

Biodiversity and Functional Ecology of Mesophotic Coral Reefs

Michael P. Lesser,¹ Marc Slattery,²
and Curtis D. Mobley³

¹Department of Molecular, Cellular and Biomedical Sciences, and School of Marine Science and Ocean Engineering, University of New Hampshire, Durham, New Hampshire 03824, USA; email: mpl@unh.edu

²Department of BioMolecular Science, University of Mississippi, Oxford, Mississippi 38677, USA; email: slattery@olemiss.edu

³Sequoia Scientific, Inc., Bellevue, Washington 98005, USA; email: curtis.mobley@sequoiasci.com

Annu. Rev. Ecol. Evol. Syst. 2018. 49:49–71

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

<https://doi.org/10.1146/annurev-ecolsys-110617-062423>

Copyright © 2018 by Annual Reviews.
All rights reserved

**ANNUAL
REVIEWS CONNECT**

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Keywords

mesophotic coral reefs, biodiversity, deep reef refuges, connectivity, phase shifts, sponges

Abstract

Mesophotic coral reefs, currently defined as deep reefs between 30 and 150 m, are linked physically and biologically to their shallow water counterparts, have the potential to be refuges for shallow coral reef taxa such as coral and sponges, and might be a source of larvae that could contribute to the resiliency of shallow water reefs. Mesophotic coral reefs are found worldwide, but most are undescribed and understudied. Here, we review our current knowledge of mesophotic coral reefs and their functional ecology as it relates to their geomorphology, changes in the abiotic environment along depth gradients, trophic ecology, their reproduction, and their connectivity to shallow depths. Understanding the ecology of mesophotic coral reefs, and the connectivity between them and their shallow water counterparts, is now a primary focus for many reef studies as the worldwide degradation of shallow coral reefs, and the ecosystem services they provide, continues unabated.

INTRODUCTION

Worldwide declines of shallow water scleractinian corals have occurred and are linked to recurring sources of disturbance such as eutrophication, hurricanes, and coral bleaching. Significant gaps in our knowledge of the fundamental structure and function of coral reef ecosystems remain, especially when we look at deep fore reef communities at depths > 30 m, where, until recently, fewer studies have been done (Turner et al. 2017). These deep fore reef coral communities have been mistakenly referred to as the twilight zone, which is actually synonymous with the mesopelagic zone of the open ocean that extends beyond the euphotic zone from a depth of 200 to 1,000 m. These deep coral reefs are now known as mesophotic coral ecosystems (MCEs) with a depth-dependent definition of 30–150 m. However, this definition is not based on any ecological or environmental characteristics, and we discuss below whether a new definition of MCEs can be established on the basis of the characteristics of the underwater light environment and its effects on MCE communities (Lesser et al. 2009).

It has been suggested that MCE communities exhibit long-term stability and are rarely affected by anthropogenic stress compared with shallow coral reefs (Lesser et al. 2009), but recent studies have shown that MCEs can be susceptible to rapid biological (Lesser & Slattery 2011) and environmental change (Smith et al. 2016a) that can result in significant shifts in community structure. This perceived stability has also been used to hypothesize that MCEs may represent a refuge for a variety of coral reef taxa that exhibit broad depth distributions and may be potential seed-banks to restore coral reef community structure and function (Bongaerts et al. 2010, Lesser et al. 2009). In contrast, several studies suggest that some MCE coral species represent distinct populations, even in taxa with broad depth distributions, with unique genetic and physiological adaptations (Bongaerts et al. 2011, 2015a; Brazeau et al. 2013; Lesser et al. 2010). It is increasingly clear that MCEs represent extensive, and understudied, areas of coral reef ecosystems worldwide, and our lack of knowledge about MCEs has impacted our broader understanding of the biodiversity, ecology, and connectivity of all coral reef communities. Additionally, the data we have to date begs the question: What are the mechanistic underpinnings for the observed patterns of function and biodiversity that contribute to MCE ecology over the shallow-to-mesophotic depth range?

ABIOTIC DRIVERS OF MESOPHOTIC CORAL REEF ECOSYSTEMS

Geomorphology

The emerging picture is that MCEs are communities structured by gradients of abiotic factors such as downwelling irradiance and upwelling nutrients (Lesser et al. 2009). But other factors may have a significant influence on the structure and function of MCEs. Modern biogenic coral reefs, whether shallow or MCEs, include both geological history and geomorphology as critical factors that determine their growth, structure, and function. For example, the geomorphology of MCEs is affected by changes in sea level caused during glacial and interglacial periods. Their geomorphology is also affected by depositional and erosion processes that can profoundly influence the amount, and stability, of substrate available for MCE development. Modern reefs, both shallow reefs (< 30 m) and upper MCE reefs (30–60 m), of the Holocene epoch in the western Atlantic and Pacific Oceans are largely built upon drowned, Pleistocene epoch reefs submerged by changes in sea level (Macintyre et al. 1991, Montaggioni 2005). Lower MCEs (> 60 m) exhibit no biogenic reef accretion (e.g., Grigg 2006), and fauna from these depths is comprised of scleractinian corals and taxa such as sponges and soft corals not usually found in shallow waters (Bridge et al. 2012, Lesser & Slattery 2011, Slattery & Lesser 2012). Changes in geomorphology over time also influence the slope of that substrate, which can introduce reef-to-reef variability in community composition

(Locker et al. 2010, Sherman et al. 2010). Substrate angle also has an important influence on downslope stability secondary to bioerosion in shallow waters <30 m (Weinstein et al. 2014) and subsequent sedimentation affects that influence the structure and function of shallow and mesophotic coral reefs (Sherman et al. 2016).

Another important consideration related to geological history is the concept of high-relief islands and coastal habitats with well-developed terrestrial vegetation and watersheds [e.g., Curaçao, Jamaica, Puerto Rico, the United States Virgin Islands (USVI), Hawai'i, Mooréa, and Palau], compared with coastal habitats and islands with lower relief and little or no well-developed terrestrial vegetation or watersheds (e.g., the Bahamas, Cayman Islands, and Palmyra Atoll). These differences could cause significant alterations in the amount of nutrients coming from runoff, the attenuation of light, and rates of sedimentation, all of which are known to affect the communities of both shallow (Fabricius 2005) and mesophotic coral reefs (Sherman et al. 2016). Therefore, understanding how geological history and geomorphology effect the structure, function, and ecology of MCEs is important.

Temperature

Temperature is the most pervasive abiotic factor in biology affecting the physiology and ecology of all organisms. Seawater temperatures below 18°C are considered prohibitive for net coral reef accretion, whereas elevated temperatures and high solar irradiances can result in the phenomenon known as coral bleaching, which causes coral morbidity and mortality in shallow waters (Lesser 2011). Temperature profiles generally decrease by ~5°C from the surface to 100 m (Lesser et al. 2010, Pyle et al. 2016), with the lower depth limits for photoautotrophic coral growth in the mesophotic zone well within the favorable temperature range (Kahng et al. 2010). However, recent studies have shown that *Orbicella* spp. occurring in upper mesophotic reefs of the Caribbean Sea may actually be more sensitive to elevated seawater temperatures, as observed when warmer water is advected downward through the water column, because these corals have a lower threshold for temperature-induced bleaching than conspecifics from shallow depths (Smith et al. 2016a).

The temperature at deeper depths is generally less variable, but it can be influenced by hurricanes and internal waves (Lesser et al. 2009, Wolanski et al. 2004). The colder upwelled waters resulting from internal waves can provide food and nutrient subsidies (Leichter et al. 2003) that result in enhanced organismal performance (Leichter & Genovese 2006), and these cold waters can also reduce the impact of thermal stress from elevated seawater temperatures (Schmidt et al. 2016). In areas where large-amplitude internal waves occur (e.g., Palau), these waves can be a source of significant biological disturbance in the mesophotic zone by affecting the lower depth limit of MCE corals when anomalously low seawater temperatures simultaneously occur, causing repeated episodes of mortality (Wolanski et al. 2004).

The Underwater Light Environment

The light environment is the critical abiotic factor driving the structure and function of coral reefs generally and MCEs in particular (Lesser et al. 2009). In the optically clear waters of the tropics, the attenuation of solar radiation, both ultraviolet radiation (UVR, 290–400 nm) and photosynthetically active radiation (PAR, 400–700 nm), is modified by the angle of incident light at the surface and decreases with increasing depth as a function of the optical properties of the water. Additionally, the spectral composition of the underwater light field also contracts as depth increases, with UVR, blue, and red wavelengths exhibiting the most significant decreases (Eyal et al. 2015, Lesser et al. 2009). Bulk attenuation coefficients for PAR (K_{dPAR} m⁻¹) are adequate to

Table 1 Bulk attenuation coefficients (K_{dPAR} m^{-1}) and optical depths (1% = bottom of euphotic zone; 10% = midpoint of euphotic zone) for selected locations and using a surface irradiance of 2,100 μmol quanta $m^{-2} s^{-1}$

Location	K_{dPAR} m^{-1}	1% Optical depth (m)	10% Optical depth (m)	Relief
Hawai'i (Au'au Channel)	0.0475	97	48	High
Puerto Rico	0.065	71	35	High
Jamaica	0.06	77	38	High
Curaçao	0.063	73	37	High
Belize	0.08	58	28	High
Bahamas (Bock Wall)	0.057	81	40	Low
Red Sea	0.047	98	49	Low
Marshall Islands	0.045	102	51	Low
Bermuda	0.0485	95	47	Low
Okinawa	0.046	100	50	Low

Data from table 4 in Kahng et al. (2010), Banaszak et al. (1998), and Lesser et al. (2010). Differences between high- and low-relief K_{dPAR} m^{-1} are significant (ANOVA: $F_{1,9}$, $F = 6.53$, $P = 0.033$) as is the 1% optical depth (ANOVA: $F_{1,9}$, $F = 7.44$, $P = 0.026$).

describe the general optical characteristics of the water column and can also be used to derive other metrics including the 10% light level, considered to be the midpoint of the euphotic zone, and the 1% light level, or the bottom of the euphotic zone where photosynthesis equals respiration (i.e., the compensation point). If we look at a selection of K_{dPAR} m^{-1} values from reefs in the Caribbean Sea, Bermuda, and the Pacific Ocean (**Table 1**), we see values for the 1% light level that are significantly different between high- and low-relief settings, with an average depth of 95 m (± 8 m [SD]) for low-relief-associated reefs and 75 m (± 14 m [SD]) for high-relief-associated reefs. Differences in topographical relief, through its effect on water column optics, consequently have an effect on the community structure of reefs along a shallow-to-mesophotic depth gradient.

Solar radiation interacts with the benthos depending on whether the substrate is sloping or vertical in nature (Brakel 1979), which results in different irradiances during the same time of day for differently sloped substrates, with vertical surfaces estimated to receive $\sim 25\%$ of the irradiance that horizontal surfaces are exposed to (Brakel 1979). These differences in irradiance, based on substrate angle, could result in completely different communities occurring at the same depths in different MCE habitats. To further explore this interaction between light and substrate slope, we undertook an optical analysis to describe these effects. The radiometric quantities typically used in optical oceanography are for horizontally infinite water bodies, which correspond to a one-dimensional (1D) radiative transfer problem with depth being the only spatial variable. For example, commonly used models such as HydroLight are limited to 1D geometries in which the water absorption and scattering properties depend spatially only on depth and for which the surface and bottom boundary conditions are treated as horizontally homogeneous. However, the light field next to a vertical wall is coming from the water in front of the wall such that the models needed for understanding and predicting the underwater light field on the varying substrate angles of MCEs, but especially vertical walls, are inherently 3D.

