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EDITORIAL

Theme section on "Mesophotic Coral Ecosystems: Characterization, Ecology, and Management"

L. M. Hinderstein · J. C. A. Marr · F. A. Martinez · M. J. Dowgiallo · K. A. Puglise · R. L. Pyle · D. G. Zawada · R. Appeldoorn

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Abstract Mesophotic coral ecosystems (MCEs) are characterized by the presence of light-dependent corals and associated communities that are typically found at depths ranging from 30 to 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. Because working in this depth range is constrained by traditional SCUBA limits, less is known about corals and associated organisms there compared to shallower coral communities. Following the first-ever gathering of international scientists to review and discuss existing knowledge of MCEs, this issue focuses on the ecological characterization, geomorphology, and concept of MCEs as refugia for shallow-water populations. The review and research papers comprising this special issue reflect the current scientific understanding of these ecosystems and the underlying mechanisms that regulate them, as well as potential resource management implications. It is important to understand the value and role of mesophotic coral ecosystems in tropical and subtropical regions as these areas face increasing environmental change and human impacts

Keywords Mesophotic coral ecosystem · Biodiversity · Geomorphology · Connectivity · Community structure · Resource management

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L. M. Hinderstein (✉) · F. A. Martinez ·
M. J. Dowgiallo · K. A. Puglise
Center for Sponsored Coastal Ocean Research, National Oceanic and Atmospheric Administration, 1305 East-West Highway, Silver Spring, MD 20910, USA
e-mail: lara.hinderstein@noaa.gov

J. C. A. Marr
Perry Institute for Marine Science, 100 North US Highway 1, Suite 202, Jupiter, FL 33477, USA

K. A. Puglise
Office of Ocean Exploration and Research/NOAA's Undersea Research Program, National Oceanic and Atmospheric Administration, 1315 East-West Highway, Silver Spring, MD 20910, USA

R. L. Pyle
Department of Natural Sciences, Bishop Museum, 1525 Bernice St., Honolulu, HI 96817, USA

D. G. Zawada
Florida Integrated Science Center, U.S. Geological Survey, 600 4th Street South, St. Petersburg, FL 33701, USA

R. Appeldoorn
Department of Marine Sciences, University of Puerto Rico, Mayaguez, PR 00681, USA

Mesophotic coral ecosystem workshop

On 12–15 July 2008, a scientific workshop was held in Jupiter, Florida, to identify critical research and resource management needs for mesophotic coral ecosystems

(MCEs) (Puglise et al. 2009). The workshop was hosted by the Perry Institute for Marine Science (PIMS) and organized by two offices of the U.S. National Oceanic and Atmospheric Administration (NOAA): the Center for Sponsored Coastal Ocean Research (CSCOR) and the Office of Ocean Exploration and Research/NOAA's Undersea Research Program (OER/NURP) and also by the U.S. Geological Survey (USGS). The workshop gathered scientists and managers from governmental and non-governmental organizations for the first time to discuss MCE-related topics. The inception for this workshop grew out of NOAA/CSCOR's Coral Reef Ecosystems Studies program, which identified the need for further investigations of MCEs.

The goal of the workshop was to review and discuss current knowledge about the characterization (biodiversity, geomorphology, microbiology), ecology (connectivity, community structure/dynamics), and management of MCEs. Three primary products resulted from the workshop: (1) this special Theme Section of *Coral Reefs*, focused on MCEs; (2) a MCEs Research Strategy (Puglise et al. 2009); and (3) a MCE information portal found at www.mesophotic.org (Bongaerts et al. 2008).

The following articles provide a description of the current state of knowledge about the science and management of MCEs. This information is intended to serve as the baseline for further research initiatives that address the characterization, ecology, and management of MCEs.

Introduction to mesophotic coral ecosystems

In the study of marine ecosystems, much attention has been devoted to the ecology of shallow-water (<30 m) coastal communities. Over the last several decades, there also has been a marked increase in the study of deep-sea environments. However, intermediate depths, particularly coastal environments in the 30–150 m depth range, have received relatively little attention.

Coral ecosystems at intermediate depths are by no means new to science; in fact, Darwin (1889) was one of the first to report the existence of hermatypic corals at depths up to 128 m, while Gardiner (1903) and Vaughan (1907) noted unique geomorphic characteristics of corals at intermediate depths. The 1960s and early 1970s saw the beginning of direct observations on deep coral environments and experimentation with new diving technologies (Stark and Stark 1972; Starck and Colin 1978). However, the physiologically imposed depth limits of sampling with conventional SCUBA, and the impracticality and expense of using submersibles in deep coral environments, limited exploration of the deeper portions of zooxanthellate coral communities (Lang 1974; James and Ginsburg 1979; Nelson and Appeldoorn 1985; Reed 1985; Hanisak and Blair 1988; Liddell and Ohlhorst 1988; Aponte and Ballantine 2001). As a consequence, fully two-thirds of the total depth range of zooxanthellate coral environments remain largely unexplored (Pyle 1996, 2000; Feitoza et al. 2005).

