Modelling Ecological Susceptibility of Coral Reefs to Environmental Stress
Using Remote Sensing, GIS, and in situ Observations:
A case study in the Western Indian Ocean

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Modelling Ecological Susceptibility of Coral Reefs to environmental stress using Remote Sensing, GIS, and in situ Observations: A case study in the Western Indian Ocean

by

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Abstract

The rate at which coral reefs are impacted by environmental and anthropogenic stressors threatens them with extinction all over the world where they are found. Understanding coral bleaching patterns and ecosystem resilience will lead to the understanding of how coral abundance will change under the influencing physical factors. This is critical to any projection of how the goods and services of a coral reef will change, and for the analysis of the socio-economic consequences. This study aims to determine relative importance of historical and short-term environmental conditions to coral bleaching, and to develop a susceptibility map of coral reef systems based on parameters which correlate with resistance to thermal stress. We investigate the interaction of these factors in the Western Indian Ocean, at a scale detectable by moderate resolution remote sensors using modelling approach. We use remotely sensed oceanography data for six environmental variables: surface currents; wind velocity; sea surface temperature (SST); UV radiation; photosynthetic active radiation (PAR); and chlorophyll-a concentration, to derive predictor variables for the observed coral bleaching. Using Spatial Principal Component Analysis (SPCA) and cosine amplitude-AHP methods, we develop two susceptibility Models (SM1&2) in GIS using fuzzy logic technique. These models predict specific areas with environmental conditions that are likely to result in low bleaching and mortality; and that have a potential of maximum recovery from environmental disturbances. Historical environmental conditions explained 56% of the variation of bleaching observed in 2005; while conditions at the time of bleaching explained 62%. When combined all environmental variables explained 67% of the variation, with variables derived from sea surface temperature (coefficient of variation; positive anomalies), surface currents, wind anomalies, PAR and UV contributing significantly to the total variation. 2005 bleaching event differed from previous events as it affected regions in southern latitudes more than in the North. Susceptibility models identified regions which are highly susceptible and less resistant to environmental stress, as mainly the reef systems along the north-west boundary of the Indian Ocean and some Indian Ocean Islands. Half of strictly no take zones in the region are situated in locations with medial to severe susceptibility. Similar studies using moderate to high resolution data should be undertaken as a basis for establishment of marine protected areas to facilitate the mitigation and recovery measures, and to safe guard global coral reef biodiversity.

Key words: susceptibility, coral bleaching, resilience, oceanography variables, Western Indian Ocean.
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Table of contents

1. Introduction ................................................................................................................... 1
   1.1. General background: reef building corals .............................................................. 1
   1.2. Threats to coral reefs .............................................................................................. 1
   1.3. Coral bleaching mechanisms, patterns and theories ............................................... 4
   1.4. Environmental Factors that enhance Coral Community Resilience .......... 6
   1.5. Modelling susceptibility of coral reefs systems ..................................................... 6

2. Study context and conceptual framework ................................................................. 9
   2.1. Problem statement and justification ..................................................................... 11
   2.2. Research objectives .............................................................................................. 11
   2.3. Research hypotheses ............................................................................................ 12

3. Methods and Materials ............................................................................................... 15
   3.1. Study Area ........................................................................................................... 15
   3.2. Data description, extraction and processing methods .......................................... 16
      3.2.1. Coral bleaching observation data ............................................................... 16
      3.2.2. Sea Surface Temperature ............................................................................ 17
      3.2.3. Ocean Surface Current velocity .................................................................. 18
      3.2.4. Ultraviolet radiation (UV) .......................................................................... 19
      3.2.5. Photosynthetically Active Radiation (PAR) .............................................. 20
      3.2.6. Chlorophyll-α Pigment concentration ........................................................ 21
      3.2.7. Wind speed ................................................................................................. 21
   3.3. Derived primary variables .................................................................................... 22

   4.1. Coral bleaching as a function of environmental variables ................................... 25
   4.2. Bleaching observation data .................................................................................. 25
   4.3. Reef base bleaching observation data .................................................................. 27
   4.4. Modeling Susceptibility ....................................................................................... 27
      4.4.1. Expert knowledge analysis ......................................................................... 27
      4.4.2. Susceptibility model 1 (SM1) ................................................................. 34
      4.4.3. Susceptibility model 2 (SM2) .................................................................. 35
      4.4.4. Models comparison, evaluation, and susceptibility gradation ..................... 38

5. Results ........................................................................................................................... 41
   5.1. Bleaching observations ......................................................................................... 41
   5.2. Conditions at the time of bleaching .................................................................... 42
   5.3. Long term environmental variables ..................................................................... 43
   5.4. Long term and short term variables ..................................................................... 44
List of figures

Figure 1: Conceptual framework for modelling the susceptibility. .......................... 10
Figure 2: Map of the study area showing coral reef areas and the coral bleaching study sites 16
Figure 3: Comparison of satellite derived skin temperature with in situ data (n = 267)....... 18
Figure 4: Membership functions and their respective equations. ................................. 30
Figure 5: Susceptibility maps based on respective environmental variables. ............. 33
Figure 6: Correlation plot of the two models, SM 1 and SM 2 ................................. 39
Figure 7: Plot of bleaching indices against latitude...................................................... 41
Figure 8: Logistic probability plot of coral bleaching intensity against latitude. .......... 42
Figure 9: A scatter plot based on the first two canonical axes................................. 47
Figure 10: Plot of mean of environmental variables against bleaching intensity categories ... 48
Figure 11: Maps showing estimated susceptibilities by (a) SM1 and (b) SM2; and the classified maps for (c) SM1 and (d) SM2 ............................................................... 49
Figure 12: Correlation of change in coral cover (%) with susceptibility indices as estimated by (a) SM1 and (b) SM2 ................................................................. 53

List of Appendices

Appendix 1: Parameters derived/aggregated from the satellite images. Units for the respective layers are: SST (°C); UV (milli-watts/m2); Chlorophyll (Mg/m³); CV (°C); Bleaching (%); Wind speed (m/s); PAR (PAR, Einstein/m2/day); currents (m/s); hotspot (°C); slope (°C) ... 77
Appendix 2: Histograms showing value ranges for respective variables. The y-axes are number of pixels while the x-axes are the value for respective variables. (Units are the same as in Appendix 1). ................................................................. 79
Appendix 3: Properties and sources of satellite modelled and point data used in this study... 81
List of tables

Table 1: Summary of environmental factors alleged to cause/influence coral bleaching .......3
Table 2: Description of the equations used in the derivation of parameters .................23
Table 3: Environmental variables separated into conditions at the time of bleaching and the long term or historical conditions) .................................................................25
Table 4: Summary of the nature of influence a parameter has on coral’s thermal stress ....28
Table 5: Estimates of control values defining points along x-axis where the variable’s threats to corals reefs are perceived to be zero (a; d) and one (b; c). ...............................................31
Table 6: Results of SPCA ..............................................................................................34
Table 7: Pair-wise parameter relation strength (rij) matrix from equation 19. ............37
Table 8: Cluster analysis results with respect to susceptibility .....................................39
Table 9: Output of a regression model performed with conditions at the time of bleaching as predictor variables. .......................................................................................43
Table 10: Model output when the long term variables are used as predictor variables. ....44
Table 11: Model output when all uncorrelated variables are factored as predictor variables in the stepwise regression model ............................................................................45
Table 12: Logistic regression output with bleaching intensity categories from reef base data as response the variable .........................................................................................47
Table 13: Susceptibility indices derived from SM1 and SM2 for selected 397 reef systems summarized by countries in the region .................................................................51
Table 14: Summary of the susceptibility indices for the marine protected areas (strictly no take zones) in the region ..................................................................................51
1. Introduction

1.1. General background: reef building corals

Coral reefs are the most diverse marine ecosystems. Geographically they are located in circumtropical shallow tropical waters along the shores of islands and continents (Buchheim, J., 1998). Scleractinian corals play a primary role in the construction and maintenance of reefs. They provide support and shelter for the many organisms that inhabit the coral reefs (Meesters et al., 1998). It is estimated that 25% of all marine species inhabit coral reefs, where the number of individual species may be as high as one million (Davidson, O. G. 1998).

Marine ecosystems contribute about 63% of the estimated value of the biosphere - $16-$54 trillion USD annually (Costanza et al., 1997). Coral reefs in particular contribute to about 1.8% of this value (Costanza et al., 1997). Given that coral reefs constitute 0.2 % of the world’s marine ecosystem (Bryant et al., 1998), these figures demonstrate that the contribution of coral reefs to the welfare of the world and the people living on it is disproportionately large (Souter and Linden, 2000).

One thing the countries which border Western Indian Ocean have in common is the high dependency on coastal resources by the population living at the coast (Muthiga et al., 1998). Resources derived from coral reefs are essential to the livelihood of millions of people who live within tropical coastal communities (Souter and Linden, 2000). Economically they support artisanal fisheries; a source of livelihood to the most of the coastal population in tropical countries. Tourism is vital to economies of most countries where coral reefs are found. Coral reefs are invaluable for protecting the beach against strong ocean waves.

1.2. Threats to coral reefs

One of the major challenges facing science today is the response of ecosystems to global environmental change, and its retroaction on climate and human societies (Reynaud et al., 2003). The frequency, diversity and the rate at which humans are impacting coral reefs are increasing to the extent that reefs are threatened globally, throughout their geographical range (Hughes et al., 2003; Shepherd, R. C, 2003).
Assessments to late 2000 are that 27% of the world’s reefs have been effectively lost, with the largest single cause being the massive climate-related coral bleaching event of 1998 (Almada-Villela, et al., 2002). Coral reef ecosystems in the Western Indian Ocean, like elsewhere in the world where they are found, have undergone a tremendous change due to environmental and anthropogenic factors (McClanahan, T. R., 2000; Turner et al., 2000; Sheppard, C. R, 2003). Though scientists do not yet know definitely what is causing the decline of some reefs (Dustan et al., 2001), factors known to contribute to this change include over fishing and removal of grazers, use of destructive gear, bleaching (the loss of algal symbionts), storm damage, disease, increasing abundance of macro algae and pollution (Hoegh-Guldberg 1999, Rogers and Miller, 2006 ).

The link between increased greenhouse gases, climate change, and regional-scale bleaching of corals, considered dubious by many reef researchers only 10 to 20 years (Sheppard and Rioja-Nieto, 2005), is now incontrovertible. Moreover, future changes in ocean chemistry due to higher atmospheric carbon dioxide may cause weakening of coral skeletons and reduce the accretion of reefs, especially at higher latitudes (Hughes et al., 2003). It is predicted that coral reefs will suffer mounting stress associated with a global increase in atmospheric carbon dioxide over the coming decades (Mumby, et al., 2001).

Coral bleaching is a very patchy phenomena (Wooldridge and done, 2004). Often, bleached and unbleached corals are found in the same reef or next to each other (McClanahan, T. R. 2004). This provides evidence that temperature alone does not account for the bleaching patterns. The sources of this variation are poorly understood and have been variously attributed to extrinsic environmental patchiness e.g. temperature, light, turbulence, solar radiation, water flow, salinity, sediments (see the respective sources in table 1), as well as phenotypic and genetic differences among corals and their micro algal symbionts (Hughes et al., 2003, Baker A. C., 2001). Average summer water temperatures differ enormously within the geographic boundaries of a typical coral species’ range (Hughes et al., 2003). Wind speed, light, and clouds are all thought to influence bleaching intensity (Table 1). Satellite-derived SST has been widely used to identify the spatial extent of coral reef bleaching (Strong et al., 1997). However, to accurately monitor and predict coral bleaching, satellite observations of additional environmental parameters such as wind, currents, cloud cover, and solar radiation are necessary as they will help to better relate environmental measurements.
Table 1: Summary of environmental factors alleged to cause/influence coral bleaching

<table>
<thead>
<tr>
<th>Variable</th>
<th>Field</th>
<th>Laboratory</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevated sea water temperature</td>
<td>Glynn, P. W. (1993); Aronson et al. (2000); McClanahan et al. (2005);</td>
<td>Hoegh-Guldberg and Smith (1989);</td>
</tr>
<tr>
<td></td>
<td>McClanahan and Maina (2003); Sheppard, R. C. (2003)</td>
<td>Glynn and DÓCroz (1990); Lesser et al. (1990); Fitt and Warner (1995);</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Warner et al. (1996); Porter et al., 1999</td>
</tr>
<tr>
<td>Solar radiation (including ultraviolet radiation) ; and clouds</td>
<td>Fisk and Done (1985); Gleason and Wellington (1993); Brown et al. (1994);</td>
<td>Hoegh-Guldberg and Smith (1989) Lesser, M. P. (1989); Lesser and Shick (1989); Lesser et al. (1990); Salih et al. (2000); Kinzie et al. (2001); Nakamura et al. (2005); Anderson et al. (2001)</td>
</tr>
<tr>
<td></td>
<td>Gleason and Wellington (1995); Mumby et al., 2001</td>
<td></td>
</tr>
<tr>
<td>Water flow/current speed</td>
<td>McClanahan et al.(2005) Finelli et al., 2006</td>
<td>Nakamura and van Woersk (2001); Nakamura et al. (2003); Nakamura et al. (2005);</td>
</tr>
<tr>
<td>Reduced/increased salinity; river sediments</td>
<td>Fang et al. (1995); Obura, D. O. (1995); McClanahan and Obura (1997)</td>
<td>Kushmaro et al. (1996); Kinzie et al. (2001); Porter et al., 1999</td>
</tr>
<tr>
<td>Modelling approach: Water flow; Habitat; community; elevated temperature</td>
<td>Wooldridge and Done (2004)</td>
<td></td>
</tr>
</tbody>
</table>

Source: modified and updated from Brown, B. E., 1996
1.3. Coral bleaching mechanisms, patterns and theories

It has been over two decades since the phenomenon of coral bleaching was first described (Brown, B. E., 1996). There is still however no simple explanation for the unusual increase in frequency and intensity of these events that have been occurring at a global scale (Huppert and Stone, 1998). Coral bleaching, defined as the loss of symbiotic dinoflagellates (zooxanthellae) from animals normally possessing them (Ware et al., 1996), is a response of tropical symbiotic corals and related cnidarians and molluscs to a variety of environmental stresses (Fitt et al., 2001).

Bleaching’ in the botanical sense usually refers to the destruction of photosynthetic pigments by photo-oxidative processes that can occur in both higher plants and algae (Venn et al., 2006). When corals are exposed to heat stress, the photosynthetic metabolism fails, a phenomenon generally known as photo inhibition. These conditions result in a decline in photochemical efficiency of symbiotic micro algae (zooxanthellae) which ultimately leads to the expulsion of these symbionts.