However, no bio-optical models are available to predict horizontal irradiances for the 3D geometry of a reef wall. Using a previously developed model from other 3D studies (Mobley & Sundman 2003), we incorporated a simple 3D reef wall geometry (**Figure 1**), the inherent optical properties for clear tropical waters, the incident sky radiance as a function of sun angle, the sky conditions, the sea surface wave state, and the reflectance properties corresponding to

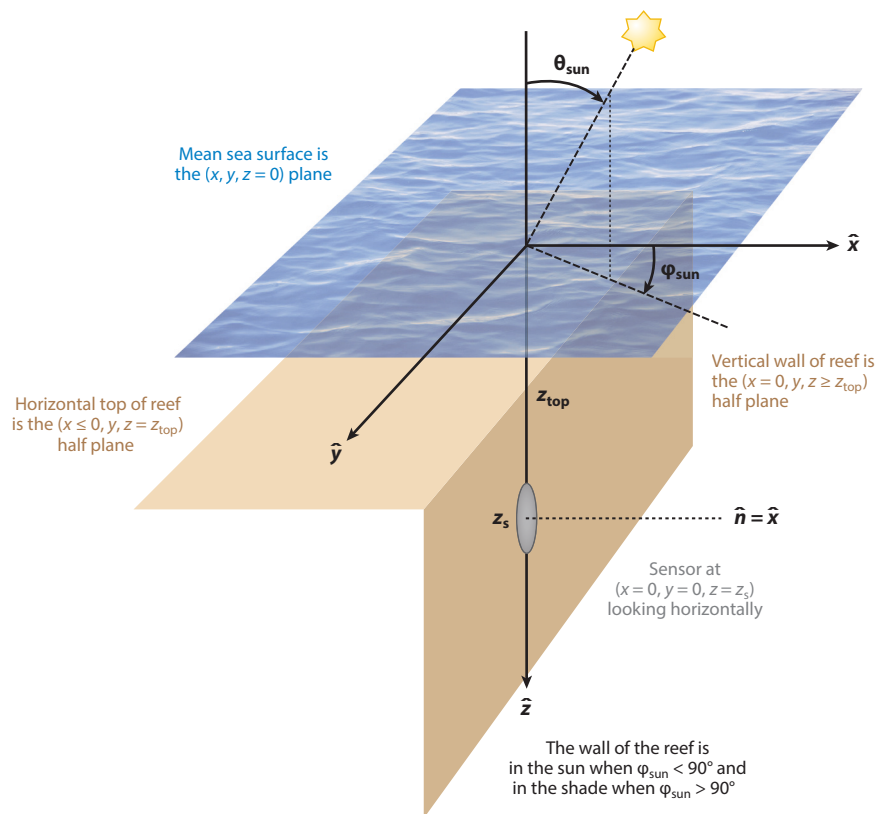


Figure 1

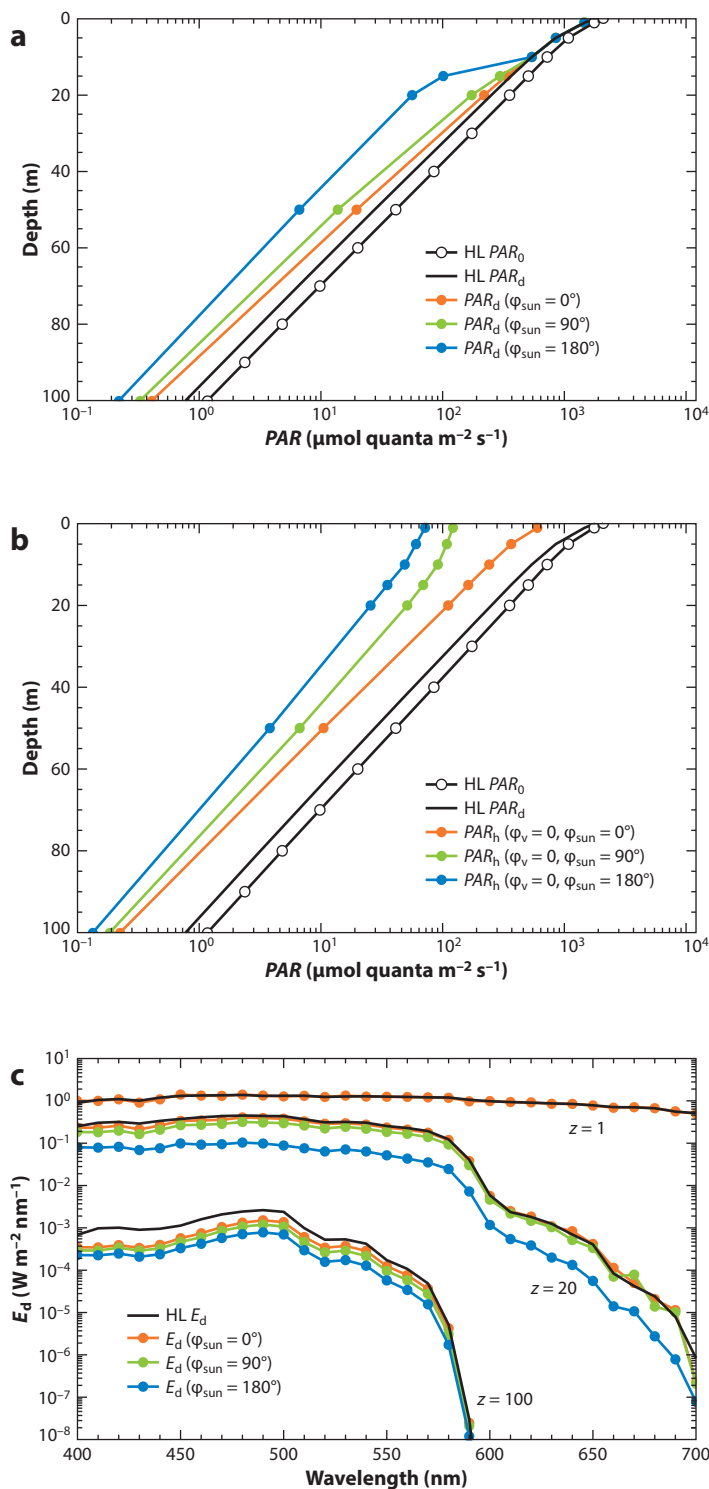
Reef geometry for modeling the underwater light field. The $(\hat{x}, \hat{y}, \hat{z})$ directions define an ocean coordinate system for the specification of the reef top, reef wall, and mean sea surface. This is a right-handed coordinate system with depth positive downward from 0 at the mean sea surface. The reef wall faces the $+\hat{x}$ direction, and θ_{sun} is the solar zenith angle. As θ_{sun} increases from 0° to 90° , the sun moves lower in the sky. φ_{sun} is the solar azimuthal angle relative to the reef wall. Here, φ_{sun} is modeled at 0° (directly in front of the reef wall), 90° (parallel to the reef wall), and 180° (behind the reef wall). For practical purposes, when $\varphi_{\text{sun}} < 90^\circ$ the reef wall is in the sun and when $\varphi_{\text{sun}} > 90^\circ$ the reef wall is in the shade. The numerical values for the depth of the reef top (z_{top}); the reflectance of the reef top (R_{top}) and of the reef wall (R_{wall}); sun geometry; sensor depth (z_s), type, and orientation; water-inherent optical properties; and chlorophyll content are specified for each run.

benthic organisms on the wall surface to run a simulation for an idealized vertical reef oriented in a north–south direction.

The results of these model simulations show that for MCEs critical differences exist between 3D and 1D models for describing the changes in the underwater light field with increasing depth. When using the 1D HydroLight (HL) model, the results show, as expected, no difference between downwelling (E_d) and horizontal (E_h) irradiances as they are attenuated with depth (**Figure 2a,b**). However, when modeled as a 3D problem using a solar zenith angle of 30° (θ_{sun}), the effect of the wall at different solar azimuthal angles relative to the reef wall (φ_{sun}) becomes apparent. Below 10 m, the top of the reef in these simulations, the PAR value at each depth is computed from a starting E_d and is denoted as PAR_d ; E_h is similarly denoted as PAR_h as seen by the wall. These values can be seen to converge with depth depending on φ_{sun} . **Figure 2a,b** shows the PAR values

Figure 2

Simulation outputs for effect of substrate angle on irradiance. (a) Plot of PAR_d with depth simulation outputs for $\theta_{\text{sun}} = 30^\circ$, chlorophyll a ($\text{Chl } a$) = $0.5 \mu\text{g l}^{-1}$, and φ_{sun} relative to the reef wall. $\varphi_{\text{sun}} = 0^\circ$ (orange line, directly in front of the reef wall), 90° (green line, parallel to the reef wall), and 180° (blue line, behind the reef wall). The black lines are the 1D HydroLight (HL) outputs for scalar (HL PAR_0) and downwelling irradiance (HL PAR_d). (b) Plot of PAR_h results for the same conditions as shown for PAR_d in panel a. (c) Plot of the E_d simulation outputs as a function of wavelength for $\theta_{\text{sun}} = 30^\circ$, $\text{Chl } a = 0.5 \mu\text{g l}^{-1}$, and φ_{sun} relative to the reef wall. $\varphi_{\text{sun}} = 0^\circ$ (orange line, directly in front of the reef wall), 90° (green line, parallel to the reef wall), and 180° (blue line; behind the reef wall) at three depths: $z = 1 \text{ m}$, 20 m , and 100 m . Points on each line represent values from Monte Carlo simulations.



decreasing from the sun in front of the wall ($\varphi_{\text{sun}} = 0$) and parallel with the wall ($\varphi_{\text{sun}} = 90$), with the lowest irradiances observed when the wall is in its own shadow ($\varphi_{\text{sun}} = 180$). In all cases, PAR_h is lower than PAR_d , and differences between φ_{sun} values grow smaller with increasing depth as the light field approaches its asymptotic distribution. For example, PAR_d ($z = 20$ m, $\varphi_{\text{sun}} = 0^\circ$) = 210 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ (**Figure 2a**), whereas PAR_h ($z = 20$ m, $\varphi_{\text{sun}} = 0^\circ$) = 110 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ (**Figure 2b**). For comparison, irradiances for all 3D model results are significantly less than the 1D outputs (**Figure 2a,b**) that represent the scalar (HL PAR_0) and downwelling (HL PAR_d) irradiances commonly measured by coral reef ecologists (**Figure 2a,b**) (e.g., Lesser et al. 2009).

The simulations above describe how sun angle and coral reef orientation change the bulk water column irradiances with depth. **Figure 2c** shows the changes in spectral downwelling irradiances at three depths ($z = 1$ m, 20 m, and 100 m). There is almost no dependence on φ_{sun} at 1 m, which is above the reef top and wall. However, at 20 m and 100 m, we see changes in the spectral composition of downwelling irradiance with depth (**Figure 2c**) as previously described (Lesser et al. 2009), but only modest effects of φ_{sun} are observed (**Figure 2c**).

We can now take these model outputs and compare them with actual data of vertical profiles for both E_d and E_h taken simultaneously using planar, cosine corrected irradiance sensors mounted in vertical and horizontal orientations along a reef wall from the surface to 61 m in Curaçao (**Figure 3**). The results of these direct measurements show that on average E_d is approximately 2–3 times greater than E_h at shallow depths (<20 m) and that values of E_d and E_h converge as depth increases (**Figure 3**), both of which are consistent with the 3D modeling results described above (**Figure 2a,b**). In the only other measurements of E_d and E_h taken simultaneously along a reef wall to depths > 50 m, we see a similar pattern (Frade et al. 2008, Vermeij & Bak 2002).

