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^{o}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.