Mesophotic Coral Ecosystems

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Abstract

Coral reefs are among the most biodiverse and productive ecosystems on the planet. However, our understanding of these ecosystems and their inhabitants has primarily been gleaned from shallow-water studies (<40 m), while light-dependent corals and the ecosystems they support extend much deeper (e.g., 150 m in some locations). In recent decades, coral reef ecosystems have substantially declined globally due to direct and indirect anthropogenic activities that differentially impact shallow-water habitats. This decline has led to the...
suggestion that surface-oriented stressors and disturbances may be mediated by
depth. The role of deeper coral reef ecosystems, called mesophotic coral ecosystems (MCEs), as refugia for shallow-water species has fueled new investigations
into this realm facilitated in part by advances in diving technology and remote
observation platforms. The increasing access to these poorly studied ecosystems
is revealing new insights into the biodiversity of MCEs as well as that of shallow
coral reefs. The upper mesophotic community is largely an extension of the
shallow-water coral reef community, much of the flora and fauna are shared
across these depths. However, there is a transition with increasing depth to a
lower mesophotic community dominated by flora and fauna that are largely
endemic to this zone. Investigations are also expanding depth and geographic
ranges for many species, and new species are being discovered regularly in
MCEs. However, caution must be taken when generalizing due to the geograph-
ically and numerically limited nature of these studies.

Keywords
Mesophotic coral ecosystems (MCEs) • Biodiversity • Deep coral reef • Commu-
nity structure • Endemism • Depth refugia

1 Introduction

Mesophotic coral ecosystems (MCEs) are light-dependent coral reef communities
starting at 30–40 m and extend to the bottom of the photic zone, which varies by
location and may reach depths of over 150 m in some regions (reviewed in Baker
et al. 2016). By virtue of the distribution of obligate zooxanthellate corals, these
communities are restricted to warm-water habitat (Kleypas et al. 1999). While high-
latitudinal MCE investigations are sparse, the latitudinal extent of MCEs (e.g., Kure
Atoll, Lord Howe Island, Bermuda) appears to mirror much of the range of shallow-
water coral reefs (reviewed in Linklater 2016; Linklater et al. 2016). MCEs represent
a direct extension of shallow-water reef ecosystems, which support a diverse abundance
of habitat-building taxa including corals, crustose coralline algae, macroalgae,
and sponges (reviewed in Kahng et al. 2010, 2014). The upper depth limit attributed
to MCEs (30–40 m) corresponds to the depth limit of conventional scuba diving and
a vast majority of coral reef research but does not represent a static physiological
boundary for marine organisms. Due to the logistical and safety constraints of
conducting research at these depths, MCE studies have lagged far behind shallow-
water reef studies (e.g., Pyle 1996).

The lower depth limit of MCEs varies by location primarily due to site-specific
attenuation of light and in some cases temperature regime (Kahng et al. 2010, 2014).
While MCEs remain largely unexplored in many regions, especially in many parts
of the Indo-Pacific, mesophotic investigations have accelerated in recent years (Loya
et al. 2016), thereby providing new insights into the biodiversity of this largely
understudied marine habitat. The recent growth in mesophotic studies has been aided
in part by advances in technology and by a growing interest in the potential role of MCEs as refugia for shallow-water reef fauna (i.e., the deep reef refugia hypothesis) which are increasingly being subject to habitat degradation (Glynn 1996; Bellwood et al. 2004; Bongaerts et al. 2010a).

This chapter provides an overview of the known patterns of MCE biodiversity to date. Caution against premature generalizations is advised due to the uneven nature of available studies across locations. Historically, the Caribbean region has been more thoroughly surveyed and studied than other regions. In recent years, a growing number of studies from Hawaii, the Great Barrier Reef, the Red Sea, and Brazil are adding fresh insights into this understudied realm. For purposes of this chapter, the terms upper and lower mesophotic refer to depth zones bordering shallow-water coral reef ecosystems and the depth zone bordering lower limit of light-dependent coral communities, respectively. The depth gradient of transition between these two communities varies by location without a uniform boundary between the two.

2 Habitat-Forming Megabenthos

2.1 Phototrophic Taxa

The habitat-forming megabenthic fauna of the upper mesophotic is largely a continuation of the shallow-water coral reef community. Many of the coral species that dominate the substrate in shallow waters can also be observed at mesophotic depths (>40 m), albeit at lower relative abundance (e.g., Van den Hoek et al. 1978; Kahng and Kelley 2007; Wagner et al. 2014; Muir et al. 2015). With increasing depth, downwelling, light irradiance, and wave energy attenuate. This vertical gradient leads to changes in coral morphology within species and vertical zonation of the dominant coral taxa (reviewed in Kahng et al. 2010). For species found across a wide depth gradient, a flattening of colony morphology occurs at greater depths. In branching and foliose corals, branches become thinner and more widely spaced, thereby reducing self-shading and facilitating ventilation in hydrodynamic conditions with lower energy (Mass et al. 2007; Hoogenboom et al. 2008). In general, dominant shallow-water species with branching, massive, and other robust morphologies are eventually replaced by more delicate, foliose, and platelike species at deeper depths (e.g., Kühlmann 1983; Fricke and Schumacher 1983); however, branching corals do extend well into the mesophotic zone (e.g., Muir et al. 2015).

