POPULATION DYNAMIC MODELING OF THE CORKSCREW SEA ANEMONE *BARTHOLOMEA ANNULATA* ON CARIBBEAN CORAL REEFS

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Michael W. Nelsen

Certificate of approval:

Stephen Kempf Associate Professor Biological Sciences	Nanette Chadwick, Chair Associate Professor Biological Sciences
Georg Hetzer Professor Mathematics and Statistics	George T. Flowers Dean Graduate School

POPULATION DYNAMIC MODELING OF THE CORKSCREW SEA ANEMONE *BARTHOLOMEA ANNULATA* ON CARIBBEAN CORAL REEFS

Michael W. Nelsen

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POPULATION DYNAMICS MODELING OF THE CORKSCREW SEA ANEMONE *BARTHOLOMEA ANNULATA* ON CARIBBEAN CORAL REEFS

Michael W. Nelsen

Signature of Author

Date of Graduation

VITA

Michael W. Nelsen, son of Gary Nelsen and Sheila Gardineer born August 22, 1983, in Fremont, Michigan. He graduated with a Bachelor of Arts degree in Biology and Mathematics in 2005 from Hope College in Holland, MI. In the Fall of 2006 he entered the Graduate School in the Department of Biological Sciences where he joined the laboratory of Dr. Nanette E. Chadwick and is currently pursuing a Masters degree.

THESIS ABSTRACT

POPULATION DYNAMICS MODELING OF THE CORKSCREW SEA ANEMONE *BARTHOLOMEA ANNULATA* ON CARIBBEAN CORAL REEFS

Michael W. Nelsen

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The corkscrew anemone *Bartholomea annulata* is a large, common sea anemone on Caribbean coral reefs. The holobiont of *B. annulata*, endosymbiotic microalgae (zooxanthellae), and ectosymbiotic cleaner shrimps may have positive cascade effects in coral reef communities by serving as fish cleaning stations. Thus, collection of *B. annulata* for the ornamental aquarium trade may indirectly impact reef fish diversity, yet this fishery is largely uncontrolled and has drastically reduced the abundance of these sea anemones in some parts of the Caribbean. The dynamics of 2 unfished populations of *B. annulata* in the US Virgin Islands were modeled here, to determine how they vary spatially (between habitats) and temporally (among 4 seasons). Seven types of demographic models were used to project future population size and structure at each of the 2 study sites.

Population dynamics differed significantly between the 2 examined study locations, with higher mortality at the outer reef site (Flat Cay) and higher rates of transition between size-classes (growth and shrinkage) at the inner reef site (Brewers Bay). There was no significant difference in the rate of total recruitment between these 2 populations, but both the number of recruits per m^2 and recruits per resident anemone per m^2 were significantly higher at Brewers Bay, while the number of recruits per resident anemone was significantly higher at Flat Cay. Light intensity, sediment grain size, percent stony coral cover, and relative water motion all were significantly greater at the outer site of Flat Cay than at the inner protected site in Brewers Bay. These differences in site characteristics may influence the demography of *B. annulata* at each site, in particular rates of anemone growth and mortality.

Matrix models based on current population trends projected the survival of these populations at both sites. Closed population models for both sites projected exponential growth and population sizes much larger than the potential carrying capacities of the sites. In contrast, the open and semi-open models projected stabilization of the anemone populations, though the equilibrium sizes of the populations varied among models. Elasticity analyses of the matrix models indicated that the smallest individuals contributed the most to population growth, and suggest a need for establishing a minimum body size for the collection for these organisms. When outside recruitment was removed from the open and semi-open models, anemone populations were projected to plummet to zero within about 3 years, revealing the importance of outside recruitment for population growth and stability. Thus, unfished marine preserves near fished areas of these anemones may be important as sources of outside recruitment. It is concluded that the establishment of unfished marine preserves adjacent to fished populations, and a minimum body size for collection, are recommended for the development of a sustainable fishery on this giant sea anemone on Caribbean coral reefs.

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CHAPTER I

INTRODUCTION

History and Applications of Population Modeling

Over the past sixty years, mathematics has become an important tool in the management of biological systems. In 1945, Patrick Holt Leslie developed a method to use matrices to represent a population of organisms if the ages of individuals in the population are known. This method has been applied to a variety of organisms ranging from black rhinos and eagles to cheetahs and everything in between (Crooks et al. 1998, Cromsigt et al. 2002, Katzner et al. 2006). Although Leslie was one of the earliest and most influential mathematicians to use matrices to model biological systems, he was not the first to use reproduction and survival rates to model population growth (Caswell 2001). In 1895, Edwin Cannan used these vital rates to analyze "The cessation of the growth of population in England and Wales", and he is credited with being the first to use vital rates in population modeling (Caswell 2001).

The first major variation on Leslie's model was introduced in 1965 by Lenard Lefkovitch. Lefkovitch took Leslie's model and modified it so that the matrix was no longer divided into age classes of equal length, but into stages that did not have to be equal in length (Lefkovitch 1965). This modification allowed for more accurate modeling of organisms, such as beetles, where life stages such as pupae and larvae describe the biology of the organism better than the age does.

The demography of marine organisms typically is modeled using either stage-based or size-based matrices for several reasons, the most prominent of which is that often it is difficult to determine the ages of individuals from their appearance. Some marine invertebrates may shrink or fragment and thus decrease in size as they age (Hughes 1984, Cropper and DiResta 1999, Hughes and Tanner 2000, and Cropper et al. 2001), so it is easier to classify them by stage/size rather than age. Secondly, it has been difficult to perform long-term studies on organisms underwater. It is much easier to observe and collect data on birds everyday with binoculars than to measure the height of gorgonian soft corals on a daily basis, using SCUBA. For example, Gotelli (1991) misses several months of data collection on a gorgonian population because the water was too cold to dive in for long periods of time. Due in part to these limitations of working on marine organisms, matrix modeling has been applied to a variety of marine invertebrates, including lobsters in Maine (Incze et al. 2006), soft-shell clams in Massachusetts (Ripley and Caswell 2006), and corals during recovery from disturbances on tropical reefs in the Florida Keys (Lirman and Miller 2003).

The above studies have used matrix modeling to manage populations of organisms. Another use of matrix models is in the development of marine preserves/sanctuaries, which have become popular tools in conservation planning. Gerber and Heppell (2004) showed that matrix modeling could improve the efficacy of marine sanctuaries. Currently, marine sanctuaries are designed in locations that provide the most protection for adult individuals. Mathematical modeling of the species that the sanctuaries are designed to protect can reveal the crucial life stages that require the most protection. Then the sanctuaries can be more properly designed so that optimal population growth is obtained. For example, in many marine species the juveniles and adults live in different habitats (Sebens 1981, Mumby and Hastings 2008), thus modeling may show that the efficacy of marine preserves may be greater near nursery habitats where juveniles occur, rather than in the habitats with contain most adults. Another benefit is that by using matrix models, populations can be better managed with less overall cost (Rose and Cowan 2003). Another advantage of modeling is that it allows for better planning. A model can project the size of future populations of target organisms, allowing for multi-year planning versus plans for only a single year.

Matrix Theory for Population Models

The matrix population model described by Leslie (1945, 1948) may be expressed as $\mathbf{b}_{t+1}=\mathbf{A}*\mathbf{b}_t$ (Eq. 1.1) where $\mathbf{A}$ is the s x s transition matrix, $\mathbf{b}_t$ is the s x 1 population vector at time t, and $\mathbf{b}_{t+1}$ is the population vector at time t+1. The elements in vector $\mathbf{b}_t$ are the number of individuals in each stage/age class in the population at time t (t=0,1,2,3,…, n). How the elements in $\mathbf{A}$ are arranged will depend on whether an age or stage based model is used. If an age-based model is used, then the top row and the subdiagonal will be the only elements of the matrix used (Fig. 1.1). If **A** is a stage-based matrix, then it is possible that any and/or every element in the matrix could be used (Fig. 1.2). The top row elements can be different from the rest of the values in the matrix. These elements can represent sexual reproduction, asexual reproduction, and new recruitment into the population combined with shrinkage of larger individuals. They can be greater than one (depending on the population being studied), whereas none of the other elements can be. Fecundity may be greater than one because it represents offspring produced from organisms currently in the population while the other elements represent a proportion of the individuals that transition from one stage/size to another. **A** is typically known as a transition matrix because the probabilities therein reveal whether or not an individual in a given class will remain in the same class or transition forward or backward. In age-based models, the transition is only from one age to the next, whereas stage-based models allow for movement of more than one stage in either direction, as well as for individuals remaining in the same stage. The vector **n**(t+1) is the result of multiplying **A*n**(t). This vector gives the composition of the population after it has transitioned from time t to time (t+1). Matrix modeling is a useful technique for the projection of future population size but it has yet to be used for tropical sea anemones, especially those in the Caribbean Sea.

Population Ecology of Caribbean Sea Anemones

The rosetip anemone *Condylactis gigantea* and the corkscrew anemone *Bartholomea annulata* (Cnidaria: Anthozoa: Actiniaria) are the largest and most common sea anemones in the Caribbean Sea, and yet little information exists on the biology of either species (Colin 1978, Kaplan 1982, Sefton & Webster 1986). This lack of information precludes a scientific basis for management of commercial fishing of these animals. Collection of sea anemones for ornamental aquarium use is a $6 million per year industry in Florida alone, with 11.8 million individuals of *C. gigantea* collected commercially, not including anemones taken by non-commercial collectors (Chiappone et al. 2001). Commercial fishing data for *B. annulata* show that the number collected in the state of Florida has sharply declined over the past decade, indicating a general decline in anemone populations (Fig. 1.3). In addition, individuals of *B. annulata* are one of the most common invertebrates collected for the aquarium trade in Puerto Rico. *B. annulata* is number 7 on the list of invertebrates collected, with 650 individuals collected by one collector in the first six months of 2002 (LeGore et al. 2005). Currently, no data exist on how these rates of fishing affect these sea anemone populations, or on the extent to which the fishery is sustainable but Chiappone et al. (2001) suggest that because of the distributional patterns of these anemones, the populations in Florida are unlikely to recover from this intense fishing pressure.

Governmental agencies that regulate collecting have assumed that both *C. gigantea* and *B. annulata* have high rates of population turnover, and thus that intensive fishing may not be a problem because many offspring are produced each year (Chiappone et al. 2001). These assumptions are not supported by the limited evidence available on the reproduction of these species. Jennison (1981) showed that individuals of *C. gigantea* are large, long-lived, and produce small numbers of large eggs. Those of *B. annulata* produce a larger number of eggs, but their planktotrophic planulae likely are susceptible to high rates of mortality due to starvation and predation during the drifting planktonic phase. As populations of these anemones decrease due to over-fishing, other problems can arise. Fertilization of gametes in both *C. gigantea* and *B. annulata* is external (Jennison 1981), thus as population size decreases, so does the concentration of their gametes in seawater and the probability that external fertilization will be successful (Levitan et al. 1992, 2004).

Individuals of *C. gigantea* and *B. annulata* serve as hosts to a diverse assemblage of ectosymbiotic fish and crustacean associates (Mahnken 1972). Obligate associates of particular importance are the cleaner shrimps. Several species of *Periclimenes* and one of *Thor* are known to be obligate shrimp mutualists with these anemones (Mahnken 1972, Nizinski 1989, Crawford 1992, Gwaltney and Brooks 1993). The anemones provide protection from predation for the shrimps, and the shrimps in some cases provide nutrients to the host anemones (Spotte 1996). Together, the holobiont of anemone host and shrimp associates fills an important niche in coral reef ecosystems (Nizinski 1989, Fautin et al. 1995).

The cleaner-shrimp *Periclimenes pedersoni* uses both species of giant anemone (*C. gigantea* and *B. annulata*) as base stations, and cleans external parasites from fish that inhabit the coral reef (Mahnken 1972, Nizinski 1989, Crawford 1992, Gwaltney and Brooks 1993, Becker and Grutter 2004). Thus, anemone-based cleaning stations may indirectly affect multiple trophic levels on the reef through positive effects on large carnivorous reef fish. Bshary (2003) conducted a long-term study that revealed how cleaners significantly impact coral reef communities. Four months after the removal of cleaners, the species diversity of client fish (small groupers [Serranidae], surgeon fish

[Acanthuridae], squirrelfish [Holocentridae], damselfish [Pomacentridae], wrasses [Labridae], dottybacks [Pseudochromidae], and cardinalfish [Apogonidae]) decreased by 18% after natural loss of cleaners and 24% after artificial cleaner removal, and did not return to normal levels for at least twenty months. Bshary also showed that the addition of cleaners to a reef can augment fish species diversity both through attraction and immigration of fishes, and through enhanced survival and retention of cleaned fish. After two to four weeks on reefs where cleaners had naturally arrived, there was a 34% increase in fish species diversity, and on reefs where cleaners were experimentally added there was a 42% increase in diversity. Increases in fish diversity due to the presence of cleaners can have a positive feedback effect on host sea anemones as well as on other zooxanthellate organisms in the community. This is because as the number of client fish increase, so does the amount of nitrogen waste excreted by these fish in the vicinity of the sea anemones, potentially providing enhanced nutrients to both the sea anemones and to nearby stony corals (Meyer and Schultz 1985a and b, Fautin et al. 1995, Spotte 1996, Porat and Chadwick-Furman 2005, Roopin et al. 2008). Over-fishing of the anemones *C. gigantea* and *B. annulata* thus potentially can cascade into major reductions of fish populations through the above indirect effects.

Research Objectives

The following research questions on populations of *B. annulata* are addressed in this thesis: (1) How do patterns of recruitment, changes in body size (growth/shrinkage), and mortality vary between two examined populations of this sea anemone? (Chapter II),

(2) What do population models predict about the crucial life stages, recovery times following disturbance, and minimum population size for recovery of this sea anemone? (Chapter III), and (3) What changes need to be made in management of this species, to support a sustainable fishery in the Caribbean? (Chapter III).

The methods employed in this study involved, firstly, collection of field data. The dynamics and stability of populations of the sea anemone *B. annulata* were examined, and patterns of recruitment, mortality, growth, and shrinkage of individuals were monitored every 3 months over a 1-year period (Mar. 07, June 07, Sept. 07, Dec. 07, and Mar. 08). *B. annulata* was the focus of this thesis, because populations of the other giant anemone in the Caribbean, *C. gigantea*, were too low at my study sites to use them for modeling. Secondly, the collected field data were used to create a stochastic population model in which a transition matrix, based on the probability of individuals transitioning among size classes, was used to make projections about future population size. Hughes (1984) created a general model for cnidarian population dynamics based on individual size rather than age, which was the basis for the models created in this study. In *B. annulata,* small individuals may be budded clonemates of older individuals produced through asexual replication, in addition to being new recruits from sexually-produced planula larvae. Because of this, an age-based model is not appropriate for this species (Jennison 1981).

The population projection model also was used to project the future condition and stability of populations of *B. annulata* at present rates of change at my field sites. I examined two unfished populations at St. Thomas, United States Virgin Islands, as a baseline to determine which vital rate was most crucial to maintain population growth, or which stage needed the most protection in order to enhance population recovery. Currently, commercial vessels are allowed to collect up to 400 sea anemones per day in some areas of the Caribbean, and declining populations indicate that this number may need to be drastically reduced (Chiappone et al. 2001).

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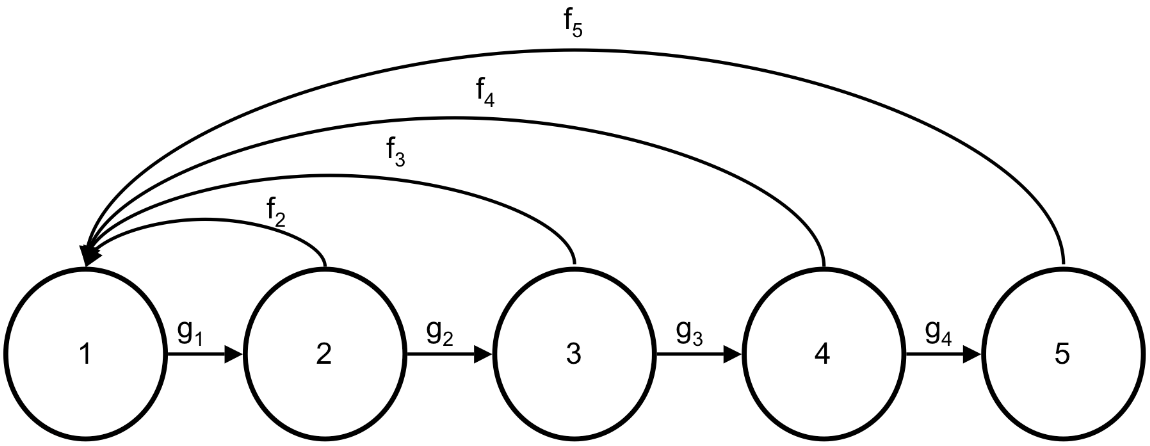
Figure Legends

Fig. 1.1. Example of an age-based life cycle graph. Arrows pointing to the right represent organisms growing older by one time period (**g**), while left-pointing arrows represent reproduction/recruitment (**f**). In this example, the organisms either grow older or die during each period (modified after Hughes 1984).

