



Recent advances in the ecology of mesophotic coral ecosystems (MCEs)

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While substantial mesophotic coral ecosystem (MCE) habitat (>30–40 m) remains uninvestigated, recent investigations show that the extent of both MCE habitat and species diversity is greater than previously thought. The depth distributions and biogeographic ranges for many shallow-water organisms have also been historically underestimated. The upper mesophotic is home to many shallow-water marine organisms and represents a transition zone between shallow-water and lower mesophotic communities. The lower mesophotic represents a distinct community with some species exhibiting special physiological adaptations. Therefore, vertical connectivity is predominantly relevant between the upper mesophotic and shallow-water reefs. In some cases vertical connectivity is restricted due to genetic adaptation to these opposing reef habitats. Horizontal connectivity between MCEs remains largely unknown and represents an important avenue for future research.

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Introduction

Aided by technological advances [e.g., [1–3]] and motivated by concerns about the welfare of coral reef ecosystems, studies on mesophotic coral ecosystems (MCEs) have begun to accelerate in recent years. MCEs are characterized by the presence of light-dependent corals and their associated communities at depths below traditional SCUBA diving (i.e., >30–40 m), and extend to the lower distributional limit of zooxanthellate, reef-building corals [4]. While the lower depth limit of MCEs varies by location due to site-specific environmental factors (predominantly light and temperature, see [5^{**},6^{*}]), the fixed upper depth limit attributed to MCEs

(i.e., 30–40 m) corresponds to the depth limit of conventional SCUBA diving and does not represent a static physiological boundary for marine organisms. Following a NOAA sponsored scientific workshop in 2008 [4], the current scientific understanding of MCEs was reviewed in a special issue of the journal *Coral Reefs* [5^{**},7^{**},8–13]. The purpose of this article is to summarize the literature on the biology and ecology of MCEs that has been published since the last MCE review [5^{**}]. For the purpose of this review, the scope is limited to tropical and subtropical MCEs and does not discuss the mesophotic habitats of temperate locations.

Recent MCE surveys and implications for biodiversity and biogeography

Given the limited exploration of MCEs worldwide, particularly in the Indo-Pacific [see [5^{**}]], recent research conducted at mesophotic depths has substantially advanced the collective understanding of coral reef ecology, especially with respect to biogeography and biodiversity. In the first detailed investigation of coral fauna at mesophotic depths (47–163 m) in the Great Barrier Reef, several new taxonomic records were reported with each representing large biogeographic range extensions [14^{*}]. Similarly, recent MCE surveys are expanding the known biodiversity of coral reef ecosystems including the discovery of new species of fish [15], invertebrates [16–19], and algae [20]. In addition to the discovery of new species, MCE investigations have documented biogeographic range expansions for fish [21], invertebrates [22–24], and algae [25]. In the first application of integrated systematics to dominant mesophotic coral genera in Hawaii, putative new species were discovered and current taxonomic definitions were found to be polyphyletic and in need of revision [26^{**}]. The depth zonation in Hawaii suggests that some species may be deep-water specialists restricted to depths >60 m.

Given the reported and forecasted degradation of shallow-water reef habitat [e.g., [27]], the depth range and connectivity of species between shallow and mesophotic depths have important conservation implications [7^{**},28]. In 2009, the Center for Biological Biodiversity petitioned to list 83 coral species as threatened or endangered under the US Endangered Species Act (ESA), based in part on the widely cited conclusions that 33% of reef-building coral species face an elevated extinction risk in the modern era [29]. This extinction risk assessment relied in part on species-specific lower depth limits, which can buffer populations from shallow-water stressors [29].

