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Assessment of Image Analysis as a Measure of Scleractinian Coral Growth

by

Steven K. Gustafson

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
College of Marine Science
University of South Florida

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Steven K. Gustafson

ABSTRACT

Image analysis was used to measure basal areas of selected colonies of *Montastraea annularis* and *Porites astreoides*, following the colonies over a three-year period from 2002 to 2004. Existing digital images of permanently-marked quadrats in the Caye Caulker Marine Reserve, Belize, were selected based on image quality and availability of images of selected quadrats for all three years. Annual growth rates were calculated from the basal-area measurements. Mean growth rates (radial skeletal extension) for *M. annularis* and *P. astreoides* were 0.02 cm yr^{-1} and -0.20 cm yr^{-1}, respectively. Basal area measurements demonstrated a large degree of variability. Increases were approximately balanced by declines giving the impression of stasis. By removing negative values and correcting by 25% to allow for comparison with vertical growth rates, mean values increased to ~0.5 cm yr^{-1} for *M. annularis* and ~0.8 cm yr^{-1} for *P. astreoides.*

Basal area as a growth measure was compared to methods used in earlier studies. A new growth index based on basal area and perimeter was proposed and modeled. This growth index can be useful for reporting growth measured from basal areas and comparable other methods. The index also measures negative growth, or mortality, which conventional methods cannot do.

1. INTRODUCTION

Introduction to tropical coral reefs

Tropical coral reefs are among the planet's most biologically diverse ecosystems. The number of species living on coral reefs has been estimated to be as high as 3 million, of which approximately ten percent have been studied and described (Adey, 2000).

High diversity makes coral reefs valuable as a biochemical resource. Tropical coral reefs are home to a diverse assemblage of sessile invertebrates such as corals, tunicates, bryozoans, and sponges. Being firmly attached to the substrate, these animals are unable to avoid environmental perturbations, predators, or other stressors. Consequently, many engage in chemical warfare, using compounds synthesized by the host, by the endosymbionts, or sequestered from the host's food. These compounds are used to deter predation, fight disease, prevent overgrowth by fouling and competing organisms, and to capture prey. Because of their unique structures and properties, these compounds are an important and, as yet, largely untapped source of natural products with enormous potential as pharmaceuticals, nutritional supplements, enzymes, pesticides, cosmetics, and other novel commercial products (Bruckner, 2002).

Many coral reefs act as protective barriers to ocean waves, providing sheltered lagoons conducive to seagrass and mangrove communities, minimizing coastal erosion and providing nurseries for a multitude of organisms. In a recent World Resource Institute research report, the value of shoreline protection provided by Caribbean reefs was estimated to be between $700 million and $2.2 billion yr^{-1} (Burke and Maidens, 2004). All coral reefs provide structure for the thousands of resident fish and invertebrate species, which, in turn, support local economies through fisheries and tourism. A study of Hawaii's coral reefs calculates their total economic value, combining the annual figures for tourism, amenities, fisheries, and biodiversity, to average $364 million yr^{-1} (Cesar et al., 2002). The average annual recreational value alone is $304 million (Cesar and van Beukering, 2004). The understanding of reef-building (hermatypic) coral growth is critical if we hope to protect and preserve the valuable resources that tropical coral reefs are.

Reefs of Belize

Charles Darwin called the Belize Barrier Reef the most remarkable reef in the West Indies (Darwin, 1846). Stretching some 250 kilometers along the Mesoamerican coast, it is the largest barrier reef in the Western Hemisphere. Major studies of the geology and morphology of the Belizean reefs have been carried out (Stoddart, 1962, Stoddart, 1963; and others (cited in McField, et al., 2001)) but studies of the community structure of this vast system are less common (McField et al., 2001). Even rarer are studies of reef communities on the numerous patch reefs in Belize's shelf lagoon. The studies of these patch reefs that do exist are virtually all restricted to the southern lagoon (Muzik, 1982; Lasker and Coffroth, 1983; Aronson et al., 1998; Aronson et al., 2002a). Indeed, an exhaustive search of the literature yielded only two studies on northern shelf lagoon patch reefs in Belize (Mazzullo et al., 1992; Burkett et al., 2002).

Community structures differ substantially from north to south. The southern patch reefs are in deeper, higher-energy water than their northern counterparts. The southern shelf lagoon reef communities were historically dominated by *Acropora palmat*a Ellis and Solander 1786 in the higher energy zones, and by *Acropora cervicornis* Lamarck 1816 in more sheltered areas (Mazzullo et al., 1992; Aronson et al., 1998). The northern shelf lagoon reefs were dominated by *Montastraea annularis* Ellis and Solander 1786 (Mazzullo et al., 1992; Burkett et al., 2002). There were, however, extensive stands of *Acropora palmat*a Lamarck 1816 and smaller stands of *Acropora cervicornis* Lamarck 1816 in the northern lagoon (Burkett et al., 2002; local residents, personal communication).

The white-band epidemic of the late 1970s and 1980s killed most *Acropora* colonies throughout the Caribbean (Aronson and Precht, 2001b; Aronson et al., 2002a). Also, during 1983-84, a mysterious pathogen decimated Caribbean populations of *Diadema antillarum* Philippi 1845, a primary reef herbivore (Carpenter, 1990; Lessios, 1995). With reduced grazing, blooms of brown algae dominated most of the shallow reefs. Local over-fishing and anthropogenic nutrification intensified this trend (McClanahan and Muthiga, 1998). Aronson and Precht (2001a) reported that at Carrie Bow Caye, Belize, coral coverage on the fore reef declined dramatically since the 1980s while macroalgal cover increased from less than 5% to more than 60%.

Aronson and Precht (2001a) proposed three causes for these dramatic shifts in Caribbean coral reef community structure. First, coral morality due to natural and anthropogenic phenomena has reduced live coverage and increased available substrate for colonization by algae. Second, the mass mortality of *Diadema antillarum* in 1983 – 1984 and local over-fishing of parrotfish and surgeonfish greatly reduced herbivory. Third, the abundance of available substrate and loss of herbivores has allowed filamentous algae and macroalgae to proliferate, preventing coral recruitment (Aronson and Precht, 2001a).

During the fall of 1995, an unprecedented mass bleaching event affected approximately 50% of Belizean scleractinian corals but with low mortality (McField, 1999). During the late summer and fall of 1998, the Belize Barrier Reef system suffered another mass bleaching. The latter event resulted in increased coral mortality in the fore reef community. On the back reef and on the patch reefs of the shelf lagoon, some areas suffered 100 percent mortality (Aronson et al., 2000; Aronson et al., 2002b).

In addition to the bleaching events, the reefs of Belize suffered further disturbance from three major hurricanes in a four-year period: Mitch (1998), Keith (2000) and Iris (2001). Mitch and Keith heavily damaged the shallow-water reefs in the northern shelf lagoon (Burkett et al., 2002; McField, M. D., personal communication). Hurricane Iris had a much reduced effect as it battered the southern reefs.

Important factors affecting coral growth

Many factors affect coral growth. Arguably, the most important is the coral-algal symbiosis. Reef-building (hermatypic) corals have a symbiotic relationship with certain dinoflagellate algae that live within the corals' tissues. The coral-algal symbiosis is best adapted to clear, nutrient-poor water (Hallock et al., 1993; Wood, 1993). Under these conditions the unicellular symbionts, called zooxanthellae, are kept in a nitrogen-deprived state. Without access to sufficient dissolved inorganic nitrogen (DIN), one of the key components of protein, the symbionts grow and reproduce very slowly. The coral host provides just enough DIN from its own waste products to maintain its symbionts' photosynthetic capabilities, and to allow the algae to reproduce at a rate that sustains a stable population size at a level that is most beneficial to the coral (Trench, 1987). As long as their photosynthetic systems remain intact, the symbionts continue producing photosynthate at rates dictated by the available light. With limited DIN, the algae cannot use all of their photosynthate. The portion that would have gone to fuel growth and reproduction, beyond what the host allows, is secreted into the host's cells where it used by the host coral for its energy needs. Most of the coral's energy budget is made up of lipids from its symbionts (Falkowski et al., 1993). This is the reason that zooxanthellate corals can do so well in highly oligotrophic waters. The occasional prey that come into contact with coral host's tentacles supply sufficient protein for the corals to grow and reproduce. Factors that reduce the flow of lipids from the symbionts ultimately cause stress in the coral host. Stressed corals grow more slowly.

Hermatypic corals are especially vulnerable to excess nutrients, particularly DIN (Koop et al., 2001). As DIN is added to the waters bathing the coral reef, several things occur which negatively affect the coral-algal symbiosis. The corals, being permeable to the seawater, cannot keep their algal symbionts as deprived of nitrogen as they can in nutrient-poor water. The symbionts are able to take up nitrogen that has permeated the host cells from the now DIN-enriched environment (Muscatine et al., 1979; Domotor and D'Elia, 1984). With more DIN, the algae can make more protein for growth and reproduction. Energy required to make protein comes from the photosynthate that would have been excreted by the algae if they were nutrient-deprived (Falkowski et al., 1993). Consequently, there is less photosynthate for the host. Also, with more nutrients available in the water column, free-living phytoplankton populations increase. This decreases water clarity and hence available light for photosynthesis by the coral's symbionts, further reducing the host's access to energy supplies (Tomascik and Sander, 1987). Furthermore, as the coral's symbiont population grows, the algae's oxygen demands, when not photosynthesizing, reduce oxygen available for the host. When the algae are producing photosynthate, they are also producing oxygen, which can reach toxic concentrations with elevated symbiont populations (Lesser and Shick, 1989). Symbiont population increases can cause stress in the host from reduced photosynthate (energy) for respiration, reduced oxygen for respiration during darkness, and oxidative stress during the photo period.

Over the last 100 years, human activity has resulted in environmental changes such as warming oceans, air and water pollution, excess dissolved nutrients, and increased ultraviolet radiation (Knowlton, 2001). These changes have been blamed for extensive disease and mortality in coral reef communities (Richardson et al., 1998). Coral reefs are uniquely vulnerable to these changes due to their close proximity to coastlines and the ocean surface. Warming oceans are the result of global warming which has been attributed largely to increasing carbon dioxide (CO_2) levels in the atmosphere (the greenhouse effect). Increased atmospheric CO_2 concentrations lead to increased concentrations in the oceans as well. This in turn acidifies the water slightly but sufficiently to dissolve scleractinian coral skeletons at rates that may exceed coral calcification capacity, causing reefs to shrink (Caldeira and Wickett, 2003; Hallock, 2005).

Chronic stress weakens corals, making them more susceptible to disease. In the past 40 years, many coral pathologies have been identified. Black Band disease was one of the first to be identified (Rutzler and Santavy, 1983) and one of most widespread (Green and Bruckner, 2000). White Band disease was also one of the earliest to be identified (Gladfelter, 1982) and is currently the only coral disease known to cause major changes in the composition and structure of reefs (Green and Bruckner, 2000).

A host of other diseases have been identified since these initial few were described. White Pox, Yellow Blotch disease, Red-Band disease, Dark-Spots disease, Yellow Band disease; the list is long and growing (Bruckner, 2001; Gil-Agudelo and Garzón-Ferreira, 2001; Green and Bruckner, 2000).

It is widely accepted that the effects of climate change are causing coral bleaching (U. S. State Department, 1999). Bleached corals appear white, or “bleached,” because they have lost symbionts, the symbionts have lost pigment, or both. Exposure to high light levels, increased ultraviolet radiation, temperature or salinity extremes, high turbidity and sedimentation resulting in reduced light levels, and other factors have been shown to cause coral bleaching (Glynn, 1996; Kushmaro et al., 1996). If the bleaching is not too severe and the conditions causing the bleaching do not persist, the bleached colonies can regain their resident symbionts within several weeks to months (Glynn, 1996). Otherwise, the corals may eventually starve or succumb to the elevated temperatures.

