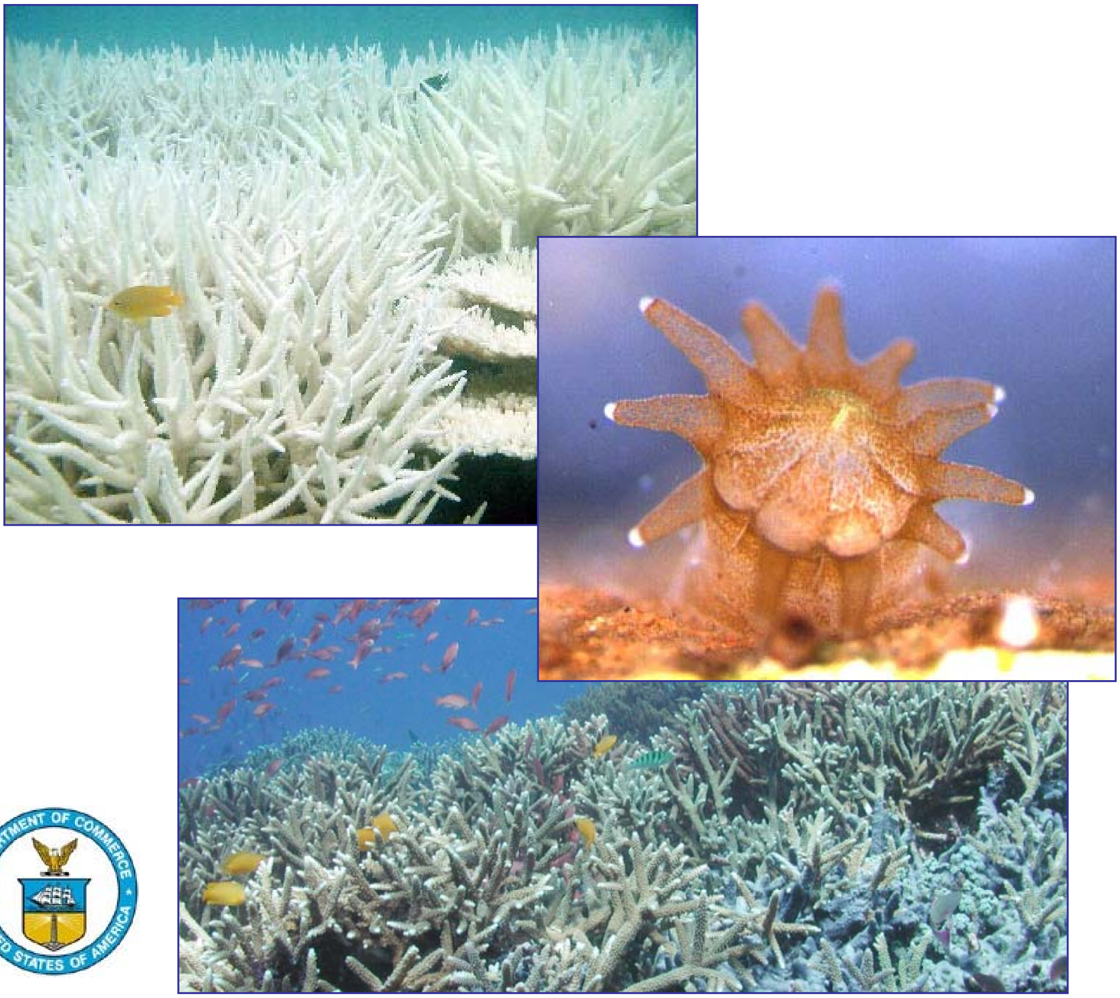
The Effects of Combined Sea Temperature, Light, and Carbon Dioxide on Coral Bleaching, Settlement, and Growth

The First Annual Combined Effects Think Tank to Support CREWS Modeling

James C. Hendee, Ph.D.
Editor



U.S. Department of Commerce
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A NOAA Research Special Report
March, 2004

Cover photographs credit:

1) Bleached corals on the Great Barrier Reef: Ray Berkelmans
2) Single coral (*Porites astreoides*) polyp: Jane Hawkridge
3) Coral seascape near Komodo Island, Indonesia: Michael Lesser

The Effects of Combined Sea Temperature, Light, and Carbon Dioxide on Coral Bleaching, Settlement, and Growth

The First Annual Combined Effects Think Tank to Support CREWS Modeling (NURP/CMRC Grant CMRC-02-PRJH-02-02A)

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March, 2004

U.S. Department of Commerce
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National Oceanic and Atmospheric Administration
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Under Secretary for Oceans and Atmosphere

Ocean and Atmospheric Research
Richard Rosen, Ph.D.
Assistant Administrator for Office of Oceanic and Atmospheric Research

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Introduction

James C. Hendee
NOAA/AOML

Researchers engaged in studies of coral bleaching, growth, reproduction and other disciplines gathered at the Caribbean Marine Research Center (CMRC) on Lee Stocking Island, Bahamas (site of the first Coral Reef Early Warning System, or CREWS stations) January 20-24, 2003, to discuss how their research problems might gain from a supplemental CREWS approach, and how the CREWS knowledge base could gain from their work. The objectives of the meeting were to, a) explain what is known of certain coral reef problem domains, that is, as they relate to anthropogenic stress and coral reef response, b) determine which *in situ* monitoring instruments would help in these research problems, and, c) to begin to provide a dialog to enhance current expert system modules, or develop new ones, to facilitate interpretation of (i.e., model) those factors thought to be conducive to stimulating a particular event (e.g., coral bleaching, coral growth). The work presented at this Think Tank represents a milestone in marking the status of important topics in coral reef research today, and indeed new research directions have already begun.

The present NOAA Technical Memorandum details the salient points of the invitees' presentations through summaries, relevant bibliographic citations, and links (*at the bottom of the first page of each presentation summary*) to their PowerPoint presentations on the World-Wide Web. The document is arranged to show the meeting agenda followed by the presentations in the order in which they were given. Based on the importance of CREWS research, we expect to conduct future Think Tank meetings to summarize current findings and identify important new coral reef research topics.

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Meeting held at Lee Stocking Island (LSI), Bahamas, January 20 - 24, 2003 to begin formulating research protocols to take advantage of CREWS monitoring stations.

“The Effects of Combined Sea Temperature, Light, and/or Carbon Dioxide on Coral Bleaching, Settlement and/or Growth (First Annual Combined Effects Think Tank to Support CREWS Modeling)”

Left to right: Joanie Kleypas, Derek Manzello, Cheryl Woodley, Caroline Rogers, Danny Gleason, Mark Warner, Michael Lesser, Lisa Rodrigues, Todd LaJeunesse, Andrea Grottoli, Mike Risk, Ilsa Kuffner, Jeff Absten, Melanie McField, Kimberly Puglise, Ray Berkelmans, William Fitt, Erich Mueller, William Skirving, Jules Craynock, Richard Zepp, Peter Glynn, Al Strong, Chris Langdon, Jim Hendee, Chris Humphrey, Geoff Chilcoat. Speakers not present in picture: Peter Ortner, Andy Hooten.

The Caribbean Marine Research Center, Lee Stocking Island, Exuma, Bahamas[*]

Kimberly Puglise, NOAA's Undersea Research Program
Craig Dahlgren, Ph.D., CMRC Science Director
John Marr, Ph.D., CMRC Director

The Caribbean Marine Research Center, NOAA's Undersea Research Program (NURP) Center for the Caribbean, is pleased to host **The First Annual Combined Effects Think Tank to Support CREWS (Coral Reef Early Warning System) Modeling** at its research station on Lee Stocking Island, Bahamas. This workshop is timely given the demands to better utilize research and monitoring techniques to improve the management of coral reef resources; and is designed to provide an opportunity for scientists to contribute ideas for future data applications, instrumentation, and monitoring techniques for the CREWS stations. We welcome all participants to CMRC for the CREWS workshop and look forward to the contributions by this very excellent cadre of coral reef scientists.

In partnership with NOAA's Coral Health and Monitoring Program and Coral Reef Watch Program, CMRC is helping to meet the environmental monitoring needs for the wider Caribbean region, as set forth by the U.S. Coral Reef Task Force. CMRC has over 15 years of history monitoring sea temperature and other environmental parameters affecting coral reef ecosystems in the wider Caribbean region. CMRC is proud that Lee Stocking Island was chosen in 2000 to be the site of the first CREWS station and to serve as a platform to test sensors and remote data transmission technologies. The CREWS stations were developed to collect oceanographic and meteorological data in near real-time to allow scientists to monitor environmental parameters affecting coral reef ecosystems in remote locations and to detect critical environmental events as they occurred, e.g. coral bleaching.

Thanks to the leadership provided by NOAA and Dr. James Hendee, many of the top coral reef experts have convened from a diversity of disciplines to focus and determine steps and improvements to the CREWS stations to further improve NOAA's capabilities to monitor coral reef ecosystems. We look forward to the outcome of the workshop and the opportunity it presents to advance marine science. It is expected that the combination of experts convened at this unique facility in the Bahamas and with the support offered by NOAA, we will advance understandings and undersea applications that translate into improved management of coral reefs for such a critical resource in the Caribbean.

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[*] Web links: http://www.cmrc.org/
http://www.nurp.noaa.gov/carib.html

~~ Schedule ~~

The Effects of Combined Sea Temperature, Light, and Carbon Dioxide on Coral Bleaching, Settlement, and Growth

(First Annual Combined Effects Think Tank to Support CREWS Modeling)
(NURP/CMRC Grant CMRC-02-PRJH-02-02A)

Lee Stocking Island (LSI), Bahamas
January 20 - 24, 2003

Monday, January 20

Arrival, Check-In, Dive Check-Outs

All Day	Arrivals, check-in, orientation, possibly some check-out dives.
Noon	Lunch
5:00pm	CMRC Laboratory and Aquaria Facilities Tour. (Meet at Lizzard Lounge.) ***Craig Dahlgren***
6:00pm	Informal introductions over cold cold beers.
7:00pm	Dinner

Tuesday, January 21

Introductions, Background, New Programs, Experimental Considerations

7:00am	Breakfast. Lunch may be packed for you, because low tide at the CREWS station will be around that time.
8:00am	Brief Introduction to CREWS station, Lizzard Lounge. ***Jim Hendee***
8:15am	Check-out dives as necessary for those new to LSI. ***Brian Kakuk*** Set-ups for later presentations at the Lizzard Lounge. ***Derek Manzello***
9:00am	Visit CREWS station, visit Rainbow Gardens, visit research sites, new CREWS location.
Noon	Lunch on the water, unless you can make it back in time
1:15pm	Meeting at the Lizzard Lounge

1:30pm	Introduction to the Combined Factors Think Tank and the CREWS concept. ***Jim Hendee***
2:00pm	CREWS station augmentation: Plankton monitoring in St. Croix, USVI. ***Peter Ortner***
2:30pm	NOAA's Coral Reef Watch program and it's role in the development of a Coral Bleaching and Climate Change program. ***Al Strong***
3:00pm	Coffee/Tea Break
3:15pm	The World Bank/Global Environmental Fund Targeted Research Initiative. ***Andy Hooten***
3:45pm	The hydrodynamics of a coral bleaching event: The role of satellite and CREWS measurements. ***William Skirving***
4:15pm	The CARICOMP Network. ***Jeff Absten***
4:25pm	Capabilities and opportunities: the SEAKEYS Network in the Florida Keys. ***Chris Humphrey***
4:45pm	A decade of SEAKEYS data: trends and patterns. ***Derek Manzello***
5:15pm	NOAA's Undersea Research Program. ***Kimberly Puglise***
5:30pm	Break for the day.
7:00pm	Dinner

Wednesday, January 22
Corals & Light

7:00am	Breakfast
8:00am	Lizzard Lounge meeting resumes
8:15am	A review of previous light studies. ***Michael Lesser***
8:45am	The sublethal bleaching response ***Bill Fitt***
9:15am	Measuring seasonal fluctuations in photosynthetic performance in reef corals: implications for long-term monitoring and coral bleaching. ***Mark Warner***

9:45am	Spillover buffer.
10:00am	Coffee break
10:15am	Zooxanthellae typing and seasonal changes. ***Todd LaJeunesse***
10:45am	Effects of light on coral reproduction and recruitment. ***Danny Gleason***
11:15am	Effects of solar irradiance on reef coral physiology and recruitment. ***Ilsa Kuffner***
11:45am	Spillover buffer.
Noon	Lunch
1:00pm	Meeting resumes
1:15pm	Lipids, isotopes, and coral bleaching.. ***Andréa Grottoli***
1:45pm	Experimental design considerations for determining bleaching thresholds**.** ***Ray Berkelmans***
2:15pm	Spillover buffer.
2:30pm	Coffee break.
2:45pm	Coral bleaching and light attenuation: Can elevated turbidity help corals?. ***Erich Mueller***
3:45pm	Factors influencing geographic and seasonal variations in light exposure of coral assemblages in the Florida Keys**.** ***Richard Zepp***
4:15pm	Assessing coral health in the Florida Keys using a cellular diagnostic system**.** ***Cheryl Woodley***
4:45pm	Discussion, and break for the day.
7:00pm	Dinner

Thursday, January 23

<u>Climate Change, Coral Growth, Anthropogenic Stress, Caribbean Status</u>

7:00am	Breakfast
8:00am	Lizzard Lounge meeting resumes

8:15am	Recruitment and biodiversity studies on ENSO-impacted coral reefs in Panama. ***Peter Glynn***
8:45am	Calcium carbonate budgets--the basic framework. ***Joanie Kleypas***
9:15am	Effects of CO_2 on coral growth and calcification. ***Chris Langdon***
9:45am	Spillover buffer
10:00am	Coffee Break
10:15am	Large-scale assessments of bleaching and potential mitigation strategies in the Mesoamerican reef. ***Melanie McField***
10:45am	Land-based sources and climate change: striking a balance. ***Mike Risk***
11:15am	Discussion on Think Tank publication, CREWS rules, etc. ***Jim Hendee***
11:45am	End of meeting. ***Jim Hendee***
Noon	Lunch
1:00pm	***Play time!***
7:00pm	Dinner

The Coral Reef Early Warning System (CREWS): Marine Environmental Monitoring to Support Research and Marine Sanctuary Management[*]

James C. Hendee, Ph.D.
NOAA/AOML

The National Oceanic and Atmospheric Administration (NOAA) has committed to the installation of meteorological and oceanographic monitoring stations at all major US coral reef areas by 2007. These stations consist of a basic suite of sensors, plus additional ones, depending upon local research the stations hope to support, and upon available funding. The basic suite of meteorological and air-based sensors measure air temperature, wind speed and direction, barometric pressure, photosynthetically available radiation (PAR) and ultraviolet radiation (UVR). The basic suite of oceanographic sensors measure salinity, sea temperature, PAR (at 1m nominal) and UVR (at 1m nominal). In addition to these sensors, a data acquisition system gathers and averages the data, then transmits the hourly averages via a GOES satellite to NOAA's National Environmental Satellite, Data and Information Service (NESDIS) data download facility at Wallups Island, Virginia, where the data are then acquired in turn via automated procedures for saving and processing at NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML) in Miami, Florida. Once the data arrive at AOML they are processed with a suite of expert systems which determine whether the data being received are within reasonable numbers, and whether certain environmental conditions are conducive to specific marine behavioral events (e.g., bleaching). The entire data collection and processing system, when used specifically to understand coral bleaching and coral reef-related events, is called the Coral Reef Early Warning System (CREWS), and is part of NOAA's larger umbrella Coral Reef Watch program.

The CREWS system has been successful in modeling and alerting to coral bleaching conditions in the Florida Keys (Hendee et al 1998; Hendee et al 2001) and the Great Barrier Reef (Hendee and Berkelmans 2003; Berkelmans et al 2002), and it is NOAA's intent to expand this alerting capability to other coral reef areas, and to better refine and enhance its alerting capabilities beyond coral bleaching (e.g., see Hendee 2000). The development of the CREWS coral bleaching and other coral reef-related alert and modeling expert systems are therefore of necessity dependent upon the expertise of problem domain experts, such as those who study coral bleaching, coral reef growth, etc.

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/hendee.pdf

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Coral Reef Early Warning System (CREWS) station near Lee Stocking Island, Bahamas.

Abundance and Diel Migrations Of Demersal Mesozooplankton And Small Reef Fishes And Their Trophodynamic Contribution to the Coral Reef Ecosystem: A Pilot Study*

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John Lamkin, Ph.D., Cynthia Yeung, Ph.D. and Dave Jones, NOAA/NMFS

Coral reefs serve as habitat for demersal mesozooplankton and small fishes that migrate into the overlying waters at night but spend daylight hours within the reef, in part because that habitat provides protection against visual predators. There is little question that these movements both affect and temporally and spatially structure energy, mass and nutrient exchange between the reef habitat and the surrounding waters. Information to date has, however, been predominately qualitative and has not taken advantage of the latest advances in biological oceanographic sampling instrumentation. Moreover, what sampling has been done has not been rigorously coupled to synoptic time series of ambient oceanographic conditions. To begin to fill this critical gap we have begun to use *in situ* multi-frequency acoustic and optical integrated environmental sensor packages that we have already tested in the FKNMS during month-long moored deployments. They are adaptations of towed systems we and others developed for using in large scale interdisciplinary oceanographic field programs (e.g.- the JGOFS and GLOBEC Arabian Sea expeditions) but have not heretofore been used in the coral reef context. The systems are capable of continuously measuring and recording the abundance and size distribution of organisms from ca. 100um to 5-10cm while concomitantly measuring water column chlorophyll fluorescence, transmittance, temperature and salinity. They would be used in conjunction with a bottom mounted ADCP yielding both vertical current structure as well as water column backscatter distributions. This kind of instrumentation will directly assess larger pelagic fish and fish schools in addition to the smaller demersal forms and their diel migration. Integrated high resolution instrument packages were deployed for a month in Sept/Oct 2002 on a relatively high relief Caribbean fore reef near the CREWS (Coral Reef Early Warning System) installed by AOML at Salt River, St.Croix in the U.S. Virgin Islands. The experiment will be repeated in May 2003 incorporating a number of technical refinements based upon the experience gained in our initial deployment. In the intervening six month interval, CREWS data, in situ video images and ADCP data are being obtained on site.

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* Web link: http://www.coral.noaa.gov/cmrc/think-tank/ortner.pdf

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NOAA’s Coral Reef Watch Program and USCRTF’s Climate Change and Coral Bleaching[*]

Alan E. Strong, Ph.D.
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NESDIS Satellite Monitoring

Over the past few years, anomalously warm Sea Surface Temperatures (SST) have led to an increased incidence of coral bleaching around the globe. Bleaching occurs as waters warm towards the coral’s upper thermal limit, corals expel their colorful symbiotic zooxanthellae leaving them devoid of any color and thus appearing to be bleached. Corals can recover from mild bleaching, however if the intensity and/or duration of the abnormally warm water is great enough, mortality will result. If severe bleaching is extensive, it could lead to permanent loss of coral from the reef.

Since 1997, the National Environment Satellite, Data, and Information Service (NESDIS) has been producing web-accessible, satellite-derived, sea surface temperature products to monitor for temperatures conducive to coral bleaching. Additionally, NESDIS has been providing technical support for coral reef mapping efforts, developing a robust and comprehensive international coral reef data management system and using paleo-climate records to describe the coral reef environment in the distant past.

As noted in the introduction the Coral Reef Watch program is part of a coordinated NOAA Coral Reef Conservation Program in partnership with NOAA’s NESDIS, National Ocean Service (NOS), the Office of Atmospheric Research (OAR), and the National Marine Fisheries Service (NMFS).

Scientists at NESDIS have developed global coral bleaching monitoring products using satellite SST data. These products are designed to provide reef environmental information in a near-real-time basis for rapid assessment of areas of concern, as well as archived information and retrospective analyses to be used for reef management, scientific research, and monitoring our changing climate.

At present our operational and experimental products include:

HotSpot Charts: depicting areas, and intensity, of thermal stress (anomalously high SSTs) conducive to coral bleaching. (Operational – Oct 2002)

Degree Heating Weeks (DHW) Charts: depicting the duration and strength of HotSpots and estimating the severity and mortality of coral bleaching. (Operational – Feb 2003)

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/strong.pdf

Bleaching Indices: being designed to provide near-real-time data of SST, HotSpot, DHW, as well as bleaching thresholds, for selected key reef sites around the globe. (Experimental/Operational – late 2003)

Retrospective analyses: Reprocessed high-quality satellite SST data, such as NOAA/NASA Pathfinder SSTs that are the most refined available, have been used to produce retrospective coral bleaching analysis products such as HotSpot and DHW charts for more accurate assessment and documentation of thermal stress conducive to coral bleaching and for refinement and development of new monitoring products, in addition to monitoring trends.

In the coming years we plan to improve the capabilities for coral reef ecosystem monitoring, develop the capabilities for understanding the past, present and future changes in coral reef environments, and transferring this technology to researchers, reef management entities and the public.

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The Hydrodynamics Of A Coral Bleaching Event:
The Role Of Satellite And CREWS Measurements[*]

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Very few mass coral bleaching events in the world are a result of advected hot water. Little to no wind, clear sunny skies and weak ocean currents characterizes these events and as such, in situ heating cause almost all hot-water mass bleaching events. It would therefore be more accurate to describe mass coral bleaching as a weather phenomenon rather than the result of climate as is currently popular. Climate is likely to modulate the frequency of these weather events, but more research is necessary before direct links between climate states (eg El Nino) and coral bleaching can be made.

During a bleaching event, spatial patterns of SST are quite complex and have a scale of hundreds to tens of thousands of metres. Given that on these scales solar radiation is homogeneous in space, hydrodynamic mixing is therefore the only other mechanism that could create such a complex SST pattern. There are four different mechanisms that can vertically mix the water column, wind, low frequency currents (eg East Australian current, Gulf Steam, etc), high frequency currents (eg tides) and swell waves.

As mentioned above, winds are effectively absent during a mass bleaching event, which leaves swell waves and currents as the only mechanisms capable of altering the spatial patterns of SST. Swell waves are very effective mixers where they exist and impinge on a reef. However, they are not capable of cooling an entire reef and will not be available for every reef since not all reefs experience swell waves and not all bleaching events have swell.

