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REVIEW

Community ecology of mesophotic coral reef ecosystems

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Abstract Given the global degradation of shallow-water coral reef ecosystems resulting from anthropogenic activities, mesophotic coral reef ecosystems (MCEs) are gaining attention because they are generally considered a de facto refuge for shallow-water species. Despite their inferred importance, MCEs remain one of the most understudied reef habitats, and basic information on the taxonomic composition, depth range, habitat preferences, and abundance and distribution of MCE taxa is scarce. The processes that structure these communities are virtually unknown. Here, we provide a review of what is known about MCEs community ecology and outline essential gaps in our knowledge of these deeper water coral reef ecosystems. The primary findings of this review are as follows: (1) many dominant shallow-water species are absent from MCEs; (2) compared to shallow reefs, herbivores are relatively scarce, perhaps due to limited habitat complexity at depth; (3) changes in the dominant photosynthetic taxa with depth suggest adaptation and specialization to depth; (4) evidence regarding the importance of heterotrophy for zooxanthellate corals at depth is conflicting and inconclusive; and (5) decreased light with depth, but not temperature, appears to be the primary factor limiting the depth of

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MCEs. The majority of research done to date has been performed in the Caribbean, where some generalization can be made about the community structure and distribution of MCEs. The larger and more diverse Indo-Pacific remains largely unexplored with no apparent generalizations from the few sites that have been comparatively well studied. For MCEs, large gaps in knowledge remain on fundamental aspects of ecology. Advanced technologies must be harnessed and logistical challenges overcome to close this knowledge gap and empower resource managers to make informed decisions on conserving shallow-water and mesophotic coral reef ecosystems.

Keywords Mesophotic · Deep coral reef · Scleractinian · Community structure · Ecology

Introduction

Mesophotic coral reef ecosystems (MCEs) are warm water, light-dependent coral reef communities starting at 30–40 m to the bottom of the photic zone, which varies by location and extends to over 150 m in some regions. MCEs represent a direct extension of shallow-water coral reef ecosystems, which support a diverse abundance of habitat-building taxa including corals, sponges, and algae (Hinderstein 2010). Despite their close proximity to well-studied shallow-water coral reefs, MCEs remain poorly understood due to the logistical difficulties and safety issues of working near or below the depth limits of recreational SCUBA diving (Pyle 1996; Menza et al. 2008). Enabled by advanced technologies (e.g., mixed gas closed circuit SCUBA, remotely operated vehicles, manned submersibles, etc.), MCE studies reveal extensive, productive habitats and rich communities, which differ significantly from their shallow-water counterparts.

In recent years, the integrity and health of coral reef ecosystems are increasingly threatened by numerous anthropogenic stresses including habitat alteration, terrigenous sources of pollution, resource extraction, and climate change (Wilkinson 1999; Kleypas and Eakin 2007). However, lack of basic knowledge about MCEs precludes accurate ecological forecasting and consequently sound resource management and conservation decisions. Important questions regarding the ecology of MCEs remain largely unanswered: How do MCE communities differ from shallow-water reefs? What environmental factors limit the distribution of reef organisms with depth? What acclimatization capabilities do mesophotic organisms possess? How susceptible are MCEs to anthropogenic disturbance and climate change? To what extent do MCEs serve as refuges for threatened shallow-water populations? Unlike shallow-water coral reefs and cold-water coral ecosystems, which have been subject to elevated research focus in recent years (Lumsden et al. 2007; Messing et al. 2008), MCEs remain relatively understudied despite the increasing availability of deep-water technologies.

This manuscript will review the knowledge to date on the mesophotic community structure >40 m and environmental factors influencing community ecology. Included in the scope of this review is the lower photic zone where the photosynthetic community transitions to non-photosynthetic. Coral communities consisting solely of azooxanthellate assemblages in both cold and warm-water habitats are excluded from this discussion. This review will be organized into the following sections: (A) mesophotic community structure for the Western Atlantic and Indo-Pacific regions; (B) factors which influence mesophotic community structure; and (C) adaptations to low light at mesophotic depths.

Mesophotic community structure

Compared to shallow-water reefs, information regarding the taxonomic composition, depth range, and habitat preferences of MCE species is scarce. Locations where MCEs have been studied to date are mapped in Fig. 1 (a comprehensive list of MCE studies below 40 m is included in the Electronic Supplemental Material). Among these

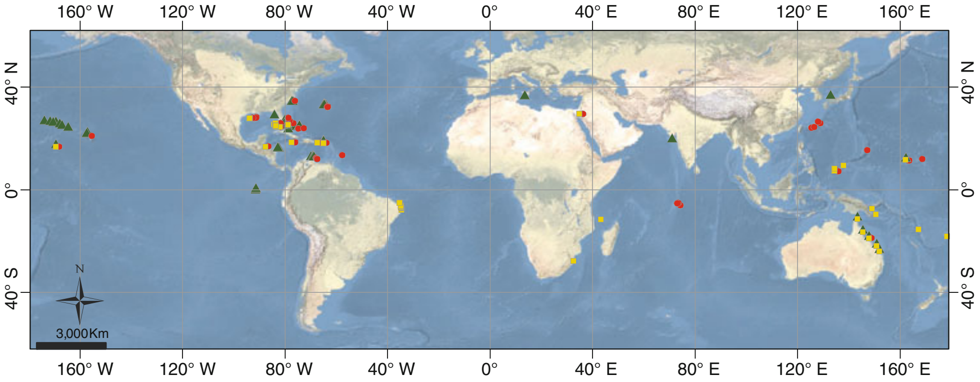

Fig. 1 Worldwide locations of mesophotic studies of corals (*red circles*), algae (*green triangles*), and reef fish (*yellow squares*)

localities, the best studied areas are generally in the Caribbean, including the northern coast of Jamaica, the Bahamas, the northern Gulf of Mexico, and Puerto Rico. Despite greater geographic coverage and biodiversity, MCE studies from the Indo-Pacific are comparatively few, with the best studied locations being the Marshall Islands, the Main Hawaiian Islands, Johnston Atoll, and the northern Red Sea. Aspects of community structures for a representative subset of well-studied MCE locations are summarized in the remainder of this section.

Western Atlantic

In general, MCEs have been found on deeper fore-reef slopes adjacent to shallow-water coral reefs, deep-water rhodolith beds, and on isolated offshore banks on the continental shelf. In shallow water, the zooxanthellate coral fauna is quite homogenous throughout the Caribbean with relatively few species dominating as major reef-builders (Glynn 1973). The zooxanthellate corals most common in the lower photic zone also appear to be shared across locations in the Caribbean (Tables 1, 2). Several of these corals are characteristically more abundant at mesophotic depths than in shallow water (Goreau and Wells 1967; Fricke and Meischner 1985).

Island fore-reef slopes

One of the best studied MCEs is the seaward fore-reef slope off the north coast of Jamaica where geomorphology changes markedly with depth (Goreau and Goreau 1973; Liddell and Ohlhorst 1988). A gentle fore-reef slope extends from 30 to ~60 m where the slope steepens to a near vertical deep fore-reef escarpment from ~60 to 120–130 m. The escarpment consists of an irregular wall incised by sediment chutes and interrupted by ledges. Near the bottom of the deep fore-reef escarpment, the slope decreases until the deep fore-reef escarpment ends in a 20–45° slope of rubble and soft substrate.

At several sites, Goreau and Goreau (1973) and Liddell and Ohlhorst (1988) reported that vertical zonation of the benthic community on hard substrata was correlated with depth-related changes in geomorphology. Dense populations of zooxanthellate scleractinian corals and macroalgae including calcareous green algae dominated the benthos within the mesophotic zone down to 60 m. From 60 to 120 m, sponges, coralline algae, and filamentous algae became dominant. Although less abundant, gorgonians and antipatharians were also common. While the lower depth limit for foliose macroalgae was around 100 m, crustose red algae were found to depths of ~250 m (Lang 1974). Below 100 m, open space was common and little evidence for space competition among sessile organisms was observed. Framework-building coralline sponges (formerly Sclerospongiae), which are cryptic in shallow water, peaked in abundance at ~100 m depth and survive til 300 m. The largest and most conspicuous sponge, *Ceratoporella nicholsoni,* covers ~25–50% of the substrata beneath ledges and inside caves at 74–98 m (Lang et al. 1975).

Using cluster analysis of benthic community composition on hard substrata, Liddell and Ohlhorst (1988) revealed well-defined bathymetric zonation with boundaries delineating the shallow-water community (≤30 m), the fore-reef slope (45 m), and the deep fore-reef (53–120 m). To a lesser degree, the deep fore-reef could be further subdivided into upper (53–75 m) and lower (90–120 m) subzones. The deep fore-reef is a biological transition zone from the shallow-water community of zooxanthellate corals and macroalgae to a deeper water community of coralline algae, azooxanthellate scleractinians and gorgonians, demosponges, endolithic sponges, and other cryptic fauna.

Within the mesophotic zone, Goreau and Goreau (1973) found that several zooxanthellate coral species were common (Tables 1, 2). Below 50 m, hermatypic coral species diversity declined rapidly. At the lower bathymetric limit for zooxanthellate corals, plate-like colonies of *Agaricia* spp. and *Leptoseris cucullata* (formerly *Helioseris cucullata*) were the most common and occurred to 99 m (Hartman 1973). In contrast, zooxanthellate gorgonians are restricted to more shallow habitats, with the deepest observation being *Pseudopterogorgia elizabethae* recorded at 75 m (Kinzie 1973).