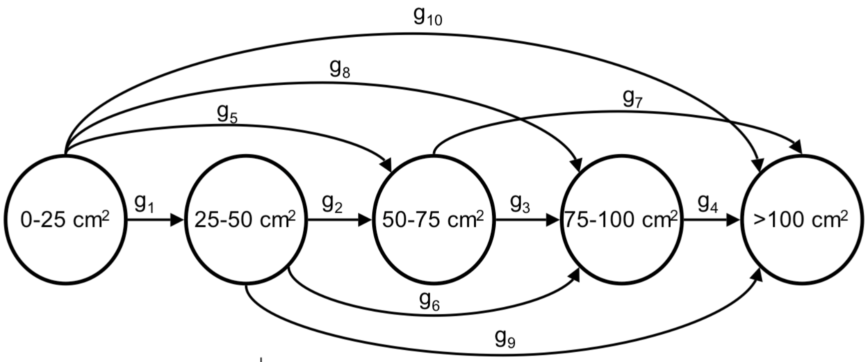
Fig. 1.2. Size-based life cycle graph for the corkscrew anemone *Bartholomea annulata*. Arrows pointing to the right represent *B. annulata* growing to a larger size-class (**g**), left-pointing arrows represent *B. annulata* shrinking to a smaller size-class and/or reproducing (**s**), and looping arrows represent *B. annulata* remaining in the same size-class (stasis, **L**). In this example, individuals of *B. annulata* either grow, shrink, remain in the same size-class, or die (modified after Hughes 1984).

Fig. 1.3. Number individuals of the corkscrew anemone *B. annulata* collected commercially per year in the state of Florida during 1990-2007. In 2005, the law changed to require individuals to purchase permits from collectors that currently possess them (data obtained from the Florida Fish and Wildlife Conservation Commission).

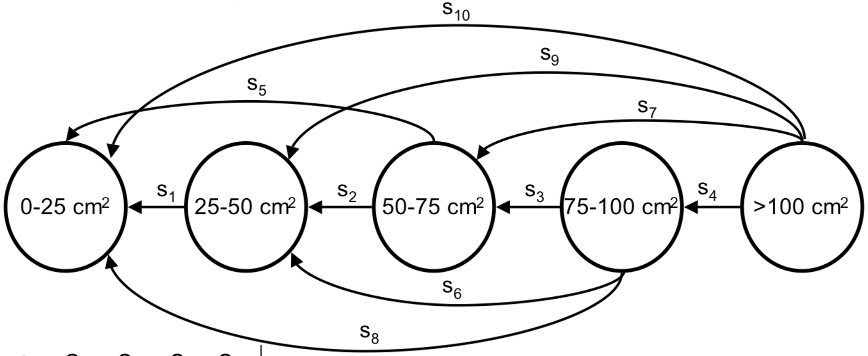


$$\begin{vmatrix} 0 & f_2 & f_3 & f_4` & f_5 \\ g_1 & 0 & 0 & 0 & 0 \\ 0 & g_2 & 0 & 0 & 0 \\ 0 & 0 & g_3 & 0 & 0 \\ 0 & 0 & 0 & g_4 & 0 \end{vmatrix}$$

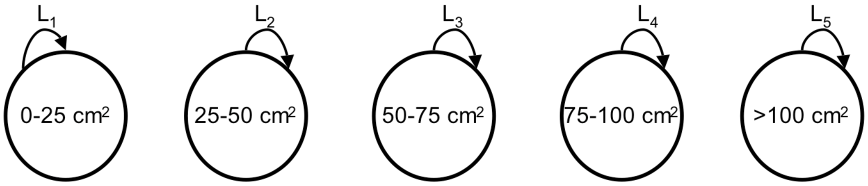
Fig. 1.1.



$$\begin{vmatrix} 0 & 0 & 0 & 0 & 0 \\ g_1 & 0 & 0 & 0 & 0 \\ g_5 & g_2 & 0 & 0 & 0 \\ g_8 & g_6 & g_3 & 0 & 0 \\ g_{10} & g_9 & g_7 & g_4 & 0 \end{vmatrix}$$



$$\begin{vmatrix} 0 & S_1 & S_5 & S_8 & S_{10} \\ 0 & 0 & S_2 & S_6 & S_9 \\ 0 & 0 & 0 & S_3 & S_7 \\ 0 & 0 & 0 & 0 & S_4 \\ 0 & 0 & 0 & 0 & 0 \end{vmatrix}$$



$$\begin{vmatrix} L_1 & 0 & 0 & 0 & 0 \\ 0 & L_2 & 0 & 0 & 0 \\ 0 & 0 & L_3 & 0 & 0 \\ 0 & 0 & 0 & L_4 & 0 \\ 0 & 0 & 0 & 0 & L_5 \end{vmatrix}$$

Fig. 1.2.

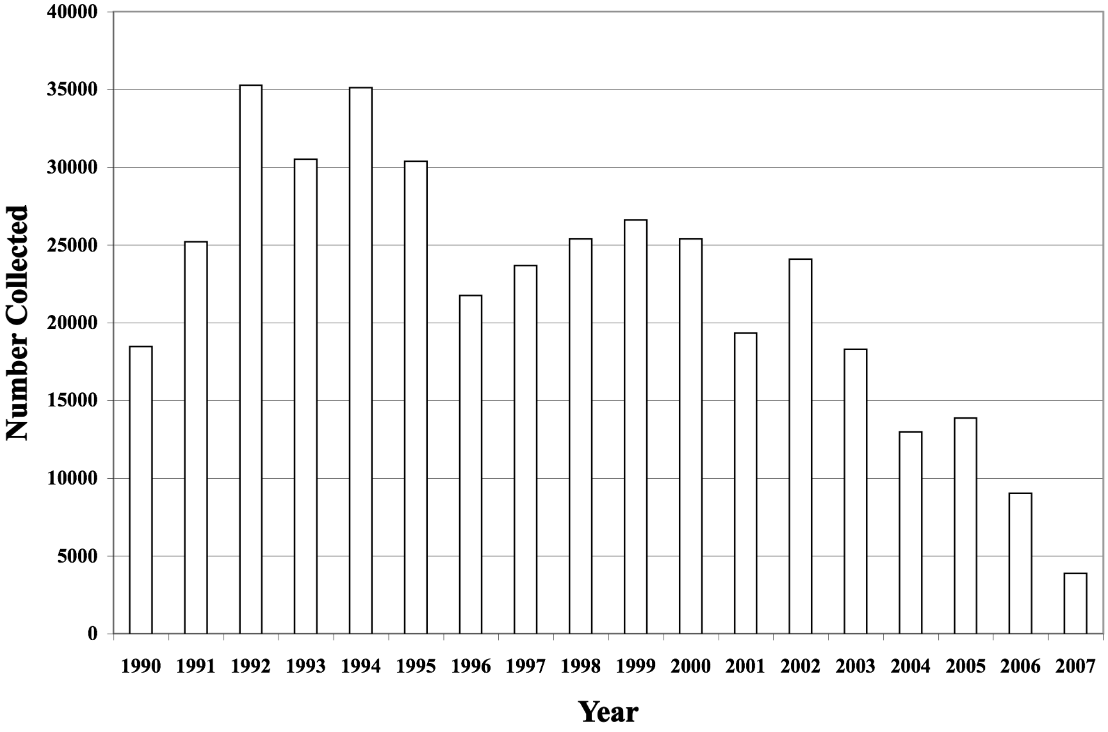

40000
35000
30000
25000
20000
15000
10000
5000
0
Number Collected
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
Year

Fig. 1.3.

CHAPTER II

POPULATION DYNAMICS OF THE CORKSCREW ANEMONE *BARTHOLOMEA ANNULATA* ON CARIBBEAN CORAL REEFS

Introduction

Giant sea anemones may be important members of coral reef communities due to their hosting of many species of obligate and facultative fish and crustacean symbionts (Fautin and Allen 1997, Bauer 2004). Large Caribbean sea anemones such as *Bartholomea annulata* and *Condylactis gigantea* serve as important symbiotic hosts to a variety of crustaceans, including the cleanershrimps *Periclemenes pedersonii* (Gwaltney and Brooks 1994) and *P. yucatanicus* (Gwaltney and Brooks 1994), and several other types of shrimp associates (Knowlton and Keller 1983, Knowlton and Keller 1985, Nizinski 1989, Crawford 1992). While most aspects of these symbioses are not fully understood, it is known that some of the crustaceans supply nitrogen to the anemone hosts (Spotte 1996, Lipschultz 2001). The holobiont of host anemone, crustacean ectosymbionts, and microalgal endosymbiont (zooxanthellae) plays an important role in the reef community, because it serves as a cleaning station for large reef fish (Bunkley-Williams and Williams 1998, Becker 2004).

Through positive cascade effects, fish-cleaning stations can influence coral reef community structure and coral-algal competition. Both Grutter et al. (2003) and Bshary (2003) showed that the removal of the cleaner wrasse *Labroides dimidiatus* causes a decrease in the diversity of both permanent and visiting reef fishes, and that the addition of this cleaner wrasse causes an increase in the fish diversity. Though this type of study has not been conducted with cleaner shrimps, it is likely that similar results would occur because changes in the cleaning process itself appear to drive reef fish diversity, rather than the type of cleaner involved. The presence of large fishes, especially visitors to the reef, influences coral-algal competition, as many migrating reef fish graze on macroalgae (McCook 2001). Thus, a decrease in the number of fishes or other grazers can result in a phase-shift to an alternate stable state in which algae rather than stony corals dominate reef areas (Hughes et al. 1987, Tkachenko 2007).

Understanding of population dynamics is important in order to gauge how environmental conditions impact populations of coral reef organisms (Chatzinkolaou and Richardson 2008). Sea anemones occur in a variety of reef habitats, and their patterns of growth, shrinkage, mortality, and recruitment/reproduction vary with the physical conditions in each habitat. Sebens (1981) showed that juveniles and adults of the temperate anemone *Anthopleura xanthogrammica* (Brandt) preferred different habitats, and that when juveniles reached a threshold body size, they moved to the preferred adult habitat.

No published information exists concerning the population dynamics of the corkscrew anemone *Bartholomea annulata*, yet individuals of this species are common on Caribbean coral reefs. In Florida, fishing of *B. annulata* for the ornamental aquarium trade is unrestricted, and the number collected has steadily declined since the mid-1990's even though fishing regulations were not changed until 2005 (Chapter I). The large decrease in *B. annulata* collected over this time period indicates that members of this species are becoming rare on Florida reefs as a result of improper management. Any decrease in the host anemone *B. annulata* will cause a decrease in the abundance of other members of this holobiont, especially the obligate cleaner shrimp associates, so this decrease likely has far-reaching cascade effects on these reefs. Shuman et al. (2005) concluded that limiting or ending the collection of giant host anemones on coral reefs in Indonesian would "reduce the indirect effects on anemonefish populations". The same principle likely holds for the host anemone *B. annulata* in the Caribbean, in that placing scientifically-based limits on the commercial collection of this species would result in positive indirect effects on its crustacean symbionts, client fish who visit these cleaning stations, and other reef organisms. In Puerto Rico, limitations have been placed on the collection of *B. annultata*: Thirty-five individuals may be collected per week per commercial collector (Hardin and LeGore 2005). Due to a lack of information on the demography of this anemone and its abundance on Puerto Rican reefs, it is not known whether current restrictions on the number of anemones collected have resulted in increase, stability, or decrease in population sizes.

Studies have been conducted on the population dynamics of a variety of stony and soft corals (Grigg 1977, Hughes and Tanner 2000, Tkachenko et al. 2007) and a few species of temperate sea anemones (Ottaway 1979, 1980, Sebens 1983), but little demographic information exists for coral reef sea anemones worldwide. I describe here how population dynamics of the corkscrew anemone *Bartholomea annulata* vary between 2 reef sites and among 4 seasons over 1 year, and discuss how the 2 types of reefs examined may influence population structure in this species.

Methods

Study site characteristics

The present study was conducted during March 2007-March 2008 at 2 coral reef sites on St. Thomas, US Virgin Islands (USVI). The study sites were selected due to their proximity to the MacLean Marine Science Center (MMSC) of the University of the Virgin Islands (UVI), which provided support for diving operations. In addition, commercial collecting of sea anemones does not occur in the USVI, thus allowing assessment of unfished populations. The two coral reef sites were: (1) Flat Cay, about 2.2 km offshore, and (2) Brewers Bay, an inshore reef about 200 m from the beach at the MMSC (Fig. 2.1). Both sites were located at 6-10 m depth below sea surface and contained abundant individuals of *B. annulata*, but differed in their physical characteristics. Flat Cay was a typical offshore Caribbean patch reef with a lower rate of sedimentation and significantly higher sediment grain size, light penetration, water flow, and percent coral cover than on the reef at Brewers Bay (Table 2.1), which was a typical inshore patch reef. The Brewers Bay site, which was enclosed partially by an airport runway since 1979 (Rogers 1990), periodically received heavy runoff after rainfall on the nearby island of St. Thomas, resulting in high sedimentation and low light levels relative to Flat Cay. Much of the reef consisted of non-living coral rock, and the few live stony corals appeared stressed and partially bleached (N. E. Chadwick, pers. comm.). Despite the apparently marginal reef conditions in Brewers Bay, individuals of *B. annulata* were abundant at this site, often attached to small patches of hard substrate surrounded by sand, including discarded shoes that had drifted close to the patch reef. The areas selected at each site for monitoring of anemone population dynamics were along the margin of the reef, where small patches of coral were interspersed with sand (see maps, Fig. 2.2A, B). This reef habitat supported maximal abundance of *B. annulata.* Similar habitat along the reef margin also supported the highest abundance of *B. annulata* sea anemones in previous studies in the USVI (Mahnken 1972)

Light intensity was measured in μE m^{-2} s^{-1} every 30 minutes during October 21-November 29, 2006 by a HOBO Pendant Temperature/Light Data Logger placed 0.5 m above the substrate on a rebar stake at about 8m depth at both sites. Light intensities were compared between the 2 sites both during peak daylight hours (11:00 AM-1:00 PM) and over the entire daylight period (6:30 AM-5:30 PM).

Sediment grain sizes were determined by collecting sediment in 50ml centrifuge tubes (N=3 at each site) that were pushed into the soft substratum adjacent to the reef at each site. Only two of the tubes were analyzed from Flat Cay because one sample was damaged prior to analysis. The sediment from each tube was rinsed with freshwater to remove salt residues, allowed to dry, and then placed in an 8-sieve with mesh sizes of 4mm, 2mm, and 850, 425, 250, 180, 150, and 63 microns, and shaken for 5 minutes. The mean grain size of sediments was calculated as a weighted average, where the percent of the total weight of the sediment on each sieve was multiplied by (mesh of sieve + mesh of sieve one size larger)/2.

Rates of sedimentation were determined by deploying sediment traps (N=3) at each site, each consisting of a PVC pipe (25 x 5 cm) attached at 1m above the soft substratum on a rebar stake. Sediment traps were collected 5 days after deployment at Flat Cay, and 6 days after deployment at Brewers Bay (after Gilmour 2002).

Relative rates of water flow at each site were determined using the clod card method (Jokiel and Morrissey 1993). Clod cards were made by placing plaster of Paris into 2 ice trays with 16 wells each of 30 ml volume per well, allowing the plaster to dry, and weighing each dried clod of plaster. The clods then were glued onto plastic sheets using epoxy, and deployed on 5 September 2007 at each site (N=10 clods per site), by attaching them to the reef near sea anemones. Only 9 clods were analyzed from Brewers Bay because 1 was lost. After 24 hours, the clod cards were retrieved and allowed to dry, then reweighed and the percent and absolute change in mass were determined for each clod.

The percent cover of major benthic organisms at each site was determined from photo-quadrats. A 50-m transect tape was deployed along the margin of the patch reef at each site at about 8m depth, where individuals of *B. annulata* are most abundant (see above). At Flat Cay, 20 photographs were taken and at Brewers Bay, 24 photos were taken, each .05 m^2 (25x20 cm) at random intervals along the transect tape. A random number generator was used to select the points on the 50 m transect. Percent cover was estimated for 6 categories of benthos: live stony corals, macroalgae, other live organisms, non-living coral skeleton, other hard substrate, and soft substrate. A grid of 25 randomly-generated points was superimposed over each photograph, and the type of benthos under each point was determined (after Walker et al. 2007).