Seven major episodes of bleaching have occurred since 1979. These events have been primarily attributed to increased sea water temperatures associated with global climate change and El Niño/La Niña events, with a possible synergistic effect of elevated ultraviolet and visible light (Hoegh-Guldberg, 1999). In 1995, a mass bleaching event affected reefs, e.g., in Belize, that had no history of bleaching. In 1998, the most severe and extensive bleaching on record occurred, resulting in mass mortality (Aronson, et al., 2000; McField, 1999).

In a report presented to the U.S. Coral Reef Task Force in 1999, the U.S. State Department (2004) warned: “In 1998 coral reefs around the world appear to have suffered the most extensive and severe bleaching and subsequent mortality in modern record. In the same year, tropical sea surface temperatures were the highest in modern record, topping off a 50-year trend for some tropical oceans. These events cannot be accounted for by localized stressors or natural variability alone. The geographic extent, increasing frequency, and regional severity of mass bleaching events are likely a consequence of a steadily rising baseline of marine temperatures, driven by anthropogenic global warming.”

Scleractinian coral reefs have existed since the late Triassic period (Achituv and Dubinsky, 1990; Stanley and Fautin, 2001). For some 200 million years coral reefs have survived the ravages of mass extinctions and climate change. Whether or not coral reefs will be able to survive the 21st century is an important and relevant question. In its 2000 report, the Global Coral Reef Monitoring Network states that approximately 25 percent of coral reefs worldwide have been effectively lost and another 40 percent could be lost by 2010 unless urgently needed action is taken (Wilkinson, 2001).

Coral growth rate as environmental indicator

Brown and Howard (1985) suggested that coral growth rate is a good individual-based parameter for measuring declining environmental quality on reefs (also see Buddemeier and Kinzie, 1976.). There is, however, conflicting evidence of how nutrification affects coral skeletal extension rates (Hudson, 1981; Cortes and Risk, 1985; Brown et al., 1990; Rogers, 1990). A possible reconciliation is the "Janus effect" (Edinger, 1991, cited in Risk et al., 2001), whereby nutrient enhancement, up to a certain critical level, can increase coral growth rates. When this level is reached, nutrification becomes deleterious and growth rates decline (Tomascik and Sander 1985, Risk et al., 1995). This increased growth in the presence of increased nutrients appears to be low-density skeletal extension (Risk et al., 2001).

Coral growth rate measurement

A majority of the published scleractinian growth studies used methods that required harvesting living coral colonies or taking core samples from living coral colonies. These methods used density bands in X-radiographs of thin cross-sections of coral skeletons, alizarin-red dye markers, or both, to measure growth rates as annual skeletal extensions (Table 1).

Using image analysis to compare basal areas offers a non-destructive method of calculating growth rates. Connell et al. (1997) used an “image-analysis” method to measure coral colony basal area, incorporating standard photography, tracing projected images and measuring the areas of the tracings with an electronic planimeter. The method used in my study improves on the Connell etal. method by eliminating the processing of photographic film and the projecting of images for tracing. Using digital photography also makes it possible to display the images immediately, saving time and resources by eliminating “wasted” shots, and since the images are already in digital format, it is not necessary to use a planimeter to measure areas. Furthermore, this method does not require harvesting, coring, dyeing or otherwise disturbing live coral colonies, nor does it require the use of X-ray equipment.

Table 1. Synopsis of published growth rates for *Montastraea annularis* and *Porites astreoides*. Growth rates are average skeletal extension in cm yr^{-1}.

Author	Year	Location	Species	Growth	Technique
Carricart-Gavinet & Merino	2001	Campeche Bank, Mexico	*M. annularis*	0.87	X-ray
Carricart-Gavinet et al.	1994	Campeche Bank, Mexico	*M. annularis*	0.86	X-ray
Dustan	1975	Dancing Lady Reef, Jamaica	*M. annularis*	0.47 – 0.68	Aliz. Red
Gladfelter et al.	1978	Buck I, V. I.	*M. annularis* *P. astreoides*	0.76 0.31	Aliz. Red
Goreau & Macfarlane	1990	Discovery Bay, Jamaica	*M. annularis*	0.62	Direct (nail)
Highsmith et al.	1983	Carrie Bow Cay, Belize	*M. annularis* *P. astreoides*	0.37 – 0.98 0.29 – 0.69	X-ray
Hubbard & Scaturo	1985	Cane Bay & Salt River,	*M. annularis* *P. astreoides*	0.2 – 0.9 0.19 – 0.31	X-ray
Hudson et al.	1994	Biscayne Bay, Fl, US	*M. annularis*	0.7 – 0.9	X-ray
Logan & Tomascik	1991	Bermuda	*P. astreoides*	0.2	X-ray
Tomascik & Sander	1985	Barbados	*M. annularis*	0.61 – 1.24	X-ray
Van Veghel & Bosscher	1995	Leeward reef, Curacao, NA	*M. annularis*	1.27 – 1.81	X-ray

Reporting growth rates for scleractinian colonies is somewhat problematic, given the large range in size. Area measurements by themselves do not give a growth rate. Change in basal area yields a rate in areal units per time unit. However, this measure is biased toward the larger colonies. A one percent change in a 1,000-cm^2 colony will add ten cm^2 in basal area while 100 percent change in a five-cm^2 colony will add only five cm^2 in basal area. Using percent change as a measure is biased toward the small colonies. A five-cm^2 change in a five-cm^2 colony is a 100-percent change while the same change in 1,000-cm^2 colony is a 0.5-percent change. Radial skeletal extension is less affected by colony size but the assumption must be made that the colonies are more or less circular, which is not necessarily the case, especially for fragmented colonies.

Proposed here is a growth index that would be useful for calculating growth rates that more accurately reflect the colony shape and size, and are more comparable to those found in the literature. This index is calculated from the area and perimeter information obtained from image analysis and is based on the assumption that coral colonies grow by increasing their basal areas in all directions whereby a one-unit “radial” increase would add approximately one areal unit for each unit of its perimeter.

Objectives

The primary goals of this study are to:

- Assess the use of image analysis to measure coral growth using existing data.
- Assess basal area as a measure of coral growth
- Develop methods to compare basal area measurements to conventional radial measurements

A secondary goal is to use the data from images analysis to address the following:

- Did growth rates differ between years?
- Did growth rates differ between species?
- Did growth rates differ between sites?
- Did growth rates differ with colony sizes?

Data Source

Data for my study were collected as part of a collaborative effort between Caribbean Coral Reef Studies (CCRS) at the University of Wisconsin-Superior (UWS) and the Caye Caulker Marine Reserve (CCMR) and its supporting agencies in Belize, C.A.

The CCMR was established 1999. This 9,670-acre reserve includes the Caribbean Sea surrounding the northern end of Caye Caulker and that portion of the Belize Barrier Reef system that lies to the east and southeast of the island between the Caye Chapel Channel and the North Channel (Fig. 1).

CCRS is a long-term undergraduate research program at UWS established in 1991 under the direction Dr. Edward Burkett. In January 2002, CCRS set up new monitoring sites in the CCMR. Ten sites were selected on back reef and lagoon patch reefs in the CCMR (Fig. 1) based on one or more of the following criteria:

- The reef community was representative of the general area.
- The site contained living coral, but damage from various sources (e.g., hurricanes, boat traffic, etc.) was evident.
- The site had the potential to be used by tourists.
- The site was located near sources of potential environmental impact.

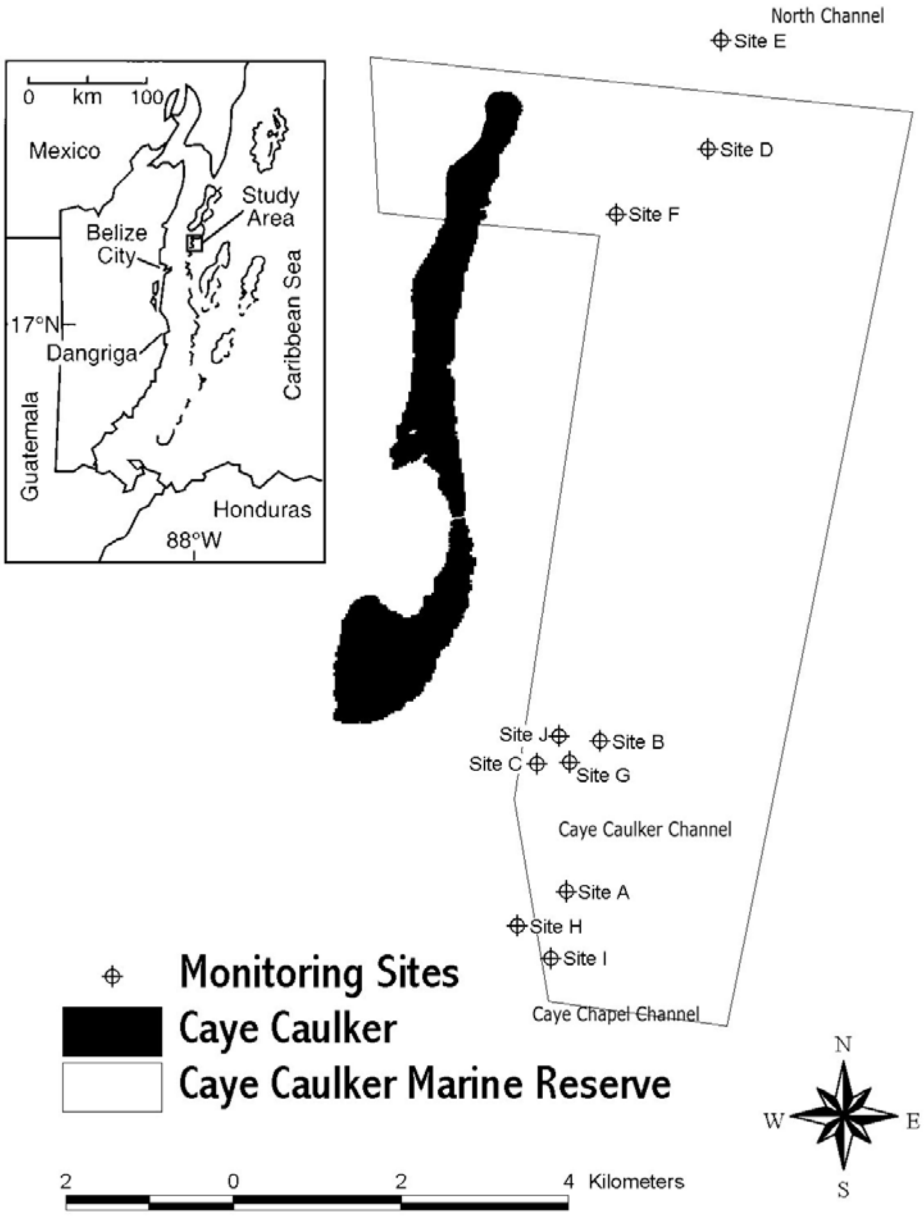


Figure 1. Map of Monitoring Sites Referenced in the Study

Sites A, H and I, near the Caye Caulker and Caye Chapel channels, sites B, C, G and J, near the most developed areas on Caye Caulker, and sites F and E, at maximum distance from the developed areas on Caye Caulker, are typical of the *M. annularis*-

dominated patch reefs in the CCMR. Site D, on the back reef, is typical of areas where large *Acropora palmata* stands were formerly common. Sites E and H are slightly outside the CCMR due to the lack of exact coordinates for the reserve boundaries at the time of site selection.

On each site, a 50-meter transect was laid out with stations at two-meter intervals. These stations were permanently marked and labeled for year-to-year location of sampling quadrats.

