Environmental Evidence

SYSTEMATIC REVIEW

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

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Abstract

Background: Globally, shallow-water coral reef biodiversity is at risk from a variety of threats, some of which may attenuate with depth. Mesophotic coral ecosystems (MCEs), occurring from 30 to 40 m and deeper in tropical locations, have been subject to a surge of research this century. Though a number of valuable narrative reviews exist, a systematic quantitative synthesis of published MCE studies is lacking. We conducted a systematic review to collate mesophotic research, including studies from the twentieth century to the present. We highlight current biases in research effort, regarding locations and subject matter, and suggest where more attention may be particularly valuable. Following a notable number of studies considering the potential for mesophotic reefs to act as refuges, it is important to know how comprehensive these sources of recruits and organisms capable of moving to shallow water reefs may be.

Methods: We search seven sources of bibliographic data with two search strings, as well as personal libraries. Articles were included if they contained species presence data from both shallower and deeper than 30 m depth on tropical coral reefs. Studies were critically appraised based on the number of species identified and balanced sampling effort with depth. Maximum and minimum depths per species were extracted from each study, along with study region and taxon. We quantified the degree of community overlap between shallow tropical reefs (< 30 m) and reefs surveyed at the same locations below 30 m. Proportions of shallow species, across all studied taxa, observed deeper than 30 m were used to generate log odds ratios and passed to a mixed-effects model. Study location and taxon were included as effect modifiers. Funnel plots, regression tests, fail safe numbers, and analysis of a high validity subgroup contributed to sensitivity analyses and tests of bias.

Results: Across all studies synthesised we found two-thirds of shallow species were present on mesophotic reefs. Further analysis by taxon and broad locations show that this pattern is influenced geographically and taxonomically. Community overlap was estimated as low as 26% and as high as 97% for some cases.

Conclusions: There is clear support for the hypothesis that protecting mesophotic reefs will also help to conserve shallow water species. At the same time, it is important to note that this study does not address mesophotic-specialist communities, or the ecological forces which would permit refuge dynamics. As we limit our analysis to species only present above 30 m it is also possible diversity found exclusively deeper than 30 m warrants protection in its own right. Further research into relatively ignored taxa and geographic regions will help improve the design of protected areas in future.

Keywords: Depth, Community structure, Biodiversity, Coral reefs, Twilight zone, Refuge

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Background

Mesophotic coral ecosystems (MCEs) occur between 30 and 40 m at their shallowest in tropical and sub-tropical regions [1] and can be found deeper than 150 m [2]. MCEs are considered understudied in comparison to shallow reefs [3], likely because of difficulties of access [4], yet when accounted for they may greatly increase global reef area [5]. MCEs may be protected from commonly cited threats in comparison to shallow reefs [6–9], and additionally may provide recruits to aid shallow reef recovery [10, 11]. The amount of research published on mesophotic reefs is increasing [12] as technology advances and research groups grow [13].

Research efforts are attempting to increase awareness regarding MCEs, while calling for their conservation [14]. Protecting MCEs is often justified by the hypothesised existence of deep reef refuges [13] as shallow reefs continue to suffer damage [15]. In areas where there is a substantial degree of community overlap between shallow reefs and MCEs, species may persist locally on MCEs despite extirpation in the shallows [16, 17]. If these deep populations are reproductively active [18] then shallow reefs may be able to recover through vertical connectivity [10, 19].

Some studies have found that MCEs support high levels of endemism [20], offering alternative justification for protecting MCEs as they may harbour distinct geographical communities. Similarly, some researchers now argue MCEs could be identified by their own depth-specific ecological communities [21, 22]. These studies bring into question the general degree of community overlap between MCEs and shallow reefs [8] as currently defined by a 30–40 m depth limit based on SCUBA regulations. Understanding how many shallow reef species may be protected on reefs at depths greater than 30 m will aid the future decisions of conservation managers [23].

Narrative reviews of the MCE literature have been conducted a number of times [2, 13, 24–28], highlighting older studies and changes of key terms used to describe MCEs historically [1, 29]. Narrative reviews, however, may be subject to subconscious biases in article selection [30]. It is also difficult to ensure older studies, without keywords relating to depth ranges which fit in the modern framework, are re-discovered. Recently the bibliographies of a number of key reviews, publications from an online MCE database (www.mesophotic.org), and broader databases were systematically collated to show the state of the field [12]. However, existing reviews have stopped short of quantitatively synthesising the results of past studies.

As shallow reefs globally are increasingly threatened [15], we conduct a meta-analysis quantifying the extent of community overlap between shallow and mesophotic reefs across all taxa. We determine the proportion of shallow species which are present on MCEs, while highlighting the variation which can be ascribed to the study location and focus taxon. If species present below 30 m are protected from impact, then the higher the proportion of overlap the more effectively the conservation and management of MCEs will protect shallow water species. We collate the research field [29], depositing a bibliography of all identified MCE research online (www.mesophotic.org) to ensure wide and easy accessibility for future studies.

Stakeholder engagement

Invited discussion with our advisory committee generated our research question [29], which aims to quantify shallow water taxa present on MCEs that may contribute to refuge dynamics. The need for this information, and the raising of awareness in management circles, was expressed in a recent United Nations Environment Programme report [13]. The stakeholders on our advisory committee are researchers active in the mesophotic filed, from a geographical spread of universities and research institutions. Committee members are listed as authors following further involvement in generating the screening criteria, assisting with full-text retrieval, and commenting on this manuscript.

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 (an ecosystem of conservation concern)	Reefs deeper than 30 m	Reefs shallower than 30 m	Species presence or absence

Secondary questions consider effect modifiers:

Does the extent of community overlap vary by region or between broad taxonomic groups?

