Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems

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Abstract

Mesophotic coral ecosystems (MCEs) and temperate mesophotic ecosystems (TMEs) have received increasing research attention during the last decade as many new and improved methods and technologies have become more accessible to explore deeper parts of the ocean. However, large voids in knowledge remain in our scientific understanding, limiting our ability to make scientifically-based decisions for conservation and management of these ecosystems. Here, we present a list of key research and conservation questions to enhance progress in the field. Questions were generated following an initial open call to MCE and TME experts, representing a range of career levels, interests, organizations (including academia, governmental, and non-governmental), and geographic locations. Questions were refined and grouped into eight broad themes: (1) distribution, (2) environmental and physical processes, (3) biodiversity and community structure, (4) ecological processes, (5) connectivity, (6) physiology, (7) threats, and (8) management and policy. Questions were ranked within themes, and a workshop was used to discuss, refine, and finalize a list of 25 key questions. The 25 questions are presented as a guide for MCE and TME researchers, managers, and funders for future work and collaborations.

Keywords: mesophotic, mesophotic coral ecosystems, temperate mesophotic ecosystems, research priorities, research questions

Introduction

In the 21st century, marine systems—including tropical, subtropical, and temperate reef ecosystems—are facing escalating threats from human-induced and natural pressures (Pandolfi et al. 2011; Hughes et al. 2017). The future of these ecosystems now largely depends on establishing innovative partnerships, redefining management and conservation goals, and building institutions for effective governance (Hughes et al. 2017; Mumby 2017). To do this appropriately and effectively, researchers and policymakers must have a fundamental understanding of reef ecosystems, and how humans interact with them. A sound scientific comprehension of ecosystem functioning and the ability of reef-associated organisms to adapt to environmental change are essential (Hume et al. 2016; Torda et al. 2017). To achieve these goals the key areas of knowledge that need to be researched must be identified (Sutherland et al. 2011; Parsons et al. 2014).

Compared to shallow-water reef ecosystems, mesophotic coral ecosystems (MCEs) and temperate mesophotic ecosystems (TMEs) have received relatively little research attention. Knowledge of their distribution, biodiversity, community structure, and ecological processes remains limited (Baker et al. 2016; Puglise and Colin 2016; Turner et al. 2017). MCEs are defined as light-dependent reef communities in tropical and subtropical waters ~30–150 m depth, containing diverse assemblages of corals (including Scleractinia, Octocorallia, and Antipatharia), algae, sponges, and fishes (Hinderstein et al. 2010; Kahng et al. 2010; Loya et al. 2016; Baldwin et al. 2018). While corals are present on MCEs, they are not necessarily the dominant benthic taxa (Hinderstein et al. 2010; Kahng et al. 2010). In temperate areas, TMEs are also defined as light-dependent communities located at ~30–150 m depth, and are mainly dominated by algae generating complex three-dimensional structures with a high-diversity of anthozoans, sponges, fishes, and other associated species (Ballesteros 2006). While the number of MCE and TME studies has increased substantially in the last decade (Loya et al. 2016), research in these systems remains problematic, with increased logistical and financial challenges accessing deeper depths. As a result, our knowledge of MCEs and TMEs is still limited and localized to specific geographic locations (Puglise and Colin 2016; Turner et al. 2017). For the purpose of ease and clarity, the term mesophotic ecosystems (ME) will be used when statements address both MCEs and TMEs.

Research identification exercises are useful tools for scientific disciplines and have been successfully used in ecological conservation related fields (Sutherland et al. 2011, 2013; Parsons et al. 2014; Ockendon et al. 2018). For example, efforts combining open solicitations of research questions have helped create consensus on important research issues in management and conservation (Parsons et al. 2014). The first MCE workshop (Jupiter, Florida, U.S.A., 12–15 July 2008) focused on assessing the current state of MCE knowledge, developing a research strategy, and identifying management-driven research needs (Puglise et al. 2009). This was followed by the second MCE workshop (the Interuniversity Institute for Marine Sciences in Eilat, Israel, 26–31 October 2014), which highlighted the research addressed in the interim and that broad knowledge gaps still remain (Loya et al. 2016; Puglise and Colin 2016). Here, we present results of an exercise conducted during October-December 2017, including an open workshop at the European Coral Reef Symposium (ECRS; Oxford, U.K., 14 December 2017). The aim was to identify key questions that, if answered, would increase substantially the understanding of ME functioning and the ability of resource managers to make effective ME decisions.

Methods

Stage 1: Open Invitation of Initial Questions

In October 2017, questions were solicited from researchers and managers with expertise in MEs using a number of different methods. The methods included contacting the ECRS 2017 delegate list, mesophotic.org members (www.mesophotic.org/members), authors' personal contacts, the membership of the public Coral-List (http://coral.aoml.noaa.gov/mailman/listinfo/coral-list), and making announcements on social media networks. Using these methods, we were able to cover a broad geographic area and reach a wide network to encourage the participation of people working on MEs.

Participants were asked to submit ≥ 3 to 10 questions. For a proposed question to be considered, it had to meet the following criteria adapted from Sutherland et al. (2011, 2013) and Parsons et al. (2014), it must be: (1) of global importance, (2) impeding a wider understanding of ME processes and/or management/conservation progress, (3) answerable (or significant progress should be possible) through a realistic research design and within the scope of a large ($1–5 million USD) research grant (at least for a specific geographic region, where underlying information is already available), (4) not be answerable by a simple yes or no, and (5) answerable with research using a measurable outcome, and not based on value judgement. Participants submitted questions that met this criteria using an online web form that allowed for suggestions to be entered with no restrictions (e.g., no specific number of characters). In total, 287 suggested questions were received from 43 individuals.

Stage 2: Initial Question Classification

Submitted questions were screened and questions that clearly failed to meet the above criteria were removed and questions that were similar were merged, resulting in a list of 131 unique questions (Supplementary Table X.1). The 131 questions were classified into eight broad themes to aid discussion at the ECRS Workshop (Parsons et al. 2014). Decisions on the themes and question allocations by theme were made by consensus by the workshop theme chairs following a series of calls and discussions via email. The themes were: (1) distribution, (2) environmental and physical processes, (3) biodiversity and community structure, (4) ecological processes, (5) connectivity, (6) physiology, (7) threats, and (8) management and policy. Theme order does not represent their relative importance and there is overlap between these broad themes and the identified questions. The themes were designed to enable workshop participants to be easily parsed among the themes, and closely align with the main knowledge gaps identified by Puglise and Colin (2016).

Stage 3: Question Ranking

Questions were circulated via the methods described in Stage 1 and to the 43 individuals that submitted questions. Submission of questions in Stage 1 was not a prerequisite to participate in Stage 3. Individuals were directed to a web-based survey tool (SurveyAnyplace: www.surveyanyplace.com) where information on the study's goals and the question inclusion criteria were displayed. Participants were required to identify their affiliation, which was classified during analysis into one of the following: conservation [non-governmental organization (NGO) and/or charity], consultant, government, research institution, or university. Then, for each theme, a random subset of questions was shown to each participant in a random order. Participants were required to rank each question with whole integers from 0 (no importance) to 10 (critical importance). Participants could rank multiple questions within each theme with the same score. Mean scores were used to order questions by rank prior to the ECRS workshop. As a result of differing numbers of questions per theme, the number of random questions shown to participants was either four (themes with fewer than 10 questions: Distribution, Environmental and Physical Processes, and Physiology), six (theme with 15 questions: Connectivity), or eight (themes with more than 20 questions: Biodiversity and Community Structure, Ecological Processes, Threats, and Management and Policy).

Stage 4: Workshop

The ECRS 2017 was held on 14 December 2017 to discuss and rank the questions. In advance of the workshop, ME researchers on the delegate list were directly invited to attend the workshop, in addition to an open call in the conference program for any delegates with ME interests. The aim for the ECRS workshop was to reduce the total number of questions from 131 to 25 (or by 20%). It was arbitrarily determined that: (1) the list should contain less than 25 questions (including the highest-ranked questions per theme) to be manageable and targeted for the workshop, and (2) each theme must have a minimum of two questions to get a spread of questions and safeguard against a specific research area dominating the discussion. Mean scores per theme were compared and used to weight the final number of questions for each theme. For themes with ≥ 10 questions (Biodiversity and Community Structure, Ecological Processes, Connectivity, Threats, and Management and Policy) only the scores of the highest 10 ranked questions were taken into account so that no single theme would have > 10 questions to enable more equitable comparisons between themes. Mean scores were not used to remove questions, but instead to determine the order in which questions were presented to workshop participants.

At the start of the workshop, participants were provided with an overview of the process, and asked to self-divide into one of the eight theme groups (based upon their expertise and personal preference). Each theme had an assigned chair that led the discussion and summarized any recommendations. The theme chair was briefed in advance with the target number of final questions for the theme (≥ 2, but ≤ 10) and the question inclusion criteria. Each theme group was provided with the questions for their theme in rank order from highest to lowest (see Stage 3 for ranking process). Discussions within theme groups (and comments sent to theme chairs by researchers that could not attend the workshop) allowed for the questions to be merged and rephrased. Theme chairs encouraged their group to consider questions in rank order, and ensure that merged and/or reworded questions still met the question inclusion criteria (see Stage 1). Thus, preventing groups from expanding the scope of questions.

