Review Article

Deep thinking: a systematic review of mesophotic coral ecosystems

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Mesophotic coral ecosystems (MCEs) occur at depths beyond those typically associated with coral reefs. Significant logistical challenges associated with data collection in deep water have resulted in a limited understanding of the ecological relevance of these deeper coral ecosystems. We review the trends in this research, covering the geographic spread of MCE research, the focus of these studies, the methods used, how MCEs differ in terms of species diversity and begin to assess connectivity of coral populations. Clear locational biases were observed, with studies concentrated in a few discrete areas mainly around the Atlantic region. The focus of MCE studies has diversified in recent years and more detailed aspects of MCE ecology are now being investigated in particular areas of research. Advances in technology are also reflected in the current range of research, with a wider variety of methods now employed. However, large information gaps are present in entire regions and particularly in relation to the threats, impacts and subsequent management of MCEs. Analysis of species diversity shows that initial definitions based on depth alone may not be appropriate globally, while further taxonomic resolution may also be required to deduce the full biodiversity of major groups in certain regions. Genetic studies to date show species-specific results, although distinct deeper populations do appear to exist, which raises questions regarding the potential of MCEs to act as refugia.

Keywords: connectivity, coral reefs, mesophotic coral ecosystems, twilight zone.

Introduction

Coral reefs are in worldwide decline, due to increased mass disturbance events brought about by climate change and anthropogenic activities (Hughes et al., 2003; Bellwood et al., 2004; Hoegh-Guldberg et al., 2007). However, a majority of the data on which these projections are based are from coral reefs shallower than 20–30 m, while the trends below this depth remain unknown (Bak et al., 2005; Bridge et al., 2013). Deeper mesophotic coral ecosystems (MCEs) are defined as tropical and sub-tropical light-dependent communities occurring from approximately 30 m to the lower limit of the photic zone, extending as deep as 150 m in some locations (Hinderstein et al., 2010). These reefs are perceived as continuations of the shallow reef communities, with a similarly diverse range of taxa (Lesser et al., 2009; Hinderstein et al., 2010). Communities are primarily structured by light (Sheppard, 1982; Lesser et al., 2009) although there are other factors at play, including topography (Bridge et al., 2010), temperature (Kahng et al., 2012), sedimentation, and water movement (Goreau and Goreau, 1973; Sheppard, 1982).

Mesophotic communities have been broadly described (Busby, 1966; Goreau and Goreau, 1973; Bouchon, 1981; Sheppard, 1982; Fricke and Meischner, 1985; Colin et al., 1986; Fricke and Knauer, 1986; Thresher and Colin, 1986) but remain relatively unexplored compared to shallow water reefs, particularly in relation to ecological characteristics and functions. This is primarily due to their location, lying beyond recreational SCUBA diving limits, and therefore posing increased logistical challenges (Lesser et al., 2009; Kahng et al., 2010). Mesophotic reefs are starting to

gain more attention as modern technological advances make them increasingly accessible (Lesser *et al.*, 2009; Kahng *et al.*, 2010). Advances in habitat mapping and technologies such as Remotely Operated underwater Vehicles (ROVs) and Autonomous Underwater Vehicles (AUVs) can provide a useful platform for monitoring these systems (Singh *et al.*, 2004; Armstrong *et al.*, 2006; Bridge *et al.*, 2011a). Increased interest in MCEs is evident in the exponential increase in publications following recent workshops and special journal theme sections (Loya *et al.*, 2016). During the past decade in particular, knowledge of these systems has moved on significantly.

MCEs have only been studied in a few areas of the world resulting in little generalizable knowledge of the drivers of their structure, function, connectivity and refugia role for shallow reefs globally. There is a poor understanding of the role environmental factors have in influencing spatial patterns in community structure, and therefore how MCEs respond to anthropogenic threats and climate change (Puglise *et al.*, 2009; Kahng *et al.*, 2014). MCEs can harbour diverse biological assemblages of corals, fish and other invertebrates consisting of a range of "deep-specialist" and "depth-generalist" species (Bongaerts *et al.*, 2010a; Kahng *et al.*, 2014). Some species are endemic to these systems, highlighting the importance of MCEs in contributing to and maintaining global biodiversity (Heyward *et al.*, 2010; Bridge *et al.*, 2011b; Kane *et al.*, 2014; Muir *et al.*, 2015). As more studies are completed, the limitations to our current knowledge have become evident. For example, studies investigating mesophotic areas of the Great Barrier Reef identified that submerged reef habitat may have been underestimated by as much as 100% (Harris *et al.*, 2012) and new species records for Australia have also been found (Muir *et al.*, 2015).

It has been suggested that MCEs function as refugia, where communities are sheltered from perturbations in shallow waters including high temperature, sedimentation, storm damage and fishing and so may re-seed more frequently disturbed shallow reefs (Bongaerts *et al.*, 2010a; Hinderstein *et al.*, 2010). Larval connectivity needs to be understood, in order to assess the extent of re-seeding potential, including whether species are present in deep and shallow water and how they are connected through the movement of currents (Lesser *et al.*, 2009; Slattery *et al.*, 2011; Baker *et al.*, 2016). A zone that harbours both shallow reef and mesophotic species appears to occur in a number of the locations studied, generally between 30 and 60 m (Lesser *et al.*, 2009; Slattery *et al.*, 2011), often termed the upper-mesophotic. However, in deeper areas, high levels of depth-endemism would suggest greater habitat specialization, and possibly limited larval exchange with shallower waters and a reduced ability to replenish shallow habitats (Slattery *et al.*, 2011). If the community structures between deep mesophotic and shallow coral reefs are different then re-seeding will not be possible.

