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TITLE PAGE

Understanding Environmental Controls and Predicting Climate Change Effects on the Health and Occurrence of Coral Communities and their Constituent Organisms

Thesis submitted by

John Michael Guinotte, Master of Arts (Geography), Bachelor of Science (Geography)

June 2006

for the degree of Doctor of Philosophy

in the School of Tropical Environment Studies and Geography

James Cook University

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STATEMENT OF THE CONTRIBUTION OF OTHERS

Most research higher degrees are accomplished with the help of others. The research presented in this thesis is no exception to this rule. The majority of the work presented here is in the form of jointly-published papers with numerous co-authors. An alphabetical list of colleagues who contributed to publications stemming from my research and provided theoretical input is listed below. My personal contributions to each paper are listed at the beginning of each chapter.

Contributors: J. Bartley, R. Berkelmans, G. Bohling, R. Buddemeier, S. Cairns, T. Done, D. Fautin, R. Feely, R. George, D. Gillieson, A. Heyward, A. Iqbal, J. Kleypas, A. Lewis, L. Morgan, J. Orr, M. Rees, W. Skirving, L. Smith, J. Veron, M. Wakeford.

Supervision from Robert Buddemeier, Joanie Kleypas, Terry Done, and Dave Gillieson were instrumental in seeing this work to fruition.

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ABSTRACT

Research presented in this thesis provides insight into important environmental controls on coral occurrence and survival, potential climate related problems coral ecosystems face in the coming decades, the probable temporal and spatial progression of these problems, and provides tools that will aid the science community in anticipating range shifts and in identifying areas for protection. These topics are addressed by investigating four research foci, which follow a logical progression from shallow-hermatypic, to deep-hermatypic, to deep-ahermatypic corals. This is due largely to the success of early model predictions for shallow-hermatypic corals and the fact that new applications of the methodologies were quickly recognized for deep-hermatypic and ahermatypic coral ecosystems. The latter two are breaking novel ground and opening new fields of study. Model results indicate both hermatypic and ahermatypic coral ecosystems, which are presently under intense anthropogenic stress, will face even greater challenges within the century. Research findings presented in this thesis show the primary drivers behind the 1998 coral bleaching event on the Great Barrier Reef were a combination of low winds, clear skies, and neap tides. These conditions caused sea surface temperatures to rise and resulted in significant coral mortality. Coral bleaching events have persisted post 1998 and will continue to occur in the future. Model projections indicate that rising atmospheric CO^2 concentrations will significantly reduce the saturation state of carbonate minerals in the surface ocean and the deep sea within the century. By 2070, nearly all reefs in the Pacific basin will be “marginal” with respect to aragonite, which will probably result in long-term, gradual decreases in calcification, reef accumulation, and changes in community structure. The projections indicate this “saturation stress” will be compounded by rising average sea surface temperatures throughout much of the Pacific, including the Indo-Pacific center of coral diversity. Decreases in aragonite saturation state will not be limited to the surface ocean and will probably have negative affects on the calcification rates/mechanisms of deep sea scleractinian bioherms and marine plankton throughout the world's oceans. Modeling suitable reef habitat from environmental data successfully predicted numerous uncharted deep-hermatypic reefs within the Great Barrier Reef Marine Park and Timor Sea. Identifying the location of deep-hermatypic reefs will become increasingly important in the coming decades as these areas are less likely to experience coral bleaching events. Light availability and average nitrate were the most important variables in determining where reefs (both modeled and documented) occur. Temperature, salinity, and phosphate concentration were also statistically significant. An online spatial analysis tool was developed to predict potential ranges of marine organisms (e.g. sea anemones and anemonefishes) and areas which could be susceptible to marine species invasions. These predictions were derived by examining the environmental characteristics of waters surrounding known locations of constituent reef organisms. Documented locations of anemonefishes and their sea anemone hosts were used as a case study, but this tool is applicable for all marine taxa that live within relatively well defined environmental limits. A promising future application of this tool is to predict species range shifts due to climate change.

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Introduction

Context of the Research

The world's oceans are changing rapidly both physically and chemically from the addition of anthropogenic CO_2 to the atmosphere (Kleypas et al. 1999a, Feely et al. 2004, Sabine et al. 2004). Shallow-water hermatypic and deep-sea ahermatypic coral communities will not be immune from these changes, nor will the constituent organisms (e.g. sea anemones, fishes, etc.) that depend on them for survival. Earth's shallow-water coral reefs have experienced unprecedented severe bleaching events in recent decades, which have caused massive coral mortality and warranted concern in the science community (Wilkinson 2000, Wilkinson 2002). Nearly 30% of all hermatypic corals have disappeared since the beginning of the 1980s and there are no indications this trend is showing signs of slowing down or reversing itself in the near future (Hoegh-Guldberg 2005). Sea temperatures will continue to rise and bleaching events will probably become more frequent and/or the severity of the events will increase (Buddemeier et al. 2004, Hoegh-Guldberg 2005). These acute high temperature events, which have caused significant coral mortality in relatively pristine areas devoid of other human induced stressors, will occur in concert with other chronic, climate change induced stress.

High temperature events are not the only threat coral ecosystems face from global climate change. The chemistry of the world's oceans, from surface waters to the abyssal plains, is changing rapidly due to an influx of anthropogenic CO_2 (Caldiera and Wickett 2003, Feely et al. 2004, Sabine et al. 2004, Orr et al. 2005). The resultant decreases in seawater pH will probably impact marine ecosystems at all trophic levels and could potentially alter the global distribution of coral ecosystems (Guinotte et al. 2006). These human-induced threats to coral ecosystems are legitimate and point to the need for a thorough understanding of the environmental controls that influence coral growth and occurrence. By understanding these controls, it may be possible to project and/or predict how, when, and where these changes are likely to impact coral ecosystems and the organisms that depend on them.

This thesis is an applied research project with products designed to provide insight and practical application to the problems coral communities face in the age of global climate change. Research presented here is at the intersection of climate change science and the causal effects theses changes may have on marine organisms, specifically coral ecosystems. Climate model projections described here are based on uncertain data with respect to future atmospheric CO_2 concentrations and it is likely that some of the results and conclusions presented in this thesis will not be testable for several decades. Nevertheless, the health of marine ecosystems depends on the science community’s ability to proactively anticipate the temporal and spatial effects of climate change and take active steps to protect vulnerable areas from non-climate induced threats and permanently protect areas that are less likely to experience the negative effects of climate change. Findings reported here will aid in predicting these threats and the methodologies and tools developed during the course of this research will provide valuable information to the management community.

Understanding environmental controls and predicting climate change effects on the health and occurrence of coral communities and their constituent organisms requires a thorough understanding of ecological processes and threats which operate at multiple spatial and temporal scales. Remote Sensing and Geographic Information Systems (GIS) are tools that enable researchers to process and analyze scientific data across these scales and were relied upon heavily to produce the findings presented in this thesis. In some cases new GIS tools, methods for processing remotely sensed data, and methodologies for integrating/analyzing data were developed during the course of this research to address four research questions.

Purpose of the Thesis

The purpose of this thesis is to provide insight into four research foci (RF):

RF1) What are the important environmental controls on coral community occurrence and their constituent organisms?
RF2) What are the potential climate related problems coral ecosystems face in the coming decades?
RF3) What will be the probable temporal and spatial progression of these climate related problems?
RF4) What tools are available, or will need to be developed, to answer the foregoing questions?

The four research foci listed are addressed in seven chapters. Four of these chapters were published in peer-reviewed journals and a fifth was published as a book chapter. The two remaining chapters are in preparation for publication and/or have been submitted for publication. The research of higher degree candidates is often team-based and collaborative in nature. Research presented here is no exception to this trend in contemporary scientific research with five of the seven publications having more than one author. Clear statements of my personal contribution, as well as the contribution of co-authors, can be found at the beginning of each chapter.

Structure of the Thesis

This thesis follows a logical progression from shallow-hermatypic (Chapters 1-3 and Chapter 5), to deep-hermatypic (Chapters 3-5), to deep-ahermatypic corals (Chapters 6 and 7). This is due largely to the success of early model predictions for shallow-hermatypic corals (Chapter 3) and the fact that new applications of the methodology were quickly recognized for deep hermatypic and ahermatypic coral ecosystems. The chapters fall into three categories: Descriptive Analysis, Methods Development and Application, and Operational Integration into Predictive Analysis. Thesis chapters also address four research foci or objectives. Figure 1 illustrates the category and the research foci addressed in each chapter.

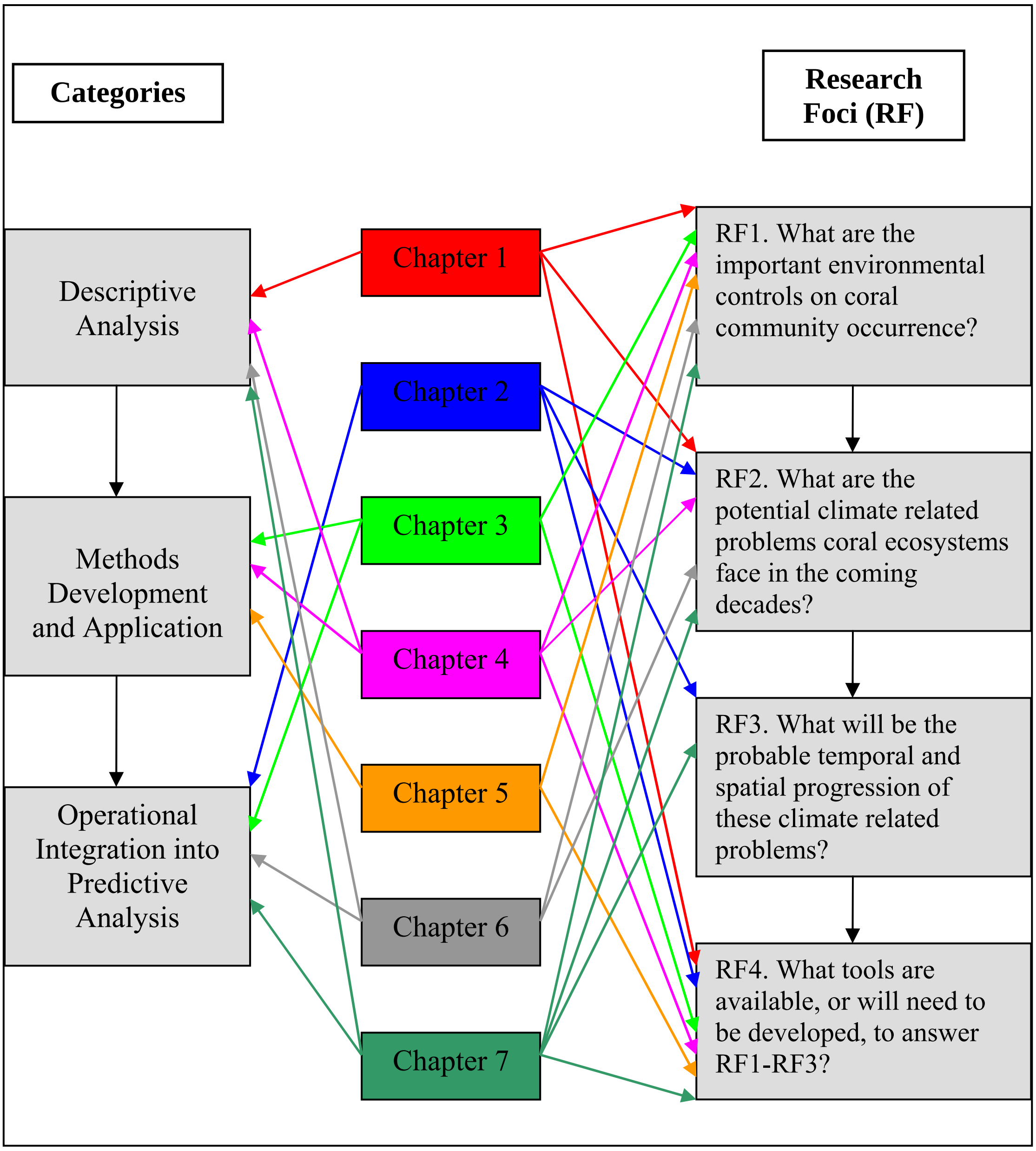


Figure 1**.** General diagram illustrating where chapters fit within the overall scheme of the research. Citation information for C1-C7 is listed below.

C1. Skirving W, Guinotte J (2001) The Sea Surface Temperature Story on the Great Barrier Reef during the Coral Bleaching Event of 1998. In E. Wolanski (ed.), Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef. CRC Press, Boca Raton, Florida, pp.301-313

C2. Guinotte JM, Buddemeier RW, Kleypas JA (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. Coral Reefs 22:551-558

C3. Guinotte JM (submitted) Predicting present day coral reef habitat from measured environmental data: a diagnostic model for the Great Barrier Reef. Marine Ecology Progress Series

C4. Heyward A, Smith L, Rees M, Guinotte JM (in prep) Depth provides refuge for coral reefs. [Target journal = Note submitted to Science or Nature]

C5. Guinotte JM, Bartley JD, Iqbal A, Fautin DG, Buddemeier RW (2006) Modeling habitat distribution from organism occurrences and environmental data: a case study using anemonefishes and their sea anemone hosts. Marine Ecology Progress Series 316:269-283

C6. Guinotte JM (2005) Climate change and deep-sea corals. Current: the journal of Marine Education 21:48-49

C7. Guinotte JM, Orr J, Cairns S, Freiwald A, Morgan L, George R (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Frontiers in Ecology and the Environment 4(3):141-146

Chapter 1

The Sea Surface Temperature Story on the Great Barrier Reef during the Coral Bleaching Event of 1998

Photo Credit: Associated Press

Citation:

Skirving W, Guinotte J (2001) The Sea Surface Temperature Story on the Great Barrier Reef during the Coral Bleaching Event of 1998. In E. Wolanski (ed.), Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef. CRC Press, Boca Raton, Florida, pp.301-313.

Abstract:

This paper describes the primary drivers of the 1998 GBR coral bleaching event and provides detailed maps and animations illustrating the warm-up, hot water, and cool-down phases of the event within the GBRMP. The primary significance of this work was that it provided the first detailed time series and spatially comprehensive documentation of a major bleaching event on the GBR. This was accomplished using remote sensing technologies (AVHRR) and Geographic Information Systems, tools that were not readily available or accessible for past bleaching events. The primary drivers of the 1998 coral bleaching event on the GBR were low winds, clear skies, and neap tides. This combination of factors will likely occur in the future, but the larger question regarding the background influence of climate change and whether or not it will make these drivers more or less prevalent in the future remains uncertain.

Personal Contribution and Context within the Thesis:

My personal contribution to this research was to investigate Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature (SST) data for patterns and/or anomalies and to formulate hypotheses addressing the issue of patchiness (why some coral areas bleached and others experiencing similar environmental conditions did not). This early work contributed to findings and implications contained in the report "Global Climate Change and Coral Bleaching on the Great Barrier Reef" (Done et al. 2003). My personal contribution to this effort was approximately 40% and lead author, William Skirving's contribution was 60%.

This research was my first experience working in a multi-disciplinary team environment with researchers from AIMS, JCU, and GBRMPA. I learned a great deal about the environmental controls driving bleaching events on the GBR, which gave me an early perspective into exciting future research possibilities. This work demonstrated that bleaching events were probably going to be a recurring phenomenon on the GBR and the science community needed to understand which coral areas were less likely to experience the negative effects of bleaching.

This work directly addresses Research Foci 1, 2, and 4. (Figure 2). Analyses of AVHRR data allowed our team to formulate hypotheses regarding the upper thermal limit of corals within the GBRMP (RF1). This was especially useful in areas of the GBRMP which had not been surveyed post-bleaching. Investigation of the environmental factors which induced bleaching in 1997-1998 allowed us to formulate hypotheses about the future spatio-temporal occurrence of this phenomenon on the GBR (RF2). Finally, new processing algorithms were developed to obtain accurate estimates of skin temperature from AVHRR and cluster analysis techniques were conducted to identify areas that had historically experienced the hottest temperatures (RF4).

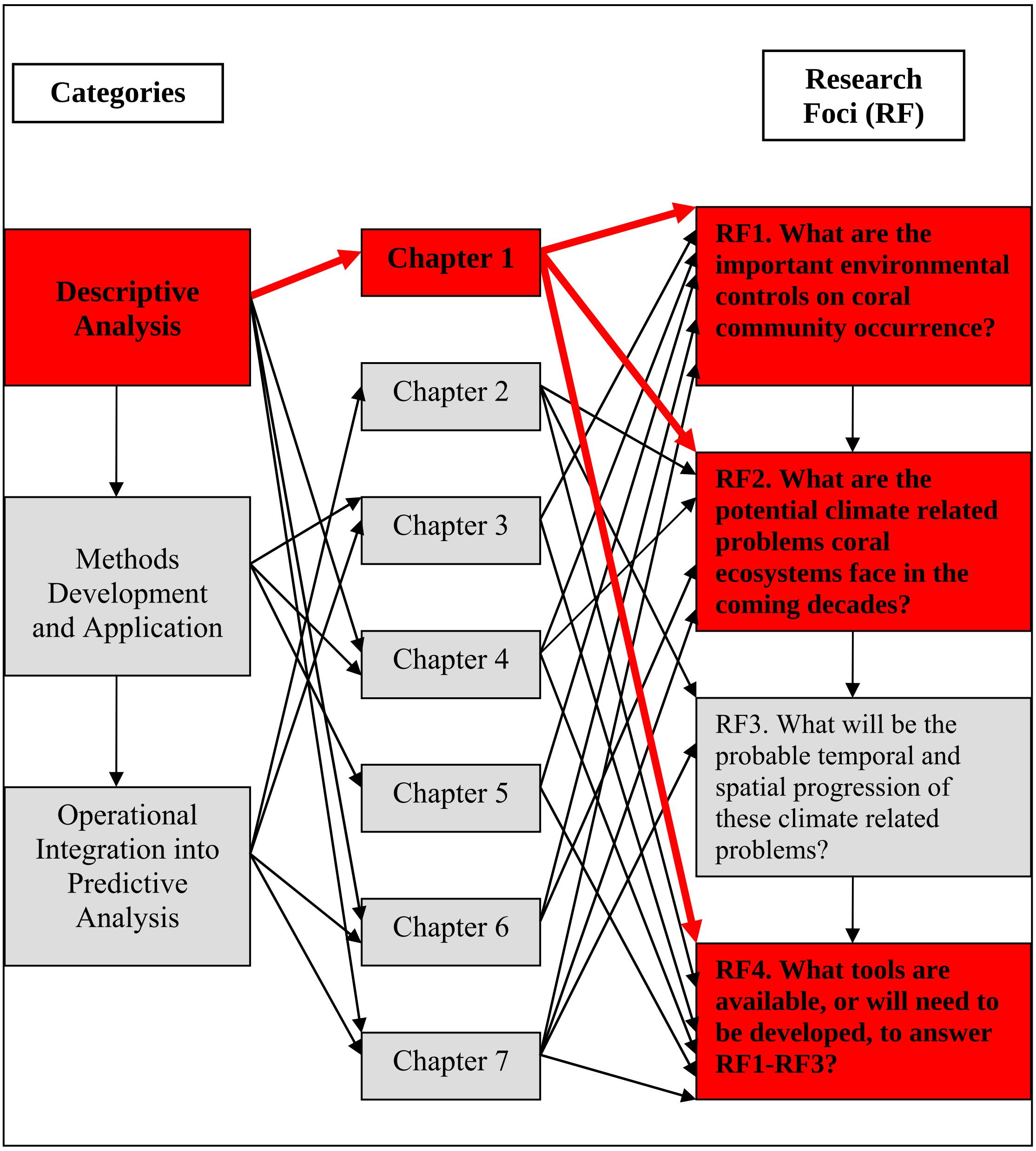


Figure 2: The relevance of Chapter 1 to the overall scheme of the research.

The Great Barrier Reef (GBR) experienced it's most intensive and extensive coral bleaching event on record in early 1998 (Berkelmans and Oliver 1999). Bleaching occurs when there is widespread loss of pigment from coral, due mainly to the expulsion of symbiotic algae (Yonge and Nicholls 1931). The algae are usually expelled in times of stress, often caused by sea surface temperatures (SST) which are higher than the coral colony's tolerance level. This may be as little as 1 to 2 ^{o}C above the mean monthly summer values (Glynn et al. 1988, Drollet et al. 1994, and Berkelmans and Willis 1999). Other causes of stress are above-average amounts of solar radiation, high turbidity, and low salinity. Generally, high SSTs and high levels of solar radiation go hand in hand, and are occasionally accompanied by low tides. This is due to the fact that elevated solar radiation is often a contributing factor to elevated SST, and low tides create shallow semi-enclosed lagoons on individual reefs, allowing the sun to heat the water in absence of any significant flushing from the surrounding cooler waters. Low salinity and high turbidity are often coincident, and are a result of high discharge rates from coastal rivers.

Although most of these causes have been implicated at some sites for the 1998 mass bleaching event (especially some coastal sites where low salinity and high turbidity conditions resulted from floods in January, 1998), the main cause has been identified as elevated SST. The occurrence of bleaching at many locations was patchy with more severe bleaching recorded in shallow waters than at deeper offshore sites. Corals can recover from bleaching but death may result if environmental stresses are extreme and/or prolonged (Done and Whetton 1999).

There is concern among environmental scientists and GBR-based industries, especially tourism industries, that widespread death and bleaching of corals caused by extremely high temperatures and flooding during 1997-98 may occur more frequently in the Great Barrier Reef region if global climate change unfolds as expected during the 21st Century (Done and Whetton 1999).

The need for accurate environmental monitoring techniques that are of use in monitoring coral bleaching is of utmost importance among coral reef researchers. The National Oceanic and Atmospheric Administration (NOAA) National Environmental Satellite, Data, and Information Service (NESDIS) have gone some way towards developing a useful tool with their 'coral bleaching hot spot' maps. These maps are developed from NOAA Advanced Very High Resolution Radiometer (AVHRR) data and are provided via the internet at 50 km resolution. A current version of this product can be seen at http://psbsgi1.nesdis.noaa.gov:8080/PSB/EPS/SST/climo&hot.html.

The "hot spot" maps show temperature anomalies, which are derived by subtracting recent images from a "satellite only" 25-year climatology. The "daily" climatology used an interpolation of the two monthly climatologies closest in time. The July 30, 1999 anomaly chart was calculated by linearly interpolating the July and August climatologies. This 'daily' climatology is subtracted from the operational 50- km SST analysis to produce the July 30 SST anomaly chart labeled 7.30.1999. For a complete description of the process see http://psbsgi1.nesdis.noaa.gov:8080/PSB/EPS/SST/climodoc.html.

This ‘hot spot’ analysis seemed to provide a useful tool for monitoring the onset of the GBR bleaching in 1998. An animation of the progress of the 1998 anomaly through the bleaching period can be found at http://psbsgi1.nesdis.noaa.gov:8080/PSB/EPS/SST/data/ane98e.gif. The onset of the bleaching in early February 1998 seemed to be predicted by the hot spot anomaly for 31 January, 1998 (see Figure 3).

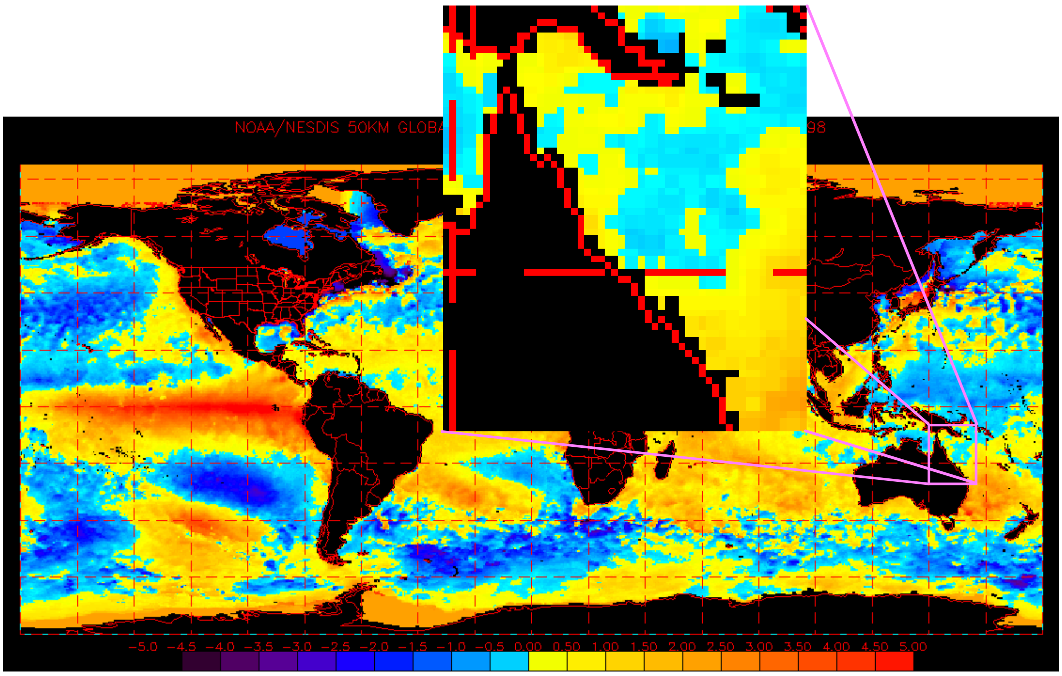


Figure 3. NOAA NESDIS SST anomaly chart for 31 January, 1998.

However, there are resolution problems. The resolution of 50 km and the use of monthly averages do not allow the complete story to be told. Figure 4 is a SST map we produced at 1km spatial resolution using the NOAA non-linear SST (NLSST) algorithm. The NLSST is NOAA’s current operational SST algorithm. Overlaid on this image are the results of coral bleaching intensity map produced by Berkelmans and Oliver (1999). This figure shows in detail the spatial variability in the SST and the bleaching and the correlation between these. This is not apparent in the 50-km NOAA hot spot map (Figure 3). Furthermore, Figure 3 is a snapshot on 31 January, 1998, whereas Figure 4 is a composite for 4 to 5 February, 1998, almost a week later.

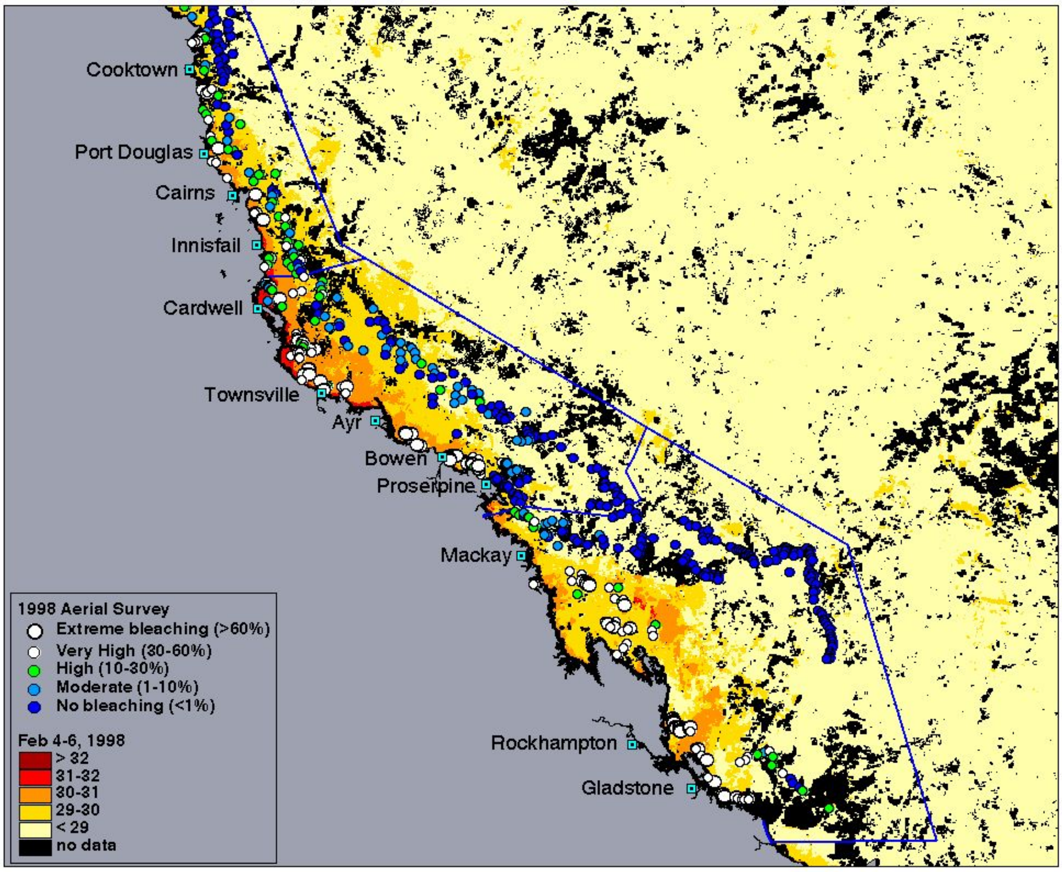


Figure 4. Coral bleaching survey results overlaid on an SST (°C) composite image for 4 to 6 February, 1998. The bleaching data were adapted from Berkelmans and Oliver (1999).

Figure 5 is the same NOAA 50-km temperature anomaly product as shown in Figure 3, but for 7 February, 1998. This image does not match the broadscale spatial variation of SST, depicted in Figure 4, as does the hot spot product for 31 January, 1998. The NOAA NESDIS product requires better spatial and temporal scales to be of significant use for monitoring of coral reef bleaching events in the GBR region.

Figure 4 shows that the severity of bleaching is highly correlated with the AVHRR SST local area coverage (LAC) product. This is due to the fact that the corals have thermal thresholds (Berkelmans and Willis 1999). After their threshold has been reached then they are likely to bleach. The problem with these thresholds is that they are not well understood. It is known that they vary between species and between different geographic sites (Berkelmans and Willis 1999). An accurate satellite-derived SST product would be invaluable for studying bleaching.

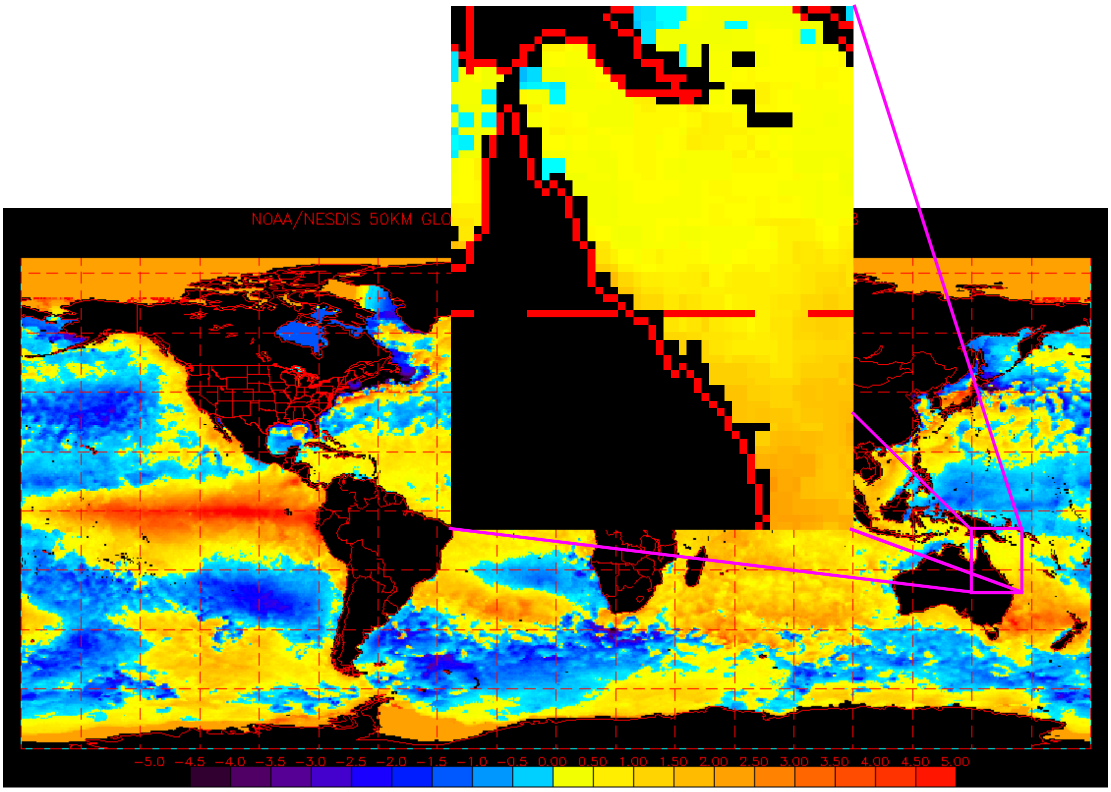


Figure 5. NOAA NESDIS SST anomaly chart for 7 February, 1998.

The NOAA NLSST algorithm is employed by NESDIS and is considered to be one of the most accurate algorithms to date (Barton 1995). This algorithm is designed to provide an estimate of the SST value at a depth of 1 m, from AVHRR data. When applied to the GBR region, the NLSST algorithm slightly underestimates the bulk temperature below about 27°C, and significantly overestimates the bulk temperature above this temperature (Figure 6). The overall root mean square (rms) value is 0.82°C. Figure 7 shows the time series of temperature between 1 September, 1997 and 30 December, 1998 for Kelso Reef (80 km north of Townsville). Note that the NLSST algorithm significantly overestimates the bulk temperature for temperatures above 29.5°C (indicated by the dashed line). The first section of temperatures over 29.5°C in Figure 7 represents the coral bleaching period of 1998 (around day 450).

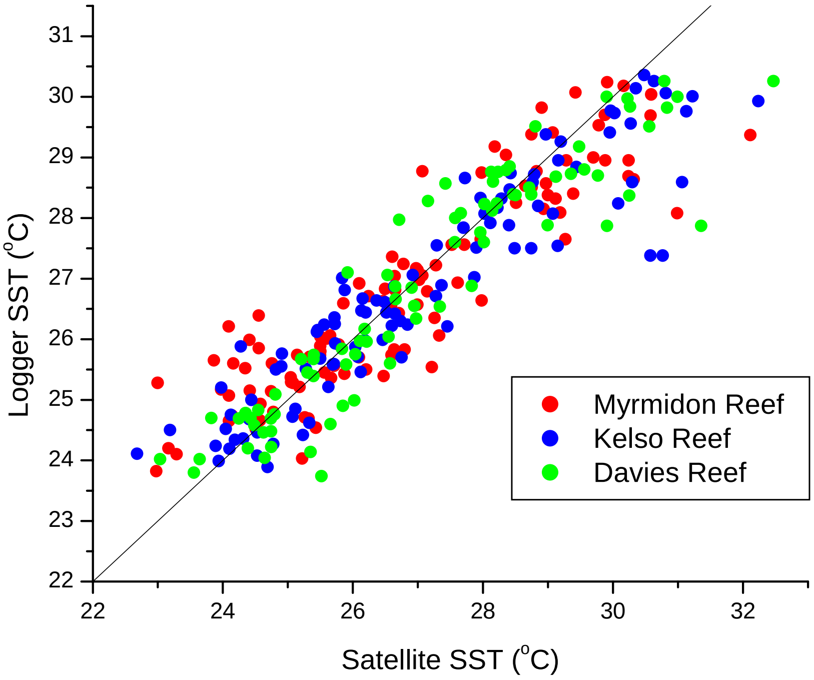


Figure 6. Plot of *in situ* SST logger data (taken in the top few meters of the water column) against coincident satellite SST data (derived by applying the NLSST to AVHRR data collected at the Australian Institute of Marine Science, AIMS). These data were collected between December 1996 and December 1998 and include the coral bleaching event of February 1998.

The reasons for the NLSST algorithm overestimation of temperatures are easily explained for the GBR region. SSTs in excess of 30°C mostly occur during periods of cloudless days with light winds. The lack of cloud allows the sun to heat up the upper few centimeters of the sea surface. The wind-induced mixing would normally mix the cooler, deeper waters with the warmer surface, thus distributing the heat through the water column rather than allowing it to be concentrated at the surface. A lack of mixing creates a stratified water column within the first few tens of centimeters of the surface, making the skin temperature atypically higher than the temperature at a depth of 1 m (the depth at which the NLSST is tuned). Yokoyama et al. (1995) described similar effects on satellite SSTs in Mutsu Bay, Japan.

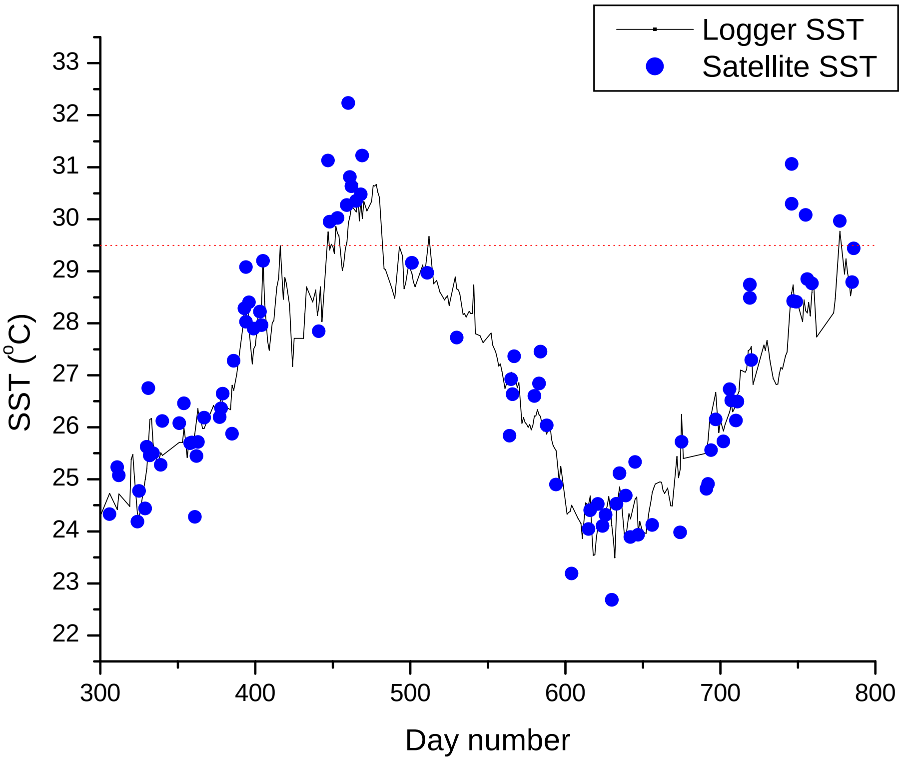


Figure 7. Time series of SSTs derived from logger and satellite data for Kelso Reef for the period 1 September, 1997 to 30 December, 1998.

Typically, the skin temperature (that measured by the satellite) will be between 0 and 0.5 ^{o}C cooler than the temperature at a depth of 1 m (Wick et al. 1992). This is due to two mechanisms. The “skin effect” (Saunders 1967, Mobasheri 1995) is the term associated with a cool skin due to loss of heat via the process of evaporation. The second mechanism is due to wind waves, which are the main mechanism for mixing within the top few meters of the sea surface (Massel 1996). Wave-induced mixing decreases the temperature gradient through the first meter of water (Mobasheri 1995). By not explicitly taking account of these two effects in the NLSST, Walton et al. (1998) effectively built an average temperature gradient into their algorithm based on the average amount of mixing and evaporation implicit in the ground truth data used to derive the algorithm. This is the main reason for the poor performance of the NLSST in the GBR region during the 1998 coral bleaching event. The performance of the NLSST algorithm can be seen in Figure 8.

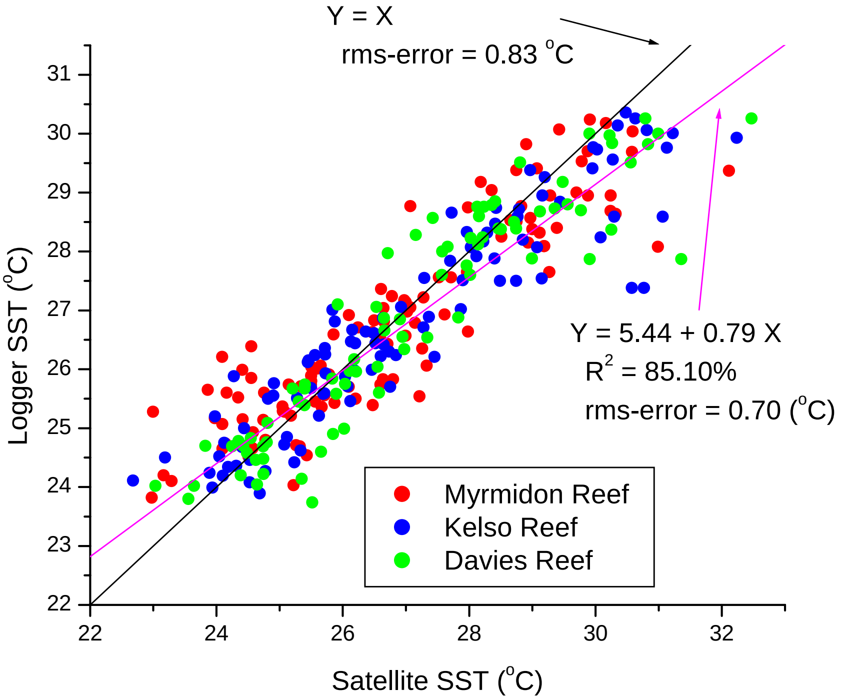


Figure 8. Scatter plot of logger SSTs against NLSST-derived AVHRR SSTs. The solid line is the one-to-one relationship and the dashed line is the linear least-squares fit.

The rms error of the one-to-one line is 0.83°C. This error can be decreased to 0.7°C if we fit a least squares' linear function to the data. Although this is only a modest improvement, it will greatly improve the SST estimates above 30°C. This function can be used as a "regional fix" for NLSST-derived SST values for the GBR. The function is:

$$Y = 4.55 + 0.79\,X,\ R^2 = 85.10\%,\ \text{St-error} = 0.70\ ^{o}C \qquad (1)$$

where Y is the corrected SST and X is the AVHRR SST derived with the use of the NLSST.

In an attempt to improve on the accuracy of the NLSST, we derived a new SST algorithm for the GBR. This is a skin SST algorithm which overcomes the problems of the skin/bulk temperature variations by avoiding its use in the first instance. The new algorithm is

$$SST = A + B\,bt4 + C\,bt45 + D\,(bt45)^2$$

where $A = 9.21083 - 6.74323\,sec\theta + 9.09126\,(sec\theta)^2$

$B = 0.9676 + 0.02535\,sec\theta - 0.0292\,(sec\theta)^2$

$C = 1.1246 + 0.3183\,sec\theta - 0.228\,(sec\theta)^2$

$D = -0.22123 + 0.73108\,sec\theta - 0.35553\,(sec\theta)^2 + 0.06464\,(sec\theta)^3$

$bt4$ is the brightness temperature of AVHRR channel 4

$bt45$ is the difference between AVHRR channels 4 & 5

θ is the satellite look angle as measured at the surface

This algorithm uses AVHRR channels 4 and 5 to derive a skin SST, and is applicable to the GBR. Without testing, it would not be wise to assume that this algorithm will be accurate outside this region.

Figure 9 shows a plot of the results of this algorithm against data collected on board a ferry, just north of Townsville, over a period of two years (1997-1998). This algorithm has an rms error of 0.4 ^{o}C when compared to the radiometer data. This is a significant improvement on the NLSST performance. The difference between these two errors associated with each of the algorithms can be largely explained by the variation in the skin/bulk temperature difference.