Publication trends within ME themes

Separately from the key question identification process, the representation of each theme in the scientific literature was analyzed. Trends in the number of scientific publications within each theme were investigated by using the database compiled on mesophotic.org (accessed 19 Jan 2018). Each publication was assigned to the most appropriate theme based on the mesophotic.org topic label and the article's title and abstract. The total number of studies by theme per year were calculated. Gray literature (e.g., government reports) are underrepresented in this database. Thus, the total number of publications per theme are not accurate, and merely demonstrate general trends in the themes across time. This database was also used to identify the approximate size of the ME research community. A total of 664 unique authors were identified, however, the database likely underrepresents governmental organizations and NGOs.

Results

A total of 287 questions were submitted by 43 individuals from a range of affiliations (Table X.1). Of the 287 questions, 131 were deemed unique and allocated to one of eight themes to form the question list for ranking at Stage 3. The number of questions within each theme ranged from 26 (Management and Policy) to 8 (Environmental and Physical Processes) (Table X.2).

In total 84 individuals participated in the exercise. Not all participants were involved at every stage, 43 participants provided questions, 39 ranked them (during Stage 3), and 39 attended the ECRS workshop (some of the attendees did not rank questions during Stage 3). This represented a response rate of approximately 13% of the ME research community. There was no significant difference in the mean score assigned by participants based on question theme (χ^2 (7)=6.550, p=0.477).

The final number of questions for each theme reflected a similar proportion to the number of submitted questions (Table X.2). The themes with a larger number of submitted questions (in particular Ecological Processes and Biodiversity and Community Structure) may be slightly underrepresented as their list had to be substantially reduced, however, this is balanced by the fact that these workshop themes were overrepresented with regards to participant's area of expertise. The balancing of the number of questions by theme was necessary to ensure that themes with fewer questions were not discounted due to a smaller proportion of experts working in those areas. It is important to note that given the primary list-serve used for polling (coral-list) and the venue where the workshop was held (ECRS) are focused on coral reef research, the list of questions generated is biased towards coral-related themes. In an effort to reduce bias, we reworded questions that specifically mentioned scleractinian corals to encompass other taxonomic groups.

All themes show an increasing trend in the numbers of scientific publications with time (Fig. X.1). The proportion of studies focused on each theme differs from 52.0% (Biodiversity and Community Structure) to 2.7% (Management and Policy). The dominance of Biodiversity and Community Structure in the literature was not observed in the number of submitted questions (Fig. X.2). Higher proportions of questions were submitted for the themes on Management and

Policy (19.8%), Threats (16.8%), and Ecological Processes (16.0%), which make up less than 16% of the literature in total. There was very little difference in the relative proportions of studies in total. Since 2010, the largest shifts in scientific publications occurred between Environmental and Physical Processes (-2.9%) and Connectivity (+3.8%) (Fig. X.2). Themes that fall below the line y=x could possibly be considered to be underrepresented in the literature or overrepresented in the submitted questions (Fig. X.2).

A final list of 25 questions (labelled herein as Q1, Q2, etc.) was produced by consensus within each theme group at the workshop. Themes are ordered broadly from the largest to the smallest spatial scale, followed by themes relating to Threats, and Management and Policy. Neither the final theme order, nor the final question order, represents any judgment on their relative importance. Given the inclusive and multi-stage approach, all questions are considered to be important for progressing our understanding of MEs and their overall conservation and management.

Theme 1: Distribution

To manage MEs effectively, it is imperative to know their spatial distribution both regionally and globally. Only a small proportion of the global seabed has been mapped and an even smaller proportion has high-resolution imaging (Brown et al. 2011). The full distribution of MEs is largely unknown, and under-sampling is one of the greatest issues facing ME research (Q1). Current information on ME distribution is patchy with research focused in specific geographic areas, particularly in the Caribbean, Great Barrier Reef, Red Sea, Mediterranean, and Hawaiʻi (Puglise and Colin 2016; Turner et al. 2017). Unlike shallow-water reefs, ME distribution cannot be derived from satellite-based surveys. Studies to estimate regional extent of MEs rely on multibeam mapping and predictive habitat modelling with sparse georeferenced

ME identification and bathymetric classifications (e.g., Locker et al. 2010; Bridge et al. 2012). Technologies, including remote operated vehicles (ROVs), autonomous underwater vehicles (AUVs), acoustic instruments (e.g., multibeam echosounders and side-scan sonars), enable mapping of wide-areas at high-spatial resolution (Armstrong et al. 2018). Knowledge of ME distribution is also needed to understand their temporal dynamics, particularly in relation to future changes (Q2).

Q1: How are MEs distributed globally?

Q2: Will the extent of MEs change in the future?

Theme 2: Environmental and Physical Processes

Understanding of the biotic and abiotic interactions in MEs, in the context of past and present variability and projected environmental change, lags behind what is known about shallow reefs. Mesophotic environmental conditions (e.g., light limitation) and associated physiology and geomorphology often differ from shallow reefs (Lesser et al. 2010), suggesting a difference in the environmental drivers of ME functions. These drivers include increased dependence on heterotrophy (Slattery et al. 2011), differences in bioerosion processes (Weinstein et al. 2014), and the contribution of relict reefs to their overall structure (Sherman et al. 2010). Light and depth have received most of the research attention (Lesser et al. 2010; Pyle et al. 2016). However, other environmental, physical, and biological characteristics, such as temperature (Baker et al. 2016), sediment production (Weinstein et al. 2015b), cementation (Weinstein et al. 2015a), and antecedent topography (Sherman et al. 2018), remain largely unknown. Moreover, biological limits of ME organisms and differences from shallower systems in terms of various ecosystem functions (e.g., calcification rates, inorganic carbon metabolism, and biogeochemical cycling) are not well characterized (Q3). Thus, limiting our ability to generalize the major controls on fundamental factors such as ME distribution and carbonate accretion.

Large knowledge gaps exist over present-day and past biogeochemical cycling in MEs (Q4) and, in particular, the carbon/carbonate budget. Despite a notable account of MEs in the geologic record (Sherman et al. 2018), our understanding about the geochemical resilience and sustainability of ME carbonate structures to past environmental changes, such as reduced carbonate saturation state, remains poorly constrained. Additionally, while the role of shallow-water coral reefs in the biogeochemical cycling of sulphur (e.g., Burdett et al. 2013) and nitrogen (e.g., Rädecker et al. 2015) is well recognized, there is a paucity of knowledge regarding the role of modern and past MEs in marine biogeochemical cycling. This limits our ability to accurately understand historic, current, and/or projected biogeochemical dynamics, the response of ancient MEs to paleoenvironmental change (Morsilli et al. 2012; e.g., Abbey et al. 2013) and to predict ME responses to future environmental changes.

> Q3: What are the biological, environmental, and geological factors controlling ME distribution, accretion, and function across space and time?
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> Q4: What is the role of MEs in biogeochemical cycling across space and time?

Theme 3: Biodiversity and Community Structure

Taxonomic surveys of MEs continue to return high rates of species discovery and geographic-endemism (Kosaki et al. 2017). Our understanding of ME biodiversity is biased regionally and taxonomically (Baker et al. 2016; Turner et al. 2017), with the most information available for fishes followed by scleractinian corals. This, coupled with difficulties and expense in accessing MEs, has hampered the ability to address global biodiversity questions. Based on the current rate of discovery (Pomponi et al. 2018; Pyle et al. 2018; Spalding et al. 2018), there is a high proportion of biodiversity to be found in MEs and more knowledge of community structure across vertical and horizontal scales is needed (Q5 and Q6). Research focus is often on more charismatic species such as corals and fishes. Other organismal groups likely harbor high, undiscovered biodiversity, e.g., meiofauna (e.g., Bianchelli et al. 2013), macroalgae (e.g., Ballantine and Aponte 2003, 2005; Spalding et al. 2016) coralline algae (e.g., Brasileiro et al. 2015), and other invertebrates (Pyle et al. 2016). Quantifying biodiversity across taxa and community structure will also provide an improved understanding of fundamental ME functional processes. Detailed information on the biotic and abiotic variables is required to identify the drivers and processes affecting the biodiversity patterns observed on MEs (Q7). It is also important to understand how biodiversity differs between shallow-water, mesophotic, and the deep-sea ecosystems (Q8), and the degree of overlap.

Q5. What proportion of global reef biodiversity, is attributed to MEs?

Q6. How does holobiont (including microbial) community structure change across vertical and horizontal scales?

Q7. What are the variables that influence community structure and biodiversity across depths and regions?

Q8. How does biodiversity (taxonomic and genetic) change across depths and regions?

Theme 4: Ecological Processes

Difficulty accessing MEs has limited the assessment of basic ecological processes (Kahng et al. 2010). These types of studies usually require in situ manipulation and repeated sampling through time, which can be logistically difficult to perform at 30–150 m in depth. Studies of growth rates (Littler et al. 1991; Spalding 2012; Kahng 2013; Weinstein et al. 2016; Groves et al. 2018) and the reproductive ecology (Gori et al. 2012; Holstein et al. 2015; Eyal-Shaham et al. 2016; Goldstein et al. 2016; Goodbody-Gringley et al. 2018) are limited to a small number of mesophotic species and areas. Increased knowledge about life history (Q9) and the functional traits and responses (Q10) of key mesophotic species is paramount to understanding overall ecosystem functioning and assessing ME vulnerability to climate and anthropogenic impacts (see theme on Threats).

