SCLERACTINIAN CORAL MORTALITY AND COLOR CHANGE ON CENTRAL BAHAMIAN REEFS: 1991-1995

Thesis by

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Austin, TX
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ASSESSMENTS OF SCLERACTINIAN CORAL MORTALITY AND COLOR CHANGE ON CENTRAL BAHAMIAN REEFS: 1991-1995

APPROVED BY
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The University of Texas at Austin, 1997
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The causes of partial-colony *vs.* whole-colony mortality, and assessments of color change, were examined for three species of scleractinian corals (*Montastraea* cf. *annularis*, *Montastraea* cf. *franksi*, and *Porites astreoides*) on two central Bahamian reefs near Lee Stocking Island in the Exuma Cays. Partial-colony mortality was due primarily to bioerosion by endolithic sponges, and overgrowth by epibenthic sponges or macroalgae. Mortality from bleaching, sedimentation, or disease was negligible. Cumulative whole-colony mortalities (mostly a consequence of basal detachment) after four years were higher on the deeper reef due to burial of colonies by sediment.

Three 'mass bleaching' events occurred during the course of this study in 1991, 1993 and 1995, following prolonged periods of higher water temperatures (above 29.5°C on the deep reef, and 30°C on the shallow reef). Three techniques were used to assess 'bleaching'. The number of affected colonies was always greatest during fall observational periods, and bleaching was more severe on the deeper reef during each event. Differences in bleaching response were found between the three species, by reef and temporally. The relative advantages and disadvantages of each method were compared.

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Chapter 1

Causes of scleractinian coral mortality on central Bahamian reefs: 1991-1995

1.1 Introduction

1.1.1 *Overview of coral reefs*

Coral reefs are complex and diverse ecosystems that can only survive in a narrow range of physical and chemical environments. Hermatypic corals of the Order Scleractinia, also called hard or stony corals, are the basic constructive units of such reefs. Corals are colonial invertebrate animals, usually made up of thousands of individual but interconnected polyps, which secrete calcium carbonate to form hard cups called *corallites*. These cups provide protection for the corals' delicate tissues, and contribute to the reef structure. Species are generally distinguished by the size and shape of their corallites, in addition to overall colony morphologies and life histories. Colonies increase in size by the asexual budding of additional polyps, and by successive generations overgrowing one another.

Hermatypic corals get their coloration from the photosynthetic pigments of single-celled dinoflagellates called *zooxanthellae*, which live inside the polyps' tissues. The symbiotic relationship between zooxanthellae and corals, and the breakdown of this relationship during periods of stress (*i.e.*, bleaching), is discussed further in Chapter 2.

Many coral reefs located near large human populations are declining from anthropogenic stresses such as nutrient loading, sedimentation, overfishing, mining and tourism. Even remote reefs have been directly and indirectly affected by overfishing, or by mass mortalities associated with disease and bleaching, some of which may be signs of global climate change (Glynn 1991; Glynn 1993). Therefore, long-term physical and biological data on the dynamics of reef communities are greatly needed to better understand reef ecology, and to help distinguish human-induced changes from those that occur naturally (Rogers 1988; Hughes 1993).

For many purposes, non-invasive methods of investigation have become preferable to traditional collection-based research, so that damage to reef organisms is minimized or eliminated, leaving organisms intact for long-term study. Although identification of unfamiliar organisms is often difficult without the collection of specimens, successive *in situ* visual observations, combined with photographs or videotapes, can provide useful and permanent records on multiple levels, ranging from individuals to communities (Rogers 1988; Porter and Meier 1992). Particularly valuable insights may be obtained by tracking 'indicator species', which display greater sensitivity to local stresses (Gomez and Yap 1988).

Reefs near the Caribbean Marine Research Center (CMRC) facility on Lee Stocking Island, in the Exuma Cays, central Bahamas are considered ideal control study sites because they are relatively unaffected by human activity, yet mass bleaching/recovery has occurred repeatedly within the last decade (Lang et al. 1988; Lang et al. 1992). The scleractinian species *Montastraea annularis* and *Porites astreoides* were chosen as study organisms for the following reasons: 1) they are the dominant corals on the reefs of interest, and; 2) they are known to be good local indicators of bleaching (Lang et al. 1988).

1.1.2 *Objectives*

The original focus of this study was to provide long-term observations of natural seasonal color variation, as well as color changes brought about by bleaching (Chapter 2), using still photography. In addition, the photographic series have provided data on mortality which was also of interest. I used these data to address the following questions: 1) What mechanisms of coral mortality are at work in shallow vs. deep reef environments?, 2) Do the sources of mortality show any variation in their occurrence through time, for example, are there seasonally-correlated patterns or perhaps correlations with other factors?, 3) Does bleaching appear to be an important cause of mortality in corals in this area?, and 4) Does the stress of repeated bleaching make corals more susceptible to these other sources of mortality, thereby indirectly causing increases in mortality events?

Observations of mortality causes for this four-year study spanned three bleaching events in 1991, 1993, and 1995 (Chapter 2), and the close passage of three hurricanes (1991, 1992, 1995) as well as numerous smaller storms. Earlier observations during the 1990 bleaching event (Lang, pers. comm.) indicated that larger amounts of bleaching occurred on the deeper reef (especially in *Porites astreoides*), so I expected that any effects of the stress of repeated bleaching would be reflected by an increasing incidence of mortality on the deep reef.

1.2 Materials and Methods

1.2.1 *Study sites*

For replication, two adjacent sites were chosen on each of two reefs, one deep and one shallow. The nearshore, shallow fringing reef along the northeast side of Norman's Pond Cay (NPC) is directly exposed to breaking waves (Fig. 1.1). Small stony corals (maximum cover <10%, J.C.Lang pers. obs.), fire corals, gorgonians, and sponges occur on a low-relief hardground at approximately 2-4 m depth. Due to the high wave energy of this area, there are few colonies larger than 0.5 m in diameter (J.C. Lang pers. obs.). Larger colonies that are present are generally not attached to the substratum.

At 16-18 m depth on the North Perry (NP) fore reef near the northeast end of Lee Stocking Island (Fig. 1.1), 3-4 m high spurs and low (<1 m) lobes mark a transition area between a gentle shoreward (<30°) slope and a sand-covered seaward terrace. Stony corals here have maximum cover of 25% (A.J.King pers. obs.); macroalgae

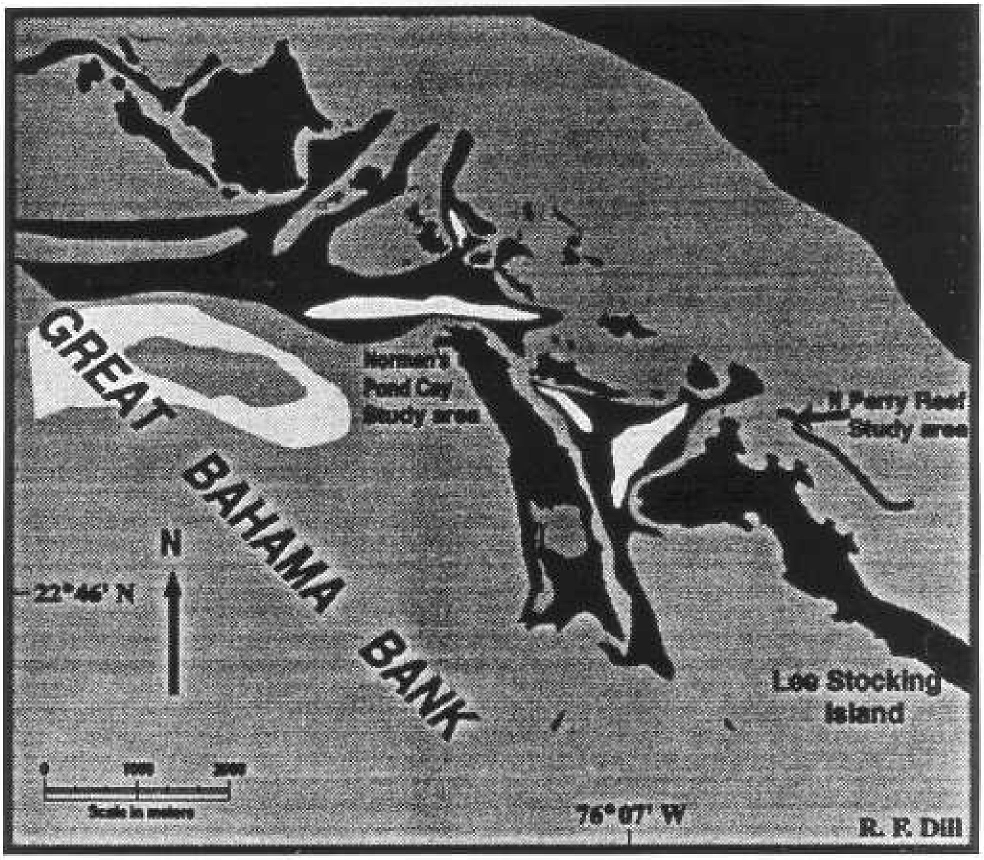


Fig. 1.1: Location of study sites near Lee Stocking Island, Exuma Cays, Bahamas.

(in amounts which vary seasonally), gorgonians, and sponges are common.

1.2.2 *Study organisms*

At the beginning of this study, the *Montastraea annularis* complex was still thought to consist of a number of morphotypes with overlapping habitats. The *Montastraea* spp. on both reefs were thus all initially included as *M. annularis*. However, there is much recent evidence that the shallower morphotypes may actually be three very closely related, but separate, species (Weil and Knowlton 1994). Using these later criteria, all but one of the photographed colonies on the shallow reef were informally renamed as *Montastraea* cf. *annularis* (which predominates in shallow-water environments), while the colonies on the deeper North Perry reef were found to be a mixture of *Montastraea* cf. *franksi*, *Montastraea* cf. *faveolata*, and possibly several hybrids. To simplify the analyses, data from the non-*M.* cf. *annularis* colony on the shallow reef was excluded, and only the species with the greatest number of photographed colonies on the deep reef (*Montastraea* cf. *franksi*) was retained.

Significant variations in color are found within *Porites astreoides*: the two main types are a yellow-green variety which occurs mostly in shallow waters, and brownish-colored colonies which are found at depth. Despite much controversy, all colors are currently considered to be one species by Caribbean taxonomists (Lang pers. comm.). Although all corals were initially chosen randomly irregardless of color, for simplicity, data from the one *P. astreoides* on each reef that differed in coloration from the majority were discarded, leaving all yellow-green colonies at Norman's Pond Cay, and all brown colonies at North Perry.

The shallow-water *Montastraea* cf. *annularis* and *Porites astreoides* colonies are mound-shaped corals, while *Montastraea* cf. *franksi* on the North Perry reef is generally very flat, growing in sheets or plates. Colonies of *Porites astreoides* also have a more 'platey' growth form on the deep reef, but there is much between-colony variation in the extent of flattening.

1.2.3 *Selection of colonies*

For each species at each site (*Montastraea* cf. *annularis* and *Porites astreoides* at Norman's Pond Cay; *Montastraea* cf. *franksi* and *Porites astreoides* at North Perry), up to 16 randomly- chosen corals (~10-40cm^2 in diameter) were permanently marked by nailing a numbered tag into the adjacent non-living substratum (regardless of color, shape, appearance, orientation, or ease of photography). Additional colonies were tagged in 1992 to increase the sample size. A colony was defined as any physiologically isolated area of live tissue (Jackson 1985), regardless of whether or not it had apparently at one time been part of a larger coral. If a coral disappeared, died, or was later renamed (as happened for 11 *Montastraea* cf. *franksi* at North Perry), it was replaced by the nearest colony of the same species.

1.2.4 *Photography*

Colonies were photographed up to four times a year from a fixed distance of 0.6 m, using B. Maguire's stereo-pair camera/strobe system with attached Macbeth or Kodak gray scale, compass and goniometer (Lang et al. 1993; Maguire et al. 1996). Sketches, along with goniometer and compass directions, helped ensure that all photographs of any given coral were taken at approximately the same angle and orientation; however, some variation was unavoidable, particularly in heavy surge. A flashgun (strobelight) was used with each camera, and for uniform illumination of the coral and gray scale, a second diver held a sheet of black plastic over the entire setup to block out spatially variable ambient light (see Chapter 2).

Photographs were taken from August 1991 through October 1995 at the two deeper North Perry sites, to March 1994 at the northern Norman's Pond Cay site and, with two interruptions in 1994, to October 1995 at the southern Norman's Pond Cay site. No photographs were taken in spring of 1995 for any site. As the photography of individual corals was occasionally unsuccessful, sample sizes varied among observation periods for each species at all sites.

1.2.5 *Visual slide analysis*

The complete temporal series of color slides for each colony was examined visually on a light box, using a 10x magnifying lens. For each observational period, the apparent physical or biological agent (see the following section) responsible for any newly-detected tissue loss was recorded. When no obvious cause of mortality could be discerned, the loss was categorized as 'unknown'. Once a part of the colony had died, the dead area was no longer included in future analyses.

Mortality events were also classified as partial-colony or whole-colony, depending on the relative amount of tissue lost. Partial-colony mortality events involved the death of smaller areas of tissue which usually did not recover, but in which the remainder of the colony was left intact. Whole-colony mortality was defined as an entire colony dying during one inter-observational period. In a few instances, chronic loss of large amounts of tissue over a longer time period eventually led to whole-colony mortality.

Physiological remnants (Jackson 1985) were created by fission of five of the corals (2 *M.* cf. *annularis* and 1 *P. astreoides* at Norman's Pond Cay; 1 *M.* cf. *franksi* and 1 *P. astreoides* at North Perry); all remnants were considered subsets of the original colonies. Fusion with an adjacent conspecific was noted on 10 occasions (1 *M.* cf. *annularis* and 1 *P. astreoides* at Norman's Pond Cay; 6 *M.* cf. *franksi* and 2 *P. astreoides* at North Perry); however, the additional tissue area was not considered in the mortality events analysis.

1.2.6 *Sources of mortality*

Those physical factors which could be identified as causes of tissue loss included smothering by sediments present on the colony, bleaching, and detachment from the substratum leading to abrasion (shallow) or burial in sand (deep). The apparent causes of biologically-induced tissue loss included endolithic and epibenthic sponges, macroalgae, grazing by other invertebrates or corallivorous fish, and disease. (Endolithic sponges invade and bioerode coral skeletons until they eventually erupt at the surface and spread over living tissues. Epibenthic sponges and macroalgae can quickly overgrow other organisms, and cause death to coral tissues through shading or physical contact.) Based on the very low percentages of coral cover at the study sites on both reefs, and on *in situ* observations, intraspecific and interspecific competitive interactions among corals appeared to be negligible.

1.2.7 *Statistical analysis*

If the stress of bleaching makes corals more susceptible to invasion or infection by various coral diseases and other causes of mortality, the frequencies of mortality events from individual causes, and hence the overall frequency (*i.e.* all causes combined), should increase significantly over time (Peters 1993). Using this statement as our alternate hypothesis, and no significant change through time as the null hypothesis, I performed a Fisher's exact test of independence (Sokal and Rohlf 1994) for each category of factors to detect any significant differences from initial patterns (expected amounts) after 5, 10, and 15 observations. Supporting Chi-square tests (with Bonferroni corrections) were also run for each category, since a Fisher's exact test was not always practical for larger sample sizes.

1.3 Results

1.3.1 *Partial-colony mortality of attached corals*

Endolithic sponges (*Cliona delitrix* >>>*Siphonodictyon coralliphagum*) were the predominant source of partial-colony mortality on both reefs throughout the duration of the study (Figs. 1.2-1.9). Their impact is greatly increased if the number of 'unknowns' (most of which were suspected to result from internal sponge boring prior to visible detection) are added to the endolithic sponge category. However, at the shallow southern Norman's Pond Cay site, overgrowth by several species of epibenthic sponges (*Ircinia felix, Spongia* cf. *tubulifera, Aplysina* cf. *fistularis*) (Wiedenmeyer 1977) was either the most common cause of tissue loss (*M.* cf. *annularis*; Fig. 1.2), or was co-dominant with endolithic sponge activity (*P. astreoides*; Fig. 1.3).

