Coral
Reef Targeted Research &
Capacity Building for Management

Bleaching and Related Ecological Factors

CRTR Working Group Findings 2004-2009

www.gefcoral.org

Acknowledgements

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Cover Photo: Ove Hoegh-Guldberg

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The Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program is a leading international coral reef research initiative that provides a coordinated approach to credible, factual and scientifically-proven knowledge for coral reef management.

The CRTR Program is a partnership between the Global Environment Facility, the World Bank, The University of Queensland (Australia), the United States National Oceanic and Atmospheric Administration (NOAA) and approximately 50 research institutes and other third-parties around the world.

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Foreword

Coral reefs are the most biologically diverse marine ecosystems on Earth. In addition to their role in providing habitat for over a million species, coral reefs also provide goods and services to over 500 million people across tropical and subtropical regions. These provisions include food, building materials, income, cultural benefits and the protection of coastlines from ocean waves. They also drive billion-dollar fishery and tourist industries, which provide much-needed income to communities and nations.

Unfortunately, the health of coral reefs is in steep decline, and studies over the past 40 years have indicated coral cover decline by over 40% in many regions of the world. These changes have come about because of the expanding activities of humans along the coastlines adjacent to coral reefs. These activities include the overexploitation of reef species, destructive activities associated with tourism and fishing, pollution and declining water quality as urban areas, coastal agriculture, and aquaculture have expanded.

Climate change is now exacerbating the pressures on coral reefs, with increasing stress from elevated sea temperatures and acidity as atmospheric carbon dioxide has increased. In 1998, coral reefs in all the world's tropical regions experienced mass coral bleaching and mortality. Some regions lost over 90-95% of their coral cover with an average loss of 17.7% of corals from reefs worldwide.

The devastation of coral reefs during this period triggered a number of initiatives. One of these was the formation of the IOC-UNESCO working group on coral bleaching, which brought together a group of marine scientists to explore the causes and solutions to the impacts of coral bleaching. At the same time, the World Bank coastal program began to evolve a research program aimed at exploring the decline of coral reefs. The two initiatives came together with the incorporation of the IOC-UNESCO into one of six scientific Working Groups within the Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program.

Photo: A. Zvuloni

Following success with applications to the World Bank and the Global Environment Facility (GEF), the CRTR began the first phase of a 15 year project in 2004 which aims to address knowledge and technology gaps, promote learning and capacity building, and link scientific knowledge to management and policy. The Bleaching Working Group (BWG) has focused on key gaps in our understanding of mass coral bleaching and related ecological phenomena, and has pursued research projects that range from establishing a better understanding of why corals bleach and get diseased, to the impacts of coral mortality on fish populations and human dependents. The associated research has been conducted across four Centres of Excellence (COE's) within the CRTR Program: Heron Island (Australia), Zanzibar (Tanzania), Bolinao (Philippines) and Puerto Morelos (Mexico). In addition to producing over 230 peer-reviewed papers, the BWG has trained 17 postgraduate students and has supported many more through its regional workshops and research projects.

Photo: A. Zvuloni

While the contribution of new knowledge and understanding of the impacts of global climate change by the BWG has been significant, the project has also contributed to a series of new technologies useful to the management of coral reefs. Development of low cost colour cards for detecting bleaching (in partnership with Justin Marshall and Uli Seibeck at the University of Queensland) as well as ecological methods for detecting sub-chronic change on coral reefs will provide important contributions. The ecological studies undertaken by the BWG, for example, produced a 'Common Sampling Protocol' outlining ecological techniques used at all Centres of Excellence. These techniques allowed us to determine which vital rates were responsible for the state of the reef and allowed us to derive novel yet pragmatic

Photo: A. Zvuloni

models that predict population changes and the future state of the reefs. It is expected that these contributions will flow naturally into the more applied program of the second phase of the CRTR Program.

The BWG has also played a very significant role in influencing policy development at a national and international level. Papers such as that published by BWG members in December 2007 (now ISI's hottest and most cited paper over the past two years in the areas of "climate change" and "ocean acidification") are playing an important role in the climate change issue. The results of papers like this are playing very significant roles in helping policy makers understand the serious consequences of approaching or exceeding atmospheric carbon dioxide concentrations of 450 ppm. Attendance of members of the BWG at the recent Copenhagen conference, visits by the Chair to Capitol Hill and a strong presence at the recent World Oceans Conference in Manado, Indonesia, have ensured that the results of the research are now being included in many of the discussions that are occurring as we lead up to crucially important climate change COP15 negotiations in Copenhagen at the end of 2009.

This final report describes the scientific outcomes, major training achievements, and the outreach activities and outputs undertaken by the BWG within the CRTR Program. Most importantly, this report describes a series of exciting and innovative contributions to the understanding of how climate change is, and will, affect the world's most diverse and important marine ecosystem. We hope that you will enjoy reading about the activities and contributions from the BWG over the past five years (2004-2009).

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Introduction

Coral reefs play critically important roles as sources of income and resources from fishing, tourism, building materials, coastal protection and biodiscovery (Bryant 1998; Hoegh-Guldberg et al. 2009). They also have significant cultural and spiritual value to coastal communities, which often include some of the most disadvantaged people who are heavily dependent on marine resources (Bryant 1998). Approximately 15% of the world's population (0.5 billion people) live within 100 km of coral reef ecosystems (Pomerance et al. 1999). Coral reefs play a vital role in directly supporting at least 500 million people worldwide, despite only representing 0.1% of the world's ocean area. The Coral Triangle in south-east Asia, for example, includes over 100 million people who are almost entirely dependent on coastal resources (Hoegh-Guldberg et al. 2009). In many cases, the precise evaluation of these resources is hard to define given that much of it is associated with providing food to people who forage in shallow coastal waters for food and involve commodities that do not involve monitored fisheries or markets.

Photo: T. McClanahan

In addition to direct support to subsistence fishers, commercial fishing in the rich waters of coral reefs sustains 25% of the total annual fish catch globally (Moberg and Folke 1999). In regions like the Coral Triangle, fisheries (including aquaculture) earn over $10 billion each year in exports (Hoegh-Guldberg et al. 2009). Coral reefs also provide a rich source of income from tourism, with people travelling thousands of miles, in many cases, to dive, fish and swim in the scenic locations offered by coral reefs. Reef associated tourism, for example, adds $89 billion to the gross development product (GDP) of the Caribbean region (Jameson et al., 1995 cited by Pomerance 1999). In Australia, tourism generated by the Great Barrier Reef brings in over $5 billion per annum and employs over 65,000 people (Hoegh-Guldberg and Hoegh-Guldberg 2004).

The extraordinarily high biodiversity of coral reefs is inherently difficult to value formally. The sheer scale of coral reef biodiversity, with its thousands of unexplored gene pools, perhaps negates the need to calculate this formally. About 100,000 species have been described from the world's 375,000 km² of coral reef. This is a tiny fraction of an estimated 0.5 to 2.0 million species that live on coral reefs (Spalding et al. 2001). Other estimates range as high as 9 million species being associated with coral reefs (Reaka-Kudla 1997). This biodiversity has an increasing value as a storehouse of potential novel compounds. Recent advances in the molecular sciences (e.g. robotic sequencing and screening, microarrays and molecular databases) are making gene and pharmaceutical discovery many hundreds of times faster than it was even a decade ago. New medicines, chemicals and materials can be realistically discovered within these vast ecosystems. Economic wealth is being built upon these discoveries (e.g. conotoxins from *Conus* sp., (Livett et al. 2004); pocilloporin from reef cnidarians (Dove et al. 2001); anti-cancer drugs from sponges (Wallace 1997). While this exploration is in its infancy, it is significant to note that half of the potential pharmaceuticals being explored at present are from the oceans, and many of these are from coral reef ecosystems. It should be recognised that while corals and their allies (cnidarians) were one of the earliest multicellular animal groups to evolve, their genome is as large and complex as humans (Miller et al. 2007). The original forms and functions of genes that were later adapted by mammals might therefore be determined from cnidarians. Coral reefs are valuable in ways that are often unappreciated. By reducing the force of ocean waves, corals reefs provide critical protection along tropical coastlines over the planet. This protection is critical for coastal cities and towns, and for other ecosystems such as sea grass and mangrove communities that require calm waters in which to grow and proliferate. For example, Hurricane Wilma, which sat over Cancun for 36 hours in October 2005, generated 12-14 m waves on the outer reef which were reduced by the reef barrier to 3 m waves within the lagoon (Ruíz, Escaleante and Iglesias-Prieto, unpublished data). The role of coral reefs in protecting coastlines was also clearly demonstrated across areas affected by the Asian Tsunami of December 29, 2004. In this devastating event, coastal regions lacking a well-developed coral reef in front of them suffered the greatest damage. Physical protection aside, coral reefs and associated habitats such as mangroves also have enormous value as critical nursery grounds within the network of coastal habitats (Mumby et al. 2004). Many commercially important species spend their early life-history stages in these rich habitats.

Reef-building corals: The framework builders of coral reefs

Reef-building corals are critical to coral reef ecosystems and are unique in being a mutualistic symbiosis between a simple multicellular animal and a single-celled dinoflagellate protist. The greatest diversity of reef-building corals is located closest to the equator. Light, temperature and the carbonate alkalinity of seawater decrease in a poleward direction, making the formation of carbonate reefs more difficult at higher latitudes (Kleypas et al. 1999a). In many ways, the productivity and biodiversity of coral reefs is at odds with the nutrient depleted waters of the earth's tropical oceans. Starting with Charles Darwin, visitors to coral reefs have marvelled at how these productive ecosystems exist in waters that otherwise support only the most sparse phytoplankton populations (Darwin 1842; Odum and Odum 1955). Coral reefs support, or did in the past (Jackson et al. 2001b), massive populations of fishes, birds, turtles and marine mammals (Maragos et al. 1996). Akin to the cactus gardens of tropical nutrient deserts, coral reefs tightly recycle nutrients between often closely associated mutualistic partners. This has been identified as the key feature that allows coral reefs to maintain high productivity in this otherwise desolate setting of tropical oceans (Muscatine and Porter 1977; Hatcher 1988).
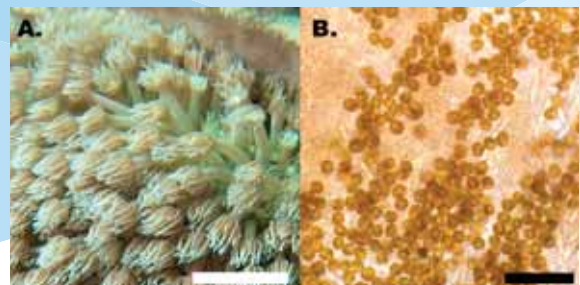

Figure 1. A. Polyps of the reef-building coral Goniopora tenuidens (scale bar = 2 cm) B. *Symbiodinium* from tentacle squash of G. tenuidens (scale bar = 50 µm).

Reef-building corals are fundamentally important to coral reefs and are responsible for the framework of coral reefs. This framework is in turn cemented together via the activity of calcareous algae to create habitat for thousands of animals, plants, fungi and protists. Much of the diversity of coral reefs depends on their three-dimensional topography and complexity. Reef-building corals live in a mutualistic symbiosis with single-celled dinoflagellate algae from the genus *Symbiodinium* (Trench 1979). These tiny (8-10 μm in diameter) plant-like protists live inside the cells of the coral host and photosynthesize in the light. Instead of retaining the sugars and amino acids that result from this activity for their own growth and reproduction, *Symbiodinium* export more than 95% of their photosynthetic production to the coral host (Muscatine 1967,1990). In return, *Symbiodinium* have direct access to the waste products of animal metabolism, which are lacking in the surrounding waters. The close association of animal (heterotroph) and plant (phototroph) means that the problem of nutrient/particle dilution within a nutrient-poor water column is avoided. The success of coral reefs in the otherwise nutrient deserts of tropical oceans is seen as a direct consequence of the mutualism exemplified by corals and their *Symbiodinium* (Muscatine and Porter 1977). More recently it has been recognised that reef corals also engage in close associations with a range of micro-organisms including cyanobacteria (Lesser et al. 2007b) and in total, the association is termed the coral 'holobiont' (Rohwer et al. 2002).

All reef-building corals were thought to contain a single species of symbiotic dinoflagellates called *Symbiodinium microadriaticum* (Freudenthal 1962; Taylor 1974). Starting with Robert Trench and associates at the University of California at Santa Barbara (Trench 1979; Schoenberg and Trench 1980c,a,b), this view changed however, as results accumulated that showed that *Symbiodinium* in reef-building corals was a collection of many taxa (Rowan et al. 1997; Loh et al. 2001). A recent survey (done as part of the World Bank Block B activities associated with the current project) of the molecular identity of symbionts from 86 host species from the Great Barrier Reef representing 2 genera from Class Hydrozoa, 6 genera from Subclass Alcyonacea, and 32 genera from Subclass Zoantharia (28 Scleractinian, 1 Actiniarian, 2 Zoanthidean, and 1 Coralimorpharian) revealed at least 23 distinct types of *Symbiodinium* (LaJeunesse et al. 2003). Many hosts may also have 2 or more genetic varieties of *Symbiodinium* in their tissues. Several research groups have tried to link this diversity to the different tolerances between reef-building corals, albeit without much success. Given the importance of understanding why some corals differ in their sensitivity to thermal stress, understanding the diversity of *Symbiodinium* and how it relates to climate-change impacts is a major objective of the Bleaching Working Group.

Human impacts on coral reefs

Coral reefs have persisted for over 200 million years even after global catastrophes that caused mass extinction, such as that which occurred 65 million years ago. They show enormous resilience in geological time (i.e. over millions to tens of millions of years). Paradoxically then, coral reefs appear to be highly sensitive to the increased pressure that human activity has brought to bear on them. Global surveys of coral reef health indicate that coral reefs are in decline in almost all areas of the world (Bruno and Selig 2007; Wilkinson 2008). The implications for global biodiversity and functional coral reef ecosystems are likely to be severe if these trends continue.

A range of human activities have impacts on coral reefs. These are listed with a brief description in Table 1. Understanding these stressors (especially the interactions) is critical if we wish to develop strategies to reduce or even reverse the current rapid decline in coral reef health across the world's tropical oceans.

Coral bleaching and climate change

The algal symbionts of reef-building corals exist at high densities within the host tissues. Under normal conditions, the population densities of symbionts range from between 0.5 to 5 x 10^6 cells cm^2 of host surface (Drew 1972). Reef-building corals maintain low rates of migration or expulsion of their symbionts to the water column (Hoegh-Guldberg et al. 1987). Symbiotic dinoflagellate population densities in the coral vary in response to seasonal changes in light and temperature (Jones 1997a; Fagoonee et al. 1999; Fitt et al. 2000). These changes represent gentle adjustments between the two symbiotic partners to optimize their integrated physiological performance as the environment changes.

Under a variety of stresses, abrupt changes can occur to the density of *Symbiodinium* in symbiotic corals and other invertebrate hosts (Brown and Howard 1985; Hoegh-Guldberg and Smith 1989). These stresses include changes in salinity (Goreau 1964; Egana and DiSalvo 1982), light (Vaughan 1914; Yonge and Nichols 1931; Hoegh-Guldberg and Smith 1989; Lesser et al. 1990; Gleason and Wellington 1993), toxin concentrations (e.g. cyanide, (Jones and Hoegh-Guldberg 1999); copper ions (Jones 1997b), microbial infection (e.g. *Vibrio*, (Kushmaro et al. 2001) or temperature (Coles and Jokiel 1977; Coles and Jokiel 1978; Hoegh-Guldberg and Smith 1989; Glynn and D'Croz 1990). This phenomenon has been referred to as 'bleaching' because corals rapidly lose their brown colour (because of the *Symbiodinium*) and turn a brilliant white, because most of the pigments are gone and the white calcareous skeleton is revealed (Figure 1A, B).

Bleaching at local scales (10-1000 m^2) has been recorded for almost a century (e.g. Yonge and Nichols 1931). Bleaching at larger geographical scales, however, is a relative new phenomenon. Prior to 1979, there are no formal reports of mass coral bleaching in the scientific literature. Since that date, however, the number of reports has risen dramatically. Mass bleaching events have a number of possible outcomes. In mild cases, reefs will recover their colour within months. At the other end of the spectrum, mass bleaching events can result in large numbers of corals dying across vast areas of coral reef. In 1998, for example, coral reefs off the Australian coastline recovered from wide-spread bleaching, with minimal loss of reef-building coral (Berkelmans and Oliver 1999). In the same year, reef communities lost up to 95% of their corals across large areas of the Indian Ocean, Palau, Okinawa and north Western Australia (Wilkinson and Hodgson 1999).

While localized bleaching can arise as a result of any number of stresses, mass coral bleaching is tightly correlated with short excursions of sea temperature above summer maxima. Over the past 20 years, there have been six major global cycles of coral bleaching ("mass coral bleaching events"). A combination of the intensity and length of periods of elevated sea temperature provides an accurate prediction of mass coral bleaching and mortality (Strong et al. 1996b; Strong et al. 2006a). Thermal thresholds for bleaching generally begin at approximately 1°C above the sea temperature maxima for a region, but will vary with latitude, species, clone, other physical factors (e.g. light and water flow rate) and history (Edmunds 1994; Jones et al. 1998; Hoegh-Guldberg 1999a; Coles and Brown 2003). Understanding the sources of this variability was a major objective of the first five years of the research program of the Bleaching Working Group (BWG).

Despite this secondary source of variability, satellite measurements of sea-surface temperature anomalies can be used to predict bleaching events several weeks in advance with more than 90% accuracy (review: Hoegh-Guldberg 1999). Sea surface temperature measurements also appear to deliver information on the intensity and outcome of bleaching events. Table 2 outlines information from the global event in 1998 in which anomaly intensity and exposure duration were multiplied together to give a degree heating month (akin to degree heating weeks of Strong et al 2000; see also Hotspot program, coordinated by the United States National Oceanic and Atmospheric Administration, NOAA: http://orbit-net.nesdis.noaa.gov/orad/coral_bleaching_index.html). The four sites that experienced major post-bleaching mortalities had three-fold higher degree heating month indices. While there is some fine-tuning that needs to be done with regard to the influence of other factors (e.g. Mumby et al. 2001; Berkelmans 2002; Berkelmans 2006), the relationship between sea surface temperature (SST) anomalies and exposure time gives a strong indication of the bleaching progression to mortality as heat stress increases over the next century. Significantly, Hoegh-Guldberg (2000) has pointed out that a doubling of CO_2 (IS92a scenario) will lead to 'degree heating months' in most tropical regions over three-fold higher than those previous increases which caused large scale mortality events in Palau, Okinawa, Seychelles and Scott Reef.

Heat stress and mechanisms of coral bleaching

There is a considerable amount of information on the underlying physiological mechanisms involved in coral bleaching. Coles and Jokiel (1977) were among the first researchers to investigate heat stress in reef-building corals during a project looking at the affect of heat effluent flowing from a power plant in Kaneohe Bay in Hawaii. Coles and Jokiel (1977) noted that corals that were warmer than normal were bleached. Those that were warmest soon died. In their investigation of the physiology of heat stressed corals, they noted the rapid reduction in photosynthetic activity early in the bleaching syndrome. Some of this decrease was due to reduced *Symbiodinium* numbers as the corals bleached. However, subsequent work has revealed that photosynthetic decreases occur prior to the onset of the loss of *Symbiodinium* (Hoegh-Guldberg and Smith 1989; Iglesias-Prieto et al. 1992 -a; Fitt and Warner 1995; Warner et al. 1996; Jones et al. 1998). Heat stressed corals develop an increased susceptibility to the phenomenon of photoinhibition, which is very similar to the mechanisms that are faced by all plants when they become temperature stressed. This mechanism, in which light becomes a liability, also explains the important role that light plays as a secondary factor (Iglesias-Prieto et al. 1992 -b; Jones et al. 1998; Hoegh-Guldberg 1999a). Resolving the detail of the mechanism underlying coral bleaching and understanding the role of secondary factors like light and flow regimes, are major research goals of the current project.

A key observation regarding heat stress in reef-building corals is that not all corals are equally sensitive to temperature. Corals with thicker tissues (e.g. *Porites* spp., and *Goniopora* spp.) tend to be more tolerant than corals that have thinner tissues (e.g. *Acropora* spp., *Stylophora* spp., *Pocillopora* spp.). Some species of *Symbiodinium* may also be more thermally tolerant although the evidence is equivocal at this point (Hoegh-Guldberg 1999). The thermal threshold above which corals and their symbionts will experience heat stress and bleaching also varies geographically, indicating that corals and *Symbiodinium* have evolved over evolutionary time to local temperature regimes (Coles et al. 1976), (Table 2, Hoegh-Guldberg 1999).

Table 1. Principal threats to coral reefs worldwide. References are intended as samples of key literature and are not meant to be exhaustive. Further details on these threats can be gained from Bryant et al. (1998), Spalding et al. (2002) or from Wilkinson (1999)

Activity	Description	Reference
Coastal development	Expansion of urban centres, townships, tourist activities, shipping, aquaculture and agricultural activities have resulted in major changes to coastal regions. This has in turn led to increased amounts of sediments and nutrients entering coastal waters, which has triggered the pollution, algal overgrowth and outbreaks of coral predators such as the Crown-of-Thorns Starfish.	(Bryant et al. 1998; Wong 1998; White et al. 2000; Harborne et al. 2001; McClanahan et al. 2001; Lipp et al. 2007)
Overexploitation	Both local subsistence fishers and fishing industries are putting large pressures on fish stocks associated with coral reefs. As a result, many fish stocks are in major decline. Changes to reef community structure have occurred as functional groups (herbivore and key predators) have disappeared.	(Hughes 1994; McManus 1997; Boersma and Parrish 1999; White et al. 2000; Jackson et al. 2001b)
Destructive fishing	Destructive methods employed to catch fish have also had major impacts on coral reefs. In many parts of the world, fishermen use cyanide to poison, and dynamite to stun fish, often with devastating impacts on reef structure and function.	(Jones and Hoegh-Guldberg 1999,2001; McClanahanan et al. 2002; Edinger et al. 2008)
Marine-based pollution	Chemicals and trash dumped by shipping or coastal developments leads to a build up of compounds that poison corals and associated organisms, as well as leading to the choking of fauna such as fish, turtles and dugongs. Another form of trash of significance is the discarded fishing nets ("ghost nets"), which can continue to cause the death of thousands of fish long after decommissioning.	(Abelson et al. 1999; Bastidas et al. 1999; Wilkinson 1999; Edinger et al. 2000; Edinger et al. 2008)
Climate change	Rising ocean temperatures and acidities are changing the conditions under which coral reefs have prospered for at least 740,000 years. In 1998 alone, a single worldwide episode of warmer than normal water temperatures, led to an estimated 16% of the world's corals dying. This is seen by many as the number one threat to coral reefs now as oceans undergo sustained warming over the next century. Recent work in Australia and Thailand has revealed that coral reefs are accreting at 15% of the rate that they were prior to 1980. This decline is unprecedented in over 400 years of records available so far.	(Glynn 1991; Brown 1997; Hoegh-Guldberg 1999a; Done et al. 2003)

Table 2. Comparison of recent Degree Heating Months and mass bleaching mortality estimates from incidents of bleaching within the 1998 mass bleaching event (adapted from Hoegh-Guldberg 2002).

Severe events (mortality > 80%)

Location	Degree heating months	Mortality	Source
Palau	3.9	70-90%	J. Bruno, unpublished data
Seychelles	3.1	Up to 75%	Spencer et al. (2000)
Okinawa	3	90-95%	Loya et al. (2001)
Scott Reef	3	90-95%	L. Smith and A. Heyward, unpublished data
Mean + 95% CI	3.2 + 0.47		

Mild events (mortality < 10%)

Location	Degree heating months	Mortality	Source
Southern GBR (reef crest)	1.7	10-30%	(Jones et al. 2000)
Central GBR (inner reefs)	1.4	1-16%	Marshall and Baird (2000)
Moorea (outer reef crest)	0.9	0% mortality	Personal observation (10% bleached)
Cook Is (Southern; reef crest)	0.4	0% mortality	Personal observation (5% bleached)
Mean + 95% CI	1.1 + 0.49		

Corals closer to the equator have thermal thresholds for bleaching that may be as high as 31°C while those at higher latitudes may bleach at temperatures as low as 26°C. Thresholds may also vary seasonally. Berkelmans and Willis (1999) revealed that the winter maximum upper thermal limit for the ubiquitous coral *Pocillopora damicornis* was 1°C lower than the threshold for the same species of coral in summer. These shifts are evidence of thermal acclimation, a physiological adjustment that can occur in most organisms up to some upper or lower thermal limit.

Why corals are sitting so close to their thermal threshold for bleaching has been a subject of considerable interest given the importance of adaptation in future scenarios. The explanation is also important to perspectives as to why mass bleaching events appear to be more frequent and intense. Several factors are involved in the latter. The first factor involved is the increase in tropical/subtropical sea temperatures over the past 100 years. Tropical and subtropical oceans are about 0.7–1.0°C warmer (minimum estimate, some estimates range up to 2°C) than they were 100 years ago (Hoegh-Guldberg 1999a; Lough 2000). The second factor is associated with the timing and intensity of El Niño Southern Oscillation (ENSO) events (Glynn 1988,1991; Glynn 1993; Hoegh-Guldberg 1999a).

Figure 2. Sea surface temperatures and triggers for coral bleaching for offshore reefs near Townsville, central Great Barrier Reef (latitude 18.3S, longitude 146.3E). Dataset from the Comprehensive Ocean Atmosphere Data Set (COADS) and satellite observations (1990 – present), compiled from operational data produced by the National Environmental Satellite, Data and Information Service (NESDIS). Horizontal dashed line indicates the thermal threshold for 3-4 week exposure times (Hoegh-Guldberg 1999). Arrows indicate when bleaching was reported on the Great Barrier Reef (emphasized arrows indicate years in which intense bleaching occurred).

The effect of these events is that they combine to produce short periods during the summer months in which sea temperatures rise above the thermal tolerance of reef-building corals and their *Symbiodinium*. The last factor is the apparent stability of the thermal threshold of corals. It appears that rates of adaptation to changing conditions over the past 30 years are much slower than the rate of increase in stress levels affecting coral reefs. This is a critical observation that underpins the development of projections of the future for reef systems.

Mortality estimates of reef-building corals following bleaching

As discussed above, mortality following mass bleaching ranges from zero, in cases of mild bleaching, to close to 100% as seen at many sites in recent global events (Table 2; (Wilkinson and Hodgson 1999). The Global Coral Reef Monitoring Network, GCRMN (supported by more than 30 countries, IOC-UNESCO, UNEP, IUCN and the World Bank) has produced a series of annual reports on the state of coral reefs since the mid 1990s. These reports, though of varying qualities, are an attempt to get a yearly snapshot of coral reef health across the planet. The numbers from 1997 to 1998 (Table 3) indicate the scale of mortality that can occur in a global cycle of mass coral bleaching. Prior to 1998, the GCRMN surveys reported a loss of 9.5% of living corals from six regions. During 1998, one of the warmest years on record, regions lost an average of 17.7% of their living reef-building corals. The range of mortality estimates is perhaps the most interesting detail hidden within the average. While some regions (e.g. Australia and Papua New Guinea) lost an estimated 3%, regions like the Arabian Gulf and Wider Indian Ocean lost 33% and 46% respectively during the single event in 1998.

Table 3. Summary of net estimates of the disappearance of reef-building corals during surveys carried out by the Global Coral Reef Monitoring Network (adapted from GCRMN 2000).

Location	% destroyed pre 1998	% destroyed in 1998
Arabian Region	2	33
Wider Indian Ocean	13	46
Australia, Papua New Guinea	1	3
Southeast & East Asia	16	18
Wider Pacific Ocean	4	5
Caribbean Atlantic	21	1
Average (region)	9.5	17.7

The novelty of recent changes on coral reefs is an important part of understanding global events. Several studies have looked into the past behaviour of reefs and have come up with some compelling data that indicates that recent mass mortalities of the 1990s have not been seen for at least the last 3,000 years. *Acropora cervicornis*, for example, was a dominant species across the central shelf lagoon of Belize up until 20 years ago. In the 1980s, however, disease (white-band disease) resulted in almost the complete mortality of *A. cervicornis*. Stands of the foliose (scroll-like) coral *Agaricia tenuifolia* quickly replaced *A. cervicornis* in the early 1990s but were wiped out by the high-water temperatures of 1998. The mortality of *A. cervicornis* in the 1990s left an unambiguous layer of coral branches in the sediments of reefs throughout the Caribbean. Investigation of reef deposits reveals that the scale of these mortality events appears to have been unique in the past 3,000 years (Aronson et al. 2002). Indeed, Aronson and his colleagues analysed 38 cores from across the 375 km^2 central lagoon basin and could not demonstrate the existence of a similar layer in sediment cores stretching back at least as far as 3,000 years ago. While the focus of Aronson et al. (2002) was specifically responding to a disease event that may or may not have a direct relationship to thermal bleaching, the results indicate that catastrophic events such as that which occurred in 1998 were extremely rare or absent prior to industrialization.

Chronic impacts of thermal stress

Often forgotten from the discussion of impacts of climate change on coral reefs are the chronic or sub-lethal effects of thermal stress that may or may not be associated with bleaching and/or death. These may be as important as changes in mortality and have the potential to bring about huge changes in growth, calcification and age structure. These in turn can fundamentally affect reef function, resilience and survival.

Reef-building corals that experience thermal stress have reduced growth, calcification and repair capabilities (Goreau and Macfarlane 1990; Meesters and Bak 1993). Not surprisingly, as thermal stress reduces the amount of photosynthetic activity and as *Symbiodinium* are lost from reef-building corals, the amount of energy available for these fundamental processes is reduced. In addition, the amount of energy available for reproduction is also potentially compromised under thermal stress. Coral species utilise a variety of reproductive modes including brooding of larvae and broadcast spawning of gametes for external fertilisation (Harrison et al. 1984). Coral reproduction is generally sensitive to stress (Harrison and Wallace 1990) and measures of reproductive output or fecundity can be used as indicators of reactions to various stressors such as mechanical damage (Ward 1995), nutrients (Tomascik and Sander 1987; Harrison and Ward 2001; Koop et al. 2001; Ward et al. 2002) and oil (Guzman and Holst 1993).

The evidence for the sub-chronic impact of thermal stress on reef-building corals is very strong. Mass coral bleaching has been reported to affect coral reproduction. Szmant and Gassman (1990) examined a limited number of corals (due to marine park restrictions) following a bleaching event in Florida in 1987 and found that bleached colonies did not complete gametogenesis in the season following the bleaching event. They also found that bleached colonies had 30% less tissue carbon and 44% less tissue nitrogen biomass per skeletal surface area than unbleached colonies. Harrison and Ward (2001) and Koop et al. (2001) demonstrated a failure of gametogenesis in a large number of corals that were affected in the southern Great Barrier Reef by the 1998 mass-bleaching event. This is similar to observations made for soft corals by Michalek-Wagner and Willis (2001). They also demonstrated that fertilization, settlement and juvenile growth were all compromised at the end of 1998, even though the bleaching event occurred in March of that year. The implications for reef dynamics are considerable as recovery of affected reefs can be heavily dependent on larval recruitment. There are a growing number of observations that have linked low levels of larval recruitment to earlier periods of thermal stress on coral populations. For example, severe bleaching also occurred on the Western Australian coast in 1998 and was followed by a year of failed recruitment at Scott Reef (L. Smith, Australian Institute of Marine Science, pers. comm.). Because of the importance of this linkage within the biology of reef-building corals, a major focus was placed on the sub-chronic impacts of thermal stress (e.g. on growth and reproduction) within the first five years of the project. The general effect of increasing stress on other aspects such as disease susceptibility, age structure and ecological traits such as partial-colony mortality was also explored.

Projections of change under rapid climate change

The conditions under which coral reefs have prospered are changing rapidly. Global temperatures and carbon dioxide concentrations are now higher than they have been for at least the last 400,000 years. There is now very strong evidence that coral reefs have already experienced major impacts from climate change. Current projections of changes to the earth's climate suggest that sea temperatures may be 2-5°C higher by 2100 than they are right now. Some studies suggest that tropical and sub-tropical reefs will not be coral dominated by the middle of the current century (Hoegh-Guldberg 1999a; Hoegh-Guldberg 2002a; Done et al. 2003; Hoegh-Guldberg 2004; Donner et al. 2007; Hoegh-Guldberg et al. 2007b). The implications of these types of scenarios for tropical near shore communities and the humans that interact with them are enormous and must be considered in any serious exercise to plan for the future.

Even under mild climate change scenarios, coral reefs will undergo major increases in coral bleaching and mortality. Drawing together the responses of reef-building corals to El Niño Southern Oscillation (ENSO) related excursions in sea temperature over the past 20 years, Hoegh-Guldberg (1999) derived a series of simple thermal thresholds for a series of sites and compared these threshold values to future sea temperatures. As discussed previously, some variation surrounds thermal thresholds because of the influence of other secondary factors (e.g. light, history, exposure time). However, despite the influence of these secondary factors, thermal thresholds can be used to predict bleaching events from passing satellites

and hence (for exposure times of 3-4 weeks) are fairly good indicators whether a reef will bleach or not (Strong et al. 1996a; Strong et al. 2006b). Estimates of past and future sea temperatures were generated by a range of General Circulation Models of areas of Tropical Ocean and compared to these threshold values. From these analyses it is clear that sea temperatures under a doubling of atmospheric carbon dioxide quickly rise above the known thermal stress thresholds of reef-building corals. When this is combined with estimates of the atmospheric carbon dioxide content required to drive carbonate ion concentrations down below levels necessary for maintaining calcification and reef accretion, it becomes apparent that we are headed for conditions on planet Earth in which coral reefs will struggle to survive as functional ecosystems (Hoegh-Guldberg et al. 2009).

Biological consequences of declining coral reef health

While corals form a primary response, the biological consequences of thermal stress fall into two basic categories. These are:

A. Reefs that bleach but recover: Reefs that experience 0.5 Degree Heating Months (DHM) during the summer months will experience mass bleaching. They will recover if stress levels return to previous levels. It is important to note that bleaching is just a visual sign of stress and that the recovery of colour does not imply that there have not been physiological consequences. As discussed above, these can manifest themselves in the form of reduced growth and reproduction.

B. Reefs that experience almost total coral mortality: Reefs that are exposed to 3.2 DHM per year or more will experience almost complete mortality of their coral populations. This is conservative as reefs probably experience major mortality events at lower Degree Heating Month values (e.g. Scott Reef, 2.6 DHM in 1998; Table 2).

From here, we can assume that reefs that are experiencing bleaching every second year will also experience a decrease in reef quality and that reefs with total mortality events three times per decade will be no longer coral-dominated reefs. The latter is also conservative as coral communities take anywhere from 10-50 years to recover after a mass mortality event. Consequently one event per decade (let alone three events) is probably enough to tip the balance in favour of non-coral dominated systems. This was recently recognised by Done et al. (2003) in a useful scheme that defines the types of ecological impacts on coral reefs with an estimate of return times. "High level" and "catastrophic" ecological impacts each have return times of 20 and 50 years. Clearly, even three "High level" events per decade would clear reefs of coral cover (let alone three "catastrophic" impacts which is probably closer to that posed by a 3.2 DHM event). Recent community modelling work has reinforced this conclusion. Using a cellular automaton model developed for coral communities, (Johnson et al. 2002) have demonstrated that merely having an event with a DHM value of 1.2 every 10 years into the next century is enough to reduce coral cover by 50%. Adding stress levels like those seen when events (similar to that of 3.2 DHM) occur every 3-4 years produces outcomes in which coral cover is extremely remnant (Johnson et al. 2002).

As part of the current project, present-day conditions were compared with those that have occurred over the past 420,000 years (Hoegh-Guldberg et al. 2007a). This study revealed that current conditions on coral reefs in terms of pH, carbonate ion concentrations and sea temperature are well outside those experienced by corals in the past. Further analysis of the literature revealed that conditions are fast approaching critical thresholds, one associated with high sea temperatures and the other approaching with the critical carbonate ion concentration. The conclusion from this study was that coral reefs will soon become non-coral dominated, with important consequences across the globe for the many millions of species that live on and depend on corals. Naturally, these changes have serious consequences for the people and communities that depend on coral reefs and other coastal ecosystems for their food and livelihood.

Important to evaluating these potential scenarios is an integration of the information generated from this project on the underlying mechanisms, sources of variability and potential roles of adaptation and acclimation. In integrating the knowledge across four sites in the world's tropical oceans, it is anticipated that a stronger basis will be developed for understanding and projecting the changes that have been proposed to occur. These perspectives on the nature and health of future reef systems under a warming world are critical for human societies to assess the likely cost or plan adaptive responses to rapid climate change in our tropical oceans.

Escape clauses: can genetic adaptation save the day?

Faced with rising sea temperatures and corals with tolerances that are being exceeded, genetic adaptation to these rising stress levels has been suggested as one scenario (Done 1999; Baker 2001a; Hoegh-Guldberg 2002b; Done et al. 2003; Baker et al. 2004). Simplistically, if thermal tolerance increased through adaptation at the same rate as seawater temperature increased, the rate of coral bleaching and mortality would remain constant and not increase (Hoegh-Guldberg 2002b). There is, however, no evidence of a rapid adaptive response by reef-building corals to the increase in thermal stress. The problem, as outlined above, is that the rates of environmental change may be much higher than the adaptive capacities of reef organisms. The current growth of greenhouse gas concentrations is two orders of magnitude greater than even that seen during the transitions from ice age to warm period. Future rates of change are predicted to be even higher than those seen over the last hundred years.

There is also very little, if any, evidence that suggests that corals and their *Symbiodinium* have adapted to the changes in sea temperature over the past 20 years. As mortality appears to be increasing not decreasing, and thermal thresholds appear to be in similar places as they were 20 years ago, all evidence appears to favour the suggestion that rates of change are exceeding the rates at which reef-building coral populations can adapt. This is not surprising given that corals are largely slow growing, asexual organisms that are involved in a complex intracellular symbiosis.

In future scenarios, dependence on the notion that more tolerant genotypes will arise via mutation is extremely risky, since the probabilities of the appropriate mutations arising in the time required are vanishingly small. This leaves three possibilities. The first is that populations contain individuals that are more tolerant and that these are selected as stress increases. The second is that a more tolerant population stock recruits from areas (e.g. lower latitudes) that are historically warmer. The last is by swapping their algal symbionts for other more tolerant varieties. This research program explores all three of these possibilities.

Inherent variability as a source of tolerant genotypes

Within any given population of corals, there will be differences among individuals with respect to genetic make-up. As thermal stress increases, more heat tolerant individuals will be selected in favour of those that are less heat tolerant. Conceivably then, the population would eventually become more heat tolerant even if genetic variability had decreased. There are two necessary properties that need to be established before the reality of this possibility can be established. The first is inherent variability in thermal tolerance within coral populations. The second is that selection acts to eliminate some but not all genotypes within a population.

There is little doubt that different individuals within a coral species have different tolerances. Edmunds (1994) noted differences in bleaching sensitivity among individuals of *Montastraea annularis* during mass bleaching events in the Caribbean. Similar differences across populations of corals within a single location have been noted by Glynn, Brown and others (Glynn 1993; Brown 1997). Some of these differences are due to the variation in secondary factors like light quality, which varies across and between colonies and can strongly affect the susceptibility to bleaching (Jones et al. 1998; Mumby et al. 2001). Other studies have shown differences may be due to different genotypes of *Symbiodinium* (Rowan et al. 1997). At present, these studies are in their infancy. A demonstration that differences between corals are genetically based as opposed to being phenotypic (because of acclimation) is lacking.

The demonstration of a strong role of selection across coral populations during mass bleaching events is equally speculative at this point. While there is no firm data outlining the possibility of mass bleaching events selecting more tolerant corals, two studies hint at the fact that this may have already occurred within populations in the Eastern Pacific and Okinawa. Peter Glynn and co-workers have noted that the impact of the 1997-98 event was smaller than the impact of the 1982-83 event, even though the size of the thermal anomaly was suggested to be the same (Glynn et al. 2001). The authors suggest that the reason lies in the 1998 population having become tougher because of selection of more tolerant individuals in the earlier event. While this is provocative, the data to say that the stress levels were identical is lacking. Most critically, light was not considered in both cases. As Jones et al. (1998) have demonstrated in laboratory trials, shading corals can dramatically reduce their tendency to bleach at a given temperature. The important influence of light on the outcome of a given level of thermal stress was highlighted by Mumby et al. (2001). In their study, much less bleaching occurred around Tahiti and Moorea in 1998 than expected from the calculated exposure to temperature stress. Most notably cloud cover was unusually high in 1998 at these locations, which most likely led to lower levels of stress.

Immigration of warm adapted genotypes

If the variability required for adaptive change is not present within a reef, then the second possibility is that it arises as part of the input from other reefs or reef systems. On the Great Barrier Reef, this might mean that larvae from more northerly, warm-adapted reefs are transported southward to reef systems where corals are being eliminated by thermal stress. In this way, there might be a southward movement of genotypes to replace those that were finding southern locations too warm. There are two components that are critical to whether or not this process is likely to occur or not. The first is a healthy source of larvae. The second is reef connectivity such that larvae can travel in substantial numbers between reefs.

Changes in climate are being felt on all coral reefs, irrespective of latitude (Hoegh-Guldberg 1999). This is due to the fact that corals and their symbionts are adapted to local conditions and sea temperatures are increasing across the planet. Consequently, there are no safe havens for corals. Given the impact of stress on reproduction (see discussion above), the possibility of large numbers of gametes flowing from warm-adapted reefs to reefs where corals are being eliminated by thermal stress is unlikely.

Differences in the connectivity of reef systems and the life histories of corals have been shown to be crucial for determining patterns of recovery or decline in Caribbean reef systems (Hughes et al. 2000). Recent evidence that coral populations may be largely self-seeding, and connected at the scale of the village, despite relatively high levels of genetic connectivity (Ayre and Hughes 2000) also challenges the idea that reef systems may rapidly be repopulated after the removal of adult corals. While reefs may remain connected genetically, the actual number of migrants that need to travel between reefs to maintain this connectivity may be higher than the few individuals per generation. Given that recovery of reefs would require large numbers of migrants arriving to rebuild coral populations, the demonstration of genetic connectivity does not imply connectivity on the level to rapidly repopulate a reef.

Other pieces of information also appear to indicate that reefs may be more self-seeding than first appreciated. Hughes et al (2000) demonstrated that the fecundity of adult corals and the establishment of larval recruits at a particular site are tightly correlated. In their study, the variation in space and time of the fecundity of three common Acropora species explained most of the variation (72%) in Acroporid (staghorn coral) recruitment. The dependence of recruitment on the size and health of the adult population also suggests that the direct effects of temperature (or any anthropogenic factor) on the fecundity of corals will have direct impacts on the abundance of new recruits and hence of adult reef-building corals.

Migration of warm-adapted genotypes of coral will occur as seas warm. The issues, as with other parts of this discussion, are that the speed at which migration can occur may fall short of the rapid rate of change. For example, warm-adapted coral species and genotypes may migrate to high latitudes but coral communities may still decline because the rate of invasion and subsequent growth of migrants fail to match the ever increasing level of thermal stress and mortality at any particular location.

Given the critical role that variability plays in determining rates of change within coral populations, assessing genetic variability and tolerance at different sites was a priority of the project. The development of population level genetic markers will also provide critical information on the interrelatedness of coral populations within regions and hence insight into whether there is potential for the rapid genetic change within populations that is required if adaptation is to keep pace with the rapid pace of current climate change.

Remaking the Holobiont (the Adaptive Bleaching Hypothesis)

It is highly likely that the properties that enable a coral to survive a given environmental circumstance will involve both coral and *Symbiodinium*. Both partners contribute genetic potential to the overall capabilities of the combination (or holobiont). Recent work has shown that *Symbiodinium* are highly diverse genetically, with many species being represented on coral reefs. One potential way to improve fitness would be to swap one genetic variety of *Symbiodinium* for another with a view to adopting a more tolerant genetic variety. Buddemeier and Fautin (1993) proposed that bleaching might be an adaptive behaviour that allows reef-building corals and other symbiotic invertebrates to adopt new genetic characteristics as regards to thermal tolerance. Although this idea continues to attract discussion (e.g. Baker 2001b versus Hoegh-Guldberg 2002b), it has yet to be unambiguously demonstrated.

As with any valid argument, the assumptions of this proposal must all be true if the argument's logic is sound. Ware (1996) formally state the assumptions of the Adaptive Bleaching Hypothesis (ABH). This has been a useful exercise as it allows detailed scrutiny of the hypothesis and its assumptions. While some of the assumptions underlying the ABH are true (e.g. *Symbiodinium* are genetically diverse), several critical assumptions are not supported by available evidence. For example, the hypothesis critically requires that "bleaching provides an opportunity for the host to be repopulated with a different type of partner". To date, the invasion of a bleached host by a new species of *Symbiodinium* has not been reported. While there is evidence that this has happened in geological time frames, the required observation that it can operate on the time scale of a bleaching event has not been observed. Attempts to infect aposymbiotic coral larvae (Weis et al. 2001) with the *Symbiodinium* of other coral hosts always resulted in ineffective establishment of a new symbiosis compared to that of the native symbiont. Similar results have been observed for other symbiotic hosts (Trench 1979).

The proponents of the hypothesis have now shifted emphasis to the potential that multicladal symbioses (those that contain more than one type of *Symbiodinium*) that shift the ratio of different clades or types of algae is proof of the Adaptive Bleaching Hypothesis. But as argued by Hoegh-Guldberg (1999), the observation of a change in the proportion of pre-existing genotypes also does not qualify as "the host to be repopulated with a different type of partner". Remixing may extend the thermal range of corals but it will not result in the rapid shifts in the genetic potential of coral populations that are required if coral populations are to keep up with climate change under even the mildest scenarios.

The ABH is a potential source of rapid genetic change in the composition of the holobiont. Given the importance of this type of change in determining how coral and symbiont populations respond to climate change, the BWG critically investigated whether or not there is evidence for this mechanism operating at ecologically relevant timescales.

What will be the state of the world's coral reefs in 2050?