This leaves currents as the only reliable mechanism for altering spatial patterns of SST. The vertical temperature profile is determined by heating from above via incoming solar radiation and cooling from below via upwelling, breaking internal waves and cold-water intrusions. Currents then mix this vertical profile via bottom friction and 3D mixing behind reefs and islands. Advection can be a horizontal mixing mechanism associated with these currents in some situations. The spatial pattern of mixing interacts with the spatial pattern of vertical temperature profiles to create patterns of low to high SST during a bleaching event. To date, coral bleaching has occurred in regions of high SST, with the regions of cool water remaining relatively stress free.

Although the vertical profile of temperature can change slightly from event to event, the mixing parameters change very little, since the tidal and low frequency currents are cyclic and effectively predictable. The result is that for any given area, the SST pattern during a severe bleaching event is effectively static from one bleaching event to another, the only thing that changes is how hot and cool the patches become.

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/skirving.pdf

The hydrology of a bleaching event makes monitoring the marine environment during a bleaching event quite challenging. *In situ* measurements from a single static station such as CREWS installations give good temporal coverage, potentially very high accuracy and a much better range of measurements than satellite based sensors. The down side of this system is that it can only give measurements from a profile in a single point in space, which may be a well mixed or a stratified patch of water. It would take a considerable number of CREWS stations to cover a single region sufficiently during a bleaching event.

Satellites on the other hand give a very good spatial coverage, however they have a spatial coverage of only 1 to 4 km, are effected by clouds and do not have a good temporal coverage when compared to *in situ* measurements.

It would seem that neither CREWS nor satellites are capable of satisfactorily monitoring the marine environment during a bleaching event and yet they provide highly complimentary measurements. We can successfully combine these data sets to provide full 3D data with good temporal and spatial resolution with 3D hydrodynamic models. These models can be kept accurate and on track by the inclusion of the combination of CREWS and satellite data, neither of which would be sufficient to keep the models accurate on their own. It would even be possible to use this combination of data and models to forecast.

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A Decade of SEAKEYS Data: SST Trends and Patterns[*]

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The SEAKEYS (Sustained Ecological Research Related to the Management of the Florida Keys) program was initiated in the early 1990's to complement the National Data Buoy Center's (NDBC's) Coastal Marine Automated Network (C-MAN) (Ogden 1994). C-MAN stations transmit hourly data via the Geostationary Operational Environmental Satellites (GOES) (NDBC 1992) providing researchers with long-term *in situ* data records. Elevated sea surface temperature (SST) has been repeatedly identified as the primary causative agent of coral bleaching events on a global scale (Glynn 1993; Brown 1997; Hoegh-Guldberg 1999). It is well accepted that hermatypic corals live near their upper thermal tolerances and small increases in temperature (i.e., 1 ^{o} C) result in physiological stress to the maintenance of the animal-plant symbiosis (Glynn and D'Croz 1990). Generally speaking, Goreau and Hayes (1994) propose that sustained SSTs of 31 ^{o} C for one month will result in significant coral bleaching and mortality. Mean monthly SSTs were analyzed for August from *in situ* thermistors on 5 SEAKEYS/C-MAN stations located on the Florida Reef Tract (Fowey Rocks, Molasses Reef, Sombrero Reef, Sand Key, Dry Tortugas) from 1992 - 2002. All 5 locations displayed a warming trend (regression analysis) and imply that reef-building corals in the Florida Keys have and are already experiencing significant thermal stress with mean SSTs for August (1992 – 2002) greater than 30 ^{o} C at Sombrero Reef, Sand Key, and the Dry Tortugas. SST records correlate with reported coral bleaching at Sombrero Reef in 1998 (Hendee *et al.* 2001) in that mean August SSTs were 31.1 ^{o} C. Elevated SSTs worldwide in 1998 have been attributed to the El Nino-Southern Oscillation (ENSO) event (Wilkinson *et al*. 1999) that was unique in that it affected virtually all reef areas of the world with high coral mortality in many locations. Furthermore, regression analysis showed that SSTs are on pace to sustain and exceed 31.0 ^{o} C for the entire month of August by the year 2057 for the Dry Tortugas, 2061 for Molasses Reef, and 2063 for Fowey Rocks. These results concur with the work of Hoegh-Guldberg (1999) who predicts by the year 2050 that global, mass coral bleaching events with unsubstantiated degrees of mortality will occur annually. Data from Sombrero Reef display a strong slope predicting annual mean SSTs of 31 ^{o} C by 2008 for August and 2009 for July. Higher SSTs recorded for Sombrero Reef are likely due to the influence of warm Florida Bay waters exiting the wide channels in the middle Florida Keys and washing out over the reefs (Smith 1994). Continued long-term, *in situ* monitoring of SSTs in the Florida Keys is vital given the dynamic nature of climate and the short time frame over which this analysis was performed. Despite the short time frame of analysis, the results were conclusive in showing a warming trend for the Florida Reef Tract.

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Response of Corals to Solar Radiation and Temperature[*]

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Over the past several years, and with increasing regularity, coral reefs around the world have been affected by a phenomenon known as "coral bleaching" which principally involves the mass expulsion of their symbiotic dinoflagellates also know as zooxanthellae, but can also include the loss of photosynthetic pigments within individual zooxanthellae (Glynn 1991). These events closely follow oceanic warming that results in elevated seawater temperatures of 30°-33°C (Glynn 1991). Field and laboratory studies on bleaching in corals and other symbiotic cnidarians have established a causal link between temperature stress and bleaching (Jokiel and Coles 1990, Lesser *et al.* 1990, Glynn and D'Croz 1990, Fitt *et al.* 1993). Other studies have implicated UV radiation (UV-A: 320-400 nm, UV-B: 290-320 nm) as a cause of bleaching either alone (Jokiel 1980, Lesser *et al.* 1990; Gleason and Wellington 1993) or synergistically with elevated temperature (Lesser *et al.* 1990, Glynn *et al.* 1992). During 1998 the geographic extent and intensity of bleaching events world-wide caused a significant shift in the thinking of the coral research community that resulted in a clear statement that global warming is occurring, will get worse, and will result in more bleaching events (Hoegh-Guldberg 1999). The extent of bleaching and any subsequent mortality are directly related to the degree of temperature elevation and the duration of exposure for each event.

The decrease of stratospheric ozone from anthropogenic inputs of chlorinated fluorocarbons has resulted in an increase in the amount of harmful UV-B radiation reaching the sea surface. The combination of a higher solar angle and the generally thinner layer of ozone near the equator (Cutchis 1982) is such that tropical ecosystems have a long evolutionary history of exposure to higher irradiances of total UV radiation, and UV-B in particular (Frederick *et al.* 1989). In absolute terms, even small percentage decreases in ozone that may occur in the tropics would be important because the UV-B irradiance there is already high (Madronich *et al*. 1994). Many subtropical coral reefs (Caribbean, Hawaii, northern Red Sea) lie within latitudes where modeling predictions suggest that UV-B irradiances will increase in the future and before the recovery of stratospheric ozone concentrations in the next half-century (Madronich *et al*. 1994). In general, the high transparency of tropical ocean waters allows UV radiation to penetrate to depths of 15 m or more or more (Gleason and Wellington 1993; Shick *et al.* 1996). Ultraviolet radiation is known to have a detrimental effect on photosynthesis and growth in zooxanthellae and the survival of coral reef epifauna (see Shick *et al*. 1996 for review). The harmful effects of UV radiation may involve damage to DNA, various proteins, and membrane lipids. The damage is the result of both the direct and indirect effects of UV radiation on several cellular targets. For sessile corals, exposure to solar UV radiation in shallow tropical waters is unavoidable.

An important protective response of corals during exposure to UV radiation includes the synthesis of UV-absorbing compounds and enzymes involved in the protection of both the host and symbiont from oxidative stress (Dykens and Shick 1984, Lesser and Shick 1989, Lesser 1996). The concentration of protective UV-absorbing compounds (mycosporine-like amino

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/lesser.pdf

acids [MAAs]) within the coral *Montastraea faveolata* shows an exponential decrease with depth (Lesser 2001) and has been shown to decrease upon exposure to elevated temperatures (Lesser *et al.* 1990, Glynn *et al.* 1992, Lesser 1996). Several other species of coral from Hawaii and the Caribbean also show a similar decrease in MAA concentration with depth that is significantly correlated with the irradiance of UV radiation (Banaszak *et al.*1998). UV radiation absorbing compounds are believed to provide protection from the high energy wavelengths within the UV portion of the spectrum. A protective role for these compounds has been inferred from their UV absorbing properties (Karentz *et al.* 1991, Gleason 1993), their decrease in concentration with increasing depth (Dunlap *et al.* 1986) or, after artificial shielding from UV (Jokiel and York 1982, Shick *et al.* 1991).

Climate change is happening. Recent studies have provided crucial evidence that the greenhouse effect is occurring and that it is anthropogenic in nature (Crowley 2000, Stott *et al.*2000). Biological indicators of the resulting warming are also evident in terrestrial and marine systems (Hughes 2000). Nowhere is this more evident than the recent (last 20+ year) increase in the incidence of bleaching events on coral reefs. Some investigators have suggested that thermal stress and the resulting bleaching in corals may be "adaptive" in nature (Buddemeier and Fautin 1993, Ware *et al.* 1996) that is supported by some lines of evolutionary theory (Hoffmann and Hercus 2000). However, it is more commonly believed that adaptive evolution under global climate changes will be severely constrained (Etterson and Shaw 2001). The important question is; will reef corals be able to acclimatize or undergo adaptive evolution at the present and predicted rates of environmental change (Gates and Edmunds 1999, Fitt et al. 2001)?

Mechanism of Coral Bleaching: Oxidative Stress Caused by Elevated Temperatures and UV Radiation

Exposure to sublethal temperature perturbation alone (Iglesias-Prieto *et al.* 1992) or UV radiation alone (Lesser and Shick 1989) does result in photoinhibition of photosynthesis in zooxanthellae. Photoinhibition occurs as a result of the reduction in photosynthetic electron transport, combined with the continued high absorption of excitation energy (Osmond 1981). This can lead to the production of reactive oxygen species (ROS; singlet oxygen [$^1O_2$] superoxide radicals [O_2^-] and hydrogen peroxide [H_2O_2]) for which there are many cellular targets including photosystem II and the primary carboxylating enzyme, Rubisco (Lesser 1996). Damage to PSII, following exposure to elevated temperatures and solar radiation, is believed to be an important initiator of bleaching (Iglesias-Prieto et al. 1992, Lesser 1996, Warner et al. 1996, Warner et al. 1999).

Recent data provided by fluorescent measurements (PAM) and quenching analyses supports the result described by Lesser (1996), that there is damage to both the light and dark reactions (Jones et al. 1998). Brown et al. (1999) suggested that the diurnal patterns in quantum yields and xanthophyll cycling they observed in corals were indicative of photoinhibition followed by photoprotection. Recent results using an instrument similar to the PAM (fast repetition rate fluorometer or FRRF) has shown that quantum yields of chlorophyll fluorescence change with depth and that diel changes in fluorescence yields are not coupled to photosynthetic activity, measured as oxygen flux, but are linked to non-photochemical quenching (Lesser and Gorbunov 2001). Work by Warner *et al.* (1999) has clearly shown that the changes in the patterns of fluorescence upon exposure to thermal stress are caused by damage at the D1 protein of PSII in the zooxanthellae. Other experiments have shown that corals exposed to elevated temperature and varying irradiances of solar radiation exhibit a pattern of differential D1 expression consistent with a significant role for "light" in the initiation of damage to the D1 protein (Lesser and Farrell submitted). Additionally, fluorescence measurements are capable of detecting incipient bleaching in reef corals before visible signs (i.e., colony paling) actually occur (Lombardi *et al*. 2000).

The measurement of chlorophyll *a* fluorescence using active, versus passive (= solar induced), techniques is becoming the preferred, non-destructive, *in situ* method to assess how well PSII is functioning in benthic marine photoautotrophs under a variety of environmental conditions. Instruments have been developed that measure chlorophyll fluorescence yields of PSII using multiple photochemical turnover (pulse amplitude modulated [PAM]), and single photochemical turnover protocols (pump and probe or fast repetition rate) in the laboratory and in the field. These instruments also allow detailed quenching analyses to be performed on photoautotrophs under a variety of environmental conditions (thermal, nutrient, and UV radiation stress) to understand the dynamics between photochemical and non-photochemical quenching. Use of these instruments has greatly enhanced our understanding of the dynamics of the response of zooxanthellae in corals to changes in solar radiation and seawater temperatures (Brown *et al.* 1999, Warner *et al.* 1999, Gorbunov *et al.* 2001, Lesser and Gorbunov 2001).

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The Sublethal Bleaching Response[*]

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Salient points:

1. Zooxanthellae in corals are in the genus *Symbiodinium*, with several different types identified via molecular techniques (see Todd LaJeunesse's talk) and a wide range of physiological capabilities.

2. We have been monitoring seven species of reef-building corals in the Bahamas (LSI) in comparison to the same corals living at the same depths (1-3 m, 13 m) in the FKNMS in terms of tissue biomass and zooxanthellae density and pigment content.

3. Seasonal cycles in the above parameters are somewhat counter-intuitive:

    a. Symbiont densities and pigment peak in winter (coldest months,lowest light intensities and duration)
    b. Tissue biomass typically peaks in the spring sample times
    c. Lowest density of *Symbiodinium* and tissue biomass in the late summer/fall (end of warm season, highest light intensity and duration)(especially in El Nino years)

4. The relationship with the host appears to be very important in determing density of zooxanthellae in corals:

    a. Number of symbionts per host cell is positively correlated to size of the host cell
    b. Division of zooxanthellae in cnidarian hosts is synchronized to host feeding, peaking at the night-morning transition
    c. Appearance of moribund symbionts (and their disappearance from the host cell) is also on a diurnal cycle, peaking in the dark period, ususally before symbiont division but after host feeding begins at the beginning of the dark cycle.
    d. "Constancy" in number of zoox per unit host tissue is found, with particular ranges associated with particular corals-symbiont combinations (=holobiont). Note that this ratio can change depending on changing environmental conditions (light, temperature, food availability, etc)

5. Physiological stresses drive decreases in density of symbionts and host tissue biomass:
    a. Temperature stress acts on respiration rates of host tissue and symbionts, and especially on photosystems of the symbionts, and varies with:
        (1) season
        (2) time of day
        (3) location on reef

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[*] No presentation available.

Note that we know very little about the last two variables here, and that temperature stress probably acts most significantly on the organismal level at relatively short periods of time on a diel cycle.

b. Light stress varies seasonally as far as:

(1) quantity
(2) quality
(3) duration
(4) time of day
(5) location on reef

Reef organisms (coral tissue and/or symbionts) typically have one to several mechanisms to protect themselves from light stress (UV-MAA's, xanthophyll cycle, etc)

6. Conclusion: correlates with light and temperature help explain differences in physiological responses of corals and their symbionts over various temporal scales (daily, seasonal, PDO, El Nino).

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Seasonal Fluctuations in Photosynthetic Performance in Reef Corals: Implications for Long-Term Monitoring and Coral Bleaching[*]

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Over the past eight years, there has been resurgence in investigating the photobiology of reef building corals. This is due, in part, to the recent discoveries that some environmental stressors such as elevated seawater temperature, excessive photosynthetically active radiation (PAR), and ultraviolet radiation can have serious impacts on corals and their endosymbiotic dinoflagellates (*Symbiodinium sp.,* commonly called zooxanthellae). Previous work has confirmed an important link in patterns of widespread coral bleaching events, correlated to elevated sea surface temperature, and the loss in photosynthetic activity of zooxanthellae in several species of corals. In this regard, there has been much interest in using instrumentation that measures active chlorophyll fluorescence to discern pathways of photodamage as well as photoprotection in zooxanthellae during experimental and natural bleaching. Kinetics of chlorophyll fluorescence, recorded by the saturation pulse technique, are easily measured with laboratory based or submersible pulse amplitude modulation (PAM) fluorometry. This technique was used in order to follow seasonal shifts in the quantum yield of charge separation (F_V/F_M) in two primary Caribbean reef-building corals, *Montastraea annularis* and *Montastraea faveolata,* at three different depths near Lee Stocking Island in the Bahamas. The results from this four-year study, briefly summarized here, provide valuable insight into the long term dynamics and stability of zooxanthellae symbioses. A synopsis of this work shows several advantages to long term monitoring of chlorophyll fluorescence coupled to other measurements (e.g. above and below water PAR, temperature), with the caution that reef biologists must understand that this technique provides only a glimpse of one aspect of photosynthesis and that further work at the biochemical and molecular scale is needed if we are to fully interpret such data.

Six colonies of *M. annularis* and *M. faveolata* were sampled at 1.5, 3, and 14 m at three reef locations surrounding Lee Stocking Island, South Normans Patch, Rainbow Gardens, and South Perry Reef respectively. Samples of each colony were taken four times per year from March 1995 to January 1999. There were significant seasonal fluctuations in the activity of photosystem II (PS II) as measured by F_V/F_M , with the highest values consistently noted in the late autumn to early winter time points while lowest F_V/F_M values were recorded during the mid to late summer. The greatest seasonal fluctuation occurred in corals sampled at the shallow site, with a range in F_V/F_M from 0.43–0.66, while corals from the 3 and 14 m sites did not show as much variation. Zooxanthellae within both species of coral at the shallow site showed a similar response in PS II activity over the course of the study, while significant interactive effects were noted at the other sites. In particular, F_V/F_M values recorded in *M. faveolata* were significantly lower than those from *M. annularis* in the summer sampling times of 1996 and 1998 at 3 m, and *M. faveolata* typically had a faster summer decline in F_V/F_M compared to *M. annularis* at 3 and 12 m. Visual signs of bleaching were noted during three sampling times, October 1995, and March and June 1998. Zooxanthellae density was significantly reduced at these time points relative to the preceding sampling times before the noted bleaching. However, F_V/F_M values did

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/warner.pdf

not always correspond to dinoflagellate number. Nevertheless, there was a significant correlation between the photosynthetic capacity of PS II and the maximum daily temperature recorded at each site, with the peak temperature corresponding to the lowest F_V/F_M values. Similar analyses of F_V/F_M to the total daily light recorded on Lee Stocking Island yielded significant correlations between these variables at the shallow and deep sites, while no significant correlation was noted for the intermediate depth (3 m). This trend may have been due increased turbidity at the 3 m site, yet without a complementary data set for *in situ* PAR, this conclusion is speculative. When fluorescence data is compared to zooxanthellae density and host biomass (expressed as ash-free dry weight), a clear temporal trend is apparent wherein algal populations, and then coral biomass follow recovery of PS II activity.

The seasonal fluctuation in photosynthetic capacity of PS II is most likely due to a number of biochemical changes in the zooxanthellae. Seasonal shifts in light contributed to normal patterns of photoacclimation (e.g. increased levels of chlorophyll *a* declines in chl $a{:}c_2$ noted in the winter) that can significantly influence fluorescence measurements. It is further hypothesized that the summer decline in F_V/F_M is due to a combination of photodamage and photoprotective processes. We hypothesize that a fraction of PS II reaction centers become non functional and are down regulated during the summer months. If normal summer time water temperatures are extended or if temperatures rise above normal summer maxima, more zooxanthellae will show signs of chronic photoinhibition. When zooxanthellae density and fluorescence values are presented together, coral bleaching represents the end point of a physiological continuum within what appears to be normal seasonal variation in which the photosynthetic capacity of PS II and zooxanthellae are reduced to lower levels than during non-bleaching years. Of notable interest is the fact that we know very little concerning the biochemical pathways involved in the homeostasis of daily and seasonal photosynthetic processes in zooxanthellae, yet these may provide valuable insight for interpreting patterns of chlorophyll fluorescence and predicting future bleaching response.

This work has shown that there is much utility in using active chlorophyll fluorescence for monitoring the long-term stability of potential photosynthetic activity in reef building corals. PAM fluorescence holds several advantages over other methods (e.g. respirometry, ^{14}C analysis), yet one must understand that these methods are complementary, and patterns of dark acclimated quantum yield (F_V/F_M) or light acclimated effective quantum yield ($\Delta F/F_{M'}$) are not synonymous with other values traditionally recorded from photosynthesis to irradiance curve analyses (e.g. maximal photosynthesis, P_{max}). Thus, chlorophyll fluorometry measures one aspect of photosynthesis. Future work with *in situ* fixed fluorescence monitoring stations coupled with real-time monitoring of PAR and temperature could hold great promise for furthering our understanding of zooxanthellae photosynthesis, provided that continued biochemical and molecular work is undertaken to supplement these ongoing efforts.

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Zooxanthellae Typing And Seasonal Changes[*]

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A community ecology approach to the study of the most common group of zooxanthellae, dinoflagellates in the genus *Symbiodinium*, was applied to symbiotic invertebrate assemblages on coral reefs in the western Caribbean, off the Yucatan peninsula (Puerto Morelos, Mexico) and over 1000 km away in the northeastern Caribbean, at Lee Stocking Island, Bahamas. Sequence differences and intragenomic variation, as determined by denaturing gradient gel electrophoresis and sequencing of the internal transcribed spacer 2 (ITS 2) region, were used to classify these symbionts. Twenty-eight genetically distinct *Symbiodinium* types were identified, eleven of which were found in hosts from both Caribbean locations. A single symbiont population was detected in 72% of hosts from the Yucatan and 92% of hosts from the Bahamas. The reef-wide community distribution of these symbionts is dominated by a few types found in many different host taxa, while numerous rare types appear to have high specificity for a particular host species or genus. Clade or lineage A *Symbiodinium* was restricted to compatible hosts located within 3-4 m of the surface, while *Symbiodinium* types from other lineages displayed differences in vertical zonation correlated with ITS type but were independent of clade designation. A comparison of the symbiont types found in field-collected hosts with types previously cultured from these hosts indicates the existence of low density or "background"-symbiont populations and cryptic, potentially nonmutualistic types in some hosts.