Methods

A protocol paper for this systematic review details the search strings used, databases searched, and the screening process amongst other information [29]. Here, we reiterate our methods while detailing deviations from the protocol. The final sets of screening criteria used are reported along with the statistical analysis selected as suitable after the retrieval of studies. We report our review following the reporting standards for systematic evidence syntheses in environmental research (ROSES) [31].

Deviations from the protocol

JSTOR (all years) was not searched as a database, despite being detailed in our protocol. This was because an information request was declined as a result of the high volume of enquiries. Journal articles were still retrieved from JSTOR through a Google Scholar search.

Articles were categorised by type as part of a supporting narrative synthesis. We generated a word cloud based on term frequencies from included titles and abstracts, in consultation with the advisory committee. The five, objectively derived, tags were: ecology, disturbance, trophic interactions, symbionts, and reproduction. Tags were assigned manually while screening on outcome at abstract level. Our full text screening for the primary review question, and quantitative synthesis, use studies tagged as ecology.

Method of data collection was not extracted, despite being identified in the protocol paper [29], as many articles used a mixture of different survey methods for shallow and deep sampling. AIC are not compared between models fitted to the full dataset and the high validity subgroup as the metric is affected by sample size.

Search strategy

We use two search strings to balance capturing relevant literature against articles captured after name changes in the field over time, as detailed in our protocol [29]. "Mesophotic" from 01/01/2010 to 31/12/2016, and "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*))" from the start of the source to 31/12/2009. The scoping exercise and search string development are reported in the protocol paper. The final search strings were successful in retrieving 87% of our test library.

We conducted our literature search in ISI Web of Science, Science Direct, Proquest, AGRICOLA and Scopus in English, with a full list of databases presented in our protocol [29]. We downloaded all bibliographic data from mesophotic.org at the end of 2016 and used Google Scholar for a complimentary search, capable of capturing grey literature [32]. The Google Scholar search was conducted using web-scraping software in R [33]. A detailed methodology can be found in Additional file 1, based on work by Haddaway et al. [34], retrieving up to the first 1000 entries. Following our literature search the personal libraries (Private collection of manuscripts) of authors and advisory committee members were checked for missed publications. Additional publications were also provided by the reviewers of this manuscript. Literature searches were conducted in the period from 19/04/2015 to 28/02/2017.

Article screening and study inclusion criteria

Before screening based on exclusion criteria occurred in the software EPPI Reviewer 4 [35], duplicate entries resulting from the use of multiple databases were removed. We set EPPI Reviewer to automatically mark as duplicates full bibliographic entries with 95% similarity. This level of similarity generally corresponded to the identical entries with differing capitalisation, or entries with one database field left blank in comparison to the master entry. Other possible duplicates were checked manually. When retrieving full-text articles for detailed screening not all were readily available. The lead author was contacted for any manuscripts the screening team could not find available online. A final list of full texts not retrieved after two attempts at contact with the authors was circulated to the advisory committee. If full texts were not present in personal libraries after these checks the articles were excluded. The screening was conducted by authors who had no publications in the list screened, preventing bias in the inclusion of data.

The original screening and validity appraisal criteria were reviewed to reconcile disagreements during Kappa analysis, at each level of screening, between the two reviewers. 1000 articles were coded by both reviewers at title and abstract level, 50 full texts were coded by both reviewers. Any differently assigned articles were discussed. The final criteria were as follows:

Title and abstract criteria:

1. Relevant subject: Extant Tropical and Subtropical coral reefs (exclude Mediterranean and palaeobiological studies).
2. Relevant exposure: Sampling at depths greater than 30 m.
3. Relevant outcome: Ecological data such as richness, biodiversity, species lists and abundance. (Other study types were tallied for discussion of the broader field, but omitted from the primary review question).

Full text criteria:

1. Relevant subject: Mention of reefs containing photosynthetic stony (scleractinian) corals (exclude non-biology studies i.e. geology).
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.

Critical appraisal

External validity considers the generalisability, and the fairness of comparison between different studies. Internal validity considers the risk of bias within a specific study. A number of methods exist to critically assess these concepts, but most are developed with randomised control trials in mind, or at least observational studies with a level of randomisation in allocation and blinding rarely found outside of the medical sciences [36].

We have no reason to believe the observation of a species depth range from one article is any more important than that from another [29]. By including geographical area and taxon as effect modifiers, we have controlled for the primary confounding sources of variability when comparing studies. We therefore consider the spatial scales of different studies are the primary remaining threat to external validity. A key based on a whole ocean region is likely to find a greater depth range for a given species than a study at a specific location, because the key is likely based on data from a broader range of abiotic conditions.

With respect to internal validity, our primary concern with mesophotic research is that sampling effort may decline with increasing depth. This can lead to an underestimate of the number of species present deeper than 30 m as rarer species are found in shallow water, but are missed at depth. Similarly, studies reporting only a small number of species may provide a less reliable estimate of community level overlap. This is because the importance of a single species depth range is elevated, when community overlap is calculated as a proportion. Our critical appraisal is therefore based on the following criteria:

Validity appraisal criteria:

1. More than 10 species are identified within a taxon.
2. The study is not a regional taxonomic key.
3. Even sampling effort is reported across depths.

Studies passing all these criteria were included in a high validity sub-group for sensitivity analysis. We choose to limit our high validity group to studies with more than ten species to avoid undue influence of single species over community level overlap values.