Information on the distribution and extent of MCEs, the factors that determine their distributions, and the organisms found in these ecosystems, are all critical to inform biodiversity management (Puglise *et al.*, 2009; Baker *et al.*, 2016). The spatial distributions of rare and ecologically important habitats are required to adequately design networks of Marine Protected Areas and ensure representation of all habitat types (Bridge *et al.*, 2016a). Mesophotic reefs are likely to provide similar ecosystem services to those of shallow water reefs and can contribute to fisheries, tourism, and pharmaceutical uses (Eyal *et al.*, 2015; Baker *et al.*, 2016). Identifying the key ecosystem services provided by these

systems is important in order to gain support for their protection (Puglise *et al.*, 2009). Adopting a broad, ecosystem-wide approach that encompasses deep reefs is most likely to have many environmental, social and economic benefits (Bridge *et al.*, 2013).

This review investigates the current literature regarding MCEs. The term "deep coral reef" is often used to refer to much deeper water ecosystems of aphotic species associated with colder water, e.g. *Lophelia pertusa*, defined as living without light (Freiwald *et al.*, 2004). While these ecosystems may occasionally occur in mesophotic depth ranges at high latitudes, such as in Norwegian fjords, or at similar latitudes but at much greater depths (Roberts *et al.*, 2006), they function differently from shallower coral ecosystems; with the term cold-water corals coined to differentiate them from tropical coral reefs (Freiwald and Roberts, 2005). For this review, MCEs will be defined as in Hinderstein *et al.* (2010) as light-dependant coral-dominated systems in tropical regions that form extensions of shallow coral reefs. The aims are to: (1) Characterize study locations and global hotspots of MCE research, (2) Identify trends in MCE research topics, (3) Identify the methods used, including how they have changed over time, (4) Describe how mesophotic biodiversity may differ between locations, and (5) Describe connectivity trends across shallow reefs to mesophotic depths. Assessing the work done so far will allow us to identify and characterize the key aspects of MCEs as well as identifying the key gaps in our understanding to inform future research direction.

Methods

A literature review was carried out following the systematic methods outlined in Pickering and Byrne (2014) and Pickering *et al.* (2015). The databases Google Scholar, Web of Science, and Scopus in May 2016 and February 2017 were searched using the search terms:

mesophotic

AND

reef OR coral OR fish OR sponge OR connectivity OR ecolog* OR community OR recruit* OR impact OR disturbance

The specialist database at mesophotic.org (http://www.mesophotic.org/publications/), maintained by field experts, was also utilized, and all papers were screened for content. As "mesophotic" is a relatively new term to be applied to reef ecosystems, defined in Puglise *et al.* (2009), we further checked references from recent review articles (Lesser *et al.*, 2009; Kahng *et al.*, 2010; Kahng *et al.*, 2014; Baker *et al.*, 2016; Loya *et al.*, 2016) to ensure all relevant papers were acquired. Still, the search was conservative and some papers that did not use the search terms we utilized would not have been identified. Results were limited to those with an English title and abstract.

Studies were screened to ensure relevance in a two-step process outlined below, and results are shown in Figure 1.

(1) Titles and abstracts were required to mention or contain information on:
   (a) mesophotic or deep/twilight reef,
   (b) tropical habitats, and
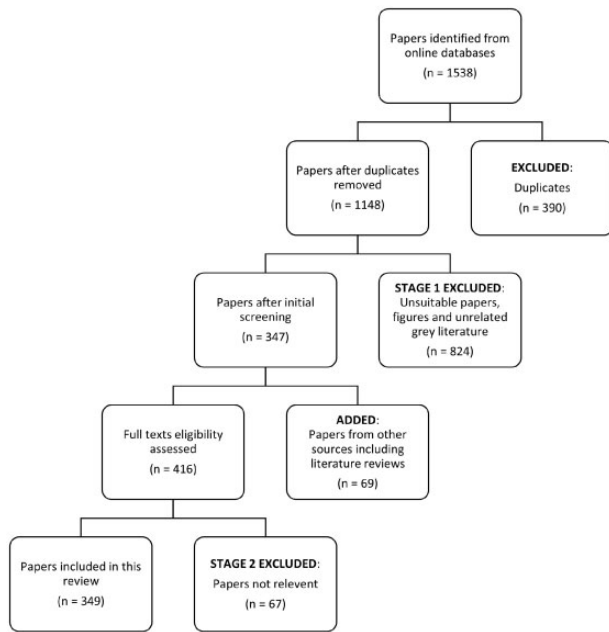   (c) coral reef ecology.

Figure 1. Summary of numbers of papers included/excluded in the process.

(2) Following screening, the full texts of relevant articles were obtained and reviewed. Studies were excluded if the main aims did not concentrate on mesophotic depths and communities (e.g. "deep" areas can relate to less than 10 m in some studies and so would not meet the aims of this review). A study had to encompass a proportion of the 30–150 m depth band defined for mesophotic areas in order to be considered relevant.

In order to gather data to meet Aims 1–3 the following information was recorded for all papers:

- Authors and Title
- Geographic location (including coordinates), split into region [based on those used by Burke *et al.* (2011)], country and study area
- Year
- Primary research focus (Table 1)
- Methods used for data collection
- Depth range investigated

Only a subset of papers provided information to investigate Aims 4 and 5. Mesophotic species diversity, deepest records, or the depth at which significant changes in community structure occur was included in the database when available. Any study that concentrated on genetic differences was investigated for Aim 5. This is currently the most effective method to quantify connectivity between deep and shallow areas: we extracted information on species, whether there was a genetic change with depth and if so what depth the changes occurred.

