

REPORT ON THE 2005 MASS CORAL BLEACHING EVENT IN TOBAGO

PART I. RESULTS FROM PHASE 1 SURVEY



Prepared by the BUCCOO REEF TRUST and CORAL CAY CONSERVATION
In collaboration with the TOBAGO HOUSE OF ASSEMBLY and the TRAVEL FOUNDATION



Executive Summary

In the second half of 2005, the Caribbean region experienced a widespread coral bleaching episode. As such episodes have previously caused widespread mortality amongst reef building corals, there was a great deal of concern amongst the scientific community, fisherfolk, tourism organisations and other interested stakeholders. In order to determine the extent and nature of the impacts of the episode on the reefs of their island, the Buccoo Reef Trust (BRT) and the Tobago House of Assembly (THA) decided to invite a team of 5 scientists from Coral Cay Conservation (CCC) to assist in undertaking targeted surveys of the coral bleaching in Tobago.

Over a three week period commencing in October 2005, a two-phase campaign was launched: in Phase 1 the reefs were assessed to establish the extent and severity of the coral bleaching on Tobago's main reef systems, in Phase 2, an appropriate long-term monitoring programme was designed and installed to examine the recovery of bleached corals. The content of this report deals mostly with Phase 1, as the data from Phase 2 will not be complete until May 2006.

Phase 1 involved surveys of 22 discreet sites, which were assessed using a Point Intercept Transect method, utilising a 20m transect chain marked at 25cm intervals. At each site, two deep and two shallow surveys were completed, producing over 7000 data points from 88 transects. Overall mean bleaching of hard corals was found to be 66% (71% on deep transects and 63% on shallow sites). Bleaching by geographic region was found to be largely consistent, with sites exhibiting greater than 85% bleaching dispersed throughout the target area. However, of the 9 transects exhibiting less than 20% bleaching, 5 were located near Speyside in the northeast of Tobago, perhaps indicating either localised tolerance to bleaching or superior water quality (lower temperatures, less silt and fewer nutrients).

Bleaching by species was found to be highly variable, both between and within species. *Agaricia agaricites* ('leaf') and *Siderastrea radians* ('rough starlet') were the most impacted species, with 93% of the observations for both species being bleaching. *Madracis mirabilis* ('yellow pencil') and *Acropora palmata* ('elkhorn') were the least impacted species (3% and 0% respectively). Although the low number of observations recorded for *A. palmata* (n=7) reflects the low abundance of the species, many additional stands were observed by the surveyors during the campaign and all appeared to be unbleached. Very high variability was found amongst the species of the *Montastrea annularis* complex ('boulder/mountainous star'), which demonstrated overall bleaching impacts of 73%. For example, at one site in Buccoo Reef, two adjacent stands of *M. annularis* (*annularis*) exhibited 97% and 6% bleaching impacts respectively, implying the existence of bleaching resistant combinations of the coral species, its algal symbionts, or both.

It is not possible to predict the nature and extent of any subsequent mortality/recovery to the reefs of Tobago. Whilst cyanobacterial overgrowth was observed on the colonial zoanthids of the *Palythoa* genus, there were no recorded observations of coral disease, tissue necrosis or turf-algal/cyanobacterial overgrowth on bleached scleractinian corals. However, the incidence of opportunistic coral diseases may be expected to peak at the end of the warm season, and thus remain to be quantified. The monitoring programme installed during Phase 2 has been designed to gather these data.

Table of Contents

Acknowledgements	4
List of Figures.....	5
1 Introduction.....	6
1.1 Study Background and Objectives.....	6
1.2 The Phenomenon of Coral Bleaching.....	7
1.3 Causes of Bleaching.....	8
1.3.1 Sea Temperature	9
1.3.2 Solar Irradiance.....	9
1.4 Mechanisms of Bleaching.....	12
1.4.1 Physiological Bleaching.....	12
1.4.2 Algal-Stress Bleaching.....	12
1.4.3 Animal-Stress Bleaching.....	13
1.5 Effects of Bleaching.....	13
1.6 Recovery from Bleaching	14
2 Methods.....	15
3 Results	17
3.1 The Caribbean-Coast Reefs of Tobago.....	18
3.2 Benthic Cover	20
3.3 Coral Disease	20
3.4 Variability in Bleaching by Geographical Location	21
3.5 Variability in Bleaching by Depth	21
3.6 Variability in Bleaching by Coral Species.....	22
4 Discussion.....	24
5 Conclusions and Recommendations.....	28
References	30
Appendix I	32
Summary of dominant corals (and their status with regard to bleaching) at each site	32
Appendix II.....	40
Summary of benthic cover by class at each site and depth.....	40

Acknowledgements

This study was supported with grants from the **Tobago House of Assembly** and **The Travel Foundation** (www.thetravelfoundation.org.uk). All personnel costs and survey equipment were provided by **Coral Cay Conservation**¹ and the **Buccoo Reef Trust**². The survey team consisted of **Shay O'Farrell**¹, **Rebecca Korda**¹, **Hayley Rose**¹, **Christian Williams**¹, **James Comley**¹, **Barry Lovelace**², **Hyacinth Armstrong**², **Rolland "Saga" Guillard**², **Joseph Benjamin**² and **Owen Day**². The authors would like to thank **Andrew Lovell** and **Ricky Knowles** for providing a consistent supply of air tanks during the course of the survey.

Authors and Profile of Executing Organisations

This report was produced jointly by **Shay O'Farrell** (so@coralcayconservation.com) from Coral Cay Conservation and **Owen Day** (o.day@buccooreef.org) from the Buccoo Reef Trust.

Coral Cay Conservation

Founded in 1986, CCC is dedicated to 'providing resources to help protect livelihoods and alleviate poverty through the protection, restoration and sustainable use of coral reefs and tropical forests'. All of our projects are operated in collaboration with governmental and non-governmental organisations within each host country. CCC is primarily self-financed through a pioneering volunteer participatory scheme whereby international volunteers are given the opportunity to join a phase of each project in return for a financial contribution towards the project costs. Under the guidance of qualified and experienced project scientists, the volunteers undergo an intensive training programme in marine life identification and underwater survey techniques, prior to assisting in the acquisition of data. Finances generated from the volunteer programme allow CCC to provide a range of services, including data acquisition, assimilation and synthesis, conservation education, technical skills training and other capacity building programmes. Marine ecological information gathered by CCC volunteers was used in the successful bid to have the Belize Barrier Reef designated as a UNESCO World Heritage Site and in the creation of Danjungan Island Marine Reserve in The Philippines. This year so far, CCC has been instrumental in the implementation of four new community-based Marine Protected Areas in The Philippines and in the assessment of the tsunami damage to the reefs of Mu Ko Surin Marine National Park in Thailand. CCC is associated with the Coral Cay Conservation Trust, the only British-based charity dedicated to protecting coral reefs. For further information, please visit us at www.coralcay.org

Buccoo Reef Trust

The Buccoo Reef Trust (BRT) is a non-profit company registered in Trinidad and Tobago (since 1999) that has been developing programs aimed at building capacity for science-based marine conservation. With financial support provided by a number of donor agencies, the BRT has succeeded in implementing education, research and conservation programs. The BRT has forged an effective working relationship with the governing body of Tobago, the Tobago House of Assembly, and collaborates with the Department of Fisheries and Marine Resources in developing and executing projects aimed at improving the protection of Tobago's coral reefs. Members of the Buccoo Reef Trust have successfully implemented a number of initiatives in collaboration with local, national and international agencies. Key activities undertaken by the Buccoo Reef Trust up to January 2005 include island-wide water quality and reef health monitoring, installation and maintenance of reef demarcation buoys throughout Tobago's reef complex, training of reef tour operators, advice on marine park management, environmental and cultural awareness videos for incoming European flights, environmental and mapping workshops, and overseeing the completion of 11 MSc research projects by UK students. The activities of the BRT are executed by a compliment of 13 full-time staff and have received recognition both nationally (T&T Environmental Management Authority, 2004 Green Leaf Award) and internationally (World Association of Non-Governmental Organizations 2004 Environment Award). For further information, please visit us at www.buccooreef.org

List of Figures

Figure 1	Degree Heating Weeks (source NOAA/NESDIS) indicating the accumulation of thermal stress to which corals have been subjected over a 12 week period.	11
Figure 2	Locations of survey sites.....	17
Figure 3	Distribution of hard coral cover. Red stars indicate transects with hard coral cover values of $\geq 34\%$, with the letters A, B and C indicating the three transects with the highest values.	19
Figure 4	Linear regression plot of Shannon-Wiener diversity index against hard coral cover, showing a positive correlation.	20
Figure 5	Distribution of sites exhibiting greater than 85% hard coral bleaching.....	21
Figure 6	Coral bleaching as a percentage of observations for 15 selected species.....	23

List of Tables

Table 1	Coral abundance by species as a percentage of overall coral cover.....	19
Table 2	Coral bleaching as a percentage of observations for 15 selected species.....	22

1 Introduction

1.1 STUDY BACKGROUND AND OBJECTIVES

In the early summer months of 2005, anecdotal reports about the appearance of the phenomenon of coral bleaching began circulating amongst coral reef scientists in the Caribbean. As the year progressed, these reports became more and more widespread, with bleaching being observed throughout the greater part of the Caribbean. As there is literature to support the belief that mass bleaching can induce mass mortality in reef-building corals (see, for example, Goreau et al, 2000) there was widespread concern amongst various stakeholders that the 2005 episode may follow the 1998 episode in its extent and severity.

In early September 2005, reports of widespread bleaching of hydrocorals (fire corals) began to filter in to the Buccoo Reef Trust from diving and reef tour operators, which were confirmed by Buccoo Reef Trust personnel. By the later half of September, BRT staff observed that other species of coral were also visibly bleached, notably species of brain corals, and reports from tour operators suggested that the situation was worsening in many areas, especially Mt Irvine, Arnos Vale, Castara and Englishman's Bay. Concerned by the implications of the bleaching threat to the island, the BRT discussed the issue with the Tobago House of Assembly. Several international agencies involved with coral reef protection were then contacted for advice and support, and Coral Cay Conservation responded with an immediate offer of technical assistance.

A proposal was developed by BRT and CCC to survey Tobago's reefs in order to determine the extent, severity and nature of the impacts on the reefs of Tobago and presented to the THA on 14th October 2005. On receiving written approval from the THA on the 21st October that the proposal would receive financial support, the BRT purchased tickets and a team of 5 coral reef biologists from CCC was dispatched to Tobago.

The field surveys with CCC, which started on the 28th October and lasted three weeks, were divided into Phase 1 and Phase 2. Phase 1 involved rapid survey techniques to assess the extent and severity of the bleaching around Tobago. Phase 2 was designed as a long-term monitoring programme in order to gather data on the extent and nature of any subsequent recovery, and to highlight possible impediments to that recovery, such as land-based sources of pollution or silt. After the departure of CCC, the BRT has continued to expand and monitor Phase 2. All of the data generated have been linked to an ArcView GIS to facilitate interactive access for the resource managers of Tobago. The methods used are described in detail in Section 2.

1.2 THE PHENOMENON OF CORAL BLEACHING

Although 'modern' coral reef organisms and their associated communities have an evolutionary history of 40 -55 million years, present day coral reefs have accumulated during the past 10,000 years or so (Buddemeier et al 2004). Hermatypic (or 'reef building') corals are organisms of the exclusively-marine animal phylum, Cnidaria. Their body plan is virtually identical to that of their close relatives, the sea anemones, although the hermatypes possess a hard exoskeleton composed of calcium carbonate. It is the accumulation of these skeletons over time that creates the physical matrix of coral reefs, providing a substrate and habitat for most of the other reefal and reef-associated organisms. Living within the colourless, translucent tissue of the coral animals are microscopic, single-celled algae. Although these algae are of varying taxa, they are collectively known as *zooxanthellae*. Packed in at a density of around 30,000 organisms per mm³, it is the pigments in these algae that give the corals their colour. The coral and the algae tightly recycle nutrients between them. Most reef building corals gain around 80% of their energy requirements directly from their symbiotic algae, and make up the balance by feeding with their tentacles. The coral/algae symbiosis effectively allows corals to harness the energy of the sun and it is because of the passive nature of this that they can spare energy to create the limestone skeletons of which reefs are composed.

Although there are natural (especially seasonal) variations in the density of the microscopic algal symbionts present within a host coral's tissue, the term "coral bleaching" is used to describe the loss of abnormally large quantities of these algae, leaving the host organism to appear paler than usual or, in extreme cases, white. By the time the human eye is capable of detecting any change in colour associated with coral bleaching, the coral may have already lost more than half of its zooxanthellae although, conversely, when corals are reported to be 'severely bleached' or even 'white', they may still retain 20-50% of their original algal population (Fitt et al, 2001).

Bleaching episodes have been observed since the 1870s (Glynn, 1993) and are known to have occurred in most of the Earth's oceans; within the Caribbean region, bleaching has been documented since before 1940. It can be assumed that the phenomenon predates even these records. However, extensive or regional bleaching appears to be a relatively new phenomenon, with a significant increase in the levels and extent of bleaching recorded in the past 20 years or so (Winter et al, 1998). During the 1997/1998 ENSO (*El Niño* Southern Oscillation) event, corals in over 42 countries were affected, with wide-scale mortality reported in many areas (Fitt et al, 2001; Goreau et al, 2000). Despite advances in technology, especially with regard to satellite remote sensing of sea surface temperatures, accurate predictions of bleaching episodes remain elusive, partially because satellites are only capable of measuring sea-surface

temperatures (the top few millimetres) which may not accurately reflect the temperature of the underlying water column (Schluessel et al, 1990).

