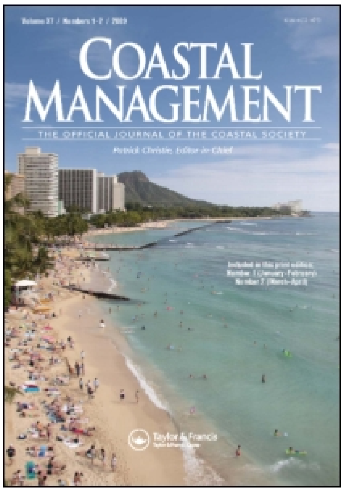

Coastal Management
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713626371

Warming Seas in the Coral Triangle: Coral Reef Vulnerability and Management Implications

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First published on: 26 August 2010

To cite this Article McLeod, Elizabeth , Moffitt, Russell , Timmermann, Axel , Salm, Rodney , Menviel, Laurie , Palmer, Michael J. , Selig, Elizabeth R. , Casey, Kenneth S. and Bruno, John F.(2010) 'Warming Seas in the Coral Triangle: Coral Reef Vulnerability and Management Implications', Coastal Management, 38: 5, 518 — 539, First published on: 26 August 2010 (iFirst)

To link to this Article: DOI: 10.1080/08920753.2010.509466

URL: http://dx.doi.org/10.1080/08920753.2010.509466

Coastal Management, 38:518–539, 2010

ISSN: 0892-0753 print / 1521-0421 online
DOI: 10.1080/08920753.2010.509466

Warming Seas in the Coral Triangle: Coral Reef Vulnerability and Management Implications

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The highest diversity coral reefs in the world, located in the Coral Triangle, are threatened by a variety of local stresses including pollution, overfishing, and destructive fishing in addition to climate change impacts, such as increasing sea surface temperatures (SSTs), and ocean acidification. As climate change impacts increase, coral reef vulnerability at the ecoregional scale will have an increasingly important influence on conservation management decisions. This project provides the first detailed assessment of past and future climatic stress, thermal variability, and anthropogenic impacts in the Coral Triangle at the ecoregional level, thus incorporating both local

We are grateful to Alison Green, Eddie Game, Scott Heron, and Mark Eakin for providing useful input on an earlier version of this manuscript. We would also like to thank two anonymous reviewers for improving the manuscript. Financial assistance was provided by the National Oceanographic and Atmospheric Administration's (NOAA) Sector Applications Research Program (SARP). This publication is the University of Hawaii's School of Ocean and Earth Science and Technology (SOEST) publication #7977 and the International Pacific Research Center (IPRC) publication #712. The opinions expressed herein are those of the author(s) and do not necessarily reflect the view of NOAA.
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(e.g., pollution, development, and overfishing) and global threats (increasing SSTs). The development of marine protected area (MPA) networks across the Coral Triangle is critical for the region to address these threats. Specific management recommendations are defined for MPA networks based on the levels of vulnerability to thermal and local stress. For example, coral reef regions with potentially low vulnerability to thermal stress may be priorities for establishment of MPA networks, whereas high vulnerability regions may require selection and design principles aimed at building resilience to climate change. The identification of climate and other human threats to coral reef systems and ecoregions can help conservation practitioners prioritize management responses to address these threats and identify gaps in MPA networks or other management mechanisms (e.g., integrated coastal management).

Keywords Coral Triangle, climate change, coral reef, marine protected area (MPA), sea surface temperature (SST), management

Introduction

The Coral Triangle spans provinces in Indonesia, Malaysia, the Philippines, East Timor, Papua New Guinea, and the Solomon Islands. It includes over 75% of the world's hard coral species (Veron et al., 2009) and is considered a global conservation priority (Baird et al., 2002; Roberts et al., 2002; Bellwood et al., 2005; Briggs, 2005; Carpenter & Springer, 2005). The Coral Triangle's coral reefs directly and indirectly support the livelihoods of 100 million people (Hoegh-Guldberg et al., 2009), and the economic value of coral reef fisheries in Southeast Asia alone is estimated to be US$2.3 billion per year (adapted from (Burke et al., 2002)).

Despite their diversity and value, coral reefs in this region are threatened by a combination of climate change impacts (e.g., increasing sea surface temperatures [SSTs], ocean acidification, and sea-level rise; IPCC, 2007) as well as a variety of other anthropogenic impacts (e.g., coastal development, overfishing, destructive fishing, and pollution; Burke et al., 2002). More than 80% of the reefs in Southeast Asia are considered at risk from anthropogenic threats (Burke et al., 2002); and studies suggest that Indo-Pacific coral reefs are disappearing at a rate of 1% per year (Bruno & Selig, 2007). By 2050, reefs globally may no longer be dominated by hard corals (Hoegh-Guldberg et al., 2007).

Elevated SSTs combined with high solar irradiance have been linked to large scale, or mass coral bleaching (Glynn, 1996; Hoegh-Guldberg, 1999). Specifically, increases in SST of 1°C above normal summer maxima and sustained for at least 2–3 days appear to provide a potentially useful predictor of subsequent bleaching (Goreau & Hayes, 1994; Glynn, 1996; Strong et al., 1998). Mass bleaching refers to an entire community of corals that has become partly or totally bleached (Glynn, 1993). Coral bleaching is a stress response usually associated with both anthropogenic and natural disturbances, because corals can tolerate only a narrow range of environmental conditions and live near the upper limit of their thermal tolerance (Glynn, 1993). Bleaching is caused by the temporary or permanent loss of endosymbiotic algae (zooxanthellae) and their associated pigments from host coral tissue (Jokiel & Coles, 1990; Gleason & Wellington, 1993; Glynn, 1996; Podesta & Glynn, 1997, 2001). When the stress decreases, corals may recover, but if the stress is sustained, coral mortality can occur. Local scale bleaching may be caused by changes in environmental conditions (e.g., extreme low/high temperatures, subaerial exposure, sedimentation, contaminants, and diseases; Glynn, 1996).

