Population Dynamics of Hurricane-Generated Fragments of Elkhorn Coral *Acropora palmata* (Lamarck, 1816)

by

Antonio L. Ortiz Prosper

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Approved by:

Nilda E. Aponte, Ph.D. Member, Graduate Committee	Date
Paul M. Yoshioka, Ph.D. Member, Graduate Committee	Date
Fernando Bird-Picó, Ph.D. Member, Graduate Committee	Date
Ernesto Weil, Ph.D. President, Graduate Committee	Date
Mónica Alfaro, Ph.D. Representative of Graduate Studies	Date
Nilda E. Aponte, Ph.D. Chairperson, Department of Marine Sciences	Date
José A. Mari Mutt, Ph.D. Director, Department of Graduate Studies	Date

ABSTRACT

Fragmentation and local dispersion of hurricane-generated fragments have been considered an important feature in the life history, population dynamics and genetic structure of the elkhorn coral *Acropora palmata*. The significance of fragmentation as a strategy of this species to maintain local populations in the time of their recent decline was assessed by studying the dynamics and size structure of Hurricane Georges (1998) generated fragments in three reefs (Media Luna Reef, Laurel Reef and San Cristóbal Reef) within La Parguera coral reef system on the southwestern coast of Puerto Rico. Two belt transects (30 m long and 2 m wide) were established across the largest patch of living *A. palmata* in each reef. All fragments with living tissue were counted, labeled and measured. Additional information collected included: 1) maximum length and width of living tissue on the fragment at three time intervals (one month, one year and three years after fragmentation), 2) type of reef substrate where the fragment landed (hard bottom, rubble, sand, live standing coral), and 3) condition of the fragment (loose, slightly stable or cemented to the substrate) was recorded in time. No significant difference in mean fragment densities was observed among reefs ($p > 0.05$; Tukey-Kramer). Fragment abundance after a year was 369 (1.02 ± 0.35 fragments/m^2). No significant relationships were observed between fragment density and coral cover or with the types of reef substrates observed in each transect. However, there was a significant difference ($p < 0.05$, Tukey-Kramer) in mean fragment size (length, width and surface area) among reefs. The mean overall mortality within the first year was 28.24 ± 3.68 % (n= 151 fragments from San Cristóbal Reef only), after 3 years was 47.96 ± 17.71 % (n= 254 fragments from all reefs). Fragment mortality at San Cristóbal Reef was significantly lower (22.92 ± 10.42 %) than at Media Luna and Laurel Reefs (60.54 ± 6.13 %, 60.43 ± 8.43%, respectively; $p < 0.025$, ANOVA). Mean percentage of colonies with partial tissue mortality in the first year was significantly higher (85.92 ± 4.94 %) compared to 3 years (50.81 ± 12.53 %; $p < 0.05$, t-test). The mean percentage of loss tissue per fragment was 61.74 ± 9.97 % after the first year, and did not increase after 3 years (57.56 ± 6.69 %; $p>0.05$, t-test). After three years, loose fragments were significantly ($p< 0.05$, Tukey-Kramer) more abundant than cemented fragments, and the major mode of cementation was by means of coralline algae calcification (average= 29.92 %, n= 254 fragments). No significant differences were found in mean fragment survivorships across different conditions (loose, slight stable or cemented fragments). Substrates had a moderate effect on the survival rate of the fragments within the first year, but after three years, a significant ($p< 0.05$, Tukey-Kramer) lower survivorship was observed in those fragments that landed over sand compared to those that landed over hard substrates and standing live colonies. A positive and significant relationship (Regression, $p< 0.01$; $R^2= 0.63\text{-}0.77$) was observed between fragment size (length and surface area) and mortality with a possible threshold size (20-25 cm length) above which fragments are less likely to die in the first year. While initial fragment size was an important factor determining the early survival of the ramet, the effect of continuous tissue loss by partial mortality (disease, predation, sedimentation) produced fragments with reduced size, affecting future survival. The predicted decline of populations by the fragment size-based models suggests a complex response of populations to recent environmental change and may be related to the recent demise of this species in the wider Caribbean.

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RESUMEN

La fragmentación y dispersión local de fragmentos generados por huracanes ha sido considerada una característica importante en la historia de vida, dinámica poblacional y estructura genética del coral cuerno de alce, *Acropora palmata*. El papel de la fragmentación como estrategia de esta especie para mantener poblaciones locales fue evaluado estudiando la dinámica y estructura de tamaños de fragmentos generados por el Huracán Georges en tres arrecifes (Arrecife Media Luna, Arrecife Laurel y Arrecife San Cristóbal) dentro del sistema de arrecifes de La Parguera, en la costa suroeste de Puerto Rico. Se establecieron dos transectos de banda (30 m de largo por 2 m de ancho) sobre el parche más grande de colonias de *A. palmata*. Todos los fragmentos con tejido vivo fueron contabilizados, marcados y medidos. Información adicional incluyó: 1) largo y ancho máximo de la porción de tejido vivo del fragmento en tres intervalos de tiempo (un mes, un año y tres años después de producido), 2) tipo de sustrato en que cayeron los fragmentos (sustrato duro, escombros, arena, sobre colonias vivas), y 3) la condición de los fragmentos (sueltos, moderadamente estabilizados o cementados al sustrato) fue medida. No se observó diferencia significativa en densidad promedio entre los arrecifes ($p > 0.05$; Tukey-Kramer). La abundancia de fragmentos después de un año fue 369 (1.02 ± 0.35 fragmentos/m^2). No se observaron relaciones significativas entre la densidad de fragmentos y la cobertura de coral vivo o con algunos de los tipos de substratos del fondo del arrecife observado en cada transecto. Sin embargo, hubo una diferencia significativa ($p < 0.05$, Tukey-Kramer) en el tamaño promedio del fragmento (largo, ancho y área de superficie) entre los arrecifes. El promedio general de mortalidad durante el primer año fue 28.24 ± 3.68 % (n= 151 fragmentos solamente del Arrecife San Cristóbal), después de 3 años fue 47.96 ± 17.71% (n= 254 fragmentos encontrados en todos los arrecifes). La mortandad de fragmentos en el Arrecife San Cristóbal fue significativamente menor (22.92 ± 10.42%) que en el Arrecife Media Luna y el Arrecife Laurel (60.54 ± 6.13 %, 60.43 ± 8.43 %, respectivamente; $p < 0.025$, ANOVA). El promedio porcentual de colonias con mortalidad parcial de tejido durante el primer año fue significativamente mayor (85.92 ± 4.94 %) comparada con 3 años (50.81 ± 12.53 %; $p < 0.05$, prueba t). El promedio porcentual de perdida de tejido por fragmento fue 61.74 ± 9.97 % después de un año, y no aumentó después de 3 años (57.56 ± 6.69 %). Después de tres años, los fragmentos sueltos eran significativamente más abundantes ($p < 0.05$, Tukey-Kramer) que los fragmentos cementados y el principal modo de cementación fue por medio de la calcificación de algas (promedio= 29.92 %, n= 254 fragmentos). No se encontraron diferencias significativas entre los promedios de sobrevivencia de fragmentos en distintas condiciones (fragmentos sueltos, moderadamente estabilizados o cementados). Los substratos duros tuvieron un efecto moderado en el ritmo de sobrevivencia de los fragmentos durante el primer año, pero después de tres años se observó una baja y significativa ($p < 0.05$, Tukey-Kramer) sobrevivencia en aquellos fragmentos que aterrizaron sobre arena comparados con aquellos que aterrizaron sobre sustratos duros y colonias vivas. Una relación positiva y significante (Regresión, $p<0.01$; $R^2= 0.63-0.77$) fue observada entre el tamaño (largo y área de superficie) y mortalidad con un posible umbral de tamaño (20-25 cm largo) sobre el cual los fragmentos son menos propensos a morir durante el primer año. Mientras que el tamaño inicial resultó ser un factor importante que controla la sobrevivencia temprana de la colonia, la continua pérdida de tejido por mortalidad parcial (enfermedad, depredación, sedimentación) tiende a disminuir el tamaño afectando así su futura sobrevivencia. El descenso poblacional pronosticado por los modelos a base del tamaño del fragmento sugiere una compleja respuesta de las poblaciones ante los recientes cambios ambientales que podría estar relacionada con la reciente merma de esta especie en todo el Caribe.

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Antonio L Ortiz Prosper
May 15, 2005

This work is dedicated to my wife *Rebecca* and my three little pieces of coral: *Taina del Mar, Coral del Mar* and *Katia del Mar*.

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CHAPTER 1
INTRODUCTION

1.1. - INTRODUCTION

The ability to form physiologically-separated organisms of identical genetic composition (= ramets: sensu Harper, 1977) by different asexual mechanisms is a common feature in the life history of a wide variety of plants (Cook, 1985; Selander, 1985) and benthic marine organisms (Highsmith et al., 1980; Jackson and Winston, 1981; Highsmith, 1982; Lasker, 1984,1990; Lasker and Coffroth, 1985; Heyward and Collins, 1985; Wallace, 1985; Wulff, 1985, 1991; Dahan and Benayahu, 1997). Asexual reproduction can provide modular organisms with a considerable advantage through numerical abundance, size and persistence in local populations. For example, the evolutionary and ecological success of clonal plant species that predominate in many ecosystems (arctic and alpine regions, grasslands and savannas, wetland and coastal communities, shrublands, boreal forests, and temperate and tropical herbaceous communities) have been related to the maintenance of both modes of reproduction, sexual and asexual (Selander, 1985). Since asexual reproduction plays an important role, its pervasiveness in many organisms of different taxonomic groups implies an evolutionary advantage (Sebens and Thorne, 1985; Lasker and Coffroth, 1995, 1999).

A coral reef community can be described as a clonal community because most of its principal components are modular organisms. This clonality occurs at two levels: (a) the colony level (polyps within a colony) and, (b) the population level (ramets). Asexual reproduction at the colony level occurs by binary fision of the polyps. At the populations level, scleractinian corals have been reported to reproduce asexually by the propagation of broken fragments of individual colonies (Tunnicliffe, 1981; Highsmith, 1982; Lasker, 1984, 1990; Lasker and Coffroth, 1985, 1995), asexually-produced planulae (Stoddart, 1983), single polyp bail-out (Sammarco, 1982), polyps expulsion (Kramarsky-Winter et al., 1997), detachment of groups of polyps (Rosen and Taylor,

1969) and gemmae (Weil et al., 2000). The resulting propagules of asexual reproduction have attributes that are different from the products of sexual reproduction (Lasker, 1984). Some suggested advantages of asexual propagation are: (1) rapid colonization of available space by a locally successful genotype, (2) increased genetic survivorship by escaping from multiple biological and physical processes (Knowlton et al., 1981), (3) the ability to become established on substrata not directly colonizable by larvae; (4) increased genet (all genetically identical colonies) fitness by stimulating genet growth rates and indirectly increasing its fecundity (Highsmith, 1982; Coffroth and Lasker, 1998). Another benefit of spreading copies of the genets across the reef, not documented in the literature, is that it may increase the probability of different genotypes to be close together at the moment of release of the sexual gametes (coral spawning) therefore promoting crossbreeding. By far, asexual reproduction exploits the fact that particular genotypes can be successful repeatedly in both time and space if the conditions remain more or less the same. In this sense, genets may be virtually immortal if the rate of clonal reproduction equals or exceeds ramet mortality (McFadden, 1997). Therefore, organisms that reproduce using both mechanisms may be able to make use of asexual propagation of short-dispersing ramets to preserve locally well-adapted genotypes, while sexual reproduction may improve fitness by forming new genetic recombinations prior to the colonization of new habitats (Williams, 1975) and usually have a long distance dispersal capability.

Despite the relative advantage of clonal propagation, an optimal balance between recruitment of new genets and asexual propagation may be needed to adapt to variable environmental conditions. With vegetative propagation alone, clonal taxa may respond to environmental change through a variety of mechanisms, some of which mitigate disturbance effects and some of which amplify it (Lasker and Coffroth, 1999). Mechanisms that allow populations to mitigate the effects of disturbance are those related with their capacity to escape from the disturbance or to reduce the effects. For example, when a hurricane hits a reef, exposed populations with a large number of well-dispersed colonies may survive these catastrophic events and at the same time, allow populations to expand following the perturbation. Amplification of disturbance effects will be expected to occur when populations are dominated by genetically uniform ramets of a small number of asexually prolific clones (Ayre, 1985). Therefore, the mortality of a single genet by a clone specific factor (i.e. disease) becomes an important ecological event when the affected genet is the dominant one within the population and community (Bak, 1983). For example, Lasker (1990) observed a clone-specific mortality among *Plexaura kuna* (Lasker, Kim and Coffroth, 1996) clonemates that declined in abundance while an adjacent clone did not respond in the same manner (i.e. did not suffer any mortality). Similarly, Schick et al. (1979) suggested that a depauperate genetic structure in concert with clonal variation in thermal tolerance, explains the numerous examples of population-wide catastrophic mortalities of the anemone *Haliplanella luciae* (Verrill, 1898). This suggests that persistence of local populations largely depend on the contribution of both modes of reproduction. Failure or decrease in any one of these reproductive mechanisms can result in significant changes in the population (genet, clone) susceptibility, resistance, and resilience to disturbances.

Given the importance of understanding the contribution of asexual and sexual reproductive mechanisms for the long-term survival of coral populations, the purpose of the present study was to evaluate the relevance of fragmentation as a major controlling and structuring factor in populations of the elkhorn coral *Acropora palmata* (Lamarck, 1816). The elkhorn coral, *A. palmata* is a large arborescent coral that usually forms monospecific thickets and patches on shallow and high-energy portions of reefs throughout the Caribbean (Goreau, 1959; Geister, 1977; Rogers, et al., 1982). This species has several adaptations that enable it to dominate and persist in the high-energy zone of the reef (Schuhmacher and Plewka, 1981). Some of these adaptations include a strong skeleton, a thick basal attachment to the substratum, and branches usually oriented parallel to the prevailing currents (Shinn, 1966; Schuhmacher and Plewka, 1981). Although, *A. palmata* is an important species in most modern shallow reefs

(Jordán-Dahlgren, 1992), it apparently did not evolve until the earliest Pleistocene (Lewis, 1984; Budd et al., 1994; Jordán-Dahlgren, 1997). This species is an extremely important reef builder and its rapid accretion rates allowed shallow reef zones to keep up with sea level rise (Aronson and Precht, 2001a, 2001b). The structural complexity formed by the branching morphology is another important feature that provides essential reef habitat for many associated organisms (Lirman, 1999; Bruckner, 2003). Unlike acroporid species in the Indo-Pacific, which exhibit high sexual recruitment rates (Wallace, 1985), the main local propagation mechanism of *A. palmata* in the Caribbean has been considered to be by means of colony fragmentation (Bak and Engel, 1979; Highsmith, 1982; Rylaarsdam, 1983; Lirman and Fong, 1997). The assumption that this species uses mostly asexual reproduction to persist locally, with sporadic sexual recruitment, is considered a general trait of its life history strategy.

During the last decades, populations of acroporids in the Caribbean have been greatly reduced throughout their range as a result of at least two major factors: hurricanes (Glynn et al., 1964; Knowlton et al., 1981, 1990; Woodley et al., 1981; Rogers et al., 1982, 1991; Woodley, 1992; Vicente, 1994; Jaap and Sargent, 1994; Lirman and Fong, 1996, 1997) and coral diseases (Bak and Criens, 1981; Gladfelter, 1982; Ogden and Ogden, 1994; Garzón-Ferreira and Kielman, 1994; Sheppard et al., 1995; Bruckner and Bruckner, 1997; Zea et al., 1998; Weil et al., 2002). White-band disease was probably the most important cause of geographic declines of *Acropora* populations (Aronson and Precht, 2001a, 2001b). Although, paleontological data suggests that populations of *Acropora* spp. have died off locally in the past (Shinn et al., 1981; Lewis, 1984), a Caribbean-wide mass mortality of these corals has not occurred during the Holocene (Hubbard et al., 1994; Aronson and Precht, 2001b). This unprecedented decline changed the composition of shallow reef communities and the complete loss of this keystone resource represent a significant loss of reef structure and function (Bruckner, 2003). As a result, in January 23, 1999, *A. palmata* and *Acropora cervicornis* (Lamarck, 1816) were submitted to evaluation as possible candidates to be added to the List of Endangered and Threatened Species under the Endangered Species Act of 1973 (Federal Register: Vol. 64(120)). The general perception for this act was that acroporid species were no longer able to increase or sustain local populations by means of asexual propagation due to a constant reduction of populations size and recent environmental changes which have affected the survivorship and regrowth of coral fragments (Bruckner, 2003). Consequently, as the remaining populations decline, a further reduction in sexual reproductive success may also take place due to an Allee effect resulting from low adult densities, possible low genetic diversity and patchy distribution that can reduce the chance of fertilization (Bruckner, 2003). Therefore, understanding the conditions that promote local proliferation of this species may provide insights into the adaptive significance of clonal propagations as a strategy to maintain local populations to the present decline. This may provide valuable information to predict population changes in response to natural or human-induced disturbances.

In this project, the dynamics and structure of asexually-derived ramets in several populations of *A. palmata* produced during Hurricane Georges (September 21, 1998) were studied for three years. Although, the effects of hurricanes on *A. palmata* populations was previously studied (Highsmith et al., 1980; Woodley et al., 1981; Rogers et al., 1982; Fong and Lirman, 1995; Lirman and Fong, 1996, 1997; Jordán-Dahlgren and Rodríguez-Martínez, 1998; Lirman, 2000a, 2000b), including survivorships studies (≈ 1year) of resulting fragments (Highsmith et al., 1980; Rogers et al., 1982; Lirman and Fong, 1997; Lirman, 2000a), this is the first time that large numbers of hurricane-generated fragments naturally dispersed over different reef substrates, were followed for 3 years (cohort of 1998). The information gathered in this study aid to previously conflicting results about the relationship between fragment size and survivorship. For example, while some studies reported positive relationships between fragment size and survivorships (Highsmith et al., 1980; Rogers et al., 1982) others reports claim a non-significant relationship (Lirman and Fong, 1997; Lirman, 2000a). Size as well as other different factors (reef location, substrate, conditions or combination of those) that influence the survival of these naturally generated fragments was evaluated in the present study. Two main questions were addressed:

(1) Is fragmentation by hurricanes an important structuring force regulating the recent dynamics and structure of populations of *A. palmata*?

(2) Are there significant differences in the structure and dynamics of hurricane-generated ¨populations¨ of *A. palmata* fragments across different reefs?

To answer these questions, several specific objectives were proposed. First, the structure and dynamics of different ¨populations¨ of hurricane-generated (Georges) fragments in different reefs were characterized by assesing:

1a- The densities and size structure of different populations of hurricane-generated fragments in different reefs.

1b- The rates of growth, tissue mortality and overall survivorship of the fragments in the different populations.

1c- Correlations of these parameters with the initial size of the fragment.

1d- The spatial (within and across reefs) and temporal (one and three years) variability of growth and mortality rates (d_x) and the overall survivorship of the fragments.

Secondly, how different types of substrate affected the survivorship of different fragment sizes were determined by:

2a- Characterizing the different types (hard, rubble, sand, standing coral) of the substrate where the fragments landed and conditions (loose, slightly stablized or cemented to the substrate) .