Data extraction

Maximum and minimum depths for each species reported in an article were extracted manually. A subset of 12 articles were checked for consistency of data extraction by a second reviewer. Discussion of these extractions produced the following clarifications. Depth ranges for adults and juveniles of a species were combined into a single depth range. For the purposes of defining multiple studies within an article, locations were considered different when across multiple countries, when provided. Australia and the USA were exceptions because of their size, here we took into account the seas around Australia, and the islands/coastlines sampled of the USA. The review was conducted by authors who had no publications in the list screened at full text, preventing bias in the inclusion of data. Data were restricted to species occurring on tropical and sub-tropical reefs when multiple habitats were studied in a single article, such as mangroves and reefs. If these data were not available, the corresponding author was contacted. Contact was attempted twice before asking members of the advisory committee to try a third time with any researchers they knew personally. Failure to respond to these contact attempts led to exclusion of the data set from the analysis (Additional file 2). A list of all articles contributing data to the final meta-analysis can be found in Additional file 2 [37–68], a list of the studies resulting from these articles can be found in Additional file 3.

Potential effect modifiers/reasons for heterogeneity

The location and broad taxonomic group were extracted from articles as effect modifiers, following consultation with the advisory committee [29], as different regions may have different transition depths and taxa may respond differently to depth.

Data synthesis

After reviewing the retrieved articles, a meta-analysis for the primary review question was deemed appropriate. The list of observed depth ranges was limited to species observed shallower than 30 m. Of these species, the proportion also present deeper than 30 m was calculated, grouped by article, site, and taxon. Log odds ratios were calculated in R [69] in the package metafoR [70] and passed to a mixed-effects model. A maximum-likelihood estimator with Knapp and Hartung adjustments [71] was used with location and taxon as effect modifiers. Likelihood-ratio tests assessed the statistical significance of model elements and determined whether to retain an interaction term.

Our sensitivity analysis and tests for bias follow our protocol [29], and were as follows. Funnel plots were used to identify potential outliers [72], and a regression test for asymmetry assessed the chance of publication bias affecting the dataset [72]. As a sensitivity analysis, Rosenthal's fail-safe number [73] was calculated for the model to determine how many studies, averaging to null results, are required to lose statistical significance. To check sensitivity further, the analysis was repeated on a subset of high validity studies and the effects compared to a full model.

The broader research field was summarised using the bibliographic data from papers retained at full text level. Articles by year, categorisation, geographical area, and the mesophotic depth limit used were counted and plotted.

Results

Review descriptive statistics

Our methods retrieved almost 170,000 articles, with 3011 screened at full text (Fig. 1). Kappa analysis was used for consistency checking and refining of the inclusion criteria by two reviewers for 1000/122,305 at title and abstract level and 50/311 at full text level. A list of all ecology articles screened at full text level, with decisions, can be found in Additional file 4. The following summary and figures of the systematic review, as opposed to the meta-analysis, are created from the data extracted from all articles; not excluded on outcome at the abstract level and verified as mesophotic at full text level. This brief discussion provides context of the wider field of mesophotic research, before we address the primary review question with a meta-analysis. The bibliographic data for these 461 articles were deposited with mesophotic.org.

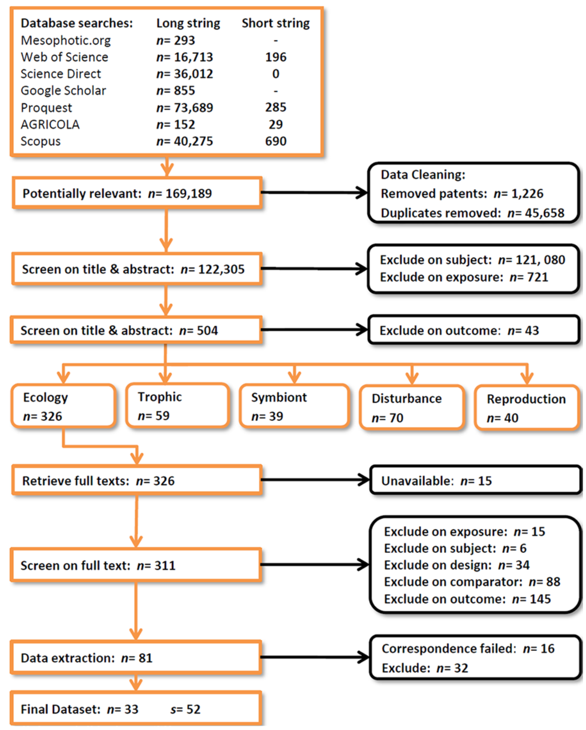

Fig. 1 Screening report. The number of articles (n) assigned to each screening criteria is reported. Black boxes are articles removed from consideration. Orange boxes contain articles included for the next level of screening. Note that a single article could be excluded for multiple reasons i.e. not reporting data shallower than 30 m and not containing the right type of data. Short and long string refer to the two search strings defined in our protocol paper. Our five tags were assigned to articles while screening by outcome at abstract level. At data extraction multiple studies (s), data from combinations of taxa and locations, were reported in some articles. A list of studies can be found in Additional file 3

There was a notable acceleration in the number of articles per year as we entered the twenty first century (Fig. 2a). Publication levels were relatively stable during the twentieth century with only 1 year yielding more than 10 papers. The earliest article we identified was from 1960.

After more than half a century of research, the mesophotic field is still largely descriptive and focussed on pattern. This is supported by the majority of studies being assigned an ecology tag during our screening process (Fig. 2b). The next most common tag was assigned six times less frequently and indicates articles considering disturbance or damage on mesophotic reefs. Other common MCE study types refer to trophic interactions, symbioses, and reproduction.

This exercise was used as an opportunity to see how researchers define mesophotic reefs. 27% of articles include a depth limit in their introductions. The overwhelming majority of papers providing a definition state MCEs start at 30 m depth (89%), however, some papers exist claiming the upper bound is 20 m or even as deep as 60 m.