Corals and their zooxanthellae are vulnerable to a variety of environmental stressors that can disrupt the symbiotic relationship (Reaser et al., 2000). If the stress is severe and prolonged, most of the corals on a reef may bleach, and many may die (Hughes et al., 2003). Competing hypotheses for the cause of coral bleaching include: nutrient enrichment, disease, increase in temperature, and excess light/ultraviolet exposure (Yentsch et al., 2002; Brown, B. E., 1996; and Table 1). Of all these factors, sea surface temperature (SST) has received the most attention (Ware et al., 1996), and has generally been considered as the primary stress which causes coral to bleach worldwide when their thermal tolerance is exceeded (Fitt et al., 2001; McClanahan et al., 2005; Liu, G., 2003, Hoegh-Guldberg and Smith 1989; Glynn and DeCroz, 1990; Hoegh-Guldberg 1999; Jokiel, P., 2004).

The last major occurrence of coral bleaching was in 1998, when corals bleached extensively as a result of elevated Sea surface temperatures, destroying about one-sixth of the world’s coral colonies (Dennis, C., 2002). This event coincided with the largest El Niño–Southern Oscillation (ENSO) on record (West and Salm, 2003). But the 2002, 2004 and 2005 bleaching is out of phase with El Niño, raising concerns that bleaching events are growing in frequency and intensity in response to climate change (Dennis, C., 2002, Glynn, P. W., 1993, McClanahan et al., 2005). This has stimulated research into modelling potential future scenarios of sea temperatures in reef regions e.g. Sheppard, R. C., 2003, Hoegh–Guldberg, O., 1999. Based on the
temperature thresholds and a predicted recurrence of the El Niño events, Sheppard (2003) predicted that corals in the Western Indian Ocean’s southern hemisphere will become ecologically extinct within the next 20 to 40 yrs. However, recent developments in Zooxanthelae genetics suggest that resilience of coral reefs, through acclimation of the coral animal and the symbiotic algae may prevent extinction to occur (Sheppard, R. C., 2003; McClanahan et al., 2005). Andrea et al. (2006) observed that some species of bleached corals were able to adapt to bleaching state by increasing their feeding rates; suggesting that coral species with high Cnidarians feeding capability during bleaching and recovery, will be more resilient to bleaching events over the long term and may help to safeguard affected reefs from potential local and global extinction (Andrea et al., 2006).

Published projections of a baseline of increasing ocean temperature resulting from global warming have suggested that annual temperature maxima within 30 years may be at levels that will cause frequent coral bleaching and widespread mortality leading to decline of corals as dominant organisms on reefs (Coles and Brown, 2003, Hughes et al., 2003). However, these projections have not considered the high variability in bleaching response that occurs among corals both within and among species (Coles and Brown, 2003). The ‘adaptive bleaching hypotheses’ as described by Buddemeier and Fautin, 1993; Ware et al., 1996; Kinzie et al., 2001; stipulates that with coral bleaching, corals first lose their dinoflagellate symbiont’s and then regain a new mix of symbionts that are better suited to the imposed stress regime. It was formulated explicitly to account for the varied observations and experiments on bleaching (Ware et al., 1996). Several studies have carried on the debate through field and lab experiments. Baker, A. C. (2001) through molecular studies of corals noted that bleaching offers an ecological opportunity for reef corals to rid themselves rapidly of suboptimal algae and to acquire new partners. This infers that bleaching may sometimes help reef corals to survive environmental change (Hoegh-Guldberg, et al., 2002, Baker, A. C., 2001). In support of the adaptive bleaching hypotheses is the long-term data sets on mass coral bleaching and mortality, which reveals that far fewer corals in the far-eastern Pacific Ocean died after the 1997–98 El Niño event (0–26%) than after the 1982–83 El Niño event (52–97%) even though the magnitude and duration of sea-surface temperature anomalies in the region in 1997–98 exceeded those of 1982–83 (Glynn et al., 2001; Enfield, D. B., Baker, A. C., 2001). McClanahan et al. (2004) analyzed the frequency of four possible responses to anomalous warm water (not bleach and live; not bleach and die; bleach and live; bleach and die). He observed similar frequencies for the taxa that bleached and died, and those that bleached and lived. To support the adaptive bleaching hypotheses
based on his study, the frequency of survival after bleaching should be high than those that beached and died (McClanahan, T. R., 2004).

1.4. Environmental Factors that enhance Coral Community Resilience

It is imperative that historical environmental conditions do shape the community structure of the population and their response to disturbances. The challenge for coral reef researchers and managers is to identify specific locations with environmental conditions that enhance the coral community resilience, i.e. resistance to heat stress, survival during bleaching, and reef recovery after bleaching-related mortality (Marshall and Schuttenberg, 2006; Obura, D. O., 2005). Coral resistance to heat stress; their tolerance to disturbances, and potential to recover from large scale disturbances are determined by the ecosystem conditions; biological diversity; connectivity between areas; and the local environmental conditions (Marshall and Schuttenberg, 2006; Obura, D. O., 2005). From the perspective of modelling resilience, biological diversity and ecological conditions can be represented by estimates of species richness, coral abundance and the management status of a reef system. Connectivity or location of an area with respect to the ‘transport network’ of the larvae can be estimated using the current vectors and the network of marine protected areas (Roberts, C. M., 2006; Cowen et al., 2000; Dawson et al., 2006; Cowen et al., 2006).

West and Salm (2003) in their review compiled environmental factors which are likely correlates of resistance and resilience to coral bleaching. These factor included cloud cover, temperature variability, turbidity, absorption, wind, high wave energy, up welling and adjacent to deep water. They listed broad size and species distributions and history of corals surviving bleaching events as indirect indicators of bleaching tolerance.

1.5. Modelling susceptibility of coral reefs systems

A modest number of studies have attempted to model coral reef processes including coral bleaching using different approaches: e.g. Wooldridge and Done, 2004; Langmead and Sheppard, 2004; Sheppard R. C., 2003; Sheppard and Rioja-Nieto, 2005.

The modelling of coral reef ecological processes, like in many ecosystem modelling is complicated by the imprecise nature of ecological interrelationships, and the subjectivity inherent in the judgments by field observers (Bosserman and Ragade,
Traditional models of reef processes often require unavailable data and precision (Meesters et al., 1998). Frequently important observations are lacking, and potentially valuable information may be non quantitative in nature (Silvert, W., 1997). This may limit the success and usefulness of these models.

Fuzzy set theory, first introduced by Zadeh (1965) offers a methodology for dealing with these problems, and provides an alternative approach to modelling highly complex systems. It is an extension of classical set theory where elements of a set have grades of membership ranging from zero for non-membership to one for full membership. A ‘fuzzy set’ is a collection of paired numbers that consist of members and degrees of support or the level of confidence for those numbers (Juang et al., 1992). In classical set theory, every element can be classified as to whether or not it belongs to a particular set.

In considering the modelling of coral reef resilience, defining strong resilience of a reef system in terms of crisp sets for attributes presumes the ecosystem manager can make a sharp, unambiguous distinction between an ecosystem that is strongly resilient and one that is not by comparing measured attributes to resilience thresholds for those attributes. A crisp set is a set in which all members match the class concept and the class boundaries are sharp, and allow only binary membership functions (Burrough and McDonnell, 2005). However, fuzzy set theory deals with situations where membership in a set is unclear and allows for this division to be removed. Instead, the uncertainty of the boundary between these regions, and the measurements on which they are based, can be modelled (Malins and Metternicht, 2006; Burrough and McDonnell, 2005). The boundaries or control points of a membership function for some fuzzy set A are defined as the region of the universe containing elements that have non zero membership function but not complete membership (Burrough and McDonnell, 2005, Ross, T. J., 2004). The control points along the x-axis bound the elements of the universe with some degree of fuzziness, or only partial membership in fuzzy set A in the form $0 < \mu_A(x) < 1$ (Ross, T. J., 2004). Fuzzy modelling provides a framework which allows a greater ability to make decisions about ecosystems and to develop ecosystem concepts (Bosserman and Ragade, 1982).

In literature, application studies of fuzzy logic concept to modelling coral reef processes include the work of Meesters et al., 1996. They constructed a coral reef model that predicts changes in coral cover and diversity under anthropogenic stress.
Hendee et al., 1998 constructed an expert system application, termed the coral reefs early warning system (CREWS) to identify oceanographic conditions conducive to coral bleaching. This application is programmed to send bleaching alerts in fuzzy terms when the real time input oceanography data is favourable for bleaching (Hendee et al., 1998). CREWS use SST, wind speed, and PAR as input parameters.
2. Study context and conceptual framework

In 2003, a major initiative was launched by the World Bank other partners to support coral reef resource managers with the best available scientific advice on coral reefs response to human disturbances and climate change (Hatziolos et al., 2003). A Modelling and Decision Support working group was established within this framework, with a mandate to:

‘to develop a coordinated information base that can improve the accuracy and reliability of forecasting and predictive modelling, and to develop modelling tools to handle data on aspects such as community dynamics, oceanography, climate, as well as socio-economic data on fisheries, tourism, and coastal development’ (Hatziolos et al., 2003).

This research is part of a larger study that aims to develop indicators of stress on reefs from in situ data and satellite based observations of sea surface temperature, wind speed, solar insolation, radiation (UV&PAR), and chlorophyll. The ultimate goal is to identify areas less prone to stress at meso scale, based on environmental parameters. In situ bleaching survey data is used here together with environmental parameters as the basis of modelling susceptibility of coral reef systems within WIO. The outcome of this research aims to contribute to the decision-support system for establishments of marine protected areas to conserve biodiversity.

This study adopted a general conceptual model as outlined in figure1. The initial step involved selection of variables which are known to influence coral bleaching and resilience of coral reef ecosystems. Data were then retrieved and pre-processed to obtain the primary variables. The primary variables and/or their respective derived parameters were used in statistical analysis together with coral bleaching observation data as the response variable. Based on a regression equation a coral bleaching map for the entire region was generated. This map, together with derived parameters maps was used in a fuzzification process to yield respective susceptibility membership grade maps. These maps were integrated to obtain two susceptibility models (SM1&2). Validation could not be performed and instead, the models were calibrated using coral mortality data. The outcome of the calibration may lead to a reiteration process and if need be, a lurking variable added. Accuracies of all the data used were explored and taken into account in the assessment of model uncertainties.
Figure 1: Conceptual framework adopted for modelling susceptibility and analysis coral bleaching. Rectangles represent data; tanks represent models; and hexagons represent data/model analysis.
2.1. **Problem statement and justification**

Coral reefs are declining at an alarming rate all over the world. It is suspected by many researchers that multiple stressors, including direct and indirect anthropogenic effects, are the root cause of the problem. Deterioration of these ecosystems has led to the loss of livelihood of many coastal inhabitants, mostly in the developing countries where they depend entirely on these habitats for food. This has aggravated poverty levels in these countries. While managers can regulate coral stressors of anthropogenic nature, those related to physical environment are difficult, if not impossible, to manage. Understanding the interactions of oceanographic factors in relation to bleaching and use of the remotely sensed data in monitoring them will increase our predictive capacity over a large area. When used as a basis to determine areas less prone to stress, it may also serve as a decision support system for their management. This could be further used as the criteria for establishment of marine protected areas to facilitate the mitigation and recovery measures, and to safeguard biodiversity. Understanding coral bleaching will lead to the understanding of how coral abundance will change under the influencing physical factors. This is critical to any projection of how the goods and services of a coral reef will change, and for the analysis of the socio-economic consequences.

2.2. **Research objectives**

The overall objective of this study is to determine the relative importance of environmental factors to coral bleaching and the general health of the ecosystems at a geographical scale. Interaction of these factors in the Western Indian Ocean, at a scale detectable by moderate resolution remote sensors, will be investigated using a modelling approach, and their capacity to predict similar events in the future will be assessed. In effect specific areas with environmental conditions that are likely to result in low bleaching and mortality, and that have a potential of maximum recovery from environmental disturbances will be identified. Recommendations will be made to the management to possibly incorporate these areas into a strategic networks of marine protected areas designed to maximize conservation of global coral reef biodiversity.

In order to achieve this broad objective, specific objectives were formulated as follows:
1. To determine the relative importance of environmental variables as factors which trigger, aggravate, or are conducive to coral bleaching while assessing the relative roles of both short term and long term variables in explaining the bleaching pattern
2. Identify specific areas with environmental conditions that are likely to result in low bleaching and mortality, and that have a potential of maximum recovery from environmental disturbances (resilient areas)
3. To determine the suitability of remotely sensed oceanographic variables, obtained at a moderate to low spatial resolutions, in predicting biological processes in marine ecosystems

Given the above research objectives, the following research questions were formulated:
1. Which environmental variables explain the spatial variation in observed bleaching events; at what time scales is the variability best explained; and how are these events distributed in the Western Indian Ocean region?
2. Which specific areas have environmental conditions that enhance resilience of coral reefs to warm water anomalies and are more likely to experience low mortality?
3. Is remotely sensed oceanography data at a moderate to low spatial resolutions suitable for estimating susceptibility of coral reef systems to environmental stress?

2.3. Research hypotheses

Based on the stated research questions, three sets of hypotheses are derived:

Hypotheses 1

Sea surface temperature is known to be the main cause of coral bleaching. It has been suggested that other environmental variables play a major role in shaping the response of corals to thermal stress. Here investigate the role of all oceanographic variables, historical and at the time of bleaching observation, on the coral bleaching patterns in the region. We also assess their relative importance:

\( H_0: \) Variation in coral bleaching is explained sufficiently by only the ocean temperature at the time bleaching observations were made.

\( H_1: \) Variation in coral bleaching is explained sufficiently by not only the ocean temperature at the time bleaching observations were made, but also by other environmental variables at the time of bleaching and the historical conditions.
Hypotheses 2
Here we investigate if there is a spatial pattern of bleaching in the region, mainly along latitudinal gradient. Due to the varying oceanography conditions with latitude, a hypothesis to test if there is latitudinal gradient of coral bleaching is formulated:

\( H_0: \) There is no spatial variation in coral bleaching in WIO region.
\( H_1: \) There is spatial variation of coral bleaching in WIO region.

Hypotheses 3
Susceptibility of coral reefs and their resistance to thermal stress is modelled. Susceptibility here is defined as magnitude of risk a reef system is exposed to with respect to its ability to resist and tolerate increased positive thermal anomalies. We test if there are variations in environmental variables; combine these variables using fuzzy theory to predict the resistance, tolerance, and susceptibility. Coral mortality data is used to evaluate the models, hence:

\( H_0: \) Coral mortality does not significantly correlate with the susceptibility map.
\( H_1: \) Coral mortality correlates significantly with susceptibility map.

