To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest?

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Abstract

Background: Mesophotic coral ecosystems (MCEs) are tropical and sub-tropical reefs between 30 m and potentially >150 m depth, the maximum for photosynthetic hard corals. The definition's upper boundary is ecologically arbitrary. Recently, research has focused on the deep reef refugia hypothesis suggesting MCEs can be protected from shallow-water threats, potentially acting as a local source for re-colonisation of shallow reefs. This led to recent calls to increase their protection. It remains unclear whether the current MCE definition reflects changing biodiversity with depth, and so whether protecting MCEs based on this definition will protect shallow reef species. We ask where shifts in ecological community structure occur across the shallow-mesophotic depth gradient. We consider to what extent MCEs as currently defined protect shallow reef taxa. Research on coral reef depth gradients has a long history. Research relevant to MCEs has been published under a variety of terms. We will use the systematic review framework to collect older data sources, increasing accessibility by depositing the meta-data in an online library for researchers and managers.

Methods: A systematic review will be conducted, searching online databases, grey literature and personal libraries of experts. The primary question was formulated after consulting an advisory committee. Inclusion criteria discriminate among studies by sampling depths and community data. Critical appraisal of studies will consider key criteria concerning internal validity. We shall identify where more biodiversity and community-level data are required, determined by whether a meta-analysis is possible. Considering how to structure a meta-analysis once community metric and variability data have been collected will help to advise future data collection. Provided enough data are extracted, we shall conduct a meta-analysis examining changes in species richness, abundance and biomass across the depth gradient. If ecological community level data are present, we shall conduct an additional meta-analysis looking at community turnover with depth.

Keywords: Mesophotic coral ecosystems, Depth, Community structure, Biodiversity, Coral reefs, Twilight zone

Background

Mesophotic coral ecosystems (MCEs) are currently defined as reefs 'characterised by the presence of light-dependent corals and associated communities typically found at depths ranging from 30–40 m and extending to over 150 m in some tropical and subtropical regions with high water clarity' [1, 2]. MCEs are more difficult to access than their shallow reef counterparts, yet harbour distinct communities adapted to living under low-light conditions [3]. These ecosystems have been observed almost everywhere shallow reefs are found, and significantly increase global coral reef area [4]. Despite their broad distribution, it is clear that MCEs remain highly understudied [5]. MCEs are of conservation interest in part because they can be protected from certain disturbances that affect shallow reefs, such as storm damage

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and rising sea surface temperatures [6, 7]. In some cases however MCEs may be susceptible to damage [8]. When a MCE survives the damage occurring on an adjacent shallow reef, recruits from depth could settle in the shallows and support recovery [9]. This is known as the deep reef refugia hypothesis (DRRH). To what extent the DRRH applies is dependent on: the degree of community overlap between shallow and mesophotic reefs and, the ability of offspring from the deeper reefs to survive in the shallows, the fecundity of deeper reefs and the assumption deeper reefs are protected from pressures.

The accessibility of MCEs has been increasing as a result of technological advances in diving, acoustic mapping and autonomous and remote vehicles [10], as well as expanding interest because of the suggested links to shallow-water reef conservation [6]. The field has received a body of new work following the original foundation in the 1980s [11] with a marked increase over the last few years. Kahng et al. [2] reported 26 papers from 16 regions in their 2010 review of MCEs for zooxanthellate corals, as well as papers on fish and algae. Additional data are now available from: the Red Sea [12, 13], the Caribbean [14, 15], the central Pacific [16–18], the Great Barrier Reef [19, 20], and others. However, the techniques employed, the questions asked and the taxa considered are variable. As a result, following the second International Workshop on Mesophotic Coral Ecosystems in 2014 at the Interuniversity Institute for Marine Science, (Eilat, Israel), the need for synthesis has been acknowledged [21]. In order to maximise productivity in this new phase of MCE exploration, it is necessary to draw together the multiple sources of existing data into a single synthesis. The current upper limit of MCEs is considered as approximately 30 m [2], determined primarily by limits of conventional SCUBA diving techniques. The lower limit coincides with the record of the deepest zooxanthellate coral for a site. These two depth limits are fundamentally different, the second has its roots in ecological observation and is variable by location, whereas the first is a definition based on a lack of study effort resulting from technological difficulty and is fixed.