2b- Spatial and temporal variability of growth and survivorship of the fragments on the different substrates within and across reefs.

Third, the population dynamics of hurricane-generated fragments was described by using a size-specific demography approach. To describe temporal trends in survivorships of hurricane-generated fragments, two size-based population matrix models were developed to describe separately the survivorship and growth of colonies within the first year after fragmentation (early population matrix model) from those that occur two years later (late population matrix model).

CHAPTER 2

DENSITY AND SIZE STRUCTURE OF HURRICANE-GENERATED *Acropora palmata* FRAGMENTS

2.1. - INTRODUCTION

Modern Caribbean reefs probably began to grow over Pleistocene substrate about 8,500 yeas ago (Adey, 1978). Since then, reefs have experienced different developmental phases influenced, in part, by changes in their environment. Disturbances like hurricanes have the potential to produce significant environmental changes to the shape and community assemblages of reefs. This natural and recurrent perturbation is a common event in the evolutionary history of all Caribbean coral ecological assemblages and affects coral reef structure in a variety of ways. Heavy swells and surge produced by hurricanes can dislodge, fragment and remove reef structural organisms (Glynn, et al., 1964; Woodley et al., 1981). In addition, heavy runoff associated with hurricanes can affect coral reefs through lowering salinity, high sedimentation and increasing nutrient concentrations (Johannes, 1972; Goenaga and Canals, 1979). Most organisms living in the shallow areas of the reef are more susceptible to this type of perturbation (Rogers et al., 1982; Lirman and Fong, 1996). The dynamics of these communities can be described as a shifting equilibrium between development, maintenance and a deterioration process caused by disturbances (Bak and Criens, 1981). Long-term persistence of local populations within this unstable environment can be achieved by being resistant to change or by being resilient and capable of rapidly recovering before the next disturbance (Grime and Wissel, 1997). Sexual and asexual recruitment play an important role in this recovery process (Highsmith et al., 1980; Jordán-Dahlgren, 1992).

The elkhorn coral, *Acropora palmata* is a large arborescent coral that usually forms monospecific thickets on the shallow and high-energy portions of reefs throughout the Caribbean (Goreau, 1959; Geister, 1977; Rogers, et al., 1982). This species has several adaptations that enable it to dominate and persist in this high-energy zone of the reef (Schuhmacher and Plewka, 1981). Some of those adaptations include a strong skeleton, a thick basal attachment to the substratum, and branches usually oriented parallel to the prevailing currents (Shinn; 1966; Graus et al., 1977; Schuhmacher and Plewka, 1981). However, dislodgment and fragmentation of colonies of this species following hurricanes have been widely reported (Highsmith et al., 1980; Woodley et al., 1981; Rogers et al., 1982; Fong and Lirman, 1995; Lirman and Fong, 1996, 1997; Jordán-Dahlgren and Rodríguez-Martínez, 1998; Lirman, 2000a, 2000b). After disturbance, the recovery process of a local population may take place by healing and regrowth of survivors, recruitment of hurricane-generated fragments, and by recruitment of sexually-produced planulae. Due to the apparent low recruitment success of planulae (Bak and Engel, 1979; Rylaarsdam, 1983), recruitment and growth of asexually generated fragments play a significant role in the recovery process of local populations (Lirman and Fong, 1997), and at the same time can bring an important competitive strategy to expand their territory. This ability to propagate by fragmentation is an adaptive process (Highsmith, 1982) in which fragmentation is likely to occur with some frequency related to the probability of survival of the fragments. It implies that the relationships between the growth form, growth rate, and skeletal strength of *A. palmata* could be such, that fragmentation produces new colonies of a shape or size likely to survive (Highsmith et al., 1980; Highsmith, 1982).

In September 21, 1998, Hurricane Georges passed over the island of Puerto Rico and caused extensive fragmentation of the elkhorn coral in southwestern reefs. The main goal of this study was to characterize the features of different hurricane-generated populations by determining and comparing their distribution, densities and size structure to test the hypothesis that hurricanes produces ramets of similar size and density among populations comparatively with the intensity (i.e. maximum sustained winds) of the storm.

2.2. - METHODOLOGY

2.2.1. - Study Area and Hurricane Description

Three reef areas within the La Parguera Natural Reserve coral reef system, at the southwestern coast of Puerto Rico, were selected (Figure 2.1); Media Luna Reef (N 17º 56.433 W 67° 02.345), Laurel Reef (N 17° 56.609 W 67° 03.308) and San Cristóbal Reef (N 17° 56.450 W 67° 04.659). This part of the island is characterized by a dry climate, moderate wave energy and an extensive insular shelf (approximately five miles wide (Almy and Carrión-Torres, 1963). Reefs of La Parguera Natural Reserve have a predominantly east-west orientation which roughly parallels the coast. The prevailing wind-generated waves are from the southeast, establishing unidirectional currents that flow over the reef crests and towards the back reefs. Supratidal rubble bars composed primary of storm generated *A. palmata* fragments form small islets on three reefs studied. These reefs were selected because of the high abundance of *A. palmata*, and due to their proximity (1.5 – 2.2 km) these reefs were exposed to similar hurricane effects. In September 21, 1998, Hurricane Georges, a category III hurricane with sustainable winds of up to 177 kph and maximum gusts to 208 kph, passed over the Island of Puerto Rico (Bennett and Mojica, 1999), causing significant damage to the island coast and to the exposed reefs. Hurricane Georges moved generally westward at 24 kph, from its landfall on the southeast coast until it exited the island on the southwest coast and entered the Mona Passage.

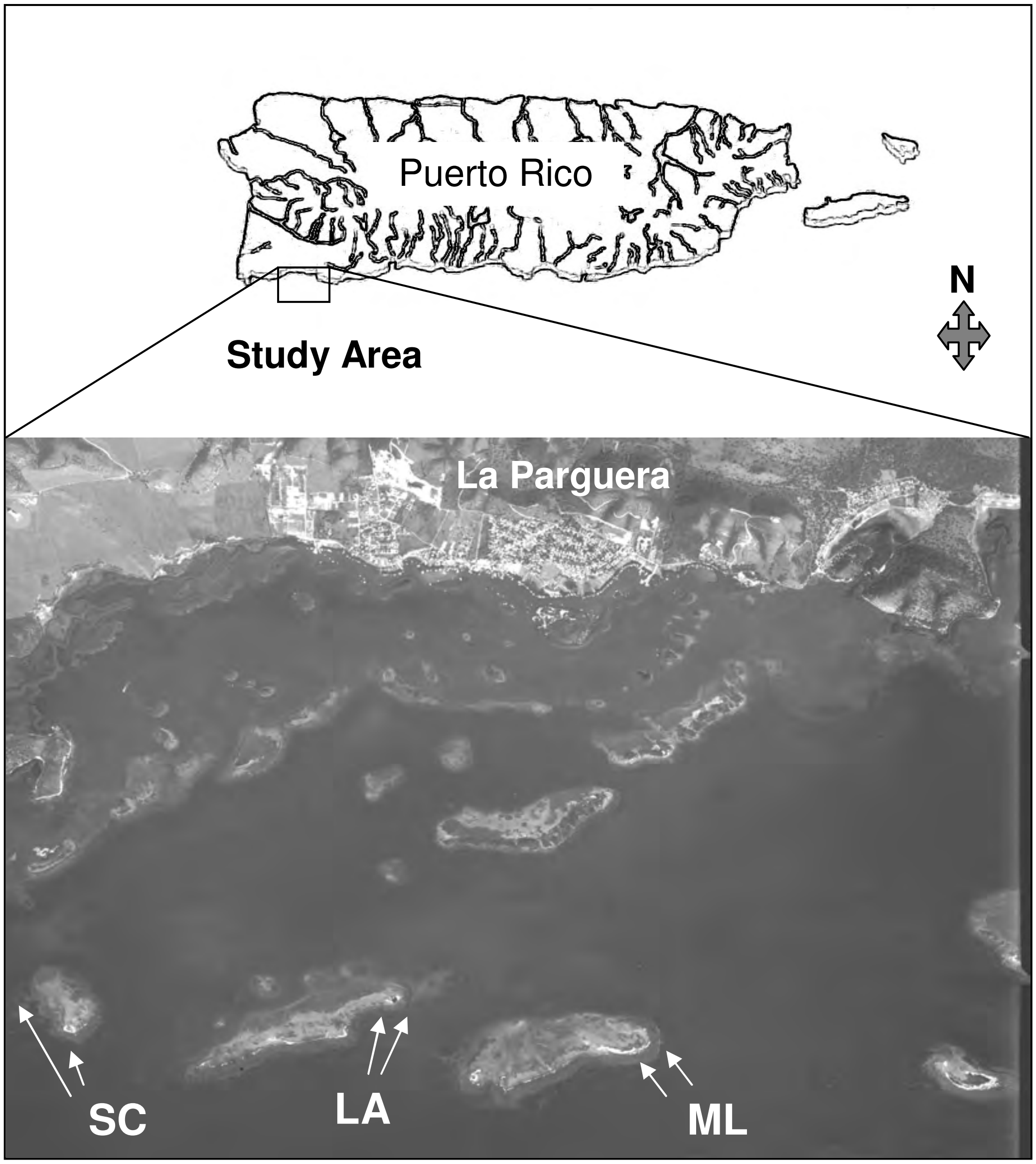

Figure 2.1. - Location of La Parguera Natural Reserve coral reef system and sampling localities. Arrows and letters indicate study sites: (ML) Media Luna Reef, (LA) Laurel Reef, and (SC) San Cristóbal Reef.

2.2.2- Field Survey

Preliminary surveys to determine damage and distribution of fragments were conducted in the three selected reefs after the storm. Permanent belt transects of 30 m long and 2 m wide (60 m^2) were established across the largest patch of live *A. palmata* in all studied reefs. Transects were permanently marked at each end with stakes. Two belt transects were marked within each study site (Figure 2.1). All fragments with living tissue found along the belt transects were counted, labeled with numbered aluminium tags and measured with a plastic metric ruler (maximun length and width of the fragment to the nearest cm). All fragments were left in the same place and position found. San Cristóbal Reef was surveyed before and after the hurricane. In the other two reefs, Laurel Reef and Media Luna Reef, transects were established and surveyed several months after the hurricane.

A line intercept transect (30 m long) bisecting the belt transect was surveyed to determine the composition of major reef substrates (fragments, standing colonies and other reef bottom substrate). The cover of fragments, standing colonies, as well as the cover of the types of reef bottom substrates (hard, rubble or sand) were estimated at a meter-intervals by calculating the fraction of the length of the line they intercepted (Loya, 1978).

2.3. - RESULTS

2.3.1. - Fragment Densities

Fragment density in San Cristóbal Reef prior to the hurricane event was 0.32 ± 0.28 fragmets/m^2 (n= 38 fragments). One month after the hurricane fragment density increased to 1.26 ± 0.31 fragments/m^2 (n=151). One year later, the density dropped to 0.90 ± 0.25 fragments/m^2 (n= 107), after the mortality of 44 fragments. Fragment density, coral cover and cover area of other types of substrates (hard, rubble and sand) were estimated in each transect using data collected a year after the disturbance (Table 2.1). The mean fragment densities observed in Media Luna Reef and Laurel Reef were 0.95 ±0.60 (n=113) and 1.25 ±0.25 fragments/m^2 (n=149), respectively. No significant difference in mean fragment densities were observed among reefs after a year ($p>0.05$; Tukey-Kramer). The overall mean density of surviving fragments after one year was 1.02 ± 0.35 fragments/m^2 (n=369). No significant relationship ($p>0.05$) was observed between fragment density and coral cover or one of the other three types of reef bottom substrates (hard, rubble or sand) in each transect. Also, no significant difference among reefs (p>0.05; ANOVA) was observed in mean percent cover of the common substrates (coral cover, hard, rubble, or sand substrates).

Table 2.1.- Density of living fragments (fragments/m^2) observed one year after Hurricane Georges (sample size = 60 m^2) and relative percent cover of three common substrates and live standing colonies, using a line intercept method (30 m long) (Loya, 1978).

Reef	**TR**	**Mean Depth (m)**	**Fragment Density (frag./m^2)**	**Percent Cover**			**% Standing colonies**
				Hard	Rubble	Sand	
Media Luna	A	3.35	0.52	45.5	29.17	5.0	12
	B	3.35	1.37	44.7	22.0	16.3	16.3
Laurel	A	1.95	1.42	25.8	28.6	9.2	16.8
	B	1.65	1.07	51.0	17.3	6.3	11.67
San Cristóbal	A	1.80	1.07	41.8	5.0	5.0	20.3
	B	3.35	0.72	44.9	19.0	2.0	16.8

2.3.2.-Fragment Size Structure and Distribution

Fragment size data (length, width and surface area) was log-transformed to adjust data to normality requirements of ANOVA. There was a significant difference in mean fragment size (length, width and surface area) among studied reefs (Table 2.2). Fragments from San Cristóbal were significantly smaller (Table 2.2) than those from the other two reefs (p<0.0001 using LS Means Adjusted for Multiple Comparisons: Tukey-Kramer). Although, overall mean of length was 40.36 ± 21.13 cm, a large proportion of fragments in the cumulative frequency were within the size interval of 20-35 cm (Figure 2.2). The size frequency distribution of fragments from San Cristóbal reef showed a typical bell shape distribution with a mode in the size interval of 25-30 cm and a slight skewness to large sizes (Figure 2.3). The other two reefs showed an irregular size frequency distributions with more than one mode. Fragments under 10 cm long were not observed (Figure 2.2-2.3).

Table 2.2.- Average values and standard deviation for length, width and surface area of hurricane-generated fragments observed in the study localities.

Size Category	Media Luna Reef (n= 111)	Laurel Reef (n= 139)	San Cristóbal Reef (n= 107)
Length ± std (cm)	45.23 ± 21.82	42.07 ± 22.98	33.08 ± 15.36***
Width ± std (cm)	17.00 ± 11.56	16.50 ± 11.27	11.10 ± 5.69***
Area ± std (cm^2)	925.14 ± 1084.76	828.01 ± 1091.27	403.21 ± 354.80***

*** Significant among reefs ($p < 0.001$, Tukey-Kramer test)

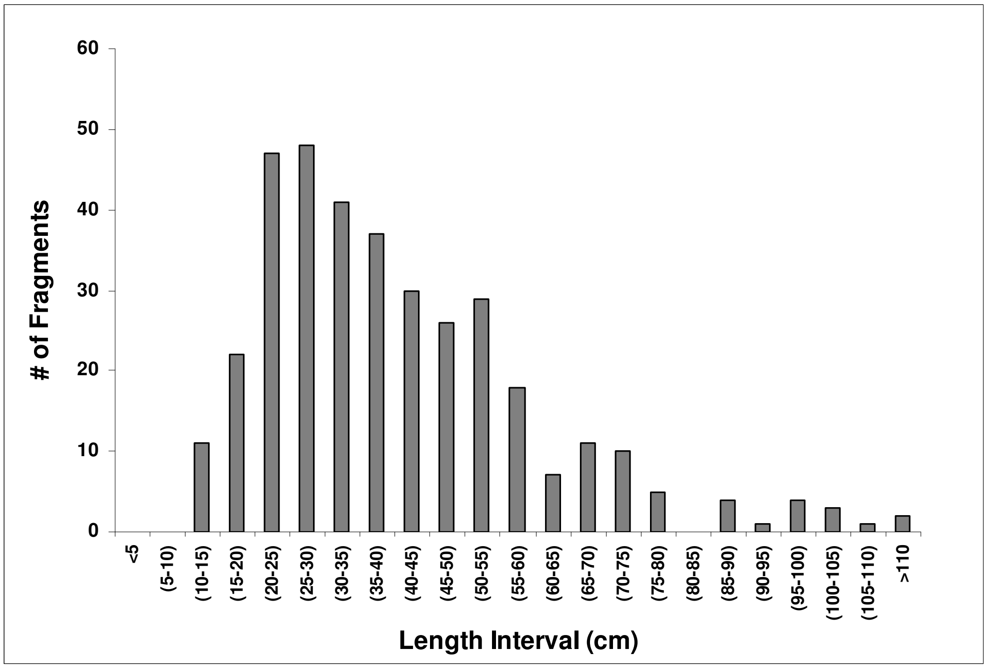

Figure 2.2. - Size frequency distributions of all fragments of *Acropora palmata* measured in all surveyed reefs (n= 357).

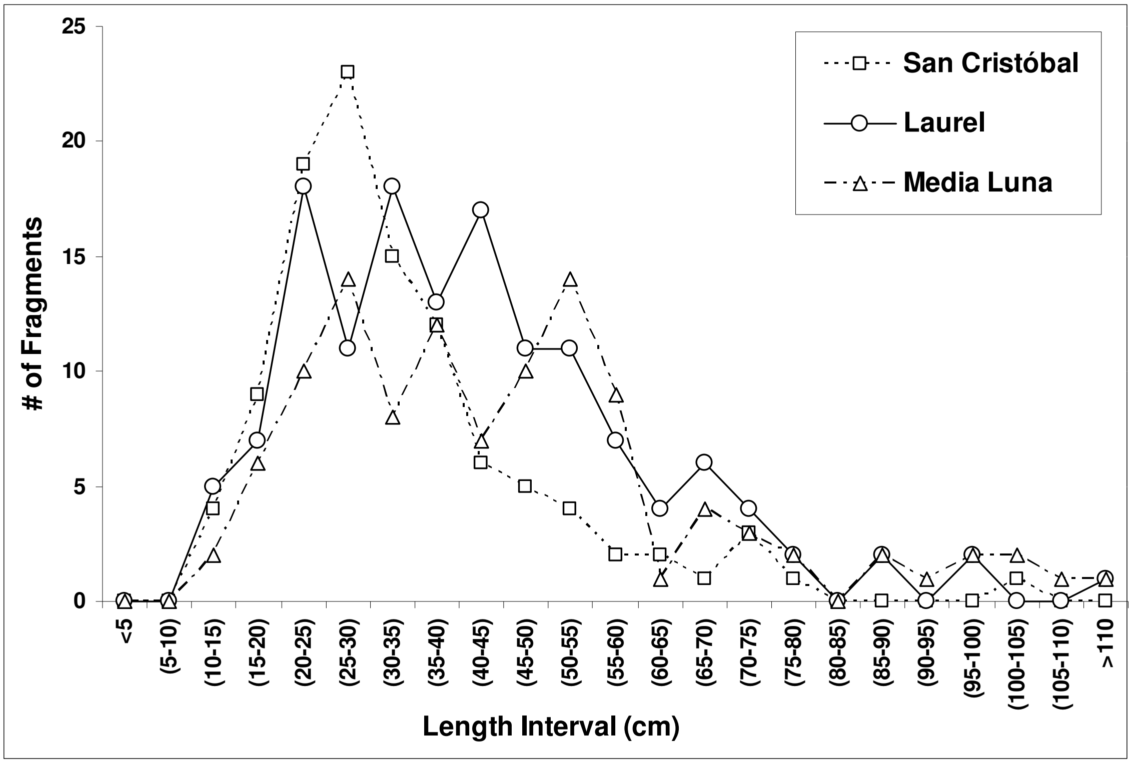

Figure 2.3. - Comparative size frequency distributions of fragments of *Acropora palmata* among the three reefs surveyed.