The susceptibility of corals to bleaching varies between species, within species (particularly with regard to spatial variation on the reef) and even within individual colonies (Iglesias Prieto and Trench, 1994; Rowan and Knowlton, 1995; Brown, 1997a). Some researchers have suggested that bleaching can act as an adaptive mechanism, allowing the coral host to 'select' those algal symbionts most tolerant of the prevailing environmental conditions (Buddemeier and Fautin, 1993; Ware et al, 1996). Fitt et al (2001) consider that corals may achieve an improved tolerance to higher temperatures through experimental or seasonal acclimatisation. In the 1970s, it was believed that coral reef ecosystems existed in equilibrium, mediated by competition for limited resources, and that the effects of periodic disturbances would dissipate once the 'acute' stressor was removed (Oxley, in English et al, 1997). However, it has since been established that reefs are in fact dynamic, and that both acute and chronic stressors can produce irreversible changes in the biological assemblages of the system, a phenomenon labelled "disturbance adapted" by Connell (1997). Although research into this topic is still in its infancy, it does seem likely that some form of selection may be occurring during such periods of stress. However, the ability of most corals to adapt in this way (if at all) remains unknown (Brown, 1997a).

1.3 CAUSES OF BLEACHING

Environmental stressors which may be considered to induce and/or exacerbate coral bleaching include (but are not limited to) elevated/decreased sea water temperature, solar radiation (including ultraviolet radiation), reduced salinity, sedimentation, bacterial and other infections, exposure at low tide, or combinations of these factors (Fitt et al, 2001; see Brown, 1997, and Glynn, 1993, for reviews of laboratory and field work examining the impacts of various stressors). However, determining exactly which factors have what effects in bleaching episodes is very difficult, with Brown (1997a) attributing this to the lack of accurate long-term data sets and the complex and variable nature of coral reefs; Fitt et al (2001) point out that it is impossible to isolate cause and effect between a single stressor and a single symptom with regard to the causes or severity of bleaching episodes. Some broad observations can, nonetheless, be made. Of the stressors which have been shown to instigate widespread bleaching, the most important triggers are considered to be elevated sea temperature and solar irradiance (Fitt et al, 2001; Brown, 1997a), and thus these are briefly discussed herein.

1.3.1 Sea Temperature

Long term data sets imply that the increasing frequency of bleaching events may be as a result of steadily increasing sea temperatures, which are correlated with increases in atmospheric carbon dioxide (Brown, 1997a; Strong et al 2000; Buddemeier et al, 2004). Much of the literature reflects the belief that this will positively influence the incidence of bleaching episodes (Burke and Maidens, 2004). Furthermore, as coral reefs are ‘carbon sinks’, acting to lay down carbon in the form of calcium carbonate, they can be considered to play some part in the moderation of atmospheric carbon levels. If coral reefs continue to degrade because of bleaching episodes, this may have a positive feedback effect, accelerating the accumulation of atmospheric carbon dioxide, and consequently increasing the frequency and severity of bleaching episodes.

Fitt et al (2001) point out that it is not possible to specify a single critical temperature at which bleaching will occur without specifying the length of exposure to the elevated temperature; Burke and Maidens (2004) suggest that, within the Caribbean, a sea temperature increase of 1 °C in above summertime maximum with a duration of 2 – 3 days is sufficient to act as a trigger. It should be noted, however, that during the Caribbean bleaching event of 1987, sea surface temperatures did not actually exceed their normal summertime maximum levels, but the elevated temperatures were unusual in their duration (Attwood et al, 1992). With this in mind, it is useful to note that Winter et al (1998) propose three temperature-related factors which can be considered instrumental in bleaching: absolute temperature (acute temperature stress), duration at some temperature (cumulative heat stress), and rate of change in temperature (temperature shock), although the effects of these are variable in the extent and severity of their influence.

One of the most common methods of estimating the cumulative effects of elevated sea temperatures over a period of time is ‘Degree Heating Weeks’ (Figure 1). One DHW is equivalent to one week of sea surface temperatures 1°C greater than the expected summertime maximum. Two DHWs are equivalent to two weeks at 1°C above the expected summertime maximum OR one week of 2°C above the expected summertime maximum. The orange to purple colours in the images (where DHWs are greater than 10) indicate the existence of high and persistent sea surface temperatures. Under these conditions, coral reefs may be undergoing severe bleaching, and possibly mortality. From Figure 1 it can be seen that the Caribbean region surrounding Tobago has experienced 10 – 13 consecutive DHW prior to 25th October 2005.

1.3.2 Solar Irradiance

The literature reflects a widespread belief that solar irradiance may play a significant role in the bleaching process, especially when combined with elevated sea temperatures (Fitt et al, 2001; Brown, 1997a;

Schick et al, 1996), although a paucity of long-term data sets and difficulties with *in situ* monitoring make quantification difficult. It is known, however, that irradiance acts both to increase the sea temperature and to interfere with the biochemical pathways involved in photosynthesis. Glynn (1993) notes that increased levels of bleaching have been observed by many researchers during periods of low winds, calm seas and decreased turbidity, conditions that augment the penetration of solar radiation into water and the heating of shallow waters (although, paradoxically, Fitt et al 2001 note that factors which lead to decreased 'water clarity' may negatively influence photosynthesis, again triggering bleaching).

Solar radiation may, even in isolation, play a very important role in the instigation of coral bleaching. For example, in field studies conducted in Thailand, the distribution of symbiont density within the host organism varied considerably, with those cells nearer the surface of the colony experiencing a greater loss of zooxanthellae than those located 'deeper' within the coral (Brown, 1997a). As it is assumed that the temperature of both deep and surface tissues would be very similar, Brown suggests that variation in symbiont density is due to the decreased intensity of solar irradiance experienced by the deeper tissues as a result of the shading offered by the outer layers of tissue.

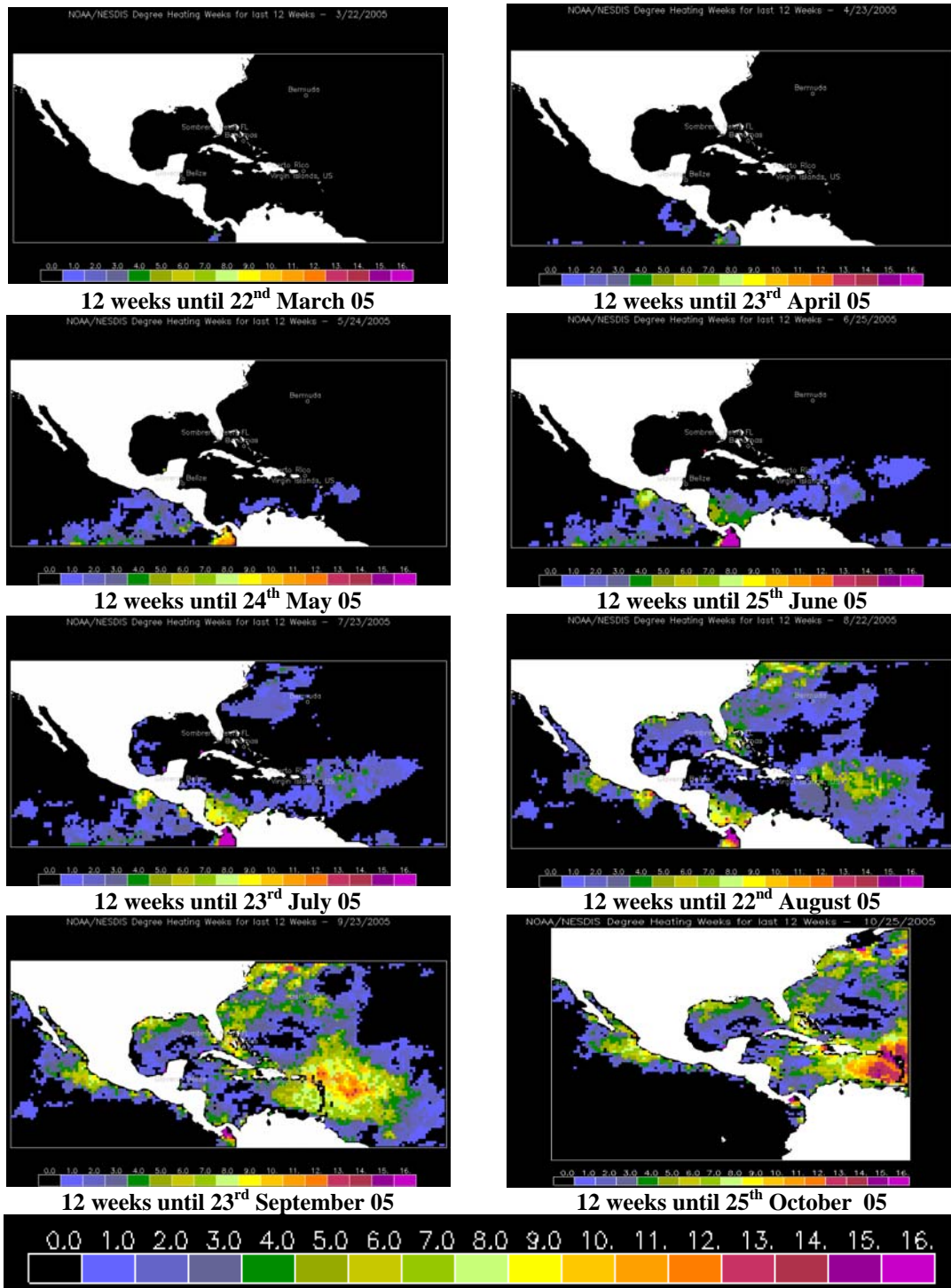


Figure 1 Degree Heating Weeks (source NOAA/NESDIS) indicating the accumulation of thermal stress to which corals have been subjected over a 12 week period.

1.4 MECHANISMS OF BLEACHING

Many researchers agree that in most cases it is the reaction of the algae (with particular regard to their photosynthetic apparatus) to the stressors which is instrumental in the phenomenon, rather than the reaction of the coral host; many studies have shown that in most cases, corals are more resilient to these stressors than are their algal symbionts (Fitt et al, 2001).

The advanced stages of coral bleaching are often quite apparent to the human eye. However, the actual mechanisms underlying the phenomenon are varied and complex, although it appears that zooxanthellae are, in most cases, instrumental in the initiation of bleaching. Whilst noting that the exact mechanisms underpinning the phenomenon are not fully understood, Fitt et al (2001) propose three general types of 'high-temperature' bleaching: physiological bleaching, algal-stress bleaching, and animal stress bleaching.

1.4.1 Physiological Bleaching

It is established that there is a maximum number of algal symbionts that any given amount of coral tissue can hold, and therefore the more tissue a coral has, the greater the potential number of zooxanthellae that it can contain. The amount of tissue (and therefore zooxanthellae) varies seasonally, with the maximum generally discovered during the coolest period of the year with the lowest levels of solar radiation, and the minimum at the end of the warmest season with the highest levels of solar radiation; there is an inverse correlation between temperature/solar radiation and the density of zooxanthellae (and therefore tissue biomass). It is hypothesised that this is an adaptive mechanism, allowing the coral host to benefit from the increased metabolic activity permitted by elevated temperatures and availability of Photosynthetically Active Radiation (PAR), through a reduction in the energy budget outputs required by the maintenance of elevated levels of tissue biomass. Interestingly, increasing zooxanthellate densities typically precede increases in tissue biomass, and are considered to be causative in that increase. It is assumed that the reverse is also true, with a decrease in seasonal zooxanthellate density leading to a decrease in tissue biomass and subsequent bleached appearance of the coral host.

1.4.2 Algal-Stress Bleaching

This describes the effects of above-normal levels of solar radiation on the seasonal cycle outlined previously. Although 'normal' diel changes in the routing of PAR photons occur at midday (probably to prevent damage to the photosynthetic pathway), excessively high levels of PAR can cause degradation in components of this photosynthetic pathway, resulting in the death of the algal symbionts affected. This

process, known as ‘photoinhibition’, takes place when excessive PAR causes irreparable malfunctions within the biochemical pathways involved in photosynthesis. Many researchers (e.g. Brown, 1997; Fitt et al, 2001) agree that this may be the primary mechanism responsible for bleaching associated with elevated seawater temperatures and/or solar irradiance. Furthermore, Brown (1997) suggests that this may be followed, at least in some cases, by exocytosis of the damaged cell from the endodermic tissue into the coelenteron of the host organism.

1.4.3 Animal-Stress Bleaching

Laboratory studies have shown that corals exposed to rapid, large changes in temperature may shed the gastrodermal tissue layer containing the algal symbionts, the latter being passive ‘victims’ of bleaching, rather than instigators (Gates et al, 1992). However, Fitt et al (2001) conclude that this type of extreme reaction is unlikely to occur in most sea conditions, and that the effect does not play a significant role in widespread bleaching events.

1.5 EFFECTS OF BLEACHING

Dissolved carbon dioxide increases the acidity of the upper layers of the water column, which affects the solubility of other compounds, such as aragonite which is required by hermatypic corals in reef building. Dissolved aragonite levels are decreasing, reducing the abilities of corals to create their limestone skeletons and pointing to a slowdown (or even reversal) of reef building (Burke and Maidens, 2004). In the eastern Pacific, Eakin (1996) quantified the rate of decline of calcium carbonate deposition at Uva Island: prior to the 1982-83 El Niño event, calcium carbonate was being laid down at a rate of 8600 kg per annum; after the bleaching caused by this event, the reef began eroding at a rate of 4800 kg per annum.