Though generally poorly protected [7], MCEs are beginning to be incorporated into marine protected areas [22] because of the possibility they may shelter unique biodiversity and shallow reef species. For example, the existing Coral Beach Nature Reserve in Israel was expanded in order to incorporate MCEs down to a depth of 50 m. It is unclear how this expansion in protection will impact MCEs and shallow-water reefs, as conditions may alter species depth distributions from site to site and affect the degree of community overlap between the shallow reefs and MCEs. In other instances, MCEs may have been serendipitously protected by the establishment of large off-shore no-take reserves [23].

Recently a "faunal break" has been described at approximately 60 m between the 'upper' and 'lower' MCEs, based on site-specific ecological community composition observations, as well as genetic and physiological data for corals [3, 14, 24, 25]. It appears that in some locations, the lower MCEs may harbour a distinct community of depth-specialists. The upper MCEs may represent a transitional zone containing species specialised for both the shallows and lower MCEs. This may mean MCEs require protection across their whole range to capture distinct assemblages as these reefs are subject to their own pressures [26].

We seek evidence of natural break points in community structure, which may lead to a biological definition of both depth limits. Site-specific environmental conditions such as turbidity can modify the depths at which reefs, and particular communities, occur. The logical comparison across sites requires that the upper limit accommodates the variable nature of species occurrence. We consider changing biodiversity and community composition as potential definitions, as they allow researchers with taxonomic experience to recognise the vertical zonation of the reef. The occurrence of a species can be viewed as a signal which integrates multiple environmental factors. Measuring the environmental factors directly, while possible, would require expensive monitoring equipment housings and extensive operational capability to maintain equipment, download and impose quality control on the data and archive it for general use. Such issues may be circumvented by the use of ecological data.

Identifying the upper boundary of MCEs in terms of community composition has implications for assessment of whether the DRRH may apply at a given site, though we concede this is not the only factor of importance. In order for a shallow reef to be repopulated by a deeper reef, or vice versa, there must be an overlap in the species present on both reefs. A deeper boundary between shallow reefs and MCEs resulting from, for example, high water clarity at a given site, may increase the applicability of the DRRH. The field may have been asking the wrong question of "can MCEs act as a refuge for shallow reefs?" rather than "what is the best way to define the shallow boundary of MCEs?". A larger depth range for the shallow reef would allow shallow-water corals to exploit the same protection MCEs are theoretically afforded [7]. Upper MCEs may be the depth zone in which the DRRH applies [27], while lower MCEs should become of conservation interest in their own right [15]. Should the transition occur relatively shallow, then upper MCEs may not be protected by depth. The scientific and management community can then recognise MCEs as a special biological assemblage and make logical cross-site comparisons. To begin with this approach, however, it is important to

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determine the extent to which shallow reef species are present in MCEs as currently defined.

Conservation managers in charge of existing MPAs, or government organisations considering the establishment of new reserves, will benefit from this evidence base. Quantifying the degree of community overlap between protected mesophotic reefs and shallow reefs may help inform the urgent decisions which must be made in the face of mass climate change and other threats. Marine protected area authorities, without this information, would otherwise be unable to prioritise the boundaries of reserves based on biological resource at depth for insurance purposes or for their own uniqueness. The need to answer these questions for, and raise awareness within, the management community has recently been raised [28].

Objective of the review

Primary question:
To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest?

This can be broken into the following structure:

Subject (population)	Exposure	Comparator	Outcome
Tropical and subtropical coral reefs	Reefs deeper than 30 m	Reefs shallower than 30 m	Biodiversity, abundance and biomass measures

Secondary questions may be attempted dependent on the literature retrieved. Possible questions could either identify the depths at which the new boundaries may be set, or are exploratory questions based on effect modifiers.

Secondary questions:
What is the impact of increasing depth on community structure?

Can biodiversity and community data from coral reefs be used to naturally define the depth limits of MCEs?