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/lajeunesse.pdf

Effects of Light on Coral Reproduction and Recruitment*

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Coral reefs are currently in a state of crisis from the impact of multiple stressors that include physical (e.g., elevated temperature, sedimentation, and ultraviolet light), chemical (e.g., pesticides, nutrients, and metals), and biological factors (e.g., disease, bleaching, and competition with algae). Declines in reefs, especially the coral component, have been observed worldwide and many reefs may be functionally gone within the next 30-50 years (Hughes and Connell 1999, Hoegh-Guldberg 1999, Wilkinson 1999, 2000). The persistence of coral-dominated reef communities and the continued accretion of reefs depend on the ability of corals to maintain high fertilization success, produce viable offspring and recruit successfully. Despite the critical link between coral reproduction and adult population structure (Hughes et al. 2000, Hughes and Tanner 2000), our understanding of the effects of physical factors on the reproductive output of adult colonies, viability of dispersing larvae, and the growth and survivorship of newly settled recruits is tenuous at best.

Most sessile marine species have a pelagic larval stage that results from spawning of eggs and sperm into the water column followed by fertilization, or release of fully mature brooded larvae (Pechenik 1999). This is also true in reef-building corals whereby broadcasting species, such as *Montastraea faveolata* and *M. cavernosa* in the Caribbean, release gametes into the water column. In contrast, brooding species, such as *Porites astreoides* and *Agaricia agaricites*, broadcast sperm that is taken up by female or hermaphroditic colonies. Once fertilization takes place, development to the planula larva stage occurs within the polyp and release of a fully mature larva ensues. If we are to paint a more accurate picture of the factors impacting reef sustainability, it is imperative that we gain insight into the proximal controls on coral reproduction and subsequent larval dispersal and recruitment.

Over the last several years we have been investigating the effects of light (both ultraviolet radiation and photosynthetically active radiation) on the survival and growth of coral planulae and recruits. More recently we have begun to investigate the impact of differences in the availability of photosynthetically active radiation (PAR, 400-700 nm) on reproductive output of reef-building corals. Many of our investigations have concentrated on the effects of ultraviolet radiation (UVR, 280-400 nm) because it has previously been found to cause stress in both adult and larval corals (e.g., Lesser et al. 1990, Gleason and Wellington 1993, 1995, Lesser 1996, Kuffner 2001) and its intensities are highly dependent on the clarity of the water column (Gleason and Wellington 1993). The specific goals of our recent investigations are as follows:

1) To determine if coral planulae can detect and avoid high intensities of ultraviolet radiation (UVR, 280-400 nm).
2) To determine if UVR sets controls on the patterns of coral recruitment observed on the reef.
3) To determine if high intensities of UVR affect the health of newly settled coral recruits and, if not, how they acclimate to UVR.

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* Web link: http://www.coral.noaa.gov/cmrc/think-tank/gleason.pdf

4) To determine if the change in PAR intensity observed along a depth gradient, or with long-term variation in water column clarity, affects both absolute and relative abundances of ova and spermaries in hermaphroditic corals.

Our studies have been conducted with the Caribbean coral *Porites astreoides* because it is common, hermaphroditic, and provides a ready source of brooded planulae. Experiments addressing objectives 1-3 above have been completed and results of these studies are outlined below. Objective 4 is under investigation currently, but results are not yet available.

The ability of larvae spawned by *P. astreoides* to detect and avoid UVR was assessed in petri dishes filled with seawater where one-half of the dish was shielded from UVR and the other exposed to ambient levels. Observations made every 30 minutes between 1030 and 1330 h showed significantly higher densities of larvae swimming in regions shielded from UVR indicating that these planulae possess UVR receptors.

To further determine how this UVR avoidance behavior affects recruitment patterns in *P. astreoides*, larvae were placed in chambers that were divided into three light regions: PAR (PAR = 400-700 nm) only, PAR + UVAR (UVAR = 320-400 nm), and PAR+UVAR+UVBR (UVBR = 280-320 nm). Larvae obtained from adults at 17 m and placed in chambers at 2 m depth recruited equally to all three regions. In contrast, larvae placed in chambers at 17 m depth were more often found as recruits in the region where UVAR and UVBR were reduced. This somewhat counterintuitive result, i.e. avoidance of UVR in deeper water where its intensities are lower, can be explained when viewed within the context of two additional results. First, mortality was significantly greater for larvae in chambers at 2 m depth as opposed to 17 m and was probably attributable to the extremely high light intensities (both UVR and PAR) present in shallow water. Thus, at 2 m depth, even larvae settling in regions of the chamber where UVR was reduced experienced PAR levels that could induce photooxidative and photoinhibitory stress that ultimately resulted in mortality. Second, more detailed analysis of recruitment patterns at 17 m depth revealed that recruits more often settled on vertical, as opposed to horizontal, substrate when UVR was present. Settling on vertical substrate can reduce UVR exposure substantially (see figures in Browne et al. 1994). These results indicate that UVR may set limits on dispersal and settlement patterns of *P. astreoides* larvae and that at depth these larvae are maximizing their PAR exposure while minimizing UVR exposure.

Results presented above indicate that *P. astreoides* larvae have UVR receptors and can actively avoid high intensities of this radiation while dispersing in the water column or at the time of settlement, but what happens if larvae are duped into making a bad choice? For example, if cloudy skies or low water clarity are present at the time of settlement a planula may be duped into settling in an area where the mean UVR conditions do not favor survival over the long term. We tested this possibility by settling *P. astreoides* on coral rubble and then exposing them to the same three light regimes outlined above (PAR only, PAR+UVAR, and PAR+UVAR+UVBR). Health of newly settled *P. astreoides* recruits; measured as survival, growth, and total chlorophyll and protein concentrations; was not affected by the light regime. This lack of effect can be explained by the ability of these recruits to quickly increase concentrations of a suite of UVR absorbing compounds known as mycosporine-like amino acids (MAAs). After only 20 days, MAAs with absorbance maxima around 330 nm were in significantly higher concentrations in all larvae exposed to UVBR. These results suggest that exposure to high intensities of UVR forces coral larvae to expend energy to combat UVR damage that could otherwise be used for growth and development (Gleason 2001).

The results of our studies with *P. astreoides* indicate that changes in the clarity of the water column may have a significant impact on the settlement patterns of corals. As a consequence, changes in environmental conditions that alter the light regime, such as increased or decreased suspended sediment loads, may have a direct positive or negative impact on coral recruitment. Clearly water column parameters affect UVR intensities and increases in the amount of UVR reaching corals can be more than double the mean annual maximum if the water column changes from its normal state to a sustained period of extreme calm and exceptional clarity (Gleason and Wellington 1993). Thus, for example, land use patterns impacting sediment run-off may indirectly affect coral recruitment dynamics in waters immediately offshore by altering the photic regime of the water column. Having CREWS stations established to monitor long-term patterns of light intensity on the reef and combining these data with hypothesis-driven research, such as outlined above, may allow us to better estimate the consequences that human-induced alterations in water column clarity will have on patterns of coral recruitment.

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Effects of Solar Irradiance on Reef Coral Physiology and Recruitment*

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Opportunity Statement

In this presentation I highlight key results from my dissertation work at the University of Hawaii (Zoology Dept., Committee Chair: Paul L. Jokiel) that contribute to our understanding of coral bleaching and the effects of ultraviolet radiation (UVR) on coral recruitment. The talk was divided into three parts discussing 1) An annual cycle of mycosporine-like amino acids (MAAs – UV-absorbing compounds) and photosynthetic pigments in two species of reef coral, 2) Colony-specific patterns of MAA composition and response to UVR in *Porites compressa*, and 3) The effects of UVR on coral recruitment. I then finished with suggestions for an *in situ* experiment testing the hypothesis that decreased solar irradiance can mitigate bleaching during a natural high-sea-surface temperature event. I am planning to conduct this experiment during a natural bleaching event in the proximity of a CREWS station.

Methods

The data presented in item 1) are in review (Kuffner submitted), and thus are presently available only as part of my published dissertation (Kuffner 1999). Methods involved collecting n = 3 samples of *Porites compressa* and *Montipora verrucosa* on a monthly basis for 14 months on the shallow (<1 m) reef flat of Coconut Island (Kaneohe Bay, Hawaii). This was a population-side survey; coral samples were taken from different colonies at every collection data. MAAs and photosynthetic pigments were separated and quantified using HPLC, and UVR was monitored continuously at the Hawaii Institute of Marine Biology weather station. It is important to document seasonal fluctuations in MAAs and pigments because natural variability in these compounds can better our definition of coral bleaching and may help reveal mechanisms involved in the bleaching process. Data presented in item 2) are published in Kuffner (2002), and present evidence for colony-specific patterns in MAA composition and UVR-response. Methods for the transplantation experiment and the analyses can be found in the published manuscript. Data presented in item 3) are also published (Kuffner 2001), and provide evidence that the larvae of *Pocillopora damicornis* are inhibited by UVR during the settlement and recruitment process.

Results

1) Annual variation in MAA composition revealed that only two MAAs (shinorine in *Porites compressa* and palythene in *Montipora verrucosa*) exhibited a significant positive relationship with UVR radiation. One MAA exhibited a negative relationship (concentration of mycosporine-glycine in *P. compressa* decreased in June – August, 1998), suggesting an antioxidant role as suggested by Dunlap (1995). All photosynthetic pigments (Chl a, Chl c_2,

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/kuffner.pdf

diadinoxanthin and peridinin) in both species of coral decreased in summer months to levels around half of wintertime values. In *P. compressa*, the proportion of diadinoxanthin contributing to the total pigment pool increased in summer months, suggesting an up-regulation of a xanthophyll cycle during high irradiance periods. In *M. verrucosa*, Chl $\underline{a}$:Chl $\underline{c}_2$ decreased in winter months, suggesting photoacclimation to lower light levels.

2) Data from a field transplantation experiment (Kuffner 2002) show that colony-specific patterns in MAA composition and UVR response were surprisingly strong. Another interesting result was that the two female colonies in the experiment (*Porites compressa* is a dioecious species) did not show a response to UVR and had elevated levels of the MAA asterina-330; Michalek-Wagner (2001) found similar sex-specific patterns during the spawning period for soft corals. My data suggest that corals in close proximity to one another can have very different faculties with regards to UVR resistance. Given that increased UVR can cause bleaching (Gleason & Wellington 1993, Grottoli-Everett & Kuffner 1995), colony-specific patterns in MAA composition could be partially responsible for colony-specific bleaching responses. These results suggest that changes in community distributions of different host-zooxanthellae genotype combinations may be possible, and give rise to hope that coral-zooxanthellae populations have genetic differences that may allow for adaptation to increased SST and solar irradiance stress.

3) The results of all three coral recruitment experiments in Kuffner (2001) showed that the presence of UVR in the larval chambers decreased recruitment levels of *Pocillopora damicornis*, but did not increase mortality. A higher proportion of larvae were found still swimming in the water column in chambers with UVR as compared to chambers without UVR. Also, initial levels of MAAs did not play a significant role in the outcome of the experiments. Larvae from deep and low UVR conditions did just as well as those from shallow and high UVR conditions, even though MAA levels in deep and low corals and larvae were about half those from shallow and high UVR. Thus, MAA levels within the range tested here did not affect recruitment. The implications of these results are that UVR is an important variable affecting recruitment of *P. damicornis* in shallow water, and that the role of MAAs in coral recruitment warrants closer examination.

Summary

Data presented here suggest that further investigation into the role of solar irradiance (particularly UVR) in the bleaching process is warranted, and I highly suggest that UVR and PAR sensors, both surface and sub-surface, be part of the CREWS instrumentation ensemble. Also, UVR has been shown to be important in the coral recruitment process (Kuffner 2001). The success or failure of coral recruitment will determine if reefs can regenerate after the high levels of mortality that we are presently observing around the world.

Recommendation for future research

I am presently planning an *in situ* shading experiment during a natural bleaching event in proximity to a CREWS station; this workshop was highly valuable in fostering collaborations for this work. The hypothesis that decreased irradiance can mitigate the bleaching response to high SST will be tested using neutral density shading Plexiglas (treatment) and UVR-transparent Plexiglas (control) placed over corals naturally residing on the reef. CREWS will support this work by supplying data on SST, wind conditions, attenuation coefficients for PAR and UVR, and absolute values of solar irradiance.

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Effect Of Bleaching On The Coral Host Total Lipid Content, Lipid Class Composition, And Skeletal Stable Isotopic Composition[*]

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Mass coral bleaching events occur on a global scale throughout the world's tropical oceans and can result in large-scale coral mortality and degradation of coral reef communities and structure (Glynn, 1996; Reaser *et al*., 2000; Wilkinson, 2000). For any given event, bleaching severity and mortality varies between individual corals, coral species, depths and geographic locations (i.e.: (Edmunds, 1994; Fisk and Done, 1985; Hoegh-Guldberg and Salvat, 1995; Marshall and Baird, 2000; Wilkinson, 2000). Much research has concentrated on the variation in the *Symbiodinium* zooxanthellae type to explore this variation in bleaching. However, less research has been oriented towards examining the effect of bleaching on the animal fraction. In the absence of their zooxanthellae and/or photosynthetic pigments that normally supply the coral animal with up to 100% of its daily metabolic energy requirements (eg.: (Muscatine and Cernichiari, 1969; Muscatine *et al*., 1984; Patton and Burris, 1983), bleached corals may have to rely heavily on lipid stores to supplement and/or to support their daily metabolic energy needs. In bleached Caribbean corals, translocation of fixed carbon from zooxanthellae to coral host is estimated to decreased by ~50% (Porter *et al*., 1989). Decreases in the total amount of carbon, nitrogen, lipid, and tisuue biomass in some species of bleached Caribbean corals suggest that some species of corals consume their own structural material to survive bleaching periods without nutritional input from their zooxanthellae (Szmant and Gassman, 1990; Fitt et al 2000). However, in other coral species, energy reserves (protein, biomass, and glycerol) do not change when bleached (Grottoli-Everett 1995; Fitt et al. 2000; Edmunds et al. 2003). In addition, skeletal stable carbon isotopic composition ($\delta^{13}C$) in symbiotic corals is primarily influenced by metabolic fractionation (Grottoli, 1999; Grottoli, 2002; Grottoli and Wellington, 1999) during photosynthesis and respiration (Grottoli, 2002; Grottoli and Wellington, 1999; McConnaughey, 1989a; McConnaughey, 1989b; McConnaughey *et al*., 1997; Muscatine *et al*., 1989; Swart, 1983). Changes in the skeletal $\delta^{13}C$ in corals during bleaching may lend further insight into the metabolic activity in the coral. Here we show that bleaching in two species of Hawaiian corals results in species-specific responses in total lipid concentrations, lipid class composition, and skeletal stable isotopic values.

Approximately ten weeks after the onset of a natural bleaching event on the coral reefs of Kaneohe Bay, Hawaii in 1996, several *Porites compressa* and *Montipora capitata* corals were collected. Corals ranged from totally white in appearance (bleached) to dark brown (non-bleached). Chloropyll *a* (Chla), total lipid concentration, and lipid class composition was measured in each coral. $\delta^{13}C$ of the skeleton immediately underlying the animal tissue was also measured. Naturally bleached *P. compressa* corals depleted their total lipid stores while *M. capitata* corals maintained them. Further investigation into unevenly bleached corals revealed that *P. compressa* depleted total lipid stores in bleached areas but maintained lipid levels in non-bleached portions of the colony while *M. capitata* maintained lipid concentrations throughout

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/grottoli.pdf

bleached and non-bleached portions of the colony. Together, these results suggest two things: 1- *M. capitata* may be better able to conserve its lipid reserves because it has a 25-30% lower respiration relative to *P. compressa* at both normal (25°C) and elevated (30°) seawater (Coles and Jokiel 1977), and 2- *P. compressa* does not re-allocate existing lipid resources from the non-bleached portion of the colony while *M. capitata* may be able to.

Close examination of the lipid class composition in both bleached and non-bleached corals revealed that both *M. capitata* and *P. compressa* depleted their storage lipids (triacylglycerol and wax esters) and increased their phospholipids as would be expected in stressed animals (Lee *et al*., 1974; Sargent *et al*., 1977). However, a distinct lack of diacylglycerol was observed in *P. compress* regardless of bleaching status whereas the same class of lipids increased in *M. capitata* when it was bleached. Perhaps the absence of diaglycerol is diagnostic of corals that consume their lipids when bleached. Mean skeletal $\delta^{13}C$ in both species decreased when bleached. Such a decrease in $\delta^{13}C$ is consistent with a decrease in photosynthesis (Grottoli, 2002; Grottoli and Wellington, 1999), some observations in bleached Caribbean *Montastrea annularis* (Porter *et al.*, 1989), Costa Rican *Porites lobata* (Carriquiry *et al.*, 1994), and Japanese and Australian *Porites* corals (Suzuki *et al*., in press), indicating that bleaching has a detectable effect on the isotopic composition of the coral skeleton.

Overall, the present study shows that *P. compressa* consumed its total energy reserves when bleached. The complete lack of diacylglycerol in *P. compressa* at that time of year may be responsible for the overall decrease in total lipids observed following bleaching stress and may be diagnostic of corals that consume their lipid stores when bleached. While total lipid concentrations in bleached and non-bleached *M. verrucosa* did not differ, their lipid class composition did. Differences in the reported P/R values may influence whether or not corals consume energy reserves, and may identify corals more likely to survive a bleaching event. In addition, lower skeletal $\delta^{13}C$ in bleached corals may also be useful for identifying past bleaching events in coral paleoclimate proxy records.

This type of research would greatly benefit from the *in situ* data that a CREWS station would provide. Continuous monitoring of seawater temperature, salinity, wind speed and direction, downwelling irradiance, current speed and current direction, would be invaluable for identifying the physical parameters associated with a natural bleaching event. A clear understanding of the physical conditions that resulted in a bleaching event would enhance the interpretation of the biological data.

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Determining Bleaching Thresholds: Separating The Effects Of Light And Temperature For Species-Specific Tolerance Limits*

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Early warning of environmental conditions likely to cause stress to coral reefs has become an important piece of information to reef managers, researchers and the general public. These early warning systems have been operating in the USA and Australia for a number of years (e.g. Hendee 1998, Berkelmans et al. 2002) and demand for these systems is increasing. Despite the fact that "nothing can be done" to prevent large-scale coral bleaching, early warning of bleaching conditions is important to reef managers to help them keep abreast of reef health in their parks and answer questions from the media, politicians and the public. Researchers also need this information, not only to document an unfolding disturbance, but to learn more about the function and physiology of reef organisms and the reef system as a whole.

Despite the fact that the cause and contributing factors to bleaching have been known for decades, there is a surprising lack of information on exactly how much temperature, light (PAR and UV) and time is required to initiate a bleaching response in corals. To advance an early warming system beyond 'best guesses', controlled experiments are required to determine how much and how long of each factor (alone and in combination) is required to cause a bleaching response. I propose that determining bleaching thresholds be done in a two-step process:

1. Construct time-temperature curves for bleaching based on field observations.
2. Use the above time-temperature curves as a guide in setting levels of experimental treatments in controlled laboratory experiments. These experiments are designed to tease out the effects of each treatment alone and in combination.

Time-temperature curves for bleaching are based on in-situ observations of bleaching and water temperatures in years where bleaching did and did not take place (see Fig 1). These curves are not species specific, but in mild bleaching years, will tend to represent bleaching thresholds in relatively sensitive coral species. Because these curves are based on field observations, they represent the sum of environmental conditions that caused the bleaching (Berkelmans, 2002).

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/berkelmans.pdf

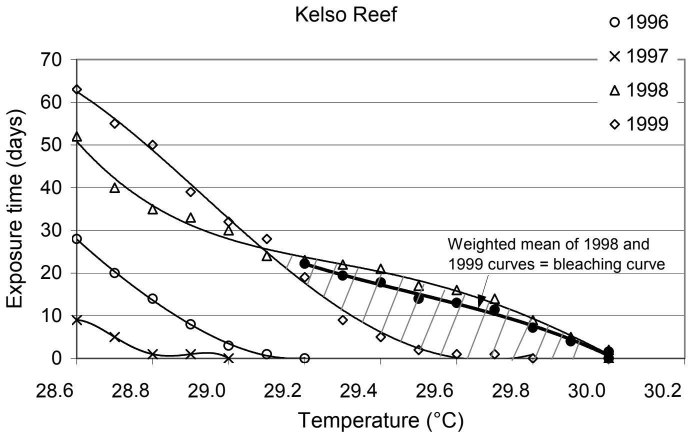

Fig 1. Example of how time-temperature bleaching curves are constructed at the scale of reefs (or regions) for from years where no bleaching took place and years where bleaching did take place. The hatched area is the time-temperature space within which the bleaching curve could fall. The heavy line is estimated position of the bleaching curve based on a weighted mean between the warmest non-bleaching year and the coolest bleaching year, weighted according to the intensity of bleaching on a 4-point scale.

Although these conditions are represented by temperature and time, these data naturally incorporate an unquantified component of light and possibly other factors. This is because moderate to high light conditions almost always accompany high water temperatures. Over the scale of the GBR (2000km), satellite SST's (1km resolution) was able to predict bleaching with 73% accuracy in the 1998 and 2002 bleaching events.

The experimental component should try to determine: (i) what the bleaching curve might look like for individual species of coral, and (ii) the level of variation around the bleaching curve due to PAR and UV light. This could be done in a 3-factor controlled experiment where the factors are temperature, PAR light and time. Due to logistic constraints, UV light might be included in follow-up experiments where PAR light is kept constant and UV light and temperature are manipulated. The final result may be time-temperature curves with known envelopes of variation depending on PAR and UV light levels, as illustrated in Fig 2.

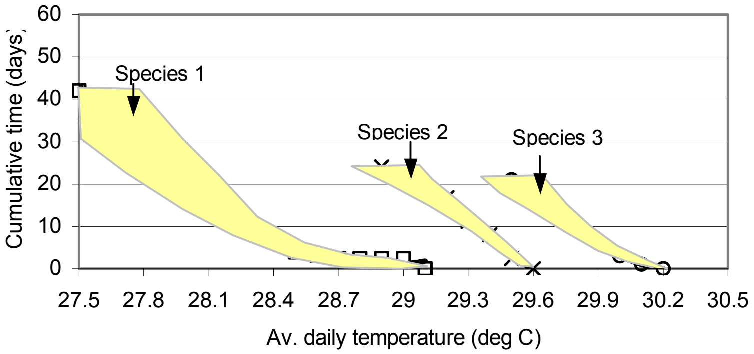

Fig 2. Hypothetical time-temperature curves for coral bleaching and their range of variation depending on PAR and UV light levels for a range of species of interest.