If there is not a strong case for evolutionary adaptation playing a role in modifying the thermal tolerances of the reef-building corals that make up today's coral reefs, then under the scenarios, the only conclusion is that reef-building corals will no longer dominate today's "coral" reefs by the middle of this century. In this intervening period, reefs will have progressively lower amounts of reef-building corals. There are several serious ramifications of coral reefs that are no longer dominated by reef-building corals. The first is that much of the productivity and nutrient dynamics of reefs and coastal waters is likely to change as corals become rare. Secondly, because of the combined effects of thermal stress and increased carbon dioxide, the calcification on coral reefs is likely to be much reduced. This may lead to the net erosion of reefs among other issues. The third is that the biodiversity of coral reefs will be substantially reduced. And the fourth is that coral reef associated fisheries are likely to change as waters warm and benthic habitats change.

Productivity, nutrient dynamics and benthic habitats

Coral reefs are regions of high productivity within otherwise low productivity waters of the tropics. While some reefs prosper in turbid, high nutrient waters inshore, most coral reefs are located in low nutrient waters. As stated at the outset, the highly evolved associations that typify coral reefs are central to their success. Reef-building corals are the basis for the high levels of primary productivity of coral reef ecosystems. Photosynthetic energy captured by the *Symbiodinium* of corals is released directly to the water column as mucus or is consumed directly by filter-feeders, particle feeders and corallivores. Coral reefs also have highly evolved nutrient dynamics, with most coral reefs acting as sinks for inorganic nutrients (Hatcher 1988,1990,1997). The net effect of these nutrient dynamics is that coral reefs often support primary production values that may be as much as several hundred fold higher than those of surrounding tropical oceans (Hatcher 1988).

While it is hard to generalise, reefs that lose reef-building coral cover undergo fundamental changes in the types of organisms that dominate the substratum. Red coralline algae, macrophytes and cyanobacteria tend to dominate reef substrates following the loss of reef-building corals. While little has been done so as to understand how these new ecosystems function, primary productivity is almost certain to have varied from the original coral dominated ecosystem. Surfaces also play a key role in the nutrient dynamics of coral reefs and hence changes are likely within the nutrient dynamics of coral reefs. All of these changes are likely to have implications for organisms living on coral reefs.

A potentially important link between these types of changes and other organisms that are likely to be important to humans is the link between coral bleaching and the incidence of the fish toxin, ciguatera. In French Polynesia, the benthic dinoflagellate, *Gambierdiscus* spp., is the primary causative agent when people eat poisoned fish. *Gambierdiscus* produces a toxin that builds up in the tissues of fish that graze the reefs where it lives. Chateau-Degat et al. (2005) studied the seasonal abundance and toxicity of *Gambierdiscus* spp. on reefs around Tahiti and found peak densities of the dinoflagellate following a severe bleaching event in 1994. The authors speculated that coral morbidity may be another critical factor in the coral bleaching leading to blooms of *Gambierdiscus* spp. by providing "new surfaces" for colonization by opportunistic species of macroalgae that are ideal hosts for *Gambierdiscus* spp. cells. The recent review of ciguatera by Lehane and Lewis (2000) also concludes that the link between global climate change, mass coral bleaching and incidences of ciguatera is strong and may explain the growing numbers of cases of poisoning in the Pacific and elsewhere.

These types of changes could have major ramifications for the way that coastal ecosystems function and may have major implications for such critical aspects as food and water quality. Trying to develop a better understanding of these changes is central to the current project. The understanding of how coral abundance will change under global warming is critical to any projection of how the goods and services of a coral reef will change. This is important for understanding the socio-economic consequences of change within coral reef ecosystems.

Calcification

Calcification is one of the most important processes occurring on coral reefs. Through the energy expensive process of calcification, calcium carbonate deposition has built reefs through time. The net effect is the large areas of carbonate reefs that dot the world's oceans and the large deposits of calcium carbonate (limestone) dating from previous periods of reef growth. Through this process, the physical structure of the habitats in which thousands of species live has been created, and at a larger scale, coastlines are protected by coral reef barriers.

Reef-building corals and other symbiotic organisms produce the large amounts of calcium carbonate rock that are required to counter the significant forces of erosion. A fairly well supported hypothesis is that the dinoflagellate symbionts of these organisms produce the large amounts of energy needed to precipitate calcium carbonate (Barnes and Chalker 1990). The addition of CO_2 to seawater will lead to the formation of carbonic acid and a decrease in the calcium carbonate saturation state. Gattuso et al (Gattuso et al. 1998) and Kleypas et al. (1999b) calculated the doubling of atmospheric concentrations of carbon dioxide will lead to a 30% decrease in calcium carbonate saturation state (Ω). As calcification is directly dependent on the available pools of ions for calcification, these authors proposed that there would be a direct decrease in calcification. Since this work, several studies have shown unambiguously that calcification is essentially linearly dependent on Ω (Marubini et al. 2001; Leclercq et al. 2002; Reynaud et al. 2003; Langdon and Atkinson 2005; Kleypas and Langdon 2006).

As coral reefs represent a fine balance between calcification and erosion, decreases of this magnitude are potentially problematic and could result in the net erosion of existing coral reef matrices. Normal rates of calcium carbonate deposition by corals range up to 20 cm per year (or its equivalent of 10 kg $CaCO_3$ m^{-2} year^{-1}). Rates of reef growth (which is essentially the balance between deposition and erosion) are about 1-2 cm year^{-1} (Done 1999). This implies that ~90% of the calcium carbonate deposited is removed by erosion. Within this simple perspective, a decrease of 30% in deposition should place reef systems into net erosion (by 20%). Recent works in the Great Barrier Reef (De'ath et al. 2009) and Thailand (Tanzil et al. 2009) have revealed that coral reefs are calcifying at 15% lower rates today than they were three decades ago. Most importantly, this degree of downturn in calcification is unprecedented over the past four centuries.

Given the key roles that reefs play in providing habitat and protecting coastlines, the implications of the net erosion of coral reef structures is enormous. At this point in time, the process and potential rates of erosion (through physical and biological agents) is little understood. Clearly illuminating on these processes and their relationship to the rates at which calcium carbonate is likely to be deposited in the future should be a priority for research. Consequently, the targeted research group on coral bleaching is exploring the impact of thermal stress and decreasing alkalinity to gain a better perspective on how changing conditions will affect the fundamental processes of reef accretion and erosion. These studies have been extended in the field to investigate how changes to the abundance of reef-building corals under a variety of reef systems affect the net balance of calcium carbonate on coral reef erosion.

Figure 3. The Orange-spotted File fish (*Oxymonacanthus longirostris*) largely disappeared from Okinawan reefs after the collapse of coral populations during the 1998 mass bleaching event (Kokita and Nakazono 2001). Some fish stocks appear relatively unaffected by the loss of coral communities; others (probably obligate corallovores like *O. longirostris*) show rapid responses to the loss of coral stocks. Photo: O. Hoegh-Guldberg

Biodiversity

The impact of the reduced coral abundance on biodiversity is still in its infancy. Even the mildest climate change scenarios project substantial decreases in the amount of coral cover and consequently coral associations. Community changes like those seen by Loya et al. (2001) in Okinawa may be commonplace within the next few decades. How these changes will affect the thousands of other organisms on coral reefs is still being examined. Organisms that depend on corals for food or shelter and which reproduce via external fertilization might be predicted to face extinction as their primary habitat, corals, become extinct. The response of fish communities over the short term has yielded some surprises. In the Seychelles, for example, Spalding and Jarvis (2002) found that the overall structure of fish communities had changed very little despite massive decreases (3-20 fold) in living coral cover after the 1997-98 bleaching event. Counter to this is the observation of rapid decreases in the abundance of species that are obligate corallivores. The Orange-spotted filefish (*Oxymonacanthus longirostris*, Figure 3), a coral obligate, rapidly disappeared from Okinawan reefs after the 1998 bleaching event (Kokita and Nakazono 2001). Abundances of some fish also appear to increase following the loss of reef-building corals from reef communities. Lindahl et al (2001), for example, showed an overall increase in fish abundance after the 1998 mass bleaching event on Tanzanian reef systems. This was largely linked to an increase in herbivores. Similar conclusions have been seen in studies at other sites (Chabanet 2002). Recent reviews showed that coral-bleaching events lead to unequivocal reductions in fish densities and diversity, which lagged behind the thermal event by up to 2-3 years (Munday 2004; Wilson et al. 2006; Munday et al. 2007; Pratchett et al. 2008).

Other organisms are also likely to respond to changes in coral cover. For example, over 55 species of decapod crustacean are associated with living colonies of a single coral species, *Pocillopora damicornis* (Abele and Patton 1976; Black and Prince 1983). Nine of these are known to be obligate symbionts of living pocilloporid coral colonies. Branching corals of the genus *Acropora*, for example, have at least 20 species of obligates symbionts that depend solely on *Acropora* to provide habitat. It is important to point out that the spacing of corals on a habitat may be critical for the reproductive success of coral associates that require sexual reproduction to proceed to the next generation. As corals become rare (i.e. spaced farther and farther apart), these organisms may be threatened as the chance of finding a partner or attaining successful fertilization becomes smaller. While the pathway and time course of this change is undefined, few experts are suggesting that biodiversity will be unaffected by a rapid loss of reef-building corals from the system. Our understanding of the impacts of climate change on biodiversity, however, is in its infancy and is a high priority of studies to be undertaken within the BWG projects.

Research
directions
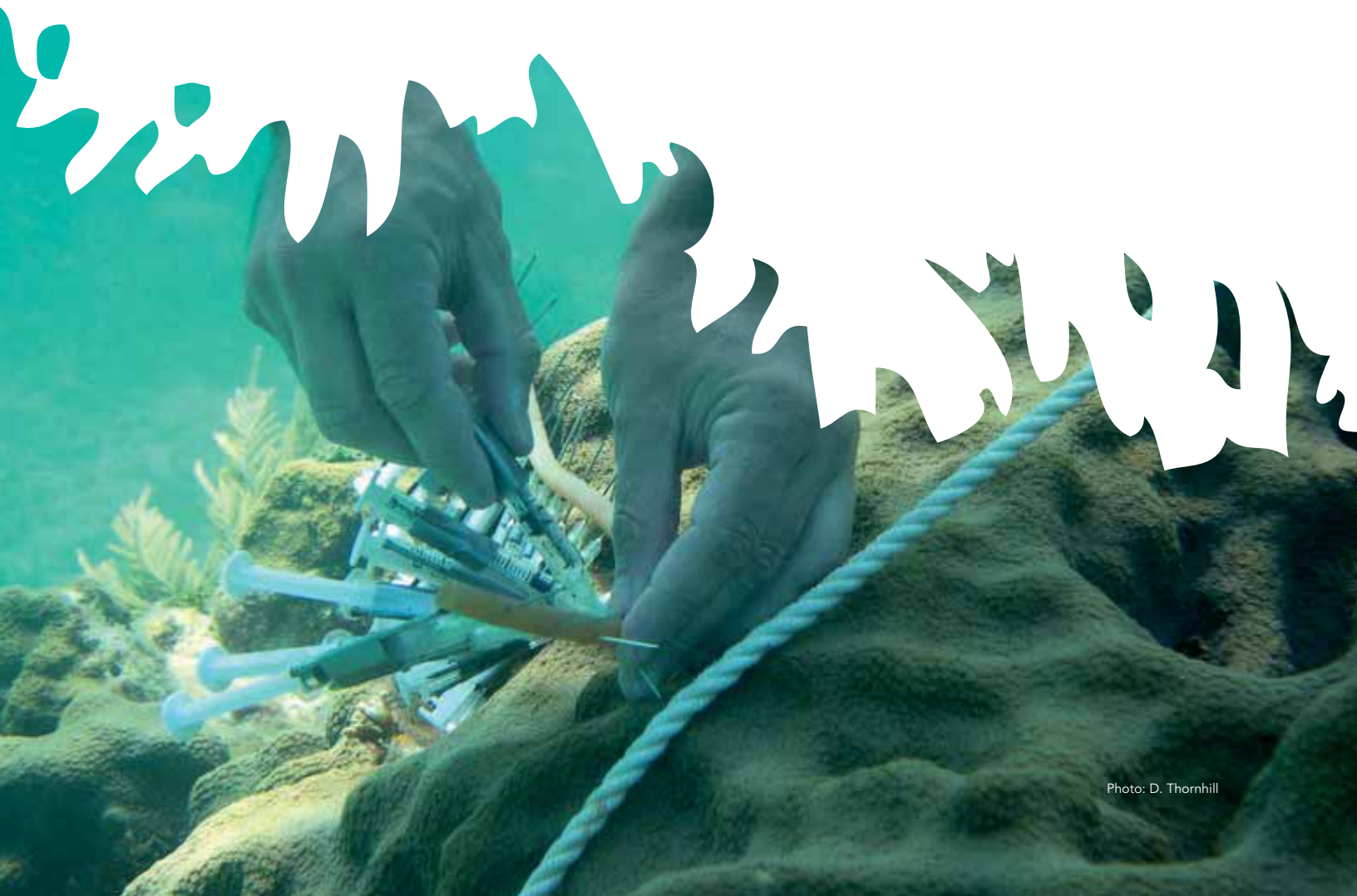
As outlined in the Introduction, there are many gaps in our understanding of coral reefs and change. In the design stage of the BWG workplan, a number of research priorities for management and policy development were identified. Given the funding, expertise and research priority, the BWG identified a number of key research themes on which it focused during the initial five-year period. It was very clear from the start that it would be impossible to tackle all questions at all sites where reefs are in decline. In keeping with the major part of its theme – mass coral bleaching – the major focus of the BWG research program was climate change, coral bleaching and its interaction with local ecological factors. In this regard, the BWG was set to contribute heavily to four major themes. These themes formed a major research focus, along with studies that explored their relationship to each other, and the need for a better understanding of the likely changes as the climate warms and carbonate in our oceans declines. This led to consideration of a number of strategies that we must implement as a society to counter the real impacts on coastal human society.

Programs

Coral-symbiont responses to thermal stress

What is changing?

Organismal mechanisms to ecological outcomes

Biomarkers of stress

How fast and where is change occurring?

Projections of change and socio-economic impact

Adaptive responses

In the original BWG research plan, 13 projects were identified. These projects brought together several of the BWG members along with their postdoctoral fellows and postgraduate students and were completed by the middle of year five of the project. As these projects were pursued, several were merged to form ten final projects. An overview of the activity, successes and products from each of these research projects are described in the section entitled scientific outcomes. In other sections, research training, conference presentations and workshop activities are also described.

Member
biographies

Ove Hoegh-Guldberg
(University of Queensland, Australia; CHAIR)

Ove Hoegh-Guldberg is Professor and Director of the Centre for Marine Studies at the University of Queensland. He completed his BSc. Hons at the University of Sydney and PhD at UCLA in 1989, and was recognized in 1999 with the Eureka prize for Scientific Research into the physiological mechanisms of coral bleaching. Specialising in the impact of climate change on biological systems, Professor Hoegh-Guldberg has worked in polar, temperate and tropical regions, particularly on the impacts of ocean warming and acidification on coral reefs. He has produced over 160 peer-reviewed publications and has mentored over 30 postgraduate students. Professor Hoegh-Guldberg is currently a Queensland Smart State Premier's Fellow, works closely with several industry and NGO groups on climate change related issues, and is a reviewing editor at Science Magazine. In mid 2009, he became Director of the Global Change Institute at the University of Queensland. Details of his laboratory group can be found at: www.coralreefecosystems.org.

Yossi Loya
(Tel Aviv University, Israel; CO-CHAIR)

Yossi Loya is a Professor at the Department of Zoology, Tel Aviv University, Israel and incumbent of the Raynor Chair for Environmental Conservation Research. He completed his PhD at the Department of Ecology and Evolution, State University of New York at Stony Brook in 1971. He has published over 200 papers on a wide range of coral reef subjects including Ecology and Evolution, Biodiversity; Conservation and Management; Theoretical Ecology; Competitive networks; Marine pollution; Coral diseases; Reproductive strategies of corals, and Global climate changes and their effects on reef corals. In recognition for his significant contribution to coral reef science he was awarded the quadrennial Darwin Medal by the International Coral Reef Society in 2000. Yossi has been the mentor of 25 PhD and 45 MSc students comprising today the backbone of coral reef researchers in Israel. Most recently (2009) he has been elected as the first member in the field of Ecology to the Israeli Academy of Sciences.

John Bythell
(University of Newcastle, United Kingdom)

John Bythell's PhD research was based at the West Indies Laboratory (WIL), St. Croix from 1985-88 working on a nitrogen and carbon budget for *Acropora palmata*. He then took up a lectureship at WIL and stayed on at St. Croix up to 1991. He was involved in establishing the coral reef monitoring programme at Buck Island on St Croix, run by the National Park Service since it was established in 1988. Since 1991 he has been at Newcastle, which houses a centre for tropical research and teaching. He was director of the Master's degree programme in Tropical Coastal Management from 1999-2003, which has some 200 graduates working in coastal management worldwide. His research spans community-level dynamics to cellular and molecular stress responses in corals and related organisms. Recent work has focussed on culture-independent analysis of bacterial communities associated with corals and investigating the structure and function of the coral surface mucus layer that protects the coral from pathogen invasion.

William Fitt
(University of Georgia, Athens, USA)

William Fitt is a Professor of Ecology and Marine Science at the University of Geórgia. He did his PhD at the University of California at Santa Bárbara on how zooxanthellae get into their hosts, and several postdocs, including one on giant clams and another on the jellyfish *Cassiopea*. He works primarily in the Western Atlantic doing research at several sites and monitoring the health of coral reefs. In the past five years Dr Fitt has worked with postdoctoral student and now Assistant Professor Todd LaJuenesse and students Dusty Kemp (the role of different clades of zooxanthellae in the same species of coral), Jennifer McCabe Reynolds (photo-protection of zooxanthellae), and Tom Shannon (symbionts in flatworms).

Ruth Gates
(University of Hawaii, USA)

Ruth D. Gates is an Associate Research Professor at the Hawaii Institute of Marine Biology (HIMB), a research unit embedded within the School of Earth and Science and Technology at the University of Hawaii, Manoa. HIMB combines close proximity to a living reef with the capacity to support a full range of research activities that span field operations to functional genomics. Her research focuses on the mechanisms by which reef corals sense and respond to changes in the marine environment, and spans a range of scales from ecological to molecular. Within this context, her current research is aimed at understanding how the biological complexity added by the intimate associations between corals and a diverse range of other organisms map onto the environmental resilience of corals. This research is implemented in the context of a dynamic training program involving undergraduates, graduate students, postdoctoral scholars and junior faculty members.

Roberto Iglesias-Prieto
(Universidad Nacional Autónoma de México)

Roberto Iglesias-Prieto obtained his PhD at the University of California, Santa Barbara. After two years of postdoctoral training at UCSB, he accepted a position as a senior research scientist at the Center for Scientific Research and Higher Education of Ensenada in northwest Pacific coast of Mexico. Since 1996 Roberto moved to the Puerto Morelos Academic Unit of the Institute of Marine Science and Limnology of the Universidad Nacional Autónoma de México, where he is a full research professor and chair of the Academic Unit and of the Centre of Excellence of Mesoamerica within the CRTR Program. Roberto's research interests range from the basic photobiology of corals to the ecological and evolutionary consequences of specificity in algal-invertebrate symbioses. When Roberto is not studying the responses of algal-invertebrate sea monsters to climate change, he enjoys sailing and playing traditional Mexican music.

Michael Lesser
(University of New Hampshire, USA)

Michael P. Lesser is a Research Professor at the University of New Hampshire where he also obtained his BSc and MSc degrees. He earned his PhD. at the University of Maine working on the effects of ultraviolet radiation on marine organisms, and then was a postdoctoral fellow at the Bigelow Laboratory for Ocean Sciences. He has worked extensively in the area of ultraviolet photobiology in the Antarctic, Gulf of Maine, and tropical coral reefs around the world as well as the physiological ecology of marine invertebrates in temperate subtidal and intertidal systems. Dr. Lesser has spent most of his research career studying oxidative stress in marine organisms and in particular he has studied extensively the role of oxidative stress in the coral-bleaching phenomenon. His current research focuses on the physiology and ecology of sponges and corals in the mesophotic zone (30-150 m) of coral reefs.

Tim McClanahan
(Wildlife Conservation Society, Kenya)

Tim McClanahan is a Senior Conservation Zoologist at the Wildlife Conservation Society, where he has worked for the past 17 years. He works on the ecology, fisheries, climate change, social-ecological systems, and management of coral reefs and also enjoys interdisciplinary research with a view to solving broader conservation and science issues. During the past 25 years his research has evolved from a focus on prioritizing the effects of human disturbance on coral reefs, the role of marine protected areas, developing theoretical and simulation models of coral reefs, practical means to restore degraded reefs through manipulation of the food web and management, and understanding human organization around resources and management. Most recently he has been investigating the interaction between climate change, coral reef management and human adaptive capacity.

Robert van Woesik
(Florida Institute of Technology, USA)

Robert van Woesik is a professor in the Department of Biological Sciences at the Florida Institute of Technology. He did his PhD at the James Cook University, Australia. His research interests are broad but ultimately linked to population ecology of scleractinian corals. Research includes the spatial and temporal assessment of coral assemblages and the application of that ecology to the management of coral reefs. Robert's approach is often multi-disciplinary utilizing a combination of empirical and mathematical techniques. He is interested in understanding vital rates and key processes that underlie and drive state variables on coral reefs. Most recently, he has become interested in ecological questions related to thermal stress, coral bleaching and predictive modelling of coral population trajectories under different climate change scenarios.

Christian Wild
(University of Munich, Germany)

Christian Wild received his PhD in 2003 from Max-Planck Institute for Marine Microbiology in Bremen, Germany. He then worked as the focal point for coral reef issues at IOC-UNESCO in Paris, France. Since 2006, he leads the junior research group Coral Reef Ecology (CORE) at the University of Munich, Germany. His group investigates biogeochemical processes and ecological functioning in coral reef ecosystems in the light of environmental change. A special focus thereby is put on understanding the role of hermatypic corals as reef ecosystem engineers in comparison to other key organisms, in particular reef algae. Research in the last 5 years was mainly carried out at the Mexican and Australian CoEs along with seasonal studies in the Northern Red Sea.

Lianne Cook
(University of Queensland, Australia; Administrator)

Lianne has more than 20 years administration and project management experience, having been an Army Officer both in Australia and overseas. During that time she wrote and delivered training packages at the Army Training Centre in Bandiana, worked as a consultant with the British Army in Germany, designed warehousing projects and administered a Logistics Group of more than 700 staff. She has also worked for not-for-profit organisations working with youth and children at risk. She is an accredited and practicing Life Coach and has worked as a consultant for Government, charity organisations and private enterprise including Boeing Australia. Her interests include photography and art, and she has won several prizes for her poetry and has held several photography exhibitions as well as producing a calendar and book. She is now the Research Manager for the Hoegh-Guldberg lab at Centre for Marine Studies, UQ.

Past members (2004-2008)

David Obura
(CORDIO-East Africa; Kenya)

David Obura is the coordinator for the Coral Reef Degradation in the Indian Ocean (CORDIO) East Africa, supporting activities in mainland Africa and the island states, including research, monitoring and capacity building of coral reefs and coastal ecosystems. A primary focus is the implications of global and local threats to coral reef health and their long term prospects and provision of socio-economic benefits. He received a PhD from the University of Miami in 1995 on coral bleaching and life history strategies, which has developed into a primary research interest in climate change, coral bleaching and resilience of coral reefs. Other areas of work include the development of participatory monitoring and research tools with artisanal fishers in East Africa, and remote-reef surveys such as in the Phoenix Islands, central Pacific, and in the central and western Indian Ocean.

Ron Johnstone
(University of Queensland, Australia)

Ron Johnstone is an Asssociate Professor who currently heads a research team engaged in coastal ecosystem function, sustainability and management projects for the University of Queensland. He has a long professional history in coastal nutrient and ecosystem function research and a longstanding international reputation, having worked in over 13 countries. Current work on the expanded emergence of toxic algal blooms and the functional ecosystem outcomes on coral death all focus on adaptation to climate change and the ecosystem elements underpinning this.

Glossary

ABH: Adaptive Bleaching Hypothesis

BWG: the Bleaching Working Group

CRTR: Coral Reef Targeted Research & Capacity Building for Management

CoE: Centre of Excellence

DHM: Degree Heating Months

ENSO: El Niño Southern Oscillation

EST: Expression Sequence Tags

GBIF: Global Biodiversity Information Facility

GCRMN: the Global Coral Reef Monitoring Network

GEF: the Global Environment Facility

IOC-UNESCO: Intergovernmental Oceanographic Commission

IUCN: the International Union for Conservation of Nature

SST: Sea Surface Temperatures

UNEP: United Nations Environment Programme

WIO: The Western Indian Ocean

Photo: A. Zvuloni

Scientific outcomes

As outlined above, reef-building coral and their symbionts are critical to coral reefs as the principal frame-builders and habitat forming organisms of these vast ecosystems. They are also among the organisms most affected by climate change. Several gaps in our knowledge limit our understanding of the likely changes facing coral reefs, and whether or not corals and their symbionts will adapt to climate change. Consequently, 10 projects listed on the following pages were undertaken to improve our understanding of these key aspects. This number does not include the many MSc and PhD projects that were associated with the Project.

Photo: A. Zvuloni

Theme 1
Coral-symbiont responses to thermal stress

Understanding the responses of corals and their symbionts to thermal stress lies at the heart of understanding the differences between corals in terms of their sensitivity to climate change, as well as opening the door to particular management strategies that aim to protect more resilient coral communities as part of the response to climate change. Six projects were developed which sought to rapidly improve our understanding of this important area.

Project 1. Resolving the Adaptive Bleaching Hypothesis

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The Adaptive Bleaching Hypothesis (Buddemeier and Fautin 1993) proposes that corals have the ability to rapidly evolve tolerance to changes in ocean temperature that are likely by the end of the current century. This has split the professional opinion into two camps. Those researchers who support this idea (e.g Baker 2001b; Little et al. 2004; Rowan 2004) propose that bleaching promotes a rapid exchange of dinoflagellate symbionts such that corals will rapidly evolve greater tolerance to climate change driven impacts on ocean temperature. In this regard, the Adaptive Bleaching Hypothesis (ABH) holds that "evolutionary switching" occurs within ecological time frames which may enable corals to swap their symbionts for more heat tolerant ones. The other research groups (e.g. Hoegh-Guldberg 2002b; Goulet and Coffroth 2003; Goulet 2006; Goulet 2007) have concluded that the symbiosis between reef-building corals and dinoflagellate symbionts is not flexible to any real extent in ecological time, and that bleaching does not allow the rapid evolution of thermal tolerance.

This project had three main components. The first was the production of a critical review regarding the state of understanding and an evaluation of the evidence for and against the ABH. This was published in the journal *Perspectives in Plant Ecology, Evolution and Systematics* (Stat et al. 2008). The second was a workshop which was held in May 2005 at the Centre of Excellence (CoE) at Puerto Morelos. The workshop included researchers from both camps, representing all points of view. The major outcome of this workshop was a consensus statement on the issues associated with the ABH, which was agreed to by the 58 discussants at the Puerto Morelos meeting in May 2005. This consensus statement appears below. The third was a series of studies aimed at exploring the flexibility of host-*Symbiodinium* combinations in different environments. In the latter case, reciprocal transplant studies from one environment to another were explored in terms of whether or not these combinations could change over time.

Photo: D. Obura

Two significant studies were undertaken during the project, both demonstrating that coral-*Symbiodinium* combinations were not flexible when transferred between environments (Iglesias-Prieto et al. 2004; Sampayo et al. 2007). This and the high degree of fidelity observed between coral hosts and particular genotypes of *Symbiodinium* (Project 3) indicate that the symbiosis is relatively inflexible in the short time frames associated with ecological changes such as mass coral bleaching. This suggests that the Adaptive Bleaching Hypothesis is incorrect.

Photo: T. McClanahan

Key literature generated with full/partial project support:

1. Stat M, Carter D, Hoegh-Guldberg O (2006) The evolutionary history of Symbiodinium and scleractinian hosts-symbiosis, diversity, and the effect of climate change. Perspectives in Plant Ecology, Evolution and Systematics 8:23-43
2. Hoegh-Guldberg O (2009) Climate change and coral reefs: Trojan horse or false prophecy? A response to Maynard et al. (2008). Coral Reefs, in press

Consensus statement on the current understanding of the diversity, specificity, and flexibility of *Symbiodinium* symbioses

Statement agreed to by participants at Puerto Morelos meeting (May 17 2005)

Dinoflagellates in the genus *Symbiodinium* are the principal symbionts of reef-building corals as well as hosts from several other phyla. These single-celled photosynthetic organisms generally occur intracellularly within host cells. Once thought to represent a single species, *Symbiodinium microadriaticum*, they are now considered phylogenetically diverse and include a number of described species.

Corals and their dinoflagellate symbionts exhibit a range of specificities. Some coral species transfer symbionts directly between generations, while others acquire symbionts from the environment anew at each generation. In the latter case, the events that lead to the establishment of *Symbiodinium* symbioses are relatively specific despite the fact most genotypes can be taken up by host cells initially.

The initial types of *Symbiodinium* that enter newly settled corals appear to be a subset of those available in the environment. This set of *Symbiodinium* types is further narrowed down to the complement dominant within the adult host and its environment, although some types may persist at background levels within the tissues of the host coral.

The processes by which one or several symbionts become dominant within the host have yet to be described, but probably involve host-symbiont recognition, specific host factors and competition between *Symbiodinium* genotypes. Future studies need to focus on understanding these mechanisms and their relative importance.

Adult corals may change their symbiotic complement in response to environmental change. 'Shuffling' and 'switching' are two non-exclusive mechanisms by which this may be accomplished. 'Shuffling' is a quantitative (compositional) change in the relative abundance of symbionts within a colony; 'switching' is qualitative change involving symbionts acquired from the environment. These exogenous symbionts may represent types that are new to the colony but not the species, or may be truly novel to the host species which is referred to as 'evolutionary switching.'

While evolutionary switching is assumed to explain the phylogenetic patterns of symbiont distribution within hosts, such events are thought to be very rare. Shuffling and/or switching of existing symbionts are thought to be more common. However, distinguishing between evolutionary (and truly novel) switches, and those that involve existing symbionts, is a methodological challenge.

Some corals routinely shuffle symbionts as a consequence of seasonal regulation of symbiont numbers with or without visual signs of bleaching. Corals can also shuffle symbionts during and after bleaching. Switching is also likely to be promoted by seasonal regulation and bleaching. Both shuffling and switching may be important mechanisms that extend the ability of corals to acclimatise to changes in the environment but requires further investigation to demonstrate true physiological advantages of the change involved.

Bleaching probably did not evolve directly as a mechanism for shuffling or switching symbionts, and has clear pathological effects. A potential side effect of bleaching is an acceleration of symbiotic change, which has the potential to elevate the tolerance threshold of coral reefs to environmental change. However, without evolutionary switching, there will be no change in the tolerance threshold for any particular coral-*Symbiodinium* symbiosis.

Widespread concern persists within the research community over the future of coral reef ecosystems. Increasing temperatures as well as ocean acidification and other anthropogenic challenges continue to pose grave threats to the future of these ecosystems and the people who depend on them. Unless these threats are addressed as a priority soon, coral reefs will continue to degrade.

This project and the publications stemming from it has concluded that rapid changes to the thermal sensitivity from the symbionts 'shuffling' are limited, and that evidence of novel symbioses forming (and changing the thermal threshold of corals) at ecological timescales is nonexistent.

Figure 4. Scott Santos addresses the BWG workshop on "Diversity, flexibility, stability, physiology of *Symbiodinium*, and the associated ecological ramifications."

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Bleaching and Related Ecological Factors:
CRTR Working Group Findings 2004-2009
Theme 1: Coral-symbiont responses to thermal stress

1

List of participants at the Puerto Morelos meeting continued

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Project 2. Understanding the fundamental mechanisms of coral bleaching

Erika Díaz-Almeyda, Florencia Colombo, Sophie Dove, Susana Enríquez, Paul Fisher, William K. Fitt, Luis González-Guerrero, Xavier Hernández-Pech, Ove Hoegh-Guldberg, Roberto Iglesias-Prieto, Dusty Kemp, Michael P. Lesser, Robin Smith, and Patricia Thomé.

Location: Australasian CoE and Mesoamerican CoE

Key results

In this project we explored the early responses to thermal stress by the symbiotic algae and the coral host. This led to a major breakthrough in terms of our understanding of how light is amplified by scattering within coral skeletons that are undergoing mass bleaching. This also led to a physiological model that is onset with a relatively mild imbalance in the rate of energy capture by the algae, and the rate of utilization of this energy. The initial compensatory photoprotective mechanisms fail to protect as the host skeleton increases the internal light fields leading to the collapse of the symbiotic association. This phenomenon leads to the propagation of oxidative stress in the animal host resulting in increasing levels of DNA damage and eventually in cell death. The results of this model helped explain the sharp tipping point observed for coral bleaching, as well as why corals differ in their thermal tolerance and sensitivity to coral bleaching.

Figure 5. Bleached (left hand side) versus normal (right hand side) Acropora near Great Keppel Island, Southern Great Barrier Reef in January 2006.
Photo: O. Hoegh-Guldberg

Background

Coral bleaching can be defined as the disassociation of the symbioses between marine invertebrates and symbiotic dinoflagellates. This phenomenon manifests itself as a loss of coral pigmentation, resulting from reductions in symbiont densities and/or cellular photosynthetic pigment concentrations (Figure 5). While coral bleaching can be elicited as a response to several environmental insults, most massive bleaching events have been associated with the prolonged presence of sea surface temperatures (SST) above the regional long-term summer average (Thompson and van Woesik 2009a; Thompson and van Woesik 2009b). The observed increases in frequency and severity of coral bleaching events during the last couple of decades is a direct result of global climate change and therefore is considered a major threat for the future of coral reefs. Despite its obvious importance, our understanding of the molecular and cellular mechanisms responsible for coral bleaching is far from complete (van Oppen and Gates 2006). Some areas of research such as the study of early effects of thermal stress on the photosynthetic responses of symbiotic dinoflagellates and the subsequent propagation of damage by the formation of free radicals are relatively well documented (Lesser 2006; Fitt et al. 2009), while others, such as the mechanisms behind the loss of symbiotic dinoflagellates from host tissues are less clearly understood.

Coral bleaching is a complex phenomenon that involves the responses of at least two organisms with different evolutionary histories. This phenomenon is initiated after a stressful stimulus is perceived by one or the two members of the symbioses and propagates through the intact symbiotic association (holobiont) after many interconnecting steps, probably following different pathways, all of which terminate with the breakdown of the symbioses, and in some extreme cases results in massive coral mortality (Muller et al. 2008). In this project we explored the mechanistic basis behind the propagation of thermal stress of relatively small amplitude, into significant light and oxidative stressful conditions in the holobiont. We place particular emphasis on the role played by solar radiation in the reception and magnification of the stress generated by exposure to elevated temperatures. The description of cellular and molecular events connecting stressful conditions with the disassociation of the symbiosis is a prerequisite for the development of models capable of predicting the possible ecological responses of these organisms under future climatic scenarios.

Methods

Throughout the project we employed an extensive suite of methodological approaches that allowed us to:

a. Define the optical properties of coral skeletons.

b. Provide a functional definition of the bleaching phenotype.

c. Characterise possible sites of damage for thermal stress.

d. Identify the physiological and biochemical signaling pathways linking the initiation of thermal stress in both members of the symbiosis, and the induction of the characteristic loss of pigmentation.

We used state-of-the-art spectroscopic techniques, in conjunction with classical methods for the determination of the basic biometric descriptors of coral physiology to describe the optical properties of intact coral surfaces with different densities of photosynthetic pigments. In addition, we evaluated the effect of the presence of different algal symbionts on the responses of the holobiont to thermal stress, using molecular techniques that allowed us to identify different *Symbiodinium* types at a level equivalent to species.

The identification of possible targets for thermal stress in *Symbiodinium* required the use of various types of techniques based on analyses of the chlorophyll a (Chl *a*) fluorescence signals, in combination with numerous biochemical techniques such as different chromatographic analyses of pigments and lipids, and the use of several different inhibitors of specific cell functions.

The preliminary description of the signaling pathways involved in coral bleaching required the use of multiple biochemical and physiological approaches to detect responses. These ranged from changes in the patterns of abundance of several key enzymes involved in scavenging radical oxygen species; expression of all chromophore proteins; light harvesting complexes; to spectroscopic techniques to evaluate the role of multiple scattering by different coral skeletons in the amplification of the internal light fields.

In collaboration with several members of the Remote Sensing Working Group, we are currently developing a model to predict the intensity of coral bleaching at large geographical areas based on satellite determinations of SST and solar radiation in conjunction with an explicit physiological model of coral bleaching. This product has the potential of increasing the sensitivity of the current bleaching predictions based only on sea surface temperature.

Photo: O. Hoegh-Guldberg.

Results and discussion

This project has achieved its research goals and has significantly advanced our understanding of the fundamental mechanisms underpinning coral bleaching.

a. Functional definition of coral bleaching

In the absence of acute thermal stress, reef corals respond to seasonal variations in temperature and solar radiation adjusting their physiology and biochemistry in a process that is very similar to the photoacclimation observed in corals growing in a vertical depth gradient. In summer chlorophyll a (Chl *a*) densities are significantly lower than in winter. Although corals look pale to the naked eye they are perfectly functional (Figure 6); actually, maximum growth rates are achieved under these circumstances (Fitt et al. in press). Analyses of the optical properties of intact corals revealed a non-linear variation of coral absorptance (% of incoming light absorbed by the tissue) as a function of coral pigment density (Enríquez et al. 2005; Rodríguez-Román et al. 2006). Corals can reduce up to 70 percent of their Chl *a* density in summer with only a minor change in their apparent coloration (Anthony et al. 2007; Apprill and Gates 2007; Fitt et al. in press). It is only when pigment densities fall below a threshold that the coral colonies experience coral bleaching. In this context, coral bleaching describes a condition in which a catastrophic reduction in pigment density results in a dysfunctional holobiont (Dove et al. 2006).
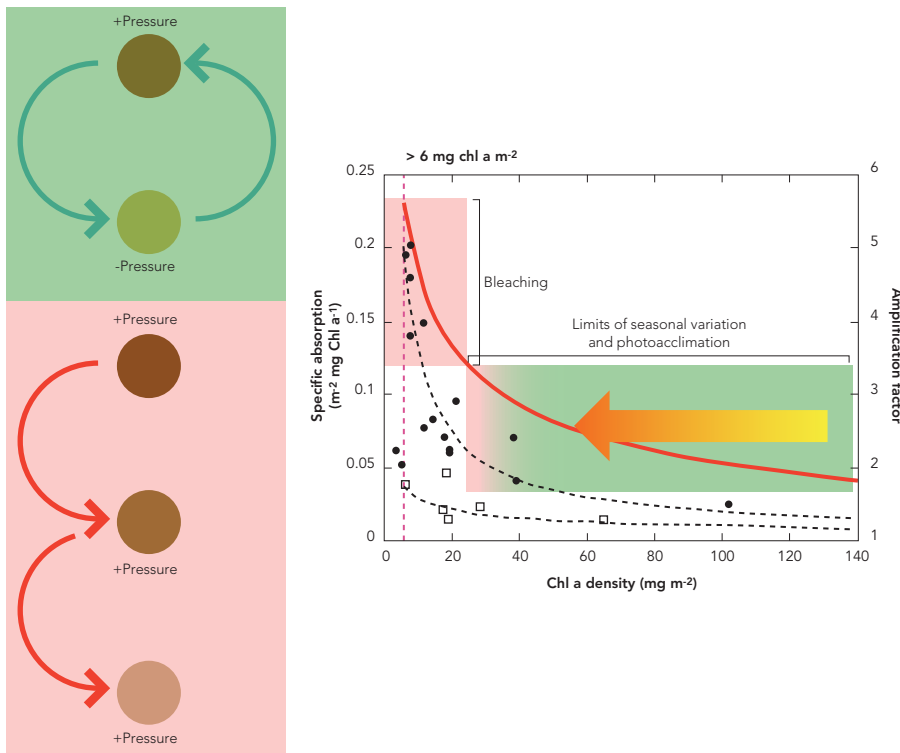

Figure 6. Effect of multiple scattering by coral skeletons on the efficiency of energy collection at different Chl *a* densities. Left-hand diagram depicts the interaction under normal circumstances (green) where small losses of pigmentation occurs to adjust light harvesting without a major increase in internal light fields, and stress situations where the loss of pigment leads to a positive feedback loop in terms of pigment and amplifying light fields. The right-hand diagram reveals where these conditions lie in the spectrum of densities of chlorophyll. The y-axis indicates the specific absorption by chloroform as well as the amplification factor.

b. Identification of the initial target of thermal stress

One of the most general responses to thermal stress in symbiotic corals is a reduction of the photosynthesis to respiration ratio, suggesting that algal photosynthesis is probably the most thermo-labile component of the holobiont (Franklin et al. 2006; Ainsworth et al. 2008b). Early work on this area revealed that thermal stress uncouples light harvesting and photochemistry and that event is sufficient to trigger several compensatory mechanisms to restore normal energy flow (Dove et al. 2006; Dove et al. 2008). To date, several possible targets for the observed uncoupling have been identified: lipid phase transition, damage of photosystem II or its repair cycle, and inactivation of key enzymes in the carbon fixation pathway (Jones et al. 1998). Although there is still controversy about the initial target of thermal stress, all studies concur that the loss of alga photosynthetic function is one of the earliest signs of thermal stress (Fitt et al. 2009).
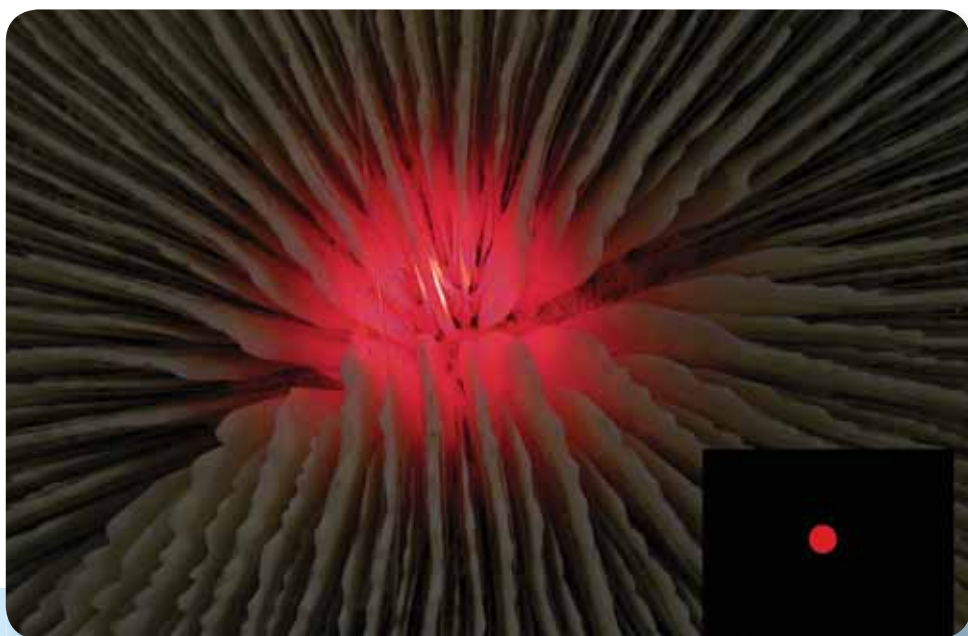
c. Compensatory mechanisms and the propagation of thermal stress

Upon the onset of thermal or any other stress condition (Nakamura et al. 2005; Dove et al. 2006; Leggat et al. 2006; Shenkar et al. 2006; Anthony et al. 2008; Dove et al. 2008), the reduction in the photosynthetic activity of the symbiotic algae is sensed as an imbalance between the total solar radiation collected by the photosynthetic antenna and the amount of sinks for this solar energy. The first response to this imbalance is the down regulation of the photosynthetic antenna and the up regulation of the enzymes acting as sinks, in a process very similar to high-light photoacclimation (Rodríguez-Román et al. 2006; Papina et al. 2007). At this stage thermal stress has been sensed as light stress that triggers a reduction in the optical cross section of the algae (Dove et al. 2006). Coral bleaching may be the result of an uncontrolled high-light photoacclimation mediated by the optical properties of the coral skeleton.

d. Multiple scattering by the coral skeleton increases light stress

Multiple scattering by the aragonite coral skeletons (Figure 7) increases dramatically the efficiency of solar radiation collection (Enriquez et al. 2005). Depending on the Chl a densities of the tissue, the amplification of the internal light fields results in an 8-fold increase in the efficiency of solar collection (Figure 6). In this context, when the reductions in the optical cross section of the symbiotic algae respond to thermal stress, they further propagate the damage as cells are exposed to a more intense solar radiation field in a positive feedback loop (Rodríguez-Román et al. 2006). The deleterious effects of light amplification by multiple scattering by the coral skeleton are not restricted to the algae and to visible radiation; higher ultra violet exposures are responsible for the accumulation of DNA damage under bleaching conditions and to the propagation of oxidative stress (Lesser 2006; Fitt et al. 2009). Uncontrolled oxidative stress is responsible for the induction of apoptosis or necrosis that leads to coral mortality (Dunn et al. 2004).