Overgrowth by fleshy macroalgae, notably *Microdictyon marinum*, *Dictyota spp.*, and *Halimeda spp.*, was the primary identified cause of partial-colony mortality in *M.* cf. *franksi* at the southern North Perry site (Fig. 1.8). Relatively few instances of tissue loss were attributable to the effects of sediment accumulation, and even fewer to bleaching (Figs. 1.2-1.9). With the

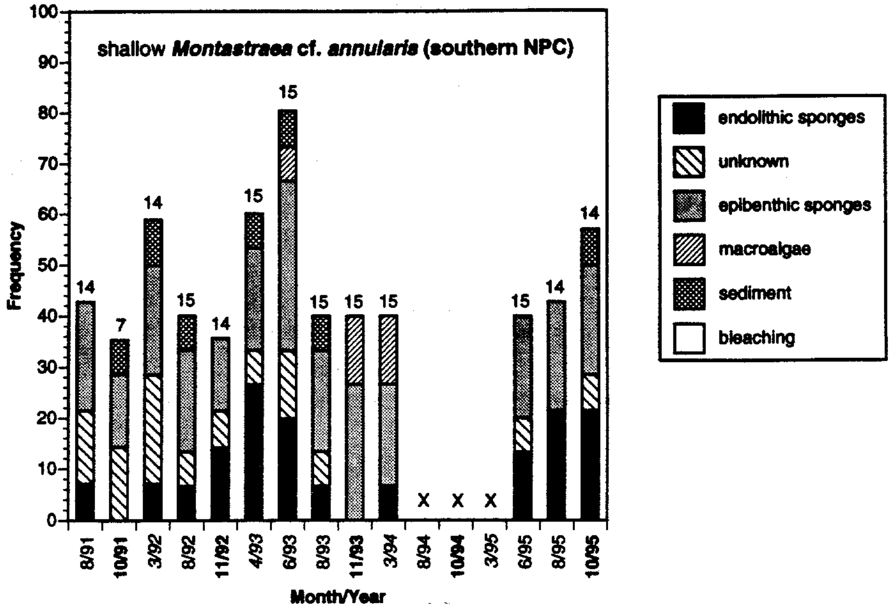


Figure 1.2: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Montastraea* cf. *annularis* at the shallow southern NPC site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

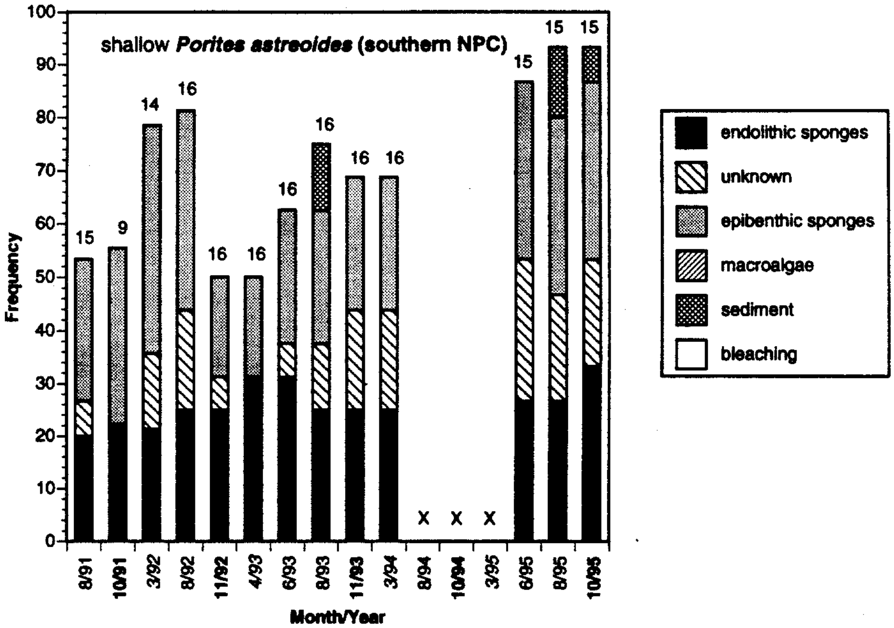


Figure 1.3: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Porites astreoides* at the shallow southern NPC site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

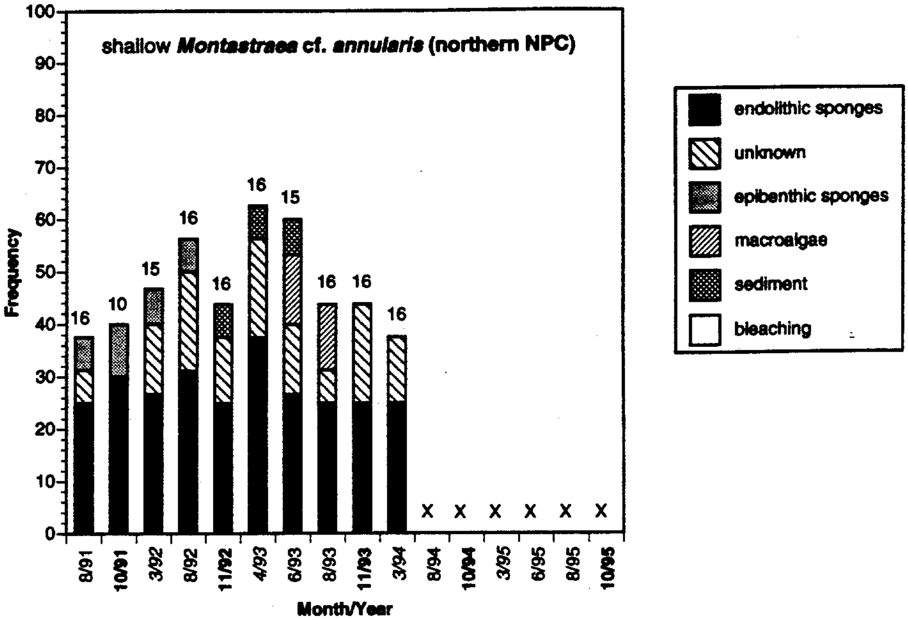


Figure 1.4: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Montastraea* cf. *annularis* at the shallow northern NPC site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

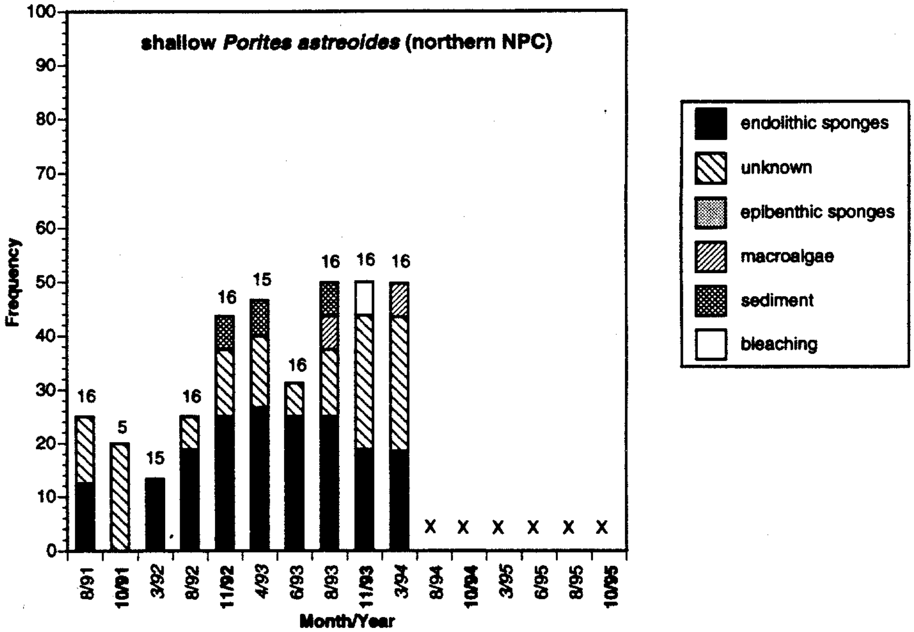


Figure 1.5: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Porites astreoides* at the shallow northern NPC site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

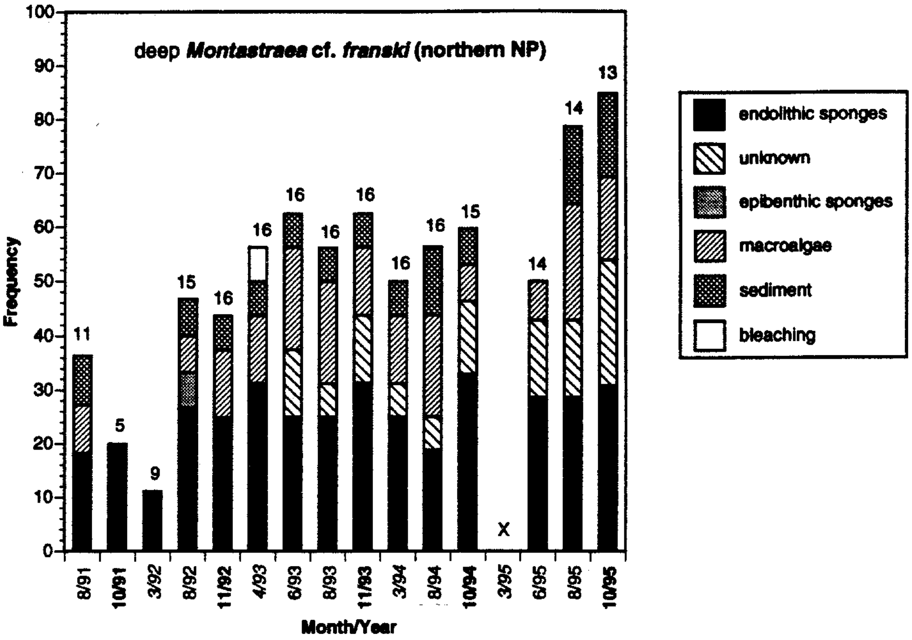


Figure 1.6: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Montastraea* cf. *franksi* at the deep northern NP site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

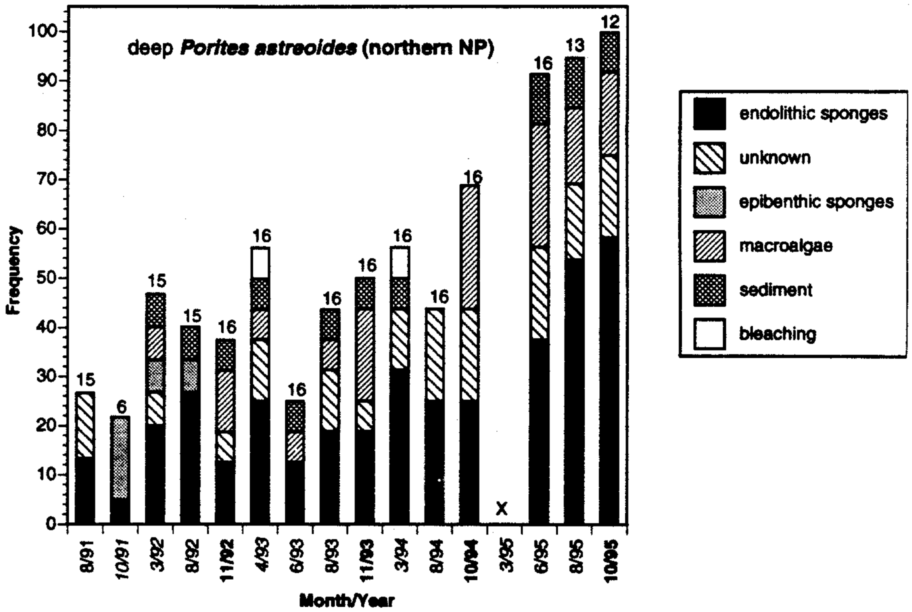


Figure 1.7: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Porites astreoides* at the deep northern NP site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

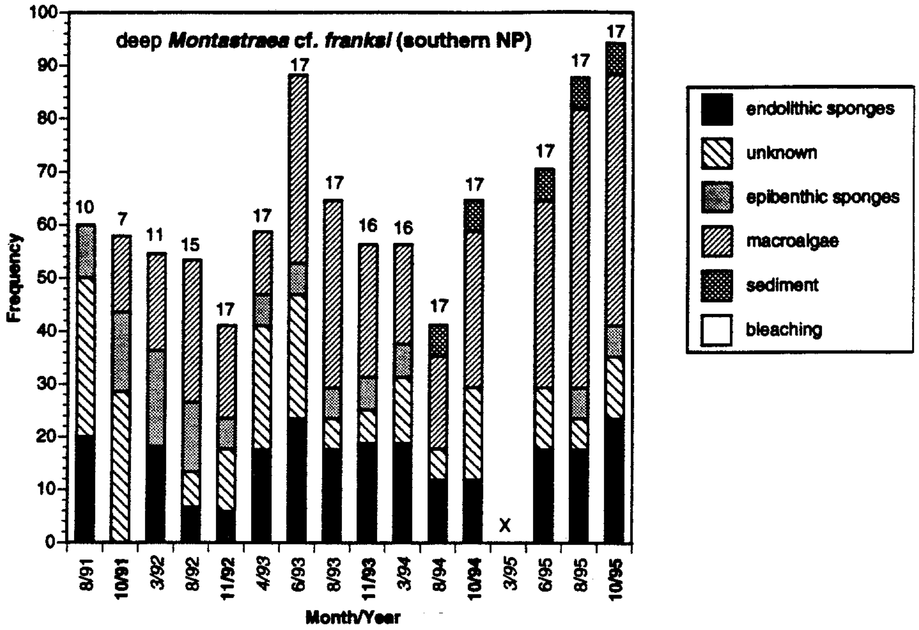


Figure 1.8: Variation in the relative and total frequenices of causes of partial-colony mortality over a four-year time period for *Montastraea* cf. *franksi* at the deep southern NP site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

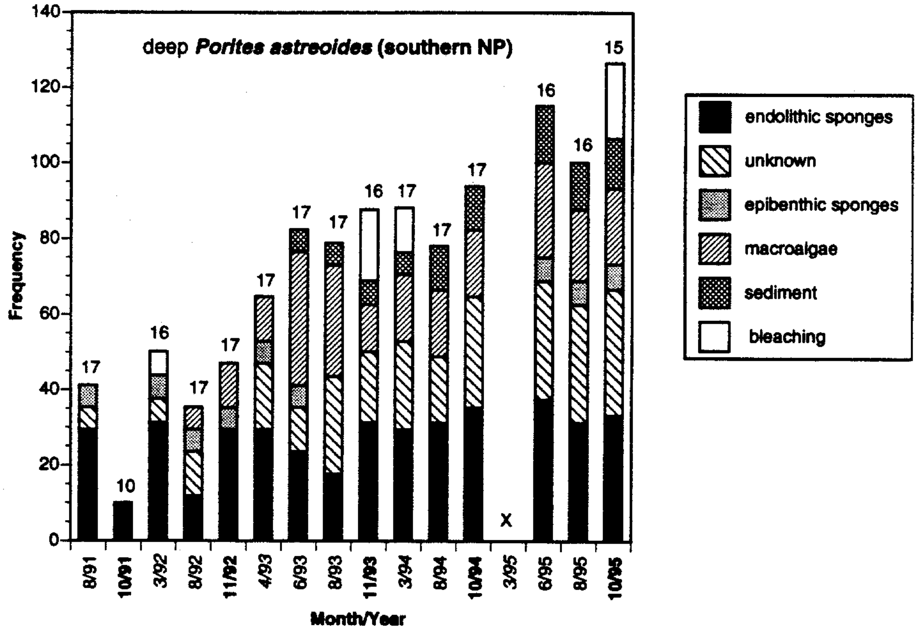


Figure 1.9: Variation in the relative and total frequencies of causes of partial-colony mortality over a four-year time period for *Porites astreoides* at the deep southern NP site. The number of photographed corals at each observation time is shown at the top of the respective column. X means no photographs taken.

exception of mass bleaching events, which occurred in the late summer and fall (Chapter 2) and occasionally resulted in mortality by late fall or spring (Figs. 1.5-1.7, Fig. 1.9), no seasonal-specific trends in the occurrence of any mortality source were noted. This was unexpected since *in situ* observations indicated that large macroalgal blooms occurred intermittently during the spring and summer months in several years. Additional causes that were found to be negligible are outlined further in the Discussion.

The overall frequencies of mortality events fluctuated over time in *M.* cf. *annularis* at Norman's Pond Cay and *M.* cf. *franksi* at southern North Perry, but gradually increased in *M.* cf. *franksi* at northern North Perry and in *P. astreoides* on both reefs (Figs. 1.2-1.9). The greatest increases in partial mortality events occurred on the deeper reef. (Colonies could incur more than one form of tissue loss simultaneously, so total proportions may exceed 100%).