2.4. - **DISCUSSION**

Hurricane Georges is considered one of the most powerful hurricanes to hit Puerto Rico in many decades (Bennett and Mojica, 1999). After the hurricane, colony fragmentation, dislodgedment and colony overturned were observed everywhere, but at a higher frequency in the shallower, high-energy zones where *Acropora palmata* is one of the dominant species. The effects of the hurricane over this species in terms of average density were similar in all reefs surveyed. One possible explanation for this similarity is that the hurricane affected *Acropora* populations uniformly at the geographical scale of the present study (< 2.2 km between reefs). The assumption of similar effects at a small space-scales is not necessarily the rule. Rogers (1993) showed that the impact of Hurricane Hugo and Hurricane Andrew over local *Acropora* populations within the

Virgin Island National Park and within the Biscayne National Park, were highly variable. In both sites, significant losses of coral were reported at some reefs whereas others reef were left intact. Similar fragment densities among reefs could also be expected if reefs did not differ in the size structure or relative colony abundance of existing (before storm) populations (Jordán-Dahlgren and Rodríguez-Martínez, 1998). However, information of previous coral populations in these study areas was incomplete and inferences using information of succeeding coral populations (i.e. percent of living coral cover) would be inconsistent. For example, although reefs did not differ in percent of living coral cover after the hurricane, no relationships between coral cover and fragment densities were observed. In addition, fragment density cannot be predicted solely from wind speed. For example, high abundances of fragments (3.7-5.9 fragments/m^2) were generated after Hurricane David and Frederic, with winds gusting up to 86 km/h when passed near St. Croix (Rogers et al., 1982), while Lirman and Fong (1997) reported 4.56 fragments/m^2 after Hurricane Andrew passed over the Florida Reef Tract with maximum sustained winds of 224 km/h. This supports early findings that the effects of hurricanes over reefs cannot be predicted solely from wind speed (Rogers, 1993; Lirman and Fong, 1996). Many other factors include: the speed of hurricane movement, the magnitude and direction of the swells, the topography of the reef, and the size structure and/or relative abundance of present population when the event happens. For example, Lirman and Fong (1996) showed that a storm with lower intensity but longer duration (low speed) may cause more damage to the reef, than a more powerful, but very rapidly moving storm. A low speed storm may increase the possibility of generated fragments to be removed from the zone and prolonged the time of tumbling and shattering. Compared to hurricane Andrew (speed of 40 kph), hurricane Georges was less powerful and a slow moving storm (speed of 24 kph). Therefore, hurricane Georges might have caused less fragmentation or more fragment remotion (≈ low fragment density) in Puerto Rico reefs than Andrew did over the Florida Reef Tract.

The size of hurricane-generated fragments may also follow the same trends of fragment density. In a general sense, the size of the generated fragments may depend on both the intensity of the storm and size structure of existing (before storm) populations. Another explanation for the observed difference in the mean size of fragments across reefs could be to a high survivorship of much smaller fragments at San Cristobal Reef compared to the other reefs after 1 year. However, sampling in Laurel Reef and Media Luna Reef began between January and May 1999 (4 months after the hurricane) and no information exists regarding earlyer mortality of small fragments before sampling. Although, variable size distribution was observed among reefs, a small proportion of fragments were observed within sizes classes under 20 cm in length. This may imply a major transportation process of smaller size fragments from the main coral patch or rapid mortality. Nevertheless, this differed from the findings of Lirman and Fong (1997), who reported a higher frequency of fragments within the next three smallest size classes (5-20 cm). However, in this study, the size of generated fragments were not based on the total length of the fragments because the authors used the length of the remaining living tissue after 9 months of generated as a measure of size. Tissue mortality is usually observed in hurricane-generated fragments after several months (Ortiz-Prosper and Ruiz, 2000) and this might explain the observed reduction in the population size structure of the generated fragments reported by Lirman and Fong (1997).

Fragment distribution over the reef bottom depends on the direction and force of the hurricane-produced swells and the topography of the reef. Several fragments tagged prior to the hurricane were moved to the shallow portion of the reef platforms, more than 30m from their original place, and were aggregated with other fragments in new sites. Rogers et al. (1982) reported similar differential transportation of broken fragments into shallower water after hurricanes David and Frederic passed over St. Croix. Lirman and Fong (1996, 1997) have also shown that a large number of fragments aggregated in the shallower portion of the reef after hurricane Andrew and also after a strong winter storm (The Storm of the Century) passed over the Florida Reef Tract. If recruitment of those generated fragments occurs, it may explain in part the high aggregation pattern of this species observed within the shallow and high-energy zone of the reef. In this case, colony aggregation would depend mostly on physical phenomena and not necessarily on biological properties as expected by larvae recruitment (Bak and Engel, 1979; Jordán-Dahlgren, 1992). However, for fragmentation to be an adaptive reproductive trait in *A. palmata*, these hurricane generated-fragments have to survive, stabilize and cement themselves to the reef bottom, and grow to reproductive size, before the next major disturbance. In the absence of compounding impacts from diseases, bleaching, sedimentation, predation and other factors (i.e. pollution) between disturbances, recruitment of generated fragments may enable this species to rapidly recover from previous hurricane damage. Thus, it is important to follow the dynamics of hurricane-generated fragments (cohort of 1998) for more than a year to evaluate the importance of fragmentation as a mechanism to persist within this narrow and unstable zone of the reef.

2.5. - **CONCLUSION**

This study confirmed that fragmentation and local dispersion of *A. palmata* is a common process during hurricanes. This study rejects the hypothesis that hurricane effect (fragment size and density) can be predicted solely from wind speed. According to this and previous studies, the abundance (i.e. fragment densities), distribution over the reef bottom and probably, the size structure of the resulting fragments depend on factors such as: duration of the storm (hurricane speed), the magnitude and direction of the swells, the topography of the reef, and the size structure and/or relative abundance of present population when the event happens.

CHAPTER 3

SURVIVORSHIP OF HURRICANE-GENERATED *Acropora palmata* FRAGMENTS

3.1. - INTRODUCTION

Several studies have demonstrated that survivorship of many modular marine organisms increases with colony size (Connell, 1973; Hughes and Jackson, 1985; Hughes and Connell, 1987; Jackson, 1985; Lasker, 1990; Yoshioka, 1994; Bruckner and Bruckner, 2001). Small colonies are more susceptible to sources of mortality such as sedimention and predation than larger colonies. Nevertheless, the relationship between size and survival are not necessarily linear (Highsmith et al., 1980). A possible ¨refuge size¨ has been proposed for many colonial organisms above which colonies escape from major sources of mortality (Hughes and Jackson, 1985; Yoshioka, 1994). Therefore, it is possible that effective clonal propagation by means of coral fragmentation could be related to the size of the resulting propagules. Compared with larvae, hurricane-generated fragments are larger, which may result in higher survivorship after recruitment (Jackson, 1979) and the ability to colonize substrata not directly colonizable by larvae (Highsmith, 1982; Heyward and Collins, 1985). However, the size of asexual propagules produced by fragmentation is not ultimately an intrinsic mechanism and may depend on both, the nature of the disturbance and the size structure of the original population.

Fragmentation and local dispersion of hurricane-generated fragments have been considered an important reproductive process for *A. palmata* (Bak and Engel, 1979; Highsmith et al., 1980; Highsmith, 1982; Lirman and Fong, 1996, 1997), more often in the absence and/or low sexual reproductive capability reported in this species (Bak and Engel, 1979; Rylaarsdam, 1983).

The present study had the objective to monitor the dynamics of fragments generated after Hurricane Georges passed over Puerto Rico (September, 1998). The hypothesis that Elkhorn populations produced particular-adaptive sizes that can survive after fragmentation was further evaluated by assessing the spatial (within and among reefs) and temporal (one to three years) variability of growth and mortality rates (d_x) and the overall survivorship of the fragments. The correlation of these parameters with the initial size of the fragment was explored. A second objective was to determine how different types of substrate (hard bottom, rubble, sand, live standing coral) and condition (loose, slightly stabilized or cemented to the substrate) affect the survival rate of the fragments and their potential relationships with the initial size of the fragments.

3.2. - METHODOLOGY

This study was carried out in three reef areas within La Parguera Natural Reserve coral reef system, located at the southwestern coast of Puerto Rico: 1) Media Luna Reef, 2) Laurel Reef and 3) San Cristóbal Reef. Site map and site description were discussed in Chapter 2 (Figure 2.1). Within each reef, two belt transects of 30 m long and 30 m wide were established across the largest patch of live *A. palmata* in the shallow platform. All fragments with living tissue were counted, labeled and measured as described in Chapter 2. Additional information included: 1) maximum length and width (to the nearest cm) of the living tissue portion of each tagged fragment at three intervals of time (one month, one year and three years after Hurricane Georges), 2) the type reef substrate where the fragment landed, and 3) condition of the fragment (loose, slightly stabilized or cemented to the substrate) were recorded. Data from measurements of the live coral tissue was used to calculate tissue surface area (cm^2) (area = maximum length x width of the live tissue portion of the fragment in cm). Because the underside of most fragments were already dead (Figure 3.1), their surface area (fragment and tissue area) was estimated and compared using collected data from the upper side of the fragment.

Transects at San Cristóbal Reef were set up and surveyed in mid-August 1998 and were surveyed again to take measurements at three time intervals (one month, one year and three years) after the hurricane impact. Sampling in Laurel Reef and Media Luna Reef began between January and May 1999 (4-8 months after the hurricane). Tissue mortality and growth (defined respectively as live tissue area reduction or increase) were estimated by measuring the live tissue area (1 and 3 years after the hurricane impact) divided by the initial surface area. The fate of the hurricane-generated fragments, such as, proportion of survivorships and proportion of coral tissue loss due to partial mortality, was related to the initial size, substrate type and fragment stability conditions. Proportion of tissue mortality (**PTM**) of a fragment, defined as a percent reduction of live coral tissue area was estimated using:

$$\mathbf{PTM} = \frac{\mathbf{TA_1 - TA_2}}{\mathbf{TA_1}} \times 100$$

where $\mathbf{TA_1}$ is the live tissue area at time 1 and $\mathbf{TA_2}$ is the live tissue area at time 2.

The types of reef substrate where the fragments came to rest were categorized as hard ground (H), rubble (R), sand (S), combination of rubble and sand (RS), and over a live standing colony (OC). The conditions of all fragments that were still alive 3 years after the hurricane were classified as: (a) loose (LF), (b) those that were stabilized by their own weigh or by being trapped beneath the rubble were classified as slightly stabilized (SS), and (c) cemented to the substrate (Figure 3.1). Three modes of cementation were also identified: self-cemented to the substrate by means of coral calcification alone (CC), cemented by calcification of reef organisms such as coralline algae (AC) or cemented by both modes (CA-coral and algae).

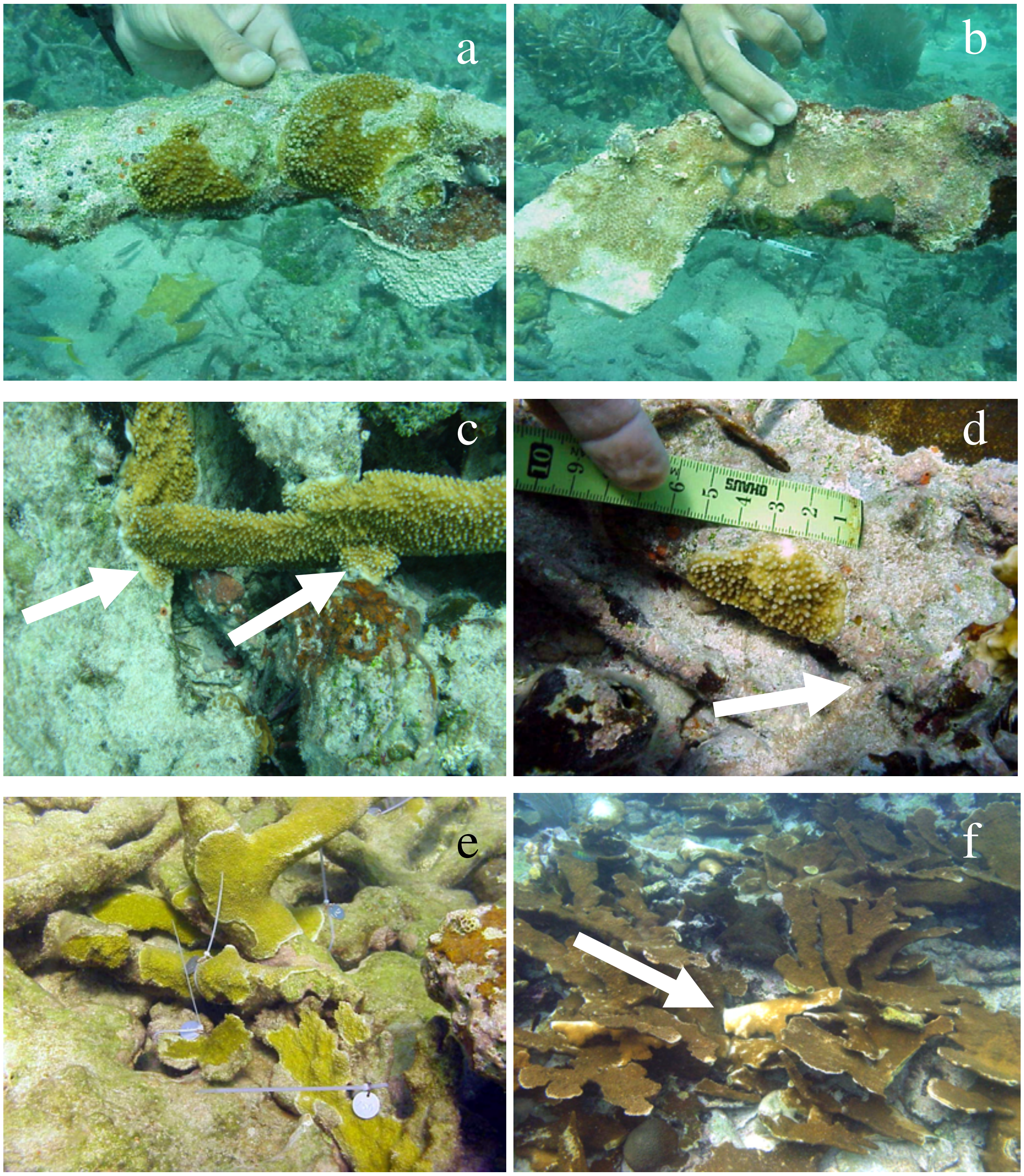

Figure 3.1. - Fragment evaluation (one-year fragment): a. upper side of the fragments with remaining coral tissue, b. underside of the fragment without living coral tissue, c. cemented to the substrate by means of coral calcification (white arrows), d. cemented to the substrate by means of coralline algae calcification (white arrow), e. fragments on rubble, f. fragment (white arrow) on live standing colony.

3.3. - RESULTS

3.3.1. - Fragment Mortality

Before Hurricane Georges, waves generated by a depression in mid-August 1998 (Tropical Storm Alex), that moved along southern of Puerto Rico, produced 38 fragments of *Acropora palmata* at San Cristóbal Reef. In October, one month after Georges, 50 % of the 24 fragments found, were dead. Some of the old fragments and new ones generated by Hurricane Georges were found aggregated 30 m away from the northwestern part of the western transect of San Cristóbal Reef (Figure 3.2). After Hurricane Georges, 151 new fragments appeared in both transects. After one year, 31.91% (n= 94) of the fragments at the western transect (SC-A) were dead, while only 24.56% (n=57) died in the eastern transect (SC-B) (Figure 3.2). Two years later, 33.33% of the remaining fragments (n=33) had died at SC-A, while only 12.50% of the remaining fragments (n=24) died at SC-B. The mean overall mortality within the first year was 28.24 ± 3.68 % and was not significant when compared with the mean mortality rate observed in the time interval of 1 to 3 years (22.92 ± 10.42 %) ($p > 0.05$, t-test); although differences in accumulative time of observations exists (1 year compared with 2 years of observations), the expected rate of mortality in the time interval of 1 - 3 years would be lower than observed (i.e. < 12 %).

The overall mean percent of mortality observed between the intervals of 1-3 years was 47.96 ± 17.71 (254 fragments). Missing fragments (n=115) may be due to missing tags, burying under the sand or rubble, displacement by surge or overgrowth by coralline algae. Assuming that all missing fragments were already dead, the overall mean mortality at the time interval of 1-3 years could increase to 66.64 ± 5.85 %. Differences in fragment survivorship were observed among reefs (Table 3.1). The observed $X^2_{(2)}$ (22.57) was significantly ($p<0.05$) than $X^2_{0.05(2)}$ (5.99). Fragment mortality at San Cristóbal Reef (22.92 ± 10.42 %) was significantly lower (ANOVA, $p< 0.05$) than Media Luna Reef (60.54 ± 6.13 %) and Laurel Reef (60.43 ± 8.43 %).

However, the mean percentage of death for Laurel Reef and Media Luna Reef seems very similar.

