony corals, so I compared my *Palythoa* population data to the historical stony coral mean percent live data from the Broward County Yearly Monitoring Project in southeast Florida (Gilliam et al. 2006, 2007) for all 16 sites (2002-2005) (Figures 38-40). When the mean percent live covers were compared for all sites, stony coral cover was greater than *Palythoa* each year. For the majority of both the High and Low cover sites, stony corals had a higher mean percent live cover than *Palythoa* each year (2002-05). Both populations seem to be maintaining size which suggests stabilization in the system.
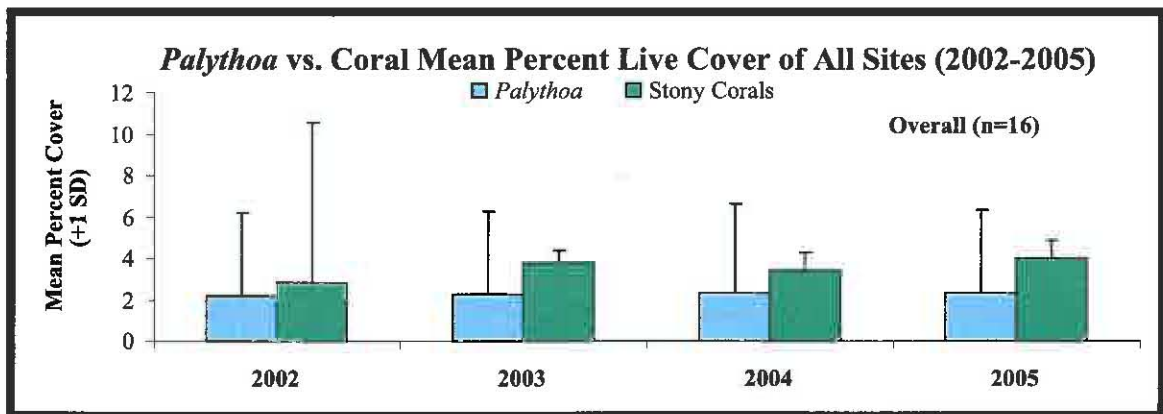
Figure 38: Comparison of *Palythoa* and stony coral mean percent live cover (+1SD) for all 16 sites.
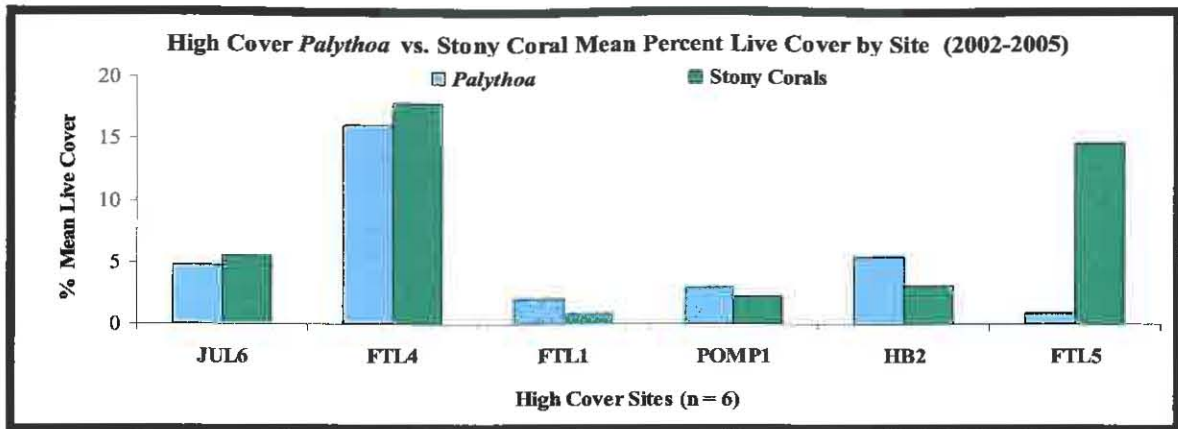
Figure 39: High cover *Palythoa* vs. stony coral mean percent live cover by site (n = 6).
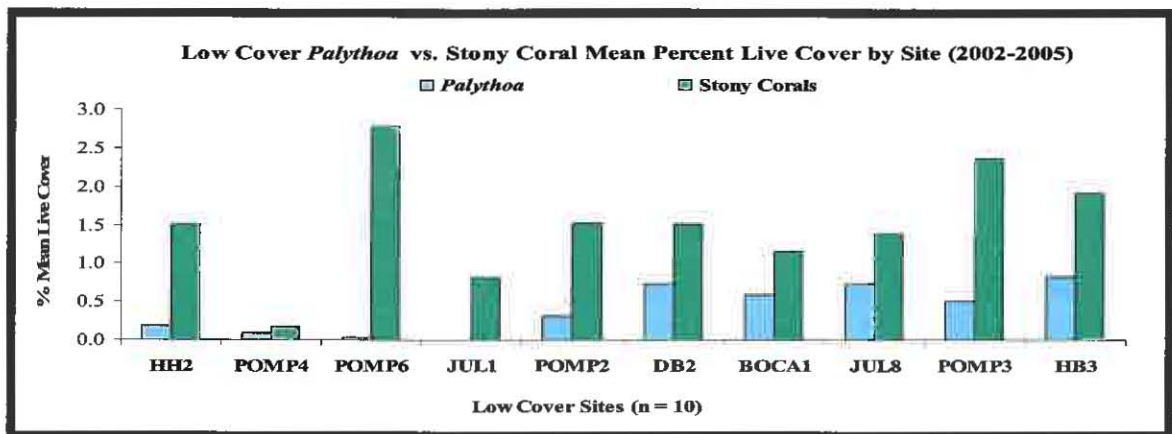
Figure 40: Low cover *Palythoa* vs. stony coral mean percent live cover by site (n = 10).