Table 1.1 summarizes the resultant P-values for each category after performing Fisher's exact tests ($\alpha = 0.05$) and comparative Chi-square tests ($\alpha = 0.0167$, with Bonferroni correction) to determine whether there

Table 1.1: Probabilities (of significance) of change through time of partial mortality event frequencies caused by various factors. Only Chi-square values are shown in cases where Fisher's exact was not used (see text). Values were not calculable for either test if the number of occurrences in a category for any observational period was equal to 0.

North Perry Reef (all observational periods)

FACTOR	P-values Chi-square	Fisher's
endolithic sponges	0.446	---
epibenthic sponges	0.373	0.481
macroalgae	0.612	0.611
sediment	0.218	0.235
bleaching	---	---
unknown	0.079	0.083

Norman's Pond Cay (after 10 observational periods)

FACTOR	P-values Chi-square	Fisher's
endolithic sponges	0.704	---
epibenthic sponges	---	---
macroalgae	---	---
sediment	0.620	0.874
bleaching	---	---
unknown	0.293	0.310

Norman's Pond Cay (all observational periods, southern site)

FACTOR	P-values Chi-square	Fisher's
endolithic sponges	0.623	0.624
epibenthic sponges	0.519	0.514
sediment	0.085	0.157
unknown	0.129	0.128

were significant changes in the frequency of partial mortality events from individual causes over time. For those rows in which only the Chi-square P-value is shown, the sample sizes were too large to perform a Fisher's exact test. In rows where values aren't shown for either test, no statistical analysis was done due to the summed value of one of the observational periods being equal to zero (*i.e.*, there were no observations of that cause in that time interval).

Although the figures do reflect changes in the overall frequency of partial mortality events, the results from Table 1.1 indicate that there were no significant differences in the number of events from individual causes for either reef when entire data sets (after 13 or 15 observations; August 1991 - October 1995) were compared with those terminating after 5 observations in November 1992, or after 10 observations in March 1994 (*i.e.*, each cause was responsible for the same relative number of mortality events at any given observational period).

1.3.2 *Whole-colony mortality of attached corals*

Between August 1994 and October 1995, two of the *Montastraea* cf. *franksi* and one *Porites astreoides* at

North Perry had completely died as a result of overgrowth from an endolithic sponge (*Cliona delitrix*), and a second *P. astreoides* was apparently killed by repeated bleaching (summary data in Table 1.2). Three colonies of *P. astreoides* (two at North Perry and one at the southern Norman's Pond Cay site) were more than 95% dead from endolithic sponge boring by October 1995, and the remaining tissue was in decay. An additional *Porites astreoides* at the northern Norman's Pond Cay site is also suspected to have died by this time, but this was not confirmed. No other sources of partial-colony mortality was responsible for the elimination of intact corals. Epibenthic sponges either receded or disappeared (*Spongia* cf. *tubulifera*), or grew into the water column (*Ircinia felix, Aplysina* cf. *fistularis*) after establishing a foundation with coral tissues. The cover of macroalgae at North Perry was observed to be periodically reduced, sometimes substantially, by storms.

1.3.3 *Partial-colony mortality of detached corals*

Excavating sponges, bivalves, etc., likely contributed to the loosening of coral bases from the substratum, thereby increasing susceptibility to detachment in areas of routinely higher wave energy (shallow reef) or during

Table 1.2: Whole-colony mortality of attached *vs*. detached colonies at three sites by October 1995.

Site	Attached Number Dead/Total	Detached Number
S-NPC, shallow		
M. cf. *annularis*	0/12	0/3
P. astreoides	*1/12	0/4
N-NP, deep		
M. cf. *franksi*	2/16	0/0
P. astreoides	*2/14	*1/2
S-NP, deep		
M. cf. *franksi*	0/17	0/0
P. astreoides	*0/14	1/2

*One additional colony was >95% dead at each of these sites by October 1995.

storm activity (both reefs). Three of the 15 detached colonies (from *all four sites* combined) are thought to have fallen during the close passage (<280 km) of a major storm (one *P. astreoides* each at Norman's Pond Cay and North Perry during Hurricane Andrew in August 1992; one *P. astreoides* at North Perry during Hurricane Erin in

July 1995). It is possible that smaller storms, which are frequent in this area, also facilitated the detachment of corals on these reefs.

Bioerosion and eventual collapse of coral bases is extremely common at Norman's Pond Cay, yet tissue loss in the detached colonies was rare, as seen for the southern site in Table 1.2. Six of the seven dislodged *M.* cf. *annularis* became wedged among other corals or in small depressions in the hardground. Five of the six comparably affected *Porites astreoides* remained loose, incurring only minor amounts of tissue abrasion after being moved around on the substratum (usually <1 m horizontally from their original locations). Despite extensive searching, one colony of each species vanished at the southern Norman's Pond Cay site, hence, their ultimate fates are unknown.

1.3.4 *Whole-colony mortality of detached corals*

Three of the four fallen *Porites astreoides* at North Perry landed in the sand surrounding the reef spurs. Two died within 2 - 6 months from progressively deeper burial (their skeletons eventually being completely covered by sand), and the third was more than 95% dead in October 1995, less than three months after detachment. Still alive at that time was a fourth *P. astreoides* colony that had landed in a crevice on the reef three years previously. No detachment of tagged *Montastraea* cf. *franksi* was observed at North Perry (Table 1.2).

1.4 Discussion

Small-scale, partial mortality/recovery events lasting only a few days or weeks are likely to have been underrepresented in the data set. However, fresh lesions were rarely observed on any tagged colonies in the field, even though *Coralliophila abbreviata* and other corallivorous snails are common along colony margins of *M.* cf. *annularis* at Norman's Pond Cay. Only one occurrence of grazing was observed on tagged corals (at Norman's Pond Cay, a parrotfish scrape on a shallow *P. astreoides* which was subsequently repaired). The presence of other organisms in or near the corals (specifically *Spirobranchus giganteus*, a serpulid polychaete) did not appear to be an important source of mortality during the course of this study.

Black band disease, occasionally noted in other faviid corals on both reefs, was not seen on any of the tagged *Montastraea*. (Poritids appear to be highly resistant to this disease (Rützler et al. 1983).) An entire colony (a *Porites astreoides* at North Perry) and patches of tissue on 16 corals appeared 'sick' (*i.e.*, having discolored, damaged and/or abnormally contracted polyps) during one or more observational periods, but later recovered without noticeable losses of tissue.

Very little observed mortality could be directly attributed to bleaching (Figs. 1.2-1.9) during, or immediately after, the mass bleaching events of 1991, 1993, and 1995. Photographed colonies on the deeper reef were more likely to be affected than those on the shallow hardground (Chapter 2), but recovery from bleaching appeared to be almost total. (However, it was apparent from follow-up *in situ* observations of North Perry corals in June of 1996, that many of the more severely bleached colonies had lost tissue.)

Although the greatest increases in overall frequency of mortality did occur in those corals and sites for which bleaching was greatest (Chapter 2), there is a lack of conclusive evidence from this study to support the hypothesis that this bleaching led to increased susceptibility from other sources of mortality. Some alternatives might be that partial-mortality events themselves weaken the coral, thereby increasing its vulnerability to subsequent colonization, invasion, or overgrowth from the same source or other sources, resulting in additional mortality.

General patterns of chronic partial-mortality events for attached corals were established within the first year of the study (Table 1.1, Figs. 1.2-1.9). Nevertheless, any cumulative effects of bioerosion from 'encrusting endolithic sponges' (common) and bleaching (rare) occurred so gradually that several years were required before the more frequent occurrence of whole-colony mortality of attached corals on the deeper fore reef became apparent (Table 1.2). (Larger sample sizes are needed in order to confirm these conclusions.) In addition, the occasional disappearance of detached colonies at Norman's Pond Cay, in contrast to the more common burial of *P. astreoides* in sand at North Perry, could have been easily missed by a short-term study.

Epibenthic sponges that cover naturally-exposed skeletal surfaces, rather than overgrowing live coral polyps, may inhibit the colonization and spread of endolithic organisms (Goreau and Hartmann 1966; J. Wulff pers. comm.). At North Perry, encrusting *Mycale* *laevis* and *Chondrilla nucula* are more common on the undersides of lobate colonies of *Montastraea* cf. *franksi* than below foliaceous *P. astreoides* (7/30 vs. 2/26 colonies, respectively, in October 1995). Protection by the presence of these encrusting sponges may partially explain the lower incidence of detachment at the North Perry reef relative to Norman's Pond Cay, particularly in the *M.* cf. *franksi* (Table 1.2), even though their presence has not yet appeared to affect susceptibility to partial-colony mortality in photographed corals. (Further *in situ* examination of affected corals on a larger scale would be needed to detect encrusting sponges whose presence may not be visible in the photographs.)

Patchiness in the spatial distribution of epibenthic organisms capable of overgrowing reef corals (macroalgae at depth and certain sponges in shallow water) created site effects that disallow other simplistic comparisons between the two reef habitats (see also Bythell et al. 1993). For example, most of the tagged *Montastraea* cf. *franksi* that are associated with *Mycale laevis* (see above) inhabit a single reef lobe at the southern North Perry site. In addition, the trend of increasing overgrowth by macroalgae at the southern North Perry site (Fig.1.8) matched *in situ* visual impressions of gross increases in the cover of fleshy and filamentous macroalgae on the deeper reef after 1992, but this was not clearly supported by the northern North Perry site data (Fig. 1.6).

Coral cover and diversity have declined in many areas of the wider Caribbean, especially near high human population densities (e.g. PEMEX 1987; Bak and Nieuwland 1995; Cortés 1993; Ogden and Ogden 1993; Hughes 1994; Wilkinson and Buddiemeier 1994). The specific natural causes attributed to these changes, where addressed, have varied according to choice of study organisms, geographic location, habitat, timing relative to outbreaks of disease or the passage of major storms, and terminology used to describe causes of mortality (e.g. Bak and Luckhurst 1980; Porter and Meier 1992; Bythell et al. 1993). For example, had *Diploria* spp. (good indicators of bleaching but less common) been chosen in the study, results (based on *in situ* observations) might have shown that black band disease was a major cause of mortality on both reefs. Hence, one must be cautious not to overgeneralize the results of any given study.

Relative to catastrophic impacts (such as storms, disease outbreaks, bleaching, etc.) little is known about chronic sources of mortality in reef corals. Even in areas that are considered relatively 'pristine', long-term comparative data are crucial for unraveling the natural complexities of reef coral population dynamics.

Chapter 2

Color change and bleaching on central Bahamian reefs: a comparison of three techniques

2.1 Introduction

2.1.1 *Overview of bleaching*

As previously mentioned in Chapter 1, scleractinian coral tissues contain single-celled photosynthetic dinoflagellates called *zooxanthellae*. Bleaching is commonly defined as the loss of these symbiotic dinoflagellates (zooxanthellae) from and/or a reduction of their photosynthetic pigments in the scleractinian coral hosts (Glynn 1993). The mechanisms involved are only partially understood; however, it is thought that stressful changes in environmental conditions lead to a breakdown in the symbiotic relationship (Gates et al. 1992). Since most coral polyps are almost transparent without the symbionts' pigments, the calcium carbonate skeleton is revealed, leaving part or all of the colony pale or white in color. (Other factors that can cause a whitened appearance of corals, e.g. strong tissue contraction induced by subaerial exposure at low tides (Brown et al.

1994) and production of masking pigments (D.K. Hagman, pers. comm.), are sometimes included under the heading of bleaching; however, the definition for this paper is restricted to examination of changes in the total pigment color of the zooxanthellar populations.)

The direct effect of bleaching on reef corals is a decreased amount of energy (in the form of various photosynthates) being provided to the host (Hoegh-Guldberg and Smith 1989; Banaszak and Trench 1994); this in turn can reduce tissue biomass (Porter et al 1989; Szmant and Gassman 1990; Fitt et al. 1993) coral skeletal deposition (Goreau and Macfarlane 1990) and fecundity (Szmant and Gassman 1990). If the length of the bleaching period is extended, the affected coral tissue may eventually die (Glynn and D'Croz 1990). Due to these negative consequences, most researchers view bleaching as a detriment to reef 'health'. However, Buddiemeier and Fautin (1993) have proposed that bleaching may be an adaptive mechanism by which corals 'switch' between specific symbionts under stressful or changing environmental conditions.

Many external variables can induce bleaching, including extremes in temperature, salinity, and oxygen, high UV radiation levels, sedimentation, pollution, changes in visible light regimes, disease, exposure at low tide and hurricane damage (Goreau 1964; Rogers 1983; Siebeck 1988; Hoegh-Guldberg and Smith 1989; Glynn and D'Croz 1990; Lesser et al. 1990; Muscatine et al 1991; Brown et al. 1992; Glynn 1993; Kushmaro et al. 1996). Of all these parameters, prolonged high sea surface temperature has the most well-documented support as the cause for many recent localized mass bleaching events (Cook et al. 1990; Gates 1990; Glynn and D'Croz 1990; Jokiel and Coles 1990; Brown and Suharsono 1992; Hagman and Gittings 1992; Dennis and Wicklund 1993; Glynn 1993; Goreau et al. 1994).

Infrequent occurrences of localized bleaching have been noted throughout the last century, but 'mass bleaching' events have been observed only within the last decade and a half (Glynn 1993). ('Mass bleaching' is defined as the conspicuous bleaching of reef-building corals over large geographical areas. In the western Atlantic it has simultaneously affected reefs in several parts of the Caribbean, Bahamas, Florida, Gulf of Mexico and/or Bermuda) This has led to speculation about the possible relationship of bleaching to global warming

(Williams et al. 1987; Williams and Bunkley-Williams 1990; D'Elia et al. 1991; Glynn 1991; Goreau et al. 1994). Whatever the cause, the increasing frequency of these events, as well as the unprecedented levels of severe bleaching and resultant mortality or local extinctions of corals in several remote or relatively 'pristine' areas (Harriot 1985; Williams and Bunkley-Williams 1990; Glynn 1993; Burke 1997), are currently of great concern to reef scientists.

2.1.2 *Objectives*

The scleractinian species *Montastraea* cf. *annularis*, *Montastraea* cf. *franksi* and *Porites astreoides* were chosen as study organisms for the following reasons:
1) they are the dominant corals on the chosen reefs, and
2) they are known to be locally good indicators of bleaching (Lang et al. 1988). I wanted to assess whether there were differences in bleaching response within each species as well as between species/genera, and between the deep and shallow reefs. Earlier *in situ* observations during the 1990 bleaching event (Lang, pers. comm.) indicated that, among the species present, proportionately more colonies of *Montastraea* spp. were noted to be 'pale' on reefs at both ~3m and ~18m, but the

deep colonies of *Porites astreoides* were more severely affected, with areas of white as well as pale.

Previous *in situ* surveys of bleaching (Lasker et al. 1984; Cook et al. 1990; Goreau and Macfarlane 1990; Bythell and Bythell 1992; Lang et al. 1988; Fitt et al. 1993) have generally used arbitrary indices to measure changes in coral color, which (theoretically) reflect the amount of zooxanthellae and/or photosynthetic pigments lost. In this chapter, I assess the effectiveness of three different techniques in estimating color change/bleaching over different temporal scales. I also compare bleaching patterns on several levels (from populations to reefs), and look at the possible association of bleaching events to increased water temperatures.

Long-term photographic observations of seasonal color changes (spanning three bleaching events in 1991, 1993, and 1995) were analyzed visually, using a novel indexing method. B. Maguire's original digital slide analysis method (Lang et al. 1993; Maguire et al. 1996) was also used to detect seasonal color change in 25 colonies of *Montastraea* cf. *franksi* from the deep reef; these results were compared to those from the visual slide analysis. A complimentary short-term study, using the same bleaching index as that of the visual slide analysis method for 2 m wide belt transects, was executed in the fall of 1995 during a mass bleaching event.

2.2 Materials and Methods

2.2.1 *Study sites*

For replication, two adjacent sites were chosen on each of two reefs, one deep and one shallow. The shallow (~3 m depth) sites were located on a nearshore fringing reef along the northeast side of Norman's Pond Cay (refer to Fig. 1.1), which is directly exposed to breaking waves. The substrate consists of a low-relief hardground sparsely covered by small stony corals (<10%, J.C.Lang, pers. obs.), fire corals, gorgonians, and sponges. There are few scleractinians larger than ~0.5 m in diameter still securely attached to the substratum.