Data collected by CCRS indicated post-disturbance recruitment. These reefs appeared to be in an early successional stage (e.g., Grigg and Maragos, 1974; Grigg, 1983) as most of the scleractinian colonies studied were 0 – 4 cm in radius (Burkett et al., 2002). The majority of *M. annularis* colonies measured by Burkett et al. (2002) were also in the 0 – 4 cm range. Growth rate studies indicate that *M. annularis* grows at a rate of approximately 0.4 – 1.2 cm yr^{-1}, radially, depending on environmental conditions (Dustan, 1975; Gladfelter et al., 1978; Hudson et al., 1994; and others). Growing at 1.2 cm yr^{-1}, these colonies would have been approximately 3 years old when measured, indicating that they recruited after Hurricane Mitch and the 1998 bleaching event, but before Hurricane Iris (after Edmunds, 2000).

Porites astreoides Lamarck 1816 grows radially at a rate of approximately 0.2 – 0.7 cm yr^{-1}, dependent on environmental conditions (Gladfelter et al., 1978; Highsmith et al., 1983; Hubbard and Scaturo, 1985; Logan and Tomascik, 1991). Most *P. astreoides* colonies measured by Burkett et al. (2002) had radii in the 0-4 cm range. The implied 0.2 – 0.7 cm yr^{-1} radial increase indicates that it is likely that these colonies also recruited between Hurricanes Mitch and Iris.

2. METHODS

Image Collection

On each site (Fig. 1), a 50-meter transect was laid out with stations at two-meter intervals. These stations were permanently marked and labeled for year-to-year location of sampling quadrats. Each January in 2002, 2003 and 2004, CCRS divers drew maps of each quadrat (Fig. 2). A 0.5-m^2 (70.7cm x 70.7cm) reference frame, made from ¾- inch PVC pipe and strung with a heavy monofilament nylon reference grid, was placed on the substrate at each tag on the transects, taking care to align the grid with the axis of the transect. All life forms were drawn to scale, identified and recorded on Mylar® data forms which were pre-printed with a grid matching that of the reference frame (Fig. 3). A short video sequence of each quadrat was recorded using a Canon Elura 10® digital video camera mounted in a Quest DH-3P Delfin Pro® underwater housing. Where depth allowed, the camera view angle was held perpendicular to the quadrat at the minimum distance that allowed the entire reference frame to be included in the image. In shallower locations where it was not possible to include the entire reference frame in the image, the quadrats were videographed in sections. The video sequences recorded by CCRS were examined and the one best frame for each quadrat was captured as a JPEG image using Adobe Premier®. For quadrats where the depth was too shallow for a single image, several partial images of the quadrat were captured.

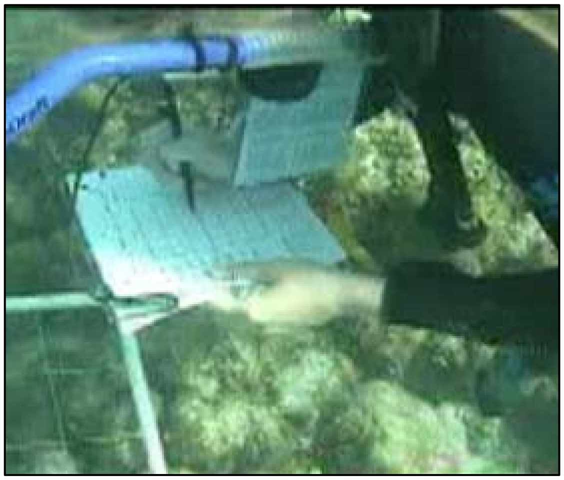


Figure 2. CCRS diver mapping a quadrat.

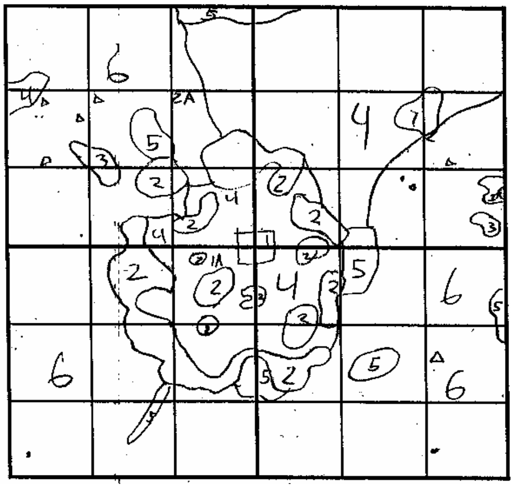


Figure 3. CCRS quadrat map. Numbers and symbols indicate coverage type.

Image Selection

The images vary in quality. Only those with proper focus, lighting and orientation were selected for analysis. Furthermore, only quadrats with images from all years were included in the study so that the fate of individual coral colonies could be tracked. No suitable images from site A were available. Among the images that were suitable for analysis, only *M. annularis* and *P. astreoides* colonies appeared in numbers sufficient to yield meaningful information. Therefore, my study included only these species. A total of 162 quadrats (54 from each year) were selected for image analysis.

The images of the quadrats were processed using Adobe Photoshop®. For the shallow quadrats represented by multiple images, a single complete image was assembled by scaling and edge-matching the partial images. For each quadrat image, contrast and color were optimized for edge definition, and a measurement scale was determined by measuring the distance in pixels between the sides of the reference frame along the grid line that best represented the scale of the quadrat. In some cases the tension of the grid caused the sides of the frame to distort. In images where this had happened, it was necessary to draw lines from corner to corner along the sides that are perpendicular to the measurement axis in order to obtain an accurate scale (Fig. 4).

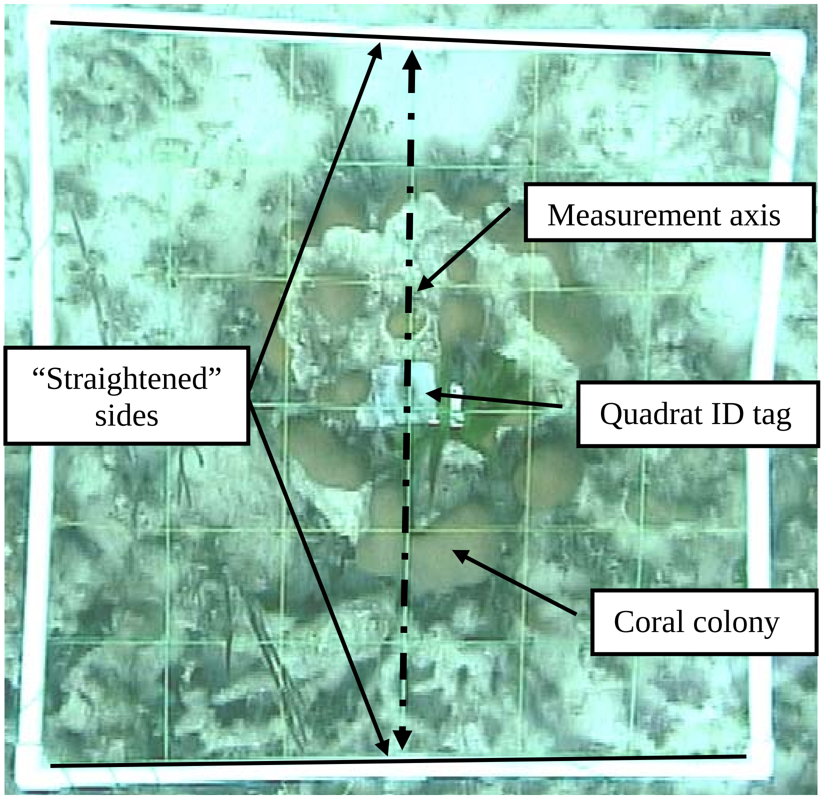


Figure 4. Image of quadrat with reference frame and grid

A transparent layer was then added to the image, on which each colony under study was labeled and outlined, resulting in a monochrome polygon representing the area of the colony (Fig. 5). The quadrat maps corresponding to selected images were used to aid species identification where necessary. Any areas not covered by the colony, but completely bounded by the colony (e.g., dead spots, cover by other organism, etc.) were also outlined so that they were not included in the basal area calculation. This layer was then exported as a bitmap image for use in calculating basal area. Only colonies that were completely visible in images from all years were analyzed. A total of 915 colonies (305 from each year) were analyzed.

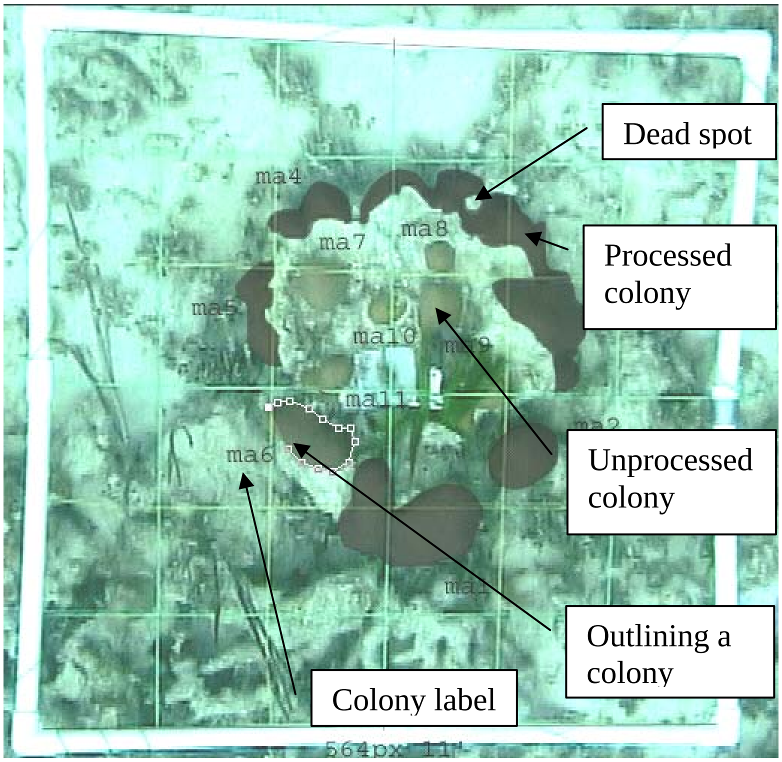


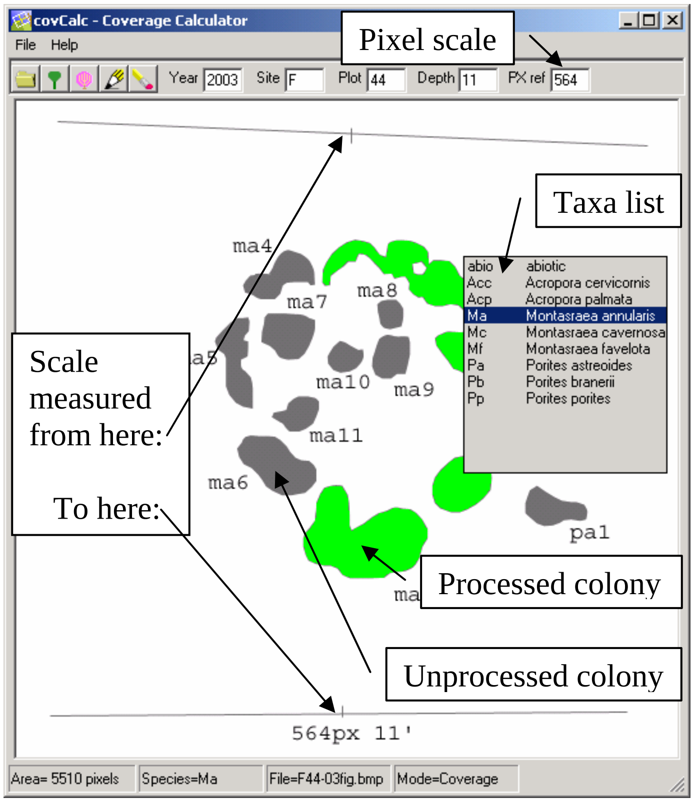
Figure 5. Partially processed image of a quadrat.

