

IOC *ad hoc* Study Group on Coral Bleaching and Related indicators of Coral Reef Health

Intergovernmental Oceanographic Commission of UNESCO
9-11 April 2001, Paris

Initial planning meeting & Presentation abstracts
Executive summary

Objectives

The first meeting of the IOC *ad hoc* Study Group on Coral Bleaching and Related Indicators of Coral Reef Health was held 9-11 April 2001 at IOC, Paris. The objectives of this new initiative are to: 1. Develop possible molecular, cellular, physiological, and community indicators of coral bleaching that are reliable in their ability to detect stress responses due to changes in variables such as SSTs, PAR, UV radiation, pCO₂, hydrodynamics, etc.; 2. Examine potential mechanisms of reef corals for adaptation/ acclimatization to global environmental change; and 3. Investigate long-term responses of coral reefs to large-scale changes in environmental variables, thereby addressing the call for development of indicators of sustainable use of ocean ecosystems of Agenda 21, Chapter 40 (Terms of Reference, Appendix I). The initiative also address the specific work plan on coral bleaching under the programme of work on marine and coastal biological diversity of CBD (SBSTTA/6/4).

More specifically, the objective of the initial planning meeting was to integrate current information, compare existing techniques, and establish research directions and studies to identify indicators of stress in corals leading to coral bleaching and subsequent effects.

Each member of the group (List of participants, Appendix II) was invited to present and discuss individual research fields and ideas of relevance to the Terms of Reference to initiate the discussions (Presentation abstracts, Appendix IV).

Summary of discussions

During the presentations physiological aspects of coral bleaching, techniques to measure stress response and their potential to serve as indicators was discussed. The complexity of the problem and a diverse range of aspects to investigate in order to effectively address it were outlined. The group identified key issues and gaps in the existing knowledge on the causes and consequences of coral bleaching and related effects. Overall, it was recognised that the potential to develop techniques and analytical tools to assess and possibly predict coral stress exist, although it was noted firstly that while some techniques may work at local level under controlled conditions, these may be too advanced and costly to operate well on larger scales as part of global monitoring systems, and secondly that critical gaps in the existing understanding of key processes related with bleaching exist and that targeted research addressing those issues are needed.

The World Bank, represented by Mr. Andy Hooten, was invited to present a World Bank proposal of a GEF targeted research program on corals sustainability currently under preparation. He informed the Group that the program, under the guidance of a scientific panel that will develop and oversee the program, aims to: 1) Identify gaps in scientific understanding of coral reef, including the ongoing degrading of corals, and 2) Prioritise needed investigations that have applied benefit and can enhance accuracy in assessment, and possibly, prediction in developing countries. The scientific panel should further facilitate a systematic application of research by involving ongoing studies, where possible, and recommending new ones; inventory and enhance networks of existing investigations, with a focus on developing countries; and synthesize information and results from this framework to improve longer term credibility and to better understand the processes that are going on. The desired results from the program are to discern effects of local stressors from broader ones (anthropogenic against climatic); test specific hypothesis based on gaps in understanding; and affect national policy and management with a more reliable information base when assessing status and trends. The program will support activities at three levels: from overall 'screening'

(assessments, inventories); to more applied experimental work at targeted sites (Caribbean, Southeast Asia); and detailed field experiments to test specific hypotheses.

A number of subcommittees will be set up to address specific issues, provide guidance to the overall panel, help formulate and priorities specific research questions to be addressed, and work in greater detail on specific problems. It is suggested that some members of the subcommittees serve on the overall panel. A number of disciplines have been identified, such as: general coral reef ecology, coral reef physiology, coral diseases, genetics, larval recruitment, coral reef fisheries, biometric analysis, ecological risk assessment, remote sensing, socio-economic aspects, coral reef management and more. None of the subcommittee's has yet been established.

Block A of the project will be finalised in May/June 2001. Based on a literature review it will contain a preliminary identification of hypothesis to be tested and describe the frame for the longer-term work. The Block B project, to be submitted concurrently, will describe the experimental design for each activity in the project, define and establish the initial network of sites and institutions where investigation will occur, and put a framework in place to operate for an extended period in the target regions. Development of the full project will occur over 2001-2002.