Hypotheses 4
Use of remote sensing in coral reef studies is limited to mainly deriving sea surface temperature, chlorophyll and studies of submerged ecosystems. The capability of long term moderate resolution oceanography data to predict coral reef processes is assessed, hence:

\( H_0: \) Moderate resolution remotely sensed data is not capable to predict coral reef processes at a meso-scale.
\( H_1: \) Moderate resolution remotely sensed data is capable of predicting coral reef processes at a meso-scale.
3. Methods and Materials

3.1. Study Area

The Western Indian Ocean (WIO) region is bounded to the West by the mainland states of eastern Africa, and comprises the island states of the Indian Ocean (Fig. 2). Nations within the region include Kenya, mainland Tanzania, Zanzibar and Mozambique, Comoros, Madagascar, Mauritius, Reunion and Seychelles, Maldives, with South Africa in the southwest and Somalia in the northwest. The marine ecosystems of the region are dominated by extensive coral reefs, mangrove forests, and seagrass beds (Muthiga et al., 1998). These ecosystems support a large proportion of the coastal population and affect millions of lives in one of the poorest and most densely populated regions in the World (Souter and Linden, 2000).

Generally the climate is tropical to sub-humid and is mostly influenced by two monsoon seasons each year. The monsoons have a major influence on wind direction and strength, air temperature and rainfall. They compose the multitude of forces that shape the structure of inter annual SST patterns in the Indian Ocean, rendering it more complex than tropical SST variations elsewhere (Nagar et al., 2005). The recently identified Indian Ocean Zonal Dipole Mode (IOZDM) (Saji et al., 1999) is another basin-scale SST pattern that affects the climate system.

Indian Ocean currents are seasonal and widely controlled by the monsoon. The dominant currents include the West flowing North Equatorial Current and South Equatorial Current, with the weaker, eastward Equatorial Counter-current flowing between them (Swallow et al., 1983). As the South Equatorial Current approaches the coast of Africa, it curves toward the southwest, part of it flowing through the Mozambique Channel between Madagascar and the mainland, and part flowing along the East coast of Madagascar. Other major currents include Southwest Monsoon Currents which form the Somali current in June-July (Nagar et al., 2005); and the Agulhas Current (Bryden and Beal, 2001).

Coral reefs in the western boundary comprise the continuous fringing reefs and patch reefs. In the WIO island states, reefs circumscribe these islands and form the main ecosystems. Since the threats to these ecosystems are common, these countries have
formed regional management initiatives such as the Regional Environment Program of the Indian Ocean Commission (Muthiga et al., 1998) and Western Indian Ocean Marine Science Association. They also have memberships and are host to international organizations such as the Global Coral Reef Monitoring Network (GCRMN) and International coral reef initiative (ICRI).

Figure 2: A map of the study area showing coral reef areas and the coral bleaching study sites

3.2. Data description, extraction and processing methods

3.2.1. Coral bleaching observation data

The Wildlife Conservation Society’s (WCS) coral bleaching intensity point data is available for Mozambique, Kenya, Tanzania, Maldives, South Africa, Mauritius, Seychelles, Re-union and Madagascar. A total of 33,405 coral colonies were sampled in reef systems of these countries between April and July 2005. Mauritius data was collected in March 2004. Bleaching estimates were made by different observers during this period using a standardized method first described by Gleason, M. G. (1993); and more recently by McClanahan et al., 2001; McClanahan, T. R., 2004; Edmunds et al., 2003; McClanahan et al., 2005. Coral mortality was also estimated alongside the bleaching intensity.
A second set of coral bleaching data is hosted on reef base website (Appendix 3). This global bleaching data is based on status reports mainly by organizations involved in coral reef research e.g. Global Coral Reef Monitoring Network (GCRMN), CORDIO, and CRCP among others. In this dataset, information on the occurrence and severity of coral bleaching is provided in categories of no bleaching, low bleaching, moderate bleaching and high bleaching. A total of 216 points data for different times between 1998 and 2005 were found within the study area. Reef base data differs from WCS data on the collection method and the data type. While reef base data if categorical and entirely based on secondary data from reports, publications and informal field observations, WCS’s bleaching index (%) is continuous and its collection was coordinated during the summer of 2005.

3.2.2. Sea Surface Temperature

Sea surface temperature data was retrieved from the NOAA website (Appendix 3). This Pathfinder version 5 data has been processed from NOAA-11, 14, 16, and 17 polar orbiting satellites. The 16 bit ‘all pixel SST files in Hierarchical Data Format (HDF), containing monthly averaged sea surface temperature data from 1985 to 2005, at 4km resolution were downloaded; alongside the corresponding overall quality flag files for filtering out clouds or other sources of error. A total of 1008 files were retrieved. Data processing included the retrieval; sub setting the files to the study area coordinates; masking; back-scaling and offsetting the data from 16 bit unsigned integer format to geophysical units using equation 1. A quality flag value of 4 was used for masking (Kilpatrick et al., 2001).

\[
\text{SST (°C)} = 0.075 \times \text{image value} - 3 \quad \text{[Equation 1]}
\]

In most instances, satellite measurements fell short of covering the coastal areas by 1-2 pixels. To interpolate measurements to these areas, and to the areas with missing values as a result masking, a 3 x 3 filter which calculates the average value of 8 pixels adjacent to the pixel being considered was applied. In effect, pixels adjacent to the missing value maintained their original values while the missing pixel was assigned the resulting value from the filter.

WCS in situ data from temperature loggers (Hobo temperature gauges, Onset Corporation, Pocasset, MA, USA) deployed at about 5 m depth in the reef lagoons in Kenya and Mauritius was used for comparison with satellite data. These loggers were programmed to record temperature every 30 minutes continuously for six to 12
months for intermittent periods between 1997 and 2005. Their estimated accuracy is within 0.35-0.4°C at room temperature (McClanahan and Maina, 2003). In situ data was aggregated into 274 monthly averages for comparison with satellite data (fig. 3). When compared to the in situ measurements, a root mean square error (RMSE) of the residuals of 0.87°C was obtained, indicating a satisfactory agreement between the two data sets. Values on either side of the diagonal line reveal that satellite measurements tend to overestimate sea surface temperature. This is expected since in situ instruments are based on bulk measurements at about 5m depth, while satellite measures the skin (surface) temperature.

Other sea surface temperature data available for use include the NOAA optimally interpolated sea surface temperature (Reynolds et al., 2002). It is served monthly on a 2-degree grid back to 1854, weekly on a 1-degree grid back to 1981, daily on a 1/4 degree grid back to 1985 (Barton and Casey, 2005). For this study, Level 3 SST data was chosen over NOAA Optimally interpolated data in recognition of the need to maintain spatial variability of sea surface temperature, some of which is lost when interpolation is performed.

Figure 3: Comparison of satellite derived (skin) temperature with in situ (bulk) data. n = 267.

3.2.3. Ocean Surface Current velocity

Ocean surface currents mean monthly velocity (cm/s) data (surface layer of thickness \( h = 30m \)), from 1992-2005 was downloaded from OSCAR website (Appendix 3).
This data is a model output with estimates of surface horizontal velocity directly from sea surface height (TOPEX/POSEIDON; ERS 1-2, Envisat, JASON-1); surface vector wind (SSMI and QuikScat scatterometers) and sea surface temperature (NOAA optimum interpolation v.2 analysis) (Lagerloef, G.S.E., 1999; Bonjean and Lagerloef, 2002; Bonjean et al., 2006). It is a representation of the low frequency surface current variability (time scales longer than 20 days), and does not contain shorter term variability that would be associated with tides or shorter period meso-scale variability. It is like a low-pass filtered version of the surface currents. The data has two components, \( u \) and \( v \), which represent the East/West (zonal) and North/South (meridional) components of total velocity, each of which have periods of positive and negative values as the total velocity vector transits into different quadrants. Because of the low-pass filter this surface currents data has lower magnitudes than one might see if measuring the currents directly in the ocean (Bonjean et al., 2006).

The drifting buoys deployed globally are used to calibrate the OSCAR diagnostic model within a certain time period (Bonjean et al., 2006). Bonjean and Lagerloef, 2002 performed a validation test and reported a standard deviation of difference between observed and estimated velocity fields to be 8 and 3 cm/s for zonal and meridional components respectively. In their recent work (Bonjean et al., 2006), Bonjean and co-worker’s report that accuracy issues were identified which mainly concerned the accuracy of the velocity meridional structure across the equator.

For this study, information on direction i.e. negative and positive velocities was discarded and only absolute magnitude values are used.

3.2.4. Ultraviolet radiation (UV)

Daily global maps of UV-erythemal irradiance (290–400 nm, milli-watts/m\(^2\)) at the Earth’s surface (Herman et al., 1999) were downloaded from the NASA’s website (Appendix 3). This data is estimated using the ozone and aerosol amounts, cloud transmittance, surface reflectivity and the solar UV radiation backscattered from the Earth’s atmosphere as measured by the total ozone mapping spectrometer (TOMS) (Herman et al., 1999, Krotkov et al., 2001, Vasilkov et al., 2001). TOMS orbit is sun synchronous which makes it possible for the fields of view to be combined into a global map of the UV irradiance at the same solar time every day (Herman et al., 1999). The solar zenith angles are adjusted so that the irradiance values are for local solar noon (minimum solar zenith angle for the day).
Herman et al., 1999 compared TOMS derived UV monthly average surface irradiance data with spectroradiometer in situ measurements. He reported an accuracy of within 6% under normal conditions; and within 12% under conditions of UV-absorbing aerosol plumes.

3650 maps of daily noontime irradiance (milli-watts/m$^2$) in a 1x1.25 degree grid were retrieved from TOMS website. The data was converted from FORTRAN based ASCII formats to conventional ASCII for use with image processing software. Since most GIS/RS software do not support rectangular pixels, they were changed into square pixels with the sides equal to the smallest extra division, i.e. 0.25 x 0.25. They were then subset to the spatial extent of the study area.

3.2.5. Photosynthetically Active Radiation (PAR)

Photosynthetically active radiation (PAR, Einstein/m$^2$/day) data from Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) over the global ocean surface is available since the October 1997, a month after SeaWiFS instrument was launched on board the OrbView-2 spacecraft. PAR is defined as the quantum energy flux from the Sun in the spectral range 400-700 nm, or the visible wavelength range (Frouin et al., 2000). SeaWiFS is on a synchronous orbit, and has 8 bands placed between 412 and 865 nm. The instrument has a spatial resolution of 1 km at nadir but is converted to 4 km resolution so as to provide global area coverage (Vasilkov et al., 2001).

Level 3 9km spatially binned monthly PAR data, in HDF format were downloaded from SeaWiFS website (Appendix 3). A total of 100 files were retrieved (Oct 97-Dec 2005). The images were spatially subset to the study area and back-scaled by multiplying the PAR pixel values with 0.3, to convert the 8 bit unsigned integers to geophysical units.

The algorithm used to convert water leaving radiance to PAR is described in Frouin et al., 2000. Frouin et al., 2000 describe the evaluation of this algorithm using several years of PAR in situ data for Canada, and report a good agreement with in-situ measurements. They observed differences of 6.2 (15.0%), 3.7(9.1%), and 3.3(8.1%) on daily, weekly, and monthly time scales, suggesting that monthly averaged data is more accurate than daily or weekly data. It is believed that SeaWiFS water-leaving radiances have an uncertainty of 5% in clear-water regions (Hooker and McClain, 2000).
3.2.6. Chlorophyll-a Pigment concentration

Satellite remote sensing of ocean colour is the only realistic way to measure near-surface chlorophyll-a concentration (chl-a), on regional scales (Lavender et al., 2004).

The SeaWiFS mission has provided the first continuous long-term observations of global ocean chlorophyll from space (Gregg et al., 2005). Chlorophyll a surface concentration is derived from SeaWiFS using OC4v4 chl-a algorithm (O’Reilly et al., 2000). SeaWiFS sensor is rigorously calibrated (Gregg et al., 2005), with a goal to measure chlorophyll-a in the range of 0.01 – 64 mgm-3 to within 35% accuracy (Hooker and McClain, 2000). Wardell et al., 2003, and more recently Barbini et al. (2005) confirmed that the accuracy is indeed within this specified goal. Other SeaWiFS validation work includes Lavender et al. (2004) who compared shipboard chlorophyll-a measurements with those of satellite. They reported that SeaWiFS over-estimated chlorophyll-a concentration relative to in situ values by a factor of three on average.

Level 3 chlorophyll a data is available from ocean colour website from 1997 (Appendix 3). Data in HDF format was retrieved and spatially subset before back-scaling the byte values using the expression:

\[
\text{Chlorophyll-a, mg/m}^3 = 10^{(0.12*\text{byte value} - 1.4)} \quad \text{[Equation 2]}
\]

3.2.7. Wind speed

Satellite remote sensing using active and passive microwave sensors have provided an opportunity for wind data acquiring at a global scale over long period of time (Mears et al., 2001). Winds data was obtained from on Special Sensor Microwave Imager (SSM/I) (see Hollinger, J., 1989 for a complete description). The first in the series of 7 SSM/I's was launched in June 1987 onboard the Defence Meteorological Satellite Program satellites (Bentamy et al., 1999). These satellites have provided large datasets of surface winds over global oceans from 1987 to present (Atlas et al., 1996).

The SSM/I is a passive multifrequency microwave sensor which consists of seven separate sensors providing measurements of brightness temperature at 19.35, 37.0, and 85.5 GHz. The SSM/I infer brightness temperatures from the ocean surface passively, receiving microwave radiation emitted by the ocean surface and passed through the atmosphere (Gemmill et al., 1999). The emission is effected by the
surface wind speed and sea surface temperature, with wind speed changing the
roughness of the ocean surface, wave structure and foam coverage (Pringent et al.,
2000).

Atlas et al. (1996) described SSM/I wind data as being characterized by high
resolution coverage (0.25 x 0.25), and accuracy. They however noted that the
application if this data has been limited by the lack of directional information.
Bentamy et al. (1999) examined the consistency of surface wind speeds estimated
from the European Remote Sensing Satellite (ERS-1) scatterometer, ERS-1
altimeter, and the special sensor microwave/imager (SSM/I). They compared satellite
measurements with buoy wind measurements and reported that the root mean square
errors (RMSE) of the three wind estimates were all within 2 m/s. The RMSE values
of the differences between the scatterometer and the altimeter and between the
scatterometer and the SSM/I were 1.67 and 1.45 m/s, respectively. Mears et al.
(2001) compared wind speeds derived from microwave radiometer measurements
made by SSM/I series of satellite instruments to those directly measured by buoy-
mounted anemometers. For a given satellite-buoy pair, they reported a mean error
range of between −1 to +1 m/s, with standard deviations <1.4 m/s. These evaluation
tests suggest that SSM/I data has a satisfactory accuracy, which underpins the
extensive applications it has been employed in. e.g. it is used in models to estimate
surface currents velocity e.g. Bonjean et al., 2002; analysis of hurricanes e.g. Alliss
et al., 1993, among others uses.