Many Caribbean MCEs, including the Bahamas and Belize, exhibit similar geomorphology and community structure patterns as Jamaica (James and Ginsburg 1979; Liddell et al. 1997; Reed and Pomponi 1997). Below the fore-reef, near vertical escarpments are characteristic at many locations and represent drowned sea cliffs formed during the Wisconsin low stillstand (Goreau and Land 1974; Ohlhorst and Liddell 1988).

MCEs in the Bahamas exhibit a similar community structure as Jamaica but have a higher dominance of algae, less coral, and a deeper bathymetric distribution of photosynthetic taxa (Reed 1985; Liddell et al. 1997). Liddell et al. (1997) and Aponte and Ballantine (2001) reported that benthic algae exhibited vertical zonation by taxa. Macroalgae (*Halimeda* spp. and *Lobophora* spp.) dominated the fore-reef slope with >50% cover to 60 m but declined sharply with increasing depth. Filamentous/turf algae remained abundant to 75 m. Calcifying algae, particularly *Peyssonnelia* spp., increased with depth and co-dominated the upper portion of the deep fore-reef escarpment at 75–100 m with endolithic green algae. Below 100 m, calcifying algae declined in abundance and endolithic algae dominated hard substrata to at least 200 m.

Table 1 Zooxanthellate corals that are relatively abundant and dominate the coral community structure at mesophotic depths (>40 m) at Western Atlantic locations

Common Mesophotic Zooxanthellate Corals	Bermuda	Florida	Bahamas	North Gulf MX	Belize	Jamaica	Puerto Rico/USVI	Curacao	Barbados
Scleractinians									
Agaricia fragilis	x	x			x				
Agaricia grahamae			x		x	x	x		x
Agaricia lamarcki		x		x			x	x	x
Agaricia undata						x		x	
Agaricia spp.	x	x	x	x	x	x	x	x	x
Colpophyllia sp.				x					
Dichocoenia stokesi				x					
Leptoseris cailleti							x		x
Leptoseris cucullata		x	x	x		x			x
Madracis brueggemanni				x					x
Madracis decactis	x	x	x						x
Madracis formosa				x				x	
Madracis mirabilis				x					
Madracis myriaster				x					
Madracis pharensis^{a}			x			x		x	
Madracis senaria								x	
Madracis spp.	x	x	x	x	x	x		x	x
Montastraea annularis			x		x	x	x	x	
Montastraea cavernosa	x	x	x	x	x	x	x	x	x
Mycetophyllia aliciae						x			
Mycetophyllia reesi					x	x			
Oculina vericosa^{a}		x							
Porites astreoides								x	
Porites divaricata		x							
Scolymia sp.	x	x	x	x		x			
Solenastrea sp.					x				
Stephanocoenia sp.				x	x				
Hydrocoral									
Millepora sp.	x			x					
Octocorals									
Eunicea claigera						x			
Pseudopterogorgia elizabethae						x			x

Corals marked with a superscript (a) denote species that are facultatively zooxanthellate. References for each location are as follows: Bermuda (Fricke and Meschner 1985); Florida (Phillips et al. 1990; Jarrett et al. 2005; Reed 2006); Bahamas (Reed 1985; Avery 1998); Northern Gulf of Mexico (Bright et al. 1984, Rezak et al. 1985); Belize (James and Ginsburg 1979); Jamaica (Goreau and Wells 1967; Goreau and Goreau 1973; Kinzie 1973); Puerto Rico and U.S. Virgin Islands (García-Sais et al. 2008); Curacao (Van den Hoek et al. 1978; Vermeij and Bak 2003), and Barbados (Macintyre et al. 1991)

Throughout the Caribbean, abundance of sponges generally increases with depth (Lang et al. 1975; Liddell and Ohlhorst 1988; Liddell et al. 1997; Lesser 2006). In the Bahamas, Reed and Pomponi (1997) described the biodiversity and distribution of sponges with depth. The deep fore-reef escarpment (60–150 m) exhibited the highest species diversity and was characterized by massive species in several orders in the class Demospongiae. While a number of sponge taxa were ubiquitous over the entire depth range, 46% of species found on the deep fore-reef escarpment occurred exclusively within this zone (Pomponi et al. 2001). In Jamaica, Lang et al. (1975) found slow-growing sclerosponges, which secrete aragonite, to be the primary substrate builders at depths of 70–100 m. However, most sponges are siliceous with spicules that dissolve in undersaturated waters and therefore do not contribute to the reef framework despite their abundance (Rützler 2004).

Table 2 Zooxanthellate corals that are relatively abundant and dominate the coral community structure at mesophotic depths (>40 m) at Indo-Pacific locations

Common Mesophotic Zooxanthellate Corals	Red Sea	Chagos/ Maldives	Ryuku Islands	Marshall Islands	Johnston Atoll	Hawaii	Society Islands
Scleractinians							
Alveopora verrilliana							x
Coscinaraea sp.		x		x			x
Cycloseris sp.				x			
Diaseris sp.		x		x			
Echinophyllia aspera				x			
Favia speciosa			x				
Goniopora muscosa				x			
Leptoseris explanata							x
Leptoseris fragilis	x						
Leptoseris hawaiiensis				x	x	x	
Leptoseris mycetoseroides							x
Leptoseris papyracea				x		x	
Leptoseris porosa							x
Leptoseris scabra				x			
Leptoseris solida				x			
Leptoseris yabei						x	
Leptoseris spp.	x	x	x	x	x	x	x
Montipora sp.				x	x		
Mycedium elephantotus							x
Oxypora lacera				x			
Pachyseris speciosa			x				
Porites eydouxi				x			
Porites lobata						x	
Psammorcora sp.		x			x		
Stylophora kuehlmanni							x

Corals marked with superscript (a) denote species that are facultatively zooxanthellate. References for each location are as follows: Red Sea (Fricke and Knauer 1986); Chagos Islands (Sheppard 1980); Maldives (Gardiner 1903); Ryuku Islands (Yamazato 1972); Marshall Islands (Wells 1954; Colin 1986); Johnston Atoll (Maragos and Jokiel 1986); Hawaii (Kahng and Maragos 2006; Kahng and Kelley 2007); and Society Islands (Kuhlmann 1983)

Offshore banks on the continental shelf

Along the Texas and Louisiana shelf in the northern Gulf of Mexico, several offshore banks support MCEs (Rezak et al. 1985). The best studied of these features are the East and West Flower Garden Banks, which rise from the sea floor at 100–140 m to 18–28 m and are located near the outer edge of the continental shelf. For these banks, Rezak et al. (1985) identified a number of depth-related zones named for dominant taxa based on benthic community structure. The *Stephanocoenia* zone at 36–52 m is dominated by *Stephanocoenia intersepta* (formerly *S. michelini*) and *Millepora* sp. Compared to shallower depths, this zone has less live coral cover, more crustose coralline algae (CCA), and exceptional numbers of the thorny oysters *Spondylus americanus.* At reef margins atop gravel deposits at 28–46 m, the *Madracis* zone is dominated by thickets of branching coral *Madracis mirabilis*, leafy algae, and sponges. At 46–98 m, an algal-sponge zone covers sand, unconsolidated rhodoliths, and rocky outcrops colonized by saucer-like colonies of *Leptoseris cucullata* and *Agaricia* spp. Small *Madracis* spp. are unevenly distributed among the algal nodules. Calcareous green algae (*Halimeda* and *Udotea*) occur in patches within the upper portions of this zone. Below 80 m, zooxanthellate corals are generally absent, and coralline algae become limited. Instead, the community (an antipatharian-transitional zone) consists primarily of antipatharians, azooxanthellate gorgonians, azooxanthellate scleractinians, sponges, and crinoids. Below this zone lies the nepheloid zone of turbid bottom water subject to frequent resuspension of sediments.

MCEs exhibiting similar zones are found at other nearby hard substrata banks (Rezak et al. 1985). Many of these banks are less elevated above the seafloor and/or are located closer to the coast, both of which increase the influence of the turbid nepheloid layer on the biota. Mid-shelf banks exhibit a minor reef-building *Millepora*-sponge zone at 18–52 m, which supports hermatypic corals including *Stephanocoenia* spp. at low densities just above the nepheloid layer. The deeper, outer shelf banks support algal-sponge and antipatharian-transitional zones, which also support zooxanthellate coral communities with locally abundant aggregations of agariciids and *Madracis* spp. corals (Rezak et al. 1990).

Deep-water rhodolith reefs

Rhodoliths are unattached accretions of coralline red algae that can form extensive beds and are a common type of hard substrate at mesophotic depths. Rhodolith beds are widely distributed in the world's oceans including the tropics where they form large concentrations to depths of 150 m (Foster 2001) and can actively grow to 268 m (Littler et al. 1985). Although rhodolith beds are relatively featureless at spatial scales greater than centimeters, their coralline algal surfaces can be colonized by megabenthic organisms such as macroalgae and zooxanthellate corals (Littler et al. 1991). On a rhodolith-covered seamount near San Salvador, Bahamas, Littler et al. (1986) recognized vertical zonation of four deep-water algal assemblages each dominated by specific taxa: *Lobophora* zone (81–90 m), *Halimeda* zone (90–130 m), *Peyssonnelia* zone (130–189 m), and crustose coralline zone (189–268 m). This zonation of algae from brown → green → red with increasing depth is consistent with other studies in clear oceanic waters (Kirk 1994).