Figure 7. Multiple scattering of light by the aragonite crystals of the coral skeleton. Both panels were illuminated by a laser beam.
Photo: R. Iglesias-Prieto

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Key literature generated with full/partial project support:

1. Ainsworth TD, Hoegh-Guldberg O, Heron SF, Skirving WJ, Leggat W (2008) Early cellular changes are indicators of pre-bleaching thermal stress in the coral host. Journal of Experimental Marine Biology and Ecology 364:63-71

2. Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. Proceedings of the National Academy of Sciences USA 105:17442-17446

3. Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics and coral mortality risk: effects of temperature, light and sediment regime. Limnology and Oceanography 52:716-726

4. Apprill AM, Bidigare RR, Gates RD (2007) Visibly healthy corals exhibit variable pigment concentrations and symbiont phenotypes. Coral Reefs 26:387-397

5. Biel KY, Gates RD, Muscatine L (2007) Effects of free amino acids on the photosynthetic carbon metabolism of symbiotic dinoflagellates. Russian Journal of Plant Physiology 54:171-183

6. Dove S, Ortiz JC, Enríquez S, Fine M, Fisher P, Iglesias-Prieto R, Thornhill D, Hoegh-Guldberg O (2006) Response of holosymbiont pigments from the scleractinian coral Montipora monasteriata to short-term heat stress. Limnology and Oceanography 51:1149-1158

7. Dove SG, Lovell C, Fine M, Deckenback J, Hoegh-Guldberg O, Iglesias-Prieto R, Anthony KRN (2008) Host pigments: potential facilitators of photosynthesis in coral symbioses. Plant Cell and Environment 31:1523-1533

8. Dunn SR, Thomason JC, Le Tissier MD, Bythell JC (2004) Heat stress induces different forms of cell death in sea anemones and their endosymbiotic algae depending on temperature and duration. Nature - Cell Death & Differentiation 11:1213-1222

9. Edmunds PJ, Gates RD (2008) Acclimatization in tropical reef corals. Marine Ecology Progress Series 361:307-310

10. Edmunds PJ, Gates RD, Leggat W, Hoegh-Guldberg O, Allen-Requa L (2005) The effect of temperature on the size and population density of dinoflagellates in larvae of the reef coral Porites astreoides. Invertebrate biology 124:185-193

11. Fitt WK, Gates RD, Hoegh-Guldberg O, Bythell JC, Jatkar A, Grottoli AG, Gomez M, Fisher P, Lajuenesse TC, Pantos O, Iglesias-Prieto R. ,Franklin DJ, RodriguesLJ, Torregiani JM, van Woesik R, Lesser M.P. (2009) Response of two species of Indo-Pacific corals, Porites cylindrica and Stylophora pistillata, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. Journal of Experimental Marine Biology and Ecology 373:102-110

12. Fitt WK, Kemp DW, Hernadez-Pech X, Iglesias-Prieto R, Thornhill DJ, Bruns BU, Schmidt GW (in press) Bleaching, El Niño, and la Niña: 13 years of seasonal analysis of reef-building corals in Florida, the Bahamas, and the Caribbean. 11th International Coral Reef Symposium, Ft Lauderdale, USA

13. Franklin DJ, Cedrés CMM, Hoegh-Guldberg O (2006) Increased mortality and photoinhibition in the symbiotic dinoflagellates of the Indo–Pacific coral Stylophora pistillata (Esper) after summer bleaching. Marine Biology 149:633-642

14. Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S, Strong A (2005) Coral bleaching following wintry weather. Limnology and Oceanography:265-271

15. Hoegh-Guldberg O, Muller-Parker G, Cook CB, Gates RD, Gladfelter E, Trench RK, Weis VM (2007) Len Muscatine (1932–2007) and his contributions to the understanding of algal-invertebrate endosymbiosis. Coral Reefs 26:731-739

16. Leggat W, Ainsworth TD, Dove S, Hoegh-Guldberg O (2006) Aerial exposure influences bleaching patterns. Coral Reefs 25:452-452

17. Lesser MP (2006) Oxidative stress in marine environments: biochemistry and physiological ecology. Annual Review Physiology 68:253-278

18. Muller EM, Rogers CS, Spitzack AS, van Woesik R (2008) Bleaching increases likelihood of disease on Acropora palmata (Lamarck) at Hawksnest Bay, St. John, US Virgin Islands. Coral Reefs 27:191-195

19. Nakamura T, van Woesik R, Yamasaki H (2005) Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral Acropora digitifera. Marine Ecology Progress Series 301:109-118

20. Obura DO (2009) Reef corals bleach to resist stress. Marine Pollution Bulletin 58:206-212

21. Papina M, Meziane T, van Woesik R (2007) Acclimation effect on fatty acids of the coral Montipora digitata and its symbiotic algae. Comparative Biochemistry and Physiology B 147:583-589

22. Rodríguez-Román A, Hernández-Pech X, Thomé PE, Enríquez S, Iglesias-Prieto R (2006) Photosynthesis and light utilization in the Caribbean coral Montastraea faveolata recovering from a bleaching event. Limnology and Oceanography 51:2702-2710

23. Shenkar N, Fine M, Kramarsky-Winter E, Loya Y (2006) Population dynamics of zooxanthellae during a bacterial bleaching event. Coral Reefs 25:223-227

24. Thompson DM, van Woesik R (2009a) Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. Proceedings of The Royal Society B 10.1098/rspb.2009.0591

25. van Oppen MJ, Gates RD (2006) Understanding the resilience of reef corals: the roles of molecular biology and genetics. Molecular Ecology 15:3863-3883

26. van Oppen MJH, Leong JA, Gates RD (2009) Coral-virus interactions: A double-edged sword? . Symbiosis:1-8

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Project 3. Geographical diversity of *Symbiodinium*

Leonard Chauka, William K. Fitt, Ove Hoegh-Guldberg, Dusty Kemp, Todd LaJeunesse, and Daniel T. Pettay.

Locations: Australasian CoE, Mesoamerican CoE, East African CoE, Palau International Coral Reef Center, Phuket Thailand, Hawaii Institute of Marine Biology, Australian Institute of Marine Science, Florida Keys, Caribbean Marine Research Center, *João Pessoa Brazil, *Curaçao Dutch Antilles (Figure 8).
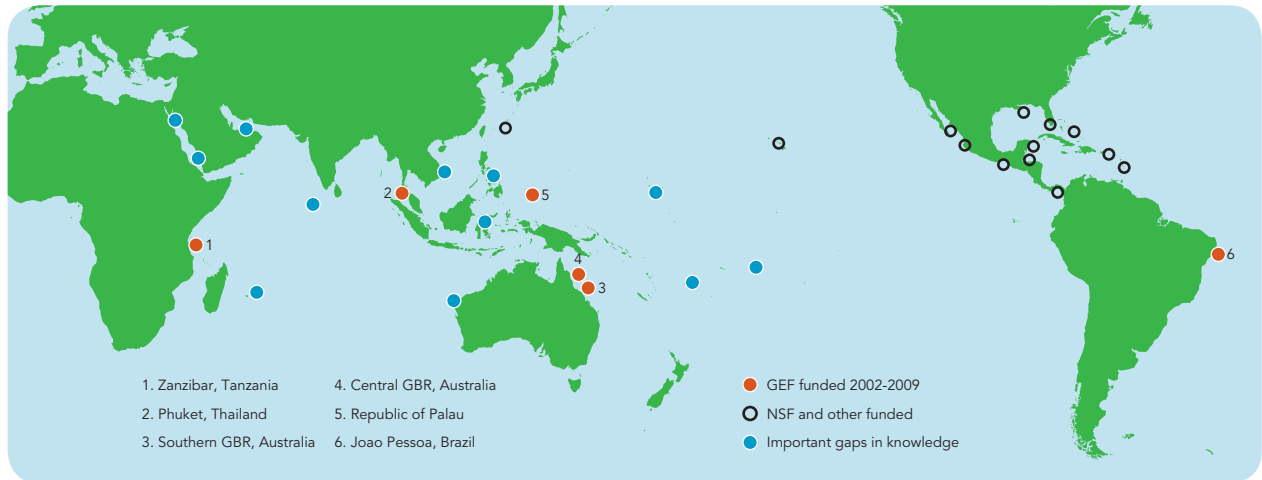

1. Zanzibar, Tanzania   4. Central GBR, Australia
2. Phuket, Thailand   5. Republic of Palau
3. Southern GBR, Australia 6. Joao Pessoa, Brazil

● GEF funded 2002-2009
○ NSF and other funded
● Important gaps in knowledge

Figure 8. Sampling locations to assess the diversity of *Symbiodinium* on a broad scale.

Key results

This project provided direct support for and played a significant role in the establishment of a worldwide database of *Symbiodinium* genetics. The results indicated that there are marked regional differences in the diversity and ecological dominance of symbiotic algae. These patterns are probably influenced by long-standing environmental conditions and/or from historical changes in climate during transitions between geological periods. Coral-algal symbioses are highly responsive to change through partner recombination but these processes may require time scales of centuries or more in duration. While there is high host-symbiont specificity, most Indo-Pacific coral communities are often dominated by one, or sometimes two, host-generalist symbionts and therefore many coral colonies on a particular Indo-Pacific reef often harbor the same species of symbiont.

Background

Any thorough investigation into the biology of reef-building corals must account for the fact that they are first and foremost symbiotic organisms that require internal algae for their growth and survival (Figure 9). These very combinations are sensitive to environmental stressors, especially episodes of high sea surface temperatures. While much is known about the diversity and distribution of corals, virtually nothing was known about the diversity and distribution of their essential symbionts until now. This project set out to accurately describe the symbiont diversity and distribution among various host taxa from reef communities all over the world. Conducting diversity surveys in different regions of the tropics provides insight into how geographic isolation, environmental conditions, and host biology influence the evolution between endosymbionts and their coral hosts (LaJeunesse 2005a).
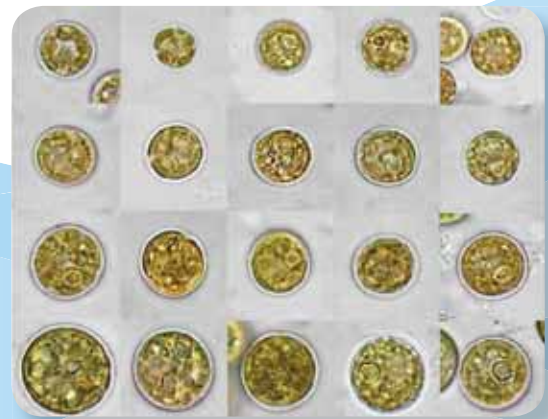

Figure 9. *Symbiodinium* cells under light microscope. Scale bar = 5 µm Photo: T. Lajeunesse

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For example, many western Pacific reef systems are periodically impacted by episodes of thermal stress resulting in mass bleaching and mortality. In contrast, coral communities in the Eastern Indian Ocean (i.e. Andaman Sea) have suffered little from these episodes. Do differences in the diversity and physiology of symbionts between these regions explain in part their resilience to stress? The biogeographic and ecological patterns produced by this work provide critical information regarding how symbioses from various regions will respond to global warming over decadal time scales. Furthermore, these data provide the basis for comparative physiological analyses and developing testable hypotheses regarding the tolerance and resilience of particular partner combinations to increased temperatures.

Methods

We conducted general surveys of the zooxanthellae biodiversity found across the community of symbiotic invertebrates (especially stony corals, but included soft corals, anemones, zoanthids etc) from reef systems around the world. In order to maximize the characterisation and identification of biodiversity, we sampled from the widest diversity of hosts as was possible. We learned that most hosts show remarkable specificity for particular symbionts at certain depths/environments. Small fragments or clippings (2-3 square cm in area) from various symbiotic reef invertebrates including hard corals, soft corals, anemones, and corallimorphs were collected by free diving or SCUBA at several sites within each regional location. Upon return to the field station, samples were processed in one of two ways. The fragments were either preserved directly in a high salt buffer containing EDTA and DMSO or the living tissue was airbrushed off the skeleton, homogenized, and centrifugation to pellets of 10-50 mg of *Symbiodinium* cell material which was then preserved in the preservation buffer (LaJeunesse et al. 2003). DNA extractions and molecular genetic analyses were conducted at the home research laboratories of Fitt and LaJeunesse. PCR-denaturing gradient gel electrophoresis analysis targeting the internal transcribed spacer regions (ITS 1 and ITS 2) was used to determine the genetic identity of the symbiont population in each sample.

Following the completion of the project, data are to be included in a worldwide database of symbiont diversity available online to researchers (www.auburn.edu/~santos/sd2_ged.htm).

Results and discussion

This study has provided fundamental and exciting knowledge about the diversity and biogeography of coral symbionts. The global perspective still remains very limited but these studies have generated an informed perspective regarding the extent of diversity and how these systems evolve in isolated regions with different long-standing environmental conditions. A total of seven reef systems were surveyed including the southern GBR (2002, ~190 samples); the central GBR (2003, ~300 samples); Zamami Island, Japan (~120 samples); Phuket, Thailand (2007, ~500 samples); Zanzibar, Tanzania (2007, ~350 samples); Joao Pessoa, Brazil (2008, ~100 samples); and The Republic of Palau (2009, ~500 samples). While each region differs in coral diversity, the symbioses for approximately 70 to 90 percent of host genera found in each region were preliminarily described. Much of the *Symbiodinium* diversity characterised by this work was new to science and comprised well over 100 ecologically and genetically distinct symbiont taxa. Each community contained numerous regionally unique species as well as a few host-generalists that exhibited broader ecological and geographic distributions. The similarity and differences between symbiont community assemblages correspond to distances separating each location. For example, there was a clear biogeographic break in the symbiont diversity between the southern and central GBR. However these communities were far more similar to each other than when compared to symbiont communities from the Andaman Sea, Thailand. Preliminary analyses of Brazilian corals indicate that it is very similar to the Caribbean, but these communities possess some notable differences in host-symbiont associations.

Figure 10. Mass coral bleaching in the Caribbean in 2005. Bleached and unbleached colonies were surveyed. Photo: H. Oxenford

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All the Pacific coral communities surveyed were dominated by symbiont species in Clade C. Many of these symbionts exhibit greater sensitivity to thermal stress. Members of Clade D *Symbiodinium* were very common among hosts in the Andaman Sea. The prevalence of Clade D in certain coral dominated ecosystems correlates with environments experiencing extreme seasonal changes in temperature and turbidity. The long-standing environmental conditions characteristic of the Andaman Sea including low water flow, wide fluctuations in turbidity, and exposure to higher sea surface temperatures relative to most regions in the Pacific, may explain the ecological success and dominance of this thermally tolerant *Symbiodinium* lineage.

Key literature generated with full/partial project support:

1. Apprill AM, Gates RD (2007) Recognizing diversity in coral symbiotic dinoflagellate communities. Molecular Ecology 16:1127-1134

2. Gómez-Cabrera MC, Ortiz J, Loh W, Ward S, Hoegh-Guldberg O (2008) Acquisition of symbiotic dinoflagellates (*Symbiodinium*) by juveniles of the coral Acropora longicyathus. Coral Reefs 27:219-226

3. Iglesias-Prieto R, Beltran VH, LaJeunesse TC, Reyes-Bonilla H, Thome PE (2004) Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. Proceedings of the Royal Society B 271:1757-1763

4. Kemp DW, Fitt WK, Schmidt GW (2008) A microsampling method for genotyping coral symbionts. Coral Reefs 27:289-293

5. Kemp DW, Hernadez-Pech X, Iglesias-Prieto R, Schmidt GW, Fitt WK (in press) Micro-niche partitioning and the photobiology of *Symbiodinium* associated with Montastraea faveolata 11th International Coral Reef Symposium, Ft Lauderdale, USA

6. LaJeunesse TC (2005) "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the miocene-pliocene transition. Molecular Biology and Evolution 22:570-581

7. Lajeunesse TC, Bhagooli R, Hidaka M, DeVantier L (2004) Closely-related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. Marine Ecology Progress Series 284:147–161

8. LaJeunesse TC, Loh W, Trench RK (2009) Do introduced endosymbiotic dinoflagellates 'take'to new hosts? Biological Invasions 11:995-1003

9. LaJeunesse TC, Loh WKW, van Woesik R, Hoegh-Guldberg O, Schmidt GW, Fitt WK (2003) Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. Limnology and Oceanography 48:2046-2054

10. LaJeunesse TC, Pettay DT, Sampayo EM, Phongsuwan N, Brown BE, Obura D, Hoegh-Guldberg O, Fitt WK (submitted) Regional differences in diversity and dominance of endosymbiotic dinoflagellates among Indian Ocean reef coral communities. Journal of Biogeography

11. LaJeunesse TC, Reyes Bonilla H, Warner ME, Wills M, Schmidt GW, Fitt WK (2008) Specificity and stability in high latitude eastern Pacific coral-algal symbioses. Limnology and Oceanography 53:719-727

12. LaJeunesse TC, Reyes-Bonilla H, Warner ME (2007) Spring "bleaching" among Pocillopora in the Sea of Cortez, Eastern Pacific. Coral Reefs 26:265-270

13. Manning MM, Gates RD (2008) Diversity in populations of free-living *Symbiodinium* from a Caribbean and Pacific reef. Limnology and Oceanography 53:1853-1861

14. Pettay DT, LaJeunesse TC (2007) Microsatellites from clade B *Symbiodinium* spp. specialized for Caribbean corals in the genus Madracis. Molecular Ecology Notes 7: 1271-1274

15. Pettay DT, Lajeunesse TC (2009) Microsatellite loci for assessing genetic diversity, dispersal and clonality of coral symbionts in 'stress-tolerant' *Symbiodinium* clade D Molecular Ecology Resources 9:1022-1025

16. Sampayo EM, Franceschinis L, Hoegh-Guldberg O, Dove S (2007) Niche partitioning of closely related symbiotic dinoflagellates. Molecular Ecology 16:3721-3733

17. Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proceedings of the National Academy of Sciences 105:10444-10449

18. Stat M, Gates RD (2008) Vectored introductions of marine endosymbiotic dinoflagellates into Hawaii. Biological Invasions 10:579-583

19. Stat M, Loh WKW, Hoegh-Guldberg O, Carter DA (2008) Symbiont acquisition strategy drives host-symbiont associations in the southern Great Barrier Reef. Coral Reefs 27:763-772

20. Stat M, Morris E, Gates RD (2008) Functional diversity in coral-dinoflagellate symbiosis. Proceedings of the National Academy of Sciences 105:9256-9261

21. Stat M, Pochon X, Cowie ROM, Gates RD (in press) Specificity in communities of *Symbiodinium* in corals from Johnston Atoll. Marine Ecology Progress Series

22. Thornhill DJ, Daniel MW, LaJeunesse TC, Schmidt GW, Fitt WK (2006a) Natural infections of aposymbiotic Cassiopea xamachana scyphistomae from environmental pools of *Symbiodinium*. Journal of Experimental Marine Biology and Ecology 338:50-56

23. Thornhill DJ, Kemp DW, Bruns BU, Fitt WK, Schmidt GW (2008) Correspondence between cold tolerance and temperate biogeography in Western Atlantic *Symbiodinium* (Dinophyta) lineage. Journal of Phycology 44:1126-1135

24. Thornhill DJ, LaJeunesse TC, Kemp DW, Fitt WK, Schmidt GW (2006b) Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion. Marine Biology 148:711-722

Project 4. Functional diversity of *Symbiodinium* (diversity and function)

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Sophie Dove, Ruth Gates, Ove Hoegh-Guldberg, Bill Leggat, Michael Lesser, Roberto Iglesias-Prieto, and Eugenia Sampayo.

Location: Australasian CoE, Mesoamerican CoE, and East African CoE

Key results

The key symbionts of reef-building corals are dinoflagellate protists belonging to the genus *Symbiodinium*. Recent genetic studies have identified large differences between *Symbiodinium* occupying different host species, indicating potentially hundreds of different species. At the outset of this project our understanding of the differences between species of *Symbiodinium* was confined to a number of non-coding sequences such as 18S, 28S and ITS ribosomal sequences. This project made a major contribution to filling this particular gap in our understanding of *Symbiodinium* by expanding the number of sequenced genes from a little over 10 to over 1450. While the function of many of these proteins remains to be identified, the function of over 560 unique genes were identified into broad categories. These included functions within areas such as post-translational modification, protein turnover, stress chaperones (12.3%) and energy production and conversion (12%). The results of this project have established an important platform for exploring the major responses of *Symbiodinium* to stresses such as those arising from climate change, and for exploring the underlying differences between reef-building corals in their response to environmental stress.

Background

Much of the discussion about the evolution of *Symbiodinium* (the key symbiont of reef-building corals) has occurred without considering the functional differences that may or not occur between different strains. The pioneering work of Trench, Schoenberg, Blank, Fitt, Iglesias-Prieto, Chang and others has been set aside by many studies that now focus on diversity using non-functional genetic differences (e.g. 18S, 28S, ITS ribosomal sequences; (Rowan and Powers 1992; Rowan et al. 1996; Baker 2001b). These studies have equated the detected genetic differences with functional differences despite the lack of firm evidence to confirm this.

However, understanding the functional behaviour of the different genotypes is also extremely important. For example, differences in tolerance have been equated to differences between *Symbiodinium* clades. It is possible, however, that the differences are because of the coral host and are unrelated to differences in ribosomal gene sequences between *Symbiodinium* clades. Quite clearly, documenting the differences that exist between the different clades (A-F) is a priority if we are to understand the underlying driving forces for evolutionary change.

To do this, an expressed sequence tag (EST) library was constructed from a stressed coral (*Acropora aspera*) and the resulting library extensively sequenced. The full details of the method is described in Leggat et al (2007a). This project began with a planning workshop in Mexico in May 2005. This workshop reviewed the available data and established a number of collaborative projects among BWG members, drawing on appropriate expertise from the international community of experts on *Symbiodinium* and related organisms.

Results and discussion

Information on the genetic makeup of the key symbiont of reef-building corals, *Symbiodinium*, was extremely limited. At the start of the BWG project, only 35 unique genes had been characterized from symbiotic and nonsymbiotic dinoflagellate species, and a number of these genes (e.g., form-II RUBISCO, peridinin-chlorophyll-binding protein [PCP]) had illustrated how dissimilar dinoflagellates are from other phototrophs. This led to a major focus within this project on improving our understanding of gene expression patterns of *Symbiodinium*. The full results were published in 2007 (Leggat et al. 2007a). As a result of this focus, the project directly identified 1456 unique expression sequence tags (ESTs) for *Symbiodinium* (clade C3) from the staghorn coral *Acropora aspera* exposed to a variety of stresses. Of these, only 10% matched previously reported dinoflagellate ESTs, suggesting that the conditions used in the construction of the library resulted in a novel transcriptome.

The function of 561 (44%) of these ESTs were identified. The majority of these genes coded for proteins involved in post-translational modification, protein turnover, and chaperones (12.3%); energy production and conversion (12%); or an unknown function (18.6%). Table S1 outlines Heat shock and related expression elements, while Table S2 lists the major groups found.

The most common transcript found was a homologue to a bacterial protein of unknown function. This algal protein is targeted to the chloroplast and is present in those phototrophs that acquired plastids from the red algal lineage. An additional 48 prokaryote-like proteins were also identified, including the first glycerol-phosphate antiporter from dinoflagellates. A protein was also found with similarity to the fungi–archael–bacterial heme catalase peroxidases. A variety of stress genes were identified, in particular heat-shock proteins and proteins involved in ubiquitin cascades. This study represented the first transcriptome from the unicellular component of a eukaryote–eukaryote symbiosis. The complete results have been made available to the research community through Gene Bank, and have generated considerable research activity within the BWG and in the broader research community. It is next to impossible to concisely describe the complete set of activities that have been stimulated by this project because of the large number of satellite projects that spawned from these investigations.

Table S1. *Symbiodinium* Hsp proteins and their co-chaperones and those proteins involved in the ubiquitin degradation cycle. Expressed during the application of heat, light, nutrient and inorganic carbon stress conditions.

Gene Name	No. of sequences	Length (bp)	Best Match	Bit score	e-value	Accession number
SyHsp100	1	519	Arabidopsis thalina AtC1pC	133	2x10^{-30}	DQ144975
SyHsp90 1[a]	1	826	*C. cohn ii* Hsp90	419	1x10^{-116}	DQ144976
SyHsp90 2[a]	1	788	*C. cohn ii* Hsp90	427	1x10^{-118}	DQ144977
SyHsp90 3	15	1326	*C. cohn ii* Hsp90	722	0	DQ144978
SyHsp70	9	1147	*C. cohn ii* Hsp70	545	1x10^{-154}	DQ144979
SyDNAJ 1	8	1185	*Apis mellifera* DNAJ	324	2x10^{-87}	DQ144980
SyDNAJ 2	3	994	*Plasmodium chabaudi* DNAJ	101	3x10^{-20}	DQ144981
SyDNAJ 3	1	1022	*Mus musculus* DNAJ	257	4x10^{-67}	DQ144982
SyDNAJ 4	1	719	*Thermosynechococcus elongatus*	119	1x10^{-25}	EH036974
Syp23	1	517	*Crytosporidium parvum* p23 co-chaperone	82	8x10^{-15}	DQ144983
Poly-ubiquitin (SyUb)	1	583	*Encephalitozoon cuniculi* ubiquitin	337	1x10^{-91}	DQ144984
Ubiquitin-conjugating enzyme (SyUbc1)	2	641	*Plasmodium falciparum* ubiquitin – conjugating enzyme (putative)	231	2x10^{-59}	DQ144985
Ubiquitin-conjugating enzyme (SyUbc2)	1	401	*Plasmodium yoelii yoelii* ubiquitin-conjugating enzyme	145	5x10^{-34}	DQ144986
Ubiquitin-conjugating enzyme (SyUbc3)	2	805	*Phytophthora infestans* ubiquitin-conjugating enzyme	133	7x10^{-30}	DQ144987
Ubiquitin-conjugating enzyme (SyUbc4)	1	618	*Phytophthora infestans* ubiquitin-conjugating enzyme	191	6x10^{-48}	DQ144988
Ubiquitin ligase (SyUbr1)	1	459	*H. sapiens* ubiquitin ligase protein CHFR	50	2x10^{-5}	DQ144989
Ubiquitin ligase (SyUbr2)	1	557	*D. rerio* ubiquitin ligase Siah2	68	3x10^{-10}	DQ144990
Ubiquitin-specific protease (SyUbp1)	4	976	*H. sapiens* ubiquitin specific proteinase 40	81	6x10^{-14}	DQ144991
Ubiquitin C-terminal hydrolase (SyUbch1)	1	722	*Oryza sativa* putative ubiquitin C-terminal hydrolase	189	2x10^{-46}	DQ144992

a These two ESTs both code for the same region of Hsp90; the identity at the amino acid level is 99.6%, (215/216 a.a. identical), while at the NDA level, identity is 89%.

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Table S2. *Symbiodinium* ESTs that match best to bacterial genes (see Leggat et al. 2007a for full description).			
Tentative protein identification	Present in other dinoflagellate ESTs (e-value)	Accession number	Present in other eukaryote ESTs (e-value < 1 × 10–5)
Bacl-1	Yes (2 × 10^{-90})	EF138814	Yes
Bacl-2	Yes (4 × 10^{-94})	EH037640, EH058151, EH037638, EH037639, EH037641, EH058149, EH037642, EH037643, EH037644, EH037645, EH037647, EH037650, EH037646, EH058148, EH037652	Yes
Sugar permease	No	EF138816	Yes
Heat caspase 1–containing protein	Yes (1 × 10^{-13})	EH036199, EH036200, EH036201	No
Lipoprotein	Yes (2 × 10^{-24})	EH036655, EH036656	No
Uncharacterized conserved bacterial protein	No	EH037155	Yes
Serine/threonine protease	Yes (8 × 10^{-7})	EH037135	Yes
Syringomycin synthesis regulator	Yes (5 × 10^{-21})	EH058140	Yes
Streptavidin	No	EH036842	Yes
Pirin	Yes (1 × 10^{-62})	EH037858, EH037857, EH037856, EH057961	Yes
Xanthine/uracil permease	No	EH037487, EH058028	Yes
Transporter	No	EH037119	Yes
Cytochrome p450	Matches to Apicomplexa (3 × 10^{-9})	EH036606, EH036607	Yes
Ammonium transporter	Yes (8 × 10^{-15})	EH037820, EH037819	Yes
Sulfate transporter	No	EH036081, EH036083, EH036084, EH036085	No
ß-lactamase inhibitor	Yes (3 × 10^{-48})	EH037946,	Yes
ß-lactamase inhibitor	Yes (1 × 10^{-48})	EH037520, EH037519	Yes
ß-lactamase inhibitor	Yes (4 × 10^{-48})	EH037943, EH037944	Yes
ß-lactamase inhibitor	Yes (8 × 10^{-48})	EH037945	Yes
Cyclophilin-peptidyl propyl isomerase	Yes (3 × 10^{-17})	EH036698	Yes
DNAJ	No	EH036974	Yes
Cell-surface protein	No	EH037161	Yes
Glycosyl transferase	Yes (4 × 10^{-45})	EH038071, EH038066	Yes
Ribonuclease H1	No	EH036802	Yes
Modification methylase	Yes (7 × 10^{-8})	EH037728, EH037730	Yes
DNA modification methylase	Yes (4 × 10^{-4})	EH038195	No
Acetyl transferase	No	EH036135, EH036134	Yes
Diacylglycerol transferase	Yes (2 × 10^{-24})	EH036135, EH036134	Yes
L-carnitine dehydratase	No	EH058162	Yes
Phosphoserine aminotransferase	Yes (4 × 10^{-102})	EH037087	Yes
Glycosyl transferase	Yes (5 × 10^{-47})	EH037619, EH037620, EH037618, EH037617, EH037614, EH037612, EH037616, EH037610, EH037609, EH037611	Yes
Glycosyl transferase	No	EH037613	Yes
Glycosyl transferase	Yes (9 × 10^{-39})	EH037621	Yes
Pyruvate orthophosphate	No	EH038113, EH038114, EH038116	Yes

Table S2. *Symbiodinium* ESTs that match best to bacterial genes (see Leggat et al. 2007a for full description).			
Tentative protein identification	Present in other dinoflagellate ESTs (e-value)	Accession number	Present in other eukaryote ESTs (e-value < 1 × 10–5)
Glycosyl transferase	Yes (2×10^{-38})	EH036023, EH036024, EH036025, EH036026, EH036028	Yes
Phosphoglycerate mutase	Yes (2×10^{-64})	EH036823	Yes
Citrate lyase	No	EH036930	Yes
Polysaccharide deacetylase	No	EH037190	Yes
Thymidine kinase	Yes (4×10^{-21})	EH037522	Yes
Keto-acid reductoisomerase	Yes (8×10^{-22})	EH036341, EH036342	Yes
Aminotransferase	Yes (3×10^{-63})	EH058166	Yes
Glucose-inhibited division protein	No	EH037376	No
ATPase domain–containing protein	Yes (9×10^{-74})	EH036068, EH036069, EH036070, EH036072	No
Cytochrome oxidase	Yes (3×10^{-53})	EH037670, EH037672, EH037673	Yes
Salicylate monoxygenase	No	EH037952, EH037953, EH037954, EH037955	Yes

Key literature generated with Full/partial project support:

1. Kvennefors ECE, Leggat W, Hoegh-Guldberg O, Degnan BM, Barnes AC (2008) An ancient and variable mannose-binding lectin from the coral Acropora millepora binds both pathogens and symbionts. Developmental and Comparative Immunology 32:1582-1592

2. Leggat W, Dixon R, Saleh S, Yellowlees D (2005) A novel carbonic anhydrase from the giant clam Tridacna gigas contains two carbonic anhydrase domains. FEBS Journal 272:3297-3305

3. Leggat W, Hoegh-Guldberg O, Dove S, Yellowlees D (2007b) Analysis of an EST library from the dinoflagellate (Symbiodinium sp.) symbiont of reef-building corals. Journal of Phycology 43:1010-1021

4. Weis VM, Davy SK, Hoegh-Guldberg O, Rodriguez-Lanetty M, Pringe JR (2008) Cell biology in model systems as the key to understanding corals. Trends in Ecology & Evolution 23:369-376

Project 5. Host-symbiont mutualism, close associates, metabolic communication and environmental change

John Bythell, Ove Hoegh-Guldberg, Mike P. Lesser, Ron Johnstone, and Christian Wild.

Location: Mesoamerican CoE, Australasian CoE, and Northern Red Sea

Key results

Understanding of the interactions of reef-building corals and *Symbiodinium*, with the broader range of symbiotic organisms associated with them, is critical to understanding not only the basic biology of corals, but also their response to stress and disease. This project set out to describe host symbiont mutualism between corals, dinoflagellates and bacteria, and resulted in a large number of new observations and discoveries. The research identified the critical role of the mucus layer on corals (Figure 11) as a barrier to microbial invasion, and concluded after extensive studies that bacteria are rare within the tissues of corals. That said, some corals do host specific bacteria. In this regard, members of the BWG discovered the presence of nitrogen-fixing bacteria within coral tissues. These organisms appear to be able to contribute inorganic nitrogen to the metabolism of the resident *Symbiodinium*, avoiding the inhibiting high levels of oxygen by restricting their nitrogen-fixing activities to dawn and dusk. Members of the group

Figure 11. Branching staghorn coral releasing mucus strings used in feeding and surface sediment cleaning. Southern Great Barrier Reef. Photo: J. Bythell

also explored the potential role of bacteria in causing bleaching, discovering that *Vibrio* and other bacterial infections are most likely secondary rather than primary causes of bleaching and disease. It became clear that thermal stress increases the incidence and susceptibility of corals to disease, which echoes results discovered within the Disease Working Group of the CRTR Program. Research undertaken during this project also identified a series of coral host shutdown reactions that were mediated by programmed cell death or apoptosis. In a series of ecosystem engineering projects, mucus released by coral was identified as a critical energy carrier and particle trap, thereby preventing loss of essential elements from the oligotrophic reef system. Changes to reef processes were also identified. These included changes to the coral derived organic material release during bleaching and the escalation in nitrogen fixation rates which occurred on the surfaces of newly dead coral skeletons.

Background

The project has investigated two main themes a) the importance of microbial associates of coral in maintaining health and in affecting the bleaching and disease processes, and b) identification of the large-scale biogeochemical processes that coral holobiont and external bacteria mediate on coral reefs and how these are changed following bleaching and coral mortality. We now know that corals are very effective at preventing microbial penetration of the tissues using effective surface mucus layer cleansing in a similar way to the human gut mucosa (Brown and Bythell 2005). They also possess effective antimicrobials and innate immunity systems (Palmer et al. 2009) in case the mucus barrier is penetrated. The normally benign microflora of the outer mucus layer also releases antimicrobials that can suppress the growth of potential pathogens. In combination, this results in typically very low numbers of bacteria in the tissues, with the exception of specific cases of putative microbial symbiosis (Bythell et al. 2002; Lesser et al. 2007b; Ainsworth et al. 2008a). Many studies have shown that this situation changes dramatically under stress, with a consistent increase in potentially pathogenic microbes dominated by *Vibrios* (Lesser et al. 2007a). Following stress, the microbial population may therefore exacerbate the bleaching process and is instrumental in the post-bleaching disease processes that lead to death of the coral. Further research is needed to analyse these processes to determine what microbial processes may lead to death or survival of the coral following a stress event and whether there are any management interventions that can influence this outcome.

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In addition, hermatypic corals are known to release large amounts of organic matter into their surroundings, in quantities that often dominate the suspended matter in coral reefs. Mucus release, like coral bleaching, is an unspecific response to environmental stress. The goal of this project was therefore to study (1) the dynamics of coral holobiont-derived organic matter release, (2) assess its general ecological role for reef functioning and its effect on associated microbial diversity, and (3) examine the activity as well as the link between organic release and coral bleaching.

Methods

The work to examine microbial associates of corals has mainly focussed on culture-independent 16S rRNA gene analysis by PCR-DGGE (denaturing gel electrophoresis) and fluorescence in situ hybridisation (FISH). These techniques have been applied to a wide range of natural and experimental manipulations.

A series of interconnected experiments were carried out in order to assess biogeochemical processes and element cycles in the investigated coral reef ecosystems (Figure 12). This included measurements of benthic oxygen fluxes using stirred benthic chambers. Benthic community structure was determined by the use of line-point-intercept transects. Dissolved and particulate organic matter release by reef organisms was quantified using diverse incubation techniques with subsequent dissolved organic carbon (DOC), particulate organic carbon (POC) and nitrogen (PN) analyses in combination with stable isotope measurements (δ 13C, δ 15N).

For the molecular diversity analyses of fingerprinting techniques (ARISA and TRFLP) were used in combination with clone libraries and quantitative analyses (FISH). Microbial activity was measured by quantification of oxygen fluxes in incubation experiments.

Several methodological papers (Holmes 2008; Laforsch et al. 2008; Naumann et al. 2009) have been produced in order to increase the accuracy of coral surface area quantification as a critical reference unit for process measurements.

Figure 12. Experiment carried out at Heron Island to determine longer-term effects of heat stress on microbial communities associated with corals (*Acropora Formosa*) Photo: J. Bythell

Results and discussion

We have substantially addressed all our initial hypotheses, H1: Predictable shifts in microbial communities associated with coral occur because of environmental stress (Pantos et al. 2003; Guppy and Bythell 2006); H2: Corals are at increased risk of developing microbially-mediated disease during and following bleaching (Lesser et al. 2007a; Fitt et al. 2009); H3: Healthy corals have symbiotic microbial communities that may be lost due to changing environmental conditions or be out-competed (Lesser et al. 2007b); H4: Populations of specific pathogens (e.g. Vibrios) associated with corals are promoted during environmental stress (Pantos and Bythell 2006; Ainsworth et al. 2007a; Ainsworth et al. 2007b). This has led to some important syntheses (Leggat et al. 2007b; Lesser et al. 2007a) and new directions of research funded by other agencies to investigate coral surface mucus layer dynamics, the specific relationship between temperature stress and antimicrobial defences and coral innate immunity mechanisms.

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This project also revealed a variety of new findings related to coral-algae-microbe interaction and the important role of hermatypic corals as engineers of entire reef ecosystems. Via complex habitat generation and the release of organic materials, corals not only affect the diversity of associated fauna and flora, but this also takes place for the microbial level (Allers et al. 2008; Schöttner et al. in press). Inorganic matter production by corals considerably affects pelagic-benthic coupling and the ensuing processing involving recycling of organic matter in reef ecosystems. This highlights the role of coral-generated reef sands as biocatalytical filter systems with their typically high abundances of heterotrophic microbes (Wild et al. 2006). In addition, organic matter released by corals initiates metabolic communication to a variety of other reef organisms and element cycles, which contribute to rapid processing of organic matter pulses and to conserving essential nutrients within the reef ecosystem (Wild et al. 2004a; Wild et al. 2004b; Wild et al. 2004c; Wild et al.

Figure 13. Mucus strings between the branches of a staghorn coral at Heron Island. This mucus is primarily released by corals in order to clean their surfaces. However, this material can also function as an energy carrier and particle trap. Photo: C. Wild
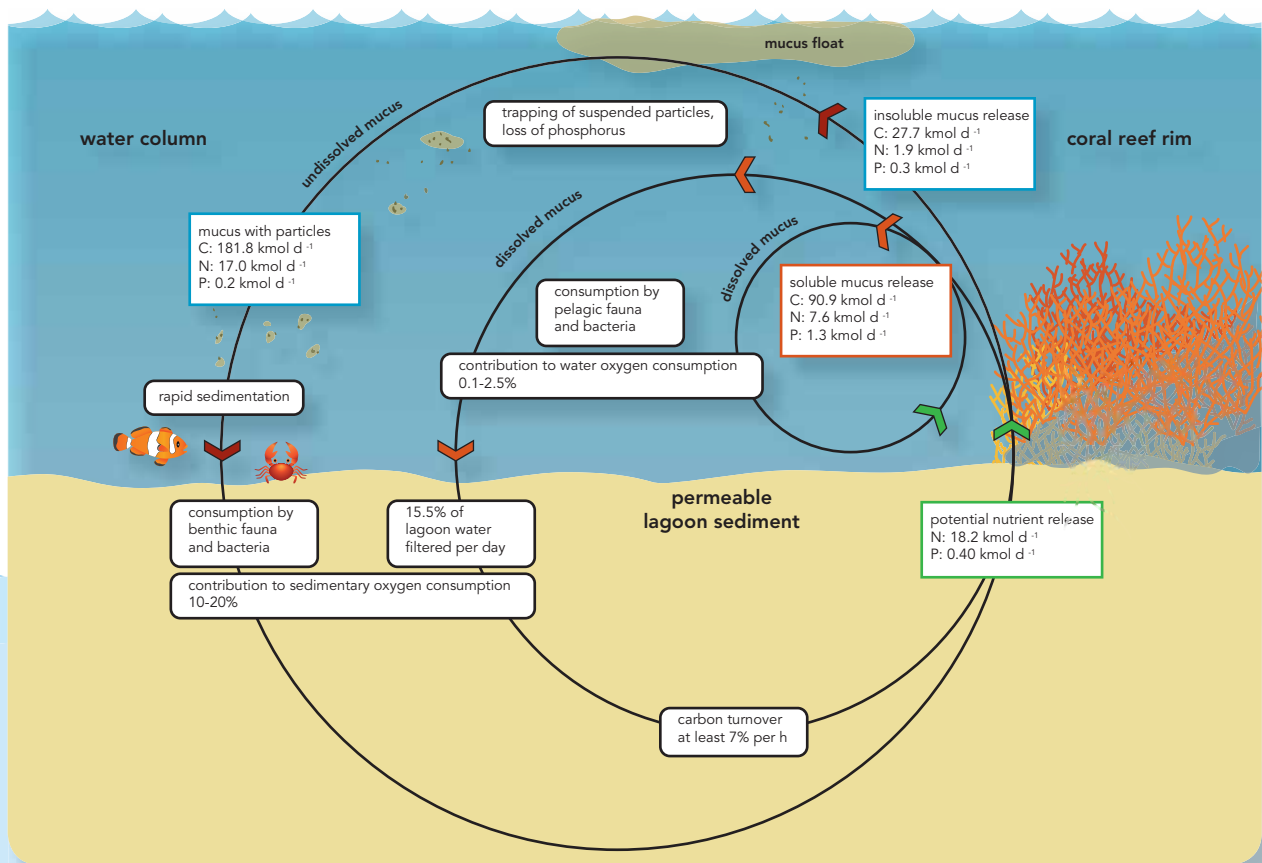
2005; Huettel et al. 2006; Wild et al. 2008) – see Figure 14. Phase-shifts from corals to benthic algae following mass bleaching events also include quantitative and compositional changes in organic matter production and release with biogeochemical consequences (Wild et al. in press).

Figure 14. Biogeochemical element cycles initiated by the release of coral mucus (suggested for Heron Island). Wild et al. (2004a).

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Key literature generated with full/partial project support:

1. Ainsworth TD, Fine M, Blackall LL, Hoegh-Guldberg O (2006) Fluorescence in situ hybridization and spectral imaging of coral-associated bacterial communities. Applied and Environmental Microbiology 72:3016-3020

2. Ainsworth TD, Fine M, Roff G, Hoegh-Guldberg O (2007a) Bacteria are not the primary cause of bleaching in the Mediterranean coral Oculina patagonica. International Society for Microbial Ecology 2:67-73

3. Ainsworth TD, Hoegh-Guldberg O (2008) Cellular processes of bleaching in the Mediterranean coral Oculina patagonica. Coral Reefs 27:593-597

4. Ainsworth TD, Hoegh-Guldberg O (2009) Bacterial communities closely associated with coral tissues vary under experimental and natural reef conditions and thermal stress. Aquatic Biology 4:289-296

5. Ainsworth TD, Hoegh-Guldberg O, Leggat W (2008) Imaging the fluorescence of marine invertebrates and their associated flora. Journal of Microscopy 232:197-199

6. Ainsworth TD, Kramasky–Winter E, Loya Y, Hoegh-Guldberg O, Fine M (2007b) Coral disease diagnostics: What's between a plague and a band? Applied and Environmental Microbiology 73:981-992

7. Ainsworth TD, Kvennefors EC, Blackall LL, Fine M, Hoegh-Guldberg O (2007c) Disease and cell death in white syndrome of Acroporid corals on the Great Barrier Reef. Marine Biology 151:19-29

8. Allers E, Niesner C, Wild C, Pernthaler J (2008) Microbes enriched in seawater after the addition of coral mucus. Applied and Environmental Microbiology 74:3274-3278

9. Brickner I, Oren U, Frank U, Loya Y (2006) Energy integration between the solitary polyps of the clonal coral Lobophyllia corymbosa. Journal of Experimental Biology 209:1690-1695

10. Brown BE, Bythell JC (2005) Perspectives on mucus secretion in reef corals. Marine Ecology Progress Series 296:291-309

11. Bythell JC, Barer MR, Cooney RP, Guest JR, O'Donnell AG, Pantos O, Le Tissier MDA (2002) Histopathological methods for the investigation of microbial communities associated with disease lesions in reef corals. Letters in applied microbiology 34:359-364

12. Bythell JC, Pantos O, Richardson LL (2004) White plague and other 'white' diseases. In: Rosenberg E, Loya Y (eds) Coral health and disease. Springer-Verlag, New York

13. Davey M, Holmes G, Johnstone R (2008) High rates of nitrogen fixation (acetylene reduction) on coral skeletons following bleaching mortality. Coral Reefs 27:227-236

14. Davy SK, Burchett SG, Dale AL, Davies P, Davy JE, Muncke C, Hoegh-Guldberg O, Wilson WH (2006) Viruses: agents of coral disease? Diseases of aquatic organisms 69:101-110

15. Efrony R, Loya Y, Bacharach E, Rosenberg E (2007) Phage therapy of coral disease. Coral Reefs 26:7-13

16. Fine M, Meroz-Fine E, Hoegh-Guldberg O (2005) Tolerance of endolithic algae to elevated temperature and light in the coral Montipora monasteriata from the southern Great Barrier Reef. Journal of Experimental Biology 208:75-81

17. Fine M, Roff G, Ainsworth TD, Hoegh-Guldberg O (2006) Phototrophic microendoliths bloom during coral "white syndrome". Coral Reefs 25:577-581

18. Guppy R, Bythell JC (2006) Environmental effects on bacterial diversity in the surface mucus layer of the reef coral Montastraea faveolata. Marine Ecology Progress Series 328:133-142

19. Haas A, al-Zibdah M, Wild C (submitted-a) Seasonal in-situ monitoring of coral-algae interaction stability in fringing reefs of the Northern Red Sea Coral Reefs

20. Haas A, el-Zibdah M, Wild C (submitted-b) Effects of inorganic and organic nutrient addition on direct competition between hermatypic corals and benthic reef algae in the Northern Red Sea. Journal of Experimental Marine Biology and Ecology

21. Hoegh-Guldberg O, Dove S (2007) Chapter 7 "Primary production, nutrient recycling and energy flow through coral reef ecosystems". In: Hutchings P., Kingsford M., Hoegh-Guldberg O. eds) Great Barrier Reef: Biology, Environment and Management. CSIRO Press.

22. Huettel M, Wild C, Gonelli S (2006) The mucus trap in coral reefs: formation and temporal evolution of aggregates caused by coral mucus. Marine Ecology Progress Series 307:69-84

23. Hutchings, P. A. and Hoegh-Guldberg O (2007) Chapter 8 "The carbonate balance of coral reefs". In: Hutchings P., Kingsford M., Hoegh-Guldberg O .(eds) Great Barrier Reef: Biology, Environment and Management. CSIRO Press.