These results suggest that even though the reefs in southeast Florida seem to be such a prime location for *Palythoa* to dominate, the *Palythoa* population is simply maintaining size. With high growth rates, a lack of predation, and the potent neurotoxin PTX, *Palythoa* should have been able to out grow/compete the majority of its spatial competitors (Karlson 1980; Suchanek and Green 1981; Sebens 1982). The relatively low live covers for the majority of the study sites suggest that there is an unknown regulatory factor (e.g. nutrient, spatial, etc.) involved. With an estimated 41km² of shallow reef habitat in Broward County and 140 MGD of nutrient-laden treated wastewater pumped into (or near to) the study area (Koopman et al. 2006), this

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seems to challenge the Lapointe et al. (2002) theory that heavy nutrient loading leads to uncontrolled *Palythoa* growth. Although factors such as disease and bleaching were not captured in this data set, it may prove that they and/or an unknown self-regulated population size are factors in keeping the *Palythoa* population size from dominating southeast Florida.

4.2. Part Two: Transition Matrix Model

The goal of Part Two was to use digital analysis to determine if it was possible to create an accurate stage transition matrix model for *Palythoa*. The model was then tested by comparing the predicted model results with the observed results from the digital image analysis. Any statistically significant differences between the observed and predicted observations were examined and the subsequent sensitivity and elasticity analyses were run on the appropriate results. Finally, I provided recommendations for the data and duration of monitoring needed for future studies, and explored any limitations of the current study.

Accurate predictive models of ecological communities are greatly needed (Keddy, 1992). The scientific community has only in the last 25 years begun to recognize the importance of modeling as a way to accurately predict the future states of communities (Keddy, 1992). So, in order to begin to understand the complex and stochastic population dynamics of *Palythoa*, it was necessary to look at these data on another level then just the population density of individuals. First, I created stage-based transition matrices for the years 2002-2006 (e.g. 2002-03, 2003-04, etc.). By taking the mean of all four transition matrices, I was able to determine the population growth rate

(λ=1.0) for the overall population. This suggests that the population is maintaining size since a lambda value equal to 1.0 signifies stability (Hughes 1984), which agrees with the Part One results that the *Palythoa* population is maintaining size, rather than growing or shrinking.

In order to test the accuracy of the model, the predicted results of the model and the actual observed results from the digital image analysis were analyzed using a standard chi-square test. The only significant differences between the observed and predicted vector chi-square results were for the Low Cover, Middle Reef, and Outer Reef sites in 2005. This may be explained by the severe high energy hurricane seasons that southeast Florida experienced in 2004 and 2005. Crossing directly over the reefs, Hurricanes Francis (August 25th – September 8th) and Jeanne (September 13th – 28th) both made landfall in Broward County, FL in 2004. In 2005, Hurricanes Katrina (August 23rd – 30th) and Wilma (October 17th -25th) hit south Florida, and although they did not directly cross the reefs of the study area, they are two of the six most intense storms ever recorded in the Atlantic basin. In 2004, five of the nine sites were sampled after the hurricanes passed, and all of the sites in 2005 were sampled either between hurricanes or after both had passed. *Palythoa*'s reaction to the disturbances was obvious as was the year that it took to regain population stability/equilibrium. This was shown by the significant difference between the observed and expected outcomes of the model for the Low Cover, Middle Reef, and Outer Reef in 2005, but not in 2006. The data suggests that the lower cover *Palythoa* population didn't regain full normal distribution again until the 2006 sampling period. The most interesting aspect of these results is that only the Low Cover sites and deeper (Middle and Outer) reefs were