In Puerto Rico, García-Sais et al. (2008) reported rhodolith reefs at 45–60^{+} m, which were dominated by benthic algae, particularly *Lobophora variegata*. Sponge cover was moderate, whereas cover by scleractinian corals was relatively low and consisted primarily of *Agaricia* spp. attached to rhodoliths. In Bermuda, rhodoliths agglutinated into solid banks were heavily colonized by corals and other sessile benthic invertebrates, whereas fields of unconsolidated rhodoliths remained uncolonized and relatively homogeneous by comparison (Fricke and Meischner 1985). On the west coast of Florida, areas of exposed hard substrata at 60–80 m consist primarily of fused rhodolith pavements colonized by *Agaricia* spp. and *Madracis decactis*, crustose red algae, and the green alga *Anadyomene menziesii*. Along the outer shelf at 100–200 m, the benthic community is non-photosynthetic consisting of crinoids, antipatharians, azooxanthellate gorgonians and scleractinians, and hexactinellid sponges (Phillips et al. 1990).

Fish community structure

The composition and numerical dominance of fish species associated with mesophotic habitats at sites across the Caribbean varies across the same depth gradient as the sessile benthic fauna. Dennis and Bright (1988) and García-Sais et al. (2008) both document a marked decrease in the overall species richness, number of species per unit area, and individual fish abundance across the same depth range over which benthic community composition shifts. In general, fish species richness correlates strongly with live coral cover; however, the abundance of several numerically dominant species varies independently from live coral cover. Instead of live corals, the abundance of crevices on escarpments is thought to promote a comparatively high abundance of species adapted for secretive habitats (e.g., basslets, basses, squirrelfishes and gobies) and facilitate penetration of deep-water predators into the MCE (Colin 1974, 1976). Both richness and abundance tend to decrease uniformly with increasing depth at sites throughout the Caribbean (Lukens 1981; Nelson and Appeldoorn 1985; Itzkowitz et al. 1991). Feitoza et al. (2005) reported that deep flat zones were occupied primarily by small fishes, whereas the larger demersal fishes were associated with the large crevices and ledges present on the steep portion of the reef slope.

Indo-Pacific

The mesophotic benthic community structure in the Indo-Pacific has been less studied compared to the Caribbean (Fig. 1). Unlike the Caribbean, consistent patterns of geomorphology and community structure are not apparent across the Pacific MCEs studied to date. One consistent finding, however, is that zooxanthellate *Leptoseris* spp. appear to be ubiquitous in the deepest parts of the mesophotic zone across the Indo-Pacific (Tables 1, 2). Despite its high biodiversity and central role as a major reef builder in the Indo-Pacific (Veron 1995), *Acropora* spp. are relatively scarce in the lower photic zone. Although numerous coral species have been reported at mesophotic depths, relatively few to date are reported as abundant (Tables 1, 2). Throughout the Indo-Pacific, MCEs are best studied in the Marshall Islands, Hawaii, Johnston Atoll, and the northern Red Sea.

Marshall Islands

In the Marshall Islands, the coral community structure has been studied at Enewetak, Bikini, and several nearby atolls.

Using extensive dredge samples, Wells (1954) defined three depth-related zones seaward of the fore-reef based on the relative abundance of coral species. Along the moderately sloping (~25°) shelf at Bikini Atoll, the *Echinophyllia* zone extended from 18 to 91 m and was dominated by *E. aspera* and *Oxypora lacera*. Over 20% of the hermatypic coral species, which occured in shallow-water, also occured within this zone or deeper. The *Leptoseris* zone extended from 91 to 146 m and was dominated by several species within the genus (Tables 1, 2). Several solitary azooxanthellate scleractinians (Caryophylliidae) were also recorded from this zone. Below 146 m, the *Sclerhelia–Dendrophyllia* zone contained only azooxanthellate corals.

At nearby Enewetak, Colin et al. (1986) reported the seaward island slope angle increasing with depth to 45° at 60 m, to 60° at 90 m, and even steeper (>60°) at 150–200 m with no significant terraces or shelves to at least 360 m. Branched corals were found to 60 m. Below 60 m, plate-like *Leptoseris* spp. predominated. Less than 1% coral cover was reported at 90 m, although individual colonies at this depth were often large. The deepest zooxanthellate coral at Enewetak was observed at 112 m. Azooxanthellate gorgonians and nephtheids dominated the coral community below 100 m. At 120–160 m, small caves protected from downwelling sediments were colonized by sponges and antipatharians. On the deep fore-reef, Hillis-Colinvaux (1986a, b) reported *Halimeda* spp. as the most conspicuous algae with high abundance (30–50% cover) from 45 to 80 m, modest abundance (10–25% cover) extending to 110 m, and a lower limit of 140 m. Inside the atoll lagoon, Colin (1986) reported a deep-water solitary coral community on soft substratum at 50–60^{+} m consisting of fungiid species in high densities (~100/m^{2}) intermixed with patches of algae.

At Enewetak, Thresher and Colin (1986) reported that fore-reef fish communities varied with depth. Relative abundance of zooplanktivores increased with depth from ~50% in shallow water to almost 100% at depth due in part to a steady decline of other trophic groups except piscivores, which peaked in abundance at 60–75 m. At mesophotic depths, the most common piscivores and consumers of large invertebrates belonged to the families Serranidae, Scorpaenidae, Tetraodontidae and Lethrinidae, whereas the primary zooplanktivorous fishes were members of the Serranidae, Labridae, and Pomacentridae. Despite locally abundant prey species, top predators such as sharks and barracudas (Sphyraenidae) were observed only in shallow water. As with Caribbean sites, herbivores declined sharply with increasing depth, both in abundance and species richness. For example, at Enewetak, herbivorous fishes comprised 40% of the community at 30 m, but declined to almost zero by 90 m.

Red Sea

Along the northwestern coast of the Red Sea, the shallow-water coral reef ends at ~65 m and is replaced by a wide sandy plain, which ends abruptly at 90–100 m where the slope increases (to 13°) and rocky terraces protrude from the sand. From 100 to 210 m, Fricke and Knauer (1986) defined three depth-related coral community zones. The uppermost zone at 100–130 m was dominated by small plate-like colonies of *Leptoseris fragilis*, the only zooxanthellate coral observed below 100 m. *L. fragilis* abundance peaked at 110 m but colonies were observed to 145 m. Scleractinian coral diversity peaked in the zone from 130 to 170 m where azooxanthellate corals, particularly *Dendrophyllia horsti* and *Javania insignis* became dominant. In the zone below 170 m, *D. horsti* continued, while *Javania insignis* declined in abundance and *Madracis interjecta* increases, forming warm-water azooxanthellate coral bioherms (Fricke and Hottinger 1983; Fricke and Knauer 1986).

Patterns of fish distribution and abundance were similar to that of Enewetak, with a steep decline in number of species to 65 m. Zooplanktivores increased with depth to almost 100% at 65 m where Serranidae and Labridae species dominated (Brokovich 2008; Brokovich et al. 2008). Herbivore species abundance and richness declined sharply with depth (Brokovich et al. 2010). Unlike Enewetak, piscivores declined to their minimum values at 65 m in the Red Sea. Typical piscivores and benthic invertebrate predators throughout the Red Sea include Serranidae, Scorpaenidae, Tetraodontidae, and Lethrinidae. Top predators such as sharks and barracudas were not observed on the deep reefs of the Red Sea.

Hawaiian Archipelago and Johnston Atoll

In the Au'au Channel in Hawaii, Kahng and Kelley (2007) reported depth-related zonation based on the relative abundance of the dominant megabenthic taxa. From 50 to 80 m, foliose macroalgae, particularly *Halimeda* spp., dominated the biota although corals within the genus *Leptoseris* were locally abundant on hard substrata. The major reef-building corals that dominate shallow-water Hawaiian reefs were conspicuously rare below 60 m. From 80 to 90 m, abundance of macroalgae declined rapidly and hard substrata was often dominated by monospecific aggregation of *Leptoseris* spp. From 90 to 120 m, live benthic cover was uniformly low and exposed hard substrata were often uncolonized by megabenthic organisms. On rugose features exposed to enhanced currents, black corals and the invasive octocoral *Carijoa* sp. were locally abundant with the latter often overgrowing large black coral colonies (Kahng and Grigg 2005). From 120 to

140 m, much of the substrata were covered by sand, but patches of small antipatharians were locally abundant on elevated features.

At nearby Penguin Bank, Agegian and Abbott (1985) described three slightly different mesophotic algal zones based on submersible surveys. The shallow zone (45–70 m) contained a diverse assemblage of algae (*Lobophora variegata*, *Dictyota friabilis*, *Halimeda* spp., coralline algal rhodoliths, *Mesophyllum mesomorphum*, and *Peyssonnelia rubra*). The mid-depth zone (90–110 m) was characterized by *Codium mamillosum* and crustose coralline algae (CCA), while the deep zone (110–182 m) was composed primarily of CCA.

