

Mesophotic coral reefs: a global model of community structure and function

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Abstract. Mesophotic coral reefs (MCRs) are an understudied continuum of shallow coral reef communities at depths of 30 to 150 m. These reefs are subject to gradients of light and nutrients that results in changes to the community structure and function with increased depth. The upper mesophotic reef is comprised of many of the same species that are found in shallow coral reef systems. However, the lower mesophotic reef, below about 60 m, has reduced photosynthetic biodiversity and often a replacement of corals and algae with sponges. The fish fauna is largely specialized to these intermediate depths, and to the available food resources. Thus, MCRs have the potential to function as refugia for shallow benthic reef species that are subject to disturbances in the upper 30 m of the water column. However, MCRs may be less stable than previously reported. Recent evidence from Caribbean reefs indicate that MCR community structure can change in as little as 3 years after decades of stability. Studies of fish spawning aggregations on MCRs have demonstrated the ecological importance of these sites to larval connectivity with shallow reefs, but recent evidence documents limited genetic diversity between MCR corals and shallow conspecifics. Despite site-specific differences in MCR community distribution and abundance, our data support a general model of structure and function that is equally applicable to MCRs in the Atlantic and Pacific.

Key words: Caribbean, mesophotic reefs, Pacific, sponges, geomorphology

Introduction

Reef-building corals, and their associated benthic community, are primarily found in shallow water (<30 m) throughout the tropics, due largely to light limitation of photosynthesis of their endosymbiotic dinoflagellates (*Symbiodinium* sp.), also known as zooxanthellae. We know, however, that many of these species are not as depth-limited as previously thought (e.g., Lesser et al. 2010). The use of submersibles, SCUBA and technical diving provided an early glimpse into the structure of deep reef communities (Goreau and Wells 1967; Fricke and Meischner 1985; Lehnert and Fischer 1999), now commonly known as “mesophotic coral ecosystems” at depths from 30 to 150 m (MCE; Lesser et al. 2009).

There is renewed interest in MCE communities because many researchers believe that these sites represent potentially important refugia, nursery habitats, and sources/sinks for shallow-water populations of many coral reef taxa, including corals, sponges, and fish (Lesser et al. 2009; Bongaerts et al. 2010; Slattery et al. 2011). Often these deeper reefs represent extensions of the nearby shallow reef communities that result in a unique community structure (Rützler and Macintyre 1982; Khang and Kelley 2007). One of the most obvious abiotic

differences on MCE reefs is the lower irradiance of photosynthetically active radiation (PAR). The irradiance of PAR in the Bahamas is 2100 $\mu\text{mol quanta m}^{-2} \text{sec}^{-1}$ at the surface and only 45 $\mu\text{mol quanta m}^{-2} \text{sec}^{-1}$ at 100 m: Lesser et al. 2009, 2010). A few deep-adapted zooxanthellate corals and algae exist in this community, but overall percent cover of photosynthetic organisms is significantly lower than on the nearby shallow reefs (Smith et al. 2004; Grigg 2006; Lesser et al. 2009). In the Caribbean, sponges dominate these deeper reefs, and their size typically exceeds that of shallow reef conspecifics (Reed and Pomponi 1997). In addition, geomorphology and hydrodynamic processes can have a significant impact on MCE ecology (e.g., Liddell et al. 1997; Khang and Kelley 2007) and resilience (Bak et al. 2005). To date, the mesophotic zone remains relatively understudied compared to other reef habitats (Menza et al. 2008), although recent reviews document potentially important biodiversity at a number of MCE sites worldwide (Khang et al. 2010; McClain and Barry 2010; Rooney et al. 2010). Additional studies have begun to provide information on the crucial question of how shallow water scleractinian corals can extend their range in to mesophotic depths (Lesser et al. 2010; Slattery et al. 2011).