Mesophotic reefs in the western Atlantic, Caribbean, and Gulf of Mexico, are the focus of most published studies, followed by those on archipelagos in the Pacific (Fig. 2d). Australian reefs represent another hot spot of activity, but are nonetheless not as well studied. The Red Sea has provided a relatively large number of articles for its area, while the Indian Ocean has been comparatively understudied.

Data-synthesis

Across the whole dataset, the median proportion of shallow species also present below 30 m is 0.67. The meta-analysis was performed on articles assigned as Eco at abstract level screening, and subsequently passed full-text level screening, as well as two further publications provided as titles at the review stage. Of these 81 + 2

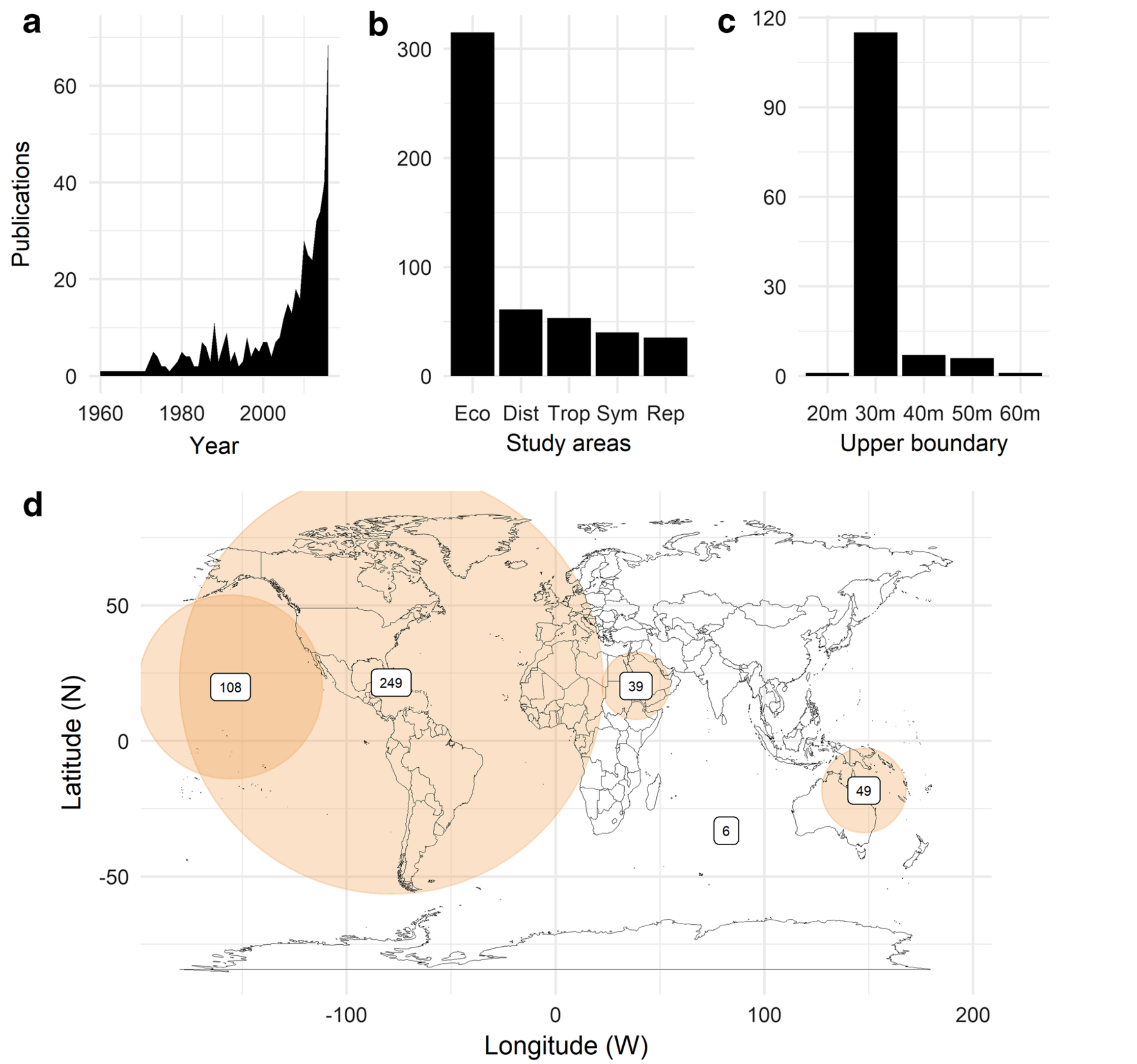

Fig. 2 Literature base summary. A graphical summary of mesophotic research since 1960. **a** The number of articles published in a given year. **b** The number of articles identified as considering ecology, disturbance, trophic interactions, symbionts, and reproduction. Article categories were chosen from a word cloud generated from abstracts, then assigned manually. **c** The number of articles reporting an upper depth limit for mesophotic reefs. If a range was reported the shallowest value was extracted. **d** The geographical distribution of research effort on MCEs. The size of the orange circles indicates the number of articles in the region, also displayed in text labels

articles (Fig. 1), data were successfully extracted from 35, yielding 52 studies (combinations of broad taxon and locations within articles) after contacting corresponding authors (Additional files 2). The consistency of data extraction was checked by a second reviewer for 12/35 articles included. The data can be found in Additional file 3. Ecology papers we could not source a full text for are listed in (Additional file 5).