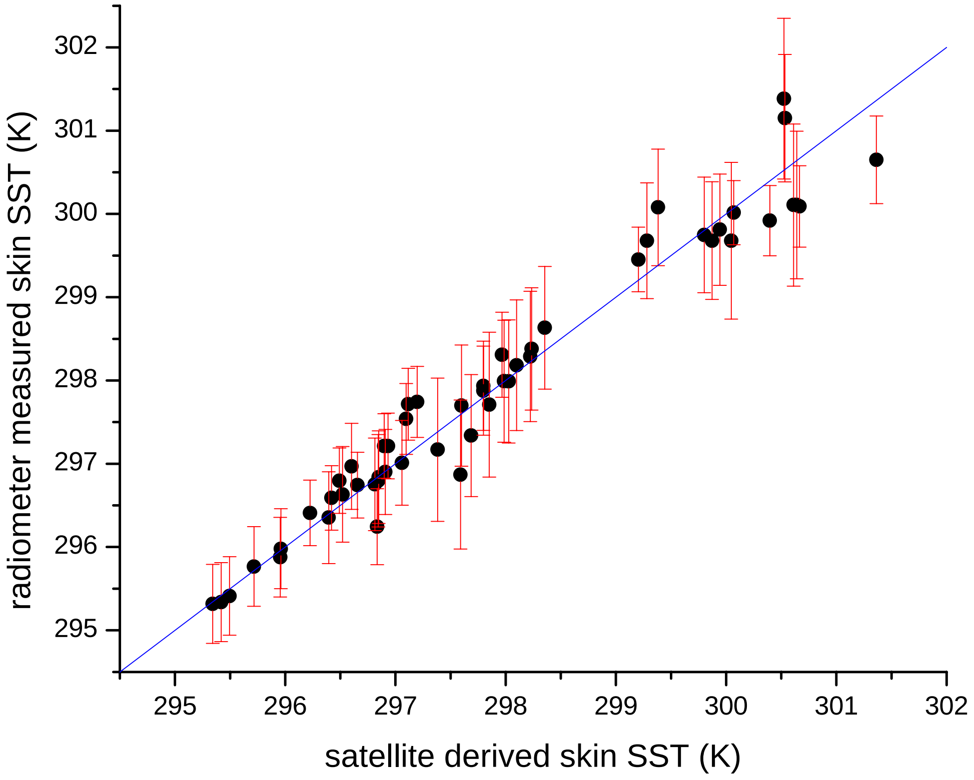


Figure 9. Radiometer-measured skin SST vs. satellite-derived skin SST. The error bars represent two standard deviations (95% of variance) as estimated from the AIMS algorithm (which includes the ability to derive an estimate of error).

The skin/bulk temperature difference is not well correlated with SST, but is likely to be explained via the two main mixing mechanisms, wind and tidal currents. Future work is being directed towards relating the skin SST (derived using their AVHRR regional skin algorithm) to the bulk water temperature with the use of local wind and tide data.

Until this work is complete, the best method for deriving bulk SSTs for the GBR from the NOAA AVHRR sensor is the NOAA NLSST algorithm with the "regional fix" applied.

Water Movement within the GBR

In gaining an insight into the causes of the 1998 GBR bleaching event, first an understanding of the mechanisms which cause water movement, both vertical (mixing) and horizontal (advection), is necessary. Vertical exchange of water due to turbulence causes the cooler bottom waters to become mixed with the warmer upper waters, effectively distributing the heat throughout the water column and thus cooling the sea surface. When currents circulate around reefs, the secondary circulation around reefs provides an efficient mechanism for mixing the cooler bottom waters with the warmer top waters in and around the reefs (Wolanski et al. 1996).

Horizontal movement, or advection of water by currents, is an important mechanism for moving hot or cold water from its place of origin to another geographic location. The water circulation within the GBR is affected by the wind, the tides, and by the East Australian Current (EAC) and the Hiri Current (Andrews and Clegg 1989).

The latter are western boundary currents, flowing, respectively, southward and northward, and are a result of the bifurcation of the South Equatorial Current as it is deflected by the Australian continent between latitude 14 and 18°S (Church 1987, Andrews and Clegg 1989, Burrage 1993). The exact location of the bifurcation point varies seasonally and also inter-annually. These low frequency currents exert most of their influence over the waters of the outer shelf (Wolanski 1994, Burrage et al. 1996, also see Spagnol et al., Chapter 14, this book).

Tidal currents vary in strength along the length of the GBR (King and Wolanski 1996). The tides in the northern and central GBR have ranges of up to about 3.5 m, whereas the southern GBR is a region of macro tides, parts of which experience tidal ranges exceeding 6 m (Wolanski 1994).

The most influential forcing mechanism, on time scales of 2 to 20 days, for currents within the GBR lagoon is the wind (Wolanski and Thomson 1984, Burrage et al. 1991, Wolanski 1994). During the winter (the dry season) the dominant winds are the southeast trades, which create a northward current over the shelf. During the summer monsoon, the winds can be more fickle. In general the wind induced currents north of the monsoon trough will have a southward component and those south of the trough will have a northern component.

GBR Weather and SST during February 1998

Since the beginning of instrumental records in 1856, 1998 was the warmest year on record (Karl et al. 2000, also see Lough, Chapter 17, this book). Clearly the highest

SSTs occurred during February 1998, as can be seen in Animation 1, which shows monthly satellite-derived SST for the GBR between January 1997 and December 1999.

In the northern GBR region (north of the Whitsunday Islands) the majority of bleaching occurred during the first week of February 1998. Between the 1 and 5 February, 1998, low winds and neap tides (Figure 10) combined to create a period of little to no mechanical mixing of the top few meters of water. These conditions when combined with little or no cloud, allow the sun to efficiently heat up the top few meters of water to remarkably high temperatures. In the absence of significant vertical mixing, this results in a stratified temperature structure. This layer will continue to get hotter until the layer is mixed with cooler bottom waters as a result of wind and/or tidal mixing processes.

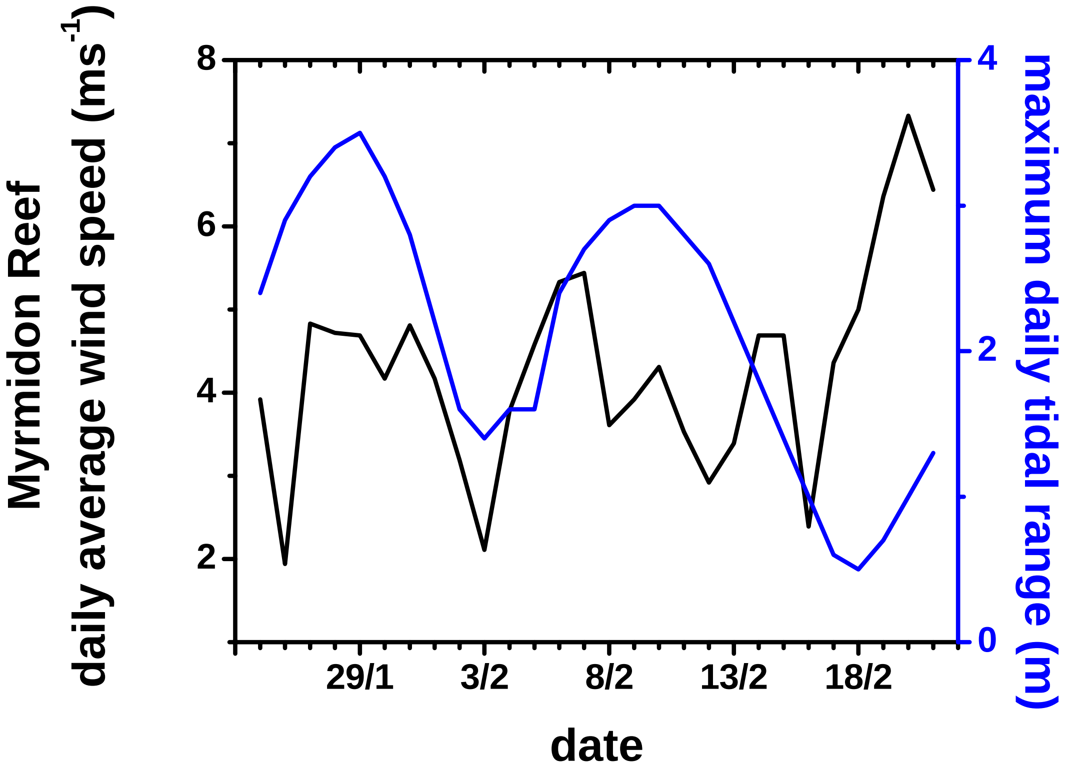


Figure 10. 1998 plot of tidal range (maximum tide height less the minimum tide height for each day) on the right axis (dashed line) and wind speed on the left axis (solid line).

This almost happened again during the next set of neap tides (two weeks later), however the lull in the wind was for a considerably shorter period and the low winds and neap tides did not align themselves quite as well as they did earlier in February.

The 3-day Averaged SST

We shall now concentrate on the period between 25 January and the 21 February, 1998. The following three sections will make use of animations based on three days running means of satellite SST images. These images are derived from AVHRR LAC data (Advanced Very High Resolution Radiometer, Local Area Coverage).

Animation 2 shows the SST distribution for this period. There are three main features to be drawn from this animation. Firstly, there are two separate regions of hot water genesis, one near Townsville and the other south of Mackay. Secondly, the timing, growth and movement of these two hot water masses differed. Lastly, the southern Whitsunday Islands (adjacent to Proserpine) remained relatively cool throughout the bleaching period. Possible reasons for this will be examined later.

There appears to be a separate story concerning the water which caused bleaching in the central and northern GBR as apposed to the story in the southern GBR. As a result, these two regions will be examined separately.

The Central and Northern GBR Story

Animation 3 shows the distribution of 3-day averages of satellite SSTs for the GBR north of the Whitsunday Islands between 25 January and 21 February, 1998. Figure 10, showing the tidal range and wind speed, has been imbedded into this animation. A red bar has been positioned over the imbedded graph which indicates the central date associated with the 3-day average for each frame of the animation. The date associated with the three day animation is also indicated at the top of the key in the lower left of the screen.

As shown in Animation 3, the beginning of the warm period corresponded to 2 to 4 February, when both the wind and tidal range were at a minimum. This represents a period of little to no mixing and maximum heating (no cloud). Immediately following this period, the wind and tides increased the mixing, and the skin temperature (the temperature sensed by the satellite) cooled down as the cooler bottom waters were mixed with the warm upper water. By 7 February, the wind speed had reached a maximum and the tidal range had increased. This increased vertical mixing and resulted in a minimum for water temperatures. This period of high average winds was characterized by strong winds from the southeast intertwined with periods of low winds with a more easterly direction. These strong winds generated a northward coastal current. This current took some time to generate and manifests itself in Animation 3 after a few days when the hot water around Innisfail was advected northward along the coast and past Cairns towards Port Douglas. The end of this advection corresponded to a period of lower winds, providing the mechanism for another period of high surface temperature.

By the 14th February, the winds had picked up again, cooling the surface waters. The period around the 16 February had the potential to cause the most bleaching of this entire period. The wind speed and tidal range were smaller than during the initial hot water period around 3 and 4 February. However, due to cloud cover, significant amounts of direct solar heating were missing. This saved the reef from record high temperatures. This cloudy period marked the end of the bleaching event in GBR north of the Whitsunday Islands.

The Southern GBR Story

The story in the southern GBR, south of the Whitsunday Islands, was somewhat different to that of the north. There was considerably more cloud cover throughout this whole period, as can be seen in Animation 4. This animation also shows a plot of winds and tidal range for this region between 25 January and the 21 February, 1998. The initial low in wind speeds occurred 1 day earlier than it does in the northern region, creating a slight mismatch with the neap tides which occurred on 3 February. This meant that the mixing depth would have been deeper through this initial warming period than it was in the northern region. Cloud amounts in the southern region were also still quite high, preventing any significant heating. Consequently, during the initial bleaching period in the northern region, water temperatures in the southern section were considerably lower than in the north.

After this period of low wind, the winds picked up substantially and the mixing process cooled the surface waters (Animation 4). As with the northern region, there was another period of low winds only a week later, but unlike the northern section, this coincided with a maximum in the tidal range in the south, effectively maintaining mixing and preventing any significant heating.

Animation 4 demonstrates that the major heating period for the southern GBR was between 15 and 17 February, during which time the winds and tidal range were sufficiently low during a period of relatively low cloud cover.

Discussion

The SST stories during the 1998 coral bleaching event in the GBR demonstrate the importance of mixing. The wind waves, when they occurred, appeared to cool the surface water surface and prevent bleaching.

The tidal currents also were important in decreasing surface temperature. These currents vary in strength along the length of the GBR, with the strongest currents in the south. North of the Whitsunday Islands, the tidal currents associated with neap tides were small enough to create no discernable mixing. This is demonstrated in Animation 3 during neap tides, when the temperature of the water over and near the reefs was the same as in the surrounding waters. This can only happen if there was negligible mixing.

The same was not the case for the southern GBR where the tides are much larger. Even during neap tides, the tidal excursion remains considerable. The effect of this is for the waters around reefs in this region to be well mixed, as is shown in Figure 11. This image suggests tide-induced mixing, because the temperatures in the waters surrounding the southern GBR were high (exceeding bleaching thresholds), whilst the waters in and around the reefs were considerably cooler. This suggests that the tide-induced mixing enabled these reefs to escape bleaching during this period.

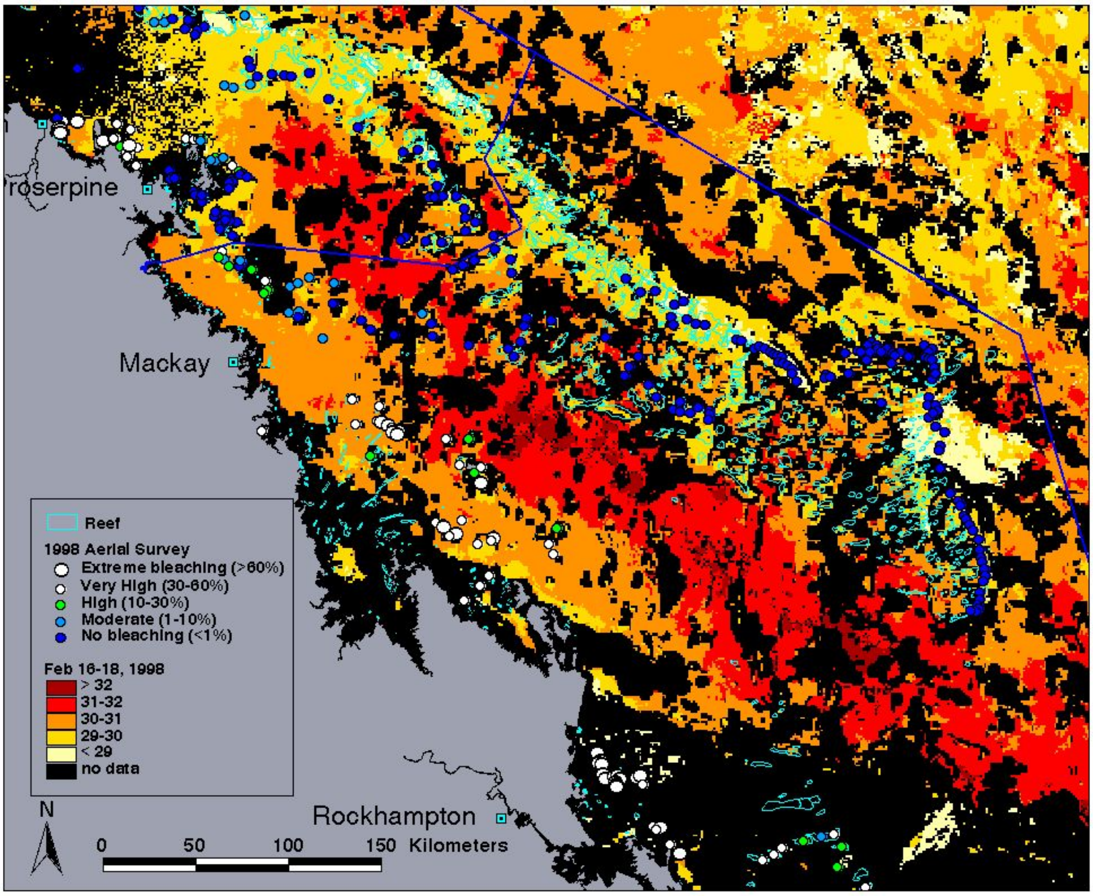


Figure 11. Average SST (°C) for 16 to 18 February for the southern GBR region. Reefs and bleaching are also depicted.

To illustrate the importance of tide-inducing mixing, we will focus on a cross-shelf transect in the northern part of this region. Figure 12 shows details of the SST distribution, while the bathymetry for this same region is shown in Figure 13. Figure 14 is the plot of depth and SST along a cross-shelf transect. This figure shows that the SSTs were highest in deep water and lowest in shallow water in and around the reefs. This is a striking demonstration of how the tides create mixing around the reefs.

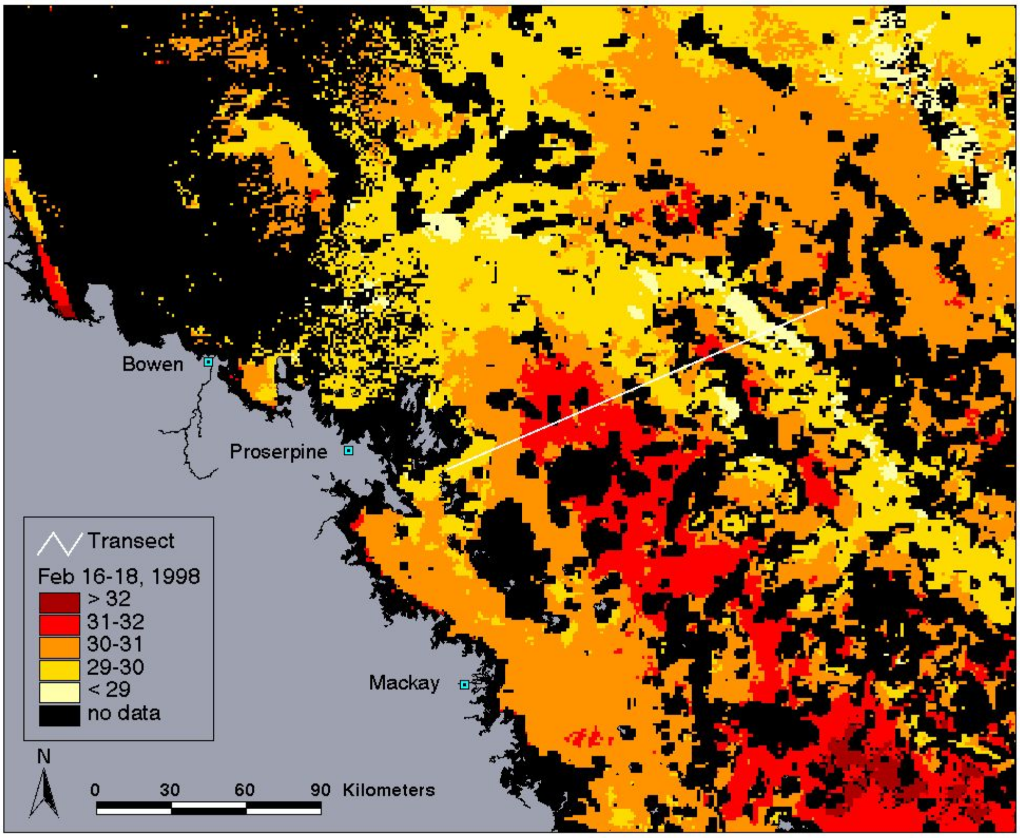


Figure 12. Subset of Figure 11, showing location of an SST (°C) transect (white line).

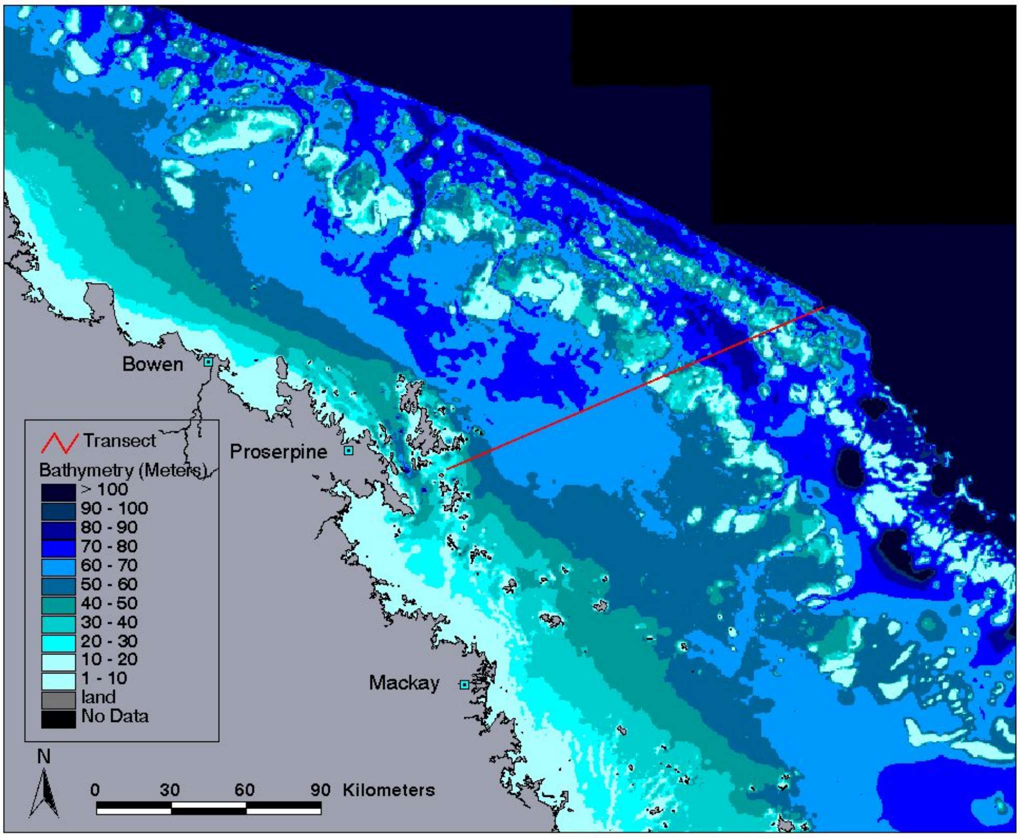


Figure 13. Subset of Figure 11, showing the location of bathymetric transect (red line)

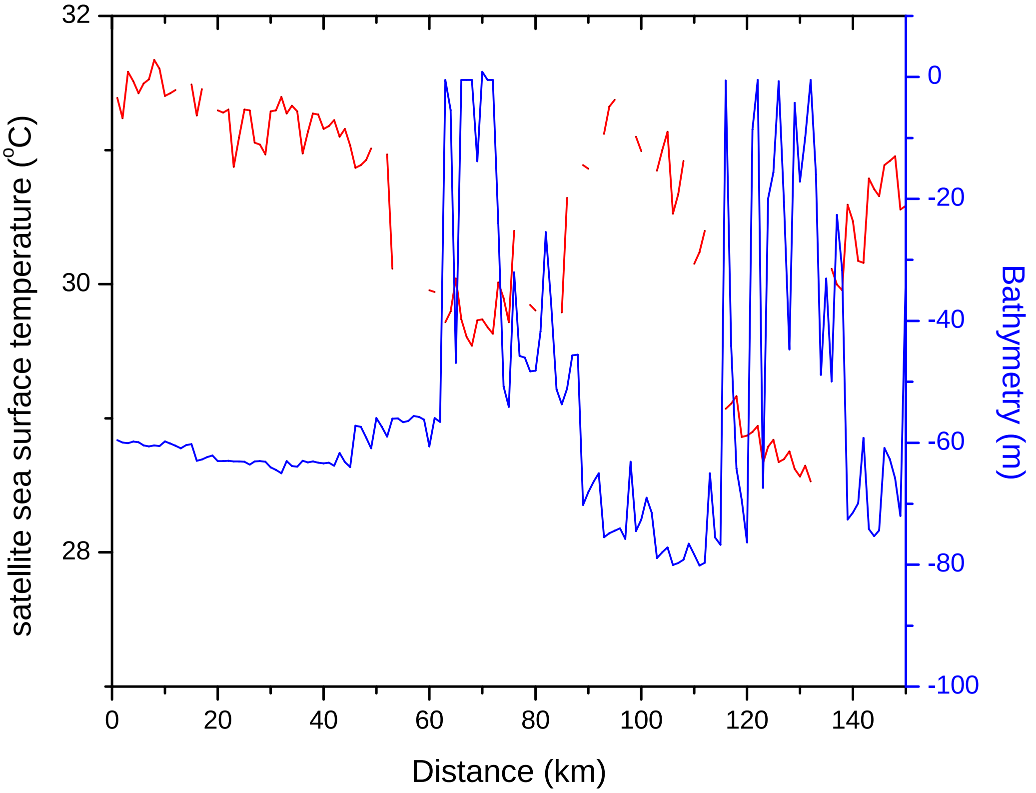


Figure 14. Transect plot (from Figures 12 and 13) of satellite SST (thick red line) and the bathymetry (thin blue line).

Figure 11 also suggests that isolated reefs are vulnerable to bleaching, while reefs in the wake of others may benefit from the mixing that occurred around the leading reef. Indeed, the reefs around the Capricorn Bunker Group (southeast of Rockhampton, in Figure 11) are an example of this. The outside reefs were severely bleached whilst the middle reefs were only moderately bleached.

Lastly, the southern Whitsunday Islands seemed to escape bleaching due to a combination of mixing due to the interaction of the tidal currents with the many islands in the region and considerably more clouds than most other parts of the GBR (Animation 4)

Conclusion

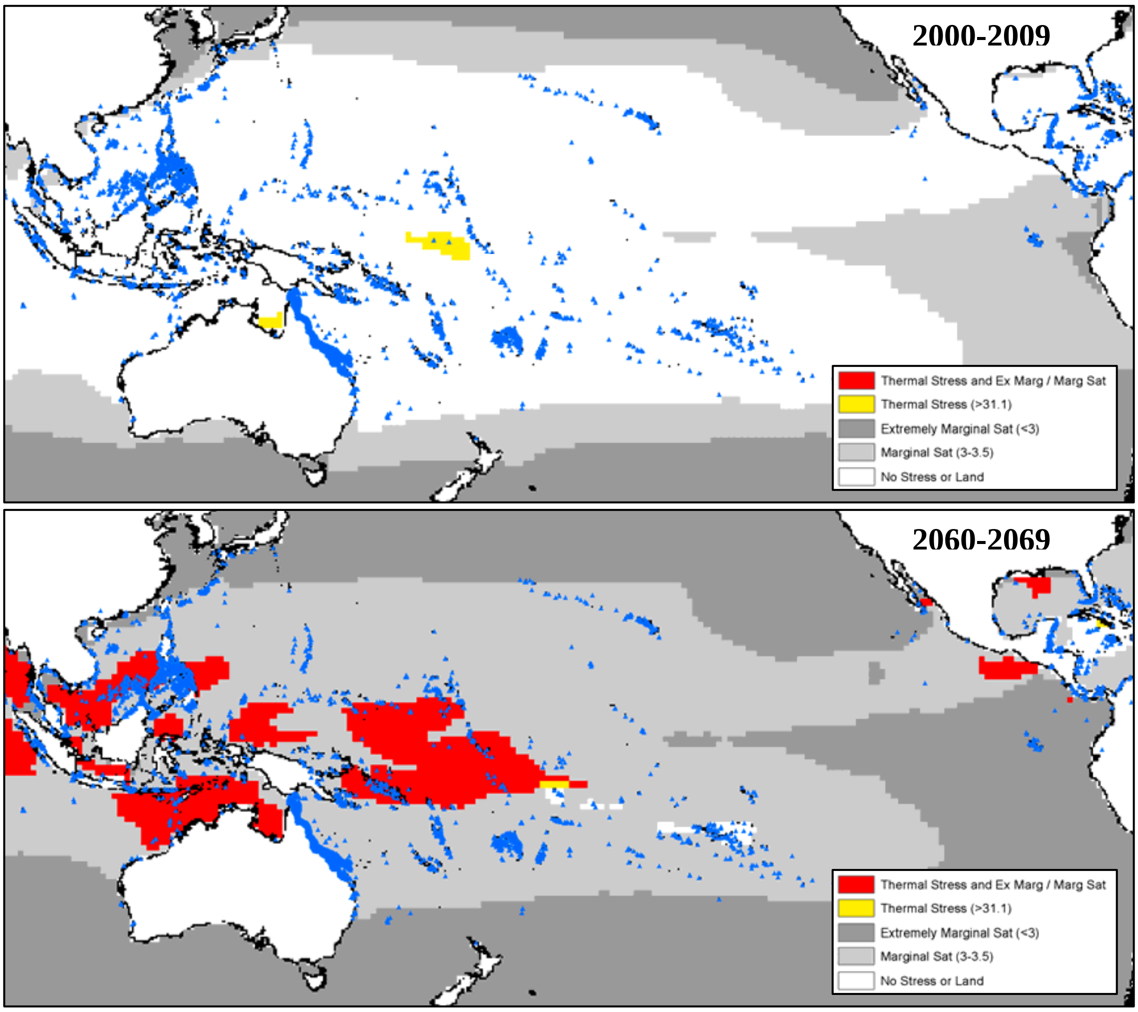
The GBR bleaching event during 1998 was caused by a coincidence of three local variables: neap tides, low winds, and clear skies. These conditions were not all that unusual and could have happened at any time in the past, and will definitely happen again. The link to climate is not clear. Global warming may provide the conditions for these three variables to coincide more frequently in the future and hence cause more bleaching more often.

During the GBR 1998 bleaching event, bleaching only occurred in the absence of mixing. In all bleaching cases, the winds were low. Many reefs seemed to escape the bleaching temperatures by interacting with the tidal currents to induce vertical mixing and hence cool the hot surface waters by mixing them with the cooler lower waters.

Based on the 1998 bleaching event, it would appear that some reefs are less likely to bleach due to their exposure to strong currents. Clearly, processes of mixing around reefs deserve further detailed investigation.

Chapter 2

Future Coral Reef Habitat Marginality: Temporal and Spatial Effects of Climate Change in the Pacific Basin



Citation:

Guinotte JM, Buddemeier RW, and Kleypas JA (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. Coral Reefs 22:551-558.

Abstract

Marginal reef habitats are regarded as regions where coral reefs and coral communities reflect the effects of steady-state or long-term average environmental limitations. We used classifications based on this concept with predicted time-variant conditions of future climate to develop a scenario for the evolution of future marginality. Model results based on a conservative scenario of atmospheric CO_2 increase were used to examine changes in sea-surface temperature and aragonite saturation state over the Pacific Ocean basin through 2069. Results of the projections indicated that essentially all reef locations are likely to become marginal with respect to aragonite saturation state. Significant areas, including some with the highest biodiversity, are expected to experience high-temperature regimes that may be marginal, and additional areas will enter the borderline high temperature range that have experienced significant ENSO-related bleaching in the recent past. The positive effects of warming in areas that are presently marginal in terms of low temperature were limited. Conditions of the late 21st century do not lie outside the ranges in which present-day marginal reef systems occur. Adaptive and acclimative capabilities of organisms and communities will be critical in determining the future of coral reef ecosystems.

Personal Contribution and Context within the Thesis:

My personal contribution to this work included obtaining relevant temperature and chemical data from various sources and synthesizing the two data sets into a cohesive and meaningful time series. Significant writing input including full responsibility for manuscript revisions and coordination among co-authors. Contribution percentage: John Guinotte (45%), Bob Buddemeier (45%), Joanie Kleypas (10%).

Chapter 2 builds on the scientific information gained from Chapter 1 (threats from elevated SST) by plotting projected SSTs throughout the Pacific Basin and introducing another CO_2 related threat, decreasing aragonite saturation state. This chapter directly addresses Research Foci 2, 3, and 4. (Figure 15). High SSTs and decreasing aragonite saturation state were identified as being significant threats to coral ecosystems in the Pacific Basin and coral communities globally (RF2). GIS was used to plot the spatial and temporal progression of each threat individually and the overlap of both threats was plotted to determine which coral areas in the Pacific Basin will experience the synergistic effects of both high SST and low saturation state (RF3). Finally, implications for reef research, management and conservation are identified and recommendations of future tool development are made (e.g. a methodology to quantify the spatial overlap between regions of high coral biodiversity and projected marginality in terms of future sea surface temperature and aragonite saturation state) (RF4).

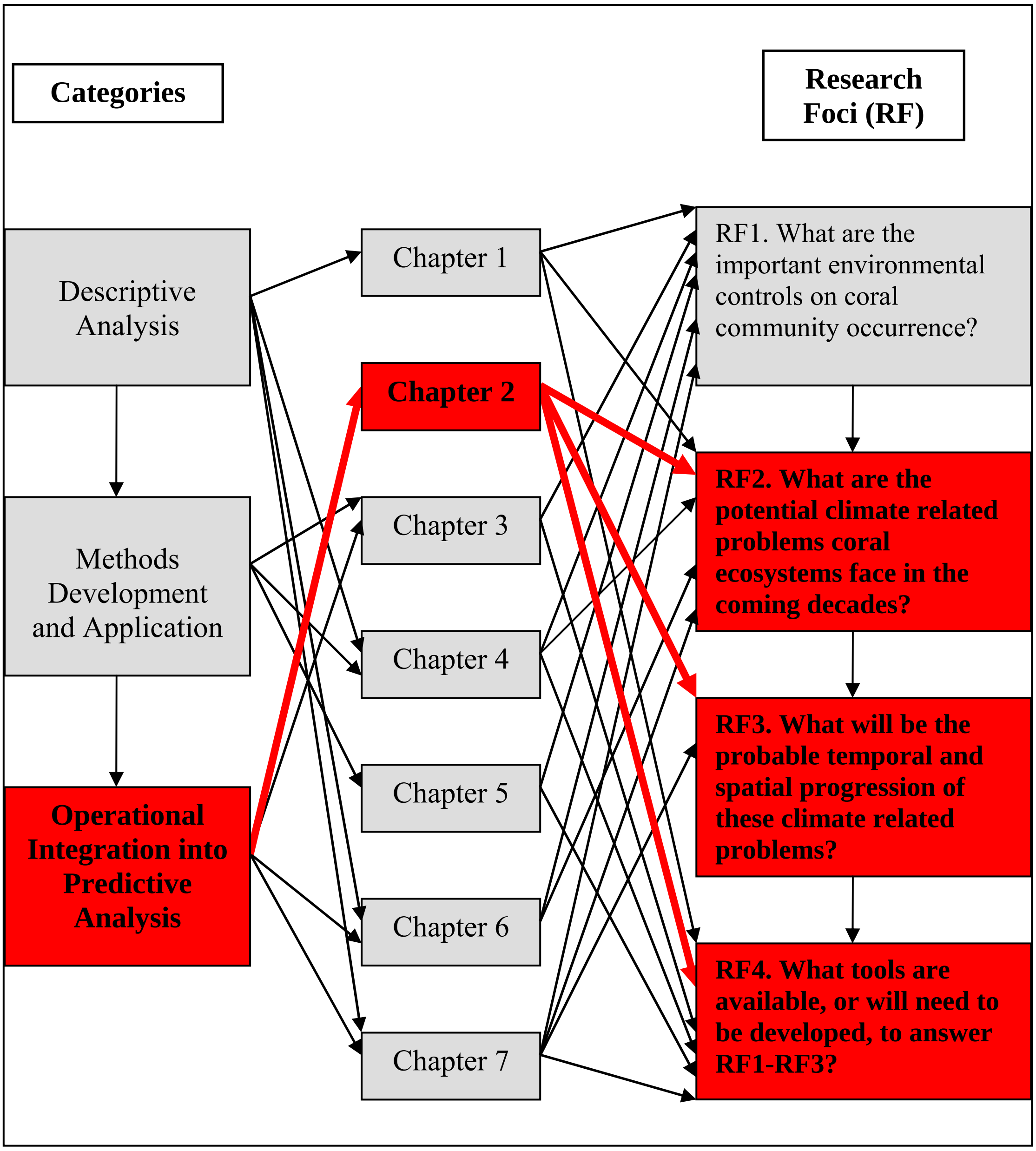


Figure 15: The relevance of Chapter 2 to the overall scheme of the research.

Introduction

Coral reefs and reef communities have been defined in many different ways (Kleypas et al. 2001), and there is no consensus for determining the condition under which a coral assemblage is judged marginal in terms of ecosystem function, nor for assessing marginality of habitat independent of what happens to be living there at any given moment. Similarly, the term 'marginal' is itself subject to different definitions and interpretations. Marginality may be defined:

(1) in a purely statistical sense, identifying the subset of reef communities or conditions that are near the extreme of a particular suite of environmental variables or community conditions;

(2) on the basis of proximity to an environmental condition known or reasonably assumed, based on physiological or biogeographic evidence, to place an absolute limit on the occurrence of reef communities or key classes of reef organisms; or

(3) in terms of organism and community condition (cover, composition, diversity, health) or metabolism. We address the interacting concepts of community and marginality below.

Kleypas et al. (1999b) used cluster analysis to define marginal reef categories at a global scale in the statistical sense. Many of the marginal categories defined coincide well with marginality in terms of definition 2 and 3 above. These marginal groupings generally represent the low ends of the environmental distributions – low temperature, low salinity, low light, and low aragonite saturation state. At the global scale, high-value clusters generally do not abut or grade into areas of clear absolute limitation, although high extremes of temperature, salinity, and light (or their combinations) can be shown to be stressful (hence potentially limiting) at local scales or in the laboratory. This emphasizes the importance of specifying spatial and temporal (both duration and frequency) scales in discussions of marginality. The definition of future marginality used here refers to those reefs that are in danger of becoming marginal (i.e. being pushed beyond their “normal” environmental limits (Kleypas et al. 1999b) due to increasing sea surface temperatures and decreasing aragonite saturation state).

A community with high cover and high diversity of healthy, zooxanthellate, scleractinian corals, with hydrocorals and reef-associated calcifying algae, would meet almost any standard for a non-marginal reef community. As diversity, cover, and health decline, the community itself becomes more marginal; this may or may not mean that the habitat (local or regional environment) is necessarily more marginal in a general or long-term sense. One specific example may be drawn from the observations of Done (1999), who described coral communities on the Great Barrier Reef (GBR) as a "shifting steady-state mosaic." Overall, the GBR is far from most people's concept of a marginal reef environment, but it is one with a high level of dynamic disturbance and recovery. Over decadal averages or spatial scales of 100s to 1000s of km the reefs are healthy – but at any given moment a specific reef site may look very marginal as the result of cyclone damage, *Acanthaster* predation, or bleaching (definition 3). By contrast, Harriott and Banks (2002) describe the systematic and consistent increase in marginality with increasing latitude south of the GBR. The latter case – a large-scale geographic marginality gradient that clearly relates to habitat characteristics – has the potential to help us understand biogeography and physiological limits on climatic and evolutionary time scales.

In the present “coral reef crisis” (Wilkinson 2000) there is great concern that many reef communities are passing very rapidly from healthy to marginal (in the sense of definition 3 above) to dead. These transitions are generally associated with increased stresses, which may be local anthropogenic, large-scale climatic and environmental, or both. The acute local forms of stress are readily identified (e.g., physical destruction, eutrophication, etc.), and are potentially controllable. What is less clear is the role of “background” environmental change in increasing marginalization (definition 2 above) – particularly the effects of changing ocean chemistry and temperature. The roles of temperature, salinity, nutrients, light, water motion, and carbonate saturation state in defining the geographic limits of coral and reef occurrence are well established (Smith and Buddemeier 1992, Veron 1995, Kleypas 1997, Kleypas et al. 1999b, Guinotte 1999), although for most of these, the mechanisms of how they limit coral reefs (both environmentally and geologically) are not necessarily well understood.

Among current concerns is the question of how these environmental controls will change over time and space, and of the significance of the changes to ecosystems. Within the present century, Earth is predicted to attain conditions of temperature and carbon dioxide concentration that have not co-occurred since the evolution of modern reef systems after the Eocene (B. Opdyke pers. comm., Wood 1999); our present and future environment has been referred to as the no-analog earth (Steffen and Tyson 2001). Throughout Earth history, low temperatures have placed an absolute limit on reef development. Today, high as well as low temperatures place an absolute limit on reef occurrence, or create marginality in the cases of definitions 2 and 3. Much effort is currently being devoted to conservation, threat mitigation, and management, however, without some basis for estimating future environmental baselines and probable changes in marginality of local habitats, long-term success is unlikely in a rapidly changing world (Buddemeier 2001).

We systematically extend the work of Kleypas et al. (1999b) on contemporary marginal environments (definitions 1 and 2) to consider the global-scale effects of CO_2 increase and global warming through 2069. Kleypas et al. (1999b) found that contemporary geographic variations in light, temperature and aragonite saturation state accounted for most of the variation in reef occurrence at the global scale. Since day length and sun angle (two of the major controls on available subsurface light) will not change over this time, and the effects of changing cloud cover or water transparency cannot be predicted at the global scale, we consider only the effects of temperature and saturation state.

CO_2 concentration in the surface ocean is largely controlled by the combination of atmospheric concentration and temperature; and since CO_2 is well-mixed in the atmosphere, aragonite saturation state is highly correlated with sea surface temperature. Temperature has long been considered the factor limiting reef development to tropical and subtropical environments, but recent evidence indicates that calcification rates of reef building corals and algae are positively correlated with aragonite saturation state (reviewed by Gattuso et al. 1999, Gattuso and Buddemeier 2001, Kennedy et al. 2002, Langdon in press). There is no evidence that high saturation state limits coral growth or reef development, but low saturation state, can be limiting at biological, ecological, and geological levels. Reef-building corals and algae are obligate calcifiers, and reduced skeletogenesis will not only reduce their ability to compete for space and withstand erosion, but can be expected to interact with other aspects of life history and ecological function. The three-dimensional structures and resultant niche diversity provided by corals are important factors in the high general biodiversity of reef communities, and these depend heavily on coral skeletal growth. At geological scales, carbonate accumulation and lithification – the processes that distinguish true reefs and coral communities (Buddemeier and Smith 1999) – would be reduced by lowered calcification rates.

Although low temperature and low saturation state appear to represent 'marginal' conditions by both definitions 1 and 2 above, high temperature is a more complicated issue. Elevation of temperature is clearly stressful to corals, and there are clear metabolic responses to temperature and its change (Gates and Edmunds 1999). However, there is also evidence that corals can adapt and acclimatize to temperature (reviewed by Jokiel and Coles 1990, see also Gates and Edmunds 1999), and there is currently no solid basis for determining an absolute upper temperature limit. In view of the abundant evidence for thermal stress as a factor in bleaching and mortality, we chose the statistical definition of high temperature marginality used by Kleypas et al. (1999b) to illustrate patterns of change over time and to assess habitat change.

We examine a time-series of changing saturation state and temperature conditions in the Pacific Ocean region, and specifically the expansion of these conditions that we currently associate with reef marginality, to identify specific regions that may experience early, extreme, or multiple stresses as a result of climate change. The Pacific region reefs vary broadly in diversity, geographic connectivity, and anthropogenic impacts, and provide an opportunity to examine pronounced gradients in both climatic and non-climatic factors associated with habitat marginality.

Methods

Future ocean sea-surface temperature (SST) was calculated from the NCAR Community Climate System Model CCSM v 1.0 (Boville and Gent 1998). The CCSM is a non-flux corrected model with fully coupled atmosphere, ocean, ice and land components, and has a spatial resolution of 2.4 deg longitude and 1.2–2.4 deg latitude. Future changes in SST were determined as the difference between SSTs from the 'B2' computation, which used the IPCC SRES B2 emissions scenario (Nakicenovic and Swart 2000), and a control computation that used constant atmospheric conditions set at preindustrial levels. SRES B2 is based on relatively slow population growth, a rapidly evolving economy, and an increasing emphasis on environmental protection (Nakicenovic and Swart 2000). It therefore projects low-to-moderate increases in CO_2 levels (increasing from approximately 375 ppm at present to 517 ppm by 2069). These increases are more conservative than the 'classic' IS92a scenario, and in fact is one of the most optimistic scenarios.

Model SSTs were averaged over decadal intervals between 2000 and 2069. Monthly averages were calculated for each 10-year average, from which the 10-year minimum and maximum values were determined. Differences between the B2 and control computations were determined and resampled to a 1x1° grid. Future SSTs were determined by adding the CCSM B2-Control SST differences to present-day SSTs derived from the Reynolds optimally interpolated SST data set (Reynolds et al. 2002). This data set incorporates remotely-sensed and ship-board observations, and has provided both weekly and monthly averages since mid 1981. Monthly data were used to calculate decadal averages for the periods 1982–1991 and 1992–2001, as was done for the model data. Because the 1992–2001 averages are warmer than the 1982–1991 averages, and may be contaminated by global warming, the 1982–1991 averages were used as the ‘baseline’ SST data set, keeping in mind that this decadal average may also have significant warming relative to preindustrial SSTs. Aragonite saturation state was calculated at 10-year intervals and 1x1° spatial resolution, using projected CO_2 levels from the IPCC SRES B2 scenario (Nakicenovic and Swart 2000), and the CCSM-derived projections of SST change as described above. Saturation state calculations were the same as those described by Kleypas et al. (1999a). The 1870 pCO_2 conditions were used to calculate the preindustrial baseline for this data set.