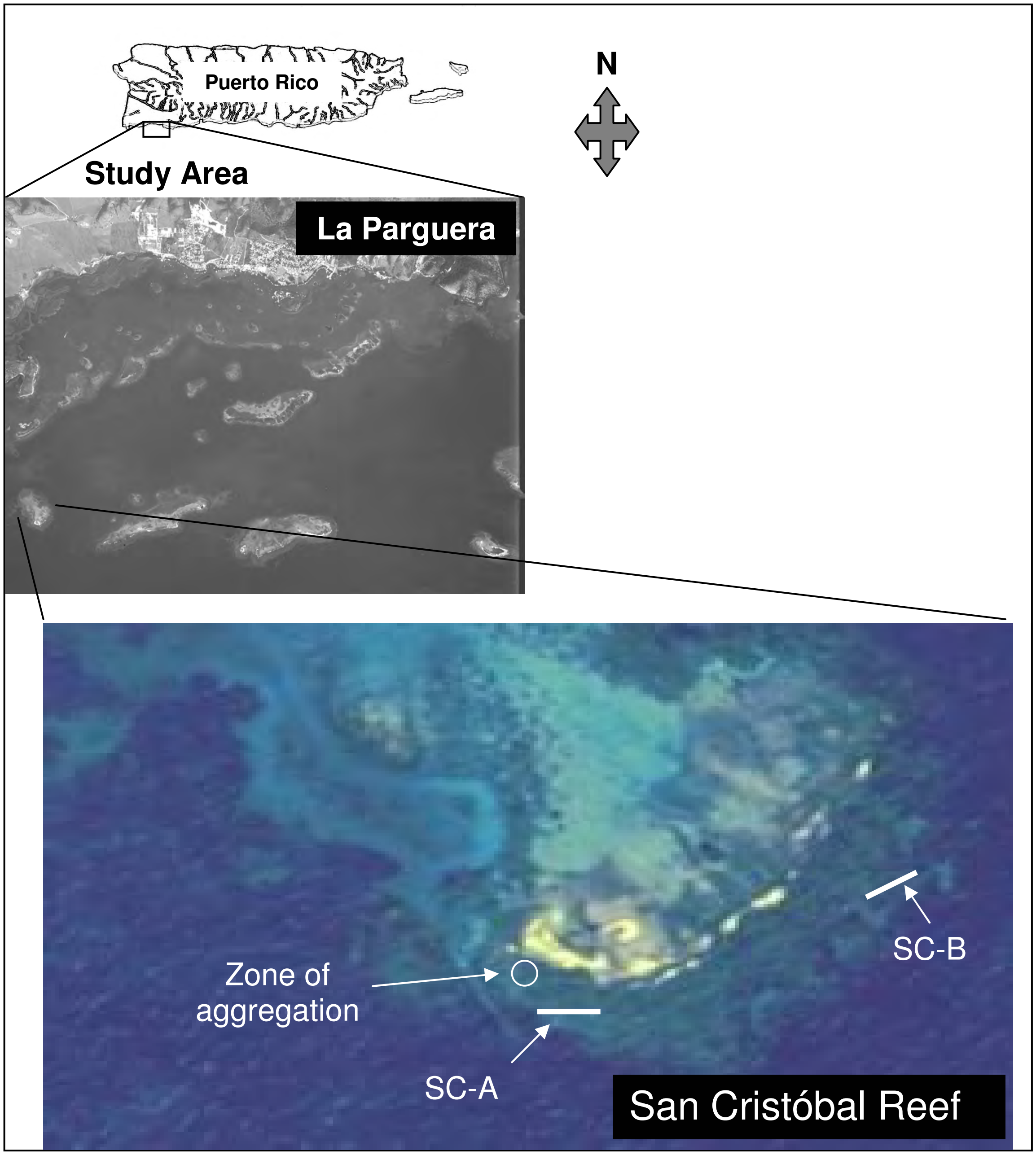

Figure 3.2.- Location of the western transect (SC-A) and eastern transect (SC-B) in San Cristóbal Reef at La Parguera Natural Reserve coral reef system. After Hurricane Georges, old and new fragments were aggregated at the northwestern part of the SC-A (white circle identified the zone of aggregation).

Table 3.1.- Observed and expected live and dead fragments at the time interval between 1 to 3 years after Hurricane Georges.

REEF	**LIVE**		**DEAD**		**TOTAL**
	Observed	**Expected**	**Observed**	**Expected**	
Media Luna	**37**	**41.3**	**49**	**44.7**	**86**
Laurel	**42**	**53.3**	**69**	**57.7**	**111**
San Cristóbal	**43**	**27.4**	**14**	**29.6**	**57**
TOTAL	**122**	**122**	**132**	**132**	**254**

3.3.2. - Partial Mortality

Tissue loss due to partial mortality was commonly observed among surviving fragments. After the first year, partial mortality was observed in more than 85 % of the fragments and no significant difference in mean percentage of fragments with partial mortality was observed across reefs ($p > 0.05$, Tukey-Kramer Test) (Figure 3.3). However, two years later, a steady decrease (toward San Cristóbal Reef) in terms of mean percentage of colonies showing partial mortality was observed. The mean percentage of colonies that showed partial mortality was significantly higher at Media Luna Reef compared to San Cristóbal Reef ($p < 0.05$, Tukey-Kramer Test). Overall, the mean percentage of colonies with partial mortality in the first year was significantly higher (85.92 ± 4.94 %) when compared with the observed in the time interval of 1 - 3 years (50.81 ± 12.53 %) ($p < 0.05$, t-test).

Mean percentage of tissue mortality (PTM) was also reef dependent (Figure 3.3). Data was arcsine transformed to meet normality requirements of the ANOVA test. A significant lower percentage of PTM was observed in San Cristóbal Reef during the first year ($p < 0.05$, Tukey-Kramer Test). The overall mean of PTM was 61.74 ± 9.97 % after the first year, which was not significantly different from the observed in the time interval of 1 - 3 years (57.56 ± 6.69 %; t-test, $p > 0.05$), although there were differences in cumulative time of observations. Therefore, the last partial mortality rate resulted from two years of observations (no observations were taken within the interval of 1 to 3 years); the expected PTM in the time interval of 1 - 2 or 2 - 3 would be lower than observed. In addition, coral fragments that died three years after the hurricane event were also those that showed a significant loss of tissue ($p<0.05$, ANOVA) during the first year (68.35 ± 25.63 %, n=113) compared with those that were still alive after the three years (56.72 ± 24.70 % of tissue lost during the first year, n=95). This reduction of live tissue over the fragment had negative effects on the size frequency distribution of the generated fragments. For example, in 1998 the peak of fragment distribution was within the interval of 200 to 400 cm^2, but one year later, most surviving colonies suffered significant and progressive partial tissue mortality causing the displacement of the fragment size distribution to the smaller size classes (Figure 3.4).

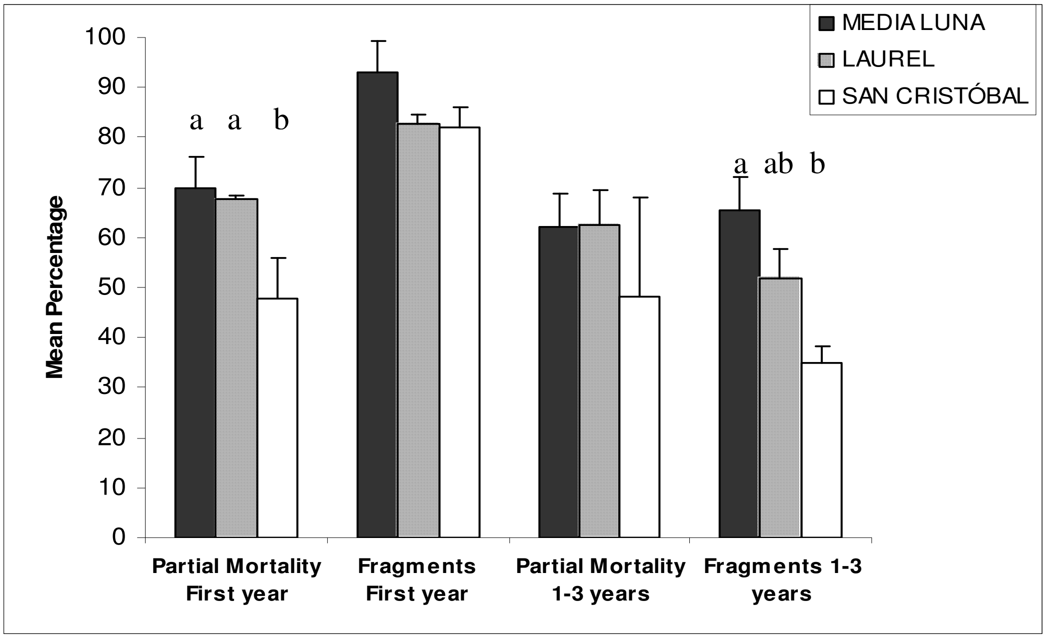

Figure 3.3.- Distribution of mean percentage partial tissue mortality per fragment, and the mean percentage of fragments observed with partial tissue mortality at two time intervals within each reef. Different letters represented significant difference between means ($p < 0.05$, Tukey-Kramer Test). A line above each bar represents one standard deviation.

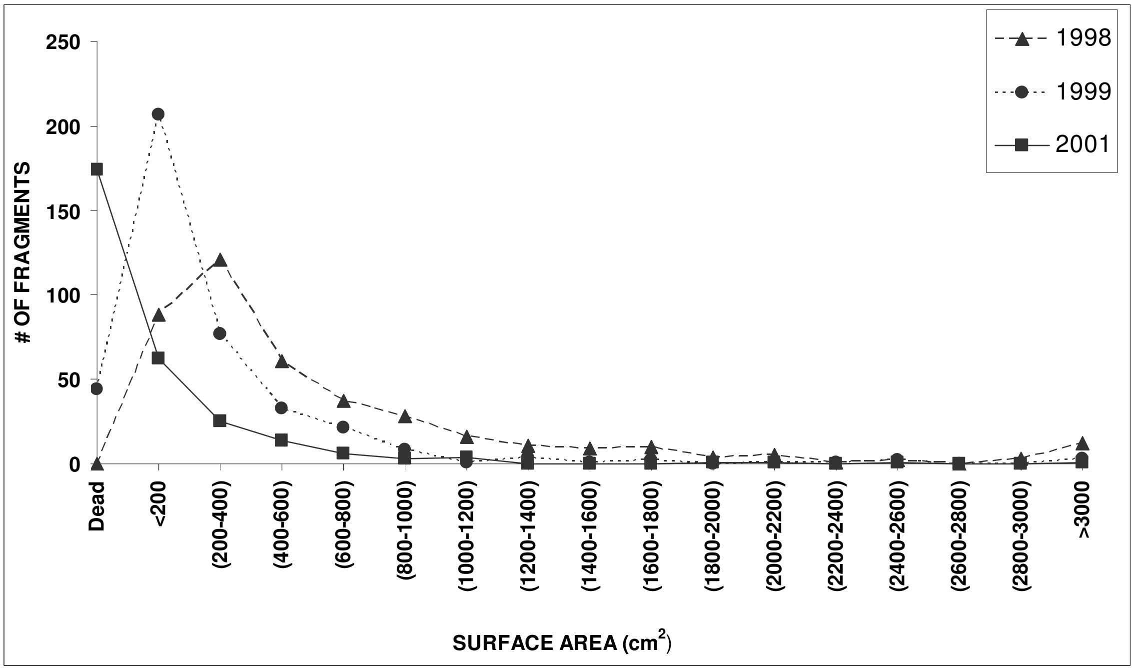

Figure 3.4. - Size frequency distributions of 401 fragments observed at three-time intervals.

3.3.3. - Tissue Growth vs. Tissue Reduction

Colony growth, defined as the increase in live coral surface area, was observed after a year in San Cristóbal Reef and after 3 years in all three reefs (Table 3.2). Within the first year, a small proportion of fragments (13 %) showed an increase of more than 128 % of their live surface area with a total amount of 1,112 cm^2 of new coral tissue gained by growth. However, this increment was overwhelmed by the large proportion of fragments (81.3 %) that showed a mean decline of more than 46.5 % of their live surface area due to partial tissue mortality. The total amount of lost tissue (16,854 cm^2) was 14 times larger when compared to the amount gained by growth. In addition, the mean surface area of lost tissue by fragments was significantly higher ($p < 0.05$, t-test) compared with the mean surface area gained by coral growth. During the time interval of 1 to 3 years, the mean surface area lost by partial tissue mortality was also significantly higher when compared with the mean surface area gained by colony growth

($p < 0.05$, t-test). However, the total amount of lost tissue was only two times higher than the amount of tissue gained by growth.

Table 3.2. - Overall results of coral increase (growth) or decrease (partial tissue mortality) of the surviving fragments at each time interval. Separate data from San Cristóbal Reef was also included.

Category	Time Interval (years)	Increase (n)	Decrease (n)	Probability
% Fragments	0-1	13.08 (14)[a]	81.31 (87)[a]	n/a
	1-3	39.84 (49)	49.59 (61)	n/a
	0-3	20.33 (25)	71.54 (85)	n/a
Mean Surface Area (cm^2/fragment)	0-1	79.47 ± 112.50 (14)[a]	193.73 ± 212.78 (87)[a]	*
	1-3	218.59 ± 229.24 (49)	369.68 ± 572.56 (61)	*
	0-3	185.88 ± 190.14 (25)	730.37 ± 899.57 (85)	*
Total amount of Surface Area (cm^2)	0-1	1,112.0 (14)[a]	16,854.8[a]	n/a
	1-3	10,711.0 (49)	22,550.5 (61)	n/a
	0-3	4,647.0 (25)	64,272.5 (85)	n/a
Mean % of Surface Area	0-1	128.54 ± 28.25 (14)[a]	46.49 ± 28.14 (87)[a]	*
	1-3	329.41 ± 419.67 (49)	59.11 ±28.74 (61)	*
	0-3	158.60 ± 69.05 (25)	70.52 ± 25.79 (85)	*

[a] Data from San Cristóbal Reef only.
n/a- not applied.
* Significant (t- test, $p < 0.05$).

3.3.4.-Reef Substrate Types

Rubble was the major constituent of the reef bottom substrate (59.95 ± 8.99 %) where the fragments came to rest, while hard substrate (24.65 ± 9.06 %) and sand (8.58 ± 2.47 %) were the second and third major constituents respectively. Despite the variability of relative percentage observed across reefs, the relative proportions of major substrate types, such as rubble, hard and sand were constant accross reefs (Figure 3.5).

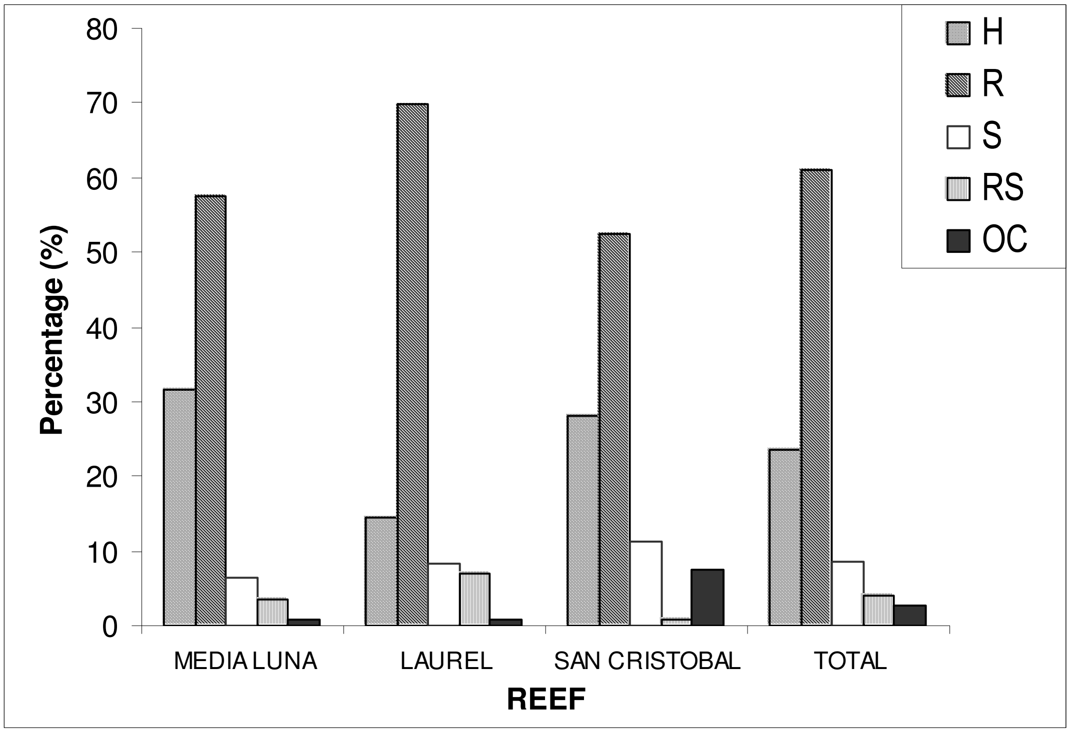

Figure 3.5. - Relative percentage of fragments that landed over the different reef substrates types (H- consolidated hard ground, R- rubble, S- sand, RS- combination of rubble and sand, and OC- over live standing colony).

3.3.5. - Fragment Conditions

After 3 years, loose fragments were significantly ($p<0.05$, Tukey) more abundant than the other conditions (Figure 3.6). Only 48.43 % (CL= 41.85 – 54.20 %) of the total fragments (n= 254) were cemented to the reef bottom three years after the hurricane. The major mode of cementation was by means of coralline algae calcification (average= 29.92 %, CL= 24.54 – 35.93 %). Coral self-attachment represents only a minor proportion with only 6.30 % (CL= 3.51 - 9.58 %) and the combination of both modes of cementation in the same fragments (coral and algae) played also a minor role with 4.33 % (CL= 2.02 – 5.34%) of the total remaining fragments (n=254). Large and heavy fragments and those beneath the rubble (slightly stablized), represented 11.02 % (CL= 7.53 – 15.42 %) of the total fragments. Coral self-attachment and the combination of coral and algae were more common in San Cristóbal Reef than in Laurel Reef or Media Luna Reef.

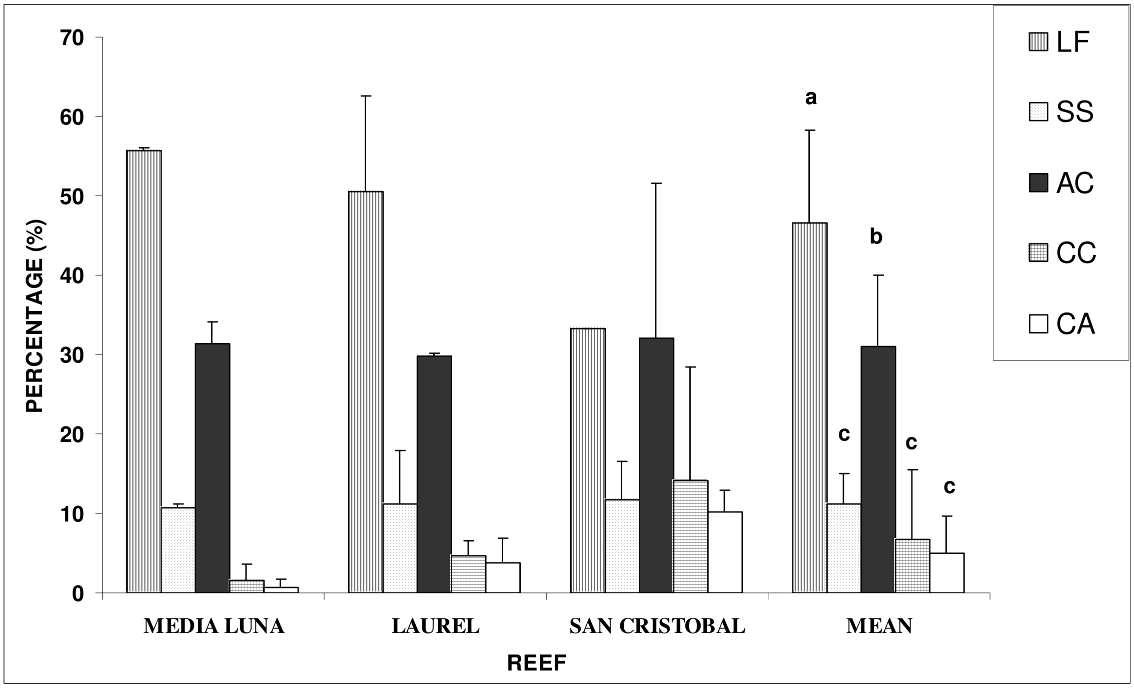

Figure 3.6. - Mean percentage distribution of different fragment conditions within and across reefs. Fragment conditions were categorized as LF- loose fragment, SS- slightly stabilized by their weigh or by being beneath rubble, CC- cemented to the substrate by means of coral calcification alone, AC- cemented by calcification of coralline algae and CA-cemented by both modes. Different letters on top of each bar ($p < 0.05$, Tukey) represented significant differences between conditions. A line above the bar represents one standard deviation.