However, recent MCE surveys suggest that the reported lower depth limits of many species may be grossly underestimated. For example, *Euphyllia parancora*, one of 66 species proposed for ESA listing by NOAA Fisheries, was recently reported in high abundance at 60–80 m in Saipan [30], well below its previously reported lower depth limit of 30 m [29]. A comparison of the recent MCE data from the Great Barrier Reef [14•] with previously reported data [29] extends the lower depth range for 17 species by an average of 37 m, thereby reclassifying several shallow-water species as depth generalists. A similar comparison of the seven *Leptoseris* spp. in Hawaii [31] with previously reports [29] extends the lower depth range by an average of 64 m. Almost all Indo-Pacific MCEs remain chronically undersampled if not entirely unsampled [32]. Given the lack of sampling, these examples help demonstrate that the absence of observations at mesophotic depths is not evidence for the absence of organisms. The often cited conclusion that 40% of reef-building coral species are restricted to shallow-waters <20 m [29] is clearly premature. To date, the depth-related environmental limits for reef-building corals have not been adequately investigated. Therefore, whether species found in shallow waters also live at mesophotic depths will remain largely unknown until MCE are comprehensively surveyed.

The amount of potential MCE habitat available depends on local geomorphology, has been historically underestimated [33,34], and can greatly exceed that of shallow-water (<30 m) coral reef habitat in some regions [8•,10,11]. Predictive modeling within the Great Barrier Reef suggests that coral reef habitat has been underestimated by as much as 100% [34]. In the absence of direct observations, predictive modeling can be used to estimate coral reef habitat using remotely collected geophysical and environmental data [35]. For MCEs, predictive models based on geophysical data are more robust than those based on environmental data [36•]. Because broad spatial data sets are required, most environmental data used in predictive modeling are derived from georeferenced satellite observations of sea surface or shallow-water optical characteristics [35,36•,37]. However, sea surface conditions such as temperature do not correlate with *in situ* environmental conditions at mesophotic depths [6•].

Recent deep-water surveys of the US Pacific Islands have confirmed the widespread presence of MCEs adjacent to shallow-water coral reef habitat [30]. In American Samoa, corals were reported to depths of 101 m, with coral cover dominated by *Leptoseris* spp. and *Pachyseris* spp. to 70 m. In the Marianas Archipelago, corals were reported at depths >150 m, with the highest coral cover of branching and foliose morphologies at 60–80 m and areas with appreciable coral cover to 100 m. Analogous deep-water surveys in the Hawaiian Archipelago suggest that the depth limits for reef-building corals at the northern

end of the archipelago (observed to 66 m at Kure Atoll, and 55 m at Pearl & Hermes Atoll) may be substantially shallower compared to the Main Hawaiian Islands at the southeastern end of the archipelago (observed to 111 m at Nihoa, 115 at Oahu, 131 m at Maui-Nui, and 153 at Hawaii Island), where areas with high coral cover are commonly observed to at least 100 m [26•,30,38]. This depth pattern for zooxanthellate corals is likely related to a thermal degree-day threshold [*sensu* [39]] associated with the shoaling isotherms along the Hawaiian Archipelago [6•,40–42].

Mesophotic fishes

Recent findings on the community ecology of mesophotic coral reef fishes are consistent with prior studies [reviewed by [5•]], which note that species richness is strongly correlated with coral cover and that species richness and abundance decline with depth [9,43–46]. However, complex non-coral reef habitat also appears to correlate positively with fish abundances [45,47]. Non-natural structures, such as artificial reefs and oil wells, may harbor relatively complex fish communities at mesophotic depths and are capable of sustaining fish populations over many generations [47–49]. Although large fish communities are found on many mesophotic reefs, Boland *et al.* [50] reported that some reefs appear to lack these communities altogether, suggesting that the presence of MCEs alone do not control fish community distributions at these depths [30].

Recent trophic studies also appear to be consistent with past studies [reviewed by [5•]]. Off the Brazilian coast, obligate planktivorous fishes were reported to dominate the mesophotic reefs at depths between 45 and 100 m [45]. On Hawaiian mesophotic reefs (50–80 m), herbivorous fishes are relatively rare [51], adding to the emerging pattern that mesophotic reef fish communities shift from herbivory to carnivory with depth [reviewed by [5•]]. Several prey items have been noted as important in diet studies at mesophotic depths including small-sized zooplankton and larval fish in *Pseudanthias rubrizonatus* at 82–152 m [49], and smaller prey items including fish, mollusks and crustaceans in *Lethrinus rubrioperculatus* at 30–100 m [52]. However, herbivory may still play an important role in some mesophotic reefs. In the Caribbean, Lesser and Slattery [53] report a shift at 46–91 m from predominately coral and sponge-dominated to algae-dominated reefs, after the invasion of the predatory, Indo-Pacific lionfish (*Pterois voltans*) reduced local herbivorous reef fish populations.