The deeper North Perry fore reef (~18 m depth), runs along the northeast end of Lee Stocking Island (Fig. 1.1), and consists of 3-4 m high spurs and low (<1 m) lobes that form a transition area between a gentle shoreward (<30°) slope and a sand-covered seaward terrace. The maximum cover of stony corals here is ~25%

(A.J.King pers. obs.), and macroalgae, gorgonians, and sponges are also prevalent.

2.2.2 *Colony selection for photography*

For each species at each site (*Montastraea* cf. *annularis* and *Porites astreoides* at Norman's Pond Cay; *Montastraea* cf. *franksi* and *Porites astreoides* at North Perry), up to 16 randomly- chosen corals were permanently marked by nailing a numbered tag into the adjacent non-living substratum. Additional colonies were tagged in 1992 to increase the sample size. Corals (~10 - 40 cm in diameter) were chosen regardless of specific color, appearance, orientation, or ease of photography. The initially-tagged colonies were defined as physiologically isolated areas of live coral tissue (Jackson 1985). During the course of the study, as corals disappeared, died, or were renamed (11 *Montastraea* cf. *franksi* at North Perry, see Chapter 1), they were replaced by the nearest appropriate colony.

2.2.3 *Photography*

Photographs of colonies were taken at least three times a year at a fixed distance of 0.6 m, using B. Maguire's stereo-pair camera/strobe light system with attached Macbeth or Kodak gray scale, compass, and goniometer (Lang et al. 1993; Maguire et al. 1996). Although sketches and compass directions ensured that all pictures of any given coral were taken at approximately the same angle and orientation, some variation was unavoidable, particularly in heavy surge. A large (2.5 m X 2.5 m) sheet of black plastic, attached to a PVC pipe on one side for ease of handling, was held over the entire setup by a second diver. This tarp blocked ambient light so the strobes would provide an even light field for the coral and gray scale, which is important for accurate digital slide analysis (B. Maguire, pers. comm.).

Observations were made from August 1991 through October 1995 at the two North Perry sites, to March 1994 at the northern Norman's Pond Cay site and to October 1995 at the southern Norman's Pond Cay site, with two interruptions in 1994. Corresponding visual observations were recorded *in situ* on slates.

2.2.4 *Digital slide analysis*

The original Fuji color print film from each series was processed into color positive slides, which were then individually labeled and stored in an archival-quality cabinet. (The original print film is preserved in a freezer.) Each slide was scanned with a Nikon CoolScan at a resolution of 300dpi, and digitized on the RGB (Red, Blue, Green) component scale in Adobe Photoshop 2.5; scanned images were then saved as PICT files for later analysis, and stored on 128MB magneto-optical disks.

A representative rectangular area on each coral image (no greater than ~100 cm^2) was chosen for analysis after visual examination of all the digitized images for each series. (Any physiological remnants resulting from fission were retained in the analysis as subsets of the original tagged colony. Fusion with adjacent conspecifics was noted on several occasions, but additional areas of tissue were not considered in this analysis.)

Each mean Red (R), Green (G), and Blue (B) brightness level was determined by generating a histogram of the chosen area using the histogram analysis procedure in Adobe Photoshop 2.5 (Lang et al. 1993). (The color black is present when all RGB brightness levels are at 0; white occurs when they are all at 255; various shades of gray result from varying (but equally proportioned) brightness levels between 0 and 255.) The respective RD (reflection density) of each RGB brightness level was then determined by comparison to the known or interpolated RD values on the photographed gray scale which has scaled brightness values from 0 to 1.5. (It is very important to note that RD values decrease as brightness levels increase (*i.e.*, as values go toward white, indicating a loss of color (pigmentation) or 'bleaching').

RD values from each brightness level were combined into one total value of Gray (R+G+B) for 25 *Montastraea* cf. *franksi* colonies on North Perry reef (11 minimum sample size, 25 maximum sample size for all observational periods). These total RD values were ranked on an even scale from 0.6 (lowest summed value, least amount of color) to 3.6 (highest summed value, highest amount of color) using the following ranges:

RD range	Rank
3.6 - 3.0	1
3.0 - 2.4	2
2.4 - 1.8	3
1.8 - 1.2	4
1.2 - 0.6	5

2.2.5 *Visual slide analysis*

The complete temporal series of slides for each colony was also examined visually on a light box, using a

10x magnifying lens. That part of the colony which was visible in each photograph was given a classification based on the following indexing method: the amount of 'bleached' tissue surface area was visually evaluated and recorded as none, part (any visible 'bleaching' less than 100%), or all; the intensity of 'bleaching' was estimated by the colors (or lack of color) present on the colony as normal, pale, or white (and all combinations). Every possible combination of area and intensity was also ranked in the following manner:

Area/Colors	Rank
none/normal	1
part/normal + pale	2
part/normal + pale + white	3
part/normal + white	3
all/pale	3
all/pale + white	4
all/white	5

(For the purpose of this chapter, indications of 'bleaching' will include ranks of 2 - 5 for the visual slide analysis and the chain transect methods.)

The ranks produced by each of the above procedures (digital slide analysis and visual slide analysis) were compared for the same 25 colonies, for the fall observational periods of 1991, 1993, and 1995 using a two-tailed Mann-Whitney U-test for tied ranks. The null hypothesis was that the ranks of RD values from the digital slide analysis were equal to the ranks of 'bleaching' from the visual slide analysis (*i.e.*, both methods indicated the same results.).

Chi-square contingency tables (with Bonferroni corrections) of area, color, and ranking were generated to detect significant differences in 'bleaching' within species (at different sites and reefs), and between species, sites, and reefs, for all 15 observational periods. In all cases the null hypothesis was stated as no significant differences between these estimates of 'bleaching' responses.

2.2.6 *Chain transects*

A chain transect assessment procedure was performed on both Norman's Pond Cay Reef and North Perry Reef during a mass bleaching event in late October of 1995, following several weeks of elevated water temperatures (see Results and Discussion). This survey provided an opportunity to relate a broader short-term assessment of a single mass bleaching event, with longerterm observations of single colonies whose color variations are known.

At Norman's Pond Cay (NPC), a starting point was haphazardly selected that placed the sampling transects in areas where the photographically-monitored corals occurred. From that point a 50 m baseline chain was laid parallel to the shoreline. Six starting points were randomly selected along the baseline from a pool of 2 m intervals (using even meter numbers from 0 through 50) for sampling transects. Each belt transect was then laid at an orientation perpendicular to the base transect (*i.e.*, perpendicular to the shoreline), and was 2 m wide and 20 m long.

At North Perry (NP), surveyed areas were restricted to five well-defined, narrow spurs with coral cover, all in the vicinity of monitored corals (Fig. 2.1). Belt transects were set up along the length of each of these spurs, choosing as endpoints the narrowest parts of the spurs that were at least 2 m wide. A sixth transect was set up on a projecting skirt of the reef slope oriented parallel to the spurs.

For every colony of the appropriate species (*Montastraea* cf. *annularis* and *P. astreoides* in shallow

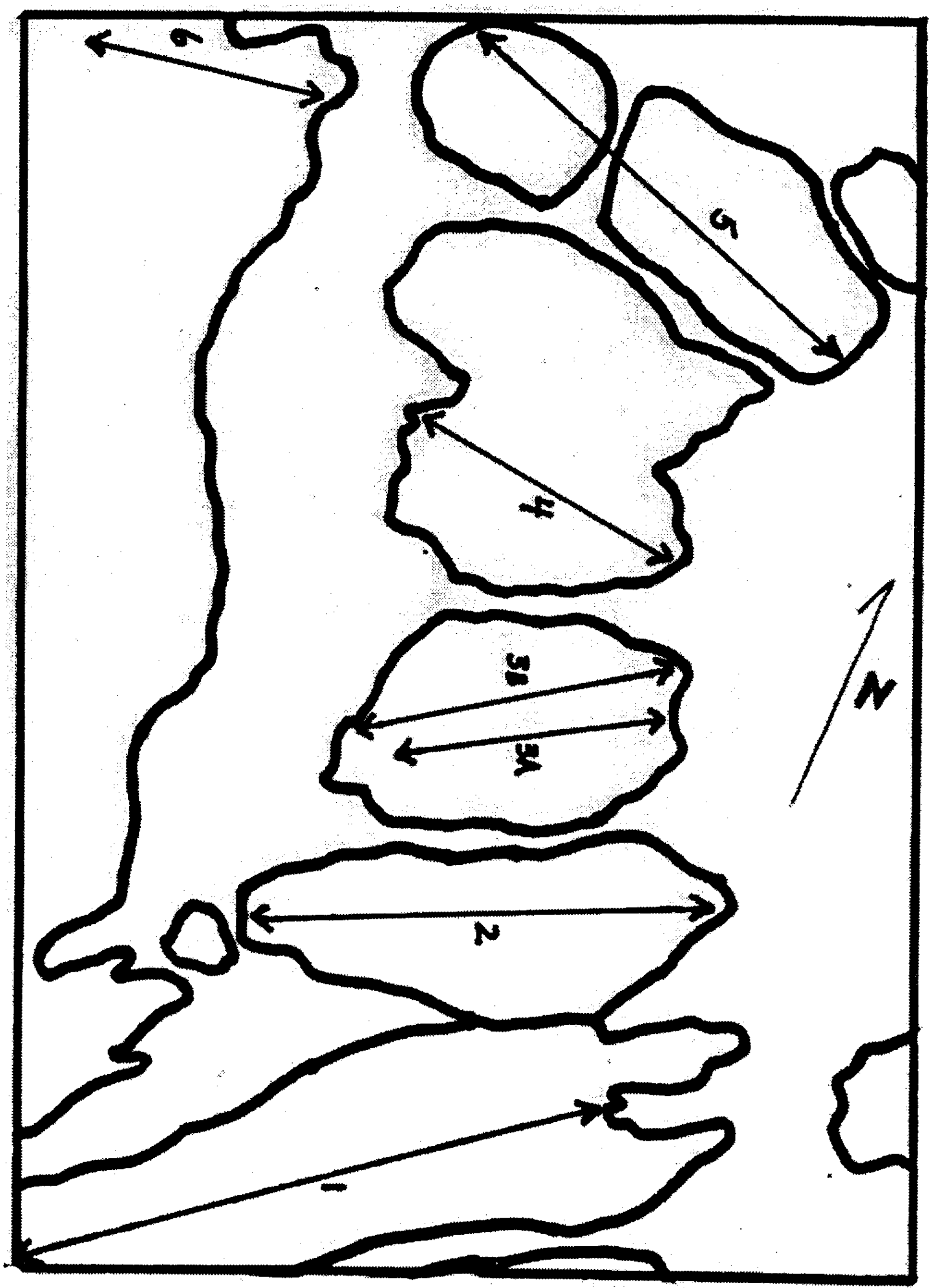


Fig. 2.1: Map of chain transects on North Perry Reef.

water; *Montastraea* cf. *franksi* and *P. astreoides* in deep) within the 2 m wide transects at all sites, I assessed 'bleaching' using the same indexing method as described in the visual slide analysis procedure. Chi-square tests (with Bonferroni corrections) of area, color, and ranks were performed to detect significant differences in 'bleaching' within species at different sites and reefs, and among species, sites, and reefs, for the corals in these transects. In all cases the null hypothesis was that there were no significant differences between 'bleaching' responses.

2.2.7 *Temperature records*

Thermographs placed at the Norman's Pond Cay reef and South Perry Reef (southern end of the same reef as North Perry, < 1 km distance, refer to Fig. 1.1) recorded hourly sea surface temperatures, which were then converted into daily average temperatures. Norman's Pond Cay data were only available from 1993 through 1995, but South Perry Reef temperature data were continuous throughout the study (1991-1995). I assumed for this study that there was no significant difference in average water temperatures between the North and South Perry reef sections.

2.3 Results

2.3.1 *Temperature records*

Three mass bleaching events occured during the late summer and fall of 1991, 1993, and 1995 (see following sections). The average daily seawater temperatures in the weeks immediately preceding these events (indicated by arrows in Figs. 2.2 and 2.3) were approximately one degree higher than in non-bleaching years. Norman's Pond Cay (Fig. 2.2) corals bleached during times of average temperatures above ~30°C, while North Perry (Fig. 2.3) showed significantly greater

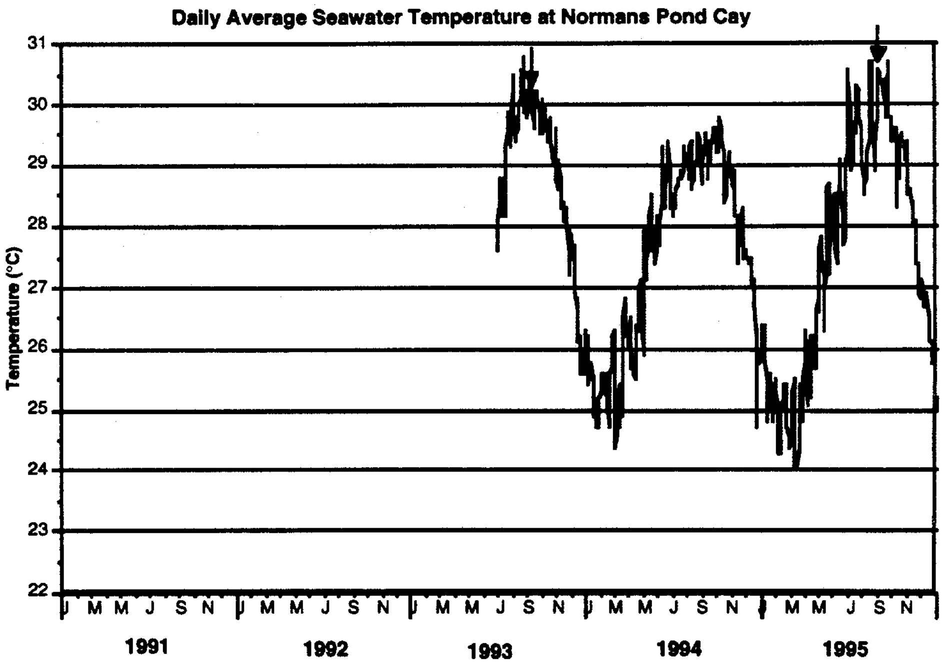


Fig. 2.2: Daily average seawater temperature at the shallow reef from 1993-1995.

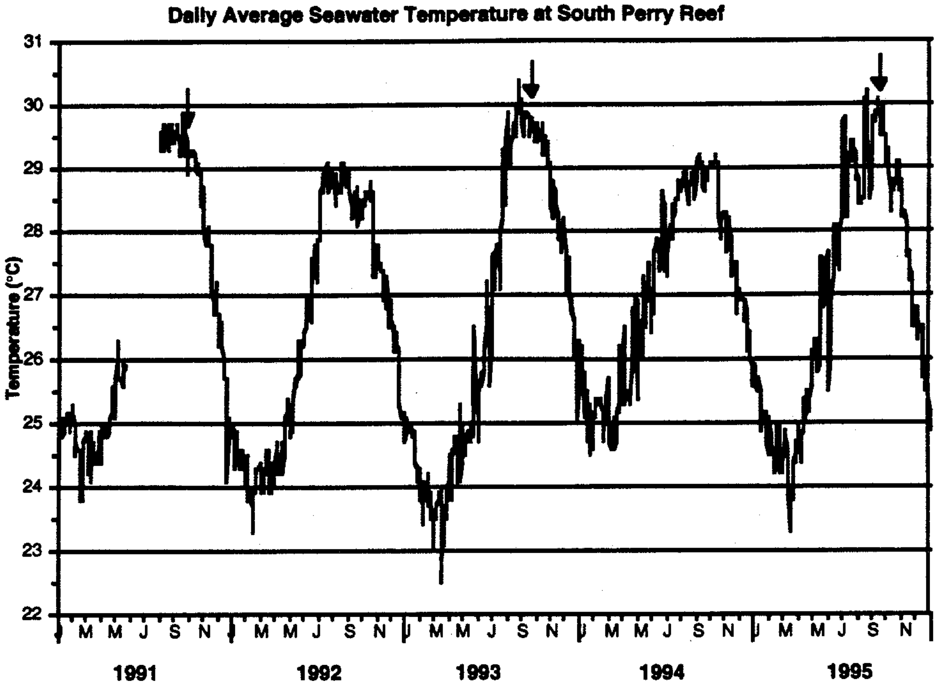


Fig. 2.3: Daily average seawater temperature at the deep reef from 1991-1995.

amounts of bleaching above ~29.5°C; these temperatures are near 29.9°C, which has been identified as a 'critical threshold' for bleaching on Jamaican reefs (Strong and Duda 1996).