Given these insights into the underwater light field that mesophotic communities experience, is there a role for water column optics in redefining what constitutes the depth range and limits of an MCE? Combining these optical approaches with geomorphology, community descriptions, and indicator species will provide a reef-to-reef understanding, from an optical perspective, of those depths where we see transitions to mesophotic communities and the potential role of light in that process. For instance, a recent study by Laverick et al. (2017) suggested that community composition patterns of scleractinian corals could be informative in defining MCEs by looking at the disappearance of shallow specialist scleractinian coral species that would vary from reef to reef on the basis of environmental factors (e.g., light). This community approach, combined with optical data, may provide a reef-to-reef definition of what constitutes being defined as either an upper or lower MCE. It may be, however, that in the absence of these types of data the broad depth definition of MCEs at 30–150 m, with subdivisions for upper (30–60 m) and lower (60–150 m) MCEs, is a reasonable starting point until additional data are incorporated to refine the definition for each specific MCE.

FUNCTIONAL ECOLOGY OF MESOPHOTIC CORAL REEF ORGANISMS

Functional Morphology

Scleractinian corals, iconic members of both shallow and mesophotic reef communities, exhibit specific depth distributions and have been the subject of many studies. Additionally, as primary photoautotrophs in coral reef ecosystems, the ability of a coral's endosymbiotic dinoflagellates (*Symbiodinium* spp.) to photoacclimatize or photoadapt is linked to their respective ecological success. The photobiology literature on corals is dominated by publications on the absorption and

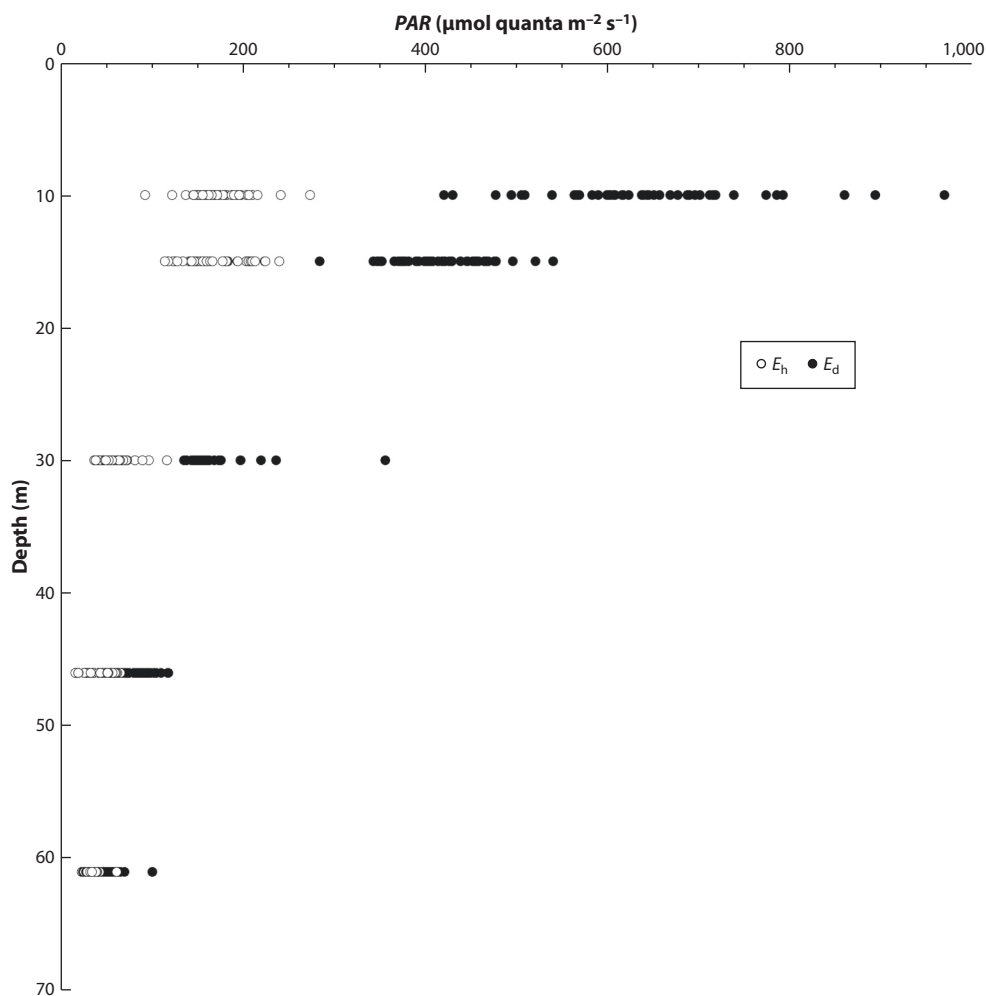


Figure 3

Plot of downwelling (E_d) and horizontal (E_h) irradiances in Curaçao down to 61 m for θ_{sun} of approximately 20° on November 15, 2017. Data were collected at approximately 10 m, 15 m, 30 m, 46 m, and 61 m using a pair of cosine-corrected Li-Cor 192 underwater quantum sensors.

utilization of light and on the regulation of the photosynthetic apparatus under varying irradiances and environmental stresses (Lesser 2011, Warner & Suggett 2016). One of the most conspicuous outcomes of photoacclimatization in many species of corals to low irradiances is to change their morphology in an effort to increase surface area for light capture. As a result, many of the zooxanthellate scleractinian corals found in MCEs exhibit a fixed plate-like morphology or change shape with depth to a flattened or plate-like morphology as a result of phenotypic plasticity (e.g., Lesser et al. 2010). Both the branching coral *Seriatopora hystrix* and the mounding coral *Montastraea cavernosa* develop flattened branches or plate-like morphologies with depth (Lesser et al. 2010, Nir

et al. 2011). In the Red Sea, the coral *Stylophora pistillata* can photoacclimatize down to a depth of 65 m by increasing its chlorophyll concentration and by changing to a more flattened, planar-like, morphology (Einbinder et al. 2009, Mass et al. 2007). However, despite these changes, the rates of photosynthesis and calcification declined significantly with increasing depth (Mass et al. 2007). Mass et al. (2007) concluded, based on these results, that corals at the deeper end of their vertical distribution were switching to heterotrophic feeding on zooplankton. Similarly, when the limits of photoacclimatizing to low irradiances have been reached in the deep mesophotic zone, *M. cavernosa* has been shown, using stable isotopic analyses, to switch to heterotrophy (Lesser et al. 2010).

Small-Scale Optics, Photoacclimatization, and Accessory Pigments

More recent work has provided critical insights into the small-scale optics of corals at the cellular level and has described the importance of the skeleton in scattering photons, which increases their path length and their potential for being absorbed (Wangpraseurt et al. 2012). The result is higher *in hospite* irradiances than the bulk measurements of E_d might suggest, making these small-scale irradiance dynamics a scalar (360°) versus planar (180°) phenomenon (Wangpraseurt et al. 2012). In fact, scattering by the skeleton and the tissues may be an important photoadaptation that could also be important for corals in MCE environments. Skeletal scattering of photons and lower pigment concentrations were suggested as mechanisms facilitating more efficient light capture in mesophotic *Leptoseris* spp. from Hawai'i (Kahng et al. 2012). Additionally, for MCE photoautotrophs, and corals in particular, complementary chromatic adaption to the spectral changes of the underwater light field in the mesophotic zone could provide an ecological advantage by maintaining photoautotrophy at deeper depths. Mass et al. (2010) provided experimental evidence that *S. pistillata* from the upper mesophotic zone (40 m) exhibited chromatic adaption to the blue wavelengths dominant at those depths and could maintain higher rates of photosynthesis with increasing depth as a result.

Many of the photoacclimatization strategies discussed above can be encapsulated into what is one of the most widely studied aspects of mesophotic coral photobiology: the diversity and depth-dependent distribution of *Symbiodinium* spp. phylotypes. Studies in the Caribbean Sea (Bongaerts et al. 2017, Frade et al. 2008, Lesser et al. 2010), Hawai'i (Pochon et al. 2015), the Red Sea (Ziegler et al. 2015), and Australia (Cooper et al. 2011) have all demonstrated depth-dependent distributions of *Symbiodinium* spp. phylotypes in several species of coral and identified *Symbiodinium* depth specialists not observed in previous studies. Additionally, a recent study showed that in the *Symbiodinium* spp. of mesophotic corals, the photosynthetic apparatus is uniquely rearranged (Einbinder et al. 2016). Different *Symbiodinium* phylotypes also exhibit variability in other physiological traits along the shallow-to-mesophotic depth gradient, including differences in lipid storage (Cooper et al. 2011) and in carbon and nitrogen acquisition strategies (Ezzat et al. 2017), that have direct ecological advantages in mesophotic habitats.

Most discussions on photoacclimatization in corals primarily involve the endosymbiotic symbionts, *Symbiodinium* spp. Others involve the host, such as the discussions above on morphology and skeletal scattering. But many early photobiological studies on deep mesophotic corals (>60 m) in the Red Sea included the discovery of a putatively adaptive host system of chromatophores that converts ambient irradiances using autofluorescence into longer wavelengths that could be utilized by their symbiotic *Symbiodinium* spp. (Schlichter et al. 1986, 1994). This conversion of ambient irradiance from short wavelengths to longer wavelengths is a potentially important photoadaptation to low irradiances, and we now know that these same chromatophores contain green fluorescent protein and that corals express a large number of fluorescent proteins with different absorption and emission characteristics (Matz et al. 2006). Many corals, including

those found in the mesophotic zone (Roth et al. 2015), express multiple fluorescent proteins. However, although nonfluorescent chromoproteins have been shown to provide photoprotective screening in corals (Smith et al. 2013), fluorescent proteins have not been shown to increase photosynthesis or provide photoprotection (Gilmore et al. 2003, Mazel et al. 2003). Mechanistically, it has recently been suggested that photoconvertible fluorescent proteins in mesophotic corals provide orange to red wavelengths *in hospite* that can be used for symbiont photosynthesis (Eyal et al. 2015, Smith et al. 2017) despite evidence showing that these wavelengths repress the photophysiology of *Symbiodinium* spp. (Wijgerde et al. 2014). Although intriguing, no direct evidence of a linkage between the emission spectra of these fluorescent proteins and increases in photosynthetic activity, or any other physiological function, has been found at MCE depths.

Macroalgae

In addition to corals, other photoautotrophs such as macroalgae exhibit depth distributions well into the mesophotic habitats and even form ecological zones based on their ability to absorb and utilize the decreasing fraction of available visible irradiance (Littler et al. 1986, Runcie et al. 2008). In San Salvador, Bahamas, a decrease in total algal cover, and distinct algal zones, is seen with increasing depth (Littler et al. 1986). Similar patterns have been observed on Lee Stocking Island, Bahamas, but the algal zones overlap and are shifted in depth upward by 30–50 m compared with San Salvador (Aponte & Ballantine 2001). Constant disturbance from sand moving down the fore reef at Lee Stocking Island is believed to result in these shallower zones (Aponte & Ballantine 2001). The depth-dependent zonation patterns observed throughout the Bahamas are reasonably consistent with the information on photosynthetic performance at low irradiances for brown, green, and red algae occurring at mesophotic depths (Runcie et al. 2008).