Wind data is stored in the SSM/I website (Appendix 3) as maps for a full day,
weekly and monthly averages in FORTRAN based ASCII format. 452 weekly
averaged maps, for the period 1997-2005 were retrieved from SSM/I ftp site
(Appendix 3). Data were converted into conventional ASCII format, and spatial
subset was performed. The stored geophysical data (0-250) was multiplied by 0.2 to
obtain 10 meter wind speed (m/s) raging from 0 -50 m/s. Interpolation to the coastal
areas similar to for SST data was performed.

3.3. Derived primary variables

Data for all environmental variables, for pixels corresponding to observation data
were exported to Excel spreadsheet. Derived parameters for environmental variables
were calculated for the extracted data and for the processed raster layers using
equations in table 2. Variables representing different aspects of environmental
parameters that are relevant to coral thermal stress were derived and used in the
analysis. Derived variables enable testing of specific hypotheses related to the
environmental parameter. For instance SST anomalies and Coefficient of variation are derived from long term SST data and used to test different hypotheses (table 3).

### Table 2: Description of the equations used in the derivation of parameters using the processed images and the data extracted to spreadsheets

<table>
<thead>
<tr>
<th>Derived variable</th>
<th>Variable used</th>
<th>No</th>
<th>Equation</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monthly Mean ((X_m))</td>
<td>UV; Wind; All other data were in (X_m)'s</td>
<td>3</td>
<td>[ \sum_{i=1}^{n_d} \frac{X_d}{n_d} ]</td>
<td>(X_d) = daily or weekly average in month (i) (n_d) = number of days or weeks in month (i)</td>
</tr>
<tr>
<td>Long term mean, ((LtM))</td>
<td>SST; PAR; Chl; current s; Wind; UV</td>
<td>4</td>
<td>[ \sum_{i=1}^{n_m} \frac{X_m}{n_m} ]</td>
<td>(X_m) = monthly mean (n_m) = number of months</td>
</tr>
<tr>
<td>Climatology ((MC))</td>
<td>SST</td>
<td>5</td>
<td>[ \sum_{i=1}^{n_c} \frac{X_m}{n_c} ]</td>
<td>(n_c) = Count of specific month (x)</td>
</tr>
<tr>
<td>Average of maximum mean monthly ((X_{m_{max}}))</td>
<td>SST, PAR</td>
<td>6</td>
<td>[ \sum_{i=1}^{n_y} \frac{X_m_{max}}{n_y} ]</td>
<td>(X_m_{max}) = maximum of the (X_m)'s for year (i=1\ldots ny) (n_y) = number of years</td>
</tr>
<tr>
<td>Coefficient of variation ((CV))</td>
<td>SST</td>
<td>7</td>
<td>(\frac{\sigma}{LtM} \times 100)</td>
<td>(\sigma) = Standard Deviation of (X_m)'s</td>
</tr>
<tr>
<td>Anomalies ((A)) ((stress index))</td>
<td>PAR; UV; SST</td>
<td>8</td>
<td>(X_m_i - MC_i)</td>
<td>(i) = months (Jan\ldots Dec) (j) = number of years</td>
</tr>
<tr>
<td>Hotspot for each month ((Hm))</td>
<td>SST, PAR</td>
<td>9</td>
<td>(X_m_i - \overline{X_m_{max}})</td>
<td>(i) = months from 1… (nm)</td>
</tr>
<tr>
<td>Long term hotspot ((Hlt))</td>
<td>SST, PAR</td>
<td>10</td>
<td>[ \sum_{i=1}^{n_y} \frac{(X_{m_{max}} - \overline{X_{m_{max}}})}{n_y} ]</td>
<td>(n_y) = Number of years NOTE: Only for years (X_{m_{max}} &gt; \overline{X_{m_{max}}}) i.e. only positive difference</td>
</tr>
<tr>
<td>Degree heating months ((DHM)) or frequency of positive anomalies</td>
<td>SST</td>
<td>11</td>
<td>[ \left[ \frac{n_{pm}}{n_m} \right] \times 100]</td>
<td>(n_{pm}) = Count of all positive hot pots ((Hm)) (n_m) = Total number of months</td>
</tr>
<tr>
<td>Slope of the regression line, (m)</td>
<td>SST</td>
<td>12</td>
<td>[ \frac{n_y \sum (xy) - \sum x \sum y}{n_y \sum (x^2) - (\sum x)^2} ]</td>
<td>(x) = time in years. (y) = average (X_m) for year (i=1\ldots n_y)</td>
</tr>
</tbody>
</table>
4. Statistical Analysis and Susceptibility Modeling

4.1. Coral bleaching as a function of environmental variables

Respective data were aggregated and derived using equations in table 2. Parameters were then separated into conditions at the time of bleaching and long term or historical conditions (table 3). Conditions at the time of bleaching are the monthly values of environmental conditions for the month preceding the date bleaching data was collected. This separation was essential so as to investigate the hypotheses relating to conditions which instigate or induce bleaching, and those relating to the role of long term environmental conditions as possible factors which shape the coral community response to bleaching. A total of 28 variables were used in the subsequent analysis (Table 3).

<table>
<thead>
<tr>
<th>Variables at the time of bleaching</th>
<th>Historical environmental conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll a - mean</td>
<td>Chlorophyll (Ltm*)</td>
</tr>
<tr>
<td>Chlorophyll a - anomaly</td>
<td>Zonal currents (Ltm)</td>
</tr>
<tr>
<td>Zonal currents - mean</td>
<td>Meridional currents (Ltm)</td>
</tr>
<tr>
<td>Zonal currents - anomaly</td>
<td>Sea surface temperature (Ltm)</td>
</tr>
<tr>
<td>Meridional currents - mean</td>
<td>SST coefficient of variation</td>
</tr>
<tr>
<td>Meridional currents - anomaly</td>
<td>Slope of SST as a function of time (nt=21 years)</td>
</tr>
<tr>
<td>Sea surface temperature - mean</td>
<td>SST - hotspot</td>
</tr>
<tr>
<td>Sea surface temperature - anomaly</td>
<td>PAR - cold spots</td>
</tr>
<tr>
<td>Sea surface temperature - hotspot</td>
<td>PAR - hotspots</td>
</tr>
<tr>
<td>PAR - anomaly</td>
<td>PAR - Ltm</td>
</tr>
<tr>
<td>PAR - mean</td>
<td>UV - Ltm</td>
</tr>
<tr>
<td>Wind speed - mean</td>
<td>Wind speed - Ltm</td>
</tr>
<tr>
<td>Wind speed - anomaly</td>
<td>Mean maximum temperature</td>
</tr>
<tr>
<td>UV - mean</td>
<td></td>
</tr>
<tr>
<td>UV - anomaly</td>
<td></td>
</tr>
</tbody>
</table>

4.2. Bleaching observation data

WCS Bleaching observation data was summarized into mean bleaching indices regardless of the coral taxa and analyzed for latitudinal gradient. Environmental data was also prepared for multiple linear regressions, with the 2005 bleaching observations as the response variable and the variables in Table 3 as the predictor
variables. Variance inflation factors (VIF) were computed within each set of environmental variables to test the assumption of perfect collinearity (Multicollinearity). VIF’s are a function of how closely the variable is a linear function of the other independent variables (Sall et al., 2005). According to Sokah & Rolf (1995), practical consequences of multi-collinearity are: large standard error of coefficients; insignificant t-values associated with very high R$^2$; estimation will not be very robust; and wrong signs for some regressors. Ryan, B. F. (1985) suggests that if the VIF is <10, the regression coefficients are poorly estimated.

For the same reasons, variables with VIF’s >10 were not included in the subsequent multiple regression analysis. If a variable had a high VIF, it was excluded from the analysis and the VIF’s computed again. In some instances, predictors were changed by taking linear combinations of them using principal components analysis.

Hierarchical Linear modelling or nested analysis (Rencher, A. C., 2002) was considered due to the hierarchical structure of the observation data i.e. data organized by countries. This would reveal any localized trends. However, observation data at each location/country were collected within 1-3 pixels of the physical environment data. The result is low spatial variability of environmental data at local level, hence several replicates of bleaching data within each pixel of physical environment data. It was therefore not possible to perform these types of analyses.

Instead, three sets of stepwise multiple linear regressions with controlled; backward elimination procedure based on Akaike’s Information Criterion (AIC) was used to select the best combination of parameters, which significantly explained the variation in observed bleaching. Stepwise-backward elimination regression is a data directed search for the variables that best explain the variation of the response variable. It is mainly used when there are no variables for which we have a priori interest in testing for significance (Rencher, A. C., 2002).

Predictor variables in the three stepwise regression models were: environmental conditions at the time of bleaching; long term environmental conditions; and the combination of these two. The latter was performed so as to investigate the combined effect of historical conditions and the conditions at the time of bleaching.

To test the validity of the models, distribution assumptions were checked by generating Studentized residuals (residuals divided by its standard error) for each model and tested for normal distribution. The residuals are not quite independent,
but one can informally identify severely non normal distributions (Sall et al., 2005). If the continuous response does not adequately meet the normal assumptions, the modelling type can be changed from continuous to ordinal and then analyzed safely, even though this approach sacrifices some richness in the presentations and some statistical power as well (Sall et al., 2005).

The prediction formula from the long term variables regression model was preserved and used to extrapolate bleaching intensity to the whole study area, to create a map of predicted bleaching.

4.3. Reef base bleaching observation data

Nominal logistic regression of bleaching intensity categories against latitude was performed to examine if there was a latitudinal gradient of coral bleaching. Logistic probability plot was generated (Fig. 8). The y-axis represents probability. For k response levels, \(k - 1\) smooth curves partition the total probability (=1) among the response levels (Sall et al., 2005).

Descriptive discriminant analysis was performed to visualize the relative contribution of the environmental variables to separation of the bleaching intensity ‘groups’. The goal of discriminant analysis for several groups is to find linear combinations of variables that best separate the \(k\) groups of multivariate observations (Rencher, A. C., 2002). In this context, the ‘\(k\) groups’ are the bleaching categories in the reef base bleaching observation data (i.e. No bleaching, low, moderate and high). The bleaching categories separation was then projected in a two-dimensional space represented by the first two discriminant functions, to obtain the best possible view of how the bleaching categories separate (Fig. 9). Variables were tested for multicollinearity before these analyses were undertaken.

Nominal logistic regression model was performed to determine which regressors were important in separating the response variable groups (Sall et al., 2005). Scatter plots of means of predictor variables which correlated well with bleaching were plotted (Fig. 10).

4.4. Modeling Susceptibility

4.4.1. Expert knowledge analysis

The first step in preparing the fuzzy model involved definition of variables and fuzzy sets. Based on the synthesis of relevant literature, statistical analysis of previous
bleaching events and consultations with coral reef experts, variables whose changes are critical to coral reef health were identified. The variables selected included those which represent thermal history i.e. the maximum upper thermal limit as estimated by the mean maximum temperature, variability of temperature; history of short wave and visible radiation, PAR, surface currents velocity, water quality and radiation attenuation, and history of wind velocity (Tables 3;4). The nature of influence a parameter has on resistance of corals to environmental stress is summarized in Table 4.

Table 4: Summary of the nature of influence a parameter has on coral’s thermal stress

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description of reference behaviour pattern in relation to thermal stress</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean maximum SST (max SST)</td>
<td>Mean maximum SST is used to estimate bleaching thresholds (Max SST+ 1°C). The higher the mean max SST the higher the bleaching threshold and resistance to thermal stress. On the other hand, regions which experience a higher maximum are more prone to heat stress than those that have lower maximum.</td>
</tr>
<tr>
<td>Temperature history (mean SST)</td>
<td>The probability of a reef system to experience heat stress increases with an increase in mean SST</td>
</tr>
<tr>
<td>Historical solar radiation at 400-700nm (PAR)</td>
<td>High solar irradiance at the surface indicates a potential to heating and photochemical damage.</td>
</tr>
<tr>
<td>Slope of SST as a function of time (21 years)</td>
<td>The regression coefficient is an estimate of annual change in temperature. Relatively high rate of increase indicates high warming rates hence more likely thermal stress will occur in the near future</td>
</tr>
<tr>
<td>Temperature fluctuation (coefficient of variation, CV)</td>
<td>Temperature variability correlates with bleaching tolerance. High water flow areas are also areas of high diversity because of the wide range of temperature.</td>
</tr>
<tr>
<td>Ultraviolet radiation (UV)</td>
<td>High solar irradiance at UV indicates a potential to heating and photochemical damage; decreased photosynthetic performance; altered community structure</td>
</tr>
<tr>
<td>Surface currents (water flow)</td>
<td>Areas with strong currents and high mixing rates indicate a potential of cooling to counter increased sea surface temperature. Other studies found that high water flow also creates a narrow environment for acclimation making corals in those high mixing places sensitive and less resistant</td>
</tr>
<tr>
<td>Wind speed (history)</td>
<td>High wind velocity enhances the water mixing. It also has a primary effect of influencing the air-water interface hence affecting solar radiation reaching water surface and the water heating mechanisms.</td>
</tr>
<tr>
<td>Chlorophyll concentration (mg/m³)</td>
<td>Chlorophyll reduces the effect of light by absorbing and scattering hence creating a shading effect. However high chlorophyll could signify poor water quality and pollution which reduces coral resistance. Here Chlorophyll is used as an absorption and scattering agent.</td>
</tr>
<tr>
<td>Map of 2005 bleaching</td>
<td>History of bleaching is an indicator of bleaching tolerance</td>
</tr>
</tbody>
</table>
The second step involved assigning a function which best represents the way the susceptibility of coral reefs changes as the attributes of the parameter change, i.e. ‘fuzzification’. It involved defining or normalizing the values of a parameter in [0, 1] using the appropriate function, to create a membership degree of susceptibility map. This was guided by empirical data and judgment based on literature review. Fuzzy membership functions of different curve shapes (linear, sigmoidal, triangular, etc) can be defined to obtain the grade of membership to a particular set, as discussed extensively in Burrough and McDonnell, 2005.

Common membership functions include linear, sigmoidal, J shaped, trapezoidal (Burrough and McDonnell, 2005), and Gaussian (Robinson, V. B., 2003). With the linear function, a given change in the attribute value (e.g., temperature) produces a given change in estimated threats between two control points. With the sigmoidal function, the change in estimated threats is smaller for a given change in attribute value near the control points than halfway between control points. With the J-shaped function the drop from high suitability is very steep, but the function is asymptotic to the 0-suitability axis. This indicates that at any value, there is still some level of suitability (Eastman, J. R., 2003). The Gaussian function produces a Bell-shaped curve and its parameters can be easily related to common statistics such as mean and variance (Robinson, V. B., 2003).