A number of parameters are useful for assessing impacts of thermal stress on coral reefs at the ecoregional scale such as measurements of SSTs and SST anomalies. SST anomalies are calculated as the difference between the current sea surface temperature and a long-term average, and therefore indicate how much temperature departs from what is expected for a given time of year. These datasets can provide valuable information on the intensity and outcome of bleaching events (Donner et al., 2007; McClanahan et al., 2007; Maina et al., 2008; Wilkinson & Souter, 2008). SST projections from climate models are useful for identifying large scale (ecoregional) patterns in temperature changes. SST variability is another important factor, although determining which geographic and temporal scales of SST variability are most relevant for assessing and predicting thermal stress impacts on coral reefs is an active area of research (Castillo & Helmuth, 2005; Leichter et al., 2006; McClanahan et al., 2007; Weeks et al., 2008). The roles of thermal history and rates of temperature change in coral physiological stress, specifically how corals are affected by exposure to high-frequency variability, are not well resolved (Castillo & Helmuth, 2005). Despite these uncertainties, numerous studies highlight the importance of thermal variability in determining coral's vulnerability to bleaching (Brown et al., 2002; McClanahan & Maina, 2003; Castillo & Helmuth, 2005; McClanahan et al., 2007; Maynard et al., 2008; Weeks et al., 2008). Corals' responses to temperature variation can be complex and depends on their history of exposure and ability to acclimate or adapt to changes. Therefore, it is not yet possible to predict future coral condition at fine spatial scales.

Marine protected area (MPA) networks have been identified as an important management tool to protect coral reefs from local threats such as coastal development, overfishing, destructive fishing, and pollution (Kelleher, 1999; Lubchenco et al., 2003; Palumbi, 2003). An MPA network is a "collection of individual MPAs operating cooperatively and synergistically, at various spatial scales, and with a range of protection levels, in order to fulfill ecological aims more effectively and comprehensively than individual sites could alone" (WCPA/IUCN, 2007). Networks of strategically placed MPAs can maintain the ecological interconnectedness within and among populations and communities, thus strengthening systems by maintaining the key functions and processes (Roberts et al., 2001, 2003). However, designing MPA networks without taking climate impacts into account could result in major investments being made in areas that will not survive the next several decades (Mcleod et al., 2009); especially considering that the frequency and severity of mass bleaching events are expected to increase as SSTs continue to warm under global climate change (Donner et al., 2005; Hoegh-Guldberg et al., 2007; IPCC, 2007; Maynard et al., 2009). Further, coral reefs in the Coral Triangle are already demonstrating signs of thermal stress (Srinivasan, 2000; Sulu et al., 2000; Raymundo & Maypa, 2002; Jones et al., 2004; Penaflor et al., 2009), which is likely to increase if ocean temperatures continue to rise as expected (IPCC, 2007).

Effectively managed MPA networks that are carefully selected for resilience to climate change may help to protect reefs from mass bleaching and related mortality. Ecosystem resilience refers to the ability of an ecosystem to undergo change and yet maintain key functions and processes in the face of stresses or pressures (Holling, 1973; Nystrom & Folke, 2001; Mcleod et al., 2009). Analyses of patterns of coral vulnerability to thermal stress introduce a key data layer for designing MPA networks for building resilience to climate change. Understanding which reef areas experience greater temperature stress could help managers to design appropriate monitoring and management strategies that take into account climate change impacts. Implementation of such strategies requires an assessment of large-scale patterns (i.e., scale of MPA networks) of environmental variation and stress (McClanahan et al., 2007). For assessments at the scale of MPA networks, ecoregions provide a useful planning unit for conservation. Ecoregions are defined as large areas containing geographically distinct assemblages of species, natural communities, and environmental conditions (Spalding et al., 2007; Green & Mous, 2008), and offer the finest resolution

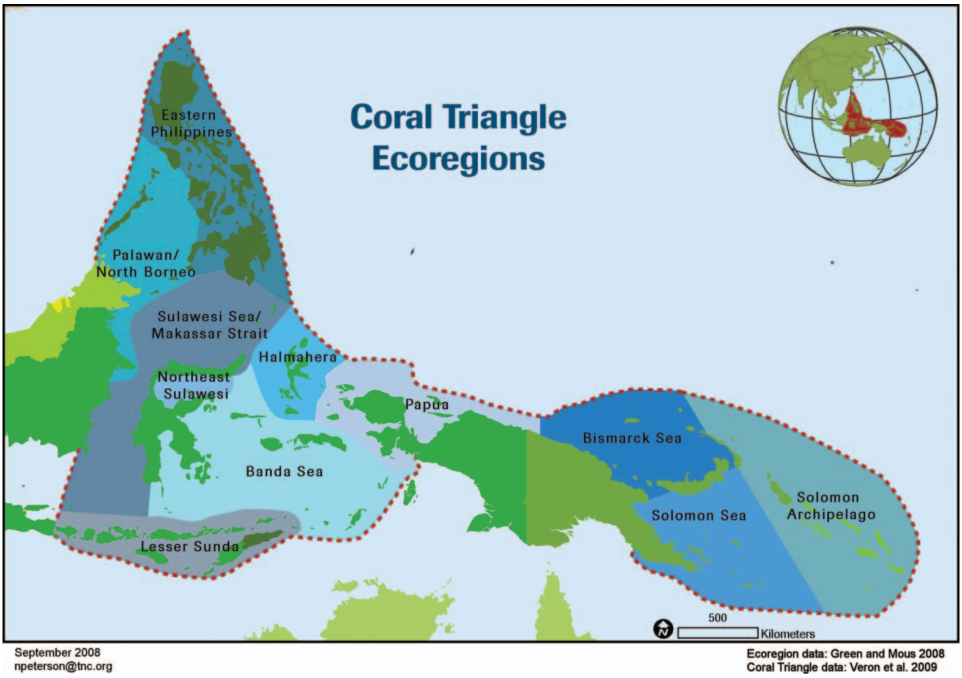

Figure 1. Ecoregions in the Coral Triangle.

planning units at which current SST data can be usefully applied. At the time of this study, eleven ecoregions were identified in the Coral Triangle (Green & Mous, 2008, Figure 1).

This study provides the first detailed analysis of the threat of warming seas and local stresses at the ecoregional scale within the Coral Triangle. An analysis of ecoregional vulnerability to thermal stress facilitates the positioning of MPA networks based on principles that relate this to historical and future patterns of thermal stress (Mcleod et al., 2009). Additionally, by presenting detailed spatial information about past thermal stress it is possible to link observed phenomena, e.g., patterns of reef decline, coral disease outbreaks, shifts in regional biodiversity, to anthropogenic warming (e.g., Selig et al., 2006). This information will help to determine how anthropogenic warming is being manifested in the Coral Triangle and through the use of climate models, how it is likely to develop over the coming centuries. Such information also can inform regional-scale policymakers and governments about probable future changes in reef functioning and valuation to aid in social adaptation planning including economic transition assistance.

Methods

Historical SST Analysis

SST data were obtained from the Coral Reef Temperature Anomaly Database (CoRTAD; Selig et al., 2010) using Pathfinder Version 5.0 data (Casey et al., 2010). The Pathfinder data have approximately 4 km resolution and are derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor series. At the time of the study, these data had the highest resolution covering the longest time period (1985–2005) of any satellite-based ocean temperature dataset (Bruno et al., 2007; Selig et al., 2010).