Data on the behavior and physiology of mesophotic fishes are sparse, but cleaning behavior of *Bodianus pulchellus* and *Elacatinus phthiropagus*, and mutualism of anemone fishes have each been reported to 60 m in Brazil and the Great Barrier Reef, respectively [54,55]. In the Red Sea, Brokovich *et al.* [56] reported that the planktivorous

damselfish *Dascyllus marginatus* exhibited greater visual acuity in low light at 40 m depth compared to shallow-water conspecifics from 5 m, thus enabling similar diurnal foraging durations despite a greater exposure to limiting light levels at depth.

Coral photophysiology and energetics

Recent studies confirm that zooxanthellate corals exhibit a variety of strategies for growing in deep water where the available light to drive photosynthesis becomes scarce [reviewed in [5**]]. Accumulating evidence suggests that mesophotic corals do not conform to a uniform metabolic strategy at depth as different species exhibit distinct and sometimes opposing photo-physiological adaptations to low light.

A common physiological adaptation to low-light intensity at depth (commonly called shade adaptation) involves high areal pigment concentration to maximize absorbance of ambient light [reviewed by [57]]. This adaptive mechanism of increasing areal chlorophyll (chl) concentrations with depth has been demonstrated for *Montastraea cavernosa* from 3 to 91 m in the Bahamas [58] and for *Seriastrea hystrix* from 20 to 60 m in the Red Sea [59]. However, in Western Australia *Pachyseris speciosa* and *S. hystrix* exhibit opposing trends in chl concentrations at depths from 3 to 60 m [60**]. In the northern Great Barrier Reef, *S. hystrix* does not exhibit a clear trend in areal chl concentrations from 2 to 27 m despite a 10-fold decrease in *in situ* irradiance along this depth gradient [61**].

Increasing evidence also conflicts with the hypothesis that symbionts increase chl *c*₂ (with a blue-shifted absorption peak compared to chl *a*) to adapt chromatically to blue light at depth [62]. Chl *c*₂/chl *a* ratios decline with increasing depths for coral species spanning mesophotic depths [58,59]. In Hawaii, mesophotic corals (>68 m) growing in predominantly blue light exhibit significantly lower chl *c*₂/chl *a* ratios than shallow-water corals (<15 m) exposed to much broader spectra [63**].

Expanding on the work of Enriquez *et al.* [64], new investigations have revealed species-specific differences in light scattering properties of coral skeletons, which enhance light utilization independent of pigment physiology [63**,65]. Despite having superior spectral absorbance, deep-water *Leptoseris* spp. (68–113 m) consistently exhibit lower photosynthetic pigment concentrations than shallow-water *Porites* spp. (2–15 m) in Hawaii [63**]. This seemingly paradoxical relationship is attributed to the micro-scale optical geometry of the coral skeleton which enables *Leptoseris* spp. to more effectively capture light despite having lower pigment concentrations. Skeletal fractal architecture at nano–microscales also influences light scattering and the amount of light available to algal symbionts [65]. Coral species with low skeletal fractality are more efficient at transporting and

redistributing light to illuminate otherwise shaded portions of the colony; however, these species are also associated with a higher risk of bleaching [65].

Given their mixotrophic capabilities, some zooxanthellate corals inhabiting low-light habitats exhibit reduced rates of photosynthesis and/or increased metabolic reliance on heterotrophy [reviewed in [5**]]. Because rates of photosynthesis and heterotrophy can be independent of each other, the photosynthesis to respiration ratio (P/R) is used as an index for the relative reliance on autotrophy versus heterotrophy. In the Bahamas, Lesser *et al.* [58] measured P/R for *M. cavernosa* from 3 to 91 m using skeleton $\delta^{13}\text{C}_s$ data transformed with $\delta^{18}\text{O}_s$ to separate kinetic effects from photosynthetic enrichment [66] and reported the lowest P/R ratios at the deepest depths (61 and 91 m).