2.3.2 *Digital slide analysis*

The mean RDs (reflection densities) of the analyzed rectangular areas for 25 out of the 33 photographed *Montastraea* cf. *franksi* from 1991-1995 are represented in the Red (Fig. 2.4), Green (Fig.2.5), and Blue (Fig. 2.6). In general, average Blue RD values were higher than

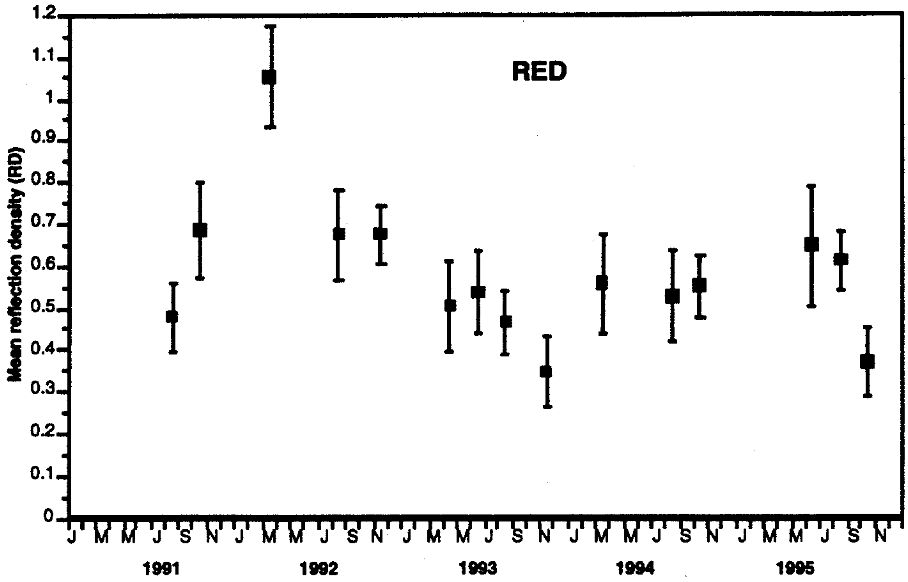


Fig. 2.4: Mean reflection densities of *Montastraea* cf. *franksi* in the RED; 1991-1995. Error bars indicate 95% confidence intervals.

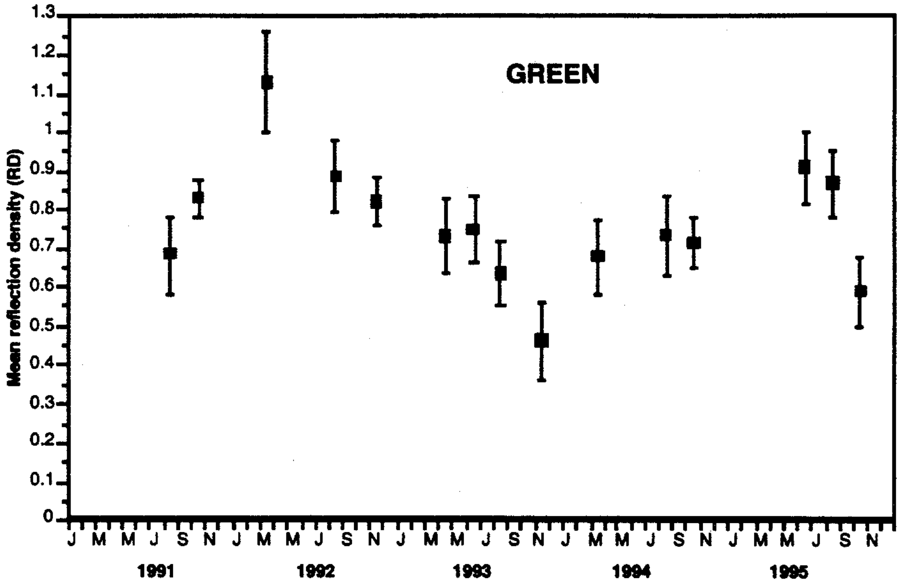


Fig. 2.5: Mean reflection densities of *Montastraea* cf. *franksi* in the GREEN. Error bars indicate 95% confidence intervals.

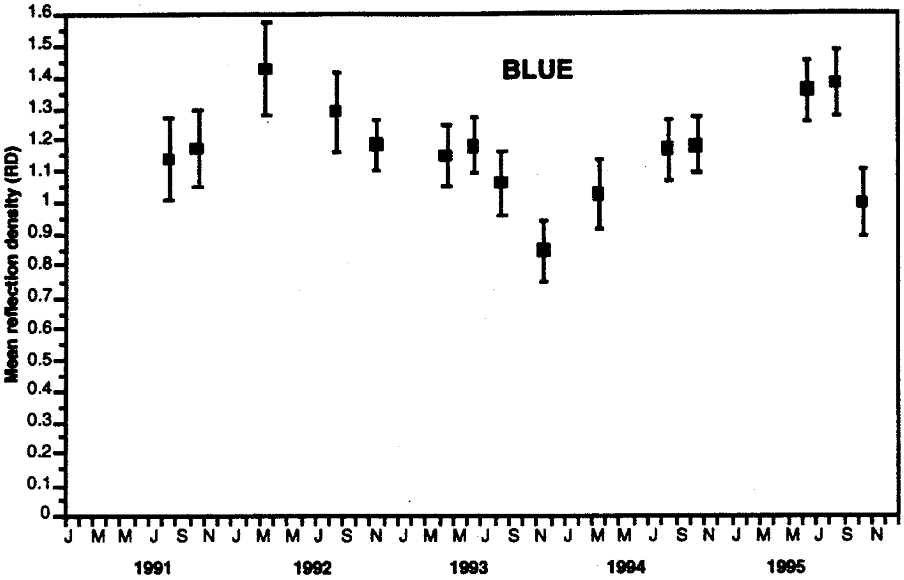


Fig. 2.6: Mean reflection densities of *Montastraea* cf. *franksi* in the BLUE; 1991-1995. Error bars indicate 95% confidence intervals.

Green and Red at any given time throughout the study, and average Red RD values were lowest; however, individual coral values occasionally deviated from this pattern. The highest reflection densities in Blue were expected as a photosynthetic response of the zooxanthellae to available wavelengths in seawater, especially at depth.

When the RD temporal patterns are compared to the temperature graphs (Figs. 2.2 and 2.3), there are certain indications that RD values may be influenced by temperature. The lowest average RD values (indicating the greatest loss of color) on all three graphs (Figs. 2.4-

2.6) did coincide with the observation periods of highest temperatures and greatest bleaching in fall 1993 and fall 1995. In addition to changes in temperature, temporal fluctuations in pigment concentrations as a result of annual patterns of change in available light levels were expected, but no clear seasonal patterns were obvious.

2.3.3 *Visual slide analysis*

Figs. 2.7-2.14 summarize the number of colonies out of the total that were affected at any time by any amount of 'bleaching' (of rank 2 or above), for all species and sites. To look for differences among species, sites, reefs, etc., Chi-square tests were performed as described in the methods. The three variables of area, color, and rank gave the same significant/not significant results for all comparisons, so for simplification, only statistics from the ranks will be presented in this paper, as both area and color are incorporated herein (χ^2-values are summarized in Table 2.1 at the end of this section).

Total amounts of 'bleaching' (combining all photographed corals) in 1991, 1993, and 1995 were each found to be significantly higher compared to 1992 and 1994, when there was almost no 'bleaching'; these results appear to associate strongly with the graphs of

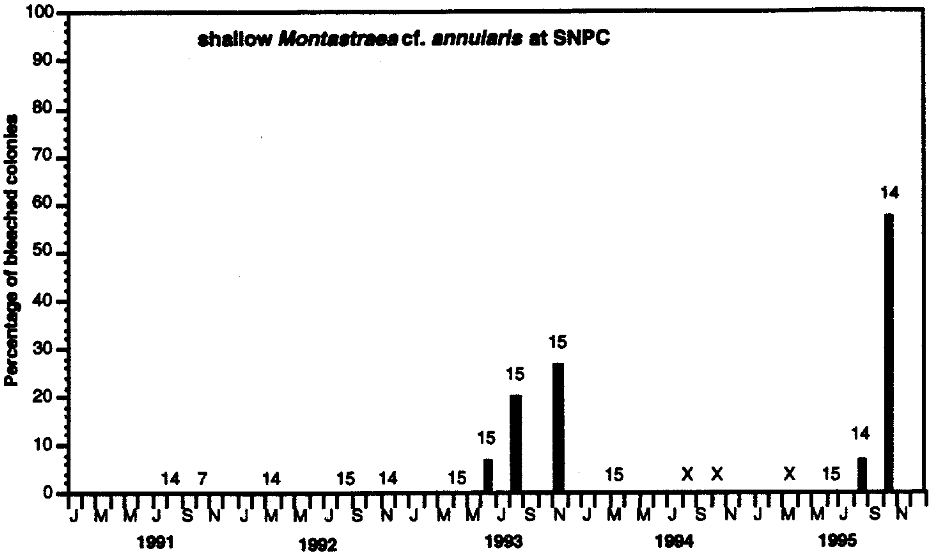


Fig. 2.7: Percent of bleached *Montastraea* cf. *annularis* colonies at the shallow southern Norman's Pond Cay site from 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

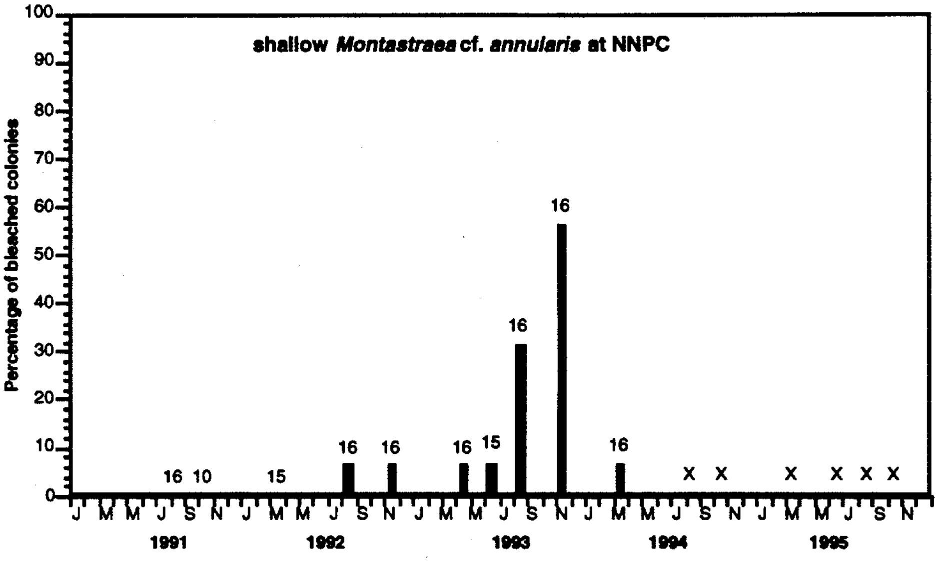


Fig. 2.8: Percent of bleached *Montastraea* cf. *annularis* colonies at the shallow northern Norman's Pond Cay site from 1991- spring 1994. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

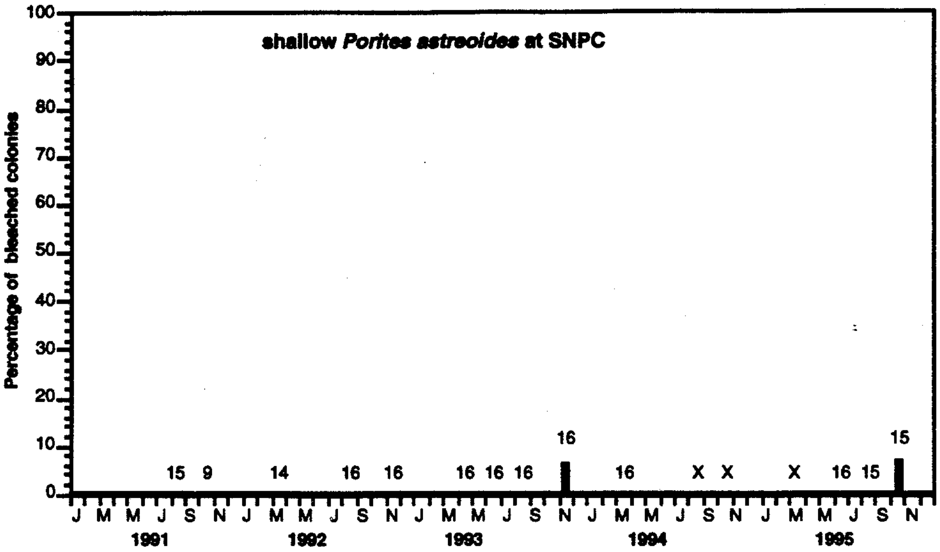


Fig. 2.9: Percent of bleached *Porites astreoides* colonies at the shallow southern Norman's Pond Cay site from 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

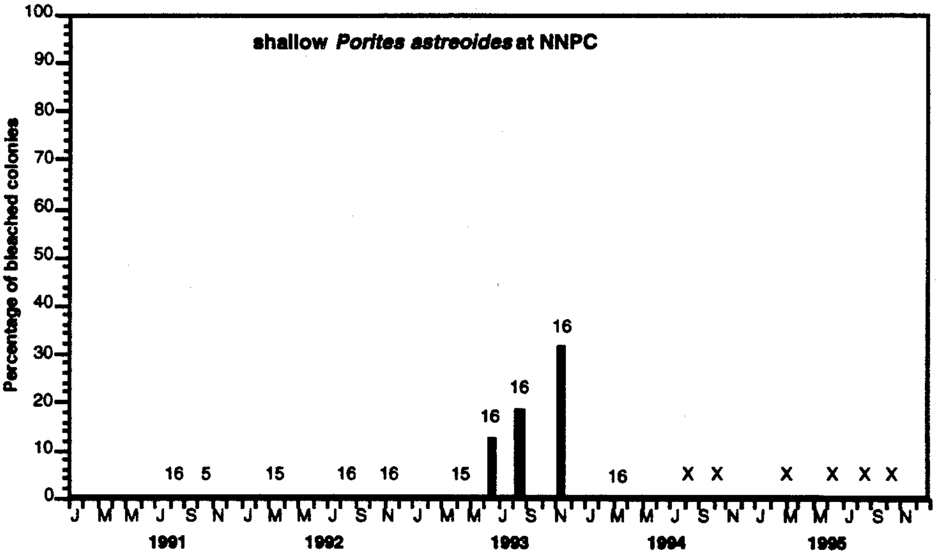


Fig. 2.10: Percent of bleached *Porites astreoides* colonies at the shallow northern Norman's Pond Cay site from 1991- spring 1994. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

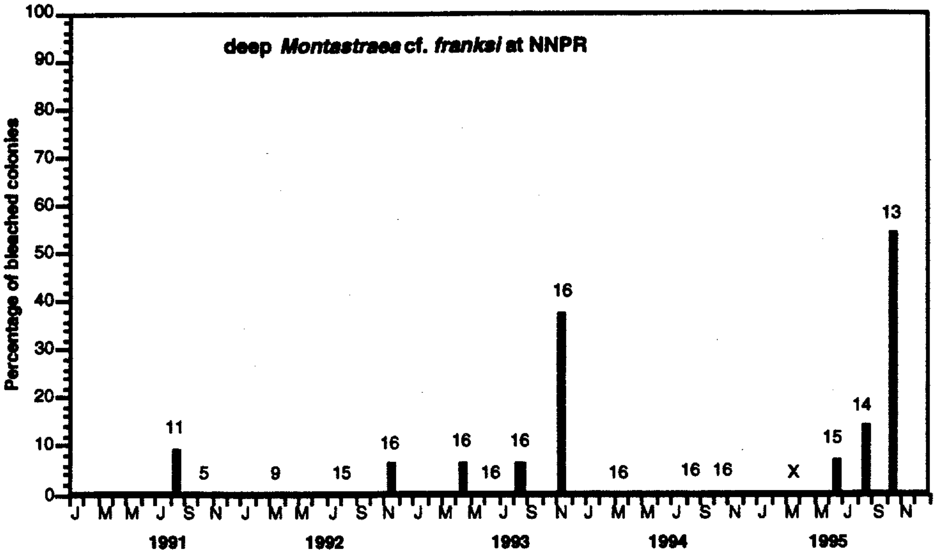


Fig. 2.11: Percent of bleached *Montastraea* cf. *franksi* at the deep northern North Perry site from 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