Macroalgae can be conspicuous members of MCEs (e.g., Hawai'i) and their depth distributions are often described as limited by physiological adaptations to the environment, but Slattery & Lesser (2014) reported the depth distribution of the brown alga *Lobophora variegata* in the Bahamas was not limited by the availability of carbon and nitrogen or by photosynthetic potential. Instead, when the invasive lionfish *Pterois volitans* removed several major trophic guilds of fish (Lesser & Slattery 2011), including herbivorous scarids and acanthurids, a trophic cascade, caused by the release from fish herbivory, increased macroalgal abundance at mesophotic depths resulting in increased competitive interactions between *Lobophora* and the coral *M. cavernosa* and the sponge *Agelas clathrodes* (Slattery & Lesser 2014). The significant allelopathy-mediated physiological impacts of these competitive interactions caused tissue bleaching and/or necrosis in 62% and 29% of the algal:coral and algal:sponge interactions, respectively (Slattery & Lesser 2014). In contrast to prior predictions (Brokovich et al. 2010), the depth distributions of mesophotic macroalgae may be limited by top-down (i.e., herbivory) control on MCEs (Liddell & Avery 2000).

Sponges

After corals, sponges are the second most dominant taxon on many coral reefs (van Soest et al. 2012). Unlike corals, however, sponges are largely dependent on planktonic food resources, both dissolved and particulate, and are primarily mixotrophic or heterotrophic (de Goeij et al. 2017). Sponges are also crucial components of mesophotic coral reef communities, where they couple water column productivity to the benthos through filter feeding, are a major component of coral reef biodiversity, and create essential habitat for many species of invertebrates and fish (de Goeij et al. 2017; Lesser 2006, 2011; Slattery & Lesser 2012). Another aspect of sponge biology related to their ecological importance is their metabolism and nutrient fluxes (de Goeij et al. 2017). For instance, the sponge *Plakortis angulospiculatus* occurs on both shallow and mesophotic reefs

(10–76 m) in the Bahamas and the Cayman Islands. But *P. angulospiculatus* from deep depths (61 m and 76 m), where fish spongivory is low, grows faster and invests more biosynthetic energy into tissue protein when wounded compared with shallow reef conspecifics (10 m and 46 m) that express enhanced chemical defenses in response to higher levels of fish spongivory (Slattery et al. 2016). Any increase in protein synthesis must be coupled to food resources also known to vary over the shallow-to-mesophotic depth range (e.g., Lesser 2006).

Our understanding of sponge ecology on coral reefs has been reframed owing to the emergence of the sponge loop pathway, a hypothesis that places sponges as a central player in the cycling of carbon and nitrogen on coral reefs (de Goeij et al. 2017). The sponge loop hypothesis postulates that sponges take up dissolved organic matter (DOM), which includes both dissolved organic carbon (DOC) and dissolved organic nitrogen (DON). This DOM is used as a food resource that is then released as detritus to be used in various detrital pathways that could have a significant impact on carbon budgets on coral reefs (de Goeij et al. 2017). Most of the studies on the sponge loop have been conducted on encrusting species in shallow waters, and very little is known about the role, if any, of the sponge loop at mesophotic depths. What is known is that the concentration of DOC generally declines with increasing depth into the mesophotic zone (Slattery & Lesser 2015, Torréton et al. 1997). We also know that DOC in the oligotrophic waters over coral reefs has a high C:N ratio ($\gg 10$; Tanaka et al. 2011), such that carbon-rich DOC could serve as carbon skeletons for protein synthesis but not without the intake of nitrogen, making the consumption of particulate organic nitrogen (PON), and potentially DON, essential. DON concentrations on coral reefs, however, are often more than an order of magnitude lower than DOC concentrations, and changes in DON concentrations generally mirror the changes in DOC concentrations (Tanaka et al. 2011). The lower DON concentrations make particulate organic matter (POM), and in particular PON, an important source of nitrogen known to vary along a shallow-to-mesophotic depth gradient to ~ 90 m (Lesser 2006). Sponges filter this POM in the form of bacterioplankton efficiently with clearance rates of 83–90% (Lesser 2006, Slattery & Lesser 2015). These bacterioplankton have low C:N ratios and are a well-known, and important, source of nitrogen for these suspension feeders (Ribes et al. 2003, 2005).

Heterotrophy in Mesophotic Corals

As discussed above, corals in the mesophotic zone must be capable of photoacclimatizing to the low irradiances at depths > 30 m. On the basis of first principals, any photoautotrophic taxa that occur at depths deeper than the 1% light level are employing other trophic strategies (e.g., heterotrophy) to offset the net loss of energy and fixed carbon previously acquired through photoautotrophy. In corals, including mesophotic corals, many species appear to shift their trophic reliance from being primarily autotrophic to an increasing dependence on heterotrophy (i.e., mixotrophy) for their carbon requirements with increasing depth (Lesser et al. 2010, Muscatine et al. 1989). The nutrient or food resources to support heterotrophy at mesophotic depths occur in the form of zooplankton (Andradi-Brown et al. 2017), picoplankton (Lesser 2006), or inorganic nutrients supplied by upwelling or internal waves (Leichter & Genovese 2006). Additionally, seasonal changes in irradiance could lead to shifts in the depths at which transitions between autotrophy and heterotrophy might occur, also affecting the energetic content of corals (Brandtneris et al. 2016).

One approach to assess whether a switch from autotrophy to heterotrophy has occurred is to measure changes in the carbon stable isotope signal ($\delta^{13}\text{C}$) of the host tissues, zooxanthellae, and skeleton of corals (Muscatine et al. 1989). Muscatine et al. (1989) used this approach to show that the increasingly depleted $\delta^{13}\text{C}$ signature of the animal tissue of corals, and its divergence from the $\delta^{13}\text{C}$ of their zooxanthellae, was evidence of increasing heterotrophy down to a depth

of 50 m, clearly demonstrating a mixotrophic strategy. In the coral *S. pistillata*, from the Red Sea, photosynthesis declines significantly with increasing depth, indicating light limitation and suggesting that these corals were growing and surviving as a result of heterotrophic feeding on zooplankton at the deeper end of their vertical distribution (Mass et al. 2007). In subsequent studies, both Alamaru et al. (2009) and Einbinder et al. (2009) used stable isotopic signatures on *S. pistillata* to discern their trophic mode and reported significant differences in both the zooxanthellae and animal tissue $\delta^{13}\text{C}$ values with increasing depth, with the animal tissue signal significantly more depleted than the zooxanthellae signal as depth increased. This pattern is consistent with increasing reliance on heterotrophy as described above and the isotopic signatures reported for zooplankton (Lesser et al. 2010, Slattery et al. 2011). Lesser et al. (2010) also used stable carbon isotope data to resolve the trophic status of *M. cavernosa* in the Caribbean Sea with similar results, but a switch to heterotrophy is also supported by the significant decrease in skeletal $\delta^{13}\text{C}$ signatures with depth in the same corals. Taken together, these data suggest that species-specific patterns of mixotrophy over the shallow-to-mesophotic depth gradient do exist, and where it has been studied an increase in heterotrophy for corals with increasing depth has been observed. Another stable isotopic approach, compound-specific isotopic analysis of carbon and nitrogen in amino acids and lipid biomarkers such as sterols, promises to enhance our understanding of food web structure on coral reefs (McMahon et al. 2016) and when transitions to heterotrophy occur (Crandall et al. 2016). But this approach is dependent on broad sampling across the shallow-to-lower mesophotic zones that include depths where photoautotrophy, mixotrophy, and heterotrophy are known to occur because small differences in isotopic signals are used to differentiate between different trophic strategies.

Finally, perhaps one of the most interesting aspects of coral biology is the emerging role of nitrogen (N_2) fixation by diazotrophic bacteria living symbiotically in corals in the nitrogen metabolism and budgets of corals (Benavides et al. 2017). Acquiring nitrogen through N_2 fixation is directly related to the role of heterotrophy in corals in the context that if a coral is getting sufficient nitrogen from its diazotrophic symbionts, its reliance on heterotrophic resources is likely to decrease. For instance, a study by Bednarz et al. (2017) showed that upper mesophotic (~45 m) *S. pistillata*, which were more heterotrophic, also required diazotroph-derived nitrogen for up to 15% of their nitrogen budget compared with 1% for conspecifics from shallow waters. These intriguing differences in the trophic strategies of corals from shallow and mesophotic depths, relative to the available carbon and nitrogen resources, require significantly more study before we can say whether generalizable patterns occur in the trophic ecology of MCE corals.

COMMUNITY ECOLOGY OF MESOPHOTIC CORAL REEFS

Several reviews of MCE community structure and function are available (e.g., Lesser et al. 2009), and as with other ecosystems, the community structure of coral reef ecosystems is determined by both top-down and bottom-up processes (Kahng et al. 2010, Lesser & Slattery 2011, Smith et al. 2016b), but we have far less knowledge about these processes for MCEs (Bridge et al. 2013; Slattery et al. 2011, 2016). 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 distinct bathymetric zonation patterns with a clear break in living cover occurring between 75 and 100 m. In particular, coral cover shallower than 50 m is 3–23% followed by significant declines with increasing depth to <5%, coupled with an increasing percent cover of sponges. In Jamaica, Liddell & Ohlhorst (1988) showed a clear break in community structure at >50 m where sponges became the dominant members of the community; they recognized the role of decreasing irradiance, and the important effects of reef wall topography and slope, from the work of Brakel (1979) on

community structure. And on the Great Barrier Reef, the scleractinian fauna was more diverse and common at depths <60 m, whereas the Octocorallia were more abundant at depths >60 m (Bridge et al. 2012).

In some MCEs, the pattern of decreasing coral cover with increasing depth is not observed, and dense beds of scleractinian corals occur at depths >60 m, such as in Curaçao, where these deep coral communities consist of mostly *Agaricia* spp. (Hoeksema et al. 2017). In Hawai'i, another MCE with extensive coral cover at deep mesophotic depths, a comprehensive survey of the Au'au Channel revealed that *Leptoseris* spp. were rare in shallow water (<60 m) but were abundant in areas of hard and stable substrate between 60 and 120 m, below which azooxanthellate wire coral, black coral, and sponges increased (Kahng & Kelley 2007). The authors attribute the decline of coral cover beginning below 90 m to a combination of changes in irradiance with depth, daily temperature fluctuations ($\pm 2\text{--}4^\circ\text{C}$) associated with changes in the depth of the seasonal thermocline, and lack of stable substrate. Similarly, Pyle et al. (2016) conducted a multiyear study of MCE habitats in the Hawaiian Archipelago and found that *Leptoseris* spp. cover up to 100% is extensive between 50 and 90 m throughout the archipelago.

For sponges, a gradient of increasing percent cover and biomass from shallow (<30 m) to mesophotic depths throughout the Caribbean Sea and the Pacific Ocean has been well described (Lesser & Slattery 2011; Lesser et al. 2009; Slattery & Lesser 2012, 2019). Evidence has also been found that MCEs contain many undescribed sponge species and increased diversity relative to shallow reefs (Diaz et al. 2010). Interestingly, the cover of corals and macrophytes decreases with increasing depth on coral reefs, whereas sponge percent cover and biomass increases along the shallow-to-mesophotic depth gradient (Lesser & Slattery 2011, Slattery & Lesser 2012). Slattery & Lesser (2012) found no increase in sponge biomass with increasing depth in the Pacific Ocean, compared with the sponge fauna in the Caribbean Sea, because the Caribbean sponge fauna consists of massive sponges with large volumes (**Figure 4a**), whereas the Pacific sponges are thin, encrusting, low-volume species (**Figure 4b**).