Both location and taxon were included as effect modifiers to aid biological interpretation and reduce the variance assigned to between study heterogeneity (I^2 of 10.1% reallocated). An interaction term was not included as intended in our protocol. This decision was made as studies were not evenly distributed across all factor-level combinations (Additional file 6) and a likelihood-ratio test failed to distinguish the two models ($\chi^2=10.8$, $P=0.14$). A Q-test detected significant between-study heterogeneity ($QE=182.2$, $df=27$, $P<0.0001$). An I^2 of 72.3% can be interpreted as "substantial" under Cochrane review guidelines [74], but does increase with study number [75] and may be less important for an ecological synthesis. The R^2 of our model is 75.9%. A forest plot of effect size contributions from individual studies can be found in Additional file 7.

Figure 4 visualises the proportion of shallow species present deeper than 30 m, predicted from the model, for each modifier level. The central Pacific has the highest community overlap between shallow and mesophotic reefs at 72% (95% CI 53–85%). Studies off the cost of Brazil report the lowest at 30% (7–72%) when ignoring areas represented by a single study. For taxa, models of algal groups all returned predictions of over 75% overlap. 86% (37–98%) of shallow-water Antipatharia were found on mesophotic reefs, while octocorals were predicted to have the lowest overlap of all factor levels at 38% (15–68%). The amount of studies retrieved for a given factor level does influence the width of the confidence interval. Scleractinia with 18 studies has a prediction ranging by 29%, whereas Octocorallia with three studies ranges by 53%. Data underlying the figure can be found in Additional file 8.

As part of the sensitivity analysis 22 studies were excluded from the high validity group, following our validity appraisal criteria. The analysis was then re-run to quantify the influence of these studies over our synthesis (Fig. 4). These studies are indicated in the comments column of Additional file 2. The dataset-wide estimate of community overlap dropped by 10 percentage points to 0.57. No change in broad pattern is noted, only a slight increase in the range of predictions, and a slight decrease in estimated overlap. We would generally expect a high validity sub-group analysis to narrow the prediction intervals. Our results suggest that the overriding influence may be the reduction in sample size, and that studies outside of the high validity group are largely similar to those retained. This is despite low validity studies operating at larger spatial scales and with unbalanced sampling effort with depth. A regression test provides no evidence for publication bias in the dataset ($t=0.5382$, $df=33$, $P=0.594$), also visualised with a funnel plot (Additional file 9). This is further supported by a Rosenthal's fail safe number [73] of 1612 studies, it is highly unlikely this many mesophotic surveys remain unpublished given the number we retrieved.

Discussion

Quantitative results

Two-thirds of shallow-water species can be found on MCEs (Fig. 3). This suggests MCEs should potentially be considered as a significant conservation target when protecting shallow reefs. This observation is in broad agreement with expert opinion regarding the Caribbean; suggesting over 40% similarity for shallow and mesophotic benthic taxa and approximately 60% for fish [8]. Semmler et al. [8] use Jaccard similarity and will therefore estimate lower similarity than this study. Jaccard similarity returns a lower score for reefs with mesophotic-specialist taxa while in this study community overlap was calculated excluding species not observed on shallow reefs.

As individual studies would lead us to expect, community overlap varies by region (Fig. 4, Additional file 8). The highest proportion of shallow species present on mesophotic reefs was predicted for the central Pacific at 72% (95% CI 53–85%). Brazilian reefs and the Coral Sea with the Great Barrier Reef both harbour less than half of shallow reef taxa on MCEs at 31% (7–72%) and 41% (20–65%) respectively. A number of drivers may explain these patterns but there are two likely candidates.

Reefs located in biodiversity hot spots, such as the Coral Triangle and Red Sea [76], may experience greater competition and subsequent specialisation [77]. This may lead to narrower depth ranges and so less community overlap in comparison to species-poor regions such as the Caribbean and Hawai'i. Additionally, the boundaries between mesophotic communities and shallow reef communities may vary between sites [22]. This is likely underpinned by abiotic factors interacting with species physiology. The current use of an arbitrary 30 m depth limit, derived from recreational SCUBA limitations, may be limiting our ability to accurately report on ecological pattern. If the transition depth occurs deeper, a larger portion of shallow water species will be present below 30 m. The deviation in community transition depth from 30 m between sites may explain some of the variability in our estimates of community overlap. The maximum depth limits of photosynthetic corals are known to vary by region [78] and with light [2] and loosely correlate with our findings.

Community overlap can be broken down further by predicting the effect of different taxon levels (Fig. 4, Additional file 8). The two taxonomic groups with the largest number of studies contributing to the synthesis, fish and Scleractinia, are estimated as having 64% (46–79%) and 57% (42–71%) of shallow taxa on MCEs respectively. These values are relatively close to our synthesis-wide estimate. Other taxonomic groups have relatively large confidence intervals, but all three algal taxa return high community overlap of over 75%. This may be surprising for autotrophic taxa, but it appears a 30 m boundary is within the physiological envelope of most algal species identified. The high estimate of 86% (37–98%) for Antipatharia, though unintuitive for a taxon traditionally considered 'deep' [79], likely results from limiting the analysis to species observed shallower than 30 m. For the most part, if a black coral is observed shallower