Given the rather narrow range of variation in temperature, temperature treatments will need to be allocated within a range of 1 – 1.5ºC. This is means target temperatures will need to be precisely controlled (≤0.1ºC), which is best done indoors and with a computer controlled process control system (e.g. Turner et al. 2002). Indoor experiments will also allow light levels to be precisely controlled by metal halide lamps (aquarium type). However, the spectral properties of the lamps need to be quantified and evaluated. Light variation within each tank can be reduced by placing coral nubbins on rotisseries that are manually rotated several times per day. Logistic constraints in terms of power supply and costs may limit the number of treatments undertaken in each experiment, in addition to the number of tanks, lighting etc.

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Coral Bleaching And Light Attenuation: Can Elevated Turbidity Help Corals?*

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Problem Statement: Numerous laboratory and field observations have implicated high sea surface temperatures and irradiance as the primary causes of coral bleaching. This results in reduced coral growth and may lead to coral mortality. High turbidity is often considered another stressor of reef corals but reefs living under chronically turbid conditions are being discovered and may be less susceptible to bleaching. Can a reduction in light intensity due to modest increases in turbidity effectively increase the temperature threshold for bleaching?

Methods: A variety of studies have found that exposure of corals living in clear water to high turbidity generally results in increased respiration rates and, by reducing available light, decreased photosynthesis. There is no literature directly addressing the question posed above but a variety of observations suggest that corals can tolerate higher temperatures when irradiance is reduced. For example, reefs exposed to temperatures considered capable of causing bleaching (>30º C) may not if there are cloudy or windy conditions. An integral question is whether ultraviolet (UV) or visible light are more important in the bleaching process.

The following general approach has been proposed with particular reference to reefs of the Florida Keys. Here reefs exist in several habitats as one travels from the Keys themselves across Hawk Channel (6-12 km wide) to the continental shelf break. The water deepens to 10-13 m in Hawk Channel as one proceeds offshore where it shoals before plunging to the depths of the Florida Straits. Patch reefs forming in Hawk Channel are typically exposed to higher turbidities than the bank/barrier reefs along the shelf break. The turbidity of Hawk Channel makes these reefs harder to find and the low water clarity results in few recreational divers visiting them. However, recent data suggest that these reefs may be in better condition than the highly visited bank/barrier reefs just 1-2 nm further offshore (Wheaton et al, 2001). Although bleaching has been observed on the Hawk Channel reefs, it may not be as severe as that seen on the bank/barrier reefs which suffered considerably during the 1997-1998 El Niño. Other diseases may also be less prevalent though this remains to be tested (Santavy et al, 2001). Finally, coral growth rates appear to be slower in Hawk Channel (Cook, et al, 2001). Is this due to turbidity and, if so, is the effect mediated primarily by light attenuation (reducing photosynthesis) or by increased sedimentation (increasing respiration)?

Along with several colleagues, we have proposed monitoring matched pairs of Hawk Channel patch and offshore bank/barrier reefs in the Lower Keys. The reefs would be characterized with respect to the light field and the factors that affect it. These factors include turbidity and its components (plankton, particulate organic matter and inorganic sediments) as well as dissolved materials. Chromophoric dissolved organic matter (CDOM) is a potent

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* Web link: http://www.coral.noaa.gov/cmrc/think-tank/mueller.pdf

absorber of UV radiation and recent results indicate that its concentration is considerably higher in Hawk Channel that at the shelf break where the bank/barrier reefs are found (Anderson et al, 2001). Selected coral colonies (*Montastrea faveolata*) at each site would be examined to determine the zooxanthellae densities, photosynthetic pigment concentrations, genetic make up of the zooxanthellae communities, coral condition (healthy, diseased), photosynthetic performance and growth rates.

Because turbidity is itself very difficult to manipulate, the experimental component of the proposed research focuses on changing the light environment and assessing the coral's responses. Using a reciprocal transplant design, corals from the Hawk Channel site would be moved to a bank/barrier reef site (which has lower turbidity) and placed under conditions that attenuate UV and/or visible light. Some would be exposed to light similar to that in Hawk Channel where they were collected and others to ambient lighting conditions. Conversely, coral from offshore would be placed at a Hawk Channel reef site under ambient conditions at the same depth that they were collected and others placed at a depth where they would receive similar light as that where they were collected. It is possible that increased sedimentation associated with higher turbidity will have some effects and this will not be directly answered with this approach. If light attenuation at the offshore site results in similar growth rates to those seen at the Hawk Channel sites, one might conclude that it is the effect of turbidity on light attenuation, rather than sedimentation, that affects coral growth.

Unfortunately, to really test the original question, bleaching conditions would be needed. Then, it would be most interesting to see if corals on the bank/barrier reef that are under light-attenuated conditions bleach to the same degree as those under ambient conditions.

Relevance to CREWS: As visible light (PAR) is a likely co-factor in bleaching, the recording of PAR should be included without doubt on every CREW station. Further, because light attenuation due to changes in water clarity could be possibly be photoprotective (if the aforementioned hypothesis is correct) or deleterious (if turbidity is very high) to corals, two PAR sensors at different depths are recommended. This allows the calculation of the diffuse attenuation coefficient (K_D), a proxy for turbidity that is more biologically relevant that traditional turbidimeters (nephalometers). Finally, UV radiation may be an important bleaching factor that is changing with climate. Again, two sensors are ideal to calculate the attenuation coefficient, here relating most directly to the CDOM content of water. At least one set of light sensors should be at the depth of the reef so that absolute light available to corals can be estimated. The incorporation of light factors into a predictive bleaching model or expert system (Hendee, et al, 2001) should increase its accuracy. Having both PAR and UV data may allow answering the question: What are the relative contributions of visible or UV light, as co-factors with temperature, to coral bleaching?

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Factors Influencing Geographic and Seasonal Variations in Light Exposure of Coral Assemblages in the Florida Keys[*]

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Introduction

Various studies have implicated both the UV-R (280 – 400 nm) and PAR (400-700 nm) components of solar radiation in various responses of coral reefs to global change (Gleason and Wellington 1993; Drollet, Faucon et al. 1994; Drollet, Faucon et al. 1995; Fitt and Warner 1995; Glynn 1996; Lesser and Lewis 1996; Shick, Lesser et al. 1996; Warner, Fitt et al. 1996; Jones, Hoegh-Guldberg et al. 1998; Hoegh-Guldberg 1999; Anderson, Zepp et al. 2001; Gleason 2001). In this paper we consider various factors that contribute to the exposure of corals to solar radiation, with emphasis on our recent results from the Florida Keys (Figure 1). Our research in the Keys examined in some detail the geographic, inter-annual, seasonal and diurnal variation in penetration of solar UV and PAR radiation into the ocean waters close to the coral reefs. Results of these studies indicate that variations in the optical properties of the water caused by changes in water composition have pronounced effects on UV exposure. We provide new information about the nature and dynamics of the substances in the Florida Keys water that control UV-R and PAR penetration. Our research included measurements of downwelling vertical profiles of UV and visible radiation that were obtained at sites located at the Upper, Middle and Lower Keys and the Dry Tortugas. Absorption spectra of the filtered water samples from these sites also were measured. In addition, we obtained continuous observations of underwater UV-B (305 nm) radiation at a SeaKeys tower (Sombrero) that provided useful insights into the diurnal and seasonal variations of UV penetration that can be directly compared to other meteorological parameters that are measured at this location. Finally, we conducted field and laboratory studies to help elucidate the effects of changes in temperature and solar irradiance on the sources and sinks of light-absorbing substances in the waters over the coral reefs.

Experimental

Underwater irradiance measurements - Depth profiles of underwater irradiance were measured at sites around the Florida Keys primarily using a Satlantic Free Fall MicroPro profiling instrument. Also, profiling was conducted by K. Patterson using a Biospherical PUV instrument equipped with 305, 320, 340, 380 and PAR channels (Patterson 2000). Typically, 5 to 6 casts were conducted at each profiling station. The free falling velocity during these casts was typically 0.3-0.4 m/s, which permitted irradiance acquisition at depth intervals of 5-7 cm, ideal for the turbid coastal shelf waters (Hawk Channel) near the Florida Keys reefs. The instrument was equipped with an OCR-504UV downwelling irradiance sensor with UV-R channels at 305, 325, 340, and 380 nm [spectral bandwidth 2 nm and 10 nm (at 380 nm)], an OCR-504I downwelling irradiance sensor equipped with visible channels at 412, 443, 490 and 555 nm (spectral bandwidth 10 nm), and an OCR-504R upwelling sensor equipped with visible

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/zepp.pdf

channels at 412, 443, 490 and 555 nm (spectral bandwidth 10 nm). The MicroPro was also equipped with pressure sensor (for depth measurements); water temperature sensor and tilt angle sensor were measured during deployment. Calibrations indicate that the accuracy of the cosine response of the OCR-504UV instrument for irradiance incident within 0 – 60^{o} of normal is 8%, and for the OCR-504I it is 3%. Downwelling irradiance was also simultaneously measured at these same wavelengths on the ship deck by an OCR-504UV and OCR-504I sensors. Measurements were logged using Satlantic's Satview software and the data were processed using Satlantic's ProSoft software (see www.satlantic.com). In addition to the depth profiling measurements, downwelling UV-B irradiance also was continuously measured using two OCR-504UV sensors equipped with UV channel at 305 nm; the sensors were mounted on one of the legs of Sombrero Tower at depths separated by 1.50 meters and were set to log data hourly from 0900 to 2000 over a 10 second observation period. Data were downloaded during bi-monthly service visits to the tower. To check for changes due to fouling the sensors were brought to the surface during the service visits and data were logged with the sensors placed in close proximity. Changes in the ratio of the irradiance measured by the two sensors were used to assess the effects of fouling on relative sensor response. These data indicated that fouling became significant over a two-week interval during the cooler times of the year (November – February). For optical equipment at the CREWS sites, use of automated covers with antifouling capability (such as copper strips) would be highly desirable.

UV-visible spectra - UV-visible spectra were measured in duplicate for the filtered water samples that were collected at the same stations where the profiling casts were conducted. Samples were analyzed over the wavelength range of 250 - 800 nm on an Agilent 8453 UV-visible Spectroscopy System in 10.00 cm quartz cells. Spectral slope coefficients were calculated by fitting absorption coefficients to the equation $a_{\lambda} = a_{\lambda o} \exp(-S(\lambda - \lambda_o))$, where $a_{\lambda o}$ is the absorption coefficient at λ_o (i.e., 290 nm) and S is the spectral slope coefficient (Zepp and Schlotzhauer 1981; Blough and Green 1995), using a non-linear least squares method (Sigma Stat, SPSS Inc.). Slopes were calculated over the 290 - 500 nm spectral region.

Chromophoric dissolved organic matter (CDOM) source and sink experiments - The investigation of CDOM derived from seagrass (*Thalassia testudinum*) was performed in the field using sealed acrylic chambers (volume 150 L) that were placed over either dead or living seagrass patches in shallow regions north of Looe Reef. The temperature dependence of CDOM production from freshly-collected dead *Thalassia testudinum* litter added to oligotrophic seawater collected near the Looe Key coral reef in the Lower Keys was determined in the laboratory by using six temperature-controlled, continuously mixed aquaria. Similar studies were conducted in the aquaria using freshly collected mangrove leaf litter from a site in Summerland Key, Florida. Other laboratory experiments involved the exposure of selected filtered water samples in quartz tubes to simulated solar radiation or to natural sunlight. The simulated solar irradiations were conducted in a temperature-controlled water bath located in an Atlas Suntest CPS solar simulator equipped with a 1 kW Xe lamp.

Results and Discussion

Background- There is pronounced geographical, diurnal and seasonal variations in solar radiation that reaches the Earth's surface. These variations are due mainly to changes in the angle of the sun and atmospheric composition with time and place but also to regional and local factors such as surface reflection and terrain. Generally, solar irradiance increases from high latitude to low latitude regions. Thus, the tropics and sub-tropics are exposed to the most intense sunlight. UV-R is the most energetic part of sunlight reaching the Earth's surface, and it has been shown to contribute to the detrimental effects of elevated sea surface temperatures on corals health. UV-R is the sum of two spectral sub-regions referred to as UV-B (280 – 315 nm) and UV-A (315 – 400 nm). The UV-B component (280-315 nm) has been of particular interest in recent years because it is strongly absorbed by ozone, and increases when the atmospheric ozone amount decreases (Shick, Lesser et al. 1996; Madronich, McKenzie et al. 1998; Kerr, Seckmeyer et al. 2003). Total ozone (the sum of ozone in the stratosphere and troposphere) is thinnest over the tropics and sub-tropics and this factor enhances exposure to this biologically active part of solar radiation compared to other part of the globe. However, the UV-B component of solar radiation has been enhanced over high- and mid-latitudes since the late 1970's by the pronounced depletion of stratospheric ozone that has occurred over this region(Madronich, McKenzie et al. 1998; Kerr, Seckmeyer et al. 2003; McKenzie, Bjorn et al. 2003). Changes in cloud cover and haze also can affect the level of solar radiation reaching the Earth's surface. Future trends in clouds and haze are uncertain, but recent data indicate that it became significantly less cloudy in the tropics during the late 1990's (Wielicki, Wong et al. 2002; McKenzie, Bjorn et al. 2003).

In addition to the solar radiation reaching the ocean surface, the light exposure of underwater corals is also strongly affected by the penetration of solar radiation into seawater (Haeder, Kumar et al. 2003; Kerr, Seckmeyer et al. 2003; Zepp, Callaghan et al. 2003). The transmittance of light through seawater at a particular wavelength λ can be described in terms of an empirically-defined parameter referred to as the diffuse attenuation coefficient, $K_d(\lambda)$(Smith and Baker 1981; Kirk 1994; Siegel and Michaels 1996; Vodacek, Blough et al. 1997). $K_d(\lambda)$ is an "apparent" optical property of seawater that is derived from underwater light measurements in the sea. For a region of uniform composition in the sea, the irradiance at depth z and wavelength λ, $E_d(z, \lambda)$, can be approximately related to the downwelling irradiance immediately below the sea surface, $E_d(0, \lambda)$ by:

$$E_d(z, \lambda) = E_d(0, \lambda)\, e^{-K_d(\lambda) * z} \tag{1}$$

Because the irradiance immediately beneath the surface can be related to that reaching the surface (e.g. using equations that describe reflective loss and refraction of light at the air-sea interface), eq. 1 is of great importance in quantitatively relating the irradiance reaching the sea surface to underwater solar spectral irradiance reaching the surface of a coral reef. We computed $K_d(\square)$ values from underwater depth profiles in the UV-R and visible spectral region at a number of sites located at the reefs, outside the reefs in deep oligotrophic waters, and in the coastal shelf region between land and the reefs. Many of the stations coincided with sites that are part of the Southeast Environmental Research Center (SERC), Florida International University's Water Quality Monitoring Network (see http://serc.fiu.edu/wqmnetwork/) which regularly characterizes water chemistry parameters. Our instrument also concurrently logged the changes in temperature with depth in the water. In addition to these experimental approaches, recent research has resulted in the development of a variety of numerical models that can simulate changes in spectral irradiance with increasing ocean depth; these have been reviewed in some detail by several authors (Mobley, Gentili et al. 1993; Kirk 1994; Mobley 1994). These models use inherent optical properties for absorption and scattering of light in seawater in their computations.

Nature of the UV-absorbing substances - To learn more about the nature of the light-absorbing substances in the ocean water around the Florida Keys, we also measured the absorption coefficients for filtered water samples that were collected at the stations where the depth profiling took place. Absorption coefficients a_λ for the dissolved substances were calculated as: $a_\lambda = 2.303\ A_\lambda / \lambda$, where A_λ is the measured absorbance at wavelength λ, and λ is the pathlength of the quartz cell (in meters). Figure 2 provides a comparison of the diffuse attenuation coefficients and absorption coefficients in the UV-B spectral region (305 nm) for various stations located around the Florida Keys. The close correlation between these two coefficients shows that the dissolved substances in the water generally control the penetration of UV-B radiation.

The wavelength dependence of the absorption coefficients can be used to help infer the nature of the UV-absorbing substances in the water. Spectral slope coefficients that describe the relationship between absorption coefficients and wavelength were calculated as described in the Experimental section. The observed spectral slope coefficients were in the same range as those assigned in other studies to CDOM in the water (ref). These results are consistent with other recent studies in ocean waters which indicate that, in the UV-R spectral region, CDOM is generally the most important determinant of $K_d(\lambda)$ (DeGrandpre, Vodacek et al. 1996; Vodacek, Blough et al. 1997; Nelson, Siegel et al. 1998; Nelson and Siegel 2002; Haeder, Kumar et al. 2003; Zepp, Callaghan et al. 2003). CDOM recently has been shown control the penetration of short-wavelength UV-A radiation even in the highly-oligotrophic waters of the Sargasso Sea around Bermuda (Nelson, Siegel et al. 1998; Nelson and Siegel 2002). CDOM has also been referred to as "gelbstoffe" or "yellow substance," "gilvin," and "humic substances." In addition to its important role in attenuating UV-R, CDOM also strongly absorbs in the visible spectral region (Kirk 1994). Thus, it interferes with the remote sensing of ocean color and strongly affects the penetration of PAR in the blue spectral region.

Although CDOM plays the dominant role in attenuating UV-B radiation in the waters around the Florida Keys, it is clear that other substances can play an important role in light attenuation in the UV-A and PAR region. For example, comparisons between the K_d and absorption coefficient spectra for the turbid mid-Hawk Channel region showed that the K_d values in the long-wavelength and blue region (340-443 nm) were typically considerably larger than the absorption coefficients of the dissolved substances in the water (Figure 3). It is likely that these differences are caused by suspended particles in the shallow Hawk Channel waters.

Geographic and current-induced change in UV penetration - The results shown in Figure 2 also demonstrate the great variability in UV-B penetration that we observed at various sites around the Florida Keys. This is further illustrated by the change in absorption spectra that we observed along south to north transects from the oligotrophic Atlantic Ocean waters south of reefs in the Lower Keys to the shallow, coastal shelf waters in Hawk Channel (Figure 4). Generally, the absorption of the water increased sharply along these transects, and the largest change often occurred over a narrow region that represented the interface between the green-yellow waters in Hawk Channel and the blue Atlantic water. The tidal movement of the more-opaque Hawk Channel waters over the reefs can cause very large diurnal changes in UV-B penetration at the reefs. This diurnal effect is demonstrated by the change in K_d values for 305 nm light during mid-August. The K_d values were computed from the irradiance data observed using sensors mounted on the Sombrero Tower , a SEAKEYS/C-MAN station in the Florida Keys (Figure 5). The highest values of K_d corresponded to low tide when the more opaque waters of Hawk Channel were transported out over the reef line. Figure 6 illustrates the impact of such changes in K_d values on light exposure where it can be seen that a 3-fold decrease in the K_d value can result in over an order of magnitude increase in light exposure at a depth of 4 meters.

Seasonal changes and stratification effects- Irradiance vs. depth profiles were measured at deep sites located south of the coral reefs in the Florida Keys (Figure 7). During most of the time the water from these deep sites is transported over the reefs. Hence, seasonal changes in the surface waters of these deep sites are an important determinant of the light exposure of the reefs. As shown in Figure 7, the depth dependence of both the light as well as temperature differs greatly between the warm summer months and cold winter months. The upper ocean water is generally much colder and more opaque to UV-R during the cold winter months than during the summer.

Moreover, although the temperature is almost depth-independent and depth dependence of the downwelling irradiance is close to exponential during the winter, a much more complex depth dependence of temperature and light develops during the warm summer months. The temperature profiles during the summer indicate that the water has stratified; *i.e.* that it has developed a poorly-mixed thermocline that blocks upward transport of cooler, deep waters to the surface layer. The thermocline is the region where temperatures rapidly decrease with depth. The pronounced stratification effect of the water is accompanied by a substantial increase in UV-R penetration in the surface waters above the thermocline compared to that below it. This is evidenced by a change in the slope of log plots of the irradiance versus depth in the vicinity of the thermocline. We attribute this effect to combined photobleaching and microbial degradation of the CDOM (Vodacek, Blough et al. 1997; Moran, Sheldon et al. 2000; Nelson and Siegel 2002; Haeder, Kumar et al. 2003; Zepp, Callaghan et al. 2003) in the upper water column coupled with reduced inputs of cooler, more opaque deep water. The term “photobleaching” refers to the decrease of absorption coefficients of the CDOM in the UV-R and visible spectral regions in irradiation. This effect also has been observed at other locations in the ocean (Siegel and Michaels 1996; Vodacek, Blough et al. 1997; Nelson, Siegel et al. 1998; Nelson and Siegel 2002). This result suggests that the extensive stratification which occurs under ENSO conditions may be greatly increasing exposure of the reefs to UV-R. Indeed, it has previously been suggested that increased UV exposure may result as a consequence of clarification of the seawater during the doldrums conditions that accompany El Niño events (Gleason and Wellington 1993; Shick, Lesser et al. 1996; Gleason 2001). This possibility appears to be confirmed by the comparison of the inter-annual K_d values for 305 nm radiation at various sites in the Dry Tortugas (Figure 8). During August 2002, a moderate El Niño year, the waters around the Dry Tortugas had significantly lower K_d values than during the early La Niña period of mid 1998 to 1999. Moreover, during the transition from El Niño to La Niña conditions in the eastern equatorial Pacific during summer of 1998, a large increase in CDOM concentrations was observed as cooler, CDOM rich subsurface waters upwelled to the ocean surface (Figure 9) (Siegel, Moritorena et al. 2002). These observations suggest that UVR penetration and sea surface temperatures in this region of the open ocean were unusually high during El Niño conditions and that a return to usual conditions occurred as the El Niño ended. Additional research is required to confirm this possibility.

Sources and sinks of CDOM – This study was performed in a coastal region of the Florida Keys with CDOM content that is impacted by terrestrial runoff, marine production in the shallow Florida Bay and Hawk Channel region, and a tidal driven mixing with low organic content 'blue' waters from the Florida Straights of the Atlantic Ocean. Terrestrially derived CDOM originates through the decomposition of dead plant material such as mangrove leaves, grasses and other land-based plants and it is introduced into water via leaching and runoff from land. Clearly, human activities on land such as land use change and hydrologic control measures can impact the release of CDOM from this source. Currents move the water from Florida Bay south into Hawk Channel and over the coral reefs (Figure 1). CDOM also can be produced through the decay of algal detritus; this source of CDOM has been referred to as "microbially-derived" (McKnight, Boyer et al. 2000). The CDOM in the oligotrophic waters of the Florida Straits likely is mainly microbially derived. In shallow coastal shelf regions such as Florida Bay and Hawk Channel, large amounts of biomass are produced by submerged aquatic vegetation. Around the Florida Keys and other global locations where coral reefs are located, turtlegrass (*Thalassia testudinum*) is a major source of biomass (Peterson and Fourqurean 2001) and thus potentially a significant CDOM source.