A possible role of the IOC Coral Bleaching Group in the WB initiative was discussed. It was noted that the Coral Bleaching Group could fit well into the program framework and could serve as a subcommittee under the scientific research panel, with the specific aim to address coral physiology and provide guidance and recommendations. The participants felt the Group could serve the overall purpose by initiating and integrating research on physiological mechanisms leading to coral bleaching, which could contribute to the fundamental understanding of coral functioning and coral degradation, and in parallel direct this knowledge into the development of indicators and predictive models.

Discussions on specific issues to be included in a larger research effort on coral degradation followed. An overall question identified was: **what controls the possible recovery of damaged coral reefs?** Or, as Loya and co-workers (2001) have formulated it: **“Who are the winners and the losers of coral bleaching?”** A brainstorm along those lines identified a number of research questions addressing fundamental mechanisms and future scenarios, which would ultimately feed into development of indicator tools and predictive models:

- Are coral reefs resilient in the face of projected climate change over the next 100 years?
- How fast will change occur within coral reefs ecosystems?
- Can coral reefs recover and if so, how fast?
- What will the final state of the ecosystem be if coral abundance decreases dramatically over time?
- What is the relationship between distance and larval transport?
- How is the primary factor temperature affected by other secondary factors?
- Why are some corals more immune than others?
- How rapidly do reefs get repopulated by larvae coming from other reefs?
- Do other species depend on structure created by corals?
- Is a phase shift permanent?
- Do reefs erode when corals are no longer present?
- How fast can reefs recover if conditions improve?
- What factors influence the ability of reefs to recover?
- Can we help reefs recover?
- Loss of species and habitat (how much? biodiversity lost?)

Conclusions and recommendations

In order to address these questions four overall research themes including a number of subtopics was identified and central work hypothesis formulated (Appendix V). An overall model for how this knew information could be linked with the development of indicators and predictive models of coral bleaching and related effects was outlined (see Appendix VI).

It was recognised that some of the identified questions and research topics reached beyond the current scope of the group. However, within the overall framework of a joint research effort the specific role of the group could be to: 1. Specifically address issues related with coral physiology and bleaching, and 2. Integrate this information with relevant information from other research fields and direct it towards the development of indicators and predictive models. The critical task of integrating and directing the information towards development of indicators could run parallel with the targeted research program.

A number of future activities and experiments were discussed. It was decided that the next meeting should take place at a field laboratory to allow comparative studies of techniques. Concern was expressed that some knowledge gaps on certain physiological disciplines existed in the group and that additional members should be identified. The group should also aim to include more participants from developing countries, and it was argued that future field activities could well take place in developing countries.

It was agreed to conduct field studies at the following three sites:

- Sydney University Field Station, Heron Island, Australia, February 2002
- Universidad Nacional Autónoma de México, Cancun, Mexico, September, 2002
- Philippines/Indonesia/Thailand (Phuket)?

The possibility of additional support for carrying out these activities was discussed. It was noted, that the World Bank might be able to contribute with resources to the further development of the project and that support from other institutions might be available.

It was suggested that one of the outputs of the IOC Study Group should be of manual on techniques that might be used as indicators of reef health that would identify the strengths and pitfalls of the methods described.

Ole Vestergaard
IOC/UNESCO, May 2001

Appendix I

IOC Ad Hoc working group on coral bleaching and related indicators of coral reef health

Terms of Reference

Under the auspices of the UNESCO/IOC Ocean Sciences programme a Study Group has been organized to develop physiological techniques methods to assess the condition (or health) of coral reefs. This initiative is pursuant to Chapter 40 of Agenda 21, which calls for the development of indicators for sustaining healthy ocean ecosystems. This coral reef initiative also relates to the Health of the Ocean Module of IOC's Global Ocean Observing System as health indicators can serve as an early warning signal of changes in the quality of the ocean environment.

The major objectives of this initiative are

1. To develop possible molecular, cellular, physiological, and community indicators of coral bleaching that are reliable in their ability to detect stress responses due to changes in variables such as SSTs, PAR, UV radiation, pCO₂, hydrodynamics, etc.
2. Examine potential mechanisms of reef corals for adaptation / acclimatization to global environmental change;
3. Investigate long-term response of coral reefs to large-scale changes in environmental variables.

The activities of the Study Group will involve consideration of current physiological research and encouragement of molecular and biochemical techniques that may lead to the recognition of indicators of stress on corals and early detection of coral bleaching. The stress signals of interest may be manifest in biochemical and cellular biomarkers, enzyme expression, cellular pathology and abnormal physiology. The Group will engage in open discussion of ongoing research relating to the topic both in meetings and intersessional periods that may include as appropriate agreements for replication of experiments and field tests of laboratory developed techniques.

