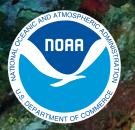
MESOPHOTIC CORAL ECOSYSTEMS RESEARCH STRATEGY:

INTERNATIONAL WORKSHOP TO PRIORITIZE RESEARCH AND MANAGEMENT NEEDS FOR MESOPHOTIC CORAL ECOSYSTEMS

JUPITER, FLORIDA • 12-15 JULY 2008



NOAA Technical Memorandum NOS NCCOS 98 and OAR OER 2



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Cover Photo: Black grouper, *Mycteroperca bonaci*, at 62 m off La Parguera, Puerto Rico. Photo Credit: Hector Ruiz.

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This document summarizes the results of the first Mesophotic Coral Ecosystems Workshop held in Jupiter, Florida on July 12-15, 2008. The workshop was hosted by the Perry Institute for Marine Science (PIMS) and organized by the National Oceanic and Atmospheric Administration (NOAA) National Centers for Coastal Ocean Science's Center for Sponsored Coastal Ocean Research and the Office of Ocean Exploration and Research's NOAA Undersea Research Program, and the U.S. Geological Survey (USGS). This meeting brought together researchers, managers, and nongovernmental agents active in mesophotic coral ecosystem issues to determine the current state of knowledge and establish research priorities for these ecosystems. NOAA, USGS, and PIMS offer their gratitude to participants and their organizations for a very successful workshop. Their enthusiasm, knowledge, and input were integral to the achievements discussed herein and we look forward to future collaborations. We especially would like to thank Tori Redinger of PIMS for her expert assistance with the planning and execution of the workshop; Lynn Dancy for editing this document; and all the photo contributors for sharing their images.



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Executive Summary

MESOPHOTIC CORAL ECOSYSTEMS WORKSHOP JUPITER, FLORIDA — 12-15 JULY 2008

OVERVIEW

On July 12-15, 2008, researchers and resource managers met in Jupiter, Florida to discuss and review the state of knowledge regarding mesophotic coral ecosystems, develop a working definition for these ecosystems, identify critical resource management information needs, and develop a *Mesophotic Coral Ecosystems Research Strategy* to assist the U.S. National Oceanic and Atmospheric Administration (NOAA) and other agencies and institutions in their research prioritization and strategic planning for mesophotic coral ecosystems. Workshop participants included representatives from international, Federal, and state governments; academia; and nongovernmental organizations.

The Mesophotic Coral Ecosystems Workshop was hosted by the Perry Institute for Marine Science (PIMS) and organized by NOAA and the U.S. Geological Survey (USGS). The workshop goals, objectives, schedule, and products were governed by a Steering Committee consisting of members from NOAA (National Centers for Coastal Ocean Science's Center for Sponsored Coastal Ocean Research, the Office of Ocean Exploration and Research's NOAA Undersea Research Program, and the National Marine Fisheries Service), USGS, PIMS, the Caribbean Coral Reef Institute, and the Bishop Museum.

Mesophotic coral ecosystems are characterized by the presence of light-dependent corals and associated communities typically found at depths ranging from 30-40 m and extending to over 150 m in tropical and subtropical regions. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species.

ACCOMPLISHMENTS

The workshop resulted in three products: (1) a special issue of the peer-reviewed journal *Coral Reefs* reviewing the state of understanding of mesophotic coral ecosystems and the management needs associated with these ecosystems, as well as primary research articles focused on mesophotic coral ecosystems; (2) mesophotic.org, a online resource for scientists, resource managers, and others interested in the research, management, and conservation of mesophotic coral ecosystems; and (3) a *Mesophotic Coral Ecosystems Research Strategy* to help guide the path forward towards understanding these ecosystems.

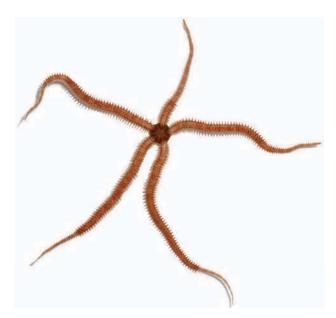
Research Priorities

Research priorities were identified to improve the understanding of mesophotic coral ecosystems to enable effective ecosystem-based management. Priorities were divided into three themes: characterization, ecology, and values and threats.

CHARACTERIZATION

Mesophotic coral ecosystems are far more extensive than previously thought with some experts estimating that their linear extent could rival or exceed that of shallower reefs. Suitable habitat for these ecosystems is dependent on several factors including light availability, substrate, temperature and other parameters. To what extent these factors control the distribution of these ecosystems is unknown.

The varied depths and topographies of mesophotic coral ecosystems present challenges for research sampling. Thus, there is a great disparity in the extent of knowledge for different taxonomic groups and geographic regions. Major components of the biotic assemblage are unknown, underscoring a critical need for basic taxonomic and systematic characterization.



Resource managers need to know where mesophotic coral ecosystems are found and their extent, what determines where these ecosystems are located, and what organisms are there.

Research priorities to address the needs are to:

- » Determine the distribution and occurrence of these ecosystems, and the geological and physical processes that control their distribution.
- » Characterize mesophotic coral ecosystem biodiversity and endemism.
- » Understand the biotic and abiotic factors that influence and regulate biodiversity.

Ecology

Mesophotic coral ecosystems support an abundant reef fauna, some of which are shared with shallower coral ecosystems. However, many of the inhabitants of these ecosystems and the processes which regulate their community structure and dynamics are currently unknown. These ecosystems may be an extension of shallow coral biota, a unique assemblage, or a combination of shallow and deep biota. If there is connectivity between shallow and mesophotic coral ecosystems, then mesophotic coral ecosystems might be a potential source of propagules to restore depleted shallow populations.

Resource managers need to know what key species are present in these ecosystems, what ecological role these ecosystems play, and if they are connected to shallow, other mesophotic, and deep-sea coral ecosystems. Research priorities to address the needs are to:

- » Characterize community structure.
- » Understand the specific processes and mechanisms that underlie the ecological dynamics of these ecosystems.
- » Determine their ecological role.
- » Understand the trophic, ecological, and genetic connectivity of mesophotic coral ecosystems with shallow, other mesophotic, and deep-sea coral ecosystems.