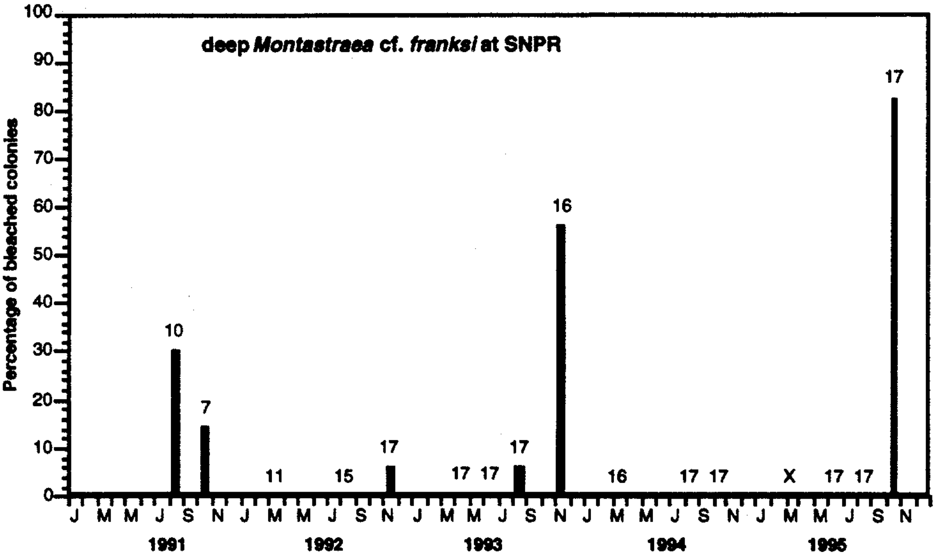


Fig. 2.12: Percent of bleached *Montastraea* cf. *franksi* colonies at the deep southern North Perry site from 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

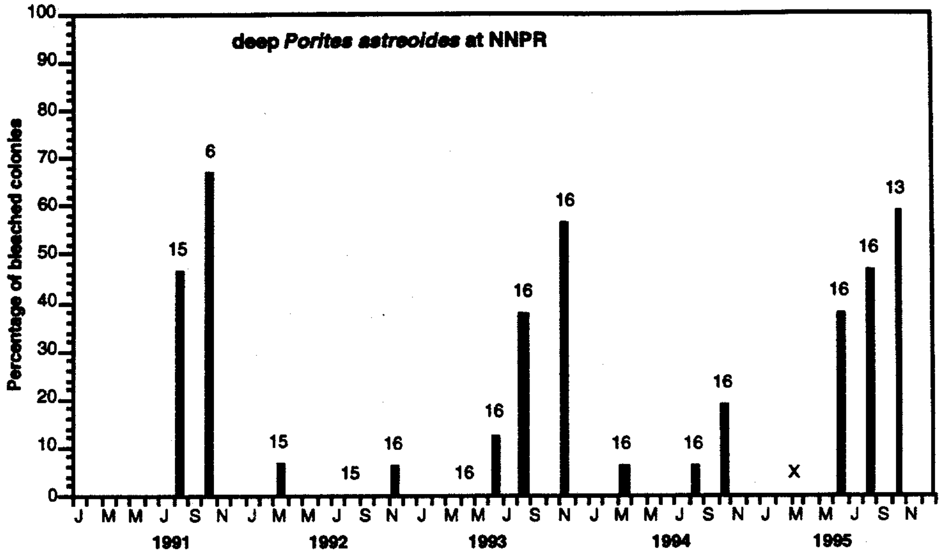


Fig. 2.13: Percent of bleached *Porites astreoides* colonies at the shallow northern North Perry site from 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

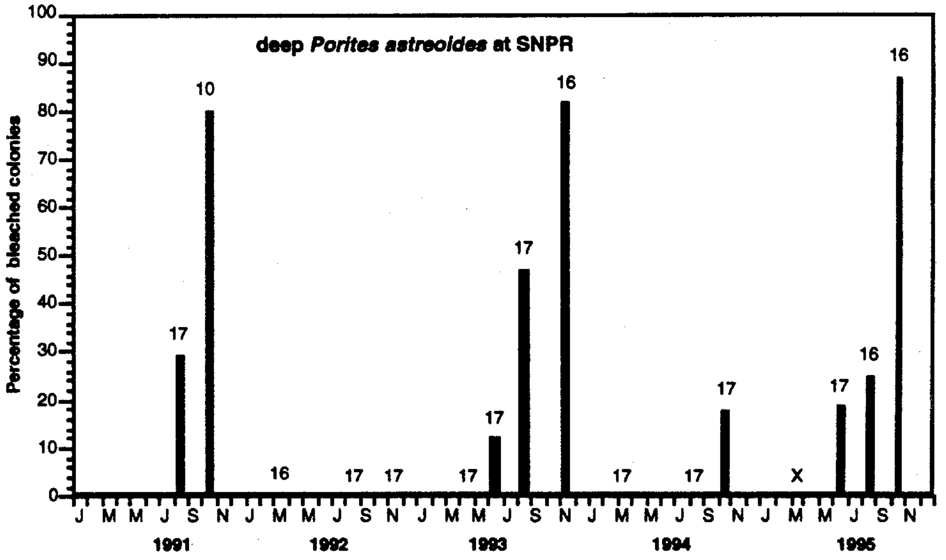


Fig. 2.14: Percent of bleached *Porites astreoides* colonies at the deep southern North Perry site from 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

temperature, as previously discussed. Overall, the fall observational period of 1995 had the highest percentage of 'bleached' colonies (50/88; Figs. 2.7-2.14), but this number was not found to be significantly different from total 'bleaching' in fall of 1993 (56/127) ($\chi^2 = 8.143$, $P = 0.0865$).

Such is not the case if *Montastraea* and *Porites* colonies are analyzed separately; the total number of affected *Montastraea* increased significantly from 1993 to 1995 ($\chi^2 = 12.133$, $P = 0.0081$), but *P. astreoides* did not ($\chi^2 = 4.143$, $P = 0.1521$). Photographed corals in 1993 ($\chi^2 = 10.876$, $P = 0.0347$) and 1995 ($\chi^2 = 19.454$, $P = 0.0002$) 'bleached' significantly more than in 1991 for all colonies at all sites (Figs. 2.7-2.14).

In those years that exhibited significant levels of 'bleaching' (1991, 1993, 1995), the highest levels always occurred during the fall (Oct/Nov) observation periods (1991: $\chi^2 = 9.643$, $P = 0.0081$; 1993: $\chi^2 = 23.637$, $P = 0.0001$; 1995: $\chi^2 = 38.747$, $P = 0.0001$). The 'occurrence' of 'bleaching' during spring observations was thought to be due to the slower relative recovery of individual colonies from an earlier bleaching event (Lang et al. 1992), and was not considered to be the start of a new event. The most extensive 'bleaching' occurred following prolonged periods of water temperatures at least 1°C higher than in non-bleaching years (Figs. 2.2, 2.3).

During any given mass bleaching event, the pattern of 'bleaching' between reefs was always the same. Deep North Perry colonies consistently exhibited significantly higher levels of 'bleaching' than the shallow corals at Norman's Pond Cay throughout the study (only fall obs. periods reported here: 1991/ $\chi^2 = 22.995$, $P = 0.0001$; 1993/ $\chi^2 = 17.993$, $P = 0.0004$; 1995/ $\chi^2 = 16.786$, $P = 0.0008$); these results concur with previous *in situ* observations, as well as data from the chain transects (see following section). Neither of the reefs exhibited significant differences in 'bleaching' response between sites for either species at any time throughout the study. Therefore, the data from each site will be combined by reef for the following comparisons.

As seen in Figs. 2.7-2.14, it is apparent that, in 1991, both deep-water species 'bleached' significantly more than their shallow counterparts. This pattern remained consistent for *Porites astreoides* in both 1993 ($\chi^2 = 21.446$, $P = 0.0001$) and 1995 ($\chi^2 = 18.368$, $P = 0.0004$). However, *M.* cf. *franksi* did not 'bleach' significantly more than *M.* cf. *annularis* for either 1993 (χ^2 = 3.022, P = 0.2207) or 1995 (χ^2 = 3.129, P = 0.2149).

In 1991, for the deep reef only, *Porites astreoides* 'bleached' more than *Montastraea* cf. *franksi* (χ^2 = 17.823, P = 0.0001). This was not the case in either 1993 (χ^2 = 3.29, P = 0.193) or 1995 (χ^2 = 1.086, P = 0.7803), when both species on the deep reef had similar numbers of affected colonies. *Montastraea* cf. *annularis* on the shallow reef did not show a significantly different response from *Porites astreoides* in the fall of 1993 (χ^2 = 6.271, P = 0.0992), but did 'bleach' at a higher level in the fall of 1995 (χ^2 = 9.176, P = 0.0102).

Both *Montastraea* cf. *annularis* (Figs. 2.7 and 2.8) and *M.* cf. *franksi* (Figs. 2.11 and 2.12) increased in the total number of affected colonies with each subsequent bleaching event, while the number of 'bleached' *Porites astreoides* stayed constant during all three events (Figs. 2.9, 2.10, 2.13, and 2.14). In 1991 (deep reef only), *P. astreoides* 'bleached' more severely than *M.* cf. *franksi*, but by 1993, the total relative numbers of affected corals were approximately equal between species on either reef (χ^2 = 1.355, P = 0.7162); this result remained consistent for 1995 (reefs combined: χ^2 = 4.973, P = 0.1738).

Table 2.1: Summary of Chi-square analysis results (with Bonferroni corrections) for visual slide analysis data.

Comparison	χ^2-value	P-value	d.f.
Total amount of 'bleaching':			
1991 *vs.* 1993	10.876	0.0347	3
1991 *vs.* 1995	19.454	0.0002	3
1993 *vs.* 1995	8.413	0.0865	4
***Montastraea*:**1993 *vs.* 1995	12.133	0.0081	4
***Porites*:**1993 *vs.* 1995	4.605	0.1521	4
Fall *vs.* Summer obs. periods			
1991 *vs.* 1993	9.643	0.0081	2
1991 *vs.* 1995	23.637	0.0001	3
1993 *vs.* 1995	38.747	0.0001	3
North Perry *vs.* Norman's Pond			
(fall obs. period only)			
1991	22.995	0.0001	2
1993	17.993	0.0004	3
1995	16.786	0.0008	3
M.* cf. *annularis* *vs.* *M.* cf. *franksi			
1993	3.022	0.2207	2
1995	3.129	0.2149	2
***Porites* (shallow) *vs.* *Porites* (deep)**			
1993	21.446	0.0001	2
1995	18.368	0.0004	3

Table 2.1 (cont.): Summary of Chi-square analysis results (with Bonferroni corrections) for visual slide analysis data.

Comparison	χ^2-value	P-value	d.f.
Shallow reef (NPC)			
M.* cf. *annularis vs. P. astreoides			
1993	6.271	0.0992	3
1995	9.176	0.0102	2
Deep reef (NPR)			
M.* cf. *franksi vs. P. astreoides			
1991	17.823	0.0001	2
1993	3.290	0.1930	2
1995	1.086	0.7803	3
All *Montastraea vs.* All *Porites*			
1993	1.355	0.7162	3
1995	4.973	0.1738	3

2.3.4 *Digital slide analysis vs. visual slide analysis*

According to visual slide analysis of only the 25 *Montastraea* cf. *franksi* colonies used in the digital analysis, the mass bleaching event in 1991 was less severe for *Montastraea* cf. *franksi* (as depicted in Fig. 2.15) than the bleaching events of 1993 and 1995 (1991/1993: χ^2 = 7.73, P = 0.021; 1991/1995: χ^2 = 23.156, P = 0.0001). (This may partially account for the somewhat higher than expected average RD values seen during the two

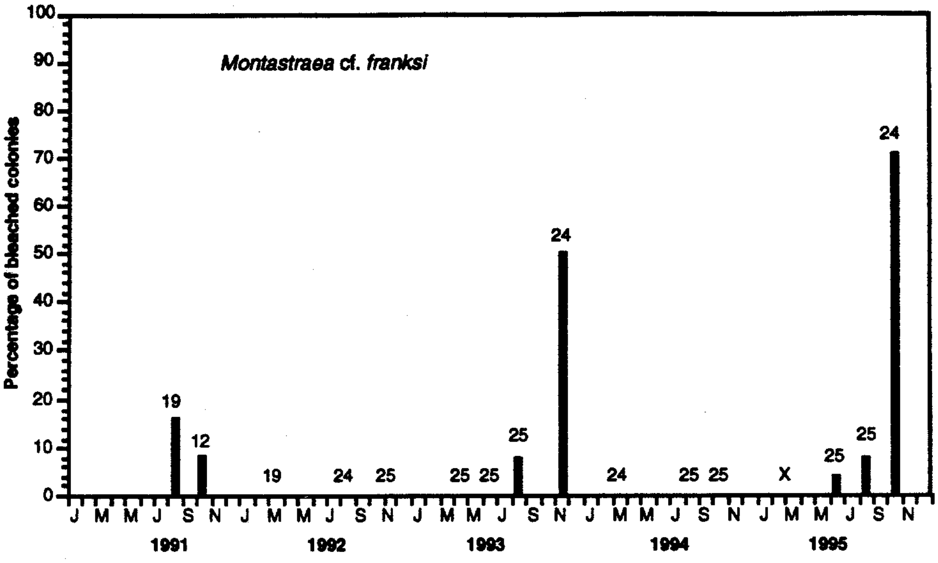


Fig. 2.15: Percent of bleached *Montastraea* cf. *franksi* colonies according to visual analysis of the same 25 colonies used in the digital analysis, 1991-1995. Numbers above spaces or columns indicate sample sizes for observational periods. X means no photographs taken.

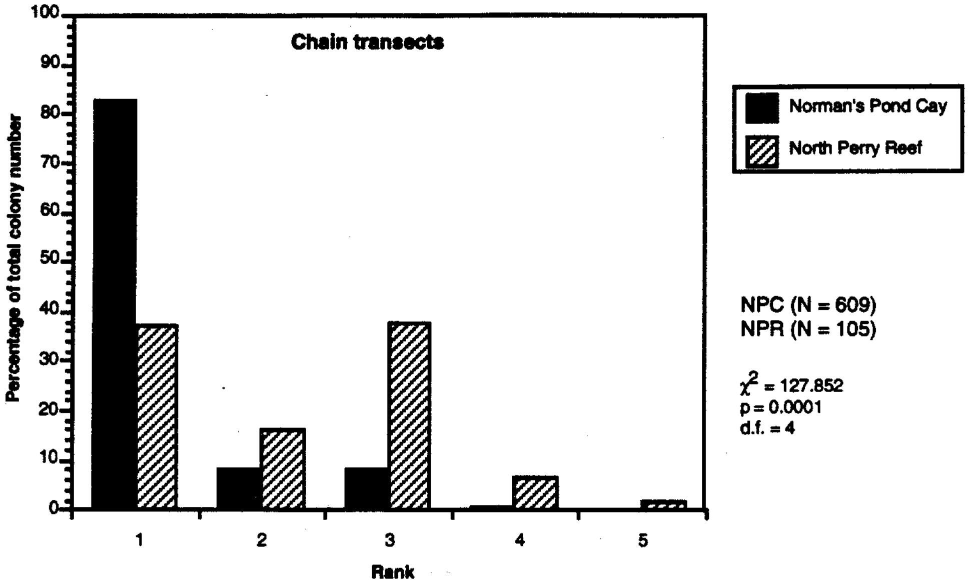
1991 observational periods (Figs. 2.4-2.6).)

A survey of the visual slide analysis data, as well as *in situ* observations, indicated that certain colonies were more sensitive to 'bleaching' than others, with some corals 'bleaching' consistently during all three events (3/25), in both the 1993 and 1995 events (7/25), only in the most recent event (9/25), or not at all (6/25). However, these 'bleaching' response patterns were not always reflected by the digital slide analysis.