Data manipulation and analysis was conducted in R (R Core Team, 2010) and figures were constructed using the ggplot2 package (Wickham, 2009). Aims 1–3 involved summarizing the information by location (map produced in ArcGIS 10.4), research focus and method. To address Aim 4 summary statistics were calculated for species diversity and transition depths between

regions. Due to the relatively few data points, a rigorous statistical analysis was not possible for Aims 4 and 5.

Results

A total of 349 papers were classified in this study, spanning from 1966 to 2017. A majority of the studies on mesophotic reefs have been completed since 2010 (56%) (Figure 2), with 54 studies (15%) completed in 2016 alone. Research is concentrated in specific regions and countries (Figure 3) with over half (57%) of global mesophotic studies having been carried out in the Atlantic region, particularly in the Caribbean.

Research into mesophotic reefs is globally very regionally localized. For example, while research spans a number of countries in the Atlantic (Table 2) effort is disproportionally split across them. Additionally, studies can concentrate in specific countries; with Israel (Middle East) and Hawaii, USA (Pacific) contributing to 91 and 71% of the entire studies for that region respectively. A single country, the USA has the greatest number of studies (18%, split over two regions) although they are focussed in geographically small areas with almost all studies occurring in Hawaii (Pacific) and Florida (Atlantic). Australia (13% of global studies) has observed significant modern research interest with 70% of Australian studies occurring since 2010. Again, studies are localized with 50% occurring on the Great Barrier Reef. The Indian Ocean and Southeast Asia are significantly under-represented (1 and 2% of global studies, respectively).

Descriptive studies dominate the MCE literature (Table 3). However, research focus has shifted over time (Figure 4). The proportion of descriptive studies drops from 92% before 1980 to 33% post-2010. Research focus has also diversified, with increases observed in all other research categories between 2001 and 2011 onwards. Studies investigating molecular ecology have seen the largest increase, from zero before 2000 to 7% then 16% in 2001–2010 and post-2010, respectively. These studies are mostly conducted in the Atlantic (47%, exclusively in the Caribbean), Australia (24%) and the Pacific (21%). Life history studies and research focussing on impacts are in their infancy, only occurring since 2000. This work is currently highly concentrated in the Atlantic region with 78% of life history and 59% of impact (including natural and anthropogenic) studies taking place there.

A variety of methods are used to study MCEs (Figure 5). Although lying beyond recreational diving depths, SCUBA diving is the most common method used for most year categories (Second to Submersibles in the 1980s and 1990s). Even prior to 1980, 69% of the studies were completed using SCUBA-based observations, before advances in technical diving such as closed-circuit rebreathers (CCRs), and when health and safety regulations were less conservative. Methods have diversified widely since 2001 as more techniques have become available. Recent studies appear to be utilizing a number of methods as the research focus diversifies. Experimental and genetic labwork are now used more widely, as finer ecological details of MCEs are explored, with large increases in the use of these methods observed from 2011. Technological advances are observed with the arrival of ROVs, AUVs, and Baited Remote Underwater Video (BRUVs) from 2001 onwards. SCUBA remains the most popular method, accounting for 33% of studies post-2010 although labwork, including identification, experiments, and genetics, totals 31%.

Table 1. Primary research focus categories and descriptions.

Category	Description
Anthropogenic impact	Study focuses on identifying the effects of a specific anthropogenic impact (e.g. dredge disposal, fishing) on the ecosystem
Descriptive	A characterizing study, identifying the communities present
Ecosystem function	Study focuses on specific aspects of the ecosystem or the biology of a particular group/taxa
Geomorphology	Study focuses on physical structural features relating to the underlying geology
Life History	Study focuses on life history parameters, such as reproduction and growth characteristics
Management	Study focuses on the ecosystem from a management perspective
Methods	Study focuses on comparing two or more methods
Molecular ecology	Investigation of macromolecules, specifically including genetic studies
Natural impacts	Study focuses on identifying the effects of a specific natural impact (e.g. bleaching, storms) on the ecosystem
Review	Study is a review paper
Structuring variables	Study specifically investigates abiotic or biotic variables that structure the community along a gradient
Taxonomy	Study is specifically focussed on the identification of (new) species
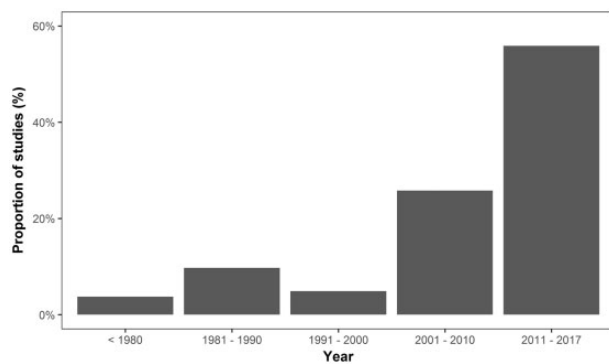
Figure 2. Frequency of publications focussing on MCEs.