The intention is to encourage physiologists and ecologists through discussions at meetings and intersessional activities to direct part of their research efforts towards development of stress indicators. A chairperson who in consultation with IOC will convene a small group of 10 to 12 active coral researches that will meet annually for these focused discussions.

Goals:

1. Integrate current information and establish research directions, develop techniques and studies to identify useful indicators of stress in corals leading to coral bleaching and subsequent effects
2. Demonstrate the effectiveness of the indicators through application in the field at selected sites;
3. Promote the use of the indicators by the user community through dissemination of results in reports, publications, symposia, web sites or other forums.

Paris, September 18, 2000

Appendix II

Ad Hoc working group on coral bleaching and related indicators of coral reef health

1st Meeting in Paris, 9 – 11 April 2001

Agenda

Monday 9 April	09.15	Registration
	09.30 – 10.00	Opening
	10.00 – 12.30	Individual presentations
	12.30 – 14.00	Lunch
	14.00 – 16.00	Presentations cont.
	16.00 – 16.30	Coffee
	16.30 – 18.00	Presentations cont. + discussion on Terms of Reference, meeting objectives and topics to be addressed
	20.00	Dinner
Tuesday 10 April	9.00 – 10.30	Presentation of the World Banks targeted research proposal
	10.30 – 11.00	Coffee
	11.00 – 13.00	Discussion
	13.00 – 14.00	Lunch
	14.00 – 16.00	Discussion
	16.00 – 16.30	Coffee
	16.30 – 18.00	Discussion
	20.00	Dinner
Wednesday 11 April	9.00 – 10.30	Discussions
	10.30 – 11.00	Coffee
	11.00 – 13.00	Discussions
	13.00 – 14.00	Lunch
	14.00 – 16.00	Discussions
	16.00 – 16.30	Coffee
	16.30 – 18.00	Wrapping up, departure

Presentations:

Roberto Iglesias Prieto	Coral Bleaching: a Cellular Perspective of a Global Phenomenon
Ove Hoegh-Guldberg	Indicators of coral reef health
Bill Fitt	Bleaching, starvation and the health of reef corals
Ruth Gates	Osmotic stress: A potential marker for monitoring coral bleaching
Michael Lesser	Coral Reef Bleaching: Early Warning, Monitoring, and Long-term Recovery
John Bythell	Community to molecular indicators of coral reef stress
Yossi Loya	Coral bleaching: individual and community aspects
Robert van Woesik	Coral bleaching: differential survival and recovery
Barbara Brown	Environmental cues and the quest to find coral 'stress' indicators

Appendix III: List of participants

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Appendix IV: Presentations and abstracts

Barbara Brown	Environmental cues and the quest to find coral 'stress' indicators
John Bythell	Community to molecular indicators of coral reef stress
Bill Fitt	Bleaching, starvation and the health of reef corals
Ruth Gates	Osmotic stress: A potential marker for monitoring coral bleaching
Ove Hoegh-Guldberg	Indicators of coral reef health
Roberto Iglesias Prieto	Coral Bleaching: a Cellular Perspective of a Global Phenomenon
Michael Lesser	Coral Reef Bleaching: Early Warning, Monitoring, and Long-term Recovery
Yossi Loya	Coral bleaching: individual and community aspects
Robert van Woesik	Coral bleaching: differential survival and recovery

Barbara Brown, Dept. Marine Sciences & Coastal Management, University of Newcastle

“Environmental cues and the quest to find coral 'stress' indicators”

This account summarises our work in the last 20 years at Ko Phuket, Thailand where we have looked at the effects of environmental stress at the community, organism and cellular level. It is a reflection on our results with respect to the terms of reference of this study group.

The shallow reef flats of the eastern Indian Ocean are extremely well adapted to environmental stress with many coral species being able to tolerate aerial exposure, high irradiance, high sea temperatures and high sediment loads. Indices of stress have been developed at the community level for these habitats but these indices, sensitive as they are, reflect the effects of perturbation rather than predict its occurrence. Over the last 22 years two environmental events have caused significant effects on the coral communities - a major dredging event in 1986-87 and anomalously low sea levels in 1997-98. Widespread bleaching events in 1991, 1995 and 1998 have not caused any significant loss of coral cover or alteration of the community structure at a selection of sites on the southeast corner of Ko Phuket.