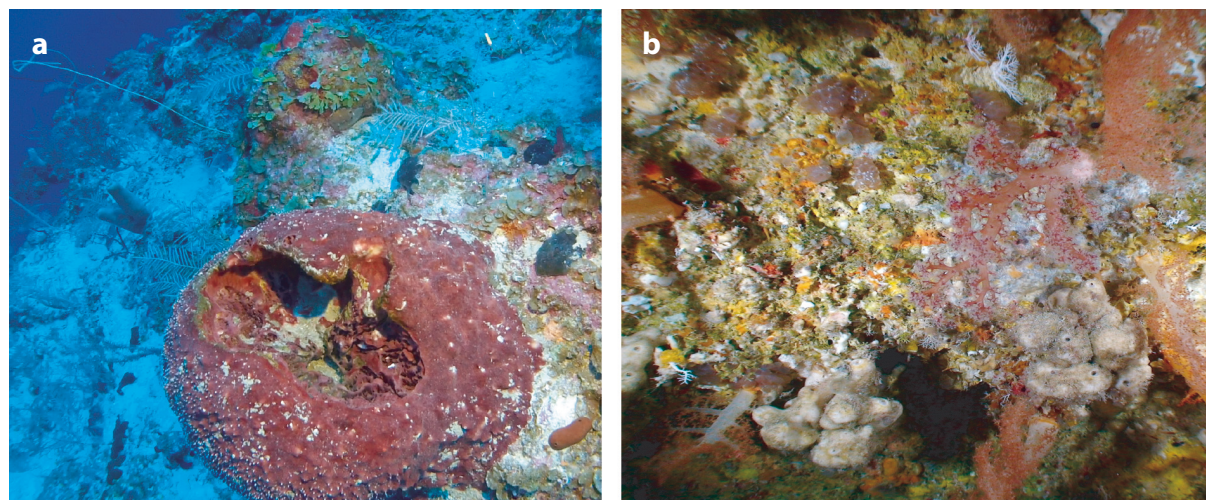


Figure 4

Typical mesophotic communities in the Cayman Islands and Palau. (a) Photograph of a mesophotic community on Grand Cayman at a depth of ~61 m showing a community of massive sponges including *Neofibularia nolitangere* and *Agelas tubulata*. (b) Photograph of mesophotic community on Palau at a depth of ~61 m showing the encrusting sponge community with soft corals.

One of the most interesting questions on MCE structure and function is the observation of distinct faunal breaks in mesophotic communities at ~60 m depth. Many MCEs within the Caribbean Sea exhibit a clear demarcation between the upper mesophotic community (30–60 m), with biodiversity that overlaps with the shallow coral reefs, and the ecologically distinct lower mesophotic community (60–100 m), which includes unique species (Slattery & Lesser 2019, Slattery et al. 2011). This pattern is supported by multiple studies that show consistent changes in community composition driven by changes in the diversity and abundance of corals, macroalgae, sponges, and fish (Bejarano et al. 2014, Lesser & Slattery 2011, Reaka et al. 2010, Rooney et al. 2010, Sherman et al. 2010, Slattery & Lesser 2012). Nonetheless, there is resistance to the use of any general ecological rule for MCEs related to faunal breaks based on studies of fish biodiversity with increasing depth (Pyle et al. 2016). Despite studies showing that mobile taxa such as Pacific MCE reef fish assemblages appear to be homogeneous to a depth of ~100 m (Pyle et al. 2016), suggesting no faunal break in fish assemblages, recent studies have clearly shown that fish assemblages from Hawai‘i and elsewhere do differ significantly as depth increases into the mesophotic zone (Andradi-Brown et al. 2016, Asher et al. 2017, Bejarano et al. 2014, Brokovich et al. 2008, Pinheiro et al. 2016). Additionally, for many sessile taxa, faunal breaks have been a consistent feature of historical MCE biodiversity surveys (corals, Liddell & Ohlhorst 1988; sponges, Reed & Pomponi 1997; algae, Aponte & Ballantine 2001) and more recent studies on both corals and sponges (Lesser & Slattery 2011, Slattery & Lesser 2012). The observation of a 60-m faunal break on MCEs also occurs across ocean basins as shown in a comparison between MCEs in the Caribbean Sea and the Pacific Ocean (Slattery & Lesser 2012). Even *Symbiodinium* phylotypes change with depth into the lower mesophotic zone at ~60 m (e.g., Lesser et al. 2010), as does the microbiome of sponges (Morrow et al. 2016). The underlying causes, and variability, in this faunal break at 60 m requires significantly more research.

THE DEEP REEF REFUGIA HYPOTHESIS

One of the main themes of MCE research efforts has centered around the vertical connectivity of species over the shallow-to-mesophotic depth range, and the identification of refugia where mesophotic species exhibiting overlapping distributions with shallow water conspecifics could provide planktonic larvae to shallow populations. Shallow populations are affected by disturbance events such as hurricanes, thermal stress, pollution, sedimentation, and eutrophication resulting in significant mortality and lowered resilience (Bongaerts et al. 2010, Lesser et al. 2009). The term refugia should be discontinued in this context, as discussed in Bongaerts et al. (2017), and replaced with the term refuges, which denotes the restricted spatial extent of a population over ecological timescales of minutes to decades.

Vertical connectivity is a requirement for the success of the deep reef refuges hypothesis (DRRH), and it can vary spatially, temporally, and across species (Bongaerts et al. 2017). The most significant factor affecting the connectivity of populations between shallow and mesophotic depths is their reproductive life history, which includes fecundity, reproductive mode, and recruitment (Holstein et al. 2015). Recruitment patterns for scleractinian corals with broad depth ranges, both broadcast spawners (*Montastraea* spp.) and brooders (*Agaricia* spp., *Porites* spp.), showed that maximum recruitment occurs between 20 and 75 m in the Bahamas, demonstrating the potential for vertical connectivity (Avery & Liddell 1997). But some coral species are endemic to mesophotic habitats and therefore have little or no potential for vertical connectivity. For example, in the Red Sea, two species of *Alveopora* (Poritidae) are exclusively found in MCE habitats from 40 to 60 m, and although these congeners are very fecund at these depths, they exhibit reproductive isolation in MCE habitats and are therefore considered depth specialists (Eyal-Shaham et al. 2016). A study

in Curaçao from 2 to 60 m showed that coral species segregate on the basis of depth with *Agaricia lamarcki* and *Agaricia grahamae* being the mesophotic depth specialists (Bongaerts et al. 2013). Bongaerts et al. (2013) also identified unique *Symbiodinium* spp. phylotypes associated with these mesophotic species. Similarly, species assemblages of mobile brachyuran crabs also segregated by depth, with lower abundance overall with increasing depth and the presence of depth specialists in shallow and mesophotic depths (Hurley et al. 2016).

In addition to recruitment potential, adult corals at mesophotic depths must both be fecund and exhibit some degree of reproductive synchrony with their shallow conspecifics. In the USVI, Holstein et al. (2015) found increased gonads/polyps in deeper (~40 m) *Orbicella faveolata*, compared with shallow depths, suggesting increased fecundity in mesophotic corals and connectivity between shallow and deep populations. Similarly, Holstein et al. (2016a) found a decrease in planulae production with increasing depth in the coral *Porites astreoides*, a brooder from shallow and upper mesophotic (~40 m) depths, but owing to an increase in coral populations with depth, these corals may still serve as a source of propagules for shallow reefs if they could be vertically advected. In Okinawa, Japan, upper mesophotic (~40 m) populations of the coral *Acropora tenella* exhibited reduced fecundity and less synchronous gamete maturation compared with their shallow water counterparts (Prasetia et al. 2016), but mesophotic *S. hystrix*, which has a shorter reproductive season and smaller planula, showed a similar reproductive periodicity, suggesting some potential for vertical connectivity (Prasetia et al. 2017). However, populations of *S. hystrix* on the east and west coasts of Australia as deep as 60 m show strong evidence of genetic structuring with increasing depth and in western Australia (Scott Reef) show vertical connectivity, whereas in eastern Australia (Yonge Reef) no evidence of vertical connectivity was detected (van Oppen et al. 2011). Finally, several species of scleractinian coral from the Red Sea also show decreasing fecundity with increasing depth compared with shallow water conspecifics (Shlesinger et al. 2018).

Another mechanism by which mesophotic corals could contribute to shallow water populations through vertical connectivity is by synchronized spawning across the depth distribution. It is generally understood that gametogenic cycles, spawning, and/or planulation are controlled by a combination of environmental cues over a variety of temporal scales including temperature (seasonal), lunar (monthly), and solar (seasonal and daily) cycles. Of particular interest for MCEs are the implications for connectivity between deep and shallow populations, as the available evidence shows that spawning synchrony between shallow and mesophotic conspecifics from the same reef can occur, although indirect evidence showing a lack of spawning synchrony also exists (Shlesinger et al. 2018). Specifically, in the Caribbean Sea, the massive broadcast spawning corals *M. cavernosa*, *Montastraea franksi* (now *Orbicella franksi*), and *Diploria strigosa* (now *Pseudodiploria strigosa*) all synchronously spawn within 30–60 min of conspecifics for populations at depths of 16 m and 30–42 m (Vize 2006). Temporal regulation of spawning would be essential to support high rates of fertilization for those coral species that broadcast spawn and span the shallow-to-mesophotic depth range. The observed variability in fecundity and spawning synchrony for different coral species and locations strongly suggests that quantitative studies on the variability in light and food supply, two factors that strongly influence reproduction and spawning, need to be undertaken.

One approach to examine the DRRH is to undertake a population genetics study over the entire depth distribution of occurrence for a specific species. One of the best-studied species of scleractinian coral in the Caribbean Sea using this approach is *M. cavernosa*. Serrano et al. (2014) found genetic differentiation by depth (<10 m, 15–20 m, and ≥25 m) in Florida but not in Bermuda or the USVI. Brazeau et al. (2013), working on *M. cavernosa* from shallow (3–10 m), medium (15–25 m), deep (30–50 m), and very deep (60–90 m) populations, also found significant genetic

differentiation between populations: Shallow and medium depths were significantly different than deep depths, which were significantly different than very deep depths at both Little Cayman Island and the Bahamas, indicative of low vertical population connectivity. They also found, analyzing the same samples as those used for the host genetics, specific *Symbiodinium* spp. phylotypes at the same depths as the respective hosts. A genetic break point was found at ~60 m, below which unique phylotypes not previously observed were found in the deepest populations of *M. cavernosa* (Lesser et al. 2010), similar to what has been reported for the *Madracis* spp. complex and the *Agaricia* spp. complex in Curaçao (Bongaerts et al. 2013, Frade et al. 2008).

In a comprehensive study on the depth distribution of *Symbiodinium* spp. phylotypes, Bongaerts et al. (2015b) analyzed the 25 most common scleractinian coral species over a depth range down to 60 m in Curaçao. They found that *Symbiodinium* spp. phylotype zonation was most common in coral species with the broadest depth distributions and concluded that, when considering both the coral host and their photosymbionts, coral reefs can exhibit highly structured communities over depth, which suggests low rates of vertical connectivity between shallow and mesophotic habitats. This finding indicates that strong gradients of environmental selection, and potentially coevolution of host and symbionts, are important drivers of these zonation patterns (Bongaerts et al. 2013, Pochon et al. 2015).