Our studies using chambers over grass beds in the field as well as with dead grass litter suspended in temperature-controlled aquaria indicated that *Thalassia* does indeed produce CDOM that has a featureless exponential absorption spectrum with about the same spectral slope coefficients as that of water samples obtained from Florida Bay and the northern part of Hawk Channel (Figure 4). Within experimental error the absorption spectrum of this CDOM was insensitive to the temperature at which it was produced. However, the rate of CDOM production under laboratory conditions increased with increasing temperature (Figure 10). The *Thalassia*-derived CDOM, like the water samples from Hawk Channel, also was susceptible to photobleaching by solar radiation. The half-life due to photodegradation alone (under irradiation equivalent to that derived at mid-afternoon during July in the Florida Keys) was also dependent on the temperature of CDOM production with the shortest being 22.4 ± 1.7 hr for material produced at 32.3 ± 0.2 C and the longest half-life observed as 35.2 ± 2.3 hr for material produced at 21.9 ± 0.2 C. During photodegradation the spectral slope coefficient of the CDOM solution also increased. A similar increase in slope is observed in a typical transect from coastal to offshore regions. These results indicate that a portion of the observed increase in spectral slope coefficient in these transects may be attributed to photobleaching of a near shore seagrass derived CDOM during transport offshore.

We also found that mangrove leaves are another potentially important source of CDOM in the Florida Keys. Like the seagrass CDOM, the mangrove derived CDOM also was susceptible to photobleaching by solar radiation. Specific absorption coefficients (absorption coefficients normalized to dissolved organic carbon) for mangrove CDOM solutions were about twice as high as those for the seagrass CDOM solutions.

Conclusions

Evidence is presented in this paper that UV exposure of coral reefs in the Florida Keys is controlled by CDOM in waters overlying the reefs. Diffuse attenuation coefficients were determined using downwelling vertical profiles of UV and visible radiation that were obtained at sites located at the Upper, Middle and Lower Keys and the Dry Tortugas and absorption spectra of the filtered water samples were measured. Absorption and diffuse attenuation coefficients were highly correlated ($r^2 > 0.9$) in the UV-B (290-315 nm) spectral region. These results support the hypothesis that UV attenuation at these sites is predominately attributable to absorption by CDOM. Absorption coefficients of water samples collected at the sampling sites could be closely described by a non-linear exponential function in the UV-R and blue region of PAR (300 – 500 nm). The absorption spectra of CDOM freshly derived from decaying detritus from seagrasses and mangroves closely matched those of the CDOM in the shallow regions of the study region that were close to land, indicating that these are major CDOM sources in the Florida Keys. The CDOM photobleached with loss of UV absorbance and an increase in spectral slope coefficient when exposed to simulated solar radiation. Under summer conditions with low winds a pronounced stratification effect on UV-R transmission occurred in the deep water just outside the reefs, the net effect of which was to substantially increase UV penetration in the surface waters above the thermocline. This effect is ascribed to combined photobleaching and microbial degradation of the CDOM in the upper water column coupled with reduced upwelling of cool, more opaque waters from the deep ocean. Because this surface water is often laterally transported over the reefs by the action of currents, this stratification effect enhances reef UV exposure compared to well-mixed conditions. This result suggests that the extensive stratification which occurs under ENSO conditions may be greatly increasing exposure of the reefs to damaging UV. We conclude that CDOM concentrations and UV penetration over the reefs are modulated by a complex interplay between this stratification effect coupled with transport and photobleaching of CDOM-rich waters from shallow waters close to the reefs.

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Figure 3. Diffuse attenuation coefficient spectra compared to absorption spectra for mid-Hawk Channel, the coastal, shelf region between land and the reefs in the Florida Keys. The comparison shows that absorption and scattering by suspended particles make a significant contribution to UV-A and PAR light attenuation, but CDOM controls UV-B attenuation.

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Figure 10. Temperature effects on the production of CDOM from seagrass (*Thalassia testudinum*) litter. These experiments were conducted in the laboratory in temperature-regulated aquaria.

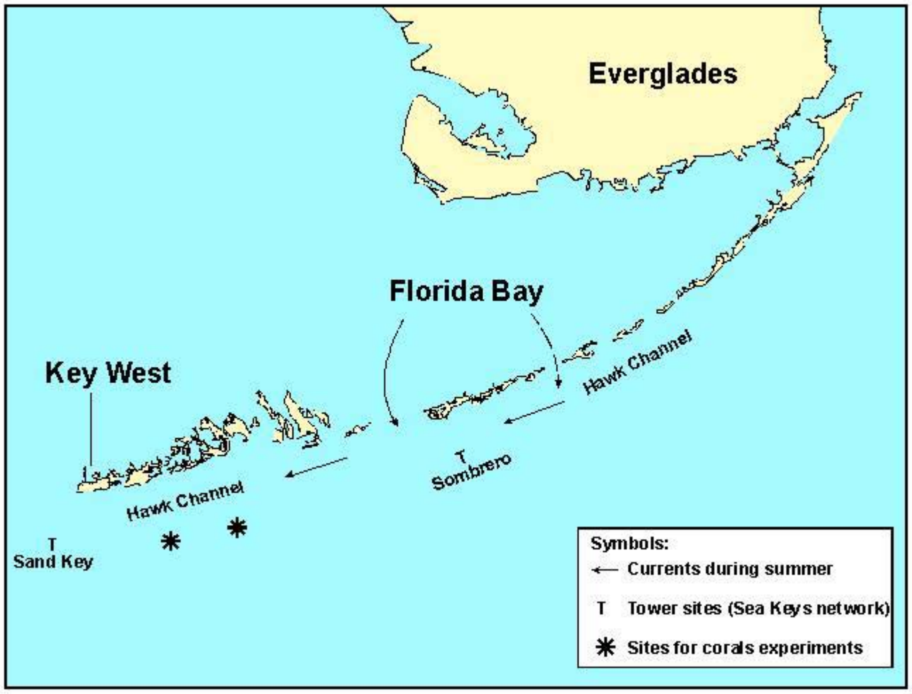


Figure 1

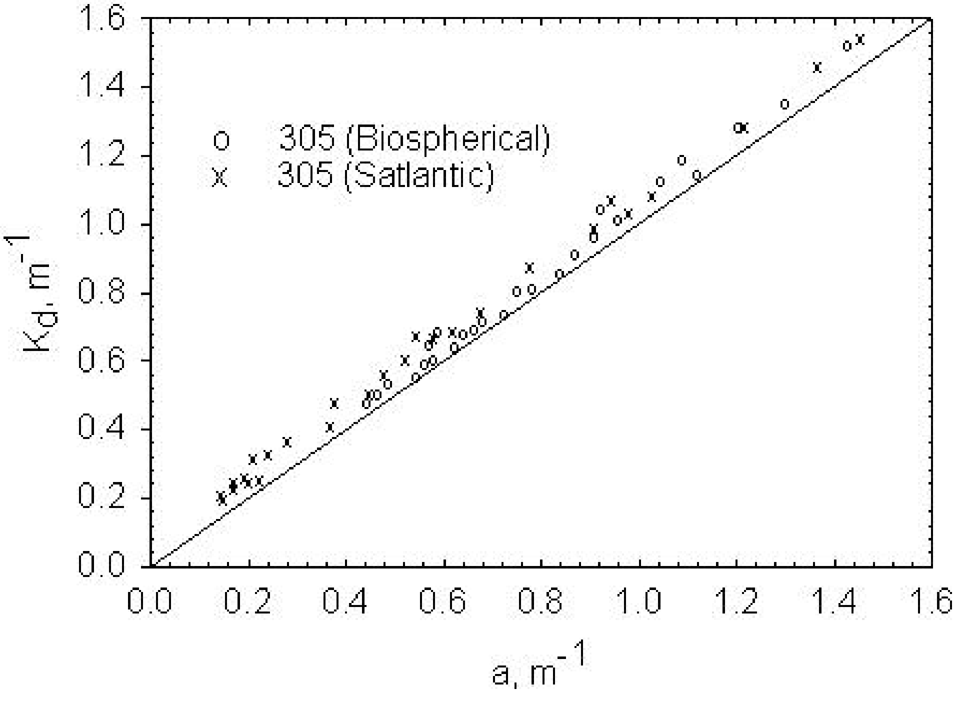
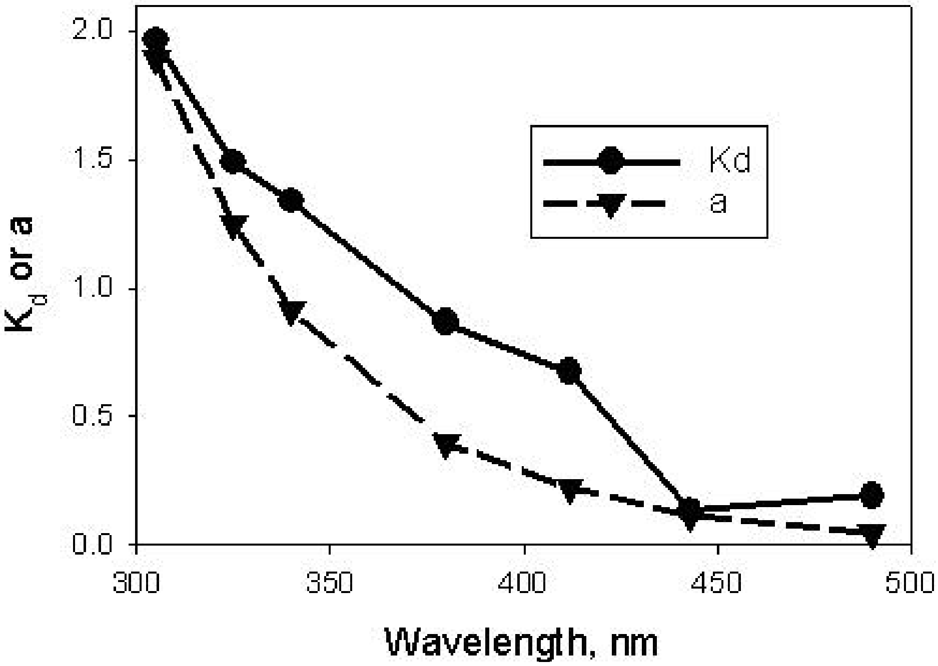


Figure 2



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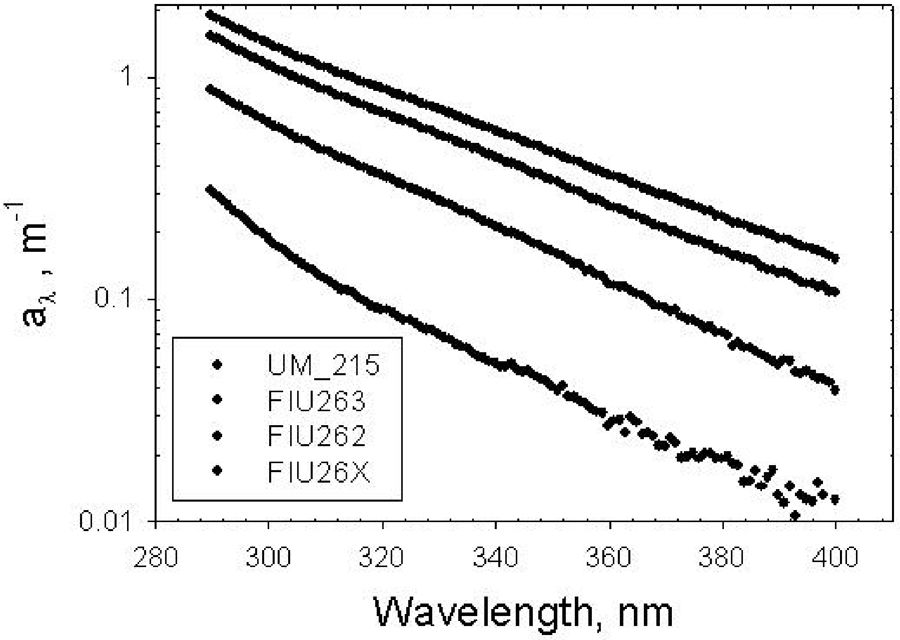

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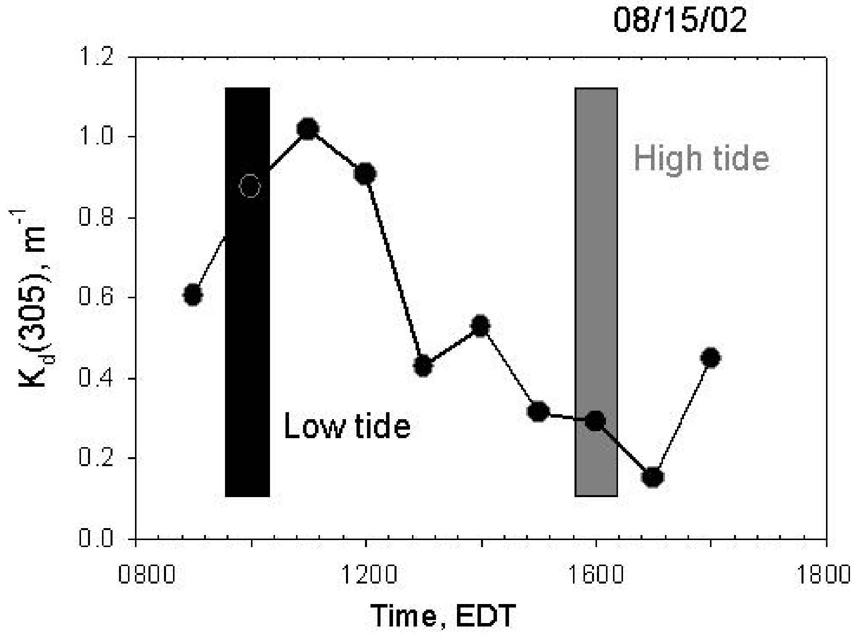

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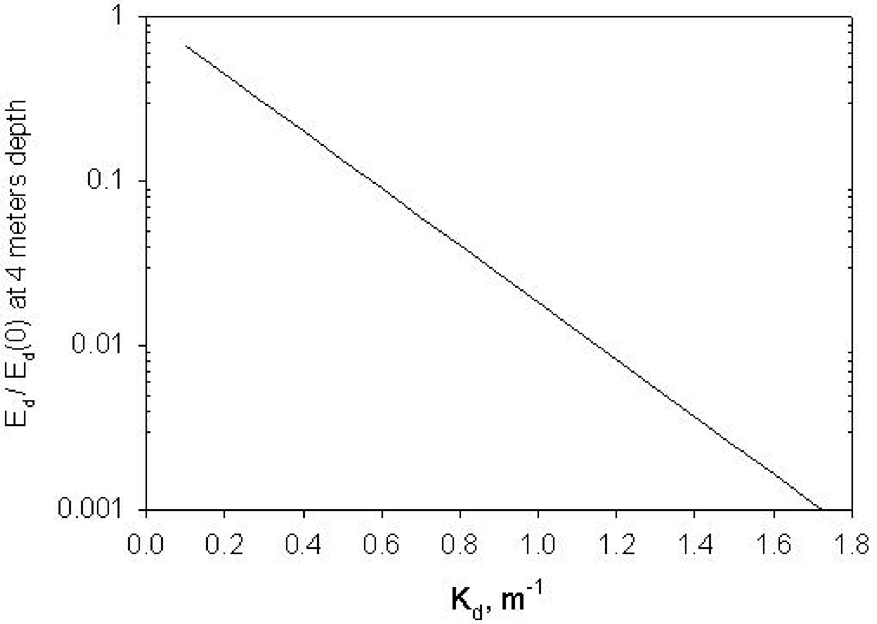

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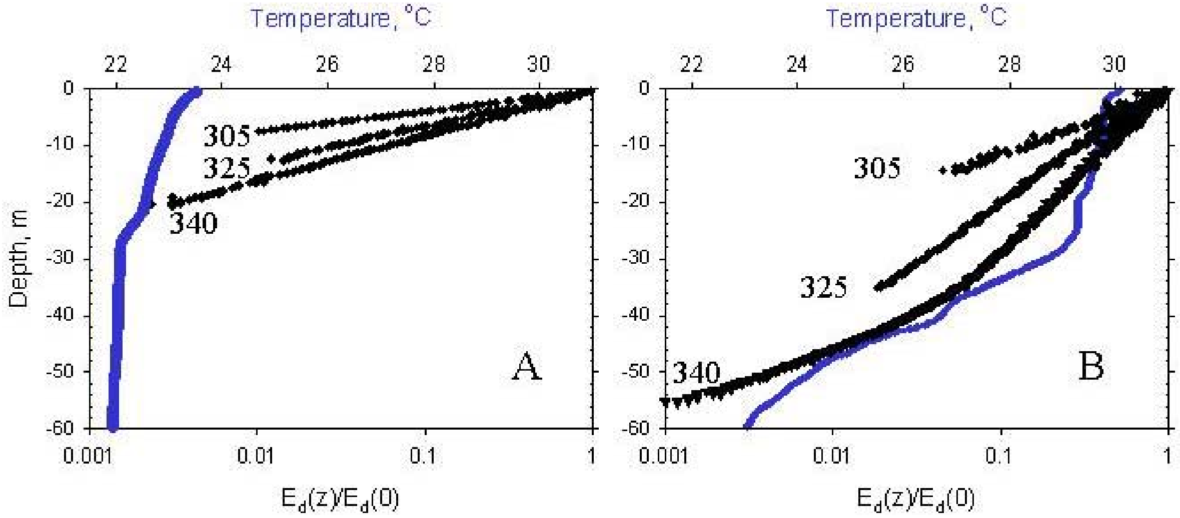

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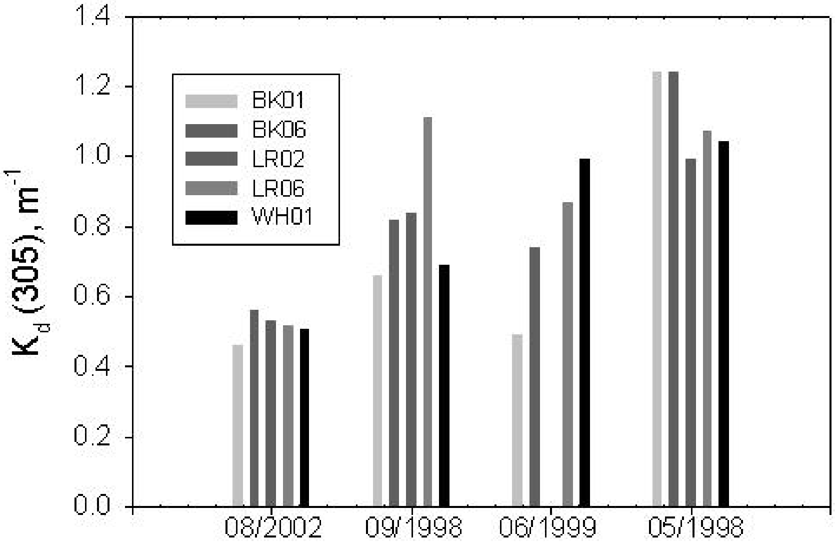

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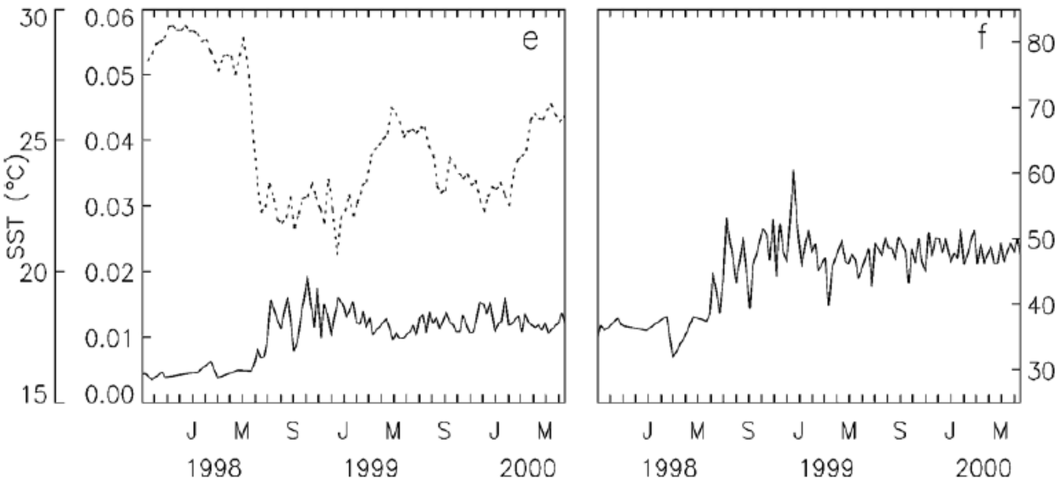

Figure 9

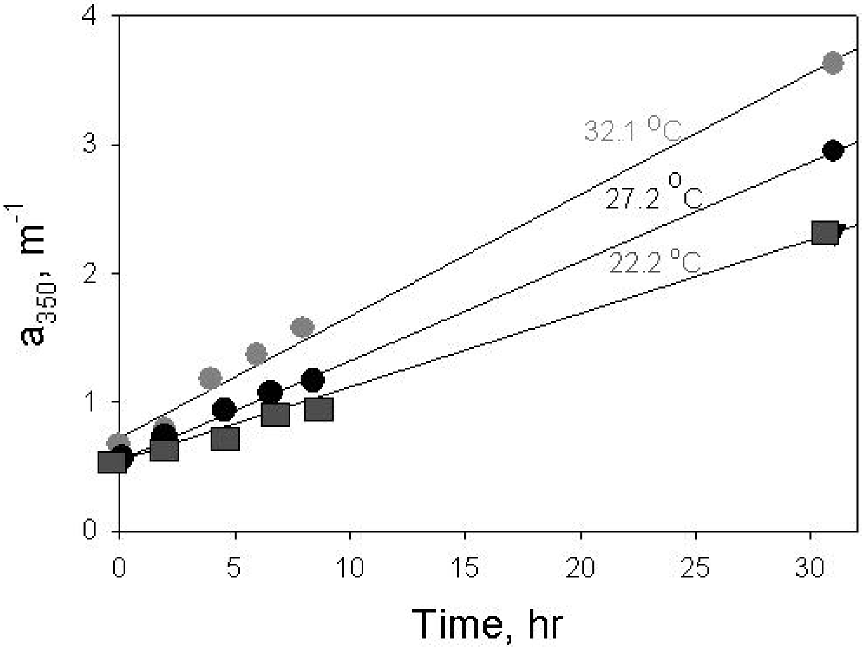

Figure 10

Assessing the Health of Coral Reef Ecosystems in the Florida Keys Using an Integrated Molecular Biomarker System[*]

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Abstract

We are using a novel cellular diagnostic system (CDS) to assess the physiological status of corals by assaying specific parameters of cellular physiology. In a recent series of papers, we demonstrated how this technology can be used to characterize coral health. In laboratory studies, diagnostic cellular parameters distinguished the separate and combined effects of heat and light on a star coral (*Montastraea faveolata*) and its symbiont (zooxanthellae), and provided evidence that oxidative stress plays a central role in bleaching. In defined areas of south Florida (Biscayne National Park) and the upper Florida Keys, colonies of *M. annularis* showed a strong correlation between oxidative stress parameters and bleaching. Under non-bleaching conditions, analysis of these colonies provided evidence for local stressor effects and possible types of stressors. Thus the CDS is allowing us to (1) diagnose whether corals are physiologically stressed, (2) discriminate between global-level stressors (e.g., El Nino/La Nina effects) and local-level stressors (e.g., agricultural runoff) and (3) possibly predict the condition of corals several months before more obvious symptoms appear (e.g., coral bleaching or coral death).