Although corals have mechanisms to defend against bleaching, such as natural ‘sunscreens’ called mycosporine-like amino acids (Schick *et al*, 1996) and the rerouting of excess photons away from Photosystem II via the xanthophyll cycle (Fitt et al, 2001), these are considered to be costly in terms of the organism’s energy budget. Szmant and Gassman (1990) consider that this alone is likely to decrease the reproductive abilities of corals, with Brown (1997a) pointing out that this effect may be exacerbated by increasing anthropogenic influences, such as sedimentation. Aronson and Precht (1997) conclude that the increasing incidence of coral diseases imply that corals may now be more stressed than they have ever been in the past 5000 years or more. Additional anthropogenic stresses can be considered to further worsen the situation and to increase the susceptibility of corals to bleaching, and to hinder their recovery from such episodes.

1.6 RECOVERY FROM BLEACHING

The relatively recent emergence of coral reef science (and increases in the extent and severity of coral bleaching episodes) has resulted in a lack of long-term data sets on the phenomenon of bleaching. The capacity of corals to recover from such episodes is thus poorly understood, with little available data on the subject (Fitt et al, 2001). The fact that predictions based on climate change models indicate that bleaching may become an annual event in the Caribbean by 2020 (Burke and Maidens, 2004), implies an urgent need to understand the implied threats to the viability of reef systems and the development of strategies that can be used to help mitigate these threats. Although reefs show ‘natural’ variation in time and space, reef decline can be considered to have two components: the initial damage or mortality and the failure of the ecosystem to recover (Buddemeier et al, 2004). There is general agreement that the ability of reefs to recover from acute stresses (such as bleaching events) will depend, at least partially, on the range and severity of other anthropogenic stresses to which present-day reefs are subject (Burke and Maidens, 2004; Kinsey, 1988; Brown et al, 1996). Other factors which will come into play will include the duration of the ‘recovery interval’ between one period of bleaching and the next and the incidence of disease which may follow such an event. As Fitt et al (2001) observe, it is as yet unclear whether corals slowly ‘starve to death’ during repetitive bleaching events, or become the victims of opportunistic diseases. One way or the other, this threat to the long-term viability of the coral reefs of the Caribbean is one that must be addressed immediately. Although many of the triggers of bleaching are beyond the control of individual nations (such as increasing atmospheric carbon dioxide levels), the 2005 bleaching event creates an opportunity within Tobago (and the wider Caribbean) to explore links between the susceptibility of corals to (and recovery from) bleaching with regard to additional stressors (such as anthropogenic impacts). Steps towards mitigating these factors can (and must) be taken at a national and local level in order to reduce as much as possible the stresses to the reefs, if bleaching is not to severely threaten the long-term viability of the coral reefs of Tobago.

2 Methods

In order to rapidly assess the benthos, the Point-Intercept Transect method was adopted, as outlined in Oliver et al (2004). In this method, a 20m-long lightweight transect chain is placed on each area of benthos under investigation, with marks (points) fixed at predetermined intervals along the chain. The survey diver swims above the chain and records the nature of the benthos found directly below each of the points. This minimises observer bias in the data.

The point interval resolution was determined by laying the 20m-long chain on the benthos, along which point cover observations were made at 12.5cm, 25 cm and 50 cm intervals. From these data, percentage live hard coral cover and percentage bleached coral cover were calculated for each of the three intervals. Using ANOVA, it was found that there was no significant difference in the values for live hard coral cover returned by the three techniques. However, the percentage of bleached coral calculated from the 25cm intervals was significantly different ($p = 0.031$) than that collected at the 50cm intervals. As there was no significant difference ($p > 0.05$) between percentage bleached coral calculated from data collected every 25 cm versus those collected every 12.5cm, the 25 cm interval was determined to be the most appropriate and efficient interval for the purposes of this study. This gives a total 80 point observations from each 20m transect assessed. The presence and abundance of sea urchins belonging to the genera *Diadema* and *Echinometra* were also recorded within a 2m wide belt, 1m on either side of the transect line.

22 sites were surveyed around Tobago (Figure 2) to quantify the spatial extent, distribution by depth and taxonomic nature of bleaching around the island. At each site, two transects were surveyed along two depth contours, 12m and 7m approximately. The resultant pairs of 'deep' and 'shallow' transects were considered to be replicates.

Cover categories of each point included both abiotic (substrate) classes and biotic or live benthic cover, with hard corals being identified to a species level, and with sponges, soft corals, zoanthids identified to a lifeform level. Furthermore, both hard and soft corals were differentiated into the categories 'bleached' or 'unbleached', as appropriate to the status of the point directly located below each interval mark rather than to the colony as a whole. Although this allows for the estimation of percentage bleaching by species and overall, it does not allow for the determination of the nature of bleaching in each colony (full, partial, patchy etc). This will be investigated during the long-term monitoring programme which follows this study.

Field data were entered into a dedicated Access (Microsoft Corp) database which was live- linked to an ArcView (ERSI Software) Geographic Information System (GIS) to facilitate real-time data

analysis and display. The GIS was also used to generate data contours through the Inverse Distance Weighted function in the Spatial Analyst of ArcView, with a fixed search radius of 4km and power =2. Shannon-Wiener diversity indices were generated in PRIMER-5 (Plymouth Routines in Multivariate Ecological Research), with ANOVA and Linear Regression Plots generated in MiniTab 13.

3 Results

During a two week period in October/November of this year, a total of 88 transects were surveyed along the length of the Caribbean coast of Tobago at 22 discreet sites (Figure 2). The surveys were biased towards areas of known reef, as established from personal communication with the Buccoo Reef Trust and from the interpretation of a Landsat 7 ETM image. The aims were to determine the extent and severity of the bleaching, as well as the existence of variability in bleaching by geographical location, by depth and/or by coral species. Appropriate sites for the installation of a long-term monitoring programme were identified, with a view to determining whether such variability may also affect the subsequent mortality and/or recovery of the reefs.

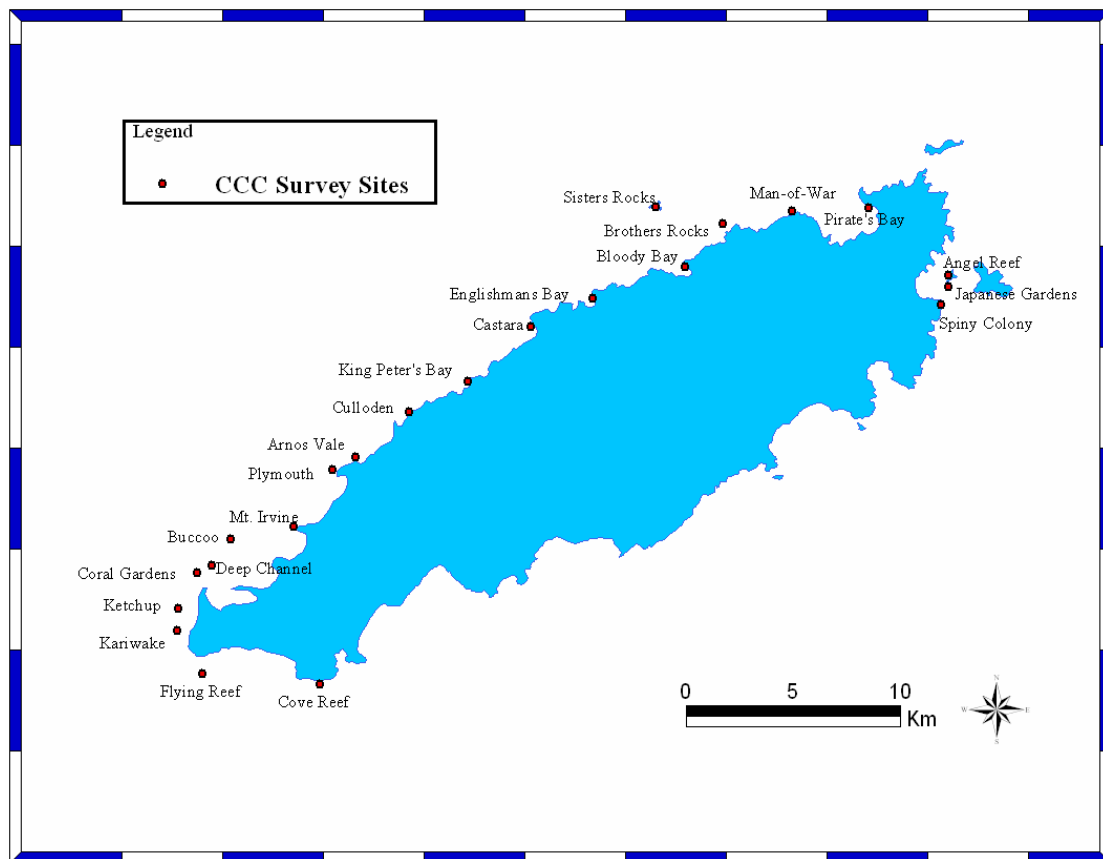


Figure 2 Locations of survey sites

3.1 THE CARIBBEAN-COAST REEFS OF TOBAGO

The reefs of the Caribbean coast were found to be a mixture of biogenic reefs (built by corals and coralline algae) and geological reefs (bedrock of a non-biological origin, colonised by hard corals). All of the reefs were found to be 'shallow' in their nature, ending abruptly in a sand seabed at depths of around 14m. Coral cover was found to be highly variable (std dev \pm 12.9%), with a mean overall value of 21.4%. The regions with the highest mean percentage cover (combining replicates and depths) were recorded at Angel Reef (41%) and Coral Gardens (40%). The highest single values for any transect were at Pirates Bay (60%), Culloden (54%) and Angel Reef (48%) – sites marked A, B and C respectively in Figure 3. Overall mean coral cover was 24% between all 'deep' transects and 19% between all shallow transects. The results of a one-way ANOVA of deep sites versus shallow sites indicate that variation in coral cover between 12m and 7m depth contours is not significant ($p=0.547$).

Figure 3 shows a GIS output of coral cover around Tobago. The colour ramp shows Inverse Distance Weighted contours, wherein the GIS compares the hard coral cover values for every transect (irrespective of depth) against all of those within a fixed search radius of 4km and assigns a value to each transect based on the hard coral cover values of its 'neighbouring' transects; regions that are highlighted towards the green end of the spectrum can be considered to have higher overall coral cover than those highlighted towards the orange end of the spectrum. The transects with the highest coral cover ($\geq 34\%$) are represented on the GIS output as red stars. Note: as the surveys conducted for this assessment were biased towards areas of higher coral, it should be noted that this output is not intended as a definitive map of the distribution of coral cover, but is used herein as an illustration of trends; a more spatially extensive dataset will be required in order to allow for robust assumptions about inter-site variations in coral cover.

The most commonly occurring species of corals were those of the *Montastrea annularis* complex, which accounted for 37% of all coral observations (Table 1), with fire corals (*Millepora* spp.) contributing 12% and the 'brain' corals, *Colpophyllia natans* and *Diploria strigosa* contributing 11% and 9% respectively. It is noteworthy that *Agaricia* spp. and the branching species of *Porites* (*P. porites*, *P. furcata* and *P. divaricata*) are far less abundant on these reefs than in many other modern Caribbean reefs.

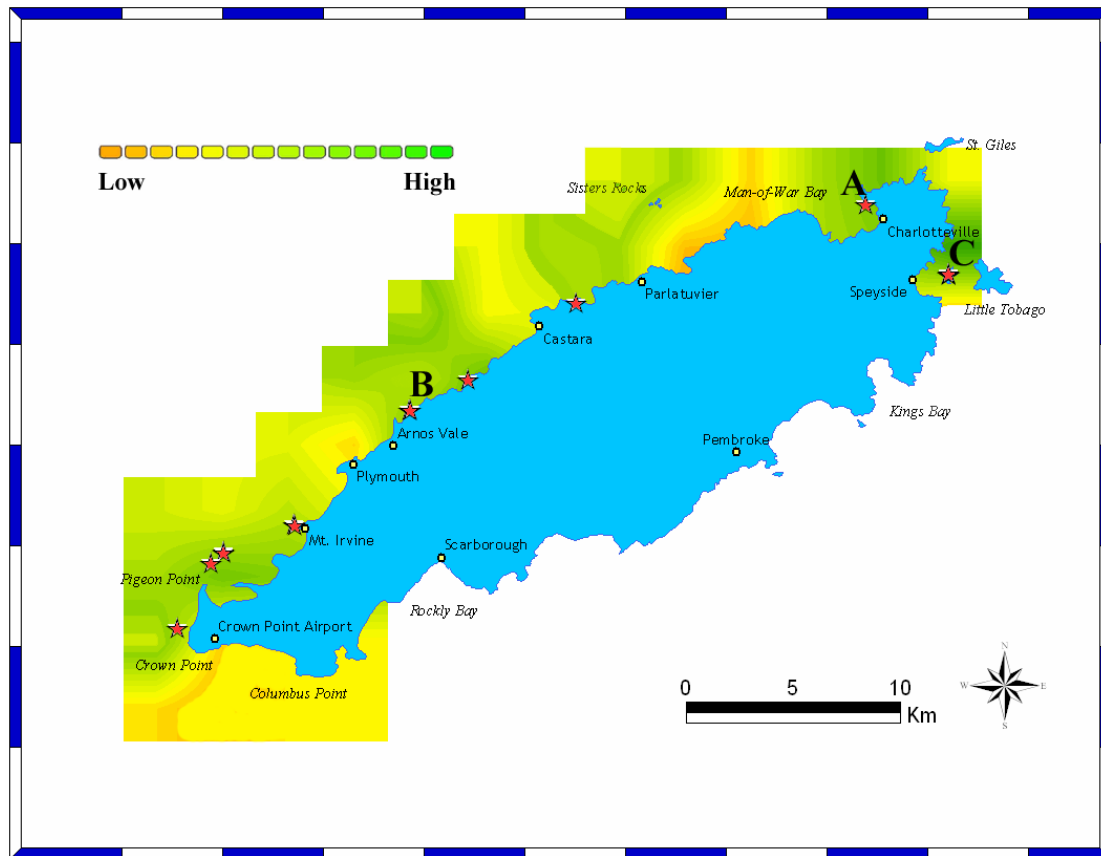


Figure 3 Distribution of hard coral cover. Red stars indicate transects with hard coral cover values of $\geq 34\%$, with the letters A, B and C indicating the three transects with the highest values.