To identify the long-term temperature patterns over the SST dataset from 1985–2005, weekly climatologies were obtained for each 4 km grid cell. Climatologies represent the long-term average temperature that would be expected for each 4 km grid cell. The climatology was generated using a harmonic analysis procedure that fits annual and semi-annual signals to the time series of weekly SSTs at each grid cell (Selig et al., 2010). Similar approaches have been used for generating climatologies because they are more robust than simple averaging techniques, which can be more susceptible to data gaps from periods of cloudiness (Podesta et al., 1991; Mesias et al., 2007).

The climatological SST maximum, climatological SST minimum, and climatological SST ranges were calculated for all grid cells in the Coral Triangle, and for all coral reef grid cells in each ecoregion. The climatological SST maximum corresponds to the highest weekly SST value from the CoRTAD climatology. The climatological SST minimum corresponds to the coldest weekly SST value in the climatology. The climatological range (i.e., annual cycle range) identifies the expected annual variability in temperature that one would expect for a given 4 km grid cell and is computed from the difference of the maximum and minimum climatological temperature.

Degree heating weeks (DHW) were used to determine patterns of variability from 1996–2005 for the study region. DHWs are measurements that combine the intensity and duration of thermal stress in order to predict coral bleaching (Liu et al., 2003). They are calculated by taking the sum of the SST anomalies that exceed the maximum climatological temperature by more than 1°C over the previous 12 weeks. To identify patterns in thermal stress at the ecoregional scale, annual maximum DHWs were calculated for all 4 km grid cells in the Coral Triangle from 1996–2005, the annual maximum DHWs were then averaged over the 10-year time period.

A map of MPAs in the Coral Triangle was developed by combining data from global coral reef and MPA databases and from nongovernmental organizations and government agencies including Reefbase, World Conservation Monitoring Center, World Database on Protected Areas, The Nature Conservancy, and the Indonesian Government. The map of Coral Triangle ecoregions was derived from Green and Mous (2008).

Climate Projections

Coupled general circulation models (CGCMs) are commonly used to simulate the climate system and its response to past and future perturbations (IPCC-TGICA 2007). To assess changes in SST by the end of the century, an ensemble of 20 state-of-the art climate model simulations were analyzed. The simulated multi-model ensemble mean SST response to an increase of atmospheric CO_2 to 700 ppmv (parts per million by volume) by year 2100 (Figure 2) predicts relatively greater equatorial warming (Liu et al., 2005).

To determine regional patterns of thermal stress over the next century, the following CGCMs were analyzed for projections of future surface warming in the Coral Triangle: BCCR, ECHO-G, GFDL-CM2.1, IPSL, and MIROC-HIRES (see Meehl et al., 2007 for details on model performance). These models are produced by different groups, and have been spatially resolved for particular areas of interest with resolutions ranging from less than $1° \times 1°$ to nearly $5° \times 5°$. They were selected in this analysis because they represent tropical climate dynamics reasonably well in comparison to other CGCMs (Guilyardi et al., 2009). Specifically, the models used in this analysis have regional features represented such as major current patterns (e.g., Indonesia Throughflow). These models were forced using the IPCC SRES A1B greenhouse emission scenario (prescribed emissions from 2001 to 2100), as part of the Coupled Model Intercomparison Project 3 (Meehl et al., 2007). The A1B

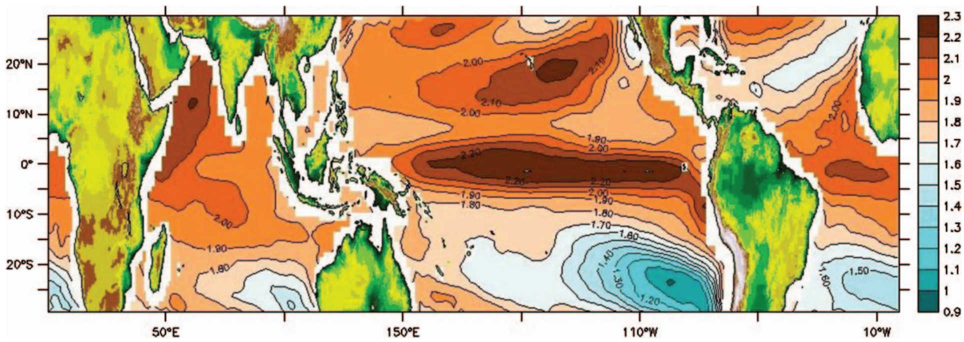

Figure 2. Multi-model ensemble mean difference of SST between 2090–2099 and 2001–2010 [°C] using 20 state-of-the-art climate model simulations forced by increasing greenhouse gas concentrations following IPCC scenario A1B.

scenario is a mid-line scenario for carbon dioxide output and economic growth (Nakicenovic et al., 2000). Recent evidence suggests that the growth rate of CO_2 emissions since 2000 was greater than for the most fossil-fuel-intensive IPCC scenario (Raupach et al., 2007), thus the results presented here are likely to represent an underestimate of future changes.

Statistical downscaling of CGCMs based on historical SST patterns can increase the resolution of coral bleaching projections, and Donner et al. (2005) developed a method of statistically interpolating SSTs from the coarse CGCM resolutions to the resolution of the satellite data. Building on Donner et al. (2005), the model results presented here were downscaled using a an Empirical Orthogonal Functions (EOF) based statistical downscaling technique using the high-resolution SST data from the AVHRR Pathfinder (4 $\times$ 4 km) and the coarse-resolution HadISST SST product ($1^\circ \times 1^\circ$). It was assumed that the statistical relationship derived from present-day observations can also be used for future climate change projections.

To test the validity of this downscaling approach, an out-of-sample prediction was made (i.e., covariance matrices were estimated using AVHRR and $1^\circ \times 1^\circ$ grid) for an independent 20-yr time period. The overall spatial correlation between the predicted SST field on the 4 $\times$ 4 km grid and the observed AVHRR data was statistically significant beyond the 95% confidence level. Based on these findings, this approach was deemed valid for the purposes of this analysis.