Introduction

Monitoring projects such as the Coral/Hardbottom Monitoring Project (CRMP, US EPA/National Marine Sanctuary, 2001) have documented recent, severe declines in coral cover and diversity in the Florida Keys; but causality has not been determined. Current health assessment methods tend to focus on either the abiotic components of a reef ecosystem (i.e., contaminant analyses) or ecological responses (i.e., species richness, percent cover) because these are well developed (e.g., Otte et al., 1993; Wilson et al., 1996). Health assessment methods using ecological responses, however, detect disturbances only after the community has been altered; thus measuring indirect effects of environmental stressors. While traditional water and sediment analyses, for example, can document the quality and quantity of a contaminant in the environment, they cannot readily describe (and therefore cannot predict) biotic responses to that contaminant. The presence of a particular contaminant does not necessarily decrease ecosystem health, because compensatory mechanisms operating at the cell, tissue and organ levels may ameliorate the stress before it reduces the fitness of an individual organism, or alters its functional role in the community.

Initial and direct effects of environmental stressors target molecular and cellular components of biologically hierarchical systems. Technologies that measure changes in cellular parameters

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/woodley.pdf

have been largely been unavailable to coral researchers. This creates a gap in our understanding of how stressors affect ecosystems. A cellular diagnostic system (CDS), based on a medical paradigm, has been developed that targets the cellular end of the biological hierarchy. This system provides an ability to diagnose health status by assaying specific cellular and molecular parameters that govern organismal health and fitness (Downs *et al*. 2000, Downs, Fauth & Woodley 2001, Downs, Dillon & coauthors 2001, Downs, Shigenaka & coauthors 2002, Downs, Fauth & coauthors 2002, Woodley *et al*. 2003).

Although this approach is amenable to a variety of different ecosystems, we specifically tailored it to coral physiological health and discerning the causes of coral reef system declines (Downs et al., 2000; Woodley et al., 2001). The specific cellular and molecular parameters used to assess physiological condition, include (but are not limited to) membrane integrity and composition (e.g., lipid peroxidation products), anti-oxidant redox potential (e.g., glutathione redox status), molecular chaperone activity (e.g., heat-shock proteins 60 & 70), enzymatic anti-oxidants (e.g., catalase, superoxide dismutases, glutathione peroxidases), stress-signaling pathways (e.g, MAPK, JANK), xenobiotic detoxification pathways (e.g., cytochrome P450 family, P-glycoprotein 160), metal-regulatory proteins (e.g., metallothionein, ferritin, porphoryn), protein status and turnover (e.g., ubiquitin, protein carbonyl formation), and genomic and translational integrity (e.g., DNA abasic phosphate site formations). These parameters quantify specific cellular physiological functions, including (1) whether the structural integrity of the cell is compromised, (2) the type or nature of the stress (e.g., oxidative stress, metal stress, salinity stress), and (3) whether defenses have been mounted against a particular stress (i.e., pesticide, acidity, heavy metal, PAH).

In laboratory experiments, explants of *Montastraea faveolata* demonstrated significant physiological changes in response to heat stress both in the light and in the dark (Downs, et. al, 2000). Changes in several cellular parameters indicated significant differences in physiological status when corals were heat stressed in the dark versus those heat stressed in the light, thus providing an ability to distinguish separate and combined effects of the stressors. Lipid peroxide (LPO) levels, for example, differed significantly among all three treatments. Mean production of LPO was 4.4 and 5.9 times greater when corals were heat-stressed in the dark and light, respectively, than in controls. This increased LPO production in the light indicated that antioxidant defenses were overwhelmed, probably by light-dependent generation of active oxygen species. The CDS also contains assays that are specific to either the anthozoan coral or it s symbiotic algae. For example, αB-crystallin is found only in the cytosol of animals, where it protects cytoskeletal elements during stress (Derham and Harding, 1999). As expected, αB-crystallin levels increased significantly in heat stress treatments compared to the control, and were unaffected by the light regime. In contrast, levels of the chloroplast small heat shock protein (chlpsHsp), produced only by the algae, responded strongly to photosynthetically active radiation. Levels of chlpsHsp were significantly higher (5X) in corals exposed to both heat-stress and PAR than to either control conditions or heat-stress in the dark; thus allowing evaluation of the effects of compound stressors.

In 1999, coral colonies (*Montastraea annularis* species complex) sampled off Key Largo, FL, were exposed to elevated ocean temperatures for several months. We observed strong positive correlations between accumulation of oxidative damage products and subsequent bleaching throughout the sampling period. Corals with high levels of chloroplast small heat shock proteins (chlpsHsp) and anti-oxidant enzymes, superoxide dismutases (SODs), had low levels of oxidative damage products, and did not bleach. In contrast, corals with low chlpsHsp and SODs – most colonies in deeper water – experienced oxidative stress, had higher chaperonin levels and protein turnover activity, and bleached in late summer. Thus, bleaching was intimately coupled to the anti-oxidant and cellular stress capacity of coral colonies, suggesting bleaching was a final defense against oxidative stress (Downs et al. 2000, Woodley et al. 2003). Laboratory experiments on a sister species (*M. faveolata*) supported this mechanism of heat-induced coral bleaching.

Continued seasonal evaluation of corals at our Florida Keys study sites demonstrated that the CDS could distinguish whether a local coral population of *Montastraea annularis* was being stressed by a global stressor (e.g., high sea-surface temperatures; Fig. 1) or by a stressor that is local in nature (Fig. 2). In conjunction with other technologies and monitoring methods, this biotechnology was able to identify potential stressor(s) responsible for the decline (Fig. 3). The CDS also possesses the ability to predict the progression of a health condition based on key diagnostic markers (Fig. 4).

In Figure 1, *M. annularis* scleractinian Hsp60 and ubiquitin data from the 1999 sampling project can be diagnostically interpreted that corals at all four depths were experiencing a protein denaturing stress, as indicated by increased ubiquitin levels (a key component of a pathway for degrading 80% of the proteins in the cell), that is positively correlated with abnormally high sea surface temperatures that peak in the months of July and August (Downs et al., 2002). Hsp60 (for description of function, see Downs et al., 2000) data in 1999 corroborate this diagnostic interpretation. Though the extent of cellular damage differed significantly with depth, the data support the argument that coral cellular damage at all four sites was the result of a global stressor (La Nina sea-surface temperature effects). In 2000, the patterns of both parameters are radically different than that of observed for 1999 and are not correlated with sea-surface temperatures (Woodley et al., in preparation). In March 2000, corals at 3 meters were not experiencing a protein denaturing cellular condition, but were experiencing non-adverse changes in mitochondrial function. In June 2000, corals at the 3m site indicated that they were experiencing a cellular stress that was adversely affecting mitochondrial function. The diagnostic interpretations for both 1999 and 2000 are corroborated by other diagnostic biomarker data. In summary, the cellular stress experienced by corals in 1999 at all four sites was the result of global stressor while cellular damage experienced by corals at the 3.1m and 9.1m sites in 2000, support the argument that a local stressor is impacting these two sites (and that the stressor is different for these two sites – Woodley et al., in preparation). In 2000, using only three diagnostic markers (out of 24 biomarkers assayed for each coral sample), we determined that a coral reef site in Biscayne National Park (BNP) was experiencing a severe cellular stress and that it was most likely generated by an electrophillically-modifiable xenobiotic (e.g., a fungicide, an organometalloid, endosulfan) (Fig. 2 & 3). The extremely high-level of ubiquitin indicates severe rates of protein turnover; this interpretation was corroborated by five other cellular biomarkers. The level of ubiquitin in March 2000 at the BNP site has been suggested to be near the maximal threshold capacity for this coral species – massive cellular deterioration is beginning to occur and coral death could be predicted. In August 2000, significant, punctuated coral coverage loss at the BNP site was observed – no observable coral coverage degradation was observed in March 2000. This partially unidentified stressor adversely affected both the scleractinian cellular physiology and the dinoflagellate cellular physiology (Fig. 2). Data presented in Fig. 3 can be interpreted that corals at the BNP site were responding to a xenobiotic stressor and that the response pathway included a monooxygenase catalytic reaction at the site of olefinic double bonds of the xenobiotic, the conjugation of glutathione to the xenobiotic by glutathione-s-transferase, and cellular exclusion of the GSH-conjugated xenobiotic by a P-glycoprotein 140/160 pump action (a.k.a. MDR: multi-drug resistance gene) (Woodley et al., in preparation; Downs et al., in preparation; not all data shown for this interpretation).

We are continuing to assess the condition of the corals at selected sites in Biscayne National Park (BNP) and in the upper Florida Keys National Marine Sanctuary (FKNMS) at multiple scales in order to compare the precision, sensitivity and prognostic capabilities of the CDS with measures traditionally used to assess ecosystem health. These include 1) community-scale condition of selected patch reefs was assessed using the well-established Atlantic and Gulf Rapid Reef Assessment (AGRRA, Ginsburg et al., 2000); 2) the condition (i.e., mottling or bleaching) of populations of a key symbiont-bearing foraminifer (*Amphistegina gibbosa)*, living in the vicinity of the corals, is also being monitored according to Hallock et al., 1995; 3) individual-scale studies, include monitoring lesions on the coral (Meesters et al., 1997) and the assessment of the overall condition (i.e., bleaching, disease, overgrowth, etc.) of the sampled corals. These assessments will be compared to measures of health status taken at the cellular physiological level in coral (*Montastraea annularis*), fish (*Haemulon plumieri* and *Stegastes partitus*), algae (*Halimeda opuntia*), and snails (*Coralliophora abbreviata*) using CDS (Downs et al., 2000; 2001). Environmental data, including continuous water temperature measurements (using HOBO data loggers) and nutrient levels (taken at the time of biological sampling), sediment-trap data, and data from other ongoing monitoring studies, (i.e., CREWS monitoring stations) are also being collected and are critical to the overall interpretation of the data. The environmental data will be analyzed in conjunction with community, population, coral condition and molecular data to develop a more comprehensive overview of coral ecosystem health and provide evidence for the underlying stresses.

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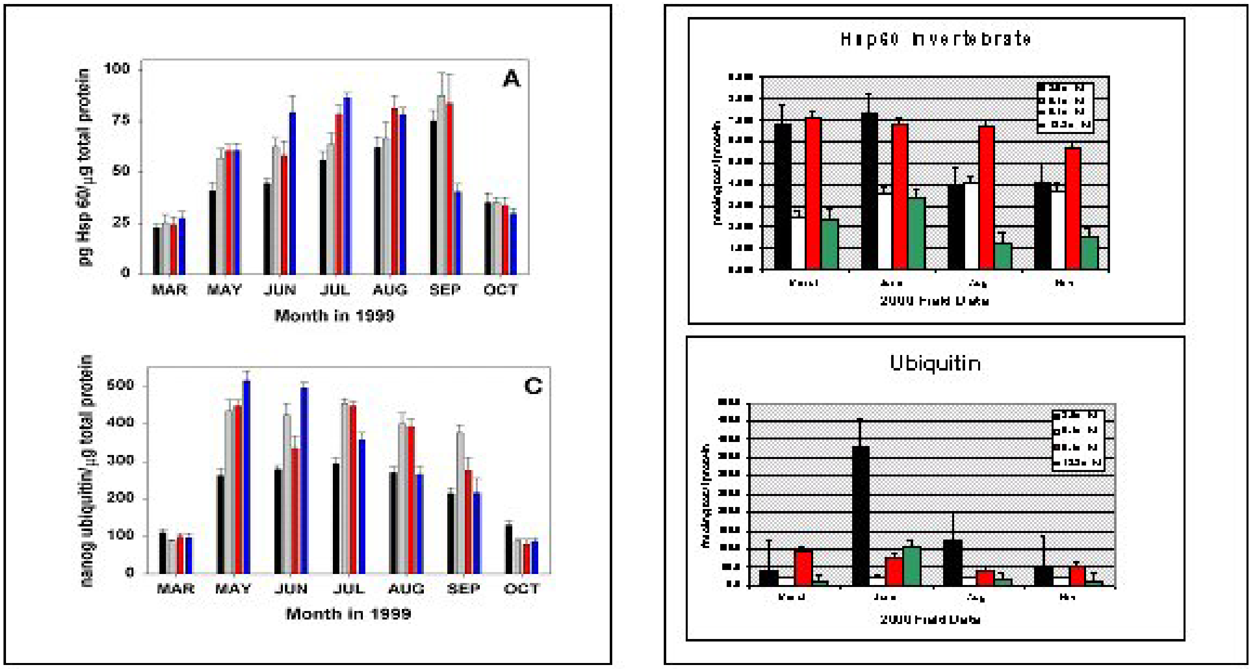
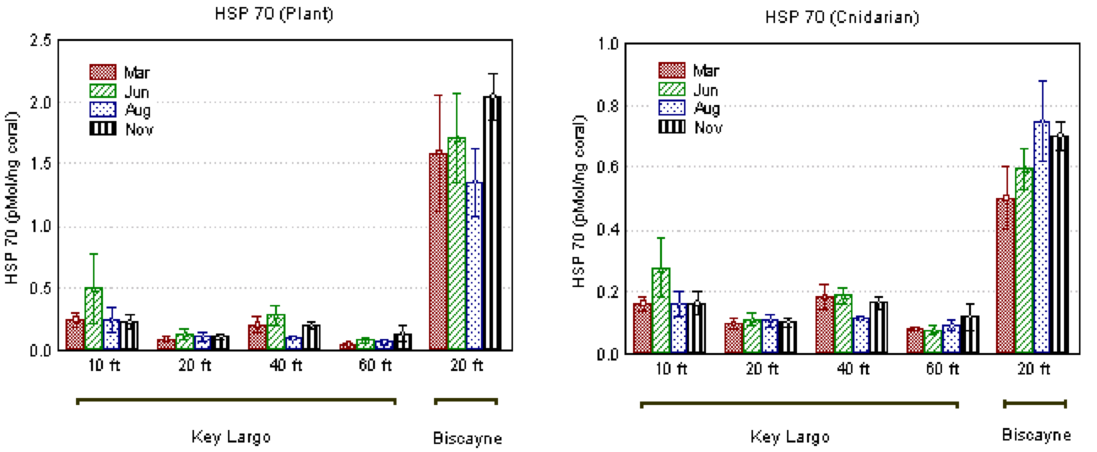


1999

2000

Figure 1. The same coral colonies from four depth sites were sampled on a monthly basis in 1999 and a quarterly basis in 2000. Hsp60 reflect chaperonin levels in the scleractinian; mean concentrations varied significantly with depth, month, and the depth x month interaction in 1999 (repeated measures MANOVAs: all *F* > 2.56, *P* < 0.02;). Ubiquitin levels reflect the rate of protein degradation, which varied significantly with depth, month, and the depth x month interaction (repeated measures MANOVA: all *F* > 8.80, *P* < 0.0001). Bars show untransformed mean (+ 1 SE) biomarker concentrations at each depth: for 1999 panel, black = 3.0 m, grey = 6.1 m, red = 9.1 m, blue = 18.3 m. Sites are from a four-mile long transect off the eastern shore of Key Largo.



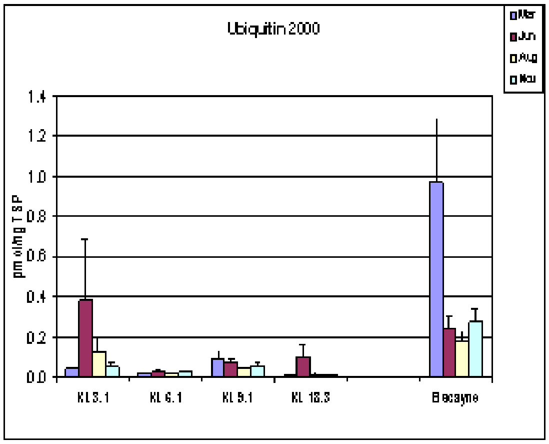


Figure 2. Data from 2000 field collections. Hsp70 is a ubiquitous chaperone, necessary for life. It functions to fold newly synthesized proteins into their active state and refold denatured proteins (resulting from a stressor) into functional enzymes. If a protein is severely damaged and cannot be refolded into a functional enzyme, it must be degraded. Protein degradation occurs mostly through the ubiquitin-proteolytic pathway. Damaged proteins are conjugated with ubiquitin, which designates to the cell that this specific protein is to be degraded. We have developed individual assays that are specific for the Hsp70 homologues found in both the dinoflagellate and scleractinian. Key Largo sites are the same as in 1999. Biscayne site is a patch reef found in southern reaches of Biscayne National Park, 15 nautical miles north of the Key Largo depth transect.

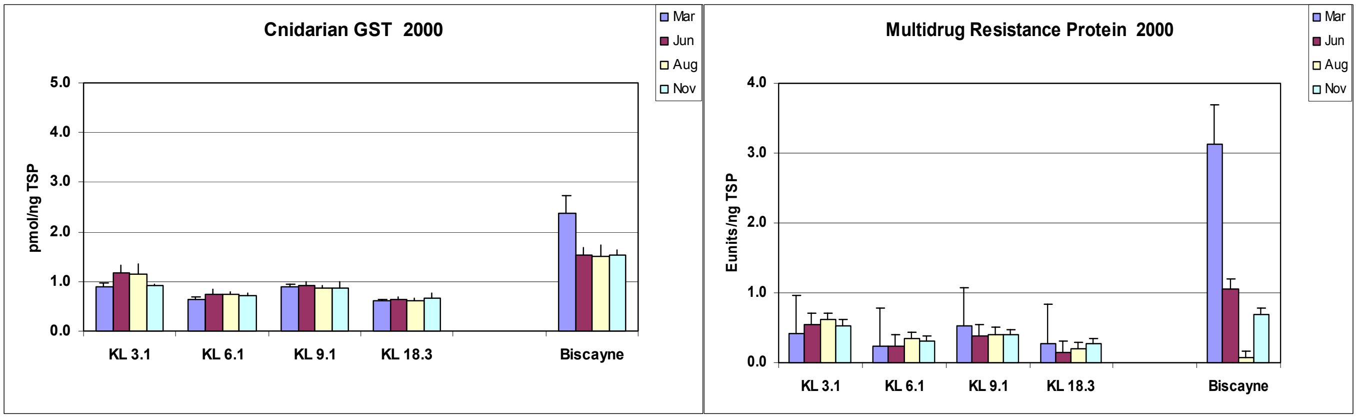
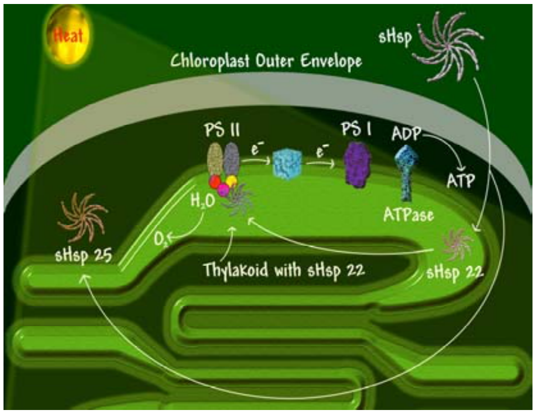


Figure 3. Data from 2000 Field collections. GST Invertebrate = scleractinian homologues of glutathione-S-transferase. GST is an enzyme that will conjugate a xenobiotic with reduced glutathione so that the xenobiotic can easily managed by the cell. MDR = P-glycoprotein 160, a member of the ABC family of proteins that is up-regulated when an organism has been exposed to specific classes of xenobiotics. Its function is to detoxify the cell of xenobiotics by pumping these xenobiotics out of the organism. Site locations are the same as described in Figure 2.