The only times at which any agreement in rankings occurred between the digital slide analysis and the visual slide analysis were during the fall observations of 1991 (8/11), 1993 (1/20 colonies) and 1995 (11/23 colonies). Results from the Mann-Whitney U-test indicated that although the ranks from both methods were approximately equal for fall of 1991 (N = 11) and fall of 1995 (N = 23), they were significantly different for fall of 1993, with the digital slide analysis indicating a higher level of 'bleaching'.

2.3.5 *Chain transects vs. visual slide analysis*

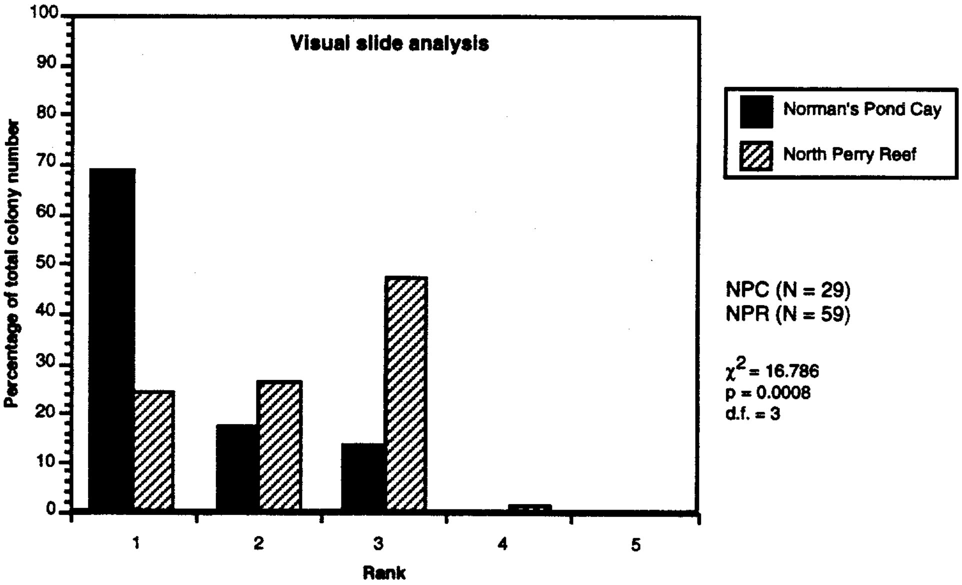
Chi-square tests of area affected, color(s) present, and rank (combined area and color) were run for the data collected in late October of 1995 using the same visual index of 'bleaching' for the chain transect assessment. As was the case in the visual slide analysis, the variables of area, color, and rank gave the same significant/not significant results for all chain transect Chi-square comparisons; hence, only values from the ranks will be presented here. Since transect lengths were not consistent on the deep reef, results depicted in Figures 2.16-2.27 are better represented as relative percentages of the contingency table row totals. (A comparative summary of the statistics from each method is presented in Table 2.2 at the end of this section.)



NPC (N = 609)
NPR (N = 105)

$\chi^2 = 127.852$
p = 0.0001
d.f. = 4

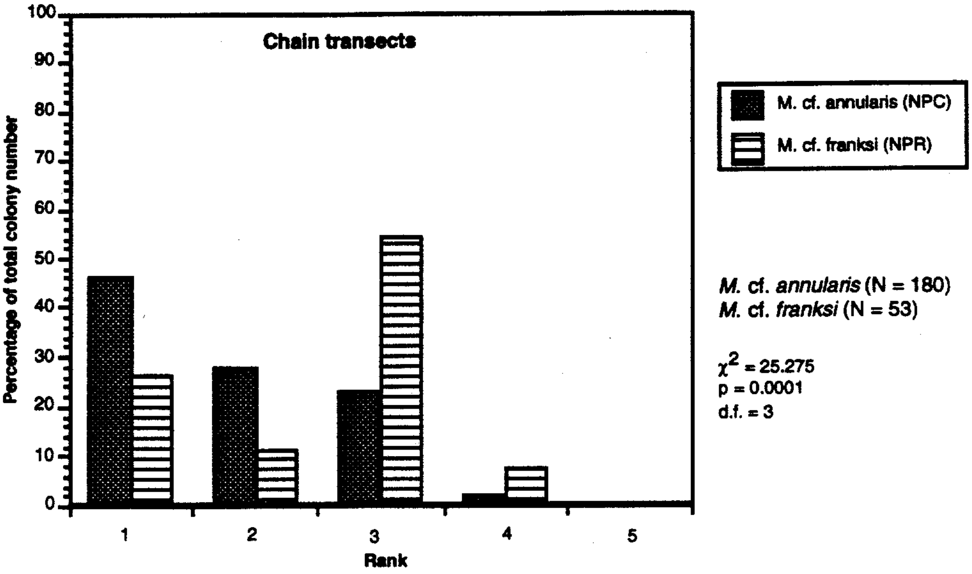
Fig. 2.16: Ranked comparison of bleaching levels by reef (chain transects); October 1995.



NPC (N = 29)
NPR (N = 59)

$\chi^2 = 16.786$
p = 0.0008
d.f. = 3

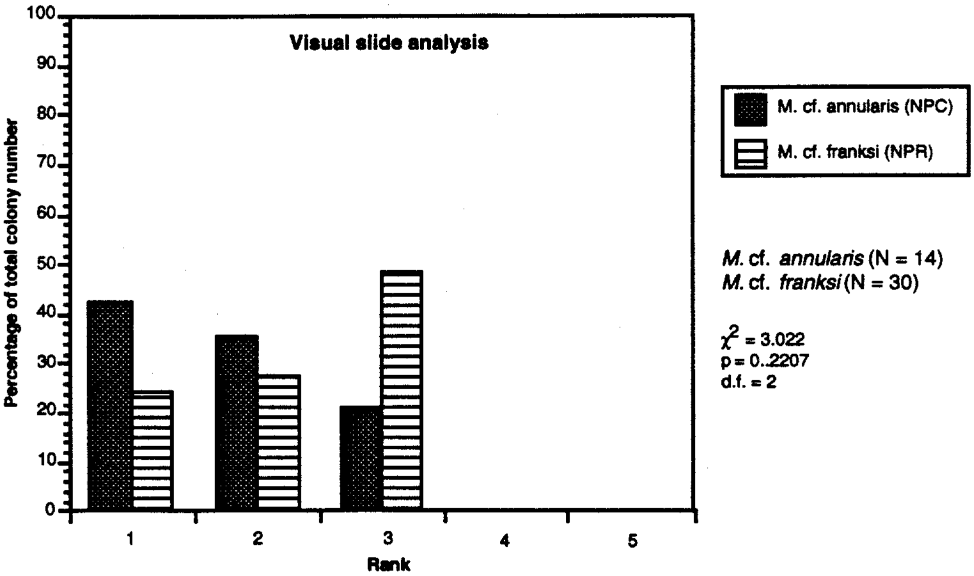
Fig. 2.17: Ranked comparison of bleaching levels by reef (visual slide analysis); October 1995.



M. cf. *annularis* (N = 180)
M. cf. *franksi* (N = 53)

$\chi^2 = 25.275$
$p = 0.0001$
d.f. = 3

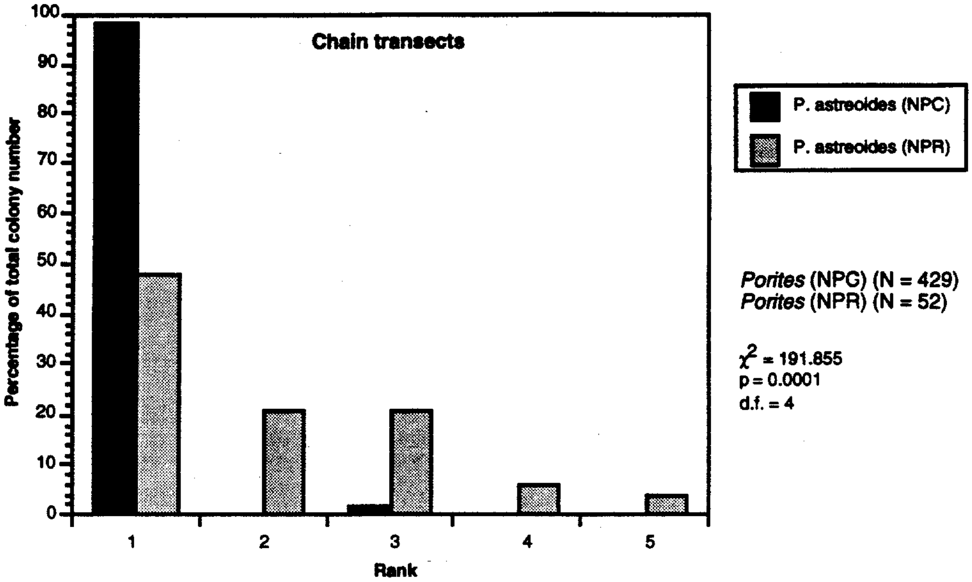
Fig. 2.18: Ranked comparison of bleaching levels in *Montastraea* spp. by reef (chain transects); October 1995.



M. cf. *annularis* (N = 14)
M. cf. *franksi* (N = 30)

$\chi^2 = 3.022$
$p = 0..2207$
d.f. = 2

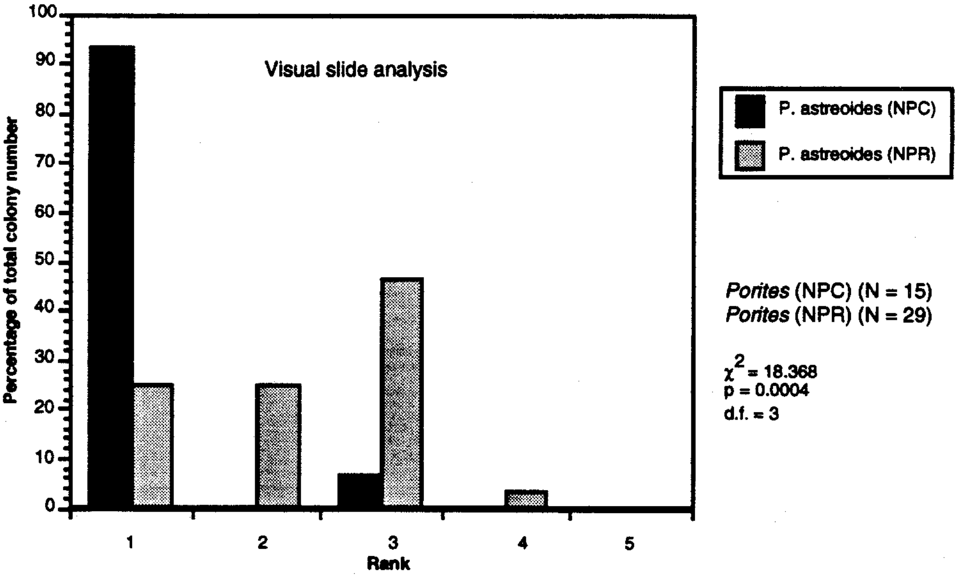
Fig. 2.19: Ranked comparison of bleaching levels in *Montastraea* spp. by reef (visual slide analysis); October 1995.



Porites (NPC) (N = 429)
Porites (NPR) (N = 52)

$\chi^2 = 191.855$
$p = 0.0001$
d.f. = 4

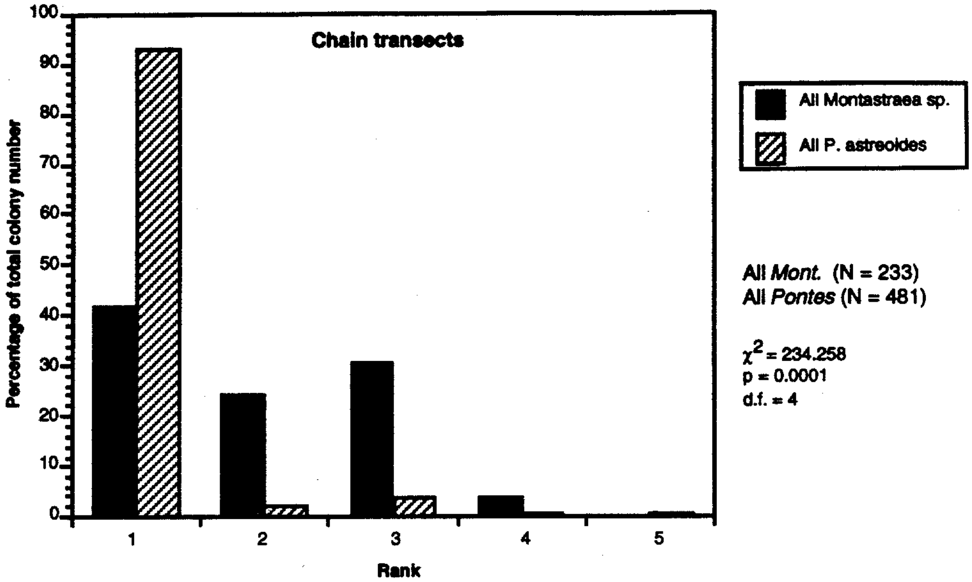
Fig. 2.20: Ranked comparison of bleaching levels in ***Porites astreoides*** by reef (chain transects); October 1995.



Porites (NPC) (N = 15)
Porites (NPR) (N = 29)

$\chi^2 = 18.368$
$p = 0.0004$
d.f. = 3

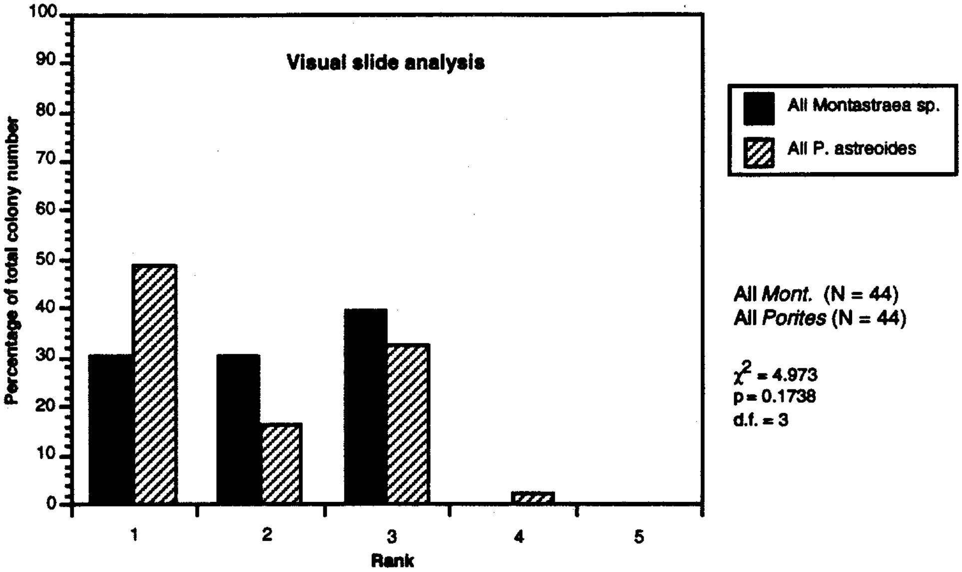
Fig. 2.21: Ranked comparison of bleaching levels in ***Porites astreoides*** by reef (visual slide analysis); October 1995.