The following zooxanthellate anthozoan taxa have been reported as abundant or dominant at mesophotic depths in some locations (Kinzie 1973; Zlatarski and Estalella 1982; Sanchez 1999; Zlatarski 2007; Kahng et al. 2010, 2014, and references therein; Bridge et al. 2012a; Friedlander et al. 2014; Magalhães et al. 2015; Eyal et al. 2016; Eyal-Shaham et al. 2016). To date, mutualistic endosymbiosis with *Symbiodinium* has only been reported for a single antipatharian species from Indonesia (*Cirrhipathes* sp., Bo et al. 2011).
Indo-Pacific
- Antipatharia: *Cirrhipathes*
- Hydrozoa: Milleporidae (*Millepora*), Stylasteridae (*Distichopora*)
- Octocorallia: Alcyoniidae (*Sarcophyton*), Xeniidae (*Cespitularia*)
- Zoantharia: *Palythoa*
- Actiniaria: *Entacmaea*

Western Atlantic
- Scleractinia: Agariciidae (*Agaricia, Helioseris*), Astrocoeniidae (*Madracis, Stephanocenia*), Faviidae (*Solenastrea*), Meandrinidae (*Dichocoenia*), Montastreaidae (*Montastrea*), Mussidae (*Myctophyllia, Scolymia, Colpophyllia, Manicina*), Poritidae (*Porites*),
- Octocorallia: Gorgoniidae (*Pseudopterogorgia*), Plexauridae (*Eunicea, Muricea, Plexaura, Plexaurella*)
- Hydrozoa: *Millepora* (Milleporidae)

At the deepest depths in the lower mesophotic, the coral community bears little resemblance to shallow-water coral reefs. Obligate zooxanthellate octocorals appear to be absent in the lower mesophotic due to higher sensitivity to light limitation and less efficient light harvesting than their scleractinian counterparts (Kinzie 1973; Enriquez et al. 2005). In both the Indo-Pacific and Western Atlantic, species in the family Agariciidae have been reported as depth specialists dominating the coral community, presumably due to superior adaptations to the environment at depth (Zlatarski and Estalella 1982; Kahng et al. 2010, 2014; Hoeksema et al. 2016). The Indo-Pacific coral species capable of inhabiting the deepest depths (e.g., *Leptoseris hawaiiensis, L. fragilis, L. scabra*) appear to be depth specialists and are typically not observed in shallow water (Fricke et al. 1987; Luck et al. 2013; Pochon et al. 2015). However, in the Caribbean, a few coral species (e.g., *Montastrea cavernosa, Madracis pharensis, M. senaria*) appear to be depth generalists, able to inhabit both shallow water (<5 m) and the lower mesophotic zone (60–90 m) (Frade et al. 2008a; Lesser et al. 2010; Bongaerts et al. 2015a). The depth range of obligate zooxanthellate corals extends significantly deeper in the Indo-Pacific compared to the Western Atlantic, likely due in part to superior optical water quality associated with more oligotrophic conditions (Kahng et al. 2010; Baker et al. 2016).

To date, the deepest in situ observations of obligate zooxanthellate corals are small colonies of *Leptoseris hawaiiensis* growing widely spaced on barren fossil reef at 165 m at Johnston Atoll and at 153 m off the southwest coast of the Big Island of Hawaii (Maragos and Jokiel 1986; Kahng and Maragos 2006) (Fig. 1). These observations suggest stunted growth consistent with marginal habitat and light limitation of obligate photosynthetic organisms. Although more extreme depth ranges have been
reported in the literature, caution must be applied when interpreting early records that are based solely on dredge hauls, as the exact depth that specimens were collected by dredges is often unknown (Kahng and Maragos 2006).

