

Impact of Global Warming on Coral Reefs

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Received: 7 March 2011, Revised: 23 June 2011, Accepted: 29 June 2011

Abstract

In this paper, we review coral reef responses to climate variability and discuss the possible mechanisms by which climate impacts the coral reef ecosystem. Effects of oceanographic variables such as sea temperature, turbulence, salinity, and nutrients on the coral reef are discussed in terms of their influence on coral growth, reproduction, mortality, acclimation and adaptation. Organisms tend to be limited to specific thermal ranges with experimental findings showing that sufficient oxygen supply by ventilation and circulation only occurs within these ranges. Indirect effects of climate change on the food web are also discussed. Further integrative studies are required to improve our knowledge of the processes linking coral reef responses to future climate change scenarios.

Keywords: Coral reef, climate change, sea temperature, coral bleaching

Introduction

Coral reefs are marine ecosystems of great biodiversity—the “rainforests of the sea”. Coral reefs are found predominantly in the tropics, often in areas of great poverty, but also exist in other specialised locations, for example Bermuda [1,2]. Coral reefs provide an environment in which one-third of all marine fish species and tens of thousands of other species are found, and from which six million tons of fish are caught annually. The reefs act as barriers to wave action and storms by reducing the incident wave energy through wave reflection, dissipation and shoaling, protecting the land and an estimated half a billion people who live within 100 kms of the nearest reefs.

Coral is directly related to the acquisition of dinoflagellate endosymbionts that enable the symbiosis to survive in oligotrophic and high solar irradiance habitats. Coral acquires the majority of its energetic and nutrient requirements by two mechanisms: photosynthesis by its zooxanthellae and heterotrophy or direct ingestion of

zooplankton and other organic particles in water by the cnidarian host [3]. Its growth and survival are related to fluctuations in physio-chemical parameters such as light [4-6], temperature [4,7], water turbulence [8], degree of sedimentation [9], water pH, water turbidity, calcium carbonate saturation, salinity and nutrients [4]. These variables influence the physiological processes of photosynthesis and calcification as well as coral survival [4]. Coral calcification rates and extension rates are highly correlated with sea surface temperature and to a lesser extent with incoming solar radiation [4,10-12].

Climate change-related coral bleaching currently constitutes the greatest threat to coral reefs the causes and consequences of which are reviewed by a number of authors in [13-15]. Substantial loss in coral cover, due to anomalously warm water, has occurred throughout the world's coral reefs during the past three decades [16-23]. Within this paper, we briefly review various processes through which climate influences the

coral reef ecosystem. We then discuss what is needed to improve our knowledge of the mechanisms linking climate to coral reef change. Finally, based on our present understanding, we comment upon our ability to predict coral reef responses to future climate change scenarios.

Factors affecting coral responses

Coral reef ecosystems are particularly sensitive to climate induced changes in their physical environment [24]. In this section, we provide examples of coral reef impacts mostly in response to climate variability and the possible mechanisms by which the response is generated. Major physical factors affecting coral responses are temperature, irradiance, water flow, salinity, nutrient, and sedimentation (**Table 1**). An increase in temperature and irradiance and a decrease in salinity tend to increase the coral bleaching events and coral mortality (**Table 1**). Increases in water flow can lessen the effects of high temperature, irradiance and salinity, and sedimentation. High levels of nutrients and sedimentation tend to intensify changes in the community structure. The complex interplay of all these physical factors determines the overall effect of climate on the coral reef ecosystem. However, changes in all these factors result in a weakening of the coral reef in general and eventually lead to the destruction of coral ecosystems. Many factors contribute to the

weakening of coral reef such as decrease in host resistance, coral reproduction, offspring settlement, reef growth and photosynthesis, and increase in changes in coral community as well as competitor coral growth (**Table 1**).

Bleaching weakens corals and, in combination with other secondary stressors, may lead to a series of problems that result in an overall decline in coral health, including increased incidence of disease [24,29]. Coral diseases have been observed to correlate with bleaching and/or heat stress. As corals undergo thermal stress [4,24] bacteria can increase in virulence and antibiotic resistance [24,49-51]. One of the most significant changes for coral reefs along the Florida Keys Reef tract and in the Caribbean generally has been the emergence of diseases and the potential relationship to global climate change [4,52-54].

In the 1990s, it appeared that a suite of new coral diseases had emerged. Some of these diseases are associated with elevated nutrients, either from agricultural runoff or from human sewage [4]. Currently, there are nearly 30 proposed names for coral diseases, although most have not been properly classified and many may refer to the same or similar diseases. The status of the new diseases is confused [29, 52]. The better described diseases of scleractinian corals are shown in **Table 2**. Most coral diseases are caused by bacterial infection (**Table 2**).