24. Iwase A, Sakai K, Suzuki A, van Woesik R (2008) Phototrophic adjustment of the foliaceous coral Echinopora lamellosa in Palau. Estuarine, Coastal and Shelf Science 77:672-678

25. Jantzen C, Wild C, Roa-Quiaoit H, El-Zibdah M, Richter C (2008) Photosynthetic performance of giant clams, Tridacna maxima and T. squamosa, in the Gulf of Aqaba, Red Sea. Marine Biology 155:211-221

26. Kaniewska P, Anthony KRN, Hoegh-Guldberg O (2008) Variation in colony geometry modulates internal light levels in branching corals, Acropora humilis and Stylophora pistillata. Marine Biology 155:649-660

27. Kaniewska P, Campbell PR, Fine M, Hoegh-Guldberg O (2009) Phototropic growth in a reef flat acroporid branching coral species. Journal of Experimental Biology 212:662-667

28. Kelman D, Kashman Y, Rosenberg E, Kushmaro A, Loya Y (2006) Antimicrobial activity of Red Sea corals. Marine Biology 149:357-363

29. Klueter A, Loh W, Hoegh-Guldberg O, Dove S (2006) Physiological and genetic properties of two fluorescent colour morphs of the coral Montipora digitata. Symbiosis 42:123-134

30. Kramarsky-Winter E, Harel M, Siboni N, Ben Dov E, Brickner I, Loya Y, Kushmaro A (2006) Identification of a protist-coral association and its possible ecological role. Marine Ecology-Progress Series 317:67-73

31. Laforsch C, Christoph E, Glaser C, Naumann M, Wild C, Niggl W (2008) A precise and non-destructive method to calculate the surface area of living scleractinian corals using X-ray computed tomography and 3D modeling. Coral Reefs 27:811-820

32. Leggat W, Ainsworth TD, Bythell JC, Dove S, Gates RD, Hoegh-Guldberg O, Iglesias-Prieto R, Yellowlees D (2007a) The hologenome theory disregards the coral holobiont. Nature Reviews Microbiology 5

33. Lesser MP, Bythell JC, Gates RD, Johnstone RW, Hoegh-Guldberg O (2007a) Are infectious diseases really killing corals? Alternative interpretations of the experimental and ecological data. Journal of Experimental Marine Biology and Ecology 346:36-44

34. Lesser MP, Falcón LI, Rodríguez-Román A, Enríquez S, Hoegh-Guldberg O, Iglesias-Prieto R (2007b) Nitrogen fixation by symbiotic cyanobacteria provides a source of nitrogen for the scleractinian coral Montastraea cavernosa. Marine Ecology Progress Series 346:143-152

35. Mayer FW, Duewel S, Haas A, Jantzen C, Naumann M, Jeschke JM, Wild C (in press) A web-based information management solution for experimental data from the field of coral reef ecology 11th International Coral Reef Symposium Ft. Lauderdale, USA

36. Mayer FW, Manasrah R, Mayr C, Wild C (submitted) Coral mucus via particle trapping initiates short linked element cycles in fringing reefs of the Northern Red Sea. Coral Reefs

37. Middlebrook R, Hoegh-Guldberg O, Leggat W (2008) The effect of thermal history on the susceptibility of reef-building corals to thermal stress. Journal of Experimental Biology 211:1050-1056

38. Moore RB, Obornik M, Janouskovec J, Chrudimsky T, Vancova M, Green DH, Wright SW, Davies NW, Bolch CJS, Heimann K, Slapeta J, Hoegh-Guldberg O, Logsdon JM, Carter DA (2008) A photosynthetic alveolate closely related to apicomplexan parasites. Nature 451:959-963

39. Naumann M, Haas A, Struck U, Mayr C, el-Zibdah M, Wild C (submitted) Organic matter release by the dominant hermatypic corals of the Northern Red Sea. Limnology and Oceanography

40. Naumann M, Niggl W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification – evaluation of established methods by comparison with computer tomography. Coral Reefs 28:109-117

41. Naumann M, Richter C, el-Zibdah M, Wild C (in press) Coral mucus as an efficient trap for picoplanktonic cyanobacteria -implications for pelagic-benthic coupling in the reef ecosystem Marine Ecology Progress Series

42. Niggl W, Glas M, Laforsch C, Mayr C, Wild C (in press) First evidence of coral bleaching stimulating organic matter release by reef corals 11th International Coral Reef Symposium Ft. Lauderdale, USA

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43. Olson ND, Ainsworth TD, Gates RD, Takabayashi M (2009) Diazotrophic bacteria associated with Hawaiian Montipora corals: Diversity and abundance in correlation with symbiotic dinoflagellates. Journal of Experimental Marine Biology and Ecology 371:140-146

44. Pantos O, Bythell JC (2006) Bacterial community structure associated with white band disease in the elkhorn coral Acropora palmata determined using culture-independent 16S rRNA techniques. Diseases of aquatic organisms 69:79-88

45. Rasheed M, Wild C, Franke U, Huettel M (2004) Benthic photosynthesis and oxygen consumption in permeable carbonate sediments at Heron Island, Great Barrier Reef, Australia. Estuar Coast Shelf Sci 59:139-150

46. Rasheed M, Wild C, Jantzen C, Badran M (2006) Natural matter mineralization in the reef sediments of the Gulf of Aqaba. Chem Ecol 22:13-20

47. Reed K, Muller EM, van Woesik R (submitted) Coral immunology and resistance to disease. Diseases of aquatic organisms.

48. Reimers CE, Stecher HA, Taghon GL, Fuller CM, Huettel M, Rusch A, Ryckelynck N, Wild C (2004) In situ measurements of advective solute transport in permeable shelf sands. Cont Shelf Res 24:183-201

49. Reshef L, Koren O, Loya Y, Zilber-Rosenberg I, Rosenberg E (2006) The Coral probiotic hypothesis. Environmental Microbiology 8:2068-2073

50. Roff G, Hoegh-Guldberg O, Fine M (2006) Intra-colonial response to Acroporid "white syndrome" lesions in tabular Acropora spp.(Scleractinia). Coral Reefs 25:255-264

51. Roff G, Kvennefors ECE, Ulstrup KE, Fine M, Hoegh-Guldberg O (2008) Coral disease physiology: the impact of Acroporid white syndrome on *Symbiodinium*. Coral Reefs 27:373-377

52. Roff G, Ulstrup KE, Fine M, Ralph PJ, Hoegh-Guldberg O (2008) Spatial heterogeneity of photosynthetic activity within diseased corals from the Great Barrier Reef. Journal of Phycology 44:526-538

53. Schöttner S, Hoffmann F, Wild C, Rapp HT, Boetius A, Ramette A (in press) Inter- and intra- habitat bacterial diversity associated with cold water corals. The ISME Journal

54. Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL (2006) Indirect effects of algae on coral: Algae-mediated, microbe-induced coral mortality. Ecology Letters 9:835-845

55. Todd BD, Thornhill DJ, Fitt WK (2006) Patterns of inorganic phosphate uptake in Cassiopea xamachana: A bioindicator species. Marine Pollution Bulletin 52:515-521

56. Torregiani JH, Lesser MP (2007) The effects of short-term exposures to ultraviolet radiation in the Hawaiian Coral Montipora verrucosa. Journal of Experimental Marine Biology and Ecology 340:194-203

57. Werner U, Bird P, Wild C, Ferdelman T, Polerecky L, Eickert G, Johnstone R, Hoegh-Guldberg O, deBeer D (2006) Spatial variability of aerobic and anaerobic mineralization in coral reef sediments (Heron Island, Australia). Marine Ecology Progress Series 309:93-105

58. Wild C (2004) Sediment-water coupling in permeable shallow water sediments, Vol 1. Peniope VLG, Munich, Germany

59. Wild C (2007) Faszination, Bedeutung und Gefährdung von Korallenriffen in einer Zeit der globalen Veränderung. In: Höfer A, Rath D (eds) Deutschlands wahre Superstars - 50 Zukunftsperspektiven junger Wissenschaftler. Heel Verlag, Königswinter, p 46-49

60. Wild C (in press) Reef-building scleractinian corals as ecosystem engineers. In: Wolanski E, McLusky D (eds) Treatise of Estuaries and Coastal Ecosystems, Vol 7. Elsevier

61. Wild C, Haas A, Naumann M, Mayr C, el-Zibdah M (in press) Comparative investigation of organic matter release by corals and benthic reef algae – implications for pelagic and benthic microbial metabolism 11th International Coral Reef Symposium, Ft. Lauderdale, USA

62. Wild C, Huettel M, Klueter A, Kremb SG, Rasheed M, Jørgensen BB (2004a) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428:66–70

63. Wild C, Jantzen C (2008) Baumeister der Meere - Korallen als Ingenieure von Warm- und Kaltwasserriffen. In: Moldrzyk U, Heiss G (eds) „abgetaucht"- Begleitbuch zur Sonderausstellung zum internationalen Jahr des Riffes 2008. Museum für Naturkunde der Humboldt-Universität, Berlin, p 171-182

64. Wild C, Jantzen C, Niggl W, Haas A, Mayer FW, Naumann M (2008a) Konsequenzen des Klimawandels für Korallenriffe - mögliche Lösungsansätze. In: Moldrzyk U, Heiss G (eds) „abgetaucht"- Begleitbuch zur Sonderausstellung zum internationalen Jahr des Riffes 2008 Museum für Naturkunde der Humboldt-Universität, Berlin, p 148-170

65. Wild C, Jantzen C, Struck U, Hoegh-Guldberg O, Huettel M (2008b) Biogeochemical responses on coral mass spawning at the Great Barrier Reef: Pelagic-benthic coupling. Coral Reefs 27:123-132

66. Wild C, Laforsch C, Huettel M (2006) Detection and enumeration of microbial cells in highly porous calcareous reef sands. Marine & Freshwater Research 57:415-420

67. Wild C, Mayr C, Wehrmann L, Schöttner S, Naumann M, Hoffmann F, Rapp HT (2008c) Organic matter release by cold water corals and its implication for fauna-microbe interaction. Marine Ecology Progress Series 372:67-75

68. Wild C, Naumann M, Haas A, Struck U, Mayer FW, Huettel M (submitted) Coral sand O2 uptake and benthic-pelagic coupling in a subtropical fringing reef, Aqaba, Red Sea. Aquatic Biology

69. Wild C, Rasheed M, Jantzen C, Cook P, Struck U, Huettel M, Boetius A (2005a) Benthic metabolism and degradation of natural particulate organic matter in silicate and carbonate sands of the Northern Red Sea. Marine Ecology Progress Series 298:69-78

70. Wild C, Rasheed M, Werner U, Franke U, Johnstone R, M. H (2004b) Degradation and mineralization of coral mucus in reef environments. Marine Ecology Progress Series 267:159-171

71. Wild C, Røy H, Huettel M (2005b) Role of pelletization for mineralization in fine-grained coastal sediments. Marine Ecology Progress Series 291:23-33

72. Wild C, Tollrian R, Huettel M (2004c) Rapid recycling of coral mass spawning products in permeable reef sediments. Marine Ecology Progress Series 271:159-166

73. Wild C, Woyt H, Huettel M (2005c) Influence of coral mucus on nutrient fluxes in carbonate sands. Marine Ecology Progress Seriers 287:87-98

Theme 2
Organismal mechanisms to ecological outcomes

Project 6. Population dynamics of coral populations under environmental change

2

Eran Brokovich, Omri Bronstein, Jessica Gilner, Yossi Loya, Juan Carlos Ortiz, Rob van Woesik, and Assaf Zvuloni.

Location: Mesoamerican CoE, Australasian CoE, East African Coe, and Philippines CoE

Key results

This project examined the population dynamics of coral populations at a scale which is highly novel relative to previous studies. In addition to establishing the monitoring of coral reefs at the four Centres of Excellence across the CRTR Program, this project delivered a number of important research outcomes and conclusions. Outcomes included corrections developed to eliminate biases that occur because of boundary effects when measuring the size of benthic organisms, as well as a series of relationships between 2-dimensional and 3-dimensional estimates of coral growth. Several important ecological phenomena were also identified, including two modes of partial mortality affecting coral species in the Caribbean; with some species rapidly losing colony integration while others maintained integration and sacrificed marginal tissue. Research within this group also identified the critical observation that mild thermal stress events showed different responses than extreme events: during extreme events, small colonies do better than larger colonies, while during mild events, colony size did not influence bleaching. In both cases massive corals were found to be more sensitive than branching corals. The research within this project also identified the important influence of substrate reflection, for example from sand, increasing available light and exacerbating the risk of coral bleaching. Indeed, corals growing on and near sand showed more intense bleaching than those growing on or near substrate with lower reflectivity. The group also made some interesting long-term observations, such as sea urchin densities on the western reefs of Zanzibar increasing 6 to 10-fold since 1996; with fish on the same reefs increasing considerably in the last three years.

Background

The overall objective in this project was to assess coral-population dynamics within the context of coral bleaching and subsequent effects. Given the importance of comparing between regions, in terms of the ability to generalise about the ecological behaviour of coral reefs, the team decided to focus work around 3 CoEs in the initial stages: Puerto Morelos (Mexico), Heron Island (Australia), and Zanzibar (Tanzania). This project also undertook activities in the Philippines and Palau. This CoE-centered approach allowed for a focus on coral dynamics which were easily accessible, and where the research activity could evoke collaboration among the other working groups with the Coral Reef Targeted Research Program.

We focused on quantifying both state (i.e., coral cover, macroalgal cover, size-frequency distributions) and process (or vital-population rates) variables (including coral recruitment rates, individual growth rates, partial mortality rates, and survival). We were also interested in the macro-processes, such as predation, herbivory, and oceanography that influenced the corals' vital-population rates. Our approach allowed us to determine which vital rates were responsible for the state of the reef, and allowed us to derive novel yet pragmatic models that would predict population changes and the future state of the reefs.

Objectives

One of our primary goals was to understand: Which coral species were physiologically more tolerant to thermal stresses than others, and why? Which interacting variables and processes are driving coral population structure? Which processes are primarily responsible for coral population change? Does differential coral population response to, and recovery from, thermal stress vary among regions and habitats? What role do remnants play in recovery processes? Is annual recruitment vital in all habitats? Which habitats recover more rapidly than others? Which coral species will adjust to global climate change? Can differential and local management practices influence thermal-stress response and recovery?

Our primary task was to assess the dynamics of coral populations and associated coral reef organisms by defining the key ecological processes that regulate the populations (Figure 15). Understanding these processes, assessing their spatial variation and their relationship with state variables, including size-frequency distributions, leads to predictive models of population trajectories, relative population size distributions, and community change under different climate change scenarios. We predicted that size-frequency distributions coupled with partial mortality information could provide a reliable indicator of coral stress and provide insight into the future of coral reefs.

Specifically we examined:

1. Spatial patterns in coral population size-frequency distributions and temporal changes of the populations at three CoEs;

2. Scale dependence of key process variables, including rates of recruitment, partial mortality, and mortality;

3. Relationships between processes and state variables and whether size-frequency distributions reflected population performance;

4. Effect of macro-processes, including herbivory (i.e., density and composition of urchins and fishes), on coral population vital rates and diseases.

Figure 15. Total mortality of a coral colony over a year period. Photo: R. van Woesik

Methods

The sampling strategy captured state and process variables at a spatial scale of 10s of kilometers (herein called a Location). Sampling aimed at establishing 6-7 sites per location. Sites were spaced approximately 2 km apart, representing a 103 m spatial scale, with random stations nested within sites. Sites were systematically selected based on the targeted depth regime where sampling efforts were focused on one depth zone (2-5 m), rather than stratifying the design by depth and reducing the spatial area to be sampled. Stations were randomly selected and nested within sites, representing a 104 m spatial scale and were 75 x 25 m. However, these dimensions remain plastic depending on the reef morphology, while maintaining a total area of 1875 m^2. Stations were the effective sampling units. Within each station we ran at least 5, 50 m transects that were re-randomized each sampling period, and used to estimate state variables (i.e. size frequency distributions, benthic composition). Three randomly selected 16 m^2 quadrats were placed in each station, and marked for relocation purposes (Figure 16), and used to assess processes (i.e. recruitment, growth, partial mortality, mortality etc.) across time (repeated measures design). Both quadrats and belt-transects are effectively sub-samples from which we derived estimates of means for each station at each sampling event (because the station was the effective sampling unit).
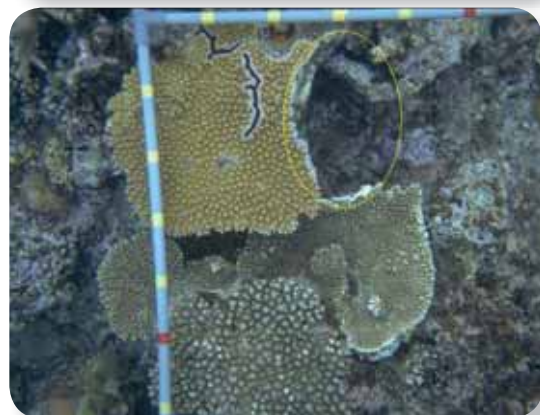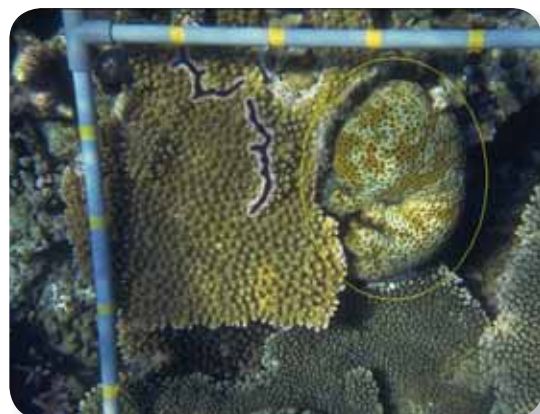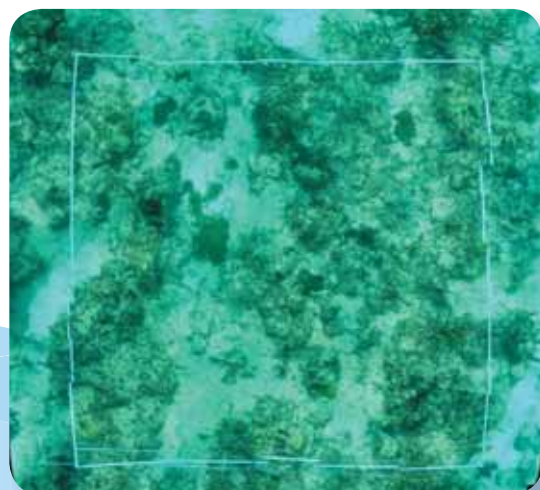

Figure 16. Permanent quadrat in Puerto Morelos, Mexico (~ 50, 1 m^2 photos were overlapped to generate a 16 m^2 mosaic using Matlab® software). Photo: Nuno Garcia

Results and discussion

a. Advancements in coral reef sampling

Throughout this project various techniques for monitoring populations have been used and tested. Zvuloni et al. (2008) elucidated the biases that can arise in the application of popular and traditional sampling methods (e.g. quadrat, belt-transect, and line-intercept). Simple mathematical corrections were developed that provide unbiased estimations for previously collected data acquired by these widely used methods. In addition, alternative sampling methods were identified that do not suffer from these shortcomings. Eliminating these types of sampling errors provide better assessments of the status of a given coral reef, and provide precise comparisons among coral reefs in different regions. This work is equally relevant in other ecological contexts, not just corals.

Limitations with photographic analyses have also been recognized as a 3-dimensional (3-D) reef is turned into a 2-dimensional (2-D) photo. For some growth morphologies such as branching corals, this significantly affects growth measurements. Holmes et al. (2008) found a significant difference in growth when comparing 2-D and 3-D measurements for two branching species. These findings suggest that growth measurements are only reliable when measured in 3-D, and 2-D measurements can be corrected to provide reliable coral estimations.

b. Population dynamics

Key process variables (i.e. partial mortality, whole colony mortality, recruitment, and growth) have been identified and investigated to some degree in each region. In the Caribbean, partial mortality appears to be a primary mechanism of coral-cover degradation (Figure 17). Two modes of partial mortality were identified: (1) peripheral-partial mortality, occurring between live tissue and substrate, and (2) centralised-partial mortality, occurring within the colony, completely surrounded by live tissue. All species investigated (*Diploria strigosa*, *Siderastrea siderea*, *Porites astreoides*, *Agaricia agaricites* and *Montastraea cavernosa*) were affected by peripheral mortality, while *P. astreoides* and *S. siderea* were more likely to also exhibit centralized mortality.
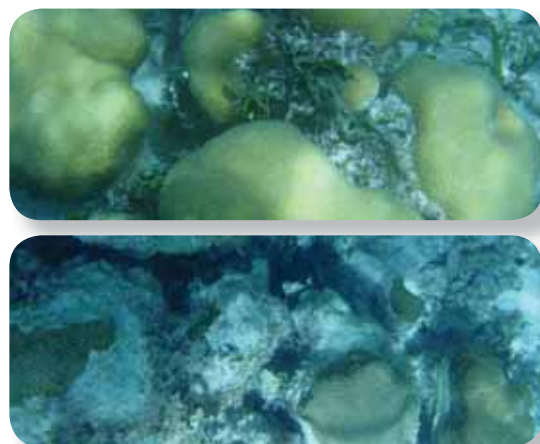

Figure 17. Partial mortality of *Montastraea* one year to the next in Puerto Morelos, Mexico. Photo: J. Gilner

c. Response and recovery from bleaching events

These same process variables were investigated on Heron Island in response to a mild thermal stress event. Mortality, recruitment, and growth were examined for four targeted coral taxa (*Pocillopora damicornis*, *Stylophora pistillata*, *Favites/Goniastrea*, and *Favia* spp.) to determine sensitivity to a mild thermal-stress event (in January-May 2006 on Heron Island in the Great Barrier Reef). The mild thermal stress event showed a different response than major thermal stress events. The mild stress showed that coral-colony size did not influence bleaching response, and massive corals were more affected by bleaching than branching corals. Because massive corals were primarily surrounded by sand, it was hypothesized that light reflectance from sand increased incoming irradiance and hence elevated stress. During extreme thermal-stress events small-coral colonies were least effected, as were massive and encrusting colonies. Therefore, various thermal stress anomalies show different bleaching responses.

d. Thermal stress, bleaching, and diseases

The prevalence of black-band disease (BBD) was strongly associated with high-water temperature. BBD infected coral colonies exhibited aggregated distributions on small spatial scales (up to 1.9 m). Newly-infected corals appeared in proximity to existing infected corals. Previously infected corals were more susceptible the following summer season. Therefore, water-borne infection is likely to be a significant transmission mechanism of BBD.

e. Coral-community structure

The patterns of coral community composition and diversity were examined around Zanzibar at three spatial scales ranging from transects (≤ 20 m), stations (< 100 m), to sites (< 1000 m). Two sites of the four, Chumbe and Mnemba, are located within marine protected areas (MPAs) and the other two sites, Bawe and Changuu, are not protected.

Additive partitioning was used to examine diversity within and between the three spatial scales, where individual-based rarefaction was used as a null model. We show that each of the sites is different in species composition, except Bawe vs. Changuu. Chumbe and Mnemba, the most diverse sites, exhibited α (local) and β (turnover)-diversity as expected by random, whereas Bawe and Changuu were different than expected. In general, given the regional species pool, diversity among sites was significantly higher than expected. These results suggest that nonrandom processes interact on an among-sites scale (i.e., ca. kilometers), and in Bawe and Changuu they also interact on a within - and between-transects scale. The nonrandom outcome helps identify appropriate boundaries for studying mechanisms that generate and maintain biodiversity within this region. In considering coral diversity in Bawe, the number of rare species and singleton species (only found in one locality) suggests that Bawe should be declared a Marine Protected Area (MPA).

Figure 18. Permanent quadrat to assess coral-community structure and herbivory by sea urchins in Zanzibar. Photo: A. Zvuloni

f. Macro-processes

i. Herbivory by sea urchins

We assessed the impact of sea urchin populations on coral communities around the island of Zanzibar. Twice a year, between 2007 and 2008, surveys of urchin populations (species, densities and size-frequency distributions) were performed at the same six locations used for coral and fish monitoring. Urchin bioerosion experiments were conducted separately for each of the study sites. Dominance of two urchin species was evident: *Diadema setosum* and *Echinometra* sp., in five out of six stations, with *D. setosum* dominating the western side of Zanzibar and *Echinometra* sp. dominating the eastern side (Figure 19). Average densities of *D. setosom* and *Echinometra* sp. ranged from 0-30 and 0-88 individuals m^{-2}, respectively. Eastern sites showed 2-4 times more sea urchins than the western sites. Urchin species assemblage did not change significantly throughout the duration of the study, nor did it change in comparison to 1996 (McClanahan et al. 1999), whereas sea urchin densities at Changu and Chumbe increased 6-10 fold since 1996. Mnemba showed the lowest sea urchin densities (1.2 urchins m^{-2}) and the highest abundance of urchin-preying fish. Molecular and morphological studies conducted on *Echinometra* sp. from 8 locations around the island of Zanzibar and 3 locations in the northern Red Sea suggest that urchins from the genus *Echinometra* are a suite of new species.

Figure 19. Dominant sea urchins in Zanzibar.
A *Echinothrix diadema*, B *Echinometra* sp, C *Diadema savignyi* and D. *setosum*. Photos: O. Bronstein

ii. Fish communities

Zanzibar's economy relies heavily on fishes, which are used both for food and as an attracting component in the coral reef tourism industry. We studied the coral reef fish community structure around Zanzibar to establish a baseline for future monitoring of fish interactions with corals and sea urchins (herbivory, predation). In April 2009 we compared four sites around the island. Two sites are marine reserves (Chumbe in the west side of the island and Mnemba in the east) and another two (Changu and Bawe, located on the west side) are not protected and are heavily fished. We visually sampled fish in replicated 25 by 2 m transects, identifying fishes to the species level and estimating their abundance and length (Figure 20). We used point sampling along transects to estimate habitat parameters. We sampled 7046 individuals from 153 species belonging to 30 fish families. Using a null model we found

Figure 20. The grunt fish Blackspotted rubberlip (*Plectorhinchus gaterinus*) is a component of the reef fisheries in Zanzibar. Photo: E. Brokovich

that alpha diversity was lower than expected by chance but also that the sites were highly heterogeneous. The fish community structure differed remarkably between the sites with the two non- managed sites being the most similar. The fish-community structure was influenced by the amount of living coral cover, particularly branching coral colonies and substrate structural complexity. Regardless of low coral cover, the number of fish species was highest at Mnemba (a protected site). The amount of large exploitable fish (> 20 cm) was highest in the protected sites (16% of all fish in Chumbe and 6% in Mnemba as oppose to ca. 3% in the non protected sites). Mnemba had the highest number of sea urchin predators and the fewest sea urchins. Comparing this study with previously reported data from the same area which was affected by the 1998 bleaching event, we show that fish density increased dramatically in the last three years.

2

Key literature generated with Full/partial project support:

1. Brokovich E, Zvuloni A, Bronstein O, Loya Y (in prep) Changes in fish assemblages around Zanzibar Island (Tanzania) with respect to habitat complexity and management practices.

2. Bronstein O, Loya Y (in prep) A new sea urchin species of the genus Echinometra from the Red Sea and western Indian Ocean.

3. Bronstein O, van Woesik R, Loya Y (in prep-a) Population shifts of sea urchins on the coral reefs of Zanzibar.

4. Bronstein O, van Woesik R, Loya Y (in prep-b) Spatial patterns of sea urchin bioerosion on the coral reefs of Zanzibar.

5. Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLoS ONE 4:e5239

6. Fabricius KE, Wild C, Wolanski E, Abele D (2003) Effect of transparent exopolymer particles and muddy terrigenous sediments on the survival of hard coral recruits. Est Coast Shelf Sci 57:613-621

7. Field SN, Glassom D, Bythell JC (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. Coral Reefs 26:279-289

8. Fleitmann D, Dunbar RB, McCulloch M, Mudelsee M, Vuille M, McClanahan TR, Cole JE, Eggins S (2007) East African soil erosion recorded in a 300 year old coral colony from Kenya. Geophysical Research Letters 34:L04401

9. Gilner JE, Van Woesik R (in prep) Partial mortality of Caribbean corals: modes, trends and consequences. Marine Biology

10. Gleason DF, Edmunds PJ, Gates RD (2006) Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral Porites astreoides. Marine Biology 148:503-512

11. Golbuu Y, Victor S, Penland L, Idip D, Emaurois C, Okaji K, Yukihira H, Iwase A, van Woesik R (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26:319-332.

12. Holem L, Koksal S, van Woesik R (in prep) Vital rates influencing population dynamics of Indo-Pacific reef corals. Oecologia

13. Holmes G (2008) Estimating three-dimensional surface areas on coral reefs. Journal of Experimental Marine Biology and Ecology 365:67-73

14. Holmes G, Ortiz JC, Kaniewska P, Johnstone R (2008) Using three-dimensional surface area to compare the growth of two Pocilloporid coral species. Marine Biology 155:421-427

15. Houk P, Bograd S, van Woesik R (2007) The Transition Zone Chlorophyll Front acts as a trigger for Acanthaster planci outbreaks in the Pacific Ocean: a historical confirmation. Journal of Oceanography 63:149-154

16. Houk P, van Woesik R (2008) Dynamics of shallow-water assemblages in the Saipan Lagoon. Marine Ecology Progress Series 356:39-50

17. Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook LJ, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365

18. Jupiter S, Roff G, Marion G, Henderson M, Schrameyer V, McCulloch M, Hoegh-Guldberg O (2008) Linkages between coral assemblages and coral proxies of terrestrial exposure along a cross-shelf gradient on the southern Great Barrier Reef. Coral Reefs 27:887-903

19. Kleypas, JA, and O. Hoegh-Guldberg (2007) Coral reefs and global climate change, Chapter 3 in Wilkinson, C. (ed.) Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005. GCRMN, Townsville.

20. Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641-653

21. Obura DO (in press) Bleaching as a life history trait in coral-zooxanthellae holobionts - relevance to acclimatization and adaptation 11th International Coral Reef Symposium, Ft. Lauderdale, USA

22. Ortiz JC, Gomez-Cabrera MD, Hoegh Guldberg O (submitted) Effect of colony size and surrounding substrate on corals experiencing a mild bleaching event on Heron Island reef flat (southern Great Barrier Reef, Australia). Coral Reefs

23. Ortiz JC, Holmes G, Gomez-Cabrera MD, Hoegh Guldberg O, van Woesik R (in prep-a) Using population's demographic dynamics as early indicator of communities' response to subtle stress: A coral reef case study. Ecological applications

24. Ortiz JC, van Woesik R, Hoegh-Guldberg O (in prep-b) Interpreting coral reefs evenness dynamics in a changing environment.

25. Ortiz JC, van Woesik R, Marshall D, Hoegh-Guldberg O (in prep-c) 'The balance between how much we should do and How much we can do: Maximizing the power and accuracy of a monitoring program dataset'.

26. Ridgway T, Gates RD (2006) Why are there so few genetic markers available for coral population analyses? Symbiosis 41:1-7

27. Ridgway T, Riginos C, Davis J, Hoegh-Guldberg O (2008) Genetic connectivity patterns of Pocillopora verrucosa in southern African Marine Protected Areas. Marine Ecology Progress Series 354:161-168

28. Rongo T, Bush M, van Woesik R (2009) Voyages of discovery or necessity: harmful algal blooms cause ciguatera poisoning in fishes and contribute to the contemporary and late Holocene Polynesian migrations. Journal of Biogeography doi:10.1111/j.1365-2699.2009.02139.x

29. Rosenberg E, Kushmaro A, Kramarsky-Winter E, Banin H, Loya Y (in press) Role of microorganisms in coral bleaching. Environmental Microbiology

30. Rosenfeld M, Shemesh A, Yam R, Sakai K, Loya Y (2006) Impact of the 1998 bleaching event on Ð18O records of Okinawa corals. Marine Ecology Progress Series 314:127-133

31. Rusch A, Huettel M, Wild C, Reimers CE (2006) Benthic oxygen consumption and organic matter turnover in organic-poor, permeable shelf sands. Aqu Geochem

32. van Woesik R, Ganase A, Sakai K, Loya Y (in prep) Coral bleaching: the winners and the losers, ten years on. Ecology Letters

33. van Woesik R, Koksal S (2006) A coral population response (CPR) model for thermal stress. In: Phinney J.T. et al (ed) Coral reefs and climate change: science and management. American Geophysical Union, Washington DC, p 129-144

34. van Woesik R, Lacharmoise F, Koksal S (2006) Annual cycles of solar insolation predict spawning times of Caribbean corals. Ecology Letters 9:390-398

35. Wagner D, Mielbrecht E, van Woesik R (2008) Application of landscape ecology to spatio-temporal variance of water-quality parameters along the Florida Keys reef tract. Bulletion of Marine Science 83:553-569

36. Weeks SJ, Anthony KRN, Bakun A, Feldman GC, Hoegh-Guldberg O (2008) Improved predictions of coral bleaching using seasonal baselines and higher spatial resolution. Limnology and Oceanography 53:1369-1375

37. Wehrmann LM, J. KN, Pirlet H, Unnithan V, Wild C, Ferdelman TG (2009) Carbon mineralization and carbonate preservation in modern cold-water coral reef sediments on the Norwegian shelf. Biogeosciences 6:663-680

38. Yarden O, Ainsworth TD, Roff G, Leggat W, Fine M, Hoegh-Guldberg O (2007) Increased prevalence of ubiquitous ascomycetes in an acropoid coral (Acropora formosa) exhibiting symptoms of brown band syndrome and skeletal eroding band disease. Applied and Environmetal Microbiology 73:2755-2757

39. Zvuloni A, Armoza-Zvuloni R, Loya Y (2008a) Structural deformation of branching corals associated with the vermetid gastropod Dendropoma maxima. Marine Ecology Progress Series 363:103–108

40. Zvuloni A, Artzy-Randrup Y, Stone L, Kramarsky-Winter E, Barkan. R, Loya Y (2009) Spatio-temporal transmission patterns of black-band disease (BBD) in a coral community. PLoS ONE 4 e4993

41. Zvuloni A, Artzy-Randrup Y, Stone L, Loya Y (in prep-a) Spatio-temporal relations between two coral diseases: black-band and white plague-like.

42. Zvuloni A, Artzy-Randrup Y, Stone L, van Woesik R, Loya Y (2008b) Ecological size-frequency distributions: how to prevent and correct biases in spatial sampling. Limnology and Oceanography: Methods:144-153

43. Zvuloni A, Brokovich E, Hosgin I, van Woesik R, Loya Y (in prep-b) Porites micro-atolls are diversity hot spots.

44. Zvuloni A, Mokady O, Al-Zibdah M, Bernardi G, Gaines SD, Abelson A (2008c) Local scale genetic structure in coral populations: A signature of selection. Marine Pollution Bulletin 56:430-438

45. Zvuloni A, Stone L, Loya Y (in prep-c) Obtaining ecological count-based measures of sessile organism distributions from line-intercept data.

46. Zvuloni A, van Woesik R (in prep) Spatial patterns of coral diversity around Zanzibar Island.

Project 7. Effects of bleaching on coral and fish communities in the Western Indian Ocean – and effects of bleaching on coastal coral communities in East Africa

Mebrahtu Ateweberhan, Juliet Karisa, Tim R. McClanahan, David Obura, and Shakil Visram

Location: Kenya and East African CoE

Key results

The study within this project compiled ~2000 site-time combinations of coral cover for the whole Western Indian Ocean (WIO) for the period 1958-2005 and analyzed regional patterns and identified the 1998 climatic oscillation as the most significant factor in affecting regional variation in coral cover. Further analysis of change in coral cover and community structure and their relationship with environmental properties indicated that the impact of the disturbance was variable in space in association with region-specific environmental properties; primarily the background temperature, light condition and water current. This has been mapped and provides the basis for identifying least/most vulnerable reefs and predicting the spatial distribution of future coral reefs and developing management priorities that are most appropriate for their future. The coral recruitment study in Kenya indicated higher recruit density and generic composition in Mombasa (MPA) than in fished reefs.

Background

The Western Indian Ocean (WIO) is home to millions of coastal people who directly or indirectly depend on coral reefs for goods and services (Figure 21). Many coral reefs in the region are already under excessive pressure from the effects of overfishing, coastal development and pollution. Climate change will interact and probably reinforce the negative effect of these other stress factors. The region suffered one of the highest rates of coral mortality during the 1998 climatic oscillation (Wilkinson et al. 1999; Goreau et al. 2000).

The future of corals and coral reefs in the region and globally will depend on their vulnerability to environmental changes associated with climate change. This will be influenced by the background environmental conditions and community structure that will eventually affect their

Figure 21. Fishermen in Mtwara, Tanzania.
Photo: T. McClanahan

tolerance to extreme anomalous events, their ability to recover from the impacts and their overall resilience. A better understanding of the relationship between the regional environmental change and the background environmental properties and the status in coral reef community structure is required. Recent studies in the Caribbean (Gardner et al. 2003) and the Pacific and Eastern Indian Ocean regions (Bruno and Selig 2007) indicated significant long-term region-wide changes in coral cover because of many interacting stress factors. This leaves a gap in information for understanding the global patterns; particularly the WIO region, which remains one of the main reef regions where little is known about the timing, rate and spatial variability of change in coral cover.

East African reef systems are among the most poorly studied on a regional scale yet face some of the greatest environmental threats globally. Measuring recruitment patterns and mortality of corals is important for understanding mechanisms that regulate their populations and mediate species coexistence. The East African project focuses on ecological and eco-physiological aspects of coral bleaching biology, and aspects of symbiotic biology and *Symbiodinium* dynamics.

Objectives

- Compile coral cover from published and unpublished sources and conduct a meta-analysis of regional patterns.

- Investigate the relationship of the regional change in cover with environmental properties, and sea surface temperature in particular.

- Gather additional information in coral and other benthic community structure and investigate changes in relation to the effects of the 1998 ENSO and other minor bleaching events.

- Investigate the effect of the changes in benthic structure and reef fish populations and vice versa.

- Identify reefs of high/low environmental vulnerability to future climate change scenarios and for prioritising conservation, based on their environmental properties and community responses.

- Investigate coral and zooxanthellae population dynamics and responses in physiology related to management, seasonality and depth.

Materials and methods

a. Regional patterns in coral cover, community structure and species diversity

We compiled a cover database based on published and unpublished data for ~2000 site-time combinations gathered between 1958 and 2005. We constructed box plots and compared cover distributions between time periods for the whole WIO and between regions for three time periods, some time before 1998 (1985-1997), immediately after the 1998 event (1999-2000) and the recovery period (2001-2005). We calculated relative change in coral cover for 36 major reef areas in WIO for periods immediately before and after 1998 in order to compare regional variation in the impacts of the 1998 bleaching event. Coral species richness data was compiled for the whole region by including recent taxonomic surveys that focused on the southern part of WIO (Tanzania, Mozambique, Madagascar) and the Southern Red Sea

Figure 22. Partially bleached colony of *Porites lutea* in the WIO during 2005 bleaching event.
Photo: T. McClanahan

(Eritrea) that were less surveyed previously. Coral community structure was investigated for 8 countries and 91 sites for data gathered in 2005 when a minor bleaching event was observed in the southern part of WIO (Figure 22). Similar analysis had been conducted for Kenya and NE Madagascar (1998) and the Maldives (2000) which enabled comparison between the two periods for those areas. The quick survey also enabled analysis of taxon and site-specific susceptibilities based on the number of coral colonies, sites and bleaching response.

b. Changes in size structure of coral populations on Kenyan reefs

The interactive effect of management and bleaching on the size structure of coral population was analysed by comparing haphazard colony size measurements for 21,000 of 26 common coral taxa collected annually between 1992 and 2006 on Kenyan reef lagoons of different management levels.

c. Relationship between coral cover, thermal stress and the background SST properties

The relationship between the level of thermal stress, expressed in degree heating weeks/months (number of weeks/months that the temperature is 1 °C above the warm-season baseline), experienced in 1998 and the background SST properties was investigated for 40 HADISST cells in the East African Coastal Current System (McClanahan et al. 2007a). A similar analysis was made for the 36 major reef areas in the region where change in coral cover due to the 1998 thermal stress was analysed. The latter analysis included areas in the Red Sea and Arabian regions. In addition, the predictive ability of a multivariate stress model (Maina et al. 2008) that included 11 SST and other environmental properties was investigated.

d. Change in benthic reef structure and reef fish populations

Changes in reef fish populations belonging to different size classes and trophic composition in relation to the change in reef benthic structure and topographic complexity was investigated on reefs in several countries in the region by comparing fish community structure before and after 1998. In addition, the role of management in influencing the response to bleaching was studied by comparing MPAs and fished reefs.

e. Spatial-temporal patterns in coral recruitment and mortality and zooxanthellae density

The East African project studied spatial and temporal patterns of coral recruitment and mortality in four lagoonal reefs in Kenya with the aim of comparing coral recruit densities and juvenile mortality between sites, months, seasons and years. In addition, differences in zooxanthellae densities among coral taxa were compared for the four main seasons in East Africa (NE Monsoon, Dec-Mar; SW Monsoon, Apr-Oct, and the transitional seasons in between, Nov-Dec).

Results and discussion

a. Regional change in coral cover, community structure and species richness distribution

Investigations of the spatio-temporal patterns indicated that the 1998 climatic oscillation was the single most important factor in influencing temporal change in coral cover in WIO (Ateweberhan and McClanahan in review-b). It resulted in a 'stepped change' of a strong decline in 1999-2000 and recovery in 2001-2005 unlike in the Caribbean (Gardner et al. 2003) and the Eastern Indian Ocean-Western Pacific (Bruno and Selig 2007), where continuous declines have been observed even before 1998. Analysis of frequency distributions indicated that median coral cover was 38.8% before 1998, 18.13% immediately after the 1998 ENSO and 28.13% in 2001-

Figure 23. Branching coral Acropora sp. in Kenyan reefs. Photo: T. McClanahan

2005. The most severely affected reef areas were southern India, Sri Lanka, central atolls of the Maldives and Granite Seychelles. Northern Arabian/Persian Gulf, Gulf of Oman, Chagos, Kenya, southern Tanzania and southern Seychelles were also greatly affected. Southern Arabian/Persian Gulf, Arabian Sea (Socotra and Gulf of Kutch), southern Maldives, northern Tanzania, northern and central Mozambique and Aldabra suffered moderate effects. The Red Sea, Mayotte, Comoros, southern Mozambique, South Africa, Madagascar, Reunion, Mauritius, and Rodrigues were the least affected.
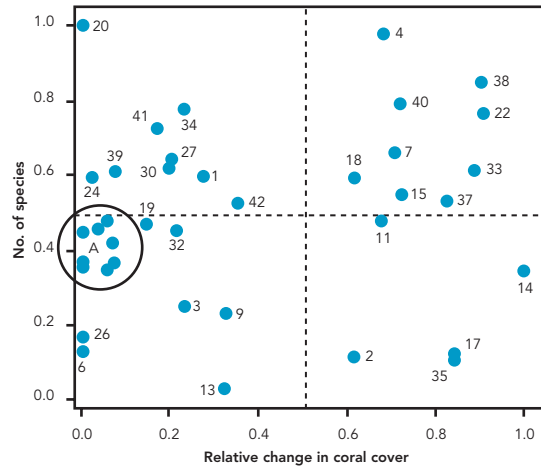
The study on coral communities and diversity in the WIO found evidence that most of the northern Indian Ocean communities were considerably changed from the pre-1998 communities (McClanahan et al. 2007b). These reefs, previously dominated by branching and plating species, such as *Acropora* (Figure 23) and *Montipora*, are now dominated by massive and submassive corals, such as *Porites* and faviids. In contrast, the southern Indian Ocean community has more of the branching forms. The same study also calculated extinction probabilities of coral taxa in the region by incorporating information on geographic distribution, abundance and bleaching susceptibility. Some of the rare and bleaching-susceptible taxa, such as *Plerogyra, Plesiastrea, Gyrosmillia, Physogyra* and *Seriatopora*, were predicted to be more vulnerable to local extinction while some of the sensitive taxa such as *Montipora, Acropora,* and *Pocillopora* are widely distributed and likely to persist over climate change disturbances, although they could suffer localised population declines.

A scatter plot of diversity-mortality relationship (Figure 24) can be used to show which areas of high diversity are the most susceptible and which are not (Ateweberhan and McClanahan in review-a). North-western Australia; Gulf of Oman; southern Kenya; Mafia and Mnazi Bay in Tanzania; Lakshadweep, India, Sri Lanka; Maldives; Seychelles and Chagos were areas of high diversity that suffered high mortality in 1998. High diversity areas that had lower mortality were northwestern Madagascar; Thailand-Mergui; Mayotte;Mozambique; Rodrigues; Socotra; Songo Songo, central Tanzania; southern Red Sea; Zanzibar and northern Tanzania. If the 1998 event represented vulnerability in the region then we can expect that these patterns may repeat themselves in the future and that the high diversity-low mortality sites listed above are a priority for protective management.

Figure 24. Scatterplot of coral diversity-mortality relationship in the western Indian Ocean.

Values are standardized from 0 to 1 relative to the lowest and highest values. High and low areas are separated at a conventional 50% cut level (dashed lines). Sites are 1. Aldabra, Cosmoledo, Faarquhar, 2. Arabian Gulf, 3. Arabian Sea, 4. Australia NW, 5. Australia SW, 6. Bangladesh, 7. Chagos, 8. Cocos Keeling, 9. Comoros, 10. Djibouti (Gulf of Aden), 11. Gulf of Oman, 12. India (Andaman-Nicobar), 13. India (Gulf of Kutch), 14. India (Gulf of Manar), 15. India (Lakshadweep), 16. India (West coast patches), 17. Kenya- N, 18, Kenya- S, 19. Madagascar- NE, 20. Madagascar- NW, 21. Madagascar- SW, 22. Maldives, 23. Mauritius, 24. Mayotte, 25. Mozambique S (Pemba), 26. Myanmar (Burma), 27. Red Sea- C, 28. Red Sea- N, 29. Red Sea- S, 30. Reunion, 31. Rodrigues, 32. Seychelles, 33. Socotra, 34. Somalia, 35. South Africa, 36. Sri Lanka, 37. Tanzania- C (Mafia), 38. Tanzania- C (Songo Songo), 39. Tanzania- N (Zanzibar), 40. Tanzania- S (Mnazi Bay), 41. Thailand-Mergui Archipelago. When a number is not shown it is in the circle marked A.

b. Relationship between change in coral cover community structure and environmental properties

Analysis of the relationship between seawater temperature properties and coral mortality identified areas with flat and weak bimodal SST distributions and moderate SD SSTs as the most resistant to these large-scale disturbances (Ateweberhan and McClanahan in review-b). These are mostly situated in high retention areas (e.g. the triangle between southern Tanzania, northern Mozambique, and northern Madagascar), or on leeward sides of islands (e.g. inner Zanzibar) and the subtropics (e.g. South Africa and northern Red Sea). The relative abundance of *Acropora* and *Montipora* declined in direct proportion to the cumulative warm seawater temperature experienced in 1998 (Figure 25).