Analytical tools

The gridded SST and saturation state files were imported as ArcInfo Grids using Environmental Systems Research Institute’s (ESRI) ArcInfo software. Geographic Information System (GIS) analysis and cartographic displays were generated using ArcMap 8.1 and ArcView 3.3. Guinotte (1999) describes methods for spatial analysis in marine environments, mapping functionality, and visualization techniques in more detail.

Threshold identification

Saturation state – “Low saturation state reefs” were identified as those occurring where aragonite saturation state (Ωarag) values were between 3 and 3.5 (Kleypas et al. 1999b). Since no reefs occurred at calculated values <3, we identify that as the threshold for “extremely marginal,” and further subdivide the values of Ωarag >3.5 into "adequate" (3.5–4.0) and "optimal" (>4.0) categories based on preindustrial saturation state (see Results) and coral and community calcification responses (see Discussion).

Temperature – Kleypas et al. (1999b) based their temperature classifications on maximum and minimum weekly values, while the CCSM 1.0 model results are reported at monthly resolution. Weekly and monthly averages of maximum, minimum, and average SST values for the latitude range 35°N–35°S were consistently highly correlated. Mean differences did not exceed 0.41°C and variances were less than 0.05°C. For the purposes of this investigation we used monthly data and adjusted the values presented in Table 5 of Kleypas et al. (1999b) according to the comparison presented in Table 1: the high monthly average temperature is > 31.1°C, and low monthly average temperature is < 18.4°C. Mean monthly and mean weekly temperatures are essentially identical.

Table 1: Weekly minus Monthly average values for Reynolds SST data sets, 35^{o}N-35^{o}S, 1982-2001.

Parameter	Mean difference	Variance
max SST	0.41	0.044
min SST	-0.38	0.035
avg SST	0.00	0.000

Results

Sea Surface Temperature Maxima

Projected future monthly SST maxima for the Pacific region (Figure 16) illustrate progressive warming relative to the 1982–1991 observations of Reynolds et al. (2002). Contour intervals in Figure 16 were selected to reflect the marginality cluster identified by Kleypas et al. (1999b); i.e., their maximum weekly value of 31.5°C corresponds to a maximum monthly value of 31.1°C. High temperature regions are identified as those where maximum monthly temperatures >31.1°C, transitional regions as 30–31.1°C, and "high normal" regions as 29–30°C.

It is not our intention to imply that 31.1°C is a magic number in terms of the upper thermal tolerance of corals. This value was used because it highlights regions that are near the thermal maxima experienced by present-day coral reefs in non-enclosed oceanic regions (Kleypas et al. 1999b). The responses of coral ecosystems to temperatures above this value, particularly to episodic increases, are largely unknown. Severe past bleaching events have been recorded in regions where 1982–1991 maximum monthly SSTs were significantly cooler than 31.1°C; in 1998 several Pacific reefs experienced bleaching where maximum monthly SSTs were in the 29–30°C range.

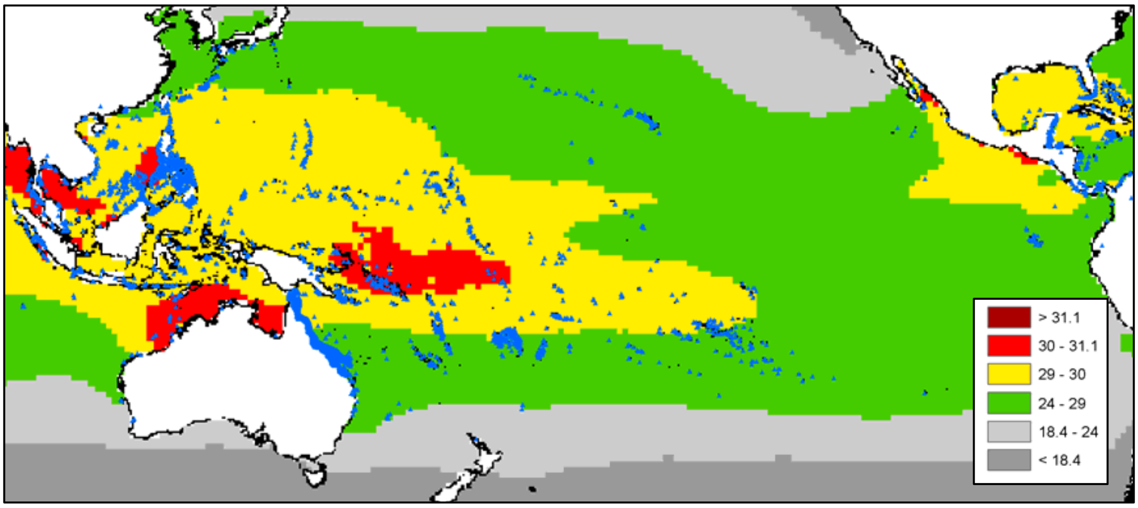


Figure 16a. Maximum monthly sea surface temperature values (ºC). Observed 1982-1991 temperatures (Reynolds et al. 2002).

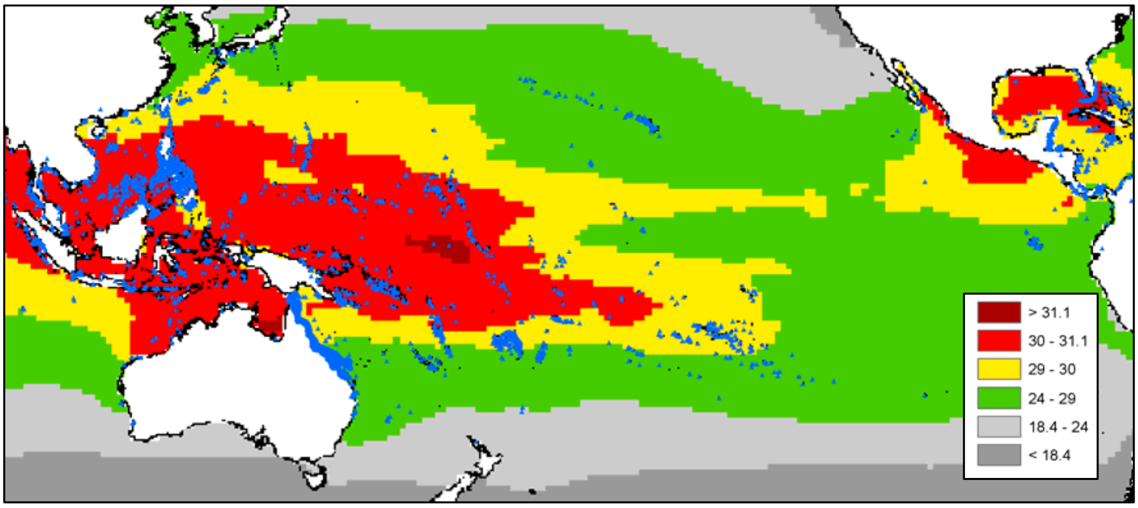


Figure 16b. Maximum monthly sea surface temperature values (ºC). Projected values, 2000-2009; pCO_2 = 375 ppmv (see text for description of methods).

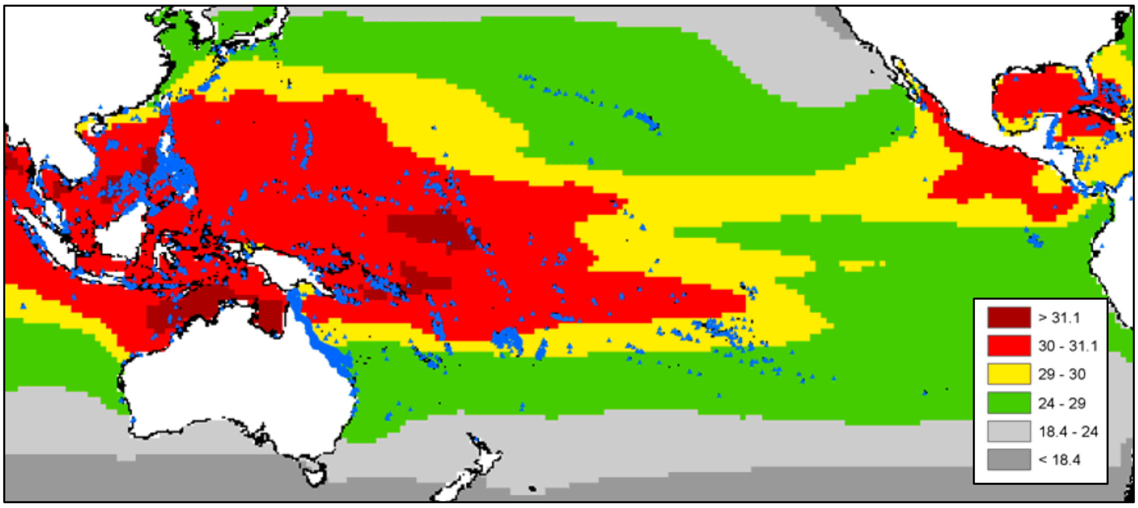


Figure 16c. Maximum monthly sea surface temperature values (ºC). Projected values, 2020-2029; pCO_2 = 415 ppmv.

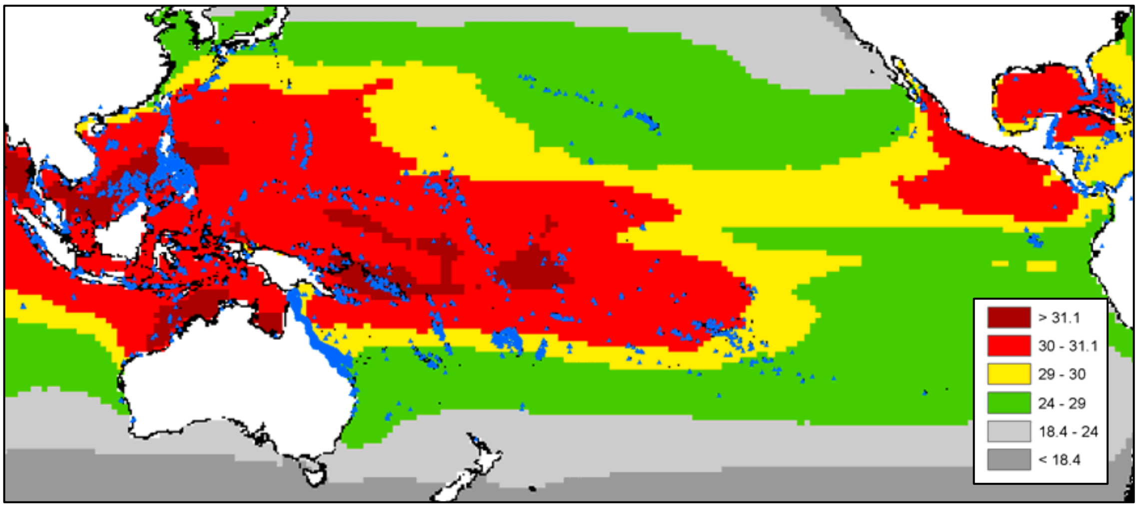


Figure 16d. Maximum monthly sea surface temperature values (ºC). Projected values, 2040-2049; pCO_2 = 465 ppmv.

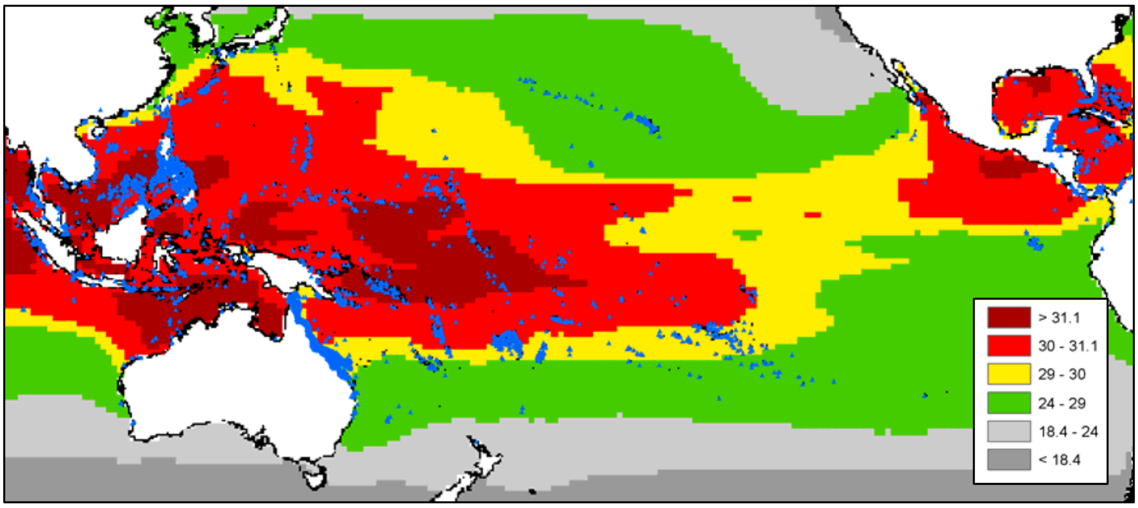


Figure 16e. Maximum monthly sea surface temperature values (ºC). Projected values, 2060-2069; pCO_2 = 517 ppmv.

The regions with maximum temperatures in the 24–29°C range encompass optimal and suboptimal (but not low marginal) regions of reef growth; the 24°C monthly maximum isotherm corresponds fairly closely to the 18.4°C monthly minimum isotherm (which in turn corresponds to the low temperature marginality threshold of 18°C for the weekly minimum temperature, determined by Kleypas et al. 1999b). Extreme SST maxima under the B2 scenario is projected to expand within the Pacific with both temporal and spatial variations. Coral areas showing the greatest probability of extreme SST maxima through 2069 are the Philippine Islands, Gulf of Thailand and Andaman Sea regions, the Arafura and Timor Sea regions, Tuvalu and the Solomon and southern Marshall Islands, and some areas adjacent to the West coast of Central America (Figure 16e).

Aragonite Saturation state

Results of the aragonite saturation state calculations show the same general trends as past studies (Figure 17, Kleypas et al. 1999a, Kleypas et al. 2001) – the pools of optimal and adequate saturation states contract inward from higher to lower latitudes and from the ocean basin margins toward the center. This analysis also highlights some additional important features for the Pacific region:

(1) Only the very high latitude reefs (generally those presently deemed marginal) fall into the "extremely marginal" (Ωarag <3.0) category by 2069 (Figure 17e).

(2) By 2069, only a few regions in the tropical oceanic south Pacific remain in the "adequate" category (Figure 17e).

(3) The Indo-West Pacific center of reef biodiversity enters the "marginal" saturation state category over the period 2020–2049 **(**Figures 17c and 17d).

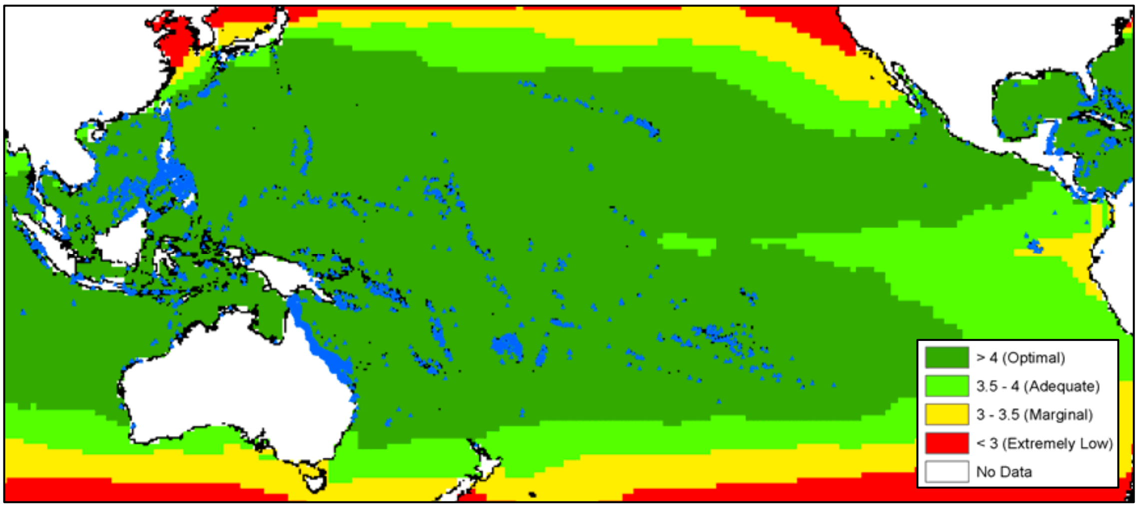


Figure 17a. Aragonite saturation state. Calculated preindustrial (1870) values; pCO_2 = 280 ppmv.

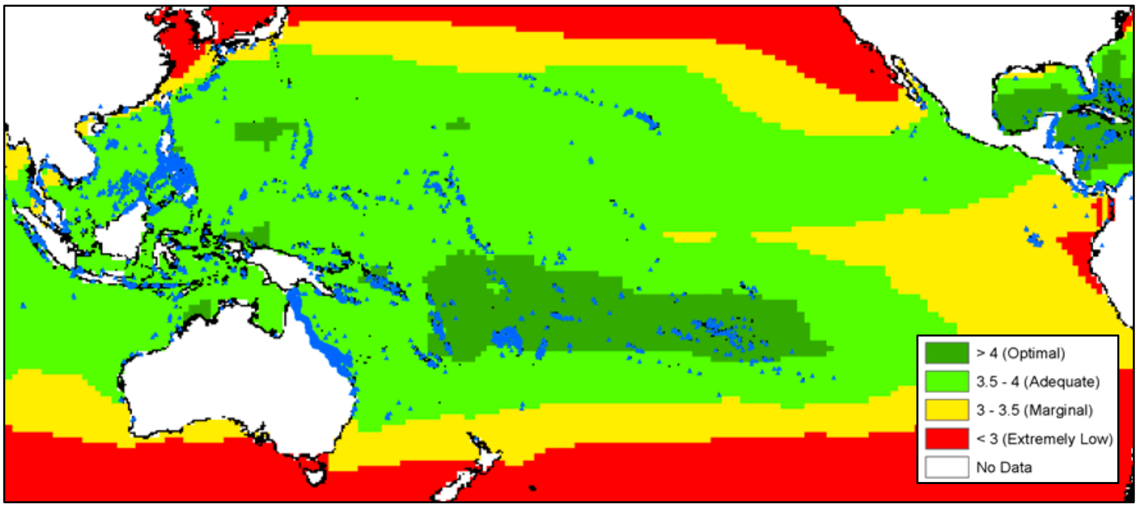


Figure 17b. Aragonite saturation state. Projected values, 2000-2009; pCO_2 = 375 ppmv (see text for description of methods).

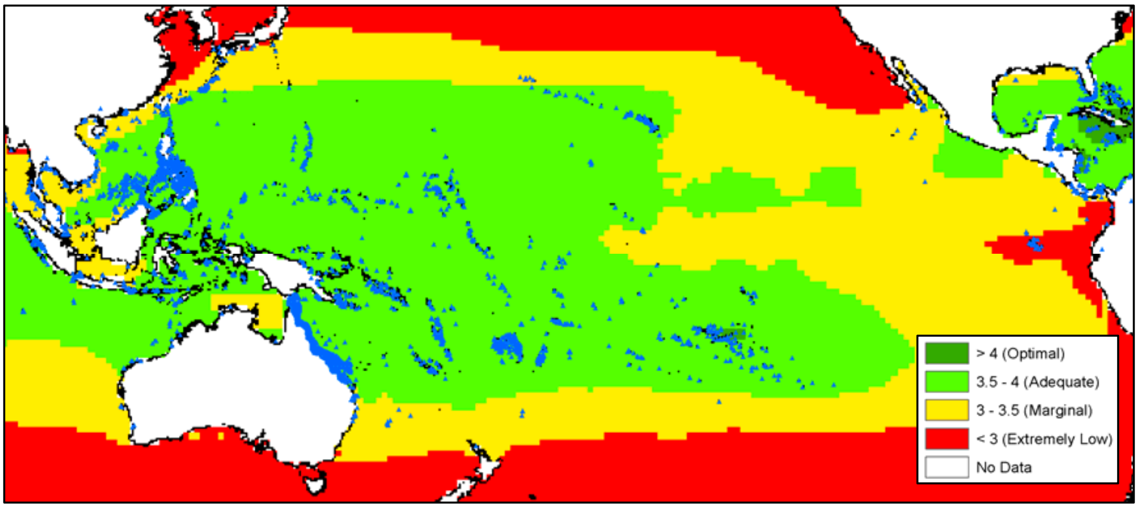


Figure 17c. Aragonite saturation state. Projected values, 2020-2029; pCO_2 = 415 ppmv.

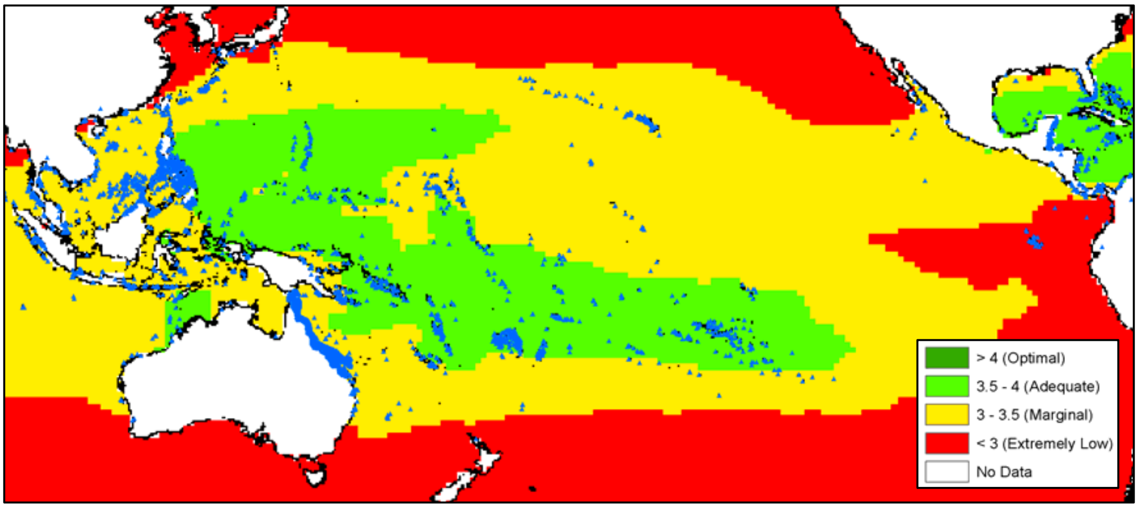


Figure 17d. Aragonite saturation state. Projected values, 2040-2049; pCO_2 = 465 ppmv.

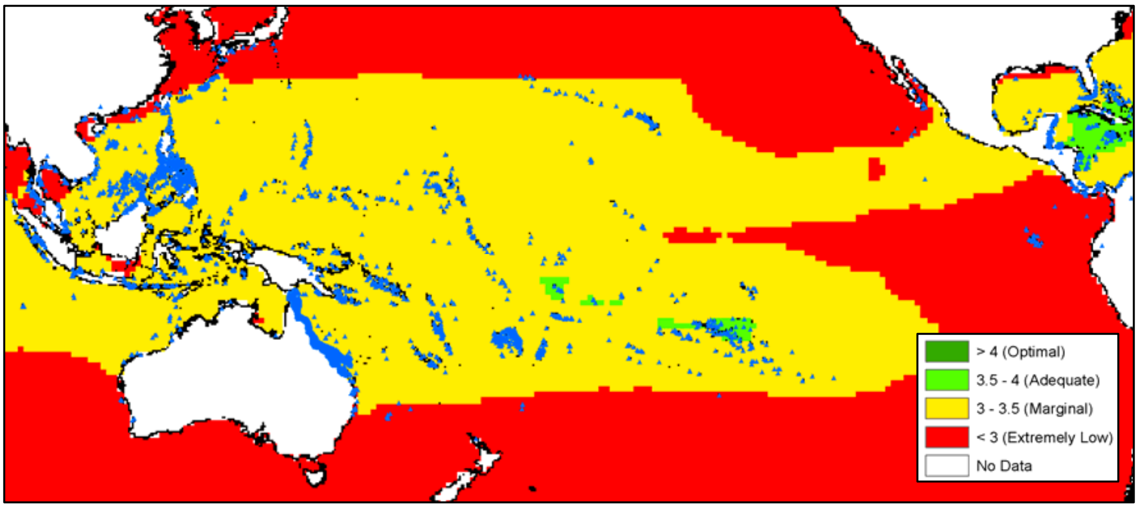


Figure 17e. Aragonite saturation state. Projected values, 2060-2069; pCO_2 = 517 ppmv.

Discussion

Projections, predictions, and uncertainty

The future scenarios presented in this paper are projections of what is likely to occur if the assumptions and models used are valid. At a general level of accepted physics and oceanography, saturation state and temperature will almost certainly continue to decrease and increase respectively, and broad latitudinal and longitudinal features of the patterns are probably realistic. Exact rates, final extent, and detailed geographic distributions of change are much less certain. Also, the models and data sets used are primarily oceanic, and are less likely to accurately predict coastal zone conditions.

Controversy surrounds the issue of whether rising atmospheric CO_2 will reduce calcification or buffer the system by dissolving existing carbonate reservoirs in the ocean. Halley and Yates (2000) have conducted field experiments demonstrating that elevated CO_2 may enhance dissolution of high- Mg calcite sediments, which could in turn partially buffer saturation state reductions. This process is likely to be significant only in areas of permeable sediments and restricted circulation (e.g. reef flats), not in the well-flushed areas of highest calcification (e.g. reef slopes).

Future behavior of other climatic and oceanographic factors should also be considered when interpreting these results. For example, recent major bleaching events occurred during El Niño years, but it is not clear if El Niño intensity and duration will change in response to global climate change (Enfield 2001). Future changes in circulation, wave energy and storm regimes, and upwelling intensity; are less predictable features of climate change.

Optimism vs. pessimism

At the global scale, most climate system models show significantly less warming in the tropics than elsewhere on the globe. There is also evidence that various ocean-atmosphere feedbacks will regionally limit the extent of open ocean warming. The "thermostat hypothesis" (Ramanathan and Collins 1991, Collins et al. 2000), for example, states that once SSTs rise above a threshold temperature of ~30ºC, convective processes produce both storms and cirrus clouds which shade the surface and curtail further heating. Recent studies suggest that ocean dynamics also play an important role in regulating tropical SSTs (e.g. Li et al. 2000, Loschnigg and Webster 2000). At the reefal scale, a number of reef areas in nearshore regions or within enclosed seas currently tolerate weekly maximum temperature values ranging from 31.5 to 34.4°C (Kleypas et al. 1999b). Temperatures within the middle of that range should be within the adaptive and acclimative ranges of at least some reef communities and organisms.

We have used a conservative (= optimistic, from the standpoint of environmental impacts) CO_2 increase scenario, which influences both the rate and extent of temperature and saturation state change. Such a scenario could be a realistic projection, since either coherent international action to reduce emissions or the disruptive consequences of wars or economic depression could act to reduce rates of energy generation from fossil fuels. For the environmental pessimists this holds out the image of a possible future worth working toward; for the environmental (or economic) optimists, it portrays the minimum level of risk and impact that can be expected.

Overview of findings and implications

Based on SST and Ωarag thresholds for reef marginality, essentially all present-day reef habitats in the Pacific Ocean will be "marginal" within the next several decades (Figure 18). The poleward shift of the 18°C isotherm represents only a small increase in potential reef habitat "gained" by global warming. However, the finding of increased reef marginality is not the same as predicting the complete demise of reefs. Within all of the "marginal" categories of Kleypas et al. (1999b), there are significant reef occurrences. Further, the two dimensions of marginality considered represent very different types of stresses. Saturation state reduction will gradually lead to less carbonate accumulation on average, probably to slower extension rates or weaker skeletons in some corals, and possibly to reduced cementation and reef structure stabilization. This suggests that the future will hold more non-framebuilding communities and fewer net accretionary reefs (Kleypas et al. 2001). The expected gradual shift in organism and community behavior due to saturation state change contrasts with the typically episodic response of coral reefs to high temperature stress.

Increasing temperature thus represents an acute stress, whereas lowering of saturation state is a chronic reduction of habitat suitability. Their effects will play out over different time periods, and although they will certainly interact, neither humans nor corals have any experience with that interaction. Under the conditions of the last several million years, temperatures at the upper limit of coral tolerance would seldom if ever have had widespread occurrence at the same times and locations as aragonite saturation states below 4.0.

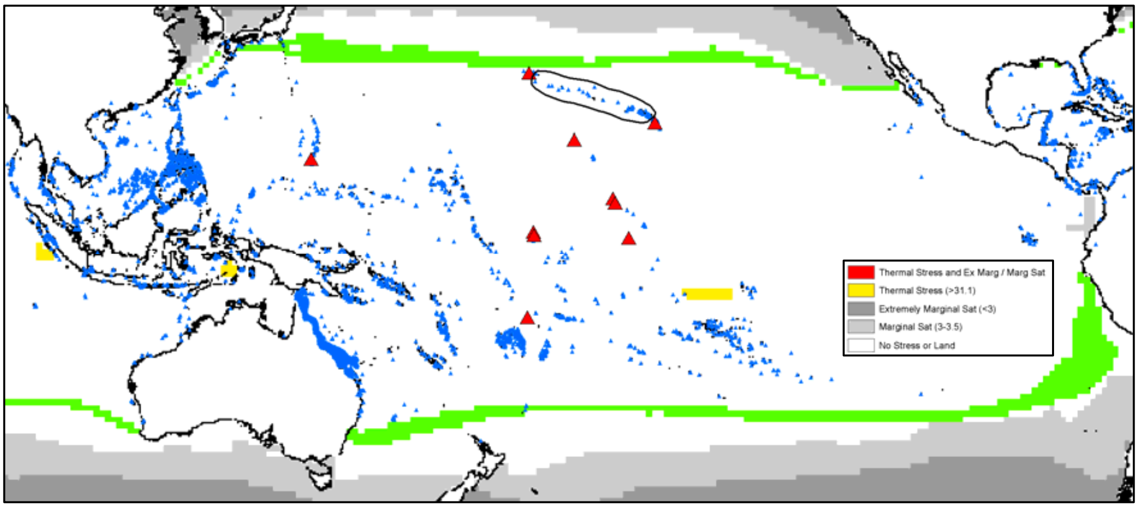


Figure 18a. Index map and composite marginality. Map of preindustrial SST (°C) and Ωarag marginal ranges, showing locations of US National Wildlife Refuges and Marine Sanctuaries (red triangles) and range of pole-ward shift of the 18 °C low temperature marginality isotherm (green area), present to 2069.

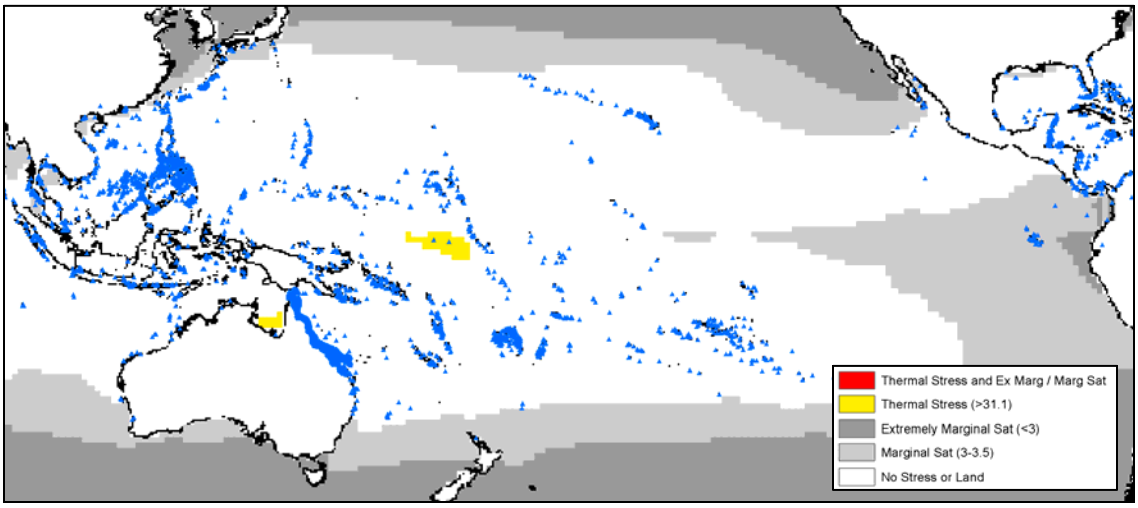


Figure 18b. Index map and composite marginality. Projected values, 2000-2009; pCO_2 = 375 ppmv, temperature units (°C).

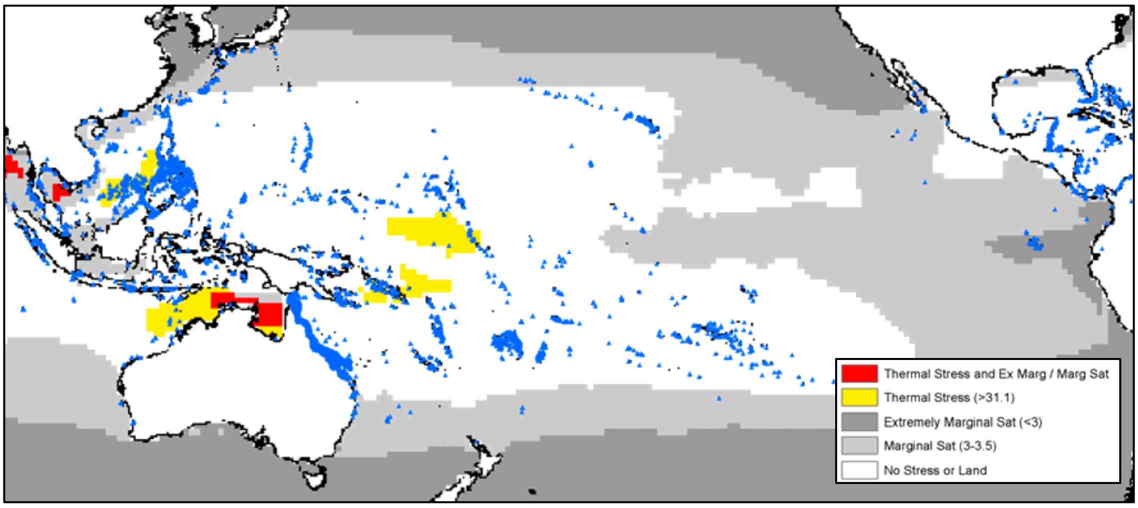


Figure 18c. Index map and composite marginality. Projected values, 2020-2029; pCO_2 = 415 ppmv, temperature units (°C).

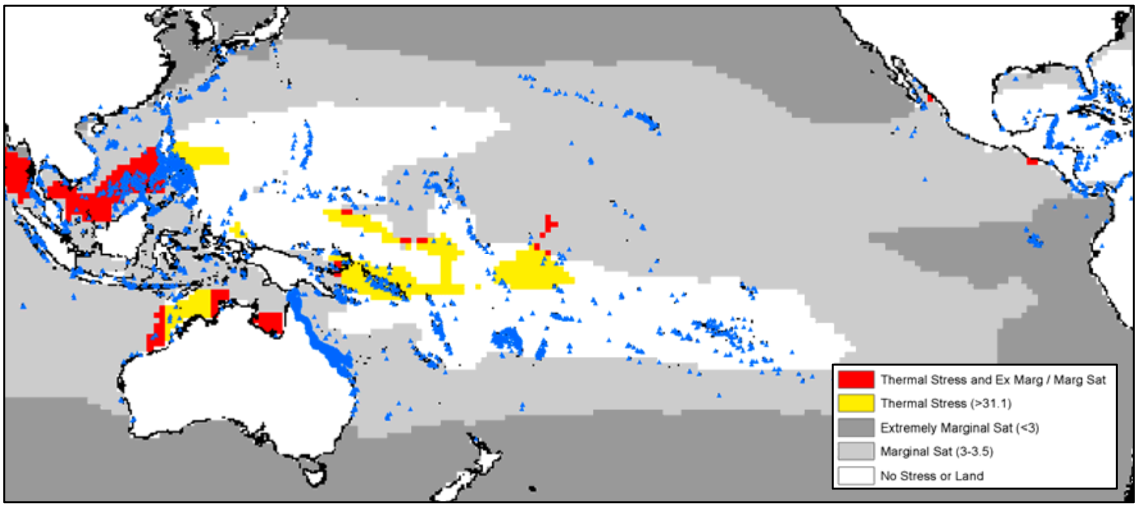


Figure 18d. Index map and composite marginality. Projected values, 2040-2049; pCO_2 = 465 ppmv, temperature units (°C).

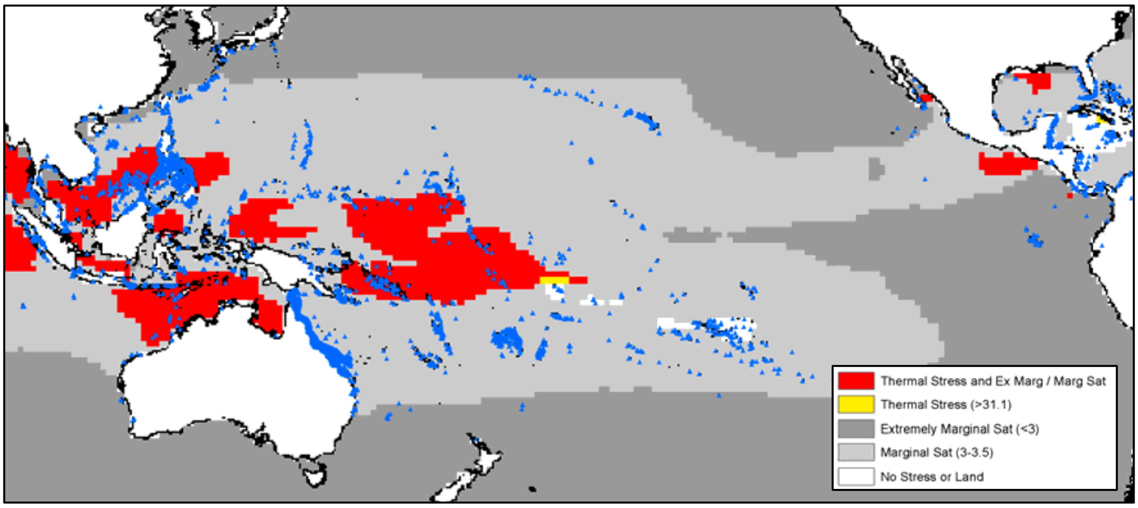


Figure 18e. Index map and composite marginality. Projected values, 2060-2069; pCO_2 = 517 ppmv, temperature units (°C).

Implications for reef research, management, and conservation

Human alteration of the oceanic climate is a biophysical experiment that, although unplanned, is neither unpredictable nor lacking in opportunities for adaptive research, monitoring, and management of the affected ecosystems. The projections illustrated in this chapter depict a shift in saturation state which will gradually modify reef carbonate accumulation and probably community structure, and which has a distinctive geographic time course. They also show a probable development of regions where maximum temperatures will exceed the normal tolerances of present-day reefs. If these regions also experience episodic extremes (e.g. as associated with El Nino events), then we can also expect increases in mortality. The spatio-temporal evolution of reef marginality that results from the overlapping of these two variables offers some guidance toward understanding the responses of reef organisms and ecosystems to global change, and for incorporating that understanding into management and conservation plans. We suggest four specific areas for development of critical sustained research efforts:

1. Biodiversity: An important research step will be to quantify the spatial overlap between regions of coral biodiversity (“hotspots”) in the Indo-Pacific region (Roberts et al. 2002) and projected marginality in terms of future sea surface temperature and aragonite saturation state. This undertaking would have two products: (1) to identify regions with high biodiversity at risk; and (2) to identify regions of low biodiversity where reef occurrence may be at risk due to lack of functional replacements for specific vulnerable organisms or guilds.

2. Terrigenous vs. Oceanic effects: Terrestrial influences play a large role in determining community structure of nearshore reefs that are distinct from those associated with oceanic reefs (see, Buddemeier and Fautin 2002). The oceanic models used in this study are less reliable in nearshore environments, where terrestrial runoff and local climatic differences can result in local conditions that are significantly modified from those of the adjacent open-ocean water mass. The Australian Great Barrier Reef spans a wide range of latitudes and has well-characterized differences between inner- and outer-shelf reef communities (Harriott and Banks 2002, Ninio and Meekan 2002). The GBR is an ideal location to investigate the spatio-temporal distributions of environmental conditions and their effects on coral communities.

3. ‘Space for time’ longitudinal studies of climate change effects: Across the oceanic central Pacific, marginal temperature and saturation conditions develop with different rates and patterns. Systematic observation of conditions and ecosystem responses at a network of relatively undisturbed reef sites (e.g. the system of US National Wildlife Refuges and Sanctuaries in the Pacific, illustrated in Figure 18a) would enhance future evaluations of the individual and synergistic effects of changing temperature and saturation state.

4. Development of a tool that can identify deep-water hermatypic reef habitat by exploring environmental data known to limit their distribution would enable researchers and management agencies to identify uncharted deep coral habitat that may serve as potential refugia areas in the future.

Conclusions

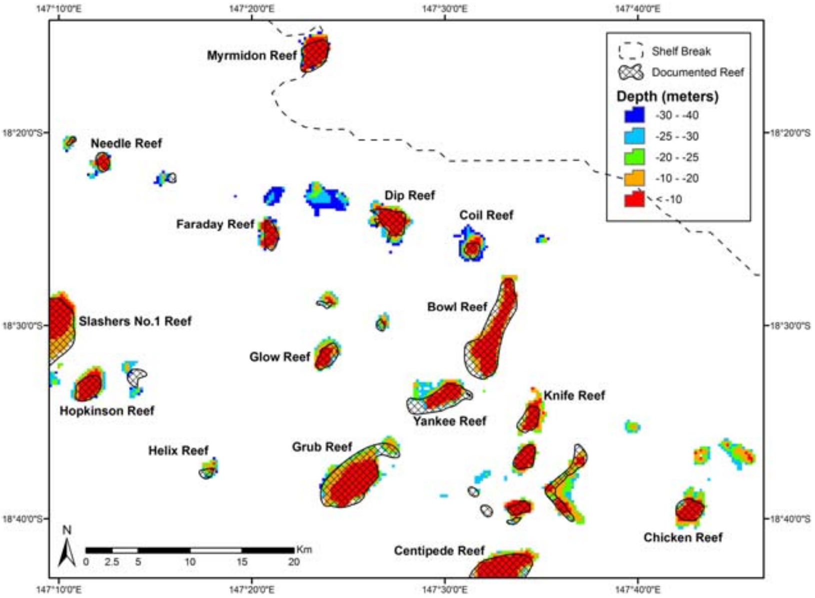
Rising atmospheric CO_2 concentrations will reduce the saturation state of carbonate minerals in the surface ocean over the next 70 years until nearly all locations are in the category identified as marginal by Kleypas et al. (1999b). This will probably result in long-term, gradual decreases in calcification, reef accumulation, and changes in community structure.

Rising oceanic SSTs will place a number of areas into a temperature category that may be marginal in terms of a maximum threshold, including much of the Indo-Pacific center of reef biodiversity. Most of the tropical Pacific will be in a borderline temperature category based on either absolute temperatures or ranges of variation (Kleypas et al. 1999b).

Probable caps on SST and the gradual reduction in saturation state mean that organisms and communities may be able to adapt or acclimatize to changing conditions. A major caveat in this regard concerns regions of high temperature and low saturation state; this combination of stresses has probably not occurred in evolutionary history, at least over the Plio-Pleistocene.