Obligate zooxanthellate octocorals and other anthozoan taxa do not appear to extend as deep as their scleractinian counterparts, nor do they appear to be as abundant in the lower mesophotic (reviewed in Kahng et al. 2010; Kinzie 1970; Bridge et al. 2012a,b). In contrast, phototrophic sponges have been reported as abundant at mesophotic depths (e.g., *Carteriospongia*) in the Indo-Pacific (Bridge and Guinotte 2013). While less studied than their anthozoan counterparts, phototrophic sponges are potentially widely distributed at mesophotic depths in the Indo-Pacific (Kahng et al. 2014 and references therein) with varying levels of contribution from their cyanobacterial symbionts (Keesing et al. 2012). However, phototrophic sponges are much less prevalent in the Caribbean and have not been reported as common at mesophotic depths (e.g., Wilkinson and Cheshire 1990). Given the more oligotrophic conditions associated with many Indo-Pacific reefs, food limitation is likely responsible for the greater prevalence of phototrophic sponges and lower biomass of heterotrophic sponges compared to Caribbean reefs, where food may not be limiting (reviewed in Pawlik et al. 2015a,b; Slattery and Lesser 2015).

### 2.2 Symbiont Biodiversity

For *Symbiodinium* found in MCEs, there are both depth-generalist subclades with broad depth distributions and depth-specialist subclades which may be adapted to...
the deep-reef environment (Frade et al. 2008a, b; Chan et al. 2009; Lesser et al. 2010; Bongaerts et al. 2011a; Pochon et al. 2015). Since biogeographic and habitat-specific host-symbiont associations have been reported for several coral species (Iglesias-Prieto et al. 2004; Bongaerts et al. 2010a, b, 2013; Thornhill et al. 2014), the discovery of depth-specialist Symbiodinium types is not unexpected. Given the energetic dependence of corals on autotrophy and the photo-physiological differences associated with Symbiodinium genotypes, the vertical zonation of Symbiodinium with depth could contribute adaptive value to the coral host (Iglesias-Prieto and Trench 1994; Hennige et al. 2010). For corals with conserved, vertical symbiont acquisition, these patterns may also reflect coevolutionary processes of both symbionts and hosts (Bongaerts et al. 2013).

In addition to depth-specialist subclades not found in shallow water, depth-related partitioning of Symbiodinium types has been reported within several depth-generalist coral species spanning across mesophotic depths (Lesser et al. 2010; Cooper et al. 2011; Schizas et al. 2012; Bongaerts et al. 2013). This partitioning includes depth-associated changes in host-symbiont associations in terms of subclades and their relative frequencies (Bongaerts et al. 2015b). Most depth-generalist coral species host distinct endosymbionts at different ends of their depth spectrums (Rowan and Knowlton 1995; Toller et al. 2001; Frade et al. 2008c; Bongaerts et al. 2015b). In Curacao, depth-generalist coral species with symbiont zonation exhibit significantly broader depth distributions than those without, highlighting the potential role of symbiont zonation in shaping the vertical distributions of the coral host (Bongaerts et al. 2015b). However, in some cases the depth-related partitioning of Symbiodinium types is only localized within a host species, as Symbiodinium types found at the lower end of one coral species’ depth distribution may be found in shallow water in another coral species (Bongaerts et al. 2015a, b).

Depth-generalist Symbiodinium types are also common in MCEs (Bongaerts et al. 2011a). In some cases, depth-specialist coral species (e.g., Leptoseris spp.) host Symbiodinium types which are also commonly found in shallow water in other coral species (Chan et al. 2009; Bongaerts et al. 2011b; Pochon et al. 2015). For several depth-generalist coral species, the same Symbiodinium types can be maintained across a large depth range (Bongaerts et al. 2011a; Cooper et al. 2011; Nir et al. 2011; Bongaerts et al. 2015b; Ziegler et al. 2015).

In general, most reef-building corals host a single Symbiodinium type which does not appear to change over time (Goulet 2006). In the Great Barrier Reef, reciprocal transplants of Seriatopora hystrix colonies (which vertically transmit symbionts) between depth-partitioned host and symbiont genotypes did not result in novel host-symbiont recombinations after 14 months (Bongaerts et al. 2011c). Whether depth-related Symbiodinium partitioning within a species with horizontal transmission would be maintained after analogous reciprocal transplants is not yet known.

The substantial overlap in Symbiodinium community between shallow-water reefs and MCEs reinforces the idea of the upper mesophotic as a transition zone between the shallow and lower mesophotic reef (Kahng et al. 2010, 2014). However, in the lower mesophotic zone, there is growing evidence for specialized host-endosymbiont associations including Symbiodinium types either not observed or
rarely observed in shallow water (Bongaerts et al. 2015b). Additional sampling of MCEs’ Symbiodinium types will likely uncover additional, depth-specialist Symbiodinium types, novel host-symbiont associations, polygamy in previously reported host-specialists, and bathymetric range extensions (Bongaerts et al. 2011a, 2015b).