Like their shallow-water counterparts, MCEs vary with respect to their location around the globe (Baker *et al.*, 2016). While accurate species numbers are rarely reported, results that could be extracted are summarized in Table 4. No data were available for the Indian Ocean and South-East Asia regions but MCEs harbour high benthic and fish biodiversity in all other regions. Atlantic MCEs are less species-rich in terms of scleractinian corals, but macroalgal and sponge diversity is high. Challenges in species identification are a likely cause of low numbers of sponge and algal studies, particularly as remote methods become increasingly used. Reported transition depths, defined as the boundary where significant changes in species composition are observed, thus representing the transition between upper and lower mesophotic communities, appear variable (Table 5). Fish transition depths appear shallower, however, this is probably an artefact of most fish studies including surveys at shallower depths (Mean start depth $= 22.7 \pm 4.4$ m) with 61% of studies completed using SCUBA. This could be interpreted better as the transition between shallow and "mesophotic associated" fish communities. Most mesophotic benthic studies start at greater depths (Mean start depth $= 40.5 \pm 4.6$ m) covering the entire mesophotic range (Mean end depth $= 218.3 \pm 37.6$ m). Benthic communities in the Atlantic transition to more deep-specialized communities at 60 m. This does not hold globally, with this change occurring at greater depths in the Pacific and Australia.

We have reviewed studies looking at genetic differences between corals and their associated *Symbiodinium* to describe connectivity patterns between MCEs and shallow reefs, and these studies showed distinct differences with depth (58% of records), between and within genera (Table 6; Figure 6). Most genetic differences appear to occur below 30 m potentially implying shallow and deep populations. Six genera (*Acropora, Eusmilia, Helioseris, Meandrina, Montipora,* and *Mycetophyllia*) showed no genetic differences across depth, though most were only sampled in a single study (except $n = 2$ for *Helioseris*).

Discussion

Studies of Mesophotic coral ecosystems (MCEs) are currently highly location and region specific and not represented in all oceans globally. While this is also the case with shallow reefs (Fisher *et al.*, 2011) the imbalance is not as great. A result of the strong locational bias is that there is not enough evidence to suggest an understanding of the ecological role of MCEs in a global context. Data collection in these ecosystems is still relatively expensive, as most methods require specialized equipment and training. It seems likely that this is the main reason why mesophotic studies are concentrated in areas where the initial investments have been made and equipment is available to enable specific research groups to explore these ecosystems. Huge regional gaps are apparent, showing that almost no studies have been conducted in the Indian Ocean and South-East Asia regions. This is of particular concern given the known high biodiversity of shallow coral ecosystems in these regions and the threats they face (Burke *et al.*, 2011).

MCE research has been mainly focussed in the exploratory phase, aiming to characterize the communities in different locations. What we know from these descriptive studies is that there is a common depth/light attenuation pattern in MCE benthic community structure indicating that upper mesophotic depths have a dominance, in terms of percentage cover, of phototrophic taxa, predominantly corals, shifting to primarily heterotrophic communities, made up of sponges and octocorals, of the lower mesophotic (Lesser *et al.*, 2009; Bongaerts *et al.*, 2010a; Kahng *et al.*, 2010; Baker *et al.*, 2016). It is also well understood that light, topography, and temperature stand out as three main factors that influence the structure of MCE communities. Light is the major factor, with the deepest zooxanthellate coral records associated with areas known for clear water (Kahng *et al.*, 2010; Baker *et al.*, 2016). Topography is also important, with local bathymetric features, such as slope, influencing benthic community structure (Bridge *et al.*, 2010; Locker *et al.*, 2010; Sherman *et al.*, 2010; Englebert *et al.*, 2017). Temperature is influenced by local upwelling (Bridge *et al.*, 2010) and internal waves (Kahng
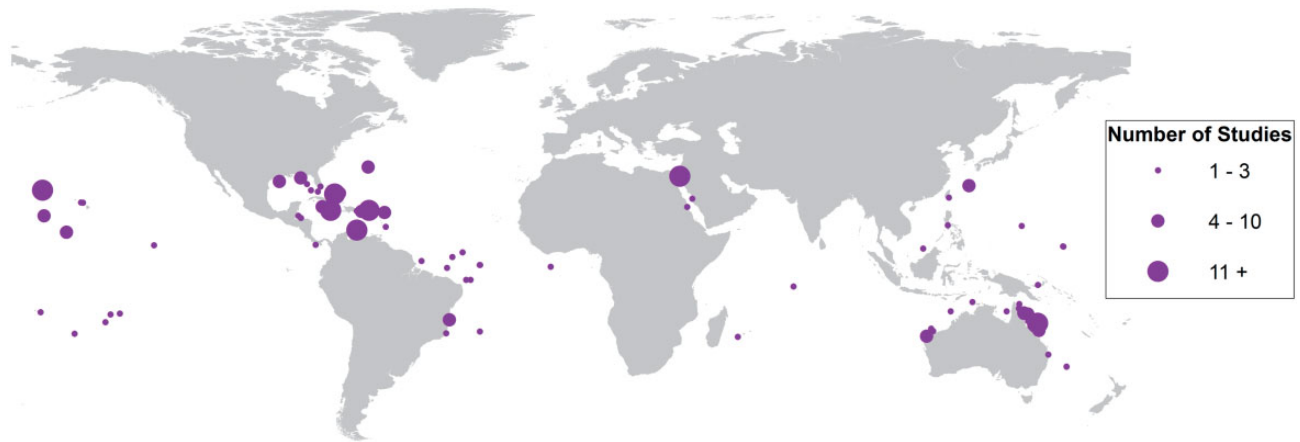
Figure 3. Global MCE research distribution (number of studies per country).

Table 2. Studies completed on mesophotic reefs by region and country.