VALUES AND THREATS

Mesophotic coral ecosystems possess considerable natural, social, and economic values, and are believed to face similar threats as shallower coral ecosystems do. To protect the values of mesophotic coral ecosystems and mitigate the threats to them, we need to better understand, from an ecological and human dimension, how these systems are characterized, which factors control the processes that regulate them, and what the key values, threats, and impacts are.

Resource managers need to know what the threats and their subsequent impacts are to these ecosystems, as well as an improved understanding of their intrinsic and extrinsic values.

Research priorities to address the needs are to:

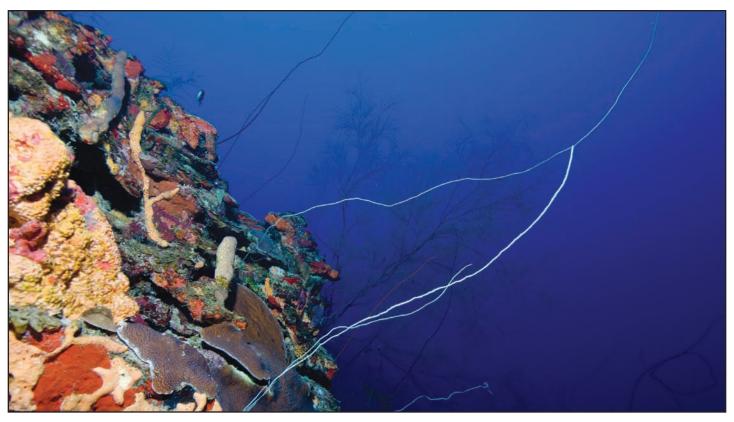
- » Understand anthropogenic and natural impacts to these ecosystems.
- » Determine the benefits of mesophotic coral ecosystems.

WORKSHOP ACCOMPLISHMENTS

- A special issue of *Coral Reefs* reviewing the state of knowledge regarding these ecosystems.
- Creation of mesophotic.org as a resource for individuals interested in mesophotic coral ecosystems and to enhance collaborations.
- A Mesophotic Coral Ecosystem Research Strategy.

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Introduction



Mesophotic coral ecosystems are found occupying both flat and slope substrates. Pictured is a mesophotic coral ecosystem off La Parguera, Puerto Rico at a depth of 45 m. Photo Credit: Hector Ruiz.

On July 12-15, 2008, researchers and resource managers met in Jupiter, Florida to discuss and review the state of knowledge regarding mesophotic coral ecosystems, develop a working definition for these ecosystems, identify critical resource management information needs, and develop a *Mesophotic Coral Ecosystems* Research Strategy to assist the U.S. National Oceanic and Atmospheric Administration (NOAA) and other agencies and institutions in their research prioritization and strategic planning for mesophotic coral ecosystems. Workshop participants included representatives from international, Federal, and state governments; academia; and nongovernmental organizations. The purpose of this document is two-fold: (1) to summarize the workshop results and (2) to present a research strategy to further the understanding of mesophotic coral ecosystems.

ABOUT THE WORKSHOP

The Mesophotic Coral Ecosystems Workshop was the outgrowth of a partnership between two offices within NOAA – the National Centers for Coastal Ocean Science's Center for Sponsored Coastal Ocean Research (NCCOS/CSCOR) and the Office of Ocean

Exploration and Research's NOAA Undersea Research Program (OER/NURP). The partnership began with development of the NCCOS/CSCOR Deep Coral Reef Ecosystem Studies announcement of opportunity for research projects in 2006 focused on deep water (50-100 m), hermatypic, light-dependent coral reef ecosystem¹ processes in which OER/NURP agreed to administer the operations for applicants that did not have access to deep water technologies and the necessary safety oversight through their home institutions. The Deep Coral Reef Ecosystem Studies announcement resulted in two multi-year research projects focused on mesophotic coral ecosystems, one in the Caribbean (Puerto Rico) and one in the Pacific (Hawaii). These studies administered by NCCOS/CSCOR contribute to the mission of the NOAA Coral Reef Conservation Program. Since then, the need to develop a research strategy to provide a detailed list of critical information needs to better understand these ecosystems and focus limited research dollars became apparent and thus, the Mesophotic Coral Ecosystems Workshop was born.

¹ Note: the thinking has evolved since 2006. These ecosystems are now referred to as mesophotic coral ecosystems to lessen confusion with azooxanthellate deep-sea corals.

The Mesophotic Coral Ecosystems Workshop was hosted by the Perry Institute for Marine Science (PIMS) and organized by NOAA and the U.S. Geological Survey (USGS). The workshop goals, objectives, schedule, and products were governed by a Steering Committee consisting of members from NOAA (NCCOS/CSCOR, OER/NURP, and the National Marine Fisheries Service), USGS, PIMS, the Caribbean Coral Reef Institute, and the Bishop Museum.² The workshop consisted of both plenary and breakout sessions organized around three themes: (1) characterization, (2) ecology, and (3) management. For the breakout sessions, participants were divided into one of six sub-themes:

- (1) Characterization
 - Biodiversity
 - Geomorphology and Physical Processes
- (2) Ecology
 - Community Structure and Dynamics
 - Connectivity
- (3) Management
 - Fisheries Impacts and Uses
 - Management Needs



Mesophotic corals such as Leptoseris spp. in Hawaii grow in plate-like form to maximize light capture by their zooxanthellae. Photo Credit: Dan Polhemus.