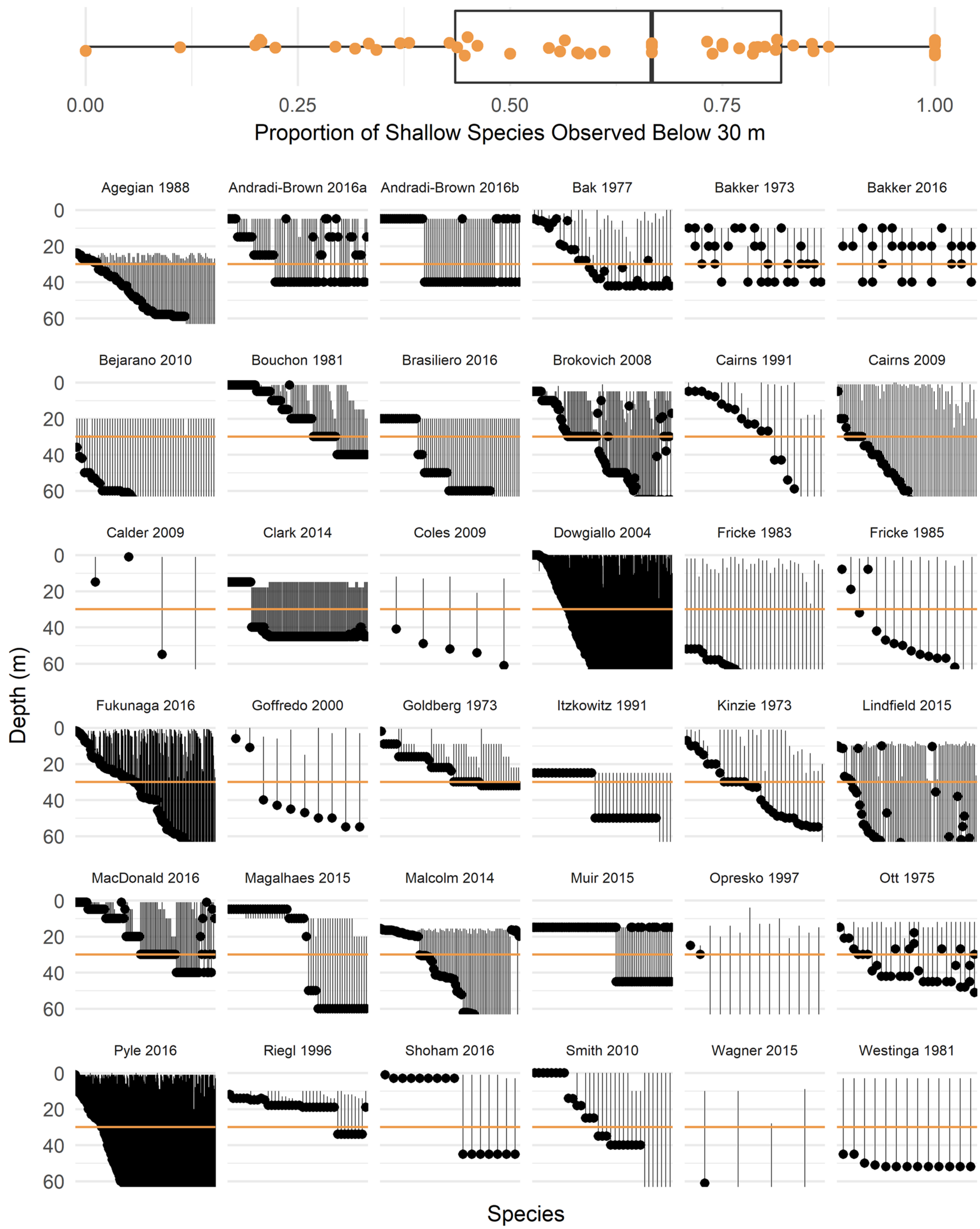

Fig. 3 Shallow reef species depth ranges by article. A box plot shows the distribution of overlap estimates from all articles contributing data to the meta-analysis. Beneath, each panel illustrates the distribution of species depth ranges within the article. The scale ends at 60 m for clarity. An orange line indicates the 30 m mesophotic boundary. 36 'articles' are shown as two time periods were sampled in Bakker 2016 and two additional articles were provided at review

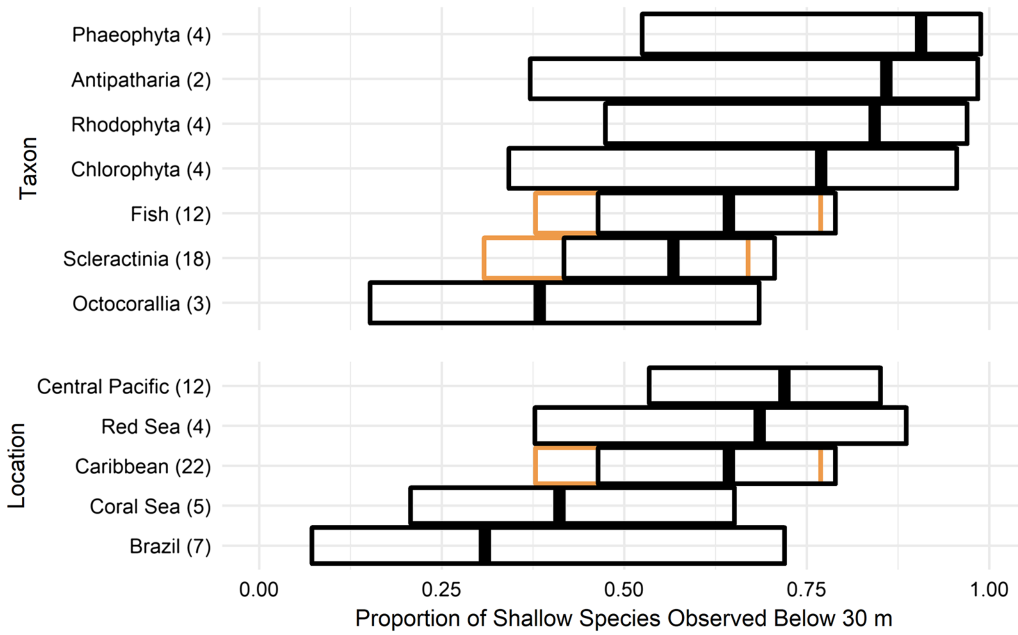

Fig. 4 Effect of modifiers on community overlap. Crossbars show back transformed model predictions of community overlap by taxon and location. The thick central bar represents the prediction, the thinner bars on either extreme are 95% confidence intervals. The bars are asymmetrical because of the scaling of the effect sizes before back transformation. The number of studies contributing to the full model for a given level are in brackets. Orange crossbars are repeat predictions for high validity subgroups; only presented for 3 factor levels because of a lack of high validity data for other levels

than 30 m it is likely a deep species encroaching on shallow reefs. Alternatively, a small number of species may have evolved towards shallow-water emergence. The smaller number of species contributing to estimates for taxa other than fish and Scleractinia highlights the need for taxonomic diversity in future mesophotic studies. It is also important to maintain shallow sampling for contemporary comparisons to allow for site to site variation.