Sea anemone population dynamics

All individuals of *B. annulata* along the reef margin were tagged and mapped at each study site. During March 2007, the population of *B. annulata* at Brewers Bay was 109 individuals and at Flat Cay 53 individuals, similar to those used by Sebens (1981) and Hattori (2006) for determination of demographic patterns in sea anemones. At Brewers Bay, the examined population was distributed over an area of 47 x 6 m (282 m^2) along the reef margin. At Flat Cay, an area of 70 x 11 m (790 m^2) was monitored along the reef margin, plus 73 x 5 m (365 m^2) of sandy area containing small patch reefs perpendicular to the reef margin (Fig. 2.2A, B). A much larger area was monitored at Flat Cay than at Brewers Bay, because the anemones were much less abundant than at Brewers. An aluminum oval tag engraved with a number was attached to a stainless steel nail and hammered into the reef substrate adjacent to each anemone. In addition, a short piece of flagging tape was tied around each nail to aid in tag relocation. During each census, encrusting organisms were removed from the tag, and the flagging was replaced. This method of marking large reef anemones appears to be accurate, because most giant anemones on coral reefs attach their bases deep within reef holes and crevices, and do not appear to locomote across the substratum (Chadwick and Arvedlund 2005). The following data were recorded for each tagged sea anemone: species, tentacle crown length and width in cm (for calculating the tentacle crown surface area [TCSA], after Hirose 1985, Hattori 2002, Chadwick and Arvedlund 2005), orientation (oral disc facing up = horizontal or oral facing sideways = vertical), microhabitat (anemone contacting live coral, non-living coral rock, and/or sand), depth below sea level, number and species of commensal shrimps, state of tentacle expansion, and notes on anything else of interest such as anemone color pattern. From the tentacle crown length and width, the tentacle crown surface area (TCSA) was calculated using the formula $((L/2*W/2)*\pi)$, where L = tentacle crown length, and W = tentacle crown width. This parameter of body size was used because the oral disk and tentacle crown of individuals of *B. annulata* are slightly oblong, as in many other coral reef sea anemones (Hirose 1985, Hattori 2002). The location of each sea anemone was recorded on a map for ease of relocation (Fig. 2.2A, B). Every 3 months for 1 year (March 07-March 08), the sites were revisited and the above data were collected on each marked anemone. The sites also were examined carefully for any new recruits of *B. annulata* during each sample period, which then were tagged and censused. Anemones that disappeared between samples were considered to have been lost to the population. No anemones were observed locomoting across the site or freely floating in the water column. Observations on other giant sea anemones indicate that if individuals leave their holes, they likely are preyed upon (N. E. Chadwick pers. comm.). Thus, substantial movement of anemones within the study sites appeared to be low. From the above demographic data, patterns of recruitment, growth, shrinkage, and mortality of the marked anemones within each site were determined.

Data Analysis

To quantify patterns of population dynamics in this sea anemone, I used size-based transition matrices (after Lefkovitch 1967, Hughes 1984). If an individual was recorded as absent during only one of the middle censes but present in the next sampling, it was considered to be alive but not sampled during that census. Sometimes tagged commensal shrimps, state of tentacle expansion, and notes on anything else of interest such as anemone color pattern. From the tentacle crown length and width, the tentacle crown surface area (TCSA) was calculated using the formula $((L/2*W/2)*\pi)$, where L = tentacle crown length, and W = tentacle crown width. This parameter of body size was used because the oral disk and tentacle crown of individuals of *B. annulata* are slightly oblong, as in many other coral reef sea anemones (Hirose 1985, Hattori 2002). The location of each sea anemone was recorded on a map for ease of relocation (Fig. 2.2A, B). Every 3 months for 1 year (March 07-March 08), the sites were revisited and the above data were collected on each marked anemone. The sites also were examined carefully for any new recruits of *B. annulata* during each sample period, which then were tagged and censused. Anemones that disappeared between samples were considered to have been lost to the population. No anemones were observed locomoting across the site or freely floating in the water column. Observations on other giant sea anemones indicate that if individuals leave their holes, they likely are preyed upon (N. E. Chadwick pers. comm.). Thus, substantial movement of anemones within the study sites appeared to be low. From the above demographic data, patterns of recruitment, growth, shrinkage, and mortality of the marked anemones within each site were determined.

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Results

Study Site Characteristics

During midday at 7-8 m depth, levels of irradiance were 3x higher at Flat Cay than at Brewers Bay (Table 2.1, 2-tailed t-test, t=14.53, p<0.0001). Irradiance levels also were >2x higher at Flat Cay for the entire daylight period (Table 2.1, t=14.96, p<0.0001). Sediment particle size also was significantly larger at Flat Cay than at Brewers Bay (Table 2.1, t=5.404, p=0.012). The sediment surrounding the reef patch was visibly fine and silty at Brewers Bay, while it was much coarser at Flat Cay. There was no significant difference in sedimentation rate between Brewers Bay and Flat Key (Table 2.1, t=0.074, p=0.945). However, this lack of difference likely was due to the very small sample sizes of sediment traps (N=3 at Flat Cay and N=3 at Brewers Bay). Both the percent and absolute loss of mass of the clod cards per unit time was significantly higher at Flat Cay than at Brewers Bay, indicating higher levels of water motion (Table 2.1, t=4.07, p<0.001 for percent change, and t=3.28, p<0.01 for absolute change). The percent live coral cover also was significantly greater at Flat Cay than at Brewers Bay (Table 2.1, t=3.037, p<0.01). Also at Brewers Bay, significantly more of the reef substratum was covered by sand that at Flat Cay (22.7±20.6% compared to 9.6±15.4%, at Flat Cay, t=2.37, p<0.05), and by macroalgae (20.7±24.3% compared to 6.2±7.8%, t=2.54, p<0.05, Fig. 2.6). Thus, the reef site at Brewers Bay had much lower irradiance, sediment grain size, water motion, and coral cover than at Flat Cay, and also more macroalgae and sand cover.

Sea Anemone Population Dynamics

At the start of the study in March 2007, the abundance of individuals of *Bartholomea annulata* was almost 10-fold greater at Brewers Bay (0.387 per m^2, or 109 individuals total per 282 m^2 area examined) than at Flat Cay (0.046 per m^2, or 53 individuals total per 1155 m^2 area examined). Anemone abundance increased by about 12% at Brewers Bay and 43% at Flat Cay during the year, and by March 2008 there were 0.433 individuals per m^2 at Brewers Bay and 0.067 individuals per m^2 at Flat Cay. In terms of microhabitat use, at both sites, most of the anemones oriented vertically, with their oral disks facing sideways, while a minority of individuals faced upwards (horizontally, Fig. 2.3A). Most of the anemones occupied holes hear the bases of small patch reefs, along the reef-sand interface. A minority of individuals occupied holes within the reef framework, with their tentacles surrounded by nonliving reef rock or in some cases touching live corals (Fig. 2.3B).

The ratio of tentacle crown length:width in individuals of *B. annulata* was on average 2.20:1 at Brewers Bay and 2.10:1 at Flat Cay in March 2007, indicating that these anemones possessed oval tentacle crowns that were about 2x as long as they were wide. Body shape did not vary significantly between the two sites (t-test, t=0.413, p=0.680). At the start of the study, the population size structure of *B. annulata* differed significantly between the two reef sites (Chi-squared test, χ^2=31.14, p<0.001, Fig. 2.4) and remained significantly different throughout the study period (June 07 χ^2=38.25, Sept.

07 χ^2=31.15, Dec. 07 χ^2=51.22, Mar. 08 χ^2=48.32, p<0.001 for all). At Brewers Bay, individuals ranged in size from 0.79 to 451.60 cm^2 TCSA (tentacle crown surface area, 1 x 0.5 cm and 25 x 23 cm respectively), while at Flat Cay they ranged from 1.57 to only 98.90 cm^2 (1 x 1 cm and 25 x 5 cm respectively). At Brewers Bay, about half the anemones occupied the smallest size-class of 0-25 cm^2 TCSA, while at Flat Cay almost 70% were in the smallest size class, and none of the individuals were in the largest size-class of >100 cm^2. Throughout the entire study period none of the anemones at Flat Cay grew into the >100 cm^2 size-class. Thus, individuals were significantly smaller at Flat Cay than at Brewers Bay (2-tailed t-test, t=2.879, p<0.01) and remained so throughout the year (Mar. 08, t=4.073, p<0.0001).

In terms of changes in body size, during all seasons examined, a higher percent of individuals in the population grew to another size-class at Brewers Bay than at Flat Cay, ranging from 13% - 30% at Brewers Bay and 3% - 29% at Flat Cay (Table 2.2). This difference in growth between the sites was significant during the summer and fall only (χ^2=19.51, p<0.001 for summer, and χ^2=12.66, p<0.001 for Fall, but χ^2=0.03, p>0.5 for Spring and χ^2=3.66, p>0.05 for Winter). On average among seasons, at Brewers Bay a higher percent of individuals grew from one size-class to another for all size-classes while at Flat Cay, no anemones grew into either of the largest 2 size-classes (Table 2.3). This difference between sites in the mean growth rate of each size class was significant only for the 50.1-75 cm^2 size class (2-tailed t-test, t=12.48, p<0.0001). During half the seasons, a significantly larger percent of individuals also transitioned to a smaller size-class (shrank) at Brewers Bay than at Flat Cay, indicating a more dynamic population at the former site (Table 2.2, χ^2=9.70, p<0.01 for Summer, χ^2=5.64, p<0.05 for Fall, but

χ^2=4.67, p=0.05 for Winter, and χ^2=1.22, >0.1 for Spring). In contrast, average shrinkage rates were higher at Flat Cay than Brewers Bay for 3 of 4 size-classes (Table 2.3). On average, 90% of anemones shrank from the 75.1-100 cm^2 at Flat Cay, but the differences were not significant. This apparently paradoxical trend resulted from the lack of large individuals at Flat Cay. Since there were no individuals of the largest size class at Flat Cay, they could not shrink, whereas, about 40% of the largest individuals shrank at Brewers Bay. The high shrinkage rate of large individuals at Brewers Bay increased the percentage of anemones that shrank during each season. Rates of retention of animals in the same size-class (stasis) also were higher at Brewers Bay than at Flat Cay during most seasons (Table 2.2), but this difference was significant only during Summer (χ^2=9.05, p<0.01 for Summer, but χ^2=2.38, p>0.1 for Spring, χ^2=1.24, p>0.1 for Fall, and χ^2=3.70, p>0.05 for Winter). The percent of individuals that remained in the same size class was similar during all seasons at Brewers Bay, but the number decreased dramatically during the Summer at Flat Cay relative to the other seasons. Average retention rates within each size class for all the seasons also were higher at Brewers Bay than at Flat Cay, in 4 of the 5 size-classes (Table 2.3) but the differences were not significant. A 2-way ANOVA of percent change in body size with site and size-class revealed no significant effects during any season except for the Fall, when anemone size change was significantly greater at Brewers Bay than at Flat Key. Thus, the population at Brewers Bay was more dynamic than the one at Flat Cay, in terms of the percent of individuals that transitioned among size-classes through growth, shrinkage, and the retention of live individuals, but there was no significant effect on the size change of individual anemones within the size classes.

Rates of mortality (loss of individuals from the population) at Flat Cay were significantly higher than those at Brewers Bay during Spring and Summer, but not during Fall and Winter (Chi^2, Spring $\chi^2=5.24$, $p<0.05$, Summer $\chi^2=51.32$, $p<0.001$, Fall $\chi^2=0.882$, $p>0.1$, and Winter $\chi^2=0.165$, $p>0.5$, Table 2.2). Peak mortality occurred during Summer at Flat Cay, when 64% of anemones died, which was >20% higher than mortality rates in other seasons. Rates of mortality were higher at Brewers Bay than Flat Cay for the largest size-classes, but were lower for the smallest individuals (Table 2.3). Differences in mortality between the 2 sites were significant only for the smallest size class (2-tailed t-test, $t=2.45$, $p<0.05$).

Recruitment rates of new individuals into the population (Table 2.4) were significantly more rapid at Brewers Bay than at Flat Cay, both in terms of recruitment per unit area (2-tailed t-test, $t=7.13$, $p<0.001$) and per resident per unit area on the reef ($t=3.64$, $p<0.05$). However, there was no significant difference in total recruitment per site ($t=1.033$, $p=0.341$), because a much smaller area was examined at Brewers Bay (see above). The opposite pattern emerged in terms of recruitment rate per resident anemone (Table 2.4), in that more recruits appeared relative to the low total number of anemones at Flat Cay, than per to the large number at Brewers Bay. However, this difference between sites in the number of recruits per resident was not significant ($t=1.594$, $p=0.162$).

Dynamic survival curves calculated from the observed loss of individuals during the study revealed that anemones survived longer at Brewers Bay than at Flat Cay (Fig. 2.5A). Static survival curves constructed from the population size-structure at each site also revealed the same trend (Fig. 2.5B).

Discussion

I show here that populations of the corkscrew anemone *Bartholomea annulata* are extremely dynamic, with high rates of mortality and recruitment during a single year, as well as large proportions of anemones transitioning among size-classes via growth and shrinkage. The highly dynamic nature of these populations has important implications for the mobility and dynamics of the obligate anemoneshrimps, including the shrimp cleaners of reef fish parasites (Nizinski 1989, Crawford 1992, Gwaltney and Brooks 1994).

Rates of stasis in *B. annulata* (10-50% of individuals remaining in the same size class per 3 months) were an order of magnitude lower than those known for some Caribbean reef-building corals: 10-60% of individuals of the massive coral *Porites astreoides* remained in the same size classes for 3 years, and up to 74% of *Montastrea annularis*, 50% of *Agaricia agaricites*, and 71% of *Leptoseris cucullata* individuals remained in the same size classes for 5 years (Hughes and Tanner 2000, Lirman and Miller 2003). Thus, stasis rates over a 3-month period for the sea anemones were similar to stasis over 3-5 years in the coral populations. Another key difference was that in these corals, larger individuals were more likely to remain in the same size-class than were smaller individuals, whereas in the sea anemone they were not. On Australian coral reefs, Babcock (1991) showed that two-year stasis rates for 3 species of brain coral ranged from 27%-90%, with a mean of 46.25% remaining in the same size-class for *Platygyra sinensis*, 56.6% for *Goniastrea aspera*, and 55.5% for *G. favulus*. Thus, stasis rates for Indo-Pacific corals also were much higher than those for this coral reef sea anemone, indicating less turnover in coral populations than for the sea anemones.

In addition to low stasis, the sea anemone populations experienced rates of mortality that were an order of magnitude higher than those known for stony corals on reefs. Mortality for *B. annulata* was 10-54% per 3 months, compared to 52-100% for *Leptoseris cucullata*, 0-89% for *Montastrea annularis*, and 27-89% for *Agarcia agaricites* per 5 years (Hughes and Tanner 2000), and 9-20% per 3 years for the massive Caribbean coral *Porites astroides* (Lirman and Miller 2003). Thus, the corals had turnover rates of individuals on the order of years, while the anemone individuals were replaced on a scale of months. Mortality rates in the above coral species decrease with colony size, but in *B. annulata* they were highly variable among seasons and did not vary significantly among size-classes. The decrease in mortality with colony size in the above coral species indicates an advantage of coloniality: when a large coral colony is damaged, most of the polyps within the colony may survive, but if a large sea anemone is damaged, the end result may be death of the entire solitary polyp. This pattern may cause mortality to decrease with size in colonial corals but not in solitary sea anemones such as *B. annulata*.

Rates of growth and shrinkage of individuals varied significantly among size classes in *B. annulata*, in that growth rates decreased and shrinkage rates increased as the anemones became larger. This pattern was similar to that observed in all other stony corals (Hughes 1984, Hughes and Jackson 1985, Hughes and Tanner 2000) and temperate sea anemones (Ottaway 1980) examined to date. In corals that rarely shrink and thus can be aged accurately, rates of growth also decrease with the age and size of individuals (Chadwick-Furman et al. 2000, Goffredo et al. 2004, Guzner et al. 2007). In all cases, reef cnidarians appear to grow rapidly when small and young, and to decrease their growth rates with age. In species with partial mortality or tissue shrinkage, such as many corals and sea anemones, shrinkage also appears to be more common in the largest individuals.