Chapter 3

Predicting Present Day Coral Reef Habitat from Measured Environmental Data: a Diagnostic Model for the Great Barrier Reef



Citation

Guinotte JM (submitted) Predicting present day coral reef habitat from measured environmental data: a diagnostic model for the Great Barrier Reef. Marine Ecology Progress Series

Abstract

The aim of this work was to identify areas where favorable coral reef habitat could occur on the Great Barrier Reef (GBR) using measured environmental data. Potential reef habitat was defined by four environmental parameters that are known to control coral reef development and survival: temperature, light availability (depth-attenuated level of photosynthetically available radiation [PAR]), salinity, and nutrients (nitrate and phosphate). The environmental parameters were queried in a geographic information system (GIS) to identify regions where present day reef growth could occur. The model most accurately predicted reef habitat in offshore regions (mid-shelf and shelf-edge regions of the GBR) remote from terrigenous inputs. Model results were highly correlated with Great Barrier Reef Marine Park (GBRMPA) reef locations and also identified numerous hermatypic deep reefs (> 20m) that have not been documented in the literature. Light availability and average nitrate were the most important variables in determining where reefs (both modeled and documented) occur. Methods described in this paper could be applied to other regions of the world where high-resolution bathymetry exists to predict coral reef habitat, undocumented reefs, and other marine ecosystems that survive within well-defined environmental limits (e.g. seagrass beds, halimeda banks, etc.).

Personal Contribution and Context within the Thesis:

Methodologies presented in Chapter 3 stem from research I conducted during my Master's thesis (Guinotte 1999) and close associations with Dr. Joanie Kleypas. Dr. Kleypas published a paper (1997) that predicted global reef habitat from environmental data. Guinotte (1999) and Chapter 3 expanded this research to develop products that could be applied to document uncharted coral habitat in the field and gain a better understanding of the environmental controls on coral reef habitat.. My personal contribution to Chapter 3 is 100% with one caveat. This research would not have been possible without important input from Joanie Kleypas, Bob Buddemeier, and Geoff Bohling. Geoff Bohling, Kansas Geological Survey, aided this research effort by providing valuable insights into the statistical analyses.

Chapter 3 builds on the scientific information gained from Chapters 1 and 2 by identifying the primary environmental controls on coral reef habitat occurrence and identifying uncharted deep coral habitat that could serve as refugia from future bleaching events. Chapter 3 directly addresses Research Foci 1 and 4 (Figure 19). Predicting potential reef habitat sheds light on the importance of environmental parameters in determining where existing reefs occur and identifies areas which may contain undocumented reefs (RF1 and RF4). This research demonstrates that methodologies presented here can be applied anywhere in the world for coral reef ecosystems and is likely to work for other marine ecosystems that live within well defined environmental limits (RF4). Future research opportunities include substituting projected future changes in environmental factors for present day data in hopes of producing outputs that will aid in identifying areas where coral growth is likely/unlikely to occur (RF4).

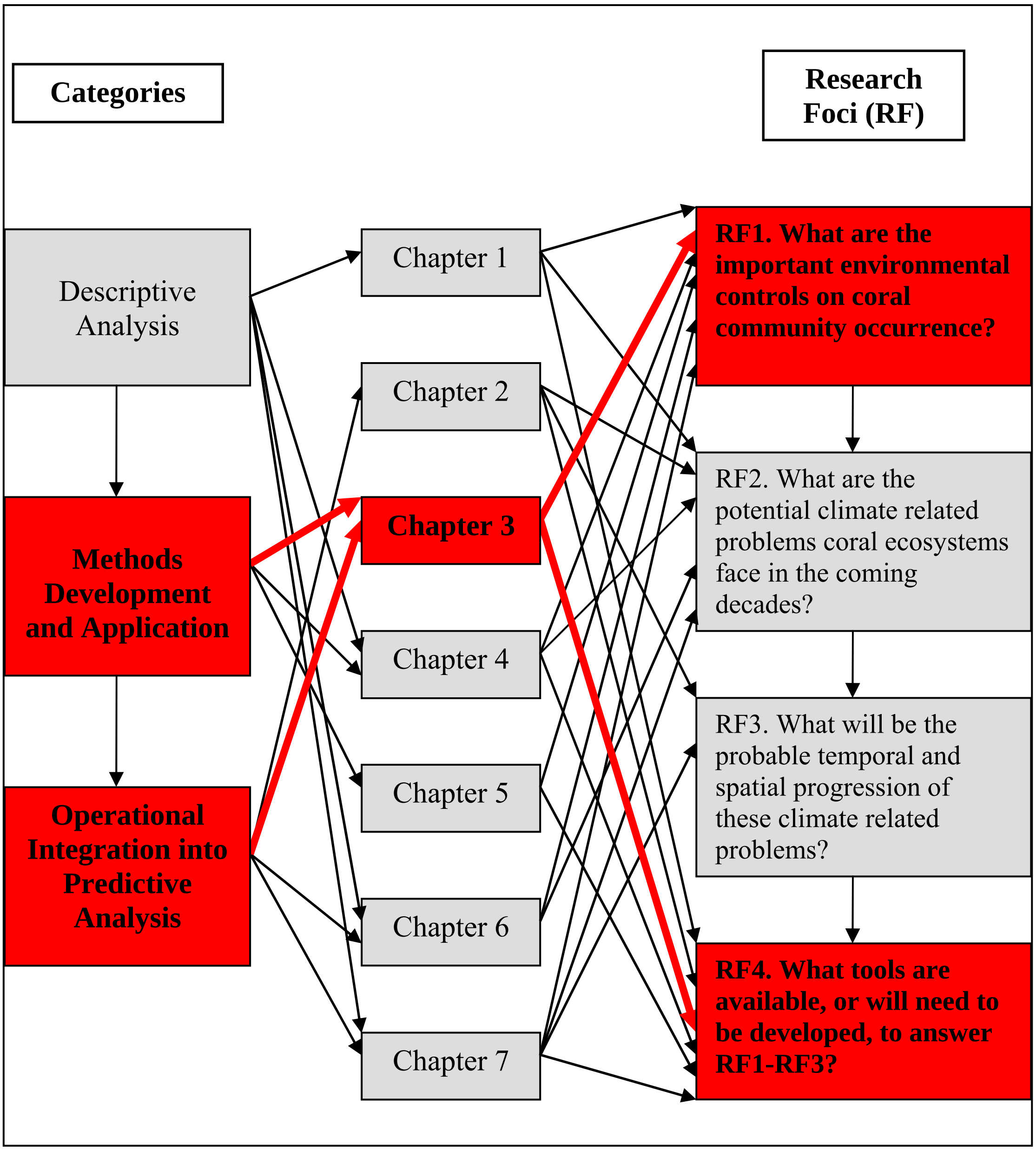


Figure 19: The relevance of Chapter 3 to the overall scheme of the research.

Introduction

Historically, coral reefs have not been well documented and were mapped only if they posed a hazard to navigation. Because deep hermatypic reefs are not hazards to navigation they have remained uncharted in many regions of the world's oceans. This is unfortunate as deep reefs often experience cooler water temperatures and are less likely to experience periodic coral bleaching episodes that have plagued shallow water reefs. In recent years, remote sensing technologies have enabled reef scientists to accurately document shallow water reef complexes at global scales (Andrefouet et al. 2003, Calpolsini et al. 2003). Remote sensing techniques have proven to be highly effective in shallow, clear-water conditions and have provided a critical inventory of Earth's shallow water reef systems. However, satellites and airborne sensors can not identify deep reef substrate due to signal penetration problems and water clarity issues resulting from suspended sediments and micro-organisms in the water column. Ongoing programs use airborne and space-based sensors to successfully map shallow water habitats, but are limited by water penetration problems and can only identify reefs to a maximum depth of ~25 m (Liceaga-Correa and Euan-Avila 2002, Andrefouet, pers com). GIS technologies fill the remote sensing void by enabling researchers to investigate environmental conditions, which are known to influence reef growth and survival, across a wide range of temporal and spatial scales. Spatial analysis techniques offer a unique means by which deep reefs can be identified.

Coral reefs live within well-defined physical and chemical limits and are most prolific in shallow, well-flushed marine environments characterized by clear, warm, low-nutrient waters that are of oceanic salinity and supersaturated with calcium carbonate minerals (Smith and Buddemeier 1992). Significant technological advances have been made in recent years, enabling researchers to collect, often remotely, detailed environmental data over large spatial and temporal scales. Since coral reefs live within relatively well-defined environmental limits and data for these environmental variables are readily available, it is possible to map areas where favorable conditions for reef growth are likely to occur.

The majority of shallow water reef systems (< 20 m) in the GBR region have been identified/mapped/documented and present an excellent opportunity to investigate the question, “Is it possible to accurately identify suitable reef habitat by exploring the physical and chemical factors that control coral reef development and survival?” For the purposes of the research reported here, suitable reef habitat is defined by the physical and chemical factors that limit coral reef development. Sea surface temperature, light availability, salinity, and nutrient concentrations all play an important role in determining where coral reefs occur in the world’s oceans (Kleypas et al. 1999, Kleypas 1997, Smith and Buddemeier 1992). By investigating the key environmental variables that control reef distribution, it is possible to predict areas that are favorable for reef formation.

Results presented here are an improvement/extension of ReefHab, the global reef habitat prediction model developed by Kleypas (1997). ReefHab used marine environmental parameters to predict global reef habitat at a spatial resolution of 5’ x 5’(~ 85 km^2). Reefhab’s resolution proved to be very useful in predicting reef habitat at the global scale and was also successful in providing estimates of calcium carbonate production since the last glacial maximum. This pioneering work illustrated that reef habitat could be identified by investigating environmental data known to influence reef growth. However, Reefhab's spatial resolution was too coarse for predicting reef habitat at local to regional scales. Global and regional bathymetric data has improved significantly in recent years and the results of the research presented here show accurate estimates of reef habitat can be determined on the order of meters, rather than kilometers.

Study Area

The Great Barrier Reef is the largest coral reef ecosystem in the world. Comprised of over 2,900 individual reefs and some 2,300 km in length, the GBR stretches across ~ 13° of latitude and 12° of longitude. This large spatial gradient causes environmental conditions to vary considerably from north to south and east to west, making it an ideal study area for investigating environmental controls on reef distribution. The Great Barrier Reef Marine Park (GBRMP) covers some 349,000 km^2 and is arguably one of the best managed, most well documented, and meticulously studied marine protected areas on Earth. The reefs of the GBR are also some of the most accurately mapped reefs in the world due to ongoing research and data collection efforts by the Australian Institute of Marine Science (AIMS), Great Barrier Reef Marine Park Authority (GBRMPA), and James Cook University (JCU). There is a wealth of high-quality marine environmental information for this region and highly-resolved positional information exists for reef location and extent, both of which are crucial for assessing the accuracy of model results presented here.

Materials and Methods

Determination of Reef Habitat

Potential habitats for reef growth were based on environmental data of sea surface temperature, salinity, nutrients, and light (as a function of solar irradiance incident on the sea surface, water depth, and water clarity; Table 1). All of the limiting values used to define reef habitat were initially determined from values quoted in the literature (Kleypas et al. 1999). Precise values were iteratively determined based on comparisons of model predictions with known reef locations in the GBRMP. The spatial resolution of model predictions is the same as the bathymetric datasets used (250m x 250m, 500m x 500m, 1km x 1km, and 2’ x 2’) in the analysis. Water depth varies over small scales and exerts a strong control over reef distribution so it was necessary to include several bathymetric datasets of varying spatial resolutions to test which resolution most accurately predicts reality. Spatial resolutions of the other environmental input variables is much coarser (e.g. 1° x 1° for temperature, salinity, nutrients); however, these data do not vary considerably within their respective resolutions.

Table 2. Limiting criteria and scale (spatial and temporal) of data used.

Parameter and Source	**Spatial**	**Temporal**	**Limiting Criteria**
Salinity, ppt *World Ocean Atlas (2001)*	1 deg	monthly	min monthly > 33.9 max monthly < 35.7
Sea surface temperature,° C *Reynolds et al. (2002)*	1 deg	weekly	min weekly > 19.4° max weekly < 31.0°
Nutrients, μmol L^{-1} *World Ocean Atlas (2001)*	1 deg	monthly	avg annual $NO_3 < 0.7$ μmol L^{-1} avg annual $PO_4 < 0.2$ μmol L^{-1}
Bathymetry, m			
CRC Reef (2001)	250 m	none	where Bathymetry < z_{max}
CRC Reef (2001)	500 m	none	z_{max} = depth of avg PAR saturation according to
Geosciences Aust. (2002)	1 km	none	$[\ln(I_{min} / PAR)] / K_{490}$
Smith and Sandwell (1997)	2 min (~4 km)	none	where I_{min} = 250 μE m-2 s-1
PAR, W m^{-2} *NASA/GSFC SeaWifs (1997-2002)*	9 km	monthly	see above
Water transparency, K_{490} *NASA/GSFC SeaWifs (1997-2002)*	9 km	monthly	see above

Minimum and maximum weekly average sea surface temperatures were calculated from 21 years of ground-truthed satellite data from Reynolds OIV2 (Reynolds et al. 2002). Modeled reef habitat was limited to areas where weekly sea surface temperatures remained between 19° and 31° C.

Monthly surface salinity data was obtained from the World Ocean Atlas 2001 (Conkright et al. 2002). Modeled reef habitat was limited to areas where average monthly salinity remained between 34 and 36 ppt.

Nutrient concentrations (nitrate and phosphate) were obtained from the World Ocean Atlas 2001 (Conkright et al. 2002). Nutrient levels acceptable for reef development vary greatly geographically and specific limits are noticeably absent from the literature. Nitrate and phosphate limits were iteratively determined by examining their respective values for known reef locations on the GBR. Modeled reef habitat was limited to areas where annual average surface nitrate remained below 0.7 μmol L^{-1} and annual average surface phosphate remained below 0.2 μmol L^{-1}.

Kleypas' (1997) method of determining "adequate" light necessary for reef growth was used to limit potential reef habitat for the GBR. Adequate light was determined by first calculating the maximum depth of light penetration (Z_{max}) at a particular point and then testing whether the topographic point lies above or below that depth.

Water depth varies greatly over small spatial scales and acts as a strong control on reef occurrence hence several bathymetric datasets of varying spatial resolutions were used to identify the optimal spatial resolution for predicting reef habitat at local to regional scales. Four bathymetric datasets spanning a range of spatial resolutions (250m – 2') were used to test model prediction sensitivity. Two digital depth models (DDM) for the Great Barrier Reef Marine Park were obtained from the CRC Reef Research Centre (Lewis 2001) with spatial resolutions of 500 m x 500 m and 250 m x 250 m. The Australian Bathymetry and Topography grid was obtained from Geosciences Australia (Petkovic and Buchanan 2002) and has a spatial resolution of 1 km x 1 km. Etopo2 bathymetry, a blended analysis of global satellite altimetry and in situ data from ship borne echo sounders, was obtained from the National Geophysical Data Center (Smith and Sandwell 1997) and has a spatial resolution of 2' x 2'. All bathymetric datasets have a vertical resolution of 1 m. It should be noted the GEBCO 1' x 1' bathymetric dataset was explored and numerous errors were discovered in the GBR region. These errors were a significant cause for concern, which led to the dataset not being used in the study.

The maximum depth of reef growth (Z_{max}) was calculated according to the Kleypas (1997) equation: $Z_{max} = (\log(I_{min}/PAR)) / K_{490}$
where I_{min} = minimum light intensity necessary for reef growth ($\mu E\ m^{-2}\ s^{-1}$); PAR = average daily PAR at sea surface ($\mu E\ m^{-2}\ s^{-1}$); and K_{490} = diffuse extinction coefficient of light of wavelength 490 nm (m^{-1}).

Daily average PAR data at the sea surface was attenuated with depth using the diffuse attenuation coefficient of light of wavelength 490 nm (K_{490}). Both PAR and K_{490} were derived from NASA's SeaWiFS satellite program and were provided by Goddard Earth Sciences Data and Information Services Center.

Hermatypic corals are limited to shallow waters and are limited to some absolute light level. The attenuation of wavelength 490 nm was assumed to be representative of the absorption spectra for zooxanthellate (Kleypas 1997) based on the fact that most zooxanthellate absorption occurs at wavelengths of 490-550 nm (blues) and less so at 650-700 nm (reds) (Falkowski et al. 1990). The 490 nm wavelength is the least attenuated in seawater and closely represents the PAR wavelength of maximum penetration, which represents the greatest depth at which photosynthesis is likely to occur (Kleypas 1997).

Kleypas (1997) tested the sensitivity of the Reefhab model by applying several I_{min} values ranging from 10 to 300 $\mu E\ m^{-2}\ s^{-1}$. We used an iterative approach to I_{min}

values and found that 250 μE m^{-2} s^{-1} produced the best correlation between model output and documented reef extent.

Analytical Tools

Environmental parameters were gridded and converted to a common GIS format (ArcInfo Grid) using Environmental Research Institute's (ESRI) ArcGIS Desktop software. Spatial queries and limiting criteria for environmental variables were input in ESRI Spatial Analyst. Statistical analyses were performed in Oracle 8i and Insightful Miner.

Results

Predicted Reef Habitat

Maps of modeled reef habitat for the GBR (Figure 20) illustrate the significant effect bathymetric spatial scale has on the accuracy of model results. Model results shown in Figure 20 were superimposed with a 1:250,000 scale reef coverage provided by GBRMPA for qualitative comparison of results. Model results using Etopo2 2' x 2' bathymetric data (Figure 1a) overpredicted mid-shelf and offshore reefs.

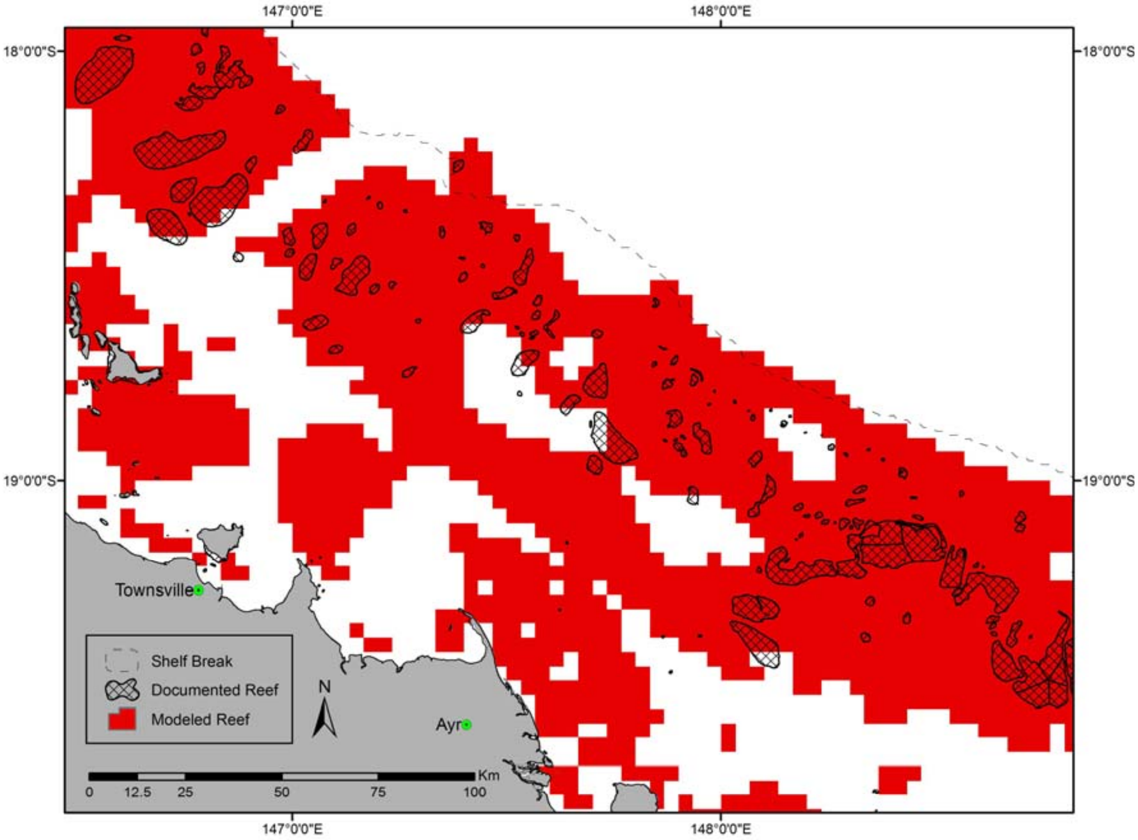


Figure 20a. Modeled reef habitat and documented reefs in central section of GBRMP. (a) spatial resolution 2’ x 2’.

Numerous false positives are evident throughout the GBR lagoon and along the mainland coast, regions where environmental conditions for reef growth are marginal due to the presence of soft sediments and frequent freshwater input from rivers and streams. False positives are evident from the mainland coast to the continental shelf break for the entire GBRMP indicating the spatial resolution of Etopo2 is not optimal for predicting reef habitat at local to regional scales. Modeled reef habitat results using Geosciences Australia’s 1 km x 1 km bathymetry (Figure 20b) show significant improvement over results obtained from using Etopo2 2’ x 2’ data. False positives remain evident throughout the inner lagoon and mainland coast, but the accuracy of model results improves dramatically in mid-shelf and shelf-edge regions.

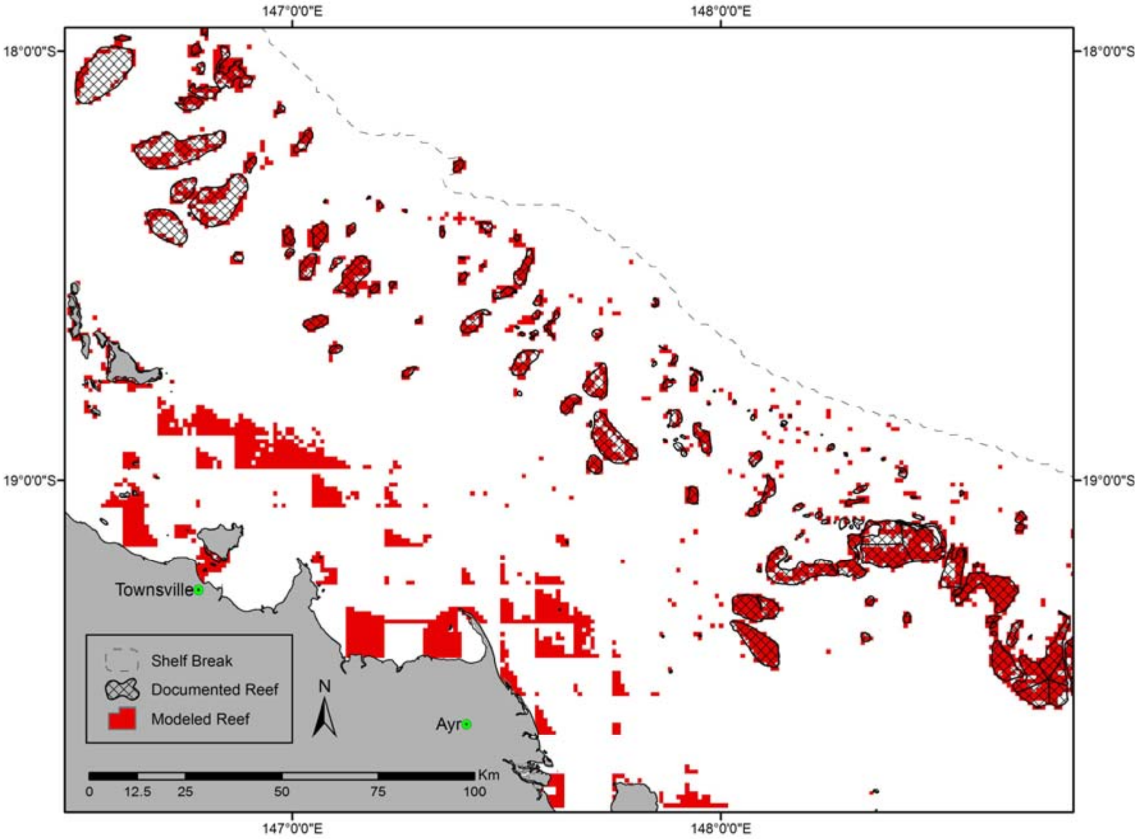


Figure 20b. Modeled reef habitat and documented reefs in central section of GBRMP; spatial resolution 1 km x 1 km, black arrows highlight false negatives.

Model runs using the 500m x 500m and 250m x 250m DDMs (Figure 20c and 20d) provided by CRC Reef Research Centre (Lewis 2001) produced the most highly correlated results between modeled reef habitat and documented reef area. False positives and false negatives are present albeit fewer in number, but with an important caveat. False positives in close proximity to the continental shelf are likely to be undocumented deep reefs. These offshore areas are far from terrigenous inputs (e.g. freshwater runoff and sediments), which are known inhibitors to reef growth. The average depth of "false positive" modeled reef habitat within ~20 km of the continental shelf is 25-40 m. Reefs in the 25-40 m depth range are too deep to be identified by satellites or airborne imagery and are unlikely to be a hazard to passing ships. Ground truthing was necessary to confirm whether these false positives really contained reefs or were in fact true false positives.

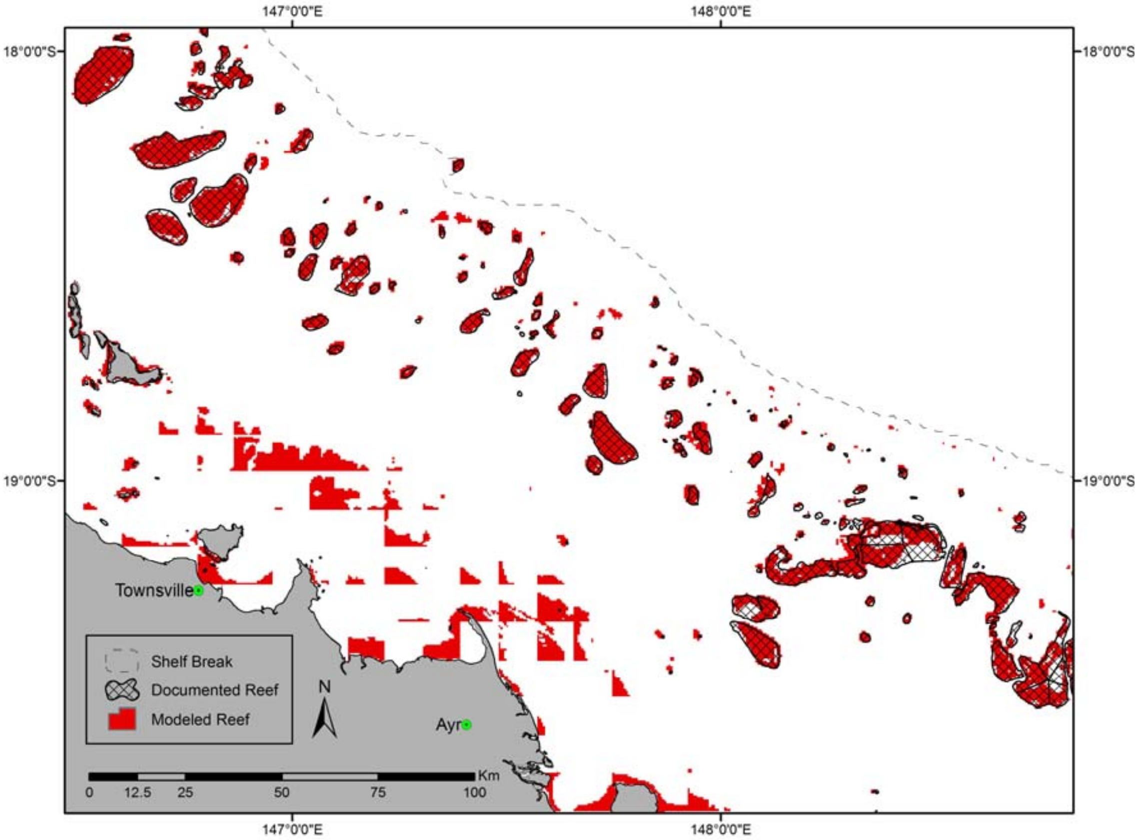


Figure 20c. Modeled reef habitat and documented reefs in central section of GBRMP; spatial resolution 500 m x 500 m.

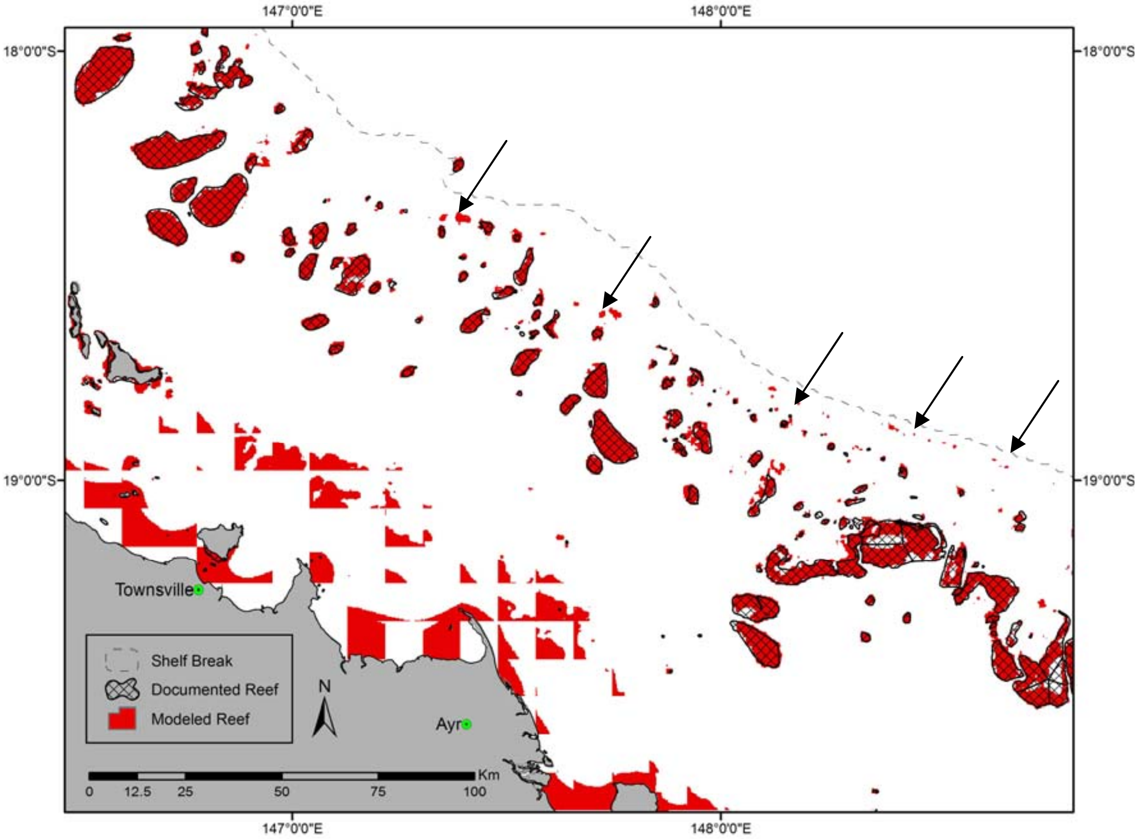


Figure 20d. Modeled reef habitat and documented reefs in central section of GBRMP; spatial resolution 250 m x 250 m; black arrows highlight offshore areas where there is a high probability modeled reef habitat identifies undocumented reefs.

Ground Truthing Predicted Reef Habitat

The Australian Institute of Marine Science (AIMS) investigated two sites where modeled reef habitat "false positives" had a high probability of being actual undocumented reefs (Figure 21). The location of the sites AIMS investigated is approximately 12 km south of Myrmidon reef or 112 km northeast of Townsville. Approximate area of site 1 is 3 km^2 and site 2 is 8 km^2, respectively. AIMS divers found healthy reefs with high coral cover at both sites in ~25-40 m of water (Figure 22). Coral at both sites showed no indication they had experienced bleaching in either the 1998 or 2002 GBR bleaching events. This is significant in that neighboring reefs (e.g.

Myrmidon) bleached in 2002 and points to the utility of the model in identifying deep reef areas that are less likely to experience the negative effects of extreme thermal events.

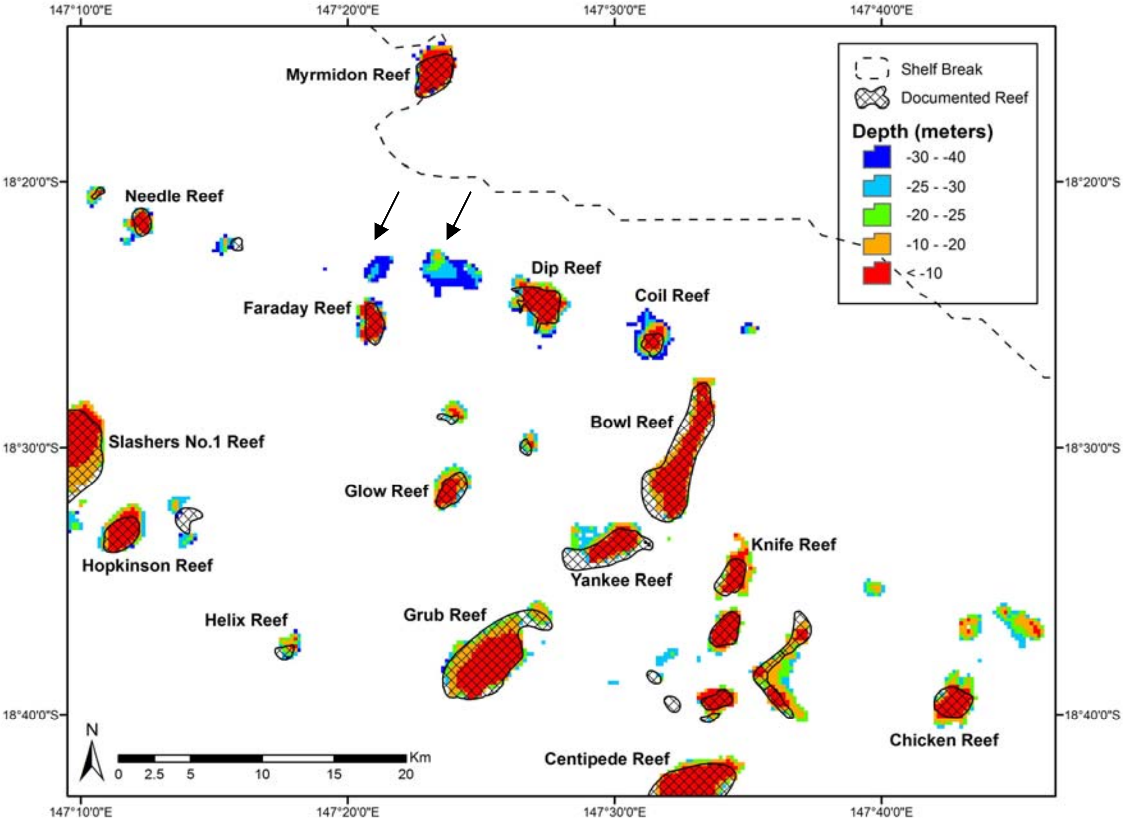


Figure 21. Location of modeled reef habitat ground truthed by AIMS divers, black arrows highlight two sites visited, legend shows depth ranges of modeled reef habitat.

Figure 22. Undocumented reef with high coral cover from ground truthed sites (Figure 21). Photo credit: M. Wakeford (AIMS).

Statistical Analyses

GBRMPA’s 1:250,000 scale reef coverage was converted to a 250 m x 250 m resolution grid so statistical comparisons could be made between model predictions and documented reefs. Table 2 shows cross validation results from 250 m x 250 m model predictions and GBRMPA’s gridded reef coverage. The model correctly predicted 76% of documented reefs and 94% of reef absences for the GBRMP. The vast majority (72%) of false negatives occurred in the extreme Far Northern Section of the GBRMP. The Far Northern Section is remote and covered in cloud for a significant portion of the year so the high number of false negatives in this region was not surprising, nor unexpected. The data quality of the 250 m and 500 m bathymetric depth models in the Far Northern Section is also questionable as this region has not been surveyed in detail. Data quality issues and concern that Far Northern Section model results could be skewing the overall performance of the prediction prompted recalculation of cross validation tables.

Table 3. Cross validation statistics for modeled reef habitat and documented reefs. Notes: These statistics were calculated for the entire extent of the 250 m DDM, which extends east of the GBRMP into the Coral Sea. Ground truthed data did not exist for Coral Sea reefs within the boundary of the 250 m DDM, thus Coral Sea reefs are reported as false positives in table 2.

		Modeled Reef		
	Frequency % Row % Col %	Absence (0)	Presence (1)	Total
Documented Reef	Absence (0)	7704944 91.0 ***Absences 94.4*** 99.1	457118 5.4 ***False pos. 5.6*** 66.5	8162062 96.4
	Presence (1)	72706 0.9 ***False neg. 24.0*** 0.9	230727 2.7 ***Presences 76.0*** 33.5	303433 3.6
	Total	7777650 91.9	687845 8.1	8465495 100.0

Cross validation statistics were recalculated excluding the northern region of The Far Northern Section of the GBRMP (the area north of 13.5° S) where most false positives occurred. Results of this recalculation (Table 4) show the model correctly predicted 90% of documented reefs and 93% of reef absences for the remainder of the GBRMP.

Table 4. Cross validation statistics for modeled reef habitat and documented reefs, excluding the northern region of the GBRMP Far Northern Section and reef containing regions of the Coral Sea within the boundaries of the 250 m DDM.

		Modeled Reef		
	Frequency % Row % Col %	Absence (0)	Presence (1)	Total
Documented Reef	Absence (0)	5190037 89.5 ***Absences 92.7*** 99.6	407927 7.0 ***False pos. 7.3*** 69.5	5597964 96.6
	Presence (1)	20463 0.4 ***False neg. 10.2*** 0.4	179311 3.09 ***Presences 89.8*** 30.5	199774 3.45
	Total	5210500 89.9	587238 10.1	5797738 100.0

Logistic regression analysis was performed to determine the importance of model input parameters in determining the locations of documented reefs (Table 5). Maximum depth of light penetration (Z_{max}) was the most important variable in determining where reefs occur, with a t-statistic of 198.5. Average nitrate was also important with a t-statistic of 78.41. The five remaining predictive parameters (min. salinity, max. salinity, max. SST, avg. phosphate, and min. SST) were significant, but not as important as light and average nitrate.

Table 5. Logistic regression showing the most important variables to reef occurrence, dependent variable is the locations of documented reefs within the GBRMP.

Variable	**Estimate**	**Std. Err.**	**t-Statistic**	**Pr(|t|)**
Light (Zmax)	1.45	0.01	198.49	0.00
Depth	3.45	0.04	80.10	0.00
Nit_Avg	0.31	0.00	78.41	0.00
Sal_Min	-0.23	0.00	-54.05	0.00
Sal_Max	-0.40	0.01	-48.05	0.00
SST_Max	-0.15	0.01	-22.80	0.00
Phos_Avg	-0.06	0.01	-8.55	0.00
SST_Min	0.04	0.01	4.86	0.00

Discussion

False Positives

Environmental parameters included in the model are statistically significant and accurate predictors of documented reefs in the GBR. High numbers of false positives along the mainland coast, inner lagoon, and Far Northern Section are likely to be the result of (1) poor data quality of input parameters in the coastal zone / Far Northern Section and (2) absence of environmental parameters that significantly influence reef growth. Poor data quality in coastal zones is common as terrestrial influences (freshwater runoff, erosion, flood events, nutrient loading, sediments) cause a high degree of environmental variability over small spatial and temporal scales. The coarse spatial resolution (1° x 1°) of some environmental parameters (salinity, sea surface temperature, nitrate, phosphate) included in the model do not capture this variability and do not accurately represent environmental conditions in the coastal zone. Higher resolution data (~ 1 km x 1 km) exists for sea surface temperature, PAR and K_{490}.

Future models will use these higher resolved datasets and will likely improve the accuracy of modeled reef habitat in inshore regions.

A reduction in false positives in the coastal zone and inner lagoon would be possible with the addition of two parameters: bottom substrate composition and freshwater inputs from flood events. Coral polyps require hard substrate for successful settlement to occur; thus, descriptive information on bottom type would be beneficial in determining areas suitable for reef growth. Unfortunately, bottom substrate data is patchy for most regions, including the GBR and non-existent in many areas. Nonetheless, if quality substrate data becomes available, a significant reduction in coastal/inner lagoon false positives would be possible.

Optimal salinity for most coral reefs is 34-35 ppt, but corals can tolerate salinities in the 25-40 ppt range (Coles and Jokiel 1992). Flood events and the resultant drop in coastal salinities are lethal to corals if the salinities remain below 20 ppt for more than 24 hours (Edmondson 1928, Vaughan 1916). Large drops in localized salinities from flood events are not sufficiently reflected in 1° x 1° monthly average salinity data used here, resulting in false positives within river flood plumes. Coral areas within the reach of river flood plumes are exposed to high levels of suspended sediments, which inhibit reef growth by causing a reduction in water clarity. This leads to a decrease in light penetration and an overall reduction in available light needed for photosynthesis. High levels of suspended sediments can also be lethal to corals if the rate of deposition is greater than the corals ability to remove the sediments, a process known as smothering (Marshall and Orr 1931, Edmondson 1928). K_{490} data used in this analysis is probably of adequate spatial resolution to detect high suspended sediments from flood events, but temporal resolution was limited to monthly average and spanned five years (1997-2002). The temporal resolution and time period covered would not capture infrequent, reef limiting flood events (e.g. 100 year flood).

Applications

The current model's greatest potential application is in identifying undocumented deep reefs. Identifying deep water areas favorable for reef growth and likely to contain reefs should be a priority as these areas are less likely to experience high temperature events that have caused significant coral mortality in recent years. These areas need to be identified and protected as there is warranted concern that coral bleaching events will occur with greater frequency and intensity due to global climate change (Done et al. 2003).

Heyward et al. (in prep) used the 1 km x 1km model and field validations of coral presence at depth to predict favorable reef habitat for the submerged shoals along the edge of the Australian continental shelf between northwestern Australia, Indonesia and Timor Leste. Model results for this region indicate approximately twice as much coral and algal dominated reef habitat occurs below 30 m as above with maximum depth of favorable reef habitat > 60 m in some areas. If model results accurately predict reefs in poorly mapped regions, it may be possible to derive more accurate estimates of local reef area.

Researchers with the Millennium Coral Reef Project, a global reef mapping initiative which used satellite data to create the first comprehensive world data resource on coral reefs, have expressed interest in using this model to identify deep reef habitat that is not detectable by satellite sensors. The model would fill the satellite depth limitation void quite well if highly resolved (1-2 km) bathymetry data were available for the World's oceans. Currently, Etopo2 (2' x 2') data is the most highly resolved bathymetric dataset that is global in extent and available to the public. A high resolution (1-2 km) global bathymetric dataset is in high demand by the marine science community in general and marine ecosystem modelers in particular.

Predicted changes in sea surface temperature and aragonite saturation state could be included in future models to identify reef areas that may become increasingly marginal due to changes in seawater chemistry and sea surface temperature. Future projections for aragonite saturation state and sea surface temperature were mapped for the Pacific Basin by Guinotte et al. (2003), but due to uncertain estimates for future atmospheric CO_2 concentration, spatial resolution of these projections remain coarse (1 - 2.5 deg or greater) and are not applicable to regional applications of the reef prediction model. Finally, a real-time high resolution version of the model could be built that would allow researchers to continually monitor environmental conditions remotely and issue alerts if and when environmental conditions exceed predetermined thresholds which are known to be detrimental to coral health (high sea surface temperatures, low salinities, or high levels of nutrients).