Our finding of over half of shallow taxa being recorded on MCEs is not in direct contention with research suggesting mesophotic-specific communities on MCEs [8, 22, 32, 80–82]. Firstly, we deliberately exclude taxa only observed on mesophotic reefs from our analysis. This is as MCEs may extend below 150 m [2] while the majority of the studies synthesised here do not sample as deep. Any estimate of the proportion of mesophotic taxa not on shallow reefs would likely be misleading because of an absence of evidence (Additional file 10). Additionally, the lower limit of MCEs is acknowledged to be variable [21, 24]. Further analyses considering overlap at the lowest limit of MCEs would therefore be inappropriate because of a similar lack of sampling. Our primary research question considers the potential for shallow water species to exploit deep reef refuges.

Secondly, we consider MCEs in a narrow sense as a 30 m depth limit. As depth increases the ratio of shallow taxa to mesophotic-specialists declines (Additional file 10) [8]. When sampling is evenly distributed across the whole depth range of an MCE it is possible to detect depth-specific community structure [22] and high levels of geographically endemic biodiversity [20]; though this likely varies between locations [22]. It is important to note consensus in the field is to recognise an upper mesophotic zone, in which shallow species are gradually lost with depth, and a lower mesophotic zone containing specialist communities [21, 25], rather than rigidly following the 30 m boundary. Any conclusions regarding shallow taxon occurrence deeper than 30 m is therefore likely driven by pattern in the upper mesophotic. We are reticent to perpetuate the definition of these zones by arbitrary depth limits because of the potential for between site variation [22].

Qualitative analysis

At the outset of this project www.mesophotic.org represented the largest publicly available compilation of mesophotic literature, with the metadata of 293 articles available. This study succeeded in boosting this number to at least 461, considerably increasing the visibility of research. Absent from this list of papers are any published in 2017 or later. The new database offered the opportunity to categorise these studies, describing the field as a whole.

Past reviews have noted the geographical bias of mesophotic research [2, 12, 78]. This is to some extent unavoidable because of the locations of research groups in developed countries near accessible reefs (i.e., Hawai'i, US Virgin Islands, and Israel among others). We confirm the bias towards studies in the central Pacific and western Atlantic region. A better global understanding of MCEs requires increased research attention in the Coral Triangle and the wider Indian Ocean to the west. Currently MCE research attention focuses on reefs with lower coral species richness [76]. Though this may be convenient for a number of reasons, it may mean ecological differences between shallow and mesophotic reefs resulting from greater competition and niche diversification are missed.

In addition to geographic biases, the mesophotic field lacks diversity in terms of study types. As expected for a field which has only recently taken off (Fig. 2a), a large proportion of the studies focus on ecological description. This has already been noted across existing research and narrative reviews [12] but we lend support to the observation with a larger literature base. This pattern has been shifting over time [12], but there is certainly room for an increase in experimental, modelling, and longitudinal studies considering processes instead of pattern.

A final interesting observation is that the term "mesophotic" has been defined differently across published work. Though the overwhelming majority of papers define mesophotic reefs as starting at 30 m, the mesophotic research strategy more loosely states they can start from 30 to 40 m [1]. This 30 m limit is rooted in recreational dive limits, rather than biological boundaries which can vary [22]. Not surprisingly the next most common definition is for mesophotic communities starting at 40 m. More interestingly, six papers within the last 10 years define MCEs from 50 m with another one at 20 m and one at 60 m. As the number of papers on mesophotic reefs increases it is important to remain consistent in the application of terminology, or specify explicitly how these boundaries may be recognised to vary.

Reasons for heterogeneity

Our analysis returns an I^2 of 72.3%, under Cochrane review guidelines this can be interpreted as 'substantial' unexplained heterogeneity [74]. However, Cochrane review guidelines were developed by the health sector, and so largely with the synthesis of controlled clinical trials in mind. In ecological studies higher degrees of residual variation are often expected, as a result of the messiness of the 'real' world and confounding variables arising outside of an experimental framework.

As already mentioned, if the 30 m boundary of shallow and mesophotic systems is not shared across all studies the estimates of community overlap could be impacted. A community transition at 20 m would result in few shallow species deeper than 30, similarly in areas of high light penetration mesophotic communities may begin deeper [24], inflating the proportion of shallow water species occurring deeper than 30 m. If this is the cause of our high between study heterogeneity, then this study may suggest the 30 m depth boundary can be misleading. Our analysis could be improved by including abiotic data believed to affect the rates of community transition for each study, such as light attenuation coefficients and topography [83]. These data are not available for the synthesised studies, and new research should ensure environmental data is collected alongside ecological surveys.