WORKSHOP ACCOMPLISHMENTS

Remarkable achievements were made during the three-day workshop, the first of its kind to focus on mesophotic coral ecosystems, with participants identifying and prioritizing critical information needs to improve the understanding of mesophotic coral ecosystems to aid resource managers in decisionmaking. Participants actively discussed and agreed to a working definition for mesophotic coral ecosystems, an accomplishment that by itself was worth having the workshop. In addition to agreeing on the definition, the workshop resulted in three products: (1) a special issue of the peer-reviewed journal Coral Reefs that reviews the state of understanding of mesophotic coral ecosystems and their management needs, and includes primary research articles focused on mesophotic coral ecosystems; (2) mesophotic.org, a online resource for scientists, resource managers, and others interested in the research, management, and conservation of mesophotic coral ecosystems; and (3) a Mesophotic Coral Ecosystems Research Strategy to help guide the path forward towards understanding these ecosystems.

RESEARCH STRATEGY FRAMEWORK

The intention of the Workshop and the Research Strategy was to identify critical research needs to help inform management. In developing this document, it became apparent that using a theme entitled "management" as one of the three themes from the workshop was not the best way to present information. For the Research Strategy, research priorities have been divided into three themes: (1) characterization, (2) ecology, and (3) values and threats. For each theme, the management needs are stated in a question format followed by the research objective(s) and activities needed to answer the management question.

IMPLEMENTING THE RESEARCH STRATEGY

The goal of the *Mesophotic Coral Ecosystems Research Strategy* is to guide NOAA-supported activities, as well as serve as a resource for other funding agencies, scientists, and managers working at local, regional, national, and international scales. To be most effective, the implementation of the research priorities identified herein should be addressed using a mixture of both short-term (1-2 years) and longer-term (3-5 years) research studies. Short-term, small-scale projects provide the ability to answer targeted questions that can feed into longer-term, ecosystem-scale studies focused on

² The Caribbean Coral Reef Institute at the University of Puerto Rico and the Bishop Museum were the awardees of the 2006 and 2007 NCCOS/CSCOR funding focused on mesophotic coral ecosystems.

understanding the patterns and processes associated with mesophotic coral ecosystems. Longer-term studies should strive to be comprehensive in nature by addressing research questions in an ecosystem context using a multi-disciplinary, multi-investigator approach.

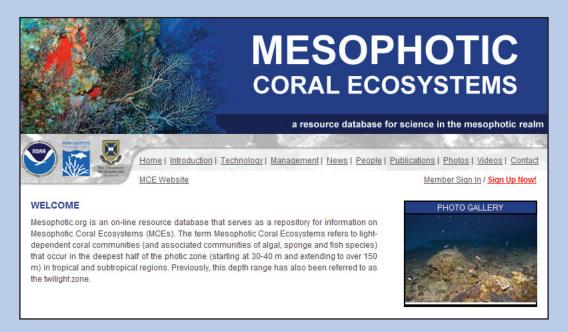
The role of research is to answer questions, not implement the results. Thus, to ensure that research conducted is relevant to resource managers, they must be entrained from the outset. One of the simplest ways to involve resource managers in a research study is to include them as part of the research or oversight team responsible for designing and guiding the research project. This will help ensure that the science performed addresses management needs. Additionally, involvement of other key stakeholders, such as Fishery Management Councils or National Marine Sanctuaries, should be addressed during the research design and execution phases so that these stakeholders are aware of the potential implications of the work being conducted and able to provide valuable feedback on the types of information that would be useful to them.

MESOPHOTIC.ORG

Mesophotic.org is an online resource for scientists, resource managers, and other parties that are interested in the research, management, and conservation of mesophotic coral ecosystems. Mesophotic.org provides a forum for collaboration and permits individuals to submit¹ their own information as it pertains to their interests and expertise in mesophotic coral ecosystems. The website is designed with the user in mind and contains contact information² to enhance collaborations, a list of publications, photos, news stories, and postings of job and educational opportunities. In addition, general information to enhance the public's understanding of these ecosystems is provided including text on the specialized underwater technologies used to study these ecosystems, as well as the threats they face.

Mesophotic.org is a collaborative effort between NOAA, PIMS, and the Centre for Marine Studies at the University of Queensland in Australia.

¹Subject to review. ²Contact information is based on user submissions.



Mesophotic Coral Ecosystems



The coral species Leptoseris provides habitat for a variety of fishes including Psuedanthias thompsoni and Cheatodon milliaris, Auau Channel, Hawaii, depth of 70 m. Photo Credit: NOAA's Hawaii Undersea Research Laboratory.

The term "coral" conjures up visions of warm, tropical waters, or, as of late, the cold, dark depths of the ocean where not a ray of sunlight penetrates. Found between these two visions is a relatively unknown and poorly understood depth realm referred to as the mesophotic zone – 'meso' for middle and 'photic' for light. Mesophotic coral ecosystems are characterized by the presence of light-dependent corals and associated communities typically found at depths ranging from 30-40 m and extending to over 150 m in tropical and subtropical regions. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species.

Investigations into the mesophotic depth realms have been hampered not by a lack of interest or importance, but by technology. The upper limit of mesophotic coral ecosystems happens to coincide with the depth limitation for conventional SCUBA diving, and is too shallow and costly for most deep-diving technologies [e.g., remotely operated vehicles (ROV) and submersibles] to operate safely without entanglement. Consequently, two-thirds of the total depth range of zooxanthellate coral environments remains largely unexplored. Advances in undersea technologies in the past decade have begun to make investigating the mesophotic zone a more tangible reality. Technologies such as, open/closed-circuit rebreather and mixedgas diving, as well as smaller ROVs and autonomous underwater vehicles designed for benthic mapping are enabling easier access to study mesophotic coral ecosystems.

Little is known or understood about mesophotic coral ecosystems. In an effort to identify the information gaps (unknowns), workshop participants and invited contributors summarized the state of knowledge regarding these ecosystems in a series of review papers to be published in a special issue of the peerreviewed journal *Coral Reefs.* The review papers focus on biodiversity, geomorphology, community ecology, biological and physical connectivity, and management issues related to mesophotic coral ecosystems. These articles, while providing a detailed account of what is known, make the large gaps which exist in our understanding of these ecosystems even more apparent.



An example of an algal-dominated mesophotic coral ecosystem community in the Auau Channel, Hawaii. Photo Credit: NOAA's Hawaii Undersea Research Laboratory.