Table 1 Physical factors affecting coral responses.

| Physical factors | Coral responses |
|------------------|--|
| Temperature | <ul style="list-style-type: none"> • increase coral bleaching events [25-28] • increase coral mortality [29] • increase changes in community structure [13] • decrease host resistance [29,30] • decrease coral reproduction [13, 31] |
| Irradiance | <ul style="list-style-type: none"> • increase coral bleaching events [32] • decrease offspring settlement [32] |
| Water flow | <ul style="list-style-type: none"> • decrease coral bleaching events [33-35] • increase coral recovering rates [35,36] |
| Salinity | <ul style="list-style-type: none"> • increase coral bleaching events [16, 37] • increase coral mortality [37-39] |
| Nutrient | <ul style="list-style-type: none"> • increase changes in community structure [40] • decrease coral reproduction [41] • suppress and extinguish reef growth [42-44] |
| Sedimentation | <ul style="list-style-type: none"> • increase coral mortality [45] • increase stimulation of competitor coral growth [9] • increase changes in coral reef community [46-48] • decrease photosynthesis [45] |

Table 2 Disease, microbial type, coral species, location, time of first documentation of scleractinian coral.

| Diseases | Microbial type | Coral species | Location | First documented | References |
|--------------------------|---|--|---|-------------------------|---------------|
| Black band | Microbial consortium of cyanobacteria and sulfide-oxidising bacteria (<i>Phormidium corallyticum</i>) | <i>Montastrea annularis</i> , <i>Montastrea cavernosa</i> <i>Diploria strigosa</i> | Caribbean Indo-Pacific | 1975 | [30,52,54-55] |
| Black band | Microbial consortium of cyanobacteria and sulfide-oxidising bacteria (<i>Phormidium corallyticum</i>) | <i>Montipora aequituberculata</i> | Magnetic Island, Australia | Summer 2001/2002 | [29] |
| White band type I & II | Gram-negative bacterium (<i>Pseudomonas</i> sp.) | <i>Acropora cervicornis</i> , <i>Acropora palmata</i> | Caribbean | 1980s | [14,30,56-57] |
| White plague type I & II | Bacterium (<i>Aurantimonas corallicida</i>) | <i>Dichocoenia stolesi</i> | Caribbean Indo-Pacific | Late 1970s mid-1990s | [30,58] |
| White pox | Enteric bacterium (<i>Seerattia marcescens</i>) | <i>Acropora palmate</i> | Florida Keys National Marine Sanctuary | 1996 | [59] |
| Yellow blotch | Bacterium (<i>Vibrio</i> spp.) | <i>Montipora faveolata</i> | Eastern Caribbean region | 1994 | [60] |

In addition to killing corals, increased temperature affects coral populations by reducing reproductive capacity [31]. In a comparison of the fecundity of 200 bleached and unbleached colonies of reef-flat corals at Heron Island after the 1998 bleaching event, it was found that bleaching reduced reproductive activity in most reef-flat species i.e. *Symphyllia* sp., *Montipora* sp., *Acropora humilis*, *Favia* sp., *Goniastrea* sp., and *Platygyra daedalea* contained no eggs at all [13,61].

Although mortality might not always eventuate, reef-building corals that undergo bleaching have reduced growth, calcification and repair capabilities following bleaching [3,62-64]. The primary effect of increased temperature is the loss of zooxanthellae from reef-building corals and other symbiotic invertebrates. As zooxanthellae are the principal engine of primary production in these organisms, the rate of photosynthetic productivity of bleached reef-building corals and other symbiotic organisms decreases dramatically [65]. The reduced ability to grow and calcify may also translate into a reduced ability to compete for space with other organisms such as macro-algae, which may eventually eliminate reef-building corals from particular reefs. Changes in community structure have occurred in coral reefs in the Caribbean and eastern Pacific [13,47,62,66]. In each case, the community structure has moved away from communities dominated by reef-

building corals to communities dominated by macro-algae.

The loss of vitality of reef-building corals is also likely to influence how coral reef ecosystems respond in the face of other anthropogenic influences. Factors such as eutrophication, increased sedimentation, tourism and destructive fishing practices may interact with global climate change to produce new and potent synergistic effects [13,67-68]. Changes in sea surface temperature can combine with other factors to completely destroy reefs (e.g. [69]) including those in the Caribbean (e.g. [61]). Increased rates of coral disease [56], the mass mortality of diademed sea urchins [70] and outbreaks of predators such as crown-of-thorns starfish (*Acanthaster planci* [54]) may also be linked to reef disturbances related to increased sea temperatures. Influences of increased temperature may be subtle and involve such things as the temperature related death of coral 'crustacean guards' normally protecting corals from predation by starfish, [62] or more rapid development of larval crown-of-thorns starfish which is temperature-dependent [13,71].