All *Mont.* (N = 233)
All *Porites* (N = 481)

$\chi^2 = 234.258$
p = 0.0001
d.f. = 4

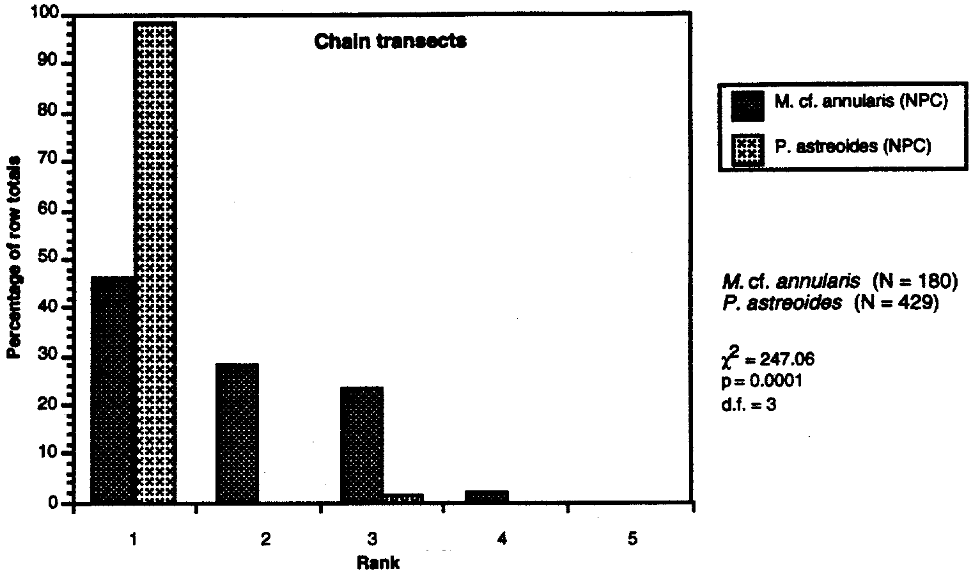
Fig. 2.22: Ranked comparison of bleaching levels between all *Montastraeas* and all *Porites* (chain transects); October 1995.



All *Mont.* (N = 44)
All *Porites* (N = 44)

$\chi^2 = 4.973$
p = 0.1738
d.f. = 3

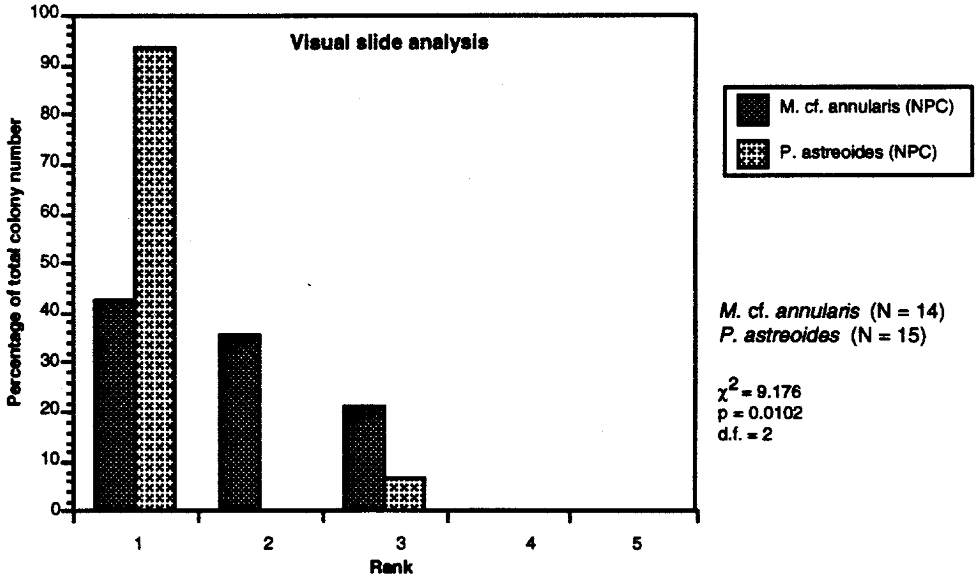
Fig. 2.23: Ranked comparison of bleaching levels between all *Montastraea* and all *Porites* (visual slide analysis); October 1995.



M. cf. *annularis* (N = 180)
P. astreoides (N = 429)

$\chi^2 = 247.06$
p = 0.0001
d.f. = 3

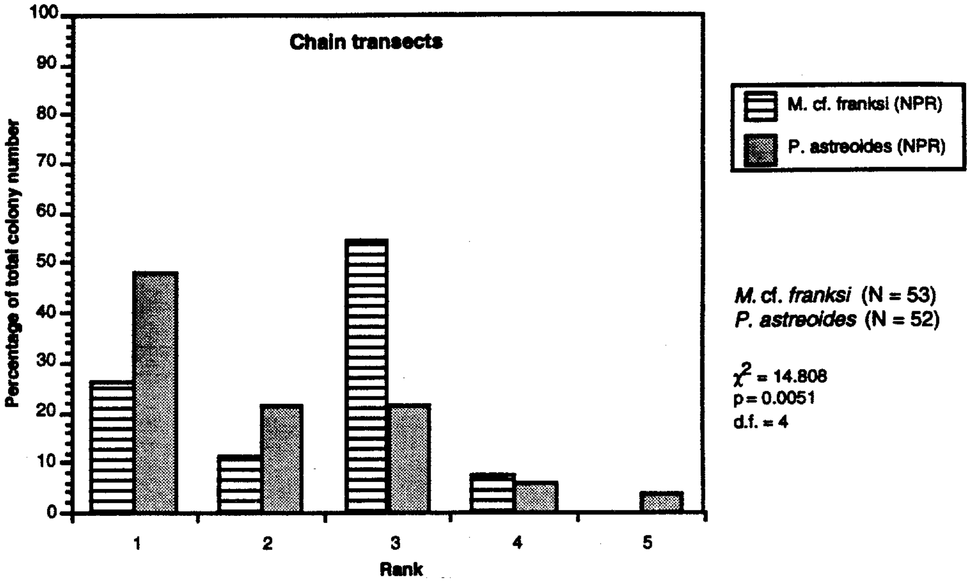
Fig. 2.24: Ranked comparison of bleaching levels between *M.* cf. *annularis* and *P. astreoides* at NPC (chain transects); October 1995.



M. cf. *annularis* (N = 14)
P. astreoides (N = 15)

$\chi^2 = 9.176$
p = 0.0102
d.f. = 2

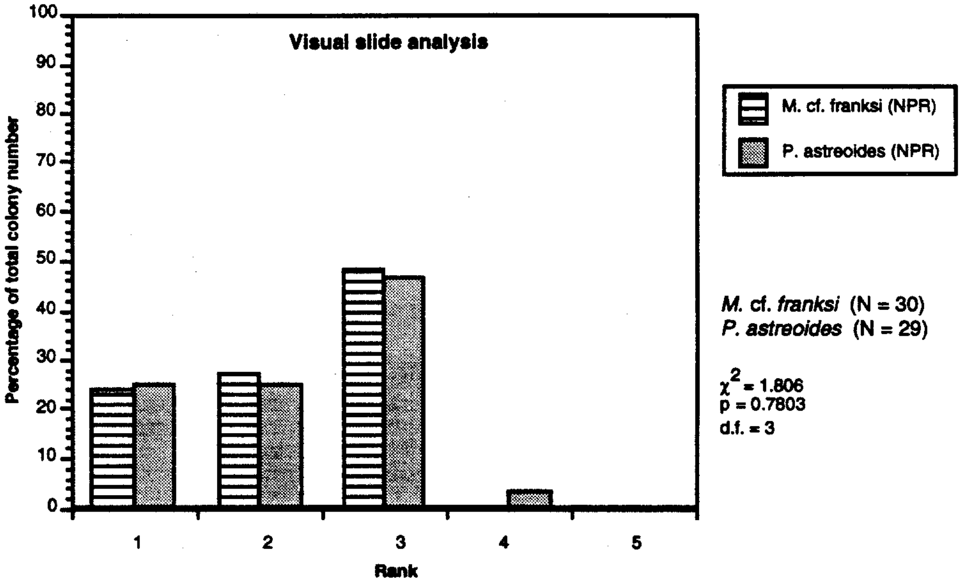
Fig. 2.25: Ranked comparison of bleaching levels between *M.* cf. *annularis* and *P. astreoides* at NPC (visual slide analysis); October 1995.



M. cf. *franksi* (N = 53)
P. astreoides (N = 52)

$\chi^2 = 14.808$
p= 0.0051
d.f. = 4

Fig. 2.26: Ranked comparison of bleaching levels between *M.* cf. *franksi* and *P. astreoides* at NPR (chain transects); October 1995.



M. cf. *franksi* (N = 30)
P. astreoides (N = 29)

$\chi^2 = 1.806$
p = 0.7803
d.f. = 3

Fig. 2.27: Ranked comparison of bleaching levels between *M.* cf. *franksi* and *P. astreoides* at NPR (visual slide analysis); October 1995.

When total numbers of corals from the chain transects were compared by reef, the statistical analysis found that the overall amount of bleaching on the deep reef was significantly greater than in shallow for October of 1995 ($\chi^2 = 127.852$, $P = 0.0001$) (Fig. 2.16). This result agrees with the visual slide analysis, which also indicated that bleaching was more severe on the deep reef for October of 1995 ($\chi^2 = 16.786$, $P = 0.0008$) (Fig. 2.17).

When comparisons were made between deep and shallow *Montastraea* colonies using the chain transect data (Fig. 2.18), *M.* cf. *franksi* showed significantly higher levels of bleaching than *M.* cf. *annularis* ($\chi^2 = 25.275$, $P = 0.0001$); this result did not agree with the visual slide analysis, which indicated no significant difference in bleaching response between the two species ($\chi^2 = 3.022$, $P = 0.2207$) (Fig. 2.19), although the trend was similar. Deep colonies of *Porites astreoides* in the chain transects also bleached significantly more than their shallow counterparts ($\chi^2 = 191.855$, $P = 0.0001$) (Fig. 2.20), and this difference was revealed by the visual slide analysis ($\chi^2 = 18.368$, $P = 0.0004$) (Fig. 2.21).

When the total number of *Montastraea* colonies from both reefs were compared to all of the *Porites* *astreoides* colonies from the chain transects, it appeared that the *Montastraeas* bleached significantly more overall (χ^2 = 234.258, P = 0.0001) (Fig. 2.22). This conflicts with the visual slide analysis, which found that the groups of combined corals showed equal bleaching responses in October of 1995 (χ^2 = 4.973, P = 0.1738) (Fig. 2.23).

At Norman's Pond Cay, chain transect *Montastraea* cf. *annularis* bleached significantly more than shallow-water *Porites astreoides* (χ^2 = 247.06, P = 0.0001) (Fig. 2.24), which does agree with the results from visual slide analysis (χ^2 = 9.176, P = 0.0102) (Fig. 2.25). Similarly, chain transect *Montastraea* cf. *franksi* colonies at North Perry bleached significantly more than deep-water *Porites astreoides* (χ^2 = 14.808, P = 0.0051) (Fig. 2.26); however, this conclusion was not supported by the visual slide analysis, which did not find a significant difference in bleaching response at depth between the two species for this observational period (χ^2 = 1.086, P = 0.7803) (Fig. 2.27).

Table 2.2: Summary of Chi-square analysis results (with Bonferroni corrections) for chain transect *vs.* visual slide analysis data; October 1995.

Comparison	χ^2-value	P-value	d.f.
North Perry *vs.* Norman's Pond			
Chain transects	127.852	0.0001	4
Visual slide analysis	16.786	0.0008	3
M.* cf. *annularis vs. M.* cf. *franksi			
Chain transects	25.275	0.0001	3
Visual slide analysis	3.022	0.2207	2
***Porites* (NPC) *vs. Porites* (NPR)**			
Chain transects	191.855	0.0001	4
Visual slide analysis	18.368	0.0004	3
Norman's Pond Cay (NPC)			
M.* cf. *annularis vs. P. astreoides			
Chain transects	247.060	0.0001	3
Visual slide analysis	9.176	0.0102	2
North Perry Reef (NPR)			
M.* cf. *franksi vs. P. astreoides			
Chain transects	14.808	0.0051	4
Visual slide analysis	1.086	0.7803	3
All *Montastraea vs.* All *Porites*			
Chain transects	234.258	0.0001	4
Visual slide analysis	4.973	0.1738	3

2.4 Discussion

All three methods were apparently sufficient to detect bleaching (or, in the case of digital slide analysis, extensive loss of pigmentation) for the more severe mass bleaching events occurring during the fall observational periods of 1993 and 1995.

According to both of the visual assessment methods (slide analysis and chain transects), 'bleaching' of colonies on the deep reef was significantly more severe than of those in shallow in October of 1995 (Table 2.2). The visual slide analysis verified that this had also been the case for the previous two mass bleaching events (Table 2.1). However, these two methods differed in that the incidence of 'bleaching' in those comparisons involving deep *Montastraea* cf. *franksi* was always significantly higher for the chain transects (Table 2.2). This may have been due to the misidentification of white 'spots', (which occur normally on *M.* cf. *franksi*), as 'bleaching' during the chain transect assessment. This problem is solved for the visual slide analysis by the historical perspective of the photographs which helps the observer distinguish 'spots' from other color changes. The difference in sample sizes (very large for chain transects *vs.* very small for visual slide analysis, Figs. 2.16-2.27) may also have affected results, as well as the fact that it was not always possible to see an entire surface of a colony from the photographs.

Savina (1991) found (for the *Montastraea annularis* complex) that once colonies had bleached, they were more susceptible to subsequent bleaching events. This may partly explain the trend of increasing numbers of affected *Montastraea* over time (see visual slide analysis, Fig. 2.8, Figs. 2.12 and 2.13).

Quantitative data collection methods able to distinguish between bleached and normal corals have previously been unavailable or unreliable (Kleppel et al. 1989). Although qualitative observations, such as those used in the two visual methods, appear to be very useful when severe bleaching has occurred, a quantitative approach (such as B. Maguire's digital slide analysis method), is especially advantageous when attempting to identify color changes on a finer scale, such as those associated with the early stages of bleaching or with recovery.

This particular digital method also provides standardization among the photographs, regardless of variations in film exposure, etc., because of the presence of the corrective gray scale, although this is not always possible in those cases where the exposures are very light or very dark. The significant difference in 'bleaching' detection between the digital and visual slide analyses for fall of 1993 may be explained by the darker than usual exposures for that set of photographs, which would have affected both analyses (especially the visual).

Both the visual and digital slide analyses potentially provide a reliable and permanent record of temporal color change/'bleaching' patterns. However, sample size is limited for both methods by the involved logistics of underwater data collection using the camera system.

The chain transect method provided the important advantage of a much larger sample size, as well as a simple and inexpensive procedure for collecting data. Chain transect data were also immediately available upon collection, and analysis was relatively easy. Problems with the chain transects arose when there were questions among observers about the definition of a colony, the identity of a species, or perhaps the discrimination of bleaching from other naturally occurring anomalies, as previously discussed for *Montastraea* cf. *franksi*.

One advance made by the two visual methods was the use of only three categories in the bleaching index for either percent (%) area affected (none, part, all) or colors present (normal, pale, white), which helped reduce bias inherent in more complex scoring systems. Although I was able to combine both 'area affected' and 'colors present' into rankings for this study, it is probably advisable to keep them separate for the detection of bleaching on as fine a scale as possible.

Regardless of the method used, it was evident in most cases that higher levels of bleaching were associated with prolonged periods of subsurface warm water temperatures in 1991, 1993, and 1995. Historical SST (satellite-derived sea surface temperature) data have indicated that surface temperatures were indeed higher than normal (Strong and Duda 1996). Other studies have also linked mass bleaching to prolonged SST temperatures greater than 1°C above average, a critical amount for environmentally sensitive corals (Cook et al. 1990; Gates 1990; Glynn and D'Croz 1990; Jokiel and Coles 1990; Hagman and Gittings 1992; Dennis and Wicklund 1993; Goreau et al. 1994).

Increased levels of ultraviolet radiation, and the combinations of high UV and high temperature, or temperature and salinity, are also thought by some to play a part in bleaching (Jaap 1985; Lang et al. 1988; Siebeck 1988; Hoegh-Guldberg and Smith 1989; Jokiel and Coles 1990; Lesser 1996). In those weeks prior to the mass bleaching events of 1991, 1993, and 1995, as well as during previously observed events (Lang et al. 1988), weather and wind conditions were unusually warm, calm, and dry (Dennis and Wicklund 1993; G.D. Dennis, pers. comm.). These conditions may have contributed to the higher temperatures, and may have increased UV levels as well.

Incoming tidal waters at both sites originate from the same source (refer to Fig. 1.1); however, the shallow Norman's Pond Cay reef area typically experiences temperatures at an average of 0.5-1°C greater than North Perry at any given time throughout the year (Fig. 2.2 and Fig. 2.3), possibly as a result of increased insolation at shallower water depth, and the relatively greater periods of exposure to warmer, saltier waters flowing off Little Bahama Bank at low tide (Smith 1995). The significantly lower levels of bleaching found in shallow corals as compared to deep may reflect an adaptive response of either the zooxanthellae or the corals, which are normally exposed to somewhat higher temperatures and greater levels of UV radiation (Cook et al. 1990; Dennis and Wicklund 1993).

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