Few studies have investigated the trophic ecology of mesophotic species. Most have focused on stable isotope compositions in corals (e.g., Alamaru et al. 2009; Einbinder et al. 2009; Crandall et al. 2016; Ezzat et al. 2017) or fishes (Bradley et al. 2016), and energy budgets (e.g., Rossi and Tsounis 2007; Gori et al. 2012; Brandtneris et al. 2016). Special attention should be dedicated to assessing population and community structure and dynamics (Bak et al. 2005; Kahng et al. 2010; Pochon et al. 2015; Pinheiro et al. 2016; Kane and Tissot 2017) particularly for species that contribute to benthic structure of MEs (Q11).

> Q9. What are the common life history traits (e.g., survival, growth, and reproduction) of mesophotic species, and do they differ from shallow systems?
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> Q10. What are the functional traits and responses of taxonomic groups in MEs, and how will they be modified under climate change?
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> Q11. What are the population and community structure and dynamics of mesophotic species, and to what extent do benthic species contribute to the three-dimensional structure of MEs?

Theme 5: Connectivity

The rapid demise of coral reefs has led to a growing interest over the past decade in identifying reef communities that can escape, or persist through, major reef disturbances (Glynn 1996; Carpenter et al. 2008). MCEs have been of particular interest, given that they are often located directly adjacent to shallow reef communities, and refuge populations may offer a local source of larval recruits aiding in shallow reef recovery (Hughes and Tanner 2000; Bongaerts et al. 2010; Bongaerts and Smith 2018). The potential of MCEs to aid in shallow reef recovery is currently unclear and has been highlighted as a key knowledge gap (Q12; Baker et al. 2016).

The ability of MCEs to act as a reproductive source for shallow reef species is dependent on the extent of overlap in species diversity. At the shallow-mesophotic transition (30–40 m depth), there can be considerable overlap with the shallow reef community (Bongaerts et al. 2010; Muir et al. 2015; Semmler et al. 2016). However, population genetic assessments, which thus far have focused primarily on scleractinian corals (e.g., Bongaerts et al. 2010; van Oppen et al. 2011; Brazeau et al. 2013; Serrano et al. 2016) and octocorals (Constantini et al. 2011; Prada and Hellberg 2013) have demonstrated that they do not necessarily form a single metapopulation over depth, and that shallow-mesophotic genetic connectivity may be hampered or strongly unidirectional. Initial assessments of more mobile species such as fish, point to greater connectivity between shallow and deeper populations, and a potential reservoir should shallow populations be greatly impacted (Tenggardjaja et al. 2014; Vaz et al. 2016). Such assessments have demonstrated that the potential for vertical connectivity can vary greatly between species (Bongaerts et al. 2017), and that within species patterns can vary between geographic regions (van Oppen et al. 2011; Serrano et al. 2014). Given the difficulty of scaling such assessments across a large number of species, detailed assessments of refuge potential and vertical and horizontal connectivity should be prioritized for species that are ecologically- and/or economically-important. Horizontal connectivity between MEs in different regions represents a further topic of interest (Q13), and in particular how such connectivity may differ from patterns observed for shallow reefs across the same regions (Pyle et al. 2018). Although horizontal connectivity is often assessed to contrast patterns of inferred vertical connectivity, we recommend that further studies consider horizontal connectivity more explicitly, as it is an important aspect in determining the resilience of MEs. Therefore, to attain a broader understanding of "reseeding" potential, it is essential to understand how physical and ecological barriers affect dispersal and selection (Q14), and how such processes relate to life history traits (Costantini et al. 2011; Holstein et al. 2016; Bongaerts et al. 2017; Turner et al. 2018).

Q12. Do MEs act as a refuge and reproductive source, particularly for ecologically- or economically-important shallow-water species?

Q13. To what extent are MEs horizontally connected to one another?

Q14. What are the relative influences of selection versus dispersal on realized connectivity?

Theme 6: Physiology

At the organismal level, understanding the similarities and differences in the survival strategies of key mesophotic sessile organisms compared to their shallow counterparts will help inform research and management priorities. Mesophotic organisms, especially in temperate areas, have to adapt to a wide range of pressure, light, and nutrient levels, which affect their physiological and metabolic processes (e.g., Grigg 2005; Pochon et al. 2015; Ziegler et al. 2015). Focus should be placed on how species residing in MEs acclimatize and adapt to the environmental conditions (Q15), taking into account all organisms, including microbes and symbionts (Olson and Kellogg 2010; Ziegler et al. 2015, 2017; Torda et al. 2017). Given that

MEs are hypothesized to be potential refuges and/or reservoir reefs for shallow-water organisms (Glynn 1996; Bongaerts et al. 2010; Bongaerts and Smith 2018), it is important to determine the physiological differences of conspecifics in shallow-water and mesophotic organisms (Roder et al. 2013; Ziegler et al. 2014, 2015; Einbinder et al. 2016).

At an ecosystem level, most knowledge on the sources and pathways of nutrient flow through reef food webs is derived from shallow-water coral reefs (McMahon et al. 2016). At present, we know little about the productivity, biomass, nutrient recycling, and nutrient flow from primary producers to organisms at higher trophic levels in MEs (Q16). Heterotrophic feeding is expected to be more pronounced and nutrients might be higher due to upwelling processes (Bradley et al. 2016; Pyle et al. 2016; Ezzat et al. 2017).

> Q15. What are the physiological limits and specialized adaptations of key sessile organisms in MEs compared to shallow-water organisms?
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> Q16. What are the energy transfer rates between trophic levels along the depth gradient from shallow to mesophotic reefs?

Theme 7: Threats

Coral reefs in general are projected to experience increased levels of stress in the future through both climate and other anthropogenic impacts (Pandolfi et al. 2011; Hughes et al. 2017). Stresses on MCEs and potential recovery have been documented for a few climate-related coral bleaching (Smith et al. 2015; Muir et al. 2017) and storm damage (Bongaerts et al. 2013; White et al. 2013) events, and ocean acidification (Bramanti et al. 2013; Cerrano et al. 2013). Despite this evidence, little is known regarding the susceptibility of MEs and the thresholds at which impacts occur (Q17). Even less is known about climate-related effects on non-coral organisms.

Environmental thresholds (e.g., temperature levels that result in bleaching of mesophotic coral populations or result in distribution changes in fish), and how they differ from shallow-water populations are important for determining whether MEs will be able to act as a refuge (Glynn 1996; Bongaerts et al. 2010; Muir et al. 2017), or not (Smith et al. 2015). Additionally, the potential for mesophotic organisms to adapt and respond to future environmental conditions is largely unknown (Q18). This information is critical for assessing the future trajectory of these ecosystems (Ziegler et al. 2015; Torda et al. 2017).

MEs are not free from anthropogenic influences (Andradi-Brown et al. 2016) though they can offer some refuge for fisheries targeted species in certain areas (Lindfield et al. 2015; Asher et al. 2017). However, the footprint and effects of human-related impacts are restricted to a handful of studies (e.g., Appeldoorn et al. 2015) and are largely unquantified globally. ME health has likely been impacted by various human stressors such as sewage outfalls, mining, cable laying, and expansion of fisheries (including trawling), but has received little scientific attention (e.g., Appeldoorn et al. 2015; Andradi-Brown et al. 2016; Baker et al. 2016). It is becoming more important to identify ME exposure to non-climate-related impacts and to quantify the effects that these activities are having on mesophotic organisms (Q19). It is critical to understand the footprint and effects of any impacts, so appropriate management actions can be taken, particularly when such activities could act synergistically and with climate-related effects (Baker et al. 2016).

Another key factor that will determine the future of these systems is the resistance and recovery potential of ME organisms (Q20). Severe impacts can lead to phase shifts and result in large-scale changes in the biological assemblage and resultant ecosystem functions (Hughes et al. 2010). Although phase shifts have been observed at mesophotic depths (e.g., Lesser and

Slattery 2011), our understanding of this process is currently severely limited and few studies have documented long-term recovery of MEs after disturbances (see Bongaerts et al. 2013; White et al. 2017).

Q17. What are the critical environmental thresholds with regard to climate-related impacts on MEs?

Q18. How quickly can mesophotic organisms adapt/acclimate to changing environmental conditions?

Q19. What is the impact of non-climate related anthropogenic stressors on MEs?

Q20. How quickly can MEs recover from severe disturbance events?

Theme 8: Management and Policy

Despite MEs receiving increased attention over the past decade (Baker et al. 2016), most are still not considered in management plans and policy decisions. MEs may be excluded for a number of reasons such as the depth-associated logistical challenges in gathering data (Pyle 1998), their unknown distribution (see theme on Distribution), lack of awareness, and a poor understanding of their ecosystem services (Millennium Ecosystem Assessment 2005; Holstein et al. 2018). Studies have been conducted on the role of MEs with respect to fisheries (Bejarano et al. 2014; Lindfield et al. 2015; e.g., Andradi-Brown et al. 2017), resource extraction (Grigg 2001; Tsounis et al. 2010; Bruckner 2016; Gress and Andradi-Brown 2017), bioprospecting for novel drugs (Eyal et al. 2015; Newman and Cragg 2015), and the aquarium trade (Andradi-Brown et al. 2016), but adequate management is now required. Additionally, ME ecosystem services studies are heavily biased to provisioning services, and there is an urgent need to consider other service types. For example, cultural ecosystem services are increasing (Mitchell and Doolette 2013; Baker et al. 2016), and large knowledge gaps remain with respect to regulating and supporting ecosystem services (Holstein et al. 2018). Obtaining a more quantitative understanding of what MEs contribute to the global ecosystem in terms of services is essential (Q21) for proper management and conservation.