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significantly impacted. Initially, this seems counter intuitive, because one would expect the shallower reefs (which received the majority of the brunt of the storm's energy) to have been impacted the most. But, *Palythoa* normally thrives in high-energy shallow areas; their conjoined polyp colony formation and ability to retain carbonate sediment in their body walls allows *Palythoa* to minimize the damaging drag of water flow. The High Cover sites and Inshore Ridge Complex may have taken the brunt of the wave action, but because of the sheer density of the population, they seemed to have faired better than the individual colonies in the Low Cover sites and deeper (Middle and Outer) reefs. The exact mechanisms involved with the hurricanes that resulted in such a large size class distribution disturbance (e.g. high energy waves damaging/stressing the colonies, lack of nutrition, turbidity, etc.) are unknown. Rather, my conclusion is that the model was accurate and sensitive enough to pick up a large-scale disturbance. In future work, the components of the study design and model will need to be fine-tuned to determine if it is possible to show small scale disturbances.

Table 12: Site visits relative to the 2004 and 2005 high energy hurricane seasons. Asterisks denote sites that were visited post hurricanes Frances and Jeanne in 2004 and either between hurricanes Katrina and Wilma or after both had passed.

Reef	Site	2004 Date Completed	2005 Date Completed
Inshore Ridge Complex	JUL6	14 Oct 2004*	09 Dec 2005*
Inshore Ridge Complex	FTL4	03 Nov 2004*	13 Jan 2006*
Inshore Ridge Complex	FTL1	30 Aug 2004	14 Oct 2005*
Middle Reef	POMP2	19 Aug 2004	09 Dec 2005*
Middle Reef	HB2	19 Aug 2004	01 Sep 2005*
Middle Reef	DB2	19 Oct 2004*	12 Oct 2005*
Outer Reef	JUL8	18 Aug 2004	07 Feb 2006*
Outer Reef	POMP3	19 Oct 2004*	01 Sep 2005*
Outer Reef	HB3	26 Oct 2004*	12 Oct 2005*

Assumptions were made as to the variable conditions of the *Palythoa* population in southeast Florida. The most important assumption was that population density plays no role in the population's dynamics. A population with a high growth rate ($\lambda > 1.0$) is predicted to exhibit an increased density (thus exhibit density dependence) (Bierzychudek, 1999). "There is a constant need for simple but general functions to describe density dependent processes; simple so that their properties may be determined analytically and general so that they are capable of describing the varied forms in which density dependence may occur" (Bellows 1981). The matrix model is ideally simple and general, but one of the main constraint assumptions of the model is that the population in question conforms to a single-step Markov process. A Markov process is a mathematical model of probabilistic processes, which generate random sequences of outcomes to certain probabilities. The basic premise of a Markov process is that if the outcomes of all of the first *t-n* events of a series of events are known, then the probabilities of outcomes in the *t-th* experiments are also known. This means that step ($t+1$) is uniquely defined by step (t). The size of t must not matter (thus, dependence of $t+1$ on t must be same after 10,000 steps as after 1). In short, transition probabilities must be totally stable. The results of the chi-square test suggest that this is not the case in the High Cover and Inshore Ridge Complex (and subsequently the mean of All) *Palythoa* sites. In general, *Palythoa* colonies have a fast initial growth rate, but as density increases, growth decreases (Tanner 1997). For the All, High Cover and Inshore Ridge Complex treatments, I observed super-adult (600+ cm²) colonies that maintained size over the four transition periods. The increased frequency of stable size super-adult colonies and the lack of major change in the population distribution after

the hurricanes passed suggest that density dependence is restricting the growth of the population. This dependence on large colonies violates the assumption of a simple Markov process, because the likelihood of transition from large into small decreases with t (i.e. as the habitat gets fuller). Therefore, the All, High Cover and Inshore Ridge Complex treatment models were excluded from the final sensitivity and elasticity analyses.

The results of the sensitivity and elasticity analyses for the Low Cover, Middle and Outer Reef treatments all showed that the stability of the *Palythoa* population in southeast Florida is dependant on the smaller size class loop transitions. Looking at each analysis individually, the Low Cover results show that growth (e.g. α_{24}) is important, while two Middle (e.g. α_{21} and α_{31}), and one Outer Reef (e.g. α_{52}) transitions show that shrinkage is important. Overall, it appears that although the *Palythoa* population in southeast Florida is mostly maintaining size (loop), there is a tendency for periodic shrinkage.

4.3. Lessons Learned Including Limitations of the Study

The size class transition matrix model works and is accurate. The sensitivity and elasticity analyses showed that population growth and shrinkage in the smaller size classes in the lower cover sites are the most important to population maintenance. One consideration is that this model does not contain any information on sexual reproduction, yet the population is somehow stable (shown by all lambda values equal to or near to 1.0). A future study would need to be specifically designed to answer the question of where the recruits are going.