3.3.6. - Factors Related to Survivorship

3.3.6.1. - Effects of Fragment Size

Fragments that died within the first year and between the intervals of 1 to 3 years were significantly smaller than those that survived at each time interval (Table 3.3). In addition, there was a significant relationship (Regression, $p < 0.01$) between initial fragment size and survivorship at San Cristóbal Reef within the first year (Figure 3.7). The same significant relationships were observed when we compared the proportion of fragment survival in terms of branch length (Figure 3.8) or surface area (Figure 3.9) within the time interval of 1 to 3 years. These results support the hypothesis that fragments survivorship is size-related. However, as observed in Figure 3.8, the logarithmic regression curve better described the relationship between size and survivorships than the straight linear regression. This indicates that total fragment mortality happened in those below a size threshold of 20 cm length or 200 cm^2 of surface area. Contrary to total mortality, the amount of tissue lost by partial mortality, at two time intervals (Figure 3.10-3.11), was not related with the initial size of the fragment (Regression, $p>0.05$). The length of the fragments alone explains less than 25 % of the coral tissue mortality observed ($r^2= 0.2385$).

Table 3.3. - Mean size comparisons between surviving and dead fragments at different time intervals. Comparisons (dead vs. living fragments) were made within each size category (length, width or surface area) and time interval.

Size Category	Time Interval (years)	Live Fragments	Dead Fragments	Probability
Fragment Length (cm)	1[a]	33.08 ± 15.36 (n= 107)	24.57 ± 14.17 (n= 44)	*
	1-3[b]	44.90 ± 25.04 (n= 119)	36.81 ± 18.17 (n= 131)	*
Fragment Width (cm)	1[a]	11.10 ± 5.69 (n= 107)	8.27 ± 5.45 (n= 44)	*
	1-3[b]	16.22 ± 11.35 (n= 119)	13.56 ± 9.01 (n= 131)	*
Fragment Surface Area (cm^2)	1[a]	403.21 ± 354.80 (n= 107)	231.59 ± 296.55 (n= 44)	*
	1-3[b]	856.23 ± 985.77 (n= 119)	610.88 ± 805.20 (n= 131)	*

[a] Only at San Cristóbal
[b] All reefs
[*] Significant (t-test, $p< 0.025$)

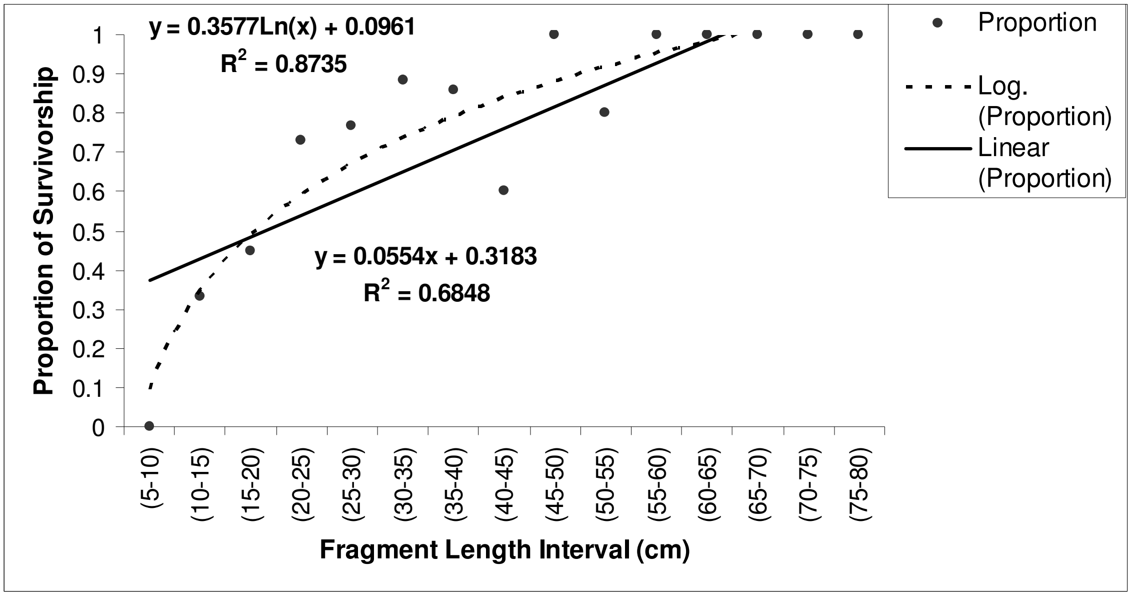

Figure 3.7. - Relationship between initial fragment size of *Acropora palmata* and proportion of fragments that survived the first year at San Cristóbal Reef (n= 151).

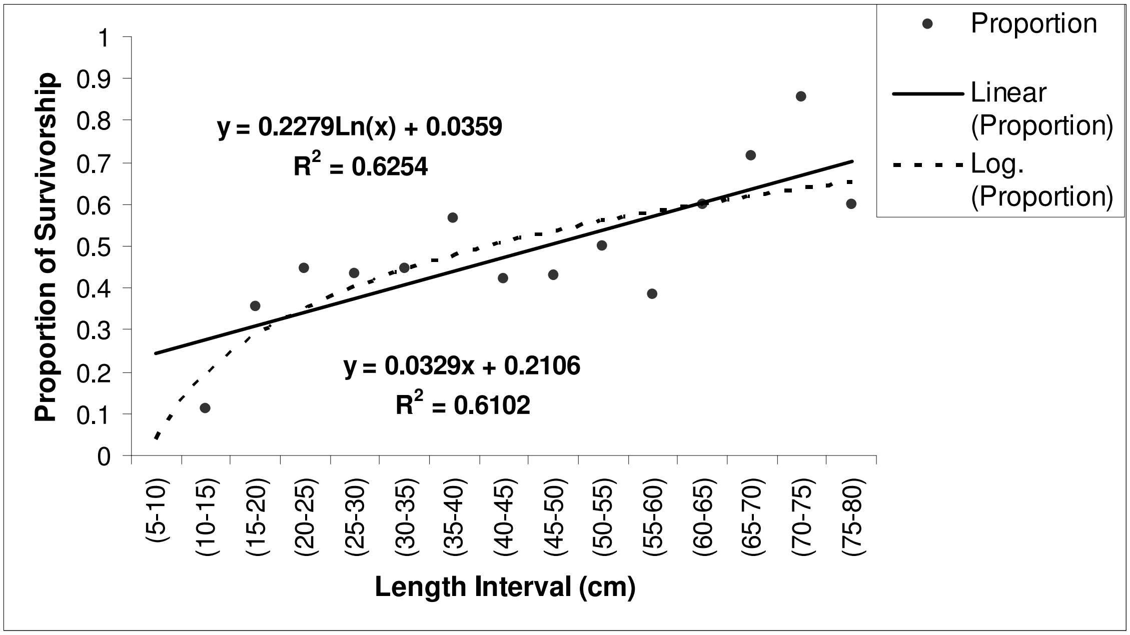

Figure 3.8. - Relationship between the initial fragment size of *Acropora palmata* and the proportion of fragments that survived between the time interval of 1 to 3 years. Only fragments with a single branch were used (n= 242).

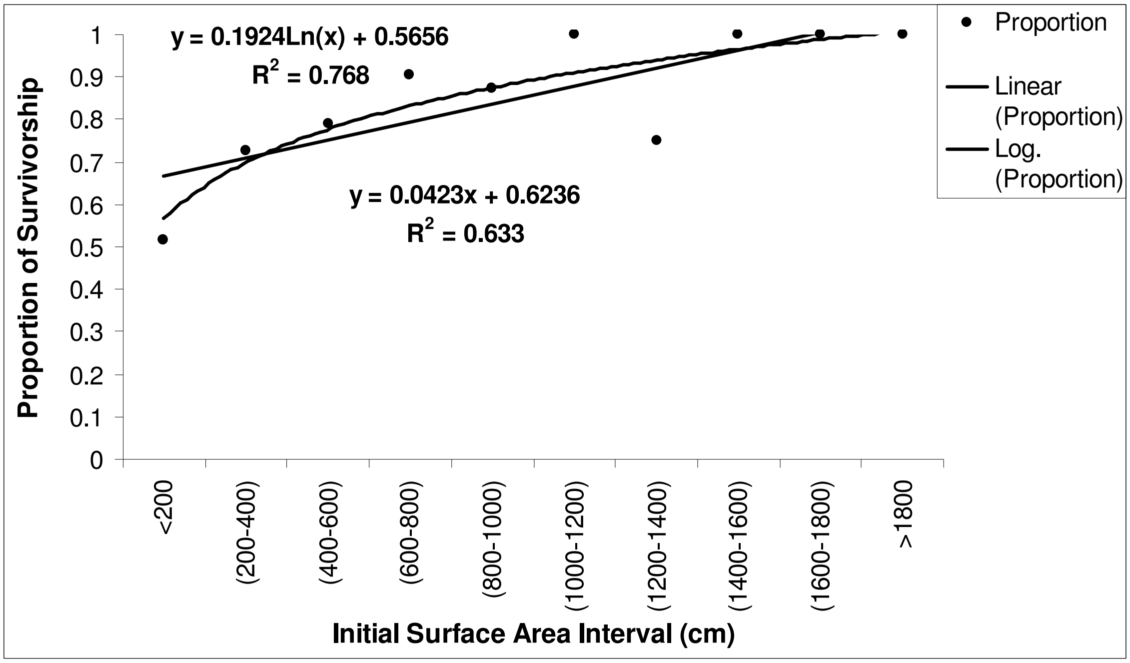

Figure 3.9. - Relationship between the initial fragment surface area of *Acropora palmata* fragments and the proportion of fragments that survived between the intervals of 1 to 3 years (n=359).

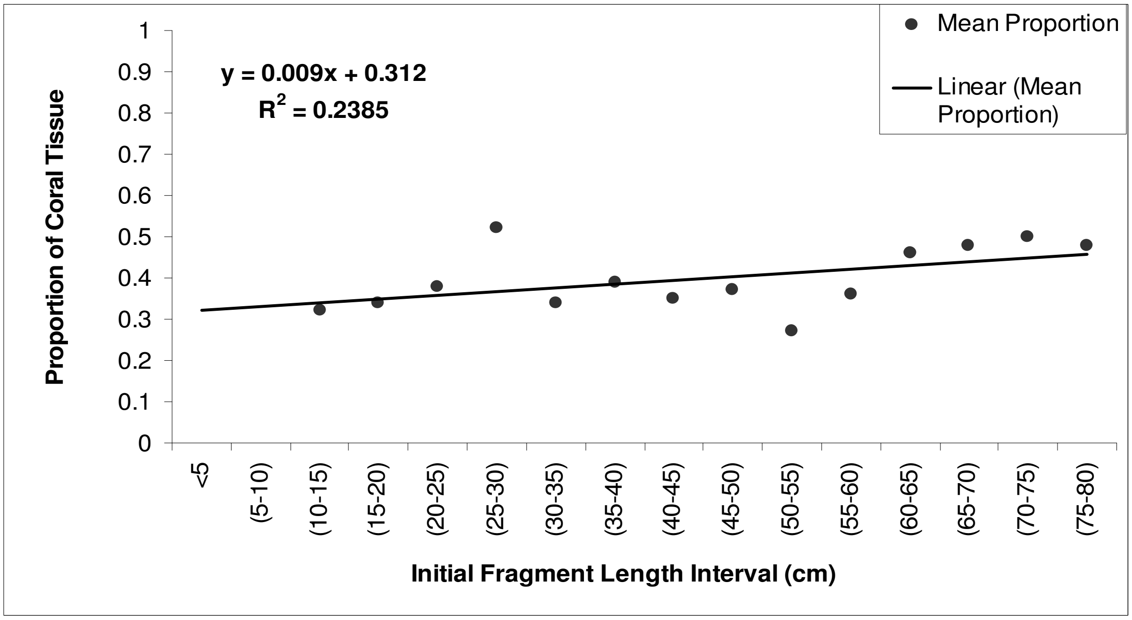

Figure 3.10. - Mean proportion of surviving coral tissue (final surface area / initial surface area) at different size intervals (initial length). Only surviving fragments with a single branch that showed partial mortality after the first year were considered (n= 314).

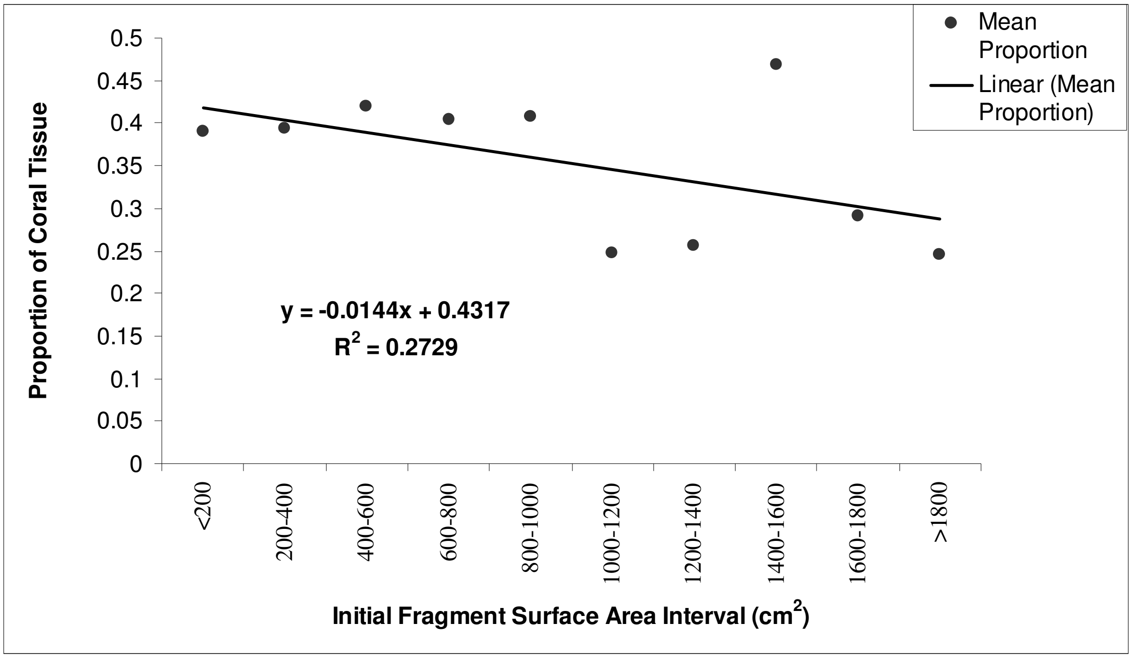

Figure 3.11. - Mean proportion of surviving coral tissue (final surface area / initial surface area) in different fragment size (initial surface area) intervals. Only fragments that showed tissue mortality the first year after the hurricane, were included (n= 314).

3.3.6.2. - Effects of Reef Substrates

During the first year, different substrates had a moderate effect on the survival rate of the fragments (Figure 3.12). Fragments that landed over standing colonies, sand or rubble/sand substrates showed a lower (not significant) survivorship than those that landed over hard or rubble substrate. This unexpected high survivorship on sand could be due to the small number of fragments observed over this type of substrate (n=9) and by the short time of observation (one year). In addition, fragments that survived the first year did not show significant differences ($p > 0.05$, Tukey test) in mean percentage of PTM across different reef substrates (Table 3.4). However, when comparing the survival of all fragments from all reefs within the interval of 1-3 years, fragments that landed over sand showed a significantly lower survivorship ($p < 0.05$, ANOVA) than those that landed over hard substrates or over standing live colonies (Figure 3.12 and Table 3.4). Although, the mean percent of survivorship over sand was the lowest one, it was not significantly different from rubble or rubble/sand substrates within this interval of time.

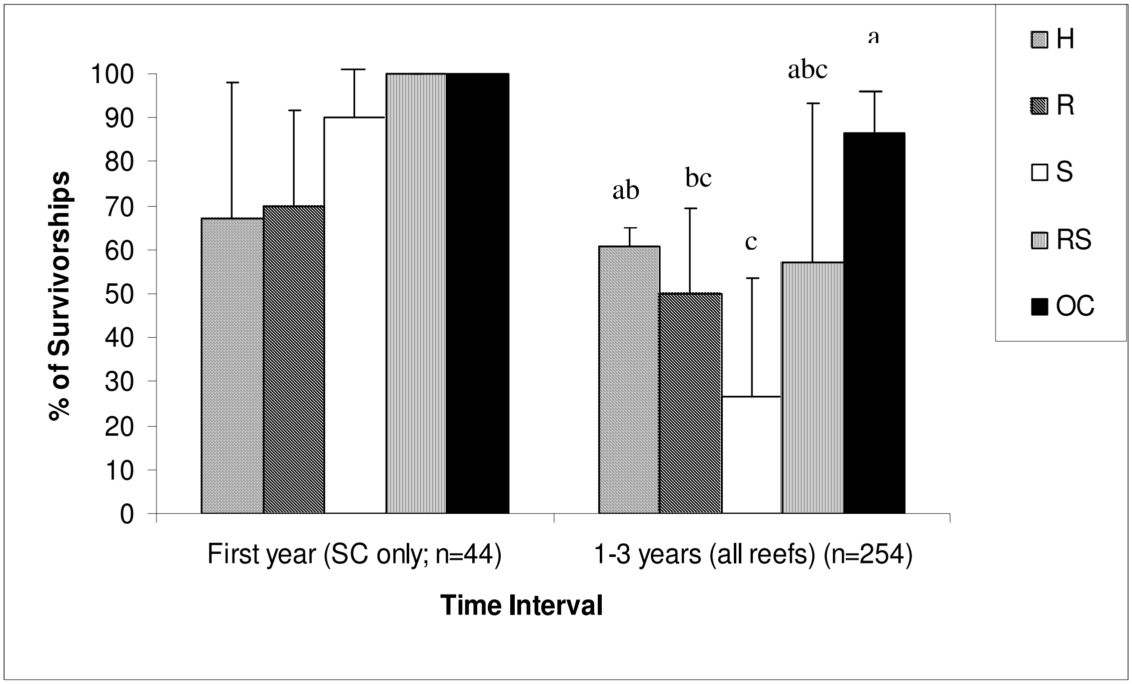

Figure 3.12.- Mean percentage of fragment survivorship observed over different reef substrate types (H- consolidated hard ground, R- rubble, S- sand, RS- combination of rubble and sand, and OC- over live standing colony) at two time intervals. Significant differences between substrates were represented by different letter on top of each bar ($p< 0.05$, Tukey). A line above each bar represents one standard deviation.

Table 3.4. Mean percentage of tissue loss (PTM) by partial mortality of *A. palmata* fragments observed over different reef substrates during the first year.

Substrate	**n**[1]	**Mean Tissue Lost ± S.E.**
Hard	41	61.66 ± 23.88
Rubble	132	65.73 ± 25.68
Sand	19	46.98 ± 29.11
Rubble/Sand	12	67.93 ± 22.82
Over colony	4	50.19 ± 16.83

[1] Only fragments that showed tissue mortality were considered.