Rates of growth in terms of both absolute surface area (up to 338 cm^2 per 3 months) and percent of total body size (an astounding 5,070% per 3 months) in *B. annulata* were much more rapid than they are for massive stony corals, which are known to grow up to 2 cm in radial growth per year (~12.6 cm^2, Hughes and Jackson 1985). They also are more rapid than rates recorded for temperate sea anemones, which in New Zealand grow only 0.6 cm in basal diameter per year (Ottaway 1980), and in the Mediterranean Sea up to 20% of basal diameter in 3 months (Chomsky et al. 2004a). Individuals of *B. annulata* may grow more rapidly than do tropical scleractininian corals because they do not need to invest energy and materials into construction of a hard skeleton as they grow. In addition, they may grow more rapidly than do temperate sea anemones, because they experience higher temperatures and light levels in the tropics, both of which correlate with more rapid growth in photosynthetic cnidarians (Chomsky et al. 2004b).

I quantify here for the first time demographic patterns in a tropical sea anemone. The population dynamics of other large coral reef anemones are expected to be more similar to those of this sea anemone than to stony corals on reefs, in that they may be quite dynamic relative to corals.

The significant differences in population size structure and dynamics between the two sites examined suggest that characteristics of the offshore site at Flat Cay restrict anemone growth rates, augment shrinkage, and reduce individual survival. Individuals of this sea anemone possess extremely long, thin tentacles and a long narrow column that are easily distorted by water motion (M. Nelsen and N. Chadwick pers. obs.). In the laboratory aquaria, individuals of this species avoid areas of high water flow, and attach their bases in areas with lower flow, where they are able to fully extend their long delicate tentacles (M. Nelsen pers. obs.). Drag, caused by the force of movement across a surface, is known to have a large influence on benthic organisms, and as body size or flow speed increases so does the amount of drag on the deformable bodies of sea anemones (Koehl 1977, 1984). Thus, the significantly higher water motion at Flat Cay than at Brewers Bay may prevent these anemones from fully extending their delicate tentacles to feed, and also to expose their zooxanthellae to light, and consequently may limit them to smaller sizes as a result of increased in mechanical stress. It is also possible that greater water motion increases energetic demands needed to maintain inflated size and for repair of tissue damage resulting from water motion. The anemones may experience equal drag overall at both locations, because the slower flow speed at Brewers Bay allows body size to become larger than at Flat Cay. During seasonal storms when water motion is especially high, many of the individuals at Flat Cay withdraw completely under rocks at the reef-sand interface, and then re-emerge a few days later after the storm has passed (S. Ratchford and N. E. Chadwick unpubl. data). In contrast, individuals at Brewers Bay remain expanded during seasonal storms, possibly due to the much lower levels of water motion that are generated at this protected inshore site.

The 20% higher growth rate of anemones at Brewers Bay than at Flat Cay in the summer when irradiance is highest and possibly zooplanktonic food supplies are as well, implies that seasonal characteristics of the latter site also restrict maximum anemone size. The higher shrinkage rates at Brewers Bay appear to result from the greater individual growth rate at this site, and thus the greater amount of larger individuals that are capable of shrinking substantially. The pattern of nearly 70% of anemones at Flat Cay occupying the smallest size class versus only 50% at Brewers Bay is explained in part by the much slower growth rates and higher mortality of small individuals at the former site. In addition, the high rates of stasis as well as growth at Brewers Bay relative to Flat Cay combined with higher survival, explain why there are relatively more individuals overall, and especially more in the largest size classes, than at the latter site. Disparities in mortality and growth are especially large during summer, when 64% of the anemones at Flat Cay die versus only 18% at Brewers Bay. The summer to fall period in the Caribbean is the season of tropical storms and hurricanes, which may greatly increase water motion at the exposed outer site of Flat Cay. Thus, I conclude that large differences in mortality and growth between the two examined sites during summer may be due in part to storm-generated water motion.

The survival curves indicated that only 5% of individuals remain alive after 26 months at Brewers Bay, thus the original population turns over almost completely within about 2 years. In contrast, only 5% of the population remains after a much shorter time of 13 months at Flat Cay, indicating a turnover time of about 1 year. Thus, if both populations were to suffer from recruitment failure, the population at Flat Cay would decrease to zero twice as fast as that at Brewers Bay, due to slow anemone growth and high mortality at the former site. Along with that, a comparison of the two survival curves indicates that not only are individuals more likely to survive longer at Brewers Bay, but they also are more likely to grow larger during the same time period as well.

Although total recruitment was similar at the two sites, the number of recruits both per m^2 and per resident per m^2 was much greater at Brewers Bay than at Flat Cay. The number of recruits per resident per m^2 was twice as high at Brewers Bay as at Flat Cay, indicating that a high abundance of large adult anemones may enhance local recruitment. This pattern occurs in many cnidarians, including reef-building corals, and indicates that self-recruitment may be common in populations of coral reef cnidarians, in that recruitment is determined largely by local population density (Hughes et al. 2000, Glassom et al. 2004). In addition, because these anemones reproduce asexually as well as sexually (Jennison 1981), the number of local residents may even more strongly influence local recruitment patterns. Sexual versus asexual recruits were not distinguished in the present study, in part because special methods need to be developed to separate these 2 types of recruits. The relative importance of these two reproductive modes to population growth is an important avenue for future research. Despite the low number of new recruits per resident per m^2 at Flat Cay, there was no significant difference in total recruits between sites. Thus, despite the overall lower population density at Flat Cay than at Brewers Bay, many recruits arrived, implying that new recruits may be coming from an outside population. Therefore, different factors may be driving each population. The Brewers Bay population may be driven largely by self-recruitment of sexual propagules and/or asexual reproduction, while the Flat Cay population may be driven largely by recruitment from an external source population.

The lack of a hard skeleton and the potential mobility of sea anemones caused some problems to arise while conducting this study. In the surveys, there were 4 possible outcomes for each tagged anemone: present with tag, present but tag lost, absent but tag still there, or both the tag and anemone gone. If the anemone and the tag were present, data were collected. If the tag was absent, either the anemone had died or had moved, and no conclusions could be drawn. In the case of anemone absence, the lack of a skeleton made it impossible to tell whether that individual at moved or died. In this study, all missing anemones were assumed deceased, because exposed anemones likely were preyed upon. For tags that were missing, anemones were considered dead if the tags were not found during two consecutive censes (had not been found in 6 months).

I conclude that demographic patterns in the corkscrew anemone *Bartholomea annulata* reveal highly dynamic populations that vary widely between in shore and off shore sites, and thus may be influenced strongly by reef characteristics. Differences is water flow, percent coral cover, irradiance, and/or particle size between the sites may explain why the anemone population at Brewers Bay was larger, had higher survivorship, and contained individuals with larger body sizes than did the population at Flat Cay. In addition, the local abundance of individuals appeared to largely influence recruitment rates, indicating that whether sexual or asexual, recruitment may be mainly local. These patterns have major implications for the stability and abundance of obligate anemoneshrimps that rely on this host anemone for essential habitat. Given the evidence on dynamics of *B. annulata* populations presented here, one would also expect that populations of their symbiotic anemoneshrimp would also be highly mobile and dynamic in order to track the rapidly changing host populations. By inference, so must the behavior of fishes that rely on anemone-associated cleaner shrimps for daily removal of ectoparasites (Sikkel et al. 2004). An additional implication of this study is that site-specific population data are needed to create a scientific basis for sustainable fisheries on this host anemone and associated anemoneshrimps.

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Table 2.1. Statistical results of 2-tailed t-tests on differences in physical characteristics between 2 coral reef sites (Brewers Bay and Flat Cay). Sediment size, irradiance at peak hours, irradiance during the entire daylight period, percent change in clod card mass, absolute change in clod card mass, and percent stony coral cover all were significantly greater at Flat Cay than at Brewers Bay, while there was no significant difference in sedimentation rate between the 2 sites.

	Sediment Size (±SD)	Irradiance Peak Hours (±SEM)	Irradiance Entire Daylight Period (±SEM)	% Change in Clod Card Mass (±SD)	Absolute Change in Clod Card Mass (±SD)	Percent Stony Coral Cover (±SD)	Sedimentation Rate (±SD)
Brewers Bay	0.53±.04 mm N=3	59.2±3.3 µE m^{-2} s^{-1} N=40	37.8±.04 µE m^{-2} s^{-1} N=40	19.1±.91% N=9	8.2±.37 g N=9	15.2±15.3 % N=20	0.06±.02 g d^{-1} N=3
Flat Cay	0.75±.04 mm N=2	194.6±8.8 µE m^{-2} s^{-1} N=40	100.9±3.8 µE m^{-2} s^{-1} N-40	20.8±1.1% N=10	8.9±.53 g N=10	31.0±19.3 % N=24	0.06±.06 g d^{-1} N=3
t-value	5.404	14.53	14.96	4.07	3.28	3.037	0.074
P-value	<.05	<.0001	<.0001	<.001	<.01	<.01	.945

Table 2.2 Variation among seasons and sites in the percent of anemones that either grew, shrank, remained in the same size class, or died (based on TCSA).

Brewers Bay	Spring	Summer	Fall	Winter
Growth	19.6%	30.5%	12.9%	16.9%
Shrinkage	13.1%	14.3%	15.6%	14.0%
Stasis	39.3%	37.1%	37.4%	29.4%
Mortality	28.0%	18.1%	34.0%	39.7%

Flat Cay	Spring	Summer	Fall	Winter
Growth	18.9%	10.5%	2.9%	9.9%
Shrinkage	9.4%	4.7%	26.5%	7.0%
Stasis	30.2%	20.9%	30.9%	40.8%
Mortality	41.5%	64.0%	39.7%	42.3%

Table 2.3. Variation among size classes and sites in the mean percent of individuals (± S.D.) that either grew, shrank, remained in the same size class, or died (based on TCSA, N=4 seasons, NA= not applicable).

Brewers Bay	0-25 cm^2	25.1-50 cm^2	50.1-75 cm^2	75.1-100 cm^2	>100 cm^2
Growth	20.2±11.6%	26.3±8.0%	23.0±3.7%	19.2±18.7%	NA
Shrinkage	NA	18.0±6.2%	37.0±19.2%	31.8±25.9%	39.7±6.2%
Stasis	50.1±6.2%	21.1±7.4%	17.1±7.9%	17.5±15.5%	37.0±10.2%
Mortality	29.7±17.2%	34.6±6.3%	22.9±16.7%	31.5±21.2%	23.3±8.5%

Flat Cay	0-25 cm^2	25.1-50 cm^2	50.1-75 cm^2	75.1-100 cm^2	>100 cm^2
Growth	10.0±6.2%	17.0±13.4%	0.0%	0.0%	NA
Shrinkage	NA	27.0±11.9%	49.2±20.6%	90.0+/14.1%	NA
Stasis	35.9±10.5%	27.9±11.6%	10.0±11.5%	0.0%	NA
Mortality	54.1±10.7%	28.1±13.9%	40.8±17.7%	10.0±14.1%	NA

Table 2.4. Variation in rates of recruitment of new anemones between 2 coral reef sites. Data are presented as mean percent of individuals ± 1 standard deviation. N=4 seasons examined.

	Total Recruitment	Recruits/m^2	Recruits/Resident	Recruits/Resident/m^2
Brewers Bay	47±9.05	.17±.03	0.42±.12	.0015±.0004
Flat Cay	39.8±10.70	.04±.01	.67±.30	.0006±.0003

Figure Legends

Fig. 2.1. Maps showing 2 coral reef sites examined for sea anemone population dynamics near the island of St. Thomas, USVI. Site #1 Brewers Bay, is 200 m from island, and site #2 Flat Cay is 2.2 km from island.

Fig. 2.2. Maps from Dec. 2007 showing locations of tagged sea anemones along the reef-sand margin at: **A.** the Brewers Bay study site. **B.** the Flat Cay study site. Numbers refer to the tag number of each anemone.

Fig. 2.3A. Percent of anemones oriented horizontally, vertically, and midway between horizontally/vertically at Brewers Bay and Flat Cay. At both locations, most of anemones were oriented vertically. Data are presented as means ± 95% CI, N=104 anemones examined at Brewers Bay and N=52 anemones examined at Flat Cay. **B.** Percent of anemones that were located in each microhabitat. Most anemones were found at the rock/sand interface at both locations. Data are presented as means ± 95% CI, N=102 anemones examined at Brewers Bay and N=52 anemones examined at Flat Cay.

Fig. 2.4. Population size-structure of the sea anemone *Bartholomea annulata* at 2 coral reef sites (Brewers Bay N=108 and Flat Cay N=53). Sea anemones were significantly larger, and populations size was significantly greater at Brewers Bay than at Flat Cay (see text for details).

Fig. 2.5A. Dynamic survival curves for Brewers Bay and Flat Cay, from observed disappearance of tagged sea anemones at each site over one year of study. Curves show that anemones are most likely to survive for one year at Brewers Bay (Brewers Bay, $y=1.007e^{-.117x}$ $R^2=.999$, Flat Cay, $y=1.027e^{-.183x}$ $R^2=.996$). **B.** Static survival curves for Brewers Bay and Flat Cay, constructed from the observed population structure of sea anemones at each site during March 2007. Static survival curves show that anemones are more likely to grow larger at Brewers Bay than at Flat Cay.

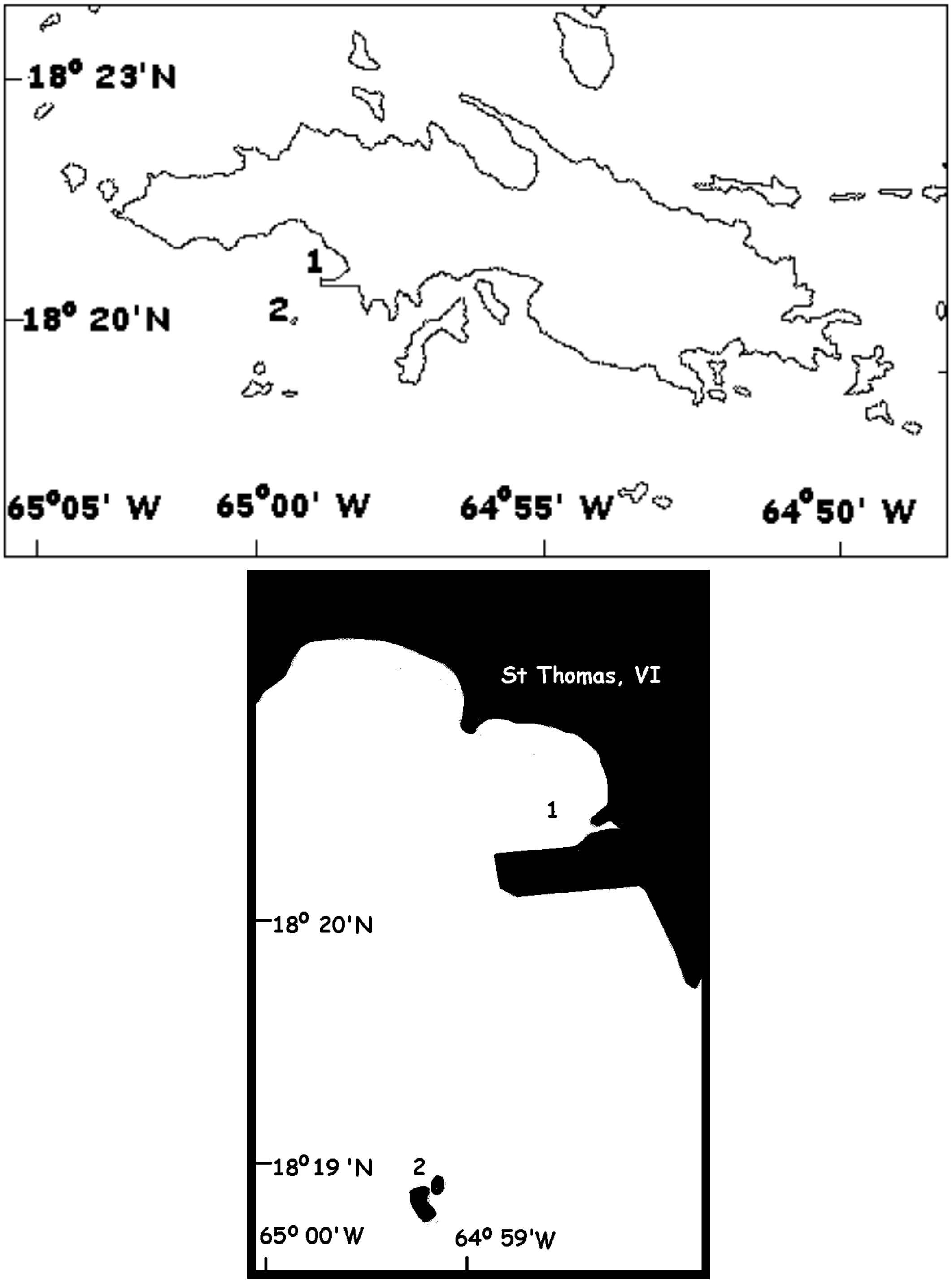
18° 23'N
18° 20'N
1
2
65°05' W
65°00' W
64°55' W
64°50' W
St Thomas, VI
1
18° 20'N
18° 19 'N
2
65° 00'W
64° 59'W

Fig. 2.1.