Coral bleaching in bio-geographical scales

Results from previous studies [13,24,55,72-74] of bio-geographical scales suggest that many coral species can be found under conditions that far exceed the thermal tolerances of the same coral species at other locations [75,76]. Bleaching temperature thresholds vary locally from 28.0-35.5

°C. Examples of bleaching threshold are at Rogotonga (28.3 °C) [13], Jamaica and Tahiti (29.2 °C) [13], Caribbean (30.5 °C) [24,55,72], Great Barrier Reef (30.8 °C) [24,55,72] and Arabian Gulf (35.5 °C) [24,73-74]. Conditions that result in coral mortality in some regions have no effect on corals in others.

Over the last three decades, coral bleaching events have been reported from every region that supports coral reefs and no region of the world's tropical and subtropical seas appears safe from coral bleaching events (**Figure 1, 2a-d**). Most bleaching events are reported from the Great Barrier Reef, Moorea, and the Caribbean (**Figure 1**) where there are likely to be more observers. The fact that coral bleaching events in some locations are not reported may be due to an absence of observers rather than an absence of bleaching events [2 are not reported 4].

The mass coral bleaching event of 1998 is considered to be the most severe on record [25,77], with bleaching affecting every geographical coral-reef realm in the world (**Figure 2a-d**). This was

the sixth major episode of coral bleaching events since 1979 to affect coral reefs across a significant portion of the world's oceans. Most evidence indicates that elevated temperature is the cause of mass bleaching events. Increasing water temperature rapidly causes zooxanthellae to leave the tissues of reef-building corals and other invertebrates resulting in a reduced number of zooxanthellae in the tissues of the host [65,78-81].

Strong bleaching episodes coincide with periods of high SST and are associated with disturbances in the El Niño-Southern Oscillation (ENSO). Most strong bleaching episodes occur during strong El Niño periods, when the Southern Oscillation Index (SOI) is negative (< -5). In 1997 - 1998, the most extensive and intense bleaching event on record coincided with (by some indices) the strongest ENSO disturbance on record [13,82]. For the first time, coral reefs in every region of the world recorded severe bleaching events (**Figure 2a-b**). In some places (e.g. Singapore, [77]), bleaching was recorded for the first time.

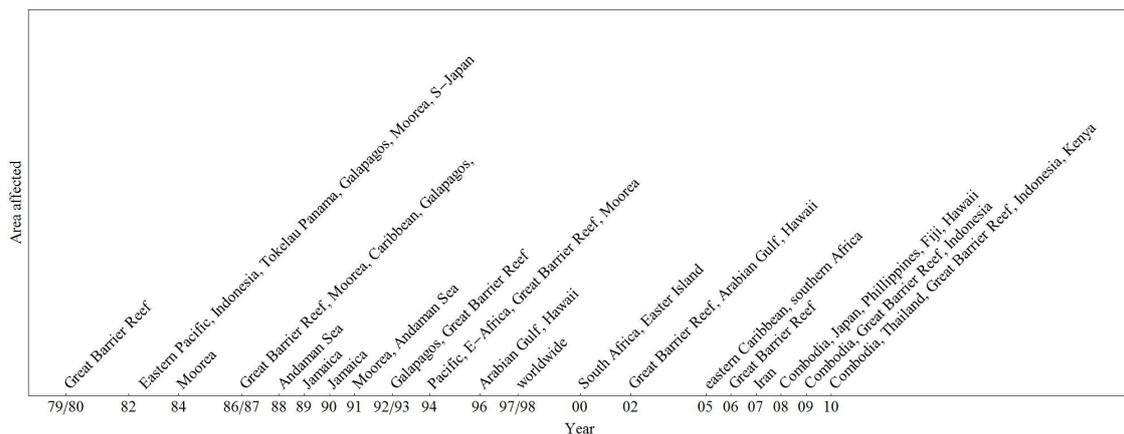
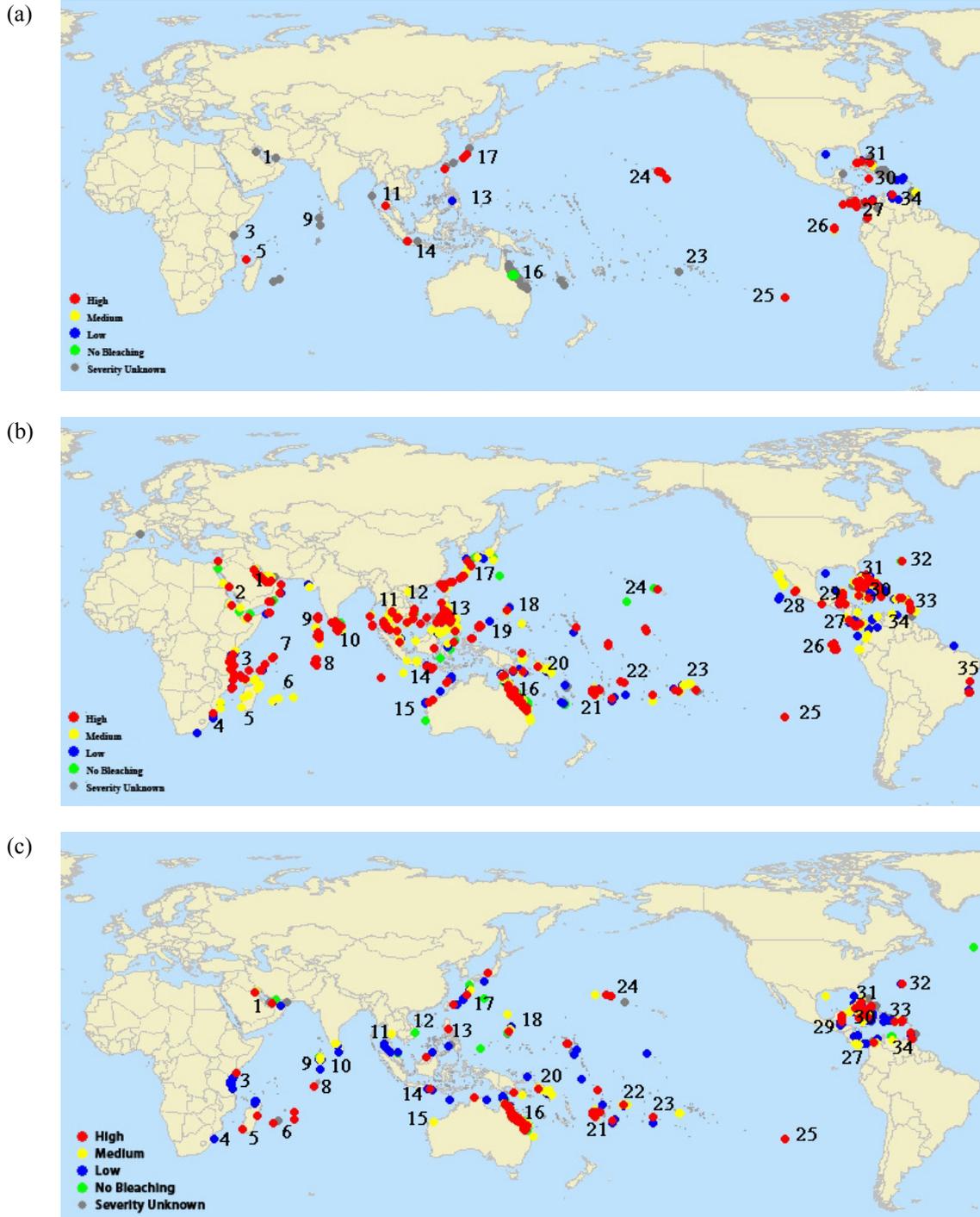