Region	Country	Number of studies	
Atlantic	Bahamas	26	7.2%
	Barbados	1	0.3%
	Belize	1	0.3%
	Bermuda	8	2.2%
	Bonaire	5	1.4%
	Brazil	19	5.3%
	Cayman Islands	7	1.9%
	Curacao	26	7.2%
	Guinea	1	0.3%
	Honduras	3	0.8%
	Jamaica	11	3.1%
	Mexico	2	0.6%
	Panama	2	0.6%
	Puerto Rico	36	10.0%
	US Virgin Islands	33	9.2%
	USA	19	5.3%
Australia	Australia	50	13.9%
Indian Ocean	Chagos	2	0.6%
	Réunion	1	0.3%
Middle East	Egypt	1	0.3%
	Israel	30	8.3%
	Saudi Arabia	1	0.3%
	Sudan	1	0.3%
Pacific	Cook Islands	1	0.3%
	French Polynesia	3	0.8%
	Marshall Islands	6	1.7%
	Micronesia	6	1.7%
	Panama	1	0.3%
	Samoa	2	0.6%
	USA	47	13.1%
Southeast Asia	Brunei	1	0.3%
	Japan	4	1.1%
	Papua New Guinea	1	0.3%
	Philippines	1	0.3%
	Taiwan	1	0.3%

and Kelley, 2007; Kahng *et al.*, 2012). This affects depth limits of organisms (Kahng *et al.*, 2012) particularly at higher latitudes (Grigg, 2005) where corals are already residing close to their physiological limits. As the processes associated with MCEs have

become better understood, fewer descriptive studies are being carried out and a greater proportion are focused on understanding ecological processes. Moving forward there is more need for studies to be targeted in locations with varying combinations of these influencing factors, as well as proving these trends hold in currently unstudied regions.

We still know little about the pressures that MCEs face, from both anthropogenic and natural sources. The "deep reef refugia" hypothesis suggests that mesophotic areas are more remote from these threats and may re-seed impacted shallow areas (Bongaerts *et al.*, 2010a; Hinderstein *et al.*, 2010). Locational differences occur for natural impacts, for example coral bleaching and disease are reported mainly in the Caribbean (Garcia-Sais *et al.*, 2007; Nemeth *et al.*, 2008; Smith *et al.*, 2015) whereas storm impacts are common in western Pacific areas (Harmelin-Vivien and Laboute, 1986; Bongaerts *et al.*, 2013b; White *et al.*, 2013). Human impacts are currently poorly documented and although localized studies are occurring (Appeldoorn *et al.*, 2015), not enough evidence is available to discuss global or regional trends and threats. Additionally, recovery rates appear to be largely unknown. This is inevitable given that current impacts on MCEs are likely unnoticed or unquantified. This kind of longitudinal information is crucial for effective management of these systems. Additional gaps lie around the direct measurements of life history characteristics and post-settlement processes of benthic organisms at mesophotic depths. Further work into life history dynamics of mesophotic organisms will give an insight into resilience and recovery when faced with disturbances. Conflicting results have been found in terms of fecundity and spawning synchrony of mesophotic coral colonies (Holstein *et al.*, 2015; Prasetia *et al.*, 2016) that also vary between species and locations (Eyal-Shaham *et al.*, 2016). These variations highlight that we know little regarding this subject, which is a concern for managers.

Technological advances have made a range of techniques available for studying MCEs; however, the cost of many of these techniques impacts on the extent to which they are used for data collection. Technical SCUBA diving, despite the training and equipment required, tends to be a cheaper option hence its popularity. The advantage of diving is that it permits investigation of organisms *in situ*, allowing easier species identification and more precise sample collection. ROVs are commonly utilized for sample collection in the more inaccessible Cold-Water Coral (CWC)
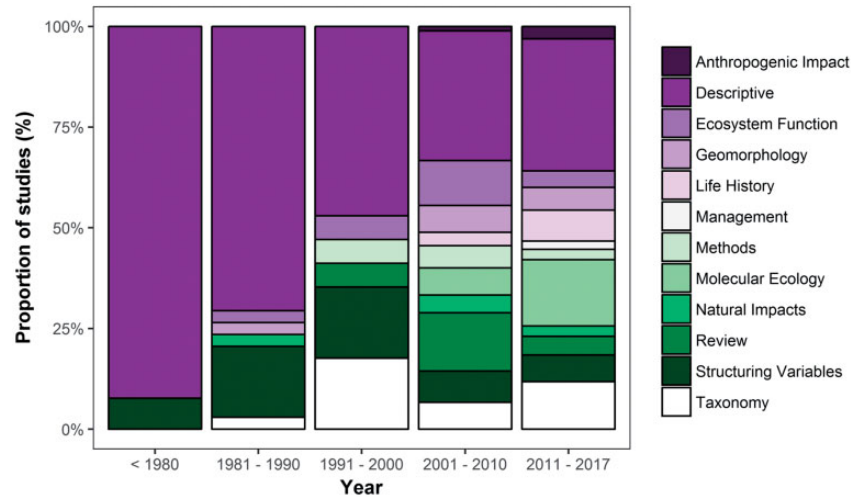
Figure 4. Research focus of mesophotic coral ecosystem studies over time.

Table 3. Primary research focus of studies on mesophotic coral ecosystems.

Research focus	Number of studies	
Descriptive	137	39.3%
Molecular Ecology	38	10.9%
Taxonomy	33	9.5%
Structuring Variables	30	8.6%
Review	23	6.6%
Ecosystem Function	20	5.7%
Geomorphology	18	5.2%
Life History	18	5.2%
Methods	11	3.2%
Natural Impacts	10	2.9%
Anthropogenic Impact	7	2.0%
Management	4	1.1%

ecosystems where the simultaneous use of video allows increased sampling precision and minimal damage (Fosså *et al.*, 2005). There is a lack of precise benthic species diversity data, in particular for difficult to identify macroalgae and sponges, so it is important that this taxonomic detail is not lost, and rather targeted to assess specific community structures. However, diving only allows small areas to be surveyed, which may not meet management goals, and additional health and safety concerns associated with technical diving may mean remote methods are more appropriate in some areas.