The multivariate stress model also predicted the change in cover and community susceptibility to bleaching reasonably well (Maina et al. 2008). Mean and maximum historical temperatures and degree heating weeks appear to be the main temperature variables that are positively associated with bleaching severity, whereas temperature variation (CV) was negatively associated with the bleaching severity. Photosynthetically active (PAR) and ultraviolet (UV) light are positively associated with bleaching severity. Winds and currents seem to play some role and the analysis indicates that bleaching is most severe in areas with low winds and north-south currents.

From both analyses of the background SST and the multivariate stress model, it is clear that the thermal stress of 1998 and its impact on coral cover and community structure were reliably predictable and that the background SST and environmental properties influence the outcome of a bleaching event. Both models provide a working tool to plan appropriate management responses for each of these regions (e.g. (McClanahan et al. 2008b).
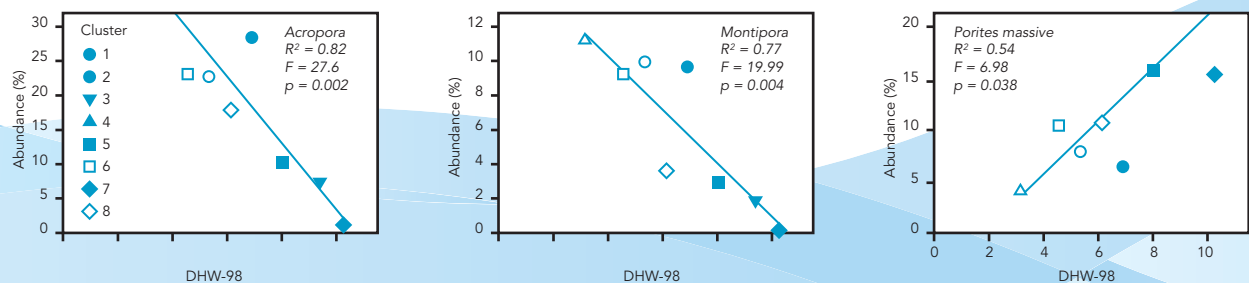
Figure 25. Relative abundance as a function of degree heating weeks in 1998 (DHW-98) for the 3 taxa with statistically significant (p < 0.05) linear relationships. JCOMM DHW was used as it gave a better fit than NOAA DHW in a previous analysis. Clusters defined as in Fig. 1. McClanahan et al. (2007a)

c. Changes in size structure of coral populations on Kenyan reefs

Analysis of size structure of coral populations also showed significant interactions between bleaching and management effects (McClanahan et al. 2008a). Seventeen taxa had statistically significant different sizes for comparison of the management regimes, with only one genus, *Pavona*, having larger sizes in the unprotected reefs. The size of eight coral genera showed significant time and management interactions, and size frequency differences that existed in management areas prior to 1998 were further reinforced after the bleaching event. Time alone was a significant factor for eleven genera, and in all cases colonies were smaller after 1998. Most taxa had right skewed size frequency distributions and these were significantly reduced after 1998 for *Acropora, Hydnophora*, and *Montipora*. Most taxa had peaky distributions and only Acropora experienced a statistically significant change from peaky to flat across the 1998 event. Generally, no taxa were tolerant to both fishing and bleaching disturbances and the combined effect was to reduce the size of all corals.

d. Relationship between change in benthic reef structure and reef fish populations

There was significant shift in the species composition of reef fishes in relation to the change in coral cover, coral and benthic community structure and spatial complexity (Graham et al. 2008). Generally corallivore and planktivore fishes suffered the highest population declines with local extinctions in some species. Effects also varied by size, the smallest size class suffering the highest (Figure 26). Herbivorous and carnivorous fishes and mixed feeders didn't show significant effects but long-term responses could be significant because of the impact on the small-size classes (recruits and juveniles). Responses also varied in accordance with management; generally protected areas suffered higher population declines and species losses. Protected areas also suffered the highest coral mortality and recovery was slower compared with fished reefs (McClanahan 2008).

Figure 26. Amphiprion on bleached anemone in Maldives, Indian Ocean Photo: T. McClanahan

e. Spatial-temporal variation in coral recruitment and mortality in coastal Kenya

Coral recruit density in the Mombasa Marine Park was significantly higher (7.45 recruits m^{-2}) than in the fished reefs. Recruit density was higher during the cold period (Southeast Monsoon) than the warm season (Northeast Monsoon) during the two study years, with 2006 having higher recruitment than 2007. A total of 16 genera were recorded; Mombasa Marine Park had the highest number of genera (13) while Kanamai had the lowest density (3.52 recruits m^{-2}) and number of genera (8). Dominating genera, in order of overall abundance were *Favia, Porites, Favites, Pocillopora* and *Pavona*, respectively. Coral genera exhibited site specific abundance and mortality rates with *Pocillopora* having high abundance in Nyali (3.46 recruits m^{-2}) and high mortality rate in Vipingo (85%). The spatial and temporal variation in recruit density, genera richness and survival of coral genera is probably related to management and sea-water temperature.

f. Temporal dynamics and species-specific differences in zooxanthellae densities

Zooxanthellae densities and mitotic index were variable depending on the coral taxa investigated (Grimsditch et al. 2008b). *Pocillopora damicornis* had the lowest zooxanthellae density and the highest taxonomic index compared to *Galaxea fascicularis, Porites cylindrica* and *Porites lutea* that had high zooxanthellae densities but low mitotic index. The results are in agreement with previous observations that showed inverse correlation between zooxanthellae density and bleaching susceptibility (Stimson et al. 2002). All the studied coral taxa displayed highest zooxanthellae densities during the northeast monsoon season and most displayed highest mitotic indices during the transitional period directly preceding the northeast monsoon (Grimsditch et al. 2008a). The higher densities found during the northeast monsoon (when temperatures and radiation levels are higher) are opposite to trends observed at higher latitudes, indicating that corals closer to the equator may be less influenced by seasonal variability of temperature and light. Other factors may have a greater influence on population dynamics.

2

Key literature generated with full/partial project support:

1. Cinner JE, Daw TM, McClanahan TR (in press) Poverty and livelihood portfolios affect decisions to exit a declining artisanal fishery. Conservation Biology

2. Cinner JE, McClanahan TR, Graham NAJ, Pratchett MS, Wilson SK, Raina JB (2009) Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. Journal of Applied Ecology 46:724-732

3. Graham NA, McClanahan TR, MacNeil MA, Wilson SK, Polunin NV, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y, Bigot L, Galzin R, Ohman MC, Garpe KC, Edwards AJ, Sheppard CR (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS ONE 3:e3039

4. Graham NAJ, McClanahan TR, Letourneur Y, Galzin R (2007) Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef. Environmental biology of fishes 78:57-69

5. Grimsditch G, Awaura J, Kilonzo J, Amiyo N, Obura D (2008a) High zooxanthellae densities and turnover correlate with low bleaching tolerance in Kenyan corals. In: Obura D, Tamelander J, Linden O (eds) Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO status report 2008. CORDIO/Sida-SAREC, Mombasa, p 235-236

6. Grimsditch G, Awaura J, Kilonzo J, Amiyo N, Obura D (2008b) Zooxanthellae densities are highest in summer months in equatorial corals in Kenya. In: Obura D, Tamelander J, Linden O (eds) Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO status report 2008. CORDIO/Sida-SAREC, Mombasa, p 237-239

7. Karisa JF, Kaunda-Arara B, Obura D (2008) Spatio-temporal variation in coral recruitment and mortality in coastal Kenya. In: Obura D, Tamelander J, Linden O (eds) Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO status report 2008. CORDIO/Sida-SAREC, Mombasa

8. Maina J, McClanahan TR, Venus V (2008a) Meso-scale modelling of coral's susceptibility to environmental stress using remotely sensed data: Reply to comments by Dunne 2008. Ecological Modelling 218:192-194

9. Maina J, Venus V, McClanahan TR, Ateweberhan M (2008b) Modelling susceptibility of coral reefs to environmental stress using remote sensing data and GIS models. Ecological Modelling 212:180-199

10. McClanahan T, Ateweberhan M, Omukoto J (2008a) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. Marine Biology 153:755-768

11. McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MMM, Bruggemann JH (2007a) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Marine Ecology Progress Series 337:1-13

12. McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007b) Effects of climate and seawater temperature variation on coral bleaching and mortality. Ecological Monographs 77:503-525

13. McClanahan TR, Ateweberhan M, Omukoto J, Pearson L (2009a) Recent seawater temperature histories, status, and predictions for Madagascar's coral reefs. Marine Ecology Progress Series 380:117-128

14. McClanahan TR, Ateweberhan M, Ruiz Sebastian C, Graham NAJ, Wilson SK, Bruggemann JH, Guillaume MMM (2007c) Predictability of coral bleaching from synoptic satellite and in situ temperature observations. Coral Reefs 26:695-701

15. McClanahan TR, Carreiro-Silva M, DiLorenzo M (2007d) Effect of nitrogen, phosphorous, and their interaction on coral reef algal succession in Glover's Reef, Belize. Marine Pollution Bulletin 54:1947-1957

16. McClanahan TR, Graham NAJ, Maina J, Chabanet P, Bruggemann JH, Polunin NVC (2007f) Influence of instantaneous variation on estimates of coral reef fish populations and communities. Marine Ecology Progress Series 340:221-234

17. McClanahan TR, Hicks CC, Darling ES (in press-a) Fishing pressure, productivity, and competition for resources: Malthusian overexplotation and efforts to overcome it on Kenyancoral reefs. Ecological Applications

18. McClanahan TR, Weil E, Cortés J, Baird AH, Ateweberhan M (2009c) Consequences of coral bleaching for sessile reef organisms. In: van Oppen MJH, Lough JM (eds) Coral bleaching: patterns, processes, causes and consequences Ecological Studies: analysis and synthesis 205. Springer Verlag Berlin, Germany, p 121-138

19. McClanahan TR, Weil E, Maina J (2009d) Strong relationship between coral bleaching and growth anomalies in massive Porites. Global Change Biology 10.1111/j.1365-2486.2008.01799.x

20. McCook LJ, Folke C, Hughes TP, Nystrom M, Obura DO, Salm R (2007) Ecological resilience, climate change and the Great Barrier Reef: an introduction. In: Johnson J, Marshall P (eds) Climate change and the Great Barrier Reef A Vulnerability Assessment GBRMPA. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia

21. Obura DO (2005) Resilience and climate change - lessons from coral reefs and bleaching in the Western Indian Ocean. Estuar Coast Shelf Sci 603:353-372

22. Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR (2008) Effects of climate-induced coral bleaching on coral reef fishes: ecological adn economic consequences. Oceanography and Marine Biology: An Annual Review 46:251-296

23. van Woesik R, Nakamura T, Yamasaki H, Sheppard CR (2005) Comment on ' Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius' (McClanahan et al 2005) Marine Ecology Progress Series 305:297-299

24. Vezina AF, Hoegh-Guldberg O (2008) Effects of ocean acidification on marine ecosystems Introduction. Marine Ecology-Progress Series 373:199-201

25. Visram S, Douglas AE (2007) Resilience and acclimation to bleaching stressors in the scleractinian coral Porites cylindrica. Journal of Experimental Marine Biology and Ecology 349:35-44

26. Visram S, Mwaura J, Obura DO (2007) Assessing coral community recovery from coral bleaching by recruitment in two reserves in Kenya. Western Indian Ocean Journal of Marine Science 6:199-205

Theme 3
Biomarkers of stress

Project 8. Biochemical stress markers in corals and *Symbiodinium*

Mayfield Anderson, Sophie Dove, Ruth Gates, Ove Hoegh-Guldberg, Paulina Kaneiwska, Michael Lesser, William Leggat, Oren Levy, Mauricio Rodriguez-Lanetty, and Caroline Palmer

Locations: Mesoamerican CoE and Australasian CoE

Key results

Developing a better understanding of the stress physiology of corals and *Symbiodinium* leads to the possibility of developing indicator tools for detecting the rates and origin of stress on reef-building corals. Building on the results of projects 1, 5 and 8, the BWG project identified potential biochemical markers for use in monitoring stress. A range of techniques were used including microarrays developed as part of the BWG project. Host pigments such as gfp-like proteins such as pocilloporin show distinct visual correlations with stress and were explored as a potential marker of both heat stress and physical damage. In the case of heat stress, pocilloporin concentrations decreased dramatically and showed a negative correlation between heat stress and their expression. Red fluorescent versions of pocilloporin were up-regulated in trematode-infected coral tissues indicating a potential diversity of complex responses. Exploration of markers associated with osmoregulation in endosymbiosis revealed a series of potentially useful biochemical markers. Lastly, a large-scale microarray project was undertaken to identify potential markers associated with light stress, given its importance in coral bleaching.

Background

Understanding and monitoring the development of physiological stress is a key aspect of understanding global change and its impacts on coral reefs. Until very recently, the number of biochemical markers for stress was extremely limited. Given this, the BWG pursued Project 8 with the objective of expanding the number of tools available to scientists working in the four Centres of Excellence. This led to the use of newly developed microarray technology. Developed around several thousand *Acropora millepora* Expression Sequence Tags (EST), this technology shows enormous promise for tracking and developing potential markers of stress.

Materials and methods

In this study, we examined the direct effect of elevated temperatures on the invertebrate host exploring the early transcriptional response of aposymbiotic (without algal symbionts) coral larvae. We explored relative changes in transcription using a cDNA microarray constructed for the scleractinian coral, Acropora millepora, and containing 18,000 EST clones / 8,386 unigenes. Our study identified 32 genes that were significantly up- and down-regulated when coral larvae were exposed to elevated temperatures. Down-regulation of several key components of DNA/RNA metabolism was detected implying inhibition of general cellular processes. The down-regulation of protein synthesis, however, was not simple and random, which suggested that the stress response was a more complicated adjustment of cellular metabolism. We identified four significant outcomes during the very early hours of the transcriptional response to hyperthermal stress in coral larvae. First, the expression of heat shock proteins increased rapidly (within 3 hours) in response to hyperthermal stress. Secondly, a fluorescent protein homolog, DsRed-type FP, decreased its expression in response to elevated temperature reinforcing a potential role as a molecular marker for monitoring hyperthermal stress in nature. Thirdly, the down-regulation of a coral
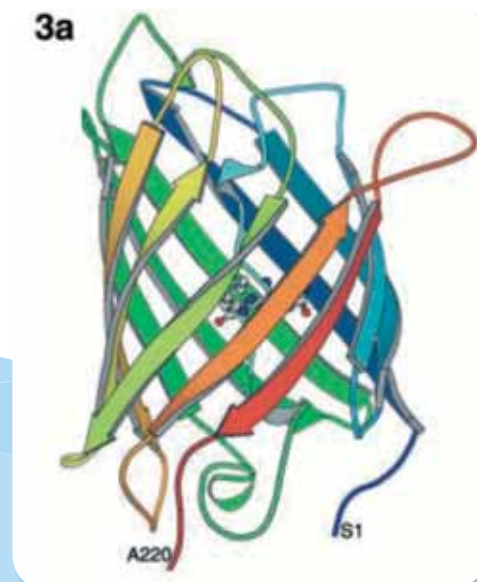

Figure 27. The bright colours of reef building corals are due to gfp-like compounds called pocilloporins first identified by Dove et al. (2001). These particular compounds show promise as biomarkers of heat and light stress, as well as damage due to parasites.

mannose-binding lectin under hyperthermal stress suggests that heat stress might compromise some components of the coral-immune defence and therefore might bring about susceptibility to pathogenic diseases. And lastly, genes involved in protecting cells against oxidative stress showed little response to heat stress, supporting the proposal that up-regulation of cnidarian host oxidative stress genes may require Reactive Oxygen Species (ROS) generated by stressed algal symbionts.

The role of pocilloporin as a host-specific biomarker of heat stress has been explored in adult corals as well. Differential display reverse transcription polymerase chain reaction (DDRT-PCR) was used to produce fingerprints of gene expression for adult reef-building corals (*A. millepora*) exposed to 33 degrees C. Changes in the expression of 23 out of 399 putative genes occurred within 144 h (Smith-Keune and Dove 2008). Down-regulation of one host-specific gene (AmA1a) occurred within just 6 h. Full-length sequencing revealed the product of this gene to be an all-protein chromatophore (green fluorescent protein [GFP]-homolog). RT-PCR revealed consistent down-regulation of this GFP-homolog for three replicate colonies within 6 h at both 32 degrees C and 33 degrees C but not at lower temperatures. Down-regulation of this host gene preceded significant decreases in the photosynthetic activity of photosystem II (dark-adapted Fv/Fm) of algal symbionts as measured by PAM fluorometry. Gene expression of host-specific genes such as GFP-homologs may therefore prove to be highly sensitive indicators for the onset of thermal stress within host coral cells. The physiology of pocilloporin within the stress biology of corals was also explored in two major studies by the BWG (Dove et al. 2006; Dove et al. 2008). These studies revealed a complex set of relationships between pigmentation, photosynthetic dysfunction and thermal stress.

Other groups within the BWG program explored the changes in expression of fluorescent proteins as a function of damage. The Pauley Program workshop run as part of the BWG activities in 2007 led to the investigation of how the Hawaiian coral species, *Porites compressa*, responds biochemically to being heavily infected with a larval trematode. In this particular case, visual signs (i.e. distinct pink nodules of tissue) are associated with infection by the trematode. This study documented up-regulation of red fluorescent compounds in trematode-infected tissue compared to healthy tissue. Additionally, the aggregations of melanin-containing granular cells observed in the trematode-infected tissue, had been previously described as an indicator of an inflammation-like response of coral, confirming the presence of an immune response to the larval trematode.

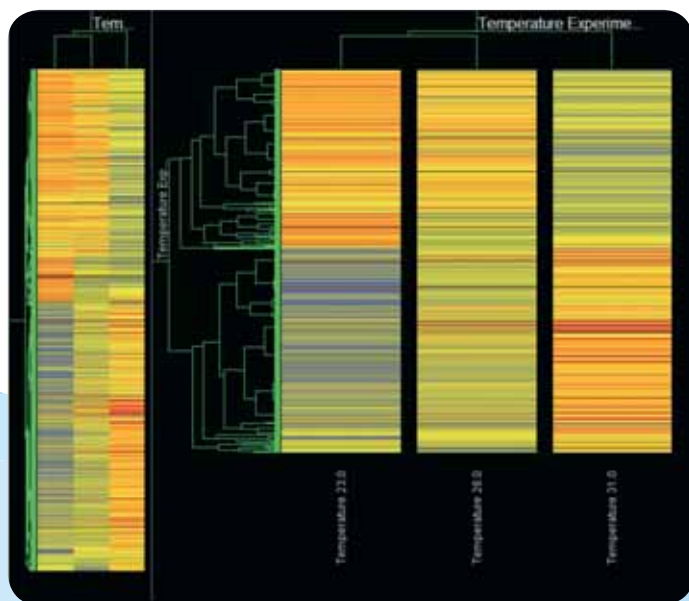Figure 28. Output from a study in which coral larvae (*Acropora millepora*) were exposed to three different temperatures over periods extending from hours to days (Rodriquez-Lanetty et al. 2009). Each bar represents an individual type of protein. Those expressed in blue indicate a decrease in expression, while those in red have been a regulator relative to controls. Proteins appearing in yellow have not changed.

3

Key literature generated with full/partial project support:

1. Dove S, Ortiz JC, Enriquez S, Fine M, Fisher P, Iglesias-Prieto R, Thornhill D, Hoegh-Guldberg O (2006) Response of holosymbiont pigments from the scleractinian coral Montipora monasteriata to short-term heat stress. Limnology and Oceanography. 2006; 51 (2): 1149-1158

2. Dove SG, Lovell C, Fine M, Deckenback J, Hoegh-Guldberg O, Iglesias-Prieto R, Anthony KR (2008) Host pigments: potential facilitators of photosynthesis in coral symbioses. Plant Cell Environ 31(11):1523-33

3. Levy O, Appelbaum L, Leggat W, Gothlif Y, Hayward DC, Miller DJ, Hoegh-Guldberg O (2007) Light-responsive cryptochromes from a simple multicellular animal, the coral Acropora millepora. Science 318:467-470

4. Mayfield AB, Gates RD (2007) Osmoregulation and osmotic stress in coral dinoflagellate symbiosis: Role in coral bleaching. Comparative Biochemistry and Physiology, Part A 147:1-10

5. Maynfield AB, Hirst MB, Gates RD (2009) Gene expression normalization in a dual-compartment system: a real-time quantitative polymerase chain reaction protocol for symbiotic anthozoans. Molecular Ecology Resources 9:462-470

6. Palmer CV, Roth MS, Gates RD (2009) Red fluorescent protein responsible for pigmentation in trematode-Infected Porites compressa tissues. The Biological Bulletin 216:68-74

7. Reynolds JM, Bruns BU, Fitt WK, Schmidt GW (2008) Enhanced photoprotection pathways in symbiotic dinoflagellates of shallow-water corals and other cnidarians. Proceedings of the National Academy of Sciences USA 105:13674-13678

8. Rodriguez-Lanetty M, Phillips WS, Dove S, Hoegh-Guldberg O, Weis VM (2008) Analytical approach for selecting normalizing genes from a cDNA microarray platform to be used in q-RT-PCR assays: A cnidarian case study. Journal of Biochemical and Biophysical Methods 70:985-991

9. Rodriguez-Lanetty M, Harii S, Hoegh-Guldberg O (2009) Early molecular responses of coral larvae to hyperthermal stress. Molecular Ecology (in review).

10. Smith-Keune C, Dove S (2008) Gene expression of a green fluorescent protein homolog as a host-specific biomarker of heat stress within a reef-building coral. Mar Biotechnol 10:166-180

Project 9. Production of colour card tool to detect and monitor coral bleaching

U. E. Siebeck, N. J. Marshall, A. Klüter and Ove Hoegh-Guldberg

Location: Developed at the Australasian CoE in association with University of Queensland-based researchers.

Key results

This project aimed to develop a rapid yet reliable technique for assessing changes in colour of reef-building corals. Initial discussions between BWG members and vision researcher, Professor Justin Marshall, revealed the viability of this idea. After several years of exploring techniques for standardising colour assessment, the team settled on the use of colour cards. After testing this technique with tourists at the Heron Island resort and other locations (Siebeck et al. 2006b), a colour card was developed that is now being used by interested amateurs and professional researchers in over 30 countries.

Background

Coral reefs worldwide have experienced coral bleaching with increasing frequency and severity over the past 30 years. Forward projections of sea temperatures suggest that this trend will continue due to rising global temperatures. A complete understanding of these changes is in its infancy and will depend in part on cheap and reliable methods to assess the extent of stress on a particular reef. To date, the assessment methods used are either expensive (remote sensing techniques), labour intensive (e.g. video transects, manta tows) or invasive (assessments of symbiont densities). We have developed a cheap, simple, non-invasive method for the assessment of coral health that makes use of changes in the colour of corals during bleaching and recovery. Results show that this method can detect multiple grades of coral bleaching including the subtle differences due to the natural environmental fluctuations.
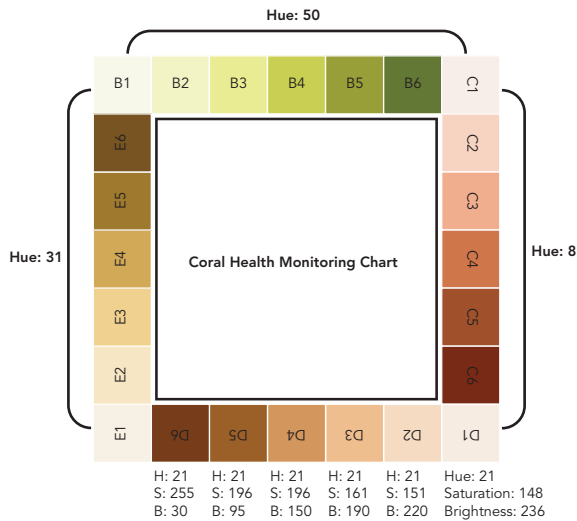
Several different methods have been used to assess coral bleaching on various different scales. Remote sensing techniques are useful as they allow us to monitor the state of large areas of reef simultaneously (Dustan et al. 2001; Hedley and Mumby 2003). However, satellite images and images obtained from aircraft are expensive, have low spatial resolution and are associated with a large error rate (Andréfouët et al. 2002; Hedley and Mumby 2003). Video transects and manta tows are probably the most widely used methods to assess the health of individual reefs (Miller and Müller 1999). However, the methods are labour intensive and time consuming and require personnel trained in scuba diving and coral species recognition. The most accurate method of investigating coral health is to measure photosynthetic activity (Fitt et al. 2001). This is often used in combination with counting the number of symbiotic dinoflagellates left in the tissue of the coral and also determining the chlorophyll a content (Hoegh-Guldberg and Smith 1989). In this way the physiological condition of individual coral colonies can be determined. However, due to their requirement of specialist equipment and the lengthy time of the process they are only useful on the scale of individual coral colonies.

This project developed a simple, cheap and non-invasive method to monitor reef health that makes use of the observed colour change of corals when experiencing stress. Our new method is sensitive enough to detect the natural fluctuations of reef colouration and it is possible to distinguish those from the colouration change during bleaching events. In testing this method, we demonstrate a finer, multi-scale method that goes far beyond widely used classifications that simply detect dead, bleached, semi-bleached or healthy corals (4-point scale). Since our method is cheap and requires minimal training, it is perfectly suited for use in a global network of places where anyone, scientist, student or any member of the community can be part of a local reef monitoring program.

Materials and methods

The colour chart method makes use of the fact that stressed corals lose their symbiotic dinoflagellates and as a consequence change colour. The aim of our method was to quantify this change and to create a chart that represents the different stages of bleaching. In order to provide a valid tool for scientific measurement the colour charts were cross-validated and calibrated with some of the standard measurements of assessing coral health. Coral health was manipulated in thermal stress experiments as well as corals in various health states collected from the reef crest at Heron Island. Full details of the methods are contained within the paper published from this project (Siebeck et al. 2006b). 2006).
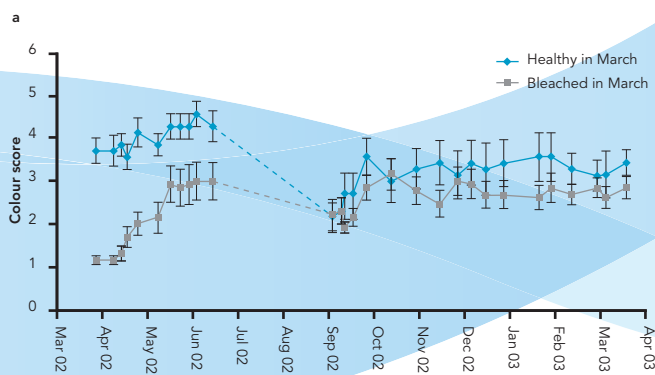
Figure 29. Colour card design. The four different colour categories are arranged in groups around the sides of the chart. Within each category, the colour squares are arranged according to their brightness and saturation values. B1, C1, D1 & E1 are identical in terms of brightness and saturation but vary in hue. Observers simply hold the waterproof chart next to a coral and determine the best colour match for the brightest and darkest area of the coral (avoiding the tips of branching corals as well as purple coloured corals).

Results and discussions

This project developed and explored the use of colour cards to measure the loss of colour during coral bleaching. In a series of field trials (the earliest began in the Block B preparatory phase of the project) outlined in the associated figures, the colour card methodology was capable of detecting very small changes in colour as corals experienced bleaching. The equipment requirements and the costs for conducting a survey are in order of magnitude less than alternative methods. In addition, the colour chart method requires almost no training, so that it is possible to post an information kit to interested people worldwide and gain data from a large variety of 'new' reefs that are not yet monitored as part of a scientific program. The partners in this project (from the Vision, Touch and Hearing Centre at the University of Queensland) have built an extensive database and involved community groups around Australia in a monitoring exercise known as Coral Watch. Further details about the method and its applicability can be obtained at www.coralwatch.org.

Figure 30. Results for the repeated colour measurements of the 20 corals on the Heron Island Reef Flat. The average colour scores (mean ± se) are given for the group of bleached corals (grey) and the group of normally pigmented corals (black). The colour scores of the two groups are significantly different during the time of the first five measurements (March-May 02). The arrow indicates the time a rainstorm coincided with a low tide. Formerly normally pigmented corals bleached more strongly than freshly recovered corals. Broken lines indicate interruption of the survey.

Key literature generated with Full/partial project support:

1. Siebeck UE, Marshall NJ, Klüter A, Hoegh-Guldberg O (2006) Monitoring coral bleaching using a colour reference card. Coral Reefs 25:453-460

Theme 4
Projections of change and socio-economic impact

Understanding how the future will unfold as climate change continues to impact tropical marine ecosystems is crucially important to both management and policy development. In the former case, understanding how reef ecosystems will be impacted will provide important foresight (and hence an ability to anticipate and prepare) for how the problems will develop over the coming decades and century. In the latter case, understanding what is at stake when it comes to important coastal ecosystems, like coral reefs, plays a very important role in determining international policy targets such as atmospheric carbon dioxide. This theme involved a single project which focused on developing credible scenarios of the future and effective responses to climate change in order to allow rational discussions about how management and policy should be poised to respond to climate change.

Project 10. Coral reefs in a century of rapid change: projections of change and effective responses.

John Bythell, William K Fitt, Ruth Gates, Ove Hoegh-Guldberg, Roberto Iglesias-Prieto, Mike P. Lesser, Yossi Loya, Tim R. McClanahan, Rob van Woesik, and Christian Wild

Location: Across all four Centres for Excellence.

Key results

Understanding how the future will unfold is critical to planning an effective response to climate change. Understanding the key drivers behind the response of coral reefs to environmental change is a primary goal of Projects 1-9. Project 10 focused on establishing credible scenarios for the future based on this information. Like the other projects, it achieved its goal and produced a number of key papers reviewing an understanding of the future. Three key steps were identified in achieving the goals of this project. These were (1) to fill the gaps in knowledge as perceived by the BWG that stand in the way of our ability to build credible scenarios of the future; (2) to convene a major workshop in association with the International Coral Reef Symposium (Fort Lauderdale, USA) in July, 2007, and

Photo: A. Zvuloni

(3) to synthesise both sets of information into projections to be published in a major Journal. All three steps were achieved. One of the outputs, published in *Science* magazine in 2007, has had a substantial impact on global policy with respect to climate change and natural ecosystems. Already heavily cited, this paper was released to coincide with the UNFCCC climate change negotiations held in Bali in December 2007. This paper plus many other similar outputs has ensured that the science of the BWG has had a major impact on policy at both regional and global levels.

Background

One of the key findings of this exercise was to identify how unusual contemporary conditions already are within tropical oceans. Comparing present day conditions to those which have occurred in tropical oceans over the past 420,000 years revealed that we have already travelled well outside the conditions under which present day coral reefs have developed. The paper also identified the newness of two critical thresholds for the temperature and carbonate ion concentration beyond which coral reefs fail to be maintained. This analysis leads to the conclusion that we must, as an international community, avoid increasing atmospheric carbon dioxide beyond 450 ppm if we are to retain carbonate coral reef ecosystems on planet Earth. The paper then proposed a series of three photographs to illustrate the types of ecosystems which will result as we travel from today's atmospheric carbon dioxide concentration, to those around 500 ppm, and beyond. As will be discussed in the section on "Contributions to Policy Development", this paper and its conclusions has had a demonstrable impact on policy development at the national and international levels.
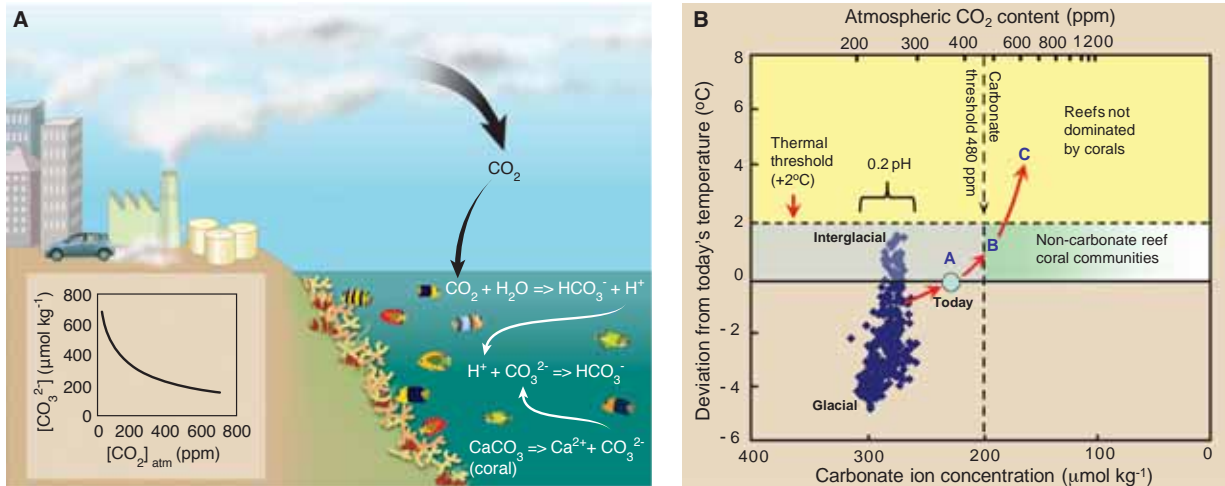
Fig. 1. (A) Linkages between the buildup of atmospheric CO_2 and the slowing of coral calcification due to ocean acidification. Approximately 25% of the CO_2 emitted by humans in the period 2000 to 2006 (9) was taken up by the ocean where it combined with water to produce carbonic acid, which releases a proton that combines with a carbonate ion. This decreases the concentration of carbonate, making it unavailable to marine calcifiers such as corals. (B) Temperature, $[CO_2]_{atm}$, carbonate ions concentrations reconstructed for the past 420,000 years. Carbonate concentrations were calculated (54) from CO_2 $_{atm}$ and temperature deviations from today's conditions with the Vostok Ice Core data set (5), assuming constant salinity (34 parts per trillion), mean sea temperature (25°C), and total alkalinity (2300 mmol kg^{-1}). Further details of these calculations are in the SOM. Acidity of the ocean varies by ± 0.1 pH units over the past 420,000 years (individual values not shown). The thresholds for major changes to coral communities are indicated for thermal stress (+2°C) and carbonate-ion concentrations ([carbonate] = 200 mmol kg^{-1}, approximate aragonite saturation ~$\Omega_{aragonite}$ = 3.3; $[CO_2]_{atm}$ = 480 ppm). Coral Reef Scenarios CRS-A, CRS-B, and CRS-C are indicated as A, B, and C, respectively, with analogs from extant reefs depicted in Fig. 5. Red arrows pointing progressively toward the right-hand top square indicate the pathway that is being following toward $[CO_2]_{atm}$ of more than 500 ppm.

Figure 31. From Hoegh-Guldberg et al. 2007b

In a second study (Hoegh-Guldberg et al. 2009), the BWG contributed to a major study of how climate change is likely to impact coastal ecosystems and communities within the Coral Triangle. The Coral Triangle spans six countries in South-East Asia (Philippines, Indonesia, Malaysia, Papua New Guinea, Timor Leste, and the Solomon Islands) and includes the highest density of coral reef organisms on the planet. For example, 76% of all coral species and 37% of all coral fishes are found along the 132,000 km of coastline in this region (Hoegh-Guldberg et al 2009). In addition to having spectacular natural ecosystems, the Coral Triangle is also home to 150 million people of which 100 million live in the coastal areas. These people are mostly economically disadvantaged, and are highly dependent on coastal ecosystems for their food and other resources. Unfortunately, coral reefs and mangrove ecosystems in this region are rapidly declining, and are disappearing at the rate of 1-2% per year. If the current rate continues, coral reefs in this region will be functionally extinct by the middle of the current century.

The study undertaken as part of Project 10 developed two scenarios of the future based on the input of over 20 experts and consideration of the conclusions of 300+ expert publications. In one case, termed the worst case, international treaties failed to constrain the rising atmospheric carbon dioxide, and attempts to deal with the many other local stresses fail. In this scenario, coral reefs and other coastal ecosystems such as mangroves, effectively disappear by 2100 as sea levels undergo rapid increases driven by soaring global temperatures and carbon dioxide contents (which reach 700 ppm by the end of the century). Under this scenario, the food security of at least 100 million people is severely threatened, while rising seas inundate coastal communities and infrastructure.

Under the so-called "best case" scenario, international efforts to obtain deep cuts in greenhouse gas emissions are successful, as are attempts to limit the impact of local stresses arising from pollution, unsustainable coastal development, overexploitation of resources and destructive fishing. While conditions are challenging up to the middle of the century, the benefits from effective action at the local and global levels means that climate change is manageable and the impacts on coastal people and their communities far less.

As described in the section on contributions to policy development, the study led to a number of policy recommendations. An illustration of these two scenarios was distributed to world leaders attending the Coral Triangle Summit meeting in Manado in Indonesia, and judging by media reports had a major impact on regional leaders and their negotiating teams.
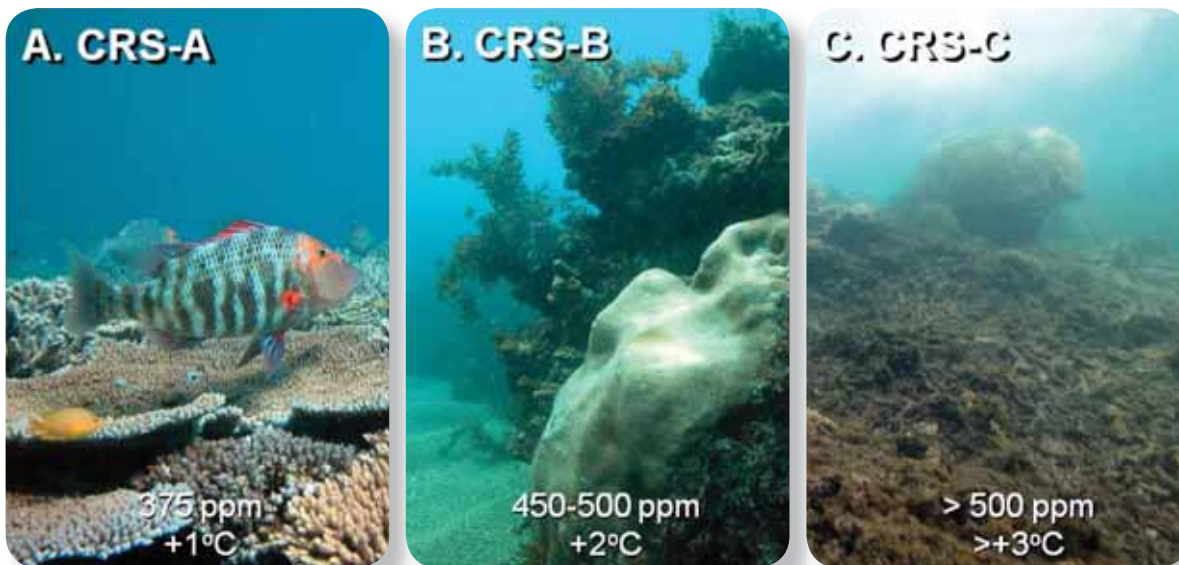
Fig. 5. Extant examples of reefs from the Great Barrier Reef that are used as analogs for the ecological structures we anticipate for Coral Reef Scenarios CRS-A, CRS-B and CRS-C (see text). The [CO2]atm temperature increases shown are those for the scenarios and do not refer to the locations photographed. (A) Reef slope communities at Heron Island. (B) Mixed algal and coral communities associated with inshore reefs around St. Bees Island near Mackay. (C) Inshore reef slope around the Low Isles near Port Douglas. [Photos by O. Hoegh-Guldberg]

Figure 32. From Hoegh-Guldberg et al. 2007b. Predicted scenarios for coral reefs under increasing amounts of atmospheric carbon dioxide. If concentrations of carbon dioxide remain at today's level, many coral dominated reefs will survive (left-hand panel) although there will be a compelling need to increase their protection from local factors such as deteriorating coastal water quality and overfishing. If carbon dioxide concentrations continue to rise as expected, reefs will become less dominated by corals and increasingly dominated by seaweeds (middle panel). If carbon dioxide levels continue to rise as we burn fossil fuels, coral reefs will disappear and will be replaced by crumbling mounds of eroding coral skeletons. In concert with the progression from left to right is the expectation that much of the enormous and largely unexplored biodiversity of coral reefs will disappear. This will almost certainly have major impacts on the tourist potential of coral reefs as well as their ability to support fisheries, both indigenous and industrial.

Other activities

As described above, Hoegh-Guldberg coordinated and led (with A. C. Baker) a special symposium entitled "Is 500 ppm CO_2 and 2°C of warming the 'tipping point' for coral reefs? If so, how should we respond?" at the International Coral Reef Symposium, Fort Lauderdale, July 2008. This meeting attracted over 50 contributors over a 3 day schedule. Christian Wild also co-chaired session 28 "Coral reefs and coral communities in a changing environment" at ASLO Aquatic Sciences Meeting, 25-30 January 2009, Nice, France. The latter will appear as a special edition in Coral Reefs and will be co-edited by Dr Wild.
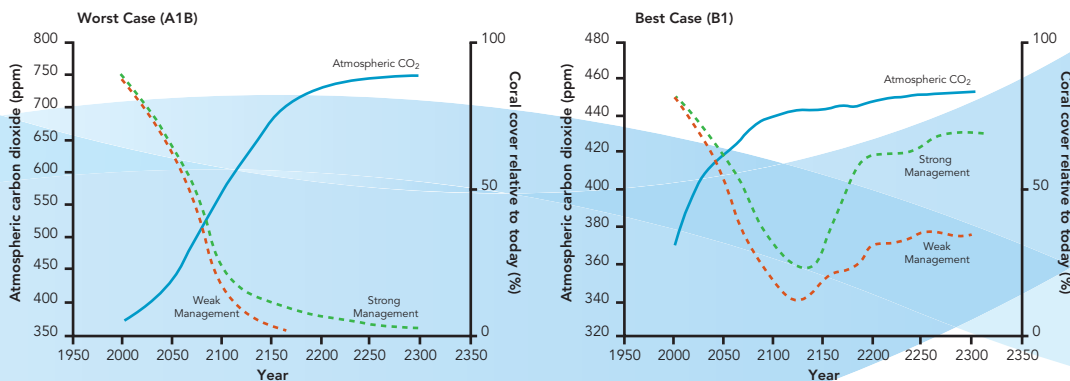

Figure 33. Hypothetical trajectory of the concentration of atmospheric CO_2 and coral cover in worst (A1B) and best case (B1) scenario. The effect of managing local stressors is shown. Hoegh-Guldberg et al. 2009

Bleaching and Related Ecological Factors:
CRTR Working Group Findings 2004-2009
Theme 4: Projections of change and socio-economic impact

4

Key literature generated with full/partial project support:

There have been a number of key publications from the BWG in this project area. These papers have generated considerable interest, and have painted scenarios of the future in a world in which we do or do not take effective action on coral reefs. Their message is very clear: continued growth in the emissions of carbon dioxide will eliminate functional coral reef ecosystems within the next 30 to 50 years. As explained elsewhere, this has serious implications for tropical marine biodiversity, as well as the food and resources for several hundred million people.

1. Caldeira K, Archer D, Barry JP, Bellerby RGJ, Brewer PG, Cao L, Dickson AG, Doney SC, Elderfield H, Fabry VJ, Feely RA, Gattuso JP, Haugan PM, Hoegh-Guldberg O, Jain AK, Kleypas JA, Langdon C, Orr JC, Ridgwell A, Sabine CL, Seibel BA, Shirayama Y, Turley C, Watson AJ, Zeebe RE (2007) Comment on "Modern-age buildup of CO_2 and its effects on seawater acidity and salinity" by Hugo A. Loáiciga. Geophysical Research Letters 34

2. Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-Third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560-563

3. Dodge RE, Birkeland C, Hatziolos M, Kleypas JA, Palumbi SR, Hoegh-Guldberg O, van Woesik R, Ogden JC, Aronson RB, Causey BD, Staub F (2008) A call to action for coral reefs. Science 322:189-190

4. Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biology 11:2251-2265

5. Fabricius K, Hoegh-Guldberg O, Johnson J, McCook L, Lough J (2007) Vulnerability of coral reefs of the Great Barrier Reef to climate change. Climate change and the Great Barrier Reef Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia:515–554

6. Hoegh-Guldberg O (2005) Low coral cover in a high-CO_2 world. Journal of Geophysical Research-Oceans 110:C09S06

7. Hoegh-Guldberg O (2006) Ecology: complexities of coral reef recovery. Science 311:42-43

8. Hoegh-Guldberg O (2006) Thermal biology of coral reefs: will coral reefs survive global warming? Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 143:S131-S131

9. Hoegh-Guldberg O (2007) Chapter 10 "Climate change and the Great Barrier Reef". In: Hutchings P., Kingsford M., Hoegh-Guldberg O. (eds) Great Barrier Reef: Biology, Environment and Management. CSIRO Press.