Basal areas of the colonies in the images were measured using a software application designed and developed by Burkett and Gustafson (1995) and modified for this project (Fig. 6). The pixels that were part of each polygon representing a colony were identified using a seed-fill, four-nearest-neighbor algorithm (Heckbert, 1990). A record of the year, site, quadrat, species, identification number, area (in pixels) and scale for each colony was written to a file for further analysis.

Basal area, in cm^2, and growth rate, in cm yr^{-1}, were calculated using the output files from the area-measurement application and Microsoft Excel®. Basal area was calculated as $colonyPixels \frac{quadArea}{imageScale^2}$ where *colonyPixels* represents the number of pixels contained in a colony polygon, *quadArea* is the area of the quadrat in cm^2, and *imageScale* is the distance between the sides of the quadrat in pixels. The quadrat size for this study is 0.5m^2 or 5000cm^2. Annual growth rate was calculated as

$$\frac{\sqrt{\dfrac{basalArea_{year}}{\pi}} - \sqrt{\dfrac{basalArea_{year-n}}{\pi}}}{n}$$

, where $basalArea_{year}$ is the basal area of a colony in cm^2 for a particular year and n is the number of years for which the rate is calculated. The growth rate is essentially the change in radius of a colony's basal area, assuming that the colony is approximately circular.



Year 2003 Site F Plot 44 Depth 11 PX ref 564

abio	abiotic
Acc	Acropora cervicornis
Acp	Acropora palmata
Ma	Montasraea annularis
Mc	Montasraea cavernosa
Mf	Montasraea favelota
Pa	Porites astreoides
Pb	Porites branerii
Pp	Porites porites

Area= 5510 pixels | Species=Ma | File=F44-03fig.bmp | Mode=Coverage

Figure 6. Screen shot of area measurement application.

Size Classification

Individual colonies were assigned to one of three classes based on size. Edmunds et al. (1998) considered colonies less than approximately 5cm in diameter to be recruits. Using this as the threshold for the small size class, again, making the assumption that individual colonies are more or less circular, colonies less than 20cm^2 in basal area ($diameter = 2\sqrt{\frac{basalArea}{\pi}}$) were classified as small. Size classes medium and large were arbitrarily chosen to represent colonies where diameter was greater than or equal to 5cm and less than 10cm, and colonies where diameter was greater than or equal to 10cm, respectively.

Data Analysis

To determine whether to use parametric or nonparametric statistical tests in the data analysis, the data were tested for meeting the assumptions of the parametric tests. Data assumptions for the parametric test, between-subjects ANOVA, are a normal distribution and homogeneity of variance. The growth-rate data for the 2002-03, 2003-04 and 2002-04 time periods were tested for normality of distribution using the Kolmogorov-Smirnov test, and for homogeneity of variance using Levene’s test. The tests indicated that none of the distributions for the three time periods were normal, but that the variance was homogenous.

To determine whether the distribution had a significant effect on the analysis, one-way ANOVA, and Kruskal-Wallis tests were run on growth rate vs. time period. The ANOVA reported no significant differences while the Kruskal-Wallis test did, demonstrating a distribution effect.

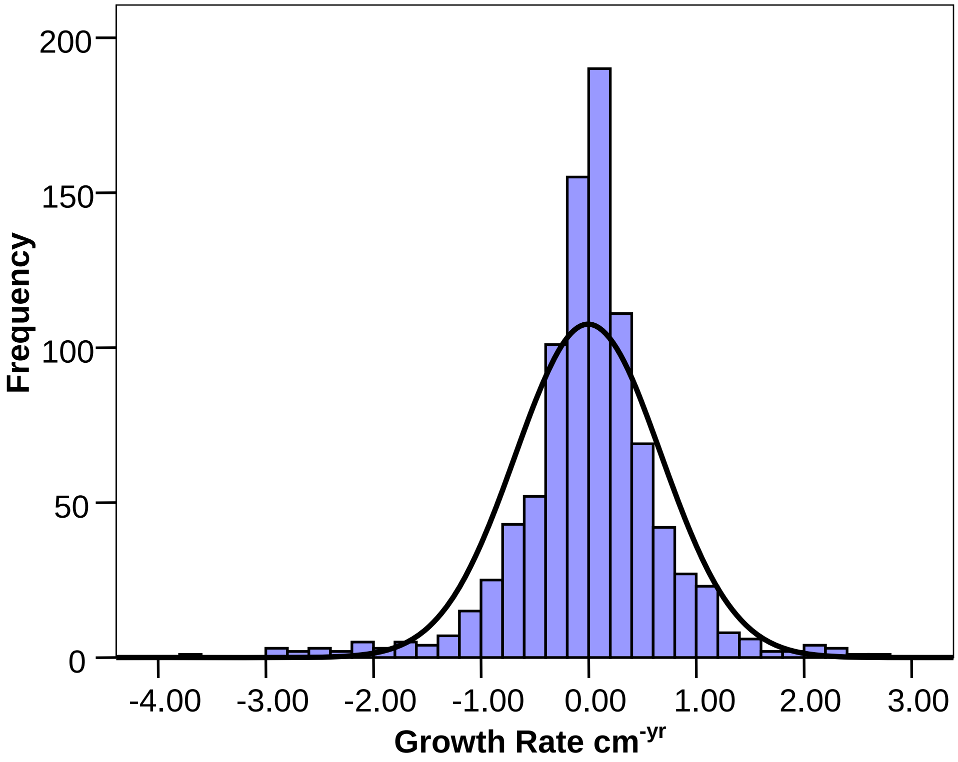


Figure 7. Growth rate distribution with normal curve superimposed.

The growth-rate data included many negative and zero values (Fig. 7). In order to natural-log transform these data, the absolute value of the data set's minimum value was added to each value in the data set. These data were then natural-log transformed and tested again with Kruskal-Wallis and ANOVA as described above. The results for ANOVA did not show significant difference, but Kruskal-Wallis did, indicating nonparametric tests were necessary. The process for determining whether to use parametric or nonparametric tests was applied to the data set for growth rate vs. species, growth rate vs. site, and growth rate vs. size class. A majority of these cases also indicated nonparametric tests.

All statistical tests were performed using SPSS® v13.0.

Growth Index Model

A series of one-unit growth rates were modeled for four different shapes, each having a basal area of approximately 40 cm^2 (Fig. 8). The shapes were constructed from simple geometric figures so that basal area increases due to one-unit, omni-directional growth could be readily calculated. One-unit growth was modeled by increasing the radii of circular portions of each shape by one unit and calculating its area and perimeter accordingly.

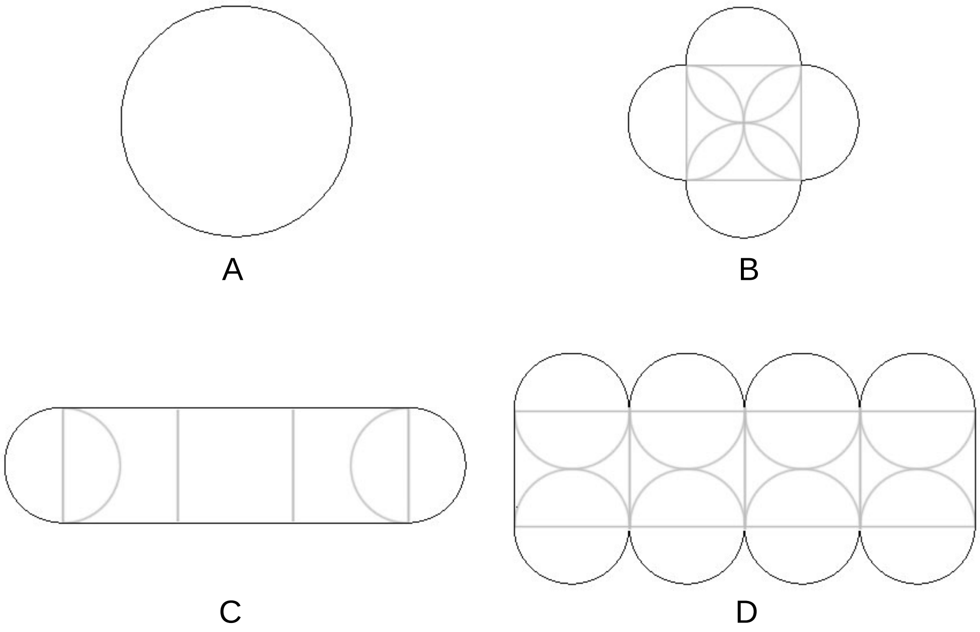


Figure 8. Basal-area shapes used in the growth-index models. "Shadow" lines added to show basic shapes used to construct the figures. One-unit growth was modeled by increasing the radii of circular shapes by one unit and calculating the area and perimeter accordingly.

For shape A (Fig. 8A), a perfect circle, the area and perimeter were calculated as πr_i^2 and $2\pi r_i$, respectively, where r_i where is radius for the model iteration.

Shape B (Fig. 8B) was constructed from four circles of radius r_i and one square with side lengths of $2r_0$ where r_0 is radius for the first model iteration (Fig. 9). The figure area was calculated as $4\mathit{circleArea} - \mathit{chord}^2$ where *circleArea* is the area of one of the circles, and *chord* is the distance between intersections of adjacent circumferences. The figure perimeter was calculated as $4\,\mathit{sectorArc}$ where *sectorArc* is the length of and arc circumscribing a sector, with a chord length of *chord*, of one of the circles.

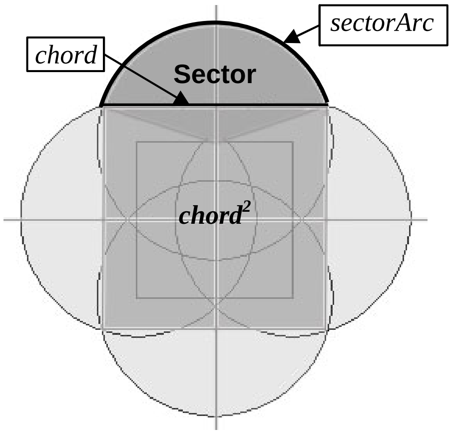


Figure 9. Construction of Figure 8B.

Shape C (Fig. 8C) was constructed from two semicircles of radius r_i and three squares with side lengths of $2r_i$. The figure area was calculated as $\mathit{circleArea} + 2r_0 6r_i$ where *circleArea* is the area of the two semicircular portions combined. The figure perimeter was calculated as $\mathit{circumf} + 12r_0$, where *circumf*, calculated as $2\pi r_i$, is the circumference of the figure's two semicircles combined.

Shape D (Fig. 8D) was constructed from eight semicircles of radius r, two squares with side lengths of $2r_0$, and two rectangles with lengths of $r_0 + r_i$ and widths of $2r_0$ (Fig. 10). The figure area was calculated as $4\,circleArea - 3\,overlapArea + rectangle$ where *circleArea* is the combined area of two of the figure's semicircles, *overlapArea* is the area where two circles, each constructed from two semicircles, overlap, and *rectangle* is the rectangular area between the semicircles, and was calculated as $(6r_0 + 2r_i)2r_i$. The figure perimeter was calculated as $4\,circumf - 6\,overlapArc + 4r_0$ where *circumf* is the combined circumference of two semicircles, and *overlapArc* is the segment of the circumference of this hypothetical circle that overlaps an adjacent hypothetical circle.