For simplicity, a linear membership function with a monotonically increasing or decreasing pattern was used (Eastman, J. R., 2003) for all parameters except for maximum SST (Fig.4 a&b). This function is sometimes called left or right shoulder trapezoidal (Robinson, V. B., 2003) and is represented using equations 13 & 14. A Gaussian function was adopted to define the nature of influence the maximum SST has on susceptibility (Fig. 4c; equation 15).

Histories for each parameter were constructed to aid in estimating the control points along the x-axis (a, b, c, d) (Appendix 2, Table 5, fig. 4). These points represent the inflection points of the line as follows: a = membership rises above 0; b = membership becomes 1; c = membership falls below 1; d = membership becomes 0. Membership functions were applied to environmental variable maps (appendix 1) to generate normalized susceptibility maps (fig. 5).
Figure 4: Membership functions and their respective equations for (a) linear monotonically increasing; (b) Linear monotonically decreasing along the x axis with positions of inflection points; and (c) Gaussian function, where \( \alpha \) and \( \sigma \) can be related to the mean and variance of \( x \), respectively.

\[ \mu_A(x) = \max\left( \min\left( \frac{b-x}{b-a} \right), 0 \right) \]

Source: Robinson, V. B., 2003

\[ \mu_A(x) = \max\left( \min\left( \frac{x-c}{d-c} \right), 0 \right) \]

Source: Robinson, V. B., 2003

\[ \mu_A(x) = e^{-\frac{1}{2} \left( \frac{x-\alpha}{\sigma^2} \right)^2} \]

Sources: Robinson, V. B., 2003; Power et al., 2001
Table 5: Estimates of control values defining points along x-axis where the variable’s threats to corals reefs are perceived to be zero (a; d) and one (b; c).

<table>
<thead>
<tr>
<th>Variable #</th>
<th>Variable</th>
<th>Units</th>
<th>Control points</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>SST</td>
<td>°C</td>
<td>26 29</td>
</tr>
<tr>
<td>P2</td>
<td>CV</td>
<td>°C</td>
<td>4 10</td>
</tr>
<tr>
<td>P3</td>
<td>PAR</td>
<td>E/m²/day</td>
<td>45 50</td>
</tr>
<tr>
<td>P4</td>
<td>Mean max SST</td>
<td>°C</td>
<td>21 27 32</td>
</tr>
<tr>
<td>P5</td>
<td>SST hotspot</td>
<td>°C</td>
<td>0.4 0.9</td>
</tr>
<tr>
<td>P6</td>
<td>UV</td>
<td>milli-watts/m²</td>
<td>230 300</td>
</tr>
<tr>
<td>P7</td>
<td>Slope (SST)</td>
<td>°C</td>
<td>0.01 0.03</td>
</tr>
<tr>
<td>P8</td>
<td>Meridional currents</td>
<td>cm/s</td>
<td>0.05 0.2</td>
</tr>
<tr>
<td>P9</td>
<td>Zonal currents</td>
<td>cm/s</td>
<td>0.1 0.5</td>
</tr>
<tr>
<td>P10</td>
<td>Wind speed</td>
<td>m/s</td>
<td>5 8</td>
</tr>
<tr>
<td>P11</td>
<td>Chlorophyll-a</td>
<td>mg/m³</td>
<td>0.05 0.2</td>
</tr>
<tr>
<td>P12</td>
<td>2005 Bleaching map</td>
<td></td>
<td>20 60</td>
</tr>
</tbody>
</table>
Country map source: ESRI world map
Figure 5: Susceptibility maps based on respective environmental variables after the application of membership functions onto original parameter maps.
Variables were weighed on the basis of how important they are with respect to coral reefs susceptibility. In literature, there are several techniques to assign weights to variables: the Indices Weight Method (IWM) (Diakoulaki et al., 1995); Analytical Hierarchical Process (AHP) (Saaty, T. L., 1980); and direct weighing methods. These methods are based entirely on expert knowledge hence the final results are directly a result of the expert’s judgments. Jiang and Eastman (2000) have illustrated the subjectivity inherent in these weighing schemes, which can be a source of uncertainty in GIS (Robinson, V. B., 2003).

Here, two empirical weighting methods were employed: component weightings were calculated using coefficients of linear correlation to weigh the contribution of factors in spatial principal component analysis (SPCA) (Li et al., 2006; Parinet et al., 2004; Tran et al., 2002); and using parametric fuzzy relations in combination with AHP to calculate respective parameter weights (Ross, T. J., 2004; Ercanoglu and Gokceoglu, 2004; Ercanoglu et al., 2006). Both methods are data driven, while the latter is only partially based upon expert knowledge.

4.4.2. Susceptibility model 1 (SM 1)

In this model, Spatial Principal Component Analysis (SPCA) is developed to build the coral reefs susceptibility map. PCA involves calculations of Eigen values and their corresponding eigenvectors of the covariance matrix to derive the new variables in a decreasing order of importance in explaining variation of the original variables (Tran et al., 2002). SPCA input consisted of the 12 fuzzy-normalized parameter raster maps (fig. 5). A matrix denoting the transformation coefficients (calculated from the covariance matrix), and a set of principal component (PC) was obtained as the output. Each variable is transformed into a linear combination of principal component with decreasing variation. The linear transformation assumes the components will explain all of the correlation in each variable. Hence each output PC carries different information which is uncorrelated with other PC’s.

<table>
<thead>
<tr>
<th>Table 6: Results of SPCA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Selected PC’s</strong></td>
</tr>
<tr>
<td>Eigen value</td>
</tr>
<tr>
<td>Contribution ratio (%)</td>
</tr>
<tr>
<td>Cumulative contribution (%)</td>
</tr>
</tbody>
</table>
Seven PC’s (I – VII) were selected (>1% variance) and used as the basis for calculating the susceptibility index. Susceptibility index (SM 1), is defined as the sum of a couple of weighted principal components shown a shown in equation 16.

\[ SMI = \alpha_1 Y_1 + \alpha_2 Y_2 + \ldots + \alpha_m Y_m \]  

[Equation 16]

Where \( Y_i \) is the number of the principal component and \( \alpha_i \) is the corresponding contribution. Using the table 6 and equation 16, SM1 was calculated as follows:

\[ SM1 = 0.5649*A_I + 0.1344*A_{II} + 0.837*A_{III} + 0.765*A_{IV} + 0.416*A_{V} + 0.366*A_{VI} + 0.272*A_{VII} \]

Where \( A_I \ldots A_{VII} \) are the seven PC’s.

The map obtained from the above model had unit-less values ranging from -1 to 2. The lowest value represented highest susceptibility and vice versa. These values were normalized and inverted such that low susceptibility became 0 and high susceptibility became 1.

### 4.4.3. Susceptibility model 2 (SM2)

Also known as the pair wise weighing, Analytic Hierarchy Process (AHP) is a general theory of measurement, widely applied in decision making process (Saaty, T. L., 1980; Saaty, T. L., 1986; Forman and Gass, 2001; Ercanoglu et al., 2006). It involves indicating for each pair of variables in qualitative terms, to what extent a variable is more important than another. Comparison of items \( i \) and \( j \) results in a positive number \( a_{ij} \) giving the strength of preference of item \( i \) over item \( j \); the larger the number the greater the preference in favour of item \( i \) while a value of 1 indicates indifference (Stein and Mizzi, 2005). It is an Eigen value approach to the pair wise comparisons, where the principal right eigenvector of variables is derived (Vaidya and Kumar, 2006). The eigenvector shows the dominance of each variable with respect to the other variables.

Instead of using the traditional AHP pair-wise comparison method, cosine amplitude, a widely used similarity method was employed (Ross, T. J, 2004; Ercanoglu and Gokceoglu, 2004; Ercanoglu et al., 2006; Dubois and Prade, 1980) to evaluate relations of input parameters in relation to susceptibility. In this method, data
samples of a set form a data array, say \( x \) and can be expressed in the following equation for \( n \) data:

\[
X = \{ x_1, x_2 \ldots x_n \} \tag{Equation 17}
\]

In this context, \( x_1 \ldots x_n \) are the number of normalized parameters being considered. Each of the parameters, \( x_i \) in the data array \( X \) is itself a vector of length \( m \), that is:

\[
x_i = \{ x_{i1}, x_{i2} \ldots x_{im} \} \tag{Equation 18}
\]

Each of the data samples can be thought as a point in \( m \)-dimensional space, where for a complete description of each point, \( m \) coordinates are required. This method calculates pair-wise relation strength (\( r_{ij} \)) using equation 19, based on the comparison of two data arrays and range of \( r_{ij} \) values that varies from 0 to 1 (\( 0 \leq r_{ij} \leq 1 \)) (Ross, T. J, 2004; Ercanoglu et al., 2006).

\[
r_{ij} = \frac{\left( \sum_{k=1}^{m} x_{ik} \times x_{jk} \right)}{\sqrt{\left( \sum_{k=1}^{m} x_{ik}^2 \right) \times \left( \sum_{k=1}^{m} x_{ij}^2 \right)}} \tag{Equation 19}
\]

Where \( x_{ik} \) and \( x_{ij} \) are the elements of the pair wise parameter.

Ross, T. J. (2004) explains that equation 19 relates to a dot product for the cosine function. When two vectors are most similar, their dot product is unity, and when they are at right angles to each other i.e. most dissimilar, their dot product is zero (Ross, T. J, 2004; Ercanoglu and Gokceoglu, 2004).

Normalized data files for all the elements (fig. 5) were used as the input for the above equation. A symmetric matrix with values indicative of the parameter relations based on their influence on the subject being modelled was developed. To determine the score (eigenvectors) of each parameter, average values for respective rows in the
normalized matrix were obtained by dividing each row sum by the number of parameters (table 7).

Table 7: Pair-wise parameter relation strength ($r_{ij}$) matrix from equation 19. The upper half of the matrix was filled with the same values before calculating the eigenvector (scores) for each parameter.

<table>
<thead>
<tr>
<th></th>
<th>P1</th>
<th>P2</th>
<th>P3</th>
<th>P4</th>
<th>P5</th>
<th>P6</th>
<th>P7</th>
<th>P8</th>
<th>P9</th>
<th>P10</th>
<th>P11</th>
<th>P12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Max SST</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UV</td>
<td></td>
<td>0.92</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chlorophyll</td>
<td></td>
<td>0.89</td>
<td>0.87</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td></td>
<td>0.51</td>
<td>0.38</td>
<td>0.43</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bleaching model</td>
<td></td>
<td>0.90</td>
<td>0.92</td>
<td>0.91</td>
<td>0.59</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td></td>
<td>0.21</td>
<td>0.01</td>
<td>0.00</td>
<td>0.61</td>
<td>0.11</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PAR</td>
<td></td>
<td>0.87</td>
<td>0.90</td>
<td>0.79</td>
<td>0.43</td>
<td>0.83</td>
<td>0.20</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zonal currents</td>
<td></td>
<td>0.79</td>
<td>0.70</td>
<td>0.90</td>
<td>0.37</td>
<td>0.78</td>
<td>0.02</td>
<td>0.66</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meridional currents</td>
<td></td>
<td>0.64</td>
<td>0.65</td>
<td>0.69</td>
<td>0.34</td>
<td>0.65</td>
<td>0.03</td>
<td>0.63</td>
<td>0.63</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td></td>
<td>0.48</td>
<td>0.66</td>
<td>0.42</td>
<td>0.66</td>
<td>0.48</td>
<td>0.59</td>
<td>0.39</td>
<td>0.41</td>
<td>0.28</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>SST Hotspot</td>
<td></td>
<td>0.49</td>
<td>0.41</td>
<td>0.55</td>
<td>0.35</td>
<td>0.57</td>
<td>0.24</td>
<td>0.50</td>
<td>0.55</td>
<td>0.44</td>
<td>0.37</td>
<td>1</td>
</tr>
<tr>
<td>Meridional currents</td>
<td></td>
<td>0.65</td>
<td>0.59</td>
<td>0.54</td>
<td>0.44</td>
<td>0.62</td>
<td>0.44</td>
<td>0.57</td>
<td>0.44</td>
<td>0.38</td>
<td>0.47</td>
<td>0.42</td>
</tr>
</tbody>
</table>

Finally, the partial membership’s i.e. fuzzified parameters were multiplied by their respective calculated weights and summed to obtain the second susceptibility model (SM2; equation 20). This method is also called convex combination or weighted sum (Ercanoglu et al., 2006; Burrough and McDonnell, 2005).

$$\text{SM2}=0.098*P1+0.092*P2+0.0e91*P3+0.080*P4+0.097*P5+0.055*P6+0.091*P7+0.084*P8+0.074*P9+0.081*P10+0.073*P11+0.082*P12$$

[Equation 20]

Robinson, V. B. (2000) observed that different fuzzy aggregation approaches can yield strikingly different results. Other common methods of aggregating fuzzy sets include the traditional ‘AND’ and ‘OR’ operators; which essentially means that for
pixel \( x_{ij} \) in maps \( X_1, \ldots, X_n \), the maximum \( x_{ij} \) in fuzzy set maps \( X_1, \ldots, X_n \) will make the final model with ‘AND’ operator. If ‘OR’ operator is used, the minimum \( x_{ij} \) is utilized (Burrough and McDonnell, 2005). The final map would only reflect the best or worst case scenario respectively (Robinson, V. B., 2003). ‘AND’ and ‘OR’ operators do not account for the effects of the other variables and instead make use of only the extreme conditions (Bone et al., 2005).

4.4.4. Models comparison, evaluation, and susceptibility gradation

The two models were compared and tested for agreement by: correlation of the continuous maps; and post-classification comparison. Using both maps, cross operation in ILWIS software was used to generate pixel values of the same position in a cross table. The 8,675,200 paired points were tested for distribution assumptions (KSL test, p<0.01), and non-parametric correlations performed based on these results (fig. 6).

In the second method, histograms for the respective maps were generated and natural breaks observed for determining the possible number of clusters. Histogram is a graphical tool which aids in determining distinct classes in the attribute of space (Li et al., 2006). Each map was grouped into five spectral clusters based on the statistical properties of all pixel values using cluster analysis/unsupervised classification (Table 8; fig. 11 c, d). In the first phase of cluster analysis operation, a multidimensional histogram of the input band is calculated (ILWIS 3.0, 2001). The multidimensional histogram is a representation of the feature space. In the second phase, this feature space is split into several boxes to obtain the desired number of clusters (ILWIS 3.0, 2001).