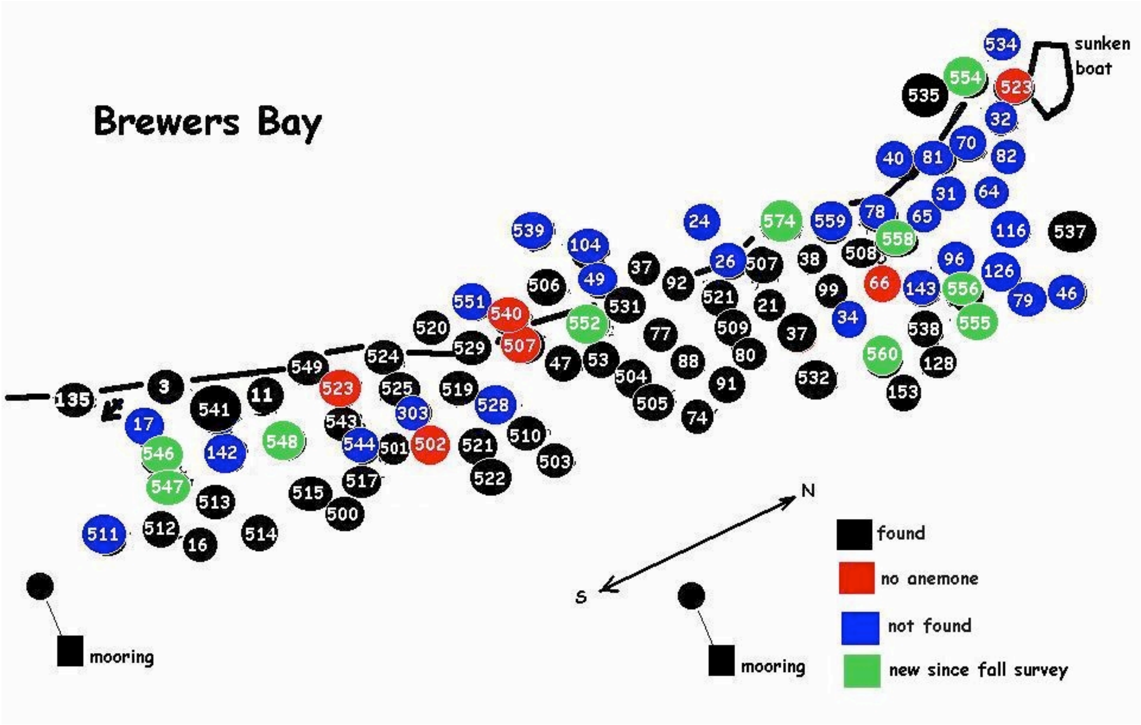
Brewers Bay
sunken boat
534
554
523
535
32
70
40
81
82
31
64
24
574
559
78
65
116
537
539
104
558
508
96
126
37
26
507
38
92
66
143
556
46
506
49
521
99
79
551
531
21
34
540
552
509
37
538
555
520
77
560
507
529
88
80
128
549
524
47
53
504
91
532
3
523
525
519
135
541
11
505
74
153
303
528
17
543
510
548
544
501
502
521
546
142
503
522
547
517
513
515
500
N
511
512
514
16
S
found
no anemone
not found
new since fall survey
mooring
mooring

Fig. 2.2A.

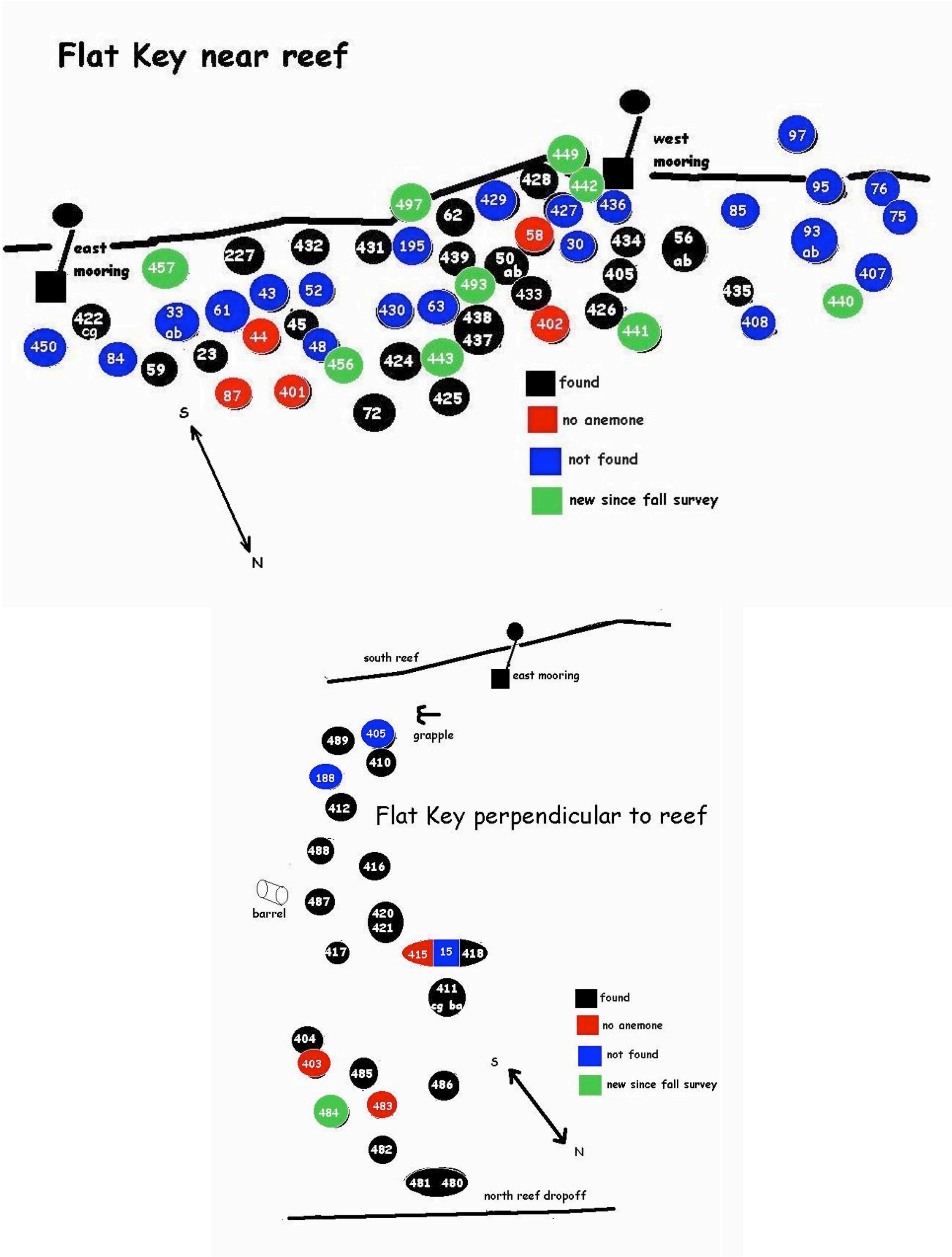
Flat Key near reef
east mooring
west mooring
450
422 cg
84
59
33 ab
23
61
44
43
45
52
48
456
87
401
227
432
431
195
424
72
430
63
443
425
497
62
439
493
438 437
50 ab
433
429
428
58
449
442
427
436
30
434
405
426
402
441
56 ab
85
435
408
97
95
76
75
93 ab
407
440
found
no anemone
not found
new since fall survey
S
N
south reef
east mooring
grapple
489
405
410
188
412
Flat Key perpendicular to reef
488
416
barrel
487
420 421
417
415
15
418
411 cg ba
404
403
485
486
484
483
482
481 480
north reef dropoff
found
no anemone
not found
new since fall survey
S
N

Fig. 2.2B.

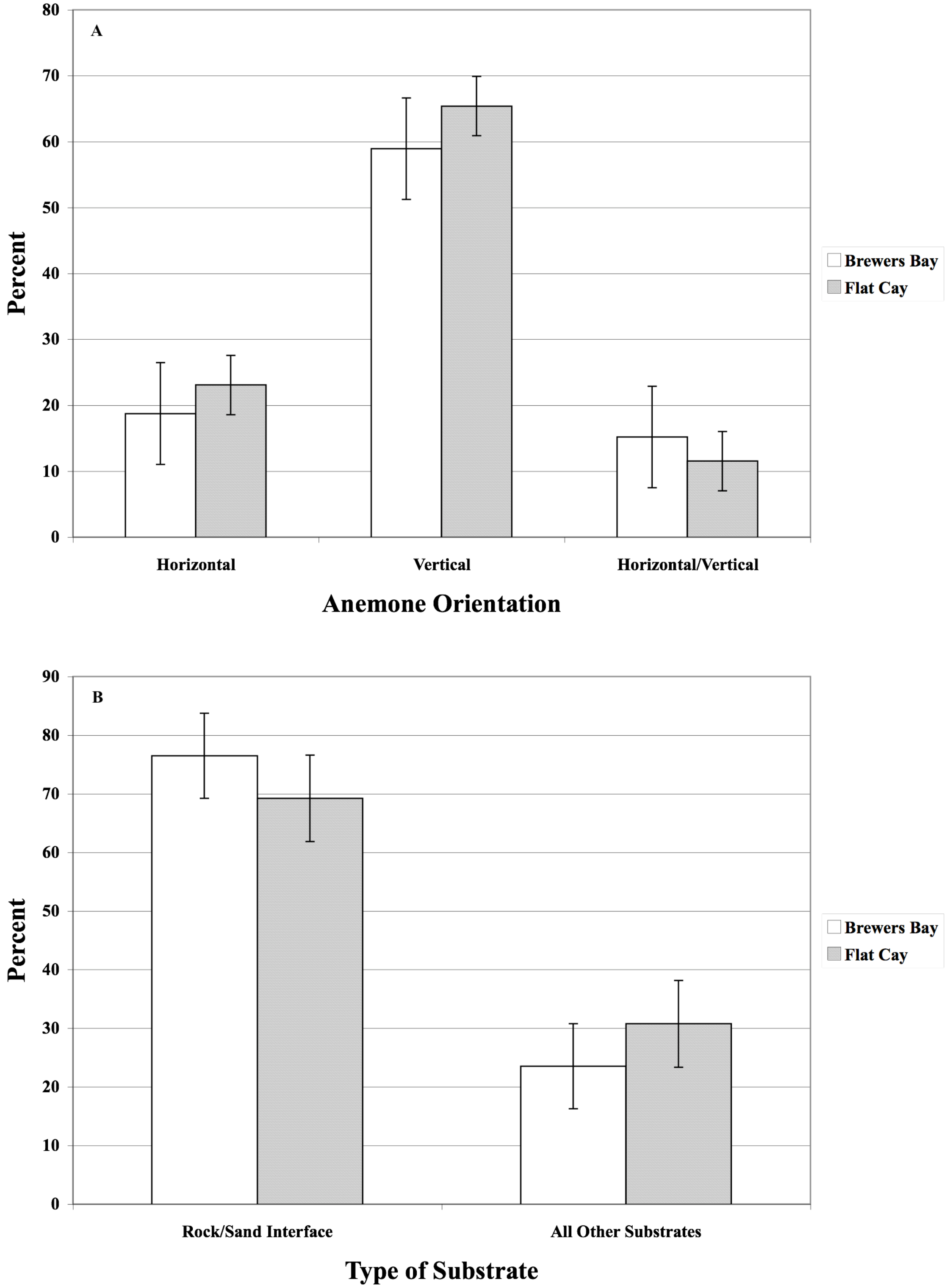
80
70
60
50
40
30
20
10
0
A
Percent
Brewers Bay
Flat Cay
Horizontal
Vertical
Horizontal/Vertical
Anemone Orientation
90
80
70
60
50
40
30
20
10
0
B
Percent
Brewers Bay
Flat Cay
Rock/Sand Interface
All Other Substrates
Type of Substrate

Fig 2.3.

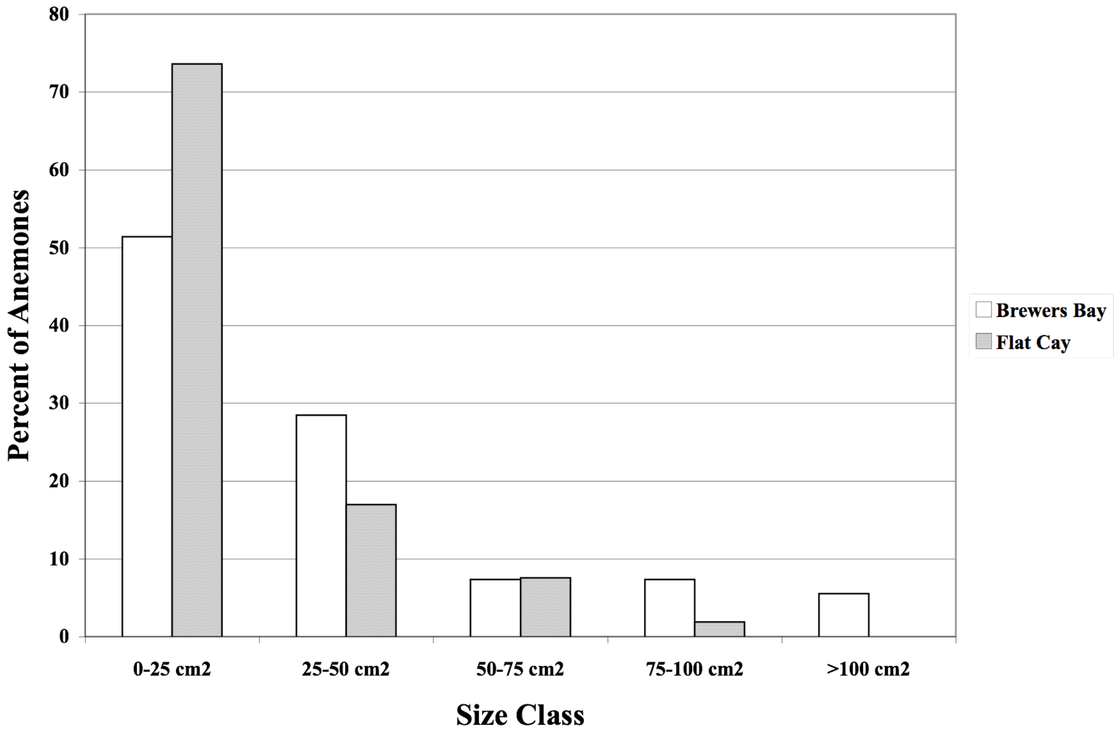
80
70
60
50
40
30
20
10
0
Percent of Anemones
0-25 cm2
25-50 cm2
50-75 cm2
75-100 cm2
>100 cm2
Size Class
☐ Brewers Bay
▨ Flat Cay

Fig. 2.4.