Taxonomic name	Common name	% bleached	% of total corals observed	N
<i>Acropora palmata</i>	Elkhorn	0	0.5	7
<i>Agaricia agaricites</i>	Leaf	93	3	40
<i>Colpophyllia natans</i>	Giant Brain	80	9	122
<i>Diploria labyrinthiformis</i>	Grooved Brain	84	1	13
<i>Diploria strigosa</i>	Smooth Brain	50	11	149
<i>Madracis mirabilis</i>	Yellow Pencil	3	4	54
<i>Meandrina meandrites</i>	Butterprint Brain	67	2	27
<i>Millepora spp.</i>	Fire Coral	53	12	162
<i>Montastrea annularis</i>	Boulder Star	73	37	502
<i>Montastrea cavernosa</i>	Cavernous Star	47	4	54
<i>Porites astreoides</i>	Mustard Hill	34	3	40
<i>Porites divaricata</i>	Thin Finger	60	1	13
<i>Porites furcata</i>	Finger	50	1	13
<i>Siderastrea radians</i>	Rough Starlet	93	1	13
<i>Siderastrea siderea</i>	Smooth Starlet	68	6	81
Other	Various	5	5	67

Table 1 Coral abundance by species as a percentage of overall coral cover

Linear regression of the Shannon-Wiener diversity index against hard coral cover by transect implies a positive correlation between species diversity and coral cover ($p=0.03$; $n=88$; $df=1$) – Figure 4. However, no significant correlation (either positive or negative) was found between species diversity and incidence of bleaching by transect ($p=0.845$; $n=88$; $df=1$).

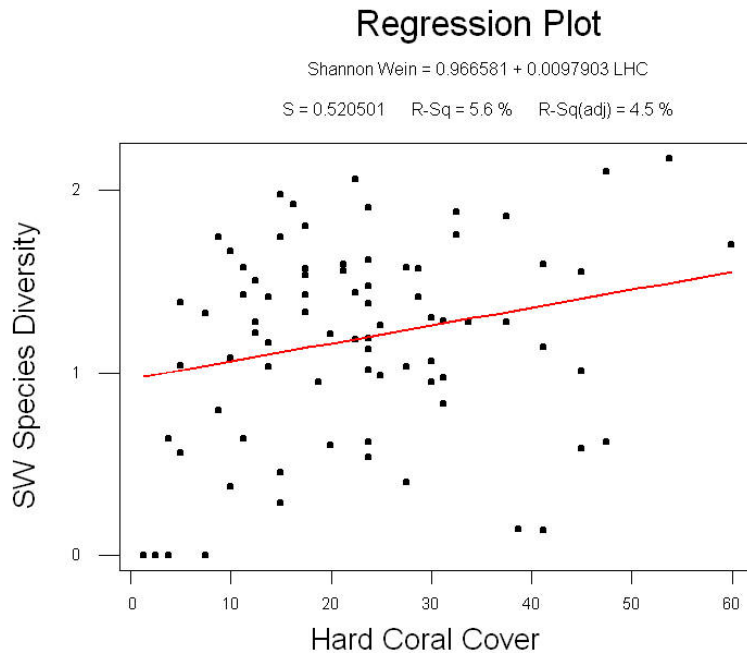


Figure 4 Linear regression plot of Shannon-Wiener diversity index against hard coral cover, showing a positive correlation.

3.2 BENTHIC COVER

A summary of dominant corals (and their status with regard to bleaching) at each site is presented in Appendix I.

A graphic summary of benthic cover by class at each site and depth is presented in Appendix II. Of considerable interest is the finding that macroalgal cover was particularly low (<3%) for the Caribbean.

3.3 CORAL DISEASE

There were zero recorded observations of coral disease, tissue necrosis or turf-algal/cyanobacterial overgrowth of bleached corals.

3.4 VARIABILITY IN BLEACHING BY GEOGRAPHICAL LOCATION

Analysis of the data does not show any general geographical trends in the distribution of bleaching, with high values being recorded at most sites. In all, bleaching was greater than 85% in 31 of the 88 sites, which are evenly distributed around the island (Figure 5). It is worth noting, however, that of the 9 transects exhibiting less than 20% bleaching, 5 are located within the same region: Angel Reef (2 transects), Spiny Colony (2 transects) and Japanese Gardens (1 transect).

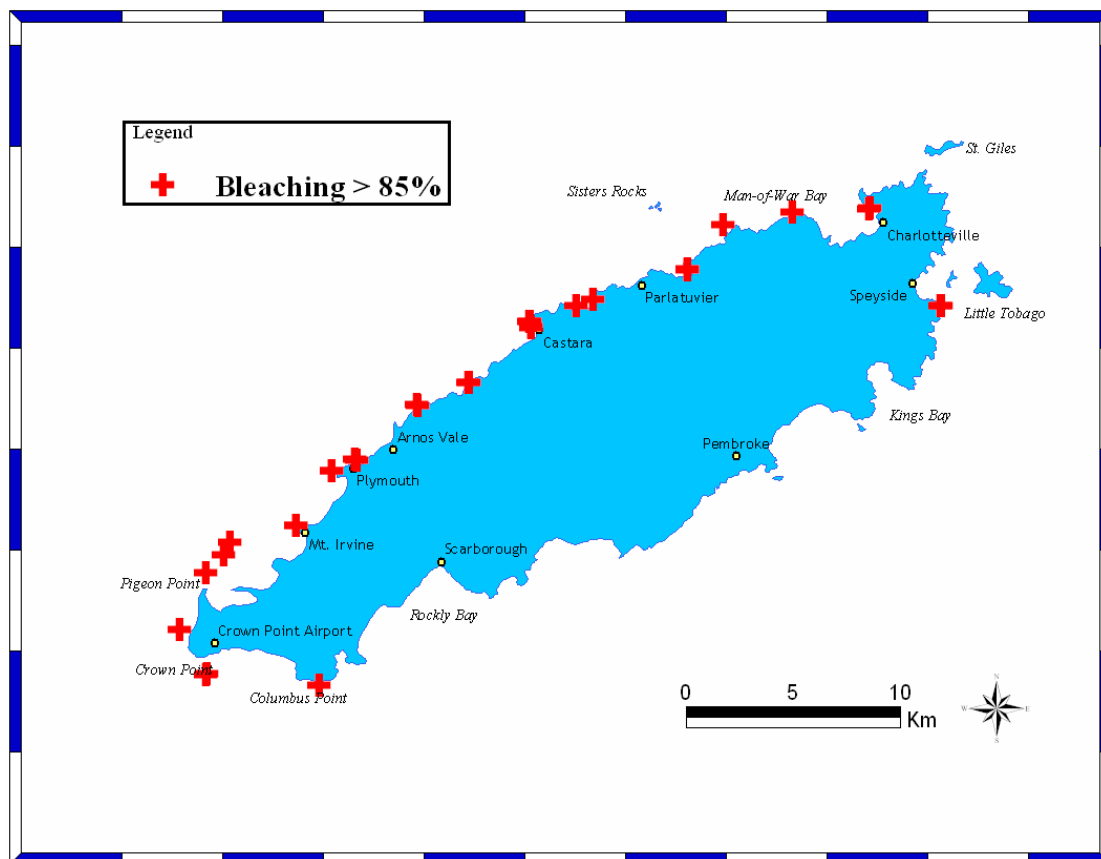


Figure 5 Distribution of sites exhibiting greater than 85% hard coral bleaching

3.5 VARIABILITY IN BLEACHING BY DEPTH

The overall mean bleaching was 66% of hard coral cover, with 71% mean at the deep sites and 63% at the shallow sites. One way ANOVA predicts that this variation by depth is significant ($p=0.016$).

3.6 VARIABILITY IN BLEACHING BY CORAL SPECIES

There are distinct variations in the data for bleaching by species (mean 66% with a standard deviation of $\pm 29\%$), with *Agaricia agaricites* and *Siderastrea radians* each demonstrating 93% bleaching (Table 2 and Figure 6). This is in marked contrast to species such as *Madracis mirabilis* and *Acropora palmata* which were 3% and 0% bleached respectively. Although there are only 7 observations of *A. palmata* in the dataset, many more stands were examined ‘off-transect’ by the survey teams, with all of them appearing visually to be completely unbleached and healthy, implying that the species may, within Tobago, be highly resistant to bleaching. The high levels of bleaching in *Colpophyllia natans* and the *Montastrea annularis* complex are of particular note, as between them they account for 46% of all coral species records (Table 1, previous). However, at Coral Gardens, there were two adjacent monospecific stands of *M. annularis* (*annularis*), one exhibiting 97% bleaching and the other only 6% bleaching. Because any micro-climactic variability between the two stands would be minimal, this may indicate the existence of genetic distinction (either within the coral species itself or within its algal symbionts), with tolerance to bleaching varying between the two.

Taxonomic name	Common name	Percent bleached	n
<i>Agaricia agaricites</i>	Leaf	93	40
<i>Siderastrea radians</i>	Rough Starlet	93	13
<i>Diploria labyrinthiformis</i>	Grooved Brain	84	13
<i>Colpophyllia natans</i>	Giant Brain	80	122
<i>Montastrea annularis</i>	Boulder/Mountainous Star	73	502
<i>Siderastrea siderea</i>	Smooth Starlet	68	81
<i>Meandrina meandrites</i>	Butterprint Brain	67	27
<i>Porites divaricata</i>	Thin Finger	60	13
<i>Millepora spp.</i>	Fire Coral	53	162
<i>Diploria strigosa</i>	Smooth Brain	50	149
<i>Porites furcata</i>	Finger	50	13
<i>Montastrea cavernosa</i>	Cavernous Star	47	54
<i>Porites astreoides</i>	Mustard Hill	34	40
<i>Madracis mirabilis</i>	Yellow Pencil	3	54
<i>Acropora palmata</i>	Elkhorn	0	7

Table 2 Coral bleaching as a percentage of observations for 15 selected species.

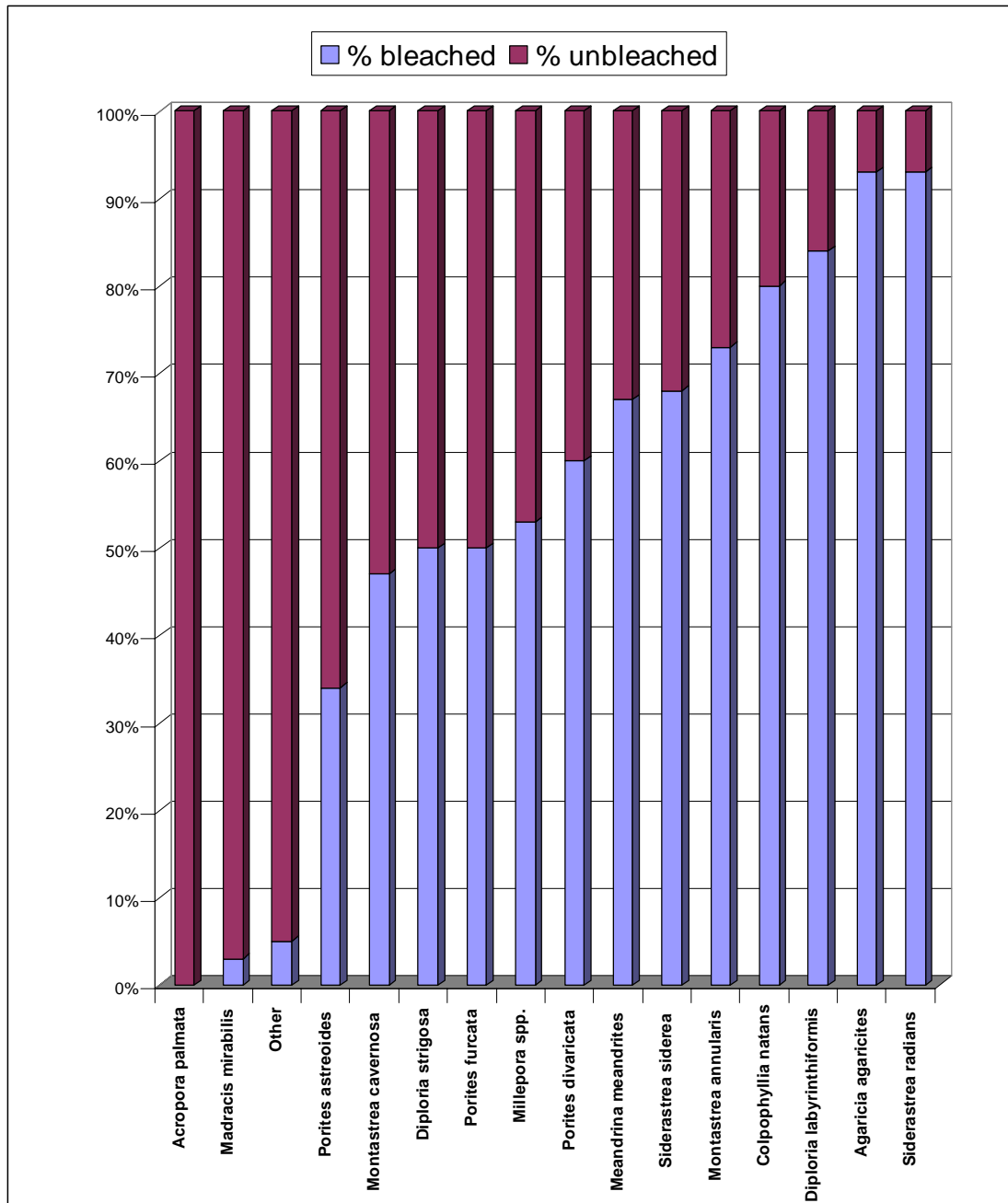


Figure 6 Coral bleaching as a percentage of observations for 15 selected species.