Important potential ecosystem services provided by MEs, combined with their intrinsic biodiversity value, indicate the need for identifying and enacting effective management (Q22). Marine protected area (MPA) management plans rarely acknowledge MEs and in many cases MPA protection is incidental resulting from shallow MPA designation extending into deeper waters (e.g., Diario Oficial de la Federación 1998). However, some MPAs have been designated explicitly targeting ME habitats (e.g., Alonso et al. 2015; Reed et al. 2018), and it is possible to capture MEs in MPAs by designing protection across biophysical gradients (Bridge et al. 2016).

To allow long-term monitoring of MEs, evaluate management effectiveness, and compare conditions between locations, a suite of appropriate indicators of ecosystem health must be developed (Q23). ME indicators should be scientifically informed, easily standardized, and logistically straight-forward to collect, including key benthic organisms, fishes, and environmental conditions (Lesser et al. 2009; Kahng et al. 2010, 2014; Woodall et al. 2018). As monitoring MEs is challenging, researchers should standardize methods. Survey protocols can be developed, as has been done for shallow coral reefs (e.g., English et al. 1997), and has begun to assess deeper habitats in some areas (Woodall et al. 2018). Broad oceanographic and bathymetric datasets can help inform mangers on likely locations containing MEs (see theme on Distribution) and spatial connectivity models may assist with MPA placement (Q24; Vaz et al. 2016; Krueck et al. 2017). Researchers developing tools to integrate MEs into management must correctly highlight these to maximize their adoption by resource managers and policymakers.

A key to the success of ME management will be the dissemination of important messages, e.g., the value of MEs economically and ecologically to stakeholders (Q25). While there is still a lack of knowledge on many MEs, often the most basic questions being asked by reef managers can be addressed, and the first step towards MEs being integrated into management and policy decisions is to build awareness of their existence (Baker et al. 2016).

Q21. What are the ecosystem services of MEs and their projected net worth?

Q22. What are the most effective management practices and long-term conservation strategies for MEs?

Q23. What are the key indicators that should be monitored to determine ME state?

Q24. What are the methods, datasets, and resources available to monitor MEs to ensure effective management decisions are made?

Q25. What are the important messages about MEs required to inform/educate stakeholders?

Discussion

While progress has been made towards increasing our knowledge of MEs, particularly in the past decade (Baker et al. 2016; Turner et al. 2017), large gaps in our understanding remain (Puglise and Colin 2016). Given the current plight of shallow-water reef environments (Carpenter et al. 2008; Hughes et al. 2017) and shifts in the composition of temperate communities (Wernberg et al. 2011; Vergés et al. 2014), there is increased urgency to fill these gaps. The questions presented here are by no means the only questions that need to be addressed in ME research, however, they do provide a useful framework and a guide to focus and encourage increased research and funding in this field for effective management, conservation, resource utilization, and general advancement in knowledge. Herein, we have identified specific knowledge gaps based on current knowledge and building upon the initial workshops that brought increased attention to these ecosystems (Puglise et al. 2009). The distribution, environmental controls, ecological roles, threats and impacts, and the connections to shallow reefs of MEs have been previously identified as (Puglise and Colin 2016) and continue to be the major gaps .

As would be the case in any exercise of this nature, participants will be biased towards their specific research areas. The methods used to communicate this study are more likely to reach coral reef scientists, as well as ME researchers. The dominance of ecological scientists in the ME field is identified in the publication numbers (Biodiversity and Community Structure make up more than 50% of the publications) meaning that specialists in other fields, e.g., Oceanography, Geology, and Management, are likely to be underrepresented. The exercise did represent a wide swath of expertise throughout, in terms of participants, co-authors, and theme chairs so as to guide the project appropriately. By allowing each theme to be adequately represented (with at least two questions), as well as keeping final questions unspecific to certain taxa, we hope to have reduced bias where possible.

This is not intended to be an exhaustive list of the gaps in ME research and may be more likely to miss important aspects of some disciplines than others. It is clear that some themes are represented more than others in the scientific literature. Management and Policy made up the smallest proportion of existing studies indexed in the mesophotic.org database. While this theme will be more prevalent in the gray literature, more thorough reviews have found similar results (Turner et al. 2017). Yet, Management and Policy had both the most questions submitted and also the highest mean ranking for the top ten questions, suggesting that the ME community recognizes the importance of this topic. Management and policy questions were ranked highly by participants and have previously been deemed critically important for marine conservation research (Parsons et al. 2014).

Threats are another theme that is underrepresented in the literature (Turner et al. 2017). A shift in focus may now occur as we start to identify the threats present in these systems (Andradi-Brown et al. 2016), as well as increase our understanding of the underlying ecology. Despite its dominance in the literature, Biodiversity and Community Structure made up 16% of the submitted questions. This highlights how much more information we require to fully understand the complex nature of these systems and how new questions are likely to emerge as further work is conducted. This is a theme that is likely to be more affected by the bias of the participants, where a larger number of coral reef scientists are likely to prioritize this theme.

We anticipate the questions presented here will aid research progress and effective conservation efforts on MCEs and TMEs. We are also optimistic that by focusing on this specific ecosystem type, we will help propel the observed upward trend in MCE and TME research. Our final question list, we hope, can act as a guide for MCE and TME researchers, managers, and funders for future work and collaborations.

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References

Abbey E, Webster JM, Braga JC, Jacobsen GE, Thorogood G, Thomas AL, Camoin G, Reimer PJ, Potts DC (2013) Deglacial mesophotic reef demise on the great barrier reef. Palaeogeography, Palaeoclimatology, Palaeoecology 392:473–494 doi:10.1016/j.palaeo.2013.09.032

Alamaru A, Loya Y, Brokovich E, Yam R, Shemesh A (2009) Carbon and nitrogen utilization in two species of red sea corals along a depth gradient: Insights from stable isotope analysis of total organic material and lipids. Geochimica et Cosmochimica Acta 73:5333–5342. doi:10.1016/j.gca.2009.06.018

Alonso D, Vides M, Cedeño C, Marrugo M, Henao A, Sánchez J, Dueñas L, Andrade J, González F, Gómez M (2015) Parque nacional natural corales de profundidad: Descripción de comunidades coralinas y fauna asociada. Serie de Publicaciones Especiales INVEMAR 88:1–20

Andradi-Brown D, Laverick JH, Bejarano I, Bridge T, Colin PL, Eyal G, Jones RJ, Kahng SE, Reed JK, Smith TB (2016) Threats to mesophotic coral ecosystems and management options. In: Baker EK, Puglise KA, Harris PT (eds) Mesophotic coral ecosystems—a lifeboat for coral reefs. The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, p 67–82

Andradi-Brown DA, Grey R, Hendrix A, Hitchner D, Hunt CL, Gress E, Madej K, Parry RL, Régnier-McKellar C, Jones OP, Arteaga M, Izaguirre AP, Rogers AD, Exton DA (2017) Depth-dependent effects of culling—do mesophotic lionfish populations undermine current management? Royal Society Open Science 4:170027. doi:10.1098/rsos.170027

Appeldoorn R, Ballantine D, Bejarano I, Carlo M, Nemeth M, Otero E, Pagan F, Ruiz H, Schizas N, Sherman C, Weil E (2015) Mesophotic coral ecosystems under anthropogenic stress: A case study at Ponce, Puerto Rico. Coral Reefs 35:63–75. doi:10.1007/s00338–015–1360–5

Armstrong RA, Pizarro O, Roman C (2018) Underwater robotic technology for imaging mesophotic coral ecosystems. In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world. Springer, New York

Asher J, Williams ID, Harvey ES (2017) Mesophotic depth gradients impact reef fish assemblage composition and functional group partitioning in the main hawaiian islands. Frontiers in Marine Science 4:98. doi:10.3389/fmars.2017.00098

Bak RPM, Nieuwland G, Meesters EH (2005) Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. Coral Reefs 24:475–479. doi:10.1007/s00338–005–0009–1

Baker EK, Puglise KA, Harris PT (eds) (2016) Mesophotic coral ecosystems—a lifeboat for coral reefs? The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, 98 p

Baldwin CC, Tornabene L, Robertson DR (2018) Below the mesophotic. Scientific Reports 8:4920. doi:10.1038/s41598–018–23067–1

Ballantine DL, Aponte NE (2003) An annotated checklist of deep-reef benthic marine algae from Lee Stocking Island, Bahamas (western atlantic), I. Chlorophyta and Heterokontophyta. Nova Hedwigia 76:113–127

Ballantine DL, Aponte NE (2005) An annotated checklist of deep-reef benthic marine algae from Lee Stocking Island, Bahamas (western atlantic) II. Rhodophyta. Nova Hedwigia 80:147–171. doi:10.1127/0029–5035/2005/0080–0147

Ballesteros E (2006) Mediterranean coralligenous assemblages: A synthesis of present knowledge. Oceanography and Marine Biology 44:123–195

Bejarano I, Appeldoorn RS, Nemeth M (2014) Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. Coral Reefs 33:313–328. doi:10.1007/s00338-014-1125-6

Bianchelli S, Pusceddu A, Canese S, Greco S, Danovaro R (2013) High meiofaunal and nematodes diversity around mesophotic coral oases in the mediterranean sea. PLoS ONE 8:e66553. doi:10.1371/journal.pone.0066553