Acoustic methods cover large areas and allow geophysical variables to be measured at fine scales, where reef corals show distinct bathymetric signatures (Brown *et al.*, 2011). Acoustic data have proven to be highly successful for identifying the extent of CWC ecosystems (Fosså *et al.*, 2005; Roberts *et al.*, 2009; Buhl-Mortensen *et al.*, 2015). Estimates of total habitat area can be deduced and the information can be used for habitat suitability modelling to identify areas of likely occurrence, which has performed well when applied to mesophotic habitats, given the knowledge of the key structuring variables (Bridge *et al.*, 2012; Costa *et al.*, 2015). Detailed bathymetric information allows for planning of future surveys and can assist with ROV navigation, particularly in areas of high rugosity (Fosså *et al.*, 2005).

ROVs are often used to provide qualitative visual information to explore new areas (Kahng and Kelley, 2007; Bongaerts *et al.*, 2011a; Blythe-Skyrme *et al.*, 2013; Englebert *et al.*, 2014), commonly prior to committing divers or to survey depths >150 m. Samples collected from ROVs have allowed the detailed taxonomy of mesophotic corals (Muir *et al.*, 2015) as well as further lab experiments (van Oppen *et al.*, 2011). CWC ecosystems have utilized ROVs to deploy additional equipment and set up *in situ* experiments (Roberts *et al.*, 2009) which are an approach that should be considered for MCEs. AUVs, while unable to collect samples, can offer a more quantitative approach to obtaining imagery. Hundreds of thousands of accurately georeferenced images may be collected, as well as accompanying environmental information (Williams *et al.*, 2012; Pizarro *et al.*, 2013), while also having the advantage of running independently to the deployment vessel. AUVs have the capability to accurately perform repeat monitoring surveys and relocate colonies (Pizarro *et al.*, 2013; Ferrari *et al.*, 2016) which enable an insight into processes such as growth rates in the future. In terms of costs per area surveyed remote methods may be cheaper, although their ability to fill data gaps surrounding life history traits may be limited; however they may be complemented by diving surveys and experiments.

High biodiversity is common across MCEs of all regions (Baker *et al.*, 2016) although there is still further biodiversity to be discovered as mentioned above. High taxonomic resolution is required to assess connectivity, as will be discussed, where species-specific differences are observed. Depths at which communities change appear to be area-specific and evidence appears to suggest that using depth alone as a basis for universal definitions may not be appropriate. The depth of the transition zone, representing a shift in upper and lower mesophotic assemblages also varies between locations. While 60 m is commonly reported (Fricke and Meischner, 1985; Liddell and Ohlhorst, 1988; Bongaerts *et al.*, 2010a; Bridge *et al.*, 2010; Slattery *et al.*, 2011) on average this only applies to the Atlantic region. In the Pacific and the Coral Sea, the transition zone depth extends past 80 m (Kahng and Kelley, 2007; Pyle *et al.*, 2016; Englebert *et al.*, 2017). Equally, mesophotic depths are shallower for locations with lower light regimes, such as Ningaloo, Australia (Rees *et al.*, 2004) or
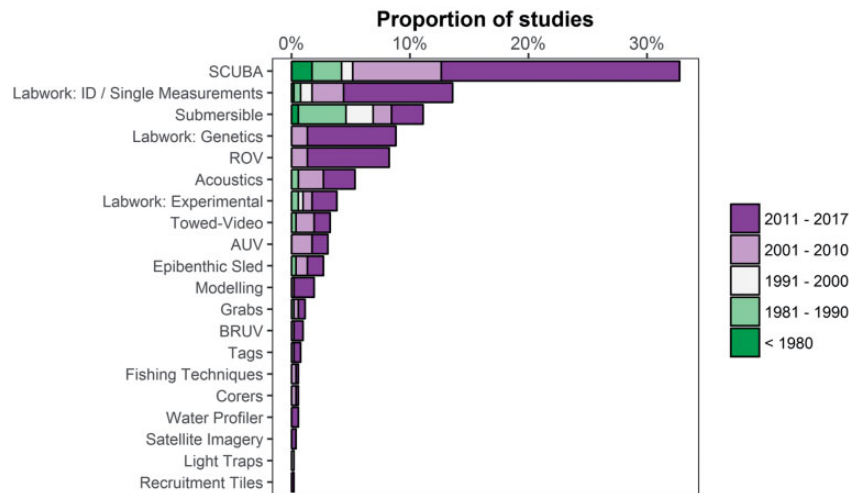
Figure 5. Methods used in mesophotic studies. SCUBA = Self-Contained Underwater Breathing Apparatus, ROV = Remotely Operated Vehicle, AUV = Autonomous Underwater Vehicle, BRUV = Baited Remote Underwater Video.

Table 4. Mean species richness at mesophotic depths (>30 m) for each region ± Standard Error.

Region	Macroalgae	Scleractinian coral	Fish	Sponge
Atlantic	90.3 (± 25.9, $n = 4$)	16.3 (±1.7, $n = 18$)	77.3 (±9.2, $n = 16$)	79.6 (±28.8, $n = 9$)
Australia		32.0 (±3.0, $n = 3$)		240.4 (±37.7, $n = 5$)
Middle East		48.0 (±20.3, $n = 3$)	139 ($n = 1$)	
Pacific	69.8 (± 7.6, $n = 4$)	27.6 (±6.6, $n = 5$)	132.7 (±6.6, $n = 7$)	

Blanks show no data available for that region.