On the northern Great Barrier Reef, Bongaerts *et al.* [61**] observed that vertically partitioned *S. hystrix* ecotypes (from 3 to 27 m) retained photo-physiological differences (i.e., symbiont density and chl/cell) 14 months after reciprocal transplantation. Despite these physiological differences, all ecotypes transplanted to the deep-slope (27 m) exhibited similar photosynthetic performance at equivalent light regimes (120–1200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). However, the deep-slope ecotype (27 m) grew faster than the shallow-water ecotypes (2–6 m) transplanted to the deep-slope habitat, suggesting that the deep-slope ecotype engages in more heterotrophy and/or exhibits higher growth efficiency [61**].

In Western Australia, Cooper *et al.* [60**] measured P/R for *P. speciosa* and *S. hystrix* from 3 to 60 m using oxygen respirometry and reported the lowest dark respiration rates and highest P/R ratios for corals from the deepest depths (55–60 m). However, these rates were measured across 15–400 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ which may exceed the *in situ* light regime at these depths. Nonetheless, these combined differences suggest that basal metabolism may contribute to differential growth efficiencies independent of rates of photosynthesis [60**].

Carbon stable isotopic ratios for coral host tissue ($\delta^{13}\text{C}_h$), zooxanthellae ($\delta^{13}\text{C}_z$), and coral skeleton ($\delta^{13}\text{C}_s$) are also used as proxies for measuring relative rates of photosynthesis and relative contributions of autotrophy versus heterotrophy. Consistent with the diffusion depletion hypothesis (*sensu* [68]), Lesser *et al.* [67] reported a decrease in $\delta^{13}\text{C}_h$ and $\delta^{13}\text{C}_z$ with depth for *M. cavernosa* from 3 to 91 m, indicating progressively lower rates of photosynthesis. Additionally, a large difference between $\delta^{13}\text{C}_h$ and $\delta^{13}\text{C}_z$ was observed at the deepest depth (91 m), indicating an equilibrium effect of eating more zooplankton with low $\delta^{13}\text{C}$ (–14 to –25‰) and less translocation of photosynthetically derived organic

carbon from symbiont to host [68]. However, little difference between $\delta^{13}\text{C}_h$ and $\delta^{13}\text{C}_z$ was observed at other depths (45 and 61 m), reflecting no clear trend of photosynthate translocation with increasing depth.

Lesser *et al.* [67] also attributed the incremental decrease in $\delta^{13}\text{C}_s$ from 9 to 46 m to the equilibrium effect of heterotrophy. However, an increase in $\delta^{13}\text{C}_s$ at 61 m conflicts with this trend and interpretation. While Grottooli [69] demonstrated that feeding shallow-water corals unnaturally high concentrations of zooplankton can increase $\delta^{13}\text{C}_s$ due to a nutrient-driven photosynthesis enrichment effect overcoming equilibrium effects, corals in low light (e.g., $80 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) do not always exhibit different rates of photosynthesis between fed and starved colonies [70]. The conflicting effects of eating zooplankton (equilibrium effect) and nutrient-driven photosynthesis enrichment, both from heterotrophy, potentially confound interpretation of $\delta^{13}\text{C}_s$ values with respect to levels of heterotrophy with depth.

Accumulating evidence suggests that the use of $\delta^{15}\text{N}$ in zooxanthellate corals as a proxy for trophic enrichment may not follow previously described relationships in pure animal systems [71]. No trend in $\delta^{15}\text{N}_h$ or $\delta^{15}\text{N}_z$ with depth was observed for *Stylophora pistillata*, *Favia fava* (both from 1 to 60 m), and *M. cavernosa* (from 3 to 91 m) [58,72]. In a controlled experiment, Reynaud *et al.* [73] reported that fed colonies of *Stylophora pistillata* actually exhibited lighter $\delta^{15}\text{N}_h$ and $\delta^{15}\text{N}_z$ compared to starved colonies across a range of light regimes ($80\text{--}300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and attributed this trend to nitrogen-recycling between host and symbiont.