Bongaerts P, Smith TB (2018) Beyond the 'deep reef refuge' hypothesis: a conceptual framework to characterize persistence at depth. In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world. Springer, New York

Bongaerts P, Muir P, Englebert N, Bridge TCL, Hoegh-Guldberg O (2013) Cyclone damage at mesophotic depths on Myrmidon Reef (GBR). Coral Reefs 32:935–935. doi:10.1007/s00338-013-1052-y

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: Focus on Caribbean reefs. Coral Reefs 29:309–327. doi:10.1007/s00338-009-0581-x

Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, Hoegh-Guldberg O (2017) Deep reefs are not universal refuges: Reseeding potential varies among coral species. Science Advances 3:e1602373. doi:10.1126/sciadv.1602373

Bradley CJ, Longenecker K, Pyle RL, Popp BN (2016) Compound-specific isotopic analysis of amino acids reveals dietary changes in mesophotic coral-reef fish. Marine Ecology Progress Series 558:65–79

Bramanti L, Movilla J, Guron M, Calvo E, Gori A, Dominguez-Carrió C, Grinyó J, Lopez-Sanz A, Martinez-Quintana A, Pelejero C, Ziveri P, Rossi S (2013) Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). Global Change Biology 19:1897–1908. doi:10.1111/gcb.12171

Brandtneris VW, Brandt ME, Glynn PW, Gyory J, Smith TB (2016) Seasonal variability in calorimetric energy content of two Caribbean mesophotic corals. PloS ONE 11:e0151953. doi:10.1371/journal.pone.0151953

Brasileiro PS, Pereira-Filho GH, Bahia RG, Abrantes DP, Guimarães SMPB, Moura RL, Francini-Filho RB, Bastos AC, Amado-Filho GM (2015) Macroalgal composition and community structure of the largest rhodolith beds in the world. Marine Biodiversity 46:407–420. doi:10.1007/s12526–015–0378–9

Brazeau DA, Lesser MP, Slattery M (2013) Genetic structure in the coral, *Montastraea cavernosa*: Assessing genetic differentiation among and within mesophotic reefs. PLoS ONE 8:e65845. doi:10.1371/journal.pone.0065845

Bridge T, Beaman R, Done T, Webster J (2012) Predicting the location and spatial extent of submerged coral reef habitat in the Great Barrier Reef world heritage area, Australia. PLoS ONE 7:e48203. doi:10.1371/journal.pone.0048203

Bridge TCL, Grech AM, Pressey RL (2016) Factors influencing incidental representation of previously unknown conservation features in marine protected areas. Conserv Biol 30:154–165. doi:10.1111/cobi.12557

Brown CJ, Smith SJ, Lawton P, Anderson JT (2011) Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuarine, Coastal and Shelf Science 92:502–520. doi:10.1016/j.ecss.2011.02.007

Bruckner AW (2016) Advances in management of precious corals to address unsustainable and destructive harvest techniques. In: Goffredo S, Dubinsky Z (eds) The Cnidaria, Past, Present and Future. Springer International Publishing, p 747–786

Burdett HL, Donohue PJC, Hatton AD, Alwany MA, Kamenos NA (2013) Spatiotemporal variability of dimethylsulphoniopropionate on a fringing coral reef: The role of reefal carbonate chemistry and environmental variability PLoS ONE 8:e64651. doi:10.1371/journal.pone.0064651

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563. doi:10.1126/science.1159196

Cerrano C, Cardini U, Bianchelli S, Corinaldesi C, Pusceddu A, Danovaro R (2013) Red coral extinction risk enhanced by ocean acidification. Sci Rep 3:1457. doi:10.1038/srep01457

Costantini F, Rossi S, Pintus E, Cerrano C, Gili J–M, Abbiati M (2011) Low connectivity and declining genetic variability along a depth gradient in *Corallium rubrum* populations. Coral Reefs 30:991–1003. doi:10.1007/s00338–011–0771–1

Crandall JB, Teece MA, Estes BA, Manfrino C, Ciesla JH (2016) Nutrient acquisition strategies in mesophotic hard corals using compound specific stable isotope analysis of sterols. Journal of Experimental Marine Biology and Ecology 474:133–141. doi:10.1016/j.jembe.2015.10.010

de Bakker DM, van Duyl FC, Bak RPM, Nugues MM, Nieuwland G, Meesters EH (2017) 40 years of benthic community change on the caribbean reefs of Curaçao and Bonaire: The rise of slimy cyanobacterial mats. Coral Reefs 36(2):355–367. doi:10.1007/s00338–016–1534–9

Diario Oficial de la Federación (1998) Aviso por el que se informa al publico en general que la secretaria de medio ambiente, recursos naturales y pesca, ha concluido la elaboracion del programa de manejo del area natural protegida con el caracter de parque marino nacional arrecifes de Cozumel. http://wwwconanpgobmx/que%7B_%7Dhacemos/pdf/programas%7B_%7Dma677nejo/AvisoCozumel.pdf. Accessed 16 Mar 2018

Einbinder S, Gruber DF, Salomon E, Liran O, Keren N, Tchernov D (2016) Novel adaptive photosynthetic characteristics of mesophotic symbiotic microalgae within the reef-building coral, *Stylophora pistillata*. Frontiers in Marine Science 3:195. doi:10.3389/fmars.2016.00195

Einbinder S, Mass T, Brokovich E, Dubinsky Z, Erez J, Tchernov D (2009) Changes in morphology and diet of the coral *Stylophora pistillata* along a depth gradient. Marine Ecology Progress Series 381:167–174. doi:10.3354/meps07908

English S, Wilkinson CR, Baker V (1997) Survey manual for tropical marine resources Australian Institute of Marine Science, Townsville, Australia, 378 p

Eyal-Shaham L, Eyal G, Tamir R, Loya Y (2016) Reproduction, abundance and survivorship of two *Alveopora* spp. in the mesophotic reefs of eilat, Red Sea. Sci Rep 6:20964. doi:10.1038/srep20964

Eyal G, Wiedenmann J, Grinblat M, D'Angelo C, Kramarsky-Winter E, Treibitz T, Ben-Zvi O, Shaked Y, Smith TB, Harii S, Denis V, Noyes T, Tamir R, Loya Y (2015) Spectral diversity and regulation of coral fluorescence in a mesophotic reef habitat in the Red Sea. PLoS ONE 10:e0128697. doi:10.1371/journal.pone.0128697

Ezzat L, Fine M, Maguer J-F, Grover R, Ferrier-Pagès C (2017) Carbon and nitrogen acquisition in shallow and deep holobionts of the scleractinian coral *S. pistillata*. Frontiers in Marine Science 4:102. doi:10.3389/fmars.2017.00102

Glynn PW (1996) Coral reef bleaching: Facts, hypotheses and implications. Glob Chang Biol 2:495–509. doi:10.1111/j.1365–2486.1996.tb00063.x

Goldstein ED, D'Alessandro EK, Sponaugle S (2016) Demographic and reproductive plasticity across the depth distribution of a coral reef fish. Scientific Reports 6:34077. doi:10.1038/srep34077

Goodbody–Gringley G, Wong KH, Becker DM, Glennon K, de Putron SJ (2018) Reproductive ecology and early life history traits of the brooding coral, *Porites astreoides*, from shallow to mesophotic zones. Coral Reefs 37(2):483–494. doi:10.1007/s00338–018–1673–2

Gori A, Viladrich N, Gili J-M, Kotta M, Cucio C, Magni L, Bramanti L, Rossi S (2012) Reproductive cycle and trophic ecology in deep versus shallow populations of the mediterranean gorgonian *Eunicella singularis* (cap de creus, northwestern mediterranean sea). Coral Reefs 31:823–837. doi:10.1007/s00338–012–0904–1

Gress E, Andradi-Brown DA (2017) Assessing population changes of historically overexploited black corals (order: Antipatharia) in cozumel, mexico. PeerJ Preprints 5:e3499v3491. doi:10.7287/peerj.preprints.3499v1

Grigg RW (2001) Black coral: History of a sustainable fishery in Hawai'i. Pacific Science 55:291–299

Grigg RW (2005) Depth limit for reef building corals in the Au'Au channel, S.E. Hawaii. Coral Reefs 25:77–84. doi:10.1007/s00338–005–0073–6

Groves SH, Holstein DM, Enochs IC, Kolodzeij G, Manzello DP, Brandt ME, Smith TB (2018) Growth rates of *Porites astreoides* and *Orbicella franksi* in mesophotic habitats surrounding St. Thomas, US Virgin Islands. Coral Reefs 37(2):345–354. doi:10.1007/s00338–018–1660–7

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on "Mesophotic coral ecosystems: Characterization, ecology, and management." Coral Reefs 29:247–251. doi:10.1007/s00338–010–0614–5

Holstein DM, Fletcher P, Groves SH, Smith TB (2018) Ecosystem services of mesophotic coral ecosystems and a call for better accounting In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world. Springer, New York

Holstein DM, Smith TB, Gyory J, Paris CB (2015) Fertile fathoms: Deep reproductive refugia for threatened shallow corals. Sci Rep 5:12407. doi:10.1038/srep12407

Holstein DM, Smith TB, Paris CB (2016) Depth-independent reproduction in the reef coral *Porites astreoides* from shallow to mesophotic zones. PLoS ONE 11:e0146068. doi:10.1371/journal.pone.0146068

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the anthropocene. Nature 546:82–90. doi:10.1038/nature22901

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution 25:633–642. doi:10.1016/j.tree.2010.07.011