Table 5. Mean transition depth between benthic and fish communities for each region ± Standard Error.

Region	Benthic	Fish
Atlantic	60.9 m (±4.68, $n = 12$)	63.1 m (± 4.9, $n = 8$)
Australia	75.3 m (±3.4, $n = 15$)	49 m ($n = 1$)
Middle East		50.0 m (±0.0, $n = 2$)
Pacific	74.7 m (±3.6, $n = 7$)	61.3 m (±16.1, $n = 9$)

Blanks show no data available for that region.

Pohnpei, Micronesia (Muir and Wallace, 2016) and reduced temperature, such as Bermuda (Fricke and Meischner, 1985). This raises questions about the ecological relevance (Laverick et al., 2016) for the global definition of the transition to MCEs of 30–40 m (Puglise et al., 2009; Hinderstein et al., 2010; Baker et al., 2016).

Most mesophotic fish surveys use SCUBA-based methods and often make use of lengthy decompression schedules to collect accompanying shallow water data (Lombardi and Godfrey, 2011; Andradi-Brown et al., 2016a) so as to allow comparisons to be made. High proportions of fish species are common to both shallow and lower mesophotic areas across regions (Bejarano et al., 2014; Wagner et al., 2014; Lindfield et al., 2015), while genetic similarities are also described (Tenggardjaja et al., 2014). Ontogenic movements are also reported (Brokovich et al., 2006; Rosa et al., 2015; Andradi-Brown et al., 2016b) suggesting movement is common across depths. Given these findings, reported transition depths seem to represent the change from shallow water to mesophotic associated fish communities, in contrast to benthic communities where transition depths represent the change from upper to lower mesophotic; having already seen a shift from shallow waters. While changes in the benthic composition are likely to affect distributions of fish species (Garcia-Sais et al., 2007; Brokovich et al., 2008; Garcia-Sais, 2010): corals may decrease but sponges and other benthic organisms can provide structural habitat (Bell et al., 2013) at depth. Other factors may be structuring fish communities, such as food availability, given the distinct changes in functional groups observed (Bridge et al., 2016b).

Assessing connectivity between shallow and deep reefs is a primary focus in the published literature, and more studies are being undertaken in this research area. Vertical connectivity will ultimately determine whether MCEs can re-seed shallow coral reefs following chronic disturbances. Questions do remain over how genetic changes in *Symbiodinium* correlate with that of their hosts. However, given that host specificity is common and specific adaptation to environmental conditions are likely to have evolved (LaJeunesse et al., 2004; Frade et al., 2008b; Finney et al., 2010) differences probably indicate genetic separation of shallow and MCEs (Bongaerts et al., 2010b,c). Populations below 30 m are reported as unconnected to shallower conspecifics, with distinct shallow and deep genetic populations found (Brazeau et al., 2013). Deeper coral populations are specialized to lower light conditions, showing changes in morphology (Fricke and Meischner, 1985; Einbinder et al., 2009; Nir et al., 2011), photosynthetic efficiency (Lesser et al., 2010; Mass et al., 2010; Nir et al., 2011; Einbinder et al., 2016), and alternative nutrient sources (Muscatine et al., 1989; Einbinder et al., 2009; Crandall et al., 2016). Isolated reefs appear to have higher vertical genetic
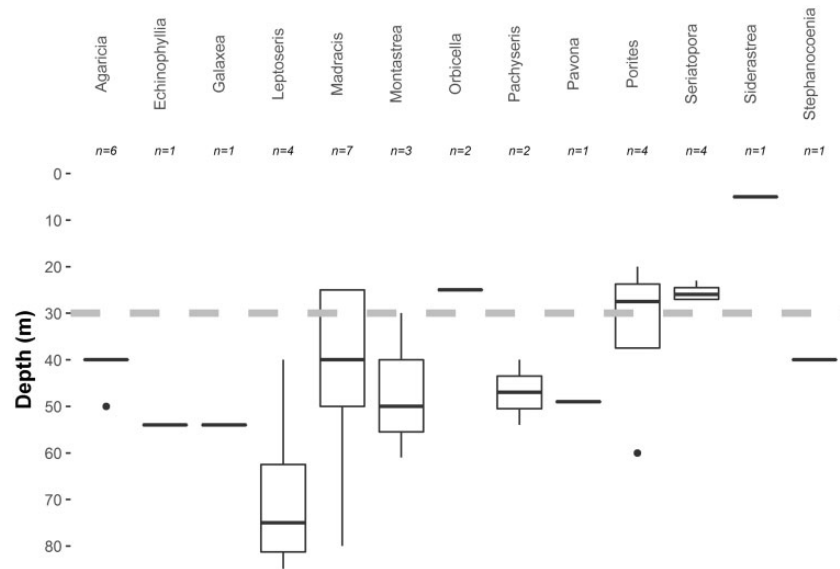
Figure 6. Depths at which genetic changes in corals and their *Symbiodinium* occur.

Table 6. Numbers of records of whether genetic differences in corals of their *Symbiodinium* occur (Yes) or do not occur (No) with depth.