Clearly, not all corals in the lower mesophotic exhibit a uniform metabolic strategy such as traditional shade adaptation. Incremental increases in pigment concentrations can be self-limiting due to declining photosynthetic efficiency per unit pigment [74]. Photosynthetic and growth efficiencies play important roles for some obligate zooxanthellate corals in the lower mesophotic zone, enabling some species to thrive deeper than others. Despite the low levels of ambient light at 90 m in Hawaii, *Leptoseris hawaiiensis* in Hawaii can sustain radial growth rates (1.0 cm/year) that are comparable to some shallow-water coral species despite completely lacking tentacles to facilitate heterotrophy [75].

Mesophotic symbionts

While most reef-building corals host a single *Symbiodinium* type and do not appear to change their symbionts over time [76], habitat-specific symbiont associations have been reported for several coral species in shallow water (<40 m) [reviewed in [7]]. Given the energetic dependence of corals on autotrophy and the photo-physiological differences associated with *Symbiodinium* genotypes [77,78], the vertical zonation of *Symbiodinium* with

depth could contribute adaptive value. For corals with vertical symbiont acquisition, these patterns may also reflect co-evolutionary processes of both symbiont and host [79].

Additional cases of depth-related partitioning of *Symbiodinium* types spanning mesophotic depths have recently been reported for *M. cavernosa* (3–91 m) and *Agaricia lamarcki* (to 70 m) in the Caribbean [58,79,80]. However, depth-generalist *Symbiodinium* types are also common in MCEs, and host specificity can be maintained across a large depth range [81]. For *S. hystrix*, a depth-related partitioning (0–60 m) of *Symbiodinium* clades was reported in Western Australia, but a stable affiliation (0–50 m) was reported in the Red Sea [59,60]. In the Great Barrier Reef, reciprocal transplants of *S. hystrix* colonies (which vertically transmit symbionts) between depth-partitioned host and symbiont genotypes did not result in novel host–symbiont recombinations after 14 months, although limited symbiont shuffling was reported in a couple of instances [61].

In general, the mesophotic *Symbiodinium* community does not appear to be distinct from shallow-water communities, although a few depth-specialist *Symbiodinium* types have been reported [58,81]. Additional sampling of MCEs *Symbiodinium* types will likely uncover novel host–symbiont partnerships, polygamy in types previously reported as host-specialists, and bathymetric range extensions [81].

For coral species with depth zonation of *Symbiodinium* types, differential photo-physiological capabilities may contribute habitat-specific adaptation to mesophotic depths. In Western Australia, the shift from *Symbiodinium* type D1 to C1 in *S. hystrix* with increasing depth (0–60 m) is accompanied by a concomitant increase in the P/R ratio [60]. Cooper *et al.* [60] suggest that colonies with *Symbiodinium* type D1 have a competitive advantage over colonies with *Symbiodinium* type C1 in high-irradiance habitats. However, at lower irradiance, the P/R ratio for *Symbiodinium* type D1 declines in contrast to that for *Symbiodinium* type C1. An analogous shift in the lipid fraction ratio, a measure of nutritional health of a coral colony, was correlated with a shift in *Symbiodinium* type [82]. In shallow water, colonies with *Symbiodinium* type D1 contained high storage lipids which declined with increasing depth from 3 to 23 m. A reversed trend coincided with the shift to *Symbiodinium* type C1 at 23 m with deeper colonies exhibiting higher storage lipids. In contrast, co-occurring *P. speciosa* with *Symbiodinium* type C3 exhibited a uniform trend of decreasing storage lipids throughout its depth range (12–61 m) [82]. These results are consistent with shallow-water studies [e.g., [83–85]] and suggest that *Symbiodinium* type affects holobiont productivity, energetics, and energy stores [60,82].