At Johnston Atoll, macroalgae were less diverse but found at greater depths. The shallow-water zone (45–120 m) contained patchily distributed siphonous green algae (*Halimeda* spp. and *Caulerpa* spp.). The mid-depth zone (120–180 m) consisted of a low abundance of *Halimeda gracilis* and CCA, and the deep zone (180–250 m) contained CCA covering 40–60% of the substratum (Agegian and Abbott 1985).

Factors that influence mesophotic community structure

Many biotic and abiotic factors vary predictably with depth and can influence the upper and lower depth distribution of mesophotic organisms. Other factors are not correlated with depth but can affect the availability of suitable substrata and the spatial distribution and abundance of benthic organisms. In shallow water, community structure and the factors, which influence distribution and abundance of key organisms are well known (Sheppard 1982; Done 1983; Grigg 1983; Huston 1985; Lüning 1990; Rogers 1990; Kleypas et al. 1999). Because of the logistical challenges of performing manipulative experiments at depth, relatively little is known about the suite of factors that influence mesophotic community structure and their relative importance. The best studied factors that differ significantly from shallow-water reefs are summarized in the following paragraphs.

Competition

Mesophotic scleractinian corals may be uncommon in exposed, shallow water due to inferior competition for space with other benthos. Fast-growing photosynthetic species may out-compete non-photosynthetic and slower growing species in areas with high-light irradiance (Huston 1985). In Hawaii from 60 to 100 m, Kahng and Kelley (2007) reported a decrease in live benthic cover and an increase in uncolonized hard substrata with increasing depth except in localized areas of high current flow where large suspension feeders were abundant. Space competition appeared less intense with increasing depths due in part to the reduction in macroalgae abundance. In the Bahamas, the relative space-acquiring competitive abilities shift phyletic dominance from macroalgae to corals to sponges and other heterotrophic invertebrates as light levels declined with depth (Liddell and Avery 2000).

Liddell and Avery (2000) also noted that the pattern of species diversity with depth was inconsistent with the intermediate disturbance hypothesis (Connell 1978). Below 50 m, grazing was greatly reduced and hydrodynamic disturbance was rare due to attenuation of wave energy. Yet megabenthic species diversity did not decline from 50 to 75 m. Lower levels of light enabled more species to coexist with photosynthetic species which out-compete them at higher levels of light. The sharp decline in recruitment for most taxa below 50 m further supports the hypothesis that competitive exclusion has less influence on diversity and community structure at depth (Avery and Liddell 1997).

Predation and herbivory

Although no studies to date quantify community-level feeding habits of mesophotic reef fishes, plankton appears to supply most of the energetic demands of fish at mesophotic depths. Inferences of trophic interactions of mesophotic fishes are based largely on studies from Caribbean shallow reefs (e.g., Randall 1967) substantiated in some cases by direct observations from submersibles and/or diving (Feitoza et al. 2005; García-Sais et al. 2008). About 22% of the fish species common or abundant in Western Atlantic mesophotic reefs are planktivores (Table 3). Some of the species are strongly schooling and appear to account for a significant proportion of the mesophotic reef fish biomass. Despite the diversity and abundance of zooplanktivores, Rodriguez-Jeréz (2004) reported a depauperate zooplankton (>200 µm) community over mesophotic reefs with fish eggs as the only moderately abundant item. High predation pressure by zooplanktivorous fishes, strong dependence upon fish eggs as food, and/or significant roles of demersal zooplankton (near the benthos), which were missed in the sampling, may account for these unexpected findings (Rodriguez-Jeréz 2004).

A common feature of many MCEs is the relative scarcity of herbivorous fishes (but see Dennis and Bright 1988; Feitoza et al. 2005), even in areas dominated by benthic algae. At 30–50 m in the Caribbean, García-Sais et al. (2008) identified over 25 species of macroalgae from mesophotic reef habitats. For example, the encrusting fan-leaf algae *Lobophora variegata*, known to be common in the diet of herbivorous fishes on shallow reefs (Colin 1978),

Table 3 Common and abundant fishes reported from mesophotic depths (>40 m) in the Western Atlantic region

Family	Genus species	Reef habitat	Sites where abundant	Trophic group
Ginglymostomidae	*Ginglymostoma cirratum*	SE, A/S	1, 2, 6	C
Carcharhinidae	*Carcharhinus perezi*	SE, A/S	1	C
	Carcharhinus limbatus	SE, A/S	1	C
Sphyrnidae	*Sphyrna mokarran*	SE, A/S	1	C
Dasyatidae	*Dasyatis americana*	SE, A/S	1, 2, 6	C
Muraenidae	*Gymnothorax funebris*	SE, A/S	1, 2	C
Synodontidae	*Synodus intermedius*	SE, A/S	1, 6	C
	Synodus synodus	SE, A/S	1, 2	C
Holocentridae	*Holocentrus adscensionis*	SE, A/S	1, 2	C
	Holocentrus marianus	n/d	3, 4, 5	C
	Holocentrus rufus	SE, W, A/S	1, 3, 6	C
	Myripristis jacobus	SE, A/S	1, 2	C
	Sargocentron bullisi	n/d	7	C
Serranidae	*Cephalopholis cruentatus*	SE, W	1, 3, 4, 5, 6	C
	Cephalopholis fulva	SE, W	1, 2, 3, 7	C
	Epinephelus guttatus	SE, W	1, 3	C
	Epinephelus morio	n/d	7	C
	Holanthias martinicensis	W	6	C
	Hypoplectrus puella	SE, W	1, 3	C
	Liopropoma eukrines	A/S	6, 7	C
	Liopropoma mowbrayi	n/d	1, 3, 4, 5	P
	Mycteroperca bonaci	SE, W	1, 2, 3, 6	C
	Mycteroperca phenax	n/d	7	C
	Mycteroperca tigris	SE, W, A/S	1, 6	C
	Serranus annularis	A/S	1, 6	C
	Serranus baldwini	SE, W	3	C
	Serranus lucipercanus	SE, W	1, 3, 4, 5	C
	Serranus tabacarius	SE, W	1	C
	Serranus tortugarum	SE, W	1	C
	Serranus phoebe	W	6	C
	Schultzea beta	SE, W	1, 3, 4, 5	P
Grammidae	*Gramma loreto*	SE, W	1, 3	P
	Gramma linki	W, C	1, 3	P
	Gramma melacara	n/d	3, 4, 5	P
	Lipogramma klayi	n/d	1, 3, 4, 5	P
Opistognathidae	*Opistognathus aurifrons*	SE, W	1, 2	P
Apogonidae	*Apogon americanus*	SE, W	2	P
	Apogon pseudomaculatus	SE, W	2	P
Malacanthidae	*Malacanthus plumieri*	SE, SD	1, 2, 7	C
Carangidae	*Carangoides bartholomei*	SE, W	1, 2	C
	Caranx crysos	SE, W	1, 2	C
	Caranx latus	SE, W	1	C
	Caranx lugubris	SE, W	1, 2	C
	Decapterus macarellus	SE, W	1	P
	Decapterus tabl	SE, W	2	P
	Elagatis bipinnulata	SE, W	1, 2	C
Lutjanidae	*Lutjanus analis*	SE, W	1, 2	C
	Lutjanus apodus	SE, W	1, 3, 6	C

Table 3 continued

Family	Genus species	Reef habitat	Sites where abundant	Trophic group
	Lutjanus buccanella	W	1	C
	Lutjanus campechanus	W	6	C
	Lutjanus jocu	SE, W	1, 2, 6	C
	Lutjanus vivanus	n/d	1	C
	Ocyurus chrysurus	SE, W	1, 3, 6	C
	Rhomboplites aurorubens	W	1, 6	C
Haemulidae	*Anisotremus surinamensis*	SE, W	2	C
	Haemulon aurolineatum	SE, W	2	C
	Haemulon parra	SE, W	2	C
	Haemulon plumieri	SE, W	2	C
	Haemulon striatum	n/d	3, 4	C
Sparidae	*Calamus pennatula*	n/d	2	C
Mullidae	*Pseudupeneus maculatus*	n/d	2	C
Chaetodontidae	*Chaetodon aculeatus*	SE, W, A/S	1	P
	Chaetodon aya	A/S	7, 1	P
	Chaetodon guyanensis	n/d	3, 4, 5	n/d
	Chaetodon ocellatus	SE, W	2	C
	Chaetodon sedentarius	n/d	3, 6	C
Pomacanthidae	*Centropyge argi*	A/S	1, 6	H
	Centropyge aurantonotus	A/S	1, 6	H
	Holacanthus tricolor	n/d	1, 3, 4, 5, 7	O
	Holacanthus ciliaris	SE, W	1, 2	O
	Pomacanthus paru	SE, W	2, 7	O
Cirrhitidae	*Amblycirrhitus pinos*	A/S	1	C
Pomacentridae	*Chromis cyanea*	SE, W, A/S	1, 4	P
	Chromis enchrysurus	n/d	1, 6	P
	Chromis insolata	SE, W	1, 4, 5	P
	Chromis scotti	n/d	3, 4, 5	P
	Stegastes partitus	SE, W, A/S	1, 6, 7	P
	Stegastes pictus	SE, W	2	H
Labridae	*Bodianus rufus*	SE, W	2, 6	C
	Bodianus pulchellus	A/S	6, 7	C
	Clepticus parrae	SE, W	1, 3, 4, 5, 6	P
	Halichoeres dimidiatus	SE, W	2	C
	Lachnolaimus maximus		7	C
	Thalassoma bifasciatum	SE, W	1, 6, 7	P
	Thalassoma noronhanum	SE, W	2	P
Scaridae	*Sparisoma atomarium*	A/S	1, 4, 5	H
	Sparisoma frondosum	n/d	2	H
Gobiidae	*Coryphopterus lipernes*	SE, W, A/S	1	C
	Coryphopterus thrix	SE, W	2	C
	Elacatinus figaro	SE, W	2	C
	Risor ruber	SE, W	2	C
Microdesmidae	*Ptereleotris randalli*	n/a	2	P
Acanthuridae	*Acanthurus chirurgus*	SE, W	2	H
	Acanthurus coeruleus	SE, W	2	H
Sphyraenidae	*Sphyraena barracuda*	SE, W	1, 2, 3, 4, 5	C
Balistidae	*Balistes vetula*	SE, W	1, 2, 5	C