Advances in technical diving methods and instrumentation, such as mixed gas diving, rebreathers, and autonomous underwater vehicles, as well as in imaging techniques, e.g., see Gleason et al. (2010), are increasingly providing easier access to study coral ecosystems in the intermediate depth realm (Pyle et al. 2008). Kahng et al. (2010) review the geographic distribution of studies of MCEs and conclude that although some generalizations may be made about community structure and distribution of MCE in the Caribbean, these generalizations cannot be made for the vastly understudied Indo-Pacific regions. In all areas, major gaps of knowledge still exist.

Coral ecosystems in this depth range have sometimes been referred to as the "upper Twilight Zone" (Fricke and Knauer 1986) or "Coral-reef Twilight Zone" (Pyle 1996; Brokovich et al. 2008), or simply "deep coral reefs". The term "twilight zone" has also been ascribed to a much deeper zone in the open ocean, depths between the euphotic zone and 1,000 m (Buesseler et al. 2007). The term "deep coral reefs" is both technically inaccurate (in the context of the geological definition of "reef"), and "deep coral" is often applied to the clearly distinct cold-water, aphotic deep-sea coral communities, which can occur at much greater depths. To avoid confusion, we follow Ginsburg (2007) in referring to the zone in deeper water where zooxanthellate corals occur as "mesophotic".

Mesophotic coral ecosystems (MCEs) are characterized by the presence of light-dependent corals and associated communities that are typically found at depths ranging from 30 to 40 m and extending to over 150 m in tropical and subtropical regions (Figs. 1, 2). The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species. The upper boundary not only reflects the limits imposed using traditional SCUBA diving, but also the depths at or below which there is the beginning of a shift in species composition (Liddell and Ohlhorst 1988; Kahng et al. 2010) as Garcia-Sais (2010) describes for fish at Isla Desecheo, Puerto Rico. Depth records for zooxanthellate corals have been documented for *Agaricia grahamae* at 119 m in the Caribbean (Reed 1985), *Leptoseris fragilis* at 145 m in the Red Sea (Fricke et al. 1987), *Leptoseris* sp. at 153 m in Hawaii (Kahng and Maragos 2006), and *L. hawaiiensis* at 165 m in Johnston Atoll (Maragos and Jokiel 1986). The lower boundary of "over 150 m" reflects the deeper extensions of these documented observations, as well as other unpublished observations in the Pacific and the documented presence of crustose coralline algae at 268 m in the Bahamas (Littler et al. 1985, 1986). This

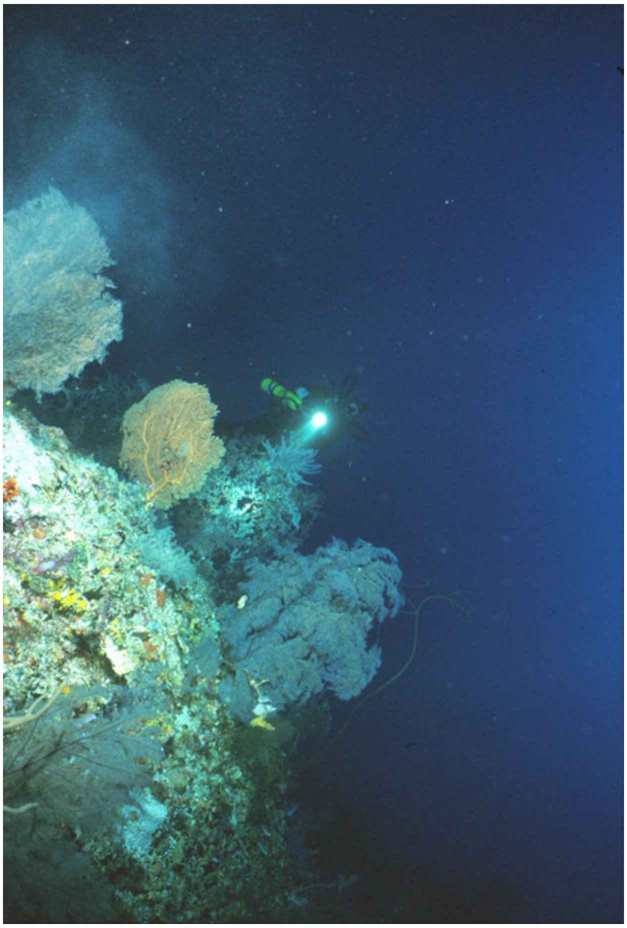

Fig. 1 A diver using rebreather technology explores a highly diverse mesophotic coral ecosystem at 120+ m in Fiji. Photo credit Richard Pyle