Here we will analyze and compare a unique data set of community composition surveys and other relevant data from the Caribbean basin and western Pacific. To add in this comparison there are community surveys available for MCE communities from Jamaica (Goreau 1967, Lehnert and Fischer 1999), Carrie Bow Cay, Belize (Rützler and Macintyre 1982), Reunion Island (Bouchon 1981), Bermuda (Fricke and Meischner 1985), St Croix, US Virgin Islands (Kühlman 1983), the Red Sea (Kühlman 1983, Fricke and Knauer 1986), Hawaii (Kahng and Kelley 2007), and French Polynesia (Kühlman 1983).

Material and Methods

Research was conducted between 2002 and 2011 at Bock Wall [28°49.55'N, 76°9.15'W] to the northeast of Great Exuma Island in the Bahamas, at Rock Bottom Wall [19°42.03'N, 80°03.25'W] off the north-shore of Little Cayman Island, at Anaw Pass (Chuuk-site A) on the northeast corner of the Chuuk atoll [151°41.27'N, 7°12.49'E] and at South Pass (Chuuk-site B) on the southern edge of the atoll [151°47.83'N, 7°34.55'E], and at Siaes Wall (Palau-site A) off the northwest coast of Koror, Palau [7°18.50'N, 134°13.20'W] and Turtle Cove (Palau-site B) off the south coast of Ngemelis Island, Palau [7°05.06'N, 134°15.32'W]. Since MCEs occur on a variety of geomorphologies, including near vertical walls and terraced slopes, we examined multiple sites within each Pacific island location to assess variation in the structural groups relative to this factor.

All dives were conducted using conventional SCUBA and/or technical diving TRIMIX gas, as well as closed circuit rebreathers using TRIMIX gas. At each site, replicate 25 x 1 m band transects were surveyed at depths of 30, 46, 61, 76, and 91 m (n= 3-9 transects per depth) for the percent cover of sponges, algae, coral, and other (= abiotic substrata and/or taxonomically rare [i.e., <1% cover] groups such as tunicates). Surveys were only conducted to a depth of 61m in Chuuk due to limitations on the availability of technical diving gas mixtures.

Additionally, in the Bahamas and Chuuk the volume of each sponge encountered at fifteen random points along the band transect was estimated using multiple areal measurements with plastic calipers (Wulff 2001). If no sponge was encountered at the predetermined point, then the nearest sponge was measured so that each transect provided a minimum of 15 replicate sponges. Time did not permit extensive volumetric sampling in the Caymans or Palau, but fewer select sponges were examined at each of the depth gradients in these sites. Data were analyzed using two-way ANOVAs with interaction.

Where interactive effects were detected independent effects were no longer considered, and these interactions were subsequently analyzed using Tukey's HSD multiple comparison testing.

Results

There were significant differences between Pacific (n=4) and Caribbean (n=2) mesophotic reefs in the percent cover of the major functional groups (Fig. 1).

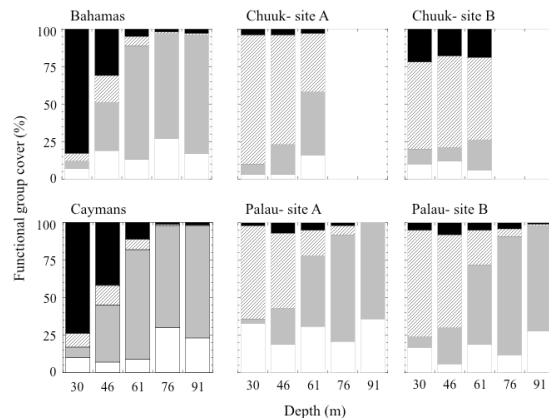


Figure 1: Percent cover of different functional groups from surveys on Pacific and Caribbean mesophotic coral reefs. Black = algae, hatched = coral, gray = sponge and white = other.