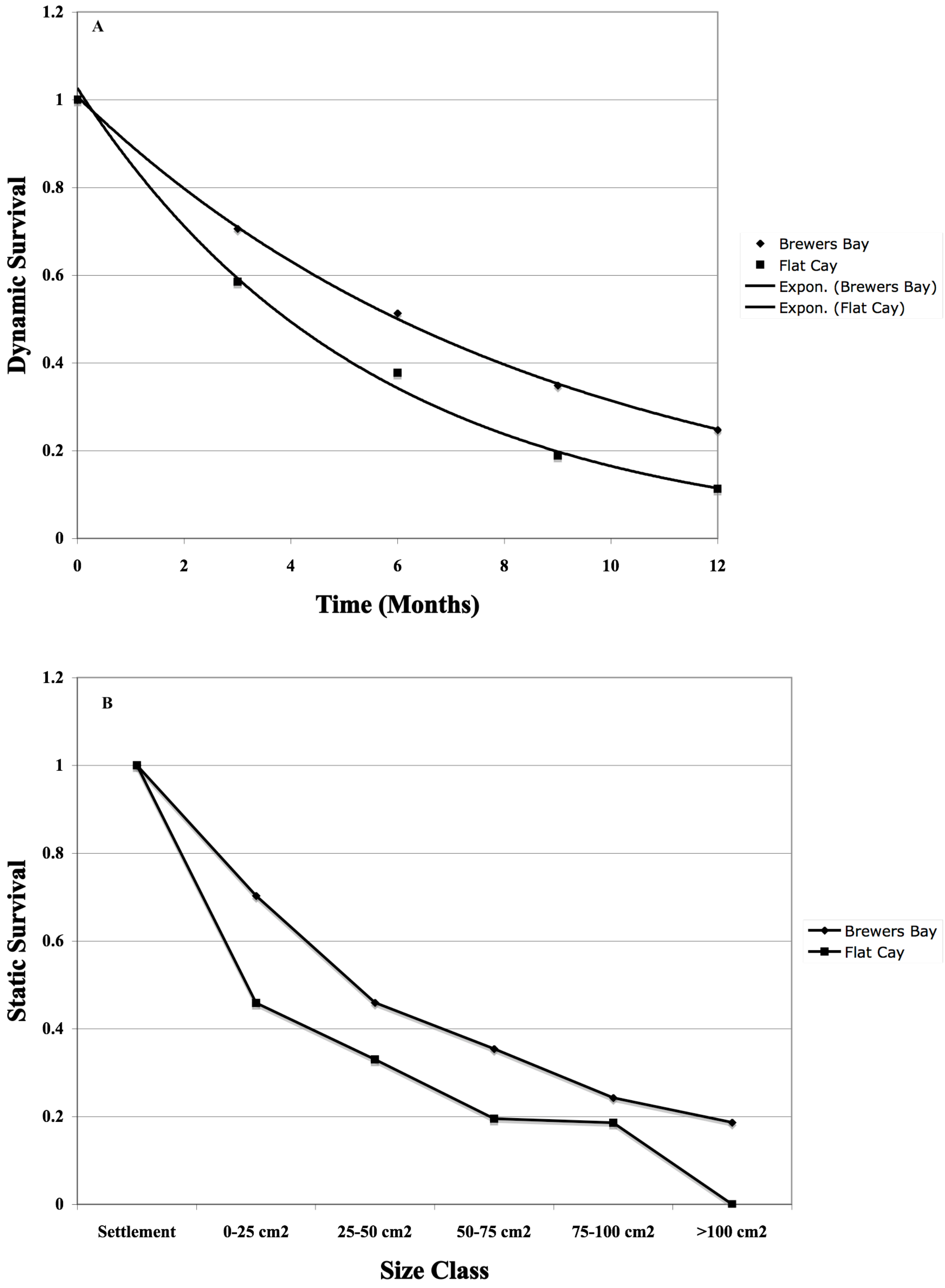
A
Dynamic Survival
1.2
1
0.8
0.6
0.4
0.2
0
Time (Months)
0
2
4
6
8
10
12
◆ Brewers Bay
■ Flat Cay
Expon. (Brewers Bay)
Expon. (Flat Cay)
B
Static Survival
1.2
1
0.8
0.6
0.4
0.2
0
Settlement
0-25 cm2
25-50 cm2
50-75 cm2
75-100 cm2
>100 cm2
Size Class
Brewers Bay
Flat Cay

Fig. 2.5.

CHAPTER III

STAGE-BASED MODELING OF POPULATINO DYNAMICS IN THE CORKSCREW ANEMONE *BARHTOLOMEA ANNULATA*

<u>Introduction</u>

Population dynamic modeling has been used to assess the changes in population size and structure for several species of stony corals (Grigg 1984, Hughes 1984, Fong and Glynn 2000, Hughes and Tanner 2000, and Lirman and Miller 2003), but has not yet been applied to actinian sea anemones. Grigg (1984) was the first to apply a standard fisheries model to stony corals. However, this type of age-based model applies only to corals that rarely fuse, fission, or shrink and thus have a strong relationship between coral size and age. Age-based models have been applied to solitary corals (Chadwick-Furman et al. 2000, Goffredo 2004), and corals that form compact colonies with little shrinkage (Guzner et al. 2007). Hughes (1984) was the first to use a stage-based model for organisms such as most stony corals that can suffer from partial mortality, and thus may shrink as well as grow. His model was a variation on the Lefkovitch model (1965) that was used initially to group beetles into life-stage classes based on their stage of development (egg, larva, pupae, etc.). These modifications of the original, age-based, Leslie model (1945) laid the groundwork for population modeling of organisms that cannot be classified by age.

The application of size-based models to sea anemones requires several modifications from those used for stony corals. For example, the corkscrew anemone *Bartholomea annulata* (Cnidaria: Anthozoa) forms clones of unconnected individuals via pedal laceration (Jennison 1981), and as a result do not produce colonies of connected units like the stony corals that have been modeled (see above). Thus, the elements of a transition matrix for this sea anemone do not represent change in the size of a colony, but rather change in the size of individual polyps. Anemones suffer from partial tissue mortality as do corals, but because they have no hard skeleton, their tissue loss is visible only as a general shrinkage of the body. Reproduction also must be integrated into the model differently than for stony corals, which can fragment to produce new asexual recruits. These asexual recruits often are clearly distinguishable from newly-settled sexual recruits due to differences in their skeletal shape, and thus can be incorporated into the model separately. In contrast, newly-budded sea anemones often are indistinguishable from new sexual recruits, due to their essentially identical appearance (M. Nelsen, personal observation). The ability to distinguish sexually versus asexually produced recruits allows for the clear integration of asexual recruits into the coral transition matrices. Because this is not possible with sea anemone recruits, it is necessary to construct 3 separate models, each with a different possible type of reproduction: (1) fully-closed recruitment, that assumes all recruits, either sexually or asexually produced, arise from within the population, (2) open recruitment, where all recruits arrive sexually from outside the population, and (3) semi-open recruitment, where relatively large individuals are considered to be asexual recruits that arise from within the population, and small individuals are assumed to be sexual recruits that arise from outside the population.

Bartholomea annulata is one of the largest and most common sea anemones on coral reefs in the Caribbean Sea, and yet the little information that exists on the biology of this species, is contained mainly in coral reef guide-books (Colin 1978, Kaplan 1982, Sefton & Webster 1986). This lack of information precludes a scientific basis for management of commercial fishing of these animals. Individuals of *B. annulata* are a major component of the ornamental aquarium trade (Chapter I), and modeling of their demographics will support the development of a sustainable fishery on this important reef species. Here I use a size-based demographic model to project population trends under various recruitment régimes for two unfished populations at St. Thomas, US Virgin Islands. Modeling of these populations reveals how unfished populations at two reef sites maintain demographic stability under various recruitment scenarios, and also highlights which life history stages are the most important for maintaining these populations (Cropper and DiResta 1999, Caswell 2001, Lirman and Miller 2003). I present here information on population growth rates, stable size distributions, and time to convergence to stable size structure for each of these two populations, and reveal how they may be influenced by local environmental conditions. Finally, I demonstrate how elasticity analysis can be used as a management tool for these sea anemones to set restrictions on fishing rates, by revealing which life history processes/vital rates (growth, shrinkage, stasis, or recruitment, also known as vital rates) most influence the pace of population growth.

Methods

Collection of Population Data

Field data on population parameters were collected during March 2007-March 2008 for individuals of the corkscrew anemone *Bartholomea annulata* at St. Thomas, US Virgin Islands (USVI). Two coral reef sites on St. Thomas were examined: (1) an offshore patch reef at Flat Cay, and (2) an inshore reef at Brewers Bay. Each 3 months during the study year, all individuals of this species were censused within mapped areas at both reef sites, and information was collected on the number of new recruits, changes in size of resident anemones, and disappearance of individuals from the populations. For details on physical characteristics of the field sites, and methods of field data collection, see Chapter II.

Population Modeling

A size-based population model was created for *B. annulata* from the above field measurements, modified after Hughes (1984, Eq. 3.1), where **A** (Table 3.1A) is the s x s transition matrix, b_t is the s x 1 population vector at time t, and b_{t+1} is the s x 1 population vector 1 time period later.

$b_{t+1}=\mathbf{A}*b_t$ (Eq. 3.1)

A model for each of the two reef sites was created from a size-based life cycle graph for *B. annulata* (Chapter I) in which the anemone life cycle was divided into 5 size-classes of tentacle crown surface area (TCSA, 0.1-25 cm^2, 25.1-50 cm^2, 50.1-75 cm^2, 75.1-100 cm^2, and >100 cm^2), that encompass the range of body sizes of the anemones at these study sites (Chapter II). Only individuals in the smallest size-class (0.1-25 cm^2) were classified as juveniles that do not reproduce; this is an arbitrary assignment based on the average size of anemones without gonads of 7.4 mm basal diameter (Jennison 1981). Transition matrices were created, in which the elements contained within were the proportions of anemones that transitioned from one size-class to another during each 3-month time step (Hughes and Tanner 2000). There were three possible transitions: an anemone grew from its size-class to a larger size-class (**G**), it remained in the same size-class (**L**), or it shrank and transitioned from its current size-class to a smaller size-class (**S**). Four seasonal matrices were created from the five sampling periods (Spring=**A,** Summer=**B,** Fall=**C,** and Winter=**D**), and from these a one-year transition matrix was created by multiplying the four seasonal matrices together (**E**=**D*C*B*A**, Caswell 2001). The one-year transition matrix (**E**) projects future populations from the beginning of one spring until the beginning of the next (March to March).

Modeling of Reproduction

Three models were created to incorporate three different possible modes of reproduction, and thus of recruitment, into these populations: completely closed, completely open, and semi-open. In a completely closed population, all new individuals arise from sexual or asexual reproduction by resident anemones within the population. In a completely open population, all new individuals are considered to originate through the arrival of sexual recruits from outside the population. Finally, in a semi-open population, small individuals are sexual recruits that come from outside the population while new large individuals are asexual recruits that come from within the population.

Treating the populations as completely closed assumes that 100% of recruitment is local, and therefore that all new individuals are either sexually or asexually produced from individuals currently in the population. Fecundity is known to increase with body size in marine invertebrates (Cropper and DiResta 1999). Here, anemones with large TCSA are expected to have high fecundity and more reproductive output relative to those with small TCSA (Eq. 3.2 and 3.3):

$N(t+1)=F_1*n_1(t)+F_2*n_2(t)+F_3*n_3(t)+F_4*n_4(t)+F_5*n_5(t)$ (Eq. 3.2)

In Eq. 3.2, N is the number of new individuals at time t+1, n_i is the number of individuals at time t, and F_i is the reproductive rate. The subscripts represent the size-classes: T=total, 1=0.1-25 cm^2, 2=25.1-50 cm^2, 3=50.1-75 cm^2, 4=75.1-100 cm^2, and 5=>100 cm^2. This equation alone does not reveal the reproductive rate of each size-class, because each F_i is unknown. Therefore, we can produce five equations based on the assumptions that fecundity is proportional to body size, and that the smallest size-class does not reproduce. The following equations were used:

$F_5=2.5*F_2$ (Eq. 3.3A)

$F_4=2*F_2$ (Eq. 3.3B)

$F_3=1.5*F_2$ (Eq. 3.3C)

$F_2=1*F_2$ (Eq. 3.3D)

$F_1=0$ (Eq. 3.3E)

The constant multipliers in Eq. 3.3A-E represent linear stepwise increases in reproductive output (fecundity) based on increases in body size in each size-class. Thus, I may underestimate here the reproductive output of very large anemones, because egg number in sea anemones increase in a linear fashion with body mass rather than with TCSA, which is a 2-dimensional rather than a 3-dimensional measure of body size (Chadwick-Furman and Spiegel 2000). Equations 3.2 and 3.3 were used to solve for F_i. To complete the transition matrix, the reproductive rates (F_i) were added to the transition probabilities. N was set equal to the number of new individuals in the smallest size-class the F_1-F_5 values were added to the first row of the transition matrix. This was repeated for each size-class (Table 3.1B).

Treating the population as being completely open requires a separate recruitment vector, r, to be added to Eq. 3.1:

$c_{t+1}=\mathbf{A}*b_t + r_t$ (Eq. 3.4)

Observed rates of annual recruitment in the field were used for r_{it}, in which r_{1t}= # recruits/m^2 of 0.1-25 cm^2 TCSA, r_{2t}= # recruits/m^2 of 25.1-50 cm^2, r_{3t}= # recruits/m^2 of 50.1-75 cm^2, r_{4t}= # recruits/m^2 of 75.1-100 cm^2, and r_{5t}= # recruits/m^2 of >100 cm^2. No published information exists on the extent to which new recruits of this sea anemone species are sexually versus asexually produced, originate locally or externally to the populations, or whether recruitment varies with physical characteristics of the reef environment. As such, in addition to the above-observed rates, simulated rates of recruitment were used, in which recruitment was classified as either maximal (r_{max}, observed recruitment was the greatest possible recruitment), or average ($r_{average}$, observed recruitment was treated as half of the potential recruitment). In each time step, r_t was determined by sampling randomly from a uniform distribution of 0 to r_{max} recruits/m^2 for maximal recruitment, and 0 to 2*r_{max} for average recruitment (after Fong and Glynn 1998, Lirman and Miller 2003). This process was repeated 30 times for each of 30 annual time steps, to project a range of possible future recruitment rates to each population.

For modeling of the semi-open populations, all large recruits are considered to be asexual, and were integrated into the transition matrix (in a similar manner as in the closed population) while all small recruits are considered sexual and assumed to come from outside of the population. Therefore, eq. 3.4 still applies for this model, but the matrix **A** is constructed differently. All new individuals < 50 cm^2 TCSA were considered to be sexual recruits, and new individuals > 50 cm^2 were considered to be asexually recruited clonemates of existing anemones from within the population. To model this process, eq. 3.2 was used for the three largest size-classes, and eq. 3.3 was modified such that (Eq. 3.5):

$F_5=5/3*F_3$ (Eq. 3.5A)

$F_4=4/3*F_3$ (Eq. 3.5B)

$F_3=1*F_3$ (Eq. 3.5C)

$F_2=0$ (Eq. 3.5D)

$F_1=0$ (Eq. 3.5E)

The values used in eq. 3.5 are the same as those used in eq. 3.3, except that they have been reduced so that the constant in eq. 3.5C is equal to 1. Budding rates are not currently known for *B. annulata*, and because of this the same rates are used here as for sexual reproduction. The budding rates then were integrated into the transition matrix in a similar manner to that used in the closed population. Asexual recruits were classified as all new individuals that were >50 cm^2 in body size, and were assumed to have arisen from large anemones >50 cm^2 in body size. Therefore the recruitment rates were added to the 3x3 bottom right corner of the matrix (Table 3.1C). Limits were set on the body size of new sexual recruits, because it was unlikely that large recruits were newly-metamorphosed from planktonic planula larvae, which are known to be 0.5-13.3 mm in column diameter for the intertidal sea anemone *Actinia tenebrosa* (Ottaway 1979). In addition, laboratory observations indicated that buds of *B. annulata* may become large (up to 180 cm^2 TCSA) while still attached to parental polyps, thus large newly-recruited anemones likely were pedal lacerated clonemates of resident anemones (M. Nelsen, personal observation). In all, 7 possible recruitment scenarios were examined: closed, open with observed rates, open with average rates, and open with maximal rates, semi-open with observed rates, semi-open with average rates, and semi-open with maximal rates. Closed population models did not require more than one model, because all recruits were considered to be local and therefore the changes made to outside recruitment did not apply. Thus, I generated seven thirty-year projections to estimate changes in population size and structure for these sea anemones at each of the two study sites (after Fong and Glynn 1998, Lirman and Miller 2003).

Data Analyses

For each transition matrix, the dominant eigenvalue (λ), right eigenvectors, damping ratio and elasticity were determined (Caswell 2001). These values revealed how population growth rate, stable size distribution, time to reach the stable size distribution, and the vital rates with the greatest influence on population growth, each varied between the two study sites and among the three different styles of transition matrices. (closed, open, and semi-open). Because each 1-year transition matrix was a combination of 4 seasonal matrices, the elasticity equation was modified to negate the compounding of elements by matrix multiplication. For details on population model analysis, see Caswell (2001). The modification to the elasticity equation revealed how each element of all of the seasonal matrices proportionally affected the dominant eigenvalue. The elasticity of each seasonal matrix was summed to determine the total contribution of any particular matrix element during the entire year.

Recruitment into both anemone populations occurred year-round (see Chapter II), so recruitment vectors were added to the populations after each season when applicable. Therefore, each one-year projection shows population size in March, but did not show the seasonal variation. All other matrix analyses were performed without outside recruitment, because recruitment values did not affect the results, so, the yearlong matrices were used instead of the 4 seasonal matrices.

Results

Dominant eigenvalues (finite population growth rate, λ) varied widely between the two examined populations of *Bartholomea annulata*, and also among the three transition matrices (closed, open, and semi-open, Table 3.2A). These differences in eigenvalues revealed to what extent the various possible modes of reproduction and recruitment affected population growth rates, because the only differences between the transition matrices were the reproductive values (Table 3.1A, B, C). The closed transition matrices representing both the Brewers Bay and Flat Cay anemone populations had eigenvalues >1, indicating population growth, whereas the open and semi-open transition matrices had eigenvalues <1, revealing that the processes represented by the matrices did not cause population growth on their own. The eigenvalues for the open model revealed that the transition between size-classes of anemones currently in the population were not enough to cause population growth, while the eigenvalues for the semi-open model indicate that these processes along with asexual reproduction also were not enough to maintain population growth. Eigenvalues for the open and semi-open models indicated the apparent importance of outside recruitment for the population growth of these anemones.