The output of the cluster analysis is a map, and a table containing statistical information on the output clusters: the average, minimum and maximum value of each cluster as found in the input maps. Clusters were defined into susceptibility levels as shown in Table 8.

The maps were then imported into IDRISI software and Validate module used to generate a kappa statistic to indicate the level of agreement between the two maps (Overall Kappa statistic = 0.48).

The models were also evaluated for performance using coral mortality data. This data is based upon published reports on percentage coral cover before the and after
the 1998 mass bleaching event. Mortality was inferred from percentage relative change in coral cover before and after the 1998 ENSO event, for 27 locations in the Indian Ocean (Goreau et al., 2000). Modelled susceptibility values for pixels corresponding to the position of the mortality observations were extracted to a spreadsheet and compared with the observed mortality (fig. 12 a&b).

![Figure 6: Correlation plot of the two models, SM 1 and SM 2](image)

Table 8: Cluster analysis results with respect to susceptibility

<table>
<thead>
<tr>
<th>Susceptibility class</th>
<th>SM1</th>
<th>SM2</th>
<th>Feature description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not susceptible</td>
<td>0 - 0.35</td>
<td>0 - 0.24</td>
<td>Locations with no susceptibility as defined by the input parameters</td>
</tr>
<tr>
<td>Low susceptibility</td>
<td>0.36 - 0.56</td>
<td>0.25 - 0.36</td>
<td>Locations which are slight susceptible to thermal stress</td>
</tr>
<tr>
<td>Medial susceptibility</td>
<td>0.57 - 0.65</td>
<td>0.37 - 0.52</td>
<td>Moderately susceptibility to thermal stress due to moderate resistance</td>
</tr>
<tr>
<td>High Susceptibility</td>
<td>0.66 - 0.71</td>
<td>0.53 - 0.62</td>
<td>Locations which have very low or no resistance to thermal stress</td>
</tr>
<tr>
<td>Severely susceptible</td>
<td>0.72 - 1</td>
<td>0.63 - 1</td>
<td>Locations with no resistance to thermal stress and severely susceptible</td>
</tr>
<tr>
<td>Average</td>
<td>0.49</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>Standard error</td>
<td>0.22</td>
<td>0.24</td>
<td></td>
</tr>
</tbody>
</table>
5. Results

5.1. Bleaching observations

Bleaching observations ranged between 0 - 50%, i.e. no bleaching to moderate bleaching (Fig. 7). Reefs North of latitude 10°S including Kenya, Tanzania, Seychelles, and Maldives experienced low bleaching (0-20%) compared to most reefs in higher southern latitudes where up to 50% bleaching was observed. Highest bleaching observations were made at the reefs in Madagascar, Mozambique and Reunion (Fig. 7).

![Figure 7: Plot of bleaching indices against latitude.](image)

Different results were observed with reef base long term bleaching data. In figure 8, the first (bottom) curve shows the probability attributed to high bleaching as latitude varies. The next higher curve shows the probability attributed to Low bleaching. Thus, the distance between the first two curves is the probability for low bleaching. The distance from the top curve to the top of the graph is the probability attributed to No bleaching. Note that as latitude increases, the model gives more probability to the high bleaching category. From about 0° - 10°N, most probability is attributed High
bleaching. Thus in countries like Kenya, Maldives, India, and Somalia; the probability of high/severe bleaching reports are relatively high. While further in the South along South Africa, Reunion and Mozambique, there is relatively higher probability of low bleaching incidents. Tanzania and Seychelles exhibit more or less the same probabilities for occurrence of the three categories of bleaching (fig. 8).

Figure 8: Logistic probability plot of coral bleaching intensity against latitude. The primary y-axis represents probability. Three smooth curves partition the total probability (=1) among the bleaching categories. N for the bleaching intensity is as follows: No bleaching = 9; Low = 56; Moderate = 57; High = 94

5.2. Conditions at the time of bleaching

Multicolinearity test revealed high correlations between some of the parameters, particularly sea surface temperature and wind speed (Table 9). Adjustments were made until all VIF’s were within acceptable range of <10. Chlorophyll anomaly and monthly mean PAR were left out in the stepwise selection of variables and were therefore not included in the final model. Sorted in descending order by the F values, Table 9 shows the relative contribution of predictor variables to the total variation of the observed bleaching. The model as a whole explained 62% of the variation, with a p value <0.001 (Table 9). While most variables contributed significantly to the total variation explained, sea surface temperature anomaly, wind speed anomaly, and hotspots contributed the most as depicted by relatively high corresponding F values. Corresponding t values for the same variables are positive indicating that they may have induced or aggravated the observed coral bleaching. Bleaching observations varied strongly and negatively with anomalous currents, while Chlorophyll and mean currents were marginally significant.
Table 9: Output of a regression model performed with conditions at the time of bleaching as predictor variables. The table is sorted in descending order by F values.

<table>
<thead>
<tr>
<th>Variable</th>
<th>VIF</th>
<th>Entered</th>
<th>t Ratio</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea surface temperature anomaly</td>
<td>2.3</td>
<td>X</td>
<td>3.7</td>
<td>13.9</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Wind speeds anomaly</td>
<td>1.7</td>
<td>X</td>
<td>3.6</td>
<td>13.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Hotspot</td>
<td>2.2</td>
<td>X</td>
<td>3.3</td>
<td>11.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Summed currents anomaly</td>
<td>3.2</td>
<td>X</td>
<td>-3.1</td>
<td>9.6</td>
<td>0.003</td>
</tr>
<tr>
<td>UV radiation</td>
<td>4.5</td>
<td>X</td>
<td>-2.8</td>
<td>8</td>
<td>0.006</td>
</tr>
<tr>
<td>UV radiation anomaly</td>
<td>2.4</td>
<td>X</td>
<td>2.8</td>
<td>7.8</td>
<td>0.007</td>
</tr>
<tr>
<td>Summed currents</td>
<td>1.9</td>
<td>X</td>
<td>1.9</td>
<td>3.8</td>
<td>0.057</td>
</tr>
<tr>
<td>PAR anomaly</td>
<td>1.9</td>
<td>X</td>
<td>-1.8</td>
<td>3.2</td>
<td>0.078</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>1.2</td>
<td>X</td>
<td>1.4</td>
<td>1.9</td>
<td>NS</td>
</tr>
<tr>
<td>Chlorophyll anomaly</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PAR</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

5.3. Long term environmental variables

Mean maximum SST; mean SST; PAR; UV; and wind speed were highly correlated causing high VIF’s. Consequently, they were used interchangeably and the best model was selected. The results of the Stepwise regression model with highest AIC is presented in (Table 10). The model as a whole explained 56% of the observed bleaching; with meridional currents contributing much of the explained variation. Regions with a history of relatively high meridional currents; high wind speed; and high UV radiation bleached less.

Temperature related variables i.e. hotspot and coefficient of variation contributed significantly to the total variation explained by the whole model. Corresponding positive t values indicate that regions which have low water fluctuation and low hotspot estimates bleached less and vice versa.
Table 10: Model output when only the long term variables are used as the predictor variables. The prediction equation is included in the table

<table>
<thead>
<tr>
<th>Whole model test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>R Square</td>
<td>0.56</td>
<td>&lt;.0001</td>
<td>350</td>
</tr>
<tr>
<td>F Ratio</td>
<td>18.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob &gt; F</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AIC</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable</th>
<th>VIF</th>
<th>Entered</th>
<th>t Ratio</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meridional currents</td>
<td>2.2</td>
<td>X</td>
<td>-5.17</td>
<td>26.8</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>UV radiation</td>
<td>8.6</td>
<td>X</td>
<td>-4.42</td>
<td>19.6</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Wind speed</td>
<td>7.8</td>
<td>X</td>
<td>-3.7</td>
<td>13.7</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>SST CV</td>
<td>8.8</td>
<td>X</td>
<td>2.46</td>
<td>6.0</td>
<td>0.02</td>
</tr>
<tr>
<td>SST hotspot</td>
<td>2.2</td>
<td>X</td>
<td>2.25</td>
<td>5.1</td>
<td>0.03</td>
</tr>
<tr>
<td>PAR</td>
<td>5.6</td>
<td>X</td>
<td>-0.8</td>
<td>0.7</td>
<td>NS</td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>1.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zonal currents</td>
<td>3.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST DHM</td>
<td>7.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PAR hotspot</td>
<td>2.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regression slope</td>
<td>7.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Prediction equation: \[ 128.3 -133.3*V\text{ currents} -7.3*\text{Wind speed} + 3.4*\text{CV} +16.4*\text{Hotspot}-0.3*\text{Long term UV} \]

5.4. Long term and short term variables

A scatter plot matrix of all 28 variables and the VIF’s revealed an existence of strong correlation between the predictor variables. After excluding variables based on VIF’s, 17 variables were used for the model. On performing stepwise regression, 10 variables were selected and used to make the final model (Table 11).

In this model, meridional surface currents had the highest F value with a negative t value. Zonal surface currents influenced the observed bleaching negatively, while the anomalies marginally influenced bleaching in a similar behaviour pattern.

Variables related to sea surface temperature and which significantly contributed to the explained variation include SST anomaly at the time of bleaching, and the long term hotspots, both increasing with increase in observed bleaching. Long term PAR
and UV at the time of bleaching also contributed significantly to the total variation (Table 11).

**Table 11: Model output when all uncorrelated variables are factored as predictor variables in the stepwise regression model**

<table>
<thead>
<tr>
<th>Variable</th>
<th>VIF</th>
<th>Entered</th>
<th>t Ratio</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meridional currents</td>
<td>6.3</td>
<td>X</td>
<td>-4.34</td>
<td>18.8</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Zonal currents (atb*)</td>
<td>3.6</td>
<td>X</td>
<td>3.8</td>
<td>14.5</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>PAR</td>
<td>4.3</td>
<td>X</td>
<td>-3.52</td>
<td>12.4</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Wind anomaly (atb)</td>
<td>2.1</td>
<td>X</td>
<td>2.8</td>
<td>7.9</td>
<td>0.01</td>
</tr>
<tr>
<td>SST Anomaly_atb</td>
<td>3.4</td>
<td>X</td>
<td>2.72</td>
<td>7.4</td>
<td>0.01</td>
</tr>
<tr>
<td>UV (atb)</td>
<td>8</td>
<td>X</td>
<td>-2.49</td>
<td>6.2</td>
<td>0.02</td>
</tr>
<tr>
<td>SST hotspot</td>
<td>2.2</td>
<td>X</td>
<td>2.34</td>
<td>5.5</td>
<td>0.02</td>
</tr>
<tr>
<td>Meridional currents anomaly (atb)</td>
<td>2.5</td>
<td>X</td>
<td>2.15</td>
<td>4.6</td>
<td>0.03</td>
</tr>
<tr>
<td>Zonal currents anomaly (atb)</td>
<td>2.3</td>
<td>X</td>
<td>-1.86</td>
<td>3.5</td>
<td>0.07</td>
</tr>
<tr>
<td>PAR (atb)</td>
<td>2.4</td>
<td>X</td>
<td>0.43</td>
<td>0.2</td>
<td>NS</td>
</tr>
<tr>
<td>Chlorophyll (atb)</td>
<td>1.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chlorophyll anomaly (atb)</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PAR anomaly (atb)</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UV radiation anomaly</td>
<td>3.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zonal currents</td>
<td>5.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST COV</td>
<td>7.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST degree heating months (DHM)</td>
<td>2.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*(atb*=at the time of bleaching)*

The whole model explained 67% of the variation, suggesting that most of the factors which explained the variation in bleaching were captured in this final model. The fact that the previous two models explained lower variation than the third model...
indicates that while environmental conditions may trigger or aggravate bleaching, long term conditions may shape their response of the corals to stress.

The Akaike’s information criteria values (AIC) give an idea of which of the three models fits better (Tables 9; 10; 11). The model that has the smallest value of AIC is considered the best (Akaike, H., 1974). Based on AIC, the suitability of the models in descending order is: all variables>short term variables>long term variables. Studentized residuals for the three models were normally distributed (Shapiro-Wilk test, p > 0.05). The lack of Fit test for all three models also indicate that there is little to be gained by introducing additional variables in the model, i.e. p>0.05.

5.5. **Reef base bleaching observation data**

Sea surface temperature was correlated with PAR and UV, and was therefore excluded from the model. Stepwise analysis utilized only four long term averaged variables to discriminate between the bleaching intensity categories i.e. Meridional surface currents, PAR, CV, and UV. The same variables had a p<0.05 in the nominal logistic regression indicating that they best separate the bleaching categories. The canonical axis plot displays graphically how these variables separate the ‘high’ and ‘medium’ bleaching categories from ‘low’ and no bleaching categories (Fig. 9).

Scatter plots of selected environmental variables against bleaching categories were made (Fig. 10). Zonal currents; PAR; UV and SST increase with bleaching intensities (Fig.10 b, d, e, and g). UV is highly correlated with SST and can be used interchangeably. Coefficient of variation is relatively low at high and moderate bleaching, suggesting that regions with high water fluctuation had a tendency not to bleach highly and vice versa (Fig.10). These results are not consistent with the 2005 bleaching data for UV, CV and PAR.
Figure 9: A scatter plot based on the first two canonical axes showing the separation of the groups based on the variables selected using stepwise discriminant analysis.

Table 12: Logistic regression output with bleaching intensity categories from reef base data as response variable.

<table>
<thead>
<tr>
<th>Whole model test</th>
<th>DF</th>
<th>Chi-Square</th>
<th>Prob&gt;ChiSq</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>27</td>
<td>100</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Effect Likelihood Ratio Tests</th>
<th>Source</th>
<th>VIF</th>
<th>DF</th>
<th>L-R Chi-Square</th>
<th>Prob&gt;ChiSq</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meridional currents</td>
<td>1.8</td>
<td>3</td>
<td>15.2</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>PAR</td>
<td>2.7</td>
<td>3</td>
<td>8.9</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>SST CV</td>
<td>4.3</td>
<td>3</td>
<td>8.7</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>UV radiation</td>
<td>7.7</td>
<td>3</td>
<td>7.8</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>SST hotspot</td>
<td>1.9</td>
<td>3</td>
<td>4.2</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Max SST</td>
<td>9.2</td>
<td>3</td>
<td>2.7</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>1.2</td>
<td>3</td>
<td>2.4</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Zonal currents</td>
<td>1.2</td>
<td>3</td>
<td>1.8</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Wind speed</td>
<td>6.2</td>
<td>3</td>
<td>1.4</td>
<td>NS</td>
<td></td>
</tr>
</tbody>
</table>
5.6. Ecological susceptibility

The two models, SM1 and SM2 display common susceptibility pattern in some regions while they differ in some (Fig. 11). SM1 model highlights the north-western region of the WIO from the Kenyan and Somali coast and extending towards the East as severely susceptible areas (Figure 11a,c). Most of the same region is classified as moderate to highly susceptible in SM2. Regions off the coast of Tanzania,
Mozambique, South Africa and the East coast of Madagascar are classified as low-moderate susceptibility classes in both models. However, the north-western coast of Madagascar falls within the moderate and highly susceptible categories in SM2, whereas, according to SM1, the same region is classified as low-moderately susceptible.