Table 3 continued

Family	Genus species	Reef habitat	Sites where abundant	Trophic group
	Canthidermis sufflamen	WC	1, 2	C
	Melichthys niger	WC	1, 2	C
	Xanthichthys ringens	SE, W	1, 4	C
Tetraodontidae	*Canthigaster rostrata*	SE, W	1, 4	C
Diodontidae	*Diodon* sp.	SE, W	2	C

Habitat: *SE* shelf-edge, *A/S* algal-sponge zone, *W* wall, *S* surface, *n/d* no data. Sites: 1, Puerto Rico; 2, Brazil; 3, Bahamas; 4, Jamaica; 5, Belize; 6, Flower Garden Banks; 7, Pulley Ridge. Trophic group: *C* carnivore, *H* herbivore, *O* omnivore, *P* planktivore

is the dominant fleshy alga at Isla Desecheo, Puerto Rico below 25 m (García-Sais et al. 2008). Despite an apparent abundance of edible algae at depth, only 7% of the fish species common or abundant in mesophotic reefs from the tropical Western Atlantic (Table 3) are known herbivores. Whether nutritional value and digestibility of algae declines with depth is unknown (Clements et al. 2009) but should be investigated further.

Conversely, the relative scarcity of deep-water herbivores may contribute to the abundance of some algal species at depth. Reduced herbivory in deep water relative to shallow water has been observed in several MCEs and associated with a low abundance of herbivorous echinoderms (i.e., *Diadema antillarum*) and herbivorous fish (Gilmartin 1960; Van den Hoek et al. 1978; Liddell and Ohlhorst 1988). In Curacao, de Ruyter van Steveninck and Bak (1986) noted that the mass *D. antillarum* mortality in 1983 had only a minor impact on the percent cover of deep-water (40 m) *Lobophora variegata* likely due to a low density of *D. antillarum* at that depth (Nugues and Bak 2008). Van den Hoek et al. (1978) concluded that the relatively high coverage of fleshy and filamentous algae on the deep algal community with presumably lower growth rates than in shallow water reflects very low grazing pressure.

In Jamaica, Belize, the Bahamas, and Cayman Islands, the scarcity of benthic algae on the vertical escarpments may cause low herbivorous abundance on MCEs (Colin 1974, 1976; Lukens 1981; Itzkowitz et al. 1991). However, on shallow reefs, low algal biomass has been associated with heavy grazing and high primary productivity of early succession algal species, which are more palatable to herbivores (Birkeland et al 1985, McClanahan et al. 2000). Alternatively, the low abundance of herbivores observed in MCEs may be related to lower structural complexity. In the Red Sea, habitat complexity declines with depth due to replacement of branching with non-ramose coral morphologies and reduces the availability of shelter for damselfish (Brokovich et al. 2008). In the Florida Keys, Leichter et al. (2008) observed herbivory halos at 50–60 m depths around ship wrecks (i.e., artificial reefs) and found that algal recruitment on settlement plates was low in close proximity to the coral reef. Away from structural refuges, heavy predation pressure on herbivores may limit their abundance and indirectly facilitate high algal cover (Parrish and Bolland 2004).

Physical factors

Hydrodynamics

Hydrodynamic regime and exposure to wave energy are major factors that influence benthic community structure and zonation patterns in shallow water (Wells 1954; Dollar 1982; Sheppard 1982; Grigg 1983). Because water movement associated with surface waves attenuates with depth, mesophotic habitats are partially buffered from rough hydrodynamic conditions, which can set the upper depth distribution limit for fragile organisms (Huston 1985). MCEs are largely sheltered from direct physical damage from episodic storm events but can be subject to indirect effects such as debris avalanches depending on the angle of the reef slope (Bongaerts et al. (2010) this issue; and references therein). In contrast, along-shore currents driven by tidal forcing and wind stress tend to increase with depth along the fore-reef slope (Done 1983), creating more favorable habitat for passive suspension feeders.

In Jamaica, these factors are consistent with the appearance of azooxanthellate gorgonians in appreciable numbers below 45 m (Kinzie 1973). In Hawaii, black corals (Order Antipatharia), which cannot retract their tentacles, generally occur below 30 m, but they can occur shallower in areas sheltered from sediment scour and surface-generated turbulence (Grigg 1976). When transplanted to shallow water, deep-water gorgonians and black corals exhibit high mortality due to rougher water movement and smothering by epiphytic algae (Grigg 1965; Kinzie 1973).

In contrast, scleractinian corals can survive well above their natural upper depth distribution where they are exposed to greater hydrodynamic forces and higher light intensity. In the Red Sea, deep-water zooxanthellate and azooxanthellate corals from 110 to 170 m experienced low mortality after being experimentally exposed to shallower depths (i.e., 40–118 m) for 1 year (Fricke and Knauer 1986). Although transplants of *Leptoseris fragilis* to the shallowest depth (40 m) survived for 1 year, they did not grow and were heavily fouled by algae and epibionts by the end of the experiment (Fricke et al. 1987).

Topography, substrata, and sedimentation

Topography, sedimentation, and availability of suitable substrata are often interrelated and influence the distribution of corals and community structure on MCEs. In general, heavy sedimentation is associated with lower coral abundance (Rogers 1990; Fabricius 2005). On deep fore-reefs, sediment accumulation negatively affects living cover of all benthic species especially on low angle and horizontal ledges (Aponte and Ballantine 2001). On the steep windward fore-reef slope of Enewetak, Colin et al. (1986) concluded that the benthic community was profoundly influenced by downwelling sediments often limiting colonization by sessile invertebrates to indentations and other surfaces protected from sediment accumulation.

Within MCEs, steeper slopes less subject to sedimentation tend to support the highest coral cover, especially at the top of vertical walls (Ohlhorst and Liddell 1988). In areas of heavy sedimentation, water movement exerts significant influence on benthic community structure. Ramose coral morphologies are more resistant to siltation but require more water movement for ventilation (Sheppard 1982; Huston 1985). In contrast, plate-like coral colony morphologies, which are poorly adapted to resist sedimentation, commonly dominate at mesophotic depths (Kühlmann 1983). The predominance of plate-like coral morphologies at depth likely increases the sensitivity of MCEs to sedimentation.

In the northern Gulf of Mexico, the mesophotic community structure of the offshore banks is influenced by the nepheloid layer of turbid bottom water. Banks that are located closer to terrigenous influence and/or are insufficiently elevated above the seafloor are subject to more sedimentation and exhibit marginal coral communities compared to higher relief banks and banks that are further offshore along the outer continental shelf (Rezak et al. 1985).

Rhodolith and rubble fields are a common feature within some MCEs (Reed 1985; Phillips et al. 1990; García-Sais et al. 2008) and influence community structure due to substratum stability. In the Caribbean, an otherwise dominant mesophotic coral, *Montastraea cavernosa,* appears to be excluded from areas of loose substrata, which are often colonized by *Madracis* spp., *Agaricia* spp., and macroalgae. Only a few gorgonian species are able to utilize unstable substratum (Kinzie 1973). In fact, toppling of colonies due to weakening of carbonate substrata from boring organisms was postulated to be a primary cause of natural mortality for large gorgonians in Jamaica and black coral in Hawaii (Grigg 1965).

Low temperature and distributional limits

At high latitudes, low seasonal temperatures are correlated with the environmental limits of zooxanthellate and hermatypic corals (Kleypas et al. 1999). Severe low temperature events (e.g., prolonged exposure to 18°C or short-term exposure to 15°C) can cause rapid mortality in some shallow-water coral species (Jokiel and Coles 1977). In general, temperatures below 15–16°C are considered the long-term lower limit for reef coral survival (Coles and Fadlallah 1991). However, hermatypic corals form communities in some high latitude locations despite prolonged exposure to minimum temperatures as low as 13°C (Yamano et al. 2001). With depth, the thermal environment of MCEs varies considerably by location (Grigg et al. 2008), suggesting that low temperatures may limit coral depth distributions at subtropical latitudes.

However, based on evidence from several tropical locations, decreasing temperature with depth does not appear to limit the depth distribution of zooxanthellate and hermatypic corals at most locations. In the Marshall Islands, Wells (1954) and Colin et al. (1986) surmised that the lower bathymetric limit of hermatypic corals was not imposed by temperature gradient based on recordings ≥20°C above 150 m. In Jamaica, Bermuda, the Red Sea, and the Ryuku Islands, favorable temperatures for coral growth extend well below the lower depth distribution of zooxanthellate corals (Yamazato 1972; Lang 1974; Fricke and Meischner 1985; Fricke and Knauer 1986). However, in Palau, Wolanski et al. (2004) suggested that thermal stress may be responsible for its biologically depauperate mesophotic community. Internal waves can induce large amplitude fluctuations of the thermocline causing temperature at 90 m to vary by 10–20°C.