2.3 Benthic Macroalgae

Benthic macroalgae are important components of MCEs and provide critical ecological functions to coral reef communities including primary productivity, substrate stabilization, carbonate sand production, and nutrient recycling and retention (Fong and Paul 2011). Benthic marine macroalgae are a highly diverse functional group comprised of members from at least four major Phyla including Cyanophyta (blue-green algae), Chlorophyta (green algae), Heterokontophyta (includes brown algae), and Rhodophyta (red algae) (Lee 2008). Most marine macroalgae require some form of hard substrata to settle, but some macroalgae, predominantly siphonaceous green algae (e.g., Halimeda, Caulerpa, Pennella, and Udotea), are able to establish in soft sediment using specialized rhizomes (Fong and Paul 2011). While exhibiting less habitat complexity than coral aggregations, rhodolith beds and algal meadows on soft substrate can provide habitat and trophic support for fishes and invertebrates (Foster et al. 2013). While less thoroughly studied than their coral counterparts, the following taxa of benthic macroalgae have been reported as abundant at mesophotic depths (reviewed in Kahng et al. 2010, 2014; Van den Hoek et al. 1978; Hillis-Colinvaux 1986a,b; Littler et al. 1986; Aponte and Ballantine 2001; Parrish and Bolland 2004; Culter et al. 2006; Peyton 2009; Bongaerts et al. 2011b; Littler and Littler 2012; Spalding 2012; Friedlander et al. 2014; Magalhães et al. 2015; Pyle et al. 2016a; Spalding et al. 2016):

**Indo-Pacific**
- Brown algae: Dictyota, Dictyopteris, Distromium, Padina
- Noncalcareous green algae: Avrainvillea, Codium, Caulerpa, Microdictyon, Neomeris, Ulva, Umbraulva
- Calcareous green algae: Halimeda, Udotea
- Noncalcareous red algae: Asparagopsis, Dasya, Veleroa
- Coralline red algae: Peyssonnelia, Mesophyllum, unspecified crustose coralline red algae

**Western Atlantic**
- Brown algae: Dictyota, Lobophora, Sargassum
- Noncalcareous green algae: Anadyomene, Avrainvillea, Cladophora, Microdictyon, Ostreobium, Plectonema, Verdigellas, unspecified filamentous algae, unspecified endolithic green algae
- Calcareous green algae: Halimeda, Pennella, Udotea
- Coralline red algae: Hydrolithon, Lithothamnion, Peyssonnelia, Sporolithon, unspecified crustose coralline red algae
Distinct depth zonation of dominant floral taxa has been reported from locations in both the Caribbean and the Indo-Pacific (Kahng et al. 2010 and references therein). In many locations, the mesophotic algal communities include species with wide bathymetric ranges which also extent to shallow waters (Agegian and Abbott 1985; Hillis-Colinvaux 1986b; Drew and Abel 1988; Hanisak and Blair 1988). However, in some locations, the mesophotic florae are dominated by depth-specialized species that are presumably adapted to deep-water environmental conditions (Agegian and Abbott 1985; Aponte and Ballantine 2001; Ballantine et al. 2015). In Hawaii, 80 m is associated with a peak in macroalgae diversity and change in community composition (Spalding 2012). In at least some Caribbean locations, the peak in algal diversity, abundance, and shifts in dominant florae occur at shallower depths in the upper mesophotic (Hanisak and Blair 1988; Ballantine et al. 2008; Leichter et al. 2008). Unlike slower-growing and longer-lived corals, mesophotic algal abundance and diversity can vary seasonally at the same location, as many species exhibit bloom dynamics (Cheney and Dyer 1974).

In general, the lower depth distributions of benthic macroalgal taxa in oligotrophic waters follow a pattern from brown (phaeophytes) to green (chlorophytes) to red (rhodophytes), suggesting phylogenetic chromatic adaptation to low light of a particular spectral character (Dring 1981; Kirk 2011). The lower depth limits for foliose macroalgae and encrusting coralline algae correspond to a light level of 0.10% and ~0.01% of surface irradiance, respectively (Markager and Sand-Jensen 1992; Runcie et al. 2008). In many locations, rhodolith beds (aggregations of unattached, nongeniculate coralline red algae) can dominate level substrate in the lower photic zone where water motion is sufficient to prevent burial from sedimentation (Foster 2001; Foster et al. 2013). The deepest in situ observations of benthic macroalgae is a crustose coralline alga at 312 m in the Pitcairn Islands (Friedlander et al. 2014).