The recent discovery of *Symbiodinium* within the gastrodermal tissues of several deep-water antipatharian corals previously described as azooxanthellate has raised questions concerning the function and role of *Symbiodinium* as mutualists or parasites [86**]. The *Symbiodinium* genotypes were either identical or closely related to those found in shallow-water scleractinians and were found in a diversity of antipatharian species from 10 to 396 m, thus surpassing previous *in situ* depth records for *Symbiodinium*, zooxanthellate corals and benthic algae [reviewed in 5**]. Similarly, the report of functional diatom plastids found in benthic foraminifera at 600 m off the coast of California demonstrates that alternative functional roles of algal symbionts are likely [87*]. Grzyski *et al.* [87*] hypothesized that algal symbionts may be used to assimilate nitrate, a capability not found in obligate heterotrophic eukaryotes. In the oligotrophic tropical and subtropical oceans, fully oxidized, dissolved inorganic nitrogen (i.e., nitrate) is readily available below the photic zone, while particulate organic nitrogen and other reduced forms decrease exponentially with depth [88].

Compared to corals, less is known about the symbionts associated with sponges; however, recent investigations suggest that microbial symbionts play important roles at mesophotic depths [89,90*,91]. A wide range of microbes are associated with mesophotic sponges, and they can account for up to 40% of a sponge's volume [reviewed by 89,92*]. On tropical reefs, 30–50% of sponges are cyanosponges, and cyanobacterial symbionts can provide >50% of their energetic requirements [92*,93*]. Cyanobacteria have a wider temperature tolerance and capture a wider light spectrum than *Symbiodinium*, and the distribution of cyanosponges exceeds both the latitudinal and depth distributions of zooxanthellate corals [93*,94].

MCE connectivity

Understanding the extent to which MCEs can seed shallow-water reefs is crucial to evaluating the deep reef refugia hypothesis and associated management implications [7**,95]. However, our understanding of connectivity remains limited [reviewed by 96]] and many factors affect connectivity including water currents, available habitat for settlement, fecundity, pelagic larval duration, larval survivorship, and larval behavior [97]. Slattery *et al.* [98] reviewed species distributions, trophic interactions, and two genetic studies between deep and shallow reefs and concluded that the upper mesophotic (30–60 m) is a transition zone or an extension of shallow-water reefs which could function to replenish shallow-water reefs. In the Caribbean, ~25% of coral species span depths from shallow to upper mesophotic depths but few extend below 60 m [7**]. In the lower mesophotic zone (>60 m), levels of depth endemism are moderate for many taxa (20–50%), thus reducing connectivity potential [9,44,47,50,98–100]. Depth partitioning of agariciid coral species in both the Caribbean (2–60 m) and Hawaii (2–

127 m) suggests that depth-related environmental gradients may have influenced the evolution of closely related species [26**,79**].

Measuring genetic structure and levels of larval exchange across depths, recent investigations show that patterns of vertical connectivity appear to be both species and location specific. Many coral species are self-seeding and characterized by limited dispersal [e.g., 7**,101]] which could limit vertical gene flow. The brooding coral *S. hystrix* exhibits strong genetic structure for host and symbiont with depth on the northern Great Barrier Reef [102,103**]; however, little structure was found in NW Australia [103**]. The broadcast spawner *M. cavernosa* exhibits significant structure with depth in Florida but not in the US Virgin Islands or Bermuda [104]. Using amplified fragment length polymorphism (AFLP) markers, Brazeau *et al.* [105] reported genetic structure with depth for *M. cavernosa* in the Bahamas and Cayman Islands.

Using an individual-based stochastic biophysical model of larval dispersal for *P. astreoides* and *M. faveolata* in the US Virgin Islands, Holstein [106] demonstrated considerable potential of mesophotic larvae to settle in shallow water. *M. faveolata* and *P. astreoides* at 35 m are gravid on the same schedule as their shallow-water counterparts with *M. faveolata* exhibiting greater ova production at depth [106].