In the context of mobile species, far less work has been done related to vertical connectivity than on sessile species. In particular, as the number of studies on fish have increased substantially, it is clear that fish assemblages are not generally homogeneous with depth and that unique fish assemblages in mesophotic zones exist (e.g., MacDonald et al. 2016). Additionally, demographic studies on fish species found throughout the shallow-to-mesophotic depth range have shown that although some fish populations found in mesophotic zones decrease in density, they are larger, have longer life spans than their shallow water counterparts, and are more fecund, resulting in higher quality larvae (Goldstein et al. 2016a); this combination of demographic characteristics for populations of mesophotic fish can lead to a substantial amount of the reproductive output of a metapopulation (Goldstein et al. 2016b). Where it has been examined, the genetic connectivity of fish that span the shallow-to-mesophotic depth gradient does not exhibit population structure, indicating that these species utilize the entire habitat from <30 m to 150 m (Tenggardjaja et al. 2014).

Are mesophotic communities distinct, and can they serve as a refuge for shallow coral reefs? In one of the largest studies conducted, Semmler et al. (2017) showed that in the Gulf of Mexico three distinct communities consisting of a broad range of benthic invertebrates and fish are evident: a shallow community from 0 to 70 m, two mid-depth communities from 60 to 120 m and from 110 to 200 m, and a deeper outer continental shelf community from 190 to 200 m. Semmler et al. (2017) also concluded that a sharp faunal break occurs at ~60 m and that it includes fish. Lastly, a recent biophysical model of vertical connectivity using data on corals in the USVI from upper mesophotic reefs showed that larval subsidies from both a broadcasting species (*O. faveolata*) and a brooding species (*P. astreoides*) to shallower depths can occur under realistic ecological conditions (Holstein et al. 2016b). Taken together, the current data suggest that lower mesophotic communities are unique and an unlikely source of propagules to assist in the restoration of shallow coral reefs for sessile taxa such as scleractinian corals.

MICROBIAL ECOLOGY OF MESOPHOTIC CORAL REEFS

Coral reef microbial ecology emerged at the same time that intense efforts at understanding the biogeochemistry of nutrients, and in particular nitrogen, were undertaken to explain Darwin's "paradox of the coral reef," in which high biodiversity is sustained in oligotrophic waters. Additionally,

the recycling of DOC through the microbial loop to higher trophic levels (Azam et al. 1983), and its relative importance, was being incorporated into coral reef ecology (Ducklow 1990). Ducklow (1990), in particular, developed a forward-looking scheme whereby the microbial loop in the overlying waters of coral reefs was connected to benthic consumers (i.e., corals) and the export of POM and DOM to sediments and lagoons. This theory led to numerous studies on the biomass, production, and grazing of bacterioplankton on coral reefs (e.g., Ferrier-Pagès & Gattuso 1998). More recently, the microbial loop has been integrated with the newly described sponge loop and the relative importance of DOM from macroalgae versus corals (de Goeij et al. 2017), DOM recycling (Rix et al. 2017), and DOM effects on the microbial metabolism of the reef benthos (Haas et al. 2013).

The preponderance of studies in the microbial ecology of coral reefs has been on the description and function of symbiotic microbiomes in multiple taxa, but primarily in corals and sponges (Hentschel et al. 2012, Hernandez-Agreda et al. 2016). For MCEs, we have very little knowledge about the roles of microbes generally or about their symbiosis with various MCE taxa (Olson & Kellogg 2010). For coral species studied across the shallow-to-mesophotic depth gradient, it has been shown that their microbiome can vary depending on whether they are depth generalists or depth specialists, and the patterns observed are similar to the *Symbiodinium* spp. phylotype distributions for the same corals (Glasl et al. 2017). Changes in the coral microbiome from shallow and mesophotic depths consist of a core community and a variable component, which are believed to provide a mechanistic basis for the success of these corals at mesophotic depths (Hernandez-Agreda et al. 2016). For the sponges *P. angulospiculatus*, *Agelas conifera* (actually *Agelas tubulata*), and *Xestospongia muta*, Olson & Gao (2013) used terminal restriction fragment length polymorphism analyses of amplified 16S rRNA genes to show that each species has a host-specific microbiome that varies significantly with depth. Using next-generation sequencing, Morrow et al. (2016) showed that samples of *X. muta* collected over the shallow-to-mesophotic depth gradient were also significantly different in their sponge microbiome communities from Little Cayman but not from the Bahamas. Again, this finding supports the important role for environmental factors in shaping the sponge microbiome from the same species in different locations. Similarly, in a study on Guam sponge species, a significant influence on the composition of the sponge microbiome was found, but the effect of depth was significant only for a species of *Callyspongia*, a low microbial abundance sponge, whereas *Rhabdastrella globostellata*, a high microbial abundance sponge, exhibited no such effect of depth (Steinert et al. 2016).

CONCLUSIONS AND FUTURE DIRECTIONS

MCEs are still vastly understudied despite increased attention over the past two decades (Loya et al. 2016). In this regard, there is still a significant need to study and understand the geological history and fundamental ecological characteristics, both biotic and abiotic, of MCEs around the world. To further this endeavor of discovery and quantitative ecology, we hope that this review illuminates the need for studies on the DRRH, ecological processes at the community level, and microbial ecology of the water column and functional ecology of microbiomes in the major MCE taxa. Given our current understanding of the optical properties of MCE habitats as it relates to the depth-dependent definition of MCE, and emerging approaches that incorporate species turnover with increasing depth, we feel that trying to redefine MCEs now would confuse the issue rather than bring additional clarity. Nonetheless, we recognize that optical properties of the water column are likely to have the strongest correlation with MCE community patterns. To improve the current definition of MCEs, which may result in regional or reef-to-reef definitions, we need more studies that include community characterization throughout the entire depth range of 30–150 m, that are combined with studies on the optics of the water column, and that include

the identification of critical taxa that characterize unique upper (30–60 m) and lower (60–150 m) mesophotic habitats.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Support for MCE research was provided by the National Science Foundation Biological Oceanography program (OCE-1632348/1632333) to M.P.L. and M.S., respectively.

LITERATURE CITED

- Alamaru A, Loya Y, Brokovich E, Yam R, Shemesh A. 2009. Carbon and nitrogen utilization in two species of Red Sea corals along a depth gradient: insights from stable isotope analysis of total organic material and lipids. *Geochim. Cosmochim. Acta* 73:5333–42
- Andradi-Brown DA, Head CEI, Exton DA, Hunt CL, Hendrix A, et al. 2017. Identifying zooplankton community changes between shallow and upper-mesophotic reefs on the Mesoamerican Barrier Reef, Caribbean. *PeerJ* 5:e2853
- Andradi-Brown DA, Macaya-Solis C, Exton DA, Gress E, Wright G, et al. 2016. Assessing Caribbean shallow and mesophotic reef fish communities using baited-remote underwater video (BRUV) and diver-operated video (DOV) survey techniques. *PLOS ONE* 11:e0168235
- Aponte NE, Ballantine DL. 2001. Depth distribution of algal species on the deep insular fore reef at Lee Stocking Island, Bahamas. *Deep-Sea Res. Part I* 48:2185–94
- Asher J, Williams ID, Harvey ES. 2017. Mesophotic depth gradients impact reef fish assemblage composition and functional group partitioning in the Main Hawaiian Islands. *Front. Mar. Sci.* 4:98
- Avery WE, Liddell WD. 1997. Sessile community recruitment patterns on Western Atlantic shallow and deep-reef hard substrata. *Proc. 8th Int. Coral Reef Symp.* 2:1179–84
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, et al. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10:257–63
- Banaszak AT, Lesser MP, Kuffner IB, Ondrusek M. 1998. Relationship between ultraviolet (UV) radiation and mycosporine-like amino acids (MAAs) in marine organisms. *Bull. Mar. Sci.* 63:617–28
- Bednarz VN, Grover R, Maguer J-F, Fine M. 2017. The assimilation of diazotroph-derived nitrogen by scleractinian corals depends on their metabolic status. *mBio* 8:e02058-16
- Bejarano I, Appeldoorn RS, Nemeth M. 2014. Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. *Coral Reefs* 33:313–28
- Benavides M, Bednarz VN, Ferrier-Pagès C. 2017. Diazotrophs: overlooked key players within coral symbiosis and tropical reef ecosystems? *Front. Mar. Sci.* 4:10
- Bongaerts P, Carmichael M, Hay KB, Tonk L, Frade PR, et al. 2015b. Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. *R. Soc. Open Sci.* 2:140297
- Bongaerts P, Frade PR, Hay KB, Englebert N, Latijnhouwers KRW, et al. 2015a. Deep down on a Caribbean reef: lower mesophotic depths harbor a specialized coral-endosymbiont community. *Sci. Rep.* 5:7652
- Bongaerts P, Frade PR, Ogier JJ, Kay KB, van Bleijswijk J, et al. 2013. Sharing the slope: depth partitioning of agariciid corals and associated *Symbiodinium* across shallow and mesophotic habitats (2–60 m) on a Caribbean reef. *BMC Evol. Biol.* 13:205
- Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O. 2010. Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral Reefs* 29:309–27
- Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, et al. 2017. Deep reefs are not universal refuges: reseeding potential varies among coral species. *Sci. Adv.* 3:e1602373

- Bongaerts P, Riginos C, Hay KB, van Oppen MJ, Hoegh-Guldberg O, et al. 2011. Adaptive divergence in a scleractinian coral: physiological adaptation of *Seriatopora hystrix* to shallow and deep reef habitats. *BMC Evol. Biol.* 11:303
- Brakel WH. 1979. Small-scale spatial variation in light available to coral reef benthos: quantum irradiance measurements from a Jamaican reef. *Bull. Mar. Sci.* 29:406–13
- Brandtneris VW, Brandt ME, Glynn PW, Gyory J, Smith TB. 2016. Seasonal variability in calorimetric energy content of two Caribbean mesophotic corals. *PLOS ONE* 11:e0151953
- Brazeau DA, Lesser MP, Slattery M. 2013. Genetic structure in the coral, *Montastraea cavernosa*: assessing genetic differentiation among and within mesophotic reefs. *PLOS ONE* 8:e65845
- Bridge TCL, Fabricius KE, Bongaerts P, Wallace CC, Muir PR, et al. 2012. Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia. *Coral Reefs* 31:179–89
- Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P. 2013. Call to protect all coral reefs. *Nat. Clim. Change* 3:528–30
- Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, et al. 2010. Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Mar. Ecol. Prog. Ser.* 399:69–80
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S. 2008. Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Mar. Ecol. Prog. Ser.* 371:253–62
- Cooper TF, Ulstrup KE, Dandan SS, Heyward AJ, Kühl M, et al. 2011. Niche specialization of reef-building corals in the mesophotic zone: metabolic trade-offs between divergent *Symbiodinium* types. *Proc. Biol. Sci.* 278:1840–50
- Crandall JB, Teece MA, Estes BA, Manfrino C, Ciesla JH. 2016. Nutrient acquisition strategies in mesophotic hard corals using compound specific stable isotope analysis of sterols. *J. Exp. Mar. Biol. Ecol.* 474:133–41
- de Goeij JM, Lesser MP, Pawlik JR. 2017. Nutrient fluxes and ecological functions of coral reef sponges in a changing ocean. In *Climate Change, Ocean Acidification and Sponges*, ed. JL Carballo, JJ Bell, pp. 373–410. Cham, Switz.: Springer Int.
- Diaz MC, van Soest RWM, Gochfeld DJ, Olson JB, Slattery M, et al. 2010. A checklist from shallow and mesophotic marine sponges from Little Cayman Island. Poster presented at the International Sponge Symposium, Girona, Spain, September 20–24, 2010
- Ducklow HW. 1990. The biomass, production, and fate of bacteria in coral reefs. In *Coral Reefs*, ed. Z Dubinski, pp. 265–89. Amsterdam: Elsevier
- Einbinder S, Gruber DF, Salomon E, Liran O, Keren N, et al. 2016. Novel adaptive photosynthetic characteristics of mesophotic symbiotic microalgae within the reef-building coral, *Stylophora pistillata*. *Front. Mar. Sci.* 3:195
- Einbinder S, Mass T, Brokovich E, Dubinsky Z, Erez J, et al. 2009. Changes in morphology and diet of the coral *Stylophora pistillata* along a depth gradient. *Mar. Ecol. Prog. Ser.* 381:167–74
- Eyal G, Wiedenmann J, Grinblat M, D'Angelo C, Kramarsky-Winter E, et al. 2015. Spectral diversity and regulation of coral fluorescence in a mesophotic reef habitat in the Red Sea. *PLOS ONE* 10:e0128697
- Eyal-Shaham L, Eyal G, Tamir R, Loya Y. 2016. Reproduction, abundance and survivorship of two *Alveopora* spp. in the mesophotic reefs of Eilat, Red Sea. *Sci. Rep.* 6:20964
- Ezzat L, Fine M, Maguer J-F, Grover R, Ferrier-Pagès C. 2017. Carbon and nitrogen acquisition in shallow and deep holobionts of the scleractinian coral *S. pistillata*. *Sci. Rep.* 4:102
- Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pol. Bull.* 50:125–46
- Ferrier-Pagès C, Gattuso J-P. 1998. Biomass, production and grazing rates of the pico-and nanoplankton in coral reef waters (Myako Island, Japan). *Microb. Ecol.* 35:46–57
- Frade PR, De Jongh F, Vermeulen F, Van Bleijswijk J, Bak RPM. 2008. Variation in symbiont distribution between closely related coral species over large depth ranges. *Mol. Ecol.* 17:691–703
- Gilmore AM, Larkum AW, Salih A, Itoh S, Shibata Y, et al. 2003. Simultaneous time resolution of the emission spectra of fluorescent proteins and zooxanthellar chlorophyll in reef-building corals. *Photochem. Photobiol.* 77:515–23
- Glasl B, Pongaerts P, Elisabeth NH, Hoegh-Guldberg, Herndl GJ, et al. 2017. Microbiome variation in corals with distinct depth distribution ranges across a shallow–mesophotic gradient (15–85 m). *Coral Reefs* 36:447–52