Thermal Stress Index

To compare thermal stress across ecoregions, a thermal stress index was developed from the results of the historical SST analysis and the climate projections by weighting and combining the following parameters: (1) mean annual maximum DHWs from 1996–2005 for reef areas; and (2) climate projections of thermal stress (decadal average of annually accumulated DHWs from 2091–2100) for reef areas. The values for the mean annual maximum DHWs from 1996–2005 were binned into low, medium, and high based on the spatial standard deviation within reef areas among the ecoregions. Low vulnerability equals <0.72 (the spatial mean, 2.53, less the standard deviation, 1.81); medium vulnerability equals 0.72–4.34; and high vulnerability equals >4.34 (the spatial mean, 2.53, plus the standard deviation, 1.81). This binning approach was also applied to the climate projections of thermal stress to calculate low (<4.60), medium (4.60–12.50), and high (>12.50) intervals

Table 1
Ecoregional comparison of thermal stress of coral reef areas in the Coral Triangle; High (H), Medium (M), and Low (L) rankings follow in brackets

Ecoregions in Coral Triangle	Historical DHWs (Decadal mean of annual maximum DHW from 1996–2005)	DHW Projections (Decadal mean of annually accumulated DHWs from 2091–2100)	Integrated thermal stress index
Northeast Sulawesi	1.84 [M]	10.43 [M]	3.90 [M]
Sulawesi Sea/Makassar	2.75 [M]	8.34 [M]	4.00 [M]
Lesser Sunda	4.01 [M]	2.81 [L]	3.65 [M]
Banda Sea	2.77 [M]	6.55 [M]	3.78 [M]
Papua	4.05 [M]	9.95 [M]	4.19 [M]
Halmahera	3.53 [M]	16.30 [H]	4.44 [H]
Solomon Sea	2.34 [M]	7.89 [M]	3.83 [M]
Bismarck Sea	4.44 [H]	11.94 [M]	4.71 [H]
Solomon Archipelago	3.59 [M]	10.85 [M]	4.21 [M]
Palawan/North Borneo	1.71 [M]	3.21 [L]	3.32 [L]
Eastern Philippines	3.48 [M]	5.78 [M]	3.80 [M]

based on the mean and standard deviation within reef areas among the ecoregions. Based on these intervals, the historical SSTs and climate projections were each reclassed in ArcGIS as a 1 (low), 2 (medium), and 3 (high) and then the re-classed layers were combined to provide an integrated thermal stress value. The integrated values were then binned into low, medium, and high based on the spatial standard deviation method described above. A thermal stress index value of 6 indicates maximum thermal stress and 2 indicates minimum thermal stress. For the integrated thermal stress index, low vulnerability equals <3.60; medium vulnerability equals 3.60–4.36, and high vulnerability equals >4.36 (Table 1).

Local Stress

Coral reef health is impacted by local stresses in addition to thermal stress. Therefore, data from the Reefs at Risk in Southeast Asia project (Burke et al., 2002) were used to compare coral reef vulnerability based on thermal stress to vulnerability based on coastal development, marine-based pollution, overfishing, destructive fishing, and sedimentation and pollution from inland sources in each ecoregion in the Coral Triangle.

Annual SST Variability

Due to the importance of background thermal variability in determining coral's vulnerability to bleaching (Brown et al., 2002; McClanahan & Maina, 2003; Castillo & Helmuth, 2005; McClanahan et al., 2007; Maynard et al., 2008; Weeks et al., 2008), the annual cycle range was calculated for all pixels in the Coral Triangle. However, because of the major uncertainties regarding how corals will respond to this variability, the annual cycle range was not included as part of the thermal stress index for this analysis.

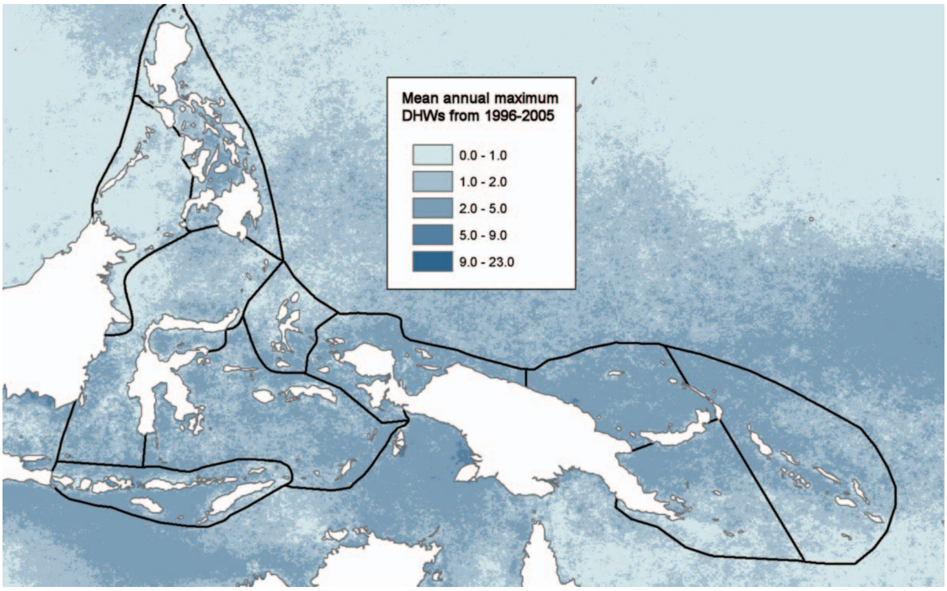

Figure 3. Mean annual maximum DHWs from 1996–2005 for the Coral Triangle based on weekly DHW data obtained from CoRTAD.

Results

Historical Patterns of Thermal Stress

Coral reef areas in the Bismarck Sea, Papua, and Lesser Sunda experienced the highest mean annual maximum DHWs over the 10 year dataset (1996–2005), followed by the Solomon Archipelago and Halmahera ecoregions (Figure 3, Table 1). Palawan/North Borneo and Northeast Sulawesi had the lowest mean annual maximum DHWs over the time series.

Climate Projections of Thermal Stress

The decadal average (2091–2100) of the annually accumulated DHWs was projected for the Coral Triangle region (Figure 4). The large area north of Sulawesi, Indonesia showing low DHWs is correlated with very deep water (Celebes Sea, >6000 m deep). The downscaling results suggest that areas further from the equator are projected to experience less thermal stress than equatorial regions. This supports findings from other studies that suggest that frequent harmful thermal stress events will occur annually after 2050 (Donner et al., 2005), if not before (Donner, 2009). The decadal average of the annually accumulated DHWs was compared for ecoregions in the Coral Triangle (Table 1). Based on these results, Halmahera and the Bismarck Sea are expected to have the highest annually accumulated DHWs, and the Lesser Sunda and Palawan/North Borneo are expected to have the lowest annually accumulated DHWs from 2091–2100.