4 Discussion

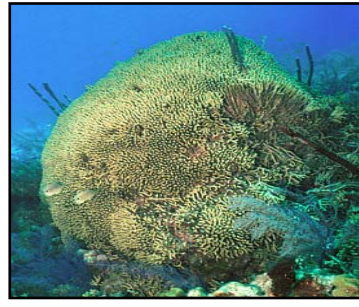
The results obtained during this survey campaign show an average of 66% of the hard coral cover has been visibly affected by the bleaching episode. The levels of bleaching varied widely, but many sites had over 85% bleaching and some 100%. The geographic extent of the bleaching was also found to be widespread, with all reefs on the Caribbean coast affected, while those at Speyside showed a reduced level of bleaching for reasons that are still unknown. The magnitude and extent of the bleaching indicate that it is a very severe mass bleaching event, which has the potential to cause profound and long-lasting effects on Tobago's reef communities.

The inter- and intra-species variability in bleaching implies that there may be taxonomic and genetic groupings in Tobago that vary in their susceptibility to such events. Of particular note are the adjacent *Montastrea annularis* (*annularis*) (Boulder star coral) stands at the 'Coral Gardens' site in Buccoo Reef, one of which was almost completely bleached (97%) and the other which was almost entirely unaffected (6% bleaching). At many sites, recent *M. annularis* and *M. cavernosa* recruits were seen (<10cm in diameter) indicating that the genus is reproducing in Tobago. This contrasts with the situation in much of the Caribbean where the genus is believed to be 'losing out' to other genera, such as *Agaricia* and *Porites*. As the *Montastrea* species (along with *Acropora* species) are historically the most important 'reef builders' in the whole Caribbean, this is quite exceptional.

Every stand of *A. palmata* (Elkhorn) that was examined by the surveyors appeared to be completely impervious to the bleaching episode, all appearing healthy (although only 7 observations were recorded 'on transect', indicating the low overall abundance of the species). As *A. palmata* is generally believed not yet to have recovered from the widespread mortality caused by the outbreak of white-band disease in the early 1980s, this gives some scope for optimism. Recent recruits of the species were frequently seen, with encrusting colonies observed overgrowing bedrock, and recolonisation of previously killed stands also in evidence. Extensive *A. palmata* rubble was observed on the reef crest at Cove Reef, indicating that the species was once far more abundant than at present. *Madracis mirabilis* (Yellow pencil coral) also appears to have endured the episode particularly well, with bleaching recorded at only 2 out of 54 point observations.



Acropora palmata
Elkhorn Coral



Madracis mirabilis
Yellow Pencil Coral

It is established that the incidence of many coral diseases peaks at the end of the warmest season, when tissues (and thus zooxanthellate densities) are at their lowest (Fitt et al, 2000) and that climate-induced physiological stresses are likely to increase the occurrence of, and susceptibility of corals to, opportunistic diseases (Harvell et al, 1999). Work by Toren et al (1998) observed that increases in water temperature correlated with increased adhesive capacity of particular bacteria, enhancing their ability to remain ‘attached’ to the coral tissue. With this in mind, it should be noted that there were zero observations of coral disease, tissue necrosis or turf-algal/cyanobacterial overgrowth on any of the bleached colonies. At the time of this study, mean sea temperature was calculated at 28.6 °C (std dev = ± 1.08 ; n=88). Although data are not currently available for seasonal variations in sea temperature around Tobago, anecdotal reports suggest that this is lower than earlier in the summer, which is to be expected. The fact that the corals appear to have ‘survived’ the duration of the elevated sea temperatures displayed in Figure 1 (previous) is positive, although whether the incidence of opportunistic diseases may subsequently increase remains to be seen. This will be quantified and documented during the long-term monitoring programme established as a result of this study.

Most scientists agree that the capacity of corals to adapt to changes in environmental conditions will depend on the level of additional ‘unnatural’ stresses with which they have to contend. As Kinsey (1998) observes, corals can endure chronic stress, and even rebuff acute stresses over a short period, but that chronically stressed reefs are less likely to be capable of successfully moderating the impacts of acute stresses. Key additional stresses are known to include unmitigated coastal development, land-based sources of pollution and overfishing (Burke and Maidens, 2004; Buddemeier et al, 2004) and it is likely that reefs that are not subject to such anthropogenic stresses will be more resilient than those that are heavily stressed and will thus be less susceptible to, and more likely to recover from, acute environmental stresses such as bleaching events. As Brown et al (1996) state, “*clearly, the interaction of anthropogenic and natural influences (elevated sea temperature/increased irradiance) will be a major factor determining not only the mortality and recovery of reefs from bleaching episodes but also*

their ability to adapt to future change given a scenario of increasing sea temperature and the likelihood of increased frequency and intensity of bleaching.”

The low levels of bleaching at Speyside strengthen the case for creating a Marine Protected Area (MPAs) in this area. In terms of the preservation of coral stocks (and therefore the maintenance of healthy reefs), experts recommend that key locations for the placement of MPAs should include those containing populations of corals that appear to be highly tolerant of bleaching stresses. If these ‘resistant’ stocks become damaged through other mechanisms (such as coastal development or sewage discharge) an invaluable opportunity to nurture bleaching ‘resilient’ reefs will have been lost. The reefs around the northeast of Tobago displayed a high concentration of sites with apparent: resilience; Angel Reef, Spiny Colony and Japanese Gardens all contained transects with less than 20% bleaching, indicating that this may be an appropriate site for the creation of an MPA. The remarkable tolerance of the *Acropora palmata* stands seen indicates that this is also highly tolerant of bleaching, and thus up-current areas with high levels of the species (which will serve as a larval source for downstream reefs) should also be identified and protected.

The low incidence of macro-algae (<3%) recorded is also of interest, with particular regard to the apparent paucity of herbivorous grazers: zero *Diadema* or *Echinometra* sea urchins were recorded within a distance of 1m on either side of the transects, although there were isolated sightings. Occasional schools of surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) were also observed. Although it was not the purpose of this campaign to quantify the abundance or biomass of such fishes, it would seem unlikely that herbivory is a limiting factor on algal growth. This is particularly noteworthy, because uncolonised bedrock accounted for a mean 41% of all surveyed transects, implying that competition for space is not a limiting factor either.

Reef communities have been described as “disturbance adapted” ecosystems but that adaptation is to natural rather than human-enhanced disturbances (Connell, 1997). The enduring effects of the 2005 bleaching event on the nature and ecosystem functionality of the reefs of Tobago cannot at this time be quantified, but the newly installed monitoring programme will provide vital data for the resource managers of Trinidad and Tobago and is intended to provide answers to questions regarding the extent and nature of any recovery from the 2005 bleaching episode, and to highlight any anthropogenic factors that may be influential.

Protection of coral reefs has a very strong economic incentive. Aside from the established benefits to fisheries and protection from shoreline erosion, the potential revenue to be generated from tourism

through the sustainable use of reef resources is enormous. Tourism is the world's largest and fastest growing industry. Reef associated tourism is typically 'high-value', with tourists in this sector typically spending 60 – 80% more than tourists in most other sectors, with the average diver spending \$2,100 per trip. Net benefits from dive tourism alone in the Caribbean region amounted to an estimated \$2.1 billion in the year 2000 (\$4.1 billion gross), and the sector is considered to have grown significantly since then (Burke and Maidens, 2004). Moreover, despite the fact that Marine Protected Areas only account for a small proportion of all Caribbean reefs, half of all tourism diving in the region occurs within these areas and it may be assumed that an increasing share of the growing market will continue to go towards well-managed reefs, with degrading reefs squabbling for the leftovers.

5 Conclusions and Recommendations

The coral bleaching event first observed on the coral reefs of Tobago in 2005 was part of a regional mass bleaching event that affected reefs throughout the Caribbean. The bleaching was caused by elevated sea-surface-temperatures (SST) recorded in the region during 2005, which also were associated with the record number of hurricanes during the season of 2005. NOAA is currently coordinating the collection and analysis of the regional datasets, including the data collected during this survey which was submitted to NOAA in December 2005. Many other teams of marine managers and scientists throughout the Caribbean are monitoring the recovery of corals, from what is now officially considered to be the worst mass bleaching event ever recorded in the Caribbean.

The data gathered during this survey show that a mean of 66% of the hard coral cover in Tobago has been visibly affected by the bleaching episode, with levels over 85% observed at many sites. The geographic extent of the bleaching was also found to be widespread, with all reefs on the Caribbean coast affected, while those at Speyside showed a reduced level of bleaching for reasons that are still unknown. The high magnitude and widespread extent of the bleaching measured in this study indicate that it is a very severe mass bleaching event, which has the potential to cause profound and long-lasting effects on Tobago's reef communities.

The recovery of the corals is still unknown, though observations at the time of writing (Phase 2) seem to indicate that mortality is highly species-dependent. For instance, most of the large brain corals affected (*Diploria strigosa* and *Colpohyllia natans* that represent 11% and 9% all coral observed respectively) appear to be dying, while the Boulder star corals (*Montastrea annularis* – 37%) appear to be regaining their colour. It is still too early to know what the long-term affects will be, but an increase in the existing levels of coral diseases is expected.

Given the economic and ecological value of Tobago's reefs, and the predicted increase in bleaching events in the forthcoming years, the authors of this study offer the following recommendations;

- **The recovery of bleached corals should be monitored for the next 6 months to provide both quantitative and qualitative data on the resilience of Tobago's corals to bleaching events. *This activity is currently being pursued by staff of the BRT as Phase 2.***

- **A spatial database (baseline data) of Tobago’s coastal areas should be developed that describes the extent and characteristics of the many ecological habitats around the island (coral reef, seagrass, mangrove, sand, mud, rock, etc.). This baseline data should be linked to a larger GIS database of the watersheds in order to inform managers, planners, policy-makers and scientists on the current status of the coastal zone around Tobago and optimal land-use strategies for the sustainable development of the island.**
- **A long-term monitoring programme should be developed that includes regular measurements of key parameters of environmental health (e.g. water quality, temperature, biodiversity, coral diseases, fish abundance) at fixed sites around Tobago’s coastline,. This data would be used to update the GIS database suggested above.**
- **Due to the likely increase in bleaching events in forthcoming years, there should be increased management efforts to reduce coastal pollution from inadequately treated sewage effluent and surface run-off contaminated with mud and silt. This will help build the resilience of corals and increase their likelihood of surviving future bleaching events.**
- **The creation of the Speyside Marine Protected Area should be made a management priority as the area contains an important stock of “bleaching-resilient” corals that provide new recruits to downstream reefs around Tobago. Particular efforts should be made to protect the watersheds around the Speyside MPA to prevent siltation and pollution impacts on the surrounding reefs.**