Genera	Species	No	Yes	Depth range investigated	References
Acropora	*Acropora elegans*	1		10–48 m	(Bongaerts *et al.*, 2011c)
Agaricia	*Agaricia agaricites*	2		5–50 m	(Bongaerts *et al.*, 2013a, 2015a)
	Agaricia fragilis		1	12–40 m	(Bongaerts *et al.*, 2017)
	Agaricia grahamae	1	1	15–90 m	(Bongaerts *et al.*, 2013a, 2015b)
	Agaricia lamarcki		3	10–70 m	(Bongaerts *et al.*, 2013a, 2015a; Lucas *et al.*, 2016)
	Agaricia undata		1	15–90 m	(Bongaerts *et al.*, 2015b)
Echinophyllia	*Echinophyllia aspera*		1	10–62 m	(Bongaerts *et al.*, 2011c)
Eusmilia	*Eusmilia fastigiata*	1		5–40 m	(Bongaerts *et al.*, 2015a)
Galaxea	*Galaxea astreata*		1	10–55 m	(Bongaerts *et al.*, 2011c)
Helioseris	*Helioseris cucullata*	2		25–45 m	(Bongaerts *et al.*, 2013a, 2015a)
Leptoseris	*Leptoseris hawaiiensis*		1	10–70 m	(Bongaerts *et al.*, 2011c)
	Leptoseris spp.	1	3	1–127 m	(Chan *et al.*, 2009; Luck *et al.*, 2013; Pochon *et al.*, 2015; Ziegler *et al.*, 2015)
Madracis	*Madracis carmabi*	1		5–40 m	(Frade *et al.*, 2008b)
	Madracis decatis	2		5–40 m	(Frade *et al.*, 2008b; Bongaerts *et al.*, 2015a)
	Madracis formosa	2	1	5–60 m	(Frade *et al.*, 2008a,b; Bongaerts *et al.*, 2015a)
	Madracis mirabilis	1	1	5–40 m	(Bongaerts *et al.*, 2015a),
	Madracis pharensis		5	5–90 m	(Frade *et al.*, 2008a,b; Bongaerts *et al.*, 2015a,b)
	Madracis senaria	2		5–40 m	(Frade *et al.*, 2008a,b)
Meandrina	*Meandrina meandrites*	1		5–40 m	(Bongaerts *et al.*, 2015a)
Montastrea	*Montastrea cavernosa*		3	3–91 m	(Lesser *et al.*, 2010; Brazeau *et al.*, 2013; Bongaerts *et al.*, 2015a)
Montipora	*Montipora spp.*	1		10–70 m	(Bongaerts *et al.*, 2011c)
Mycetophyllia	*Mycetophyllia ferox*	1		25–40 m	(Bongaerts *et al.*, 2015a)
Orbicella	*Orbicella faveolata*		1	5–25 m	(Bongaerts *et al.*, 2015a)
	Orbicella franksi		1	10–25 m	(Bongaerts *et al.*, 2015a)
Pachyseris	*Pachyseris speciosa*	1	2	1–62 m	(Bongaerts *et al.*, 2011c; Cooper *et al.*, 2011; Ziegler *et al.*, 2015)
Pavona	*Pavona spp.*		1	10–59 m	(Bongaerts *et al.*, 2011c)
Porites	*Porites astreoides*	2	3	2–30 m	(Bongaerts *et al.*, 2015a; Serrano *et al.*, 2016; Reich *et al.*, 2017)
	Porites spp.	1	1	1–70 m	(Bongaerts *et al.*, 2011c; Ziegler *et al.*, 2015)
Seriatopora	*Seriatopora hystrix*	3	4	2–57 m	(Bongaerts *et al.*, 2010b,2011b,c; Cooper *et al.*, 2011; Nir *et al.*, 2011; van Oppen *et al.*, 2011)
Siderastrea	*Siderastrea siderea*		1	2–50 m	(Bongaerts *et al.*, 2015a)
Stephanocoenia	*Stephanocoenia intersepta*	1	1	10–60 m	(Bongaerts *et al.*, 2015a, 2017)

connectivity, possibly due to the importance of localized recruitment for sustaining populations (Serrano *et al.*, 2016) or reduced competition following disturbance which may prevent localized extinctions (van Oppen *et al.*, 2011; Sinniger *et al.*, 2012; Muir *et al.*, 2015). However, using Bermuda as an example, not all species show this pattern of strong vertical connectivity (Bongaerts *et al.*, 2017). The reproductive mode may give some insight, with broadcast spawning genera generally showing reduced genetic partitioning with depth (Bongaerts *et al.*, 2011c, 2017) although this is not exclusive (Bongaerts *et al.*, 2015a). Local environmental conditions also play a role, and light levels will ultimately influence the upper and lower limits of coral species and their *Symbiodinium* types due to functional adaptations (Frade *et al.*, 2008a,c). This again calls into question the use of only depth to define deep and shallow MCEs. Overall, the findings in this review show that differences in vertical connectivity patterns at species and genera level are common across MCEs globally. These results highlight our limited knowledge, and the need for these studies to be done at both localized scales, for a detailed analysis of local populations, and across biogeographic ranges.

Conclusions

The importance of mesophotic areas is now recognized in the scientific community. There is a clear locational bias of the existing research to the Atlantic, and specifically the Caribbean, which makes the extrapolation of findings to the rest of the world difficult. Definitions coined from data in this region alone need to be redefined as more studies are completed globally. A clear priority is to collect data for MCEs in South East Asia and the Indian Ocean. Remote methods are clearly advancing research in this field, though it is important to not lose taxonomic detail, given the apparent species and location specificity of connectivity patterns. If shallow and deep populations are separate, then management plans need to accommodate this in order to conserve the different biodiversity of both of these light-mediated ecosystems. The current lack of information about the threats and impacts on MCEs needs to be addressed immediately so that they can be identified at local, regional, and global scales so that effective management can be implemented. Further prioritization of such studies, as well as those investigating connectivity at both local and regional scales, is clearly required, to ensure adequate protection of these ecosystems and their shallow water counterparts, for which relying on MCEs as refugia may not be appropriate.

Acknowledgements

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