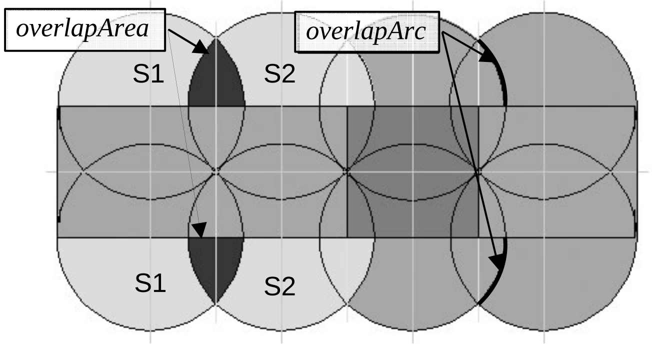


Figure 10. Construction of Figure 8D. S1 and S2 are the parts of the overlapping circles.

Growth Index

The growth index was computed as $\frac{adjRadius_{p} - adjRadius_{p-n}}{n}$ where *adjRadius* is a radius adjusted to reflect the area-to-perimeter relationship, p is the time period for which the index was calculated for a particular colony, and n is the number of years between time periods. *AdjRadius* was calculated as $\sqrt{\frac{circ \times basalArea}{\pi}}$ where *circ* is the circularity of *basalArea*, the basal area of a coral colony. Circularity is a measure of how close the shape being measured is to a perfect circle. A perfect circle has a circularity value of 1.00 while values for non-circular shapes are less than 1.00, with the least circular having the lowest value. Circularity is calculated as $4\pi \frac{basalArea}{perimeter^{2}}$ where *basalArea* and *perimeter* are the basal area of coral colony and its perimeter, respectively. The growth index is essentially a “radius” adjusted to more accurately give a growth rate appropriate for the shape of the basal area.

The correlation between area increase and perimeter was analyzed using the Pearson two-tailed correlation test. The correlation between measured basal-area-increase and modeled basal-area-increase was analyzed with the same test.

Hypothesis testing

The hypotheses tested are as follows:

Basal area increase and perimeter are not correlated, H_0: p = 0.0

Basal area increase and perimeter are correlated, H_a: $p \neq 0$

Modeled basal-area-increase and measured basal-area-increase are not correlated,

H_0: p = 0.0

Modeled basal-area-increase and measured basal-area-increase are correlated,

H_a: p $\neq$ 0

Mean growth rates did not differ between years, H_0: $\mu_{\text{year1}} = \mu_{\text{year 2}}$

Mean growth rates differed among years, H_a: $\mu_{\text{year 1}} \neq \mu_{\text{year 2}}$

Mean growth rates did not differ among species, H_0: $\mu_{\text{species 1}} = \mu_{\text{species 2}}$

Mean growth rates differed among species, H_a: $\mu_{\text{species 1}} \neq \mu_{\text{species 2}}$

Mean growth rates did not differ among sites, H_0: $\mu_{\text{site 1}} = \mu_{\text{site 2}}$

Mean growth rates differed among sites, H_a: $\mu_{\text{site 1}} \neq \mu_{\text{site 2}}$

Mean growth rates did not differ among size classes, H_0: $\mu_{\text{size 1}} = \mu_{\text{size 2}}$

Mean growth rates differed among size classes, H_a: $\mu_{\text{size 1}} \neq \mu_{\text{size 2}}$

3. RESULTS

Growth Rate

Mean growth rate for *M. annularis* ranged from -0.05 cm yr^{-1} for 2002-03 to 0.09 cm yr^{-1} for 2003-04 (Fig. 11). The overall rate (2002-04) was 0.02 cm yr^{-1}. Kruskal-Wallis tests showed significant differences in growth rates between time periods for *M. annularis.* The growth rate 2002-03 was less than the rate for 2003-04 (p=0.002). The rate for 2003-04 was greater than the rate for 2002-04 (p=0.031). The rate for 2002-03 was less than the rate for 2002-04 (p=0.046).

For *P. astreoides* growth rates ranged from -0.22 cm yr^{-1} for 2002-03 to -0.19 cm yr^{-1} for 2002-03. The overall rate (2002-04) was -0.20 cm yr^{-1}. Kruskal-Wallis tests showed no significant differences in growth rates between time periods for *P. astreoides* (Fig. 11).

Note that 2002-04 values are not averages of the 2002-03 and 2003-04 values. The 2002-04 values are derived from direct comparison of the 2002 and 2004 basal area values.

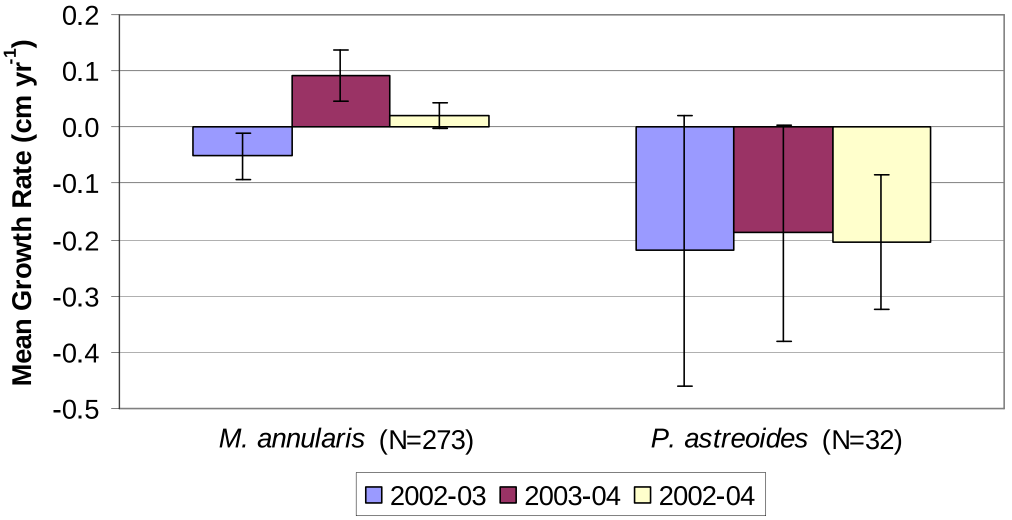


Figure 11. Mean growth rate (cm yr^{-1} radial skeletal increase) for *M. annularis* and *P. astreoides* colonies by time period ± SE[‡]. Data in appendix E.

Mean growth rates for *M. annularis* plotted by site and time span showed a wide range of values. Values for *M. annularis* were generally positive and less extreme (Fig. 12) than the values for *P. astreoides*, which were generally negative (Fig. 13). Kruskal-Wallis tests showed significant differences in the rates between years. The rate for 2002-03 was greater than the rate 2003-04 for site B (-0.37 cm yr^{-1} vs. 0.36 cm yr^{-1}, p=0.000), site F (-0.16 cm yr^{-1} vs. 0.14 cm yr^{-1}, p=0.009) and G (-0.39 cm yr^{-1} vs. 0.41 cm yr^{-1}, p=0.000), and less than the rate 2003-04 for site H (0.29 cm yr^{-1} vs. -0.06 cm yr^{-1}, p=0.029). The 2003-04 rate was greater than the 2002-04 rate for sites B (0.36 cm yr^{-1} vs. 0.00 cm yr^{-1}, p=0.000) and G (0.36 cm yr^{-1} vs. 0.01 cm yr^{-1}, p=0.005). The 2002-04 rate was less than the 2002-04 rate for sites B (-0.37 cm yr^{-1} vs. 0.00 cm yr^{-1}, p=0.000) and G (-0.39 cm yr^{-1} vs. 0.01 cm yr^{-1}, p=0.013).

[‡] Error bars represent ± standard error. Data from image analysis was statistically analyzed with non-parametric tests. It is possible that error-bar overlap can occur where there is a statistically significant difference.

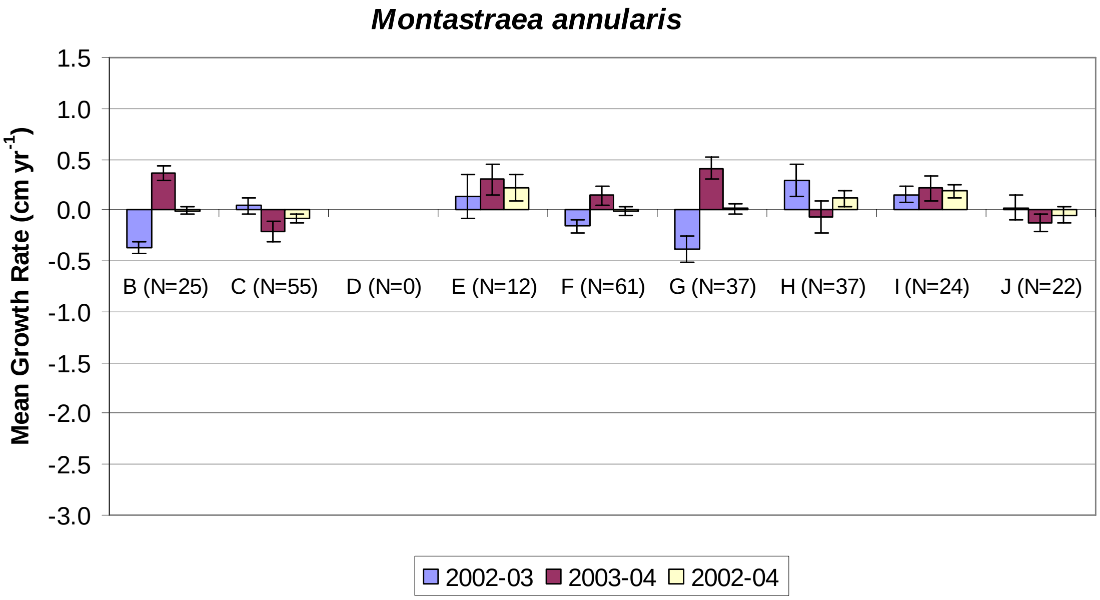


Figure 12. Mean growth rate (cm yr^{-1} radial skeletal increase) for *M. annularis* colonies by site and time span ± SE (There were no *M. annularis* colonies measured at site D). Data in appendix F.

Figure. 13 shows growth rates for *P. astreoides* plotted by site and time span. There were no significant differences in growth rates between time periods.

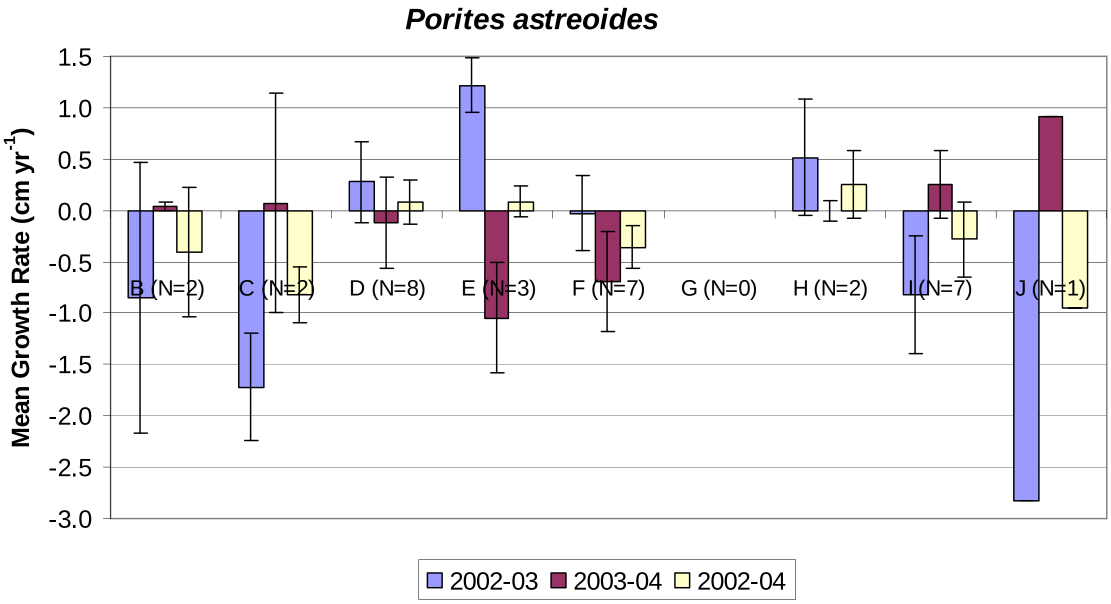


Figure 13. Mean growth rate (cm yr^{-1} radial skeletal increase) for *P. astreoides* colonies by site and time span ± SE (There were no *P. astreoides* colonies measured at site G; only one *P. astreoides* colony was measured at site J so SE was not calculated). Data in appendix F.