For macroalgae, global distribution patterns are primarily determined by temperature gradients (Lüning 1990). Tropical floras have a low tolerance for prolonged exposure to low temperatures. In west Florida, annual fluctuations of 10°C may account for the strong seasonality in the deep-water algae (Cheney and Dyer 1974). Decreasing temperature with depth may also influence the zonation and lower depth limit of tropical algae. For instance, chlorophytes of tropical origin containing siphonaxanthin may require higher temperatures than rhodophytes and phaeophyceae (Kirk 1994).

Within tropical regions, cold-water intrusions may encourage temperate algal species to thrive and increase the abundance and diversity of algae in MCEs. In the Northwestern Hawaiian Islands, temperate algal species have been found in deep water (Abbott and Huisman 2003). In the Galapagos Islands, areas with cold-water upwelling have been associated with deep-water kelp forests to 60 m and possibly deeper (Graham et al. 2007).

Despite negative effects of colder temperatures on some tropical algae, upwelling of cold, nutrient-rich water may positively influence distribution and abundance of mesophotic taxa. Modest temperature fluctuations reported from several mesophotic locations have been associated with nutrient and particulate flux to the deep reef enhancing coral growth (Leichter and Genovese 2006). In the Great Barrier Reef, tidally driven upwelling provides nutrients for deep-water *Halimeda* meadows (Drew 2001). In the Florida Keys, upwelling events increase nutrient concentrations and may be responsible for the high rates of benthic productivity in deep-water algae at 40–70 m (Leichter et al. 2008).

Light and upper depth limits

The community structure of dominant mesophotic organisms suggests that high-intensity light in shallow waters may directly limit the upper depth distribution of some species. In Bermuda, Fricke and Meischner (1985) noted that hermatypic coral species that dominate at mesophotic depths are often rare or absent in exposed, shallow-water habitat but can be common in shaded, shallow-water habitat. While space competition remains a primary consideration, intense light, particularly ultraviolet radiation associated with exposed shallow-water locations, can cause mortality of cryptic sessile fauna (Jokiel 1980). On the Great Barrier Reef, Dinesen (1980) observed colonies of cryptic *Leptoseris* spp. growing in gullies exposed to high-intensity light for limited periods and concluded that the time of exposure to high light intensity, and not light intensity itself, influences distribution patterns. Transplant experiments of deep-water zooxanthellate corals to exposed shallow water have demonstrated that if light intensity is too high or increased too rapidly, zooxanthellae of deep-water corals cannot acclimate and are damaged by high light (Dustan 1982; Fricke et al. 1987).

Light and lower depth limits

Using dredge hauls, Vaughan (1907) recorded the deepest records for zooxanthellate corals; however, these records are questionable. In Hawaii, *Leptoseris hawaiiensis* colonies were retrieved from 470 m near Kauai and from 238 m in the Pailolo Channel. The bottom temperatures (8°C) and sea floor substratum (fine sand and mud) reported from these dredge hauls are inconsistent with known environmental limits for obligate zooxanthellate corals (Kleypas et al. 1999). The deepest retrievals of *Leptoseris* spp. reported in Vaughan (1907) likely represent colonies advected to deep water. In contrast, azooxanthellate colonies of facultatively zooxanthellate scleractinians species (e.g., *Oculina vericosa*, *Madracis pharensis*, etc.) are known to inhabit deep, cold-water habitat below the photic zone (Reed 1980, 1981; Cairns et al. 1993).

The deepest in situ observations of zooxanthellate coral growing attached to immovable substrata are at 165 m at Johnston Atoll (Maragos and Jokiel 1986) and at 153 m off the west coast of the Big Island of Hawaii (Kahng and Maragos 2006). In both cases, small, heavily pigmented, horizontal plates of *Leptoseris hawaiiensis* were observed growing widely spaced on barren fossil reef. These observations suggest stunted growth consistent with marginal habitat and light limitation of obligate photosynthetic organisms. Interestingly, zooxanthellate forms of facultatively zooxanthellate corals (e.g., *Oculina* spp., *Madracis* spp., *Astrangia danae,* etc.) appear to have much shallower distributions than their obligate zooxanthellate neighbors.

Attenuation of downwelling light eventually limits the distribution of obligate photosynthetic organisms with depth (Kirk 1994). For reef corals and algae, the underwater light field controls rates of primary productivity, calcification, and growth (reviewed by Falkowski et al. 1990; Barnes and Chalker 1990). The deepest records for zooxanthellate corals by location are generally associated with the highest optical water quality (Table 4; Fig. 2) as measured by the downwelling attenuation coefficient for photosynthetically active radiation ($\mathrm{K_{d(PAR)}}$). Due to latitudinal and seasonal variations in solar insolation as well as variable atmospheric conditions, irradiance of photosynthetically active radiation at the sea surface (surface PAR) varies across time independent of optical water quality. Angle, orientation, and reflectance properties of the substrata can also influence the amount of light available to the benthos (Brakel 1979). Metabolically, the minimum amount of time above an absolute threshold of light intensity may be more relevant for determining lower depth limits than optical water quality per se.

For obligate photosynthetic benthic taxa, maximum depth records may be linearly correlated with optical water quality (i.e., $K_{\mathrm{d(PAR)}}$) where surface PAR is similar. Assuming that downwelling irradiance of light in the ocean attenuates exponentially with depth, the depth ($z_{\min}$) at which a minimum absolute threshold of light intensity ($E_{\min}$) occurs can be represented as $z_{\min} = (\ln \mathrm{E_0} - \ln E_{\min})/K_{\mathrm{d(PAR)}}$, where E_0 represents downward PAR at the ocean's surface (derived from Kirk 1994). Assuming roughly equivalent photosynthetic capabilities within taxa, $E_{\min}$ should be similar for a given taxa across locations. Therefore, the greatest viable depth $z_{\min}$ for a given taxa will vary more strongly with optical water quality ($K_{\mathrm{d(PAR)}}$)

Table 4 Deepest records of zooxanthellate corals observed growing in situ by location with corresponding values for optical water quality (i.e., attenuation coefficient of downwelling photosynthetically active radiation)

Location	Taxa	Depth (m)	$K_{d(PAR)}$ (m^{-1})	% PAR	References
Johnston Atoll	*Leptoseris hawaiiensis*	165			Maragos and Jokiel (1986)
Hawaii	*Leptoseris hawaiiensis*	153	0.0475	0.07	Kahng and Maragos (2006) and Kahng and Kelley (2007)
Red Sea, Gulf of Aqaba	*Leptoseris fragilis*	145	0.047	0.11	Schlichter et al. (1986) and Fricke et al. (1987)
Bahamas, San Salvador	*Agaricia* sp.	119	0.054	0.15	Reed (1985)
Marshall Islands, Enewetak	*Leptoseris* sp.	112	0.045	0.65	Colin et al. (1986)
Belize	*Agaricia fragilis*	107			Busby et al. (1966)
Jamaica (north coast)	*Agaricia* sp.	99	0.060	0.26	Hartman (1973) and Liddell and Ohlhorst (1988)
Puerto Rico	either *Agaricia* or *M. cavernosa*	90	0.065	0.29	Garcia-Sais et al. (2007)
West Florida Shelf	*Agaricia* sp., *Madracis decactis*	80	0.0576	1.00	Phillips et al. (1990) and Jarrett et al. (2005)
Curacao	*Montastraea cavernosa, Agaricia undata*	80	0.063	0.65	Van den Hoek et al. (1978) and Vermeij and Bak (2002)
Bermuda	*Montastraea cavernosa*	78	0.0485	2.28	Fricke and Meischner (1985)
Northern Gulf of Mexico	*Leptoseris cullata*	84			Rezak et al. (1985)
Barbados	*Agaricia* sp.	74			Macintyre et al. (1991)
Okinawa	*Pachyseris speciosa, Favia speciosa*	>70	0.046		Yamazato (1972)
Chagos Islands	Unspecificed	>60			Sheppard (1980) and Sheppard (1981)
East Florida Shelf	*Oculina vericosa* (zooxanthellate)	40	0.071	5.84	Reed (1980)

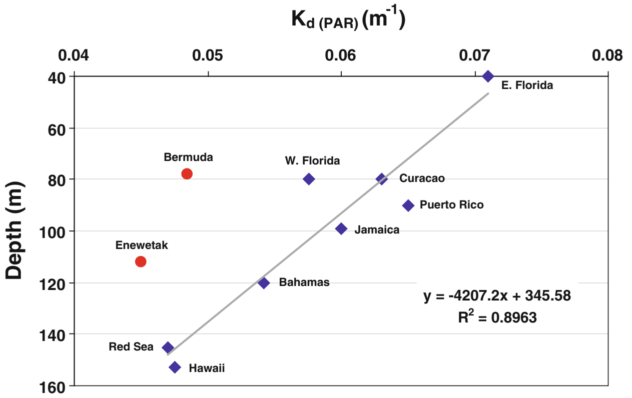

Fig. 2 Attenuation coefficient of downwelling photosynthetically active radiation ($K_{d(PAR)}$) versus depth limit by location for zooxanthellate corals. Bermuda and Enewetak have been excluded from the regression analysis calculation illustrated on the figure

than with surface PAR (E_0). Where additional environmental factors further restrict depth distribution, depth records may be shallower than those predicted by $K_{d(PAR)}$ alone.