Can a change in species richness/biodiversity/community structure coinciding with genetic and physiological observations be detected in the literature?

Do the boundaries of MCEs vary by region or between broad taxonomic groups?

Does the method used to survey MCEs influence the detected patterns in composition?

These secondary questions consider the ecology that may help inform conservation decisions. Trying to improve our ability to recognise different types of coral reef could allow more effective prioritisation of biological resources. A significant change in community composition may exist in line with other data suggesting a 60 m boundary. This compositional change may have already been detected for fishes. Fish communities have been found to change rapidly with depth at around 60 m at some sites, for example in the Red Sea [29] and Puerto Rico [13, 30]. A meta-analytical approach would allow this broad observation to be tested directly. Quantifying the effect of different surveying methodologies will also help inform future research, allowing for the correction of differences.

Methods

Searches
Searches shall be limited to studies providing an English title and abstract. Patents will also be excluded from the search. As a result of preliminary scoping of the literature two search strings will be run in conjunction, limited by year. The MCE literature is under-represented in the coral literature [5] and spread over at least four decades. The multiple name changes of the field make it difficult to generate a specific search string which remains comprehensive as other fields have since adopted the synonyms.

Early studies in the 1980s [31] simply referred to MCEs as deep reefs. With the discovery of azooxanthellate reefs as deep as 1000 m, the term deep reef was henceforth used to refer to azooxanthellate coral reefs occurring below the photic zone [32]. It was not until 2008, when an international workshop sponsored by National Oceanic and Atmospheric Administration (NOAA) brought together researchers familiar with deep coral reefs, that agreement was reached to use the term "mesophotic coral ecosystems" [1]. We aim to use the systematic review framework as an opportunity to collect older data sources using different keywords and make them readily accessible by depositing the meta-data in a central repository, (http://www.mesophotic.org). This review will utilise a broad search strategy in order to capture as much of the literature as possible prior to 2010. Previous terms such as deep reefs have since been adopted by other fields [32]. We chose to adopt a second simple search string from 2010 onwards, allowing time for the new term 'Mesophotic' to become adopted and avoiding the retrieval of a wealth of misleading modern articles from different fields as shown by Fig. 1.

Any literature detected as relevant to MCEs shall be recorded and reported to http://www.mesophotic.org, regardless of whether it is included in the final dataset concerned with ecology. This prevents the loss of physiology and genetic studies from the search and their addition to the online resource. Doing so should aid the accessibility of the literature and favour synthesis in the field.

Review scoping was conducted in order to generate and refine a search string. The scoping exercise
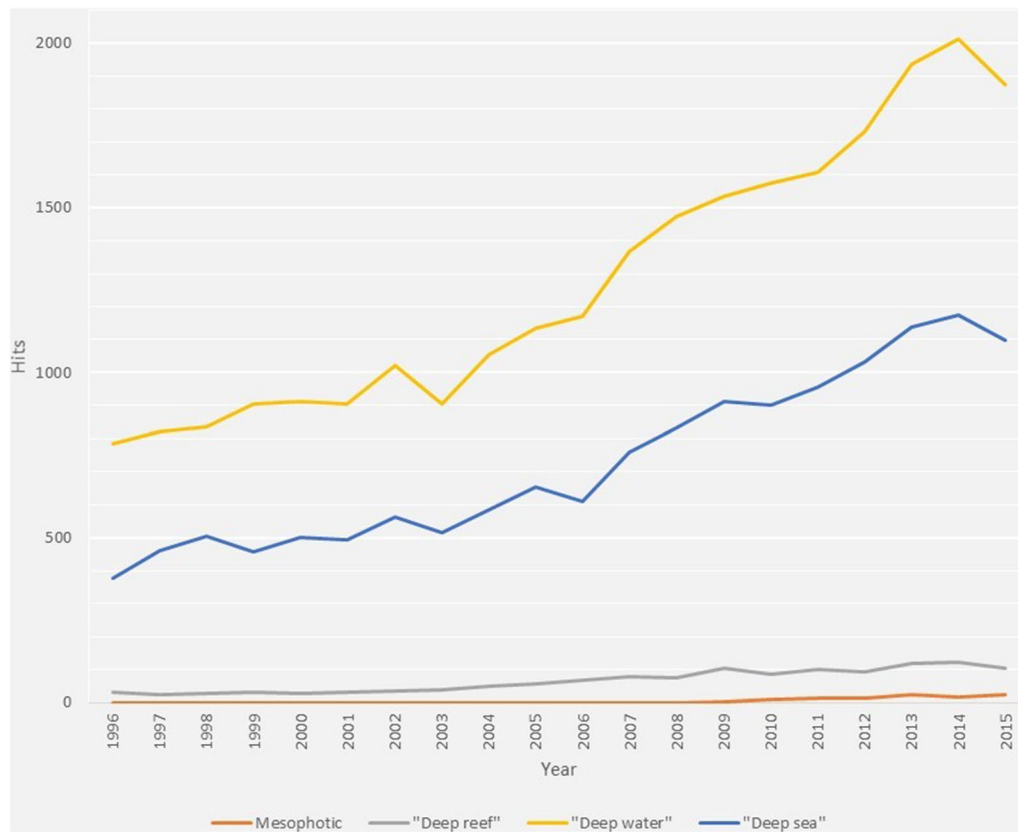
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Fig. 1 The number of hits returned in the last 20 years, by the search strings detailed in the legend, when ran in Scopus on 23/02/16. These terms can capture mesophotic research. The search was limited to English journal articles and reviews in the life sciences