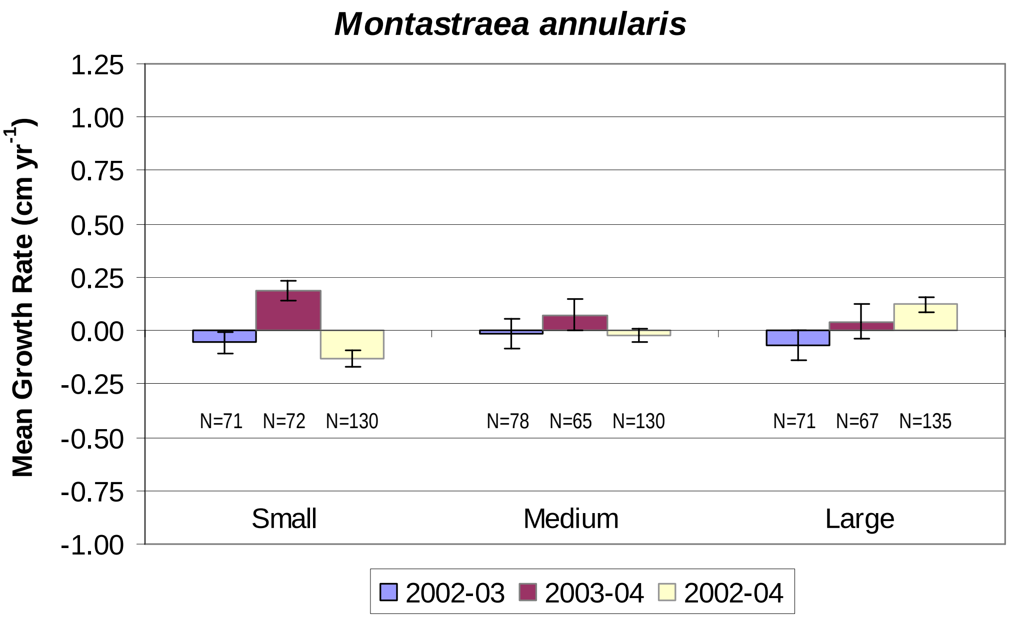


Figure 14. Mean growth rate (cm yr^{-1} radial skeletal increase) for *M. annularis* colonies by size class and time period ± SE (Small=diameter < 5cm, Medium=diameter >= 5cm and < 10cm, Large=diameter >= 10cm). Data in appendix G.

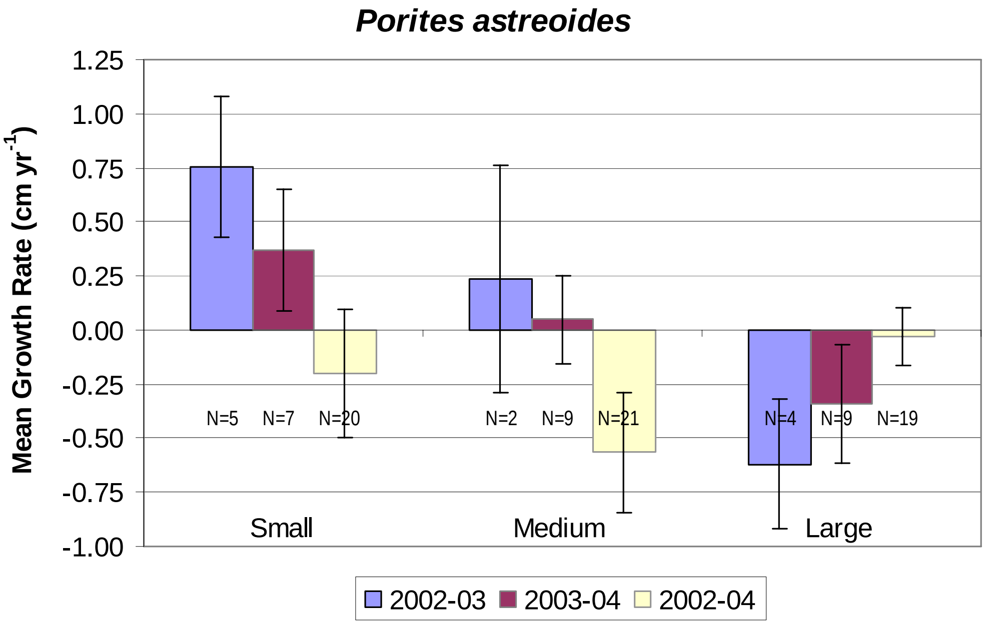


Figure 15. Mean growth rate (cm yr^{-1} radial skeletal increase) for *P. astreoides* colonies by size class and time period ± SE (Small=diameter < 5cm, Medium=diameter >= 5cm and < 10cm, Large=diameter >= 10cm). Data in appendix G.

Kruskal-Wallis tests showed significant differences in growth rates by size classes between time periods (Fig. 14, 15). For Small *M. annularis* colonies the rate for 2002-03 was less than the rate for 2003-04 (-0.05 cm yr^{-1} vs. 0.19 cm yr^{-1}, p=0.001) and the rate for 2003-04 was greater than the rate for 2002-04 (0.19 cm yr^{-1} vs. -0.13 cm yr^{-1}, p=0.000). For Medium *M. annularis* colonies the rate for 2002-03 was greater than the rate for 2003-04 (-0.02 cm yr^{-1} vs. 0.07 cm yr^{-1}, p=0.043), the rate for 2002-03 was greater than the rate for 2002-04 (-0.02 cm yr^{-1} vs. -0.03 cm yr^{-1}, p=0.382) and the rate for 2003-04 was greater than the rate for 2002-04 (0.07 cm yr^{-1} vs. -0.03 cm yr^{-1}, p=0.022). For Large *M. annularis* colonies the rate for 2002-03 was less than the rate for 2003-04 (-0.07 cm yr^{-1} vs. 0.04 cm yr^{-1}, p=0.357), the rate for 2002-03 was less than the rate for 2002-04 (-0.07 cm yr^{-1} vs. 0.12 cm yr^{-1}, p=0.052) and the rate for 2003-04 was less than the rate for 2002-04 (0.04 cm yr^{-1} vs. 0.12 cm yr^{-1}, p=0.271).

Kruskal-Wallis tests showed no significant differences in growth rates for *P. astreoides* size classes between time periods.

Modeling

Pearson correlation coefficient for basal-area increase vs. perimeter for shapes A (circle), B (elongate capsule), C (four-lobe) and D (elongate eight-lobe) were 1.00 (p=0.000), indicating a strong positive relationship (Fig. 16). Pearson correlation coefficient for modeled basal-area increase vs. measured basal-area increase was 0.986 (p=0.000) for shape A, 1.000 (p=0.000) for shapes B and C, and 0.990 (p=0.000) for shape D, indicating a strong positive relationship here as well (Fig. 17).

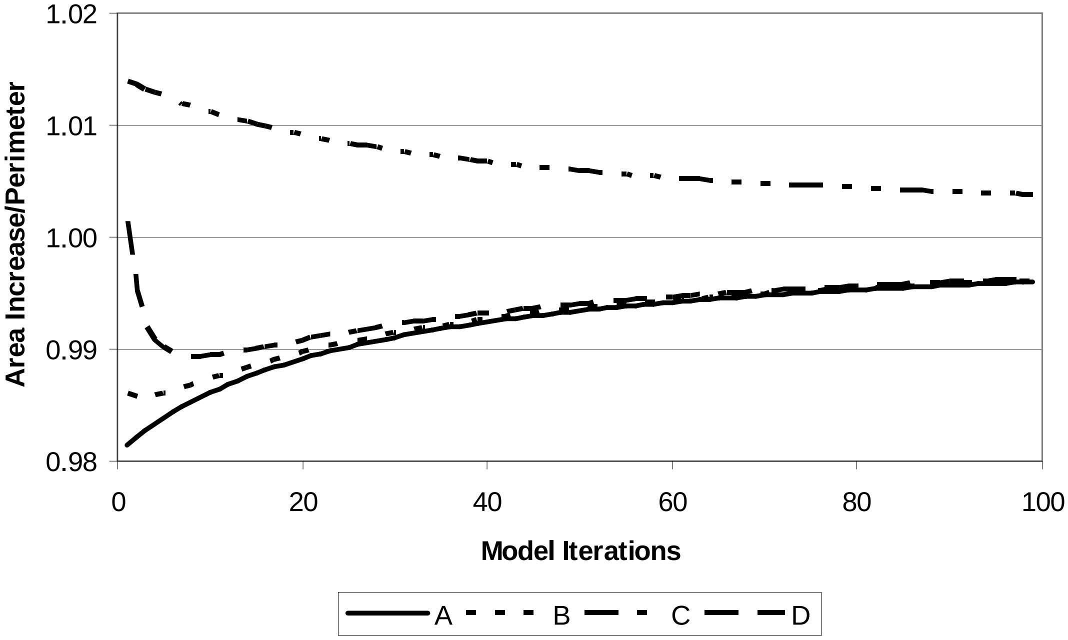


Figure 16. Ratio of basal area increase to perimeter for one-unit growth rate. A, B, C and D correspond to the shapes in Figure 7.

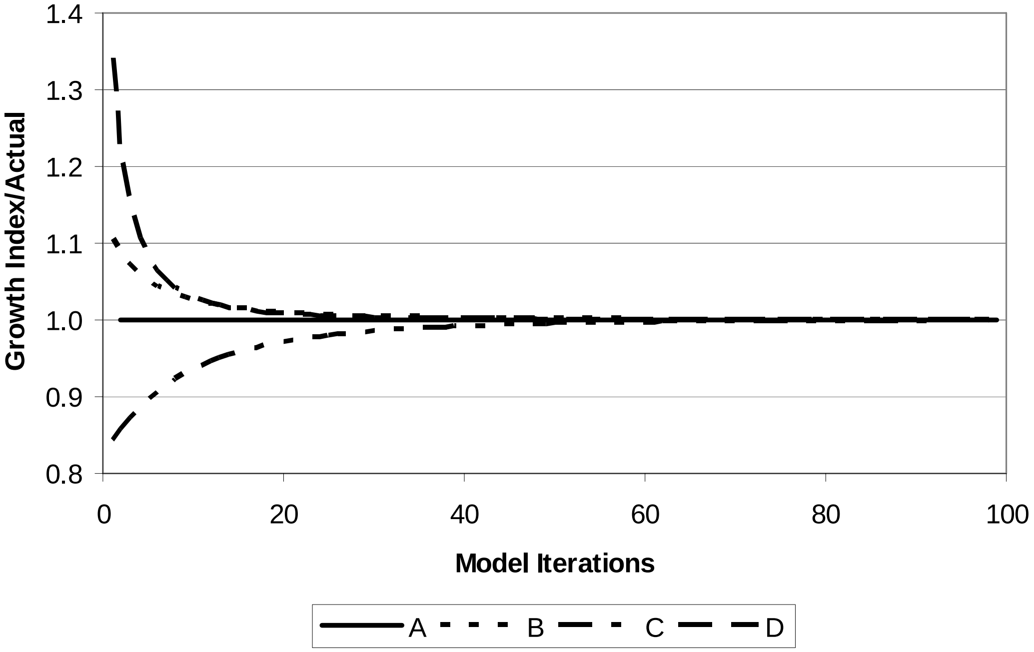


Figure 17. Ratio of growth-index-cacluated basal area increase to actual basal area increase for one-unit growth rate. A, B, C and D correspond to the shapes in Figure 7.