While chromatic adaptation arguably plays a significant adaptive role in the lower photic zone, other factors affecting efficiency of light harvesting and energetic demands may also be significant. Various calcifying algal taxa (green and red) are commonly abundant at mesophotic depths (reviewed in Kahng et al. 2010; Kirk 2011). The predominance of calcareous and coralline algae in the lower photic zone suggests that the reflective properties of calcium carbonate may play a supporting role in enhancing light-harvesting efficiency in the lower photic zone (Kahng et al. 2012). In particular, crustose coralline algae is commonly reported as the dominant phototrophic taxa at the deepest depths (e.g., > 200 m) (Agegian and Abbott 1985; Littler et al. 1986; Markager and Sand-Jensen 1992; Aponte and Ballantine 2001; Runcie et al. 2008; Friedlander et al. 2014). The superior reflectance of calcite versus aragonite particularly of short wavelength light (i.e., UVA, blue) (Gaffey 1986) may play a role in the relative depth zonation of calcareous green algae (aragonitic) and coralline red algae (calcitic). Although non-calcifying, endolithic green algae (Ostreobium) have also been reported as abundant below 200 m (Aponte and Ballantine 2001). This group inhabits calcium carbonate substrate possibly benefiting from its reflective properties and exhibits very low metabolic activity rates in extremely low-light habitats (Shashar and Stambler 1992).
2.4 Azooxanthellate Benthic Taxa

In addition to phototrophic organisms, several obligate heterotrophic taxa create habitat for a myriad of associated species and are notably abundant at mesophotic depths including azooxanthellate octocorals, antipatharians, and sponges. In general, the relative abundance of obligate heterotrophic benthic fauna increases with depth, due in part to decreased space competition with phototrophic taxa which become light limited with depth (Kahng and Kelley 2007; Bridge et al. 2012a). In several locations around the world, azooxanthellate octocorals, antipatharians, and sponges have been seen to replace obligate photosynthetics at depths below ~50 m (Grigg 1965; Sanchez et al. 1998; Sanchez 1999; Wagner et al. 2012). While less thoroughly surveyed and reported than zooxanthellate corals, abundant heterotrophic megabenthic taxa have been reported from select mesophotic locations around the globe (reviewed in Kinzie 1973; Sanchez et al. 1998; Sanchez 1999; Kahng et al. 2010 an references therein; Rivero-Calle 2010; Bridge et al. 2012a; Magalhães et al. 2015; Wagner 2015).

Indo-Pacific

- Porifera: Dragmacidon, Prosuberites, Chondrosia, Batzella, Niphatidae
- Octocorallia: Annella, Carijoa, Dendronephthya, Junceella, other nephtheids
- Antipatharia: Antipathes, Cirrhipathes, Stichopathes, Myriopathes, Aphanipathes

Western Atlantic

- Porifera: Amphimedon, Aiolochroia, Agelas, Aplysina, Ceratoporella, Xestospongia
- Octocorallia: Anthothelidae (Diodogorgia), Ellisellidae (Ellisella, Nicella, Ctenocella), Plexauridae (Hypnogorgia)
- Antipatharia: Antipathes, Stichopathes, Cirrhipathes, Aphanipathes, Plumapathes
- Bryozoa: Margaretta

In the Caribbean, the abundance of heterotrophic sponges increases with depth and constitutes a major component of the MCE community (reviewed in Kahng et al. 2010). Despite their non-phototrophic nature, the species composition of the sponge community exhibits vertical zonation including many depth-specialist species restricted to either shallow water (<40 m) or deep water (>40 m) (Lehnert and Fischer 1999) (Fig. 2). Sponge communities are particularly diverse on the deep fore-reef escarpments at depths of 60–150 m, which are common to many Caribbean island reefs and include coralline sponges (formerly called sclerosponges) which secrete aragonite and contribute to reef formation at depth (Goreau and Land 1974; Ohlhorst and Liddell 1988).

In both the Indo-Pacific and Caribbean, antipatharians are a common component of MCEs (Sanchez et al. 1998; Sanchez 1999; Wagner et al. 2012; Wagner 2015). Similar to some deep-water gorgonians, the upper depth limit of arborescent antipatharians can be limited by strong turbulence and smothering by epiphytes, as well
as being outcompeted by faster-growing photosynthetic species (Grigg 1965; Kinzie 1973). While low densities of endosymbiotic Symbiodinium have been found in several deep-water antipatharians, they are not considered phototrophic (Wagner et al. 2011). Concomitant with the transition from phototrophic to heterotrophic dominance with increasing depth, the abundance of antipatharians increases below 40 m, and antipatharian abundance typically peaks deeper than their gorgonian counterparts (Kahng and Kelly 2007; Ballantine et al. 2008; Rivero-Calle 2010; Magalhães et al. 2015).

3 Coral Reef Fishes

Growing evidence from both the Indo-Pacific and Western Atlantic suggests that the upper mesophotic fish community is largely an extension of the shallow-water coral reef fish community. At Johnston Atoll, 76% of species recorded in the upper mesophotic (30–60 m) also occur in shallow water (Wagner et al. 2014). A similar pattern has been observed in the Hawaiian Archipelago, the Mariana Islands, and Puerto Rico (Parrish and Boland 2004; Garcia-Sais 2010; Bejarano et al. 2014; Kane et al. 2014; Lindfield et al. 2016; Pyle et al. 2016a, Fukunaga et al. 2016), although the depths at which these faunal breaks occur fluctuate by location (Pyle et al. 2016a and references herein).

