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 nongovernmental), 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.

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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.

52.1 Introduction

In the twenty-first 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 to 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.

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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, USA, 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, UK, 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.

52.2 Methods

52.2.1 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 ≥3–10 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), and it must (1) be of global importance, (2) be impeding a wider understanding of ME processes and/or management/conservation progress, (3) be 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) be answerable with research using a measurable outcome, and not based on value judgment.

Participants submitted questions that met this criterion 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.

52.2.2 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 (Table 52.S1). 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).

52.2.3 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).

52.2.4 Stage 4: Workshop

The ECRS 2017 workshop 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 ten 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.

52.2.5 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 January 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 was calculated. Gray literature (e.g., government reports) is underrepresented in this database. Thus, the total number of publications per theme is not accurate and merely demonstrates 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.

52.3 Results

A total of 287 questions were submitted by 43 individuals from a range of affiliations (Table 52.1). Of the 287 questions, 131 were deemed unique and allocated to one of the 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 52.2). 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 ($\chi^2 (7) = 6.550$, $p = 0.477$).

The final number of questions for each theme reflected a similar proportion to the number of submitted questions (Table 52.2). 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 over-

Table 52.1 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 52.2 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)

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

Mean scores were calculated from the ten top-ranked questions or included all questions in themes with fewer than ten

represented with regard 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 toward 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. 52.1). 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. 52.2). 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. 52.2). 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. 52.2).

A final list of 25 questions (labeled 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 multistage approach, all questions are considered to be important for progressing our understanding of MEs and their overall conservation and management.

52.3.1 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 Hawai'i (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 modeling 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), and acoustic instruments (e.g., multibeam echo sounders and side-scan sonars), enable mapping of wide areas at high spatial resolution (Armstrong et al. 2019). 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?