Integration of Historical and Climate Projections of Thermal Stress

The Bismarck Sea is the ecoregion most vulnerable to thermal stress based on both historical and projections of thermal stress based on the parameters included above (i.e.,

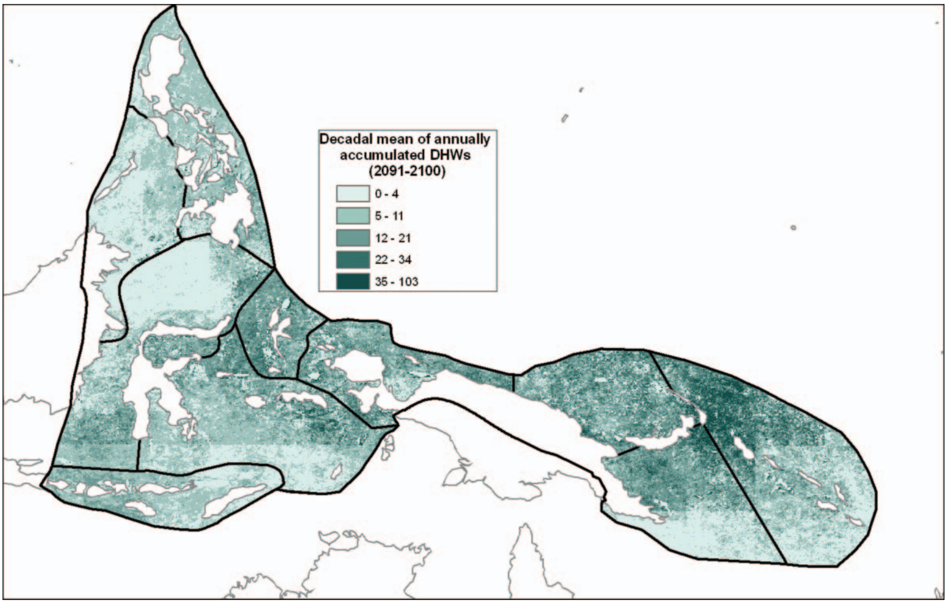

Figure 4. Projected decadal mean (2091–2100) of annually accumulated DHWs for the Coral Triangle based on CGCMs.

mean annual maximum DHWs and projections of annually accumulated DHWs), followed by Halmahera, Solomon Archipelago, and Papua. Palawan/North Borneo and the Lesser Sunda are the least vulnerable ecoregions to thermal stress based on the indicated parameters.

Annual SST Variability

Annual variability is determined from the climatological range at each grid cells (i.e., the seasonal mean swing in temperature from maximum to minimum temperatures that would be expected for a given point). Low annual temperature variability was observed throughout the West Pacific Warm Pool region, which spans the western waters of the equatorial Pacific to the eastern Indian Ocean. Annual variability was analyzed for all reef grid cells in each ecoregion from 1985–2005 (Table 2). The coral reefs in ecoregions with the largest mean climatological range of SSTs were the Solomon Sea, Lesser Sunda, Banda Sea, and the Eastern Philippines. The ecoregions that experienced the lowest mean climatological range are the Bismarck Sea and Northeast Sulawesi (Figure 5).

Patterns of Local Stress

Figure 6 shows the vulnerability of coral reefs by ecoregion in the Coral Triangle to local stresses (coastal development, marine-based pollution, overexploitation of marine resources, inland pollution, and erosion) (Burke et al., 2002). Coral reefs in the Solomon Archipelago were the least vulnerable to local stresses based on the Reefs at Risk in Southeast Asia data, followed by the Solomon Sea, and the Bismarck Sea. Reefs in the Eastern Philippines and Lesser Sunda were the most vulnerable to local stresses.

Table 2
Ecoregional comparison of annual variability of coral reef areas in the Coral Triangle, High (H), Medium (M), and Low (L) rankings follow in brackets

Ecoregions in Coral Triangle	Range of annual cycle (climatological SST range from 1985–2005; in °C) for reef areas
Northeast Sulawesi	1.19 [L]
Sulawesi Sea/Makassar	1.72 [M]
Lesser Sunda	2.87 [H]
Banda Sea	2.83 [M]
Papua	1.30 [M]
Halmahera	1.45 [M]
Solomon Sea	3.29 [H]
Bismarck Sea	0.84 [L]
Solomon Archipelago	1.65 [M]
Palawan/North Borneo	2.45 [M]
Eastern Philippines	2.83 [M]

Discussion

Uncertainties in Climate Modeling

Combining historical SST data with climate projections enhances the understanding of thermal stress impacts on coral reef systems. However, the use of climate models introduces

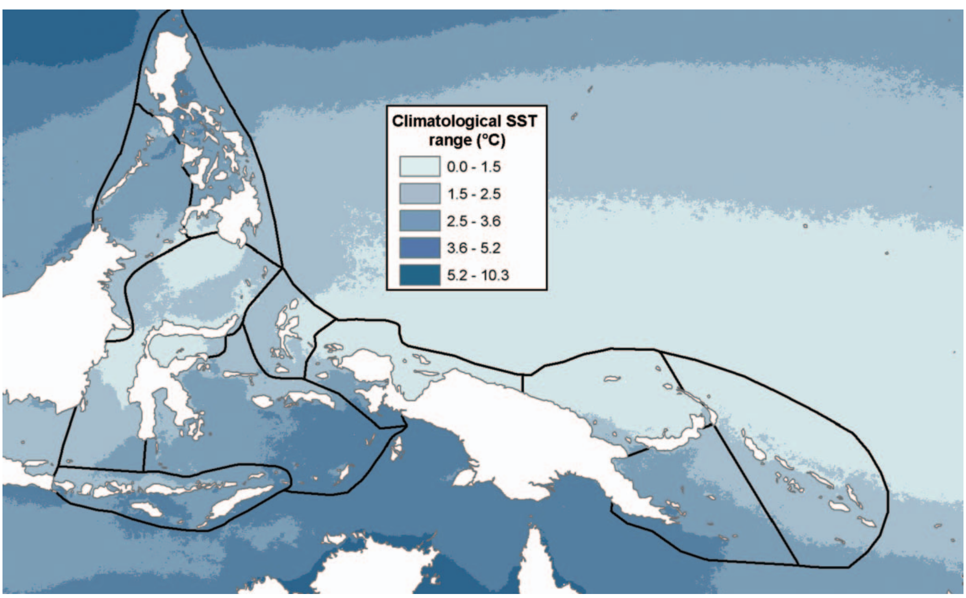

Figure 5. Climatological SST range (0–10.3°C) for the Coral Triangle region from 1985–2005 based on weekly climatologies obtained from CoRTAD.