The damping ratio (ρ), which is the ratio of the dominant eigenvalue to the 2nd largest eigenvalue in each model, revealed the time required for each population to reach the stable-size structure (Table 3.2B). Note that given the current population structure and trends at each site, the Brewers Bay population was projected to each a stable-size structure in only a few years, while the Flat Cay population was expected to require 10s to 100s of years to reach the stable-size structure. This pattern is due largely to the relative absence of both large resident anemones, and of large recruits, at Flat Cay (Chapter II). The lack of both together at this site further supports the idea that large residents may be mainly responsible for the production of large recruits through clonal replication.

The stable size structure of each population revealed the expected ratio of individuals in each size-class, if current population trends persist (Table 3.3). The population did not have to reach steady state for stable size structure to be reached; rather, once stable size structure was reached, if the population is growing or shrinking, the proportion of anemones in each size-class remained the same. The expected stable size structure for each population was based on the transition matrices for each model, therefore outside recruitment, which was incorporated into the recruitment vector, had no influence. Therefore, the actual, maximal, and average versions of the open and semi-open models shared a common size stage structure. When stable size structure was reached at Brewers Bay, >50% of the anemones would be in the smallest size-class for the closed population, and 38% and 24% for the open and semi-open populations respectively. At Flat Cay, an even greater percentage of the populations would be in the smallest size-class: >75% in the closed population, 63% in the open population, and 53% in the semi-open population. Current population size structure (Table 3.3) differed from the expected stable size structure, because time was required for these apparently growing populations before the stable size structure could be reached.

Elasticity analyses for both closed population models indicated that the smallest size-classes had the largest effect on population growth rate (Table 3.4A). Elasticity represented which aspects of the transition matrix exerted the greatest proportional changes on population growth rate. Thus, a 10% increase in the growth of the smallest size-class would increase population growth rate more than a 10% increase in the largest size-class remaining the same size. The same was true of the open population (Table 3.4B). At both locations, the smallest individuals had a greater effect on population growth rate than did the largest individuals, with the exception of the largest size-class at Brewers Bay. The sum of elasticities of the largest individuals at Brewers Bay was almost as large as the sum of elasticities of the smallest anemones (.089 and .097 respectively). This indicated that having both the largest and the smallest anemones in the population was crucial to maintaining the open population. The semi-open population, which included asexual reproduction in the 3 largest size-classes, painted a different picture than the other 2 models (Table 3.4C). In this case, in the Brewers Bay population, the elasticities were greatest for shrinkage of the largest anemones. This was because the shrinkage value in the transition matrices included asexual reproduction (See Table 3.1C). This was not true for the semi-open model for Flat Cay. At Flat Cay, there were no anemones in the largest size-class and very few in the 75-100 cm^2 size-class, resulting in very small transitions to these size-classes, and small elasticities. For the semi-open model at Flat Cay, the elasticities indicated that stasis in the 50-75 cm^2 size-class, and growth of the 25-50 cm^2 size class, both had the largest influence on population growth rate at this site.

The closed population model projected that anemone populations would continue to grow at both Brewers Bay and at Flat Cay (Fig. 3.1A and Table 3.5A and B). The 30-year population projections showed that each closed population would grow much larger than either site could maintain. The carrying capacity of these reef sites currently is unknown for these populations, but it is expected to be much less than the unrestricted population sizes projected here.

The open population model projected the Brewers Bay population to decrease to ~29% of its original population size and the Flat Cay population to decrease to ~10% of the original population after 1 year, without recruitment. This pattern was very different from the closed population model that projected large population growth each year, and indicated that recruitment/reproduction played a large role in maintaining population size. This became more apparent when the semi-open model was taken into account. In the semi-open model, the Brewers Bay population was projected to decrease to ~71% of the original population size, while the Flat Cay population was projected to decrease to ~20% of the original population size after one year, without outside, sexual recruitment. Though neither population decreased as fast as the in the open population model both populations would eventually go to zero (Table 3.2C).

The open population model for Brewers Bay, using the observed recruitment numbers, showed that the population becomes stable after a 4-year growth period at a population size of about 151 anemones (Fig. 3.1B and Table 3.5C). Integrating variation into the model changed the maximum population size. For the average model (where observed recruitment is treated as ½ of potential), a true steady state would never be reached but more of a quasi-steady state. This was because of the variable nature of the model, in which recruitment could vary from zero to twice that of observed levels. The maximum and minimum population sizes after four years were projected to 160 and 143 anemones (Fig. 3.1B). Thus, if this population did not experience recruitment failure for an extended period, it would stabilize and become similar in size to that projected by the model where the actual recruitment values were used. The maximal population model (where observed recruitment is treated as the maximum potential recruitment) reached a quasi-steady state value at a much smaller population size than did the average model (Fig. 3.1B). In this case, after a 4-year growth period, the maximum population size was projected to be about 81 anemones, with a minimum of 70 anemones.

The semi-open population model for Brewers Bay projected a 20-year growth period before the population stabilized at around 269 anemones (Fig. 3.1C and Table 3.5E). The average model projected a range of 264-276 anemones, much greater than values projected from the maximal model of 133-138 anemones in the population. After one year of population change at this site, the observed population size was 122 anemones, much larger than that projected by the open-maximal population model, but smaller than the expected steady state projected from the open-average and open-observed recruitment models. When observed rates of recruitment were used, there was a 4-year and 20-year growth period for the open and semi-open models respectively, before the population size stabilized (Fig. 3.1B and 3.1C). Thus, if current population size does not change, the maximal semi-open population model appeared to most closely project the population size of these anemones.

Population projection models for the sea anemones at the Flat Cay site yielded similar patterns to those for Brewers Bay. The open population model, using observed recruitment rates, stabilized after 3 years with a maximum population size of 83 anemones. The average model projected a range of 83-102 anemones, and the maximal model projected a range of 40-48 anemones (Fig. 3.1D and Table 3.5D). These population sizes did not differ much from those produced by the semi-open model, which projected population stabilization after 4 years at about 91 anemones, using observed recruitment rates. The average semi-open model for Flat Cay projected 83-97 anemones, while the maximal model projected 43-50 anemones in the population (Fig. 3.1E and Table 3.5F). The open and semi-open models for Flat Cay all produced similar projected population sizes, because few large anemones occurred in this population and even fewer anemones recruited to the population at large body size (i.e.: products of asexual cloning), in contrast to the reproductive patterns at Brewers Bay. Therefore, asexual reproductive rates, which varied among the above 3 models, exerted little influence on maximal population size at Flat Cay. Currently, population size at Flat Cay is 77 anemones, which is midway between future sizes projected by the average and maximal models above. A short, 3-year period of growth is expected before the anemone population at Flat Cay stabilizes. At that point, it would be possible to determine how accurately theses models project actual short-term population trends.

Discussion

We show here that based on our assumptions and given current trends in population growth and recruitment, the two examined populations of the corkscrew anemone *Bartholomea annulata* in the US Virgin Islands are expected to continue to grow and to stabilize in size over the next 30 years. Both are highly dynamic, and exhibit rapid rates of transition among size-classes and of mortality of individuals (Chapter II). Thus, these anemone populations depend on rapid influxes of a large number of small individuals, in the form of a steady supply of new recruits.

Commercial fishing for the aquarium trade is a large, profitable industry that is only beginning to incorporate scientifically-based regulations to protect ornamental organisms from over-harvesting (Chiappone et al. 2001, LeGore et al. 2005).

Unfortunately, non-coral invertebrates often are overlooked in regulations aimed at maintaining sustainable harvest of ornamental reef organisms (MyFCW.com 2008, Rule 68B-42, F.A.C.). Regulatory agencies, and indeed the fishers themselves, appear to assume that populations of non-coral invertebrates are sustainable even under intense fishing pressure (Shuman et al. 2005). Our application of seven types of population models to each of two populations of the large Caribbean sea anemone *B. annulata* reveal that given current non-fished conditions in the US Virgin Islands, anemones populations at both sites are projected to thrive. The open and semi-open population models also suggest that outside recruitment appears to play a large role in maintaining the stability of these populations.

If outside recruitment decreases or fails completely for even 1 year, then these anemone populations are expected to decline at a rapid rate, because of the observed high mortality rates in all size classes (Chapter II). Thus, due to the rapid turnover of these populations, recruitment must remain high in order to make up for the rapid and constant loss of individuals from the populations. Elasticity analysis of all models at Flat Cay, and of the closed and open models at Brewers Bay, reveals that the growth and survival of the smallest anemones have the greatest effect on population growth rates. Population growth rates in both the open and semi-open models is $<<1$, which represents no change in population size, at both study locations. Thus, in fished populations, ensuring the growth and survival of the small anemones alone may not be enough to cause population growth and stability. Protection of a steady recruitment source, in addition to ensuring the high survival of small anemones, may be needed to maintain sustainable populations of this highly-prized anemone. For successful sexual reproduction, individuals of *B.*

annulata, as in other broadcast spawners, need to reach a minimum critical abundance for adequate fertilization of gametes (Levitan et al. 1992, Quinn et al. 1993, Levitan 2004). Therefore, to maintain anemone populations in fished environments, high levels of outside recruitment are necessary. This requires large nearby source populations for the arrival of planktonic larvae.

The models presented here differ from some recent stage-based models of reef coral populations (Hughes 1984, Fong and Glynn 1998), in that they do not incorporate the potential impacts of large physical disturbances such as hurricanes or flooding. The reef sites that we examined on St. Thomas have experienced several hurricanes in recent decades (Bythell et al. 1993, Edmunds 2002). Thus, the population trends modeled here likely will be interrupted by storms and other disturbances that will reduce population sizes at unpredictable time intervals. However, these models allow projection of potential recovery rates of these anemone populations following hurricanes and other disturbances, given the size and structure of surviving populations after each type of disturbance. Based on observed demographic patterns for the corkscrew anemone *B. annulata* (Chapter II), and the model projections presented here, we predict that populations of this species will recover fairly rapidly from disturbances if a source population remains nearby. The open and semi-open models project that even if the 2 St. Thomas sites contain zero anemones, the populations could recover to current size in <3 years via an influx of planktonic recruits. The closed model projects longer recovery times (up to 25 years at Brewers Bay if the population is reduced to only 10 anemone in the smallest size-class, and 5 years at Flat Cay), with the populations never recovering if they crash to zero, because in this model, the populations rely entirely on self-recruitment.

Based on the above data, we recommend specific regulatory measures to ensure a sustainable ornamental fishery on these important Caribbean anemones. These regulations also will protect the obligate cleaner shrimps that associate with these sea anemones, and thus contribute to the maintenance of sustainable stocks of these in-demand ornamental crustaceans (LeGore et al. 2005). Firstly, a minimum anemone body size of about 50 cm^2 TCSA (~4 cm tentacle crown diameter) for collection will ensure that the smallest individuals in these populations (the ones that contribute the most to population growth and survival) will not be removed. Secondly, we recommend that anemone collection be banned altogether in selected reef areas near each fished area. High rates of juvenile recruitment depend on high levels of sexual reproduction in the local adult population, because self-recruitment appears to be the rule for most coral reef organisms (Hughes et al. 2000). The creation of marine protected areas near open fished areas, or at least nearby areas where anemone fishing is prohibited, will allow the survival of large adult individuals in nearby populations. This will maintain adequate sexual reproduction and local recruitment. Implementation of both these recommended measures (minimum collection size together with the nearby unfished areas) will enhance both anemone recruitment and survival rates, and support stable populations of *B. annulata* as the basis of a sustainable fishery (Quinn et al. 1993). Implementation of these regulatory measures is expected to produce 3 synergistic effects: (1) creation of long-term sustainable collecting sites for ornamental fishers of sea anemones and associated invertebrates such as cleaner shrimp, (2) prevention of local extinction of corkscrew anemones on Caribbean coral reefs, which appears to have already occurred in some parts of Florida due to overfishing (Chiappone et al. 2001), and (3) positive cascade effects on the diversity and abundance of large reef fishes, due to the maintenance of populations of anemone-based cleaner shrimps and thus of fish cleaning stations in adequately-regulated reef areas. The results of this research apply only to populations of giant sea anemones with similar reproductive strategies to *B. annulata* and we do not recommend extrapolation to mainly clonally reproducing populations such as those of *Aiptasia pallida* that may behave very differently in response to collection pressure.

We conclude that the application of size-based population modeling is an effective tool for projection of giant sea anemone population sizes, and that elasticity analysis can reveal the crucial life stages that most impact the growth rates of these populations. The use of these tools has the potential to provide a more scientific basis for the sustainable management of the large ornamental fishery based on these spectacular reef organisms.

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Table 3.1. Transition matrices for the sea anemone *Bartholomea annulata* in 3 types of population models (**A**, **B**, **C**). The sum of a column is equal to the survival of that size-class of anemones. (**G**) represents growth, (**S**) represents shrinkage, and (**L**) represents remaining in the same size-class (stasis).

A. Open

$$\begin{vmatrix} L_{11} & S_{12} & S_{13} & S_{14} & S_{15} \\ G_{21} & L_{22} & S_{23} & S_{24} & S_{25} \\ G_{31} & G_{32} & L_{33} & S_{34} & S_{35} \\ G_{41} & G_{42} & G_{43} & L_{44} & S_{45} \\ G_{51} & G_{52} & G_{53} & G_{54} & L_{55} \end{vmatrix}$$

B. Closed

$$\begin{vmatrix} L_{11} & S_{12}+F_{12} & S_{13}+F_{13} & S_{14}+F_{14} & S_{15}+F_{15} \\ G_{21} & L_{22}+F_{22} & S_{23}+F_{23} & S_{24}+F_{24} & S_{25}+F_{25} \\ G_{31} & G_{32}+F_{32} & L_{33}+F_{33} & S_{34}+F_{34} & S_{35}+F_{35} \\ G_{41} & G_{42}+F_{42} & G_{43}+F_{43} & L_{44}+F_{44} & S_{45}+F_{45} \\ G_{51} & G_{52}+F_{52} & G_{53}+F_{53} & G_{54}+F_{54} & L_{55}+F_{55} \end{vmatrix}$$

C. Semi-open

$$\begin{vmatrix} L_{11} & S_{12} & S_{13} & S_{14} & S_{15} \\ G_{21} & L_{22} & S_{23} & S_{24} & S_{25} \\ G_{31} & G_{32} & L_{33}+F_{33} & S_{34}+F_{34} & S_{35}+F_{35} \\ G_{41} & G_{42} & G_{43}+F_{43} & L_{44}+F_{44} & S_{45}+F_{45} \\ G_{51} & G_{52} & G_{53}+F_{53} & G_{54}+F_{54} & L_{55}+F_{55} \end{vmatrix}$$

Table 3.2. Variation in **A.** dominant eigenvalues (finite population growth rate, λ), **B.** Time in years to reach stable size structure, and **C.** time until populations reduce to zero without outside recruitment, for populations of the sea anemone *Bartholomea annulata* among 3 types of population matrices (closed, open, and semi-open) at 2 coral reef sites (Brewers Bay and Flat Cay). Dominant eigenvalues >1 represent population growth, and <1 represent population shrinkage.

A.

	Closed Population	Open Population	Semi-open Population
Brewers Bay	1.104	0.288	0.707
Flat Cay	1.381	0.101	0.206

B.

	Closed Population	Open Population	Semi-open Population
Brewers Bay	3.53	7.35	11.10
Flat Cay	975.19	138.74	25.17

C.

	Closed Model	Open Model	Semi-open Model
Brewers Bay	N/A	4 Years	15 Years
Flat Cay	N/A	3 Years	4 years

Table 3.3. Proportion of individuals of the sea anemone *Bartholomea annulata* in each size-class after projected stable-size structure has been reached. Actual observed population size-structure during the March 2007 census also is given for comparison.

		0-25 cm^2	25-50 cm^2	50-75 cm^2	75-100 cm^2	>100 cm^2
Brewers Bay	Closed Population	.536	.152	.125	.093	.094
	Open Population	.380	.148	.145	.146	.181
	Semi-open Population	.241	.101	.218	.184	.256
	March 2007 Population	.514	.284	.073	.073	.055
Flat Cay	Closed Population	.754	.168	.052	.031	0
	Open Population	.632	.278	.059	.031	0
	Semi-open Population	.534	.241	.125	.100	0
	March 2007 Population	.736	.170	.075	.019	0

Table 3.4. Elasticity values of each size class of individuals (columns) in populations of the sea anemone *Bartholomea annulata* at 2 coral reef sites (Brewers Bay and Flat Cay). Bold numbers represent the greatest elasticity values in each table. **A.** Closed populations, bold represents elasticities >0.5. **B.** Open populations, bold represents elasticities >0.01. **C.** Semi-open populations, bold represents elasticities >0.1.