Figure 1 Coral bleaching events reported during 1979 - 2010.



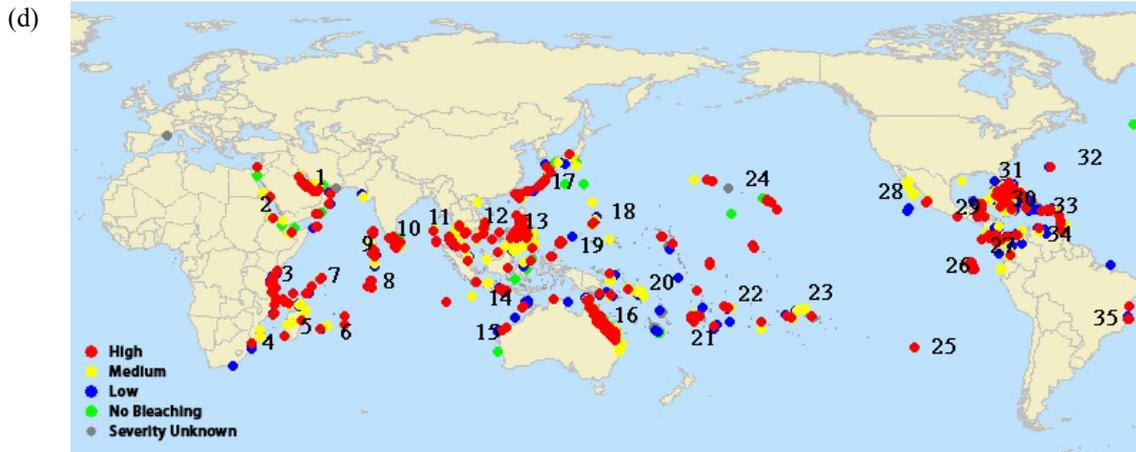


Figure 2 Incidence of coral reef bleaching on a worldwide scale: location of bleaching reports during (a) 1979 - 1990, (b) 1990 - 2000, (c) 2000 - 2010 and (d) 1979 - 2010. Maps are from ReefBase, www.reefbase.org: 1, Arabian Gulf (United Arab Emirates, Qatar, Iran); 2, Red Sea; 3, east Africa; 4, southern Africa (Mozambique, South Africa); 5, Madagascar; 6, Mauritius, Reunion; 7, Seychelles; 8, Chagos; 9, Maldives; 10, Sri Lanka/southern India; 11, Andaman Sea (Andamans, Thailand, Malaysia); 12, South China Sea (Vietnam, Paracel Islands); 13, Philippines; 14, Indonesia; 15, western Australia; 16, Great Barrier Reef; 17, Ryukyu Islands; 18, Mariana Islands; 19, Palau; 20, Papua New Guinea, Vanuatu; 21, Fiji; 22, Samoa; 23, French Polynesia (including Moorea); 24, Hawaiian Islands; 25, Easter Island; 26, Galapagos Islands; 27, equatorial eastern Pacific (Costa Rica, Cocos Island, Panama, Colombia, Ecuador); 28, subtropical eastern Pacific (Mexico); 29, Mesoamerican reef system (Mexico, Belize, Honduras, Nicaragua); 30, Greater Antilles (Cuba, Haiti, Dominican Republic, Puerto Rico, Virgin Islands); 31, Bahamas, Florida; 32, Bermuda; 33, Lesser Antilles; 34, Curaçao, Aruba, Bonaire, Los Roques; 35, Brazil.

Bleaching began in 1997-1998 in the southern Hemisphere during summer. Bleaching incidences in 1997 - 1998 were first reported on the CHAMP Network [13,83] in the eastern Pacific (Galapagos) and parts of the Caribbean (Grand Cayman) in late 1997, and spread across the Pacific to French Polynesia, Samoa, and Australia by early February 1998. Soon afterwards (March - April 1998), bleaching was being reported at sites across the Indian Ocean, with reports being received from south-east Asia in May 1998. As summer began in the Northern Hemisphere, north-east Asian and Caribbean coral reefs began to bleach in June, with bleaching continuing until early September 1998 [13].

From the previous study, the pattern associated with the 1997 - 1998 bleaching episode strongly resembles patterns seen during the strong 1982 - 1983, 1987 - 1988 and 1994 - 1995 bleaching episodes. Southern Hemisphere reefs (both Pacific and Indian Oceans) tend to

experience the major episodes of bleaching during February - April, south-east Asian reefs in May, and Caribbean reefs during July-August [13,83-84]. Bleaching events in the northern Hemisphere tend to occur after the appearance of bleaching in the Southern Hemisphere, although this is not always the case.

La Niña also formed in 1995, from 1998 to 2000, and a minor one occurred from 2000 to 2001. Recently, an occurrence of El Niño started in September 2006 [85] and lasted until early 2007 [86]. From June 2007 on, data indicated a moderate La Niña event, which strengthened in early 2008 and weakened by early 2009; the 2007 - 2008 La Niña event was the strongest since the 1988 - 1989 event. According to NOAA, El Niño conditions were in place in the equatorial Pacific Ocean starting June 2009, peaking in January - February 2010. Positive SST anomalies (El Niño) lasted until May 2010. Since then, SST anomalies have been negative (La Niña) and are expected to

stay negative for the next northern winter [87]. In addition, bleaching events have been reported from 2000 to 2010 (**Figure 1, 2c**).

An increasing amount of evidence is now accumulating of an indirect relationship between hurricanes and the coral reef ecosystem, from a direct relationship between global warming and increasing hurricane frequency [88,89]. Global warming produces significant increases in the frequency of high sea surface temperatures (SSTs) [13,90-91], and hurricane winds are strengthened by warm waters. Hurricanes and storms result in increases in rainfall, severe flooding and high levels of terrestrial runoff. High energy waves cause coastal erosion, sediment scouring, mechanical breakage, and loss of substrate. These effects can result in severe damage, or subsequent mortality, to coral colonies and loss of suitable substrate for colonisation [91-94].

The occurrence of mass bleaching events correlates well with observed increases in global sea temperatures, and particularly thermal anomalies. This relationship was clearly observed in the Caribbean basin during the 1980s and 1990s, when annual coral bleaching increased logarithmically with SST anomalies [90]. A 0.1 °C rise in the regional SST resulted in a 35 % increase in the number of areas that reported bleaching, and mass bleaching events occurred at regional SST anomalies of 0.2 °C and above. Bleaching within affected regions is not uniform, exhibiting patchy effects over micro (mm to cm) to meso-scales. Such variability results from fluctuations in environmental conditions, spatial heterogeneity of reef surfaces, genetic differences in host or symbionts, and differences in environmental history [24].

Improving our mechanistic understanding

All surveys of living resources of coral reefs should include environmental parameters which characterise the conditions at the site when the data are collected. The environmental parameters that should be measured are temperature, salinity, pH, turbidity, light penetration, cloud cover, and wind. Long term coral monitoring using underwater sensors has been popular for detecting climate change (**Table 3**).

For several years coral reef researchers have been working on coral reefs in many fields throughout the world. Studies of high-latitude reefs have yielded publications on reef geology [45];

taxonomy of the corals [47-48,129-134], ascidians [135] and sponges [136,137]; reef biodiversity [138] and community structure [136,138-140]; coral genetics [141], reproduction [107-110,142] and recruitment [111]; and responses to factors such as crown-of-thorns starfish predation [112,113], sedimentation [114,115], recreational diving [116] and climate change [114,115].