IMPORTANCE

In an era of significant coastal ocean changes, documented human impacts on shallow coral reefs, and increased efficiency of exploitation, it is important to understand the value and role of mesophotic coral ecosystems in tropical and subtropical ecosystems. Limited data on taxonomy, distribution, population genetics, reproductive biology, and life histories of species restrict our ability to address these issues and implement effective management.

Mesophotic coral ecosystems may be regarded as extensions of shallow coral ecosystems including sharing common species. It has been hypothesized that mesophotic coral ecosystems may serve as refugia for impacted shallow-water populations. If true, mesophotic coral ecosystems may serve as potential sources to reseed or replenish degraded shallow-water populations. Additionally, mesophotic coral ecosystems may contain a number of species that are endemic to this depth range, making them especially vulnerable to disturbances.

Mesophotic coral ecosystems may also serve as critical habitat for economically- and ecologically-important species that undergo ontogenetic shifts in habitat use from the larval to juvenile to adult phases. Little is known about which species may utilize these ecosystems

- Mesophotic Coral Ecosystems Research Strategy

as essential fish habitat.³ Discoveries of new species or horizontal and vertical range expansions tensions are occurring on a regular basis at these depths.

In addition, the ability to live in the mesophotic zone requires special adaptations to low-light conditions. These adaptations may increase the value of these species as bioproducts such as pharmaceuticals. Similar to their shallower-water counterparts, mesophotic coral ecosystems contain organisms with specialized defenses to ward off predators, competitors, and microbial infections. These specialized defenses often yield unique compounds that have potential as marine natural products.

THREATS

Since mesophotic coral ecosystems are part of the continuum of shallow-water reefs along a depth gradient, they are subject to many of the same threats faced by shallower coral ecosystems, such as climate change, fishing, pollution, invasive species, and coastal uses (e.g., dredging and anchoring). The degree and extent each threat poses to these ecosystems is unknown and needs to be evaluated. However, even without a quantitative measurement of the impact from threats, it is fairly safe to state that anything limiting light penetration (e.g., increased water turbidity and sedimentation) or hinders sessile organisms from performing normal functions (e.g., sedimentation impairing an organism's ability to filter feed) could have a significant impact on these ecosystems.

Increased nutrients may also pose a problem to these ecosystems. At mesophotic depths, there are less herbivores compared to shallower depths. Therefore, if an algal bloom is triggered by increased nutrients, there will not be enough herbivores present to reduce the impact of the algal bloom.

Fishing-specific impacts to productivity are welldocumented for coastal ecosystems and can result in changes in habitats, fish community dynamics, and connectivity to supportive nearshore habitats. Fisheries activities may negatively influence abundances, sizes, and the diversity of fishes, invertebrates, and corals, as well as alter food web dynamics. Loss of fisheries productivity will deleteriously affect the economic and cultural benefits derived from the ecosystem.

³ Essential fish habitat is those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity.

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Research Priorities for Mesophotic Coral Ecosystems



Fish collected at mesophotic depths in the Auau Channel, Hawaii. Many of the fish species found at mesophotic depths are endemic to the Hawaiian archipelago. Photo Credit: Heather Spalding.

Research Goal:

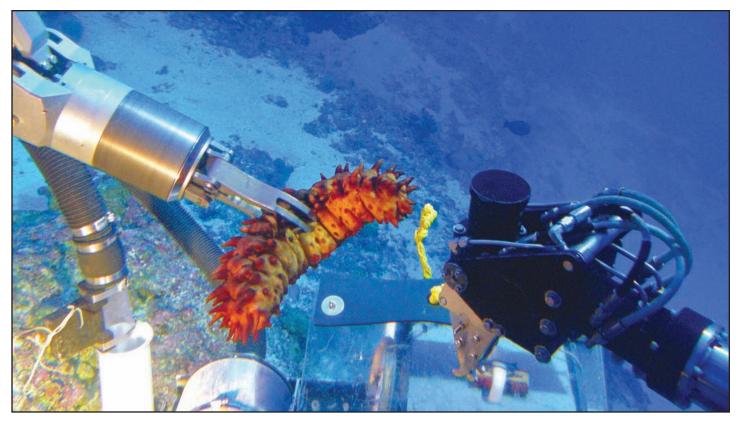
to provide sound science to enable effective ecosystem-based management of mesophotic coral ecosystems.

For resource managers to make informed decisions, they require the most up-to-date scientific information for the resources under their purview. In the case of mesophotic coral ecosystems, so little is known about them that what is needed most is baseline information on their location, characteristics, perceived threats, condition, and the causes and consequences of that condition. The highest priorities for improving the understanding of mesophotic coral ecosystems are to:

- Locate and predict where mesophotic coral ecosystems exist;
- Characterize their biodiversity and the geological and physical processes that control their distribution;

- Determine the community structure and dynamics of these ecosystems, as well as their connectivity to other coral ecosystems found in shallow, mesophotic, and deeper depths; and
- Identify threats, uses, and values of these ecosystems.





The Pisces IV and V submersibles have been critical to the study of mesophotic coral ecosystems in Hawaii. Scientists in the Pisces IV shown collecting a sea cucumber, Stichopus sp. Photo Credit: NOAA's Hawaii Undersea Research Laboratory.

CHARACTERIZATION OF MESOPHOTIC CORAL ECOSYSTEMS

Mesophotic coral ecosystems are far more extensive than previously thought with some experts estimating that the linear extent of these ecosystems could rival or exceed that of shallower reefs. Suitable habitat for mesophotic coral ecosystems will be dependent on several factors including light availability, substrate, temperature, and other parameters. To what extent these factors control the distribution of these ecosystems is unknown. Improving our ability to predict the location of these ecosystems will be vital to enhancing our understanding of them and ensuring that limited research dollars are used efficiently. Additionally, collecting coral cores could provide information on the accretion history of these systems, and enable forecasts of how current and predicted environmental changes may impact them.