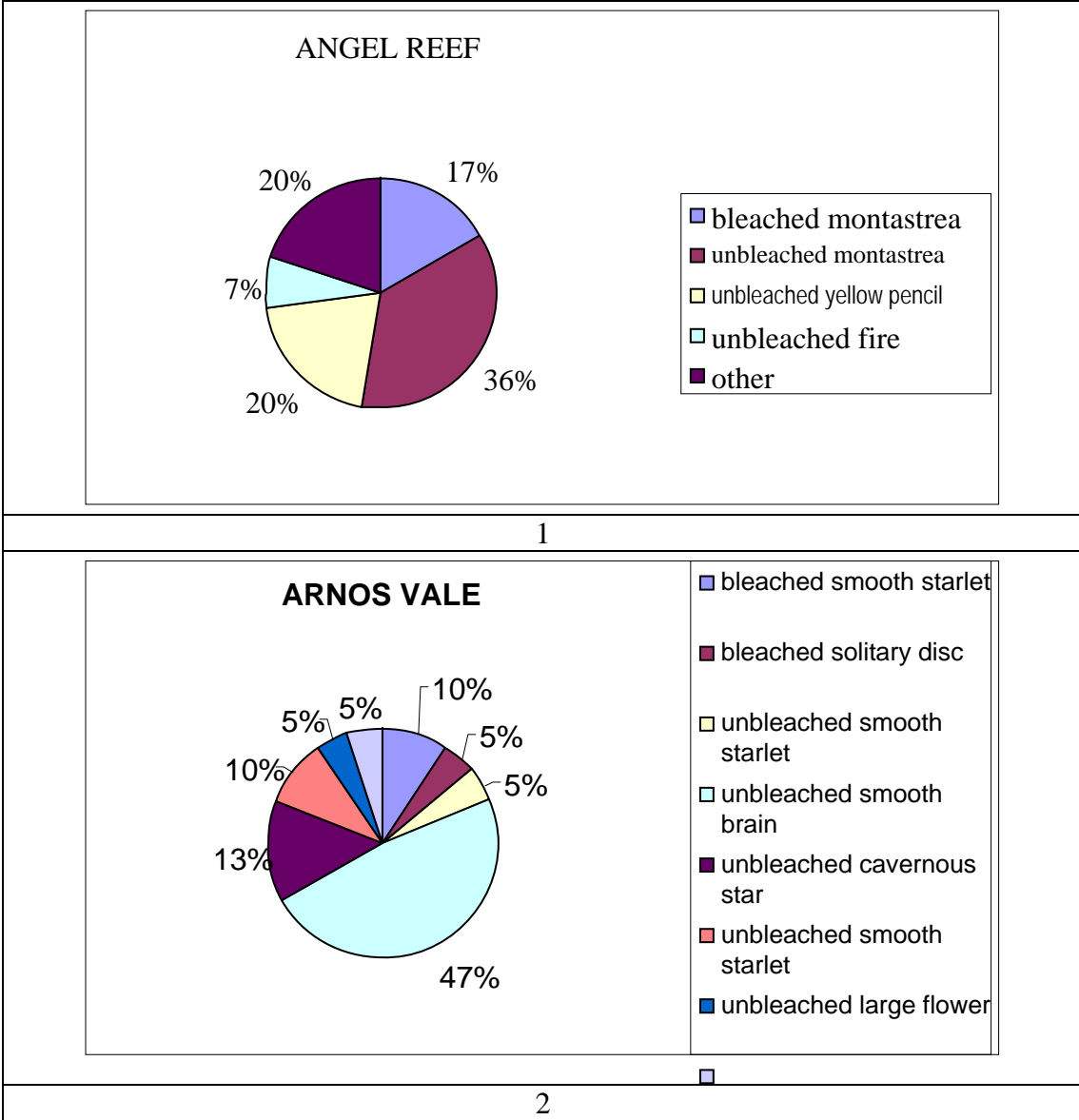
References

- Aronson, R.B. and Precht, W.F. 1997. *Stasis, biological disturbance, and community structure of a Holocene coral reef*. *Paleobiology* 23: 326-346.
- Attwood, D.K., Hendee, J.C. and Mendez, A. 1992. *An assessment of global warming stress on Caribbean coral reef ecosystems*. *Bulletin of Marine Science* 51: 118-130.
- Brown, B.E., Dunne, R.P., Goodson, M.S. and Douglas, A.E. 2002. *Experience shapes the susceptibility of a reef coral to bleaching*. *Coral Reefs* 21: 119-126.
- Brown, B.E., Dunne, R.P., Goodson, M.S. and Douglas, A.E. 2000. *Bleaching patterns in coral reefs*. *Nature* 404: 142-143.
- Brown, B.E. 1997a. *Coral bleaching: causes and consequences*. *Coral Reefs* 16: Suppl.: S129-S138.
- Brown, B.E. 1997b. *Adaptations of reef corals to physical environmental stress*. *Adv Mar Biol* 31: 221-299.
- Brown, B.E., Dunne R.P. and Chansang H. 1996. *Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years*. *Coral reefs* 15: 151-152.
- Buddemeier, R.W., Kleypas, J.A. and Aronson, R.B. 2004. *Coral reefs and global climate change: potential contributions of climate change to stresses on coral reef ecosystems*. Pew Center on Global Climate Change, Virginia, USA.
- Buddemeier, R.W. and Fautin, D.G. 1993. *Coral bleaching as an adaptive mechanism – a testable hypothesis*. *BioSci* 43: 320-326.
- Burke, L. and Maidens, J. 2004. *Reefs at risk in the Caribbean*. World Resources Institute, Washington D.C. USA.
- Connell, J.H. 1997. *Disturbance and recovery of coral assemblages*. *Coral Reefs* 16: S101 – S113.
- Eakin, C.M. 1996. *Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific*. *Coral Reefs* 15: 109-119.
- English, S., Wilkinson, C. and Baker, V. 1997. *Survey manual for tropical marine resources – 2nd edition*. Australian Institute of Marine Science, Queensland, Australia.
- Fitt, W.K., McFarland F.K., Warner, M.E. and Chilcoat G.C. 2000. *Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching*. *Limnol Oceanography* 45: 677-685.
- Fitt, W.K., Brown, B.E., Warner, M. and Dunne, R.P. 2001. *Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals*. *Coral Reefs* 20: 51-65.
- Gates, R.D., Baghdasarian, G. and Muscatine, L. 1992. *Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching*. *Biol Bull* 182: 324-332.

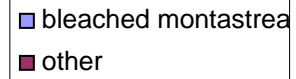
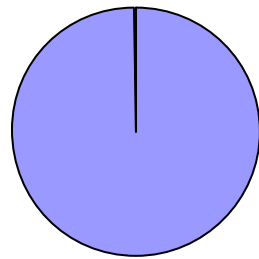
- Glynn, P.W. 1993. *Coral reef bleaching ecological perspectives*. Coral Reefs 12: 1-17.
- Goreau, T., McClanahan, T., Hayes, R. and Strong, A. 2000. *Conservation of coral reefs after the 1998 global bleaching event*. Conservation Biology 14: 5-15.
- Harvell, C., Kim, K., Burkholder, J., Colwell, R., Epstein, P., Grimes, D., Hofmann, E., Lipp, E., Osterhaus, A., Overstreet R., Porter, J., Smith G. and Vasta G. 1999. *Emerging marine diseases – climate links and anthropogenic factors*. Science 285: 1505-1510.
- Iglesias-Prieto, R. and Trench, R.K. 1994. *Acclimation and adaptation to irradiance in symbiotic dinoflagellates. Responses of the photosynthetic unit to changes in photon flux-density*. Mar Ecol Prog Ser 113: 163-175.
- Kinsey, D.W. 1988. *Coral reef system response to some natural and anthropogenic stresses*. Galaxea 7: 113-128.
- Oliver, J., Marshall, P., Setiasih, N. and Hansen, L. 2004. *Coral bleaching monitoring protocol*. World Fish Center and WWF Indonesia.
- Rowan, R. and Knowlton, N. 1995. *Intraspecific diversity and ecological zonation in coral algal symbiosis*. Proc Nat Acad Sci 92: 2850-2853.
- Schick, J., Lesser, M. and Jokiel, P. 1996. *Effect of ultraviolet radiation on corals and other coral reef organisms*. Global Change Biology 2: 527-545
- Schluessel, P., Emery, W.J., Grassl, H and Mammen, T. 1990. *On the bulk-skin temperature difference and its impacts on satellite remote sensing of sea surface temperatures*. Journal of Geophys Res 95: 13341-13356.
- Stone, L., Huppert, A., Rajagopalan, B., Bhasin, H. and Loya, Y. 1999. *Mass coral reef bleaching: a recent outcome of increased El Niño activity?* Ecology Letters 2: 325 – 330, Blackwell Science Ltd/CNRS.
- Szmant, A.M. and Gassman, N.J. 1990. *The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral Montastrea annularis*. Coral Reefs 8: 217-224.
- Toren, A., Landau, L., Kushmaro, A., Loya, Y., and Rosenberg E. 1998. *Effect of temperature on adhesion of Vibrio strain AK-1 to Oculina patagonica and on coral bleaching*. Applied Environmental Microbiology 64: 1379-1384.
- Ware, J.R., Fautin, D.G. and Buddemeier, R.W. 1996. *Patterns of coral bleaching: modelling the adaptive bleaching hypothesis*. Ecol Model 84: 199-214.
- Winter, A., Appeldoorn, R.S., Bruckner, A., Williams, E.H.(Jr) and Goenaga, C. 1998. *Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico*. Coral Reefs 17: 377-382.

Appendix I

SUMMARY OF DOMINANT CORALS (AND THEIR STATUS WITH REGARD TO BLEACHING) AT EACH SITE

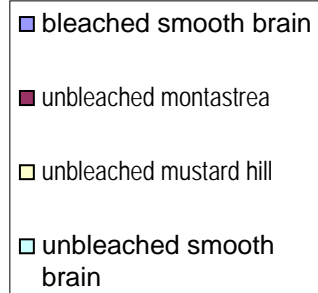
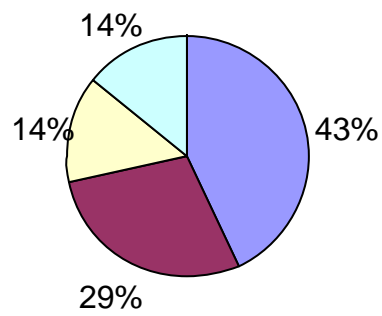


BLOODY BAY



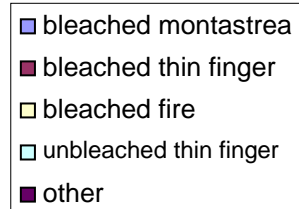
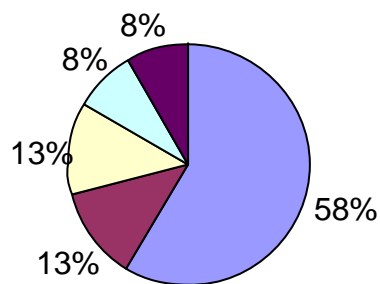
3