recorded tested search strings, the details of search results, the percentage of test library retrieved and the decision process, and can be found in the Additional file 1. Search string development was an iterative process conducted in the platforms ISI Web of Science and Scopus using an Oxford University log in, trialling against a test library of papers (Additional file 2). The test library was formed of a mix of recent papers and those predating the term "mesophotic". The chosen papers included relevant information for meta-analysis and were suggested from the personal libraries of members of the advisory committee. The final search strings are as follows:

Mesophotic
From *1 Jan 2010 to the date of search*
Mesophotic
OR
"Deep reef"
OR
((Submersibl* OR Submarine* OR "Deep water" OR Trimix)
AND

(biolog* OR Reef* OR Cora* OR Spong* OR Alga* OR Fish*))
Beginning of the resource—31 December 2009

The search strings retrieved 87 % of the test library. This was deemed suitably comprehensive given the large number of hits returned and after investigating why certain test library documents were not retrieved (Additional file 1).

Data sources
All of the relevant resources shall be downloaded with abstracts, when provided, into reference management software.

Platforms and Databases (104 total):

- ISI web of knowledge platform http://www.isiknowledge.com
- Science direct—http://www.sciencedirect.com (all years)
- JSTOR—http://www.jstor.org (all years)
- Scopus—http://www.scopus.com
- AGRICOLA—http://www.agricola.nal.usda.gov (all years)
- Proquest—http://www.search.proquest.com (all years)

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The overarching Platform names are provided. A full list of sources can be found in the Additional file 3.

Specialist sources

- Mesophotic.org http://www.mesophotic.org/publications/

Search engines

An internet search will be carried out in order to catch additional sources using the search engine:

- Google Scholar—http://www.scholar.google.co.uk

The search will be limited to Word or PDF documents and the first 1000 hits will be examined following recommendations [33]. Citation chasing, searching within the bibliographies of sources passing abstract level inclusion criteria, shall be allowed for the results from search engines and the grey literature. The bibliography of retained papers will be downloaded and reviewed using the study inclusion criteria; papers retrieved in this way shall not be subject to further citation chasing to minimise the influence of knowledge bias, the tendency of authors to cite the same paper pool repeatedly. This increases the chance our searches will bring back relevant data.

Personal libraries

The personal libraries of all advisory committee members shall also be reviewed. Any papers missed by the formal literature search post abstract level screening, which are known to contain data from MCEs shall be added for full text screening.