Chapter 4

Depth Provides Refuge for Coral Reefs

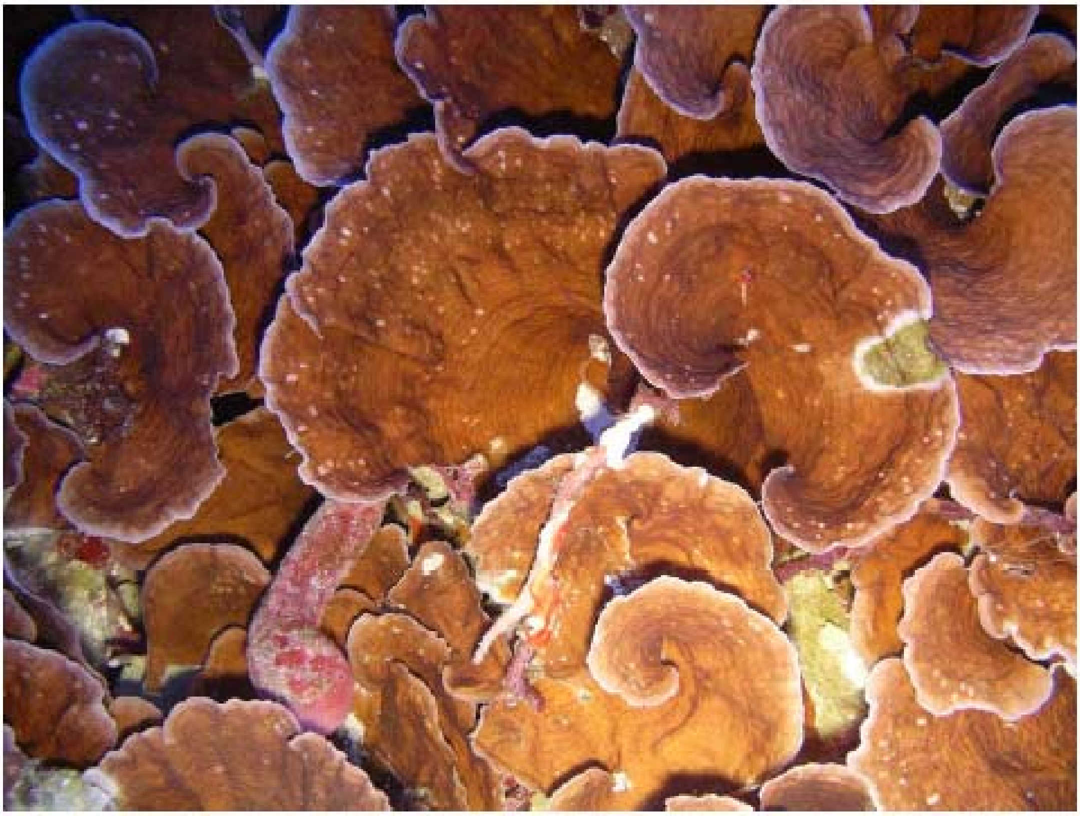


Photo Credit: Andrew Heyward

Citation

Heyward A, Smith L, Rees M, Guinotte JM (in prep) Depth provides refuge for coral reefs. [Target journal = Note submitted to Science or Nature]

Abstract

While the declining state of the world’s coral reefs has become a disturbing icon of global-scale human pressures and environmental change, here we present evidence that in some tropical regions the major components of reef coral communities can occur at depths greater than 30m and these have largely escaped both investigation and degradation. This finding suggests a risk that the true extent and nature of functional reef ecosystems is currently misrepresented due to a research bias towards waters less than 20m deep. There is comparatively little understanding of the functional links to deeper contiguous habitats, nearby submerged reefs or inter-reefal habitats beyond typical scientific SCUBA diving depths. Using imaging tools such as ROVs and towed video systems we explored the numerous submerged shoals along the edge of the Australian continental shelf between northwestern Australia, Indonesia and Timor Leste. The majority of these habitats are 15-50m deep and support a high diversity of coral reef organisms. Reef-building coral and algae communities in this region are found in shallow waters (< 30m), but are also common in depths of 30-60m. On some shoals and reefs the extent of live coral at depth greatly exceeds that in adjacent shallow water zones and appear to have escaped the global coral bleaching episode of 1998. We provide an example where the closely monitored shallow sites in the upper 20m were devastated by bleaching in 1998, yet vast reserves of live coral remained intact in depths of 30-60m. Application of a model for potential coral habitats on these shoals, using the Australian bathymetric database and field validations of coral presence at depth, indicates that approximately twice as much coral and algal dominated coral reef habitat occurs below 30 m as above for this region. This finding suggests a risk that the true extent and nature of functional reef

ecosystems is currently under-represented due to a research bias towards waters less than 20m deep. These deeper reef zones may provide refugia for some shallow water species and are likely to contribute greatly to ecosystem resilience (the capacity of an ecosystem to tolerate disturbance without collapsing) as the shallow water reef zones increasingly suffer disturbance. There is comparatively little understanding of the functional links to deeper contiguous habitats, nearby submerged reefs or inter-reefal habitats beyond typical scientific SCUBA diving depths. Other deeper shoal areas, such as in the Seychelles, Bahamas and Bermuda Banks, may harbor important coral reserves, underscoring the need to extend quantitative surveys below the readily-accessible shallow reefs.

Personal Contribution and Context within the Thesis:

My personal contribution to Chapter 4 was to obtain relevant environmental data for the region and estimate the probable area of deep coral cover. I was also involved in a substantial rewrite of an early version of this manuscript, which has since undergone extensive edits by me, culminating in Chapter 4. Contribution percentage to Chapter 4 as it appears in this thesis: Andrew Heyward (30%), Luke Smith (20%), Max Rees (10%), and John Guinotte (40%).

Chapter 4 builds heavily on methodologies developed in Chapter 3 and applies these methods to another region of the world (Western Australia). Chapter 4 directly addresses Research Foci 1, 2, and 4 (Figure 23). Results in Chapter 4 clearly show that the methodologies developed to identify deep coral habitat in the GBRMP can successfully be applied globally (RF1 and RF4). Deep coral habitat is identified off the

Western Australian coast by applying Chapter 3 methodologies (RF1) and the detrimental effects of the 1997-1998 coral bleaching event are documented for the region (RF2). Predicted deep coral regions as potential areas of refugia from coral bleaching is also discussed (RF 2 andRF4).

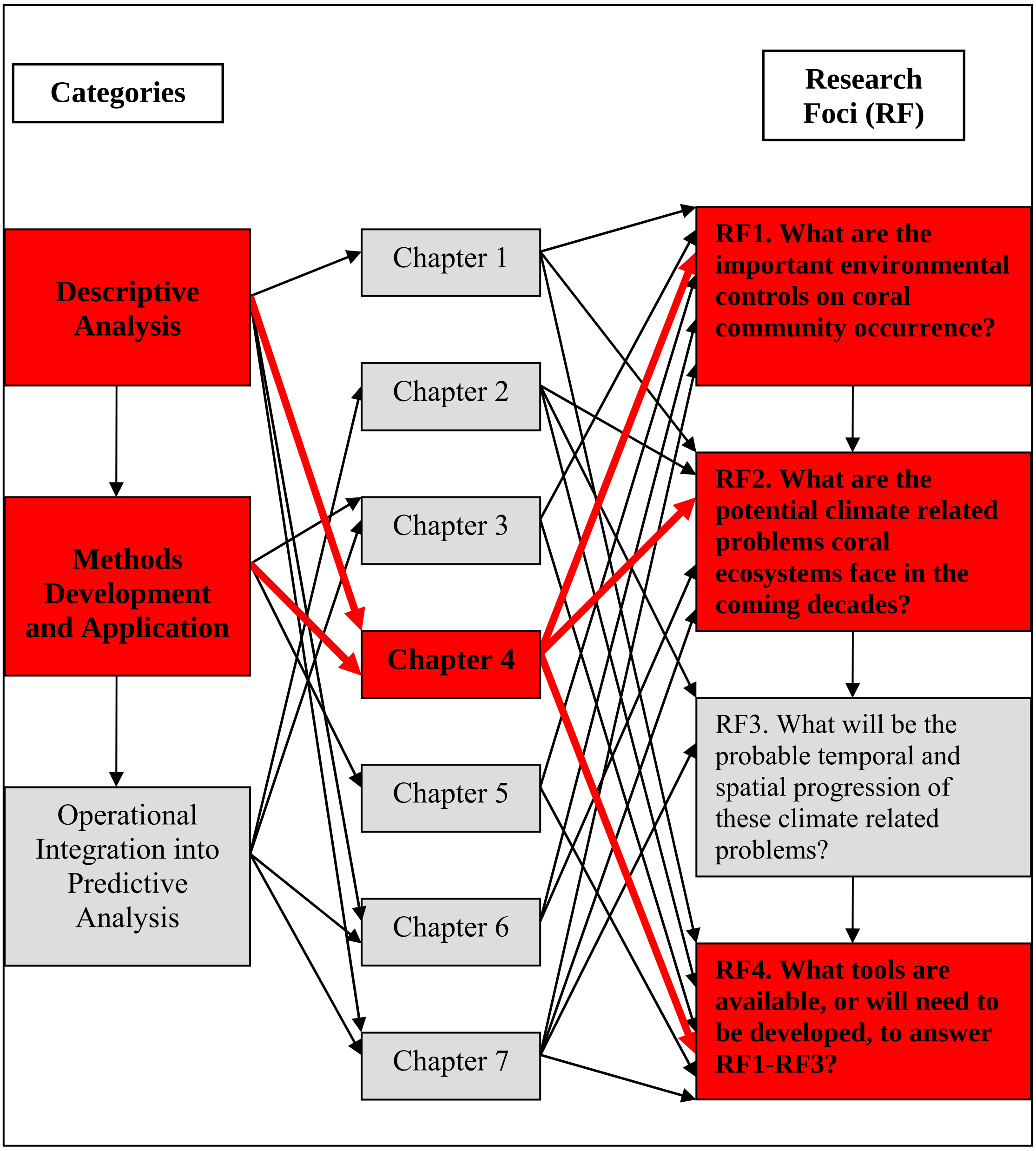


Figure 23: The relevance of Chapter 4 to the overall scheme of the research.

Introduction

Global reef monitoring programs and studies of reef ecology suggest unsustainable use by humans and a spate of regional or global scale threats are placing increasing numbers of reefs in crisis (Bellwood et al. 2004, Wilkinson 2002). Pandolfi et al. (2003) stated that coral reefs have declined over the course of human history, evidenced by a substantial increase in coral mortality and degradation in the past 20-25 years. Wilkinson (2000, 2002) estimated that 16% of the world's coral reefs had been extensively damaged by the 1997-1998 coral bleaching event alone. Much of the data underlying these irrefutable observations during the last two decades has come from SCUBA or snorkeling-based studies that focused on shallow waters. Although technical innovations are being pursued to ameliorate depth and bottom time diving constraints (Mastro and Dinsmore 1990), consideration of the contemporary literature and an indicative analysis of institutional diving logs shows that the overwhelming majority of field studies are still focused at depths of 0-20m (AIMS 2004). Major assessments of reef coral and reef fish zoogeography have acknowledged that ecosystem boundaries should be set to at least 50m depth (Bellwood and Hughes 2001, Veron 1995, Praeobrazhensky 1993). Species lists derived from taxonomic studies were made with grabs, dredges, and tows, or by divers venturing to depths in excess of present-day approved depth range (15-30m).

Methods

During the course of routine surveys of Australian coral reefs in the Timor Sea and Northwest Shelf region we established permanently marked SCUBA-survey areas in 1994 at Scott Reef, an oceanic emergent reef at the edge of Australia's Northwest Shelf in the Timor Sea, and also began analysis of ROV-based surveys of a number of submerged reefs that run along the shelf edge margin for more than 600km to the east (see Figure 1). The Scott Reef studies used existing AIMS reef monitoring protocols, which are diver based, while the assessments of submerged reefs, which were often deeper than 20m, relied on interpretation of videotape captured using ROVs or towed video systems.

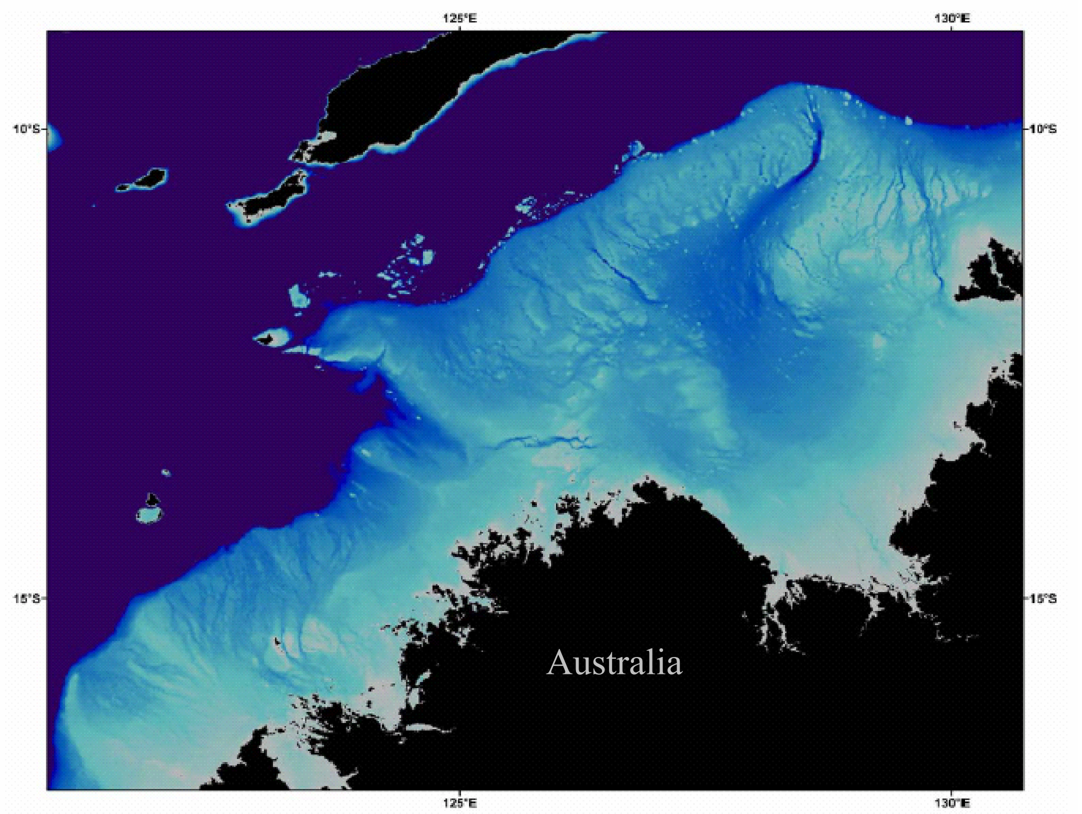


Figure 24. The Australian continental shelf and numerous submerged shelf edge reef shoals in the Timor Sea. Image is a bathymetric database reconstruction, provided by Geosciences Australia.

Results

Scott Reef consists of two main reef structures, North and South Scott Reef, rising from several hundred meters to emergent rims. Our monitoring focused on South Scott reef, where the reef rim bounds an open, horseshoe-shaped lagoon comprising both shallow lagoon habitats and a small sandy islet, together with a significant area of deeper lagoon. In South Scott Reef the estimated area of habitat <30m depth is 100km^2, while there is 300km^2 of deeper lagoon between 30-70m depth. The monitoring sites, used for annual surveys of the status of the benthic and fish communities from 1994 to the present, are located at depths less than 15m, with most sites at 6-12m depth. In 1994 all sites were in good condition and the mean abundance of live corals compared favorably with the long-term average of outer reef slope sites in the Great Barrier Reef. Annual censes indicated an overall trend of increasing coral abundance, reaching a mean across all sites of 51% in late 1997. In 1998 this reef system suffered catastrophic coral mortality due to coral bleaching, with a loss of 80% of live coral (Figure 25). Surveys in 1998 and 99 confirmed this situation and together with subsequent surveys also suggested that recovery of the shallow water communities would be slow.

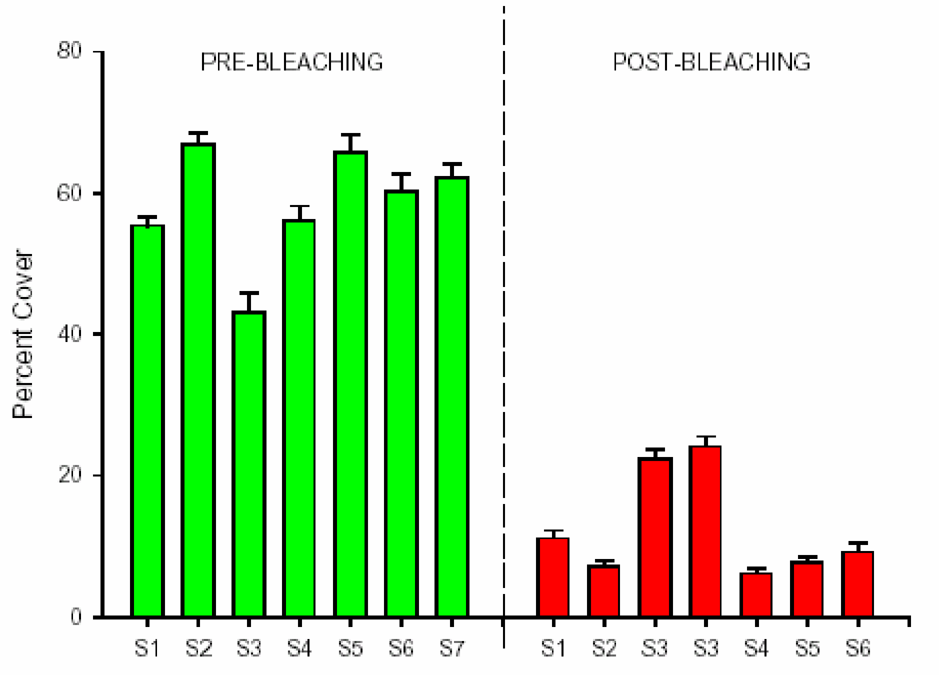


Figure 25. Impact of the 1998 global bleaching phenomenon on coral abundance at shallow-water monitoring sites on Scott Reef. Each site consists of 15 X 50 m fixed transects, permanently marked to enable repeated surveys through time

However, in 1999 we extended the quantitative census of this system to the deeper waters of South Scott lagoon and found widespread live coral and benthic algal communities, with surprisingly high abundance in places, even at depths of 50-60m (Figure 26). Based on 198 ROV survey transects in 1999 the mean coral abundance between depths of 30-70m was 21%, with some transects as high as 80% (Figure 27). Compared to traditional diver-based reef assessments the habitats deeper than 30 m had twice the mean abundance of live coral as the shallower habitats after 1998. Furthermore, when available habitat for coral growth is considered, these data indicate that for this reef system, the greater abundance of live coral will always be in deeper water (> 30 m). Although Scleractinian diversity declined with depth, we observed no reduction in the abundance of either coral or algae such as *Halimeda* at sites down to 65m (Figure 28). In terms of total ecosystem status, available habitats, or trophic links dependent on live corals or benthic algae, the deeper reef is likely to be extremely important.

Figure 26. Mix of red algae, *Halimeda* and scleractinian corals at 57 m, Timor Sea.

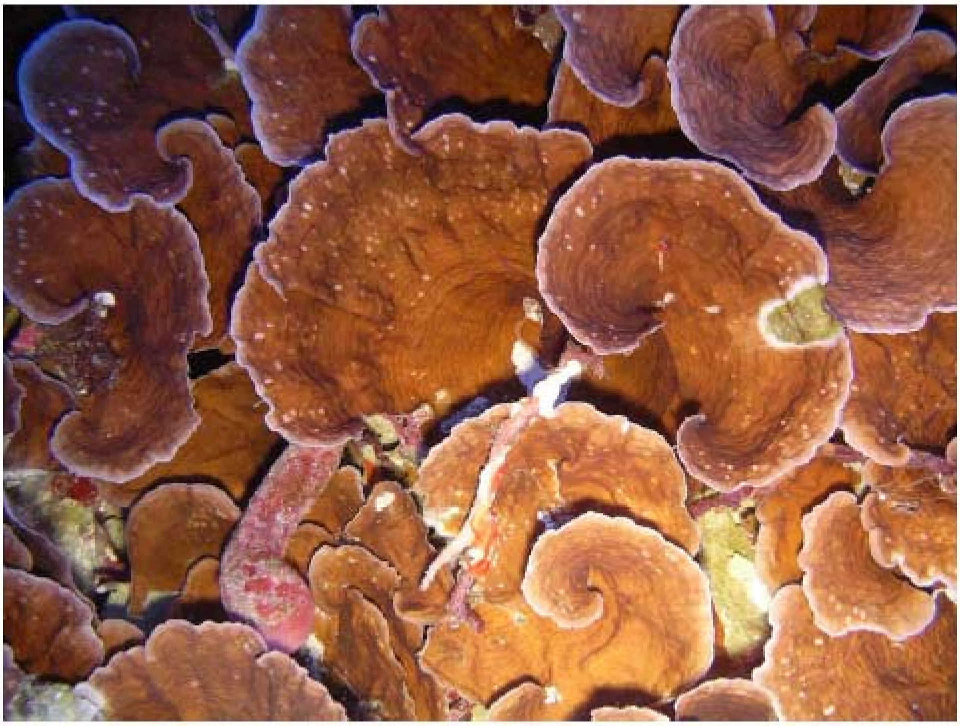


Figure 27. Scleractinian dominated habitat at 55 m, Timor Sea.

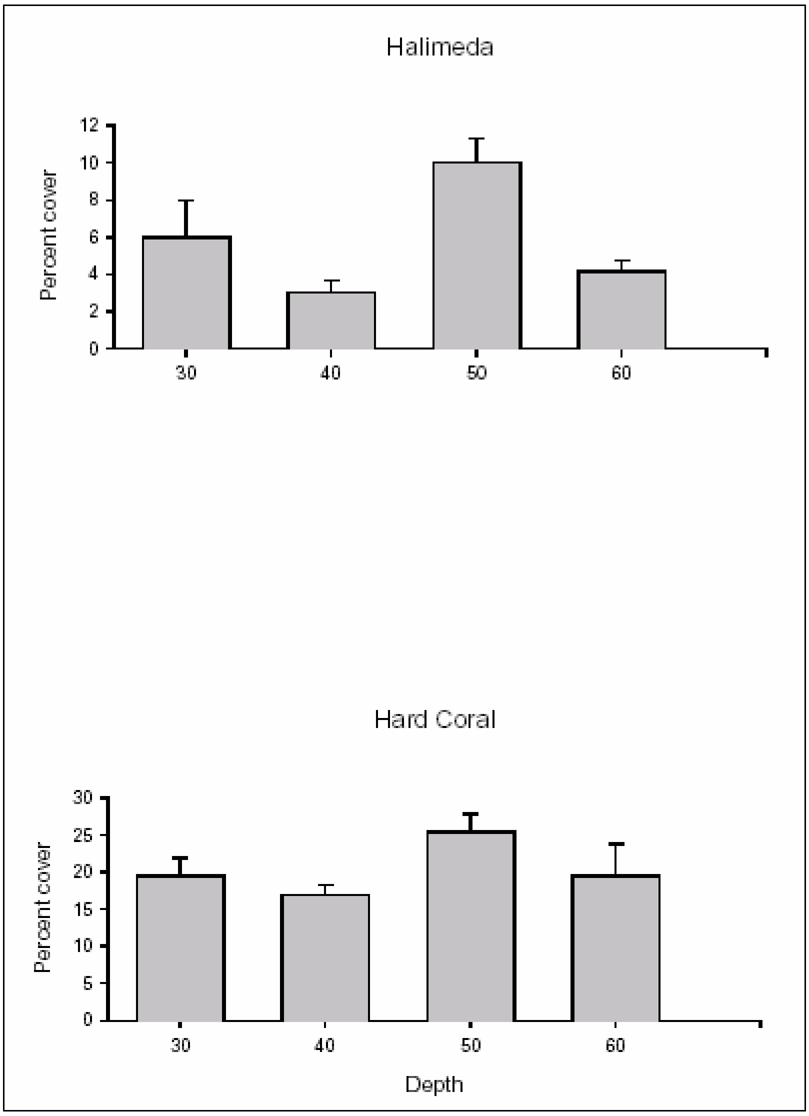


Figure 28. South Scott deeper lagoon. Mean abundance versus depth of live coral and the calcareous algae Halimeda spp. for all ROV survey transects. A total of 199 X 50m transects were captured in depths between 30 and 70m. Data was averaged for depth between replicate transects at each site and grouped into 4 depth classes: <36m, 36-45m, 46-55m and 56-65m.

The coral reefs of northwest Australia are best known from a handful of emergent reef systems located well offshore along the edge of the continental shelf, examples include the marine protected areas of Ashmore Reef, Rowley Shoals, and Scott Reef. However, this region is notable for more than one hundred subsurface carbonate reefs (Figure 24). We have analyzed data for additional subsurface reef sites in the central and eastern parts of the Northwest Shelf edge region. In all areas we have found examples of the same deep water coral and algal assemblages seen in South Scott Reef's deep lagoon, suggesting the widespread nature of this reefal habitat. Using the highest resolution bathymetric database available for the region we applied Guinotte's model (Guinotte submitted) for potential coral habitat across the region. The model was refined using light penetration data for Scott Reef and coral abundance data from several submerged reefs along the shelf edge. Results indicate almost twice as much potential coral habitat at depths in excess of 30m than at less than 30m (Figure 29). Ongoing surveys of submerged shoals across the shelf-edge region continue to reveal significant coral reefs with high coral cover at depths greater than 30 m.

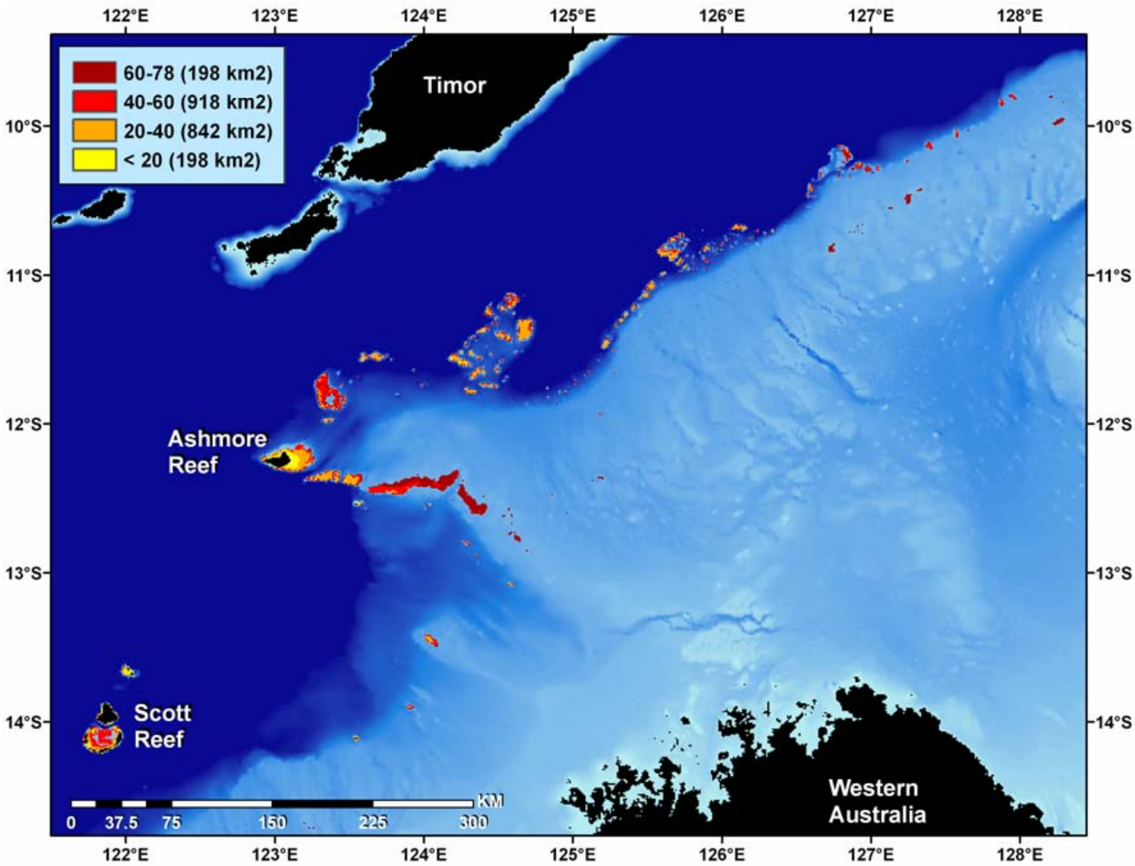


Figure 29. Available coral habitat in the central Timor Sea. Model prediction using 1km bathymetry database provided by Geoscience Australia and calibrated by field observations of significant coral abundance below 30m depth where coral communities could flourish at depths below tidal datum.

Discussion

These results indicate that diver based research in depths of 0-30m will not accurately estimate coral abundance in some regions or the status of reefs as a whole. The extensive deeper communities of Scott Reef appear to have escaped the severe disturbance of the 1998 global bleaching event, while the adjacent shallow water communities were devastated. Similar differential stability is also likely in the face of storms. This potentially large and less disturbed reservoir of phototropic benthos may be a key factor in the resilience of these systems. Reefs in depths below 30m remain the least studied and understood coral reef types and their full extent remains unknown. In this study we have focused on a large, oceanic, clearwater region. However, the recent discovery of submerged tropical reefs at 30m in nearshore turbid waters suggests still more extensive deep reef resources exist (Harris et al. 2004).

Chapter 5

Modeling Habitat Distribution from Organism Occurrences and Environmental Data: a Case Study using Anemonefishes and their Sea Anemone Hosts

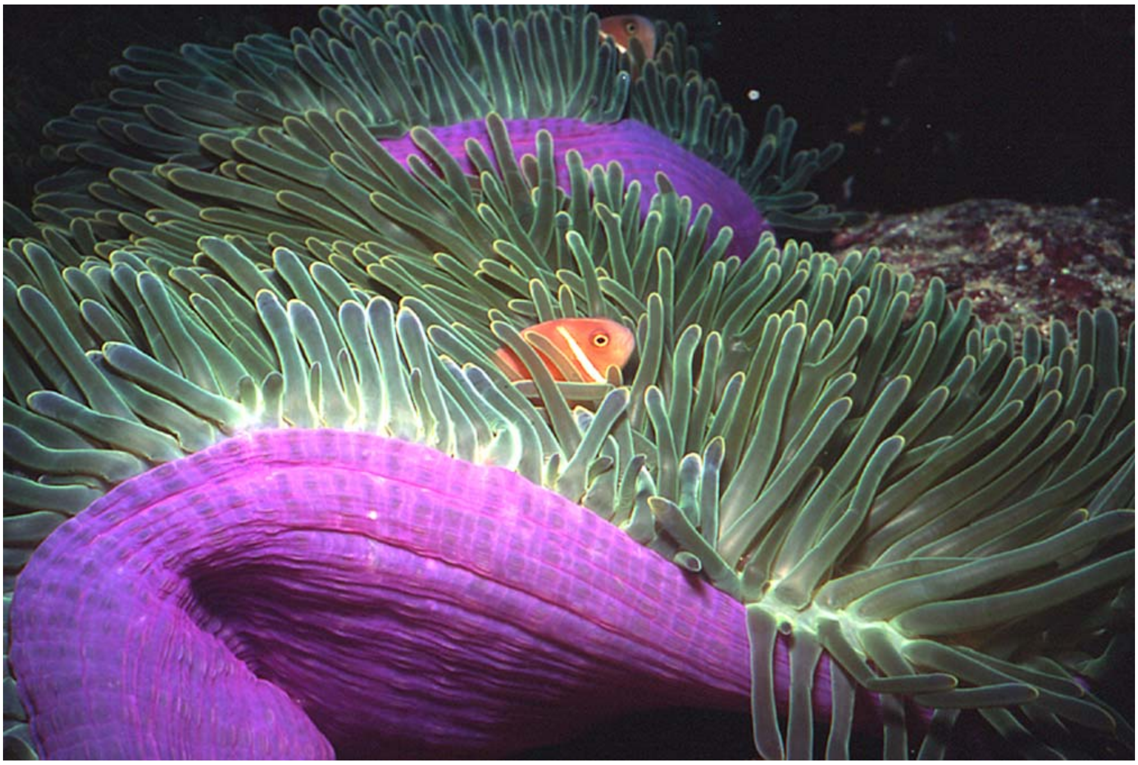


Photo Credit: California Academy of Science

Citation

Guinotte JM, Bartley JD, Iqbal A, Fautin DG, Buddemeier RW (2006) Modeling habitat distribution from organism occurrences and environmental data: a case study using anemonefishes and their sea anemone hosts. Marine Ecology Progress Series 316:269-283

Abstract

We demonstrate the KGSMapper, a straight-forward web-based biogeographic tool that uses environmental conditions of places where members of a taxon are known to occur to find other places containing suitable habitat for them. Using occurrence data for anemonefishes or their host sea anemones, and data for environmental parameters, we generated maps of suitable habitat for the organisms. The fact that the fishes are obligate symbionts of the anemones allowed us to validate the KGSMapper output: we could compare the inferred occurrence of the organism to that of the actual occurrence of its symbiont. Characterizing suitable habitat for these organisms in the Indo-west Pacific, the region where they naturally occur, can be used to guide conservation efforts, field work, etc.; defining suitable habitat for them in the Atlantic and eastern Pacific is relevant to identifying areas vulnerable to biological invasions. We advocate distinguishing between these two sorts of model output, terming the former maps of realized habitat and the latter maps of potential habitat. Creation of a niche model requires adding biotic data to the environmental data used for habitat maps: we included data on fish occurrences to infer anemone distribution and vice versa. Altering the selection of environmental variables allowed us to investigate which variables may exert the most influence on organism distribution. Adding variables does not necessarily improve precision of the model output. KGSMapper output distinguishes areas that fall within one standard deviation (SD) of the mean environmental variable values for places where members of the taxon occur, within 2 SD, and within the entire range of values; eliminating outliers or data known to be imprecise or inaccurate improved output precision mainly in the 2 SD range and beyond. Thus, KGSMapper is robust in face of questionable data, offering the user a way to recognize and clean such data. It also functions well with sparse datasets. These features

make it useful for biogeographic meta-analyses with diverse, distributed datasets that are typical for marine organisms lacking direct commercial value.

Personal Contribution and Context within the Thesis:

My personal contribution to Chapter 5 was to collaborate with Kansas Geological Survey computer programmers to make these data sets accessible to the public via the World Wide Web and help develop the online GIS functionality that made this Chapter possible. I obtained relevant environmental data sets, performed the GIS analyses for this research, participated in the joint writing of this paper, and handled all reviewer comments and edits. Contribution percentage to Chapter 5: John Guinotte (35%), Jeremy Bartley (10%), Asif Iqbal (10%), Daphne Fautin (20%) and Bob Buddemeier (25%).

Research presented in Chapter 5 is a logical next step to the methodologies developed in Chapters 3 and 4 to predict habitat for marine organisms, in this case anemones and anemonefishes, with known locations. Chapter 5 directly addresses Research Foci 1, 2, and 4 (Figure 30). Anemones and anemonefishes are constituent organisms of coral reef ecosystems and are sensitive to environmental change (RF1). New online tools were developed to map potential distributions for these organisms and can be used to predict the range of suitable habitat for any marine organism (RF 4).

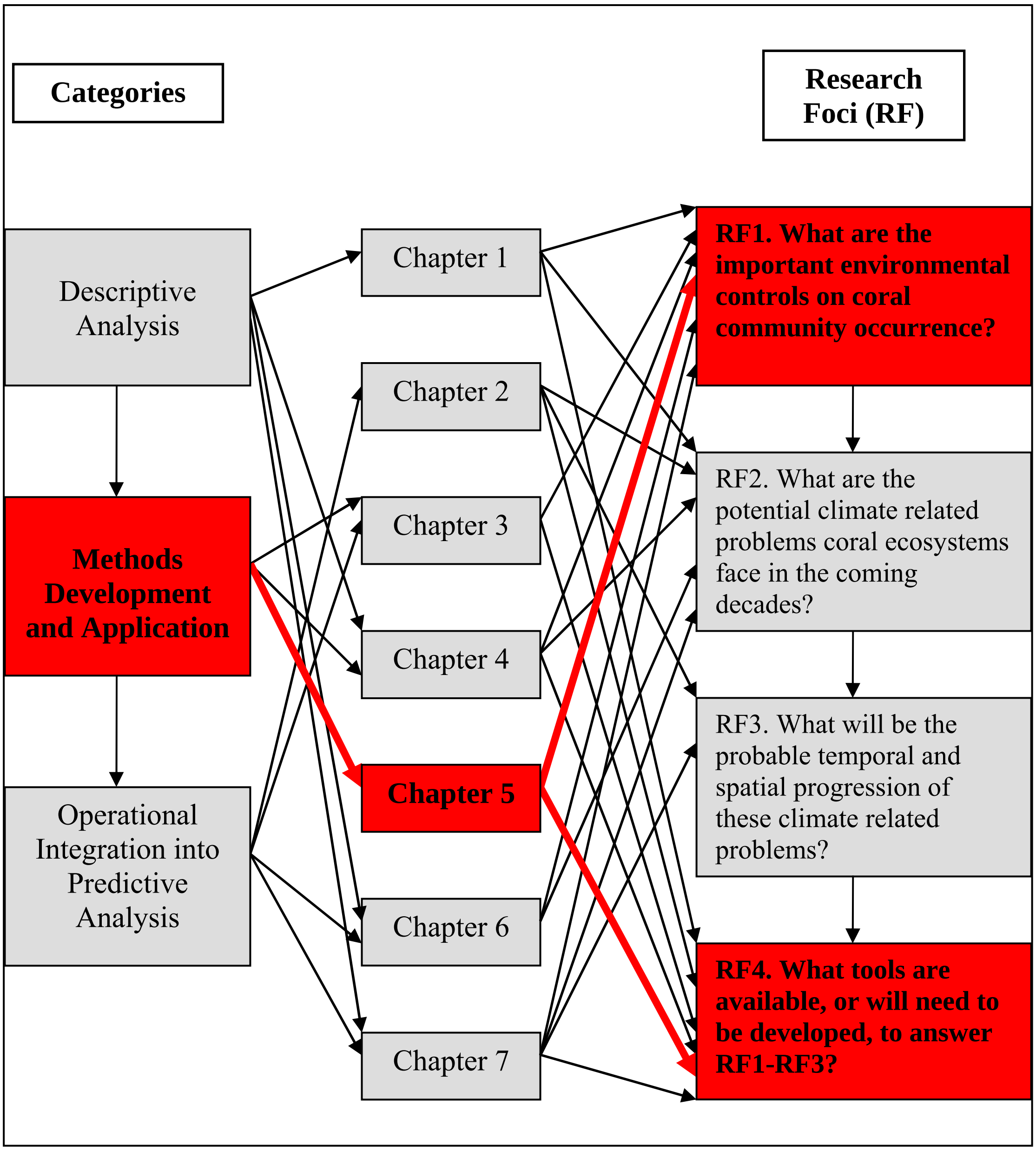


Figure 30: The relevance of Chapter 5 to the overall scheme of the research.

Introduction

Biogeographic information, whether about taxa, guilds, or groups of associated organisms, is fundamental to human use and understanding of the environment. Electronic resources are rapidly enhancing the volume and diversity of information that can be brought to bear on problems such as the identification and protection of biodiversity, actual or potential invasive species, and diagnosis and prediction of the effects of climate change (e.g. Soberón & Peterson 2004, and references cited therein). As distributed biogeographical and environmental datasets become more available and better integrated, the need for simple but flexible tools to exploit them will grow, and the outputs will be extended to more uses. It is vital to understand the nature of the data and the uses to which tools and their outputs can appropriately be put. In this proof of concept study, we explore some characteristics of mapping tools and their output.

The most fundamental of biogeographic data concern organism distribution. One convention for depicting distribution is plotting known occurrences as dots (points) on a map. With rare exceptions, these dots are not intended to represent the entire distribution of the taxon in question. A range map is commonly derived from such a dot map, the outermost bounds of a polygon representing the taxon's distribution connecting the most peripheral dots of the taxon's known occurrence or where organism density falls below a particular threshold (e.g. MacArthur 1972). Such a polygon commonly overestimates the taxon's range. In the marine realm, the range of a shallow-water species occurring throughout the tropical Pacific would cover the entire tropical Pacific Ocean, including the deep water between islands (as in, e.g., Fautin & Allen 1992). A more ecologically realistic approach is to correlate actual occurrences with physical, chemical, or biological data (e.g. MacArthur 1972), so, for example, a shallow marine species would be depicted as occurring only around land masses or on banks and shoals.

Thus, more than a collection of geographic coordinates, a range is a manifestation of characteristics of the habitat (biotic and abiotic) that limit or support the organism of interest. A range is inherently a large-scale concept based on observed occurrences; however, range analysis does not necessarily predict organism presence at any specific point. We illustrate some alternative approaches to modeling and understanding habitat distributions for marine organisms by analyzing data from three databases with the KGSMapper, an application for interactive analysis of georeferenced occurrence records of marine organisms with gridded environmental data. It is one of a class of electronic tools that, by making it progressively easier to develop correlative analyses from occurrence and environmental data, are rapidly supplanting traditional approaches to interpretive mapping, which tend to be tedious and difficult to replicate. We discuss some issues in evaluating these sorts of analyses. Computer tools and databases cannot substitute completely for knowledge and judgment, however, and the tool we discuss provides ways in which the investigator can interact with and modify the datasets used in order to explore or test hypotheses and tune the nature of the output to the question of interest, rather than simply generating a "hard-wired" occurrence prediction.

Applications such as WhyWhere (http://biodi.sdsc.edu/ww_home.html) and GARP (http://www.lifemapper.org/desktopgarp, http://biodi.sdsc.edu/Doc/GARP/Manual/manual.html) that offer computationally sophisticated approaches to associating environmental and occurrence data (e.g. genetic algorithms) provide the user limited control over datasets and particularly data processing.

Tools such as BIOCLIM (http://cres.anu.edu.au/outputs/anuclim/doc/bioclim.html) are confined to or work best in terrestrial habitats. No single approach will be optimal for all questions, or for the needs of all potential users (Fielding and Bell 1997, compare assessments of GARP by Beauvais et al. 2004, and Drake & Bossenbroek 2004); in making a choice, consideration must be given to types, scale, quality, and quantity of data available, questions to be addressed, and verifiability of the product (e.g. Fielding & Bell 1997, Manel et al. 2001, Beauvais et al. 2004, Drake & Bossenbroek 2004, Robertson ND).

We investigated the issues listed below by generating probabilistic maps of potential habitat occurrence, depicting large-scale areas suitable for survival of these organisms, not organism presence-absence inferences. We used the KGSMapper to analyze the occurrence of habitat suitable for anemonefishes (which may be referred to as clownfishes) and their host sea anemones. The fact that the fishes are obligate symbionts of the anemones (although individual anemones may be found without anemonefish) make it an ideal test case for validating model output: we did not have to go to the field to determine if the organism occurs where we inferred it would, but could compare the inferred occurrence of suitable habitat for the organism to that of the actual occurrence of its symbiont. It is also ideal as a test case in being typical of datasets available for non-fisheries marine species. We discuss model outputs often termed range, habitat, and niche predictions. Such outputs are commonly used within the natural range of a taxon to guide field work, conservation efforts, etc., and outside the natural range to identify areas vulnerable to biological invasion.

(1) Sampling issues. Datasets for a diversity of environmental parameters may be available. The outcome of occurrence predictions or range inferences will be affected by which variables are selected, and how. True niche models (e.g. Peterson 2001,

Raxworthy et al. 2003, Soberón & Peterson 2004) must include parameters of the biotic environment beyond strictly habitat characteristics.

(2) Data quality. Models must be robust in the presence of questionable or erroneous data points. Particularly for meta-analyses, which use datasets from a variety of sources, the data are likely to vary in accuracy, precision, and resolution, making it unlikely that data quality will uniformly meet the desired standards of any individual user or application. Therefore, tools are needed for evaluating and/or cleaning datasets when there is a basis for doing so, and the criteria for these actions must be clear.

(3) Data quantity. The effect of number of data points on inferences is vital to recognize (e.g. Stockwell & Peterson 2002). A common use of modeling is to infer the biogeographic range of a taxon for which the documented occurrence records almost certainly fall far short of encompassing the actual range. This situation is extremely common for marine invertebrates, particularly for analyses at the species level, but is by no means restricted to them (e.g. Beauvais et al. 2004). Models can provide insight into the areas in which it will be most economical or efficient to sample to verify the true extent of the range.

(4) Validating or testing results. Assessing predictions or inferences is a desideratum (Fielding & Bell 1997, Robertson ND) in this, as in any hypothesis-testing. The end-members on the predictive continuum are a broad-brush approach that minimizes errors of omission and a focused approach that minimizes errors of commission (Fielding & Bell 1997, Anderson et al. 2003). In dealing with the continuum of quality and/or extent inherent in habitat assessment at large spatial scales, omission and commission are not binary no-yes choices, as is typically the case in dealing with presence-absence of organisms; different tests and criteria are called for.