Horizontal connectivity of shallow-water marine organisms has been more heavily studied compared to that of mesophotic organisms, except for some commercially fished species such as Lutjanidae [e.g., 108,109]]. Recent phylogeographic data for *Lutjanus purpureus* in Brazil and *Lutjanus campechanus* in the Caribbean reveal a single red snapper species throughout the Western Atlantic [110]. Similarly, no genetic structure was found for *Pristipomoides filamentosus* across its wide Indo-Pacific range except for an isolated population in Hawaii [111]. Similarly, little genetic structure was found for the coral *S. hystrix* within the northern Great Barrier Reef [102,103**] and for *M. cavernosa* across the Caribbean [104,112**]. However, Brazeau *et al.* [105] reported genetic structure for *M. cavernosa* between locations in the Caribbean using AFLPs. Even in very well studied species, degrees of population structure can differ among studies due to the application of different molecular markers, extent of sampling, and taxonomic interpretations [e.g., 113–119]]. The restricted geographic distances in the mesophotic corals studied to date also limit the inferences that can be made about their general patterns of horizontal connectivity.

To date, two possible patterns emerge from the connectivity studies of MCEs. First, limited vertical connectivity may exist for some sessile benthic taxa. Factors affecting

this pattern include adaptations to depth-specific environmental conditions, disturbance events freeing habitat for allochthonous propagules, and reproductive behavior [e.g., [102,103^{••}]]. However, few data exist on mobile organisms able to move freely between depths. Second, high horizontal connectivity may be prevalent for many mesophotic organisms both on broad and narrow geographic scales [e.g., [102,103^{••},110,111]]. However, data on MCE horizontal connectivity are very sparse and more research is needed to support any generalized conclusions.

MCE sustainability

For MCEs, depth can buffer the impacts of episodic disturbances [reviewed by [7^{••}]]. While some MCEs can be negatively impacted by large storm events, particularly in areas directly exposed to storm waves or on steep slopes subject to debris avalanches [100,120], others appear to be well insulated from wave stress and thermal bleaching which cause coral mortality on adjacent shallow-water reefs [100,121]. Given the attenuation of light with increasing depth, MCEs are likely to be more adversely affected than their shallow-water counterparts to reductions in optical water quality associated with coastal eutrophication. The available data on the stability of MCEs remain sparse, and long-term data sets on MCEs below 50 m are virtually nonexistent. Therefore, little is known about the direct threats to MCEs and their sustainability with respect to environmental change.

Conclusions

While substantial MCE habitat has yet to be mapped and explored, especially throughout much of the Indo-Pacific, recent investigations have demonstrated that many shallow-water organisms have greater depth distributions than previously reported and for many, their biogeographic ranges have been underestimated due to lack of MCE exploration. While the depth limits of traditional SCUBA diving have prejudiced much of the available data on coral reef ecosystems, shallow-water reef communities readily extend to mesophotic depths where water clarity and warm temperatures remain favorable. Given the sheer magnitude of unsampled and under-sampled coral reef habitat at mesophotic depths, conclusions based on limited observations (e.g., species lower depth limits, exclusivity of host–symbiont associations, etc.) should be tempered with due caution.

Reports of new species and putative new species suggest that species richness will continue to expand with further MCE investigations. The identification of depth specialists and the discovery of special adaptations to low light suggest that the lower mesophotic hosts unique members of the coral reef community with little connection to adjacent shallow-water reefs. In particular, some lower mesophotic coral populations appear to be disconnected

from shallow-water counterparts due to genetic divergence, lack of interbreeding, or lack of larval exchange. The adaptations to the changes in environmental conditions with increasing depth vary by species, and evidence to date suggests that no uniform metabolic strategy applies to all mesophotic corals. Further MCE investigations will likely reveal a diversity of strategies associated with the species which dominate the lower mesophotic. The widespread presence of algal symbionts below the compensation depth for photosynthesis also indicates that much remains to be understood about the ecology of these organisms.

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- of special interest
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