In contrast, the available quantitative data to date suggests that lower mesophotic zones (~60–150 m) harbor fish assemblages which are largely unique (e.g., Thresher and Colin 1986; Bejarano et al. 2014; Pinheiro et al. 2016; Rosa et al. 2015). In the
Bahamas, Porter (1973) first reported the lower mesophotic zone as a unique zone, set apart from both the shallower water and abyssal communities and only occasionally visited by opportunistic species from above. In La Parguera, Puerto Rico, the abundance and frequency of most shallow fish decrease rapidly with depth, disappearing below 60 m (Bejarano et al. 2014). In mesophotic surveys of Bermuda and Curacao, 71% of fish species were restricted to depths <60 m, 8% were exclusive to the lower mesophotic, and only 21% were found in both upper and lower mesophotic zones (Pinheiro et al. 2016). At Enewetak, Marshall Islands, the lower mesophotic fish community (> 60 m) is composed of a higher proportion of non-shallow-water species than the fish community in both the upper mesophotic (30–60 m) and the subphotic (>150 m) (Thresher and Colin 1986). These findings imply that numerous species are restricted to the lower mesophotic depth zone, presumably due to its unique environmental conditions.

Given the largely unexplored nature of many MCEs, a high rate of discovery of new fish species has been reported across a variety of locations (e.g., Pyle et al. 2008, 2016b; Baldwin and Robertson 2014, 2015; Copus et al. 2015a,b; Baldwin et al. 2016; Pyle and Kosaki 2016; Tornabene et al. 2016; Easton et al. 2016), and there is an estimated potential for thousands of species to yet be discovered from these deep coral reef habitats (Pyle et al. 2016a). Early studies in Jamaica and Belize reported 33% of fishes between 60 and 150 m represented undescribed species (Colin 1974). During a 25 min exploratory dive in American Samoa to 113 m, over a dozen new fish species were observed (R.L. Pyle, pers. com.). Similarly, in Palau, Papua New Guinea, and the Cook Islands, 50 new fish species were reported from mesophotic dives between 60 and 126 m depth consisting of 9.9 h of bottom time (Pyle 2000). Of 144 species collected on a single dive site in Fiji, 40 were found to be undescribed (Baker et al. 2016).

As mesophotic surveys and exploration of new habitats continue, depth range extensions and new location records will continue to expand our knowledge of the distributions of many species. For example, initial mesophotic surveys of Johnston Atoll added new location records for 24 fish species (Wagner et al. 2014). Surveys of Vitória-Trindade Seamount Chain in Brazil revealed that 93% of fishes recorded on the seamounts and 11% of species at the two islands were new records for those locations, and most were found at mesophotic depths (Pinheiro et al. 2015). Depth range extensions were also recorded for 49 species along with two new species discovered. Similarly, one new record for the southwestern Atlantic and six new location records were discovered on the Abrolhos Shelf in the Western Atlantic (Simon et al. 2016). Further exploration of mesophotic depths will likely expand the known biodiversity and biogeography of coral reef species worldwide (Wagner et al. 2014).

To date, MCE surveys have been primarily limited to upper mesophotic depths due to the obvious logistical challenges of operating deeper, and quantitative mesophotic fish data are largely lacking. Despite these limitations, several taxa from the following genera have been reported as dominant on mesophotic reefs (Pyle 2000; Feitoza et al. 2005; Brokovich et al. 2008; Garcia-Sais 2010; Lesser and Slattery 2011; Bejarano et al. 2014; Wagner et al. 2014; Pinheiro et al. 2015; Rosa et al. 2015; Fukunaga et al. 2016).
Indo-West Pacific

- Apogonidae: Pristiapogon
- Chaetodontidae: Chaetodon
- Gobiidae: Trimma
- Labridae: Anampses, Bodianus, Cheilinus, Cirrhilabrus, Coris, Gomphosus, Hologymnosus, Larabicus, Labroides, Oxycirrhites, Paracheilinus, Pseudochaetodon, Pseudojuloides, Thalassoma
- Pinguipedidae: Parapercis
- Pomacentridae: Apolemichthys, Chromis, Dascyllus
- Pomacanthidae: Genicanthus
- Serranidae: Capron, Luzonichthys, Pseudanthias, Cephalopholis, Epinephelus, Variola