A.

Closed Population		0-25 cm^2	25-50 cm^2	50-75 cm^2	75-100 cm^2	>100 cm^2
Brewers Bay	Growth	**.701**	**.615**	.302	.096	
	Loop	**.648**	.379	.223	.141	.186
	Shrinkage		.253	.346	.360	**.630**

Flat Cay	Growth	**1.229**	**1.065**	.055	0	
	Loop	**.607**	**2.094**	.224	0	0
	Shrinkage		**.814**	**.910**	**.634**	0

B.

Open Population		0-25 cm^2	25-50 cm^2	50-75 cm^2	75-100 cm^2	>100 cm^2
Brewers Bay	Growth	**.031**	**.035**	**.014**	.010	
	Loop	**.066**	**.019**	.010	.009	**.043**
	Shrinkage		**.015**	**.021**	**.016**	**.046**

Flat Cay	Growth	.006	.006	0	0	
	Loop	.009	.008	.001	0	0
	Shrinkage		.004	.004	.004	0

C.

Semi-open Population		0-25 cm^2	25-50 cm^2	50-75 cm^2	75-100 cm^2	>100 cm^2
Brewers Bay	Growth	.080	**.155**	**.218**	**.121**	
	Loop	.096	.050	**.139**	**.114**	.0366
	Shrinkage		.026	.102	**.141**	**.392**
Flat Cay	Growth	.015	.027	.012	0	
	Loop	.015	.021	.031	0	0
	Shrinkage		.007	.018	,024	0

Table 3.5. Three types of transition matrices (closed, open, semi-open) used to construct population models for the sea anemone *Bartholomea annulata* at each of 2 coral reef sites (Brewers Bay and Flat Cay).

Table 10	**A.** Brewers Bay Closed Matrix					**B.** Flat Cay Closed Matrix				
	0-25 cm^2	25.1-50 cm^2	50.1-75 cm^2	75.1-100 cm^2	>100 cm^2	0-25 cm^2	25.1-50 cm^2	50.1-75 cm^2	75.1-100 cm^2	>100 cm^2
0-25 cm^2	.250	.721	.902	1.154	1.363	.041	2.786	2.901	4.508	3.236
25.1-50 cm^2	.070	.204	.256	.327	.386	.092	.612	.649	1.011	.720
50.1-75 cm^2	.055	.171	.214	.272	.323	.028	.191	.201	.311	.228
75.1-100 cm^2	.042	.127	.159	.202	.239	.014	.093	.010	.156	.228
>100 cm^2	.041	.129	.162	.206	.245	0	0	0	0	0
	C. Brewers Bay Open Matrix					**D.** Flat Cay Closed Matrix				
0-25 cm^2	.118	.103	.091	.127	.098	.045	.098	.068	.136	0
25.1-50 cm^2	.040	.041	.039	.052	.044	.019	.043	.036	.072	0
50.1-75 cm^2	.032	.042	.043	.055	.052	.004	.009	.006	.012	0
75.1-100 cm^2	.032	.042	.043	.055	.052	.002	.005	.004	.009	0
>100 cm^2	.035	.053	.055	.072	.071	0	0	0	0	0
	E. Brewers Bay Semi-open Matrix					**F.** Flat Cay Semi-open Matrix				
0-25 cm^2	.126	.141	.151	.209	.214	.052	.180	.136	.226	.112
25.1-50 cm^2	.044	.058	.065	.089	.096	.022	.079	.065	.110	.047
50.1-75 cm^2	.059	.120	.146	.195	.234	.010	.046	.033	.054	.032
75.1-100 cm^2	.056	.103	.124	.165	.193	.007	.004	.028	.046	.025
>100 cm^2	.067	.140	.172	.230	.275	0	0	0	0	0

Figure Legends

Fig. 3.1. 30-year projections for 3 types of size-based matrix models of populations of the sea anemone *Bartholomea annulata* at 2 coral reef sites (Brewers Bay and Flat Cay): **A.** Closed models for both reef sites. Anemone populations are projected to grow much larger than carrying capacity would allow. **B.** Open models at Brewers Bay. **C.** Semi-open models at Brewers Bay. **D.** Open models at Flat Cay. **E.** Semi-open models at Flat Cay. For all open and semi-open models, population sizes projected by the models that use actual recruitment and average values are slightly larger than current levels, while the maximal model projects anemone populations to be smaller. Average and maximal models are shown as means +/- SEM of N=30 replicates.

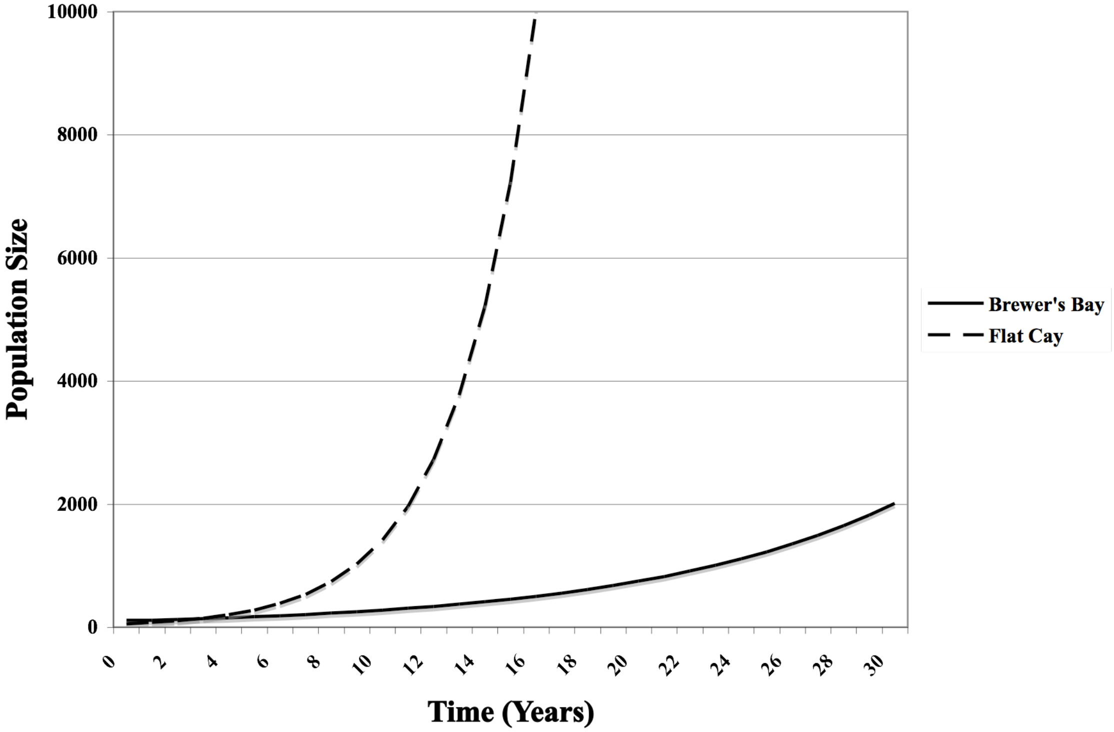
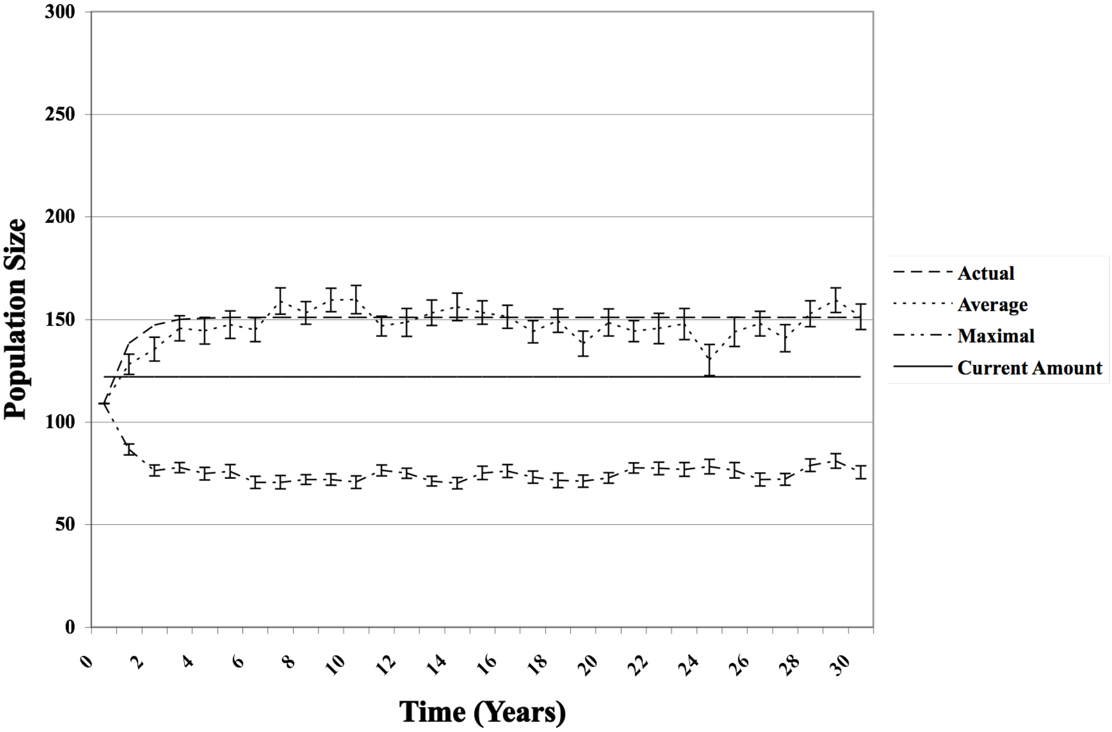
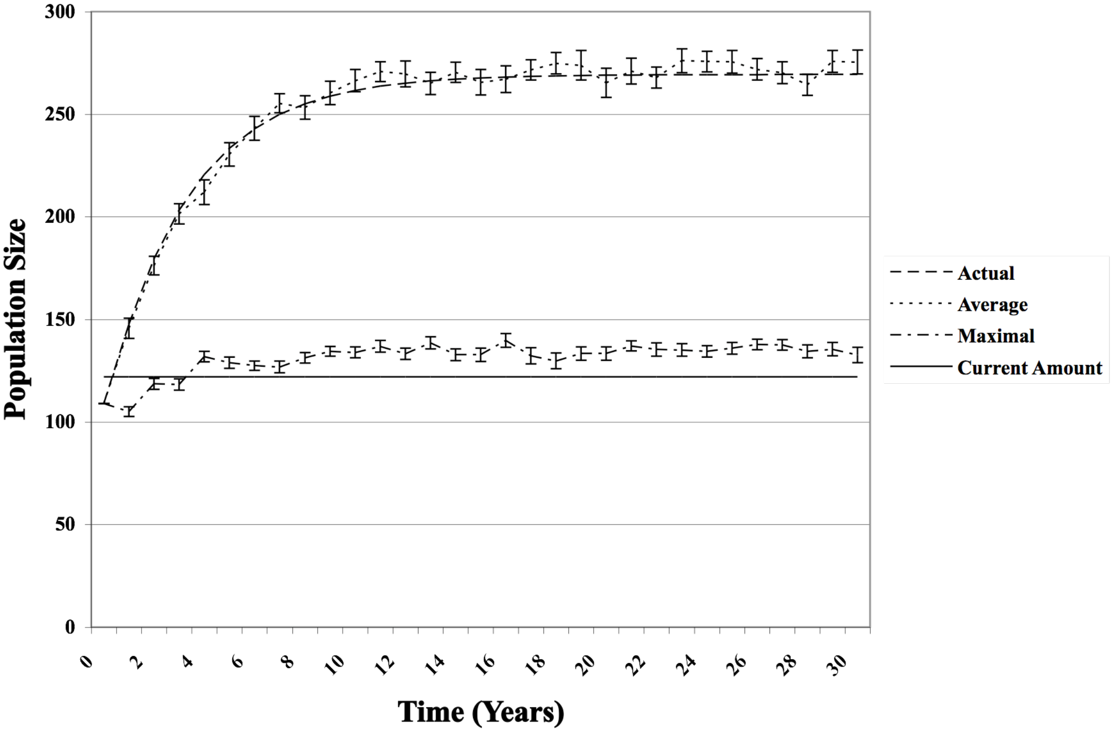

10000
8000
6000
4000
2000
0
Population Size
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Time (Years)
Brewer's Bay
Flat Cay

Fig. 3.1A


300
250
200
150
100
50
0
Population Size
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Time (Years)
Actual
Average
Maximal
Current Amount


300
250
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100
50
0
Population Size
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Time (Years)
Actual
Average
Maximal
Current Amount

Fig. 3.1B, C

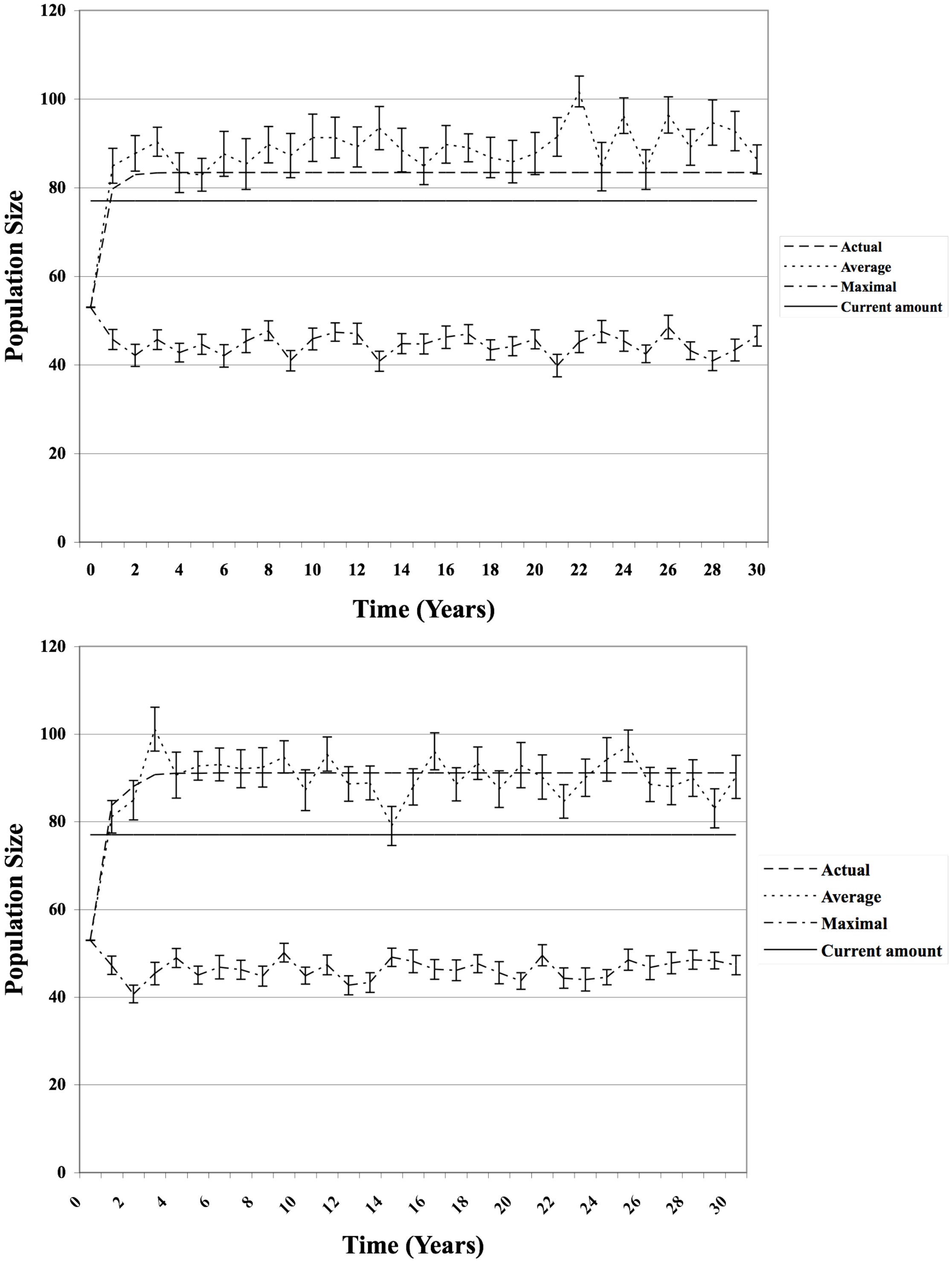
Population Size
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Time (Years)
Actual
Average
Maximal
Current amount
Population Size
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Time (Years)
Actual
Average
Maximal
Current amount

Fig. 3.1D, E