At the organism level we have looked at a variety of potential 'stress' indicators from coral algal densities to the up-regulation of stress proteins. Although algal densities and algal chlorophylls provide some idea of the status of the algal symbiosis, are relatively straightforward and inexpensive to measure and fluctuate in a now well established seasonal pattern they do not necessarily offer scope of prediction of future bleaching months ahead of the event.

The evaluation of molecular markers such as stress proteins is still in its infancy, even though heat-shock proteins (hsps) were first identified in tropical corals over six years ago. It is still unclear what the significance of hsps to bleaching might be. For the wealth of molecular markers now at our disposal we need to know, for any given species, exactly how they relate to the environmental stressors eliciting bleaching and to the bleaching mechanism. Also, what is their natural variability over time and do they offer any scope as bleaching predictors? It is likely that we are looking not for isolated indicators but rather a suite of suitable assays since the cellular and molecular processes involved in bleaching (and its prevention) are diverse.

Most importantly we need to have a much better understanding of the local oceanography of our study sites and the variation (at all scales) in the key physical parameters, which elicit bleaching. It may be that some of these physical signals offer the greatest predictive ability of bleaching events since they forecast major ocean/atmosphere changes that lead to anomalously high sea temperatures and other cues for bleaching - but only time will tell.

John Bythell, Dept. Marine Sciences & Coastal Management, University of Newcastle

“Community to molecular indicators of coral reef stress”

1. Long-term ecological community dynamics in a protected coral reef reserve

This study shows that even in a pristine site with relatively little direct local human impacts, there are a range of community dynamics and a range of responses to perturbations. The recent 1998 bleaching event resulted in damage equal to that of the major (Category 5) Hurricane Hugo in 1989. The difference was that *Montastraea sp* were mainly affected by the bleaching. This is a 'stalwart' species that has proven virtually resistant to hurricane effects over the past 12 years. Because the bleaching was directional, affecting upper surfaces only, it is likely that the affected colonies will recover by tissue regrowth. It is very difficult to predict the way coral reef communities will respond to climate change, because they are so diverse in their functional responses.

2. Mechanisms of cell death activity in *Aiptasia sp.* during bleaching

Recent work by Simon Dunn in our laboratories has shown that necrotic cell death rather than programmed cell death (apoptosis) was responsible for most of the cell death activity during temperature-induced bleaching in the laboratory. We are attempting to understand to what extent bleaching should be viewed as an adaptive response versus being simply a symptom of extrinsic stress. These preliminary trials indicate that most of the cell death should be viewed as a symptom rather than a response. Much of the zooxanthellae loss at early stages (4 days at 32C) seems to be due to host cell necrosis leading to loss of apparently healthy zooxanthellae cells. Interestingly, the only indication of apoptosis was in the zooxanthellae, not the host animal. At later stages of treatment (7 days at 32C), a percentage of the zooxanthellae underwent apoptosis. This may be an indication that the zooxanthellae are attempting to maintain the symbiosis by the rather extreme measure of 'cell suicide'.

3. Molecular characterisation of microbial community structure in diseased and bleached corals

Our recent work is showing that apparently healthy corals typically show very low populations of associated microbes. Only occasional "control" samples show any PCR product for bacterial 16Sr-DNA. Those that do, however, show a significant and diverse community that includes known pathogens. Could we use the microbial community as an indicator of the effects of stress and the breakdown of the normally very effective antimicrobial mechanisms? Diseased corals, by contrast, consistently show a suite of bacterial and fungal isolates, including those diseases, which have been attributed to single pathogens. Clearly, we at an early stage of understanding coral diseases and the question of whether emerging diseases are mainly a result of host stress or the introduction of novel pathogens.