4. DISCUSSION

Coral Growth Rate

It was clear during the analysis that images from 2003 were the most variable in quality which made it difficult to obtain an accurate scale in many cases. This is likely a key reason that the 2002-03 and 2003-04 time periods showed more variability in the values calculated from basal area than did the 2002-04 time period. Also, my data were collected for basal-area measurement and due to the limited number of suitable images available, random image selection was not possible. Therefore, my data represent only those selected images and should not be interpreted to represent the conditions in the field.

Data for *M. annularis* from sites E, H and I share attributes. The coral colonies measured at these sites had the highest overall mean growth rates and the majority of these colonies were in the Large size class (greater than 10cm in diameter). All three sites are close to channels in the barrier reef. Site E is on the southern margin of the North Channel. Sites H and I are located just north of the Caye Chapel Channel and just south of the Caye Caulker Channel.

Nutrient uptake, gas exchange, and feeding depend on the flow of water over and around the coral (Goldshmid et al., 2004). Historically, growth may have been enhanced by the channels' tidal currents, delivering nutrient necessary for growth in the form of plankton, and maintaining better water quality and stabilizing surface temperatures with daily tidal flushing.

It is widely accepted that scleractinian mortality is inversely related to size (Edmunds and Gates, 2004). Perhaps the larger colonies at these sites were able to survive disturbances better than their smaller counterparts. However, the larger colonies assessed at these sites also could be an artifact of image selection.

My data from sites C, F and I had the highest mean basal areas for *P. astreoides*. Data from Sites C, F and I had neither the highest overall mean change-in-basal-area rates nor the highest overall mean growth rates. Data from Site H had the highest rates for these measures with those from sites D and E tied for second place. Data from these three sites also were unique in that they showed positive change in basal area and growth while mean basal-area data from other the other sites declined. *Porites astreoides* is an opportunistic species capable of withstanding higher nutrient and sediment loads than *M. annularis* (Tomascik and Sander, 1987; Martin, 1998). This could account for the some of the difference in the distribution of *P. astreoides* and *M. annularis*. Site C is closest to Caye Caulker Village and could be affected by nutrient runoff and sediment resuspended by boat traffic, favoring *P. astreoides*. Another possible explanation of the distribution is that there is less competition for space at Site C. The higher basal area change and growth rates for *P. astreoides* at sites E and H could be due to the phenomena that affect *M. annularis* at these sites. Again, differences must be interpreted with caution, as , they may simply be artifacts of image selection.

The published growth rates for *M. annularis* are approximately 1 cm yr-1, radially (Table 1). Published rates for *P. astreoides* are approximately half of that (Table 1). The growth rates measured in this study for these species were 0.02 cm yr^{-1} and -0.20 cm yr^{-1}, respectively.

Improvements to Methods and Recommendations for Further Research

Growth index

A subset of the images used in my study was reanalyzed to obtain perimeter data for each colony so that circularity and growth index could be calculated. When growth indices were computed for these colonies, it became apparent that a significant change in circularity for a particular colony over a time period affected the results to the point where the growth rates were unusable (see Buddemeier and Kinzie, 1976.). Significant changes in basal circularity are not uncommon in coral colonies. Disease and trauma can change the shape of colony dramatically. Therefore, only growth rates of colonies that maintain approximately the same basal shape between measurements should be used for comparison with growth rates from “traditional” studies.

Image analysis

Image analysis measures horizontal skeletal extension while the harvesting and coring methods generally measure skeletal extension along the axis of maximum extension. This discrepancy makes it difficult to compare results of other growth studies to this study. Hubbard and Scaturo (1985) used a multi-axis method measuring skeletal extension along the maximum (vertical at depths less than approximately 20 m), intermediate and minimum (horizontal) growth axes. They show growth rates plotted against depth with the rates for the minimum-growth axis and the mean of the maximum-and minimum-growth axes falling below those of the single-axis (maximum growth) method at depths less than approximately 30 m (Fig. 18). This demonstrates that the horizontal-axis growth rates are considerably less that those for the vertical axis in this depth range. The difference between maximum- and minimum-axis growth rates shown is approximately 25 percent. Increasing the mean overall growth rates from this study by 25 percent would make the rate for *M. annularis* 0.03 cm yr^{-1} and the rate for *P. astreoides* 0.05 cm yr^{-1}, a little closer to agreement with published growth rates for these species but still quite low.

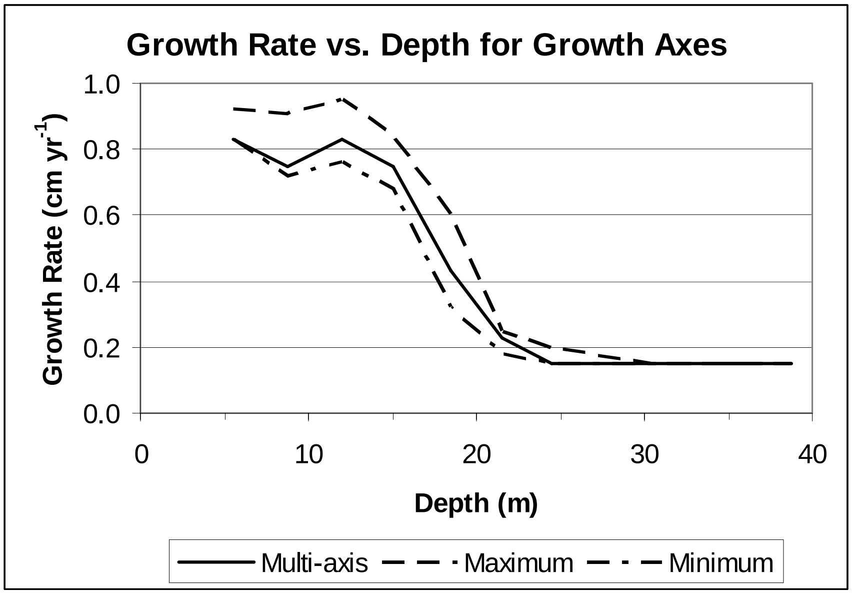


Figure 18. Growth rate vs. depth for growth axes. Multi-axis = average of minimum, intermediate and maximum axes. After Hubbard and Scaturo, 1985.

Measuring skeletal extension from cores and cross-sections cannot detect decreases in colony size, while image analysis can, as my study demonstrates. The distribution of growth-rate-area data shows that more than half the mean values were less than zero (Fig. 7). In the context of comparing growth rates with those in the literature, negative growth rates are meaningless. If growth rates are calculated only where change in basal area is non-negative, the rate for *M. annularis* is 0.41 cm yr^{-1} and the rate for *P. astreoides* is 0.61 cm yr^{-1}. Increasing these rates by 25 percent to simulate vertical growth would make the rates 0.51 cm yr^{-1} and 0.77 cm yr^{-1}, respectively. These values are comparable to published growth rates (Table1).

Image Quality

Connell, at al. (1997) reported that they were able to identify objects greater than 0.5 cm^2 in area. The smallest objects identifiable in images used in this study were approximately 2 cm^2 in area. The images of the CCRS quadrats were of varying quality in terms of lighting, focus, framing and collimation (perpendicularity to the focal plane). This being a dataset of opportunity, there was no control of these image-quality parameters. These images were originally intended to be a photographic record of the quadrats of which hand-drawn, *in-situ* maps were created for the CCRS study. While useful for this purpose, many proved unsuitable for the kind of detailed image analysis needed for my study. For species-specific growth, measurements of individual colonies for each year were required, further restricting the pool of suitable images. Furthermore, the cost of digital photography equipment at the time the images were acquired prohibited the use of a sufficiently large pixel matrix to capture the fine detail needed for accurate and precise analysis.

High-resolution equipment is now more affordable. CCRS returned to Caye Caulker in January 2005 to continue the long-term study. The photographic equipment used on this expedition, a Canon PowerShot A95 with an Ikelite #6140.80 housing, was far superior to that used previously and of lower cost. With its five-mega-pixel resolution and automatic focus, the camera was able to capture the 0.5m^2 quadrats, in ambient light, at an image size of 2,272 X 1,704 pixels, with the detail required for the identification of most scleractinians. A skilled photographer could capture close-up images with detail sufficient to identify virtually all visually identifiable species.

The major difficulty with image analysis is the lack of depth inherent in any two-dimensional representation of three-dimensional objects. The difference between actual basal area and apparent basal area can be significant in images of groups of objects with the amount of relief that can be encountered over short distances on a coral reef. Another problem encountered in image analysis is collimation error. Again, the actual basal area and the apparent basal area may be significantly different if the sight axis is not perpendicular to the plane of reference for the image. The use of dual cameras mounted on a framework could be employed to produce stereo images that could be analyzed using ray tracing and triangulation to measure depth of field. If the proposed framework had a leveling system, collimation error could also be corrected. Spring-loaded, telescoping leg extensions at the corners of the frame base with lock/unlock controls at the top of the frame, in combination with a spirit-bubble level indicator, would allow for quick and precise photography in less than optimal conditions.

Working in shallow water may prevent capturing the entire quadrat (or other subject) in one image. An accurate and relatively fast method of assembling a mosaic of image “tiles” would also be of significant benefit. Adding a height adjustment to the proposed framework so that the cameras could be raised and lowered to suit depth would allow “tiled” quadrat images to be matched easily and accurately

Basal-area Variability

Basal area appears to be a very dynamic parameter. My data show that there is substantial growth and mortality of massive scleractinians but the mean growth rates suggest very little change. High temporal and spatial variability in physiological responses, including growth or lesion healing, may be a characteristic of corals under stress, as reported by Fisher et al. (in press).

5. CONCLUSIONS

Coral Growth Rates

Mean growth rates (radial skeletal extension) for *M. annularis* and *P. astreoides* were 0.02 cm yr^{-1} and -0.20 cm yr^{-1}, respectively. By removing negative values and correcting by 25% to allow for comparison with vertical growth rates, mean values increased to ~0.5 cm yr^{-1} for *M. annularis* and ~0.8 cm yr^{-1} for *P. astreoides.*

Did species-specific growth rates differ between years?

- There were statistically-significant differences in mean growth rate for *M. annularis*. The rate for 2002-03 was greater than the rate for 2003-04 while the 2003-04 was less than the rate for 2002-04.
- The limited sample size did not reveal statistically significant differences in mean growth rate for *P. astreoides* between years.

Did species-specific growth rates differ between species?

- The overall mean growth rates for *M. annularis* and *P. astreoides* were not significantly different.

Did species-specific growth rates differ between sites?

- There were statistically-significant differences for *M. annularis* between site E and sites C and J, between site H and Site C, and between site I and sites B, C, F and G.
- The limited sample size did not reveal statistically differences in growth rates for *P. astreoides* among sites.

Did species-specific growth rates differ with colony sizes?

- There were no statistically significant differences between size classes for *M. annularis* or *P. astreoides*.

Thus, the image analysis methods detected significant differences. However, the process of selection of images was not random, thereby limiting the applicability of these results to the images analyzed. Results should not be used to interpret conditions at sites from which the images were collected.