Figure 11: Maps showing estimated susceptibilities by (a) SM1 and (b) SM2; and the classified maps for (c) SM1 and (d) SM2

While the two models generally agree on susceptibility for regions North of 5°S, they differ on the susceptibility estimates for further South (>5°S). The Indian Ocean islands of Mauritius and Re union have relatively low susceptibility estimates: in SM1 they are classified as being low-moderately susceptible while, in SM2, the same region fall under not susceptible or low susceptibility classes.
Seychelles Islands are depicted as being severely susceptible in SM1, and moderately-highly susceptible in SM2 (Fig. 11, tables 8 and 13). The models also differ for susceptibilities of some reef locations in Maldives (\(\approx 0-1^\circ N \text{to } \approx 60-75^\circ E\)), where SM1 indicates moderate susceptibility, while SM2 estimates are high to severely susceptible. However, a sample of 107 reefs in Maldives indicate similar susceptibility estimates by both models with mean susceptibility of \(0.61 \pm 0.01\) and \(0.69 \pm 0.01\) by SM1 and SM2 respectively (Table 13).

Variables differed in their influence on the final models: The weightings obtained by the cosine amplitude method indicate temperature related variables are the most important factors. Mean maximum SST is ranked the highest, followed by SST, CV and wind, while ocean currents and predicted bleaching rank the lowest (Table 7). The noteworthy point in this hierarchy is the combination of the top ranked susceptibility-reinforcing variables (SST, CV) and balancing variables (wind speed, CV).

On performing SPCA, seven PCs accounted for 96.7% of the total variation (Table 6). By looking at the key indicators associated with a PC, an approximate parameter can be associated for that particular PC (Li et al., 2006). PC 1 has high loadings in descending order with Max SST, CV, SST and UV; PC2 has high loadings with zonal current, winds, regression model and SST; while PC3 has high loadings with PAR, UV, zonal currents and chlorophyll. This infers that variables associated with SST and radiations have a significant influence on the resulting model. Apart from radiation and SST, zonal currents and wind speed have a relatively higher influence on the model.

Statistics of the susceptibility estimates by the two models reveal a similar differentiation. SM1 has a slightly higher mean of 0.49 compared to 0.45 for SM2. The standard deviation for the spread of the susceptibility estimates differ in the same manner, with a value of 0.22 for SM1 and a value of 0.24 for SM2.

To illustrate differences and similarities between the two models, and between reef locations, susceptibility estimates of 397 reef locations from the two models are listed (Table 13). It is evident from Table 13 and from the map (Fig. 11) that regions in the North (Maldives, Somalia, and Kenya) are much more susceptible than in the South (Mauritius, Madagascar, and South Africa).
Out of the 61 MPA’s in the region listed in the reef base, 28 are protected under category I and II of the IUCN Protected Area Management Categories. Susceptibilities for these no take zones are summarized in table (14).

Table 13: Susceptibility indices derived from SM1 and SM2 for selected 397 reef systems summarized by countries in the region

<table>
<thead>
<tr>
<th>Geographical region</th>
<th>n - reef systems</th>
<th>SM1</th>
<th>sem</th>
<th>SM2</th>
<th>sem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maldives</td>
<td>107</td>
<td>0.61</td>
<td>0.01</td>
<td>0.69</td>
<td>0.01</td>
</tr>
<tr>
<td>Somalia</td>
<td>2</td>
<td>0.72</td>
<td>0.01</td>
<td>0.49</td>
<td>0.01</td>
</tr>
<tr>
<td>Kenya</td>
<td>37</td>
<td>0.68</td>
<td>0.01</td>
<td>0.49</td>
<td>0.01</td>
</tr>
<tr>
<td>Chagos</td>
<td>12</td>
<td>0.68</td>
<td>0.01</td>
<td>0.50</td>
<td>0.01</td>
</tr>
<tr>
<td>India</td>
<td>22</td>
<td>0.59</td>
<td>0.01</td>
<td>0.54</td>
<td>0.01</td>
</tr>
<tr>
<td>Seychelles</td>
<td>58</td>
<td>0.63</td>
<td>0.01</td>
<td>0.44</td>
<td>0.01</td>
</tr>
<tr>
<td>Tanzania</td>
<td>32</td>
<td>0.59</td>
<td>0.01</td>
<td>0.44</td>
<td>0.01</td>
</tr>
<tr>
<td>Comoros</td>
<td>12</td>
<td>0.46</td>
<td>0.01</td>
<td>0.51</td>
<td>0.01</td>
</tr>
<tr>
<td>Reunion</td>
<td>11</td>
<td>0.49</td>
<td>0.03</td>
<td>0.35</td>
<td>0.04</td>
</tr>
<tr>
<td>Mozambique</td>
<td>29</td>
<td>0.41</td>
<td>0.02</td>
<td>0.34</td>
<td>0.02</td>
</tr>
<tr>
<td>Mauritius</td>
<td>51</td>
<td>0.51</td>
<td>0.01</td>
<td>0.16</td>
<td>0.01</td>
</tr>
<tr>
<td>Madagascar</td>
<td>13</td>
<td>0.37</td>
<td>0.02</td>
<td>0.29</td>
<td>0.03</td>
</tr>
<tr>
<td>South Africa</td>
<td>9</td>
<td>0.29</td>
<td>0.01</td>
<td>0.13</td>
<td>0.02</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>0.54</strong></td>
<td></td>
<td><strong>0.41</strong></td>
<td></td>
</tr>
</tbody>
</table>

Table 14: Summary of the susceptibility indices for the marine protected areas (strictly no take zones) in the region

<table>
<thead>
<tr>
<th>Country</th>
<th>IUCN category</th>
<th>Year of protection</th>
<th>Name</th>
<th>SM-1</th>
<th>SM-2</th>
<th>SM-1 class</th>
<th>SM-2 class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seychelles</td>
<td>Ia</td>
<td>1973</td>
<td>Aride Island</td>
<td>0.74</td>
<td>0.54</td>
<td>severe</td>
<td>high</td>
</tr>
<tr>
<td>Seychelles</td>
<td>Ia</td>
<td>1975</td>
<td>Cousin Island</td>
<td>0.72</td>
<td>0.54</td>
<td>Severe</td>
<td>high</td>
</tr>
<tr>
<td>Seychelles</td>
<td>II</td>
<td>1979</td>
<td>Port Launay</td>
<td>0.67</td>
<td>0.57</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>Seychelles</td>
<td>II</td>
<td>1979</td>
<td>Baie Ternaie</td>
<td>0.67</td>
<td>0.57</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>Seychelles</td>
<td>II</td>
<td>1979</td>
<td>Curieuse</td>
<td>0.67</td>
<td>0.57</td>
<td>high</td>
<td>high</td>
</tr>
</tbody>
</table>
### RESULTS

<table>
<thead>
<tr>
<th>Country</th>
<th>Year</th>
<th>Location</th>
<th>Susceptibility</th>
<th>Mortality</th>
<th>Susceptibility behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>British In</td>
<td>1998</td>
<td>Cow Island</td>
<td>0.69</td>
<td>0.52</td>
<td>high medial</td>
</tr>
<tr>
<td>Kenya</td>
<td>1986</td>
<td>Mombasa</td>
<td>0.68</td>
<td>0.5</td>
<td>high medial</td>
</tr>
<tr>
<td>Kenya</td>
<td>1978</td>
<td>Kisite</td>
<td>0.69</td>
<td>0.49</td>
<td>high medial</td>
</tr>
<tr>
<td>Seychelles</td>
<td>1973</td>
<td>St. Anne</td>
<td>0.71</td>
<td>0.47</td>
<td>high medial</td>
</tr>
<tr>
<td>Seychelles</td>
<td>1987</td>
<td>Silhouette</td>
<td>0.67</td>
<td>0.5</td>
<td>high medial</td>
</tr>
<tr>
<td>Eastern Peros</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>British In</td>
<td>1998</td>
<td>Banhos Atoll</td>
<td>0.66</td>
<td>0.5</td>
<td>high medial</td>
</tr>
<tr>
<td>British In</td>
<td>1998</td>
<td>Danger Island</td>
<td>0.66</td>
<td>0.48</td>
<td>high medial</td>
</tr>
<tr>
<td>Three Brothers</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>British In</td>
<td>1998</td>
<td>Eastern Peros</td>
<td>0.66</td>
<td>0.48</td>
<td>high medial</td>
</tr>
<tr>
<td>British In</td>
<td>1998</td>
<td>Nelson Island</td>
<td>0.67</td>
<td>0.47</td>
<td>high medial</td>
</tr>
<tr>
<td>Tanzania</td>
<td>1981</td>
<td>Maziwi Island</td>
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<td>Madagascar</td>
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<td>0.2</td>
<td>0.23</td>
<td>not</td>
</tr>
</tbody>
</table>

#### 5.7. Susceptibility and mortality

When the two models were evaluated using 27 mortality data points, the results indicate that there is indeed a correlation between mortality and susceptibility estimates (Fig.12). Locations with high mortality also had corresponding high susceptibility estimates in both models, and vice versa. However for a few locations – a reef in Mauritius and Madagascar in SM1 and Mauritius and Maldives in SM2, no mortalities were reported, but the susceptibility estimates are moderate. The sample of 27 is not sufficient to validate the two models. They however indicate the general behaviour pattern which could be confirmed with several data points of relative change in coral cover.
Figure 12: Correlation of change in coral cover (%) with susceptibility indices as estimated by (a) SM1 and (b) SM2.
6. Discussion

6.1. Environmental factors that explain coral bleaching

The results suggest that 2005 bleaching may have been induced or triggered by elevated sea surface temperature, represented in the model as sea surface temperature anomaly. Other environmental parameters also feature prominently, mainly wind speed and surface currents. It is surprising however that short term wind speeds had a positive influence on bleaching, considering that previous reports on bleaching have also reported calm periods preceding the bleaching events (e.g. Jokiel and Brown, 2004). They noted that solar input and wind speed work against each other in producing temperature change, while tide and currents modify local water temperature (Jokiel and Brown, 2004). Wind anomalies could have been caused by anomalous warming of the water in the southern latitudes of the Indian Ocean causing a change in winds direction and magnitude as a result of advection, a condition similar to the Indian Ocean dipole first described by Saji et al., 1999 and later by van Woesik, R., 2004. UV radiation and PAR correlate highly \((r=0.78)\). This has also been reported elsewhere e.g. in Jokiel and Brown, 2004. The regions which experienced increased UV anomalies bleached more. Converse was true for regions with a history of high UV and PAR (table 9). It is possible that short term anomalies are less likely to affect regions which are ordinarily exposed to high UV-PAR radiation. These results support the hypotheses that historical environmental conditions shape the coral community structure to the effect that short term anomalies are not likely to affect these already acclimatized coral communities, also suggested by Fitt et al., 2001.

Long term PAR and UV correlate highly with mean maximum SST. For the same reasons mean maximum SST was not included in the model due to high VIF’s to avoid multicolinearity. This relationship suggests that increased radiation results in high water temperature with high maxima. As mentioned earlier, maximum SST infers to thermal threshold of corals. This would then suggest that the higher the mean maximum SST, the higher the coral tolerance to thermal stress. Therefore during anomalous warm waters, regions with high thermal tolerance levels will bleach less than those with low thermal thresholds. However during extreme and prolonged elevated temperature similar to 1998 event, these warm regions are more
susceptible to increased water temperatures and disturbances due to geographical location among other factors. As a result these areas tend to bleach more severely as supported by the results from the logistic probability plot (Fig. 8). The data used in this plot includes data from 1998 and 2001 bleaching events and show that it is more likely to bleach highly in the North than in the South. Incidentally, temperatures in the North are usually much higher than in the South.

The results also suggest that the temperature coefficient of variation (CV) correlated positively with bleaching observations (Table 10). Temperature variation is higher in southern latitudes than in the North. It also correlates negatively with sea surface temperature. In places like Mozambique in the South where 2005 bleaching was relatively high, temperature variation is higher than for instance Maldives in the North where the variation is very low and experienced low bleaching during the same period. The 2005 bleaching event differs from previous events both in magnitude and geographical coverage. It mainly affected reefs in the southern hemisphere (Fig. 7). Results from the regressions (table 12) of the long term reef base bleaching data and figure 8 reveal that CV was low in areas where bleaching is categorized as high. In addition, CV, meridional currents, PAR and UV separate moderate-high bleaching categories from no bleaching-low bleaching groups (fig. 9). This emphasizes the importance of radiation, temperature and currents in influencing the reef systems. Based on this data, the hypothesis that regions with high CV are more resistant to bleaching is supported. However if we consider the 2005 data conversely is true. Therefore we can conclude that CV enhances resistance to thermal stress, as evidenced by the mild bleaching event which affected reef systems in the South; and the corresponding low temperature fluctuation in locations where there were reports of high bleaching since 1998. Long term meridional currents predicted much of the variation in the 2005 event. These currents are much stronger in the North than they are in the South. This can be attributed to the strong Somali current which occur in the north-western part of the Indian Ocean. This current flows two times in a year, resulting in mass water movements in the north-south direction (Nagar et al., 2005). And because corals were not as affected in the North than in the South as mentioned earlier, the north-south currents correlate negatively with the bleaching data (Table 10). This correlation may not necessarily suggest a cause-effect currents-bleaching relationship. The same parameter is positively correlated with bleaching intensity in the reef base long term bleaching data. This may be a true reflection of the influence surface currents have on bleaching intensity, as observed in the field by McClanahan et al. (2005).
This study also confirms that both long term and short term environmental conditions influence the response of the coral communities to heat stress. 67% of bleaching variation is explained when all the variables are combined (Table 11). Currents, wind speed, UV and SST anomaly at the time of bleaching played an important role in the variation of the observed bleaching. Thermal history represented in the model as long term hotspots, and long term PAR were important in shaping the response of corals to the SST anomaly. While the main variables which influence variation on bleaching may have been captured, biological conditions and community structures are not fully taken into account here, though it can be argued that long term environmental conditions greatly influence the coral communities and the zooxanthellae types, and can therefore be a proxy for community structure. The variance explained by the all variables model (67%) is acceptable considering that a lurking variable in the form of community structure and anthropogenic disturbance are not included in the model. In addition errors and uncertainties from the data used can further alter the model’s explained variance.