The varied depths and topographies of mesophotic coral ecosystems present challenges for sampling and measuring biodiversity, and there is a great disparity in the extent of our knowledge for different taxonomic groups and geographic regions. Although conventional wisdom and a few studies indicate that diversity is lower in these ecosystems than in their shallower-water counterparts, several studies show high diversity and species richness within mesophotic coral ecosystems. Additionally, major components of the biotic assemblage are unknown, thus underscoring a critical need for basic taxonomic and systematic characterization.

Mesophotic coral ecosystems may also harbor endemic species. Some species in these ecosystems have more restricted geographic ranges than those on shallow reefs and thus, are at risk of extinction if disturbed or exploited, attesting to the urgency for their study. Other species have broad geographic and depth distributions.

For resource managers, it is important to understand where and to what extent mesophotic coral ecosystems are found, what factors influence their location, as well as what organisms are found in these ecosystems. Management Need: Where are mesophotic coral ecosystems found and what is their extent?

Research Objective: Determine the distribution and occurrence of mesophotic coral ecosystems.

- Evaluate existing data sets for the presence/absence of mesophotic coral ecosystems to target mapping efforts.
- Conduct broad-scale, reconnaissance surveys to identify the presence/absence of mesophotic coral ecosystems, and site-specific, high-resolution surveys for small-scale characterizations.
- Develop or refine, test, and evaluate tools and technologies to predict where these ecosystems may occur, and assess the distribution and extent of mesophotic coral ecosystems.

Management Need: What determines where mesophotic coral ecosystems are found?

Research Objective: Understand the geological and physical processes that control mesophotic coral ecosystem distribution and characteristics.

- Characterize the environmental regime spatially and temporally (e.g., light, temperature, and carbonate chemistry) associated with mesophotic coral ecosystems.
- Determine which geomorphological features are associated with mesophotic coral ecosystems (e.g., upper shelf geology and slope gradient).
- Ascertain how physical processes influence mesophotic coral ecosystem formation (e.g., downward sedimentation, currents, and upwelling).

Management Need: What organisms are found in these ecosystems?

Research Objective: Characterize mesophotic coral ecosystem biodiversity to better understand, manage, and conserve biodiversity and endemism.

- Develop consistent sampling methods in conformance with data standards to allow for cross-study comparisons and collaborations.
- Conduct systematic, broad-scale surveys to inventory organisms present in the mesophotic zone. For each species:
 - o Collect and catalog specimens including photo documentation and tissue samples for molecular analyses.
 - o Determine relative abundance, geographic and depth distributions, and extinction vulnerabilities.
- Improve the understanding of basic taxonomy of mesophotic coral ecosystem biota.
- Determine biotic and abiotic factors which influence biodiversity.



The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species. Image taken at 60 m at Precipico on the southwest coast of Puerto Rico. Photo Credit: Hector Ruiz.

ECOLOGY OF MESOPHOTIC CORAL ECOSYSTEMS

Mesophotic coral ecosystems cover extensive areas and support an abundant community of reef fauna, some of which are shared with shallow-water coral reef ecosystems. However, many of the inhabitants of mesophotic coral ecosystems and the processes which regulate their community structure and dynamics are currently unknown.

The possibility that mesophotic coral ecosystems can replenish shallow reefs, many of which have been impacted by natural and anthropogenic disturbances, has become an issue of keen interest to resource managers. Mesophotic coral ecosystems may be an extension of shallow coral reef communities, a unique assemblage, or a combination of shallow and deep biota. If there is population genetic connectivity between shallow and mesophotic coral ecosystems, then mesophotic coral ecosystems might be a potential source of larvae to restore depleted shallow populations. If there is trophic connectivity between these habitats, then mesophotic coral ecosystems may enhance or restore ecosystem services for shallow reef habitats. Population connectivity is driven by biological processes that encompass larval supply, hydrodynamics, settlement, and movement within and among populations. The rate of exchange of these individuals determines whether mesophotic coral ecosystems are connected to shallow, other mesophotic, or deep-sea coral ecosystems. Trophic connectivity depends on the extent of biophysical coupling between habitats. Thus, reciprocal connectivity between shallow habitats and mesophotic coral ecosystems encompasses processes related to energy flux, trophic biology, and population genetics.

For resource managers, it is important to know what key species are found in mesophotic coral ecosystems, what types of ecological roles mesophotic coral ecosystems play, as well as the connectivity of these ecosystems with shallow, other mesophotic, and deep-sea coral ecosystems.

Management Need: What are the key species within mesophotic coral ecosystems?

Research Objective: Characterize community structure including patterns of distribution and abundance.

- Identify and describe the economically- and ecologically-important species from representative habitats.
- Determine spatial and temporal variability within and between mesophotic regions.
- Relate distribution and abundance patterns to biotic and abiotic factors.
- Characterize the microbial ecology of the holobiont⁴ including autotrophic and heterotrophic components.

Management Need: What types of ecological roles do mesophotic coral ecosystems play?

Research Objective: Understand the role of mesophotic coral ecosystems in supporting various life stages of living marine resources and the processes that regulate these ecosystems.

- Characterize the life history traits of economically- and ecologically-important species.
- Determine whether economically- and ecologically-important species undergo an ontogenetic shift in mesophotic habitat use from larval to juvenile to adult phases.
- Characterize the range of habitat types and their distribution, how they are utilized, and how these relationships change over time.
- Determine the reproductive output of economically- and ecologically-important species within mesophotic coral ecosystems.
- Understand the specific processes and mechanisms that underlie the ecological dynamics of these ecosystems.

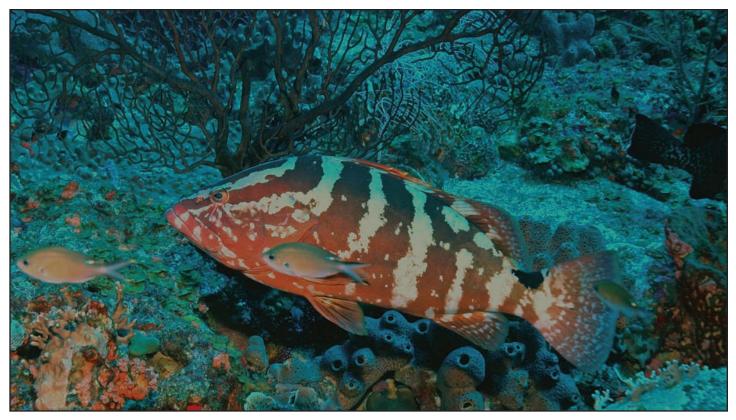
Management Need: What is the connectivity of these ecosystems with shallow, other mesophotic, and deep-sea coral ecosystems?