Researchers have been using many methods to improve knowledge about coral reefs (**Table 3**). Field survey methods include mapped quadrats (MAP), line-point transect (LPT), line-intercept transect (LIT), video transect (VIDEO), photo-quadrats methods (PHOTP and PHOTS) used to investigate population dynamics, diversity, community structure and population density etc (**Table 3**). Line-point transect (LPT) and line-intercept transect (LIT) techniques are used to assess the sessile benthic community of coral reefs (**Table 3**). The LPT and LIT are used to estimate the cover of an object or group of objects within a specified area by calculating the fraction of the length of the line that is intercepted by the object [92]. The LPT measures along a 50 m transect tape whereas the LIT measures every 10 cm along a 50 m transect tape. The MAP technique provides a detailed record of changes in individual corals and recruitment (**Table 3**). Each quadrat is mapped on to underwater paper and all coral colonies are drawn by hand. Doing this by hand is very time consuming. VIDEO, PHOTP and PHOTS methods use underwater cameras and video to photograph coral colonies. These photos and video images allow comparable photographs and video images to be taken [92].

Laboratory work is comprised of pulse amplitude modulation (PAM) and fluorometry and fast repetition rate (FRR). These methods are used to investigate changes to the photosynthetic physiology of the dinoflagellate symbionts of reef-building corals, *Symbiodinium* sp. The instruments measure non-destructively fluorescent transients that provide information on the efficiency of PSII, and can distinguish chronic photo-inhibition from dynamic photo-inhibition, the former representing damage to PSII and the latter a protective regulatory response of the photosynthetic apparatus [3]. Rowan and Powers [102,103] used molecular genetic tools, restriction fragment length polymorphisms (RFLPs) of the small ribosomal subunit (ssRNA) and sequencing of ssRNA, to show that the zooxanthellae of reef-building corals

and other symbiotic invertebrates are a highly diverse group of organisms organised at the time into three major “clades”: A, B and C.

Table 3 Methods used in monitoring coral reef ecosystem.

| Method | Application area | Measurement | Advantage | Disadvantage | References |
|--|--|---|---|---|------------|
| Field Survey | | | | | |
| Mapped quadrats (MAP) | Population dynamics - Diversity - Community structure | Coral colonies, positions of coral recruits, extent of coral damage, percent cover of benthic substrate types | - Highly accurate estimates of benthic cover, hard coral growth forms - Record significantly more genera than all survey methods - Cheap method | - Take long time to measure | [91,92] |
| Line-point transect (LPT) | Diversity, population density | Life-forms and target coral genera or species (Along the 50 m transect tape and measure every 10 cm) | - More time-efficient at assessing hard coral cover (also species richness and diversity) than LIT - Cheap method | - Overestimate the benthic substrate categories - Underestimate the coral cover - Less accurate coral growth forms | [92,93] |
| Line-intercept transect (LIT) | Diversity, population density | Life-forms and target coral genera or species (Along the 50 m transect tape) | - Cheap method | - Overestimate the benthic substrate categories - Underestimate the coral cover - Less accurate coral growth forms - Take long time to measure (require approximately 8 days/station) | [92] |
| Video transect (VIDEO) | Community structure | Abundant substrate types, coral genera | - Accurate method to estimate benthic substrate categories - Time-efficient method (requiring only 1 day/station) | - Overestimate the cover of massive corals and underestimate the cover of encrusting coral - Less accurate coral growth forms - Poor ability to detect coral genera - Expensive method (cost for purchase of equipments) | [94,95] |
| Photo-quadrats methods Photo-quadrats analysed with point counts (PHOTP) Photo-quadrats analysed by outlining coral colonies (PHOTS) | Community structure and population dynamics | Coral genera or substrate and boundary of each individual colony | - Photo-quadrats methods give highly accurate estimates of hard coral growth forms | - Underestimate the cover of both branching and encrusting coral - Expensive methods | [87] |
| Laboratory work | | | | | |
| Pulse Amplitude Modulation (PAM) | <i>In situ</i> and laboratory measurements of photosynthetic | - Non-destructively, fluorescent transients, the former representing damage to PSII and the | - Non-intrusive - Portability - Autonomous underwater equipment | - PAM fluorometry determines photosynthetic traits of individual plants | [96-98] |