3.3.6.3. - Effects of the Conditions of the Fragment

Fragment condition played a minor role in their survivorship (Figure 3.13). No significant differences ($p > 0.05$, ANOVA) were observed between mean survivorship of loose fragments, slightly-stablized fragments and the combinations of all cementation processes (algae, coral, algae & coral cementation). On the other hand, when comparing the mean percentage of tissue loss due to partial mortality, fragments attached to the substrate by coral and algae cementation showed a significantly lower tissue mortality rate ($p < 0.05$; Tukey) (Table 3.5).

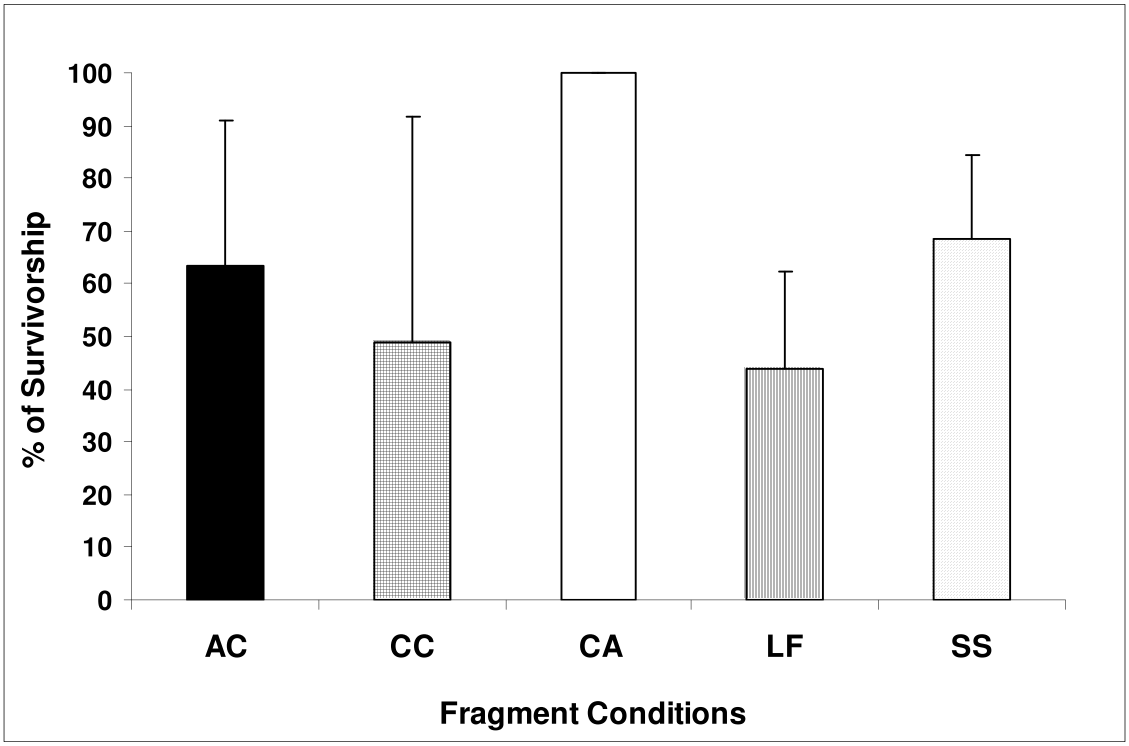

Figure 3.13. - Percentage of fragment survival in different conditions. Fragment conditions were categorized as LF- loose fragment, SS- slightly stablized by their weigh or by being beneath rubble, CC- cemented to the substrate by means of coral calcification alone, AC- cemented by calcification of coralline algae and CA-cemented by both modes. A line above each bar represents one standard deviation.

Table 3.5. - Mean percentage of tissue loss by partial mortality of *A. palmata* fragments of different conditions during the first year.

Conditions	**n**	**Mean Tissue Lost ± S.E.**	**Tukey** [1]
Loose	101	61.97 (26.05)	a
Semi-stable	23	60.60 (26.54)	a
Cemented by algal calcification	67	69.66 (24.86)	a
Cemented by coral self-calcification	10	54.68 (16.27)	ab
Cemented by coral and algal calcification	7	35.19 (18.52)	b

[1] Significant differences ($p<0.05$) between conditions were represented by a different letter.

3.3.6.4. - Other factors

Other factors such as predation, disease and overtopping by other reef organisms were observed to contribute to total or tissue mortality of the fragments. For example, 18 out of 24 fragments (75 %) infected with the boring sponge *Cliona tenuis* (Zea and Weil, 2003) were dead within 2 years. Five other fragments (1.4%) showed signs of predation by the corallivorous snail *Corallophila abbreviata*. Total cover or overgrowth by the green calcareous algae, *Halimeda* sp., was the cause of dead of other nine fragments (2.5%). In addition, tissue mortality due to ¨Patchy Necrosis¨ was observed several times during this study. In mid-November 2001, an extreme calm weather and doldrum oceanographic conditions for approximately 15 days, characterized the occurrence of this epizootic (see Weil and Ruiz, 2003; Weil et al., 2003). However, only one of nine fragments (11%) at Media Luna Reef (the only reef surveyed in this time) died due to this syndrome. None of surviving fragments (8 fragments) showed tissue regeneration, six month after the partial mortality event. Presence of fish feces over many colonies could be a causal factor of the mortality of underside tissue (Figure 3.14). However, this was not further studied.

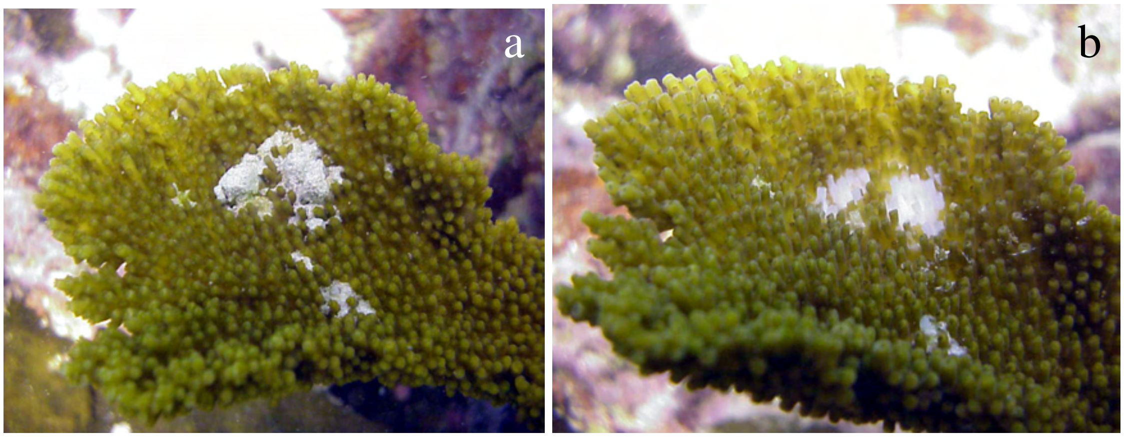

Figure 3.14. - Fish feces over a branch of *Acropora palmata* during the patchy necrosis event in mid-November 2001 (a). White spots without coral tissue after feces were removed (b).

3.4. - DISCUSSION

Fragmentation in *Acropora palmata* is an common process that can occur throughout the year due to its branching growth form and the environmental conditions prevalent in the shallow high energy zone where this species lives. Fragments generated by normal swells tend to recruit near parents, which contributes to the strength and complexity of their stands (Highsmith, 1982). However, disturbances like hurricanes can generate and disperse fragments farther away, mostly shoreward (Highsmith, et al., 1980; Rogers et al., 1982). The transportation and accumulation of *Acropora* fragments to the upper few meters of the reef has contributed to the formation of boulder ramparts in many reefs (Macintyre and Glynn, 1976; Armstrong, 1981), including the formation of many reef-associated islands observed in Puerto Rico (Glynn et al., 1964; Goenaga, 1991). Thus, the observed aggregation of fragments after Hurricane Georges contributed to the formation of new *Acropora* stands on shallow reefs zones close to the shoreline, as observed in many other places through the Caribbean (Highsmith et al., 1980; Rogers et al., 1982; Lirman and Fong, 1996, 1997; Lirman, 2000a). In addition, if most of the fragments die, their accumulation would contribute to reef growth or it may provide settlement sites for diverse coral larvae (Stoddart, 1974; Highsmith et al., 1980), crustose algae, other sessile invertebrate or recruitment of future fragments (Lirman and Fong, 1997; Lirman, 2000a).

After a hurricane event, newly generated fragments may comprise a large proportion of genetically different ramets (Highsmith et al., 1980; Highsmith, 1982; Rogers et al., 1982) and cover a large area of the reef substrate (Lirman and Fong, 1997). Although fragment cover was low in this study, recruitment of those fragments could be an important mechanism to restore a population following a disturbance as well as to increase a local population and colonize new areas. However, survival of hurricane generated-fragments is not guaranteed and may depend on many factors such as: the substrate where fragments land (Lirman and Fong, 1997; Lirman, 2000a), rate of stabilization or fusion to the substrate (Highsmith, 1982; Rogers et al., 1982; Lirman, 2000a), initial fragment size (Highsmith et al., 1980; Knowlton et al., 1981) and other ecologically-related factors such as disease, predation and competition with other reef organisms (Knowlton et al., 1981; Rogers et al., 1982; Bruckner and Bruckner, 2001). Three evident trends were observed in this study: 1) a significant spatial variability in fragment survival, 2) a size-specific mortality relationship and 3) a delayed effect of the substrate where the fragments land.

San Cristóbal Reef was the most western and remote of the three reefs studied. Although water quality was not studied, by inference this reef may be less influenced by direct human impact than the other reefs. Within this reef, the two *Acropora* species, and their hybrid, coexist in large numbers (Weil et al., 2003). These high abundances and the high genetic diversity observed in *A. cervicornis* from this reef (Vollmer and Palumbi, 2002), may indicate suitable conditions for the genus. This in part may explain the high survivorship of fragments observed in this reef, including the survival of much smaller fragments compared to the other reefs after 1 year. The other two reefs (Media Luna Reef and Laurel Reef) are closer together and near the town of La Parguera, they may be more affected by direct human impact (i.e. siltation, pollution and over-fishing).

Curiously, Bowden-Kerby (2001) reported high nitrified water conditions above the threshold level (1.00 µM/L total dissolve nitrogen) for coral growth (Marubini and Daves, 1996) in Media Luna Reef (1.70 µM/L) and Laurel Reef (1.05 µM/L), but not in San Cristóbal Reef (0.24 µM/L). Therefore, the high mortality rate observed in Media Luna Reef and Laurel Reef and their similarity in terms of the size structure of fragments (Chapter 2), indicates similar responses of fragment populations in both reefs. Thus, this suggests that local environments or ecological regimes that characterize each study site may influence the fate of generated fragments. Experimental transplantation of *A. cervicornis* and *A. prolifera* fragments within La Parguera has also showed that mortality and growth was site dependent (Bowden-Kerby, 2001).

Another trend observed was a positive relationship between fragment size and survivorship. The present study supports the hypothesis that fragment survivorship of *A. palmata* is size-related (Highsmith et al., 1980; Rogers et al., 1982; Bruckner and Bruckner, 2001). In contrast, Lirman and Fong (1997) and Lirman (2000a) did not observe any relationship between size and survivorship, possibly because of the majority of the fragments and the sample sizes (< 50 fragments) were relativately small. In this study, small fragments were less able to survive than large fragments. However, the fact that the relationship between size and survivorships was better described by a logarithmic curve suggested a possible threshold size (i.e. 20-25 cm length) above which fragments is less likely to die during the first year. Curiously, Mester and Bak (1995) proposed a decrease in capability of tissue regeneration for fragments longer than 25 cm from the distal end of the branch as a mechanism to promote the fragmentation of branches with a length sufficient to ensure high survivorship. This has profound implications for the persistence of this species within the high-energy zone of the reef where it lives. In the present study, more than 90 % of the hurricane generated-fragments measured were above this threshold size (Mester and Bak, 1995), which suggested high survivorship of fragments, at least in the first year. Considering the assumption proposed by Highsmith et al. (1980), the production of fragments of a size likely to survive can be related to the frequency of hurricanes that the coral population experiences. For example, if the mean growth rate of *A. palmata* branches is 6.8 cm per year (Shinn, 1966; Bak, 1976; Gladfelter et al., 1978; García et al., 1996; Lirman, 2000a), then local colonies are producing branches that can reach more than 75 % survival size (30.6 cm, Figure 3.6) in a period of approximately 4.5 years, the average hurricane frequency observed at Puerto Rico (Salivia, 1972; Goenaga, 1991). However, 6.5 cm/year is a low rate of linear growth for *A. palmata*. It can grow up to 12-16 cm/year.

Long-term survivorship of new asexual propagules may still be affected by their size. For example, a short time after landing, all fragments lost their underside tissue and most of them (85 %) had lost more than 60 % of their upper tissue area due to tissue mortality. The estimated overall tissue lost during the first year was 80 % and fragments continued to lose tissue over time, even though at a slower rate. The effect of this partial mortality was to reduce the living size of fragments and reduce their survival and potential for sexual reproduction. Consequently, fragmentation, the common strategy for this species local propagation, could fail to maintain or increase populations if the resulting propagules suffer extensive tissue mortality. In this study, colonies that suffered substantial tissue mortality within the first year eventually died. Delayed tissue and colony mortality was also observed in *A. cervicornis* on a Jamaican reef damaged by Hurricane Allen (Knowlton et al., 1981). In this study the length of the longest living branches was an important factor at early stages while causes of late mortality (2 to 4 months after disturbance) were attributed to post hurricane increase of predators (i.e. snail *Coralliophila abbreviata*) and susceptibility to disease. Both factors have been previously documented to produce mortality in *A. palmata* (Bak and Criens, 1981; Bruckner and Bruckner, 2001; Weil et al., 2003), as well as in the present study. However, to what extent those mortality factors are decreasing survivorship by reducing the size of the fragment remains an open question, and it may be related to the recent decline of the species.

While initial fragment size is an important factor controlling early survival, other factors such as the type of substrate where the fragment landed after the storm may influence late survival and future stability of the new asexual recruits. As reported in previous studies (Lirman and Fong, 1997; Lirman, 2000a), fragments that landed on top of live *A. palmata* colonies showed the highest survivorship compared with those that landed on sand, which showed the lowest survivorship. Fragments that landed over hard ground or rubble substrate showed intermediate survivorship. However, contrary to Lirman (2000a), the type of substratum had minor effect on the percentage of tissue retention as well as no effect in early survivorship of the colonies. In addition, not all fragments that landed on top of living standing colonies fused to the underlying tissue and no differential survivorship was observed between fragments on hard bottom and rubble. Nevertheles, substratum may still be an important factor for the stability and permanence of the colony. For example, for a long-term survivorship of a new recruit on this high-energy zone, a fragment must stabilize itself over the substrate by cementation prior to the next disturbance (Lirman and Fong, 1997). Removal of previously generated fragments has been observed in this study and elsewhere in the Caribbean (Knowlton et al., 1981; Highsmith, 1982; Rogers et al., 1982; Lirman and Fong, 1996; 1997; Lirman, 2000a; Bruckner and Bruckner, 2001) which means that fragment cementation is important before the next disturbance. Three years after Hurricane Georges, only 40 % of the surviving fragments (n= 131) were cemented to the reef. This may imply that three years may be not enough time to ensure attachment before the next disturbance. However, due to continuing loss of tissue by partial mortality, mostly at the underside and edge zone in contact with the substrate, fragments are not able to cement to the substrate by means of coral calcification. The allocation of energy towards cementation to the bottom before growth reported by Lirman and Fong (1997) and Lirman (2000b) was not commonly observed in the present study. Only a small number of studied fragments developed growing lips (yellow-pale tissue with small number of polyps) toward the substrate before new growth appear. Consequently, fragment stability depended on other biological processes, like colonization by coralline algae to attach to the reef. This may highlight another contribution of coralline algae for the recruitment of both, sexual and asexual propagules of *A. palmata*. For example, a chemical morphogen, a sulfated polysaccharide of the calcified cell walls of several tropical crustose red algae have been identified to induce settlement of coral larvae from major reef building corals (Morse et al., 1996), including *A. palmata* (Morse et al., 2000). Therefore, as coralline algae are common inhabitants of the shallow high-energy areas of the reef, the use of this chemical cue may ensure the right settlement of *A. palmata* larvae on this zone. Even if the contributions of crustose coralline algae in the overall construction of modern reefs is far less significant than other processes (Macintyre, 1997), their role as reef binder as well as coral settlement cue has been underestimated.

3.5. – CONCLUSION

This study has shown that some populations could show low success in recruitment of newly hurricane-generated fragments. Although *Acropora* populations are able to generate fragments of large enough sizes that their survival potential is high, at least during the early stages, this study found three trends that influence late survival and future stability of these new asexual recruits:

- a - significant spatial variability in fragment survival, which suggests that local environments or ecological regimens that characterize each study site can influence the fate of the fragments;
- b- delayed effect of substrate types where the fragment landed, which in combination with the observed low capability to attach to the substrate, would preclude a long-term survival and growth of asexual recruits on the unstable zone of the reef
- c- size-specific mortality relationship with a possible threshold size (i.e. 20-25 cm length) above which fragments are less likely to die during the first year

As a result, the dynamics of observed fragments was characterized by a high initial mortality presumably due to the physiological impairment and adaptation to a new site, followed by a slow but steady decline of live tissues due to partial mortality. In addition, the mortality of underlying tissue reduced the probability of self-attachment to the substrate, leading newly generated fragments to depend on other mechanisms, such as, the overgrowth or the binding ability of coralline algae to fuse and stabilize the fragment to the reef. Thus, if fragmentation by hurricanes is an important structuring force regulating the dynamics and structure of populations of *A. palmata*, the observed failure to recruit by this mechanism may result in progressive reduction of the local population that may be somewhat related to the recent demise of this species in the wider Caribbean (Bruckner, 2003).

CHAPTER 4

SIZE-BASED POPULATION MATRIX MODEL OF HURRICANE-GENERATED FRAGMENTS OF *Acropora palmata*

4.1.-INTRODUCTION

In coral reefs, as in forests, physical structure is provided by the predominant organisms, which are characterized by long life spans and indeterminate growth. As in any other system, the dynamics of these communities reflect the dynamics of their component populations. However, due to the long life spans of scleractinian corals and clonal propagation where a colony is not necessarily an individual (≈genet), the use of traditional age-specific demography for population dynamics is impractical. Simulation models based on size-specific demography (Hughes, 1984; Yoshioka, 1994; Hughes and Tanner, 2000) or stage-specific demography (Lirman, 2003) offer a better approach to the study of corals and community dynamics. The development and use of simulation models can provide a powerful tool to increase our understanding of the ecology and population dynamics of corals as well as for predicting the possible effects of biological and physical disturbance on reef ecosystems (Lirman (2003).