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long–term decline of Caribbean corals. Ecology 81:2250–2263

Hume BCC, Voolstra CR, Arif C, D'Angelo C, Burt JA, Eyal G, Loya Y, Wiedenmann J (2016) Ancestral genetic diversity associated with the rapid spread of stress–tolerant coral symbionts in response to Holocene climate change. Proceedings of the National Academy of Sciences 113:4416–4421. doi:10.1073/pnas.1601910113

Kahng SE (2013) Growth rate for a zooxanthellate coral (*Leptoseris hawaiiensis*) at 90 m. Journal of Coral Reef Studies 15:39–40

Kahng SE, Copus JM, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Current Opinion in Environmental Sustainability 7:72–81. doi:10.1016/j.cosust.2013.11.019

Kahng SE, Garcia-Sais JR, Spalding HL et al (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275. doi:10.1007/s00338–010–0593–6

Kane CN, Tissot BN (2017) Trophic designation and live coral cover predict changes in reef-fish community structure along a shallow to mesophotic gradient in Hawaii. Coral Reefs 36:891–901. doi:10.1007/s00338–017–1581–x

Kosaki RK, Pyle RL, Leonard JC, Hauk BB, Whitton RK, Wagner D (2017) 100% endemism in mesophotic reef fish assemblages at Kure Atoll, Hawaiian Islands. Marine Biodiversity 47:783–784. doi:10.1007/s12526–016–0510–5

Krueck NC, Ahmadia GN, Green A, Jones GP, Possingham HP, Riginos C, Treml EA, Mumby PJ (2017) Incorporating larval dispersal into MPA design for both conservation and fisheries. Ecological Applications 27:925–941

Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biological Invasions 13:1855–1868. doi:10.1007/s10530–011–0005–z

Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. Journal of Experimental Marine Biology and Ecology 375:1–8. doi:10.1016/j.jembe.2009.05.009

Lesser MP, Slattery M, Stat M, Ojimi M, Gates RD, Grottoli A (2010) Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: Light, food, and genetics. Ecology 91:990–1003

Lindfield SJ, Harvey ES, Halford AR, McIlwain JL (2015) Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. Coral Reefs 35:125–137. doi:10.1007/s00338–015–1386–8

Littler M, Littler D, Hanisak D (1991) Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. Journal of Experimental Marine Biology and Ecology 150:163–182

Locker SD, Armstrong RA, Battista TA, Rooney JJ, Sherman C, Zawada DG (2010) Geomorphology of mesophotic coral ecosystems: Current perspectives on morphology, distribution, and mapping strategies. Coral Reefs 29:329–345. doi:10.1007/s00338–010–0613–6

Loya Y, Eyal G, Treibitz T, Lesser MP, Appeldoorn R (2016) Theme section on mesophotic coral ecosystems: Advances in knowledge and future perspectives. Coral Reefs 35:1–9

McMahon KW, Thorrold SR, Houghton LA, Berumen ML (2016) Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach. Oecologia 180:809–821. doi:10.1007/s00442–015–3475–3

Millennium Ecosystem Assessment [MEA] (2005) Ecosystems and human well–being: Wetlands and water. World Resources Institute, Washington, DC

Mitchell SJ, Doolette DJ (2013) Recreational technical diving part 1: An introduction to technical diving methods and activities. Diving Hyperb Med 43:86–93

Morsilli M, Bosellini FR, Pomar L, Hallock P, Aurell M, Papazzoni CA (2012) Mesophotic coral buildups in a Prodelta setting (Late Eocene, Southern Pyrenees, Spain): A mixed carbonate–siliciclastic system. Sedimentology 59:766–794. doi:10.1111/j.1365–3091.2011.01275.x

Muir P, Wallace C, Bridge TC, Bongaerts P (2015) Diverse staghorn coral fauna on the mesophotic reefs of north-east Australia. PLoS ONE 10:e0117933. doi:10.1371/journal.pone.0117933

Muir PR, Marshall PA, Abdulla A, Aguirre JD (2017) Species identity and depth predict bleaching severity in reef-building corals: Shall the deep inherit the reef? Proceedings of the Royal Society B: Biological Sciences 284:20171551. doi:10.1098/rspb.2017.1551

Mumby PJ (2017) Embracing a world of subtlety and nuance on coral reefs. Coral Reefs 36:1003–1011. doi:10.1007/s00338–017–1591–8

Newman DJ, Cragg GM (2015) Endophytic and epiphytic microbes as “sources” of bioactive agents. Frontiers in Chemistry 3:34

Ockendon N, Thomas DHL, Cortina J, Adams WM, Aykroyd T, Barov B, Boitani L, Bonn A, Branquinho C, Brombacher M, Burrell C, Carver S, Crick HQP, Duguy B, Everett S, Fokkens B, Fuller RJ, Gibbons DW, Gokhelashvili R, Griffin C, Halley DJ, Hotham P, Hughes FMR, Karamanlidis AA, McOwen CJ, Miles L, Mitchell R, Rands MRW, Roberts J, Sandom CJ, Spencer JW, ten Broeke E, Tew ER, Thomas CD, Timoshyna A, Unsworth RKF, Warrington S, Sutherland WJ (2018) One hundred priority questions for landscape restoration in Europe. Biological Conservation 221:198–208. doi:10.1016/j.biocon.2018.03.002

Olson JB, Kellogg CA (2010) Microbial ecology of corals, sponges, and algae in mesophotic coral environments. FEMS Microbiol Ecol 73:17–30. doi:10.1111/j.1574–6941.2010.00862.x

Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333:418–422. doi:10.1126/science.1204794

Parsons ECM, Favaro B, Aguirre AA, Bauer AL, Blight LK, Cigliano JA, Coleman MA, Cote IM, Draheim M, Fletcher S, Foley MM, Jefferson R, Jones MC, Kelaher BP, Lundquist CJ, McCarthy J-B, Nelson A, Patterson K, Walsh L, Wright AJ, Sutherland WJ (2014) Seventy–one important questions for the conservation of marine biodiversity. Conservation Biology 28:1206–1214. doi:10.1111/cobi.12303

Pinheiro HT, Goodbody-Gringley G, Jessup ME, Shepherd B, Chequer AD, Rocha LA (2016) Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. Coral Reefs 35:139–151. doi:10.1007/s00338–015–1381–0

Pochon X, Forsman ZH, Spalding HL, Padilla-Gamino JL, Smith CM, Gates RD (2015) Depth specialization in mesophotic corals (*Leptoseris* spp.) and associated algal symbionts in Hawai‘i. R Soc Open Sci 2:140351. doi:10.1098/rsos.140351

Pomponi SA, Diaz MC, Van Soest RWM, Bell LJ, Busutil L, Gochfeld DJ, Kelly M, Slattery M (2018) Sponges. In: Loya Y, Puglise KA, Bridge T (eds) mesophotic coral ecosystems of the world. Springer, New York

Prada C, Hellberg ME (2013) Long prereproductive selection and divergence by depth in a Caribbean candelabrum coral. Proceedings of the National Academy of Sciences 110:3961–3966. doi:10.1073/pnas.1208931110

Puglise K, Hinderstein L, Marr JCA, Dowgiallo M, Martinez F (2009) Mesophotic coral ecosystems research strategy: International workshop to prioritize research and management needs for mesophotic coral ecosystems, Jupiter, Florida, 12–15 July 2008. NOAA National Centers for Coastal Ocean Science and Office of Ocean Exploration and Research, Silver Spring MD, NOAA Technical Meorandum NOS NCCOS 98 and OAR OER 2, 24 p

Puglise KA, Colin PL (2016) Understanding mesophotic coral ecosystems: Knowledge gaps for management. In: Baker EK, Puglise KA, Harris PT (eds) Mesophotic coral ecosystems—a lifeboat for coral reefs. The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, p 83–85

Pyle RL (1998) Use of advanced mixed-gas diving technology to explore the coral reef “Twilight zone.” In: Ocean pulse. Springer, p 71–88

Pyle RL, Boland R, Bolick H, Bowen BW, Bradley CJ, Kane C, Kosaki RK, Langston R, Longenecker K, Montgomery A, Parrish FA, Popp BN, Rooney J, Smith CM, Wagner D, Spalding HL (2016) A comprehensive investigation of mesophotic coral ecosystems in the Hawaiian archipelago. PeerJ 4:e2475. doi:10.7717/peerj.2475

Pyle RL, Kosaki RK, Copus JM, Whitton RK, Pinheiro HT, Rocha LA (2018) Fishes: Biodiversity In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world. Springer, New York

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Rädecker N, Pogoreutz C, Voolstra CR, Wiedenmann J, Wild C (2015) Nitrogen cycling in corals: The key to understanding holobiont functioning? Trends in Microbiology 23:490–497. doi:https://doi.org/10.1016/j.tim.2015.03.008

Reed JK, Farrington S, David A, Harter S, Pomponi S, Diaz C, Voss J, Spring KD, Hine AC, Kourafalou V, Smith RH, Vaz AC, Paris CB, Hanisak MD (2018) Pulley Ridge, Gulf of Mexico, U.S.A. In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world. Springer, New York

Roder C, Berumen ML, Bouwmeester J, Papathanassiou E, Al-Suwailem A, Voolstra CR (2013) First biological measurements of deep-sea corals from the Red Sea. Scientific Reports 3:2802. doi:10.1038/srep02802