10. Hoegh-Guldberg O (2009) Climate change and coral reefs: Trojan horse or false prophecy? A response to Maynard et al. (2008). Coral Reefs, in press

11. Hoegh-Guldberg O, Anthony K, Berkelmans R, Dove S, Fabricus K, Lough J, Marshall P, van Oppen M, Willis B, Chapter 12 "The vulnerability of reef-building corals to climate change" In: Johnson J, Marshall PA (eds) Climate change and the Great Barrier Reef. GBRMPA, Townsville p271-308

12. Hoegh-Guldberg O, Australia G (1999) Climate change, coral bleaching and the future of the world's coral reefs. Marine & Freshwater Research 50:839-866

13. Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Where Species Go, Legal Protections Must Follow Response. Science 322:1049-1050

14. Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. Science 321:345-346

15. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell DR, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2008) Coral adaptation in the face of climate change - Response. Science 320:315-316

16. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742

17. Hoegh-Guldberg, O (2007). Impacts of Climate Change on Coral Reefs. pp 59-68. In Impacts of Climate Change on Australian Marine Life. A. J. Hobday, T. A. Okey, E. S. Poloczanska, T. J. Kunz and A. J. Richardson (Eds.). CSIRO Marine and Atmospheric Research

18. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742

19. Hoegh-Guldberg, O (2007). Impacts of Climate Change on Coral Reefs. pp 59-68. In Impacts of Climate Change on Australian Marine Life. A. J. Hobday, T. A. Okey, E. S. Poloczanska, T. J. Kunz and A. J. Richardson (Eds.). CSIRO Marine and Atmospheric Research

20. Hoegh-Guldberg, O. (2006) Impacts of Climate Change on Coral reefs. In, Hobday, A.J., Okey, T.A., Poloczanska, E.S., Kunz, T.J. & Richardson, A.J. (eds) 2006. Impacts of climate change on Australian marine life. Report to the Australian Greenhouse Office, Canberra, Australia. June 2006.

21. Kleypas JA, Buddemeier RW, Eakin CM, Gattuso JP, Guinotte J, Hoegh-Guldberg O, Iglesias-Prieto R, Jokiel PL, Langdon C, Skirving W, Strong AE (2005) Comment on "Coral reef calcification and climate change: The effect of ocean warming''. Geophysical Research Letters 32: 320-323:L08601

22. Poloczanska ES, Babcock RC, Butler A, Hobday AJ, Hoegh-Guldberg O, Kunz TJ, Matear R, Milton DA, Okey TA, Richardson AJ (2007) Impacts of Climate Change on Australian Marine Life. In: Gibson RN, A ARJ, Gordon JDM (eds) Oceanography and Marine Biology: An Annual Review, p 407-478

23. Raven J, Caldeira K, Elderfield H, Hoegh-Guldberg O, Liss P, Riebesell U, Shepherd J, Turley C, Watson AJ (2005) Ocean acidification due to increasing atmospheric carbon dioxide, London

24. Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE 3:e1548

Management implications

Coral reef ecosystems are facing unprecedented stress from human activities (Jackson et al. 2001a; Pandolfi et al. 2005; Hughes et al. 2007). Until 10 years ago, local factors such as overfishing, pollution and declining water quality were seen as the greatest threats to the survival of coral reefs. Growing evidence in addition to events such as the worldwide mass bleaching and mortality event in 1998 have convinced many research scientists that global climate change represents the most serious near-term threat. (Hoegh-Guldberg 1999b). Either way, both local and global threats are combining to rapidly decrease the distribution and abundance of reef-building corals and the ecosystems they build.

Accurate knowledge and understanding of the changes occurring within coral reef ecosystems is essential to any effective management response. In this regard, the Bleaching Working Group identified several key areas in which it could contribute to the resources available to reef managers.

Coral-symbiont responses to thermal stress

By improving our understanding of the coral-*Symbiodinium*-bacterial holobiont, the BWG has identified the inherent complexity that exists between the various elements that go into making healthy reef building corals. In this respect, it is clear that reef building corals live in a delicate balance with their various symbionts, with stress leading to a breakdown of communication and synergy between the various partners. The surprising discovery of nitrogen-fixing bacteria adds an interesting layer to the complexity and biosis that makes up healthy coral communities (Lesser et al. 2007b).

The exploration of the fundamental mechanism of coral bleaching leads to a number of observations which are reviewed for reef managers. For example, the central role of light causing damage in heat stressed corals suggests a number of potential insights into the variability observed on coral reefs. For example, it is clear that reducing light levels on coral reefs could potentially act as a way of reducing the impact of heat stress (Enriquez et al. 2005). While this cannot be done at the level of entire coral reefs, it does suggest strategies for managers to protect small areas of highly valuable coral reef. Stemming from this work, there are now a number of initiatives looking at whether or not shading coral reefs during heat stress might represent an effective adaptation response.

In exploring the diversity and flexibility of coral-*Symbiodinium* associations, it has become clear from the last five years of research that these co-evolved mutualistic symbioses are not flexible on the timescale of the bleaching event. In this respect, the Working Group found little support for the adaptive bleaching hypothesis, and particularly for the ability of corals to expel one genotype of *Symbiodinium* and adopt a brand new variety with a higher thermal tolerance (Hoegh-Guldberg et al. 2007b; Goulet et al. 2008; LaJeunesse 2008; Stat et al. 2008). The observation that coral hosts tend to be found with the same subclade of *Symbiodinium* across vast areas of the Indo-Pacific or Caribbean oceans also confirms that the ability of corals to rapidly evolve a new, more tolerant symbiosis does not occur over years or decades, and that it is an evolutionary process that takes hundreds if not thousands of years to occur. It would appear that relying on these mechanisms in terms of the management of coral reefs will not generate outcomes for reef resilience. These ideas are explored further in the number of key publications and studies arising from BWG activities over the past five years (Iglesias-Prieto et al. 2004; LaJeunesse 2005c; Lajeunesse 2005b; LaJeunesse et al. 2008; Sampayo et al. 2008).

Development of tools for detecting change

Being able to detect changes in coral reef ecosystems in response to global changes is a critical part of management responses. In this respect, it is impossible to devise an effective management response without effective levels of information or tools for detecting change. The BWG has contributed to a number of different areas. Firstly, in terms of biochemical tools for understanding stress within corals, it appears there are a number of tools which could potentially be deployed to understand whether or not stress is occurring. The successful research into stress markers such as heat shock proteins, fluorescent proteins and a number of other markers will contribute to important insights that managers require when it comes to change within the ecosystem that they are managing. Colour cards used to detect and measure coral bleaching were developed in partnership with researchers from the Vision, Touch and Hearing Centre (VTHC) at the University of Queensland (Siebeck et al. 2006a). Colour cards are now being readily used in the assessment of coral health across a vast array of sites internationally. Their use is being coordinated by CoralWatch, which is an organisation based at the University of Queensland, Brisbane, Australia

(www.coralwatch.org). As part of this project, coral colour cards have been incorporated into a cheap, simple, non-invasive method for the monitoring of coral bleaching, and assessment of coral health. The charts can and are being used by anyone – scientists, school children, tourists and politicians.

Ecological responses to climate change impacts

The ecological studies undertaken by the BWG spanned the four Centres of Excellence, pursuing a set of common sampling protocols for ecological indicators of change on coral reefs. This research has refined a number of tools for detecting change on coral reefs, and has suggested a set of principles and design elements for establishing ecological monitoring of change of coral reefs. Key publications and methodologies are clearly contributing to the management of coral reefs as change occurs. As stated above, without effective and accurate ecological information, our ability to detect and respond to changes in the health of reefs will be otherwise severely limited.

Ecological studies established key linkages between the structures built by corals and other calcifiers, and other coral reef organisms such as fishes. When this structure breaks down, fish populations dwindle with the loss of some 50% of species (Graham et al. 2008; McClanahan et al. 2008b; Pratchett et al. 2008; Wilson et al. 2008). This clearly has implications for people in terms of the services that coral reefs provide, such as food and tourism. In identifying the key drivers for these populations, the research undertaken by the BWG has suggested that preserving the three-dimensional structure of reefs is an overriding important management objective. Moreover, reducing damage from boating activities, such as anchors and ship strikes on a local scale, is important so that reefs maintain the capacity to maintain themselves as oceans warm and acidify.

In concert with the results of many other research groups, the BWG has identified the important role that maintaining and improving the ecological resilience of coral reefs will play in a changing global environment (McClanahan and Cinner 2008; McClanahan et al. 2008c; McClanahan et al. 2008b; McClanahan et al. 2009). In this respect, reducing other stresses such as overfishing, pollution and declining water quality becomes an even greater priority as conditions worsen under global climate change. This suggests that strategies associated with marine protected areas, greater regulations on fishing and, control of impacts arising from poor land-use along tropical coastlines, should be stepped up in terms of their implementation. This said, any effort to improve the resilience of coral reefs to climate change will only work if effective strategies are put in place to rapidly reduce the build up of greenhouse gases in the Earth's atmosphere.

Projections of future change

One of the key contributions that the BWG has made to the management of coral reefs under rapid global climate change has been to analyse the key drivers and establish a series of credible projections on how coral reefs will change as climate change deepens (Hoegh-Guldberg et al. 2007b; Schuttenberg and Hoegh-Guldberg 2007). Understanding these futures is critically important to the management of coral reefs because it sets the context under which reef managers will be operating in the future. These studies have also provided effective policy tools and advice, which adds to the ability of reef managers to communicate and inform the governments for which they work. These aspects will be explored in the policy section.

Contributions to policy development

The research outputs of the Bleaching Working Group have made fundamental contributions to the direction of policy with respect to local and regional governments, as well as having an important impact on international climate change negotiations.

Impacts on local and regional policy development

BWG activities have spanned the four CRTR Centres of Excellence, and through their interaction with local researchers have had a direct impact on local attitudes, knowledge and policy developments. One of the most important contributions occurred recently when BWG members and other CRTR members, participated in a large-scale study of the local and global pressures associated with coral reefs in the Coral Triangle.

As described before, the Coral Triangle spans six countries in Southeast Asia and contains the most biologically rich marine ecosystems on the planet. It also contains dense coastal communities which rely heavily on the sea and coastal resources for food, income and livelihoods. As elsewhere, coral reefs are in decline and are disappearing at the rate of 1-2% per year. A large number of local and global stressors are to blame for this decline.

Broad sweeping strategies to deal with local stress factors such as pollution, poor-water quality, overexploitation of fishery stocks, unsustainable coastal development and destructive fishing are required if this steady decline in these important coastal ecosystems is to be halted. Beginning with the Bali meeting in 2007, the six leaders of the Coral Triangle countries, along with international partners such as Australia and the United States, pledged to commit to signing an original plan of action to deal with the serious threats arising from local factors.

In order to facilitate and inform the leadership teams that were headed into this meeting, Hoegh-Guldberg and 20 other authors completed a study of the atmospheric, biological, economic, and social drivers associated with both local and global threats to coastal ecosystems. This study was launched at the Coral Triangle Summit in Manado (May 11-15, 2009) by the Indonesian Environment Minister Witoelar and was distributed to leaders and their negotiating teams. Several leaders in Southeast Asia made reference to it in some of the over 900 media articles about the study, committing to the 10 key recommendations that it made.

Figure 34. Launch of the Coral Triangle study led by BWG member Ove Hoegh-Guldberg (right). The study was launched by the Indonesian Environment Minister Witoelar (centre) on May 13, 2009. Lida Pet-Soede from WWF is also shown.

The policy recommendations were (see full report, Hoegh-Guldberg et al. 2009):

1. **Create a binding international agreement to reduce the rate and extent of climate change.** To do this, emissions should peak no later than 2020, and global warming limited to less than 2°C above pre-industrial temperatures (i.e. atmospheric CO_2 < 450 ppm) by 2100. This will require steep global cuts in emissions that are 80% below 1990 levels by 2050. Inherent to this recommendation is the creation of an aggregate group reduction target for developed countries of 40% below 1990 levels by 2020, and a reduction from business-as-usual emission levels for developing countries of at least 30% by 2020.

2. **Take immediate action to establish national targets and plan to meet these commitments such that the international agreement can be achieved.** This report shows that nations in the Coral Triangle region have a great deal at stake if climate change continues unchecked. They must become part of the solution and must do this expeditiously. Lag-times and non-linear responses in the climate system mean that every day we wait to take action, the problem becomes dramatically more difficult and protracted to address successfully.

3. **Pursue the establishment of integrated coastal zone management across the region** to reverse the decline of the health of coastal ecosystems. This should include implementation of policies that eliminate deforestation of coastal areas and river catchments, reduce pollution, expand marine protected areas, regulate fishing pressures and abolish destructive practices. It is important that these actions not aim to restore or protect ecosystems for past conditions, rather they must prepare for conditions under a changing climate.

4. **Support the establishment of a global adaptation fund to meet the adaptation needs of developing countries.** While some of the cost of adapting to climate change can be met by redirecting current resources that are being used in a manner that is vulnerable to climate change, the growing challenge of climate change will result in new and increasing costs. Recent efforts to establish a fund through the Global Environment Facility (GEF) should be supported and accelerated. These funds will be required to meet these costs given the nature of the problem and that the disproportionate brunt of the hardship caused by the problem is borne by developing countries. International funds will be necessary to meet these needs.

5. **Build adjustable financial mechanisms into national budgeting to help cover the increasing costs of adaptation to climate change.** Climate change will require not only new funds, but also a reassessment of current spending so that funds are not spent in ways that are not 'climate-smart' - in other words, on efforts that are not resilient to climate change. Every effort should be made to avoid spending funds and taking actions that exacerbate the problem of climate change.

6. **Establish governance structures that integrate resource and development management to provide robust protection of both in the face of climate change.** Adaptation plans cannot be developed on a sector-by-sector basis. Doing so risks creating problems such as adaptation being effective against one issue but maladaptive against another. It will be important to plan holistically and create governance structures that can support, implement and monitor these efforts.

7. **Build the socio-ecological resilience of coastal ecosystems and develop stakeholder and community engagement processes for communities to improve their ability to survive climate change impacts.** Involving coastal people and communities in planning provides greater stability and efficacy for solutions to social and ecological systems within the Coral Triangle. Establish ecosystem-based adaptation that focuses on protecting the fundamental ecosystem processes that underline the services valuable to society—particularly local communities who depend on them for the most basic needs. Fundamentally, it will be local knowledge that generates innovative adaptation strategies which may prove most successful. Reducing the influence of local stress factors on coastal ecosystems makes them able to better survive climate change impacts. Protecting the diversity of components (communities, populations, and species) under the guidance and actions of local people strengthens the resolve of these systems in the face of climate change.

8. **Critically review and revise conservation and development efforts at the local, national and regional levels for their robustness in the face of climate change.** Business-as-usual conservation and development will not achieve success. The new mode of action requires integration between conservation and development, and the realisation that many past approaches are no longer effective due to the impacts of climate change.

9. **Build capacity to engage on planning for climate change issues – from origins to strategies and actions to address it – with civil society.** Climate change planning, both mitigation and adaptation, will require that we educate current and future practitioners, as well as the concerned constituencies. Mechanisms must be created to develop current resource managers and planners so that they can immediately implement these new approaches. As the problem of climate change is not one that will be solved in this generation, planning and responses to climate change will be iterative as the target continues to move over the coming centuries. Therefore, it will also be necessary to develop training for future capacity through education in academic settings. Informed stakeholder and community engagement is at the core of successful adaptation, so in addition to professionals and students, civil society must be given access to the information they need to understand and respond to climate change.

10. **Focus adaptation on playing a role in economic stimulus, especially in job creation and financial mobilisation.** Private-public sector incentive schemes, regional/international arrangements and investment partnerships (e.g. national insurance reform and special-access loan schemes) need to better incorporate risk management and adaptation strategies to reduce investment risk and maintain positive financial conditions.

International climate change policy

One of the goals of the Coral Reef Targeted Research Program is to provide advice to policymakers on a range of issues associated with coral reefs and rapid environmental change. Given the graphic way that coral reefs respond to warming seas (i.e. mass coral bleaching and mortality), they have played an important role in illustrating the consequences of further changes in carbon dioxide and sea temperature. One of the ambitions of the Bleaching Working Group's research agenda was to explore, verify and recommend levels of atmospheric carbon dioxide that would be considered safer for coral reefs. In this respect, several outputs of Project 12 were aimed specifically at bringing the science to the policy debates associated with the climate change negotiations culminating in the Congress of Parties (COP) 15, in Copenhagen in December 2009.

In December 2007, members of the BWG led a study which investigated the unusual nature of current conditions in tropical seas by comparing temperatures and carbonate ion concentrations to those from the past 420,000 years (using Vostok Ice Core data). This paper revealed that conditions in tropical oceans are already well outside those in which oceans have been over this period, which experienced large perturbations associated with the glacial cycle. The paper has attracted significant attention and is now ISI's hottest paper (most cited over the past two years) in both the area of "climate change" and "ocean acidification" (cited 81 times in <18 months). In addition to gaining considerable media attention, the review has had a direct impact on the perspective of safe levels of atmospheric carbon dioxide at various national and international forums.

For example, the BWG Chair was commissioned by the Australian Federal Government's Garnaut Review to submit a paper on the implications of climate change for Australia's Great Barrier Reef. This contribution led directly to the admission by the Australian Government that exceeding 450 ppm carbon dioxide in the atmosphere would have dire consequences for the Great Barrier Reef. The conclusions of the paper have also fed into World Bank dialogue (the Chair addressed audiences such as the World Bank's Country Environment Managers), and the results were recently presented at the climate change science summit meeting in Copenhagen in March 2009. This information was also used in a recent study also led by Hoegh-Guldberg which examined the impacts of a changing climate on the coastal ecosystems and people of the Coral Triangle, one of the most diverse and populated areas of the planet. This particular study received enormous attention (>900 media articles) and fed into the successful signing of the Coral Triangle Initiative, one of the most exciting regional conservation initiatives ever taken within Southeast Asia. In addition to recommending deep cuts in greenhouse gas emissions, the study linked action on local stresses to adaptation measures. These have now been included on the agenda of several countries as they head towards Copenhagen for the climate change negotiations associated with COP15, in December, 2009.

Key literature generated with full/partial project support:

1.   Hoegh-Guldberg, O (2008). Ten Commitments to Marine Ecosystems. In: Lindenmayer DB, Dovers S, Harriss Olson M, Morton S. (eds) Ten Commitments: Reshaping the Lucky Country's Environment. CSIRO Publishing: Melbourne, pp. 228-231.

2.   Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell DR, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2008) Coral adaptation in the face of climate change - Response. Science 320:315-316

3.   Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Where Species Go, Legal Protections Must Follow Response. Science 322:1049-1050

4.   Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. Science 321:345-346

5.   Hoegh-Guldberg, O (2008). Ten Commitments to Marine Ecosystems. In: Lindenmayer DB, Dovers S, Harriss Olson M, Morton S. (eds) Ten Commitments: Reshaping the Lucky Country's Environment. CSIRO Publishing: Melbourne, pp. 228-231.

6.   McClanahan T, Cinner J, Maina J, Graham N, Daw T, Stead S, Wamukota A, Brown K, Ateweberhan M, Venus V (2008b) Conservation action in a changing climate. Conservation Letters 1:53-59

7.   McClanahan TR (2007a) Achieving sustainability in East African coral reefs. Journal of the Marine Science and Environment C5:13-16

8.   McClanahan TR (2007b) Testing for correspondence between coral reef invertebrate diversity and marine park designation on the Masoala Peninsula of eastern Madagascar. Aquatic Conservation: Marine and Freshwater Ecosystems 17:409-419

9.   McClanahan TR (2008) Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. Oecologia 155:169-177

10. McClanahan TR, Cinner JE (in press) A framework for adaptative gear and ecosystem-based management in the artisanal coral reef fishery of Papua New Guinea. Aquatic Conservation: Marine and Freshwater Ecosystems

11. McClanahan TR, Cinner JE, Graham NA, Daw TM, Maina J, Stead SM, Wamukota A, Brown K, Venus V, Polunin NVC (2009b) Identifying reefs of hope and hopeful actions: Contextualizing environmental, ecological, and social parameters to respond effectively to climate change. Conserv Biol 10.1111/j.1523-1739.2008.01154.x

12. Schuttenberg H, Hoegh-Guldberg O (2007) A World with Corals: What Will It Take? Science 318:42b

13. McClanahan TR, Cinner JE, Maina J, Graham NAJ, Daw TM, Stead SM, Wamukota A, Brown K, Ateweberhan M, Venus V, Polunin NVC (2008c) Conservation action in a changing climate. Conservation Letters 1:53-59

14. McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007e) Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications 17:1055-1067

15. McClanahan TR, R. SC, Cinner JE, Maina J, Wilson SK, Graham NAJ (in press-b) Managing fishing gear to encourage ecosystem-based management of coral reefs fisheries. In: Riegl B (ed) Proceedings 11th International Coral Reef Symposium, Ft Lauderdale, USA

16. Morton SR, Hoegh-Guldberg O, Lindenmayer DB, Olson MH, Hughes L, McCulloch MT, McIntyre S, Nix HA, Prober SM, Saunders DA, Andersen AN, Burgman MA, Lefroy EC, Lonsdale WM, Lowe I, McMichael AJ, Parslow JS, Steffen W, Williams JE, Woinarski JCZ (2009) The big ecological questions inhibiting effective environmental management in Australia. Austral Ecology 34:1-9

17. Obura DO, Causey BD, Church J (2006) Management response to a bleaching event. In: Phinney P, Hoegh-Guldberg O, Kleypas JA, Skirving W, Strong A (eds) Corals and Climate Change. American Geophysical Union, Washington DC

Research training

The BWG project has provided crucial support for 17 student researchers and 2 postdoctoral fellows, through either full or partial scholarship support, support of research costs and assistance to attend the many training and research workshops that have been held during the project.

Photo: A. Zvuloni.

Amita Jatkar (India)
PhD student at the Newcastle University (UK)

I held a Leverhulme Trust studentship (2004-2008) to investigate the structure and function of mucin genes and the biophysical properties of the coral surface mucus layer. My recent work has included measuring the surface mucus layer of corals using a novel technique developed for the mammalian gut by colleagues in the Medical School at Newcastle University. I have also used bioinformatics approaches to investigate mucin (MUC) genes in coral EST databases and the Nematostella genome. To date we have identified at least 3 coral MUC genes and shown that the overall MUC gene structure is similar to humans. I completed my PhD in 2008. I was supported by the BWG to attend the joint BWG/DWG meeting in Mexico (2005) and the International Coral Reef Symposium in Florida (2008).

Assaf Zvuloni (Israel)
PhD student at the University of Tel Aviv (Israel)

In coral reef populations spatial patterns may be the result of several different processes that operate at different spatial scales. As a first stage in my work I examined and improved traditional sampling methods that were found to lead to significant biases in studying population demography (Zvuloni et al. 2008). In the next study I inferred the transmission mode of black-band coral disease from its spatial patterns in the field (Zvuloni et al. 2009). My main finding was that local transmission via waterborne infection is a significant transmission mechanism of the disease. The third aspect I explored for my Ph.D deals with additive partitioning of coral diversity around Zanzibar Island (Tanzania). The results suggest that non-random processes operating on a scale of a few kilometres affected the spatial patterns of coral diversity around the island. This insight helps identifying appropriate boundaries for studying mechanisms that generate and maintain biodiversity within this region.

Caroline Palmer (UK)
PhD student at the Newcastle University (UK)

I started my PhD in 2007 jointly with Newcastle University, UK (with John Bythell, BWG) and James Cook University, Australia (with Bette Willis, DWG). I am investigating immune defences in corals as part of a Natural Environment Research Council-funded project looking at bleaching impacts on microbial communities. Recent work has shown the importance of the melanin synthesis pathway in protecting corals against invasion by microbial pathogens. I think coral immunity research will become increasingly important in predicting corals ability to survive climate change. I was supported for travel to the Heron Island CoE to undertake research and engage in BWG group meetings and to attend the International Coral Reef Symposium in Florida (2008).

Dustin W. Kemp (USA)
PhD student at the University of Georgia (USA)

I am broadly interested in physiology of the coral holobiont (animal + micro-algae). Coral reef ecosystems are among the most productive habitats on the planet and support large amounts of biodiversity. At the base of these ecosystems are very diverse groups of endosymbiotic dinoflagellates in the genus *Symbiodinium*. My research focuses on the diversity of *Symbiodinium* and how it may relate to holobiont physiology. I work primarily in the Caribbean and use molecular-genetic techniques to identify the *Symbiodinium* associated with reef-building corals. Asking ecological questions I use photo-physiological techniques to better understand the symbiotic relationships between corals and their symbionts. My doctoral work focuses on comparing photo-acclimation and carbon transfer among genetically diverse *Symbiodinium* within the same species of coral. These complex processes are fundamental for understanding holobiont physiology and may provide important insight about the extent to which corals may respond physiologically to climate change.

Erika Díaz Almeyda (Mexico)
MSc student at the Universidad Nacional Autónoma de Mexico

I recently received a M.Sc. degree in marine sciences at the Universidad Nacional Aútonoma of Mexico (UNAM) as part of the CRTR. In addition, I received training in coral reef research in Curacao, Netherlands Antilles, sponsored by University of North Carolina at Wilmington USA, CONACyT and UNAM. My main research interest focuses in the symbioses between invertebrates and photosynthetic dinoflagellates. My work has been addressed on the effects of thermal stress in the stability of the photosynthetic membrane of different symbiotic dinoflagellates. The findings of my study clearly establish the differences in the membrane fluidities of the different symbionts in isolation. I presented my work as an oral presentation on the 11th International Coral Reef Symposium 2008 in Fort Lauderdale, USA. I recently started a PhD at the University of California under Dr. Monica Medina supervision to explore the molecular and cellular mechanisms involved in cnidarian-dinoflagellate symbioses.

Eugenia M. Sampayo (The Netherlands)
PhD student at the University of Queensland (Australia)

I completed my PhD in 2007 on the ecology of coral-symbiont associations of three common Indo-Pacific corals, Stylophora pistillata, Pocillopora damicornis, and Seriatopora hystrix under natural conditions, thermal stress, and long-term environmental shifts. The results showed that under natural conditions each coral species associated with host and depth specific symbionts. I also studied the effects of environmental disturbance such as thermal stress leading to coral bleaching. I found that patterns of differential bleaching susceptibility as well as post-bleaching mortality were related to fine-scale variability in symbionts and that changes in symbiont community diversity were not driven by the uptake of more tolerant symbiont types but by differential mortality between colonies. Corals did not acquire novel symbionts during transient bleaching stress or a three-year transplantation experiment simulating permanent shifts in environmental conditions. In conclusion, changes in the tolerance limits of adult corals by acquiring novel symbiont types may be limited, and unlikely to prevent large-scale reef degradation.

George (Jez) Roff (Australia)
PhD student at the University of Queensland (Australia)

I worked on a BWG research topic as an Honours student and now I am a PhD candidate. Together with Tracy, I pioneered the fieldwork which showed that bleaching is not triggered by Vibrio, and published extensively as a student (more than 10 papers). My research on 'white syndrome', a coral disease from the Great Barrier, provided insight into the intracolonial pathways and physiological mechanisms of the disease. Long-term ecological monitoring of affected colonies suggests that whilst white syndrome is initiated by high temperature, lesion progression in individual colonies is not directly related to thermal episodes. More recently I have research interests focused on the historical ecology of coral reefs, particularly the trajectories of decline that have been observed in coral reefs throughout the Caribbean and Indo-Pacific region. I use a range of techniques to investigate the possible synergistic effects of human induced disturbances, identify changes to coral communities across decadal, centennial and millennial scales on inshore reefs of the GBR.

Jacqueline Padilla Gamiño (Mexico)
PhD student at the University of Hawaii (Hawaii)

I am currently a graduate student enrolled in a PhD program in the Department of Oceanography at the University of Hawaii and working in the laboratory of Dr. Ruth Gates at the Hawaii Institute of Marine Biology. My research focuses on the reproductive ecophysiology of scleractinian corals from different biogeographic regions. Specifically, I am interested in how reproductive patterns (fecundity, fertilization, parental investment per ovum and larval fitness) can be influenced by a coral's exposure and ability to adapt and/or acclimatize to new environmental conditions. Coral bleaching, in response to factors such as temperature, salinity and sedimentation can reduce the reproductive fitness and influence the successful recruitment of future generations. My research seeks to understand how the coral parent and offspring can acclimatize in different environments. Having different physiological and morphological characteristics may increase or decrease the propensity of bleaching in both, parents and offspring.

Jessica Gilner (USA)
PhD student at the Florida Institute of Technology (USA)

My research has examined the coral assemblages along the northeastern Yucatan Peninsula, Mexico, and investigated fundamental links between states (i.e. size-frequency distributions and benthic composition) and processes (i.e. reproduction, growth and mortality). Focus has been on the major processes including coral growth, reproduction, partial mortality, and mortality and their effect on size-frequency distributions. These processes are not mutually exclusive; reproductive output is affected by partial colony mortality and growth because they take precedence over reproduction in resource allocation. Partial mortality affects colony size by taking resources away from growth, but also by directly shrinking the effective size of the colony. Furthermore, reproduction is clearly the 'backbone' of population persistence through ecological and evolutionary time and is susceptible to changes in life history characteristics that are governed by environmental factors. Therefore, size-frequency distributions coupled with rates of partial mortality are useful indicators of coral stress and provide insight into the future of reef corals.

Juan Carlos Ortiz (Venezuela)
PhD student at the University of Queensland (Australia)

My PhD is focused on the effect of mild thermal stress on community dynamics of reef building corals. During the summer of 2006 a mild bleaching event occurred at Heron Island on the Great Barrier Reef. The effects of this bleaching on the coral community around Heron Island were followed for 2 years. The data indicates that the substrate surrounding corals affects the degree to which thermal stress causes corals to bleach. Coral identity (taxa) is also important to determine the tolerance to bleaching and the response of certain taxa to mild thermal stress in comparison to extreme thermal stress can be highly varied. With these multiple levels of information an index of sensitivity to thermal stress was formulated. The study demonstrated that population dynamics and response of taxa with a high sensitivity can be used as informative early warning bioindicators of thermal stress.

Juliet Furaha (Kenya)
MSc student at the Moi University (Kenya)

My name is Juliet Furaha Karisa and I hold a Master of Philosophy in Fisheries Management from Moi University, Kenya. Some of the courses that I covered are aquatic ecology, research methods, fish population dynamics, systematic ichthyology and ecology and behaviour of fishes. Broadly, my thesis research was looking at the population dynamics of juvenile corals. I was particularly interested in the temporal and spatial variability of juvenile coral recruitment. To understand these dynamics, I studied the differences of juvenile coral recruitment at sites with different habitat characteristics and management levels for 15 months. Overall, the findings in my study suggest that the stochastic and seasonal dynamics of larval supply and local habitat characteristics are more important determinants of juvenile coral dynamics than is site protection.

Leonard Jones Chauka
PhD student at the University of Dar es Salaam (Tanzania)

The main goal of my proposed study is to enhance understanding on the genetic diversity of *Symbiodinium* harbored by reef building corals and their physiological performance in relation to environmental stress. Specific objectives include: 1- To determine geographical distribution and diversity of *Symbiodinium* harbored by reef building corals of Tanzania. 2- To assess effects of seasonality, depth and disturbance intensities on diversity and distribution of *Symbiodinium* in common reef building corals of Tanzania. 3- To examine how water chemistry, temperature and light intensities affect photosynthetic efficiencies of photosystem II of *Symbiodinium* harbored by reef building corals of Tanzania. I visited Dr Lajeunesse lab for approximately 6 weeks to analyze the identity of symbionts in 10 common species of coral found along the mainland coastline of Tanzania. Building on my intitial training as an attendee of the Pauly Program in Hawaii, I incorporated a variety of molecular genetic techniques including PCR-DGGE and DNA Sequencing.

Luis Alejandro González Guerrero (Mexico)
BSc student at the Universidad Nacional Autónoma of Mexico

I am currently working at Puerto Morelos on my honor's thesis after finishing my undergraduate education in Biology at UNAM. My academic interests include the effects of climate change on coral communities, and the basic photobiology of dinoflagellates. My current research is aiming to dissect the effects of elevated temperature on the photoacclimatory responses of symbiotic dinoflagellates in culture. I work with three different *Symbiodinium* isolates with contrasting evolutionary origin and photosynthetic capacities. The results of my research indicate that in all cases, thermal stress is perceived by the symbiotic algae as an increase in light intensity. In addition, I have been contrasting different analytical techniques such as respirometry and spectroscopy in an effort to establish the limits of applicability of common chlorophyll a fluorescence approaches for the study of photoacclimation. I plan to continue my training in biology to understand the molecular and cellular mechanisms behind coral bleaching.

Mauricio Rodriguez-Lanetty (Venezuela)
Postdoctoral Fellow, University of Queensland (Australia)

My research focused on the use of microarray technology to explore gene expression under stress in reef-building corals. I was co-supported by the BWG while I was an ARC funded postdoctoral fellow under the supervision of Ove Hoegh-Guldberg. I am originally from Venezuela where I obtained my bachelor degree in Biology in 1994. I moved to Australia in 1997 to pursue my PhD degree; first at the University of Sydney (1997-1999) and later at the University of Queensland where I completed my PhD in Marine Studies in 2002. From 2002 to 2008, I worked as a Postdoctoral Fellow in several Universities including Ewha Womans University (South Korea), Oregon State University (in the Weis's lab) and then in the University of Queensland (Hoegh-Guldberg's lab). I recently moved to a position in the Department of Biology at the University of Louisiana in Lafayette, USA.

Omri Bronstein (Israel)
PhD student at the University of Tel Aviv (Israel)

My name is Omri Bronstein and I am a PhD student at Professor Yossi Loya's lab, Tel Aviv University, Israel. As part of the GEF/World Bank targeted research on coral bleaching and local ecological responses, my study aims at evaluating the state and assessing the impact of sea urchin populations on coral communities around the island of Zanzibar. My work is part of a combined effort to provide a comprehensive view of the state of coral reefs through examination of the relationship between coral, fish and sea urchins. In the past two years we tracked the changes of sea urchin populations at six sites around Zanzibar, identified the key urchin species and conducted bioerosion experiments on the four most dominant urchin species. Our examination also revealed that one of the most dominant species in the region should be considered a new species.

Reia Guppy (Trinidad and Tobago)
PhD student at the Newcastle University (UK)

I completed my PhD in 2006 and continued with a 3-year post-doctoral position with John Bythell at Newcastle. I took up a Faculty position at the new University of Trinidad & Tobago in August 2009. I use an array of molecular, cellular and ecological techniques to address a range of ecological problems. Particular interests are coral host-microbe interactions, biogeography of marine microbial communities ranging from micro to macro spatial scales, and how these communities develop on healthy coral colonies over time. Recent work has compared surface mucus layer microbial communities across several spatial and temporal scales and followed the persistence and rate of development of the coral surface biofilm. I was supported by the BWG to attend the joint BWG/DWG meeting in Mexico (2005) and the International Coral Reef Symposium in Florida (2008).

Tracy Ainsworth (Australia)
PhD student at the University of Queensland (Australia)

I was Ove Hoegh-Guldberg's PhD student and worked on the BWG project until late 2007. I was awarded my PhD in 2007 and I am currently an ARC Postdoctoral Research Fellow (2008-2010), at the ARC Centre of Excellence for Coral Reef Studies, James Cook University. My research interests include stress responses, cell biology, immunity and disease of marine invertebrates. My current research focuses on investigating the cellular and molecular responses of corals to environmental stressors as a means to better understand the impact of climate change and disease in reef ecosystems. I was particularly productive during the research BWG program, producing 8 publications from this and related work.

William Leggat (Australia)
Postdoctoral Fellow, University of Queensland (Australia)

My research was co-supported by the BWG while I was an ARC funded postdoctoral fellow under the supervision of Ove Hoegh-Guldberg. I focused on the all-important symbiotic dinoflagellate *Symbiodinium*, particularly on the linkages between gene expression of *Symbiodinium* to physiology of the algae and the intact coral holobiont (its host), and subsequent ecological changes. Research of this type can broadly be called ecological genomics. In particular, I am interested in how these dinoflagellates respond to human induced stress, such as climate change, what effects these changes have on the coral host and how the responses of the alga effect the future of coral reefs as we know them. I recently took at position at James Cook University, in Townsville, Australia.

Xavier Enoch Hernández Pech (Mexico)
PhD student at at the Universidad Nacional Autónoma
of Mexico

I am currently writing my PhD dissertation at the Institute for Cell Physiology at UNAM. My research interest is focused on the responses of the photosynthetic apparatus of dinoflagellates to different stressful conditions. The main topic of this research is the characterization of the photoprotective mechanisms present in symbiotic dinoflagellates of scleractinian corals using a combination of biochemical and biophysical approaches. My work describes the effect of light stress on the dial oscillation of the efficiency of charge separation of photosystem II (PSII) reaction center and its relationship to PSII repair cycle. Chronic light stress periods have been described as one of several key stressors leading to the disruption of the coral/dinoflagellate symbiotic relationship, characteristic of coral bleaching. I plan to continue pursuing my academic interest as a postdoctoral fellow in the near future.

Workshops and outreach

The Working Group on Bleaching and Local Ecological Factors (BWG) developed a series of large regional workshops to strengthen collaborations between Working Groups and Centres of Excellence and to encompass a strategy to build expert knowledge and capacity for coral reef management. These meetings were an important opportunity to share knowledge and extend scientific capacity and learning through encouraging young research scientists and students. The workshops were also central to making good technical progress toward technologies that will support management and policy. As a result of the workshops, the BWG established a strong collaborative network which extends well beyond the discrete membership of the Working Group and was focused on linkages and synergies between developed and developing countries. This was a substantial output for a group of ten scientists.

Workshop 1
Inaugural BWG meeting and first research workshop

Date: May 4 – 27, 2005

Purpose: The Bleaching Working Group held an inaugural workshop at the MesoAmerican Centre of Excellence at Puerto Morelos from 10 May to 3 June 2005. This workshop is seen as the first of many collaborations between Working Groups and Centres of Excellence and remains consistent with the capacity building goals of the Project to provide an ideal opportunity to "share knowledge and extend scientific capacity and learning" through encouraging young research scientists and students. Approximately 70 senior scientists, graduate students and post-doctoral fellows from both developing and developed countries attended the event. The workshop was the first of a series of workshops designed to galvanise the international scientific community around problems, gaps and solutions with respect to the global issue of coral bleaching and related ecological disturbances to coral reefs. The workshop was broken into a series of smaller workshops including: Using Pulsed Amplitude Modulated Fluorescence to detect stress; Diversity, flexibility, stability, physiology of *Symbiodinium* and the associated ecological ramifications, Exploration of the Coral and *Symbiodinium* genomes, Coral Reef Targeted Research Working Group joint field methods, and integrated research on coral bleaching and disease. The workshop also conducted a major study of the molecular and physiological mechanisms underlying thermal stress with the focus being the Caribbean coral Montastraea annularis.

Location: Puerto Morelos, Meso-American CoE, Mexico.

Number of Participants: 70

Figure 35. Attendees at the inaugural BWG workshop in Puerto Morelos, Mexico.

Workshop 2
A major student training workshop for research skill development

Date: July 26 – August 11, 2005

Purpose: Training workshop for 8 advanced undergraduate students from Indonesia on methods for understanding stress on coral reefs and to attend the Australian Coral Reef Society annual meeting. The workshop involved training in library research and writing science, as well as hands-on research at Heron Island Research Station. Three students from this course have begun higher degrees.

Location: Heron Island, Australasian CoE, Australia.

Number of Participants: 8

Figure 36. Ms Lely Fika Anggraini undertaking field work as part of the research training workshop in Heron Island, 2005.

Workshop 3
Meeting on field methods for the CRTR Program: toward commonality and complementarity

Date: November 6 – 7, 2005

Purpose: Discuss how we can facilitate interaction among working groups, identify key process variables and finalize selected parameters and methods; gathering to establish a complementary approach to field methods and data collection.

Location: Melbourne, Florida, USA

Number of Participants: 8

Workshop 4
BWG Research workshop

Date: January 2 – February 16 2006

Purpose: Undertake research focused on answering fundamental mechanisms of coral bleaching and mortality.

Location: Heron Island, Australasian CoE, Australia

Number of Participants: 18

Workshop 5
BWG Research workshop – Remote sensing and thermal thresholds

Date: March 2006

Purpose: The team had a three week experimental workshop, followed by a video conference link up which was held in Brisbane.

Location: Heron Island, Australasian CoE, Australia

Number of Participants: 18

Workshop 6
BWG Annual meeting

Date: April 8 – 9, 2006

Purpose: Review of funding activities and reporting update. Discussion on first year activities and outcomes. Define position for the next 4 years.

Location: UNESCO-IOC, Paris

Number of Participants: 13

Figure 37. Member participants during the BWG annual meeting in Paris, 2003. From left to right: Y. Loya, R. Iglesias-Prieto, D. Obura, R. Johnston, O. Hoegh-Guldberg, T . McClanahan, R. Gates, M. Lesser. W. Fitt, R. van Woesik, J. Bythell, H. Chin and O. Vestegaard.

Workshop 7
Training workshop/course on coral reefs and environmental change

Date: July 9 – 11, 2006

Purpose: A training course for Indonesia and West Papua students was run at the University of Diponegoro in order to discuss significant coastal and coral reef issues.

Location: Semarang, Indonesia

Number of Participants: 45 students

Figure 38. Students and Rector (left) at the University of Diponegoro and Ove Hoegh-Guldberg (right)

Workshop 8
BWG Research workshop on meso-scale effects of coral bleaching – benthic-fish interactions

Date: November 28 – December 1, 2006

Purpose: The workshop focused on benthic-fish-fishing interactions and the medium-term (3-10 years) effects of coral bleaching and mortality on these interactions and the coral reef ecosystem. Several major reviews have been generated from this meeting.

Location: Zanzibar, East African CoE.

Number of Participants: 17

Workshop 9
BWG Research workshop

Date: January 22 – 27, 2007

Purpose: BWG/NSF/ARC workshop on Heron island "New frontiers in cellular interactions in Cnidarian/dinoflagellate symbiosis" NSF/ARC proposal (Weis, Hoegh-Guldberg, Pringle, Davy; $140k from NSF). (BWG supported 5 scholars to attend from Mexico, Kenya, Iran, and Taiwan).

Location: Heron island, Australasian CoE

Number of Participants: 57

Figure 39. Participants at Workshop 9 (supported by BWG/NSF/ARC) at Heron Island, Australia

Workshop 10
BWG Research workshop

Date: July 30 – August 3, 2007

Purpose: BWG supported workshop responding to climate change: a workshop for reef managers. Lady Elliot Island, Southern GBR

Location: Australasian CoE

Number of Participants: (Supported 9 managers to attend; $10k)

Workshop 11
BWG Research workshop

Date: April 16 – 26, 2007

Purpose: "Science for management: Understanding and protecting East Africa's coral reefs." Workshop involved BWG members as well as scholars and students from South Africa, Kenya and Tanzania. Three days of presentations and seminars – followed by 8 days of research. Several key papers were generated as a result of this interaction.

Location: Zanzibar, East African CoE.

Number of Participants: 25

Workshop 12
Molecular techniques workshop

Date: June 2 – July 27, 2007

Purpose: The BWG coordinated and taught the Edwin W. Pauley Summer Program in Marine Biology ("The Biology of Corals: Developing a Fundamental Understanding of the Coral Stress"). This 6 week program focused on developing research capacity in the biology of corals and examining the biology underlying stress responses. (see details at http://www.hawaii.edu/HIMB/Education/pauley2007.html) The BWG contributed $45,000 of the $162,000 budget to run this program. The 15 student participants were selected through a competitive application process from a pool of over 70 applicants from 27 countries. The BWG funding supported the participation of four developing country students, six BWG members as faculty in the program - Ruth Gates (Lead PI), John

Figure 40. Ruth Gates and students during the 2007 Edwin W. Pauley Summer Program in Marine Biology, Hawaii.

Bythell, David Obura, Roberto Iglesias Prieto, Ove Hoegh Guldberg and Michael Lesser and Jackie Padilla-Gamino, the GEF PhD candidate being trained in Hawaii. In addition to the BWG faculty, students were taught by an additional 10 coral biology experts (see website for details). Two short workshops were embedded in the program to expose students to management relevant science.

Location: Hawaii Institute of Marine Biology, Hawaii, USA.

Number of Participants: 15 (+ 22 lecturers/research leaders)

Workshop 13
Developing a temperature-light satellite product for predicting coral bleaching impacts

Date: June 24 – 26, 2009

Purpose: Collaboration between RSWG and BWG – aimed at refining an algorithm that uses light and temperature to predict the impact and outcome of mass coral bleaching events.

Location: HIMB, Hawaii.

Number of Participants: 12

Workshop 14
BWG Research workshop on common sampling methods

Date: October 3 – 7, 2007

Purpose: Define common-field sampling protocols for working groups at the CoE within the CRTR Program

Location: Florida Institute of Technology, Florida, USA

Number of Participants: 10

Figure 41. BWG students and Yossi Loya (front centre) and Rob van Woesik (back centre) in the sampling methodologies workshop.

Workshop 15
BWG Annual meeting

Date: December 18 – 20, 2007

Purpose: Present work to-date and set budget and work plan for 2008

Location: Amsterdam, The Netherlands

Number of Participants: 13

Workshop 16
BWG Microbial ecology workshop

Date: May 5 – 16, 2008

Purpose: Training workshop for students on microbial ecology techniques. Regional capacity building

Location: Zanzibar, East African CoE.

Number of Participants: 17

Figure 42. John Bythell and Ron Johnstone (front) and participants in the microbial ecology workshop for Western Indian Ocean and East African participants, Zanzibar CoE, May 2008.

Workshop 17
BWG Annual meeting

Date: July 13 – 14, 2008

Purpose: Discuss progress, Phase 2 Working Group activities, budgets and personnel.

Location: Fort Lauderdale, Florida, USA.

Number of Participants: 13

Workshop 18
BWG meeting and research workshop

Date: May 17 – 30, 2009

Purpose: Seminars to present the most recent results. Review, analyse and write up the project activities from the preceding 4-5 years. Focus on two major writing tasks: (1) major academic contributions aimed at synthesising the research results from past five years, and (2) public outreach documents aimed at local managers, government agencies and scientists. Also produce a number of small videos and interviews on BWG activities for target audiences.