Abstract:

A



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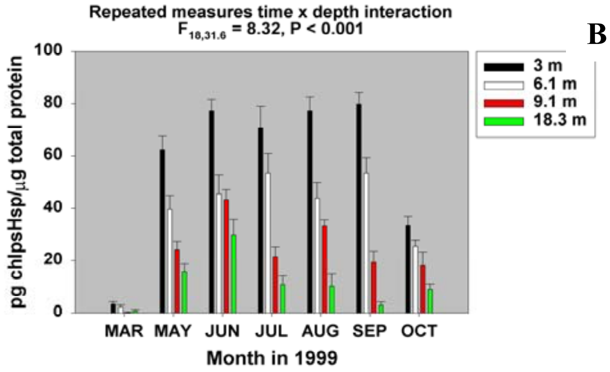

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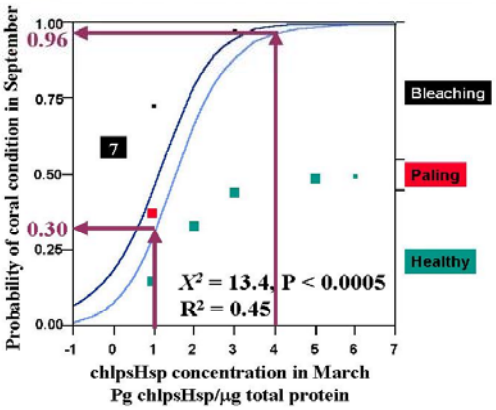

Fig. 4 Panel **A** – Function of the chloroplast small heat-shock protein (Chlpshsp). This protein is only induced when photosystem II is being damaged. It is a major adaptation of photosynthesis against heat stress, oxidative stress, and photoinhibition (Downs et al., 1999a, b) Panel **B** – Levels of ChlpsHsp in dinoflagellate of *M. annularis*. Coral samples and sampling scheme the same as in Fig. 2. (Downs et al., in rev.) Panel **C-** Logistic regression analysis of probability of the level of chlpsHsp in March to predict coral bleaching in September when sea surface temperatures reached 31ºC in August (Fauth et al., in prep.)

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Recruitment and Biodiversity Studies on ENSO-Impacted Coral Reefs in Panama[*]

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Even though hundreds of severe coral bleaching events have been documented during the 1980s and 1990s, relatively few studies are available on the extent of coral community recovery. From quantitative long-term studies, with data spanning at least 4 years, Connell (1997) listed only 8 examples of changes in coral cover following bleaching events likely caused by elevated sea water temperature or a combination of elevated temperature and irradiance. In general, coral community recovery occurred in less than 10 years at western Pacific sites, but not at the single reef reported in the eastern Pacific. A more recent analysis of the state of eastern Pacific coral reefs demonstrated no recovery on 8 of 12 reefs monitored over periods ranging from 11 to 31 years (Wellington and Glynn, in press). If coral recruitment and/or survivorship to dead reef surfaces is low, in due course bioerosion will cause the disintegration of reef framework structures. In the Galápagos Islands, intense bioerosion by sea urchins has caused the disappearance of reef structures only 8 to 10 years after the 1982-83 ENSO (Glynn, 1994; Reaka-Kudla et al., 1996).

Thus, some fundamental changes can occur to coral reefs following ENSO-related disturbances. This likely possibility raises several important questions. What is the fate of coral reef communities following a severe coral bleaching event with high coral mortality? How does bioerosion and loss of coral reef frameworks affect reef-associated biotas? What effect does reef framework loss have on the abundance and diversity of coral reef organisms? A field experiment was initiated on an ENSO-impacted coral reef in the Gulf of Chiriquí, Pacific Panamá to help address such questions. This experiment attempts to compare the macrobiota (smallest body dimension = 2 mm), both surface dwelling and cryptic species, that recruit to 3-dimensional coral structures (imitating intact reef frameworks) and to 2-dimensional rubble plains (eroded reefs). In other words, to what extent will reef-associated species recruit to 3- versus 2-dimensional coral habitats? Each of the 40 emplaced 3-dimensional coral structures consists of dead coral sticks (eroded pocilloporid corals) bound together to simulate undisturbed reef framework. Following is the fundamental null hypothesis being addressed in this study. H_o: the abundance and species diversity of vagile coral reef fauna are equal in framework and rubble plain habitats. Details of the experimental design were presented, including the construction of the coral structures, location of sampling and reference sites, field layout, sampling frequency, and visual census technique.

This experiment is expected to provide quantitative data on species abundances and growth rates, biomass, diversity, community development and recovery. It offers several advantages, namely (1) the non-destructive sampling of cryptic reef species, (2) the ability to

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/glynn.pdf

obtain quantitative measures of species abundances and diversity in terms of available habitat space (e.g., surface area and pore space), (3) the ability to manipulate the sizes of the coral structures, their location in relation to source populations, and the effects on recruitment of introduced live benthos such as corals and macroalgae, and (4) the option of performing similar experiments under different regional settings (e.g. on disturbed reefs in different oceans). If this sort of experiment were performed on disturbed Caribbean reefs, simulated reef frame structures could be assembled by employing *Porites* or *Acropora* coral sticks. The location of this type of experiment adjacent to a CREWS (Coral Reef Early Warning System) station would offer the opportunity to relate coral recruitment and community recovery to continuously monitored physical conditions such as sea water temperature, salinity, submarine irradiance (including UVR) and meteorological conditions. Under these conditions, the course of coral reef recovery could be rigorously compared with variations in the physical environment.

With documented examples of coral reef loss and the disappearance of reef-associated biotas in ENSO-impacted regions, e.g. the Galápagos Islands and equatorial eastern Pacific, it is urgent that a research initiative be developed to assess the fate of coral reefs beyond short-term coral reef bleaching events. What are the long-term prospects for coral reef survival vis-à-vis global warming? To begin to answer this question, we need information on post-disturbance recruitment and recovery. Do disturbed coral reefs have the capacity to recover or are they continuing to degrade in structure, species diversity and growth potential?

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Field Monitoring Of The Interactions Between Coral Reef Calcification And Seawater Chemistry[*]

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The Problem

As CO2 concentrations increase in the atmosphere, CO2 is driven into the surface ocean and invokes changes in the carbonate equilibrium chemistry. Most notably, the concentration of the bicarbonate ion increases, and both pH and the concentration of the carbonate ion decrease. Experimental results (see Langdon's presentation) illustrate convincingly that calcification rates of corals and coralline algae decrease in response to decreased carbonate ion concentration. Results from Chris Langdon's work in the Biosphere2 mesocosm, and that of several others, indicate that organic calcification rates will decrease by 10-30% once atmospheric CO2 concentration reaches twice those of the preindustrial period. The obvious next step in examining how coral reefs and other tropical calcifying systems might respond to these changes is to monitor the seawater CO2 system within a natural reef system in the field, together with the host of factors that are thought to influence calcification rates (carbonate system, temperature, light, oxygen, hydrodynamics).

Coral Calcification vs. Reef Carbonate Budgets

So far, studies of the potential impact of increased CO2 on reef ecosystems have centered on organic calcification by corals (and to a lesser extent, on coralline algae). Decreased organic calcification rates ultimately reduce the overall calcium carbonate budget on reefs, but reefs are also likely to experience decreased inorganic cementation and increased dissolution. Both of these processes need to be considered in the overall carbonate budget of reefs, as well as various feedbacks that ultimately determine whether a coral reef is constructional or destructional. For example, regardless of the changes in biogenic calcification, changes in inorganic cementation and dissolution can have significant effects on the overall carbonate budget, by influencing the susceptibility of the reef to bioerosion.

CREWS Applications

Controlled monitoring of the seawater chemistry of a natural reef system would yield the integrated net calcification (i.e., calcification and dissolution) of a typical system. Such monitoring has been performed in the past, but because of the difficulties of deciphering the extent of mixing with adjacent waters, has usually been performed in lagoons (i.e., work by H Kawahata and A Suzuki), or on reef flats (i.e., work by JP Gattuso). These previous studies have only been performed over short periods of time, while a CREWS station would allow monitoring over seasonal cycles as well as through cycles of reef damage and recovery. If coupled with coral records (e.g. isotopes), this type of monitoring would allow extension of the present-day monitoring information in interpretations of longer
term coral records.

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[*] Web link: http://www.coral.noaa.gov/cmrc/think-tank/kleypas.pdf

Note that a good understanding of mixing within the region of the CREWS station would be necessary if one were to model this system, as well as knowledge of the seawater chemistry of waters adjacent to the CREWS research area.

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Effects Of CO_2 On Coral Growth And Calcification[*]

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Overview

The rising level of atmospheric CO_2 is causing the pH of the surface ocean to drop. This drop has been docmented at the Bermuda and Hawaiian ocean time series stations. While this drop has not been documented at lower latitude reefs sites because of a lack of appropriate sampling, there is good reason to expect that the same tend is occurring. The drop in pH imposes a stress on reef building organisms because it causes a reduction in the carbonate saturation state of the water which serves as the thermodynamic driving force for the precipitation of calcium carbonate.

Discussion

Recent studies have provided crucial evidence that the greenhouse effect is occurring and that it is resulting from anthropogenic input of CO_2 into the atmosphere (Crowley 2000, Stott *et al.* 2000). The main fear regarding global warming and coral reefs is that increased air temperatures will result in a concomitant increase in sea water temperatures world wide and an increase in the frequency and severity of coral stress events. While debate about the role of global climate change in recent coral bleaching events continues (Glynn 1991, Hoegh-Guldberg 1999), the corresponding effects that might result from absorption of excess CO_2 in seawater have received relatively little attention (Kleypas et al. 1999 Kleypas and Langdon 2002; Langdon et al. 2000). Increased atmospheric CO_2 is predicted to result in changes in surface ocean seawater chemistry. Laboratory studies predict that the slow acidification of the surface ocean, in response to increased uptake of CO_2, will affect precipitation of calcium carbonate ($CaCO_3$) and the maintenance of reef structures as a whole. Light and temperature also affect calcification rate, yet the relative effects of these three variables (light, temperature, CO_2) on coral calcification rates are poorly quantified, which thwarts attempts to predict the response of reef calcification to future environmental change. However, some laboratory studies have found that a doubling in $[CO_2]_{aq}$ in seawater, such has been predicted to occur sometime during the 21st century (Houghton, Filho et al. 1996), can cause a 3-37% reduction in skeletal growth of corals (Gattuso, Frankignoulle et al. 1998; Marubini and Atkinson 1999; Schneider and Erez 2000; Marubini, Barnett et al. 2001; Marubini, Ferrier-Pages et al. 2002). Additionally, mesocosm and field studies have found that entire coral reef communities are even more sensitive with a doubling in CO_2 causing a 20-54% decrease in carbonate production (Langdon, Takahashi et al. 2000; Leclercq, Gattuso et al. 2000; Broecker, Langdon et al. 2001; Leclercq, Gattuso et al. 2002; Langdon, Broecker et al. 2003). Thus, elevated CO_2, although receiving relatively little attention from coral reef scientists, is an important environmental stressor that alone could cause a shift in community structure from coral to algal dominance. In addition, nothing is known about how variations in light intensity, high temperature, and high CO_2 might interact to affect coral physiology. Furthermore, scleractinian corals can be CO_2 limited under certain conditions (Muscatine et al. 1989; Lesser et al. 1994;) and an increase in atmospheric CO_2 might ameliorate any sink limitation due to CO_2 limitation. However, with the exception of LeClercq et al. 2002, very few studies have investigated if a rise in CO_2 will result in elevated coral photosynthetic

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[*] Web link: http://coral.aoml.noaa.gov/cmrc/think-tank/langdon.pdf

rates, and it is not known if such a reaction would result in increased carbon translocation rates and/or altered calcification.

Silicate Buffering

There has been some discussion on the Internet's Coral-List listserver (Coral Health and Monitoring Program, 2001) that weathering of silicate rocks buffer the oceans more than carbonate rocks, and that activities of the growing human population may have accelerated this process to a point that it might prevent a significant drop in ocean pH in the near future. Following are some calculations that I feel refute that theory.

The weathering of carbonate and silicate rocks consumes atmospheric CO_2. The chemical reactions are:

$CaCO_3 + CO_2 + H_2O \rightarrow Ca^{2+} + 2HCO_3^-$ (1)

$CaSiO_3 + 2CO_2 + 2H_2O \rightarrow Ca^{2+} + 2HCO_3^- + SiO_2 + H_2O$ (2)

The Ca^{2+} and HCO_3^- are delivered by the rivers to the ocean where eventually organisms use them to secrete $CaCO_3$ skeletons.

$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_2$ (3)

The net result of reactions 1 and 3 is zero if the rates of the two processes are balanced. The only time the precipitation of $CaCO_3$ and the weathering of carbonate rock will exert an influence on the atmospheric level of CO_2 and hence oceanic pH is if there is an imbalance between these two processes. Geochemists estimate the rate carbonate weathering and deposition of carbonate sediments at approximately 0.2 GtC/y (Kump, Kasting and Crane, 1999). Any imbalance between these processes will be much smaller. CO_2 is currently building up in our atmosphere at the rate of approximately 3 GtC/y and the total atmospheric inventory is 750 GtC. It is apparent that imbalances in the carbonate precipitation/carbonate weathering cycle can only affect atmospheric CO_2 and oceanic pH on time scales of 750/0.2 or 3700 years or longer. The weathering of silicate rocks is a little different because 2 moles of CO_2 are consumed for each mole of Ca^{2+} that is released. As a result the net reaction of equation 2 and 3 do not some to zero but to:

$CaSiO_3 + CO_2 \rightarrow CaCO_3 + SiO_2$ (4)

In other words the weathering of silicate rock on the continents consumes the CO_2 that is produced by the precipitation of $CaCO_3$ by organisms in the ocean. The net result is the uptake of one mole of CO_2 and explains how $CaCO_3$ becomes a long term sink of atmospheric CO_2. Geochemists estimate the rate of silicate weathering at 0.06 GtC/y or 30% of the rate of weathering of carbonate rock (Kump, Kasting and Crane, 1999). This rate is thought to have varied through out earth's history, however, it influences the atmospheric content of CO_2 on time scales on the order of 750/0.06 or 12,500 years. This process has immence capacity but the flux is far too small to have any impact on the present build up of atmospheric CO_2 and the consequent drop in oceanic pH. For the lastest on the role of silicate weathering in regulating atmospheric pCO_2 the reader should consult Munhoven (2002). He finds that the reduction in continental weathering associated with the glacial/interglacial transition 18 kyr ago could account for an increase in atmospheric pCO_2 of 6-12 ppm or 6-12% of the total observed increase.

Buffering by HMC Sediments

It has also been suggested (personal communication, Mike Risk) that buffering by high magnesium calcite sediments common on reefs may be important in buffering the ocean or perhaps just the waters flowing over reefs. This argument hinges on the solubility of HMC. Will it dissolve at the present or near future pHs of seawater and hence buffer ocean pH? Bischoff et al. (1987) measured the solubility of *Amphiroa rigida* tests. This red coralline algae produces HMC that is 22% $MgCO_3$ on a molar basis. This is probably the most soluble HMC that is likely to be found on reefs. Other algae produce less soluble HMC in the range of 15% $MgCO_3$. They defined the ion activity product as:

$$IAP_{Mg\text{-}calcite} = (a_{Ca2+})^{(1-x)}(a_{Mg2+})^{x}(a_{CO3=})$$

where x is the mole fraction of $MgCO_3$ in the solid phase and a is the activity of the respective ions in solution. Bischoff et al. (1987) found that the IAP for this HMC was $10^{-8.08}$. Plugging in x=0.22 and typical values for the concentrations of Ca^{2+} and Mg^{2+} and using the activity coefficients for Ca^{2+}, Mg^{2+} and CO_3^{2-} in seawater estimated using the modified Garrel-Thompson complex ion model of seawater (Garrels and Thompson, 1962) of 0.228, 0.255 and 0.029, respectively, it is possible to compute the $[CO_3^{2-}]$ at saturation with 22 mol% HMC to be 84 umol/kg. For comparison the IAP for aragonite, the next most soluble form of carbonate is 4.9×10^{-9} (Mucci, 1983). The saturation $[CO_3^{2-}]$ under the same conditions (25ºC, 35 ppt) is 67 umol/kg. In other words 22 mol% HMC is just 84/67 or 1.25-times more soluble than aragonite. HMC will not begin to buffer the drop in ocean pH until the carbonate ion concentration falls below 84 umol/kg. This will not happen until pCO_2 reaches ~1500 ppm. Until that time calculations based on the seawater carbonate/borate buffering system will provide accurate projections of the change in oceanic pH.

Andersson et al. (2003) employed a numerical simulation of a hypothetical shallow-water ocean environment consisting of a water column and a pore-water-sediment system to see if dissolution of metastable carbonate phases, such as HMCs, could restore any changes in carbonate saturation state and pH owing to increased atmospheric CO_2. They found that HMCs will begin to dissolve in the sediments but that the surface water environment will not accumulate sufficient alkalinity to buffer pH or carbonate saturation state.

Conclusions

The experimental evidence cited above indicates that the rising level of atmospheric CO_2 may pose a serious threat to the reef building capabilities of coral and coralline algae in the coming century. Work should begin now to confirm these findings in the field. Without precise measurements of carbonate chemistry and coral calcification and growth at reef sites we do not have a baseline with which to gauge future change. It may be possible to take advantage of pCO_2 changes at certain reef sites on diurnal and seasonal time scales to derive calcification-pCO_2 relationships that can be extrapolated to the larger changes we may see in the next 50-100 years due to the burning of fossil fuels. The CREWS platforms supplemented by diver based measurements of coral calcification and growth provide an excellent means of establishing a baseline and trend of change that can be related to CO_2 and other changes in the environment.

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Coral Bleaching Issues :
In Support of CREWS Station Monitoring Plans[*]

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The coral bleaching models and predictions being developed in association with the CREWS stations will only be verifiable through rapid *in situ* monitoring of the extent of coral bleaching in the vicinity of the CREWS stations (when such events are predicted, or if they occur at times when not predicted.) The quantification of bleaching should be rapid, simple and utilized at all stations so that these data will be comparable among stations, and readily useful to fine-tune the models to the real-world measured results.

Incorporating a planned, rapid "ground truthing" response to bleaching alerts produced by the CREWS models is needed to ensure that the models are verified in a compatible fashion at all CREWS sites. Such a response could be incorporated into the "general maintenance" contracts of the agency responsible for maintaining the CREWS stations. The weighted-bar swimming transect (WBST) method provides rapid quantitative information on the extent and severity of coral bleaching (McField, 1999), and may be of value in this context.

Weighted-bar Swimming-Transect (WBST) Method

A new assessment method has been developed to rapidly and quantitatively assess the extent of coral bleaching and mortality, and the incidence of coral disease. The "weighted-bar swimming-transect method" was developed as a bleaching assessment by McField (1999) and modified by Kramer and Kramer (2000) to include information on disease and mortality. It utilizes a one meter piece of small diameter PVC tubing filled with stones or sand and capped at both ends (or left open to fill with water). Each bar is marked with five strips of black electrical tape (or other marking) spaced 0.25 meters apart. Thus there are five marks per bar, including the two ends. The observer swims in a straight line along a compass bearing or depth contour (parallel to the reef crest axis), holding the bar perpendicular to the line of the swimming-transect. Every three[1] kick cycles (one full push down and up for both legs is one kick cycle) the bar is dropped/placed straight down onto the substrate. The species and condition of corals (=>10 cm) lying under the marks are recorded. Condition refers to that of the entire colony and not to the individual polyps under the mark. If a mark does not fall directly on top of a coral, record the condition of the nearest coral colony to the mark which falls within a 12.5 cm radius of the mark. This distance of 12.5 cm is fairly easy to gauge since it is half the distance between any two marks. Thus the bar demarcates five adjacent but non-overlapping circles each centered on a mark. If no coral lies within a given circle no data is recorded for that mark so sandy patches and other non-coral areas can be passed through quickly. The total number of "bar drops" and corals

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[*] http://www.coral.noaa.gov/cmrc/think-tank/mcfield.pdf

[1] Number of kick cycles can be varied according to reef configuration ad desired size of study area. Kramer and Kramer 2000 used 10 kicks.

assessed is recorded for each site. For each “bar-drop”, anywhere from zero to five corals are assessed.

For studies of coral bleaching the conditions to recorded are as follows under the Bleach column of the datasheet (sample provided in excel file):

- PA = Pale (definite loss off pigment (lighter coloration for that species)
- PB = Part Bleached (patches of fully bleached or some white tissue on the colony - not due to other coral diseases such as white band, black band, or white plague)
- WB=Wholly Bleached (over 90% of colony with totally white-bleached tissue)

In addition the following diseases are recorded if present:

- BB = Black band
- WB = White band
- WS = White spots, patches or pox
- WP = White plague
- YB = Yellow blotch (sometimes called yellow band)
- RB = Red band
- DS = Dark Spot disease
- UK = Unknown

(these are based on Bruckner’s latest disease cards and the McCarty/Peters website http://ourworld.compuserve.com/homepages/mccarty_and_peters/coraldis.htm)

The percent of old dead and recent dead (based on the intactness of non-living corallite structure) can also be recorded (as described in AGRRA methods http://www.coral.noaa.gov/agra/). Coral mortality estimates provide information to help determine transient and lethal effects of bleaching, disease or other disturbances. However, this estimation adds additional time spent examining each colony and will reduce the number of colonies surveyed per dive. If bleaching/disease is the focus of the study this information could be skipped.

If mortality estimates are included, they include the estimation of the percent (%) of the coral that is "recently dead" and the % of the coral that is "old dead" as viewed from above in "plan" or "map" view. "Recently dead" is defined as any non-living parts of the coral in which the corallite structures are white and either still intact or covered over by a layer of algae or fine mud. “Old dead" is defined as any non-living parts of the coral in which the corallite structures are either gone or covered over by organisms that are not easily removed (certain algae and invertebrates).

While swimming, observers should look into the distance along the compass bearing and avoid looking down at the substrate until the bar is resting on the bottom. The “size” of each transect can be delimited by dive time, distance traveled, or number of coral condition records desired (like 100 records per transect), depending on habitat and sampling conditions. Each transect should remain within a pre-defined depth range or habitat zone. Several observers can swim parallel to each other to increase the sample size per dive at each site. Observers should remain at least ten meters apart, and cover approximately equal distances by swimming at the same speed.

This method enables observers to cover large areas of reef in either deep water, while scuba diving or in shallow water, while snorkeling. Because no transect lines are set more data are collected for the time expended and a larger area of reef can be covered. The method also increases the number of samples of rarer and smaller coral species as compared with traditional line intercept methods. Due to the previous use of this method, further use would allow comparisons within the Mesoamerican barrier reef system.

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Land-Based Sources Versus “Global Change”: Striking A Balance In Evaluating Stresses On Modern Coral Reefs[*]

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Introduction

The past decade has seen a veritable explosion of concern about the effects of “global change” on coral reefs, ranging from widespread reports of mortality from bleaching, to concerns about lowered oceanic alkalinity leading to decreases in coral calcification (one reference, of a plethora of similar ones: Wilkinson, 1999). Occurrences of coral bleaching seem to be on the increase (although the observer phenomenon has never been quantified adequately), usually in association with increased ocean temperatures.