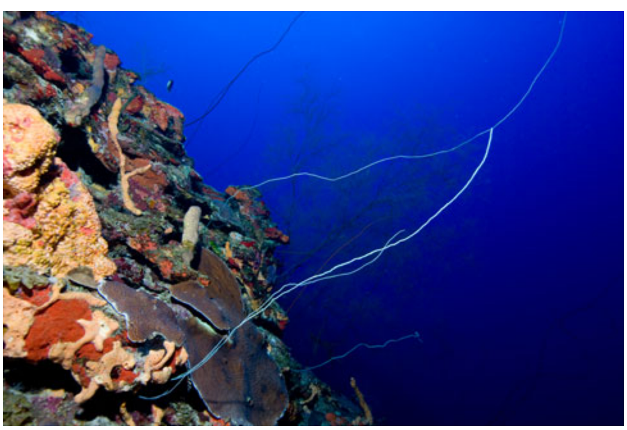

Fig. 2 This mesophotic coral ecosystem at 60+ m in Puerto Rico is characterized by an assemblage of corals, algae, and sponges. Note the flattened morphology of the *Montastrea* coral. Photo credit Hector Ruiz

depth boundary is necessarily imprecise due to differences in light penetration, patterns of thermal variation, and various other physical and ecological parameters that vary between and within geographic regions (Kahng et al. 2010; Smith et al. 2010). Furthermore, other processes structuring mesophotic coral reef communities are not well understood, particularly, as Smith et al. (2010) demonstrate the role of disturbance, e.g., disease.

Considered as extensions of shallower coral reef ecosystems, MCEs are likely to have biological, physical, and chemical connectivity with these reefs and associated communities, as well as unique assemblages, and extensions to deep biota. Although these ecosystems harbor species found in their shallower counterparts, they may also be colonized by a number of depth-restricted species of fishes, invertebrates, and algae, and a lower diversity of corals (Hanisak and Blair 1988; Pyle 2000; Ballantine and Aponte 2003, 2005; Jarrett et al. 2005; Armstrong et al. 2006; Brokovich et al. 2008; Garcia-Sais 2010). To this end, MCEs that serve as refugia for shallow and mid-depth species (Glynn 1996; Armstrong et al. 2006) may warrant special resource management attention and protection to help maintain local and regional biodiversity (Riegl and Piller 2003), However, the review by Bongaerts et al. (2010) demonstrates how little is known about deep reefs and coral reproduction over depth, and thus they propose a list of urgent research priorities to determine the extent to which deep reefs may act as a refuge in the face of global reef decline. In addition, MCEs are thought to serve as spawning grounds and may function as a larval supply for some shallow-water species (Armstrong et al. 2006; Brokovich et al. 2007; García-Sais et al. 2008).

Because MCEs are deep and can occur in remote localities (Kahng et al. 2010; Locker et al. 2010), there is a common assumption that they are less likely to be impacted by anthropogenic (e.g., overfishing, pollution) or natural (e.g., hurricanes, tsunamis, elevated temperatures) disturbances. To the extent to which such assumptions are borne out, MCEs may serve as a reference point for ecosystem condition in comparison with adjacent compromised, shallower coral reefs. For example, Bak et al. (2005) documented a lack of anthropogenically driven declines on reefs at 30–40 m in Curacao and Bonaire in contrast to the reefs at 10–20 m depth.

However, there is reason to suspect that this assumption is not valid for certain MCEs. For example, some fishing industries specifically target the larger predatory fishes that inhabit these depths. A small increase in shallow-water turbidity due to coastal development, watershed runoff, and pollution may have a greater and more devastating impact on MCEs (at the lower limits of photosynthetically viable light levels) than it would on the shallow reefs that are more directly exposed to the disturbance. While hurricanes and tsunamis have a smaller direct impact at greater depths, they may wash limestone rubble down the reef slope, potentially smothering MCEs (Bak et al. 2005).

Moreover, there is some indication that oscillations in sea temperatures, such as those caused by internal waves, cold-water intrusion, and down-welling of warmer waters, may extend to deeper depths and cause depauperate zones, stress, bleaching, and eventually death (Hickey et al. 2000; Smith 2001; Wolanski et al. 2004; Colin 2009; Smith et al. 2010). Although such potential threats are mostly speculative at this time, in certain locations encroaching threats have begun to adversely affect the condition of MCEs (Menza et al. 2007). Coral mortality events and shifting baselines at mesophotic depths have been documented by scientists, and the causes and consequences may be quite different from shallow-water reefs (Bak et al. 2005; Leichter and Genovese 2006; Menza et al. 2007; Smith et al. 2010). A better understanding of these environments is needed and will likely offer potential findings of major interest for conservation and resource management.

To determine where potential MCEs may exist and to ascertain their underlying geomorphology, Locker et al. (2010) describe regional mapping efforts that have been initiated that use a variety of manned and unmanned survey techniques. These have resulted in an increase in knowledge of the geographic extent of MCEs and a glimpse of the community structure of the MCEs found, e.g., in Hawaii, Rooney et al. (2010); and in Tutuila, American Samoa, Bare et al. (2010). Sherman et al. (2010) provide a more detailed analysis of the evolution of the underlying geological structure supporting the extant MCEs in southwestern Puerto Rico, relating their results to Caribbean sea level change models.

The results of this workshop give a glimpse of the complexity of MCEs but also emphasize the large gaps in our knowledge that currently exist. It is important to understand the value and role of mesophotic coral ecosystems in tropical and subtropical regions as these areas face increasing environmental change and human impacts.

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