Location: Heron Island, Australasian CoE, Australia.
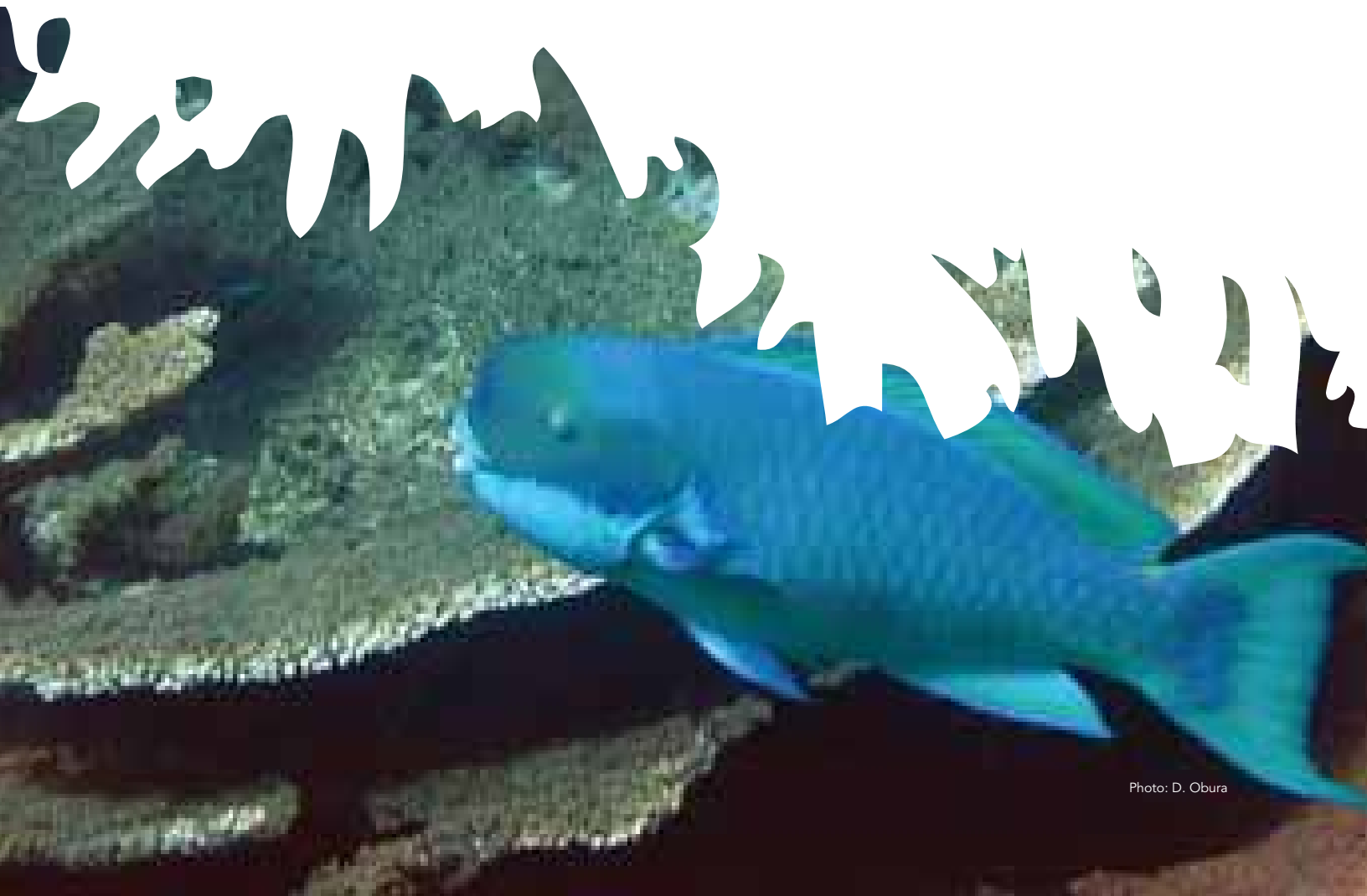
Number of Participants: 25

Figure 43. Participants at the final meeting and BWG workshop 18 on Heron Island, Australia.

Conclusions and future research

The first five years of research has been highly successful in terms of achieving the goals set by the original BWG research plan. Many of these physiological and ecological questions have been answered. These answers lead naturally to other areas of investigation, which will yield important new insights into the basic processes underpinning coral reefs and their response to rapid global change.

Beyond the four research themes

We now have a much better understanding of the diversity and flexibility of coral-*Symbiodinium* associations as a result of the first five years of investigation within Theme 1: Coral-symbiont responses to thermal stress. The notion that symbiosis is flexible enough to allow the evolution of new symbioses with higher thermal tolerances has been disproved. While there is evidence for shuffling of existing symbiont varieties (e.g., acclimatization) in the field, there is no evidence of host corals switching their existing symbionts for truly novel varieties. This leads to the conclusion (which is borne out by a large amount of ecological work) that symbiosis between corals and *Symbiodinium* are unlikely to be able to shift their thermal tolerance rapidly enough over the time frames of predicted increases in temperatures. Consequently, projections that rising sea temperatures will lead to an increase in mass coral bleaching and mortality remain the most credible conclusion regarding the future of coral reefs under rapid anthropogenic climate change.

Patterns associated with the genetic diversity of *Symbiodinium* are beginning to become coherent. While particular host species of corals tend to have the same sub-clades across most of their distribution, they often have quite different subclades at the extreme north or south of the distribution. Questions regarding how quickly these new varieties of symbiosis have arisen and how they function within these extreme environments should be a major focus for future research.

Research undertaken within Theme 1 has led to a series of new perspectives on the diversity of symbionts and close associates of reef-building corals. One of the key findings of the current project has been that corals and dinoflagellates are only two of the many organisms which are interacting to form the coral holobiont. While the function of most of the bacteria species on the surfaces of corals has yet to be identified, the discovery of the functional N-fixing bacteria within the tissues of corals indicates that many of these bacteria are likely to have key physiological roles within the coral holobiont. In addition to discovering a series of apparently benign bacterial symbionts, it is clear that the integrity of the coral surface (particularly the mucus layer) is critical to the maintenance of disease free states in reef-building corals. Understanding these relationships, particularly the role and function of mucus and other immune responses of corals, will be particularly important given recent observations of an increase in coral disease and linkage of this phenomenon to ocean warming.

Theme 2 within the BWG work plan focused on relating responses measured at the organism, population and ecosystem levels to ecological outcomes. A number of projects focused in on stony corals, algae, sea urchins and fish species diversity and community structure, as well as their population dynamics under environmental change, and the effects of bleaching on coral populations within regions, such as the Western Indian Ocean. These studies have identified a number of subtle ecological changes which suggests that changes to coral reefs occur prior to the appearance of mass mortality. This observation suggests that understanding and detecting these changes, and relating them to broad-scale physiological phenomena, such as primary productivity and calcification will be important in future studies. These types of changes currently tend to fall under the radar of reef managers, yet are likely to be fundamentally important in detecting their impact on community compositions and functional relationships of coral reefs fauna and flora. Further research in this area should also be a major priority.

Work done as part of Theme 3 (Biomarkers) has opened up an enormous set of opportunities to develop further biomarkers for detecting and distinguishing different types of environmental stress. In this regard, the discovery of around 100 stress protein candidates (many new to corals) from the microarrays studies opens up significant opportunity for future investigation. Understanding the function of each of these protein candidates, and how the expression of these proteins relates to the type and intensity of environmental stress, will help define how these important tools can be used by reef scientists and managers in the future. Being able to create less expensive technologies accessible to the developing world will be an important criterion for the development of these potentially useful tools for reef managers.

The last part of the BWG research plan was to take the knowledge from the first three themes and to incorporate these into credible projections of the future. In this respect, some progress has been made in terms of linking the physical, chemical and biological changes to the socioeconomic and political consequences. The recent multidisciplinary study within the Coral Triangle undertaken by members of the BWG has highlighted a series of important ramifications of losing coastal ecosystems under rapid changes in climate. One of these projections is the potential likelihood that the 100 million people that live in the coastal zone within the Coral Triangle are likely to see increased poverty and downwardly spiraling food security. While this has been done for the Coral Triangle, the next set of questions should focus on refining the level of precision for understanding these linkages, and extending them to other regions. In this respect, the work by BWG member Dr Tim McClanahan and others has already begun to bring important synthesis to our understanding of how climate change, coral reefs and people are linked within the Western Indian Ocean.
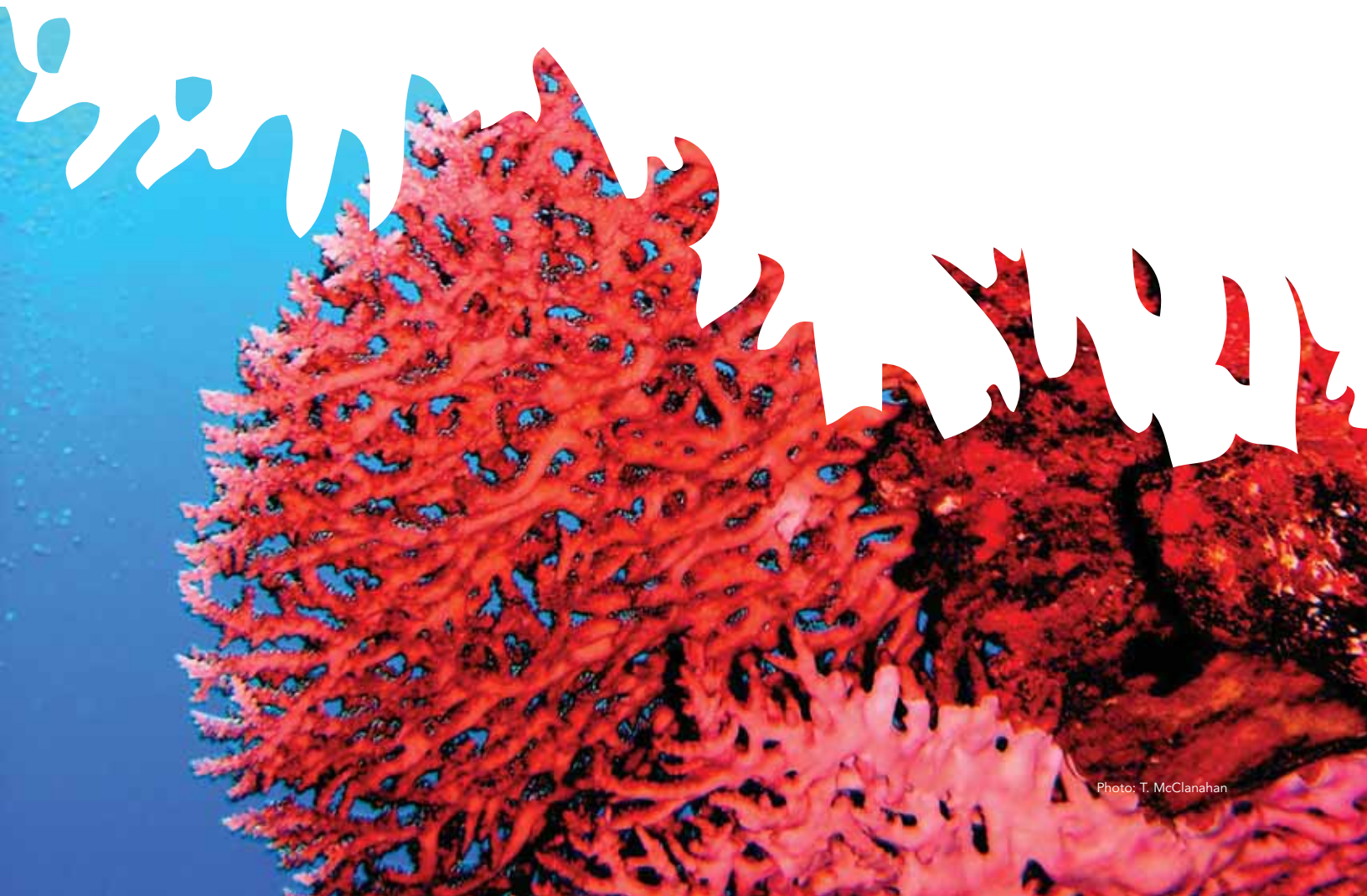
Research themes
for the future

Coral reefs are clearly facing a very difficult time as sea temperatures and acidity increase under the pressure of rising atmospheric carbon dioxide and other greenhouse gases. This leads to a number of conclusions. The first is that the current decline in reef-building corals on reefs across the planet (Bruno and Selig 2007) is likely to continue. The second is that reefs are likely to have less reef-building coral on them (Hoegh-Guldberg et al. 2007a). The third is that the majority of tropical reef systems are likely to have very different community compositions and functional relationships. Understanding how these reef systems are likely to function at the ecosystem level should be a priority of future research.

In this respect, the BWG is proposing a new focus on Reef Processes under Rapid Climate Change (RESERCC) in which understanding changes to primary productivity and carbonate accretion would form the unifying theme. These particular processes link directly into food security and human well-being. For example, it is an urgent priority that we understand how the productivity of coral reefs is likely to change as reef-building corals dwindle and other organisms such as macroalgae become more dominant within tropical reef communities. How these changes affect fisheries and other resources available to human communities in tropical coastal areas would form an important part of this research program.

Similarly, focusing on how calcification, erosion and carbonate accretion are going to change as oceans warm and acidify will also form a critical focus of this new research project. Understanding how rapidly carbonate frameworks will disintegrate (or not) under changes to the rates of calcification and erosion will be enormously useful to nations across the world's tropical regions who are trying to plan their responses to climate change. Equally, how these changes to the three-dimensional structure of coral reefs will affect the key reef ecosystem services will be critical for understanding how food security and human well-being may change in the future.

Measuring and understanding these ecological processes as part of RESERCC will require a multidisciplinary approach, which appears ideally suited to the Coral Reef Targeted Research (CRTR) Program and the scientific expertise of the BWG. This new focus will draw heavily on the first five years of research undertaken by the BWG and other Working Groups within the CRTR Program. This focus is also expected to drive a reconstitution and possible expansion of the Working Groups within the CRTR. Considering this emergent research concept, the BWG will transform into a research group that is focused on providing organismal, population, and ecosystem level models for how primary productivity, element cycles and carbonate balance of coral reefs is likely to change as carbon dioxide and other greenhouse gases continue to increase in the earth's atmosphere. In particular many coral reefs around the world have changed in their structure to "algal" dominated communities, while others have not. At a basic level the BWG would ask how are productivity, element cycles and calcification rates of these new "reefs" compare to those former reefs, which were dominated by corals. When shifts to algal dominated communities occur what coral reef ecosystem services are lost, or gained? What are the interactive roles that local anthropogenic stressors (e.g., eutrophication) play when coral reefs are faced with the effects of global climate change? The answers to these questions will continue to be the Working Group's fundamental premise that understanding the basic biology and ecology of corals leads to practical answers to applied questions that can be used by local communities and managers.

Invited presentations

Over the past five years, the BWG members, researchers and students gave more than 200 presentations in numerous meetings around the world. This involved about 65 different institutions and universities from 18 countries. Here we listed only the major international meetings and conferences in which our results were presented.

Photo: E. Brokovich

2009

Bythell J. The consequences of catastrophic events. Keynote address, 44th European Marine Biological Society meeting, Liverpool, United Kingdom.

Gates R. Evolutionary and Ecological Genetics. EPSCoR National Conference, Hawaii Institute of Marine Biology, Honolulu, Hawaii.

Hoegh-Guldberg O. Coral reefs and climate change: Is there any hope for coral reef ecosystems? Workshop: Responses of Coral Holobionts under the Impact of Climate Change: Symbiont Diversity, Coral Bleaching, Diseases, and Ocean Acidification. Plenary speaker. Tapei, Taiwan June 22.

Hoegh-Guldberg O. Coral reefs, evolution and climate change. Workshop: Responses of Coral Holobionts under the Impact of Climate Change: Symbiont Diversity, Coral Bleaching, Diseases, and Ocean Acidification; Invited speaker. Tapei, Taiwan June 23.

Hoegh-Guldberg O. Coral reefs, symbiosis and Koyaanisqatsi. Invited speaker, Archilife Research Foundation, Tapei, Taiwan June 27.

Hoegh-Guldberg O. Oceans of Change: Why we must achieve firm action on CO_2 emissions in Copenhagen. Invited Speaker, Australian Education International, Tapei, Taiwan June 23.

Hoegh-Guldberg O. Coral reefs and Rapid Climate Change: Impacts, Risks and Implications for Tropical Societies. International Scientific Congress on Climate Change, University of Copenhagen, March 12-14.

Hoegh-Guldberg O. The Coral Reef Crisis. Invited lecture to EarthStock Day at Stony Brook University, New York, USA.

Hoegh-Guldberg O. 450 ppm or bust: Copenhagen, climate change and the future of the earth's biosphere. Invited speaker, Woods Institute, Stanford University.

Hoegh-Guldberg O. Climate change and our climate. Invited speaker, Blue Visions Summit, Washington DC, March.

Hoegh-Guldberg O. Coral reefs in a rapidly heating and acidifying global ocean: reasons for hope and strategies for survival. World Ocean Congress, Manado, Indonesia May 11-15.

McClanahan T. Adaptation for tropical coral reef ecosystems in the face of climate change. Congressional staff lunch briefing, Wildlife Conservation Society, New York, USA May 20.

Padilla-Gamino J. The influence of parental conditions on coral offspring: are all gametes created equal? Best student paper award. STAR Student Symposium Department of Oceanography, University of Hawaii at Manoa. USA.

Wild C. Biogeochemical research approaches to understand coral reef engineering. Public talk at Institute de Ciéncies del Mar (CSIC), Barcelona, Spain.

Wild C. Research approaches to understand coral reef engineering and functioning in a time of change". Public talk at Center for Tropical Marine Ecology (ZMT), Bremen, Germany.

* Denotes BWG members, researches and/or students when external authors are also included.

2008

Ainsworth T, Hoegh-Guldberg O. Coral-bacterial associations vary under environmental and experimental conditions. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Ateweberhan M, McClanahan T. Historical sea-surface temperature variability predicts climate change-induced coral mortality. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Bongaerts P, Englebert N, Ridgway T, Riginos C, Hoegh-Guldberg O*. Genetic connectivity of the shallow and deep reef: intra-reef genetic structure of Seriatopora hystrix on the northern Great Barrier Reef. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Bongaerts P, Bridge T, Sampayo E*, Englebert N, Ridgway T, Rodríguez-Lanetty M, Webster J, Hoegh-Guldberg O*. Diversity of *Symbiodinium* in mesophotic coral communities on the Great Barrier Reef. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Bronstein O, Loya Y. The sea urchins of Zanzibar and their effect on local coral communities. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Bythell J*, Guppy R*, Jatkar A*, Brown B, Morris N, Pearson J. Visualising the coral surface mucus layer. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Bythell J. Reef Corals: healthy or snot? Keynote address, Reef Conservation UK Meeting, Zoological Society of London, London, United Kingdom.

Bythell J. Coral reef bleaching events, microbial communities and climate change. Invited Plenary, Society for General Microbiology, 162nd Ordinary Meeting, 'Hot Topics' Symposium on Influence of Climate Change on Disease and Microbial Environmental Processes, Edinburgh, United Kingdom.

Desalvo M, Voolstra C, Weil E, Andersen G, Iglesias-Prieto R*, Medina M. Bacterial Community and Gene Expression Profiling Using 16srrna Gene and CdnaMicroarrays: Introduction of a Dual High-Throughput Approach to the Study of Coral Disease and Bleaching. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Díaz-Almeida EM*, Iglesias-Prieto R*, Thomé PE. Differential Stability of the Photosynthetic Membrane of Symbiotic Dinoflagellates in Response to Elevated Temperature. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Díaz-Pulido G, Anthony KRN, Kline DI, Mccook L, Ward S, Hoegh-Guldberg O*, Dove S*. Effects of climate change on coral reef algae: will algae be the winners? 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Enriquez S, Mendez E, Hoegh-Guldberg O*, Iglesias-Prieto R*. Morphological Dependence of the Variation in the Light Amplification Capacity of Coral Skeleton. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Fitt W*, Kemp D*, Hernandez-Pech X*, Iglesias-Prieto R*, Mccabe J, Shannon T, Bruns B, Schmidt G. Bleaching, El Niño, and la Niña: 13 years of seasonal analysis of reef-building corals in Florida, the Bahamas, and the Caribbean. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Gates R. Comparison of endosymbiotic and free-living *Symbiodinium* diversity in a Hawaiian reef environment. Western Society of Naturalists, Vancouver, Canada.

Gates R. Developing tools for monitoring coral health. Joint Symposium (with university of Hawaii) on Ocean and Coastal Sciences, University of Tokyo, Japan.

Gates R. Do corals possess the biological flexibility to survive global climate change?. The Omics in Ocean – International Symposium for Marine Biotechnology, National Museum of Marine Biology and Aquarium (NMMBA), Taiwan.

Gates R. How flexible is the biology of corals? Long Term Ecological Research, Joint Taiwan US Symposium, Taiwan Coral Research Center, Taiwan

* Denotes BWG members, researches and/or students when external authors are also included.

Gilner J, van Woesik R. Partial mortality of Caribbean corals: modes, trends, and consequences. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Goulet T, LaJeunesse T*, Fabricus K. Symbiont specificity within and among soft coral genera during the 1998 GBR mass coral bleaching event. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Guppy R, Bythell J. Biofilms: coral surface mucus layers, settlers and their bacterial inhabitants. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Haas A, Naumann M, Mayer F, Mayr C, el-Zibdah M, Wild C*. Organic matter release by coral reef associated benthic algae - Implications for in-situ oxygen dynamics. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Hernandez-Pech X*, Iglesias-Prieto R*. In Hospite Operation of the Photosystem II Repair Cycle in Symbiotic Dinoflagellates. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Hind E*, Lindop A, Bythell J*. The unknowns in coral disease identification: an experiment to assess consensus of opinion amongst experts. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Hoegh-Guldberg O. Invited Key Note speech for opening of King Abdullah University of Science and Technology (KAUST) Symposium - "The Sustainability of Coral Reefs Faced by Unprecedented Environmental Change", Jeddah, Saudi Arabia.

Hoegh-Guldberg O. Is 500 ppm CO_2 and 2°C of warming the 'tipping point' for coral reefs? If so, how should we respond? 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Hoegh-Guldberg O. Coral reef ecosystems, climate change and human societies. Key Note Address to the World Bank's Environment Sector Board, Washington DC, USA.

Hoegh-Guldberg O. Keynote address "Coral reefs and global change". AAAS Annual Meeting in Boston on "Global Interactions between Climate Change and Microbial Activity." Boston MA, USA.

Hoegh-Guldberg O. Coral reefs and ocean acidification. Invited lecture given as part of the public symposium What's Killing the Coral Reefs? at the Marian Koshland Science Museum Coral Reefs Program, Washington DC, USA.

Hoegh-Guldberg O. Invited keynote address. Climate change, coral bleaching and the future of the world's coral reefs. International Symposium on the Effects of Climate Change on the World's Oceans, Gijón, Spain May 19-23.

Iglesias-Prieto R. Photophysiology, Bleaching and Adaptation. Plenary speaker. 11th International Coral Reef Symposium, Fort Lauderdale, USA, July 7-11.

Jatkar A*, Bythell J*, Brown B, Pearson J, Morris N, Guppy R*. Do corals possess the protective mucus encoding muc genes? 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Jupiter S, Marion G, Rof G*, Henderson M, Schrameyer V, Mcculloch M, Hoegh-Guldberg O*. Linkages between coral assemblages and coral-based proxies of terrestrial exposure along a cross-shelf gradient of the Great Barrier Reef. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Kaniewska P, Campbell P, Fine M, Hoegh-Guldberg O*. Phototropic growth and molecular basis for axial polyp differentiation in the branching coral Acropora aspera. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Kemp D*, Hernandez-Pech X*, Iglesias-Prieto R*, Schmidt G, Fitt W*. .Micro-Niche Partitioning and the Photobiology of *Symbiodinium* Associated with Montastraea faveolata. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Kline DI, Anthony KRN, Díaz-Pulido G, Dove S*, Ward S, Hoegh-Guldberg O*. Impacts of Ocean Acidification and Warming on Calcifying Coral Reef Organisms. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

* Denotes BWG members, researches and/or students when external authors are also included.

Kongjandtre N, Rodríguez-Lanetty M, Ridgway T, Hoegh-Guldberg O*. Resolving the Taxonomy of Favia Corals from Thai Waters using Morphological and Molecular Data. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Kuguru B, Nanette E. Chadwick C, Achituv Y, Dove S*, Hoegh-Guldberg O*, Tchernov D. Mechanisms of microhabitat segregation among corallimorpharians: Evidence from physiological parameters related to photosynthesis and host cellular response to irradiance. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Leggat W*, Yellowlees D, Dove S*, Hoegh-Guldberg O*. Gene Expression in *Symbiodinium* Under Stress. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Levy O, Appelbaum L, Leggat W*, Gothilf Y, Hayward D, Miller D, Hoegh-Guldberg O*. Light-Responsive Cryptochromes from a Simple Multicellular Animal, the Coral Acropora millepora. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Loya Y. Bidirectional sex change in fungiid corals. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Loya Y. The Coral Reefs of Eilat-past present and future. First International Congress Documenting, Analyzing and Managing Biodiversity in the Middle East, Aqaba, Jordan.

Marshall J, Logan D, Siebeck U, Hoegh-Guldberg O*, Joanne Marston, Jenny Miller Garmendia, Ania Budziak. CoralWatch: A Flexible Coral Bleaching Monitoring Tool for You and Your Group. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Mayer F, Naumann M, Haas A, Mansareh R, Wild C*. Coral mucus creates a short-linked energy and nutrient-cycle via particle trapping in fringing reefs of the Northern Red Sea. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Mayer F, Duewel S, Haas A, Jantzen C, Naumann M, Jeschke JM, Wild C*. A web-based information management solution for experimental data from the field of coral reef ecology. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

McClanahan T*, Ruiz Sebastian C, Cinner J, Maina J,.Wilson S. Managing fishing gear to encourage ecosystem-based management of coral reefs fisheries. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Mcdonald C, Dunbar R, Koseff J, Monismith S, Hoegh-Guldberg O*, Reidenbach M. Large-scale, In-situ Measurements of Coral Reef Community Metabolism Using an Integrated Control Volume. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Meisel J, Reef R, Rodríguez-Lanetty M, Dove S*, Hoegh-Guldberg O*. The Role of Oxidative DNA Damage and Repair in Cnidarian-Dinoflagellate Symbiosis Breakdown. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Mukherjee M, West L, Lasker H, Schmidt G, Fitt W*. Antioxidant activity of extracts and secondary metabolites from Pseudopterogorgia spp. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Naumann M, Mayr C, Wild C*. Coral mucus stable isotope composition and labeling. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Ortiz J*, Gomez-Cabrera M. Coral holobiont community structure: How much have we

missed by focusing only in the coral host?. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Padilla-Gamino J, Gates R. The Influence of Size, Morphology and Parental Conditions on Coral Reproductive Outputs. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Padilla-Gamino J, Gates R. Exploring coral reproduction in the field: do size and morphology influence the reproductive output of the hermatypic coral Montipora capitata (spawner)?. 88th Western Society of Naturalists Annual Meeting. Ventura, California, USA. Honourable mention for best student paper award.

* Denotes BWG members, researches and/or students when external authors are also included.

Palmer C*, Bythell J*, Willis B. Pigmentation as part of a general immune response in Scleractinians. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Reef R, Dove S*, Carmi M, Mooney A, Kaniewska P, Levy O, Hoegh-Guldberg O*. Climate change can supersensitise corals to natural levels of ultra violet radiation. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Rodríguez-Lanetty M, Harii S, Hoegh-Guldberg O*. Thermal regulation in coral larvae: a microarray screening. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Rosic N, Rodríguez-Lanetty M, Leggat W*, Hoegh-Guldberg O*. Effect of irradiance and increased temperature on differential gene expression in dinoflagellate. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Siboni N, Ben-Dov E, Sivan A, Hoegh-Guldberg O*, Kushmaro A. Global diversity and distribution of coral associated Archaea and the possible role in coral nitrogen cycle. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Skirving W, Iglesias-Prieto R*, Enriquez S, Christensen T, Hedley J, Eakin M, Ove Hoegh-Guldberg O*, Dove S*, Heron S, Mumby P, Strong A, Liu G, Morgan J, Gledhill D. A methodology for using satellite-based temperature and light measurements for predicting coral bleaching severity and mortality. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Smith R, LaJeunesse T*. Prevalence of background populations of an opportunistic *Symbiodinium* among Caribbean coral communities. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

van Woesik R. Characteristics of marine climate sensitive species: coral reefs. Florida Summit of climate–sensitive species, Orlando, Florida, USA:

van Woesik R. Coral reef resilience in the face of global climate change: conceptual framework for the application of resilience principles to coral reef conservation. The Florida Reef Resilience Program, Key Largo, USA.

van Woesik R. Vital processes structuring coral reef assemblages: implications for management. Endangered Acropora species in the Caribbean, Cancun, Mexico.

Ward S, Dove S*, Kline D, Anthony K, Hoegh-Guldberg O*. Ocean Acidification changes the early life history of scleractinian corals. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Wicks L, Sampayo E*, Gardner J, Hoegh-Guldberg O*, Davy S. High *Symbiodinium* diversity at high-latitude reef sites - a means of survival in the face of climate change? 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Wild C*, Naumann M, Haas A, Mayr C. Phase shifts in coral reefs – comparative investigation of corals and benthic algae as ecosystem engineers. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

Zvuloni A*, Artzy-Randrup, Stone L, van Woesik R*, Loya R*. Ecological count-based measures: how to prevent and correct biases in spatial sampling. 11th International Coral Reef Symposium, Fort Lauderdale, USA July 7-11.

* Denotes BWG members, researches and/or students when external authors are also included.

2007

Bythell J. Microbial intermediates of bleaching mortality. Centre for Marine Sciences (CMS), Departmental seminar series, University of Queensland, Australia.

Fitt W. A post-El Niño spike in zooxanthelae density – what does it mean?" Coral Reef Targeted Research and Capacity Building for Management Workshop, Institute for Marine Science, Zanzibar

Gates R. Corals and the environment. Marine Science Seminar Series, California State University Fresno, USA

Gates R. How flexible is the biology of corals? Departmental Seminar Series. Lehigh University, Pennsylvania, USA.

Gates R. Unveiling Taxonomic and Functional diversity on *Symbiodinium*-Coral Associations. All Scientists Meeting Moorea Coral Reef LTER, University of California, Santa Barbara, USA.

Hoegh-Guldberg O. Coral reefs and the impacts of rapid warming and acidification. Dutch Coral Research Symposium, Amsterdam, Netherlands

Iglesias-Prieto R*, Enríquez S. Determining algal absorptance from intact coral surfaces. AquaFluo Chlorophyll fluorescente in Aquatic Sciences Meeting. Nove Hrady, Czech Republic.

Iglesias-Prieto R. Simbiosis entre dinoflagelados y corales: perspectivas actuales. IV Congreso Mexicano de Arrecifes Coralinos. La Paz B.C.S., Mexico.

Iglesias-Prieto R. Lessons from the Yucatán and what the future might bring if we don't act now. Future Leaders Forum, Brisbane, Australia.

Iglesias-Prieto R. The photobiology of coral bleaching. Dutch Coral Research Symposium. Amsterdam, Netherlands.

Jupiter S, Marion G, Roff G*, Henderson M, Schrameyer V, Hoegh-Guldberg O*. Linkages between coral assemblages and coral-based proxies of terrestrial exposure along a cross-shelf gradient of the Great Barrier Reef. Annual Australian Coral Reef Society Conference, Fremantle, Western Australia.

LaJeunesse T. Coral Zooxanthellae as a model system for examining eukaryotic microbial evolution. Smithsonian Marine Station at Ft. Pierce, January 12.

McClanahan T. Status and Future of Indian Ocean Coral Reefs. Fifth Scientific Symposium of the Western Indian Ocean Marine Science Association WIOMSA, Durban, South Africa

McClanahan T*, Cinner JE, Maina J,. Graham NAJ, Daw TM, Stead SM, Wamukota A, Brown K, Ateweberhan M *, Venus V, Polunin NVC. Conservation action in a changing climate Society for Conservation Biology Meeting, Pt. Elizabeth, South Africa July 1-6.

Padilla-Gamino J. Sedimentation Effects on the Physiological status of P. rus in Moorea, French Polynesia. MCR LTER All Investigators Meeting. Santa Barbara, California, USA.

van Woesik R. Review of contemporary issues on coral reefs. Palau, Micronesia

Wild C. Cold water corals as engineers of their reef ecosystem. ESF Eurodiversity 1st programme conference, Paris, France.

Wild C. Corals shaping reefs in the deep. Dutch Coral Research Symposium, Amsterdam, Netherlands.

Wild C. The role of warm and cold water corals as ecosystem engineers. Talk within the interdisciplinary seminar of the LMU master program for Evolution, Ecology and Systematics (EES), Martinsried, Germany.

* Denotes BWG members, researches and/or students when external authors are also included.

2006

Ainsworth T, Hoegh-Guldberg O. Pathology and Microbial Ecology in Coral Disease and Bleaching. ACRS conference, Abstract, Mission Beach QLD, Australia.

Brown B, John Bythell*. Convenors: Stress responses in corals. International Society for Reef Studies, European Meeting, Bremen, Germany.

Bythell J*, Johnstone R*, Pantos O. Microbial mediation of coral reef responses to environmental stress. Society for Experimental Biology (SEB), Symposium on Climate Change Effects on Coral Reefs, University of Kent at Canterbury.

Bythell J*, Johnstone R*, Pantos O. Microbial mediation of coral reef responses to environmental stress. Workshop on coral bleaching and local indicators of climate change on coral reefs, UNESCO, Paris

Bythell J. Coral bleaching and disease: stress, pathogens, or a little of both? Department of Biology, Departmental Seminar series, University of Exeter, United Kingdom.

Fitt W. Thermal history of Caribbean reef corals. Society for Experimental Biology Annual Meeting, Canterbury, United Kingdom.

Gates R. Do corals possess the biological flexibility to survive global climate change?. International Symposium on Marine Environmental Research, Japan.

Gates R. The molecular biology of thermal stress in *Symbiodinium*. Society for Experimental Biology Annual Meeting, Canterbury, United Kingdom.

Hoegh-Guldberg O. Complexities of climate change for coral reefs: what are the key questions? ACRS conference, Abstract, Mission Beach QLD, Australia.

Hoegh-Guldberg O. The Great Barrier Reef – at risk? Plenary talk at the Davos leadership retreat, Hayman Island Resort, Australia August 26.

Hoegh-Guldberg O. Address to Rio Tinto Board on Coral Reefs and Climate Change, Rio Tinto, London. May 10.

Hoegh-Guldberg O. Chairman's Panel, leadership retreat on Coral Reefs, Orpheus Island, May 24.

Hoegh-Guldberg O. Climate Change and Coral Reefs: Time frames, growing risk and indecision, National University of Mexico, Mexico, December 11.

Hoegh-Guldberg O. Coral Reefs and climate change – prognosis? SEB Conference / Thermal Biology of Coral Reefs, University of Kent, Canterbury, April 5.

Hoegh-Guldberg O. Coral Reefs and Environmental Change: Workshop for Cook Islands Government, University of Queensland, CRTR GEF Program, September 11.

Hoegh-Guldberg O. Global ideas and networks: Opportunities and challenges in the international science arena. Plenary talk at INORMS Internationalization of Research Conferences, Brisbane Convention Centre, August 23.

Hoegh-Guldberg O. Global Warming and Coral Reefs: All over, except for the singing? University of Texas, Texas, November 21.

Hoegh-Guldberg O. Great Barrier Reef Research Foundation dinner, Dinner address to Board, Customs House, Brisbane, May 11.

Hoegh-Guldberg O. IOC-UNESCO Working Group on Coral Bleaching and Related Ecological Factors (Bleaching Working Group). Opening talk at UNESCO-IOC, Paris, April 10.

Hoegh-Guldberg O. Sustaining the Marine Environment, Pioneering a sustainable Queensland Talk Series, Queensland Museum, May 31.

Hoegh-Guldberg O. The Great Barrier Reef and Climate Change, UNESCO conference on climate change and World Heritage sites, UNESCO headquarters, Paris, March 15.

* Denotes BWG members, researches and/or students when external authors are also included.

Iglesias-Prieto R. Cambio climático global y blanqueamiento de coral. Simposio Cambio Climático Global y sus Consecuencias en la Península de Yucatán, Mérida Yucatán, Mexico.

Iglesias-Prieto R. Thermal stress mechanisms in corals. Society for Experimental Biology Annual Meeting, Canterbury, United Kingdom.

Iglesias-Prieto R. Arrecifes de coral y cambio climático global. Plenary 1st Congreso del Caribe: Naturaleza, Sociedad y Desarrollo. Cozumel QR, Mexico.

Kaniewska P, Sampayo E*, Anthony K, Hoegh-Guldberg O*. Exploring factors affecting within colony light attenuation at macro and micro scale in Stylophora pistillata. ACRS conference, Abstract, Mission Beach QLD, Australia.

LaJeunesse T. The evolution of coral-zooxanthellae symbioses under the influence of climate change. Congresso Mexicano de Arecifes de Coral. Cancun, Mexico March 28-30.

Lawton A, Hoegh-Guldberg O*. The effect of temperature on the photosynthetic and respiration rate of reef building corals. ACRS conference, Abstract, Mission Beach QLD, Australia.

Loya Y. Fish net pen mariculture and the coral reefs of Eilat: a sad story. Palau Coral reef workshop, Koror, Palau

Loya Y. The Coral Reefs of Eilat: Three decades of coral community structure studies. ARC Centre of Excellence - second scientific annual board meeting, Sydney, Australia

Loya Y. Net pen fish farming and coral reefs: An unhappy marriage. ISRS (International Society for Reef Studies) European Meeting, Bremen, Germany

Marion GS, Hoegh-Guldberg O*, McCulloch MT. Nitrogen isotopes (Ð15N) in coral skeleton: Assessing provenance in the Great Barrier Reef Lagoon. Geochimica et Cosmochimica Acta 70:13 (From the Goldschmidt International Geochemistry conference, Melbourne).

Marion GS, Hoegh-Guldberg O*, McCulloch MT, Jupiter SD. Coral Isotopic Records (Ð15N) of Unprecedented Land Use Stress in Great Barrier Reef Coastal Communities. Proceedings of the 2006 AGU Ocean Sciences Meeting, Honolulu, Hawaii.

Marion GS, Hoegh-Guldberg O*, McCulloch MT, Mucciarone DM, Dunbar RB. Isotopes (Ð15N) in coral skeleton: A proxy for historical Great Barrier Reef water quality. Annual Australian Coral Reef Society Conference, Mission Beach, QLD.

Marion, GS, Hoegh-Guldberg, O*, Jupiter SD, McCulloch MT. Coral isotopic records (Ð15N) of unprecedented land-use stress in Great Barrier Reef coastal communities. ACRS conference, Abstract.

McClanahan T*, Ateweberhan M *, Muhando C, Maina J, Mohammed SM. Effects of climate and seawater temperature variation on coral bleaching and mortality. International Society for Reef Studies, European Meeting, Bremen, Germany.

Schuttenberg H, Corrigan C, McLeod L, Marshall P, Setiasih N, Obura D *, Hoegh-Guldberg O*, Causey B, Drew M, Hansen L, Grimsditch G, West J, Skeat A, Eakin M, McCook L, Crawford M, Kramer P, Campbell S. Building resilience into coral reef management: Key findings & recommendations," In ICRAN and ICRI. 2007. Proceedings of the 3rd International Tropical Marine Ecosystems Management Symposium (ITMEMS3), Cozumel, Mexico October16-20.

van Woesik R. Data, sampling and experimental design for coral reef monitoring. Palau International Coral Reef Center, Palau, Micronesia.

van Woesik R. Response of coral populations to thermal stress. Seminar at the Intergovernmental Oceanographic Commission (IOC) head office in Paris, France.

van Woesik R. Response of coral reefs to thermal stress, Smithsonian Institute, Ft. Pierce, USA.

van Woesik R. Response of reef corals to thermal stress: toward a predictive ecology. Seminar at the University of Miami, Miami, USA.

* Denotes BWG members, researches and/or students when external authors are also included.

van Woesik R. The future of coral reefs, Department of Biological Sciences, Florida Institute of Technology, USA.

van Woesik R. The future of coral reefs. 2nd Annual Coral Reef Conservation and Management Conference, Miami, USA.

van Woesik R. Why we need to sample coral reefs. Environmental Protection Authority, Saipan.

Wild C. Overview on the GEF/Worldbank/IOC-UNESCO Coral Reef Targeted Research and Capacity Building for Management Project". Talk to UNESCO staff within the workshop Ecological and Socio-Economic Monitoring for Coral Reefs, Paris, France.

Wild C. Coral spawning stimulates microbial life in the reef. International Society for Reef Studies European Meeting, Bremen, Germany

Wild C. Corals as ecosystem engineers – ecological feedback scenarios after thermal stress and coral bleaching events. Society for Experimental Biology Annual Meeting, Canterbury, United Kingdom.

* Denotes BWG members, researches and/or students when external authors are also included.

2005

Bythell J*, Pantos O. Culture-independent analysis of microbial associates of coral disease. Estuarine Research Federation, Special session on Coral Diseases: An Increasing Threat to Coral Reefs Worldwide, Virginia, USA

Bythell J*, Pantos O. Experimental analysis of bacterial ecology of bleaching and disease. Integrated research on coral bleaching and disease theme, Understanding the Stress Responses of Reef Corals, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico.

Fitt W. Understanding the stress response of corals and *Symbiodinium* in a rapidly changing environment Coral Reef. Targeted Research Group on Coral Bleaching, Unidad Académica UNAM, Puerto Morelos, Mexico.

Gates R. Developing Tools for Assessing Land Based Pollution in Corals. Environmental Protection Agency, Honolulu, Hawaii

Gates R. Why do Corals Lose Their Symbionts in Response to Environmental Disturbances? California State University, Northridge, USA

Gates R. Why do Corals Lose Their Symbionts in Response to Environmental Disturbances? Department of Marine Science, University of Hawaii at Hilo, Hawaii

Hoegh-Guldberg O. Challenges for tourism in a warming world. Responding to coral bleaching and climate change. Australian Reef Tour operator's workshop, Cairns, Australia.

Hoegh-Guldberg O. Climate change and Australia's coral reefs. Participant in joint workshop on challenges for the Great Barrier Reef at the Davos leadership retreat, Hayman Island Resort, August.

Hoegh-Guldberg O. Climate change and coral reefs - the burning issues. Invited seminar, Weizmann Centre, Israel June 3.

Hoegh-Guldberg O. Coral reefs in 2050: Life in a warm acid sea. Plenary, Australian Ecological Society, Brisbane, Australia.

Hoegh-Guldberg O. Coral reefs in a warming, acidifying ocean. Invited seminar to Intergovernmental Panel on Climate Change, Canberra, Australia March 13.

Hoegh-Guldberg O. Coral-algal symbiosis in a changing environment. Invited Seminar, Interuniversity Underwater Institute, Eilat, Israel, June 3.

Iglesias-Prieto R. Coral bleaching in the Mesoamerican Barrier Reef. Tulum +8 Scientific Symposium, Cancún QR, México.

Iglesias-Prieto R, Enríquez S, Méndez E. Enhanced absorption of solar radiation by symbiotic dinoflagellates: the role of multiple scattering by coral skeletons. American Society of Limnology and Oceanography, Summer meeting, Santiago de Compostela, Spain.

Loya Y. The Coral Reefs of Eilat: Three decades of coral community structure studies. Ilanit Congress of the Federation of the Israel Societies for Experimental Biology (FISEB), Eilat, Israel.

Marion G, Jupiter S, Hoegh-Guldberg O*, McCulloch M. Mackay Whitsunday quality and coral-mangrove ecosystem linkages since European colonization. The Mackay Whitsunday Healthy Waterway Forum (MWNRM). Keynote Speaker, Sarina, Australia.

McClanahan T, Joshep Maina, R Moothien-Pillay, Andrew Baker. Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. Western Indian Ocean Marine Science Association, Biannual Meeting, Blue Bay, Mauritius.

van Woesik R. Coral spawning, monitoring and future research directions of Palau. Palau International Coral Reef Center, Palau.

* Denotes BWG members, researches and/or students when external authors are also included.

van Woesik R. Field methods for the coral reef targeted research and capacity building for management working groups (GEF-World Bank project): toward commonality and complementarity.' World Bank, Washington DC, USA.

van Woesik R. Mechanisms forcing coral population changes. National Institute of Marine Sciences, Zanzibar, Tanzania

van Woesik R. Thermal stress on coral reefs: toward a predictive ecology. Dauphin Island Research Station, University of Alabama, USA.

Wild C. IOC-UNESCO activities related to coral reefs. Summary report to Ocean Sciences Section/IOC advisory group, Paris, France.

* Denotes BWG members, researches and/or students when external authors are also included.

Co-financing

Activity associated with the Bleaching Working Group was extended through project funding attracted from a number of other sources. This funding contributed significantly to the proposed projects. The following outlines sources of co-financing research (in USD) which supported the Bleaching Working Group:

Photo: A. Zvuloni

Australian Research Council Grant (CE0561435) ARC Centre of Excellence -Innovative science for sustainable management of coral reef biodiversity-. Investigators: Prof Terence Patrick Hughes, Ove Hoegh-Guldberg and 32 other researchers ($1.9 million to O. Hoegh-Guldberg, 2005-2007; www.coralcoe.org.au).

Australian Research Council Grant (LP0562157) "New tools for managing ecosystem responses to climate change on the southern Great Barrier Reef." Principle Researcher: Ove Hoegh-Guldberg, Co-researchers: Kenneth Roald Nies Anthony, Andrew Bakun, Bradley Charles Congdon, Michael Julian Caley, Sophie Dove, Gene Carl Feldman, Malcolm Lewis Heron, Ronald Johnstone, Andrew K Krockenberger, Laurence John McCook, Alan E Strong, Paul Marshall. Partner: NOAA, GBRMPA ($1.3 million, 2005-2009).

Edwin W. Pauley Summer Program in Marine Biology. Pauley Foundation provided $117,000 to support workshop 12 "The Biology of Corals: Developing a Fundamental Understanding of the Coral Stress Response". June 2 to July 15, 2007. (See details at http://www.hawaii.edu/HIMB/Education/pauley2007. html).

Intergovernmental Oceanographic Commission (IOC) of UNESCO provided a total of $60,000 over the first three years of the project. This money assisted censuses meetings and also supported workshops 2 and 7.