Ruth D. Gates¹ and Peter J. Edmunds²

¹**Department of Organismic Biology, Ecology and Evolution, University of California**

²**Department of Biology, California State University Northridge**

“Osmotic Stress: A Potential Marker for Monitoring Coral Bleaching”

Coral symbioses are dynamic associations that are vulnerable to natural and anthropogenic disturbances. To date, most studies of these events have focused on either the ecological consequences, or the biological impact of the disturbance on the host and symbiont in isolation; few studies have addressed the response of the intact association. Here we propose osmotic stress as a novel tool with widespread application in evaluating the "health" of reef corals, and discuss an experimental test and the potential application of this tool. Physiological communication between symbiont and host remains relatively unexplored, yet the translocation of photosynthetically fixed ¹⁴C labeled glycerol to the host, and its immediate utilization as a respiratory substrate, demonstrates a high level of interaction and integration. In exploring the normal and stress related physiological integration of these symbioses, we have measured glycerol pools using a non-radioactive methodology and demonstrate that a) corals contain free glycerol, b) glycerol levels are dynamic on a time scale of hours, and c) glycerol concentrations increase in response to temperature stress. Glycerol is an important osmolyte in a taxonomically diverse group of organisms and likely plays a key role in the effective osmoregulation of corals. In this capacity, we propose that stress related changes in glycerol concentrations are a consequence of its accumulation as an osmolyte, and its function in ameliorating osmotic perturbations caused by the effect of temperature on the photophysiology of the symbionts. A literature review on the molecular control of osmoregulation has identified a genetic cascade that results in the production of glycerol, and which is induced by osmotic stress. Two elements of

this cascade, Hog1 and GPD1, appear to be highly conserved across the phylogenetic tree and we propose to exploit this conservation to develop PCR based strategies to isolate these genes from corals and explore their expression across a gradient of stress. Osmotic perturbation is a likely consequence of the environmental disturbances that elicit coral bleaching, including temperature, UV radiation, and salinity and heavy metals. If the Hog1 and GPD1 genes prove to be effective biomarkers for osmotic stress, they will represent a relatively simple and effective tool with which to monitor coral reefs and assess the "health" of intact coral-algal associations. We envision using this approach within a monitoring framework to test hypotheses concerning both the causes and consequences of changing environmental conditions.

Ove Hoegh-Guldberg, Centre for Marine Studies, University of Queensland

“Indicators of coral reef health”

Coral reefs globally are experiencing stresses that appear to be unprecedented in recent history. Global climate change has added to a background of impacts that range from physical destruction due to tourism and fishing, to more widespread and potent impacts like those associated with eutrophication and sedimentation. In 1998, approximately 10-16% of living reefs were affected by a period of unprecedented warming. Projections based on current rates of warming suggest that the conditions of 1998 will become commonplace within the next 20 years. It is almost certain (IPCC 2001) that these warming trends are associated with human driven increases in greenhouse gas concentrations. While the source of the problem (global warming) is now highly political and likely not to involve the scientist and manager, the spectre of degrading reef resources presents a new set of issues for scientists, reef users and managers. This paper concentrates on the problem of trying to find early warning systems based on physiological and biochemical parameters of reef health. Bioindicators serve two important roles. One is to allow monitoring of the impacts of climate change as it develops. Ideally, timely warnings could also give reef users and managers enough time to take either evasive action or evoke business strategies to reduce impacts on users and businesses associated with a reef. Three types of bioindicators are explored. The first, based on PAM (Pulsed Amplitude Modulated) Fluorimetry shows the most promise. It is relatively cheap, is reliable and can be used to detect a number of forms of impact. Minimal work is required to get this technique implemented as a monitoring or early warning tool. The other two, cellular markers such as dinoflagellate density, chlorophyll and protein content, and biochemical markers based on heat shock proteins (hsp 70 and hsp 50) and other enzymes (detected using Fluorescent Immuno-Absorption Assays – eg MnSOD) require considerable work before they will be ready for use in biomonitoring of climate impacts. All of them, however, should be eventually usable by the criteria for bioindicators described in this paper. The last part of the Centre for Marine Studies' studies work in this area is on linking reef based physiological and biochemical parameters to remote sensing done by low flying aircraft and satellites. This program is a major focus of the Centre and is likely to yield some extremely important monitoring tools.