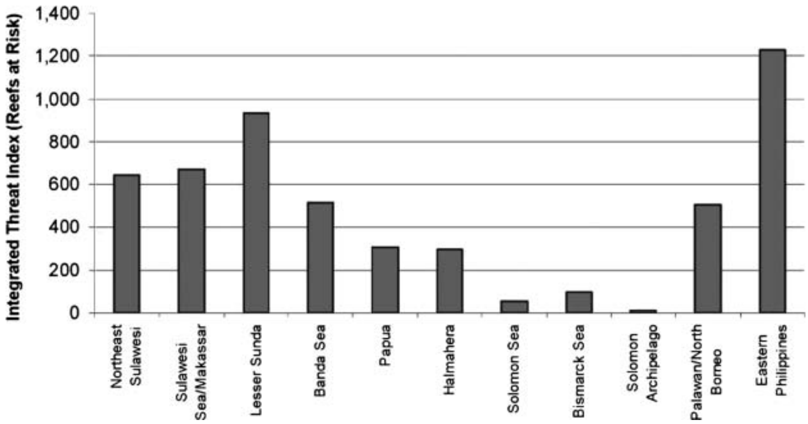

Figure 6. Integrated local threats (coastal development, marine-based pollution, overexploitation of marine resources, inland pollution and erosion; Burke et al., 2002) by coral reef area for ecoregions in the Coral Triangle.

uncertainty because certain simplifying assumptions are unavoidable when building such models (Reichler & Kim, 2008). CGCMs have limitations especially in the tropical oceans (Shukla et al., 2009). For example, they diverge strongly in the Western Tropical Pacific due to a variety of factors including the extremely complex current patterns and bathymetry and the delicate heat balance between atmospheric and oceanic transports. Many models have a tendency to produce a double Inter-Tropical Convergence Zone (ITCZ), poorly represent the annual cycle of the SSTs in the Tropics, and misrepresent the amplitude, pattern, and frequency of ENSO-like variability (Mechoso et al., 1995; Delecluse et al., 1998; Gualdi et al., 2003). To address the inconsistent predictions resulting from the use of different climate models, multi-model ensemble means (averaging across the simulations of models using equal weights) provide an effective way of improving the outcome of climate simulations and usually outperform a single model (Reichler & Kim, 2008). Multi-model ensemble means are important for long-term climate change projections, and many climate change estimates included in the International Panel on Climate Change (IPCC) 4th Assessment report are based on the ensemble simulations (IPCC, 2007). Due to the advantages of a multi-model ensemble mean approach, this study used this method.

Finally, the scale of most CGCMs is several hundred kilometers, so models do not properly resolve fine-scale features (e.g., island wake effects, Eden & Timmermann, 2004) in the Coral Triangle region. Mixing processes and regional upwelling due to island-induced wind-stress curl patterns are not captured in the models used in this analysis due to their coarse resolution, and these processes may be important for ameliorating thermal stress on coral reefs at the local scale by cooling surface waters (Goreau et al., 2000; Salm et al., 2006).

However, statistical downscaling can provide a valuable technique to increase the resolution of CGCM climate projections (Murphy, 1999), which is necessary to evaluate regional impacts of climate change. It is important to note that although downscaled projections are appropriate for regional planning and analyses (i.e., planning within or between ecoregions and for MPA networks), they are not appropriate for individual MPAs. As higher resolution data becomes available, future studies may be able to provide improved estimates of coral reef vulnerability to inform MPA zoning and management.

Uncertainties in Coral Reef Systems

Additional uncertainties exist due to the physical and biological complexity of coral reefs systems. Physical complexities include currents, tides, bathymetry, depth, and water quality, which can affect temperature and light, and thus the vulnerability of corals to bleaching. Biological complexities include the variable response of coral species to bleaching, and the interaction between corals and zooxanthellae (which themselves are differentially susceptible to thermal stress), interactions with pathogens, and acclimatization (Van Oppen & Lough, 2008; LaJeunesse et al., 2009). Even if corals are able to adapt to increasing SSTs, it is uncertain whether their adaptation could keep pace with the rate and scale of future climate change (Baker et al., 2004; Donner et al., 2005; Hoegh-Guldberg et al., 2007). Uncertainties also exist with respect to how corals will cope with the potentially synergistic impacts of climate change (e.g., increasing SSTs, changing current patterns, ocean acidification, and sea-level rise) and other anthropogenic stresses.

The understanding of how background variability in seawater temperature and frequency of thermal anomalies affect corals is limited (Berkelmans et al., 2004; Leichter et al., 2006; Castillo & Helmuth, 2005). Corals that experience higher background variability in maximum annual SST and more frequent thermal anomalies may develop a higher thermal resistance (Brown et al., 2002; McClanahan & Maina, 2003; Castillo & Helmuth, 2005; McClanahan et al., 2007; Maynard et al., 2008; Weeks et al., 2008), but this is not a universal pattern (Glynn & D'Croz, 1990). Variability in seawater temperature occurs across broad spatial and temporal scales (Leichter et al., 2006). Local scale thermal variability is unpredictable due to the influences of water column stratification, alongshore currents and their interaction with the shelf break, and local topography, and is not well captured in SST data (Leichter et al., 2006). Thermal stress and bleaching can also be highly heterogeneous across vertical (depth) and horizontal temperature gradients (Brown, 1997; West & Salm, 2003) and at the small scales of individual coral colonies (Edmunds, 1994). Quantifying *in situ* thermal variability will help to link large-scale patterns that are detectable through remote sensing and modeling techniques with physiological processes at the scale of individual reef organisms (Leichter et al., 2006). Such research is necessary to improve the use of remote sensing data to inform bleaching vulnerability analyses. Predicting bleaching at regional scales, therefore, requires an understanding of the spatial and temporal variability of temperature in different regions of the reef and how physiological responses by corals to temperature are related to thermal history (West & Salm, 2003; Helmuth et al., 2005).

Despite the uncertainties in climate model projections and the associated ecological responses of coral reef systems, conservation management and planning decisions must be made. To address these uncertainties, an adaptive management approach is necessary. Such an approach promotes flexible decision-making and supports managers in taking immediate actions using the best available information while allowing for refinements through an iterative learning process (Marshall & Schuttenberg, 2006; CCSP, 2008).