Research Objective: Understand the connectivity of these ecosystems with shallow, other mesophotic, and deep-sea coral ecosystems.

• Investigate how energy flux varies spatially and temporally.

4

- Determine the biophysical forcing factors that control nutrient and larvae distributions.
- Identify how migratory organisms use mesophotic coral ecosystems (e.g., as a trophic resource and spawning habitat).
- Describe trophic dynamics and nearshore primary productivity for these ecosystems.
- Determine the horizontal and vertical population structure of mesophotic coral ecosystems and to what extent there is genetic and ecological connectivity horizontally and vertically.
 - o Determine whether mesophotic coral ecosystems can serve as refugia and reseed shallow reefs (or vice versa).
 - o Determine the connectivity between mesophotic coral ecosystems.
- Determine the distribution overlap of key species with shallow and deep-sea coral ecosystems.
- Holobiont refers to the coral animal, its endosymbiotic zooxanthellae, and the associated community of microorganisms.



Mesophotic coral ecosystems may serve as a refuge for heavily exploited species such as the Nassau grouper, Epinephelus guttatus, photographed at 38 m off Bajo de Sico, Puerto Rico. Photo Credit: Jorge Sabater.

VALUES AND THREATS TO MESOPHOTIC CORAL ECOSYSTEMS

Mesophotic coral ecosystems possess considerable natural, social, and economic values. A few studies indicate that these ecosystems may be in relative pristine condition and less affected by current environmental and anthropogenic threats. As such, mesophotic coral ecosystems may contribute to the restoration of the much more impacted shallower coral ecosystems as sources for replenishment. However, they are still vulnerable to the same threats that affect shallowwater coral ecosystems such as climate change, fishing, pollution, invasive species, eutrophication, and coastal uses. At present, few mesophotic coral ecosystems are under some level of protection. For those under protection, resource managers assume that the needs are similar to those of shallower coral ecosystems. However, because of their remote location and greater depths, they pose unique challenges and opportunities for management.

To protect the values of mesophotic coral ecosystems and mitigate the threats to them, it is necessary to better understand, from an ecological and human dimension, how these systems are characterized, which factors control the processes that regulate them, and what the key values and threats are. Research focused on mesophotic coral ecosystems is needed to help identify which management strategies will be most effective.

For resource managers, it is important to know the threats and their impacts to mesophotic coral ecosystems and their extrinsic and intrinsic values.

Management Need: What are the known or perceived threats and their impacts to these ecosystems?

Research Objective: Understand the anthropogenic and natural impacts to mesophotic coral ecosystems.

- Determine the anthropogenic and natural threats including episodic events facing mesophotic coral ecosystems.
- Evaluate the ecological impacts and extent of these threats and the subsequent recovery from impacts/ disturbances.
- Identify the temporal and spatial variability of these threats.
- Investigate whether anthropogenic and natural disturbances disrupt the biological processes and connectivity of these ecosystems with shallow, other mesophotic, and deep-sea coral ecosystems.

Management Need: Are mesophotic coral ecosystems of value?

Research Objective: Determine the benefits of mesophotic coral ecosystems.

- Identify the ecosystem services⁵ provided by mesophotic coral ecosystems, as well as the range of current and potential future human uses of these areas.
- Analyze the various governance systems with jurisdiction over or relevance to mesophotic coral ecosystems and identify legislative and regulatory gaps.
- Develop decision support tools to help managers identify mesophotic coral ecosystems of value and in need of protection.

⁵ Ecosystem services are fundamental life-support processes upon which all organisms depend (Daily et al. 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. Issues in Ecology No. 2, Ecological Society of America).



Mesophotic coral ecosystems can be found from 30-40 m and extend to beyond 150 m. This image is taken at 40 m off Bajo de Sico, Puerto Rico. Photo Credit: Jorge Sabater.



In the Auau Channel, Hawaii, deep-sea corals, such as this azooxanthellate black coral (Antipathes grandis) at 90 m, can be found at mesophotic depths. Photo Credit: Sam Kahng.

Appendix A: Workshop Agenda

_ Mesophotic Coral Ecosystems Research Strategy

Appendix B: Workshop Participants

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Appendix C: Selected References

- Acosta CA, Robertson DN. 2002. Diversity in coral reef fish communities: the effects of habitat patchiness revisited. Marine Ecology Progress Series 227:87-96.
- Agegian CR, Abbott IA. 1985. Deep water macroalgal communities: a comparison between Penguin Bank (Hawaii) and Johnston Atoll. Proceedings of the 5th International Coral Reef Symposium 5:47-51.
- Agegian CR, MacKenzie FT, Tribble JS, Sabine
 C. 1988. Carbonate production and flux
 from a mid-depth bank ecosystem, Penguin
 Bank, Hawaii. In: Agegian, CR, editor.
 Biogeochemical cycling and fluxes between the
 deep euphotic zone and other oceanic realms.
 Washington (DC): NOAA, National Undersea
 Research Program. NURP Research Report
 88-1:5-32.
- Aponte NE, Ballantine DL. 2001. Depth distribution of algal species on the deep insular fore reef at Lee Stocking Island, Bahamas. Deep Sea Research 48:2185-2194.
- Armstrong RA. 2007. Deep zooxanthellate coral reefs of the Puerto Rico: US Virgin Islands insular platform. Coral Reefs 26(4):945.
- Armstrong RA, Singh H, Torres J, Nemeth RS, Can A, Roman C, Eustice R, Riggs L, Garcia-Moliner G. 2006. Characterizing the deep insular shelf coral reef habitat of the Hind Bank Marine Conservation District (US Virgin Islands) using the Seabed autonomous underwater vehicle. Continental Shelf Research 26:194-205.
- Austin HW. 1970. Florida Middle Ground. Marine Pollution Bulletin 1:171-172.
- Bak RPM, Nieuwland G. 1995. Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. Bulletin of Marine Science 56(2):609-619.