The percent cover of algae, scleractinian corals, and sponges were all significantly different between the Pacific and Caribbean sites (2-way ANOVAs: $P < 0.0001$), but there were also location x depth interactions (2-way ANOVAs: $P < 0.0001$) detected in all cases. A Tukey's HSD multiple comparison test on the interaction of location and depth for algal cover showed that Caribbean sites at a depth of 30 and 46 m have a significantly higher percent cover of algae than all Pacific sites and depths. Algal cover was also significantly higher at these shallow depths than at deeper depths (i.e., 61, 76 and 91 m; Fig. 1). For the percent cover of sponges a Tukey's HSD multiple comparison test on the interaction of location and depth showed that Caribbean sites at a depth of 30 and 46 m have a significantly lower percent cover of sponges than all other depths in the Caribbean. Sponge cover at depths of 61, 76 and 91 m in the Caribbean are statistically similar, and sponge cover at 76 and 91 m in the Pacific was not significantly different than similar depths in the Caribbean. Sponge cover at 61 m in the Pacific was intermediate between the statistically different levels at shallower or deeper depths (Fig. 1). Lastly, for the percent cover of corals, a Tukey's HSD multiple comparison test on the interaction of location and depth showed that Caribbean sites at a depth of 30 and 46 m have a significantly lower percent cover of corals than all

other depths in the Caribbean and the Pacific. Coral cover at depths greater than 46 m were not significantly different between the Caribbean and Pacific sites, with coral cover at 61 m being significantly higher than in the Caribbean and intermediate between shallow and deep sites in the Pacific (Fig. 1). Algae, coral, and sponge cover, in Palau, were identical at both sites and all depths.

Sponge volume differed significantly between the Bahamas and Chuuk (2-way ANOVA: $P < 0.0001$; and see Fig. 2) to a depth of 61m (maximum depth for data at Chuuk). The depth and site interaction effects were also significant (2-way ANOVA: $P = 0.0001$). In addition, sponges were significantly larger in the mesophotic zone of the Bahamas (i.e., 76 and 91m: 1-way ANOVA: $P < 0.0001$), compared to shallower depths (Fig. 2). While we did not specifically address sponge volume in the Caymans and Palau, the ocean basin and depth trends appeared similar at these two sites (Slattery and Lesser personal observation).

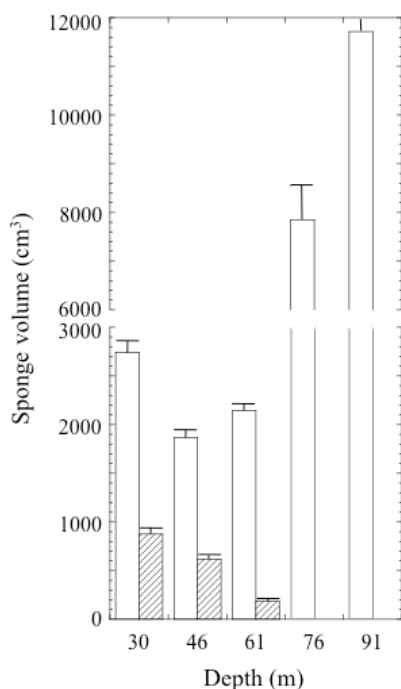


Figure 2: Sponge volume (cm³) comparison between the Bahamas and Chuuk sites. White bars=Bahamas, hatched bars=Chuuk.

Discussion

Mesophotic reefs often represent extensions of nearby shallow reef communities with a site-specific community species composition that is a reflection of regional history and variation in ecological factors such as food and light availability (Rützler and Macintyre 1982; Khang and Kelley 2007; Lesser et al. 2009). The differences in the functional groups described here for Caribbean and Pacific MCEs show