| | | | | | |
|---|--|---|--|--|--------------|
| fluorometry | efficiency at the plant level - Coral symbiont systematic and adaptation | latter a protective regulatory response of the photosynthetic apparatus - The relationship between electron transport rate and irradiance | - Possibility of continuous measurements - Fast assessment of the overall photosynthetic state - Imaging-PAM provides a high-resolution assessment of the assessment of the spatially complex regions of corals - Comparisons of photosynthetic rates based on fluorescence with standard method (oxygen evolution and radiocarbon fixation measurements) - Indicate corals exposed to bleaching conditions | - Measures light reactions Only - Does not allow respiration measurements or thus production estimates | |
| Fast repetition rate (FRR) | - <i>In situ</i> and laboratory measurements of photosynthetic efficiency of phytoplankton - Coral symbiont systematic and adaptation - Light-adaptive state of phytoplankton | - Rapid non-destructive - Real-time estimation of phytoplankton biomass - Photosynthetic rates - Photosynthetic parameters | - Accurately estimate of photosynthetic under low to middle light levels - Real-time estimation - Examining the diel cycling and dynamic versus chronic photo-inhibition of corals in shallow and deep waters - Indicate corals exposed to bleaching conditions | - Less accurately estimate of photosynthetic under high light levels | [3,96-100] |
| Restriction fragment length polymorphisms (RFLPs) | Coral symbiont systematic and adaptation | - RFLPs of small ribosomal subunit (ssRNA) and sequencing of ssRNA (to show zooxanthellae of reef building has diverse group) - RFLPs using ssRNA and large subunit ribosomal RNA (LsRNA), chloroplast 23S-rDNA sequencing, and sequencing of the internal transcribed spacer regions (ITS) | - Use in genome mapping and in variation analysis (genotyping, forensics, paternity tests, hereditary disease diagnostics, etc.) (result from RFLPs shows the zooxanthellae of reef-building corals and other symbiotic invertebrates are a highly diverse group of organisms organized at that time into three major "clades"; A, B, and C) | - Slow and cumbersome method | [3,101-106] |
| Long-term monitoring | | | | | |
| Fix site monitoring | Community structure, population dynamics, bleaching, oceanographic data collection, ocean sampling, environmental and pollution monitoring, offshore exploration, disaster prevention, tsunami and seaquake warning, assisted navigation, distributed tactical surveillance, and mine reconnaissance | - Image analysis of high resolution photographs of fixed quadrats and modelling - Water quality and its characteristics: temperature, density, salinity (interferometric and refractometric sensors), acidity, chemicals, conductivity, pH (magneto-elastic sensors), oxygen (Clark-type electrode), hydrogen, dissolved methane gas (METS), and turbidity - Ricin (poisonous protein) - DNA array for | - Long-term data of individual colony recruitment, growth and mortality - Long-term SST data can be used to detect local and macro-cyclical phenomenon - Detect the relationship between coral and climate change - Pollution monitoring (chemical, biological and nuclear) - Physical factor monitoring (ocean currents and winds), improved weather forecast, detecting climate change, understanding and predicting the | - Monitoring in small area - Expensive devices | [15,107-119] |

| | | | | | |
|--|--|--|--|--|-----------|
| | | detecting abundance and activity level of variations among natural microbial populations | effect of human activities on marine ecosystems - Biological monitoring (tracking of fishes or micro-organisms) | | |
| Remote Sensing | Community structure, population dynamics, bleaching | - Chlorophyll concentration - Global synoptic coverage of coral reefs | - Coral reefs coverage changes monitoring on large spatial and temporal scales - Assessment and management of tropical coastal resources | - Less accurate data - Data set has limitation to use | [3,120] |
| Modelling | | | | | |
| Atmosphere-ocean General Circulation Models (GCMs) | Forecast or predict frequency and intensity of coral bleaching | Sea temperature data and threshold value (generated by the model) | High level of accuracy and coherence | | [13] |
| Stress response syndrome (SRS) or General adaptive mechanism (GAM) | Bleaching and adaptation | Zooxanthellae population dynamics | - Modelling of zooxanthellae population dynamics - Evidence supporting symbiont changes following bleaching - Evidence for physiological and phylogenetic diversity among zooxanthellae - Relationships between bleaching and disease | - Less accurate prediction | [121-128] |

For large-scale monitoring, underwater sensor networks and remote sensing are used to assess changes in coral reefs. Remote sensing assesses changes in the aerial coverage of coral reefs on large spatial and temporal scales using remote sensing imagery taken from airplanes or satellite. While bleaching has long been understood as a stress response [128,143-145], the metabolic imbalance and life history arguments used here establish a novel premise for explaining its dynamics. This model is based on the stress response syndrome (SRS) or general adaptive mechanism (GAM) of Stebbing [145,146]. An SRS deals with a system under homeostatic (or homeorhetic) control by regulatory systems that sense disturbances to states or rates in the system [128,145]. To forecast the frequency and severity of bleaching events using climate models, researchers synthesise field data on bleaching temperature thresholds with coupled atmosphere-ocean general circulation models (GCMs).

Bleaching is a result of thermal stress on coral reef but it is not the only threat from global climate change. Coral reef biologists from around the world have to use new experimental tools at all levels of biological organisation in their efforts to

understand how reefs work (**Table 3**), determine which corals will survive anthropogenic-driven change, and predict what reefs will look like at the end of the next century [3,147].