A review of available metadata from the coral and algae literature partially supports this light-limitation hypothesis (Tables 4, 5). Maximum depths observed within select photosynthetic taxa do correlate with $K_{d(PAR)}$ across locations. For the green alga *Halimeda*, the relationship is significant ($R^2 = 0.744$, $P < 0.001$) (Table 5; Fig. 3). However, no significant relationship exists for CCA suggesting that other environmental factors are more important than minimum light threshold. Alternatively, reported CCA lower depth limits may be inaccurate due to their cryptic nature and difficulty in locating them in situ.

For zooxanthellate corals, the relationship between $K_{d(PAR)}$ and maximum depth is modest but statistically significant ($R^2 = 0.560$, $P < 0.001$). Excluding outlier values from Bermuda and Enewetak, where persistent cloud cover and downwelling sediments are believed to restrict the lower depth distribution of zooxanthellate corals, respectively (Fricke and Meischner 1985; Colin et al. 1986), reveals an even stronger relationship ($R^2 = 0.896$, $P < 0.001$) (Table 4; Fig. 2). This significant relationship between maximum depth and optical water quality is inconsistent with the notion that zooxanthellate corals readily substitute heterotrophy for photosynthesis with increasing depth (Anthony and Fabricius 2000). Lower optical water quality is generally correlated with higher water column productivity, which can aid heterotrophic benthos including corals (Anthony 2000).

Table 5 Deepest records of articulated green calcareous algae (*Halimeda* spp.) and crustose coralline red algae observed growing in situ by location with corresponding values for optical water quality (i.e., attenuation coefficient of downwelling photosynthetically active radiation)

Location	Taxa	Depth (m)	$K_{d(PAR)}$ (m^{-1})	% PAR	References
Articulated Coralline Algae (Chlorophyte)					
Bahamas, San Salvador	*Halimeda cryptica*	152	0.0475	0.07	Blair and Norris (1988) and Littler et al. (1985)
Enewetak	*Halimeda distorta*	140	0.045	0.18	Hillis-Colinvaux (1986a) and Colin et al. (1986)
Johnston Atoll	*Halimeda gracilis*	136	0.052	0.08	Agegian and Abbott (1985)
Bahamas, Lee Stocking Island	*Halimeda copiosa*	109	0.054	0.28	Aponte and Ballantine (2001) and Reed (1985)
Penguin Bank, Hawaii	*Halimeda copiosa*	106	0.052	0.40	Agegian and Abbott (1985)
Jamaica	*Halimeda* sp.	91	0.060	0.43	Liddell and Ohlhorst (1988)
Crustose Coralline Algae (Rhodophyte)					
Bahamas, San Salvador	Non-geniculate corallines	268	0.0475	0.0003	Littler et al. (1985)
Johnston Atoll	Non-geniculate corallines	250	0.052	0.0002	Agegian and Abbott (1985)
Jamaica	Crustose coralline	240	0.060	0.0001	Lang (1974)
Enewetak	Calcareous red algae	228	0.045	0.0035	Hillis-Colinvaux (1986a)
Penguin Bank, Hawaii	Non-geniculate corallines	182	0.052	0.0078	Agegian and Abbott (1985)
Bahamas, Lee Stocking Island	Peyssonnelia	167	0.054	0.0121	Aponte and Ballantine (2001) and Reed (1985)

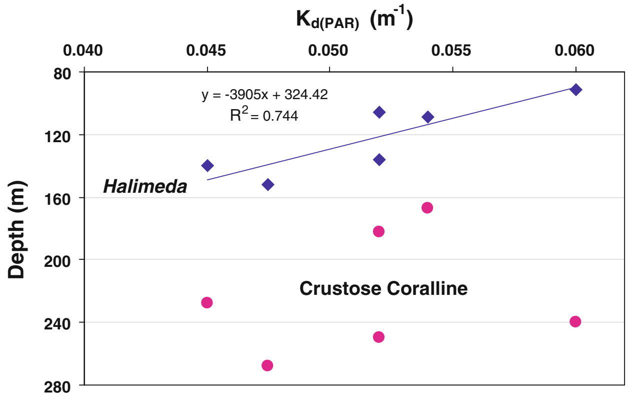

Fig. 3 Attenuation coefficient of downwelling photosynthetically active radiation ($K_{d(PAR)}$) versus depth limit by location for articulated green coralline algae (*in blue*) and crustose coralline red algae (*in red*)

Adaptation to low light at mesophotic depths

Photophysiology

The distribution and abundance patterns of zooxanthellate corals with depth suggest species are differentially adapted to low-light regimes. Zooxanthellate corals adapt to low-light conditions associated with increased depths and shaded habitats in several ways (reviewed by Falkowski et al. 1990; Kirk 1994). Shade-adapted zooxanthellae increase pigmentation at a cellular level by increasing the number and size (as absorption cross section) of the photosynthetic units, but shade-adapted corals do not significantly alter their areal zooxanthellae density. Shade-adapted corals reach their maximum rates of gross photosynthesis (P_{max}) at lower irradiance than their high-light-adapted counterparts. Per unit surface area, shade-adapted corals can exhibit greater photosynthetic capabilities than their high-light-adapted counterparts. However, photosynthetic efficiency or P_{max} normalized per unit chlorophyll *a* (chl *a*) is lower due to self-shading of light harvesting centers.

The limited studies on mesophotic coral photophysiology with depth are not consistent with expected photoadaptative response to low light. In a series of studies on *Leptoseris fragilis* in the Red Sea, zooxanthella densities, total protein, and pigment concentrations per unit area decreased with depth from 100 to 135 m, while pigment content per cell and pigment ratios remained relatively constant (Fricke et al. 1987). Zooxanthella densities per unit area in *L. fragilis* were extremely low compared to shallow-water scleractinians (Kaiser et al. 1993). Transplants from ~115 m to 70 m for 1 year resulted in no change in zooxanthella areal density, and per cell decreases in chl *a* and chl *c*, but no change in peridinin. In contrast, transplants from ~115 m to 160 m (below their natural depth limit) resulted in a sharp decrease in zooxanthella areal density, sharp per cell increases in chl *a*, chl *c*, and peridinin (Kaiser et al. 1993). While the transplant results are somewhat consistent with expected photoadaptative response, the in situ intra-species differences with increasing depth (e.g., decreasing areal pigment concentrations) are not and suggest additional physiological adaptations to low light may apply.

For zooxanthellae found in the lower photic zone, evidence suggests that there are both depth-specialist subclades adapted to the deep reef environment and depth-generalist subclades with broad photo-acclimation plasticity (Chan et al. 2009; Frade et al. 2008a, b). In sympatric, congeneric *Madracis* spp. in Curacao, Frade et al. (2008a) reported vertical zonation of zooxanthella subclades from 5 to 40 m. Within *Madracis pharensis*, relative abundance of B7 and B15 subclades was vertically zoned, and each subclade had distinct cellular properties. Compared to the depth-generalist subclade B7, the zooxanthellae of depth-specialist subclade B15 were larger, occurred in lower areal densities and had higher cellular pigments concentrations and different pigment ratios (Frade et al. 2008b). Interestingly, different light microhabitats at the same depth had no effect on symbiont distribution.

Some mesophotic corals exhibit cellular morphological adaptations with depth, which can increase photosynthetic efficiency. In Jamaica, *Montastraea annularis* complex of sibling species shifts from a multi-layer zooxanthellae arrangement in shallow water to a monolayer in deep water (Dustan 1979). In the Red Sea, *Leptoseris fragilis* in 100–145 m also exhibits monolayered zooxanthellae (Schlichter et al. 1986). Such an arrangement would minimize self-shading of zooxanthellae within the coral tissue.

Based on spectral measurements of *L. fragilis* in the Red Sea, Schlichter et al. (1986) proposed that host fluorescent proteins underlying zooxanthellae enhance photosynthesis under low-light conditions by transforming low wavelength light (which predominates at depth) into longer wavelengths within the action spectra for photosynthesis (Schlichter and Fricke 1991). However, data from Caribbean corals demonstrate that fluorescent proteins do not enhance photosynthesis under low-light conditions (Gilmore et al. 2003; Mazel et al. 2003) and fluorescence resonance energy transfer from fluorescent proteins to chlorophyll does not occur in corals (reviewed by Lesser 2004).

Metabolism

Corals appear to adapt to low-light conditions with depth by decreasing metabolic demand via reduced respiration (Anthony and Hoegh-Guldberg 2003), slower growth, and morphological adaptations. For *Porites lobata* in Hawaii, skeletal growth rate declines exponentially with PAR from 3 to 50 m (Grigg 2006). In the Red Sea, *Leptoseris fragilis* at 90–120 m exhibits skeletal extension rates of 0.5–0.8 mm per year (Fricke et al. 1987), which are much slower than typical shallow-water corals (Crabbe 2009). For several corals, areal polyp density decreases with depth (e.g., Lasker 1981; Villinski 2003; Einbinder et al. 2009), which may lower coral tissue biomass per unit surface area and metabolic demand (Dustan 1979). Coral species with large polyps respire less per unit surface area than corals with small polyps due to lower surface area to volume ratios, which influence metabolite exchange rates (Falkowski et al. 1990). For *Monitpora monasteriata* in the Great Barrier Reef, shade-adapted colonies exhibit lower respiration per unit area compared to high-light-adapted colonies due to thinner layers of tissue (Anthony and Hoegh-Guldberg 2003).