Michael P. Lesser, Dept. Zoology and Center for Marine Biology, University of New Hampshire

“Coral Reef Bleaching: Early Warning, Monitoring, and Long-term Recovery”

In recent years coral reefs have been severely degraded by a wide range of anthropogenic insults. Often times there is insufficient information available to make a case to stop this degradation or a lack of political will to put regulations and enforcement efforts in place to halt the precipitous decline in reef coverage and “health”. It has also become apparent to me that in order to provide the kind of information needed to assess and monitor coral reefs in a practical way, a multi-level approach needs to be considered. My own work has involved some but not all of the levels I've envisioned. From the perspective of cost-effectiveness and global coverage I believe that remote sensing using a variety of platforms is becoming an essential tool for coral reef biologists and managers. Being able to assess sea surface temperatures and the possibility of mapping reefs from airborne or satellite platforms is available to all nations at modest costs. To support these types of measurements several levels of ground-truthing or assessment are needed. Real-time data collection from oceanographic buoys that contain weather station, irradiance (PAR and UVR), and optical sensors will be needed. These buoys and their maintenance are not inexpensive. The number of buoys deployed will be dependent on resource availability but they are essential to realize the full potential of the remote sensing component. The next level involves

finer resolution in-water measurements. One approach that has been adopted and should be expanded is to use cheap temperature thermistor instruments that are durable, reliable, and easy to deploy and operate to obtain systematic coverage of many reefs or within reef bathymetric temperature data. At the organismal level the non-destructive assessment of PSII function using active fluorescence techniques has exploded and has the potential to provide an early signal of “stress” that could predict events such as thermally induced bleaching. These instruments are expensive, require some training, and the interpretation of the data needs to be carefully considered. At the cellular level there are several “markers” that may also have some utility. The D1 protein of PSII, heat shock proteins, and cell cycle genes are all potential candidates. Lastly, an assessment of damage and monitoring of recovery of impacted coral reefs is the unfortunate requirement for any perturbation. Combining remote sensing with rapid assessment protocols such as AGGRA promises to be the most cost-effective way to do that.

Yossi Loya, Dept of Zoology, Tel-Aviv University

“Coral bleaching: individual and community aspects”

Two studies will be presented: 1. At the community level- a recently reported account of a remarkable coral bleaching phenomenon that occurred for the first time on the coral reefs of Japan. The general question to be considered in the terms of reference of the working group is to determine factors associated with coral reef ecosystem stability and resilience to major anthropogenic or natural disturbances. Are coral community structural shifts expected following major bleaching events? 2. At the individual level – a study examining physiological constraints on energy allocation and colony integration during bleaching. Are there “bleaching thresholds” within partially affected colonies that determine energy allocation, levels of colony integration and intra-colonial translocation of energy products?

1. Coral bleaching: the winners and the losers (Y. Loya, K. Sakai, K. Yamazato, Y. Nakano, H. Sambali and R. Van Woesik, *Ecology Letters* 4:122-131,2001)

Sea surface temperatures were warmer throughout 1998 at Sesoko Island, Japan, than in the 10 preceding years. Temperatures peaked at 2.8 °C above average, resulting in extensive coral bleaching and subsequent coral mortality. Using random quadrat surveys, we quantitatively documented the coral community structure one year before and one year after the bleaching event. The 1998 bleaching event reduced coral species richness by 61% and reduced coral cover by 85%. Colony morphology affected bleaching vulnerability and subsequent coral mortality. Finely branched corals were most susceptible, while massive and encrusting colonies survived. Most heavily impacted were the branched *Acropora* and pocilloporid corals, some of which showed local extinction. We suggest two hypotheses whose synergistic effect may partially explain observed mortality patterns (i.e., preferential survival of thick-tissued species, and shape-dependent differences in colony mass-transfer efficiency). A community-structural shift occurred on Okinawan reefs, resulting in an increase in the relative abundance of massive and encrusting coral species.

2. Bleaching effects on regeneration and energy translocation in corals (M. Fine, U. Oren and Y. Loya, in progress)

Modular organisms consist of repeated building blocks. An important consequence of modularity may be reflected in the ability of a colony to continually re-allocate priority of resource transport among its units in response to stress. Hermatypic corals are prone to damage by a multitude of biotic and abiotic agents, such as storms, sedimentation, extreme temperature fluctuations, emersion at low tides, predation, diseases, anthropogenic disturbances and in recent years especially due to bleaching. During bleaching the supply of energy (photoassimilates) by zooxanthellae photosynthesis to the coral host declines. In the present study we compared regeneration capabilities of unbleached *Oculina patagonica* colonies (an encrusting Mediterranean stony coral) with those of partially bleached colonies. We also examined possible intra-colonial translocation of photosynthetic products, labeled with ¹⁴C, towards recuperating lesions in partly bleached vs. unbleached intact colonies. The percentage recovery of 2 cm² lesions inflicted on unbleached *O. patagonica* colonies was significantly higher than the percentage recovery of similar lesions within the bleached area of the partly bleached colonies. Lesion regeneration in *O. patagonica* resulted in oriented intra-colonial translocation of ¹⁴C products towards recuperating lesions located up to 4-5 cm away from them. In partially bleached colonies (50%-80%), such translocation did not occur, probably explaining the reduced recovery rates of lesions in bleached colonies. We suggest the possible existence of a bleaching threshold within *O. patagonica* colonies that determines energy allocation, levels of colony integration and intra-colonial translocation of energy products towards regions of maximal demand.