(5) Identifying controlling factors. Drake and Bossenbroek (2004:939-940) appealed to scientists to “develop methods to identify the factors that causally determine species range, and not simply make predictions based on correlations.” Characteristics of a taxon’s range or physiology may suggest that particular environmental parameters control its occurrence.

Data and Methods

Data sources and organisms

The organism distribution data for both taxa are georeferenced point occurrences; the third dataset is gridded coverages of environmental parameters. Having come from three proximate providers, all of which compiled data from multiple ultimate sources, our data are unlikely to be homogeneous in quality and scale.

Anemonefishes, which are widespread in the tropical and subtropical Indo-west Pacific but are absent from the eastern Pacific and the Atlantic, occur in nature only with sea anemones of 10 species belonging to five genera in three families; fish population is limited by the number of suitable hosts (Fautin & Allen 1992). They belong to two genera (*Amphiprion*, with 25 species, and *Premnas*, with one) in a single subfamily, and vary in host specificity, some associating with only one species of host, but most occurring with multiple hosts (Fautin & Allen 1992). Because all host anemones possess photosymbionts, they and their fish symbionts occur only in shallow water (Dunn 1981), typically in waters less than 100 m. The distribution of these animals, therefore, is constrained both environmentally and biologically.

To a first approximation, the 10 species of anemones are ecologically similar, and the 26 species of fishes are likewise similar; this allows us to use as our units of taxonomic analysis all host anemones and all anemonefishes. We extracted occurrence data for the anemones from the on-line resource “Biogeoinformatics of Hexacorals” (http://www.kgs.ku.edu/Hexacoral; hereafter referred to as “Hexacoral”). In the biological database of Hexacoral, which was assembled from the published literature, all names used to refer to a single species are linked, and names that have been applied to more than one species are distinguished. Anemonefish occurrence data were downloaded from FishBase (http://www.fishbase.org), which has been assembled from published records, museum catalogs, and other sources.

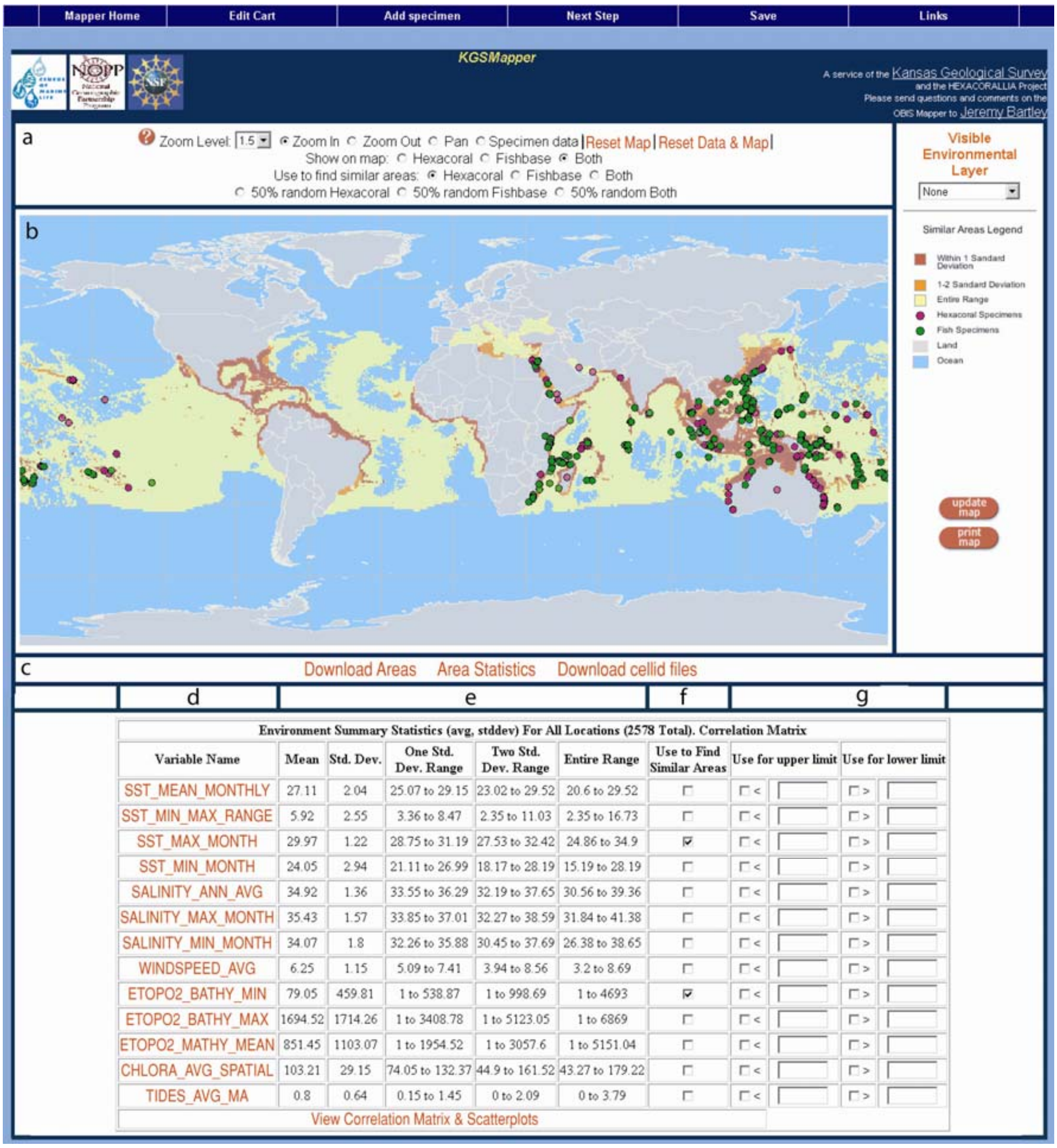
The environmental data, also served from Hexacoral, were assembled from public domain datasets (its source is identified in the metadata associated with each dataset) that are global in coverage. Data were gridded in register at 0.5^{o} resolution (~55 km on a side at the equator), which is typical resolution for global environmental datasets. Datasets with native resolutions other than 0.5^{o} were sampled or aggregated to conform to the grid; for a variable with native resolution finer than 0.5^{o} (such as the 2’ ETOPO2 bathymetry), within-cell variability and extremes were calculated. Most values are annual or monthly averages. Of the more than 200 datasets in Hexacoral, 13 especially relevant to anemonefishes and their hosts are currently available for use with KGSMapper; future versions will make the other datasets accessible. In addition to limitations imposed by size of the grid cells, a significant caveat is that the marine datasets used to generate many of the variables typically fail to represent much of the temporal and spatial variability in nearshore environments.

Tools and analytical procedures

KGSMapper is an interactive web-based mapping tool that permits a user to create maps of inferred distribution in a straight-forward manner. The basic calculations can be done in a spreadsheet, although much of the power of KGSMapper derives from its ability to display and manipulate the data in a GIS environment. Its flexibility allows a user to select approaches relevant to the goals of the study and to apply expert judgment in editing datasets. It currently uses a tightly-integrated environmental database and front end (Oracle 8i RDBMS with Cold Fusion) with, on the server side, ArcIMS web-mapping software (http://www.esri.com/software/arcgis/arcims/index.html). Occurrence records are plotted in real time on a map through an XML-coded data structure based on the OBIS Schema, an extension of DarwinCore 2 (http://iobis.org/obis/obis.xsd). KGSMapper and its associated environmental data are freely available; it is operational through the Hexacoral website (above), that of the Ocean Biogeographic Information System (OBIS: http://www.iobis.org), and those of some OBIS partners (CephBase: http://www.cephbase.org; FishBase: above).

In our analyses, locality records are the 0.5° grid cells containing organism occurrences. Thus the number of occurrences may not equal the number of locality records in the dataset. Cells with one or multiple occurrences are indistinguishable in our analyses – a single occurrence serves to qualify a cell and its environmental variable values as habitat. Conversely, for an occurrence falling on a cell boundary between two or among four cells, all cells are included in the analysis.

The advanced version of KGSMapper we used for this case study (http://drysdale.kgs.ku.edu/website/specimen_mapper/mxmapitmod_7.cfm) is a prototype that currently interacts only with the data discussed here. Table 6 summarizes the features of both prototype and operational versions, highlighting the differences between them. Figure 31 shows the prototype advanced KGSMapper web page; its functions and features are provided below and in the figure caption. KGSMapper plots organism occurrences and provides for them summary values of 13 environmental variables for all cells in which there is at least one occurrence record. Our tests were constrained by the relatively small number of variables served to this prototype from the main database, and by inherent resolution limitations of working at global scales with primarily marine parameters. These are practical matters -- neither is constrained in theory.



Zoom Level: 1.5 ● Zoom In ○ Zoom Out ○ Pan ○ Specimen data | Reset Map | Reset Data & Map |
Show on map: ○ Hexacoral ○ Fishbase ● Both
Use to find similar areas: ● Hexacoral ○ Fishbase ○ Both
○ 50% random Hexacoral ○ 50% random Fishbase ○ 50% random Both

Visible Environmental Layer: None

Environment Summary Statistics (avg, stddev) For All Locations (2578 Total). Correlation Matrix

Variable Name	Mean	Std. Dev.	One Std. Dev. Range	Two Std. Dev. Range	Entire Range	Use to Find Similar Areas	Use for upper limit		Use for lower limit	
SST_MEAN_MONTHLY	27.11	2.04	25.07 to 29.15	23.02 to 29.52	20.6 to 29.52	☐	☐ <		☐ >	
SST_MIN_MAX_RANGE	5.92	2.55	3.36 to 8.47	2.35 to 11.03	2.35 to 16.73	☐	☐ <		☐ >	
SST_MAX_MONTH	29.97	1.22	28.75 to 31.19	27.53 to 32.42	24.86 to 34.9	☑	☐ <		☐ >	
SST_MIN_MONTH	24.05	2.94	21.11 to 26.99	18.17 to 28.19	15.19 to 28.19	☐	☐ <		☐ >	
SALINITY_ANN_AVG	34.92	1.36	33.55 to 36.29	32.19 to 37.65	30.56 to 39.36	☐	☐ <		☐ >	
SALINITY_MAX_MONTH	35.43	1.57	33.85 to 37.01	32.27 to 38.59	31.84 to 41.38	☐	☐ <		☐ >	
SALINITY_MIN_MONTH	34.07	1.8	32.26 to 35.88	30.45 to 37.69	26.38 to 38.65	☐	☐ <		☐ >	
WINDSPEED_AVG	6.25	1.15	5.09 to 7.41	3.94 to 8.56	3.2 to 8.69	☐	☐ <		☐ >	
ETOPO2_BATHY_MIN	79.05	459.81	1 to 538.87	1 to 998.69	1 to 4693	☑	☐ <		☐ >	
ETOPO2_BATHY_MAX	1694.52	1714.26	1 to 3408.78	1 to 5123.05	1 to 6869	☐	☐ <		☐ >	
ETOPO2_MATHY_MEAN	851.45	1103.07	1 to 1954.52	1 to 3057.6	1 to 5151.04	☐	☐ <		☐ >	
CHLORA_AVG_SPATIAL	103.21	29.15	74.05 to 132.37	44.9 to 161.52	43.27 to 179.22	☐	☐ <		☐ >	
TIDES_AVG_MA	0.8	0.64	0.15 to 1.45	0 to 2.09	0 to 3.79	☐	☐ <		☐ >	

Figure 31. Prototype KGSMapper page; the displayed range prediction based on anemone distributions, maximum monthly sea surface temperature (SST), and minimum depth value for the grid cells containing anemone occurrences (checked in boxes below map).

(a) Zoom and pan controls on top line select region and scale. Clicking a point with "Specimen data" activated produces a pop-up window containing species name(s) and coordinates, values for environmental variables in each cell in the selected area, summary of environmental statistics for all cells containing an occurrence record, and the option of removing the point from the analysis. Second line selects sample points displayed. Third line selects sample set of cells used as the basis for prediction. Fourth line randomly selects ~50% of one or both datasets to make a prediction to be tested with the remaining cells.

(b) Map shows both datasets with localities distinguished by color of points – purple for sea anemones, green for anemonefishes – and predicted distribution of suitable habitat based on the selected environmental variables (below). Cells in areas colored dull red have values for all variables used for the prediction within one standard deviation (SD) of their means in the record-containing cells, orange is for cells between 1 and 2 SD, and yellow is for the rest of the total range.

(c) Links below map provide a download of shapefiles for the areas, a table of statistics of occurrences in both datasets relative to predicted cells in each range class, or a set of tables of the grid cell identifiers for the cells in each category of standard deviation by record contents.

(d) Link from the variable name brings up a histogram showing distribution of values and statistics for variable values from the selected locations. Environmental parameters are SST (its monthly mean, maximum, minimum, and its range), salinity (annual average, and monthly minimum and maximum), average windspeed, depth (based on ETOPO2 bathymetry, minimum, maximum, and mean), average chlorophyll a concentration, and average tidal amplitude.

(e) Statistics for each variable reflect the dataset selected by the map display (Figure 31b)

(f) Check boxes for selecting variables with which to "update map" and make predictions.

(g) Check boxes for selecting minimum and/or maximum values to restrict the locations selected, typed by the user into spaces.

Bottom line: "View Correlation Matrix & Scatterplots" link displays a correlation matrix (Table 7) showing linear regression coefficients for each pair of environmental variables, based on values selected in the map display. Values for the correlation coefficients in the matrix cells are linked dynamically to scatterplots of the selected values of each pair of variables.

Table 6. Comparison of the standard KGSMapper tool and the advanced prototype used for analyses reported here. Last three lines refer to features still being developed.

Feature	**KGS Mapper**	**Prototype**
Dynamic mapping of selected occurrences	X	X
Selectable map background	X	X
Data point identification with link to source database	X	
Short list of selectable environmental variables	X	X
Viewable environmental variable metadata	X	
Viewable distribution histogram of individual environmental variables for selected occurrences	X	X
Correlation matrix of environmental variables for selected occurrences	X	X
Pairwise scatterplots of environmental variables for selected occurrences	X	X
Map zoom controls region of analysis, occurrences selected	X	X
Environmental data table reflects selected locations	X	X
Prediction classified within 1 SD, 2 SD, and total range of selected environmental variables	X	X
Downloadable file of occurrences	X	X
Downloadable shape file of predicted areas		X
Downloadable table of relationships among occurrences, sample cells, and predicted areas		X
Downloadable table of cell IDs for all areas in analysis		X
Eliminating individual records from working dataset		X
Limiting maximum and/or minimum values for environmental variables		X
Comparing or combining two datasets		X
Prediction based on random 50% of locations, tested with others		X
User-selectable geographic localities	1	2
User can save and return to a modified dataset		
User has access to complete database of environmental variables		
User can upload an independent dataset for analysis		

Inferences of where suitable habitat occurs for members of the taxon are based on the environment of places where they are known to occur. The user selects the variables by checking the relevant boxes under "Use to Find Similar Areas" (Figure 31, area f). When the user selects "Update Map," KGSMapper builds and executes a query to find the 0.5° cells having all values within one standard deviation (SD) of the means of the environmental variables at the occurrence locations, those within 2 SD, and those within the total value range for all selected variables. The results, displayed as an interactive map (Figure 31), are also available as tabulated statistics (by clicking a link in Figure 31, area c). For 0.5° cells to be classed as within 1 SD, depicted as dull red on the map, all the selected variables must be within 1 SD of the mean of the values of the same variable in cells containing occurrence records. Orange color signifies cells in which the value for all selected variables falls within 2 SD of the mean of the values for the selected variable(s) but at least one falls beyond 1 SD, and yellow color signifies cells beyond 2 SD to the full range of the values known ("outliers"). This probabilistic approach is appropriate in dealing with habitat, which is a continuum from favorable to marginal. It also allows a user to focus attention where habitat or data are optimal, by recalculating a map that eliminates those original cells that have values in the outlier region or beyond 1 SD. This is done by selecting, respectively, "Remove All Cells Outside 2 Std. Deviation ranges from cart" or "Remove All Cells Outside 1 Std. Deviation ranges from cart," options that appear at the bottom of the statistics pop-up page.

The menu bar at the top of the page (Figure 31) offers links to other parts of the site and two editing functions. "Add Specimen" permits a user to augment the occurrence dataset; "Edit Cart" link allows a user to eliminate entries from the list of occurrences. The user can also review and edit individual location records with "Specimen Data" (Figure 31, area a). The link “Next Step” takes the user to the menu of all 200+ environmental datasets in Hexacoral – these currently do not otherwise interact with KGSMapper but a later version will allow a user to select from all datasets. The two right-hand columns (Figure 31, area g) allow selecting upper and lower limits for environmental data, eliminating from analysis cells with values outside a specified interval. Statistical analyses of both the variables and the inferred ranges can be viewed and downloaded, as can lists of cell IDs and ESRI shapefiles (Figure 31, area c). The prototype, which can show two groups of taxa concurrently, provides the option to choose which will be displayed (fish, anemones, or both) and/or used as the basis for the range inference (Figure 31, area a). In addition, the user can withhold a random selection of ~50% of the records for either dataset or both, infer a range with the remaining half, and test the product using the withheld records (Figure 31, area a).

Because organism occurrences are points (which define the 0.5° cells of analysis), not coverages, inferring the distribution of the habitat suitable for one taxon based on distribution records for the other differs from inferences using environmental data. Only qualitative matches are possible using maps. A quantitative assessment is possible by determining the number of cells inferred to contain suitable habitat for one taxon, based on occurrence records for that taxon, then determining the proportion of known occurrences for the other taxon falling within those cells.

The Analyses

We considered the effects of various aspects of the data on model outcome, addressing the issues we raised above.

Selection and effects of environmental variables (issues 1 and 5).

We investigated which variables can explain occurrence of the subjects and, if a selection is to be made among them, the basis for choice. We tested five variables individually and combined into four groups (below). Some of these are known to affect occurrence of these animals (sea surface temperature [SST], depth, salinity); others were tested to determine if they might (tidal amplitude and productivity, for which chlorophyll a concentration is a proxy). We also examined alternative parameters (maximum, minimum, and mean) of some variables (results not reported); minimum SST was chosen because the restriction of the animals to the tropics makes it likely that minimum temperature limits their distribution more than mean or maximum. The correlation matrix (Table 7) assesses the degree to which environmental variables covary within the region selected; this tool permits the investigator to explore the effects of spatial auto-correlation and covariance between variables in order to help guide variable selection for the question being addressed. The strongest correlations among variables used in this study are within the variants of SST, salinity, and depth; only one from each category was used. For example, as might be expected, maximum and mean SST are highly correlated (but minimum SST is less so).

The groups listed below were selected to determine the effect on output of number of variables:

(1) Minimum SST and minimum depth

(2) As (1) plus minimum salinity

(3) As (2) plus average chlorophyll a concentration

(4) As (3) plus tidal amplitude

Table 7. Correlation matrix (Pearson product-moment correlation coefficient) of variables for the datapoints associated with fishes and anemones.

CORRELATION MATRIX

	SST_MEAN-MONTHLY	SST_MIN_ MAX_RANGE	SST_MAX_ MONTH	SST_MIN_ MONTH	SALINITY _ANN_AVG	SALINITY_ MAX_MONTH	SALINITY_ MIN_MONTH	WINDSPEED _AVG	ETOPO2_ BATHY_MIN	ETOPO2_ BATHY_MAX	ETOPO2_ BATHY_MEAN	CHLORA_ AVG_SPATIAL	TIDES_ AVG_MA
SST_MEAN _MONTHLY	1	-0.7148	0.791	0.9466	-0.448	-0.3571	-0.2782	-0.703	-0.1105	0.0228	-0.0329	0.0153	-0.0916
SST_MIN _MAX_RANGE	-0.7148	1	-0.1629	-0.8921	0.4939	0.486	0.1148	0.56	-0.0222	-0.2255	-0.1698	0.2258	0.1446
SST_MAX _MONTH	0.791	-0.1629	1	0.5912	-0.2069	-0.0804	-0.3012	-0.4896	-0.177	-0.1759	-0.1977	0.2008	-0.0183
SST_MIN_ MONTH	0.9466	-0.8921	0.5912	1	-0.4985	-0.4341	-0.2317	-0.6907	-0.0629	0.1038	0.0482	-0.0905	-0.1266
SALINITY_ ANN_AVG	-0.448	0.4939	-0.2069	-0.4985	1	0.9494	0.4293	0.3026	0.0345	0.0938	0.0872	-0.222	-0.1283
SALINITY_ MAX_MONTH	-0.3571	0.486	-0.0804	-0.4341	0.9494	1	0.1772	0.1744	-0.0178	-0.0235	-0.0157	-0.0775	-0.1416
SALINITY_ MIN_MONTH	-0.2782	0.1148	-0.3012	-0.2317	0.4293	0.1772	1	0.3792	0.1102	0.2677	0.2382	-0.346	0.0042
WINDSPEED _AVG	-0.703	0.56	-0.4896	-0.6907	0.3026	0.1744	0.3792	1	0.1233	0.1369	0.1718	-0.2946	-0.0884
ETOPO2_ \BATHY_MIN	-0.1105	-0.0222	-0.177	-0.0629	0.0345	-0.0178	0.1102	0.1233	1	0.5028	0.7361	-0.2887	-0.1417
ETOPO2_\ BATHY_MAX	0.0228	-0.2255	-0.1759	0.1038	0.0938	-0.0235	0.2677	0.1369	0.5028	1	0.9033	-0.6949	-0.2789
ETOPO2_ \BATHY_MEAN	-0.0329	-0.1698	-0.1977	0.0482	0.0872	-0.0157	0.2382	0.1718	0.7361	0.9033	1	-0.6195	-0.2404
CHLORA_ AVG_SPATIAL	0.0153	0.2258	0.2008	-0.0905	-0.222	-0.0775	-0.346	-0.2946	-0.2887	-0.6949	-0.6195	1	0.3395
TIDES_ AVG_MA	-0.0916	0.1446	-0.0183	-0.1266	-0.1283	-0.1416	0.0042	-0.0884	-0.1417	-0.2789	-0.2404	0.3395	1

U*ncertain data quality* (issue 2).

Both organism datasets contain locations known to be inaccurate (of course, we cannot know if there are additional inaccurate locations). Inaccurate locations can sometimes be identified by their associated depth; because the subjects are constrained to live within the photic zone (operationally to ~100 m) by the photosymbionts of the host anemones, depths greater than that strongly suggest an erroneous location. We inferred potential habitats of both fish and anemones with and without eliminating cells having minimum depth >100 m.

Validating or testing range inferences (issue 4)

Inferences were made about the effects of data quantity (issue 3). We compared the outcomes of inferring habitat of each taxon based on records of the other, and inferring the habitat of each taxon based on ~50% of the records for a taxon selected randomly by the KGSMapper tool. We also demonstrated the effects of eliminating from the initial dataset points in cells with values for environmental parameters >1 SD and >2 SD.

In this case study dealing with the continuum of quality and/or extent inherent in habitat assessment, KGSMapper output ranks probability of matching habitat characteristics rather than a dichotomous occurrence or not of organisms; for this reason and because assessment of known absences at the scales used (global extents and ~2500 km^2 grid cells) are impractical, output cannot be evaluated by confusion matrix measures (Fielding & Bell 1997, Manel et al. 2001). We evaluated output by what we term “effectiveness” and “efficiency,” which assess the distribution of cells among the intervals 0-1 SD, >1-2 SD, and >2 SD. The assumption, as it is in most habitat models, is that the distribution of cells inferred to contain suitable habitat will reflect that of occurrence-containing cells. For each interval i, the number of cells containing an occurrence is a_i, and the number of cells within the range is n_i. a_T is the total number of cells containing an occurrence record over n_T (the total of cells over all n_i). “Effectiveness” is the ratio a_i/a_T – for each interval, the fraction of occurrences contained within the cells of that interval: a high value indicates inclusiveness or relative lack of false negatives. “Efficiency” is the fraction of total occurrences per area (number of cells) inferred; we use the ratio $[a_i/a_T]/n_i$. It represents the density of positive occurrences; increasing values indicate a decrease in false positives. Effectiveness and efficiency, which are related but not identical to the confusion matrix measures of predictive power, sensitivity, and prevalence, function within a run of the model; effectiveness minimizes errors of omission, and efficiency minimizes errors of commission. The data selection and editing tools permit the ratio of efficiency to effectiveness to be adjusted according to the questions and data of interest; like the output itself, evaluation of the results will necessarily be application-specific.

Results

Environmental variables

For each set of environmental variables, we did three analyses, one for each group of organisms individually and one for the two together. We illustrate examples of inferring the distribution of suitable habitat for each combination. Of datasets in the prototype KGSMapper, the parameters of chlorophyll a concentration (Figure 32a), minimum salinity (Figure 32b), and tidal amplitude and wind speed (not shown) did not discriminate suitable habitat at the geographic scale of this analysis. Combinations of two or more of these variables provided no more resolution than any of them individually. SST discriminated best for the habitat of these organisms latitudinally, with results differing somewhat depending on the parameter used (compare Figure 32c and 32d for maximum and minimum monthly SST, respectively). Two approaches were tried to consider depth, which also restricts distribution of these animals: Figure 32e is a result of using only occurrence data, whereas Figure 32f is the result of excluding cells with minimum depth >100 m. The number of cells inferred to contain suitable habitat (total range) was reduced >85% as a result of editing for depth (Table 8, Figure 32e, 32f). The outlier category (>2 SD) was most heavily affected for anemones: editing reduced the number of 0-1 SD cells by 14% and of 0-2 SD cells by 25% in the case of anemones The figures for fishes were 37% and 61%, respectively.

Table 8. Predictions of suitable habitat using minimum sea surface temperature (SSTmin) and minimum depth (Zmin) as environmental variables, and occurrence data. Edited predictions (right-hand column for each taxon) used only records in cells in which minimum depth <100 m. The line "*0-2 SD*" is total of the preceding two lines. Ctot = total number of cells predicted to contain suitable habitat; Crec = number of record-containing cells; Rec = number of occurrence records.

	Anemones: n = 641						**Fish: n =1937**					
	Unedited			**Minimum depth < 100 m**			**Unedited**			**Minimum depth < 100 m**		
	Ctot	Crec	Rec	Ctot	Crec	Rec	Ctot	Crec	Rec	Ctot	Crec	Rec
0-1 SD	6187	261	385	5331	244	385	7661	250	1281	4791	221	1211
1-2 SD	3450	103	207	1853	90	188	9150	119	538	1719	88	492
0-2 SD	*9637*	*364*	*592*	*7184*	*334*	*573*	*16811*	*369*	*1819*	*6510*	*309*	*1703*
>2 SD	49142	63	35	915	6	30	39379	58	107	731	27	20
Total range	58779	427	627	8099	340	603	56190	427	1926	7241	336	1723

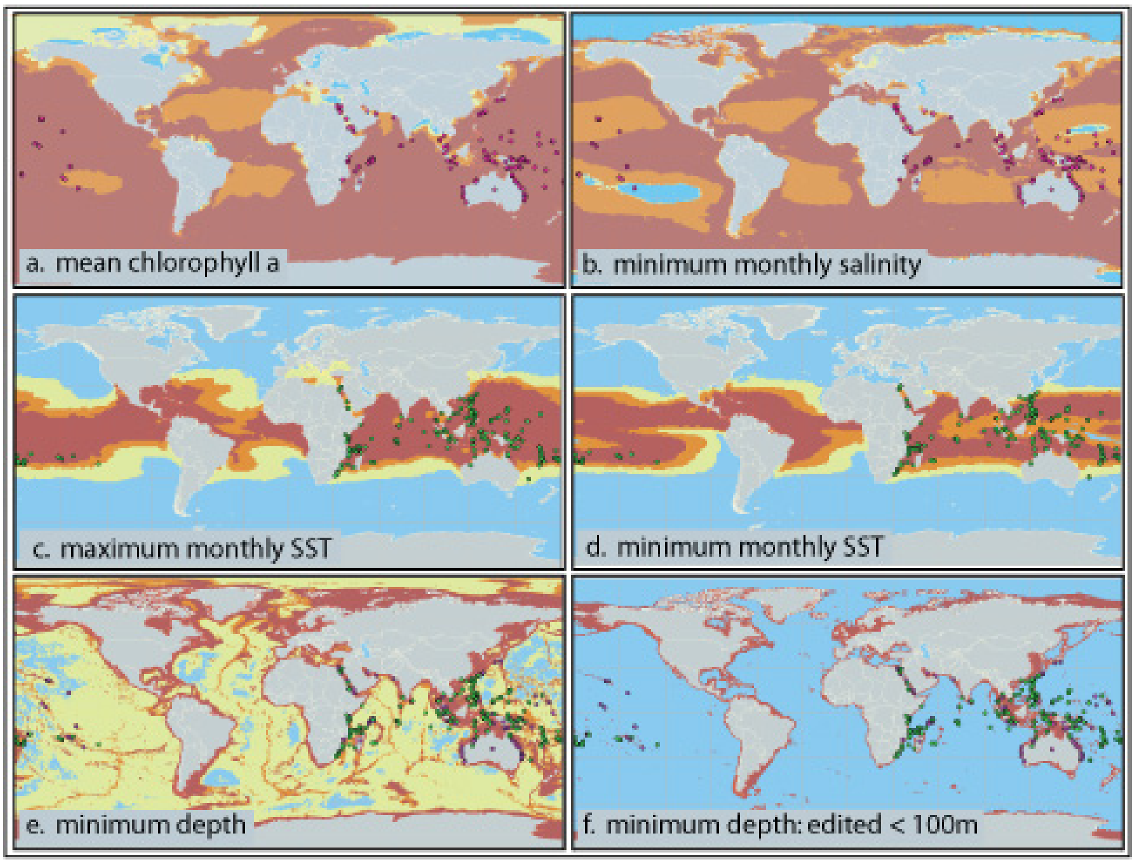


Figure 32. Predictions of suitable habitat based on single variables and organism distributions. Predictions of habitat suitable for anemones from anemone occurrences based on values from the cells containing occurrence records: (a) chlorophyll a concentration, and (b) minimum monthly salinity. Predictions of habitat suitable for fish from fish occurrences: (c) maximum monthly SST, and (d) minimum monthly SST. Combined data set predictions: (e) minimum depth, and (f) minimum depth excluding cells with values >100 m. Chlorophyll and salinity have essentially no predictive power, individually or in combination; similar results are obtained with tidal amplitude and wind speed (not shown). The depth constraints and the latitudinal controls imposed by SST provide a powerful combination (see Figures 33 and 34).

Figure 33 illustrates the capability of cleaning or editing data sets based on either specific knowledge or statistical evaluation; to allow details to be seen clearly, they show only the part of the world where most species of these animals occur, but the analyses resulting in them used global data. Figures 33a, 33b are inferences of anemone and fish habitat, respectively, based on minimum depth and minimum SST, which individually provided reasonable first approximations to defining appropriate habitat (above). Figures 33c, 33d show the improvements in both range inferred ranges generated by eliminating cells with minimum depth >100 m. Figures 33e, 33f have been remapped after elimination of all cells >2 SD in Figures 32a, 32b. Figures 33g, 33h show the effects of removing all cells >1 SD from the data sets used in Figures 33a, 33b. This rigorous cleaning shrinks the geographic range noticeably, but the 0-1 and 0-2 SD intervals remain relatively similar throughout.

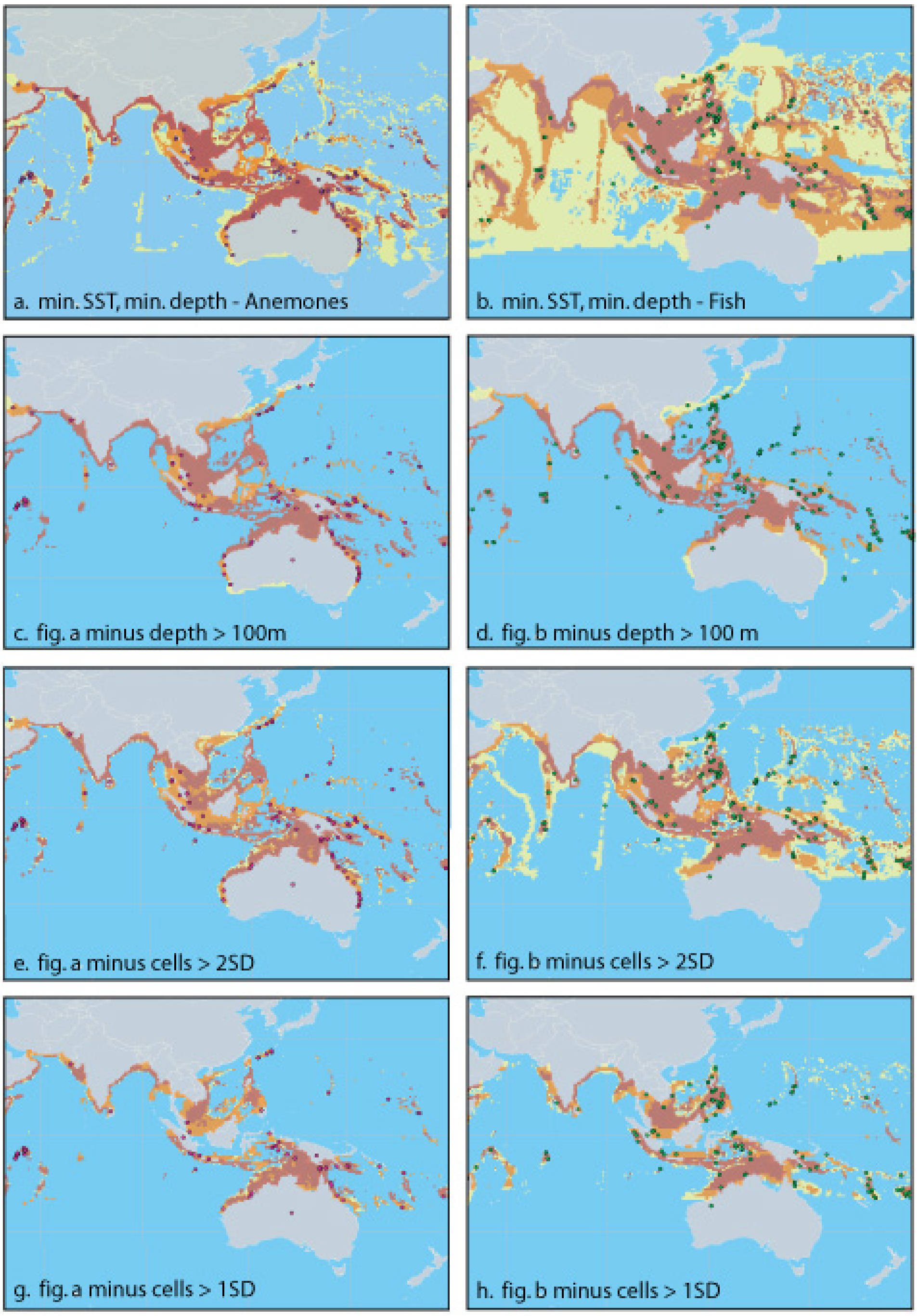


Figure 33. Dataset clean-up and editing features displaying zoomed views of the Australasian region after predicting ranges based on the global dataset. (a) Habitat suitable

for host anemones based on anemone occurrences, and (b) anemonefish habitat based on fish occurrence records using unedited datasets with minimum monthly SST and minimum depth. (c), (d) As (a) and (b), respectively, but with datasets edited to eliminate cells having minimum depth >100 m (see Figure 31g). (e), (f) As (a) and (b), but recalculated after eliminating cells in the >2 SD category in the initial analysis. (g), (h) As (a) and (b), but recalculated after eliminating cells >1 SD in the original analysis. The datasets can also be edited point by point, if desired (Figure 31, area a).

Occurrence data quantity and quality

After removal of two anemone localities in the Mediterranean Sea that were clearly due to misidentification of specimens, misapplication of a name, or misstatement of provenance, the datasets contained 641 anemone and 1937 fish records. They included some suspect data points and some of low precision; we retained all to provide a realistic test of habitat inference using the sort of data likely to be available for analysis of non-fisheries species.

Four anemone and nine fish records fell on land outside a coastal cell; because marine variables are not associated with inland cells, these points were ignored in the analyses. Points on land in a coastal cell were analyzed using the marine variables associated with that cell. Some records on land do not reflect errors: the anemone dataset (for which a precision value is assigned to each georeferenced point) contains low-precision records assigned by a convention that plots the locality in the center of a country or region given as the only location information in the original publication. This results in points on land (e.g. the centroid of Australia for localities given as “Australia”), and over water far deeper than that in which these anemones live (e.g. the center point of Fiji for localities given as “Fiji”).

Editing to eliminate occurrence-containing cells with minimum depth >100 m reduced anemone records by ~4% (24) and fish records by ~11% (203), but, because one 0.5^{o} cell may contain more than one occurrence record of a fish or anemone, the number of record-containing cells was reduced by ~20% and ~21%, respectively (Table 8).

Cross-comparison and validation

Areas of suitable habitat for anemones, as inferred using 50% of anemone-containing cells, included between 93.7% and 100% of the remaining known occurrences (Table 9) – as well as many places where the anemones are not recorded as living. Clearly, the best test of our model output would be to seek the animals in places where suitable habitat is inferred to exist and the animals are not known to occur. That being impractical, we ran an analysis using KGSMapper, appropriate environmental parameters, and the native distribution (from FishBase) of anemonefishes.

Table 9. Using 50% of anemone-containing cells and minimum sea surface temperature (SSTmin) and minimum depth (Zmin) to predict habitat suitable for the remaining anemones. After editing to exclude cells with depth >100 m, 136 cells were used in this analysis.

Trial	# and % cells used for prediction	# and % remaining anemone-containing cells predicted
1	57 / 41.91	76 / 96.20
2	63 / 46.32	73 / 100
3	74 / 54.41	61 / 98.39
4	64 / 47.06	69 / 95.83
5	65 / 47.79	71 / 100
6	69 / 50.74	67 / 100
7	63 / 46.32	72 / 98.63
8	67 / 49.26	68 / 98.55
9	62 / 45.59	71 / 95.95
10	65 / 47.79	71 / 100
11	57 / 41.91	74 / 93.67
12	66 / 48.53	70 / 100
13	65 / 47.79	71 / 100
14	68 / 50.00	68 / 100
15	73 / 53.68	63 / 100
16	71 / 52.21	65 / 100
17	75 / 55.15	61 / 100
18	62 / 45.59	74 / 100
19	66 / 48.53	69 / 98.57
20	71 / 52.21	62 / 95.38
Average	66.15 / 48.64	68.80 / 98.56
SD	5.01 / 3.68	4.44 / 2.01

On a map, known fish occurrences fell largely within areas of inferred habitat suitable for anemones and vice versa. In a quantitative assessment, using minimum SST and minimum depth (Table 10), areas inferred by anemone occurrences included virtually all places fish are known to occur, a result somewhat improved by editing both datasets for depth. Fish occurrences were less effective in identifying areas suitable for anemones, and editing had little effect (Figure 33). Thus, at the scale of this analysis, suitable habitat is inferred not to occur where it does not (at high latitude and at depth).

To explore the effects of number of environmental variables on inferred ranges, we used the four groups of environmental variables listed in “Data and Methods.” Figures 34a, 34b show the number of cells within each interval (the former for raw data, the latter for data edited to exclude cells with minimum depth >100 m), Figures 34c, 34d show effectiveness, and Figures 34e, 34f show efficiency. As single variables were added, effectiveness of the output in the 0-1 SD interval declined. However, efficiency increased because the inferred number of cells ($n_{0\text{-}1}$) decreased more rapidly than the number of occurrence-containing cells ($a_{0\text{-}1}$). We found the same pattern within groups of related variables – inferences using maximum or minimum SST plus minimum depth, and maximum or minimum SST plus the four variables used to generate Figure 34d indicate that use of maximum SST is more effective compared with minimum SST, which is somewhat more efficient.

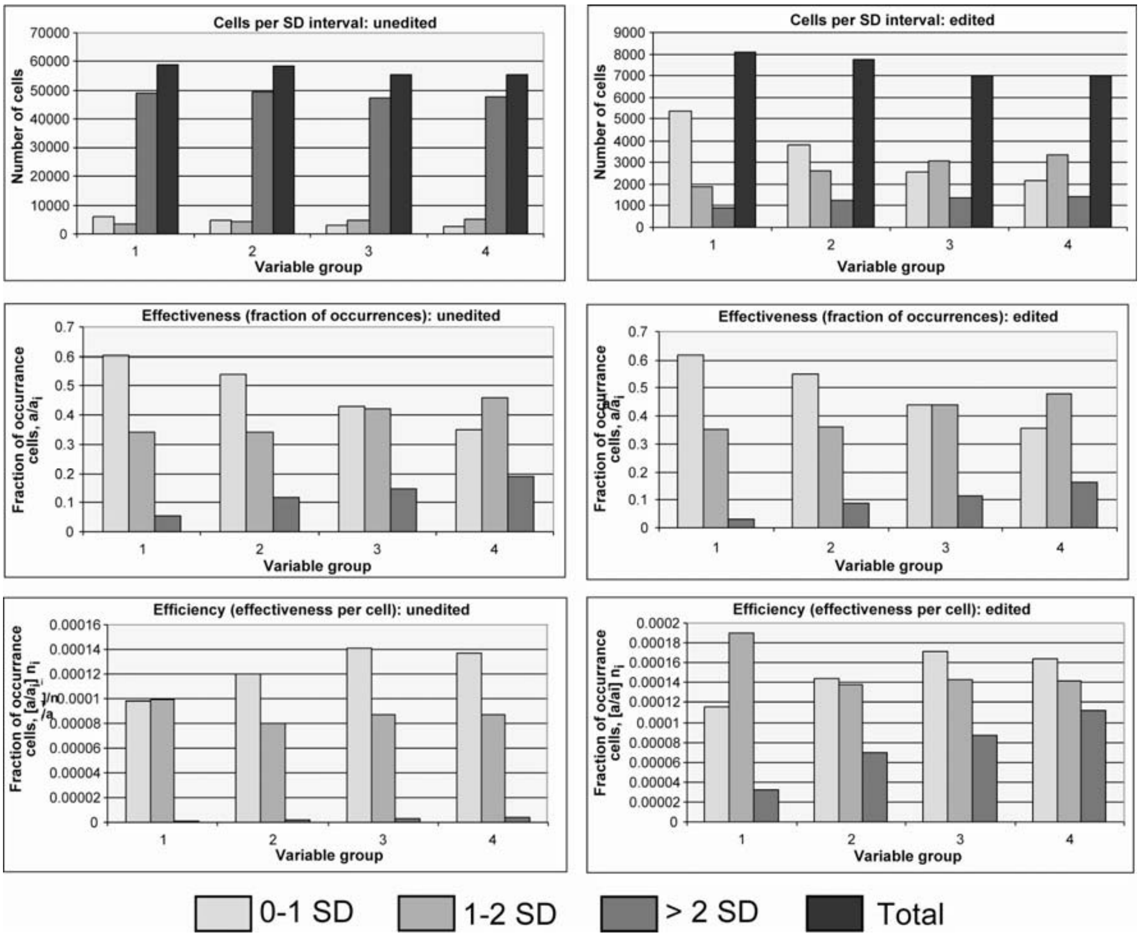


Figure 34. Distribution of cells, effectiveness, and efficiency of habitat prediction for sea anemones as functions of kind and number of variables. (a), (c), and (e) use values from all data; (b), (d), and (f) use data edited to exclude from the prediction cells having minimum depth >100 m. Numbers on abscissa are variable groups listed in “Data and methods” section. (a) and (b) show number of cells; (c) and (d) show effectiveness; (e) and (f) show efficiency.

Discussion

Environmental variables

Individually, the variables of minimum salinity, chlorophyll a concentration, tidal amplitude, and wind speed do not identify the occurrence of habitat suitable for clownfish and sea anemones (Figures 32a, 32b): much of the ocean has values equal to those of waters in which these animals occur. Although low salinity is negatively associated with anemone occurrence (most sea anemones, including the species that host anemonefishes, are stenohaline: Shick 1991), the resolution of our datasets both temporally (monthly averages) and spatially (0.5^{o} cells based mainly on oceanic measurements) is too coarse to capture its effect. Similar arguments can be made for chlorophyll a, and for the energy- and exchange-related tide and wind variables. Further, tidal amplitude is unlikely to exert systematic control because it is the relative, rather than absolute, position relative to low tide that affects anemone survival.