6.2. Estimated physical environment threats to coral reefs in WIO

6.2.1. Susceptibility, coral bleaching and mortality

The regression coefficient (slope) map (appendix 1) shows that in most locations within WIO temperature is increasing on average at 0.01°C per year. Similar results were obtained by Spencer et al., 2000. On computing SST trends from modelled data with a baseline of 1961-1990 they reported decadal increase of 0.109°C. This implies that by 2010 temperatures will increase by 1°C (Spencer et al., 2000). This is a worrying trend to coral reef conservation community, considering that most reefs within the region are experiencing temperatures near their thermal thresholds (Fitt et al., 2001).

Results obtained from the two models show some degree of spatial variability in susceptibility of coral reef systems in WIO. Generally, Kenya, Somalia, Maldives, and some of the Indian Ocean islands including Seychelles have relatively high estimates of susceptibility indices (table 13; fig 11). Environmental conditions which promote resistance and tolerance to warm water effect (Obura, D. O., 2005), mainly Winds, temperature fluctuation and chlorophyll are not sufficient to counteract the elevated SST’s. Low temperature variation, moderate SST, high UV and moderate wind speeds characterize these locations (Fig. 5; appendix 1). This implies that elevated SST events are likely to result in higher thermal stress in these locations and may induce coral mortality while curtailing their recovery. Goreau et al., 2000
DISCUSSIONS

reported that the entire African coastline was affected by the 1998 warm water event. However, mortality was higher in the North (Somalia; Maldives; Seychelles; Chagos and Kenya) than in the South (Mozambique; South Africa; Mauritius) (Goreau et al., 2000). Coral cover monitoring reports from Seychelles (Payet et al., 2005) report a moderate coral cover increase between 1998-2004 periods following the 50-90% mortality after the 1998 El Nino event. However, some reef systems experienced negative coral recovery from further coral mortality caused by 2002-3 bleaching event (Payet and Agricole, 2006). Estimates of average susceptibility for Seychelles based on 58 reefs are 0.63 and 0.44 from SM1 and SM2 respectively (Table 13). According to these estimates more than 70% of the reefs in Seychelles are in moderate to highly susceptible areas. They also reflect the mortality and recovery trends reported elsewhere for Seychelles. The geographical location of Seychelles islands (=50°-55°E and =4°-10°S) exposes it to high currents and solar radiation, less winds and low CV hence more prone to thermal stress (Appendix 1). Areas that appear resilient to past coral-bleaching events are now being protected to ensure the survival of representative coral areas in the Seychelles (Payette and Agricole, 2006).

The Kenyan reef system also suffered heavily from 1998 coral bleaching events where the main casualties were the marine protected areas (Goreau et al., 2000). Reported recovery rates are low (20-25%) between 1998 and 2002 (McClanahan et al., 2005). Average susceptibility index from 35 reef systems in Kenya is 6.8 and 5.1 (SM1 and SM2 respectively, Table 13). This corresponds to the high reported mortality (73%) and low recovery rates depicted in Kenyan reef systems. Susceptibility decreases from southern Kenya into most of Tanzania, including the reef systems of Zanzibar and Comoros Islands (fig. 11, table 13, 14). In the southern high latitudes (>15°S, South Africa and Madagascar), susceptibility index is minimal at 0.29 and 0.37 for SM1 and 0.12 and 0.29 for SM2 in South Africa and Madagascar respectively. In Madagascar the 1998 ENSO event resulted in extensive bleaching and but low mortality (26%) (Wilkinson et al., 1999; Goreau et al., 2000). South African corals did not experience significant bleaching or coral mortality in 1998 (Riegl, B., 2003; Goreau et al., 2000). However due to the high latitudes (27–28°S) and physical conditions, South Africa is considered marginal for coral reef growth (Glassom et al., 2006).

Susceptibility estimates for the reefs in Mauritius differ for the two models, where SM1 estimates are moderate susceptibility (0.5), while model SM2 estimates are low-no susceptibility (0.16). This difference can be accounted for by the fact that the region around Mauritius has relatively high wind velocity and temperature
fluctuation. These two are weighted highly in the relations matrix (Table 7) and therefore have a considerable influence on SM2, i.e. they have a balancing effect on susceptibility estimates. Moothien-Pillay et al. (2002) reported very low bleaching for Mauritius (<10%) despite the extensive coral bleaching and mortality in the region in 1998 as reported by Goreau et al., 2000. Different authors have attributed this observation (McClanahan et al., 2005) to clouds and storms (Turner et al., 2000); geography and temperature histories (Berkelmans et al. 2004); coral communities structure (McClanahan, T. R., 2004); dominant algal symbionts on these reefs (Baker et al., 2004); and water flow effects (Nakamura & van Woesik, 2001).

The differences between the two models can be attributed to different methodologies used in estimating susceptibility. These models represent two different approaches, where SM1 establishes maximum variability based on originally un-weighted parameters; while in SM2 the parameters are assigned weights prior to their integration.

6.2.2. Ecological susceptibility and Marine Protected Area’s (MPA’s)

Older MPA’s in the region were designated on the basis of mainly biodiversity indicators alone. Recently however socioeconomics aspects are beginning to gain prominence in the decision support system for the establishment of MPA’s. Ecological susceptibility based on how the ecosystems are likely to respond to future climate change needs to be integrated in the decision support system. Listed in reef base are 61 reef systems within the study area which are protected under different IUCN protection categories. 28 out of these are strictly no take zones (table 14). Based on SM1 and SM2, 5 of these MPA’s (all in Seychelles) are classified as highly or severely susceptible areas, while several others in Kenya and British islands are in high or moderately susceptible areas. Only four are located in low susceptible areas. More than a half of all strictly no take zones are situated in locations which have estimated high susceptibility to environmental change related stress. This exposes a need for the management to review the management status of existing MPA’s with respect to their respective susceptibility estimates.

6.2.3. Data assumptions and methodology assessment

A method to estimate ecological susceptibility based on the environmental variables and response of the past bleaching event, for coral reef locations in the Western Indian Ocean has been described. A few important considerations related to the
estimates obtained here include the low to moderate spatial resolution of the satellite data used. This affects variables which are highly heterogeneous over space such as ocean surface currents and chlorophyll concentration much more than those that are homogenous over large areas such as sea surface temperature. Also important to note is that these estimates do not take into account local variability and the different habitat types such as lagoons on fringing reefs, patch reefs and atolls which differ in their degree connectivity to the open ocean. For instance Kench, P. S. (1998) describe a localized wave induced currents, lagoon circulation and the spatial pattern of energy distribution as a direct effect of the morphology of a medium sized atoll in the Indian Ocean (Coco’s islands). Other equally important variables that influence coral reef resilience as explained by Obura, D. O. (2005) i.e. reef morphology, topography, tidal range, and abundance of bio-eroders and corallivores are not taken into account in these models.

Coral reefs are located a few kilometres’ from the coast where most satellite measurements do not reach. Here we assume that there is strong connectivity between coastal areas and the open ocean. Strong connectivity among areas implies that local populations may depend on processes occurring elsewhere (Roberts, C. 2006); hence we interpolated open ocean data to coastal areas with missing geophysical values.

Ecosystems are multidimensional. Individual observations may point to conflicting conclusions (Silvert, W., 1997). Lab experiments of effect of water flow on corals for example, show negative correlation with coral bleaching (Nakamura et al., 2004); while field experiments showed that conversely is true (McClanahan et al., 2005). This relates to the assignment of the membership functions to the environmental variables, and the respective control values which are a critical component of the fuzzy logic process (fig. 4) (O’Connor, J. R., 2000). Suitability of these models depends mainly on the extent to which the membership functions reflect observations in the field. This methodology allows for adjustments to the models including addition of a lurking or an overlooked variable; adjustment to the assigned membership functions and adjustments to the control points. This can be done based on new field experiments or information from scientific sources.

The models are evaluated using coral mortality data. It is assumed that mortality reflects resistance and susceptibility of corals to environmental stress. Mortality is a function of several other factors among them the environmental conditions. Physical environmental conditions are one among many coefficients required to determine the resistance, tolerance and the recovery of a coral reef system. Other equally important
parameters include community structure, variability in DNA and genetics, fishing intensity, and the connectivity of reefs.

It is also assumed here that time scale of the data used (ranges from 7-21 years) is satisfactory historical data to influence acclimation. Given that most coral reef processes are slow and takes decades to form, a much longer time series than used here may give a better impression of the reality.

6.3. Remote sensing data: scale and uncertainties

Remote sensing data is the only practical means of studying coral reef processes at meso-scale. Long term satellite data for PAR, UV, wind speeds and currents provide one of the first empirical evidence which relates these parameters at long time scale and moderate spatial resolution with regional coral bleaching events. Environmental data used here is suitable to achieve the goal of determining the general pattern of meso-scale bleaching event, and to associate this event broadly with both long term inherent oceanographic conditions and conditions when they occur. It also provides opportunity for large scale studies in biological oceanography and modelling. Wooldridge and Done, 2004 noted that low resolution data has the distinct advantage of averaging out small scale, random heterogeneity (second order effects); while still capturing the important organized component (first-order effects), and thereby facilitating inferences about a regional ecological response that are consistent with ecological heterogeneity at the reef scale. To study reef scale and colony scale processes however, high resolution data would be required (Wooldridge and Done, 2004; Hoegh-Guldberg, O., 1999). A coarse-grid model ignores significant “sub-grid” detail (Isukapalli et al., 2001).

Large scale bleaching events cannot be fully explained by localized stress factors (West and Salm, 2003), rather they have been linked to elevated sea surface temperatures at a geographical scale. The Reef check program, for example, to predict bleaching utilizes satellite-based measurements of SST at 36 km spatial resolution to identify thermal anomalies over large areas and their duration (Strong et al., 1998). In instances where bleaching does not correlate with SST (Hoegh-Guldberg, O., 1999), emphasis has been placed upon other factors mainly light intensity, zooxanthellae genotype, and historical environmental conditions.

Very often, a coarse grid resolution introduces approximations and uncertainties into model results (Isukapalli et al., 2001). Data used in this study demonstrates sufficient variability which can be used to explain large scale biological processes. The
assumptions explained in the previous section are a source of uncertainty or error to the final models. For instance, interpolation of satellite data to the coastal areas is just one source of uncertainty. In addition, satellite data used here is for different time scales and spatial resolution. Spatial and temporal aggregation, and the eventual integration increases errors from mismatch in spatial and temporal correlation structure (Burrough and McDonnel, 2005).

More uncertainties propagate from the spatial and temporal boundaries used in the models. As mentioned earlier the data used to estimate susceptibility dates 7-21 years back in time. Different results may be obtained if a longer time series is used.
7. Conclusions and Recommendations

7.1. Conclusions

Large spatial scale studies of ecological processes provide an opportunity to determine trends which otherwise would not be obviously apparent in small scale studies. The availability of various remote sensing data has enabled the application of ecosystem approach in this study in an attempt to explain complex coral reefs phenomena in the Western Indian Ocean coral reefs ecosystems.

One of the most common concluding recommendations from meetings and scientific articles, with respect to response of corals to climate change has been to integrate information on coral reef resilience as a decision support system when designating marine protected areas. However the actual methodologies of providing the manager with simplified scientific information are yet to be formulated. This work has described a methodology which breaks down information derived from satellite data and other scientific bank of knowledge into coral reefs ecological susceptibility index. It is relatively easy for managers to understand scientific Information translated into this form, and to use it for practical applications of biodiversity conservation in the realm of climate change.

The objectives of this study have largely been addressed. Conclusions to specific research goals are summarized as follows:

- Both historical and short term environmental conditions are useful in describing bleaching patterns. Historical physical oceanographic conditions result in ecological zones which constitute different community structure that respond differently to the environmental stress. While SST and derived variables explain much of the bleaching observed, other variables such as surface currents, wind anomalies, and radiation at UV and PAR play a role in shaping the response of corals to thermal stress. An approach which integrates the magnitude of all these factors; and including their temporal and spatial variations promises to increase our understanding of coral reef bleaching.

- There is variation in the susceptibilities of coral reefs systems in the WIO. Most locations currently closed for anthropogenic disturbance are exposed to...
environmental disturbance. There is low correlation between the areas which have been designated as strictly no take zones and the estimated susceptibilities. Selected regions around Tanzania, Mozambique, some parts of Madagascar, and Mauritius have been shown to be least susceptible; while most regions in the North including Seychelles, Kenya, Somalia and Maldives are highly susceptible.

- Remotely sensed oceanography data at a moderate to low spatial resolutions is suitable for estimating susceptibility of coral reef systems to environmental stress at a regional scale; and in explaining coral reef processes a meso-scale.

7.2. Recommendations

1. Moderate to high resolution satellite data should be used to test these hypotheses. High spatial resolution data will improve data spatial variability allowing hierarchical type modelling which will be more appropriate to determine variability at local scales within the context of the whole region. To estimate susceptibility, longer temporal scales should be used, within the framework of available satellite or modelled data.

2. Susceptibility models should be evaluated using sufficient coral mortality data to determine their suitability. If the models do not postdict the observed mortality, membership functions and control values should be revised using empirical values. Brain-storming workshops by coral reef scientists at all levels can be a useful forum for undertaking these revisions.

3. Managers should be encouraged to incorporate susceptibility indices in future when establishing marine protected areas. Revision of IUCN protection status for the existing MPA’s based on susceptibility indices should be undertaken to increase the number of strictly no take zones in less susceptible areas.

4. Ecosystem approach to research in marine ecosystems should be encouraged considering the complexity and high connectivity of these systems. Existence of eco-oceanographic zones should be investigated.

5. Sampling of coral bleaching should be improved such that samples are representative of a reef and are widely spaced. This way satellite data will be more useful as sample points will correspond to separate raster pixels to improve variability of satellite data with regard to the observation data.

6. While physical oceanographers have made an effort to make satellite data at all quality levels available, most marine ecologists/biologists, social scientists and resource managers do not have the knowledge to retrieve and process this data. Collaboration between these two groups should be encouraged so that data can be useful for the management and conservation of coral reefs.
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APPENDICES


Appendices

Appendix 1: Parameters derived/aggregated from the satellite images. Units for the respective layers are: SST (°C); UV (milli-watts/m2); Chlorophyll (Mg/m3); CV (°C); Bleaching (%); Wind speed (m/s); PAR (PAR, Einstein/m2/day); currents (m/s); hotspot (°C); slope (°C).
Country Map Source: ESRI world map
Appendix 2: Histograms showing value ranges for respective variables. The y-axes are number of pixels while the x-axes are the value for respective variables. (Units are the same as in Appendix 1).
### Appendix 3: Properties and sources of satellite, modelled and point data used in this study

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