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“Coral Bleaching: A Cellular Perspective of a Global Phenomenon”

Coral reefs are important and fragile tropical ecosystems, which are experiencing significant degradation on a world-wide scale mainly through direct anthropogenic activities. This trend is now compounded by the increased frequency of catastrophic coral bleaching and mortality events. There is a consensus that recent massive coral bleaching and mortality events have been triggered by the presence of Sea Surface Temperatures (SST) above the long-term summer averages. Considering that the majority of the Global Warming models predict increments in SST for the tropical oceans in the near future, there is a growing concern regarding the future of coral reef ecosystems. In this context, it is imperative to develop predictive models of how coral communities would react under possible future environmental scenarios. During my presentation, I will attempt to summarize some of the physiological and environmental information required to construct such models. Although there is still a controversy regarding the actual site of damage, most researchers agree that thermal inactivation of algal photosynthesis is a common initiator of coral bleaching. As a result of the inactivation of photosynthesis, the photosynthetic apparatus is sensitized to experience permanent photoinhibition by excess light. There are at least two other environmental factors that are known to negatively affect the photosynthetic function of symbiotic dinoflagellates, water motion and UV radiation. It will be critical to investigate the time constant for the induction of damage under a particular set of temperature, solar radiation (visible and UV) as well as water motion. This information can be generated under controlled laboratory conditions, but validation of the models requires a solid knowledge of how these environmental variables change in the field. Models need to consider that symbiotic dinoflagellates are genetically diverse and exhibit profound physiological differences, including thermal sensitivities, and capacities to dissipate excess excitation. Recent studies indicate that symbiotic dinoflagellates of the genus *Symbiodinium*, isolated from different hosts and cultured under identical conditions present dramatic differences in their thermal sensitivity. Consistent with these findings, comparative analyses of the responses of intact corals indicate the existence of up to 4°C differences in the thermal sensitivity of 14 coral species harboring distinct symbiotic dinoflagellates. The species-specific thermal tolerance range of individual coral species appears to be a function of the presence of specific algal symbionts. Finally, and considering that most of our experimental approaches stress the responses of corals to brief exposures to environmental extremes, it is important to perform long-term experiments to analyze the limits of acclimation to stressful conditions.

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“Coral bleaching: differential survival and recovery”

Coral bleaching, or the paling of corals through loss of pigmentation or loss of symbiotic algae (zooxanthellae), coincided with some of the warmest sea-surface temperatures (SSTs) on record in the western Pacific during 1998. However, there was considerable spatial variation in coral survivorship; for example, corals of the same species at different locations around the Ryukyu Islands (Japan), within kilometers of each other, showed vastly different responses. Some locations experienced 100% coral mortality while other locations, nearby, suffered little coral mortality. Coral survival was especially high in habitats with high average-water-flow rates (i.e., strong currents).

Here I show experimental evidence for high survivorship of *Acropora digitifera* coral colonies that were subjected to both high SSTs (ranging from 26.22 to 33.65°C) and high-water flow (50 to 70 cm s⁻¹), while corals that were subjected to both high SSTs and low-water flow (2 to 3 cm s⁻¹) showed low survivorship. All experiments were conducted under high irradiance (~95% photosynthetically active radiation). I also empirically show that no coral mortality occurred when SSTs were below 30°C (ranging from 26.64 to 29.74°C) under similar flow regimes. The spatial differences in coral mortality during the 1998 bleaching event may have been, in part, a result of differences in water-flow rates that induced differential rates of passive diffusion, which varied among habitats.

I also show evidence for differential selection of adult-coral colonies. The most successful survivors had encrusting and massive morphologies. The rate at which bleached corals regained their pigmentation varied in accordance with species type, colony size and depth; with small colonies in shallow waters regaining their pigmentation most quickly. Regaining pigmentation seemed to follow two patterns, either (1) stemming from remnant patches of zooxanthellae, or (2) patches appearing randomly throughout the colonies.