clear differences between the two regions. From 30 to 46 m, Caribbean reefs have a consistently greater percent cover of algae compared to the Pacific, and this follows a general trend of more phase-shifts in the Caribbean (Bruno et al. 2009). Site B in Chuuk has more algal cover from 30-61 m than the other Pacific sites; this may be a function of light availability due to slope angle since this is the sole site studied that had a terraced profile. Sponge cover and size, based on the sponge volume comparisons between the Bahamas and Chuuk, is significantly greater in the Caribbean compared to the Pacific. Sponge cover does increase with depth in the Pacific as well, except in Chuuk Site B, just not to the same extent as in the Caribbean, and the sponges are largely encrusting species (e.g., *Spirastrella*). This suggests that sponges may be a more important functional component of Caribbean MCEs (e.g., as a source of nitrogen: Fiore et al. 2010) than Pacific deep reefs. It further suggests that soft corals, representing the greatest biotic volume on deep Pacific reefs (Bridge et al. 2012, Slattery and Lesser personal observation), may fill an analogous niche to sponges on Pacific MCEs. Lastly, coral cover is significantly greater at all depths in the Pacific compared to the Caribbean; this may be due in part to greater competition with algae in the Caribbean deep reefs (e.g., McCook et al. 2001, Lesser and Slattery 2011).

How does this compare to previous studies on MCEs? Goreau and Wells (1967) described well-developed and diverse coral reefs in Jamaica down to a depth of 70 m with sea level changes and the resulting geomorphology (i.e., changes in substrate slope and rate of sedimentation) causing significant shifts in the community structure. In the Bahamas, Liddell et al. (1997) reported on the percent cover and species diversity of coral reef communities down to a depth of 250 m. Their results showed a distinct bathymetric zonation pattern consisting of coral cover of 3-23% above 50 m and significant declines with increasing depth whereas the percent cover of sponges increased with increasing depth as we report here. Until recently the results of previous community comparisons for many locations in the Caribbean basin that included mesophotic depths, as well as this study, were consistent with one another (see review by Kahng et al 2010). The bioinvasion of the Pacific lionfish into the Bahamas and its range expansion into the mesophotic zone, however, has resulted in a significant phase transition to an algal dominated community at our Bahamas site at mesophotic depths (Lesser and Slattery 2011) that is not reflected in the data presented here. In the Pacific there are fewer studies available on the community composition of MCEs (reviewed previously by Kühlmann 1983 and Kahng et al. 2010). Kühlmann

(1983) found that scleractinian coral diversity was significantly greater from shallow depths to approximately 60 m where a number of specialized taxa occur in the Caribbean basin and not in the Pacific. Interestingly, Köhlmann (1983) discounted irradiance as a primary factor affecting the depth distribution of zooxanthellate corals in these systems but felt that geomorphology and hydrodynamics, combined with differences in the underwater light field, were deterministic for many taxa at mesophotic depths.

What processes do play important roles in producing the differences between the Caribbean and Pacific MCE communities reported here and elsewhere? Certainly earth history, isolation events and subsequent evolution through time (i.e., paleoecology) contribute significantly to overall biodiversity differences between the Caribbean and Pacific. But on local scales factors such as geomorphology including substrate type, substrate angle and sedimentation environment (Goreau and Wells 1967, Liddell et al. 1997, Sherman et al. 2010, Bridge et al. 2011), as well as abiotic factors such as competition, predation, herbivory and abiotic factors such as hydrodynamics and changes in underwater irradiances are critical and interact with one another (Lesser et al. 2009, 2010, Brokovich et al. 2010, Kahng et al. 2010, Lesser and Slattery 2011) in still unknown ways. Another factor contributing to the structure of MCEs is the population connectivity, both between MCEs and between depths, for a number of taxa (reviewed in Slattery et al. 2011).

To date, MCEs are still vastly understudied compared to other reef habitats (Menza et al. 2008), although recent reviews document potentially important biodiversity at a number of MCE sites worldwide (Khang et al. 2010, McClain and Barry 2010, Rooney et al. 2010). The question of whether MCEs can be a refugia to supply propagules for a limited number of coral reef taxa to shallow water reef communities damaged by anthropogenic change remains unanswered (Lesser et al. 2009, Bongaerts et al. 2010, Slattery et al. 2011), but it is clear that deep reef research focused on the broader issues discussed here will further our understanding of MCE structure and function.

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