The information obtained in this study would not have been possible by *in situ* data collection alone. But, the data set used (Broward County Yearly Monitoring) was not designed for this kind of manipulation. Increased efficiency and integration of monitoring efforts (such as photographic and video methods) are becoming increasingly important to optimize diver time in the water (Kohler and Gill 2006). Often, biological studies are confined to good weather days and funding, but by using digital images that were taken at the same time as the *in situ* observational data, more information can be obtained from the data set than what was originally collected. There is no problem when the additional information conforms to the constraints of the original study design, but problems arise when the data is manipulated outside of that design. For example, in the case of the current study, *Palythoa* does not appear to have any impact on stony coral percent live cover; however the data did not allow for any kind of statistical comparison between the two populations.

4.4. Recommendations for Future Requirements of Data and Duration of Monitoring Needed to Accurately Model *Palythoa*

It is still unclear why or how *Palythoa* is maintaining size in southeast Florida. So, as part of this study, I have recommendations for the data and duration of monitoring needed in future studies to accurately model the dynamics of *Palythoa*. "Realistic predictions about clonal structure will require extensive knowledge of population history (e.g., the magnitude, frequency, and specific effects of past disturbances, variation in the biological and physical processes controlling normal recruitment rates, and the occurrence of episodic recruitment or mass mortality events)" (Karlson 1991). Research on *Palythoa* is additionally challenging because it is unusual

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in its ability to fluidly move between size classes as well its ability to incorporate new recruits and old ramets into mature colonies. For example, if a new recruit could immediately join a mature reproductive super-adult, then it would greatly affect the overall dynamics of the population by producing a constant reproductive (either asexual or sexual) state in the majority of the population. This is normally unrealistic for other species, but it seems that it is possible (and common) for *Palythoa*. Karlson (1991) states that the extremely long genet life spans may make it impossible to know the complete history of a population. It may not be possible to know the complete history, but by focusing future research on the most important size class transitions identified in the current study, the knowledge gained may well prove to be helpful. That being said, annual sampling periods are acceptable when focused only on less dynamic species, but especially for such an aggressive and dynamic competitor like *Palythoa*, observing the colonies only once a year greatly limits the information that can be obtained from analysis.

In the future, to truly understand what is happening in the population, a study focusing on *Palythoa* should include a longer duration of monitoring with appropriately designed sampling periods (e.g. more than once a year, seasonally focused, etc.). For example if the study were to focus on spatial competition, data could be collected monthly, but a study involving the tracking of an individual's age or stage would need observations from the inception of the original parent colony(ies), and therefore would need a more frequent sampling period. Additionally, factors such as density impacts (Tanner 1999; Caswell et al. 2004), environmental fluctuations (e.g. severe storm years) (Lirman 2003), sexual reproduction, disease (Acosta 1999), or bleaching events that are

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common to the local *Palythoa* population need to be addressed in the study design. The Gill (2006) thesis showed that image-based methodology is best used for intricate growth measurements and colony fate tracking while diver methodology is best for percent cover and recruitment studies. Combining image and diver-based methodology to form a comprehensive look at the major factors affecting the population is the only way to accurately assess the dynamics present in the population. "Though long-term studies of many individuals are expensive and laborious, they are the only way to acquire data of the quality that transition matrix models require" (Bierzychudek 1999).

Palythoa is an important component of the southeast Florida coral reef community. Although it possesses the ability to outgrow stony corals (and almost all other sessile invertebrates), the data from the current study suggests that the *Palythoa* population is actually maintaining size rather than over-growing the community. With the knowledge gained from this study, we now know that it is possible to accurately model the population dynamics present in the southeast Florida *Palythoa* population.

This study represents an initial glimpse of the dynamics involved in the *Palythoa* population of southeast Florida, but in order to form a comprehensive model more appropriately designed population dynamic studies must be completed. As research furthers our understanding of how these communities interact this information may be valuable to resource managers. Future research needs to look at all inhabitants, rather than focusing on individual components (e.g. stony corals).

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APPENDIX

Flow Chart of Major Steps to Complete Part One and Part Two

Use CPCe to trace digital images

PART ONE

Total in quad live cover (cm²) for each site

Determine mean percent live cover by year and reef

Transform data and run ANOVAs

PART TWO

Track 85 individual colonies area (cm²)

Assign size class designations by area = observed vectors

Determine size class transitions for each transition year

Results in size class transition frequencies

Transition frequencies get entered into 4 matrices (one for each transition year: 2002-03, 2003-04, etc.)

Average of the 4 transition matrices = Mean matrix

Use Matlab® to determine dominant eigenvalue (aka: population growth rate)

Multiply observed vector * Mean matrix = Next year's vector

Population growth rate determines stability of population

Chi-square test for distribution

Sensitivity and Elasticity Analyses

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