There is no doubt that bleaching reflects some profound metabolic stress on corals, from which some reefs never recover. As the future likely will bring warmer oceans, the prospects of more frequent and more severe bleaching episodes seems almost certain. On the other hand, 95% of reefs that have bleached eventually recover (Ward-Paige et al., MS). On a global scale, bleaching as a threat to coral reefs rates no higher than #4, behind eutrophication, sedimentation, and destructive fishing.

Concerns about alkalinity shifts are probably overblown. To conclude that an increase in atmospheric CO_2 will lead to more acidic oceans is not difficult, but the effects of such a shift in ocean chemistry pale in comparison with other threats. Controlled experiments show that HMC sediments of reefs effectively buffer local changes in alkalinity, and recent data on ocean circulation show that global change also brings with it increased ocean mixing-this will increase the role of the great buffers of ocean chemistry, the silicates.

In some cases, global change has become a convenient scapegoat for local managers and politicians: it is more convenient to blame events and processes over which they have no control than it is to deal with local impacts. The effects of land-based sources of pollution have been known for decades, yet mitigation is rare indeed.

At this time, in the early throes of the impact of coming climate change and the dawning appreciation of the horrible mess humans have made of the oceans, it is essential to be able to prioritise impacts. There is not enough money, and not enough time, to fix all the reefs. We will have to apply “triage”-what is more, and what may be distasteful to some: we will have to evaluate the relative roles of the stresses on reefs, and treat them in order of importance. We need the tools, and the will to use them. It is likely that the most important question now facing the coral reef research community is: which is more important, land-based sources of pollution, or global change?

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[*] http://coral.noaa.gov/cmrc/think-tank/risk.pdf

Suggestions

1. Monitoring.

Controlled experiments on infestation rates of carbonate substrates by microborers can yield water quality data quickly and easily, via an extension of the bioindicator approach. Microborers will attack submerged crystals of Iceland Spar in days, reaching virtually 100% infestation in three months (Kobluk and Risk, 1977).

2. Assessing sediment stress.

Cortes and Risk (1985) found that the acid-insoluble residue in the corals was proportional to the suspended and resuspended sediment loads. In addition, the mineral and trace element "signature" of the trapped material was sufficient to "fingerprint" specific watersheds. This technique works where the incoming sediment is largely siliciclastic (as is the case with most fringing reefs), but is ineffective on large carbonate banks, where the incoming sediment is itself carbonate.

3. Assessing sewage stress.

The cheapest, most effective way of estimating sewage stress on a reef in by $\delta^{15}N$ analyses of coral or macroalgal tissue. Methods are given in Risk et al. 2001, and have remained basically unchanged for a decade. Tissue must be analysed, not sediment:" what is in the sediment is the ashes of the fire" (Barry Hargrave, pers. comm., 1975).

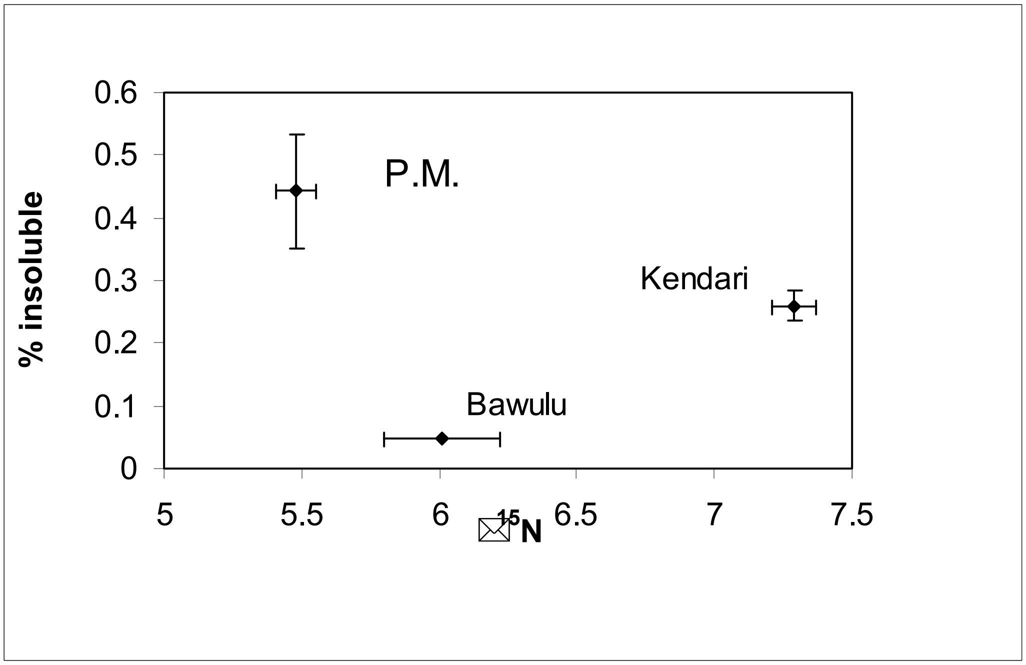
There is also the possibility of retrospective analyses of $\delta^{15}N$, in long-lived reef organisms such as gorgonians. Sequential analyses of dated gorgonian stalks from the Florida Keys show that terrestrial input has increased over the pasy few decades, and follows human densities of the adjacent shorelines (Sherwood et al., 2003).

4. Evaluating the relative importance of sewage and sediment stress.

There are no baseline date whatsoever for most of the world's reefs. A technique would be very useful that could differentiate sewage and sediment stress in the absence of any prior studies. I chose three Indonesian reefs in south Sulawesi to test whether it was possible to tease out the effects of these two stressors:

Kendari site is off the city of Kendari, pop. about one million. This was the "sewage" site.
Pulau Mapau was at the bottom of an uninhabited watershed, where clearcut logging had recently gone on. This was the "sediment" site.
Bawulu was about as remote an island as one gets in SE Asia. This was the "comparison" site.

At each site, small heads of *Porites lobata* were collected, dried, and transported back to Canada. The tissue was analysed for $\delta^{15}N$, and parts of the skeletons for insoluble residues. The results are presented below, Fig. 1:



This technique shows promise. It builds on previous work, and allows virtually instant evaluation of the relative impacts of sediment and sewage for a few dollars and a few hours' work per site.

Finally, there would seem to be a couple of research projects that have the potential of evaluating the relative impacts on reefs of global change and land-based sources. This is probably the single most important question now facing the reef research community. One of these is essentially geological, and the other geochemical.

5. Retrospective $\delta^{13}C$ analyses of coral cores

Carriquiry was the first to show that $\delta^{13}C$ in corals could be used as a measure of stress-prior to his work, it was vaguely seen as some sort of light meter. Later, Heikoop built on this work, and showed how $\delta^{13}C$ could be corrected for Kinetic Isotope Effects, allowing application of the corrected values as a stress indicator. Working with the relationship between $\delta^{13}C$ and other tracers, it should be possible to recreate the past bleaching history of an individual coral. If corals show a history of bleaching episodes on a reef with a stable and healthy population of corals, then global change has had no impact-etc.

6. Carbonate budgets revisited.

There have been three comprehensive carbonate budgets produced for coral reefs: Barbados in the 70's (Scoffin et al., 1980), the US Virgin Islands in the 80's (Hubbard et al., 1990), and Indonesia in the late 90's (Edinger et al. 2000). Each of these concluded that bioerosion rates were at least as high as calcification rates. Each has an enormous database, of production rates of all the important calcifiers, and destruction rates of the major bioeroders. Either the Barbados or Virgin Island sites should be re-occupied, and the carbonate budgets re-done. (Not enough time has passed, in the case of Indonesia.) There will be mortalities, and the pattern of these will allow us to decide how rapidly those reefs are declining, and whether the decline is largely due to global change or land-based sources.

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Think Tank Conclusions

(all authors)

The Caribbean Marine Research Center, NOAA's Undersea Research Program (NURP) Center for the Caribbean, hosted *The Effects of Combined Sea Temperature, Light, and Carbon Dioxide on Coral Bleaching, Settlement, and Growth* workshop at its research station on Lee Stocking Island, Bahamas, January 20-24, 2003. The group gathered primarily for the purpose of discussing the biology and mechanisms behind coral bleaching, growth and larval recruit health. Coral bleaching is an obvious stress to reef ecosystems, but many if not most recover, at least partially (albeit with greater susceptibility to disease in some instances), under today's climate regime. It is important to consider bleaching in the context of other stresses to coral reef ecosystems today: eutrophication (or nutrification), sedimentation, chemical contamination, destructive fishing methods and general overfishing.

Researchers discussed how their science programs might benefit by incorporating CREWS capabilities, and how the CREWS knowledge base could be improved based upon advancements in coral science. Meeting objectives included: 1) Review the current understanding of coral reef problem domains as they relate to both climate and anthropogenic stresses and associated coral reef response, 2) determine which *in situ* monitoring instruments would further aid research into these domains, and, 3) initiate dialog to either help enhance current expert system modules or develop new modules to facilitate interpretation of factors conducive to stimulating a particular event (e.g., coral bleaching, coral growth, or coral larval recruitment).

The following text outlines priorities developed by meeting attendees (*please see the individual chapters for proper referencing*).

NOAA's Coral Reef Watch program

Meteorological and oceanographic monitoring by NOAA's Coral Reef Watch program, which utilizes satellite and *in situ* monitoring methods, has resulted in effective predictions of coral bleaching through near real-time World-Wide Web and automated e-mail products. These products reflect highly spatial (satellite) and highly temporal (CREWS stations and buoys) data collection methodologies for helping to determine the causes underlying coral bleaching and other coral reef related phenomena.

The use of a suite of expert systems for CREWS stations for screening incoming data from the instrumented *in situ* arrays, together with a field program for assuring high data quality at the collection site, provides a robust system for modeling physical factors that can be measured with instruments designed for long-term deployment. The CREWS stations also provide timely feedback on the nature of the marine environment in the form of indices of stress, which can be of use to marine environmental managers and research scientists.

High sea temperatures are almost always coincident with mass bleaching episodes; however, light in the water column plays a significant facilitative role in the phenomenon. Climate is likely to modulate the intensity, duration and/or spatial extent of bleaching events through weather-related conditions (periods of no wind, clear sunny skies, weak currents). For many parts of the world, strong El Niño Southern Oscillation (ENSO) events are linked to large scale regional bleaching events, while other areas are not. A detailed analysis of the relationship between climatic trends and patterns of bleaching are warranted before direct links between climate change and coral bleaching can be made.

Preliminary analysis of environmental monitoring data acquired by the SEAKEYS network indicates an upward trend in sea surface temperatures (SST) in the Florida Keys which if maintained, would result in sustained SSTs of over 31°C by the late 2050s; today such high SSTs would be lethal for many if not most corals. These numbers appear to agree with other researchers' analyses of SSTs at other localities.

Physiology of coral bleaching

Coral bleaching represents the end point of a physiological continuum of normal seasonal variation in which the photosynthetic capacity of photosystem II and zooxanthellae are reduced to lower levels than during non-bleaching years. However, we know very little about the biochemical pathways involved in the homeostasis of daily and seasonal processes controlling densities of zooxanthellae.

Zooxanthellae in corals are in the genus *Symbiodinium*, with numerous different types identified via molecular techniques, and a wide range of physiological capabilities. In comparison studies between seven coral species in the Bahamas and the Florida Keys, at depths of 1-3 m and 13 m, seasonal cycles in tissue biomass, zooxanthellae density and pigment content revealed intriguing characteristics. Symbiont densities and pigments peaked in winter (coldest months, lowest light intensities and duration), tissue biomass typically peaked in the spring sample times, and the lowest density of *Symbiodinium* and tissue biomass was in the late summer/fall (end of warm season, highest light intensity and duration, especially in El Niño years). Coral feeding patterns, light-dark cycles and environmental conditions were found to modulate the density and number of zooxanthellae in the host tissue. Correlates with light and temperature help explain differences in physiological responses of corals and their symbionts over various temporal scales (e.g., daily, seasonal, El Niño).

Molecular methods have shown that coral endosymbiont biodiversity is high with at least seven major lineages, or clades, some comprising numerous ecologically distinctive types or species. Different combinations or "holosymbionts" (i.e., coral-algal symbioses) have different physiological attributes, and in certain situations may raise a coral's tolerance of thermal stress by several degrees. Therefore, a coral that associates with more than one symbiont species has multiple functional forms and provides an additional source of variation upon which natural selection may act. However, many hosts are specific for a particular symbiont type. A "forced" change in symbiont species due to severe environmental stress may result initially in a sub-optimal association.

Role of temperature and solar radiation in coral bleaching

While previous studies have shown that exposure to sublethal temperatures or UVR alone may cause photoinhibition, elevated temperatures coupled with solar radiation are believed to exacerbate the bleaching response of reef corals.

In many corals, compounds such as mycosporine-like amino acids (MAAs) are believed to provide protection from the high-energy wavelengths within the UV portion of the spectrum. A protective role for these compounds has been inferred from four aspects of their biology. First, MAAs have a high molar extinction coefficient in the range of environmentally relevant UVR. Second, concentrations of MAAs in coral tissues are generally higher in shallow water where UVR intensities are higher. Third, concentrations of MAAs in animal or algal tissues generally increase when UVR intensities are enhanced experimentally and, likewise, MAA concentrations decrease when UV radiation intensities are reduced. Finally, individuals containing higher concentrations of MAAs show better performance under a similar UVR regime than conspecifics with lower levels. Recent work has shown that colony-specific patterns in MAA composition are quite pronounced, giving rise to hope that coral-zooxanthellae populations have genetic differences that may allow for adaptation to increased solar irradiance stress.

A cellular diagnostic system (CDS) has been used to distinguish the separate and combined effects of heat and light on a star coral (*Montastraea faveolata*) and its zooxanthellae symbiont, and thus provide evidence that oxidative stress plays a central role in bleaching. Under non-bleaching conditions, analysis of the same colonies provided evidence for local stressor effects and other possible types of stressors. Thus the CDS provides a capability to, 1) diagnose whether corals are physiologically stressed, 2) discriminate between global-level stressors (e.g., El Niño /La Niña effects) and local-level stressors (e.g., agricultural runoff) and 3) possibly predict the condition of corals several months before more obvious symptoms appear (e.g., coral bleaching or coral death).

Ultraviolet exposure of coral reefs in the Florida Keys and possibly other regions of the sea appear to be controlled by chromophoric dissolved organic matter (CDOM) in waters overlying the reefs. Recent remote sensing studies of the global ocean have shown that >50% of blue light absorption, and presumably a higher percentage of UVR absorption, is controlled by CDOM. In the case of the Florida Keys the CDOM is derived from decaying detritus from seagrasses and mangroves. Under summer conditions with low winds, a pronounced stratification effect on UV-B transmission may occur in deep water just outside reefs, the net effect of which would be to substantially increase UV penetration in the surface waters above the thermocline. This effect might be ascribed to combined photobleaching and microbial degradation of the CDOM in the upper water column, coupled with reduced upwelling of cool, more opaque waters from the deep ocean. Because this surface water is often laterally transported over the reefs by the action of currents, this stratification effect enhances reef UV exposure compared to well-mixed conditions. Extensive stratification, which occurs more often under El Niño conditions, may be greatly increasing exposure of the reefs to damaging UV. CDOM concentrations and UV penetration over the reefs are modulated by a complex interplay between this stratification effect coupled with transport and photobleaching of CDOM-rich waters from shallow waters close to the reefs. During the transition from El Niño to La Niña conditions in the eastern equatorial Pacific during summer of 1998, a large increase in CDOM concentrations was observed as cooler, CDOM-rich subsurface waters upwelled to the ocean surface. These observations suggest that UVR penetration and sea surface temperatures in this region of the open ocean were unusually high during El Niño conditions and that a return to usual conditions occurred as the El Niño ended.

Metabolic energy needs under bleaching stress

In the absence of their zooxanthellae and/or photosynthetic pigments that normally supply the coral animal with up to 100% of its daily metabolic energy requirements, bleached corals may have to rely heavily upon lipid stores to supplement and/or to support their daily metabolic energy needs; however, they utilize those lipids differently. For instance, ten weeks following a natural bleaching event, bleached *Porites compressa* corals depleted their total lipid stores while *Montipora capitata* corals maintained them. The difference in total lipids appeared to be due to differences in the lipid class composition of each species. Close examination of the lipid class composition in both bleached and non-bleached corals revealed that: 1- both *M. capitata* and *P. compressa* depleted their storage lipids (triacylglycerol and wax esters) and increased their phospholipids, as would be expected in stressed animals, and 2- *P. compressa* appeared to lack diacylglycerol regardless of its bleaching status, while the same lipid class increased slightly in bleached *M. capitata.* In addition, over the surface of the colony, *P. compressa* depleted total lipid stores in bleached areas but maintained lipid levels in non-bleached portions of the colony while *M. capitata* maintained lipid concentrations throughout bleached and non-bleached portions of the colony.

Coral bleaching thresholds

Determining coral bleaching thresholds may perhaps best be done in a two-step process: 1) construct time-temperature curves for bleaching based on field observations, and 2) use the time-temperature curves as a guide in setting levels of experimental treatments in controlled laboratory experiments. The experimental component should try to determine: 1) what the bleaching curve might look like for individual species of coral, and 2) the level of variation around the bleaching curve due to photosynthetically available radiation (PAR) and UV light. This could be done in a three-factor controlled experiment where the factors are temperature, light and time.

Coral community recovery following bleaching

Even though hundreds of severe coral bleaching events have been documented during the 1980s and 1990s, relatively few studies are available on the extent of coral community recovery. In general, coral community recovery has occurred in less than 10 years at western Pacific sites, but not at the single reef reported in the eastern Pacific. A more recent analysis of the state of eastern Pacific coral reefs demonstrated no recovery on 8 of 12 reefs monitored over periods ranging from 11 to 31 years. If coral survivorship and/or recruitment to dead reef surfaces is low, in due course bioerosion will cause the disintegration of reef framework structures. Thus, some fundamental changes can occur to coral reefs following ENSO-related disturbances. A key requirement for understanding the fate of stressed reefs is information on post-disturbance recruitment and recovery.

Role of solar radiation in coral recruitment

Recent studies investigating the effects of UV radiation on planula larvae of brooding corals in both the Caribbean and Pacific have noted negative effects that are manifested as either mortality or delays in settlement. Despite these negative effects, all coral larvae examined thus far appear to have UVR receptors that allow them to actively avoid high intensities of this biologically damaging radiation while dispersing in the water column or at the time of settlement. In contrast, the degree to which coral larvae can acclimate to high UVR intensities by developing the chemical defenses to withstand its effects appears to vary across species.

Combined results to date suggest that changes in the clarity of the water column may have a significant impact on the settlement patterns of corals. Clearly water column parameters affect UVR intensities and increases in the amount of UVR reaching corals can be more than double the mean annual maximum if the water column changes from its normal state to a sustained period of extreme calm and exceptional clarity. As a consequence, changes in environmental conditions that alter the light regime, such as increased or decreased suspended sediment loads, may have a direct positive or negative impact on coral recruitment. For example, land use patterns causing sediment run-off may affect coral recruitment dynamics in waters immediately offshore not only through the direct negative impacts of sediments stress, but also indirectly by attenuating the intensities of UV radiation impinging on shallower areas of the reef. Such complex interactions among physical parameters must be deciphered if we are to have a complete understanding of sediment and turbidity effects on reef sustainability and community structure.

Coral calcification and calcium carbonate budgets on coral reefs

Manipulative studies have shown that exposure to elevated levels of CO_2 depresses the ability of corals and other carbonate-secreting organisms (coccolithophorids and red calcareous algae) to build their skeletons. A CO_2 concentration of 560 ppm has been found to depress the rate of skeletal growth by 10-30% relative to preindustrial rates. Projections by the Intergovernmental Panel on Climate Change (IPCC) indicate that this concentration could be reached in the next 50-80 years. One study found that net carbonate production completely stopped in a mesocosm populated with reef organisms when the CO_2 level exceeded 1200 ppmv. This level could be reached in the next century unless CO_2 emissions are dramatically reduced.

Recommendations for future research and monitoring

Bleaching predictions need to be validated rapidly and simply, and with the same methodology at all CREWS stations, so that data are comparable between stations and are readily useful to fine-tune the models to the real-world measured results. One potential methodology, the Weighted-bar Swimming-Transect method, has been employed in the Mesoamerican reef and could be used as a model. Incorporating a planned, rapid "ground truthing" response to bleaching alerts produced by the CREWS models is needed to ensure that the models are verified in a compatible fashion at all CREWS sites. Such a response could be incorporated into the "general maintenance" contracts of the agency responsible for maintaining the CREWS stations.

In future studies of the effect of light on coral bleaching, light sensors at CREWS stations should be deployed at two different depths. This would allow the calculation of the attenuation coefficient for light, and together with turbidity sensors or CDOM sensors would give an indication of the mechanism for the reduction of light. Data from the sensors could be used to great advantage in supplementing and validating remote sensing observations.

Photosynthetic function of symbiotic algae, in terms of energy flow through photosystem II, can be determined easily via Pulse-Amplitude Modulated (PAM) fluorometry. Addition of a PAM fluorometer to the CREWS instrument suite would enhance interpretations of how physical factors influence the physiological response of zooxanthellae. By providing proper maintenance of the fiber-optics probe, photochemical quenching (i.e. photosynthesis) and non-photochemical quenching (e.g., protection mechanisms) can be estimated over diel and seasonal timescales.

To better determine how changing seawater chemistry will affect coral reef calcification, the obvious next step is to monitor the seawater CO_2 system within a natural reef system in the field, together with the host of factors that are thought to influence calcification rates (carbonate system, temperature, light, oxygen, hydrodynamics). CREWS station data will provide most of the field data necessary to extrapolate experimental data to field results, including pCO_2.

Finally, participants recognized that other information important to coral reef ecosystem function would be made possible by CREWS data. For example, the movement of demersal mesozooplankton and small fishes during diurnal migrations temporally and spatially structure energy, mass and nutrient exchange between the reef habitat and the surrounding waters. Multi-frequency acoustic and optical integrated environmental sensor packages can be used to monitor the migrations, while CREWS monitoring can provide further environmental context to these measurements. The two approaches together can help to elucidate the nature of energy transfer and nutrient exchange on coral reefs.