Rossi S, Tsounis G (2007) Temporal and spatial variation in protein, carbohydrate, and lipid levels in *Corallium rubrum* (anthozoa, octocorallia). Marine Biology 152:429–439

Semmler RF, Hoot WC, Reaka ML (2016) Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? Coral Reefs 36(2):433–444. doi:10.1007/s00338–016–1530–0

Serrano X, Baums IB, O'Reilly K, Smith TB, Jones RJ, Shearer TL, Nunes FL, Baker AC (2014) Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. Mol Ecol 23:4226–4240. doi:10.1111/mec.12861

Serrano XM, Baums IB, Smith TB, Jones RJ, Shearer TL, Baker AC (2016) Long distance dispersal and vertical gene flow in the Caribbean brooding coral *Porites astreoides*. Scientific Reports 6:21619. doi:10.1038/srep21619

Sherman CE, Locker SD, Webster JM, Weinstein DK (2018) Geology and geomorphology. In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world. Springer, New York

Sherman C, Nemeth M, Ruíz H, Bejarano I, Appeldoorn R, Pagán F, Schärer M, Weil E (2010) Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. Coral Reefs 29:347–360. doi:10.1007/s00338–010–0607–4

Slattery M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ (2011) Connectivity and stability of mesophotic coral reefs. Journal of Experimental Marine Biology and Ecology 408:32–41. doi:10.1016/j.jembe.2011.07.024

Smith TB, Gyory J, Brandt ME, Miller WJ, Jossart J, Nemeth RS (2015) Caribbean mesophotic coral ecosystems are unlikely climate change refugia. Glob Chang Biol 22(8):2756–2765. doi:10.1111/gcb.13175

Spalding H (2012) Ecology of mesophotic macroalgae and *Halimeda kanaloana* meadows in the main Hawaiian Islands. Dissertation, University of Hawaiʻi at Mānoa

Spalding HL, Conklin KY, Smith CM, O'Kelly CJ, Sherwood AR (2016) New Ulvaceae (Ulvophyceae, Chlorophyta) from mesophotic ecosystems across the Hawaiian archipelago. Journal of Phycology 52:40–53. doi:10.1111/jpy.12375

Spalding HL, Amado-Filho GM, Bahia RG, Ballantine DL, Fredericq S, Leichter JJ, Nelson WA, Slattery M, Tsuda RT (2018) Macroalgae In: Loya Y, Puglise KA, Bridge T (eds) Mesophotic coral ecosystems of the world Springer, New York

Sutherland WJ, Fleishman E, Mascia MB, Pretty J, Rudd MA (2011) Methods for collaboratively identifying research priorities and emerging issues in science and policy. Methods in Ecology and Evolution 2:238–247. doi:10.1111/j.2041–210X.2010.00083.x

Sutherland WJ, Freckleton RP, Godfray HCJ, Beissinger SR, Benton T, Cameron DD, Carmel Y, Coomes DA, Coulson T, Emmerson MC, Hails RS, Hays GC, Hodgson DJ, Hutchings MJ, Johnson D, Jones JPG, Keeling MJ, Kokko H, Kunin WE, Lambin X, Lewis OT, Malhi Y, Mieszkowska N, Milner-Gulland EJ, Norris K, Phillimore AB, Purves DW, Reid JM, Reuman DC, Thompson K, Travis JMJ, Turnbull LA, Wardle DA, Wiegand T (2013) Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67. doi:10.1111/1365–2745.12025

Tenggardjaja KA, Bernardi G, Bowen BW (2014) Vertical and horizontal genetic connectivity in *Chromis verater*, an endemic damselfish found on shallow and mesophotic reefs in the Hawaiian Archipelago and adjacent Johnston Atoll. PLoS ONE 9:e115493

Torda G, Donelson JM, Aranda M, Barshis DJ, Bay L, Berumen ML, Bourne DG, Cantin N, Foret S, Matz M, Miller DJ, Moya A, Putnam HM, Ravasi T, van Oppen MJH, Thurber RV, Vidal-Dupiol J, Voolstra CR, Watson S-A, Whitelaw E, Willis BL, Munday PL (2017) Rapid adaptive responses to climate change in corals. Nature Climate Change 7:627. doi:10.1038/nclimate3374

Tsounis G, Rossi S, Grigg R, Santangelo G, Bramanti L, Gili J-M (2010) The exploitation and conservation of precious corals. CRC Press, Boca Raton (USA), vol 48

Turner JA, Babcock RC, Hovey R, Kendrick GA, Degraer S (2017) Deep thinking: A systematic review of mesophotic coral ecosystems. ICES Journal of Marine Science 74:2309–2320. doi:10.1093/icesjms/fsx085

Turner JA, Thomson DP, Cresswell AK, Trapon M, Babcock RC (2018) Depth-related patterns in coral recruitment across a shallow to mesophotic gradient. Coral Reefs. doi:10.1007/s00338-018-1696-8

van Oppen MJ, Bongaerts P, Underwood JN, Peplow LM, Cooper TF (2011) The role of deep reefs in shallow reef recovery: An assessment of vertical connectivity in a brooding coral from west and east Australia. Mol Ecol 20:1647–1660. doi:10.1111/j.1365–294X.2011.05050.x

Vaz AC, Paris CB, Olascoaga MJ, Kourafalou VH, Kang H, Reed JK (2016) The perfect storm: Match-mismatch of bio-physical events drives larval reef fish connectivity between Pulley Ridge mesophotic reef and the Florida Keys. Continental Shelf Research 125:136–146. doi: 10.1016/j.csr.2016.06.012

Vergés A, Steinberg PD, Hay ME, Poore AG, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA, Figueira W (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B 281(1789):20140846

Weinstein DK, Klaus JS, McNeill DF (2015a) Syndepositional cementation in the reef ‘twilight zone.’ Reef Encounter 30:53–56

Weinstein DK, Klaus JS, Smith TB (2015b) Habitat heterogeneity reflected in mesophotic reef sediments. Sedimentary Geology 329:177–187. doi:10.1016/j.sedgeo.2015.07.003

Weinstein DK, Sharifi A, Klaus JS, Smith TB, Giri SJ, Helmle KP (2016) Coral growth, bioerosion, and secondary accretion of living orbicellid corals from mesophotic reefs in the US Virgin Islands. Marine Ecology Progress Series 559:45–63

Weinstein DK, Smith TB, Klaus JS (2014) Mesophotic bioerosion: Variability and structural impact on U.S. Virgin Island deep reefs. Geomorphology 222:14–24. doi:10.1016/j.geomorph.2014.03.005

Wernberg T, Russell BD, Moore PJ, Ling SD, Smale DA, Campbell A, Coleman MA, Steinberg PD, Kendrick GA, Connell SD (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. Journal of Experimental Marine Biology and Ecology 400:7–16

White KN, Ohara T, Fujii T, Kawamura I, Mizuyama M, Montenegro J, Shikiba H, Naruse T, McClelland T, Denis V, Reimer JD (2013) Typhoon damage on a shallow mesophotic reef in Okinawa, Japan PeerJ 1:e151. doi:10.7717/peerj.151

White KN, Weinstein DK, Ohara T, Denis V, Montenegro J, Reimer JD (2017) Shifting communities after-typhoon damage on an upper mesophotic reef in Okinawa, Japan. PeerJ 5:e3573. doi:10.7717/peerj.3573

Woodall LC, Andradi-Brown DA, Brierley AS, Clark MR, Connelly D, Hall RA, Howell KL, Huvenne V, Linse K, Ross RE, Snelgrove P, Stefanoudis PV, Sutton TT, Taylor MW, Thornton TF, Rogers A (2018) A multidisciplinary approach for generating globally consistent data on mesophotic, deep-pelagic, and bathyal biological communities. Oceanography 31(3). doi:10.5670/oceanog.2018.301

Ziegler M, Roder CM, Buchel C, Voolstra CR (2015) Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology. Frontiers in Marine Science 2:4. doi:10.3389/fmars.2015.00004

Ziegler M, Roder CM, Büchel C, Voolstra CR (2014) Limits to physiological plasticity of the coral *Pocillopora verrucosa* from the central Red Sea. Coral Reefs 33:1115–1129. doi:10.1007/s00338–014–1192–8

Ziegler M, Seneca FO, Yum LK, Palumbi SR, Voolstra CR (2017) Bacterial community dynamics are linked to patterns of coral heat tolerance. Nature Communications 8:14213. doi:10.1038/ncomms14213

Figures

Fig. X.1. Cumulative number of scientific publications sorted by theme using the mesophotic.org database as of 19 Jan 2018.

Fig. X.2. Proportion of scientific publications (from mesophotic.org) compared to the proportion of unique submitted questions (from Stage 2, n=131) from participants by each theme. Top=All studies (since 1960), Bottom=only studies from 2010 onwards. Dashed line identifies y=x indicating equal representation in the literature and submitted questions.

Tables

Table X.1. The affiliation of survey respondents. A total of 43 respondents submitted questions at Stage 1 and a total of 39 respondents submitted rankings at Stage 3.

Affiliation	Percentage of respondents at Stage 1: Question submission (%)	Percentage of respondents at Stage 3: Question ranking (%)
University	62.8	59.0
Conservation NGO/Charity	14.0	12.8
Government	9.3	12.8
Research Institution	9.3	10.3
Consultant	4.6	5.1

Table X.2 Themes are presented in rank order based on the means cores from participants (Stage 3). Individual scores ranged from 0 (no importance) to 10 (high importance). Note: the mean score for the top 10 questions in each theme included all questions, even when there were fewer than 10 in the theme.