- Goldstein ED, D'Alessandro EK, Reed J, Sponaugle S. 2016b. Habitat availability and depth-driven population demographics regulate reproductive output of a coral reef fish. *Ecosphere* 7:e01542
- Goldstein ED, D'Alessandro EK, Sponaugle S. 2016a. Demographic and reproductive plasticity across the depth distribution of a coral reef fish. *Sci. Rep.* 6:34077
- Grigg RW. 2006. Depth limit for reef building corals in the Au'au Channel, S.E. Hawaii. *Coral Reefs* 25:77–84
- Haas AF, Nelson CE, Rohwer F, Wegley-Kelly L, Quistad SD, et al. 2013. Influence of coral and algal exudates on microbially mediated reef metabolism. *PeerJ* 1:e108
- Hentschel U, Piel J, Degnan SM, Talor MW. 2012. Genomic insights into the marine sponge microbiome. *Nat. Rev. Microbiol.* 10:641–54
- Hernandez-Agreda A, Leggat W, Bongaerts P, Ainsworth T. 2016. The microbial signature provides insights into the mechanistic basis of coral success across reef habitats. *mBio* 7:e00560
- Hoeksema B, Bongaerts P, Baldwin CC. 2017. High coral cover at lower mesophotic depths: a dense *Agaricia* community at the leeward side of Curaçao, Dutch Caribbean. *Mar. Biodiv.* 47:67–70
- Holstein DM, Paris CB, Vaz AC, Smith TB. 2016b. Modeling vertical coral connectivity and mesophotic refugia. *Coral Reefs* 35:23–57
- Holstein DM, Smith TB, Gyory J, Paris CB. 2015. Fertile fathoms: deep reproductive refugia for threatened shallow corals. *Sci. Rep.* 5:12407
- Holstein DM, Smith TB, Paris CB. 2016a. Depth-independent reproduction in the reef coral *Porites astreoides* from shallow and mesophotic zones. *PLOS ONE* 11:e0146068
- Hurley KKC, Timmer MA, Godwin LS, Copus JM, Skillings DJ, et al. 2016. An assessment of shallow and mesophotic reef brachyuran crab assemblages on the south shore of O'ahu, Hawai'i. *Coral Reefs* 35:103–12
- Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, et al. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29:255–75
- Kahng SE, Hochberg EJ, Apprill A, Wagner A, Luck DG, et al. 2012. Efficient light harvesting in deep-water zooxanthellate corals. *Mar. Ecol. Prog. Ser.* 455:65–77
- Kahng SE, Kelley CD. 2007. Vertical zonation of megabenthic taxa on a deep photosynthetic reef (50–140 m) in the Au'au Channel, Hawaii. *Coral Reefs* 26:679–87
- Laverick JH, Andradi-Brown DA, Rogers AD. 2017. Using light-dependent scleractinia to define the upper boundary of mesophotic coral ecosystems on the reefs of Utila, Honduras. *PLOS ONE* 12:e0183075
- Leichter JJ, Genovese SJ. 2006. Intermittent upwelling and subsidized growth of the scleractinian coral *Madariscus mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. *Mar. Ecol. Prog. Ser.* 316:95–103
- Leichter JJ, Stewart HL, Miller SL. 2003. Episodic nutrient transport to Florida coral reefs. *Limnol. Oceanogr.* 48:1394–407
- Lesser MP. 2006. Benthic–pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. *J. Exp. Mar. Biol. Ecol.* 328:277–88
- Lesser MP. 2011. Coral bleaching: causes and mechanisms. In *Coral Reefs: An Ecosystem in Transition*, ed. Z Dubinsky, N Stamler, pp. 405–20. Dordrecht, Neth.: Springer
- Lesser MP, Slattery M. 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biol. Invasions* 13:1855–68
- Lesser MP, Slattery M, Leichter JJ. 2009. Ecology of mesophotic coral reefs. *J. Exp. Mar. Biol. Ecol.* 375:1–8
- Lesser MP, Slattery M, Stat M, Ojimi M, Gates RD, et al. 2010. Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. *Ecology* 91:990–1003
- Liddell WD, Avery WE. 2000. Temporal change in hard substrate communities 10–250 m, the Bahamas. *Proc. 10th Intl. Coral Reef Symp.* 2:1053–58
- Liddell WD, Avery WE, Ohlhorst SL. 1997. Patterns of benthic community structure, 10–250 m, the Bahamas. *Proc. 8th Int. Coral Reef Symp.* 1:437–42
- Liddell WD, Ohlhorst SL. 1988. Hard substrata community patterns, 1–120 M, North Jamaica. *Palaios* 3:413–23
- Littler MM, Littler DS, Blair SM, Norris JN. 1986. Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance, and primary productivity. *Deep-Sea Res. Part A* 33:881–92

- Locker SD, Armstrong RA, Battista TA, Rooney JJ, Sherman C, et al. 2010. Geomorphology of mesophotic coral ecosystems: current perspectives on morphology, distribution, and mapping strategies. *Coral Reefs* 29:329–45
- Loya Y, Eyal G, Trebitz T, Lesser MP, Appeldorn R. 2016. Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. *Coral Reefs* 35:1–9
- MacDonald C, Bridge TCL, Jones GP. 2016. Depth, bay position and habitat structure as determinants of coral reef fish distributions: Are deep reefs a potential refuge? *Mar. Ecol. Prog. Ser.* 561:217–31
- Macintyre IG, Rutzler K, Norris JN, Smith KP, Cairns SD, et al. 1991. An early Holocene reef in the Western Atlantic: submersible investigations of a deep relict reef off the west coast of Barbados, WI. *Coral Reefs* 10:167–74
- Mass T, Einbinder S, Brokovich E, Shashar N, Vago R, et al. 2007. Photoacclimation of *Stylophora pistillata* to light extremes: metabolism and calcification. *Mar. Ecol. Prog. Ser.* 334:93–102
- Mass T, Kline D, Roopin M, Veal CJ, Cohen S, et al. 2010. The spectral quality of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata* colonies from different depths in the Red Sea. *J. Exp. Biol.* 213:4084–91
- Matz MV, Marshall NJ, Vorobyev CH. 2006. Symposium in-print: green fluorescent protein and homologs. Are corals colorful? *Photochem. Photobiol.* 82:345–50
- Mazel CH, Lesser MP, Gorbunov MY, Barry TM, Farrell JH, et al. 2003. Green-fluorescent proteins in Caribbean corals. *Limnol. Oceanogr.* 48:402–11
- McMahon KW, Thorrold SR, Houghton LA, Berumen ML. 2016. Tracing carbon flow through coral reef food webs using compound-specific stable isotopic approach. *Oecologia* 180:809–21
- Mobley CD, Sundman LK. 2003. Effects of optically shallow bottoms on upwelling radiances: Inhomogeneous and sloping bottoms. *Limnol. Oceanogr.* 48:239–336
- Montaggioni L. 2005. History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. *Earth Sci. Rev.* 71:1–75
- Morrow KM, Fiore C, Lesser M. 2016. Environmental drivers of microbial community shifts in the giant barrel sponge, *Xestospongia muta*, over a shallow to mesophotic depth gradient. *Environ. Microbiol.* 18:2025–38
- Muscantine L, Porter J, Kaplan I. 1989. Resource partitioning by reef corals as determined from stable isotope composition. *Mar. Biol.* 100:185–93
- Nir O, Gruber DF, Einbinder S, Kark S, Tchernov D. 2011. Changes in scleractinian coral *Seriatopora hystrix* morphology and its endocellular *Symbiodinium* characteristics along a bathymetric gradient from shallow to mesophotic reef. *Coral Reefs* 30:1089–100
- Olson JB, Gao X. 2013. Characterizing the bacterial associates of three Caribbean sponges along a gradient from shallow to mesophotic depths. *FEMS Microbiol. Ecol.* 85:74–84
- Olson JB, Kellogg CA. 2010. Microbial ecology of corals, sponges, and algae in mesophotic coral environments. *FEMS Microbiol. Ecol.* 73:17–30
- Pinheiro HT, Goodbody-Gringley G, Jessup ME, Shephard B, Chequer AD, et al. 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual census in two Caribbean locations. *Coral Reefs* 35:139–51
- Pochon X, Forsman ZH, Spalding HL, Padilla-Gamino JL, Smith CM, et al. 2015. Depth specialization in mesophotic corals (*Leptoseris* spp.) and associated algal symbionts in Hawai'i. *R. Soc. Open Sci.* 2:140351
- Prasertia R, Sinniger F, Harii S. 2016. Gametogenesis and fecundity of *Acropora tenella* (Brook 1892) in a mesophotic coral ecosystem in Okinawa, Japan. *Coral Reefs* 35:53–62
- Prasertia R, Sinniger F, Hashizume K, Harii S. 2017. Reproductive biology of the deep brooding coral *Seriatopora hystrix*: implications for shallow reef recovery. *PLOS ONE* 12:e0177034
- Pyle RL, Boland R, Bolick H, Bowen BW, Bradley CJ. 2016. A comprehensive investigation of mesophotic coral ecosystems in the Hawaiian Archipelago. *PeerJ* 4:e2475
- Reaka ML, Altman S, Ballantine DL, Dowgiallo MJ, Felder DL, et al. 2010. Biodiversity of mesophotic coral ecosystems. *Coral Reefs* 29:361–67
- Reed JK, Pomponi SA. 1997. Biodiversity and distribution of deep and shallow water sponges in the Bahamas. *Proc. 8th Int. Coral Reef Symp.* 2:1387–92
- Ribes M, Coma R, Atkinson MJ, Kinzie RA III. 2003. Particle removal by coral reef communities: Picoplankton is a major source of nitrogen. *Mar. Ecol. Prog. Ser.* 257:13–23