In this study, a size-specific demography approach was used to describe the population dynamics of hurricane-generated fragments of Elkhorn coral, *Acropora palmata*. The Caribbean Elkhorn coral is a branching coral that forms densely aggregated patches on the shallow high-energy habitats of coral reefs throughout the Caribbean (Goreau, 1959; Geister, 1977; Rogers, et al., 1982). Unlike acroporid species in the Indo-Pacific, which exhibit high sexual recruitment rates (Wallace, 1985), the main propagation mechanism of Caribbean *Acropora* has been proposed to be by colony fragmentation (Bak and Engel, 1979; Highsmith, 1982; Rylaarsdam, 1983; Lirman and Fong, 1997). Due to the apparent low recruitment success of sexually produced planulae (Bak and Engel, 1979; Rylaarsdam, 1983), the population dynamics of this species seems to be dominated by "births and deaths" of asexually produced individuals (ramets). The assumption that this species mostly uses asexual reproduction to persist locally, with sporadic sexual recruitment, is considered a general trait of their life history. During the last decades, *Acropora* populations have been greatly reduced throughout their range as a result of at least two major factors: coral diseases (Bak and Criens, 1981; Gladfelter, 1982; Ogden and Ogden, 1994; Garzón-Ferreira and Kielman, 1994; Sheppard et al., 1995; Zea et al., 1998; Bruckner and Bruckner, 1997; Weil et al., 2003) and hurricanes (Glynn et al., 1964; Knowlton et al., 1981; 1990; Woodley et al., 1981; Rogers et al., 1982; 1991; Woodley, 1992; Vicente, 1994; Jaap and Sargent, 1994; Lirman and Fong, 1996; 1997). This unprecedented decline is changing the composition of shallow reef communities. Loss of these keystone resources brought a significant loss of reef structure and function (Bruckner, 2002). Therefore, understanding the dynamics of this species through local populations may provide insights into the adaptive significance of fragmentation as a strategy to maintain local populations, and provide valuable information to predict population variation (i.e. structure, composition) in response to natural or human-induced disturbances.

The main objective of this study was to develop and describe a size-based simulation model based on data collected from three reef areas within La Parguera Natural Reserve, in the southwestern coast of Puerto Rico, after the impact of Hurricane Georges (September 22, 1998). To describe temporal trends in survivorships of hurricane-generated fragments, two size-based population matrix models were developed to describe separately the survivorship and growth of colonies within the first year after fragmentation (early population matrix model) from those that occur two years later (late population matrix model). In order to evaluate the efficacy of the size-based approaches in describing the population dynamics of hurricane-generated fragments, predictions generated by the early population matrix were compared with field data. Finally, the model results were used to further examine the importance of fragmentation as a mechanism to maintain local populations.

4.2.-METHODOLOGY

Population dynamics of hurricane generated-fragments were analyzed as a process of survivorship, growth into larger size classes or reduced to smaller size classes by partial mortalities. To examine further changes in fragment dynamics of *A. palmata*, two size classified matrix population models were developed and analyzed following those described by Hughes (1984), Yoshioka (1994), Hughes and Tanner (2000). These models were based on the Leslie matrix model (Leslie, 1945). The general formula of this model is:

$$\boldsymbol{x\ (t+1) = A \cdot x\ (t)}$$

where ***A*** is a matrix describing the probabilities of transition between different size classes and ***x (t)*** is a vector describing the number of colonies (i.e. fragments) in each size class at time ***t***. Fragments of *A. palmata* generated by Hurricane Georges (Chapter 2) were assigned to one of four size classes based on their initial live surface area. The size classes were <200 cm^2 (class I), 200-400 cm^2 (class II), 400-600 cm^2 (class III), and >600 cm^2 (class IV). If coral tissue over the fragment underwent fission during each interval time, areas of resulting patches of tissue were combined. The probabilities of a colony growth (G), shrinkage (S) or staying in the same class (L) are diagramed in Figure 4.1. In this modified size-stage matrix, the size-specific mortality rate (d_x) is one minus the sum of probabilities (i.e. probabilities of transition) in each column of the generated matrix table (d_x= 1- ΣP).

Two population matrices models based in two different time intervals after the hurricane were developed: a) an early stage model (Model 1998-1999) and b) the late stage model (Model 1999-2001). The early population stage model used data collected from San Cristóbal Reef in the first year after the disturbance. Transects at San Cristóbal Reef were set up and surveyed prior to the hurricane and surveyed again just after the disturbance and several times over a three year period.

The late population stage model was produced using values from fragments from all reefs surveyed that survived the first year (1999) and were found (dead or alive) two years later (2001). Missing fragments were excluded from the analysis. Because fragments studied had high mortality rates, the classical population growth simulation, beginning with a cohort of small colonies, was not applicable in this case. Shrinking population simulations, beginning with a cohort of large colonies, were analyzed. Both models and simulations in terms of the expected colony abundance and size-frequency distribution of cohorts were compared. The early population matrix Model 1998-1999 and the size-frequency of observed colonies in 1999 were used to calculate the expected colony abundance and size-frequency distribution of the surviving fragments in 2001. The expected size frequency distribution value obtained using this early population matrix was compared with data collected from the field in 2001. The null hypothesis here is that the observed late populations will follow a size-based frequency distribution based on the early population matrix Model 1998-1999.

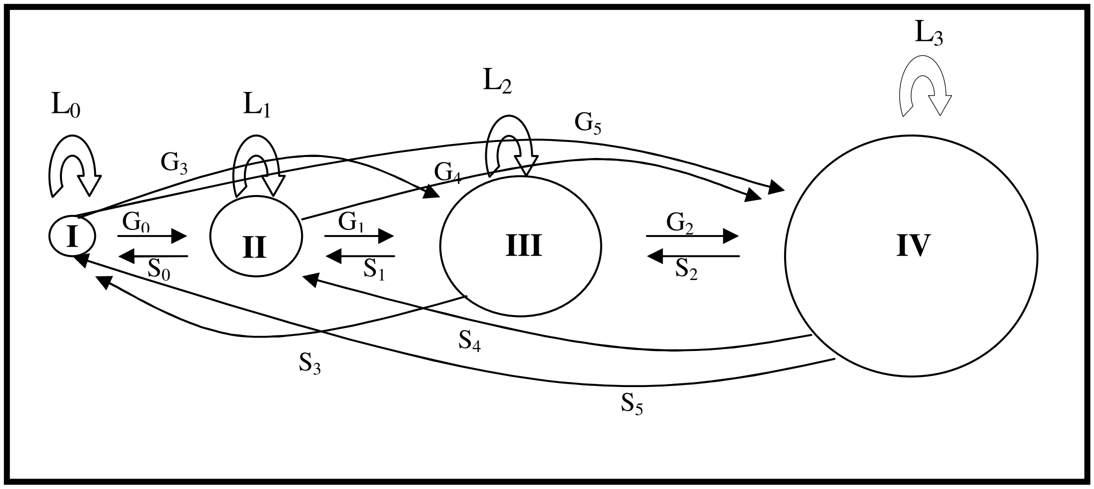

Figure 4.1.- Model of fragment size transition. Circles with roman numbers indicate different size classes (I - IV) and arrows represent the probabilities of transition: the proportion of a fragment moving from one size to another (i.e. I to II = G_0). Letters represent the probabilities of a fragment to growth (G_0-G_5), to shrink (S_0-S_5) or stay in the same class (L_0-L_3).

4.3. - RESULTS

4.3.1. - Population Matrix Model I: 1998-1999

The population matrix of the early stages after the hurricane event was characterized by high rates of transition of intermediate and large size classes with low rate of mortality (d_x), while small fragments showed low rates of transition and the highest rate of mortality (Table 4.1). This suggests that larger fragments survived better, but were more likely to shrink or contribute to smaller size classes by partial tissue mortality. Low population growth rate in terms of the transition to the highest size classes can only be observed in the two smallest size classes (<6%) and cannot be observed in size class III. This "lack of growth" or lack of contribution of size class III to size class IV can be attributed to the absence or rapid decline of the largest sizes in the classical growth simulations model (Figure 4.2). The shrinkage simulation model (Figure 4.3) also showed a more realistic population behavior, where partial mortality of the largest and medium size ramets were responsible for the increase of small size colonies in the second year, followed by a steady decrease due to high mortality rates of the small size class. If fragment populations follow the early stage matrix, most generated-fragments will die in 8 years as predicted by the growth simulations model (Figure 4.2) or 12 years if starting with large colonies as predicted by the shrinkage simulation model (Figure 4.3).

Table 4.1.- Transitional probabilities of size-specific growth (or shrinkage) and survival of *Acropora palmata* fragments based on the data collected from San Cristóbal Reef from 1998 to 1999. d_x is the size-specific probability of mortality and *N* is the total number of fragments found in each size class.

	Class I	*Class II*	*Class III*	*Class IV*
	<200	**(200-400)**	**(400-600)**	**> 600**
<200	0.4386	0.4912	0.2727	0.1667
(200-400)	0.0351	0.3158	0.4545	0.2083
(400-600)	0.0000	0.0175	0.1818	0.0000
> 600	0.0000	0.0000	0.0000	0.5000
ΣP	0.4737	0.8246	0.9091	0.8750
d_x	0.5263	0.1754	0.0909	0.1250
N	57	57	11	24

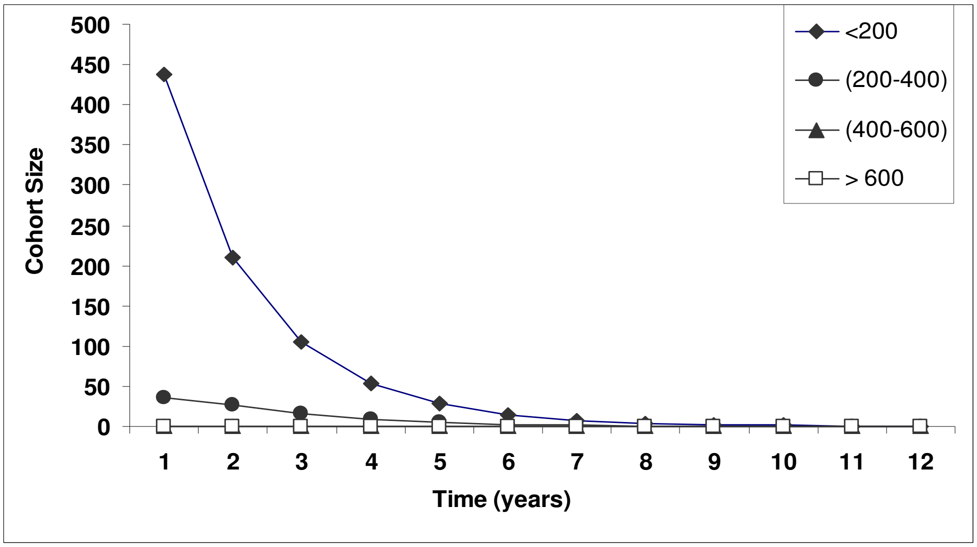

Figure 4.2.- Decline over time in the number and sizes (coral surface area) of coral fragments in a single cohort as a function of cohort age. Population growth simulation from matrix model 1998-1999 and starting with an initial settlement of 1000 fragments into smallest size class (< 200 cm^2).

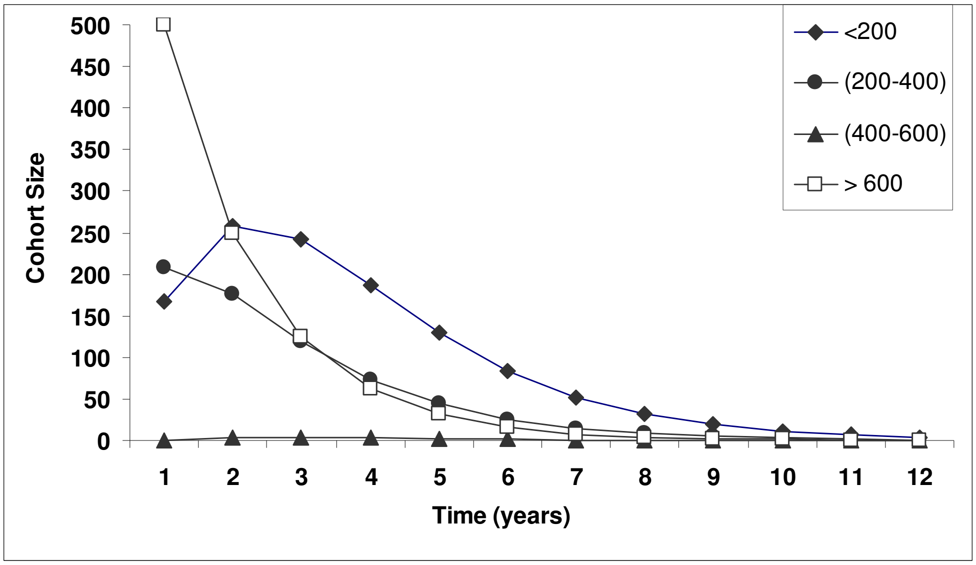

Figure 4.3.- Change over time in the number and sizes (coral surface area) of coral fragments in a single cohort as a function of cohort age. Shrinkage population simulation from matrix model 1998-1999 and starting with an initial settlement of 1000 fragments into largest size class (> 600 cm^2).

4.3.2. - Population Matrix Model II: 1999-2001

The population matrix for the late stages of the fragments after the hurricane event was characterized by an increase in mortality rate (d_x) of small and intermediate size ramets, while large fragments showed low rates of total mortality but a high rate of transition to smaller size due to partial colony mortality (Table 4.2). Population growth rate in terms of the transition to higher size classes was observed in the first three size classes (Figure 4.1). Due to the nature of the model, probability of growth of class IV was not observed because it was added to the probability of staying in the same size. Similarly, shrinkage of class I generally resulted in mortalities of the small colonies.

Given that the observed values of transitional rates of the matrix was the result of two years of observations (from 1999 to 2001), the expected probability of each stage, as well as the mortality rate, would be lower at a one-year interval. However, if fragment populations follow the late stage matrix, most colonies of initial cohort of 1000 small size fragments will die in 10 years as predicted by the growth simulations model (Figure

4.4) or more than 12 years for initially large colonies as predicted by the shrinkage simulation model (Figure 4.5). Thus, the late population simulation indicates a difference of two years persistent of fragment population compared with the early population simulation.

Table 4.2. - Transitional probabilities of size-specific growth (or shrinkage) and survival of *Acropora palmata* fragments based on the data collected from the three surveyed reefs from 1999 to 2001. d_x is the size-specific probability of mortality and N is the total number of fragments found in each size class.

	Class I	*Class II*	*Class III*	*Class IV*
	<200	**(200-400)**	**(400-600)**	**> 600**
<200	0.2245	0.3529	0.1579	0.2581
(200-400)	0.0544	0.0980	0.3158	0.1613
(400-600)	0.0272	0.0784	0.1053	0.0968
> 600	0.0136	0.0588	0.0526	0.3548
ΣP	0.3197	0.5882	0.6316	0.8710
d_x	0.6803	0.4118	0.3684	0.1290
N	207	77	33	47

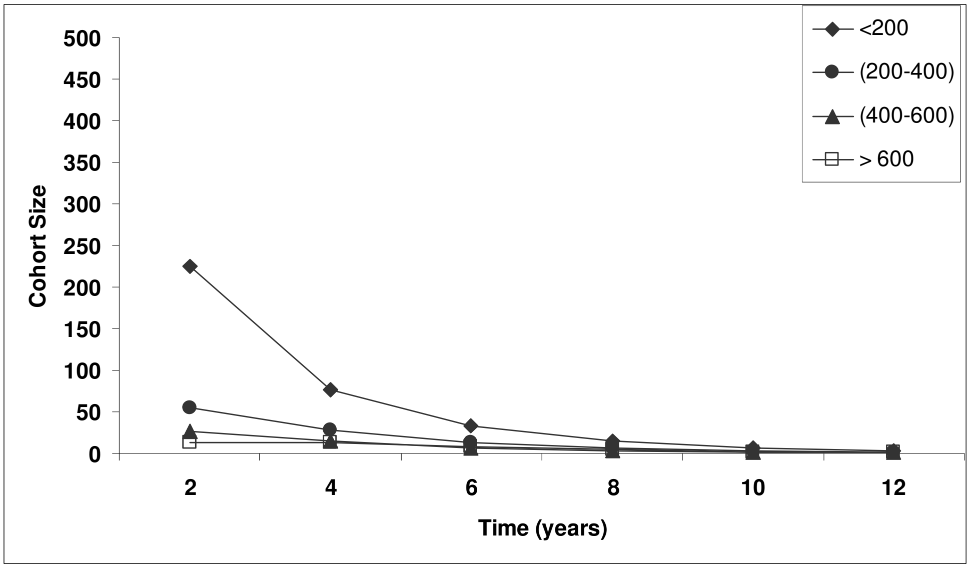

Figure 4.4. - Decline over time in the number and sizes (coral surface area) of coral fragments in a single cohort as a function of cohort age. Growth population simulation from matrix model 1999-2001 and starting with an initial settlement of 1000 fragments into smallest size class (< 200 cm^2).

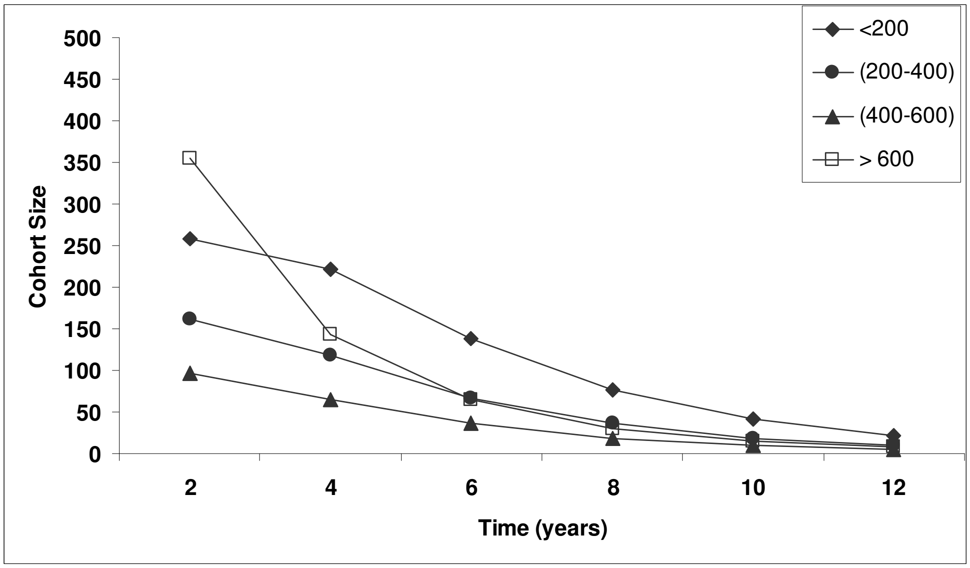

Figure 4.5. - Decline over time in the number and sizes (coral surface area) of coral fragments in a single cohort as a function of cohort age. Shrinkage population simulation from matrix model 1999-2001 and starting with an initial settlement of 1000 fragments into largest size class (> 600 cm^2).