BROTHERS ROCKS

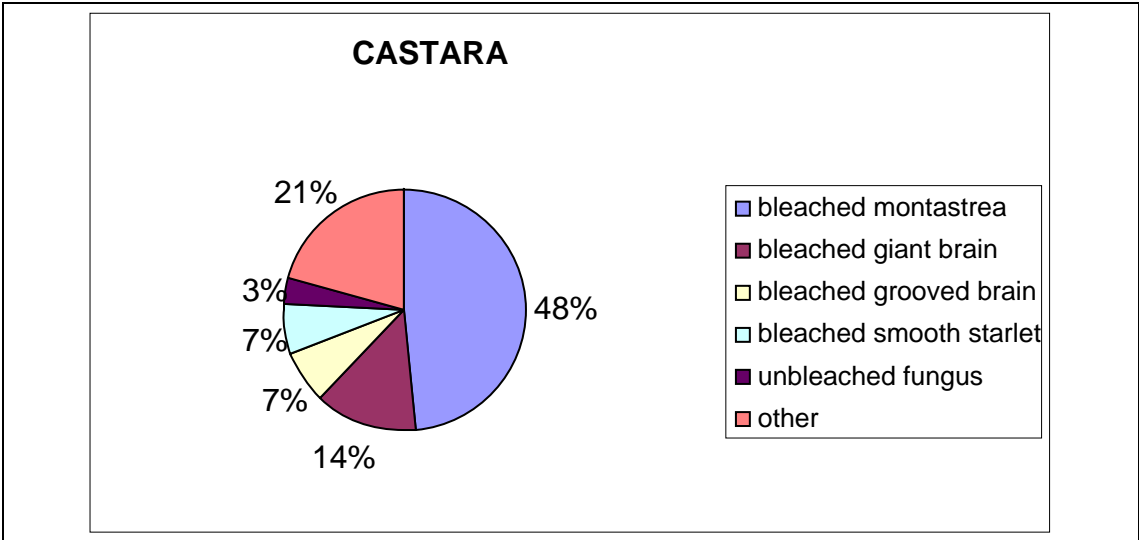


4

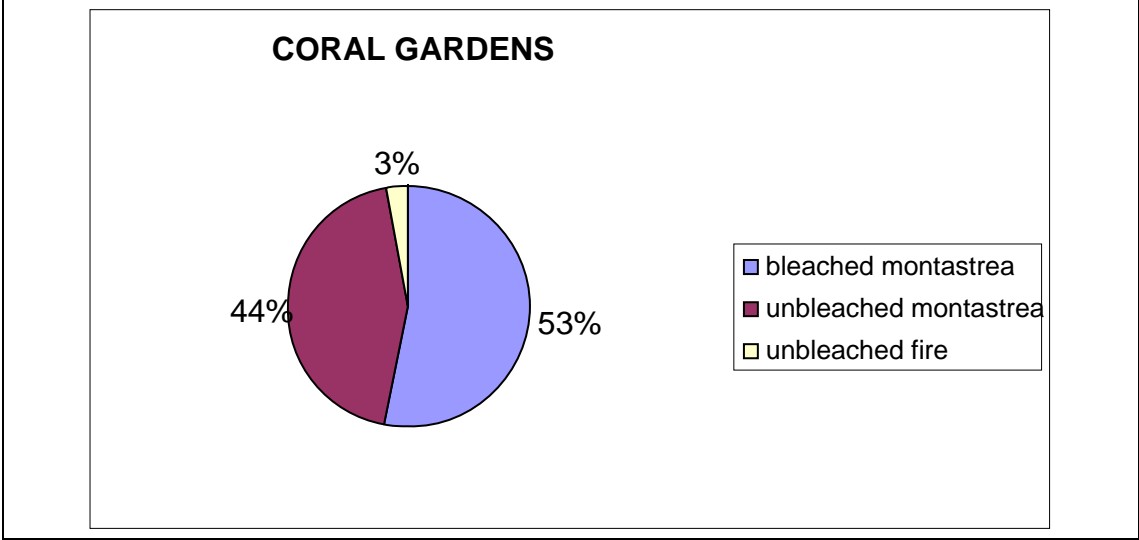
BUCCOO REEF



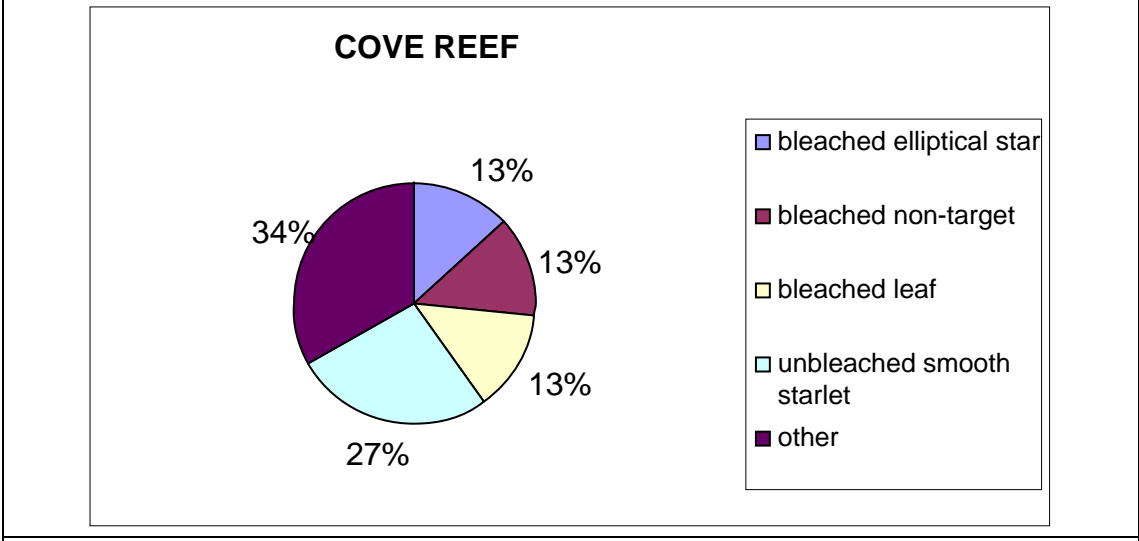
5



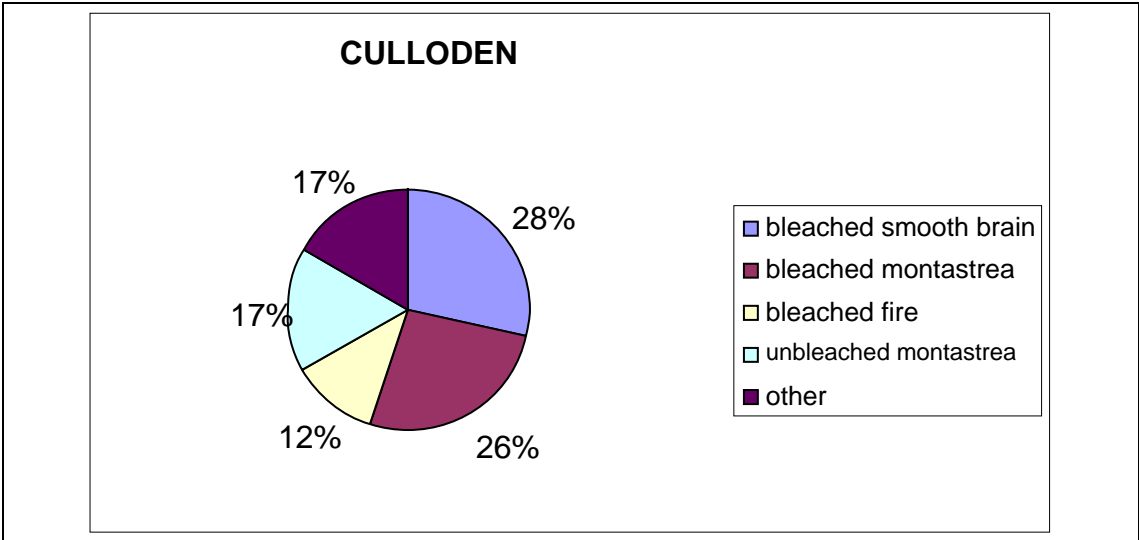
6



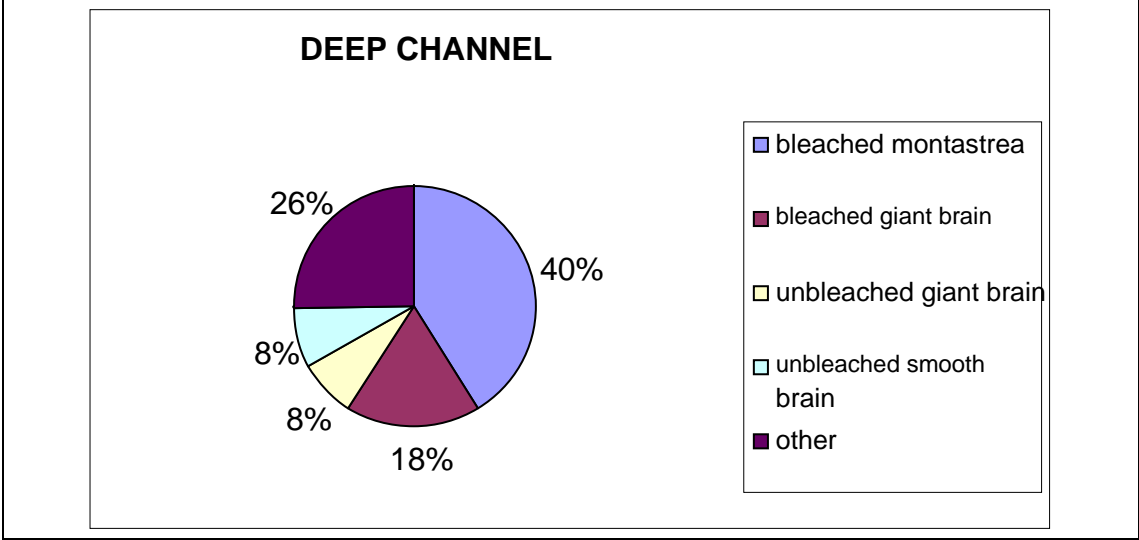
7



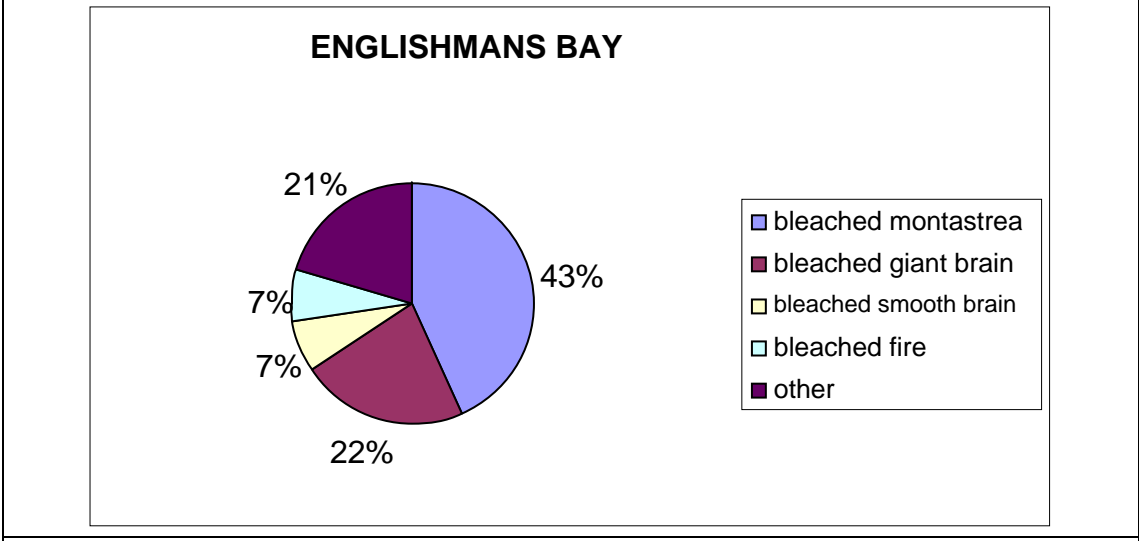
8



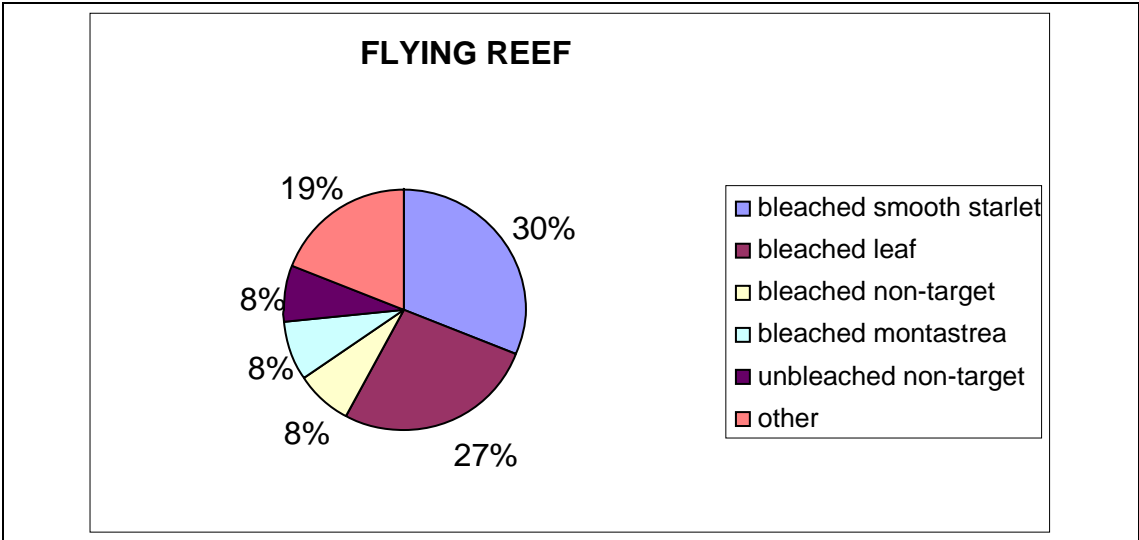
9



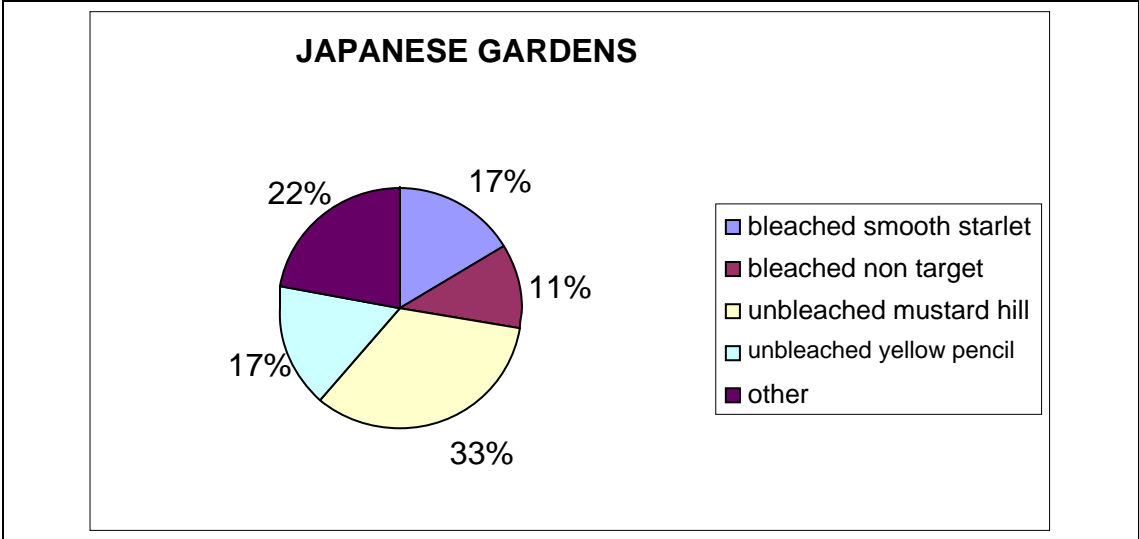
10



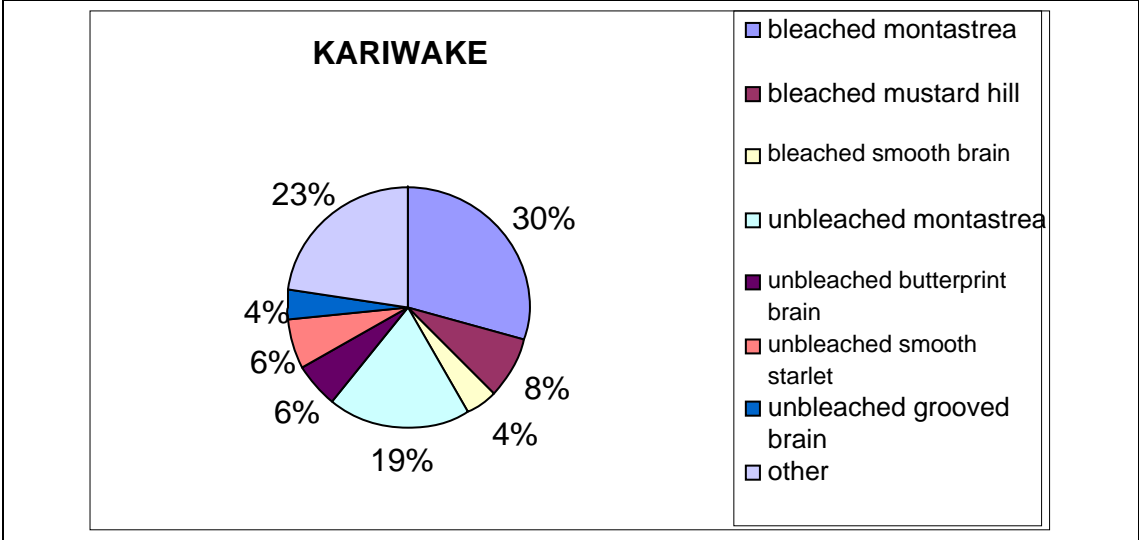
11



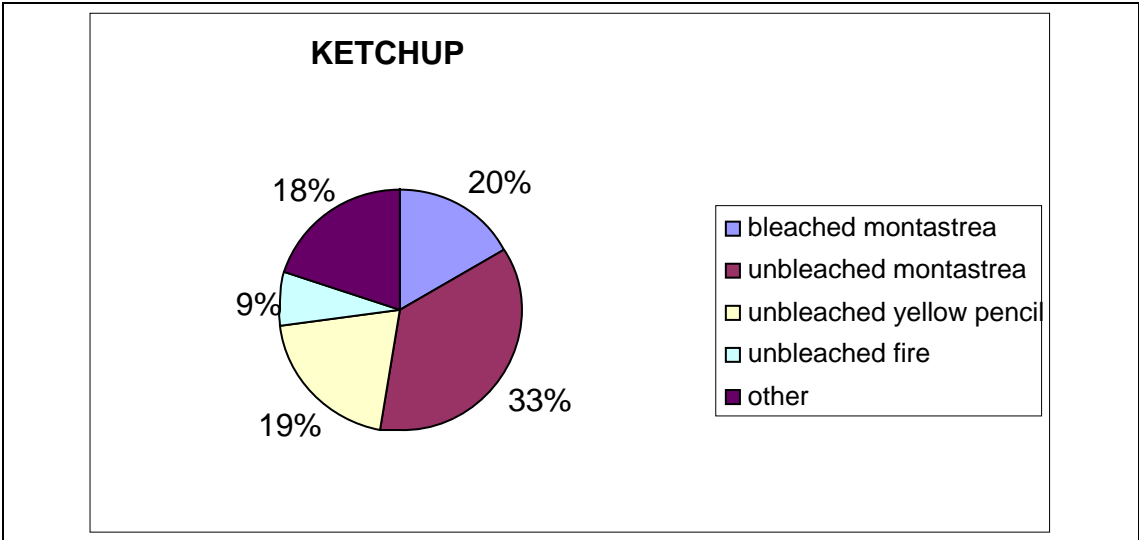