Theme	Mean Score (Top 10 ranked questions within theme ± SE)	Number of questions in theme after Stage 2	Number of questions in final list	Percentage of questions in the final list
Management and Policy	8.20 ± 0.23	26	5	19.2%
Connectivity	8.08 ± 0.30	15	3	20.0%
Threats	8.03 ± 0.53	22	4	18.2%
Ecological Processes	7.93 ± 0.27	21	3	14.3%
Biodiversity and Community Structure	7.86 ± 0.54	21	4	19.1%
Environmental and Physical Processes	7.35 ± 0.82	8	2	25.0%
Distribution	7.20 ± 0.58	9	2	22.2%
Physiology	7.01 ± 0.57	8	2	25.0%

Supplementary Information

Supplementary Table X.1. List of 131 unique questions classified by theme during Stage 2.

Theme	Unique Question
Distribution	How are MEs distributed globally?
	How different are the latitudinal range extents for MEs compared to shallow systems?
	How do we combine data to assess broader spatial patterns and processes across MCEs?
	How do we map MEs?
	What are the latitudinal range extents for MEs globally?
	Where do we draw the line between MCE and TME assemblages?
	Will the extent of MEs change in the future?
	How and why do MEs vary geographically across multiple spatial scales?
	What is the total extent of submerged/undocumented reef habitat that supports MEs?
Environmental and Physical Processes	Are MEs important carbon sinks?
	Are past mesophotic reefs the final stage in reef drowning?
	Can we utilize geological variables to predict ME location, growth and future projections?
	Do calcification processes differ at mesophotic depths?
	How variable are ME environmental conditions across time and space?
	What are the ocean environment characteristics and oceanographic processes relevant to MEs?
	What is the carbonate budget of MEs?
	What role do MEs play in coastal/benthic biogeochemical cycling?
Biodiversity and Community Structure	Are biogeographical patterns of ME diversity the same as for shallow reefs?
	Are we agreed on the definition of 'mesophotic?'
	Does the parasitic and microbial diversity of MEs differ between regions?
	How diverse are ME holobiont/microbial populations?
	How do holobiont populations change with depth?
	How do ME and shallow-water biodiversity differ?
	How do ME and shallow-water communities differ?
	How do MEs differ in biodiversity across global regions?
	How do symbiotic microbial populations change with depth?
	How do tropical and temperate MEs differ?

	How do we prioritize ME species for genome sequencing?
	How does ME and shallow-water genetic diversity differ?
	How does ME biodiversity change across latitudes?
	How does shallow-water and ME benthic diversity correlate?
	How does shallow-water and ME fish diversity and biomass correlate?
	How much marine life remains to be discovered at mesophotic depths?
	What are the diversity and distribution of key fisheries species or valuable species in the mesophotic area?
	What is the depth limit between mesophotic and deep ecosystems?
	What proportion of global coral biomass is present in MEs?
	What are the main variables that influence mesophotic community changes along a depth gradient?
	What are the main variables that influence mesophotic community changes spatially across regions?
Ecological Processes	Are recolonization dynamics in MEs the same as for shallow-water reefs?
	Do "healthier" coral reefs occur adjacent to MEs?
	Do MEs function in the same way as shallow reefs?
	Do phase shifts occur at mesophotic depths and how do we define them?
	Do symbiotic relationships between organisms differ between mesophotic and shallow depths?
	Does ME functional trait diversity mirror that of shallow reefs?
	How do ME benthic organism life history traits differ from shallow reefs?
	How do ME fish life history traits differ from shallow reefs?
	How does competition drive zonation in MEs?
	How much we know about growth rates of benthic mesophotic species?
	How much we know about population structure of benthic mesophotic species?
	How much we know about the life span of benthic mesophotic species?
	How much we know about the reproductive output of benthic mesophotic species?
	Is the lower depth limit of marine macroalgae (including calcifying marine macroalgae) becoming deeper, shallower or staying the same, over timescales of years to tens of years?
	To what extent do other organisms (not reef-building corals) contribute to ME 3D structure?
	What are the functional traits of MEs?
	What are the main roles/significances of MEs in the marine environment?
	What is the role of ME habitats to deep-sea (> 200 m) food supply?
	What will be the future functional responses of MEs to the changing world?
	Which are the key ecological functional species groups responsible for maintaining ME reef health?

	What ecological processes determine the composition of mesophotic communities?
Connectivity	Are MEs connected to deep-sea (> 200 m) areas?
	Can mesophotic reefs serve as a refugia for coral reefs?
	Do MEs play an important role in the reproduction of fish species (including commercially-important species)?
	Do mesophotic reefs provide refuge for fishery targeted species?
	How can conserving MEs improve the condition of shallower areas?
	How do mobile species utilize mesophotic areas?
	How do shallow and mesophotic populations of fisheries target species interact?
	To what extent are MEs connected to each other?
	To what extent are MEs connected to shallow-water areas?
	What are the most important factors driving the differences between ecological refuge and evolutionary refugia?
	What are the relative influences of selection versus dispersal on coral population structure across shallow coral reefs and MEs?
	What is the biomass export from MEs to shallow areas?
	What is the contribution of MEs in the recovery (and resilience) of shallow-water reefs?
	What are the differences of genetic connectivity between shallow and deep populations of ecosystem engineering species in tropical and temperate areas?
	Which coral species offer the greatest potential for replenishing shallow reefs?
Physiology	What are the environmental limits of MEs?
	Can we quantify the energy budgets of key sessile animals in MEs?
	Do organisms in MEs utilize different survival strategies to those found in shallow reefs?
	How do energy transfer rates between trophic levels differ between communities in shallow and mesophotic coral reefs?
	How does reef florescence change across shallow to mesophotic gradients and what is the significance?
	To what extent are community boundaries determined by physiology?
	What are the relative influences of genotype and environment on phenotypic adaptations in MEs?
	What environmental factors alter the coral's microbiome?
	How do individual ME organisms respond to low-light conditions (e.g., ecological plasticity vs. adaptation) particularly with respect to energetic inputs (e.g., photosynthesis and exogenous nutrient sources)?
Threats	Are mesophotic corals doing better than shallow corals in terms of resilience, resistance, and current condition?
	Can ME species adapt/acclimate to changing environmental conditions (e.g. rising sea surface temperature)?
	Can ME species adapt/acclimate to shallow-water environmental conditions?
	How are invasive species impacting MEs?
	How are MEs affected by diseases?
	How can we control invasive species impacting MEs?

	How do disease rates change with depth across a shallow to mesophotic gradient?
	How resilient are MEs?
	How resistant are MEs to sedimentation?
	How will climate change impact MEs?
	How will climate change, increased sea surface temperatures, and ocean acidification influence the distribution, richness, relative abundance, and prevalence of diseases and invasive species in MEs?
	How will global changes act on mesophotic species genetic diversity?
	What anthropogenic pressures have the highest impact on MEs?
	What are the impacts of fishing in MEs?
	What are the main threats to MEs?
	What are the main threats to MEs and how can conservation strategies tackle them (now and future)?
	What is the impact of the rising popularity of technical diving on MEs?
	What is the recovery rate and resilience potential of MEs after a disturbance event?
	What parasites are found at mesophotic depths?
	What strategies can be used to mitigate and manage the effects of the spread of existing and emergence of new marine pathogens within MEs?
	To what extent are the changing frequency, intensity, and magnitude of disturbances (both biotic and anthropogenic) altering the distribution and abundance of individual species and communities in MEs, and what are the best ways to evaluate and manage these impacts?
	What effect do severe disturbances (e.g., severe cyclones and bleaching) have on MEs?
Management and Policy	What are the ecosystem services of MEs?
	Are marine spatial planning strategies for shallow MPAs effective in MEs?
	How can we get mesophotic reefs on the Red List of ecosystems?
	How do different fisheries management methods (e.g., no take and gear restrictions) differ in their results for ME fish populations?
	How do we best raise awareness among governments/donors/funding bodies about the urgent need to conserve MEs?
	How do we best share knowledge and expertise among the ME research community?
	How do we convey the message of the importance of the MEs to decision makers?
	How do we integrate MEs consideration into national policies?
	How do we treat data from MEs in marine spatial planning (e.g., treat it differently, in regards to the target, cost, etc., or the same as data from shallow reefs)?
	How much do coastal populations depend on MEs for their livelihoods (e.g., directly from fisheries, and/or indirect ecosystem services)?
	How well known/understood are MEs by the public?
	Is artificial restoration an appropriate management choice for MEs?

	Should long-term monitoring programs of MEs be established in the near future as a priority?
	Should we prioritize areas for ME research?
	What are the key indicators that should be monitored in MEs?
	What are the main management considerations for MEs?
	What are the most adequate, long-term conservation strategies for MEs (e.g., protection level: no take or some fisheries allowed and size of MPAs)?
	What characteristics would be most appropriate to measure in order to accurately model/predict the location of known/unknown MEs?
	What considerations should go into MPA design for mesophotic benthic organisms?
	What is the economic value of ME fisheries?
	What is the status of fish populations and other marine organisms in MEs?
	What is the value of MEs (to fisheries, communities, etc.)?
	What methods, datasets, and resources are available to monitor MEs?
	What new novel methods can be utilized in ME research?
	How should uncertainty, risk, and precaution be incorporated into effective conservation policy making of MEs?
	What proportion of MEs are currently protected?