Screening process

Once the search results have been generated, the metadata will be saved in reference management software. Duplicates will be removed, as will any patents, which have not been excluded during the search. All remaining articles shall be screened. In order to select relevant resources, inclusion criteria shall be applied sequentially at three levels of scrutiny: Title-Abstract-Full text using the online resource EPPI-Reviewer 4 [34]. If it is uncertain whether a criterion is met, it is treated as fulfilled until the next level.

All researchers involved in screening shall assess the same random sample of 500 articles, pulled from the search, applying the inclusion criteria down to abstract level. Kappa analysis will be used to quantify levels of agreement and, if necessary, to refine inclusion criteria [35]. If Kappa analysis returns a value <0.6 (broad agreement threshold), the decisions shall be discussed and inclusion criteria refined.

Full text documents will be acquired and screened. If the articles are not available online, the corresponding author shall be contacted. If the full text of an article is not in English, but the study passes through the title and abstract rounds of screening, translation shall be attempted. Kappa analysis will be repeated for study inclusion at full text level. At all stages of the screening process the number of articles excluded shall be recorded and reported with justification for the decision. All articles excluded at full text shall be listed as an appendix to the final report.

Study inclusion criteria

Title and Abstract level inclusion criteria:

1. Relevant subject: Tropical and Subtropical coral reefs
2. Relevant exposure: Sampling at depths greater than 30 m.
3. Relevant outcome: Ecological data such as richness, biodiversity, species lists and abundance.

Full text criteria

1. Relevant subject: Mention of reefs containing photosynthetic hard corals.
2. Relevant study design: Observational or Experimental
3. Relevant exposure: Sampling at Depths greater than 30 m.
4. Relevant comparator: Ecological data from shallow reefs above 30 m.
5. Relevant outcome: Any of the following data are reported: taxon richness, taxon abundance, taxon biomass and biodiversity indices along with a measure of variability and number of replicates.

Potential effect modifiers and reasons for heterogeneity

The following effect modifiers shall be considered:

- Region

- Locations differ in temperature and flow dynamics. Biogeography can also result in different total richness of taxa by region, affecting the variability of community composition. We shall define regions by ocean basin.
- Taxon
- Patterns may differ between broad taxa, such as hard corals, fish or algae, because of variance in responses to environmental parameters.
- Method of data collection

- Heterogeneity between studies may result from artefacts of sampling techniques, rather than true biology. For example, fish species recorded are

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dependent on dive techniques employed [36], while taxonomic identifications by physical examination of specimens are more reliable than identifications made from video or photos.

All effect modifiers shall be considered simultaneously with interaction; provided we have at least an order of magnitude more studies than moderators and all combinations of moderators are sufficiently represented by studies. Failing this they may be considered as part of a narrative synthesis. The list of effect modifiers is the result of consultation with the advisory committee and experts.

Study validity appraisal

Once the articles for inclusion have been determined, they shall be scored as either of high or low validity by at least two independent scorers. A full list of study validity assessment criteria will be developed once we have seen the variability in the study validities identified by the inclusion criteria. Kappa analysis [35] shall be conducted on a subset of articles to ensure repeatability of the study validity assignment. Assessment will be based on the susceptibility to bias. The degree of replication, the resolution of taxonomic identification, the random placement of sampling points as opposed to haphazard sampling, and the balance of survey effort across depths shall be considered. Any meta-analysis shall be run twice. Once with all high validity studies and again with all studies. AIC values shall be compared and if there is no change in the fit of the data the inclusion of all studies in the analysis shall be deemed justified. We focus on internal validity, efforts to reduce bias within a study, rather than external validity, the potential for legitimate generalisation of a study's findings. This is as our studies of interest are largely ecological observations, rather than experimental treatments. The objective of this review, is in part to determine external validity by considering region as an affect modifier and by comparing observations at different reefs. A putative set of validity appraisal criteria are as follows:

1. Taxon ID involved a step of direct inspection, not relying on photographic information only.
2. Taxon ID was at least to the level of genus for data to be extracted.
3. Even sampling effort with at least three replicates occurred over the depth range sampled.
4. Sampling locations were chosen after a degree of randomisation.