12



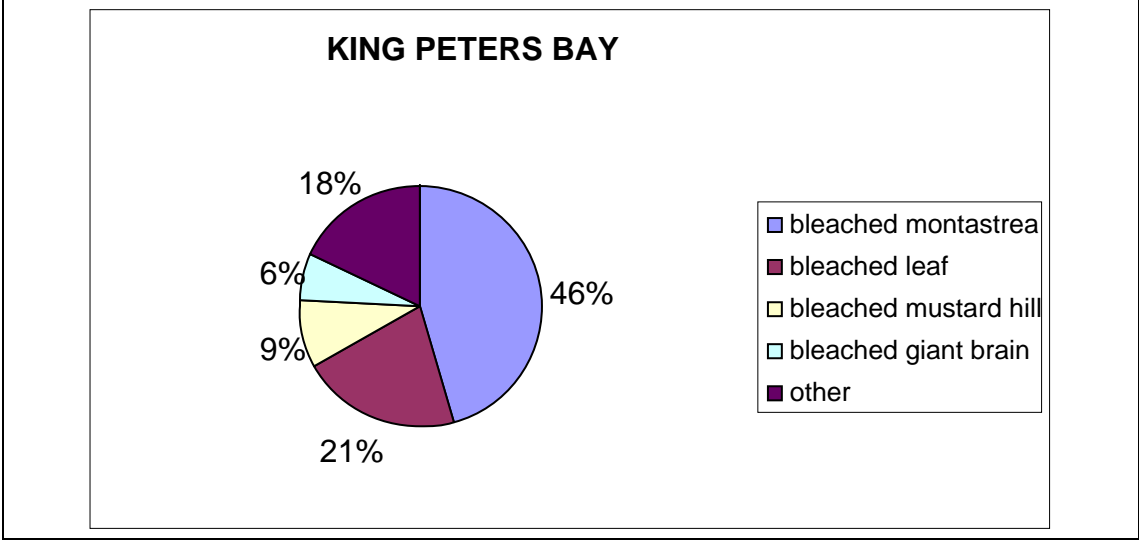
13



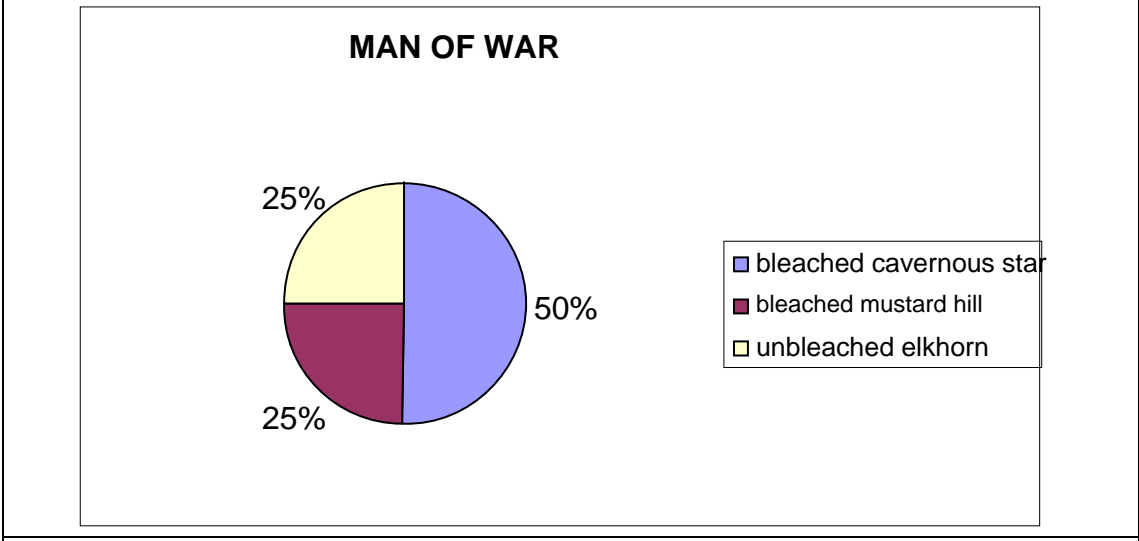
14



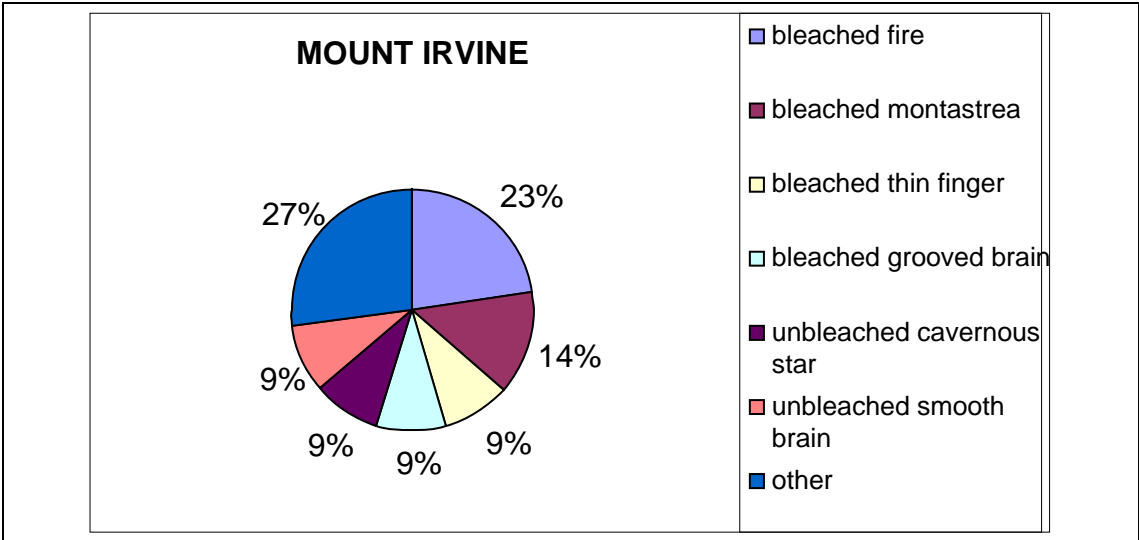
15



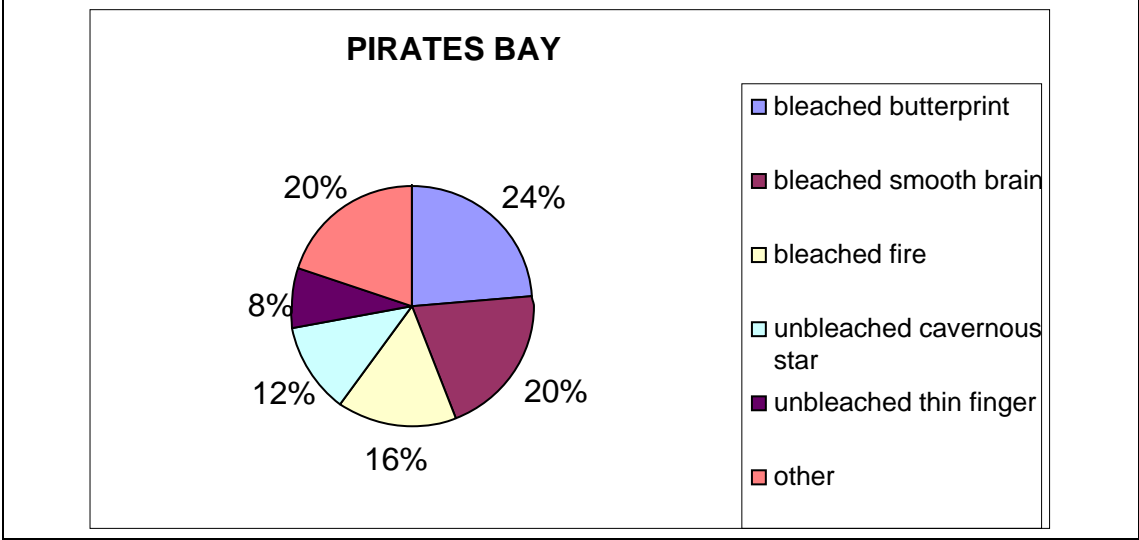
16



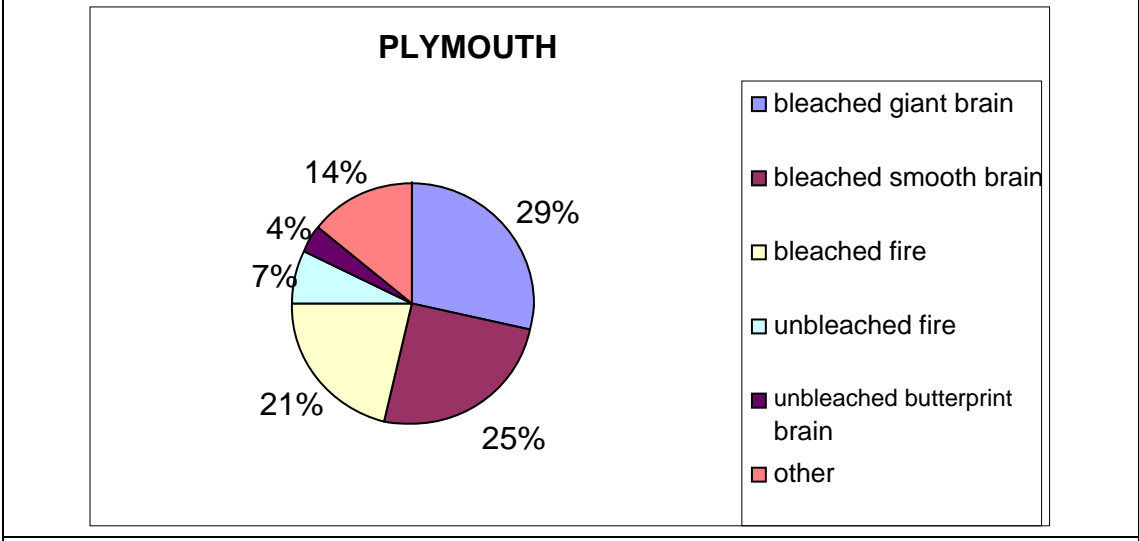
17



18

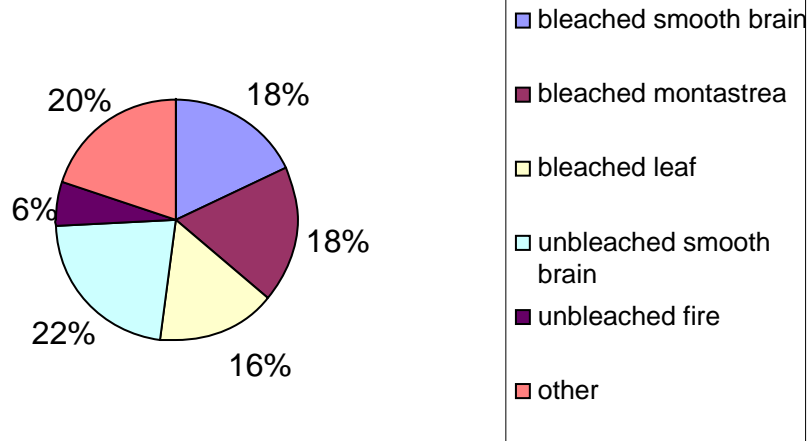


19



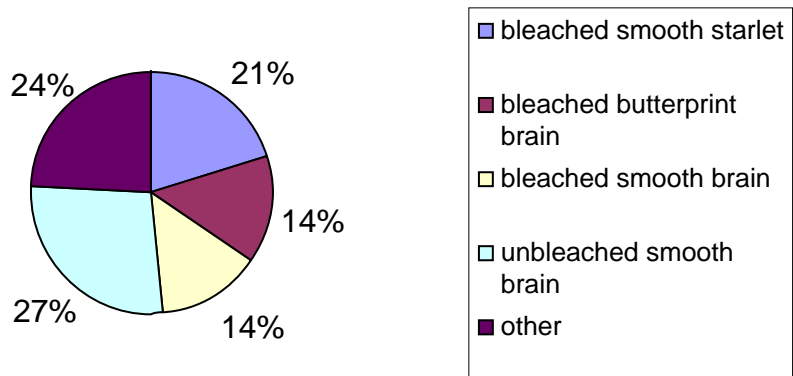
20

SISTERS ROCKS



21

SPINY COLONY



22

Appendix II

SUMMARY OF BENTHIC COVER BY CLASS AT EACH SITE AND DEPTH.