52.3.2 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 depen-
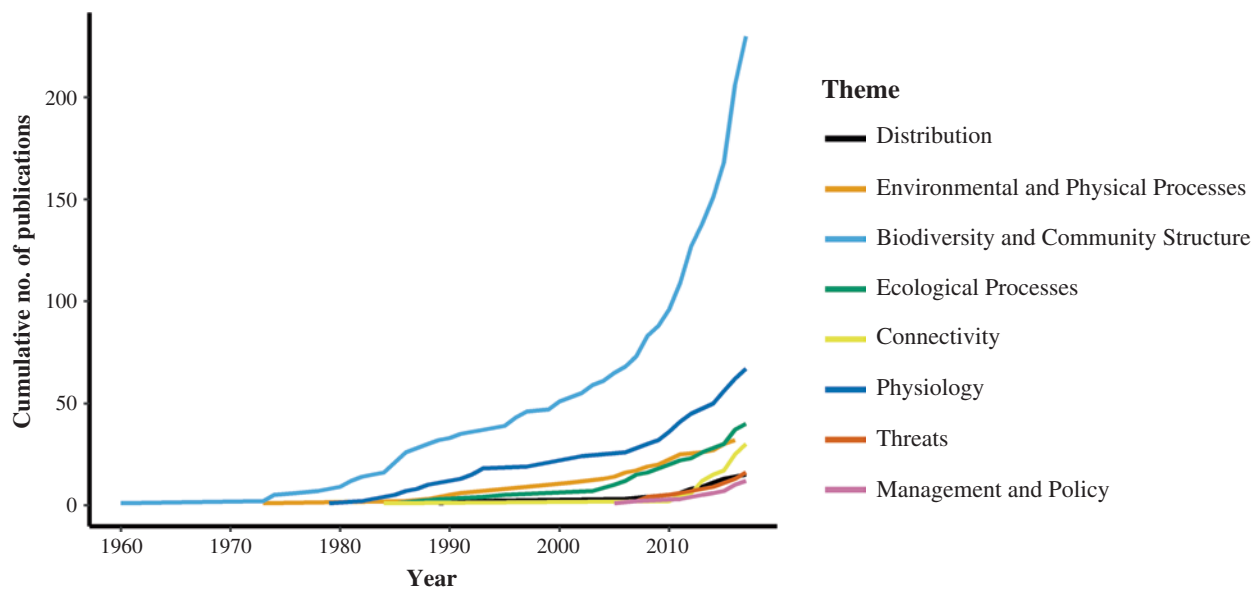
Fig. 52.1 Cumulative number of scientific publications sorted by theme using the mesophotic.org database as of 19 January 2018
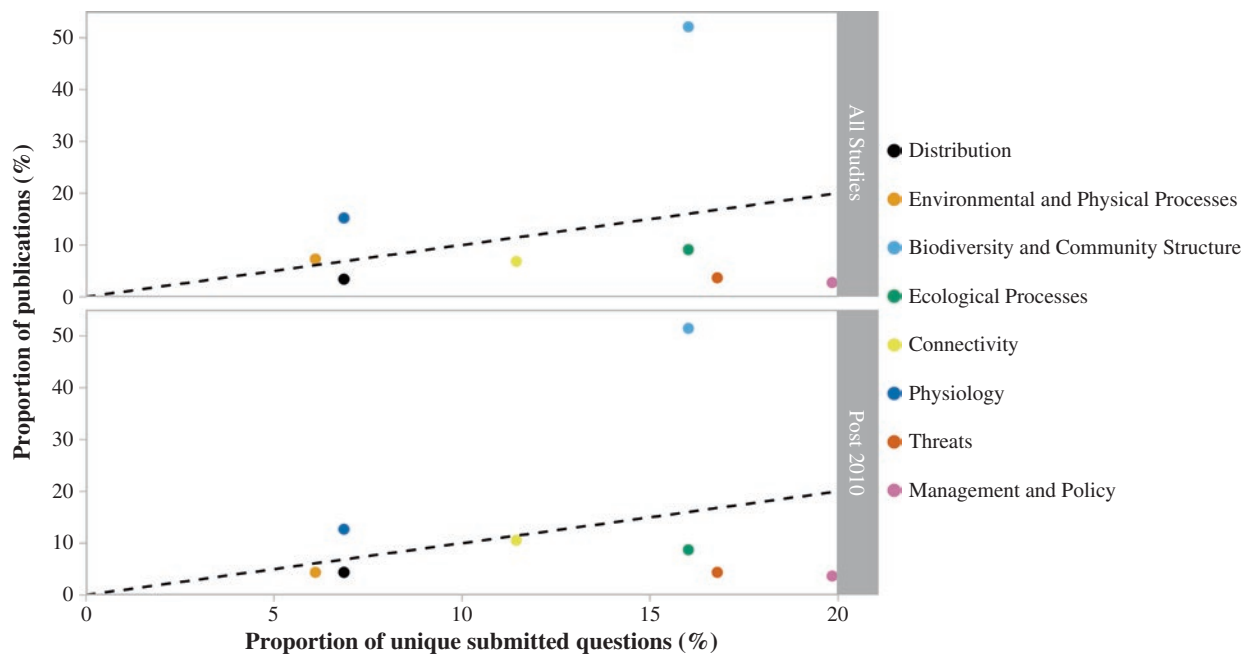

Fig. 52.2 Proportion of scientific publications (from mesophotic.org) compared to the proportion of unique submitted questions (from Stage 2, n = 131) from participants by each theme. Top = all studies (since 1960); bottom = only studies from 2010 onward. Dashed line identifies y=x indicating equal representation in the literature and submitted questions

dence 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. 2019), 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. 2019), 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 sulfur (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 and the response of ancient MEs to paleoenvironmental change (e.g., Morsilli et al. 2012; 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?

Q4. What is the role of MEs in biogeochemical cycling across space and time?

52.3.3 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. 2019; Pyle et al. 2019; Spalding et al. 2019), 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?

52.3.4 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?

Q10. What are the functional traits and responses of taxonomic groups in MEs, and how will they be modified under climate change?

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?

52.3.5 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 2019). 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 (Costantini 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), in particular how such connectivity may differ from patterns observed for shallow reefs across the same regions (Pyle et al. 2019). 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?

52.3.6 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 2019), 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?
Q16. What are the energy transfer rates between trophic levels along the depth gradient from shallow to mesophotic reefs?

52.3.7 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 (e.g., 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?

52.3.8 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. 2019). Studies have been conducted on the role of MEs with respect to fisheries (e.g., Bejarano et al. 2014; Lindfield et al. 2015; Andradi-Brown et al. 2017), resource extraction (Grigg 2001; Tsounis et al. 2010; Bruckner 2016; Gress and Andradi-Brown 2018), 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. 2019). 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. 2019), 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 straightforward 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 toward 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?

52.4 Discussion

While progress has been made toward 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 toward 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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