Meta-analysis has recently become a method of choice for describing large-scale and long-term trends in coral reefs and other ecosystems [24,148-149]. This approach is used [150-154] to document regional decline in coral cover in the Caribbean and Pacific, to study hurricane effects on Caribbean reefs [159] and bleaching in the region [24].

Coral reefs and future climate scenarios

Since the 1980s, when elevated temperatures were first recognised as the driving factor underlying episodes of mass coral bleaching and mortality, concern has grown over the likely fate of reefs in an era of continued climate change [13,156]. By synthesising field data on bleaching temperature thresholds with coupled atmosphere-ocean general circulation models (GCMs) from the 2nd assessment of the Intergovernmental Panel on Climate Change [157], Hoegh-Guldberg [13] concluded that severe bleaching events were likely to become “commonplace” worldwide by 2040,

and the Caribbean and southeast Asia regions are projected to reach this point by 2020, triggered by seasonal changes in seawater temperature rather than by EL Niño event [158].

Donner *et al* [159], in the first comprehensive global assessment of future bleaching under climate change, used models from the third assessment [160] and incorporated a bleaching prediction algorithm developed and ground-truthed by NOAA's Coral Reef Watch program. They found that, without an increase in thermal tolerance of 0.2 - 1.0 °C per decade, the majority of the world's reefs were at risk of annual or semi-annual bleaching by the 2050s. Although recognizing that advances in modelling and monitoring would likely impact forecasts for individual reefs, they concluded that the global prognosis was unlikely to change without an accelerated political effort to stabilize atmospheric greenhouse gas concentrations.

Climatic processes and extremes can influence the physiological process responsible for the growth, reproductive captivity, and coral health. Most coral reefs systems are predicted to experience near-annual bleaching events that will be a severe threat to continued coral survival for the next 30 - 50 years even under the most optimistic climate scenarios. McClanahan *et al* [4] show that corals that experience the greatest temperature variability, usually at higher latitudes, are also the corals most capable of surviving bleaching events. Coral reefs at equatorial sites that are already among the warmest might be doomed to extinction since they experience relatively little variability and have already been severely affected by past bleaching events. Nevertheless, habitat heterogeneity may limit the influence of this thermostat to specific oceanic reefs; shallow coastal reefs, particularly in restricted embayment and poorly flushed areas, are unlikely to benefit from this phenomenon.

Impact of climate change on coral reefs in Thailand

The coastline of Thailand is divided into the Gulf of Thailand (Pacific Ocean) and the Andaman Sea (Indian Ocean), both of which contain favourable conditions for coral reef development. Based on differences in environmental conditions [161]. The abnormal increase in sea surface temperature during the dry season in 1991, 1995, 1998, 2007 and 2010 caused coral bleaching in the

Andaman Sea. It was reported that the sea water temperature exceeded the seasonal maximum by 0.66 - 1.00 °C during 1991 - 2010 [19,162]. Coral bleaching events in the Andaman Sea generally caused 5 - 40 % coral mortality at each site, since most corals recovered once temperature declined [163]. However, in 1998 coral bleaching was not severe in the Andaman Sea due to a cool upwelling early in the year; thus at most sites the temperature did not increase as noted in other parts of the Indian Ocean. As a result, limited coral bleaching was only observed at a few sites. In addition, not just an increase in sea surface temperature can cause coral bleaching, in 2007, the mortality coincided with abnormally low temperatures, around 23 - 24 °C down to 30 m depth (normal temperatures are 27 - 29 °C) [164]. In the Gulf of Thailand, this phenomenon occurred in 1998, 2006, 2007 and 2010 [19,164]. Moreover, the reefs in the Gulf of Thailand were severely damaged by coral bleaching in 1998. In addition, in 2006 - 2007, soft coral bleaching was reported.

Conclusion

To date, there are several principal causes: predation by the coral-eating crown-of-thorns starfish, sedimentation from urban development and deforestation, over-fishing, destructive fishing practices, eutrophication from agriculture and sewage, pollution from herbicides and pesticides, diseases, and global warming. This paper highlights the impact of global warming on coral reefs. The global warming has now overtaken all other impacts because it is the cause of increasingly destructive and extremely widespread mass bleaching events. The multiple natures of stressors on reefs associated with climate changes are unprecedented in human history and studies of its synergisms are still in their infancy. As a result, one-third of all reef-building corals are considered to be at risk of extinction [165-167]. Unlike most ecosystems where the effects of climate change are matters of future prediction, mass bleaching of corals has been studied for 30 years and is understood in considerable detail [68,168-173].

Acknowledgements

We thank Thana na Nagara for comments on previous versions of this manuscript. This work was supported in part by Thailand Research Fund through the Royal Golden Jubilee Ph.D. Program (Grant No. PHD/0307/2550), Centre of Excellence for Ecoinformatics, the Institute of Research and Development, Walailak University and NECTEC.

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