MPA Networks as a Tool to Address Climate Change Impacts on Coral Reefs

MPAs have been identified as one of the most effective tools for conserving reefs and related marine systems (Hughes et al., 2003; Bellwood et al., 2004; Selig & Bruno, 2010), however they do not necessarily provide protection from thermal effects (Graham et al., 2008). Therefore, research is essential that helps to inform the selection of coral reef areas that may be resilient to damaging thermal impacts (West & Salm, 2003; McClanahan et al., 2007; Maina et al., 2008). Strategically placed MPAs in networks could maintain ecosystem resilience by protecting the ecological interconnectedness between and within ecosystems

(Salm et al., 2006). Specifically, MPA networks could allow species and organisms to move with changing conditions, particularly along elevation, longitudinal, bathymetric, or climatological gradients (Hansen et al., 2010). Networks of MPAs, including no-take areas, can protect coral reefs from human stresses, increase fish biomass and variability both inside and outside the boundaries of no-take areas (Halpern, 2003), and permit critical functional groups to persist, thus contributing to local ecosystem resilience (Bellwood et al., 2004; Hughes et al., 2005; Harborne et al., 2006). The ideal MPA network would be designed for resilience to climate change (Mcleod et al., 2009) and integrated with coastal management regimes to enable effective control of external threats (e.g., threats originating upstream) and to maintain high water quality (e.g., Done & Reichelt, 1998).

Through a multilateral partnership called the *Coral Triangle Initiative* (CTI), the six governments of the Coral Triangle countries have committed to protect the region's marine resources by establishing resilient networks of MPAs. Currently, less than 5% of all ecoregions, including both reef and non-reef areas, are protected in MPAs and more will need to be established and incorporated in networks. This will require a process of careful planning and prioritization that can be informed by the temperature projections described herein, because such analyses that emphasize regional and historical variability are likely to predict more accurately coral reef vulnerability to thermal stress (McClanahan et al., 2007).

Coral Reef Vulnerability to Thermal and Local Stress and Management Recommendations

Coral reef vulnerability is defined for each ecoregion by both thermal stress (weighted thermal index described above) and human activities (combination of coastal development, marine-based pollution, overexploitation of marine resources, and inland pollution and erosion; Burke et al. 2002) (Figure 7). Recognizing that all MPA networks require the

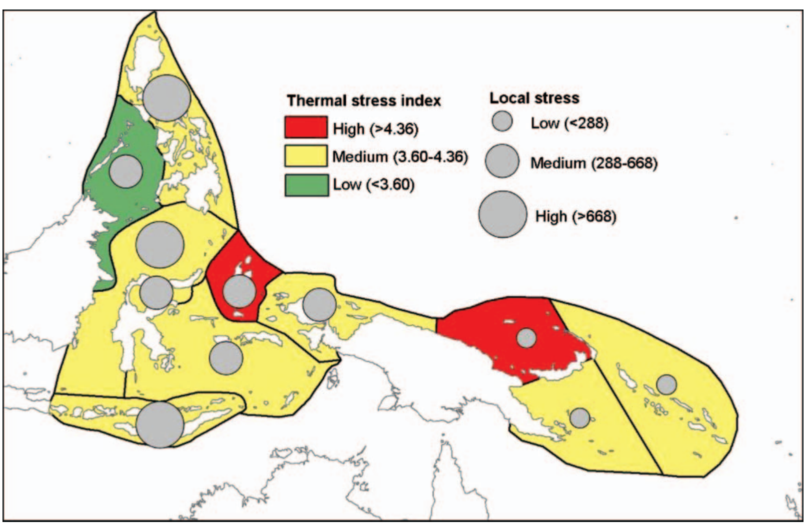

Figure 7. Assessment of vulnerability to thermal stress and local stress for coral reef area by ecoregion in the Coral Triangle. Thermal stress is estimated as the combination of historical thermal stress and projected thermal stress (Table 1), and local stress is the combination of coastal development, marine-based pollution, overexploitation of marine resources, inland pollution and erosion (from Burke et al., 2002).

application of generic design and management principles (Roberts et al., 2003; West & Salm, 2003; Mcleod et al., 2009), Table 3 identifies additional recommendations at the ecoregional level based on its specific vulnerability to thermal stress and human activities. However, within ecoregions, there will be varying levels of thermal or anthropogenic stress which will influence whether greater emphasis is placed on managing one or the other. Therefore, these recommendations are intended as broad guidelines to inform management decisions at the ecoregional scale. As a general principle, all MPA networks need to be embedded into broader frameworks, such as integrated coastal management (ICM), to address external stresses on the reefs inside MPAs and contribute to their resilience (Salm et al., 2006).

Relatively Low Coral Reef Vulnerability to Thermal Stress and Human Activities

Regions with relatively low vulnerability to thermal stress and local stress (e.g., Palawan/North Borneo, Solomon Sea) should be prioritized for implementation of resilient MPA networks if they are reinforced by management strategies that address human impacts outside of MPAs (e.g., overfishing reduction of runoff from poor land use practices). For attributes of resilient networks of MPAs, see West & Salm, 2003; Salm et al., 2006; Game et al., 2008a; Mcleod et al., 2009. Areas with low vulnerability to both thermal and local stresses should be considered good candidates for new MPA establishment.

Relatively High Coral Reef Vulnerability to Thermal Stress and Human Activities

In reef areas with moderately high vulnerability to thermal stress and local impacts (e.g., Northeast Sulawesi, Sulawesi Sea/Makassar), it is critical to reduce local stresses (Carilli et al., 2009) through effective management and rigorously apply principles for designing resilient networks of MPAs (Roberts et al., 2003; West & Salm, 2003; Salm et al., 2006; Game et al., 2008a; Mcleod et al., 2009). Strategies that facilitate coral reef recovery following bleaching events (Marshall & Schuttenberg, 2006) are likely to include the maintenance of herbivores (Mumby et al., 2006; Hughes et al., 2007), water quality (McCook, 1999; Wolanski et al., 2003; Fabricius et al., 2005), and access to coral recruits (Golbuu et al., 2007), which is often a function of the proximity of damaged reefs to healthy coral populations (Salm et al., 2006; Hoegh-Guldberg et al., 2009). Such strategies should consider restoration of damaged areas in high priority reef areas, especially when these are important to facilitate connectivity among MPAs in the network. It is also important to monitor the cumulative effects of multiple stressors, both local and climatic, in these areas. This will help managers develop an understanding of how corals respond to synergistic impacts, their survival prospects, and how to identify appropriate management responses.