Packard Foundation Grant "Managers tool package for assessing coral Reef community responses under environmental stress." Principle Researchers: Ken Anthony and Ove Hoegh-Guldberg. ($240,000; 2007-2009).

Smart State Research Facilities Funding For a Queensland Marine Science Centre; Hoegh-Guldberg secured this grant that led to funding to support CRTR project infrastructure at St Lucia ($2.55 million) and on Heron Island (0.5 million). 2005 ($3.0 million).

Israel Science Foundation (ISF) "An integrative approach of studying bacterial coral bleaching in the coral reef of Eilat". Principle Researchers: Yossi Loya and E. Rosenberg (US $ 220,000; 2003-2007).

Israel Science Foundation (ISF) "Etiology of Black Band Disease (BBD)" Principle Researchers: Yossi Loya and E. Rosenberg (US $ 220,000; 2007-2011).

Raynor Chair for Environmental Conservation Research (Y. Loya) supporting research of graduate students in Zanzibar (US $ 100,000; 2004-2009).

Natural Environment Research Council (UK) research grant to address impacts of bleaching on microbial ecology and disease susceptibility of reef corals, based at Heron Island CoE. Principal investigators: John Bythell, Ron Johnstone, Olga Pantos, Clare Lanyon, Tony O'Donnell ($666,846; 2008-10).

Natural Environment Research Council (UK) two PhD research studentships to investigate bacterial colonisation of coral surfaces at Heron Island CoE (Mike Sweet) and coral innate immunity (Caroline Palmer). Principal Investigator: John Bythell. ($184,000; 2008-10).

The Leverhulme Trust (UK) research grant to assess mucin gene expression and mucus dynamics of reef corals, based in Phuket, Thailand and Heron Island CoE. Principal Investigators: John Bythell, Barbara Brown, Jeff Pearson and Nick Morris. ($313,862, 2006-09).
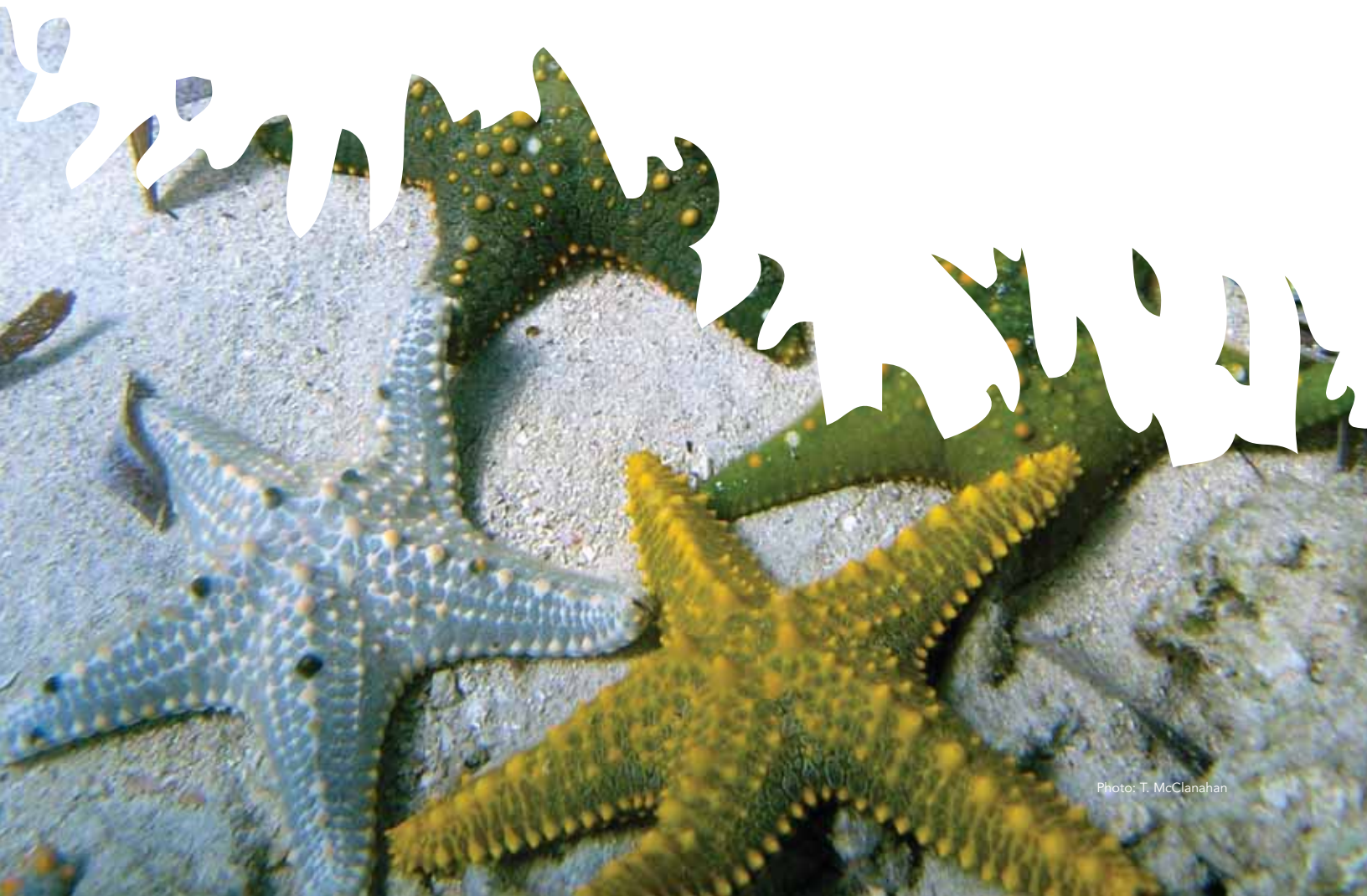
National Science Foundation (NSF) "Reef corals: symbiotic dinoflagellate/host combinations and their physiological response to environmental change". Principle Researchers: William Fitt and Schmidt (Plant Sciences). ($698,846; 2002-09).

National Science Foundation (NSF) Supplement to "Reef corals: symbiotic dinoflagellate/host combinations and their physiological response to environmental change". Principle Researchers: William Fitt and Schmidt (Plant Sciences) co-PI. ($5000; 2004).

German Research Foundation (Wi 2677/2-1a) "Element cycles in warm and cold water coral reefs – The function of organic coral exudates" Principle Researcher: Christian Wild; Co-researchers: Malik Naumann, Florian Mayer, Wolfgang Niggl, Carin Jantzen ($ 0.8 million; 2006-2010).

German Research Foundation (Wi 2677/2-1b) "Coral reefs in a time of change: Biogeochemical consequences of phase shifts" Principle Researcher: Christian Wild; Co-Researchers: Andreas Haas, Verena Witt, Christian Neukäufer ($ 0.4 million; 2007-2010).

References cited

Abele L, Patton W (1976) The size of coral heads and the community biology of associated decapod crustaceans. Journal of Biogeography:35-47

Abelson A, Shteinman B, Fine M, Kaganovsky B (1999) Mass transport from pollution sources to remote coral reefs in Eilat (Gulf of Aqaba, Red Sea). Marine Pollution Bulletin 38:25-29

Ainsworth TD, Hoegh-Guldberg O, Leggat W (2008a) Imaging the fluorescence of marine invertebrates and their associated flora. Journal of Microscopy 232:197-199

Ainsworth TD, Kramasky–Winter E, Loya Y, Hoegh-Guldberg O, Fine M (2007a) Coral disease diagnostics: What's between a plague and a band? Applied and Environmental Microbiology 73:981-992

Ainsworth TD, Kvennefors EC, Blackall LL, Fine M, Hoegh-Guldberg O (2007b) Disease and cell death in white syndrome of Acroporid corals on the Great Barrier Reef. Marine Biology 151:19-29

Ainsworth TD, Hoegh-Guldberg O, Heron SF, Skirving WJ, Leggat W (2008b) Early cellular changes are indicators of pre-bleaching thermal stress in the coral host. Journal of Experimental Marine Biology and Ecology 364:63-71

Allers E, Niesner C, Wild C, Pernthaler J (2008) Microbes enriched in seawater after the addition of coral mucus. Applied and Environmental Microbiology 74:3274-3278

Andréfouët S, Berkelmans R, Odriozola L, Done T, Oliver J, Müller-Karger F (2002) Choosing the appropriate spatial resolution for monitoring coral bleaching events using remote sensing. Coral Reefs 21:147-154

Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics and coral mortality risk: effects of temperature, light and sediment regime. Limnology and Oceanography 52:716-726

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. Proceedings of the National Academy of Sciences of the United States of America 105:17442-17446

Apprill AM, Gates RD (2007) Recognizing diversity in coral symbiotic dinoflagellate communities. Molecular Ecology 16:1127-1134

Aronson RB, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM (2002) The expanding scale of species turnover events in Belize. Ecological Monographs 72:233-249

Ateweberhan M, McClanahan T (in review-a) Linking biodiversity and climate change related impacts in coral reefs

Ateweberhan M, McClanahan T (in review-b) Relationship between historical seawater surface temperature variability and bleaching-induced coral mortality from climate change

Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54:1590-1605

Baker AC (2001a) Corals'adaptive response to climate change. Nature 411:765-766

Baker AC (2001b) Reef corals bleach to survive change. Nature 411:765-766

Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Coral reefs: corals' adaptive response to climate change. Nature 430:741

Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (ed) Coral Reefs, Ecosystems of the World. Elsevier, Amsterdam, pp109-131

Bastidas C, Bone D, García EM (1999) Sedimentation rates and metal content of sediments in a Venezuelan coral reef. Marine Pollution Bulletin 38:16-24

Berkelmans R (2002) Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. Marine ecology progress series 229:73-82

Berkelmans R, Willis B (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. Coral Reefs 18:219-228

Berkelmans R, Oliver J (1999) Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs 18:55-60

Berkelmans R, van Oppen, M. J. (2006) The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. Proc Biol Sci 273:2305-2312

Black R, Prince J (1983) Fauna associated with the coral Pocillopora damicornis at the southern limit of its distribution in Western Australia. Journal of Biogeography:135-152

Boersma PD, Parrish JK (1999) Limiting abuse: marine protected areas, a limited solution. Ecological Economics 31:287-304

Brown B, Howard L (1985) Assessing the effects of "stress" on reef corals. Adv Mar Biol 22:232

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:129-138

Brown BE, Bythell JC (2005) Perspectives on mucus secretion in reef corals. Marine Ecology Progress Series 296:291-309

Bruno JF, Selig ER (2007) Regional decline of coral cover in the indo-pacific: timing, extent, and subregional comparisons. PLoS ONE 2:e711

Bryant D (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington, DC

Bryant D, Burke L, McManus J, Spalding M (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington, DC

Buddemeier R, Fautin D (1993) Coral bleaching as an adaptive mechanism. BioScience 43:320-326

Bythell JC, Barer MR, Cooney RP, Guest JR, O'Donnell AG, Pantos O, Le Tissier MDA (2002) Histopathological methods for the investigation of microbial communities associated with disease lesions in reef corals. Letters in Applied Microbiology 34:359-364

Chabanet P (2002) Coral reef fish communities of Mayotte (western Indian Ocean) two years after the impact of the 1998 bleaching event. Marine and Freshwater Research 53:107-114

Chateau-Degat M, Chinain M, Cerf N, Gingras S, Hubert B, Dewailly É (2005) Seawater temperature, Gambierdiscus spp. variability and incidence of ciguatera poisoning in French Polynesia. Harmful Algae 4:1053-1062

Coles S, Jokiel P (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral Montipora verrucosa. Marine Biology 49:187-195

Coles S, Jokiel P, Lewis C (1976) Thermal tolerance in tropical versus subtropical Pacific reef corals. Pacific Science 30:159-166

Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. Marine Biology 43:209-216

Coles SL, Brown BE (2003) Coral bleaching--capacity for acclimatization and adaptation. Advances In Marine Biology 46:183-223

Darwin CR (1842) The structure and distribution of coral reefs. London: Smith Elder and Co

De'ath G, Lough JM, Fabricius KE (2009) Declining Coral Calcification on the Great Barrier Reef. Science 323:116-119

Done T (1999) Coral Community Adaptability to Environmental Change at the Scales of Regions, Reefs and Reef Zones 1. Integrative and Comparative Biology 39:66-79

Done T, Whetton P, Jones R, Berkelmans R, Lough J, Skirving W, Wooldridge S (2003) Global Climate Change and Coral Bleaching on the Great Barrier Reef. In: Department of Natural Resources QG (ed) Final Report to the State of Queensland Greenhouse Taskforce through the Department of Natural Resources and Mining,

Donner SD, Knutson TR, Oppenheimer M (2007) Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proc Natl Acad Sci U S A 104:5483-5488

Dove S, Ortiz JC, Enríquez S, Fine M, Fisher P, Iglesias-Prieto R, Thornhill D, Hoegh-Guldberg O (2006) Response of holosymbiont pigments from the scleractinian coral Montipora monasteriata to short-term heat stress. Limnology and Oceanography 51:1149-1158

Dove SG, Hoegh-Guldberg O, Ranganathan S (2001) Major colour patterns of reef-building corals are due to a family of GFP-like proteins19:197-204

Dove SG, Lovell C, Fine M, Deckenback J, Hoegh-Guldberg O, Iglesias-Prieto R, Anthony KRN (2008) Host pigments: potential facilitators of photosynthesis in coral symbioses. Plant Cell and Environment 31:1523-1533

Drew E (1972) The biology and physiology of algal invertebrate symbiosis. II. The density of algal cells in a number of hermatypic hard corals and alcyonarians from various depths. J exp mar Biol Ecol 9:71-75

Dunn SR, Thomason JC, Le Tissier MD, Bythell JC (2004) Heat stress induces different forms of cell death in sea anemones and their endosymbiotic algae depending on temperature and duration. Nature - Cell Death & Differentiation 11:1213-1222

Dustan P, Dobson E, Nelson G (2001) Landsat Thematic Mapper: Detection of Shifts in Community Composition of Coral Reefs. Conservation Biology 15:892-902

Edinger E, Limmon G, Jompa J, Widjatmoko W, Heikoop J, Risk M (2000) Normal Coral Growth Rates on Dying Reefs: Are Coral Growth Rates Good Indicators of Reef Health? Marine Pollution Bulletin 40:404-425

Edinger EN, Azmy K, Diegor W, Siregar PR (2008) Heavy metal contamination from gold mining recorded in Porites lobata skeletons, Buyat-Ratototok district, North Sulawesi, Indonesia. Mar Pollut Bull 56:1553-1569

Edmunds PJ (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of. Marine Biology 121:137-142

Egana AC, DiSalvo LH (1982) Mass expulsion of zooxanthellae by Easter Island corals. Pacific Science 36:61-63

Enriquez S, Mendez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnology and Oceanography. 2005; 50 (4): 1025-1032

Enríquez S, Méndez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnology and Oceanography 50:1025-1032

Fagoonee II, Wilson HB, Hassell MP, Turner JR (1999) The dynamics of zooxanthellae populations: A long-term study in the field. Science 5403:843-845

Fitt W, Brown B, Warner M, Dunne R (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20:51-65

Fitt WK, Warner ME (1995) Bleaching patterns of four species of Caribbean reef corals. The Biological Bulletin 189:298-307

Fitt WK, K. MF, E. WM, C. CG (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals. Limnology and Oceanography 45:677-685

Fitt WK, Kemp DW, Hernadez-Pech X, Iglesias-Prieto R, Thornhill DJ, Bruns BU, Schmidt GW (in press) Bleaching, El Niño, and la Niña: 13 years of seasonal analysis of reef-building corals in Florida, the Bahamas, and the Caribbean 11th International Coral Reef Symposium, Ft Lauderdale, USA

Fitt WK, Gates RD, Hoegh-Guldberg O, Bythell JC, Jatkar A, Grottoli AG, Gomez M, Fisher P, Lajuenesse TC, Pantos O (2009) Response of two species of Indo-Pacific corals, Porites cylindrica and Stylophora pistillata, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. Journal of Experimental Marine Biology and Ecology 373:102-110

Franklin DJ, Cedrés CMM, Hoegh-Guldberg O (2006) Increased mortality and photoinhibition in the symbiotic dinoflagellates of the Indo–Pacific coral Stylophora pistillata (Esper) after summer bleaching. Marine Biology 149:633-642

Freudenthal HD (1962) *Symbiodinium* gen. nov. and *Symbiodinium* microadriaticum sp. nov., a Zooxanthella: Taxonomy, Life Cycle, and Morphology. Journal of Eukaryotic Microbiology 9:45-52

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958-960

Gattuso J, Frankignoulle M, Wollast R (1998) Carbon and carbonate metabolism in coastal aquatic ecosystems. Annual Review of Ecology and Systematics 29:405-434

Gleason D, Wellington G (1993) Ultraviolet radiation and coral bleaching. Nature 365:836-838

Glynn P (1993) Coral reef bleaching: ecological perspectives. Coral Reefs 12:1-17

Glynn PW (1988) El niño warming coral mortality and reef framework destruction by echinoid bioerosion in the eastern pacific. Galaxea 7:129-160

Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. Trends In Ecology & Evolution 6:175-179

Glynn PW, D'Croz L (1990) Experimental-evidence for high-temperature stress as the cause of el-nino-coincident coral mortality. Coral Reefs 8:181-191

Glynn PW, Mat, L. J, Baker AC, Calder, n MO (2001) Coral bleaching and mortality in panama and ecuador during the 1997 1998 El Nino Southern Oscillation Event: spatial/temporal patterns and comparisons with the 19821983 event. Bulletin of Marine Science 69:79-109

Goreau T, Macfarlane A (1990) Reduced growth rate of Montastrea annularis following the 1987–1988 coral-bleaching event. Coral Reefs 8:211-215

Goreau T, McClanahan T, Hayes R, Strong A (2000) Conservation of coral reefs after the 1998 global bleaching event. Conservation Biology 14:5

Goreau TF (1964) Mass expulsion of zooxanthellae from Jamaican reef communities after hurricane Flora. Science 145:383-386

Goulet T, Coffroth M (2003) Genetic composition of zooxanthellae between and within colonies of the octocoral Plexaura kuna, based on small subunit rDNA and multilocus DNA fingerprinting. Marine Biology 142:233-239

Goulet TL (2006) Most corals may not change their symbionts. Marine Ecology Progress Series 327:1-7

Goulet TL (2007) Most scleractinian corals and octocorals host a single symbiotic zooxanthella clade. Marine Ecology Progress Series 335:243–248

Goulet TL, LaJeunesse TC, Fabricius KE (2008) Symbiont specificity and bleaching susceptibility among soft corals in the 1998 Great Barrier Reef mass coral bleaching event

Graham NA, McClanahan TR, MacNeil MA, Wilson SK, Polunin NV, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y, Bigot L, Galzin R, Ohman MC, Garpe KC, Edwards AJ, Sheppard CR (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS ONE 3:e3039

Grimsditch G, Awaura J, Kilonzo J, Amiyo N, Obura D (2008a) Zooxanthellae densities are highest in summer months in equatorial corals in Kenya. In: Obura D, Tamelander J, Linden O (eds) Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO status report 2008. CORDIO/Sida-SAREC, Mombasa, pp237-239

Grimsditch G, Awaura J, Kilonzo J, Amiyo N, Obura D (2008b) High zooxanthellae densities and turnover correlate with low bleaching tolerance in Kenyan corals. In: Obura D, Tamelander J, Linden O (eds) Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO status report 2008. CORDIO/Sida-SAREC, Mombasa, pp235-236

Guppy R, Bythell JC (2006) Environmental effects on bacterial diversity in the surface mucus layer of the reef coral Montastraea faveolata. Marine Ecology Progress Series 328:133-142

Guzman H, Holst I (1993) Effects of chronic oil-sediment pollution on the reproduction of the Caribbean reef coral Siderastrea siderea. Marine Pollution Bulletin 26:276-282

Harborne AR, Afzal DC, Andrews MJ (2001) Honduras: Caribbean Coast. Marine Pollution Bulletin 42:1221-1235

Harrison P, Wallace C (1990) Reproduction, dispersal and recruitment of scleractinian corals. Ecosystems of the world 25:133–207

Harrison P, Ward S (2001) Elevated levels of nitrogen and phosphorus reduce fertilisation success of gametes from scleractinian reef corals. Marine Biology 139:1057-1068

Harrison P, Babcock R, Bull G, Oliver J, Wallace C, Willis B (1984) Mass spawning in tropical reef corals. Science 223:1186-1189

Hatcher BG (1988) Coral reef primary productivity: A beggar's banquet. Trends in Ecology and Evolution 3:106-111

Hatcher BG (1990) Coral reef primary productivity: a hierarchy of pattern and process. Trends in Ecology and Evolution 5:149-155

Hatcher BG (1997) Coral reef ecosystems: how much greater is the whole than the sum of the parts? Coral Reefs 16:S77-S91

Hedley JD, Mumby PJ (2003) A remote sensing method for resolving depth and subpixel composition of aquatic benthos. Limnology and Oceanography 48:480-488

Hoegh-Guldberg H, Hoegh-Guldberg O (2004) Great Barrier Reef 2050: implications of climate change for Australia's Great Barrier Reef., Brisbane, Queensland 345

Hoegh-Guldberg O (1999a) Climate change, coral bleaching and the future of the world's coral reefs. Marine & Freshwater Research 50:839-866

Hoegh-Guldberg O (1999b) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839-866

Hoegh-Guldberg O (2000) Global climate change and the tolerance of corals to changes in sea temperature: Implications for reefs in the 21st Century. Proceedings of the JAMSTEC International Coral Reef Symposium. February 23-24: 197-214.

Hoegh-Guldberg O (2002a) The future of coral reefs: Integrating climate model projections and the recent behaviour of corals. Proceedings of the Ninth International Coral Reef Symposium, Bali 2:1105-1110

Hoegh-Guldberg O (2004) Coral reefs and projections of future change. Coral Health and Disease:463-484

Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals Stylophora pistillata and Seriatopra hystrix. Journal of Experimental Marine Biology and Ecology 129:279-303

Hoegh-Guldberg O, McCloskey L, Muscatine L (1987) Expulsion of zooxanthellae by symbiotic cnidarians from the Red Sea. Coral Reefs 5:201-204

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007a) Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007b) Coral reefs under rapid climate change and ocean acidification. Science 2007 Dec 14;318(5857):1737-42

Hoegh-Guldberg O, Hoegh-Guldberg H, Veron JEN, Green A, Gomez ED, Lough J, King M, Ambariyanto, Hansen L, Cinner J, Dews G, Russ G, Schuttenberg HZ, Peñaflor EL, Eakin CM, Christensen TRL, Abbey M, Areki F, Kosaka RA, Tewfik A, Oliver JK (2009) The Coral Triangle and Climate Change: Ecosystems, People and Societies at Risk. WWF Australia, Brisbane, 276 pp. Full report is available at: www.panda.org/coraltriangle

Hoegh-Guldberg O, Jones R. J., Ward S. Loh W. L. (2002b) Is coral bleaching really adaptive? Nature (London) 415:601-602

Holmes G (2008) Estimating three-dimensional surface areas on coral reefs. Journal of Experimental Marine Biology and Ecology 365:67-73

Holmes G, Ortiz JC, Kaniewska P, Johnstone R (2008) Using three-dimensional surface area to compare the growth of two Pocilloporid coral species. Marine Biology 155:421-427

Huettel M, Wild C, Gonelli S (2006) The mucus trap in coral reefs: formation and temporal evolution of aggregates caused by coral mucus. Marine Ecology Progress Series 307:69-84

Hughes T, Baird A, Dinsdale E, Moltschaniwskyj N, Pratchett M, Tanner J, Willis B (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81:2241-2249

Hughes TP (1994) Catastrophes, Phase Shifts, and a Large-Scale Degradation of Caribbean Coral Reef. Science 265:1547-1551

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 2007 Feb 20;17(4):360-5 Epub 2007 Feb 8

Iglesias-Prieto R, Matta JL, Robins WA, Trench RK (1992 -a) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate Symbiodinium microadriaticum in culture. Proceedings of the National Academy of Sciences of the United States of America 89:10302-10305

Iglesias-Prieto R, Matta JL, Robins WA, Trench RK (1992 -b) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate Symbiodinium microadriaticum in culture. Proc Natl Acad Sci U S A 89:10302-10305

Iglesias-Prieto R, Beltran VH, LaJeunesse TC, Reyes-Bonilla H, Thome PE (2004) Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. Proc Biol Sci 271:1757-1763

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001a) Historical overfishing and the recent collapse of coastal ecosystems. Science 2001 Jul 27;293(5530):629-37

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001b) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637.

Johnson C, Dunstan P, Hoegh-Guldberg O (2002) Predicting the long term effects of coral bleaching and climate change on the structure of coral communities. World Bank-UNESCO Targeted Working Group on modeling climate change, Miami Florida, USA

Jones R, Hoegh-Guldberg O, Larkum A, Schreiber U (1998) Temperature induced bleaching of corals begins with impairment to the carbon dioxide fixation mechanism of zooxanthellae. Plant, Cell and Environment 21:1219-1230

Jones R, Ward S, Amri A, Hoegh-Guldberg O (2000) Changes in quantum efficiency of Photosystem II of symbiotic dinoflagellates of corals after heat stress, and of bleached corals sampled after the 1998 Great Barrier Reef mass bleaching event. Marine and Freshwater Research 51:63-72

Jones RJ (1997a) Changes in zooxanthellar densities and chlorophyll concentrations in corals during and after a. Marine Ecology Progress Series 158:51-59

Jones RJ (1997b) Zooxanthellae loss as a bioassay for assessing stress in corals. Marine Ecology Progress Series 149:163-171

Jones RJ, Hoegh-Guldberg O (1999) Effects of cyanide on coral photosynthesis: implications for identifying the cause of coral bleaching and for assessing the environmental impacts of cyanide fishing. Marine Ecology Progress Series 177:83-91

Jones RJ, Hoegh-Guldberg O (2001) Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: photoprotection, photoinactivation and the relationship to coral bleaching. Planet, Cell and Environment 24:89-99

Kleypas JA, Langdon C (2006) Coral reefs and changing seawater chemistry, Chapter 5 In: Phinney J, Hoegh-Guldberg O, Kleypas J, Skirving W, Strong AE (eds) Coral Reefs and Climate Change: Science and Management AGU Monograph Series, Coastal and Estuarine Studies. Geophys. Union, Washington DC, pp73-110

Kleypas JA, McManus JW, Menez LAB (1999a) Environmental Limits to Coral Reef Development: Where Do We Draw the Line? American Zoologist 39:146-159

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999b) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284:118-120

Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish Oxymonacanthas longirostris (Monacanthidae) to a mass coral bleaching event. Coral Reefs 20:155-158

Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison W, Erdmann M, Harrison P, Hoegh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, O'Neil J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D (2001) ENCORE: The Effect of Nutrient Enrichment on Coral Reefs. Synthesis of Results and Conclusions. Marine Pollution Bulletin 42:91-120

Kushmaro A, Banin E, Loya Y, Stackebrandt E, Rosenberg E (2001) Vibrio shiloi sp. nov., the causative agent of bleaching of the coral Oculina patagonica. International journal of systematic and evolutionary microbiology 51:1383-1388

Laforsch C, Christoph E, Glaser C, Naumann M, Wild C, Niggl W (2008) A precise and non-destructive method to calculate the surface area of living scleractinian corals using X-ray computed tomography and 3D modeling. Coral Reefs 27:811-820

LaJeunesse TC (2005a) "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the miocene-pliocene transition. Molecular Biology and Evolution 22:570-581

Lajeunesse TC (2005b) "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. Mol Biol Evol 2005 Mar;22(3):570-81 Epub 2004 Nov 10

LaJeunesse TC, Loh WKW, van Woesik R, Hoegh-Guldberg O, Schmidt GW, Fitt WK (2003) Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. Limnology and Oceanography 48:2046-2054

LaJeunesse TC, Bonilla HR, Warner ME, Wills M, Schmidt GW, Fitt WK (2008) Specificity and stability in high latitude eastern Pacific coral-algal symbioses

LaJeunesse TCBHRWMEWMSGWFWK (2008) Specificity and stability in high latitude eastern Pacific coral-algal symbioses. Limnol Oceanogr 53:719-727

LaJeunesse TCLSBSBJF (2005c) Persistence of non-Caribbean algal symbionts in Indo-Pacific mushroom corals released to Jamaica 35 years ago. Coral Reefs 24:157-159

Langdon C, Atkinson M (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. Journal of Geophysical Research-Oceans 110:C09S07

Leclercq N, Gattuso J, Jaubert J (2002) Primary production, respiration, and calcification of a coral reef mesocosm under increased CO_2 partial pressure. Limnology and Oceanography:558-564

Leggat W, Ainsworth TD, Dove S, Hoegh-Guldberg O (2006) Aerial exposure influences bleaching patterns. Coral Reefs 25:452-452

Leggat W, Hoegh-Guldberg O, Dove S, Yellowlees D (2007a) Analysis of an EST library from the dinoflagellate (*Symbiodinium* sp.) symbiont of reef-building corals. Journal of Phycology 43:1010-1021

Leggat W, Ainsworth TD, Bythell JC, Dove S, Gates RD, Hoegh-Guldberg O, Iglesias-Prieto R, Yellowlees D (2007b) The hologenome theory disregards the coral holobiont. Nature Reviews Microbiology 5

Lehane L, Lewis R (2000) Ciguatera: recent advances but the risk remains. International journal of food microbiology 61:91-125

Lesser M, Stochaj W, Tapley D, Shick J (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs 8:225-232

Lesser MP (2006) Oxidative stress in marine environments: biochemistry and physiological ecology. Annual Review Physiology 68:253-278

Lesser MP, Bythell JC, Gates RD, Johnstone RW, Hoegh-Guldberg O (2007a) Are infectious diseases really killing corals? Alternative interpretations of the experimental and ecological data. Journal of Experimental Marine Biology and Ecology 346:36-44

Lesser MP, Falcón LI, Rodríguez-Román A, Enríquez S, Hoegh-Guldberg O, Iglesias-Prieto R (2007b) Nitrogen fixation by symbiotic cyanobacteria provides a source of nitrogen for the scleractinian coral Montastraea cavernosa. Marine Ecology Progress Series 346:143-152

Lindahl U, Öhman M, Schelten C (2001) The 1997/1998 mass mortality of corals: effects on fish communities on a Tanzanian coral reef. Marine Pollution Bulletin 42:127-131

Lipp E, Carrie Futch J, Griffin D (2007) Analysis of multiple enteric viral targets as sewage markers in coral reefs. Marine Pollution Bulletin 54:1897-1902

Little AF, van Oppen MJ, Willis BL (2004) Flexibility in algal endosymbioses shapes growth in reef corals. Science 304:1492-1494

Livett B, Gayler K, Khalil Z (2004) Drugs from the sea: conopeptides as potential therapeutics. Current medicinal chemistry 11:1715-1724

Loh WKW, Loi T, Carter D, Hoegh-Guldberg O (2001) Genetic variability of the symbiotic dinoflagellates from the wide ranging coral species Seriatopora hystrix and Acropora longicyathus in the Indo-West Pacific

Lough JM (2000) 1997-98: Unprecedented thermal stress to coral reefs? Geophysical Research Letters, 27:3901-3904

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecology Letters 4:122-131

Maina J, Venus V, McClanahan TR, Ateweberhan M (2008) Modelling susceptibility of coral reefs to environmental stress using remote sensing data and GIS models. Ecological Modelling 212:180-199

Maragos J, Crosby M, McManus J (1996) Coral reefs and biodiversity: a critical and threatened relationship. Oceanography-Washington DC Oceanography Society 9:83-99

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155-163

Marubini F, Barnett H, Langdon C, Atkinson M (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral Porites compressa. Marine Ecology Progress Series 220:153-162

McClanahan T, Cinner J (2008) A framework for adaptive gear and ecosystem-based management in the artisanal coral reef fishery of Papua New Guinea. Aquatic Conservation: Marine and Freshwater Ecosystems 18

McClanahan T, Muthiga N, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. Coral Reefs 19:380-391

McClanahan T, Ateweberhan M, Omukoto J (2008a) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. Marine Biology 153:755-768

McClanahan T, Muthiga N, Maina J, Kamukuru A, Yahya S (2009) Changes in northern Tanzania coral reefs during a period of increased fisheries management and climatic disturbance. Aquatic Conservation: Marine and Freshwater Ecosystems

McClanahan T, Cinner J, Maina J, Graham N, Daw T, Stead S, Wamukota A, Brown K, Ateweberhan M, Venus V (2008b) Conservation action in a changing climate. Conservation Letters 1:53-59

McClanahan TR (2008) Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. Oecologia 155:169-177

McClanahan TR, Hicks CC, Darling ES (2008c) Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecol Appl 18:1516-1529

McClanahan TR, Muthiga NA, Kamukuru AT, Machano H, Kiambo RW (1999) The effects of marine parks and fishing on coral reefs of northern Tanzania. Biological Conservation 89:161-182

McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007a) Effects of climate and seawater temperature variation on coral bleaching and mortality. Ecological Monographs 77:503-525

McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MMM, Bruggemann JH (2007b) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Marine Ecology Progress Series 337:1-13

McClanahanan TR, Mwaguni S, Muthiga N (2002) Management of the Kenyan coast. Ocean & Coastal Management 48:901-931

McManus JW (1997) Effects of Some Destructive Fishing Methods on Coral Cover and Potential Rates of Recovery. Environmental Management 21:69-78

Meesters E, Bak R (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. Marine Ecology-Progress Series 96:189-189

Michalek-Wagner K, Willis B (2001) Impacts of bleaching on the soft coral Lobophytum compactum. I. Fecundity, fertilization and offspring viability. Coral Reefs 19:231-239

Miller I, Müller R (1999) Validity and reproducibility of benthic cover estimates made during broadscale surveys of coral reefs by manta tow. Coral Reefs 18:353-356

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecological Economics 29:215-233

Muller EM, Rogers CS, Spitzack AS, van Woesik R (2008) Bleaching increases likelihood of disease on Acropora palmata (Lamarck) at Hawksnest Bay, St. John, US Virgin Islands. Coral Reefs 27:191-195

Mumby P, Edwards A, Arias-Gonzalez J, Lindeman K, Blackwell P, Gall A, Gorczynska M, Harborne A, Pescod C, Renken H (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature (London) 427:533-536

Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jaubert J (2001) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Marine Ecology Progress Series 222:209-216

Munday P (2004) Habitat loss, resource specialization, and extinction on coral reefs. Global Change Biology 10:1642-1647

Munday P, Jones G, Sheaves M, Williams A, Goby G (2007) Vulnerability of fishes of the Great Barrier Reef to climate change. Climate Change and the Great Barrier Reef:357–391

Muscatine L (1967) Glycerol Excretion by Symbiotic Algae from Corals and Tridacna and Its Control by the Host. Science 156:516-519

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. . In: Dubinsky Z (ed) Ecosystems of the world. Elsevier, Amsterdam, pp75-87

Muscatine L, Porter J (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. BioScience 27:454-460

Nakamura T, van Woesik R, Yamasaki H (2005) Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral Acropora digitifera. Marine Ecology Progress Series 301:109-118

Naumann M, Niggl W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification – evaluation of established methods by comparison with computer tomography. Coral Reefs 28:109-117

Odum H, Odum E (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecological Monographs:291-320

Palmer CV, Roth MS, Gates RD (2009) Red fluorescent protein responsible for pigmentation in trematode-Infected Porites compressa tissues. The Biological Bulletin 216:68-74

Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP (2005) ECOLOGY: Enhanced: Are US Coral Reefs on the Slippery Slope to Slime? Science 307:1725-1726

Pantos O, Bythell JC (2006) Bacterial community structure associated with white band disease in the elkhorn coral Acropora palmata determined using culture-independent 16S rRNA techniques. Diseases of aquatic organisms 69:79-88

Pantos O, Cooney RP, Le Tissier MDA, Barer MR, O'Donnell AG, Bythell JC (2003) The bacterial ecology of a plague-like disease affecting the Caribbean coral Montastrea annularis. Environmental Microbiology 5:370

Papina M, Meziane T, van Woesik R (2007) Acclimation effect on fatty acids of the coral Montipora digitata and its symbiotic algae. Comparative Biochemistry and Physiology B 147:583-589

Pomerance R, United States Coral Reef Task Force., United States. Dept. of State. Bureau of Oceans and International Environmental and Scientific Affairs. (1999) Coral bleaching, coral mortality, and global climate change report. U.S. Dept. of State, [Washington, D.C. 15 p.

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinnerm JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral reef fishes - Ecological and economic consequences. Oceanography And Marine Biology: An Annual Review 46:251-296

Reaka-Kudla ML (1997) Global biodiversity of coral reefs: a comparison with rainforests. In: Reaka-Kudla ML, Wilson DE (eds) Biodiversity II: Understanding and Protecting Our Biological Resources. Joseph Henry Press, pp551

Reynaud S, Leclercq N, Romaine-Lioud S, Ferrier-Pages C, Jaubert J, Gattuso J (2003) Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. Global Change Biology 9:1660-1668

Rodríguez-Román A, Hernández-Pech X, Thomé PE, Enríquez S, Iglesias-Prieto R (2006) Photosynthesis and light utilization in the Caribbean coral Montastraea faveolata recovering from a bleaching event. Limnology and Oceanography 51:2702-2710

Rowan R (2004) Coral bleaching: thermal adaptation in reef coral symbionts. Nature 430:742

Rowan R, Powers DA (1992) Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). Proceedings of the National Academy of Sciences 89:3639-3643

Rowan R, Whitney S, Fowler A, Yellowlees D (1996) Rubisco in marine symbiotic dinoflagellates: form II enzymes in eukaryotic oxygenic phototrophs encoded by a nuclear multigene family. The Plant Cell Online 8:539-553

Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388:265-269

Sampayo EM, Franceschinis L, Hoegh-Guldberg O, Dove S (2007) Niche partitioning of closely related symbiotic dinoflagellates (vol 16, pg 3721, 2007). Molecular Ecology 16:4648-4648

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc Natl Acad Sci U S A 105:10444-10449

Schoenberg DA, Trench RK (1980a) Genetic-variation in symbiodinium (=gymnodinium) microadriaticum freudenthal, and specificity in its symbiosis with marine-invertebrates .2. morphological variation in *Symbiodinium* microadriaticum. Proceeding of the Royal Society of London B 207:429-&

Schoenberg DA, Trench RK (1980b) Genetic-variation in symbiodinium (=gymnodinium) microadriaticum freudenthal, and specificity in its symbiosis with marine-invertebrates .3. specificity and infectivity of *Symbiodinium* microadriaticum. Proceeding of the Royal Society of London B 207:445-&

Schoenberg DA, Trench RK (1980c) Genetic-variation in symbiodinium (=gymnodinium) microadriaticum freudenthal, and specificity in its symbiosis with marine-invertebrates .1. isoenzyme and soluble-protein patterns of axenic cultures of *Symbiodinium* microadriaticum. Proceeding of the Royal Society of London B 207:405-427

Schöttner S, Hoffmann F, Wild C, Rapp HT, Boetius A, Ramette A (in press) Inter- and intra- habitat bacterial diversity associated with cold water corals. The ISME Journal

Schuttenberg H, Hoegh-Guldberg O (2007) A world with corals: what will it take? Science 318:42

Shenkar N, Fine M, Kramarsky-Winter E, Loya Y (2006) Population dynamics of zooxanthellae during a bacterial bleaching event. Coral Reefs 25:223-227

Siebeck U, Marshall N, Klüter A, Hoegh-Guldberg O (2006a) Monitoring coral bleaching using a colour reference card. Coral Reefs 25:453-460

Siebeck UE, Marshall NJ, Kluter A, Hoegh-Guldberg O (2006b) Monitoring coral bleaching using a colour reference card. Coral Reefs 25:453-460

Spalding M, Ravilious C, Green E (2001) World Atlas of Coral Reefs. University of California Press

Spalding MD, Jarvis GE (2002) The impact of the 1998 coral mortality on reef fish communities in the Seychelles. Mar Pollut Bull 2002 Apr;44(4):309-21

Spencer T, Teleki KA, Bradshaw C, Spalding MD (2000) Coral Bleaching in the Southern Seychelles During the 19971998 Indian Ocean Warm Event. Marine Pollution Bulletin 40:569-586

Stat M, Morris E, Gates RD (2008) Functional diversity in coral-dinoflagellate symbiosis. Proc Natl Acad Sci U S A 105:9256-9261

Stimson J, Sakai K, Sembali H (2002) Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs 21:409-421

Strong A, Arzayus F, Skirving W, Heron S (2006a) Identifying coral bleaching remotely via Coral Reef Watch—improved integration and implications for changing climate JT Phinney, et al [Eds], Coral Reefs and Climate Change: Science and Management Coastal and Estuarine Studies, Vol 61, American Geophysical Union, Washington, DC 163-180 pp,

Strong AE, Barrientos CS, Duda C, Sapper J (1996a) Improved satellite technique for monitoring coral reef bleaching. Proceedings of the eighth international coral reef symposium, Panama:1495-1497

Strong AE, Barrientos CS, Duda C, Sapper J (1996b) Improved satellite technique for monitoring coral reef bleaching. Proceedings of the eighth international coral reef symposium, Panama, June:1495-1497

Strong AE, Arzayus F, Skirving WJ, Heron SF (2006b) Identifying coral bleaching remotely via Coral Reef Watch—improved integration and implications for changing climate. In: Phinney JT, al. e (eds) Coral Reefs and Climate Change: Science and Management Coastal and Estuarine Studies. American Geophysical Union, Washington, DC, pp163-180

Szmant AM, Gassman NJ (1990) The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral Montastrea annularis. Coral Reefs 8:217-224

Tanzil J, Brown B, Tudhope A, Dunne R (2009) Decline in skeletal growth of the coral Porites lutea from the Andaman Sea, South Thailand between 1984 and 2005. Coral Reefs 28

Taylor DL (1974) Symbiotic marine algae: taxonomy and biological fitness. Pp. 245-262 in Symbiosis in the Sea , W. B. Vernberg, ed. University of South Carolina Press, Columbia, SC.

Thompson DM, van Woesik R (2009a) Past sea-surface temperature variability influences contemporary coral-bleaching severity. Proceedings of The Royal Society B

Thompson DM, van Woesik R (2009b) Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. Proceedings of The Royal Society B 10.1098/rspb.2009.0591

Tomascik T, Sander F (1987) Effects of eutrophication on reef-building corals. III: Reproduction of the reef-building coral Porites porites. Marine Biology 94:77-94

Trench RK (1979) Cell biology of plant-animal symbiosis. Annu Rev Plant Physiol Plant Molec Biol 30:485-531

van Oppen MJ, Gates RD (2006) Understanding the resilience of reef corals: the roles of molecular biology and genetics. Molecular Ecology 15:3863-3883

Vaughan TW (1914) Reef corals of the Bahamas and of southern Florida. Carnegie Institution of Washington:Year Book for 1914:1222 -1226.

Wallace R (1997) Drugs from the sea: harvesting the results of aeons of chemical evolution. Molecular Medicine Today 3:291-295

Ward S (1995) The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral Pocillopora damicornis (Linnaeus). Journal of Experimental Marine Biology and Ecology 187:193-206

Ward S, Harrison P, Hoegh-Guldberg O (2002) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future. Proceedings of the Ninth International Coral Reef Symposium 2:1123-1128

Ware JR, Fautin D. G., Buddemeier R. W. (1996) Patterns of coral bleaching: Modeling the adaptive bleaching hypothesis84:199-214

Warner ME, Fitt WK, Schmidt GW (1996) The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: A novel approach. Plant Cell Environment 19:291-299

Weis VM, Reynolds WS, deBoer MD, Krupp DA (2001) Host-symbiont specificity during onset of symbiosis between the dinoflagellates Symbiodinium spp. and planula larvae of the scleractinian coral Fungia scutaria

White AT, Vogt HP, Tijen A (2000) Philippine Coral Reefs Under Threat: The Economic Losses Caused by Reef Destruction. Marine Pollution Bulletin 40:598-605

Wild C, Tollrian R, Huettel M (2004a) Rapid recycling of coral mass spawning products in permeable reef sediments. Marine Ecology Progress Series 271:159-166

Wild C, Røy H, Huettel M (2005) Role of pelletization for mineralization in fine-grained coastal sediments. Marine Ecology Progress Series 291:23-33

Wild C, Laforsch C, Huettel M (2006) Detection and enumeration of microbial cells in highly porous calcareous reef sands. Marine & Freshwater Research 57:415-420

Wild C, Jantzen C, Struck U, Hoegh-Guldberg O, Huettel M (2008) Biogeochemical responses on coral mass spawning at the Great Barrier Reef: Pelagic-benthic coupling. Coral Reefs 27:123-132

Wild C, Haas A, Naumann M, Mayr C, el-Zibdah M (in press) Comparative investigation of organic matter release by corals and benthic reef algae – implications for pelagic and benthic microbial metabolism. 11th International Coral Reef Symposium

Wild C, Rasheed M, Werner U, Franke U, Johnstone R, M. H (2004b) Degradation and mineralization of coral mucus in reef environments. Marine Ecology Progress Series 267:159-171

Wild C, Huettel M, Klueter A, Kremb SG, Rasheed M, Jørgensen BB (2004c) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428:66-70

Wilkinson C (2008) Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, Townsville, Australia 296pp

Wilkinson C, Hodgson G (1999) Coral reefs and the 1997-1998 mass bleaching and mortality. Nat Resour 35:16-25

Wilkinson C, Lindén O, Hodgson H, Cesar J, Rubens J, Strong A (1999) Ecological and socio-economic impacts of 1998 coral mortality in the Indian Ocean: an ENSO (El Niño/Southern Oscillation) impact and a warning of future change. Ambio 28:188–196

Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. Marine & Freshwater Research 50:867-878

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biology 12:2220-2234

Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC, Rushton SP (2008) Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob Change Biol 14:2796-2809

Wong PP (1998) Coastal tourism development in Southeast Asia: relevance and lessons for coastal zone management. Ocean & Coastal Management 38:89-109

Yonge CM, Nichols AG (1931) Studies on the physiology of corals: V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. Scientific Report of the Great Barrier Reef Expedition 1:177-211.

Zvuloni A, Artzy-Randrup Y, Stone L, van Woesik R, Loya Y (2008) Ecological size-frequency distributions: how to prevent and correct biases in spatial sampling. Limnology and Oceanography: Methods:144-153