If three of the four criteria are satisfied the study shall be classed as high validity.

Data extraction strategy

We require data from multiple samples down a depth gradient within a study. The format of ecological data in the full text library, metrics or raw data, shall be reviewed to determine their prevalence. We shall extract measures of: species richness, biodiversity indices, biomass, abundances and the level of taxonomic identification. We shall also consider how often measures of variability are reported and attempt to chase data from authors when not reported. Subject to the availability of data, we will progress onto meta-analyses. Data will be extracted with variability measures and replication data from sources into a csv file. A template is included in the Additional file 4. The file will contain the study title, the extracted primary data, the depths of the samples, and potentially the following effect modifiers: geographic region of the study, taxon and method of data collection. Analyses shall be conducted in the computer programming language R, using the meta for package [37]. The extracted data files shall be made available as additional files.

Data synthesis and presentation

There are three possible outcomes for the dataset generated by the systematic review. The appropriate method of synthesis and presentation will be chosen once the available data have been collected. As a minimum, a narrative synthesis will be presented including tabulation of the data. We will identify where past research has focussed, highlight major missing geographical regions and taxa. If we find sufficient data, we will conduct a quantitative meta-analysis using effect sizes, the exact effect size used will depend on the ecological data returned by the search. Such an analysis, however, is unable to address issues of taxonomic turnover with increasing depth assuming a pool of specialist mesophotic species. Therefore, should we find sufficient community composition data, we shall attempt a meta-analysis based on community data across sites and down a depth gradient [38, 39]. Such a framework allows the incorporation of species turnover, but the data are rarer in the literature and fail to incorporate study quality and error components into the analysis. To address this, we shall generate one ordination with all data and another with data only in the high validity group. This approach involves plotting all samples of community data from all studies simultaneously in an ordination based on dissimilarity indices. We can then determine which communities can define the different reef zones.

Both quantitative analyses can incorporate effect modifiers. In the case of the classic meta-analysis, they shall be incorporated into a mixed-effect model and considered simultaneously provided enough data are present. The use of depth as a continuous effect modifier will

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be dependent on the amount of data collected. For the community data approach, centroids relating to different levels of the effect modifiers may be plotted over the ordination. Overlapping centroids and permutation tests may reveal whether there is a significant effect on similarity between samples based on the modifier.

In order to increase the robustness of our conclusions, sensitivity analyses shall be conducted and bias tested for. Publication bias considers a journal's tendency to publish papers reporting significant or positive results or those presented in a certain language, over those which do not [40]. Funnel plots shall be generated for each analysis and a regression test conducted to check for asymmetry in the plot. Forest plots will be generated to allow outliers to be identified. The outliers reflect studies with an undue influence over our conclusions. Analyses will be repeated without these studies and the resulting *P* values compared. Following this, Rosenberg's fail-safe numbers [41] for the analyses shall be calculated, reporting how many non-significant data points would be required to lose significance from the analysis. This collection of tests and plots will aid the critical assessment of our analysis.

Additional files

Additional file 1. Scoping exercise—a short report of the scoping exercise used to generate search strings. The number of returned hits for trialled search strings and the explicit decision making process of term inclusion are recorded. Uncaptured test library papers are looked at in more detail.

Additional file 2. Test library—a list of all papers used to determine the effectiveness of trialled search strings.

Additional file 3. Full database list—an expanded database list detailing all sub resources the review intends to search.

Additional file 4. Data extraction template—an annotated data extraction sheet is attached, populated with data from the test library. This example shows the type of data recorded.

Abbreviations
MCE: mesophotic coral ecosystems; DRRH: deep reef refugia hypothesis.

Authors' contributions
JHL, DAAB, ADR, DAE, PB, TCLB, MPL, RLP, MS and DW developed the review question. JHL conducted the pilot research with support from DAAB. JHL, DAAB, PB, TCLB, MPL, RLP, MS and DW reviewed the pilot research and provided the test library. JHL wrote the protocol with support from DAAB, ADR, DAE, PB, TCLB, MPL, RLP, MS and DW. All authors read and approved the final manuscript.

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