- Bak RPM, Nieuwland G, Meesters EH. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. Coral Reefs 24:475-479.
- Beets J, Muehlstein L, Haught K, Schmitges H. 2003. Habitat connectivity in coastal environments: patterns and movements of Caribbean coral reef fishes with emphasis on bluestriped grunt, *Haemulonsciurus*. Gulf and Caribbean Research 14:29-42.
- Bright TJ, Kraemer GP, Minnery GA, Viada ST. 1984. Hermatypes of the Flower Garden Banks, northwestern Gulf of Mexico: a comparison to other western Atlantic reefs. Bulletin of Marine Science 34:461-476.
- Brokovich E, Einbinder S, Kark S, Shashar N, Kiflawi M. 2007. A deep nursery for juveniles of the zebra angelfish *Genicanthus caudovittatus*. Environmental Biology of Fishes 80:1-6.
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S. 2008. Descending to the twilightzone: changes in coral reef fish assemblages along a depth gradient down to 65 m. Marine Ecology Progress Series 371:253-262.
- Brooks GR, Doyle LJ. 1991. Geologic development and depositional history of the Florida Middle Ground: a mid-shelf, temperate-zone reef system in the northeastern Gulf of Mexico. In: Osborne, RH, editor. Shoreline to abyss. Tulsa (OK): Society for Sedimentary Geology. Special Publication 46:189-203.
- Chalker BE, Dunlap WC, Oliver JK. 1983.
 Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia: II. Light saturation curves for photosynthesis and respiration. Journal of Experimental Biology and Ecology 73:37-56.
- Colin PL. 1986. Benthic community distribution in the Enewetak Atoll lagoon, Marshall Islands. Bulletin of Marine Science 38:129-143.

Mesophotic Coral Ecosystems Research Strategy.

- Colin PL, Devaney DM, Hillis-Colinvaux L, Suchanek TH, Harrison JT. 1986. Geology and biological zonation of the reef slope, 50-360 m depth at Enewetak Atoll, Marshall Islands. Bulletin of Marine Science 38:111-128.
- Craig MT, Eble JA, Robertson DR, Bowen BW. 2007. High genetic connectivity across the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). Marine Ecology Progress Series 334:245–254.
- Culter JK, Ritchie KB, Earle SA, Guggenheim DE, Halley RB, Ciembronowicz KT, Hine AC, Jarrett BD, Locker SD, Jaap WC. 2006. Pulley Ridge: a deep photosynthetic coral reef on the West Florida Shelf, USA. Coral Reefs 25(2):228.
- Dinesen ZD. 1982. Regional variation in shadedwelling coral assemblages of the Great Barrier Reef Province. Marine Ecology Progress Series 7:117-123.
- Doty MS, Gilbert WJ, Abbott IA. 1974. Hawaiian marine algae from seaward of the algal ridge. Phycologia 13:345-357.
- Dowgiallo MJ. 2004. Patterns in diversity and distribution of benthic molluscs along a depth gradient in the Bahamas [dissertation]. College Park (MD): University of Maryland. 240 pp.
- Drew AE. 1969. Photosynthesis and growth of attached marine algae down to 130 meters in the Mediterranean. International Seaweed Symposium: 161-159.
- Drew AE. 2001. Ocean nutrients to sediments banks via tidal jets and *Halimeda* meadows. In: Wolanski, E, editor. Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef. Boca Raton (FL): CRC Press. p. 255-267.
- Dustan P. 1982. Depth-dependent photoadaption by zooxanthellae of the reef coral *Montastrea annularis*. Marine Biology 68:253-264.

- Feitoza BM, Rosa RS, Rocha LA. 2005. Ecology and zoogeography of deep reef fishes in northeastern Brazil. Bulletin of Marine Science 76:725-742.
- Fredericq S, Phillips N, Gavio B. 2000. Observations on the macroalgae inhabiting deep-water hard bank communities in the Northwestern Gulf of Mexico. Gulf of Mexico Science 18:88-96.
- Fricke H, Meischner D. 1985. Depth limits of Bermudan scleractinian corals: a submersible survey. Marine Biology 88:175-187.
- Fricke HW, Knauer B. 1986. Diversity and spatial pattern of coral communities in the Red Sea upper twilight zone. Oecologia 71:29-37.
- Fricke HW, Schuhmacher H. 1983. The depth limits of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). Marine Ecology 4:163-194.
- Fricke HW, Vareschi E, Schlichter D. 1987. Photoecology of the coral *Leptoseris fragilis* in the Red Sea twilight zone (an experimental study by submersible). Oecologia 73:371-381.
- Gittings SR. 1998. Reef community stability on the Flower Garden Banks, northwest Gulf of Mexico. Gulf of Mexico Science 16:161-169.
- Graham MH, Kinlan BP, Druehl LD, Garske LE, Banks S. 2007. Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. Proceedings of the National Academy of Sciences 104:16576-16580.
- Grigg RW, Epp D. 1989. Critical depth for the survival of coral islands: effects on the Hawaiian Archipelago. Science 243:638-641.
- Grigg RW. 2003. Invasion of a deep water coral bed by an alien species, *Carijoa riisei*. Coral Reefs 22:121-122.
- Grigg RW. 2006. Depth limit for reef building corals in the Au'au Channel, S.E. Hawaii. Coral Reefs 25(1):77-84.