High Coral Reef Vulnerability to Thermal Stress and Low Vulnerability to Human Activities

In regions with high vulnerability to thermal stress, but low vulnerability to human activities (e.g., Bismarck Sea, Halmahera, Solomon Archipelago), management strategies should focus on the rigorous application of resilience principles to MPA network design, especially the identification and protection of bleaching resistant coral communities (Salm et al., 2006; Mcleod et al., 2009). These areas are important test sites for monitoring the effects of climate change on coral reefs, because the effects of climate change can be studied with minimal confounding effects from human stresses. Ecoregions with high vulnerability to thermal

Table 3
Summary of coral reef vulnerability to thermal and anthropogenic stress by ecoregion in the Coral Triangle and management recommendations

Ecoregions	Vulnerability to thermal stress	Vulnerability to human activities	Management recommendations
Palawan/North Borneo, Solomon Sea	low to medium	low to medium	• Ensure adequate representation within these areas in MPA networks • Address human activities (e.g., overfishing, pollution, coastal development) outside of MPAs that may impact these areas (e.g., through ICM)
Eastern Philippines, Lesser Sunda, Sulawesi Sea/Makassar, Banda Sea, Papua, Northeast Sulawesi	medium	medium to high	• Reduce local stresses (e.g., overfishing, destructive fishing, reduced water quality, recreational use) in MPAs • Address external anthropogenic stresses (e.g., inland erosion, destructive land use practices) that may impact coral reef systems in MPAs (e.g., through ICM) • Apply resilience principles rigorously to MPA network design and management (Mcleod et al., 2009) • Monitor cumulative effects of multiple stressors, both anthropogenic and climatic • Consider restoration in high priority reef areas
Bismarck Sea, Halmahera, Solomon Archipelago	high	low	• Apply resilience principles rigorously to MPA network design and management (Mcleod et al., 2009) • Prioritize sites in this ecoregion for monitoring coral response to increasing SSTs (e.g., recovery following bleaching, coral adaptation potential) • Prioritize research in this ecoregion for testing and refinement of resilience principles governing MPA network design and management (Mcleod et al., 2009; Green et al., 2009)

stress are important areas to monitor coral reef response to increasing SSTs because they may provide insights into how presently less vulnerable areas will respond in the future as sea temperatures warm. By monitoring coral reefs' response to bleaching events, researchers can improve the science underlying coral recovery patterns following bleaching events and assess coral adaptation potential. Therefore, research should be prioritized in reefs with high vulnerability to thermal stress and low vulnerability to human activities for the testing and refinement of resilience principles (e.g., Obura & Grimsdith, 2009) governing MPA network design and management (Green et al., 2009; Mcleod et al., 2009). It is important to anticipate potential anthropogenic stresses to the coral reef systems in MPAs resulting from distant activities and prepare for these. ICM provides a means to integrate land use practices with coral reef management and minimize negative impacts of development.

Management Implications of Temperature Variability Within Ecoregions

Ecoregions with a wide range in annual temperature (e.g., Papua with 4.5°C range in the SST climatology), may have corals that are acclimated to deal with thermal stress. In these areas, it is important to monitor the impacts of coral bleaching events and recovery following these events to determine if some coral species or reef areas are more resistant or resilient to climate change impacts. Coral communities that either resist bleaching or recover rapidly after disturbance are priorities for protection in MPAs because they provide essential sources of larvae to enhance the replenishment and recovery of reefs damaged by bleaching, hurricanes, or other events (West & Salm, 2003).

Ecoregions with a narrow range in annual temperature (e.g., Halmahera with 1.6°C range in the SST climatology) may have corals that are more vulnerable to bleaching because the corals are not acclimated to thermal stress. In these areas, multiple MPAs might be needed to create redundancy and spread the risk of coral mortality caused by a bleaching event, because if one reef area is destroyed, others may remain to provide the larvae required to replenish these areas (Salm et al., 2006). Ecoregions may have physical or oceanographic factors which either ameliorate increasing SSTs (West & Salm, 2003; Salm et al., 2006) or help maintain low ranges in annual temperature. For example, low annual temperature variability is observed throughout the West Pacific Warm Pool region (annual range of ∼0.5°C) which spans the western waters of the equatorial Pacific to the eastern Indian Ocean (includes Halmahera, Papua, Bismarck Sea, and Solomon Archipelago ecoregions). At a finer scale, physical factors can help buffer increases in SSTs such as local upwellings, which bring cold deep water to cool the warmer surface waters (West & Salm, 2003; Salm et al., 2006). It should be noted that thermal variability is only one factor, and other important biological and ecological criteria must be considered in MPA zoning and network design (Roberts et al., 2003; Mcleod et al., 2009).

Conclusion

All the ecoregions within the Coral Triangle are priorities for conservation investments (Hoegh-Guldberg et al., 2009; Veron et al., 2009). However, due to the large reef area, low mean annual maximum DHWs, moderate local threats, and lower DHW projections over the next century, the results of this analysis suggest that the Palawan/North Borneo ecoregion may be a good area for future investment in coral reef conservation, assuming that protection is directed at low risk areas (Game et al., 2008b). Coral reef areas in the Solomon Sea and Banda ecoregion may also be good choices, as these areas have moderate mean annual maximum DHWs, moderately low local stresses, and lower DHW projections by 2100 than surrounding ecoregions. Furthermore, regions with high thermal variability (such as the Lesser Sunda and Solomon Sea ecoregions) offer the opportunity to monitor the effects of thermal variability on coral bleaching at broad scales. It is important to note that conservation strategies will need to vary according to the relative vulnerability of the area to local versus climate stresses. Also, in addition to thermal stress, thermal variability, and local stress, other critical factors that affect coral reef vulnerability and appropriate management strategies include ocean acidification impacts (Kleypas et al., 2006; Guinotte & Buddemeier, 2008; Mcleod et al., 2008), surface currents, wind velocity, UV radiation, photosynthetically active radiation (PAR), and chlorophyll-a concentration (McClanahan et al., 2007; Maina et al., 2008).

Despite the deterioration of coastal ecosystems in the Coral Triangle due to human activities (e.g., coastal deforestation, declining water quality, overfishing, destructive fishing, and pollution) and climate change impacts (e.g., mass bleaching events, coastal flooding) many coral reefs areas in this region show significant ecological resilience (Hoegh-Guldberg et al., 2009). Factors such as high biodiversity combined with high levels of recruitment and fast rates of growth and recovery are likely to help coral reefs in the Coral Triangle survive climate change longer than areas that lack these attributes. Reef areas in the region that exhibit slower rates of change in temperature and acidity may provide refuges and larval sources to help damaged areas recover following mass bleaching events. Ensuring that these refuges are included in MPAs is a priority to protect the future of coral reefs in the region. Climate change brings new challenges to coral reef managers in the Coral Triangle and beyond; these are in addition to the already significant management challenges that exist. The ability of coral reefs systems to cope with climate change threats will be enhanced by mitigation measures that help slow the rate of greenhouse gas emissions, the design and management of resilient MPA networks that incorporate historical SST patterns and projections, and embedding these in ICM frameworks.

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