Endolithic algae that supply photosynthate to coral hosts may contribute to a coral's ability to inhabit low-light habitats (Odum and Odum 1955; Fine and Loya 2002). In shallow-water corals, endolithic algae commonly colonize low-light regions of the coral skeleton but are not considered a significant metabolic component (Magnusson et al. 2007; Ralph et al. 2007). However, Schlichter et al. (1997) reported a comparatively high ratio of endolithic algae to coral tissue in deep-water *L. fragilis* compared to shallow-water coral (*Mycedium elephantotus*), which is consistent with a greater metabolic role for endolithic algae at depth. For transplants of *L. fragilis* between 75 and 158 m, endolithic algal biomass adjusted to increased depth and lower light levels by increasing relative to zooxanthellae.

Gross morphology

With increasing depth, zooxanthellate scleractinians adopt flattened morphologies (Kühlmann 1983) to maximize light capture. Analogous changes in morphology with depth are not observed for azooxanthellate species (Fricke and Meischner 1985). Horizontally oriented plates are most efficient at capturing light at depth because the angular distribution of downwelling light narrows with increasing depth (Fricke et al. 1987) due to differential attenuation of scattered light in the horizontal direction. In a comparison of sympatric *Montipora monasteriata* colonies growing in different light regimes, Anthony and Hoegh-Guldberg (2003) found that shade-adapted colonies displayed a growth pattern directed towards expanding surface area rather than volume and exhibited much thinner skeletal plates. Interestingly, zooxanthellate gorgonians with arborescent morphologies well suited for passive suspension feeding exhibit substantially shallower depth limits than their neighboring scleractinian counterparts (Goreau and Wells 1967; Kinzie 1973), probably due to their less efficient light-capturing morphology.

However, not all zooxanthellate corals commonly found in the lower photic zone exhibit flattened morphologies. Species within the genera *Madracis* and *Oculina* have ramose morphologies. *Madracis* species are predominantly zooxanthellate but include species that are facultatively zooxanthellate (e.g., *M. pharensis* and *M. asperula*) and have been found below the photic zone in azooxanthellate form (Cairns et al. 1993; Veron 2000). Similarly, deep-water *Oculina vericosa* colonies are obligate heterotrophs (Reed 2006).

In macroalgae, changes in thallus morphology can also optimize light capture. Norris and Olsen (1991) noted that deep-water green algae had siphonous or giant-celled morphologies that increased total surface area and light capture for photosynthesis. Deep-water *Halimeda copiosa* increases surface area by increasing the diameter of the surface utricles by 15% when compared to shallower plants (Blair and Norris 1988). Under light limitation, thinner thalli (lower carbon content) ensures higher specific growth rates than thicker thalli (Markager and Sand-Jensen 1992). For deep-water species in the order Dictyotales, species with thin thalli have a higher photosynthetic capacity than species with thicker thalli (Peckol and Ramus 1988).

Heterotrophy

Some evidence suggests that corals readily substitute heterotrophy for photosynthesis under low-light conditions associated with depth. Based on in situ respirometry measurements of *Leptoseris fragilis* in the Red Sea, Fricke et al. (1987) determined that only a brief daily interval for positive oxygen production exists at 105 m and concluded the corals must rely primarily on heterotrophy. Based on metabolic measurements of *Stylophora pistillata* collected from 5 to 65 m in the Red Sea, Mass et al. (2007) demonstrated that rates of calcification became decoupled from photosynthesis at the lowest light levels suggesting a primarily heterotrophic metabolism. Over a depth gradient of 50 m, Muscatine et al. (1989) reported that carbon-stable isotopic composition (δ^{13}C) of coral tissue was similar to their zooxanthellae in shallow water but decreased with depth and approached that of oceanic particulate organic matter suggesting a shift to heterotrophy. Indeed, some temperate corals are facultatively zooxanthellate and rely solely on heterotrophy in deep, dark habitats (Reed 1980, 1981; Cairns et al. 1993).

However, recent evidence from stable isotopic analyses in the Red Sea suggests that heterotrophy does not readily replace photosynthesis with depth in some obligate zooxanthellate corals. For *Stylophora pistillata* from 30 to 65 m, Einbinder et al. (2009) reported a proportionate decrease with depth of δ^{13}C for both corals and zooxanthellae to values below that of zooplankton, a result that cannot be explained solely by increased heterotrophy. With increasing depth, the constant δ^{13}C offset between coral tissue and zooxanthellae suggest fast recycling of carbon between coral host and symbionts (Einbinder et al. 2009; Alamaru et al. 2009). For *S. pistillata* and *Favia favus* from 1 to 60 m, Alamaru et al. (2009) also reported no trophic enrichment with depth of nitrogen-stable isotopic composition (δ^{15}N), further suggesting that heterotrophic rates do not increase significantly with depth.

In general, morphological patterns are inconsistent with the hypothesis for increased reliance on heterotrophy with depth. Zooxanthellate corals abundant in the lower photic zone tend to exhibit features inconsistent with effective feeding: two-dimensional, plate-like morphologies, low or decreasing polyp density with depth, and polyps that lack tentacles (Dinesen 1980; Fricke et al. 1987; Goldberg 2002a, b; Einbinder et al. 2009). While some features such as irrigated gastrovascular cavities and mucus “nets” could potentially facilitate feeding (Schlichter 1991; Goldberg 2002a, b), gross morphological characteristics would reduce overall efficiency of passive suspension feeding in contrast to colonial, deep-water azooxanthellate anthozoans which all exhibit functional tentacles and either ramose and/or tall morphologies designed to penetrate the benthic boundary layer (Lumsden et al. 2007).

Differential feeding capabilities have been recorded among zooxanthellate corals, but no association with depth is evident to date. Historically, the degree of heterotrophy in corals was believed to be correlated with polyp size and increasing depth (Porter 1976). However, recent evidence indicates that corals with both large and small polyps can feed effectively (Lesser 2004; Grottoli et al. 2006), and many shade-dwelling zooxanthellate corals have small polyp sizes (Dustan 1979; Dinesen 1983). For the dominant reef-building corals in Hawaii, Grottoli et al. (2006) demonstrated that bleached and recovering *Montipora capitata* was able to meet 100% of its daily metabolic energy requirements via heterotrophy, while *Porites lobata* and *P. compressa* were not. Despite this apparent superiority in heterotrophic feeding capability, *M. capitata* does not dominate the zooxanthellate coral assemblage at mesophotic depths (Kahng and Kelley 2007). Also, the aforementioned depth records for zooxanthellate corals to date appear to be consistent with light limitation and not food availability. Overall, the existing data are inconclusive on the role and importance of heterotrophy in deep-water zooxanthellate corals.

Conclusions

While the MCEs share species distributions with shallow-water reefs, the dominant habitat forming mesophotic species and hence community structure largely differ. Compared to shallow-water reefs, herbivorous fish and invertebrates are relatively scarce possibly due to reduced structural complexity. Many mesophotic taxa appear to be largely excluded from shallow-waters by competition with faster growing photosynthetic taxa, rough hydrodynamic conditions, and/or intense light. Changes in the dominant photosynthetic taxa with depth suggest that mesophotic species have special adaptations which their dominant shallow-water counterparts lack. For obligate zooxanthellate corals, adaptations to low light at extreme depth may include flattened morphologies to maximize light capture, mono-layered zooxanthellae packaging to reduce self-shading (i.e., increase photosynthetic efficiency), and in some cases specialized zooxanthellae. Additional adaptations that minimize metabolic demand at depth include reduction in tissue biomass, thin skeletons requiring less calcification, and slow rates of growth. To date, evidence is conflicting and inconclusive regarding the role and importance of heterotrophy for zooxanthellate corals at extreme depths. With increasing depth, decreasing light but not decreasing temperature appears to limit the depth distribution of zooxanthellate corals and hence MCEs.

MCEs remain unexplored in many parts of the world, particularly in high biodiversity regions of the Indo-Pacific where oligotrophic conditions extend the photic zone to extreme depths. Taxonomy and basic life history traits remain unknown for many dominant mesophotic organisms but are needed to understand population dynamics and resilience of MCEs to disturbance. A quantitative understanding of MCE community structure is required to monitor change across time and gain insight into processes that affect change. For zooxanthellate corals and algae, which form the basis of MCEs, only a cursory understanding exists on their environmental limits and special adaptations, which enable them to survive and dominate at extreme depths. Examining environmental limits of coral reef organisms with depth and isolating individual factors will provide insight into how coral reef communities will respond to both global climate and local environmental changes.

MCEs have long been considered a de facto refuge for shallow-water coral reef ecosystems subject to greater disturbance and higher levels of resource extraction. Additional studies are needed to determine levels of connectivity and the source/sink recruitment dynamics between shallow and deep populations. While technology and operating costs associated with deep-water research remain substantial, the imperative to understand these understudied ecosystems is very high given the pessimistic forecasts on near-shore, shallow-water coral reef ecosystems (Bellwood et al. 2004).

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