- Grigg RW, Grossman EE, Earle SA, Gittings SR, Lott D, McDonough J. 2002. Drowned reefs and antecedent karst topography, Au'au Channel, S.E. Hawaiian Islands. Coral Reefs 21(1):73-82.
- Hickerson EL, Schmahl GP. 2005. The state of coral reef ecosystems of the Flower Garden Banks, Stetson Bank, and other banks in the northwestern Gulf of Mexico. In: Waddell, JE, editor. The state of coral reef ecosystems of the United States and Pacific Freely Associated States. Silver Spring (MD): NOAA, NCCOS Center for Coastal Monitoring and Assessment. NOAA Technical Memorandum NOS NCCOS 11: 201-219.
- Herzlieb S, Kadison E, Blondeau J, Nemeth RS.
 2005. Comparative assessment of coral reef systems located along the insular platform of St. Thomas, US Virgin Islands and the relative effects of natural and human impacts. Proceedings of the 10th International Coral Reef Symposium 4-2:1144-1151.
- James NP, Ginsburg RN. 1979. The seaward margin of the Belize barrier and atoll reefs. Oxford: Blackwell Scientific Publications. 191 pp.
- Jarrett BD, Hine AC, Halley RB, Naar DF, Locker SD, Neumann AC, Twichell D, Hu C, Donahue BT, Jaap WC, Palandro D, Ciembronowicz K. 2005. Strange bedfellows — a deep-water hermatypic coral reef superimposed on a drowned barrier island; southern Pulley Ridge, SW Florida platform margin. Marine Geology 214:295-307.
- Jensen PR, Gibson RA, Littler MM, Littler DS. 1985. Photosynthesis and calcification in four deep-water *Halimeda* species (Chlorophyceae, Caulerpales). Deep Sea Research 32:451-464.
- Kahng SE, Kelley C. 2007. Vertical zonation of habitat forming benthic species on a deep photosynthetic reef (50-140 m) in the Au'au Channel, Hawaii. Coral Reefs 26:679-687.
- Kahng SE, Maragos JE. 2006. The deepest zooxanthellate, scleractinian corals in the world? Coral Reefs 25:254.

- Kaiser P, Schlichter D, Fricke HW. 1993. Influence of light on algal symbionts of the deep coral *Leptoseris fragilis*. Marine Biology 117:45-52.
- Koenig CE, Coleman FE, Grimes CB, Fitzhugh GR, Scanlon KM, Gledhill CT, Grace M. 2000. Protection of fish-spawning habitat for the conservation of warm-temperate reef-fish fisheries on shelf-edge reefs of Florida. Bulletin of Marine Science 66:593-616.
- Lang JC, Wicklund RI, Dill RF. 1988. Depth- and habitat-related bleaching of zooxanthellate reef organisms near Lee Stocking Island, Exuma Cays, Bahamas. Proceedings of the 6th International Coral Reef Symposium 3:269-274.
- Leichter JJ, Genovese SF. 2006. Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. Marine Ecology Progress Series 316:95-103.
- Lesser, MP. Depth-dependent photoacclimatization to solar ultraviolet radiation in the Caribbean coral *Montastraea faveolata*. Marine Ecology Progress Series 192:137-151.
- Liddell WD, Ohlhorst SL. 1988. Hard substrata community patterns, 1-120 m, North Jamaica. Palaios 3:413-423.
- Liddell WD, Avery WE, Ohlhorst SL. 1997. Patterns of benthic community structure, 10-250 m, the Bahamas. Proceedings of the 8th International Coral Reef Symposium 1:437-442.
- Maldonado M, Young CM. 1996. Bathymetric patterns of sponge distribution on the Bahamian slope. Deep Sea Research 43:897-915.
- Markager S, Sand-Jensen K. 1992. Light requirements and depth zonation of marine macroalgae. Marine Ecology Progress Series 88:83-92.
- Menza C, Kendall M, Rogers C, Miller J. 2007. A deep reef in deep trouble. Continental Shelf Research 27(17):2224-2230.

Mesophotic Coral Ecosystems Research Strategy_

- Morrison D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69:1367-1382.
- Parrish FA, Bolland RC. 2004. Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. Marine Biology 144:1065-1073.
- Pyle RL. 1996. The twilight zone. Natural History 105:59-62.
- Pyle RL. 2000. Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained dive technology. Marine Technology Society Journal 34(4):82-91.
- Reed JK. 1985. Deepest distribution of Atlantic hermatypic corals discovered in the Bahamas. Proceedings from the 5th International Coral Reef Symposium 6:249-254.
- Riegl B, Piller WE. 2003. Possible refugia for reefs in times of environmental stress. International Journal of Earth Sciences 92:520-531.
- Schlichter D, Fricke H, Weber W. 1986. Light harvesting by wavelength transformation in a symbiotic coral of the Red Sea twilight zone. Marine Biology 91:403-407.
- Spalding H. 2008. *Halimeda* meadows in Hawaii. In: Vermeij, M, editors. Coral reefs of Maui: status, stressors, and suggestions. 60 pp.
- Trussell GC, Lesser MP, Patterson MR, Genovese SJ. 2006. Depth-specific differences in growth of the reef sponge *Callyspongia vaginalis*: role of bottom-up effects. Marine Ecology Progress Series 323:149-158.
- Van den Hoek C, Breeman AM, Bak RPM, Van Buurt G. 1978. The distribution of algae, corals, and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing reef of Curacao, Netherlands Antilles. Aquatic Botany 5:1-46.

- Vermeij MJA, Bak RPM. 2002. How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. Marine Ecology Progress Series 233:105-116.
- Vermeij MJA, Bak RPM. 2003. Species-specific population structure of closely related coral morphospecies along a depth gradient (5-60 m) over a Caribbean reef slope. Bulletin of Marine Science 73(3):725-744.
- Vize PD. 2006. Deepwater broadcast spawning by *Montastraea cavernosa, Montastraea franksi*, and *Diploria strigosa* at the Flower Garden Banks, Gulf of Mexico. Coral Reefs 25:169-171.
- Webster JM, Clague DA, Riker-Coleman K, Gallup C, Braga JC, Potts D, Moore JG, Winterer EL, Paull CK. 2004. Drowning of the – 150 m reef off Hawaii: a casualty of global meltwater pulse 1A? Geology 32:249-252.

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