I report high levels of coral recruitment on nearshore reefs despite the presence of few adult corals, which suggests that coral recruits are being supplied by offshore reefs. High recruitment nearshore does not necessarily suggest rapid community recovery at all locations because some locations show inconsistencies between coral recruitment patterns and adult coral communities. This inconsistency suggests that local environmental conditions inflict post-settlement mortality and that these processes are a vital structuring component of the recovering coral communities. I introduce some generic meta-models that may help predict spatial recovery and the extent of adaptation of different coral species to different habitats.

Annex V

Outline of four research themes with work hypothesis that address issues essential in our understanding of the mechanisms behind coral bleaching, coral degradation and the possible recovery of coral reefs, which can possibly lead to the development of indicators and predictive models.

Program 1: Tolerance of individuals and populations

Basis of tolerance (biochemical, physiological)

Environmental variability within a reef (physical and chemical variables, heterogeneity of environments within reefs; ecology, oceanographic processes)

Interspecies differences in tolerance in corals and zooxanthellae (molecular genetics, physiology and biochemistry).

Susceptibility to pathogens

Over-arching question: What is the tolerance of individuals and populations on coral reefs?

Hypotheses:

- Corals and zooxanthellae vary in their environmental tolerance.
- Coral bleaching and mortality is driven by the primary variable elevated temperature but is influenced by light, flow and other factors.
- Thermal stress will reduce growth rates, coral metabolism, regenerative capacity and colony integration
- Thermal stress will reduce reproductive output (gametogenesis, spawning)
- Other stressors (natural and/or anthropogenic) will have a compounding effect on the tolerance of corals and zooxanthellae to thermal stress.
- The tolerance of corals and zooxanthellae will determine their survival under climate change driven stress.
- The susceptibility of corals to pathogens is influenced by climate change driven stress.

Program 2: Local ecological responses

Community change, phase shifts (ecology)

Recovery process (ecology physiology)

Vulnerability of reproduction? (Reproductive biology, larval ecology)

Over-arching question: How will coral reef communities respond to climate change?

Hypotheses:

1. Increased sea temperatures will reduce reef resilience capacity by:
 - Increasing whole colony mortality on coral reefs.
 - changing differential mortality patterns (species, size)
 - reducing recruitment (loss during larval phase, failure of settlement)
 - causing a change in relative abundance of populations within the community
 - causing changes in coral abundance and in size frequency distributions
 - causing a functional shift.
 - causing net erosion (balance between accretion and bio- and chemo-physical erosion)
2. Reef complexity (e.g. physical, biological, chemical, structural) will affect the response to environmental stress.
3. Refugia (patchiness) will exist within reefs such that corals within these sub-habitats will act as important sources of re-colonization for affected reefs.

Program 3: Regional ecological responses

Population genetics (molecular genetics, population biology, modeling)

Recruitment between reefs (Larval ecology, oceanographic processes)

Larval survivorship (Larval ecology)

Over-arching question: How will refugia and reef connectivity influence the persistence of coral reefs regionally?

Hypotheses:

- Reefs are connected at a regional scale such that larvae will flow between reefs at time scales relevant to reef recovery.
- Local oceanographic processes play an important role and can be used to project how reefs will recover from disturbances like coral bleaching.
- Larval survival may be affected more than adult phase by environmental stress

Program 4: Assessing change

Remote sensing (ecology, physiology, geography, remote sensing)

Indicators (physical, physiology, biochemistry; depends on outcome from other three programs)

Over-arching question: How will coral reef communities respond to climate change?

- Potential indicators of coral health (so far):
- Thermal anomalies are a good predictor of coral bleaching.
- The multiplier of thermal, light and duration is a good indicator
- Fluorescence techniques (PAM, FRRF)
- Physiological (zooxanthellae and host parameters)
- Biochemical (e.g. MnSOD, Hsps, D1 turnover, MAA, gfps etc.)
- Molecular biology (differential gene expression)
- Potential indicators of coral reef health (so far):
- Ecological responses (ref: T. Done)
- Changes in other ecological parameters listed within programs.

Appendix VI

Conceptual model of a research program aiming to provide information for the development of indicators and predictive models of coral bleaching and related effects