Western Atlantic

- Balistidae: Melichthys
- Carangidae: Carangoides, Caranx, Decapterus, Elagatis, Selar, Selene, Seriola, Trachinotus
- Chaetodontidae: Prognathodes
- Grammatidae: Gramma
- Gobiidae: Coryphopterus, Elacatinus, Gnatholepis, Lythrypnus, Prioleps, Psilotris, Risor
- Haemulidae: Anisotremus, Haemulon
- Labridae: Bodianus, Clepticus, Halichoeres, Thalassoma, Xyrichtys
- Lutjanidae: Lutjanus, Ocyurus, Rhombopterus
- Pomacentridae: Stegastes, Chromis
- Scaridae: Cryptotomus, Scarus, Sparisoma
- Scorpaenidae: Pterois (alien species introduced from Indo-Pacific)
- Serranidae: Cephalopholis, Epinephelus, Liopropoma, Mycterochara, Paranthias, Rypticus, Serranus

In general, fish species richness and abundance tend to decrease with increasing depth (reviewed in Kahng et al. 2010; Pearson and Stevens 2015; Andradi-Brown et al. 2016; Pyle et al. 2016a). In the Western Atlantic, mesophotic species richness generally correlates with live coral cover; the abundance of crevices and ledges promotes a comparatively high abundance of cryptic species (e.g., basslets, squirrelfishes, gobies, etc.) and large demersal fishes (reviewed in Kahng et al. 2010). In Florida and Brazil, low-relief habitats are primarily inhabited by unique communities of small fishes as compared to more complex habitats (Feitoza et al. 2005; Bryan et al. 2013). At the Vitória-Trindade Seamount Chain in Brazil, mesophotic fish habitats with the highest species richness were reefs, followed by rhodolith beds, the water column, and sandy substrate (Pinheiro et al. 2015).

Across several Indo-Pacific and Western Atlantic locations, a shift in trophic guild with increasing depth has been reported, away from abundant herbivores in shallow waters toward a zooplanktivore-dominated community at mesophotic depths (Kahng et al. 2010, 2014; Bejarano et al. 2014; Pearson and Stevens 2015; Pinheiro et al. 2016; Rosa et al. 2015; Pyle et al. 2016a; Fukunaga et al. 2016).
However, mechanisms that drive trophic shifts likely vary by location as contrasting patterns have been reported. In Bermuda, a high biomass of herbivores at mesophotic depths suggests that unique oceanographic conditions may apply there (Pinheiro et al. 2016). At Enewetak in the Marshall Islands, piscivore abundance peaks at 60–75 m, whereas in the Red Sea it reaches minimum abundance at the same depth (Thresher and Colin 1986; Brokovich et al. 2008, 2010). In Honduras, with increasing depth, herbivore biomass declines and piscivore biomass increases, but zooplanktivore biomass appears to remain constant (Andradi-Brown et al. 2016).

In the Pacific, there are proportionately higher rates of endemism for fish communities on mesophotic reefs versus shallow reefs (Pyle 2000; Pyle and Kosaki 2016; Kane et al. 2014; Wagner et al. 2014; Kosaki et al. 2016). In the Northwestern Hawaiian Archipelago, 46% of fishes on mesophotic reefs are endemic to the archipelago, while only 21% of fishes found on shallow reefs are endemic (Kane et al. 2014) (Fig. 3). A comparison of fish communities between Fiji, Papua New Guinea, and Palau reveals higher rates of endemism and more restricted depth ranges for MCE fishes compared to adjacent shallow-reef fishes (e.g., 50–60% overlap in shallow fish species and only 6–10% overlap in MCE fish species) (Pyle 2000; Baker et al. 2016).

In the Hawaiian Archipelago, endemism appears to increase both with depth and with latitude. For fishes found exclusively in MCEs, 43% endemism is reported for fishes found below 30 m and increases to 51% for fishes found below 70 m (Pyle et al. 2016a). At Nihoa (23°N, 162°W), endemism in MCEs is less than 20% and progressively increases to near 100% at Kure Atoll (28°N, 178°W) (Kane et al. 2014; Kosaki et al. 2016). Given that much of the Indo-Pacific MCEs have been unexplored, contemporary rates and patterns of endemism should be interpreted with appropriate caution since these rates and patterns may change as additional MCEs are investigated.

*Fig. 3* Photo of aggregation of no fewer than 11 endemic fish species at Kure Atoll, Northwest Hawaiian Archipelago, at 100 m depth (Photo by Richard L. Pyle)
The marked differences in deep- and shallow-reef fish populations may be caused by glacio-eustatic sea-level fluctuations that periodically eliminate extensive areas of shallow coral reef habitat (i.e., gently sloping insular island and continental shelves) in many locations (Kosaki et al. 1991). Periods of low sea level would cause higher extinction rates for shallow-water fish communities that require these shallow habitats but would have less impact on deeper-water fishes that are accustomed to the vertical walls and drop-offs common to MCEs as these habitats are more likely to shift vertically and be retained during periods of low sea level.