4.3.3. - Fragment Population Trends

Cohort or coral abundance as a function of time using both models (early and late model) showed similar trends in survivorships. After a time of ≈ 10 years, most colonies went to extinction independently of the initial size (Figures 4.6-4.7). However, small differences in the magnitude of the expected abundance exist between models at each interval of time. Beginning with a cohort of small colonies, the differences in survival among models appear to decrease from 83.0 colonies after two years to 13.5 colonies after ten years (Figure 4.6). From this simulation, the estimated mortality rate at the two year interval was 73.11 ± 1.87 % (n=5) for the early population model and was significantly higher ($p<0.05$, t-test) and less variable (CV=2.56%) than predicted with the late population model (mortality rate= 56.37 ± 7.24 %, CV= 12.84%). Whereas a simulation that started with a cohort of large colonies, the difference in survival among models seems to decrease from 182.7 colonies after two years to 69.7 colonies after ten years (Figure 4.7). However, from the simulation, the estimated mortality rate at the two year interval was 55.34 ± 14.54 % (n=5) for the early population model, which was not significantly different ($p> 0.05$, t-test) from that predicted in the late population model (37.82 ± 14.56 %). In addition, the expected rate of population decline ($\lambda<1$) was highest (within the first year after the disturbance) as predicted by the early matrix (0.5716 ± 0.0634), but slowed down with time as predicted by the late matrix (0.7140 ± 0.0439).

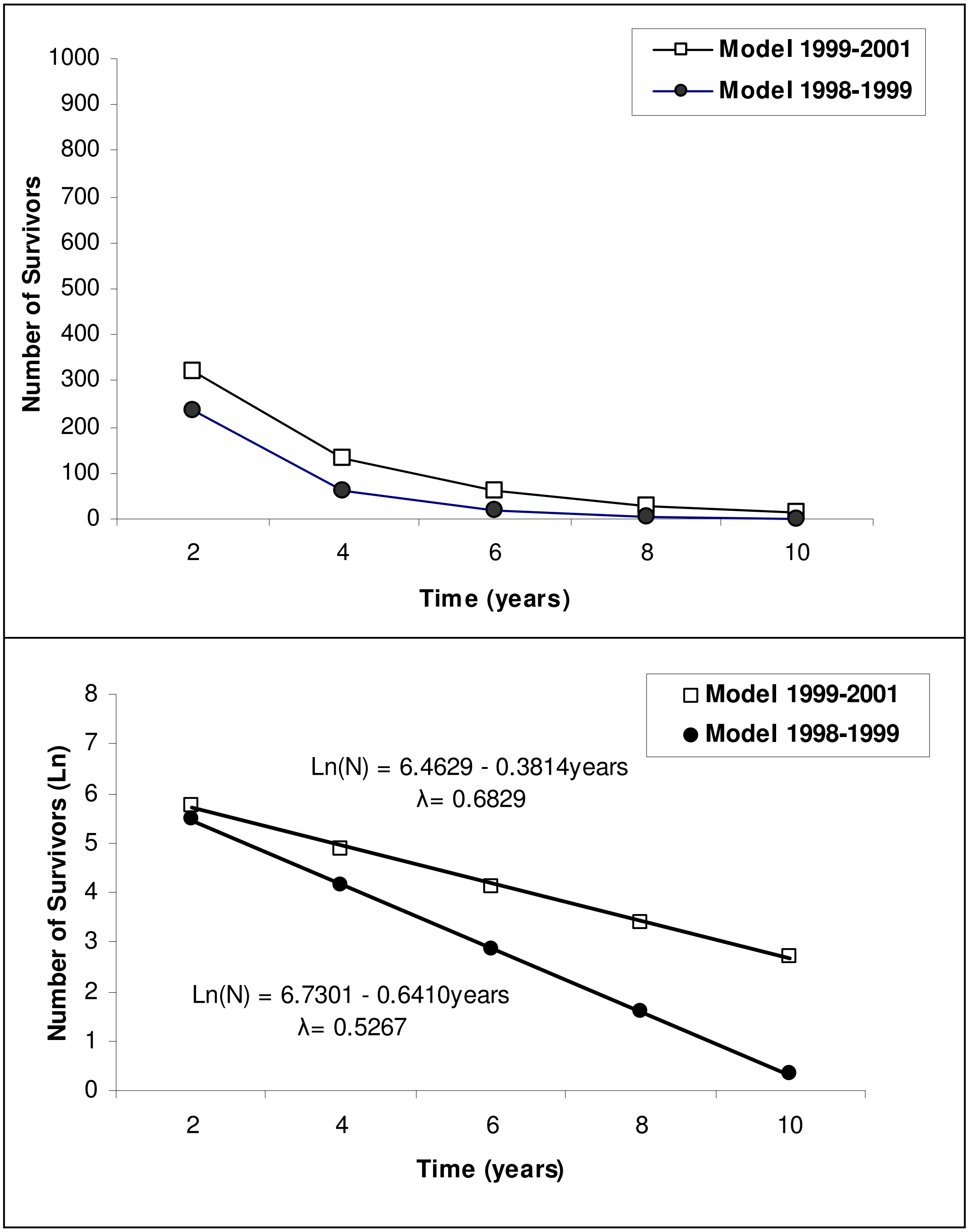

Figure 4.6.- Calculated abundance of coral fragments (survivors) in a single cohort as a function of time (years) using both matrix model (Model 1998-1999 and Model 1999-2001) and starting with an initial settlement of 1000 fragments of the smallest size class (< 200 cm^2). λ is the equilibrium growth constant (lambda of less than one indicates population decline).

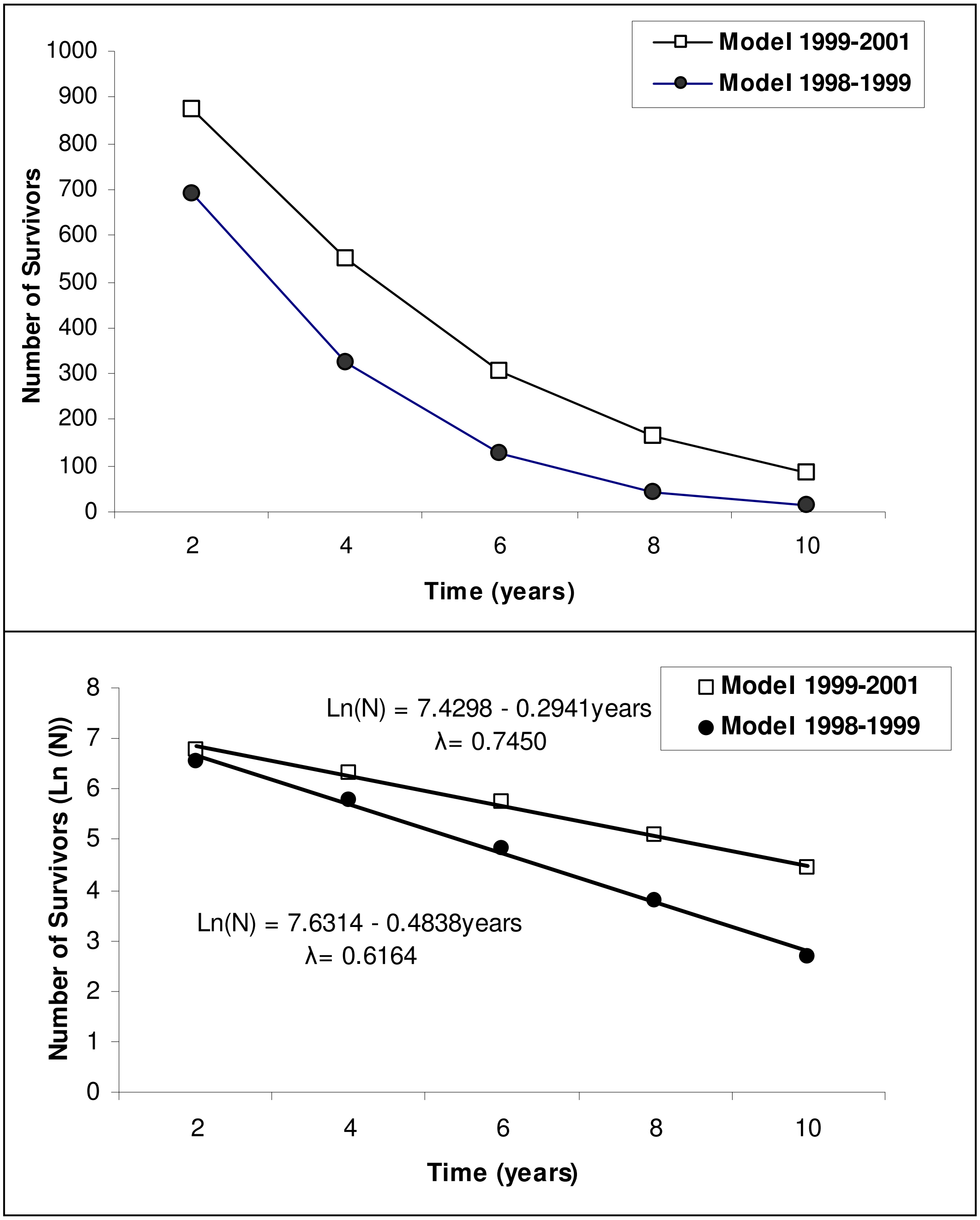

Figure 4.7.- Calculated abundance of coral fragments (survivors) in a single cohort as a function of time (years) using both matrix model (Model 1998-1999 and Model 1999-2001) and starting with an initial settlement of 1000 fragments of the largest size class (> 600 cm^2). λ is the equilibrium growth constant (lambda of less than one indicates population decline).

4.3.4. - Model Validation

The calculated size-frequency distributions of surviving fragments after 3 years from the disturbance using the early population matrix Model 1998-1999 was generally different from the observed values in 2001 (Table 4.3). Applying Williams (1976) correction to G-test for goodness of fit, to obtain a better approximation to X^2, the observed G_{adj} (25.7098) was significantly ($p<0.001$) than $X^2_{0.001(2)}$. Therefore, the null hypothesis that the late observed population followed a size-based frequency distribution based on the early population's matrix Model 1998-1999 was rejected. These significant differences suggested that the model is not correct due to: (1) information gathered to construct the early model was not representative of all populations from the study area; (2) the transitional probability (i.e. growth, shrinkage and mortality rate) was not constant and may change with time after a disturbance. In respect to the first assumption, the data used to construct the early model came from San Cristóbal Reef, while the observed values used to validate the model came from all three reefs studied. As in Chapter 3, the fate of fragments in San Cristóbal Reef (i.e. partial and total mortality) was significantly different from the other two reefs (Laurel Reef and Media Luna Reef) and this would probably incorporate variability in the transition probability of the models.

The second assumption is explained by the reduction in total fragment mortality and high partial colony mortality observed in the period between 1 to 3 years after the disturbance, followed by an increase in growing colonies within this period of time (Chapter 3). The late population matrix takes into consideration these late values but unfortunately, no other source of data exists to validate this model.

Table 4.3. - Expected and observed fragments size-frequencies in 2001 for G-test for goodness of fit analysis. A calculation of expected frequency was based on the population's matrix Model 1998-1999 and was adjusted to a sample size of 116 colonies (total surviving fragments in 2001). Frequencies (f and f_{adj}) of the last two size classes were pooled to create classes of adequate size (f >5) for the analysis.

Size Class (cm^2)	**Observed Frequency (f)**		**Expected Frequency (f_{adj})**		**Ratio (f/ f_{adj})**		**f ln f/ f_{adj}**	
<200	62		80.0632		0.7744		-15.8523	
200-400	24		24.7061		0.9714		-0.6959	
400-600	13	30	1.7480	11.2307	7.4371	2.6712	26.0842	29.4764
>600	17		9.4827		1.7927		9.9237	
Total	**116**		**116**					**ln L= 12.9282**

4.4. – DISCUSSION

This study showed that the transitional probabilities of hurricane-generated fragments vary with time and that different matrices are needed to predict temporal variation in fragments survival. Previous population models developed for *Agaricia agaricites* (Hughes, 1984) had incorporated temporal changes by alternating different matrices for two different seasons: calm and storm season. In the same way, the early population matrix was expected to incorporate the initial responce of fragments soon after the disturbance, while the late population matrix was expected to resemble the conditions years after the hurricane. Fragments generated after the hurricane came to rest on new sites followed by underside tissue death that resulted in the majority of the fragments (85%) losing more than 60% of their upper tissue area due to partial mortality (Chapter 3). This initial physiological impairment and adaptation process to new sites may affect survivorship at an early stage. Many other factors such as predation, disease and overtopping by other reef organisms have been identified to contribute to the mortality or partial mortality of the fragments soon after being generated (Knowlton et al., 1981; Rogers et al., 1982; Bruckner and Bruckner, 2001). However, to what extent some of those mortality factors are still affecting fragment survivorship at later stages is still an open question. Long-term survival was not supported by model and may have implications in the ongoing decline of the species (Bruckner, 2002).

An important observation from the population matrices is that transitional probabilities were strongly size dependent at both times and whatever the initial fragment population structure, they sharply decline to extinction in less than 15 years. Although the estimate rates of population decline (λ) were similar than reported for other Caribbean coral species (Hughes and Tanner, 2000), this trend could be somewhat offset if the rate of new growth is faster than partial mortality. However, tissue loss still exceeded new growth nearly 3 year after the hurricane. The effect of this high rate of partial mortality led fragments to reduce in size (shrinkage) which effectively reduces the probability of survivorship. As shown in Chapter 3 and by the observed size-specific probability of mortality (d_x), small colonies invariably had the highest rate of mortality. Moreover, fragments that experienced significant tissue loss during the first year eventually died after several years (Chapter 3). Consequently, this shift in tissue biomass from units with low mortality (large colonies) towards units with high mortalities (small colonies) can decrease the probability of recovery and severely affect future survivorship (see Yoshioka, 1994; Hughes and Tanner, 2000; Lirman, 2003). Therefore, if a fragment fails to recruit and grow to the threshold size before the next disturbance, fragmentation may be seen as a substantial loss of live cover and not as an alternative mechanism to maintain or increase local population (Bak and Engel, 1979; Highsmith, 1982; Rylaarsdam, 1983; Lirman and Fong, 1997; Lirman, 2003). Although recent population models suggested that *A. palmata* can still benefit from periodic storms, mostly when storms occur in 5-year intervals (Lirman, 2003), the three populations studied here do not fit whithin this expectation, especially when most fragments are still unstable, and the probability of survivorship of the remnant populations after another hurricane is 50 % (Chapter 3).

4.5. – CONCLUSION

This study have shown that the dynamics of observed fragments was characterized by a high initial mortality presumably due to the physiological impairment and adaptation to a new site, followed by a slow but steady decline of live tissues due to partial mortality. While initial fragment size is an important factor controlling early survival, the effect of this continuous partial mortality reduced the initial live size (shrinkage) affecting the future survival of the fragment (positive relationships between size and survival). Thus, if fragmentation by hurricanes is an important structuring force regulating the dynamics and structure of populations of *A. palmata*, the observed failure to recruit by this mechanism may result in progressive reduction of the local population. This previously undocumented mechanism of population decline, as predicted by the size-based simulation model suggests potentially complex responses to recent environmental change that may be somewhat related to the recent demise of this species in the wider Caribbean (Bruckner, 2003).

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

This study confirmed that fragmentation and local dispersion of *Acropora palmata* is a common process during hurricanes. According to this and previous studies, the abundance (i.e. fragment densities), distribution over the reef bottom and probably, the size structure of the resulting fragments depend on factors such as: the magnitude and direction of the swells, the topography of the reef, and the size structure and/or relative abundance of present population when the event happens. Despite the fact that newly generated fragments can potentially survive and recruit to the sea floor, this study has shown that some populations could show low success in recruitment of newly formed fragments. Although *Acropora* populations are able to generate fragments of large enough sizes with a high survival potential, at least during the early stages, this study found three trends that influence late survival and future stability of these new asexual recruits:

- a - significant spatial variability in fragment survival, which suggests that local environments or ecological regimens that characterize each study site can influence the fate of the fragments.
- b- delayed effect of substrate types where the fragment landed, which in combination with the observed low capability to attach to the substrate, would preclude a long-term survival and growth of asexual recruits on the unstable zone of the reef.
- c- high and continuous loss of coral tissue (i.e. partial mortality) which caused delayed mortality due to the observed size-specific mortality relationship and possibly prevented the attachment of the fragment to the substrate.

As a result, the dynamics of observed fragments was characterized by a high initial mortality, presumably due to the physiological impairment and adaptation to a new site, followed by a slow but steady decline of live tissues due to partial mortality. While initial fragment size is an important factor controlling early survival, the effect of this continuous partial mortality reduced the initial live size (shrinkage) affecting the future survival of the fragment (positive relationships between size and survival). In addition, the mortality of underlying tissue reduced the probability of self attachment to the substrate, leading newly generated fragments to depend on other mechanisms, such as, the overgrowth or the binding ability of coralline algae to fuse and stabilize the fragments to the reef. Thus, if fragmentation by hurricanes is an important structuring force regulating the dynamics and structure of populations of *A. palmata*, the observed failure to recruit by this mechanism may result in progressive reduction of the local population. This previously undocumented mechanism of population decline, as predicted by the size-based simulation model (Chapter 4), suggests potentially complex responses to recent environmental change that may be somewhat related to the recent demise of this species in the wider Caribbean (Bruckner, 2003).

The simulation model of the population dynamics of *A. palmata* developed by Lirman (2003) suggested that the species can still benefit from periodic storms, mostly when the storms occur at 5 year intervals (Lirman, 2003). Lirman models predict that when storm frequency increase to 5 years, the abundance of colonies by recruitment and growth of generated fragments can increase five-fold after 10 storms. However, rather than using size-based models, he used a stage-based model with transition probabilities among the different morphological stages of *A. palmata* (i.e. colony, fragment, colony from fragment, and crusts) that was not necessarily related with their age or size. The present study is not intended to refute Lirmans' prediction; this study provides a new perspective of what happens in our local populations that could be used to obtain a better resolution (i.e. incorporation of new transitional probabilities) of the Lirman model, or to develop a new model using the reported datasets of both.

Future population dynamics studies of this susceptible species need to incorporate a genetic approach. Recent genetic work on the clonal structure of *A.*

palmata populations in Puerto Rico and Mona Island (Baums et al., unpublished) has revealed a variable contribution of clonal propagation to local population genetic structure. While the compositions of *A. palmata* population at San Cristobal Reef showed a moderate level of asexual recruitment (mean ramets/genets= 1.85 ± 2.09, n= 48 colonies), other populations located at the northwestern coast of Puerto Rico (Rincón Natural Reserve), with high abundance of colonies (see Weil et al., 2003), showed a low level of asexual recruitment but high sexual recruits (mean ramets/genets= 1.02 ± 0.15, n= 48 colonies). This may suggest that the assumption that this species uses mostly asexual reproduction to persist locally is not necessarily a general trait of their life history strategy. Sexual reproduction still play an important role in certain populations, as was previously suggested by Jordán-Dahlgren (1992) in his analysis of the recolonization patterns of *A. palmata* on the Veracruz reef complex after a widespread mortality caused by a strong terrestrial input. Even if local populations of hurricane-generated fragments at La Parguera Natural Reserve went to extinction, sporadic or a mass sexual recruitment event may compensate for the loss of these colonies, and replenish the area with a population that has higher genetic variability. However, before we can accept this prediction, one question has to be answered: Can sexually-derived larvae escape from the mortality factors that usually affect the survivorship of hurricane-generated fragments? The answer may provide some insight into the dynamics of this species in the interim of recent decline.

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