Even highly correlated parameters (Table 7) may not have the same effect. For single variables, maximum and minimum SST (Figures 32c, 32d, respectively) infer somewhat different distributions of suitable habitat overall, and in the intervals 0-1 SD, 1-2 SD, and >2 SD. This is also true in combination with other parameters.

Adding parameters sequentially to minimum temperature and depth (Figure 34) did not provide increasingly good inferences, from which we conclude that more variables are not necessarily better (cf Stockwell & Peterson 2002). Quality of the variables, as judged by relevance to occurrence of the taxon in question (Fielding & Bell 1997), seems more important than the number of variables. That quality can be improved by basing the output on values that do not include the outliers (>2 SD) or >1 SD (Figure 33).

Even with the limited number of environmental variables available in the prototype KGSMapper, choosing variables expected to be relevant to the distribution of any taxon requires some expert judgment, as does determining which relevant variables to use for a given purpose. For example, although maximum SST is quantitatively more effective than minimum SST, it identifies a larger range overall and overextends the northern extent of the fish distribution (Figure 31 map result). KGSMapper can help to reveal which parameters are most closely correlated with occurrence and thus may be important in controlling, or describing, distribution.

Occurrence data quality and quantity

The linkage of taxonomic synonyms allows Hexacoral to map occurrences for the species rather than for the name; this also helps to increase the number of records for a species. Thus, rather than synonymous names being viewed as a problem (Soberón & Peterson 2004), if handled appropriately they can serve to enhance data quantity and taxonomic quality.

The two Mediterranean records we removed illustrate the need for expert judgment in selecting occurrence as well as environmental data. Machine algorithms that cleanse datasets by purging records from areas well beyond known occurrences risk removing information on range extensions or invasions. An expert may be able to differentiate among potential sources of error by considering date, similar species, taxonomic history of a name, etc. to make suspect records useful and thereby improve data quality and quantity.

Using only cells with minimum depth values <100 m resulted in a more precisely defined range (Figure 32f) than merely selecting minimum depth as a variable (Figure 32e), presumably because some actual occurrences fall in cells with minimum depth >100 m, due to either error or convention (such as using the center point of Fiji for all localities given only as "Fiji" in the anemone dataset).

Such editing for a feature relevant to organism distribution provides a crude assay of data quality. Editing produced a less dramatic change for anemones than for fishes; compare Figures 33a, 33c, 33e, and 33g with Figures 33b, 33d, 33f, and 33h, respectively. This finding is concordant with what is known of the data sources: the anemone records were assembled as a single project (by Fautin) and have been extensively checked whereas the fish records are from multiple sources with unknown and diverse authentication procedures. Thus, KGSMapper deals with suspected, inferred, or known erroneous data to provide a justifiable way to limit consideration to reasonable habitat possibilities. By doing so, it inferentially takes absences into account.

It is commonly thought that more environmental variables will improve the sensitivity or precision of a prediction. Fielding & Bell (1997) call this into question in their discussion of the issues of inappropriate variables, the 'costs' of misclassification, and the contexts in which predictive models are evaluated. Figure 34 illustrates how choice and number of environmental variables affect output in our study system. As we added single variables to the analysis, the number of cells identified as containing suitable habitat declined by ~10%, but it would be a mistake to interpret this as increasing precision; the fraction within 1 SD declined ~40% in both edited and unedited analyses. KGSMapper statistics are calculated in a univariate manner; as variables are added, the probability declines that any cell will contain values for all of them within 1 SD. Thus, adding a variable that would be expected, based on biology and analysis, to have little control over organism occurrence can eliminate cells that contain suitable habitat – a high cost for minimal return in terms of genuinely improved results.

Others have also found that quality of prediction is not necessarily improved by quantity of data. "Accuracy" of four modeling methods, including GARP, used by Stockwell and Peterson (2002) did not increase beyond about 20 data points, 10 producing 59-64% "accuracy" (90% of what could be achieved with their methods). Beauvais et al. (2004) achieved "validation success" rates of 40.0-88.2%, the lowest with a dataset of 18 records, but one of 20 records had a rate of 80.0%. The effects of geographic scale and habitat heterogeneity on quality of model output have not been addressed formally but, based on what is known, should be. The methods of Stockwell and Peterson (2002: 11) modeled "widespread species … less accurately"; Raxworthy et al. (2003) had a similar result using GARP. Attention must be paid to this issue for marine species, many of which have larger geographic ranges than is typical of terrestrial species for which predictive algorithms were developed (the animals we studied range through about 180° of longitude and 50° of latitude), and which occur through three dimensions. In one of the few published modeling studies for distribution of marine species (fish living in the Central Western Atlantic), Wiley et al. (2003: 124) also found that, using GARP, results for widespread species were "weak."

In addition to large numbers of points, a desideratum for this sort of analysis is independence of data (Fielding & Bell 1997), but many of the anemone records we used came from a small number of areas and/or investigators; we have found records for other poorly-studied marine organisms may not be truly independent, either.

Validating or testing results

Use of training data for assessing quality of model output is a common practice (e.g. Anderson et al. 2003). Such data may constitute a portion of known occurrences (e.g. 50% by Peterson et al. 2002, 75% by Beauvais et al. 2004) or areas of occurrence (e.g. states by Peterson 2001) used to predict the remainder of known occurrences. KGSMapper has a tool that randomly selects ~50% of reported occurrences and uses the associated locality records (grid cells) to infer the remainder of the localities and their associated occurrences (Figure 31, area a). If grid cells are the basis for analysis when using a gridded environmental database and there is not a one-to-one relationship between cells and occurrence records, the use of occurrence records will not be reliable. A random sample of (e.g., 50%) cells may contain far more than the stated proportion of the sample occurrences (to 75-80% in half of the tests we conducted with anemone data). This greatly increases the apparent quality of the result and provides a false indication if that level of performance is ascribed to 50% of the occurrences.

A drawback of withholding some records as training data is that “the algorithm cannot take advantage of all known locality records” (Anderson et al. 2003: 213). The symbiosis allowed us both to use all data and to implement the desideratum of incorporating interspecific information into the model (Fielding & Bell 1997); we used records of one organism to infer areas of suitable habitat for the other. We ascribe the asymmetry in our results (Table 10) to that in the relationship – although an anemonefish never occurs without an anemone in nature, individual anemones may occur without fish in some areas. Thus, anemone data will somewhat overestimate suitable habitat for fish. This result is consistent with the potential problem in modeling pointed out by Fielding and Bell (1997) of undersaturation of habitat. Accordingly, saturated symbiotic systems such as this should be particularly favorable as tests for habitat models.

Table 10. Using minimum SST (SSTmin) and minimum depth (Zmin) plus occurrence of the symbiotic partner to predict occurrence of the symbiotic partner (anemones were used in predicting fish distributions, and vice versa). Unedited predictions used all data; edited predictions eliminated records in cells in which minimum depth >100 m.

Category	**Anemones predict fish**		**Fish predict anemones**	
	Unedited	**Edited**	**Unedited**	**Edited**
0-1 SD	69.4%	74.0%	53.4%	52.4%
1-2 SD	24.4%	25.9%	27.6%	28.0%
>2 SD	5.9%	0.1%	14.2%	14.6%
Total range	99.7%	100%	94.2%	95.0%

As an indirect assessment of KGSMapper, we used environmental variables from Hexacoral with occurrence data from FishBase for the tropical Indo-Pacific lionfish, *Pterois volitans*. The inferred distribution of suitable habitat resembles that of anemonefishes, and includes the coast of the southeastern United States, where it has recently established viable populations (e.g. Semmens et al. 2004).

The addition of environmental variables that do not, and are not expected to, have any real explanatory power has the effect of increasing the apparent efficiency of the range inference. This is an artifact of constraining the basis on which cells are selected, whether or not that constraint has anything to do with organism occurrence. For a group of organisms that has been extensively sampled over most of its range, this will have little effect other than to distort the apparent quality of the range inference. However, for sparsely sampled organisms, such as most marine organisms, inclusion of gratuitous variables could significantly alter the inferred range.

Although we can readily envision application of KGSMapper to dichotomous problems, the analyses presented here cannot be usefully evaluated by confusion matrix methods (Manel et al. 2001) because of the unavailability of useful absence data at the scale of interest. A half-degree grid cell can be as much as 3000 km^2 in area; the organisms of interest range from a few cm^2 to about 1 m^2 in area, and habitat patches may be <100 m^2. The grid cell is best treated as a mosaic of potential habitats ranging from favorable to stressful to impossible. To provide some assessment of the quality and characteristics of the inferences, we use efficiency and effectiveness, which allows a user to tune the results for a particular purpose based on the relative importance or cost (Fielding and Bell 1997) assigned to errors of commission and omission. For example, a user planning an expedition to sample particular taxa or devise a scheme for protected areas would probably want to emphasize efficiency (i.e. maximize the probability of finding organisms per unit area covered), while a study concerned with invasion potential, marginal habitats, or range limits would need the most effective (complete) inventory of potential habitat. Moreover, such analysis allows a user to allocate effort where it will most enhance a product of prediction -- adding occurrences would improve the product more than adding environmental features. In an analogous manner, Graybeal (1998) found that adding taxa improved resolution of phylogenetic trees more than adding characters.

Maps and model outputs

An occurrence (or dot) map plots localities where members of the taxon have been documented (for example, Figure 31, area b, without the inferred areas of occurrence); subdividing occurrences temporally allows comparing distributions through time. An inference about where members of the taxon may occur beyond the known occurrences constitutes a range map. It, too, may be temporally defined, showing, for example, where organisms formerly occurred but do not occur currently. It may consist of discontinuous patches, as for the anemonefish and their host anemones around land masses. Done the "old-fashioned way," a range map is a simple abstraction of occurrences, an inference of where members of the taxon may occur within the same geographical region. A map generated electronically by a tool such as KGSMapper, by correlating environmental parameters with known distributions, is essentially a habitat map, plotting places compatible with life of the organism of interest.

A habitat map may contain areas of two sorts, which we advocate distinguishing. Areas on a habitat map that fall within the broad ambit of the taxon constitute, as defined above, a range map. In providing rather precise inferences about where members of a taxon may actually live by depicting realized habitat, it is useful for planning, e.g., field research and conservation strategies. Some habitat maps include areas that fall well outside the known distribution of the taxon, as illustrated in Figure 31: anemonefishes and their hosts occur naturally in only the Indo-west Pacific, but ostensibly suitable habitat for them occurs in some areas of the Atlantic (especially the Caribbean) and eastern Pacific. Such a map depicts potential habitat, which is ideal for identifying places vulnerable to invasion. Because the word “prediction” literally refers to the future, it is appropriately used for areas outside the natural range – that is for areas subject to invasion. Within the general geographical area in which members of a taxon are known to occur, where perhaps direct evidence of their occurrence is currently absent, a model actually infers – rather than predicts – appropriate habitat.

Some model outputs are said to be niche maps; whereas a habitat is defined on the basis of abiotic parameters, a niche also includes biotic parameters (e.g. Peterson 2001, Anderson et al. 2003). Including explicit biotic information in automated tools such as KGSMapper is difficult because it is rarely in the form of coverages. The one biotic parameter common in oceanographic data is chlorophyll a concentration, but it lacks discriminatory value for occurrence of most organisms such as those we studied (Figure 32a). We found that, although appropriate habitat for anemonefishes exists outside the Indo-west Pacific, when we included a vital component of the animal’s biotic environment, a host anemone, those areas were no longer identified as habitable. We therefore advocate that such relevant biotic factors be explicitly incorporated into models if they are to be considered niche models. In this case we used symbionts, some pairs of which are mutualistic, precisely because it provided a clearly relevant biotic factor with which to test model output. The relevant biotic factors in other analyses may be less obvious.

Thus, anemonefishes are less likely than lionfish to establish viable populations in the coastal southern United States: although abiotic attributes of the habitat, such as temperature and depth, appear suitable for anemonefish existence, anemones that naturally host anemonefishes do not occur there (Fautin & Allen 1992). One way to infer absence is to eliminate deep water cells (cells in which minimum depth >100 m). A second way to infer absence is to eliminate all fish habitat cells outside the Indo-west Pacific. This is justifiable based on absence of an obligate symbiont. By contrast, the potential for Hawaii to be invaded by anemonefish is real because one species of host anemone occurs in Hawaiian waters (Fautin & Allen 1992). On the other hand, for species of these anemones that can live in nature without fish symbionts (most of them), we infer the suitable habitat outside the Indo-west Pacific is vulnerable to invasion. Once individuals of a host anemone are present in a non-native place, the species of fish that can live with host anemones of that species might follow.

Modeling tools

It is difficult and/or impractical to control quality when using merged, distributed datasets. Therefore, analytical and predictive tools must have features that ensure robust output in the presence of questionable data and that offer the user ways to modify the datasets and to assess the results – by improving data quality, by testing hypotheses derived from them, or both. We have shown that the number and distribution of outlier points is an indicator of both the quality of occurrence data and the relevance of the environmental variables selected. Thus, an output that segregates results into categories of diminishing accuracy allows a user to select appropriate subsets of the output. User decisions can be based on the level of data confidence and the purposes for which the output is to be used. With KGSMapper, for example, we found the 1 SD range to be a robust initial estimate of range, even in noisy datasets.

Beyond this passive evaluative approach, KGSMapper has data-editing features that are broadly useful in assessment and research. A user can edit occurrence data (1) point by point on the map or data list, (2) by geographic area (using the zoom control), (3) by taxon, (4) by editing environmental variables. Future versions of the KGSMapper will have more versatile means of selecting geographic extent and will include explicit absence as well as presence data. In addition to selecting geographic extent, the ability to edit variables provides a means of exercising expert judgment by cleaning the datasets of points that do not conform to relevant environmental controls, and of refining the geographic limits of potential ranges; these are ways to incorporate knowledge of absence. An important means of improving the precision of the habitat inferences is provided by allowing a user to remove records that fall beyond a predetermined statistical limit. The user can then recalculate the model with the remaining cells. KGSMapper allows application of expert judgment at both input and output ends of the process; algorithms such as GARP apply it only at the output end (e.g. Anderson et al. 2003, Drake & Bossenbroek 2004)

KGSMapper outputs go beyond simple map visualizations, providing statistical analyses of the individual variables, of the relationships among the variables, and of the occurrence-environment relationships. In addition to allowing analyses in a manipulative GIS environment, KGSMapper has options that permit dynamic data assessment, which enables the user to identify covarying parameters, variables to be edited, and specific ranges of values to be included or excluded.

Models of organism occurrence may contain two types of errors: predicting the organism will occur where it does not (false positive, commission, or overprediction), and not predicting the organism to occur where it does (false negative, omission, or underprediction) (e.g. Fielding & Bell 1997, Anderson et al. 2003). Unlike many algorithms, the objective of KGSMapper is to infer the locations of habitat suitable for occurrence of organisms, not organism occurrence. Finding the organisms in the habitat clearly demonstrates it is suitable; not finding them, termed by Anderson et al. (2003) “apparent commission error,” is due to well-known contingencies in occurrence. To regard prediction of habitat in a place that has not been searched as a false positive is to imply perfect knowledge of organism occurrence. Selecting areas for fieldwork is a potential use of the output of such modeling, particularly for poorly-sampled taxa; overestimation of habitat occurrence is therefore neither unexpected nor necessarily undesirable. Moreover, a model that identifies all, but only, the places of known occurrence would be tautologous.

Chapter 6

Possible Effects of Climate Change on Deep-Sea Corals

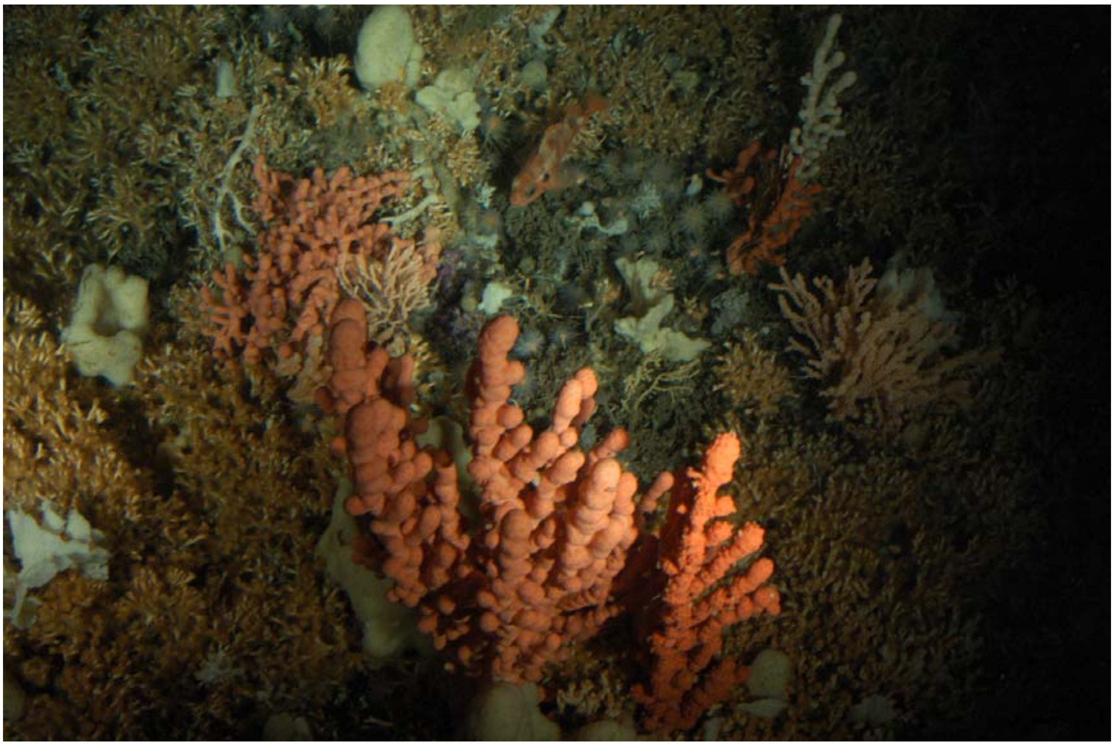


Photo Credit: Andre Freiwald

Citation

Guinotte .M (2005) Climate change and deep-sea corals. Current: the journal of Marine Education 21:48-49.

Abstract

Will climate change have negative effects on scleractinian deep-sea coral ecosystems? The answer is uncertain as very few manipulative experiments have been conducted to test how deep sea corals react to changes in temperature, salinity, seawater chemistry (pH), water motion (currents), and food availability. It is likely that the effects of climate change will not be positive for deep-sea reef ecosystems as they are highly specialized and have evolved in steady state (cold, dark, nutrient rich) conditions. Temperature, salinity, seawater chemistry, and light availability control calcification rates in shallow tropical reef systems and with the exception of light (because deep-sea corals lack the algal symbionts possessed by their shallow reef-building relatives), these factors are probably important controls on deep-sea coral calcification as well.

Personal Contribution and Context within the Thesis:

My personal contribution to Chapter 6 was the entire publication. Chapter 6 is brief and not as well referenced as Chapters 1-5, and 7 due to constraints put forward by the journal editor. Contribution percentage to Chapter 6: John Guinotte (100%).

Research presented in Chapter 6 explores the environmental controls on deep-sea corals and investigates the possible consequences of climate change on these ecosystems (RF1 and RF2). This Chapter directly addresses Research Foci 1 and 2 (Figure 37). Insights and knowledge gained from Chapters 1-5 are used to make informed statements about the possible repercussions of climate change on deep-sea coral ecosystems. Very little is known about these ecosystems due to their occurrence in the deep sea, but new applications of the methodologies and results gained in Chapters 1-5 have been instrumental in providing valuable insights and opening new fields of study regarding the possible effects of climate change on these ecosystems (e.g. Chapter 7)

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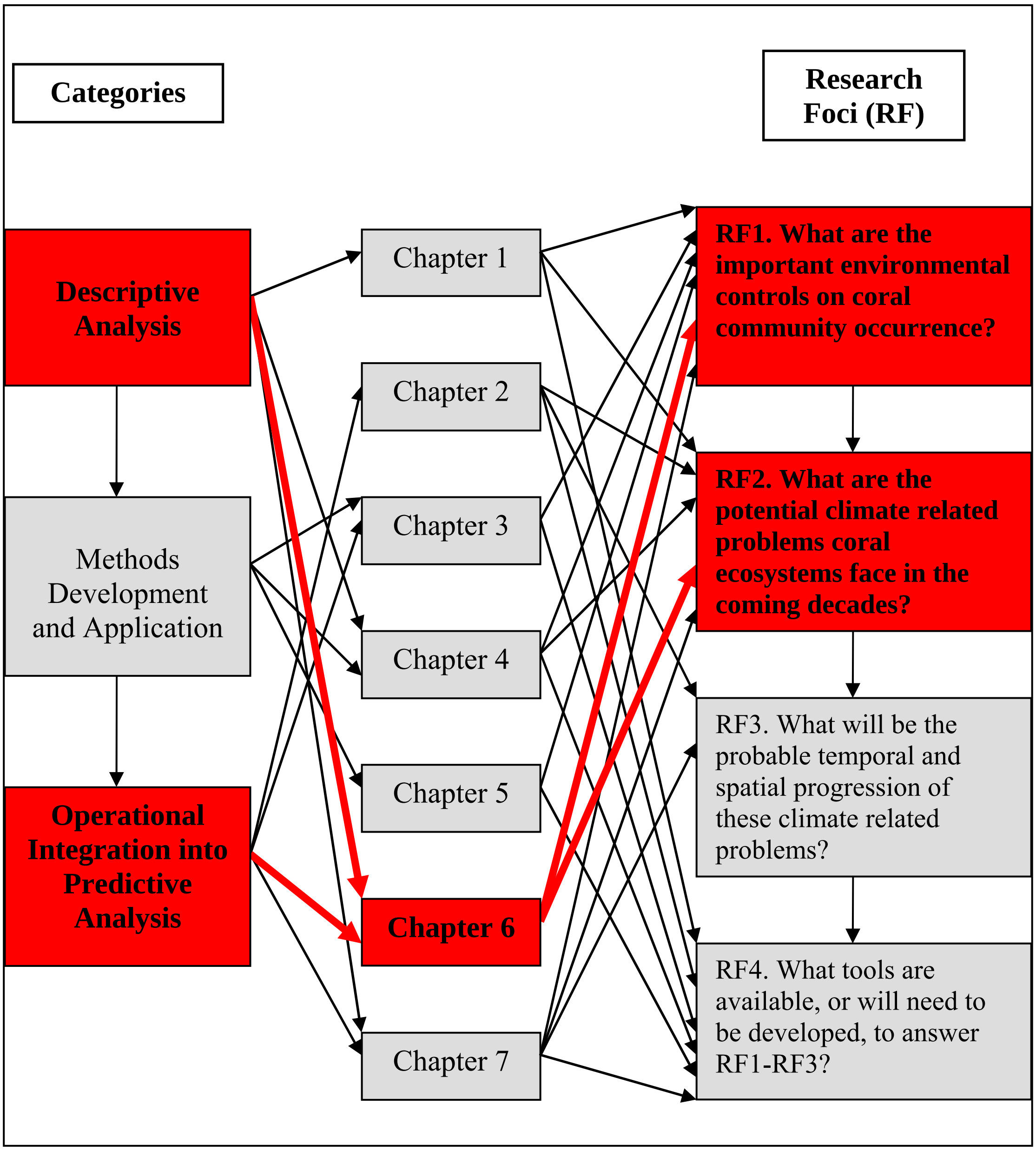

Figure 35: The relevance of Chapter 6 to the overall scheme of the research.

Environmental Variables

Temperature

Global sea temperatures are rising both in surface waters and in the deep sea due to an influx of anthropogenic carbon dioxide to the atmosphere. In the last two decades there has been a documented increase in shallow water coral bleaching events and in many cases massive coral mortality has followed. Deep sea corals cannot bleach since they lack symbiotic algae, but rising temperatures will probably influence their calcification rates, physiology and biochemistry. Deep-sea corals grow very slowly (4-25 mm/yr) (Freiwald et al. 2004), an order of magnitude slower than tropical corals. This difference is probably due to the cold temperatures in which deep sea corals live (4°-13°C). Preliminary findings suggest *Lophelia pertusa* respiration rates increase when exposed to higher ambient temperatures, but the synergistic effects of increased respiration and temperature on calcification are not known.

Salinity

Climate change is altering the salinity of the world's oceans (Curry et al. 2003). Increased evaporation in tropical waters has led to more saline conditions in lower latitudes, whereas glacial ice melt in polar waters has led to less saline conditions in higher latitudes. Deep sea corals tolerate salinity in the range of ~32-39 ppt (Freiwald et al. 2004) so any climate induced change in salinity that puts deep sea corals outside this optimal range will probably be detrimental. Physiological responses to salinities outside this optimal range are not known and warrant further study.

Seawater chemistry (pH)

Seawater chemistry and the calcium carbonate saturation state of the world's oceans are changing from the addition of fossil fuel CO_2 to the atmosphere (Feely et al. 2004, Guinotte et al. 2003, Kleypas et al. 1999). This influx of CO_2 is causing the world's oceans to become more acidic, which is bad news for corals and other marine organisms that use calcium carbonate to build their skeletons and protective shells. Although little is known about the effects of decreasing carbonate saturation state on deep-sea corals, lab experiments have conclusively shown that lowering carbonate ion concentration reduces calcification rates in tropical reef builders by 7 to 40 percent (Langdon et al. 2003, Marubini et al. 2003, Langdon et al. 2000, Gattuso et al. 1999). In fact, all marine calcifying organisms tested to date have shown a similar negative response. As the world's oceans become less saturated over time, corals are expected to build weaker skeletons (a process similar to osteoporosis in humans) and/or experience slower growth rates. If saturation state is as important to deep-sea coral calcification as it is to shallow reef builders, then this is an important issue.

Food Availability

Very little information exists on the food sources of deep sea corals. It is probable that they depend on suspended organic matter and zooplankton for nourishment (Freiwald et al. 2004). Since corals are sessile filter feeding organisms, they can obtain nourishment either from organic matter falling from the surface or via currents that bring organic matter and zooplankton to the coral. Deep sea corals occur in waters that have higher than average surface primary productivity, indicating that food falling from the surface is important to their survival. Many species of plankton (e.g. coccolithophores and foramniferans) build calcium carbonate shells and are sensitive to the seawater chemistry changes previously noted. If ecosystem changes due to climate change reduce surface productivity, food sources for deep sea corals will probably also be reduced.

Water Motion (currents)

The majority of deep sea coral ecosystems are found in relatively high energy areas and are exposed to steady currents. Freshwater inputs to high latitude waters are expected to increase as global temperatures continue to rise. The influx of freshwater causes seawater density changes, which slows down water circulation and may reduce upwelling and/or alter the trajectory of present day current patterns. Since deep sea corals are sessile organisms that depend on currents to bring them nourishment, any change in the direction and/or velocity of currents could have a significant impact on their distribution. Projections for changes in water circulation are uncertain at best, but if the Atlantic conveyor slows down as predicted, it will probably have negative consequences for deep sea corals.

Summary

Deep sea coral ecosystems have probably not experienced a combination of stresses of the types described above for a very long time. The synergistic effects of these stresses occurring in concert are uncertain, but changes in the environmental factors identified above will probably have serious implications for deep sea coral ecosystems. In situ monitoring and lab experiments are needed to help us understand and quantify how these changes might affect deep-sea coral ecosystems.

Chapter 7

Will Human-Induced Changes in Seawater Chemistry Alter the Distribution of Deep-Sea Scleractinian Corals?

Photo Credit: Steve Ross

Citation

Guinotte JM, Orr J, Cairns S, Freiwald A, Morgan L, George R (2006) Will human-induced changes is seawater chemistry alter the distribution of deep-sea scleractinian corals? Frontiers in Ecology and the Environment 4(3):141-146

Abstract

The answer to the title question is uncertain, as very few manipulative experiments have been conducted to test how deep-sea scleractinians (stony corals) react to changes in seawater chemistry. Ocean pH and calcium carbonate saturation are decreasing due to an influx of anthropogenic CO_2 to the atmosphere. Experimental evidence has shown that decreasing carbonate saturation inhibits the ability of marine organisms to build calcium carbonate skeletons, shells, and tests. Here we put forward a hypothesis suggesting that the global distribution of deep-sea scleractinian corals could be limited in part by the depth of the aragonite saturation horizon (ASH) in the world's oceans. Aragonite is the metastable form of calcium carbonate used by scleractinian corals to build their skeletons and the ASH is the limit between saturated and undersaturated water. The hypothesis is tested by reviewing the distribution of deep-sea, bioherm-forming scleractinian corals with respect to the depth of the ASH. Results indicate that >95% of 410 coral locations occurred in saturated waters during pre-industrial times. Projections indicate that about 70% of these locations will be in undersaturated waters by 2099. Lab experimentation, in situ experimentation, and monitoring efforts are needed to quantify the effects of changing seawater chemistry on deep-sea coral ecosystems.

Personal Contribution and Context within the Thesis:

My personal contribution to Chapter 7 is substantial. I collected all data sets used in the analyses, processed all remotely sensed data, performed all GIS analyses, wrote the manuscript, submitted the manuscript to the journal editor, handled all reviewer comments and edits.. Several co-authors only provided data, which accounts for their low contribution percentage. Contribution percentage for Chapter 7: John Guinotte (75%), Jim Orr (5%), Stephen Cairns (10%), Andre Freiwald (4%), Lance Morgan (5%), Robert George (1%).

Research presented in Chapter 7 is the first attempt to quantify the effects of ocean acidification on cold-water scleractinian coral ecosystems. Chapter 7 is the only chapter that directly addresses Research Foci 1, 2, 3, and 4. Results and ideas generated by Chapters 1-6 were used to formulate the hypotheses put forward in Chapter 7, namely that the distribution of present-day cold-water coral scleractinians is controlled (in large part) by the depth of the aragonite saturation horizon. The distribution of cold-water scleractinians show a strong correlation with the depth of the aragonite saturation horizon throughout the world's oceans (RF1). Calculations are conducted to quantify cold-water coral locations that are at risk due to the projected movement of the ASH to shallower depths through the year 2100 (RF2 and RF3). Recommendations for in situ monitoring and lab experimentations are made (RF4). In situ and lab experiments are needed to prove/refute that cold-water scleractinians are sensitive to changes in aragonite saturation state. New tools (e.g. landers) capable of tolerating harsh and inhospitable environments will be needed to carry out in situ experiments (RF4).

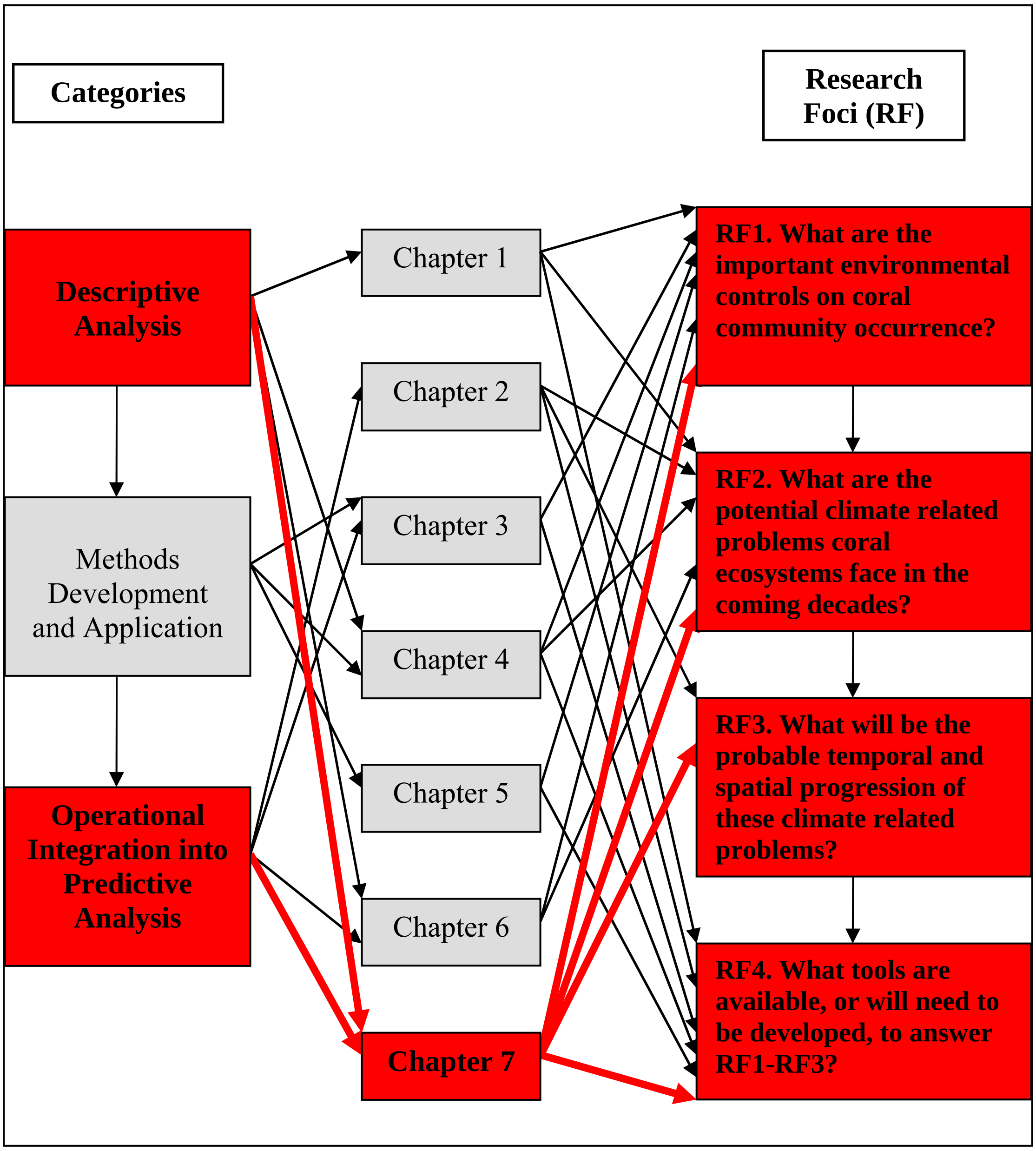

Figure 36: The relevance of Chapter 7 to the overall scheme of the research.

Introduction

Seawater chemistry and the calcium carbonate saturation state of the world's oceans are changing as a result of the addition of fossil fuel CO_2 to the atmosphere (Kleypas et al. 1999, Feely et al. 2004, Orr et al. 2005). The pH of surface oceans has dropped by 0.1 units since the industrial revolution and if fossil fuel combustion continues at present rates, the pH of the world's oceans will probably drop another 0.3 to 0.4 units by 2100 (Mehrbach et al. 1973, Lueker et al. 2000, Caldeira and Wickett 2003). This influx of anthropogenic CO_2 is causing the world's oceans to become more acidic, to the detriment of corals and other marine calcifiers, including plankton, which occupies the base of marine food webs. Corals and some species of plankton (coccolithophores and foraminiferans) use carbonate ions, obtained from the surrounding water, to build their skeletons and protective shells. As oceanic pH and carbonate ions decrease as a result of rising fossil fuel CO_2 levels, the calcification mechanisms and abilities of many marine organisms will be negatively impacted.

The oceans absorb approximately 48% of all anthropogenic CO_2 released into the atmosphere (Sabine et al. 2004), as well as an equilibrium-exchange uptake of 30% of naturally emitted CO_2 (Feely et al. 2004). This uptake initiates a series of chemical reactions, increasing the hydrogen ion concentration (H^+), lowering pH, and reducing the number of carbonate (CO_3^{2-}) ions available in seawater. All of this will make it more difficult for marine calcifying organisms to form biogenic calcium carbonate ($CaCO_3$). Although little is known about the effects of decreasing aragonite saturation state on deep-sea corals, lab experiments have conclusively shown that lowering carbonate ion concentration reduces calcification rates in tropical reef builders by 7–40% (Gattuso et al. 1999, Langdon et al. 2000, Langdon et al. 2003, Marubini et al. 2003). In fact, all marine calcifying organisms tested to date have shown a similar negative response to decreasing carbonate saturation state. As the world's oceans become less saturated over time, corals are expected to build weaker skeletons (a process similar to osteoporosis in humans) and/or experience slower growth rates (Buddemeier and Smith 1999, Gattuso et al. 1999, Kleypas et al. 1999, Guinotte et al. 2003). Both processes will make it more difficult for corals to withstand erosion and to retain a competitive advantage over other marine organisms.

Seawater chemistry: the movement of the aragonite saturation horizon (ASH)

Orr et al.'s (2005) calculated future changes in carbonate saturation state (aragonite and calcite) for the world's oceans and found that decreasing carbonate saturation state will not be limited to surface waters, but will occur in the deep sea as well. Orr's ASH (the limit between saturation and undersaturation) projections were based on the Intergovernmental Panel on Climate Change (IPCC) IS92a scenario (788 ppmv in the year 2100). The IS92a scenario is generally regarded as the "business-as-usual" scenario, where nations do very little to curb emissions. These projections were incorporated in a geographic information system (GIS) with approximately 410 records of deep-sea bioherm-forming corals (*Lophelia pertusa, Madrepora oculata, Goniocorella dumosa, Oculina varicosa, Enallopsammia profunda, Solenosmilia variabilis*) provided by Andre Freiwald, University of Erlangen, Germany (Freiwald et al. 2004; Figure 37).

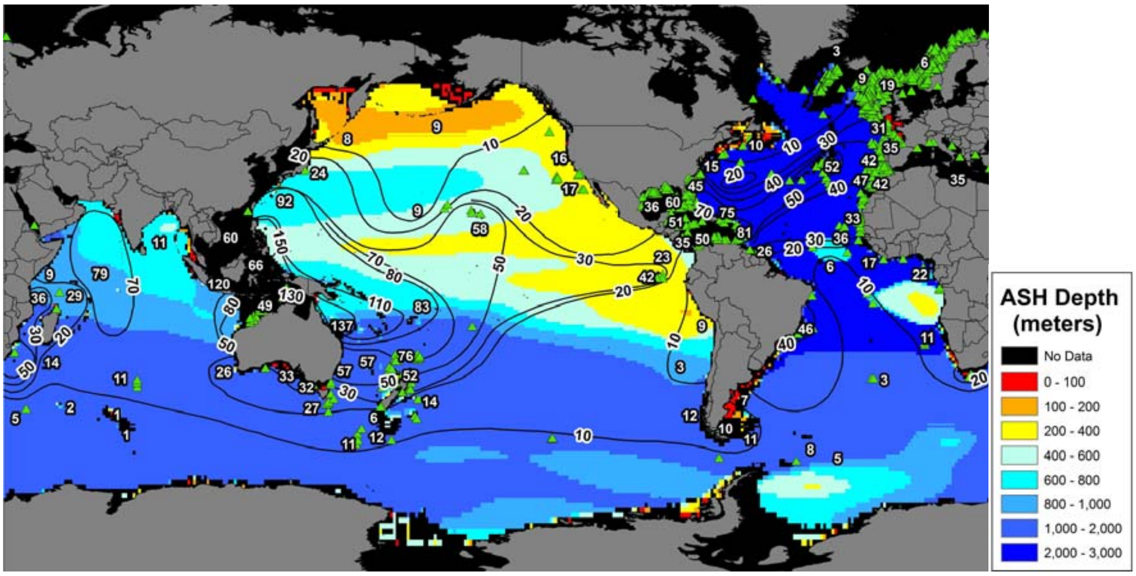

Figure 37a. Depth of the aragonite saturation horizon (ASH), locations of deep-sea bioherm-forming corals, and diversity contours for 706 species of azooxanthellate corals. (a) Projected ASH values for year 1765; $pCO_2=278$ ppmv. (b) Estimated ASH values for year 1995; $pCO_2=365$ ppmv. (c) Projected ASH values for year 2020; $pCO_2=440$ ppmv. (d) Projected ASH values for year 2040; $pCO_2=513$ ppmv. (e) Projected ASH values for year 2060; $pCO_2=594$ ppmv. (f) Projected ASH values for year 2080; $pCO_2=684$ ppmv. (g) Projected ASH values for year 2099; $pCO_2=788$ ppmv. Green triangles are locations of the six deep-sea bioherm-forming coral species. Black areas appearing in the Southern Ocean in Figures 39e–g and the North Pacific in Figure 39g indicate areas where ASH depth has reached the surface. Numerals not falling on diversity contours indicate number of azooxanthellate coral species.

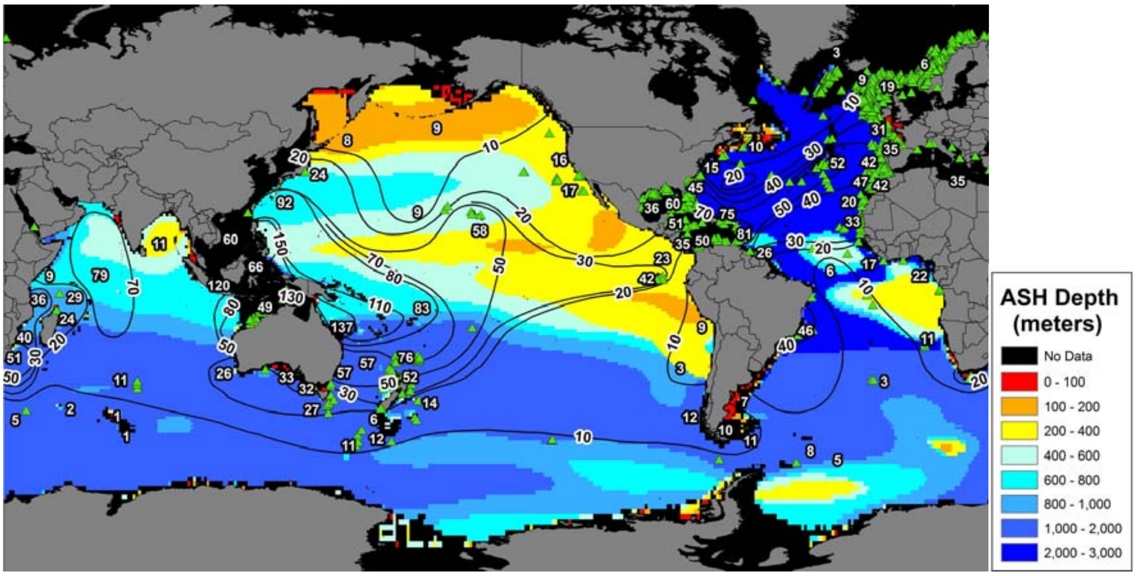

Figure 37b. Estimated ASH values for year 1995; pCO_2=365 ppmv.

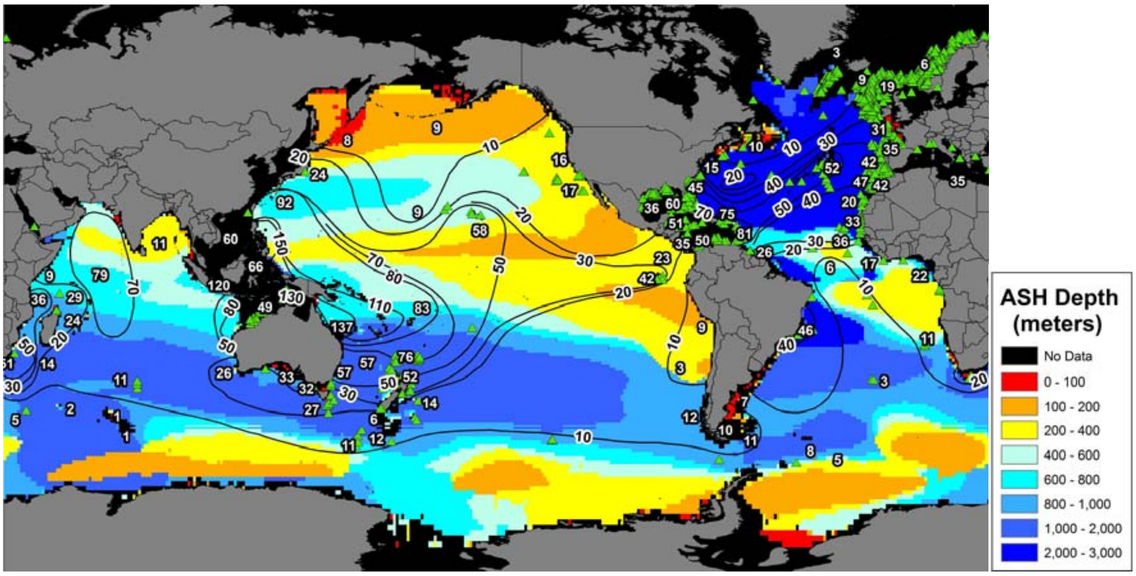

Figure 37c. Projected ASH values for year 2020; pCO_2=440 ppmv.