While the available data to date is limited due to logistical challenges, the potential role of MCEs as refugia for shallow-reef fish (i.e., the DRRH) has been supported in recent MCE investigations (Kahng et al. 2010, 2014; Loya et al. 2016; and references therein). Many MCEs are isolated from anthropogenic and natural stressors common to shallow reefs due to factors such as geographic isolation, wave attenuation with depth, and reduced fishing pressure (Baker et al. 2016). Biophysical models in the northeast Caribbean show that larvae of the damselfish Stegastes partitus spawn at 80 m can sporadically disperse to shallow reefs (Vaz et al. 2016). In fact, there is a growing list of fish species known to exhibit ontogenetic depth migrations with larvae initially recruiting to shallow habitats (i.e., seagrass beds, back-reefs, and mangroves) and then migrating as they mature to deeper reef crests and slopes (Andradi-Brown et al. 2016, and references therein). In the Hawaiian Archipelago, the damselfish Chromis verater exhibits high genetic connectivity between MCEs and adjacent shallow reefs suggesting that the species may maintain one continuous population throughout their depth distribution (Tenggardjaja et al. 2014). These studies highlight the potential for MCEs to act as a depth refuge from which shallow reefs can be repopulated following extirpation.

For targeted species facing overfishing pressure on shallow coral reefs, such connectivity can have stock management implications. For locations studied to date, the abundance of fisheries-targeted species is higher in MCEs than on adjacent shallow reefs at locations exposed to higher fishing pressure. In Bermuda and the Marianas Islands, the abundance and biomass of macro-carnivores increased with depth and distance from the coast (Lindfield et al. 2016; Pinheiro et al. 2016) suggesting that MCEs may act as refugia for fishery-targeted coral reef fish. However, large and highly mobile predatory fishes (e.g., Galapagos shark and giant trevally) can readily migrate (daily and seasonally) between MCEs and shallower depths, thereby reducing the effectiveness of the MCE to act as refugia from shallow-water fishing (Papastamatiou et al. 2015).

When assessing the utility of the DRRH, the role of MCEs is both location and species specific and related to the nature and scope of the disturbance in question (e.g., overfishing, mass coral bleaching, etc.). Although the upper mesophotic may serve as a depth refuge for several fishes, the lower mesophotic may not as there appears to be little overlap in fish communities between these depths. Recent evidence shows that diet and morphology may play a role in shaping the community structure between deep and shallow reefs (Bridge et al. 2016), thereby reducing the overlap in fish communities and increasing the likelihood of depth endemism.
4 Ongoing MCE Exploration and Implications for Biodiversity

Given the limited exploration at mesophotic depths to date, particularly in many Indo-Pacific locations, new MCE investigations are substantially expanding our understanding of coral reef biodiversity (reviewed in Kahng et al. 2014; Lane and Hoeksema 2016). Aided by advancements in technology, contemporary MCE studies are discovering many new species and cryptic diversity, as well as new taxonomic records for species that were previously unknown to many biogeographic regions (e.g., Muir et al. 2015; Magalhaes et al. 2015; Spalding et al. 2016). Some species previously reported as rare or restricted to shallow water are also being reported deeper and in greater abundance at mesophotic depths (e.g., Blyth-Skyrme et al. 2013; Englebert et al. 2014; Muir et al. 2015; Eyal et al. 2016; Eyal-Shaham et al. 2016). Therefore, inferred lower depth limits for many organisms must be interpreted cautiously until more MCEs are comprehensively surveyed (Kahng et al. 2014). Recent investigations have also identified the introduction and proliferation of alien species (e.g., Carijoa sp., Avrainvillea sp., Pterois spp.) altering mesophotic community structure at the expense of native species biodiversity (reviewed in Baker et al. 2016). The contributions from new MCE surveys along with vertical connectivity studies are steadily advancing our understanding of the effectiveness and limitations of MCEs in buffering populations from natural and anthropogenic disturbances associated with shallow-water habitat.

5 Cross-References

- Animal Forest in the Chilean Fiords: Discoveries and Perspectives in Shallow and Deep
- Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- Animal Forests of the World: an overview
- Animal Forests Through Time: Historical Data to Understand Present Changes in Marine Ecosystems
- Complexity and Biodiversity in Caribbean Coral Reefs
- Corals as Architects of the Oceans
- Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical
- Ecosystem Functions and Services of Marine Animal
- Ecosystem-based Management: Opportunities and Challenges for Application in the Ocean
- Evolution of the Marine Animal Forest
- Impact of Bottom Fishing on Animal Forests: Science, Conservation and Fisheries Management
- Limits of Photoadaptation and Photoacclimation in Symbiotic
- Octocoral and Hexacoral Diseases in a Changing Ocean
Symbiotic Versus Asymbiotic Octocorals: Physiological and Ecological Trophic Ecology and Habitat Provision in Cold-water Coral Ecosystems

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