Image analysis

- Image analysis is useful as a coral growth measure. Its utility, however, depend on image quality. Proper resolution, focus, lighting, collimation and measurement scale are critical for precise measurements.
- The proposed growth index yields growth rates more comparable to growth rates from “conventional” studies. Particular attention must be paid to changes in colony basal shapes between measurements. Substantial change in circularity can render the measurements meaningless. Also, growth indices for elongate-shaped colonies are less comparable to published rates

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APPENDICES

Appendix A. Combined mean measured basal area (cm^2) for *M. annularis* and *P. astreoides* by site and year ± standard deviation

		Year			
Site	**N**	**2002**	**2003**	**2004**	**Total**
B	27	56.70±68.62	47.41±62.17	56.74±75.48	53.62 ± 68.25
C	57	62.58±60.60	61.58±56.06	57.58±58.53	60.58 ± 58.12
D	8	55.38±17.93	63.00±21.91	60.50±25.41	59.63 ± 21.24
E	15	106.13±84.33	115.67±78.12	123.67±94.53	115.16 ± 84.26
F	68	83.01±142.81	80.71±150.18	82.94±165.95	82.22 ± 152.53
G	37	60.27±56.36	48.65±42.29	62.03±59.98	56.98 ± 53.27
H	39	244.46±378.32	258.97±386.70	258.62±399.95	254.02 ± 385.12
I	31	122.52±216.15	121.65±234.77	135.84±268.67	126.67 ± 238.30
J	23	108.17±105.38	106.57±114.20	104.52±114.66	106.42 ± 109.85
Total	305	101.08±181.83	100.46±189.02	104.23±200.66	101.92 ± 190.46

Appendix B. Mean measured basal area (cm^2) for *M. annularis* and *P. astreoides* by site and year ± standard deviation

			Year			
Species	**Site**	**N**	**2002**	**2003**	**2004**	**Total**
M. annularis	**B**	25	58.48±70.99	49.68±64.09	59.72±77.73	55.96 ± 70.33
	C	55	58.64±55.86	60.25±56.03	55.58±56.54	58.16 ± 55.83
	D	0	0.00±0.00	0.00±0.00	0.00±0.00	0.00 ± 0.00
	E	12	119.50±86.03	124.08±81.63	139.67±95.00	127.75 ± 85.64
	F	61	77.00±146.46	74.23±153.87	80.77±174.29	77.33 ± 157.79
	G	37	60.27±56.36	48.65±42.29	62.03±59.98	56.98 ± 53.27
	H	37	255.43±385.57	269.92±394.22	269.51±407.95	264.95 ± 392.46
	I	24	119.79±237.78	128.58±262.07	142.46±298.41	130.28 ± 263.62
	J	22	105.18±106.85	108.36±116.56	104.91±117.34	106.15 ± 111.93
	Total	273	101.42±189.81	101.94±198.06	106.77±210.36	103.38 ± 199.36
P. astreoides	**B**	2	34.50±20.51	19.00±12.73	19.50±12.02	24.33 ± 14.40
	C	2	171.00±113.14	98.00±60.81	112.50±113.84	127.17 ± 84.18
	D	8	55.38±17.93	63.00±21.91	60.50±25.41	59.63 ± 21.24
	E	3	52.67±60.93	82.00±62.75	59.67±72.34	64.78 ± 58.28
	F	7	135.43±98.20	137.14±104.66	101.86±57.42	124.81 ± 86.29
	G		0.00±0.00	0.00±0.00	0.00±0.00	0.00 ± 0.00
	H	2	41.50±13.44	56.50±36.06	57.00±39.60	51.67 ± 25.92
	I	7	131.86±129.38	97.86±107.05	113.14±137.07	114.29 ± 119.58
	J	1	174.00± —	67.00± —	96.00± —	112.33 ± 55.34
	Total	32	98.13±89.94	87.78±77.40	82.56±77.88	89.49 ± 81.34
Grand Total		305	101.08±181.83	100.46±189.02	104.23±200.66	101.92 ± 190.46

Appendix C. Combined mean change in basal area (cm^2 yr^{-1}) for *M. annularis* and *P. astreoides* by site and time period ± standard deviation

		Period			
Site	**N**	**2002-2003**	**2003-2004**	**2002-2004**	**Total**
B	27	-9.30±11.06	9.33±15.30	0.02±6.93	0.02± 13.78
C	57	-1.00±24.84	-4.00±21.46	-2.50±8.96	-2.50± 19.57
D	8	7.63±31.44	-2.50±36.23	2.56±16.04	2.56± 28.22
E	15	9.53±30.55	8.00±25.06	8.77±17.16	8.77± 24.31
F	68	-2.31±22.06	2.24±35.74	-0.04±19.79	-0.04± 26.74
G	37	-11.62±28.06	13.38±26.07	0.88±10.91	0.88± 24.98
H	39	14.51±56.84	-0.36±74.62	7.08±30.63	7.08± 56.80
I	31	-0.87±38.67	14.19±39.62	6.66±32.28	6.66± 37.11
J	23	-1.61±33.21	-2.04±16.36	-1.83±17.71	-1.83± 23.34
Total	305	-0.62±32.86	3.77±37.94	1.58±19.89	1.58± 31.19

Appendix D. Mean change in basal area (cm^2 yr^{-1}) for *M. annularis* and *P. astreoides* by site and time period ± standard deviation

			Period			
Species	**Site**	**N**	**2002-2003**	**2003-2004**	**2002-2004**	**Total**
M. annularis	**B**	25	-8.80± 9.11	10.04± 15.71	0.62± 5.99	0.62± 13.36
	C	55	1.62± 19.75	-4.67± 20.31	-1.53± 7.47	-1.53± 17.01
	D	0	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00
	E	12	4.58± 32.38	15.58± 21.02	10.08± 18.91	10.08± 24.53
	F	61	-2.77± 18.43	6.54± 29.83	1.89± 18.23	1.89± 23.01
	G	37	-11.62± 28.06	13.38± 26.07	0.88± 10.91	0.88± 24.98
	H	37	14.49± 58.27	-0.41± 76.66	7.04± 31.39	7.04± 58.26
	I	24	8.79± 27.24	13.88± 41.66	11.33± 31.43	11.33± 33.57
	J	22	3.18± 24.55	-3.45± 15.24	-0.14± 16.12	-0.14± 19.00
Total		273	0.52± 30.49	4.82± 37.46	2.67± 19.20	2.67± 30.02
P. astreoides	**B**	2	-15.50± 33.23	0.50± 0.71	-7.50± 16.26	-7.50± 18.03
	C	2	-73.00± 52.33	14.50± 53.03	-29.25± 0.35	-29.25± 51.39
	D	8	7.63± 31.44	-2.50± 36.23	2.56± 16.04	2.56± 28.22
	E	3	29.33± 5.69	-22.33± 15.50	3.50± 6.50	3.50± 24.07
	F	7	1.71± 44.91	-35.29± 59.50	-16.79± 26.15	-16.79± 45.96
	G	0	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00
	H	2	15.00± 22.63	0.50± 3.54	7.75± 13.08	7.75± 13.46
	I	7	-34.00± 54.57	15.29± 34.57	-9.36± 32.23	-9.36± 44.59
	J	1	-107.00± —	29.00± —	-39.00± —	-39.00± 68.00
Total		32	-10.34± 48.22	-5.22± 41.42	-7.78± 23.32	-7.78± 38.74
Grand Total		305	-0.62± 32.86	3.77± 37.94	1.58± 19.89	1.58± 31.19

Appendix E. Combined mean growth rate (cm yr^{-1} radial extension) for *M. annularis* and *P. astreoides* by site and time period ± standard deviation

		Period			
Site	**N**	**2002-2003**	**2003-2004**	**2002-2004**	**Total**
B	27	-0.41± 0.48	0.34± 0.38	-0.03± 0.27	-0.03± 0.49
C	57	-0.02± 0.68	-0.20± 0.78	-0.11± 0.33	-0.11± 0.63
D	8	0.28± 1.12	-0.12± 1.25	0.08± 0.61	0.08± 1.00
E	15	0.35± 0.82	0.03± 0.80	0.19± 0.41	0.19± 0.70
F	68	-0.15± 0.59	0.06± 0.85	-0.04± 0.40	-0.04± 0.64
G	37	-0.39± 0.76	0.41± 0.67	0.01± 0.32	0.01± 0.69
H	39	0.31± 0.94	-0.06± 0.93	0.12± 0.48	0.12± 0.82
I	31	-0.07± 0.86	0.23± 0.65	0.08± 0.56	0.08± 0.71
J	23	-0.10± 0.81	-0.08± 0.47	-0.09± 0.40	-0.09± 0.58
Total	305	-0.07± 0.77	0.06± 0.78	0.00± 0.41	0.00± 0.68

Appendix F. Mean growth rate (cm yr^{-1} radial extension) rate for *M. annularis* and *P. astreoides* by site and time period ± standard deviation

			Period			
Species	**Site**	**N**	**2002-2003**	**2003-2004**	**2002-2004**	**Total**
M. annularis	**B**	25	-0.37± 0.30	0.36± 0.38	0.00± 0.18	0.00± 0.42
	C	55	0.04± 0.60	-0.21± 0.77	-0.09± 0.30	-0.09± 0.59
	D	0	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00
	E	12	0.13± 0.75	0.30± 0.51	0.22± 0.45	0.22± 0.57
	F	61	-0.16± 0.54	0.14± 0.75	-0.01± 0.37	-0.01± 0.59
	G	37	-0.39± 0.76	0.41± 0.67	0.01± 0.32	0.01± 0.69
	H	37	0.29± 0.96	-0.06± 0.96	0.12± 0.49	0.12± 0.84
	I	24	0.15± 0.39	0.22± 0.60	0.19± 0.33	0.19± 0.45
	J	22	0.02± 0.57	-0.12± 0.43	-0.05± 0.36	-0.05± 0.46
	Total	273	-0.05± 0.67	0.09± 0.74	0.02± 0.36	0.02± 0.61
P. astreoides	**B**	2	-0.85± 1.86	0.04± 0.06	-0.40± 0.90	-0.40± 1.01
	C	2	-1.72± 0.74	0.07± 1.51	-0.82± 0.39	-0.82± 1.11
	D	8	0.28± 1.12	-0.12± 1.25	0.08± 0.61	0.08± 1.00
	E	3	1.22± 0.45	-1.05± 0.93	0.09± 0.26	0.09± 1.12
	F	7	-0.03± 0.98	-0.69± 1.28	-0.36± 0.55	-0.36± 0.97
	G	0	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00
	H	2	0.51± 0.80	-0.01± 0.14	0.25± 0.47	0.25± 0.48
	I	7	-0.82± 1.50	0.26± 0.87	-0.28± 0.98	-0.28± 1.18
	J	1	-2.82± —	0.91± —	-0.96± —	-0.96± 1.87
	Total	32	-0.22± 1.36	-0.19± 1.08	-0.20± 0.68	-0.20± 1.07
Grand Total		305	-0.07± 0.77	0.06± 0.78	0.00± 0.41	0.00± 0.68

Appendix G. Mean growth rate (cm yr^{-1} radial extension) for *M. annularis* and *P. astreoides* by size class and time period ± standard deviation

		Period							
		2002-2003		2003-2004		2002-2004		Total	
Species	**Size**	**N**	**Mean±SD**	**N**	**Mean±SD**	**N**	**Mean±SD**	**N**	**Mean±SD**
M. annularis	**S**	71	-0.05±0.42	78	0.19±0.42	71	-0.13±0.31	220	0.00± 1.16
	M	72	-0.02±0.58	65	0.07±0.58	67	-0.03±0.25	204	0.03± 1.41
	L	130	-0.07±0.82	130	0.04±0.93	135	0.12±0.40	395	0.10± 2.15
	Total	273	-0.14±1.82	273	0.31±1.93	273	-0.03±0.97	819	0.13± 4.72
P. astreoides	**S**	5	0.75±0.73	2	0.37±0.40	4	-0.20±0.59	11	0.92± 1.72
	M	7	0.23±1.39	9	0.05±0.61	9	-0.57±0.84	25	-0.28± 2.84
	L	20	-0.62±1.34	21	-0.34±1.26	19	-0.03±0.58	60	-1.00± 3.17
	Total	32	0.89±0.74	32	0.62±0.40	32	0.35±0.26	96	1.86± 1.40
Grand Total		305	0.52±0.49	305	0.49±0.50	305	0.26±0.27	915	1.28± 1.25