- Ribes M, Coma R, Atkinson MJ, Kinzie RA III. 2005. Sponges and ascidians control removal of particulate organic nitrogen from coral reef water. *Limnol. Oceanogr.* 50:1480–89
- Rix L, de Goeij JM, van Oevelen D, Struck U, Al-Horani FA, et al. 2017. Differential recycling of coral and algal dissolved organic matter via the sponge loop. *Funct. Ecol.* 31:778–89
- Rooney J, Donham E, Montgomery A, Spalding H, Parrish F, et al. 2010. Mesophotic coral ecosystems in the Hawaiian Archipelago. *Coral Reefs* 29:361–67
- Roth MS, Padilla-Gamiño JL, Pochon X, Bidigare RR, Gates RD, et al. 2015. Fluorescent proteins in dominant mesophotic reef-building corals. *Mar. Ecol. Prog. Ser.* 521:63–79
- Runcie JW, Gurgel CFD, Mcdermid KJ. 2008. In situ photosynthetic rates of tropical marine macroalgae at their lower depth limit. *Eur. J. Phycol.* 43:377–88
- Schmidt GM, Wall M, Taylor M, Jantzen C, Richter C. 2016. Large-amplitude internal waves sustain coral reef health during thermal stress. *Coral Reefs* 35:869–81
- Schlichter D, Fricke W, Weber W. 1986. Light harvesting by wavelength transformation in a symbiotic coral of the Red Sea twilight zone. *Mar. Biol.* 91:403–7
- Schlichter D, Meier U, Fricke HW. 1994. Improvement of photosynthesis in zooxanthellate corals by auto-fluorescent chromatophores. *Oecologia* 99:124–31
- Semmler RF, Hoot WC, Reaka ML. 2017. Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs. *Coral Reefs* 36:433–44
- Serrano X, Baums IB, O'Reilly K, Smith TB, Jones RJ, et al. 2014. Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. *Mol. Ecol.* 23:4226–40
- Sherman C, Nemeth M, Ruíz H, Bejarano I, Appeldoorn R, et al. 2010. Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. *Coral Reefs* 29:347–60
- Sherman C, Schmidt W, Appeldoorn R, Hutchinson Y, Ruiz H, et al. 2016. Sediment dynamics and their potential influence on insular-slope mesophotic coral ecosystems. *Cont. Shelf Res.* 129:1–9
- Shlesinger T, Grinblat M, Rapuano H, Amit T, Loya Y. 2018. Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. *Ecology* 99:421–37
- Slattery M, Gochfeld DJ, Diaz CM, Thacker RW, Lesser MP. 2016. Variability in chemical defense across a shallow to mesophotic depth gradient in the Caribbean sponge *Plakortis angulospiculatus*. *Coral Reefs* 35:11–22
- Slattery M, Lesser MP. 2012. Mesophotic coral reefs: a global model of community structure and function. *Proc. 12th Intl. Coral Reef Symp.* 1:9–13
- Slattery M, Lesser MP. 2014. Allelopathy in the tropical alga *Lobophora variegata* (Phaeophyceae): mechanistic basis for a phase shift on mesophotic coral reefs? *J. Phycol.* 50:493–505
- Slattery M, Lesser MP. 2015. Trophic ecology of sponges from shallow to mesophotic depths (3 to 150 m): comment on Pawlik et al. 2015. *Mar. Ecol. Prog. Ser.* 527:275–79
- Slattery M, Lesser MP. 2019. The Bahamas and Cayman Islands. In *Mesophotic Coral Ecosystems*, ed. Y Loya, K Puglise, T Bridge. New York: Springer
- Slattery M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ. 2011. Connectivity and stability of mesophotic coral reefs. *J. Exp. Mar. Biol. Ecol.* 408:32–41
- Smith EG, D'Angelo CD, Salih A, Wiedenmann J. 2013. Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae. *Coral Reefs* 32:463–74
- Smith EG, D'Angelo C, Sharon Y, Tchernov D, Wiedenmann J. 2017. Acclimatization of symbiotic corals to mesophotic light environments through wavelength transformation by fluorescent protein pigments. *Proc. R. Soc. B* 284:20170320
- Smith TB, Brandtneris VW, Canals M, Brandt ME, Martens J, et al. 2016b. Potential structuring forces on a shelf edge upper mesophotic coral ecosystem in the US Virgin Islands. *Front. Mar. Sci.* 3:115
- Smith TB, Gyory J, Brandt ME, Miller WJ, Jossart J, et al. 2016a. Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Glob. Change Biol.* 22:2756–65
- Steinert G, Taylor MW, Deines P, Simister RL, de Voogd NJ, et al. 2016. In four shallow and mesophotic tropical reef sponges from Guam the microbial community largely depends on host identity. *PeerJ* 4:e1936
- Tanaka Y, Miyajima T, Watanabe A, et al. 2011. Distribution of dissolved organic carbon and nitrogen in a coral reef. *Coral Reefs* 30:533–41

- Tenggardjaja K, Bowen B, Bernardi G. 2014. Vertical and horizontal genetic connectivity in *Chromis verater*, an endemic damselfish found on shallow and mesophotic reefs in the Hawaiian Archipelago and adjacent Johnston Atoll. *PLOS ONE* 9:e115493
- Torréton J-P, Pages J, Dufour P, Cauwet G. 1997. Bacterioplankton carbon growth yield and DOC turnover in some coral reef lagoons. *Proc. 8th Int. Coral Reef Symp.* 1:947–52
- Turner JA, Babcock RC, Hovey R, Kendrick GA. 2017. Deep thinking: a systematic review of mesophotic coral ecosystems. *ICES J. Mar. Sci.* 74:2309–20
- van Oppen MJH, Bongaerts P, Underwood JN, Peplow LM, Cooper TF. 2011. The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. *Mol. Ecol.* 20:1647–60
- van Soest RWM, Boury-Esnault N, Vacelot J, Dohrmann M, Erpenbeck D, et al. 2012. Global diversity of sponges. *PLOS ONE* 7:e35105
- Vermeij MJA, Bak RPM. 2002. How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. *Mar. Ecol. Prog. Ser.* 233:105–16
- Vize PD. 2006. Deepwater broadcast spawning by *Montastraea cavernosa*, *Montastraea franksi*, and *Diploria strigosa* at the Flower Garden Banks, Gulf of Mexico. *Coral Reefs* 25:169–71
- Wangpraseurt D, Larkum AWD, Ralph PJ, Kühl M. 2012. Light gradients and optical microniches in coral tissues. *Front. Microbiol.* 3:316
- Warner ME, Suggett DJ. 2016. The photobiology of *Symbiodinium* spp. linking physiological diversity to the implications of stress and resilience. In *The Cnidaria, Past, Present and Future*, ed. S Goffredo, Z Dubinsky, pp. 489–509. Cham, Switz.: Springer Int.
- Weinstein DK, Smith TB, Klaus JS. 2014. Mesophotic bioerosion: variability and structural impact on U.S. Virgin Island deep reefs. *Geomorphology* 222:14–24
- Wijgerde T, van Melis A, Silva CIF, Leal MC, Vogels L, et al. 2014. Red light represses the photophysiology of the scleractinian coral *Stylophora pistillata*. *PLOS ONE* 9:e92781
- Wolanski E, Colin P, Naithani J, Deleersnijder E, Golbuu Y. 2004. Large amplitude, leaky, island-generated, internal waves around Palau, Micronesia. *Estuar. Coast. Shelf Sci.* 60:705–16
- Ziegler M, Roder CM, Büchel C, Voolstra CR. 2015. Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology. *Front. Mar. Sci.* 2:4



Contents

Behavioral Isolation and Incipient Speciation in Birds <i>J. Albert C. Uy, Darren E. Irwin, and Michael S. Webster</i>	1
The Ecology and Evolution of Alien Plants <i>Mark van Kleunen, Oliver Bossdorf, and Wayne Dawson</i>	25
Biodiversity and Functional Ecology of Mesophotic Coral Reefs <i>Michael P. Lesser, Marc Slattery, and Curtis D. Mobley</i>	49
Evolutionary Conflict <i>David C. Queller and Joan E. Strassmann</i>	73
Evaluating Model Performance in Evolutionary Biology <i>Jeremy M. Brown and Robert C. Thomson</i>	95
Plant Secondary Metabolite Diversity and Species Interactions <i>André Kessler and Aino Kalske</i>	115
Variation and Evolution of Function-Valued Traits <i>Richard Gomulkiewicz, Joel G. Kingsolver, Patrick A. Carter, and Nancy Heckman</i>	139
Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates <i>Susanne S. Renner and Constantin M. Zohner</i>	165
Bivalve Impacts in Freshwater and Marine Ecosystems <i>Caryn C. Vaughn and Timothy J. Hoellein</i>	183
Uses and Misuses of Environmental DNA in Biodiversity Science and Conservation <i>Melania E. Cristescu and Paul D.N. Hebert</i>	209
Frontiers in Metapopulation Biology: The Legacy of Ilkka Hanski <i>Otso Ovaskainen and Marjo Saastamoinen</i>	231
Integrating Networks, Phylogenomics, and Population Genomics for the Study of Polyploidy <i>Paul D. Blischak, Makenzie E. Mabry, Gavin C. Conant, and J. Chris Pires</i>	253

Ecological Response to Permafrost Thaw and Consequences for Local and Global Ecosystem Services <i>Edward A.G. Schuur and Michelle C. Mack</i>	279
(Non)Parallel Evolution <i>Daniel I. Bolnick, Rowan D.H. Barrett, Krista B. Oke, Diana J. Rennison, and Yoel E. Stuart</i>	303
Mechanisms of Plastic Rescue in Novel Environments <i>Emilie C. Snell-Rood, Megan E. Kobiela, Kristin L. Sikkink, and Alexander M. Shephard</i>	331
Challenging Dogma Concerning Biogeographic Patterns of Antarctica and the Southern Ocean <i>Kenneth M. Halanych and Andrew R. Mabon</i>	355
Dinosaur Macroevolution and Macroecology <i>Roger B.J. Benson</i>	379
Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes <i>Joshua P. Schimel</i>	409
Using Genomic Data to Infer Historic Population Dynamics of Nonmodel Organisms <i>Annabel C. Beichman, Emilia Huerta-Sanchez, and Kirk E. Lohmueller</i>	433
The Contemporary Evolution of Fitness <i>Andrew P. Hendry, Daniel J. Schoen, Matthew E. Wolak, and Jane M. Reid</i>	457
The Deep Past Controls the Phylogenetic Structure of Present, Local Communities <i>Pille Gerhold, Marcos B. Carlucci, Șerban Procheș, and Andreas Prinzing</i>	477
Development and Evolutionary Constraints in Animals <i>Frietson Galis, Johan A.J. Metz, and Jacques J.M. van Alphen</i>	499
Indexes	
Cumulative Index of Contributing Authors, Volumes 45–49	523
Cumulative Index of Article Titles, Volumes 45–49	527

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://www.annualreviews.org/errata/ecolsys>