Review limitations

We hoped to incorporate abundance into a meta-analysis of communities [29, 84, 85], yet this approach would sharply reduce the amount of included studies because of differing measures of abundance, as well as preventing the incorporation of sessile and motile taxa into one analysis. Adopting a presence-absence approach does, however, miss the importance of population density. Our analysis could have been influenced by population overspill where a few out-lying individuals from an otherwise shallow species were observed deeper than 30 m (Bongaerts, under review). The refuge dynamics which may occur on MCEs must be underpinned by reproductively active source populations, rather than the sinks represented by outlier observations as hypothesised in deep-sea ecosystems [86]. Though such outliers are unlikely to represent source populations for a deep reef refuge, they may none-the-less protect genetic diversity [17].

Additionally, our interpretation of the impacts of effect modifiers should be taken with caution. Confidence intervals are wide because of a lack of studies across most taxonomic groups, only fish and Scleractinia predictions are based on more than five studies (Additional file 8).

Conclusion

Information for policy/management

It is clear that a notable proportion of shallow reef taxa are also present on MCEs, though this varies significantly by taxon and location. The findings of this systematic review validate conservation decisions supporting the protection of MCEs [23] as potential "lifeboats" for shallow reefs [87] based on community overlap, though further research into refuge dynamics specifically is required. It is important to note distinct mesophotic biodiversity may deserve protection in its own right, something our analysis is unable to inform.

Implications for research

The degree of overlap varies by region and taxon, however, so too does research effort and the information available to us. We recommend that in the years to come researchers conduct survey work of lesser studied, but ecologically important, taxa and also attempt to visit MCEs as yet unstudied. This extra knowledge will aid conservation prioritisation efforts and allow us to identify deeper coral reef regions currently unknown to conservation managers.

Additional files

Additional file 1. Google Scholar Web-Scraping. The following outlines the process used to extract search results from Google Scholar. The lack of a 'download results' feature on Google Scholar results pages makes the generation of a workflow necessary. This was pieced together from a number of online help files, papers, and conversations, referred to when available. We are grateful to the multiple sources of help.

Additional file 2. Data extraction report. All articles included in the final meta-analysis are reported. We also report all articles identified during full text screening as containing data of interest. The comments column provides explanations for articles which did not contribute data for the final meta-analysis, studies which were assigned to the low validity group, as well as whether the authors were contacted.

Additional file 3. Datafile. Data extracted and summarised for fitting of a meta-analytic model.

Additional file 4. Full text report. All studies with full texts retrieved and identified during the screening process as ecological are listed. Code details the screening decision for the entry based on full text screening.

Additional file 5. Unavailable full texts report. List of articles screened at abstract level and assigned an eco tag, which we could not retrieve a full text for.

Additional file 6. Distribution of studies across factor levels. The number of studies included in the full meta-analysis of 52 studies is reported for each combination of taxon and location. The total number of studies for a given factor level is in brackets after the level name. Many combinations are not represented, prompting the decision not to include an interaction term in the statistical analysis.

Additional file 7. Forest plot. The effect sizes of depth as log odds ratios of the total shallow species pool compared to shallow species present deeper than 30 m, of the 52 included studies are displayed. Studies are in the same order as in Additional file 3. Dots indicate the effect size estimate and are scaled to the number of species observed within each study. The black lines extend from the lower to upper 95% confidence limit of each study estimate. Orange lines are for reference to help interpretation. The dashed line at 0 indicates the effect size of studies finding 50% community overlap. The solid lines indicate the effect size of the largest study reporting 0% overlap (negative effect size) and 100% (positive effect size). Note that due to the scaling of effect sizes the confidence intervals become asymmetrical when back transformed to proportions (Fig. 4).

Additional file 8. Factor level effects. Predictions of community overlap between shallow and mesophotic reefs by taxon and location, as visualised in Fig. 4. Values are reported as per computer output and in descending order of estimate. The number of studies for each factor level contributing to the model is provided. Reference level indicates which factor level was held constant as the factor of interest was changed. The use of different reference levels should not affect the analysis in the absence of an interaction term in the model.

Additional file 9. Funnel plot. Funnel plot for the full meta-analysis. Dotted lines indicate the 95% confidence limit for expected deviation of study estimates from the model. Studies falling outside the triangle are potential outliers. With 52 studies we would expect fewer than 3. A lack of asymmetry to the plot provides no evidence of publication bias within the collected dataset.

Additional file 10. Proportion of mesophotic-specialists reported with maximum study depth. The proportion of all species reported, found exclusively deeper than 30 m, increases with the maximum depth of a study. An absence of deep sampling efforts does not allow us to claim there are low levels of MCE specific biodiversity. As such we limit the discussion in this paper to the shallow taxa occurring on MCEs, not of the total change in community between the two depth zones. In order for a fair comparison to be made between shallow and mesophotic biodiversity we must more strictly define the lower limit of MCEs. Data was limited to studies reporting a maximum depth < 500 m for legibility.

Abbreviation

MCE: mesophotic coral ecosystems.

Authors' contributions

In addition to the contributions to the project detailed in our protocol paper, JHL conducted the literature search. JHL and SP carried out the screening of all articles, extracted, and formatted the data. JHL and SP retrieved full texts and underlying data with help from the advisory committee (DAAB, DAE, PB, TCLB, MPL, RLP, MS and DW). JHL performed the statistical analysis and wrote the initial draft. ADR supervised the project and edited the manuscript. The advisory committee and SP also commented on the manuscript. All authors read and approved the final manuscript.

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Acknowledgements

We would like to thank all of the authors who supplied us with PDF copies of their manuscripts and underlying data when requested. We also would like to thank our editor and anonymous reviewers, who greatly helped improve the transparency of this manuscript.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

All data can be found in supporting information.

Consent for publication

All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Funding

The project has been funded by NERC (NE/L002612). DAAB was funded by a Fisheries Society of the British Isles PhD Studentship.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Received: 15 January 2018 Accepted: 30 May 2018
Published online: 11 June 2018

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