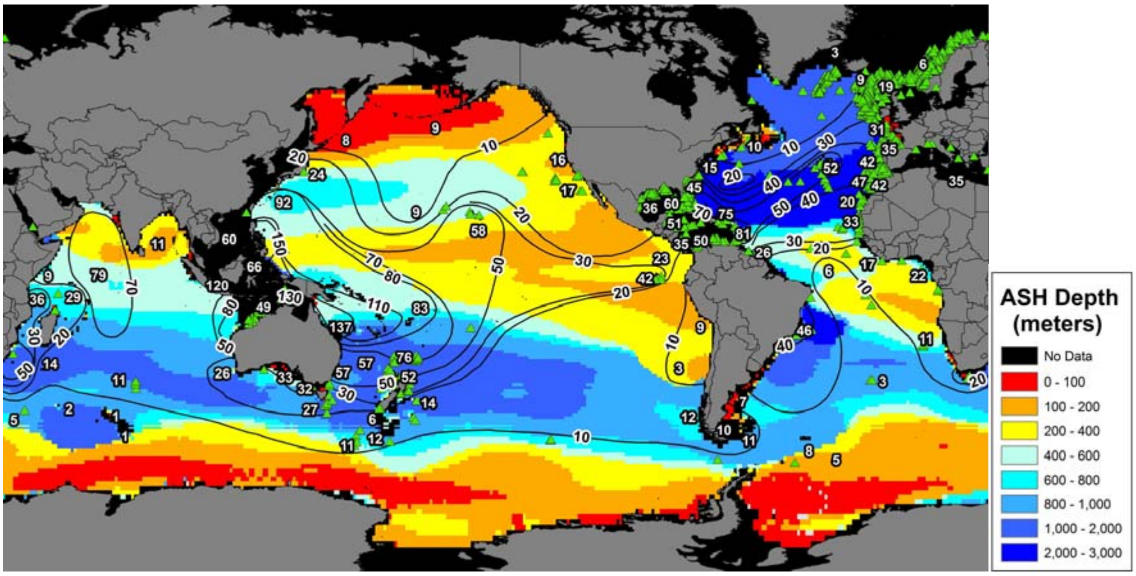

Figure 37d. Projected ASH values for year 2040; $pCO_2 = 513$ ppmv.

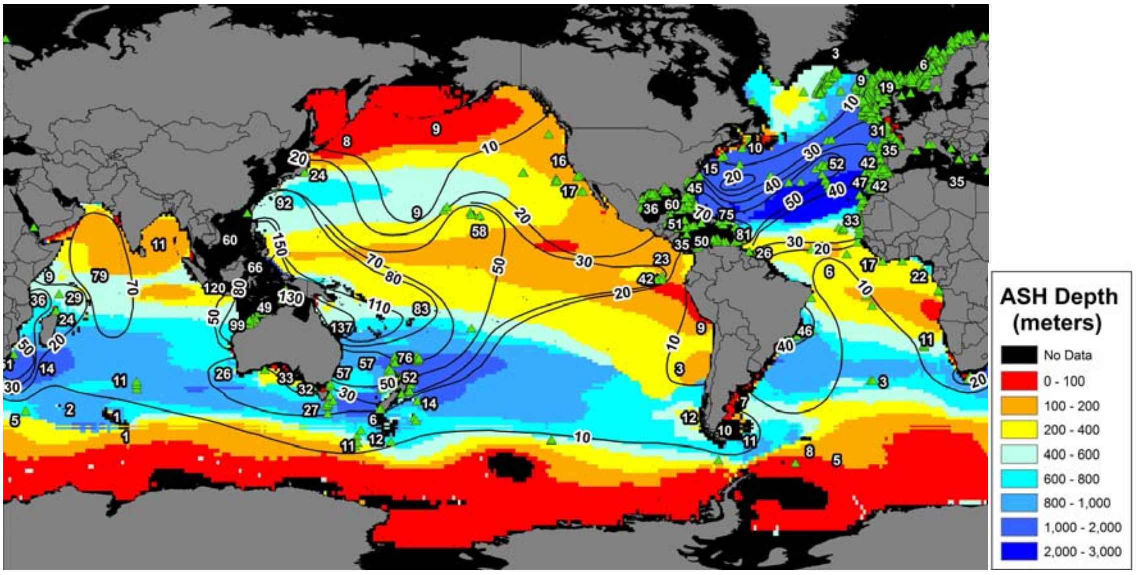

Figure 37e. Projected ASH values for year 2060; $pCO_2 = 594$ ppmv.

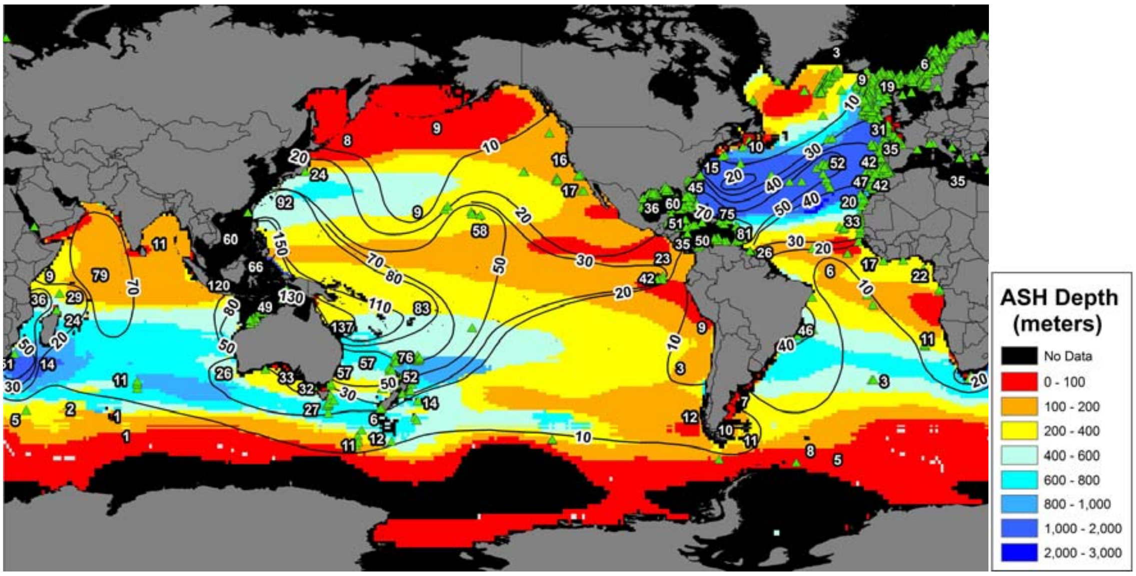

Figure 37f. Projected ASH values for year 2080; pCO_2=684 ppmv.

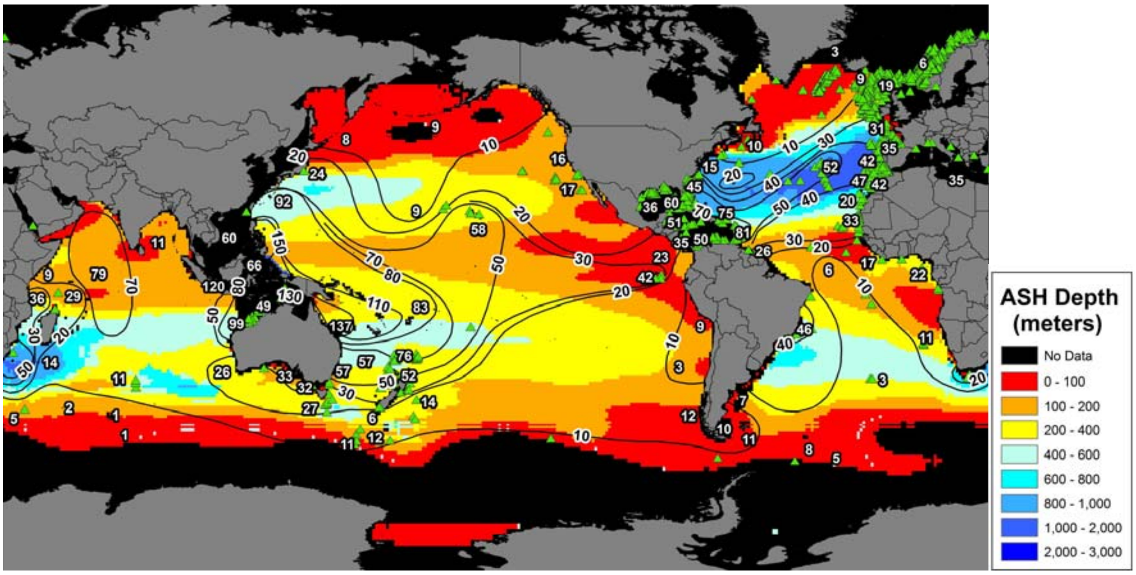

Figure 37g. Projected ASH values for year 2099; pCO_2=788 ppmv.

Bioherm is defined as an ancient organic reef of moundlike form built by a variety of marine invertebrates, including corals, echinoderms, gastropods, mollusks, and others (Encyclopedia Britannica 2006). Cairns' (in press) diversity contours for 706 species of azooxanthellate scleractinian corals were overlayed on ASH projections to highlight the relationship between coral diversity and ASH depth.

The projections clearly show the ASH moving shallower over time as atmospheric CO_2 concentrations increase. Aragonite projections were used as aragonite is the calcium carbonate mineral form deposited by scleractinian corals to build their skeletons. Calcite, the less soluble form of $CaCO_3$ used by octocorals (soft corals) and other marine organisms, is not included in this study. It should be noted that the sclerites of octocorals are calcitic, but the axes may be composed of calcite, aragonite or amorphous carbonate hydroxylapatite (Bayer and Macintyre 2001). The saturation depth for calcite is considerably greater than for aragonite because calcite is less soluble than aragonite in seawater. However, calcitic marine organisms will not be immune from saturation changes in the oceans because the depth of the calcite saturation horizon is also moving progressively shallower over time. Based on 410 known locations of deep-sea, bioherm-forming corals obtained from Freiwald (2004) and the estimated pre-industrial (year 1765) ASH depth, >95% of the coral locations were found in areas that were supersaturated (omega>1) in terms of aragonite (Figure 38).

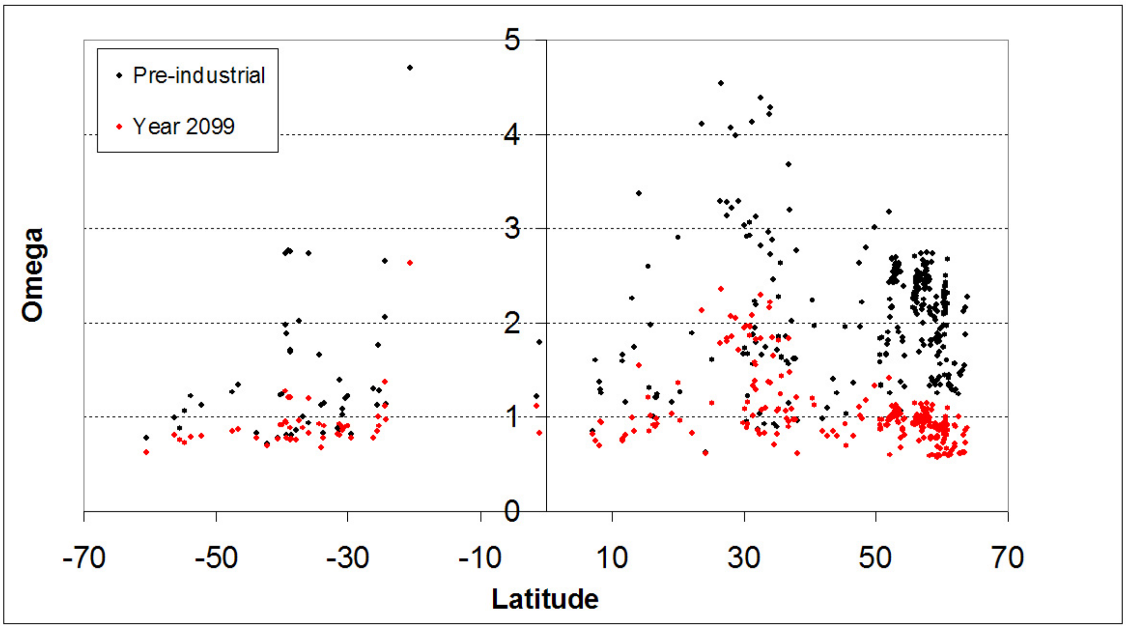

Figure 38. Projected ASH values for deep-sea coral locations in pre-industrial times (1785; black dots) and in the year 2099 (red dots). ASH (saturation boundary) is omega =1. n=410.

The mean omega value for all coral locations in pre-industrial times was 1.98 (supersaturated). By 2099, only 30% of coral locations remain in supersaturated waters, the vast majority of which are located in the North Atlantic, where the ASH remains relatively deep. Mean omega values for all coral locations in 2099 is 0.99 (undersaturated). Lab experiments performed on hermatypic, shallow-water corals in supersaturated waters have shown that relatively modest reductions in aragonite saturation state can cause substantial decreases in calcification (Langdon and Atkinson 2005, Langdon et al. 2003). If future experiments show the same is true for deep-sea, bioherm-forming corals, then calcification rates may decrease well before corals become undersaturated with respect to aragonite.

Deep-sea coral distributions in the Atlantic and Pacific

Deep-sea scleractinian corals are found in all ocean basins. Figure 37 shows that the center of species diversity for azooxanthellate scleractinian corals are the waters surrounding the Philippines (circa 160 species), followed by New Caledonia (circa 140 species), and the Caribbean Sea (circa 80 species) (Cairns in press). The majority of deep-sea, bioherm-forming scleractinians have been discovered in the North Atlantic, which is probably a function of sampling bias, but may also be connected to the ASH depth. Extensive deep water surveys in the North Pacific (Aleutian and Hawaiian Islands; Baco pers comm. 2005, Stone pers comm. 2005) have not documented deep-sea scleractinian bioherms like those found in the North Atlantic, although some records of small pieces exist from collections (Rogers 1999). One possible reason for the absence of deep-sea scleractinian bioherms in the North Pacific might be the shallow depth of the ASH throughout much of the region.

The ASH in the north Atlantic is very deep (>2000 m) and many of the deep-sea scleractinians found in these waters are bioherm-forming, robust, and cover areas several kilometers in size. The *Lophelia pertusa* bioherms off the coasts of Norway and Sweden are prime examples of such corals; they cover large areas and occur at relatively shallow depths (Fosså et al. 2002). Deep-sea scleractinian accretion in the North Atlantic produces structures several meters in height, due to the corals' ability to grow on top of the dead skeletons (coral rubble) of their predecessors. Bioherm accretion in the deep sea is a slow process; the age of North Atlantic corals vary, but recent estimates indicate they are less than 10,000 years old (Schröder-Ritzrau et al. 2005).

North Pacific deep-sea coral ecosystems are quite unlike those found in the North Atlantic. Present-day ASH depth in the North Pacific is relatively shallow (50–600 m) and scleractinian corals found there do not form bioherms. North Pacific scleractinians tend to be found in solitary colonies and the region is dominated by octocorals (soft corals, stoloniferans, sea fans, gorgonians, sea pens) and stylasterids. Octocorals and a small percentage (about 10%) of stylasterid species use calcite to build their spicules and skeletons (Cairns and Macintyre 1992). Cairns and Macintyre (1992) studied 71 stylasterid species, seven of which were from the temperate North Pacific. Remarkably, six of the seven species had calcitic skeletons (the less soluble polymorph), even though calcite is rare among the stylasterids. These calcitic stylasterids were found in abundance at depths of 50–500 m. The Aleutian Islands, a region where the approximate depth of the ASH is < 150 m, is one example of an area dominated by octocorals, stylasterids, and sponges.

The depth at which many azooxanthellate corals are found in the waters surrounding the Galápagos Islands lends further credence to the hypothesized ASH–scleractinian relationship. Figure 39 shows global diversity contours for 706 species of azooxanthellate corals, regardless of depth. Across all ocean basins, 91 of the 706 species (13%) occur exclusively in shallow water (0–50 m). However, 19 of the 42 species (45%) found in the waters off the Galápagos Islands are found in less than 50 m of water. This is interesting, given the fact that present-day ASH depth in the waters surrounding the Galapágos is quite shallow (< 300 m) due to upwelling.

Stony corals in the North Pacific are found in close proximity to, or at slightly shallower depths, than the ASH, suggesting that corals may be surviving in a marginal aragonite saturation state environment. Coral rubble fields are non-existent in the North Pacific, where aragonite dissolution rates in the upper 1000 m are twice as high as the dissolution rates of the North Atlantic (Feely et al. 2004). The shallow depth of the ASH and the high dissolution rates in North Pacific waters could work synergistically to make bioherm accretion unlikely, if not impossible. Corals may have biophysical mechanisms which allow them to survive in close proximity to the ASH, but not to flourish and form accumulated structures such as those found in the North Atlantic, where the ASH is much deeper and dissolution rates are low.

The North Atlantic is not the only region where deep-sea scleractinians form bioherms. Such structures are also found in several ocean basins, where the ASH is deep and dissolution rates are low (eg off the US east coast, Australia, New Zealand, Brazil, and the UK). Scleractinians are not known to form deep bioherms in the North Pacific or northern Indian Ocean, where the ASH is shallow and dissolution rates are high. A strong qualitative correlation exists between areas of low azooxanthellate coral diversity and areas where the present-day ASH is relatively shallow (Figure 37b). These areas include the temperate North Pacific, off the west coast of South America, the northern Indian Ocean, and off the southwest coast of Africa.

The exception to the low scleractinian diversity–shallow ASH relationship is the Southern Ocean. Scleractinian diversity in the Southern Ocean is low (< 10 species) and the present-day ASH depth is relatively deep (> 800 m) for much of the region. Low species diversity in the Southern Ocean is not due to lack of exploration in the region and it is generally accepted that the taxonomy of Antarctic scleractinians is fairly well known (Cairns pers comm. 2005). The reason(s) for this exception are not known, but possibilities include past and present barriers to coral recruitment and/or the extent of sea ice throughout geologic history.

Food availability

There is warranted concern that changing seawater chemistry could have an indirect, detrimental effect on deep-sea corals, by limiting the amount of food and nutrients available to deep-sea coral ecosystems. Very little information exists on the food sources of these organisms, but it is probable that they depend on suspended organic matter and zooplankton for nourishment (Kiriakoulakis et al. 2005). Since corals are sessile filter feeders, they can obtain nourishment either from organic matter falling from the surface or via currents that bring organic matter and zooplankton to the coral. Deep-sea corals are found in waters that have above-average surface primary productivity, indicating that food falling from the surface is important to their survival (Figures 39 and 40). There is also a strong correlation between chlorophyll-a concentration and particulate organic carbon (POC) in the world’s oceans (Legendre and Michaud 1999, Gardner et al. 2004).

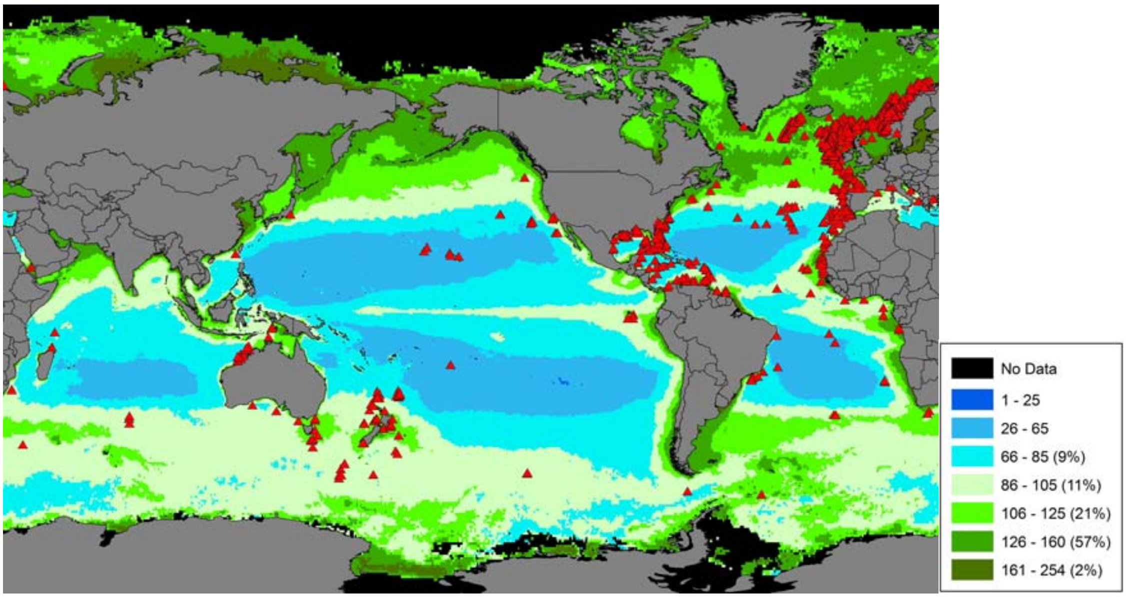

Figure 39. Coral locations and global average chlorophyll-a concentration for years 1997–2000. Red dots are 1565 locations of the six deep-sea bioherm-forming coral species. Note: legend values for chlorophyll-a concentration range from 0–255, percentages in parentheses indicate the percentage of total coral records within each concentration range. (Source: NASA.)

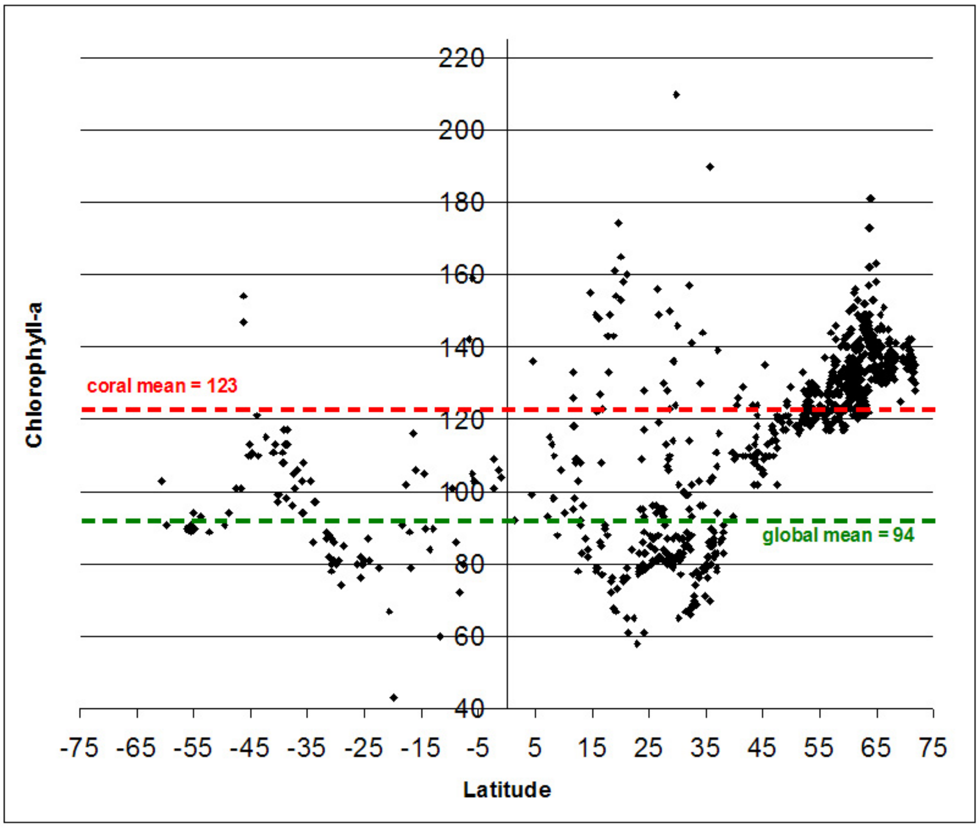

Figure 40. Chlorophyll-a concentration for 1565 locations of the six deep-sea bioherm-forming coral species plotted with latitude.

Many species of plankton (eg coccolithophores and foraminiferans) and pteropods, which form the base of marine food webs, use carbonate ions to build their $CaCO_3$ shells/tests and are sensitive to the seawater chemistry changes previously noted (Riebesell et al. 2000, Riebesell 2004, Orr et al. 2005). If changing seawater chemistry causes a reduction in phytoplankton and zooplankton production in surface waters, the feedback to deep-sea coral ecosystems will probably be a negative one, as deep-sea corals may not be able to attain their nutritional requirements.

Other factors

Changing seawater chemistry is not the only threat deep-sea corals face in the age of global climate change. These organisms have evolved in steady state, cold, dark, nutrient-rich environments and it is possible that changes in temperature, salinity, or water motion may also have negative consequences. Model projections for these variables vary considerably, uncertainties are high, and the biological feedbacks to changes in these factors are poorly understood in terms of their effects on deep-sea corals. Nevertheless, worrisome physical changes are taking place in the world’s oceans. Global sea temperatures are rising in the deep-sea, owing to an influx of anthropogenic CO_2 to the atmosphere (Barnett et al. 2005). Rising sea temperatures may influence deep-sea coral calcification rates, physiology, and biochemistry, though specific ranges and thresholds are not yet known.

Climate change is also altering the salinity of the world’s oceans (Curry et al. 2003). Increased evaporation in tropical waters has led to more saline conditions at lower latitudes, whereas glacial ice melt in polar waters has produced less saline conditions at higher latitudes. Freshwater inputs to high latitude waters are expected to increase as global temperatures continue to rise and the influx of freshwater may slow down water circulation, reduce upwelling, and/or alter the trajectory of present-day current patterns (Curry et al. 2003). Since deep-sea corals are sessile organisms that depend on currents to bring them food, any change in the direction and/or velocity of currents could influence their distribution.

Summary

The oceans are changing both chemically and physically as a result of the uptake of anthropogenic CO_2. Shallow-water corals and other marine calcifiers react negatively when exposed to reduced carbonate saturation state conditions. Biological feedbacks and the reactions of marine organisms to these changes will be complex and will probably affect all trophic levels of the world's oceans. Deep-sea coral ecosystems will not be immune from these changes and probably have not experienced the combination of chemical and physical stresses described for a very long time. The synergistic effects of these stresses occurring in concert are uncertain, but these changes will probably have serious implications for deep-sea coral ecosystems.

The effects of decreasing aragonite saturation state on deep-sea, bioherm-forming scleractinians are not well understood and further experimentation is warranted. Lab and in situ monitoring experiments are necessary to help us understand and quantify how chemical changes might affect deep-sea coral ecosystems in the future. In situ experiments are needed as they eliminate biases introduced in laboratory experiments and avoid the problem of co-variation between important parameters (temperature, saturation state, etc) (Kleypas et al. 2006). If (a) aragonite saturation state is as important to deep-sea scleractinians as it is to shallow-water hermatypic corals and (b) the depth of the ASH moves progressively into shallower waters, as projected, then, over time, deep-sea, bioherm-forming corals will be exposed to an increasingly marginal environment. If the hypothesis presented is valid and the shallow depth of the ASH in certain regions of the oceans (eg the North Pacific) is limiting deep-sea scleractinians from forming bioherms, then we can expect substantial changes in the distribution of deep-sea corals and the structures they form within this century. The upward migration of the ASH has the potential to alter the global distribution of deep-sea scleractinian bioherms and the organisms that depend on them.

Chapter 8

Discussion and Conclusions

Chapters 1-7 address four research foci (pg. 3) pertaining to the environmental controls and climate change effects on the health and occurrence of coral communities and their constituent organisms (e.g. sea anemones and anemonefishes). How each chapter addresses the four research foci is described below.

RF1 (What are the important environmental controls on coral community occurrence and their constituent organisms?) was investigated in Chapters 1, 3, 4, 5, 6, and 7.

Chapter 1 results show the primary drivers of high SSTs, which caused the 1997-1998 coral bleaching event on the GBR, were due to the combination of low winds, clear skies, and neap tides. These environmental factors have co-occurred twice (2002 and 2006) since the 1997-1998 bleaching event. The 2002 coral bleaching event surpassed the 1997-1998 event as being "the most significant GBR bleaching event on record" (Wilkinson 2002) and severe bleaching (>75 percent) was recorded in the far southern region of the GBRMP in 2006 (GBRMPA 2006). It should be noted that other environmental factors can cause coral bleaching at local scales (e.g. low salinity usually caused by freshwater input, which contributed to high coral mortality in the Keppel Islands in 2006). These factors were not investigated in Chapter 1. Findings presented in Chapter 1 show that high temperature events, caused by a combination of low winds, clear skies, and neap tides, are an important control on the health and occurrence of shallow-water hermatypic coral ecosystems.

Chapter 3 specifically identified the environmental factors that are important controls on the health and occurrence of shallow-water hermatypic and deep-water hermatypic coral habitat on the GBR. Light availability and average nitrate were the most important variables in determining where reefs (both modeled and documented) occur, but temperature, salinity and average phosphate were also significant controls on reef occurrence. Chapter 4 results showed that methodologies developed in Chapter 3 could be successfully applied to areas outside the GBRMP and illustrated that environmental parameters will have varying degrees of influence based on geography. The environmental factor with the most influence in determining where coral areas occur off the Western Australian coast was light availability. Coral areas within the WA study area are far enough offshore that nitrate and phosphate inputs from the landmass are not limiting their distribution. Chapter 5 results indicate that minimum SST and depth are the two best predictors of potential habitat for anemones and anemonefishes (constituent organisms of coral communities). Taken individually, the variables of minimum salinity, chrlorophyll a concentration, tidal amplitude and wind speed did not identify habitat suitable for clownfish and sea anemones (Figures 31a, 31b). Low salinities are known to exert a strong control on anemone occurrence (Shick 1991), but the temporal and spatial scale of salinity data used in Chapter 5 were not of sufficient resolution to capture these effects.

Chapter 6 moves away from shallow-water hermatypic corals to explore the environmental controls that influence the global distribution deep-sea ahermatypic corals and how climate induced changes in these controls might effect their distribution in the future. Temperature, salinity, seawater chemistry (pH), water motion, and food availability are either known and/or thought to be significant controls on where these ecosystems occur. The controls are reviewed in light of the changes we might expect to see due to climate change. Chapter 7 expands on the seawater chemistry (pH) control issue first introduced in Chapter 2 and discussed with respect to deep-sea corals in Chapter 6. Chapter 7 results provide strong anecdotal evidence that the depth of the aragonite saturation horizon is a significant control on cold-water scleractinian coral distribution throughout the world's oceans. Lab and in situ experiments are needed to quantify the importance of this hypothesized environmental control.

RF2 (What are the potential climate related problems coral ecosystems face in the coming decades?) was investigated in Chapters 1, 2, 4, 5, 6, and 7.

Chapter 1 identified the causal agents of the 1997-1998 coral bleaching event on the GBR and stated the 'link to climate is not clear'. This statement was valid in the context of the 1997-1998 bleaching event. However, in the ten years since this research was conducted (six years since this research was published) the climate link has become much clearer and is a significant cause for concern. The oceans are warming and this warming cannot be explained by natural internal climate variability or solar and volcanic forcing (Barnett et al. 2005). Model projections of global climate change suggest that the thermal tolerance of reef-building corals are likely to be experienced every year within the next few decades (Hoegh-Guldberg 1999). Done et al. (2003) suggest that increasing temperatures throughout the 21st Century will lead to increased levels of coral bleaching, coral mortality and biodiversity depletion that could have serious consequences for the GBR's biodiversity, ecology, and appearance. Model projections put forth in Chapter 2 (Guinotte et al. 2003) suggest that maximum monthly sea surface temperatures will likely increase to levels that have caused significant coral bleaching in the past and these levels are expected throughout many coral areas of the

Pacific Basin within decades. There is warranted concern that warming ocean temperatures may lead to a rapid increase in the frequency and severity of coral bleaching in the coming decades (Donner et al. 2005, in Donner and Potere 2007).

Chapter 2 states all reef locations within the Pacific Basin are likely to become marginal with respect to aragonite saturation state by year 2069. Figure 18 plots the spatial overlap of both projected high SSTs and low aragonite saturation state, which had not been investigated before. The synergistic effects of high temperature events and low aragonite saturation state are uncertain, but will probably be detrimental for shallow-water hermatypic corals. Clearly, the two climate related problems with the greatest potential for damage to coral reef ecosystems at the global scale are high SSTs and decreasing aragonite saturation state. The worrisome results presented in Chapter 2 also highlight the need for a tool that could predict deep-water hermatypic reef habitat.

Results presented in Chapter 4 state hermatypic shallow-water corals off the coast of Western Australia suffered high mortality (~80%) from the 1997-1998 bleaching event and subsequent surveys one year later revealed that recovery would be slow. Figure 18 (Chapter 2) identifies this region as one that will experience maximum monthly sea surface temperatures deemed marginal by Kleypas (1999b) as early as 2020. This region is a high risk area based on projections of future ‘marginal’ SSTs (Chapter 2) and will fall into the ‘marginal’ category for both high SST and low aragonite saturation state by the middle of century. These findings also highlight the need for a tool that could predict deep-water hermatypic reef habitat.

Chapter 6 summarizes potential threats deep-sea corals might face in a changing climate. Many of the statements made in Chapter 6 are hypothetical as very few manipulative experiments have been conducted to test how deep sea corals react to changes in temperature, salinity, seawater chemistry (pH), water motion (currents), and food availability. Chapter 7 expands on the seawater chemistry (aragonite saturation horizon) issue by exploring the present known distribution of cold-water scleractinian corals and the relation of these locations with the depth of the aragonite saturation horizon. The hypothesis put forth in Chapter 7 (the aragonite saturation horizon is a control on cold-water coral distribution) is reinforced by anecdotal evidence from several published papers and reports. Future projections of the aragonite saturation horizon depth indicate that approximately 70% of all known scleractinian cold-water corals will be in undersaturated waters by the end of the century.

RF3) (What will be the probable temporal and spatial progression of these climate related problems?) was addressed in Chapters 2 and 7.

Chapter 2 plots the spatial and temporal progression of future coral reef habitat marginality due to climate change. Projected changes in future maximum monthly sea surface temperatures and aragonite saturation state were used to identify where and when we might expect to see marginal conditions for coral reef habitat suitability emerge in the Pacific Basin. Results suggest that essentially all reef locations are likely to become marginal with respect to aragonite saturation state by year 2069. Significant areas, including some with the highest biodiversity, are expected to experience high-temperature regimes that may be marginal, and additional areas will enter the borderline high temperature range that have experienced significant ENSO-related bleaching in the recent past. Figures 16, 17, and 18 illustrate the spatial and temporal progression of these changes.

Chapter 7 plots the spatial and temporal progression of the shallowing of the aragonite saturation horizon throughout the world's ocean basins. Conservative projections indicate that ASH changes of 100s-1000s of meters are possible within the century, which could have detrimental impacts on marine calcifiers, including cold-water corals. Southern Ocean surface waters will begin to become undersaturated with respect to aragonite by the year 2050 and undersaturation could extend throughout the entire Southern Ocean and into the subarctic Pacific Ocean by the year 2100 (Orr et al. 2005). If aragonite saturation state or other factors (e.g. salinity, water movement) identified in Chapters 6 and 7 reduce primary productivity (plotted in Figure 39) in surface waters, cold-water coral ecosystems will likely suffer from not being able to attain their nutritional requirements.

RF4) (What tools are available, or will need to be developed, to answer the foregoing questions (RF1-RF3)?) was addressed in Chapters 1, 2, 3, 4, 5, and 7

Several tools were developed to process and analyze the AVHRR data reported in Chapter 1. William Skirving's Ph.D. research focused on developing new processing algorithms for AVHRR data so accurate values for GBR SST skin temperatures could be obtained. Mike Mahoney (AIMS) was tasked with processing all AVHRR data and wrote programming scripts to deal with AVHRR data in ENVI. I personally developed routines in ArcInfo (ESRI's GIS software) for analyzing the processed AVHRR data. These ArcInfo routines enabled me to perform cluster analyses and principal components analyses (in ArcInfo) on GBR SST data. My goal was to create a spatial index for coral bleaching thresholds in the GBRMP. The results of these analyses were the pilots for second generation clustering and PCA results published in Done et al. (2003) and I presented the results from these analyses at the 9th International Coral Reef Symposium (Guinotte et al. 2000). Researchers from AIMS (e.g. William Skirving) and NOAA have worked together for the past several years through NOAA's Coral Reef Watch Program to develop tools that can forecast bleaching events before they happen (Liu et al. 2003, 2004).

Analyses of Chapter 2 results took advantage of the standard tools within ESRI's ArcGIS raster analysis package (Spatial Analyst). No new tools were developed for this research effort. Results presented in Chapter 2 are too poorly resolved spatially to be useful for management activities. The coarse spatial resolution of projected aragonite saturation and SST data needs to be improved substantially before these methodologies could be used to identify areas for future protection. Highly resolved data for future aragonite saturation state does not currently exist, but it would be possible to substitute higher resolution SST projections.

ArcGIS spatial processing tools (Spatial Analyst and Geostatistical Analyst) were used in Chapter 3 to determine potential reef habitat. Statistics and regression analyses (Tables 3-5) were calculated on Oracle tables using Insightful Miner software. Methodologies presented here can be applied globally to predict coral reef habitat and will likely work for other marine ecosystems that live within well-defined environmental limits (e.g. *Halimeda*). Chapter 3 methods proved useful in identifying numerous offshore regions likely to contain coral reefs and/or coral communities, particularly in shelf-edge areas. Future research opportunities include substituting projected changes in environmental factors (e.g. SST, aragonite saturation state, etc) for present-day data in hopes of producing outputs that will aid in identifying areas where coral growth is likely and/or unlikely to occur. ArcGIS tools (Spatial Analyst and Geostatistical Analyst) were used in Chapter 4 to predict deep-water hermatypic reef habitat. Known deep-water coral sites on Scott Reef were used to 'train' the predictive model via the light availability parameter. Once deep-water coral sites on Scott Reef were modeled successfully, the same light availability sensitivity was used to model habitat throughout the region. This was the only change made to the methodology developed in Chapter 3.

The online tools developed in Chapter 5 were a team effort and took several years to develop. Bob Buddemeier, Daphne Fautin, Jeremy Bartley, and myself were involved in the overall design of the system. The majority of the programming was carried out by Jeremy Bartley and Asif Iqbal. Testing of the system and data entry to an Oracle database were carried out by Jeremy Bartley and myself. The KGSMapper differs from other online habitat mapping tools in that the user decides which environmental data sets are used, is able to restrict and/or edit the input data in a variety of ways, and the user has access to several statistical exploration tools to help them make decisions along the way. This tool provides the user with the added benefit of being able to quantify the environmental variables that are most/least important in determining where marine taxa can survive and choose whether or not to include them in the analysis. The development of this fully functional online analysis tool, which allows the user to upload locations of any marine taxa they wish to use, will be very useful in predicting probable range shifts (due to climate change) and in identifying areas vulnerable to biological invasions. The tools described in Chapter 5 are presently being used to predict deep-sea coral habitat globally. The distribution of deep-sea corals throughout the world’s oceans is not well documented due to the high costs of ship time and deep-sea exploration equipment. The KGSMapper is a cost effective tool that will be useful in quantifying the spatial distribution of deep-sea coral habitat and in guiding future research cruises for deep-sea corals and other marine organisms.

Research presented in Chapter 7 relied heavily on methodologies developed in Chapters 2 and 3. Existing ArcGIS tools (Spatial Analyst and Geostatistical Analyst) were used to analyze the data sets used in this chapter. Recommendations for in situ monitoring and lab experimentations are were made in Chapter 7 and this is the main area in which new tools and methods need to be developed. In situ and lab experiments are needed to prove/disprove that cold-water scleractinians are sensitive to changes in aragonite saturation state. New tools (e.g. landers) capable of tolerating harsh and inhospitable environments and able to control ocean pH will be needed to carry out these in situ experiments. Researchers and engineers at the Monterrey Bay Aquarium Research Institute (MBARI) are currently developing a lander that will be capable of controlling ocean pH at depth and quantifying calcification rates on deep-sea corals. This equipment could also be used in shallow-water hermatypic coral environments.

Utility for Management and Future Research

The tools, methodologies and results presented in this thesis provide some opportunity for adaptive research, monitoring, and management of the affected ecosystems. Chapter 1 documented the 1997-1998 coral bleaching story for the GBR, but also provided early tools and methodologies that have aided the monitoring (NOAA's Coral Reef Watch Program) and management (GBRMPA) communities. The second generation cluster analyses and PCAs reported in Done et al. (2003) were used to help identify areas within the GBRMP that are more/less likely to experience future bleaching events and this information was incorporated into GBRMPA's zoning plan in 2004.

Chapter 2 highlighted three specific areas for development of sustained research efforts: 1) Biodiversity: Quantifying the spatial overlap between regions of coral biodiversity ("hotspots") in the Indo-Pacific and marginality in terms of future sea surface temperature and aragonite saturation state. This exercise would identify regions with high biodiversity at risk and identify regions of low biodiversity where reef occurrence may be at risk due to lack of functional replacements for vulnerable organisms or guilds. 2) Terrigenous vs. Oceanic effects: Oceanic models used in Chapter 2 are less reliable in nearshore environments. The GBR is an ideal location to investigate the spatio-temporal distributions of environmental conditions and their effects on coral communities. 3) Longitudinal studies of climate change effects: Since marginal temperature and saturation conditions develop with different rates and patters, systematic observation of conditions and ecosystem responses at a network of relatively undisturbed reef sites (Fig 18a) would enhance future evaluations of the individual and synergistic effects of changing temperature and saturation state.

Methodologies developed in Chapters 3 and 4 clearly illustrate that undocumented deep-water hermatypic reefs can be identified using environmental data. GBRMPA and other management agencies could use these models to identify uncharted coral areas and take management steps to ensure they are not disturbed by human activities. Models used in these chapters would also compliment global reef mapping initiatives which cannot identify deep reef habitat due to satellite sensor limitiations. Predicted changes in sea surface temperature and aragonite saturation state could be included in future models to identify areas that may become marginal due to changes in seawater chemistry and sea surface temperature. Finally, a real-time high resolution version of the model would allow researchers and management agencies to continually monitor environmental conditions remotely and issue alters if and when environmental conditions exceed predetermined thresholds.

Tools and methodologies developed in Chapter 5 hold great potential for characterizing suitable habitat for marine species other than anemones and anemonefishes based on known locations. Future applications of these tools and methods could be used to identify areas vulnerable to biological invasions, guide conservation efforts, and plan field work. Substituting future projections of environmental data would allow researchers to predict where species ranges might contract or expand, which could be very important to a variety of management agencies, including those involved with managing global fisheries. The KGSMapper is presently being used to predict deep-sea coral habitat at the global scale.

Chapters 6 and 7 have generated a high level of interest from the scientific community and there is potential for management agencies to protect these habitats. Researchers are currently conducting laboratory experiments on cold-water corals (*Lophelia pertusa*) to determine whether or not their calcification rates decrease with lowered aragonite saturation state (Riebesell pers comm. 2007). Two teams of researchers have produced global predictive cold-water coral habitat maps. Both teams used aragonite saturation state data as environmental inputs and this data was found to be a very important predictor of cold-water coral habitat (Clark et al. 2006, Davies et al. in prep). Since the aragonite saturation horizon is moving rapidly to shallower depths, there is an opportunity to investigate those known cold-water coral locations that have become undersaturated with respect to aragonite in recent years. Field survey work in coral areas that have moved from saturated to undersaturated conditions might reveal important information about the health of these ecosystems and validate or negate the hypotheses put forth in Chapter 7. Management opportunities include taking active steps to ensure that destructive human activities (e.g. bottom trawling) are not allowed in cold-water coral areas, especially in the areas that will not become undersaturated with respect to aragonite through the year 2100 (e.g. the East coast of the U.S.).

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