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Peering into the twilight: a systematic review on visual-based investigation of worldwide mesophotic ecosystems

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ABSTRACT

Mesophotic ecosystems host high biodiversity and support a vast variety of habitats. Owing to climate change, there is a growing interest in the study of mesophotic assemblages as a possible pocket of biodiversity for species. However, due to logistic constraints, these habitats have been historically less investigated and mostly neglected in conservation planning. Thus, it is difficult to gain a global overview of the state of the art, especially with regards to sampling methodology. Here, we conducted a systematic literature review, extracting data from 1001 publications on mesophotic research at a global level, focusing on visual-based methodologies, to identify gaps, emerging trends, and to supply useful information to improve sampling methodologies of mesophotic ecosystems and their reporting. Overall, the review highlighted an evidently uneven spatial distribution and a bias towards some taxonomic groups, i.e., corals and algae. From a methodological perspective, it showed that most studies at community level were performed with no standardized protocols. Even if crucial for the understanding of the functioning of these ecosystems, baseline data and long-term monitoring projects are virtually lacking. Despite these challenges, this review clearly shows a surge in interest and research effort driven by technological development. Considering the previously underestimated vulnerability of mesophotic ecosystems to anthropogenic pressures and the current climate change scenario, there is a pushing need to study mesophotic ecosystems through a standardized framework to adequately inform conservation and restoration measures.

1. Introduction

1.1. State of the art

The mesophotic zone encompasses a variety of ecosystems and its boundaries, and thus its definition, are still debated. Pioneer research and the term mesophotic itself were first applied to Mesophotic Coral Ecosystems (MCEs), which are limited to tropical and subtropical regions. In this context, mesophotic boundaries were conventionally set below 30–40 m down to 150 m (Kahng et al., 2010). In practical terms, the upper boundary was chosen as it is close to both the limit of recreational diving and the shift from photophilous to sciaphilous organisms in tropical and subtropical ecosystems. By contrast, the lower boundary was chosen to reflect what was considered at that time the deepest record of zooxanthellate corals, that to date is at 172 m (French Polynesia, Rouzé et al., 2021). Other authors supported the definition of mesophotic ecosystems based on light penetration (Castellan et al., 2025) or on both light penetration and community composition and turnover (Lesser et al., 2019; Tamir et al., 2019; Laverick et al., 2020); for example, it was suggested that Mediterranean mesophotic ranges from the depth where ~1% of surface irradiance penetrates to the deepest extent of benthic primary producers (Cerrano et al., 2019).

At large scale, mesophotic depths have been mainly investigated through remote sensing, e.g. acoustic techniques or seismic surveys (Locker et al., 2010; Santos Filho et al., 2025), but in terms of biological characterization they are limited to habitat-level and need

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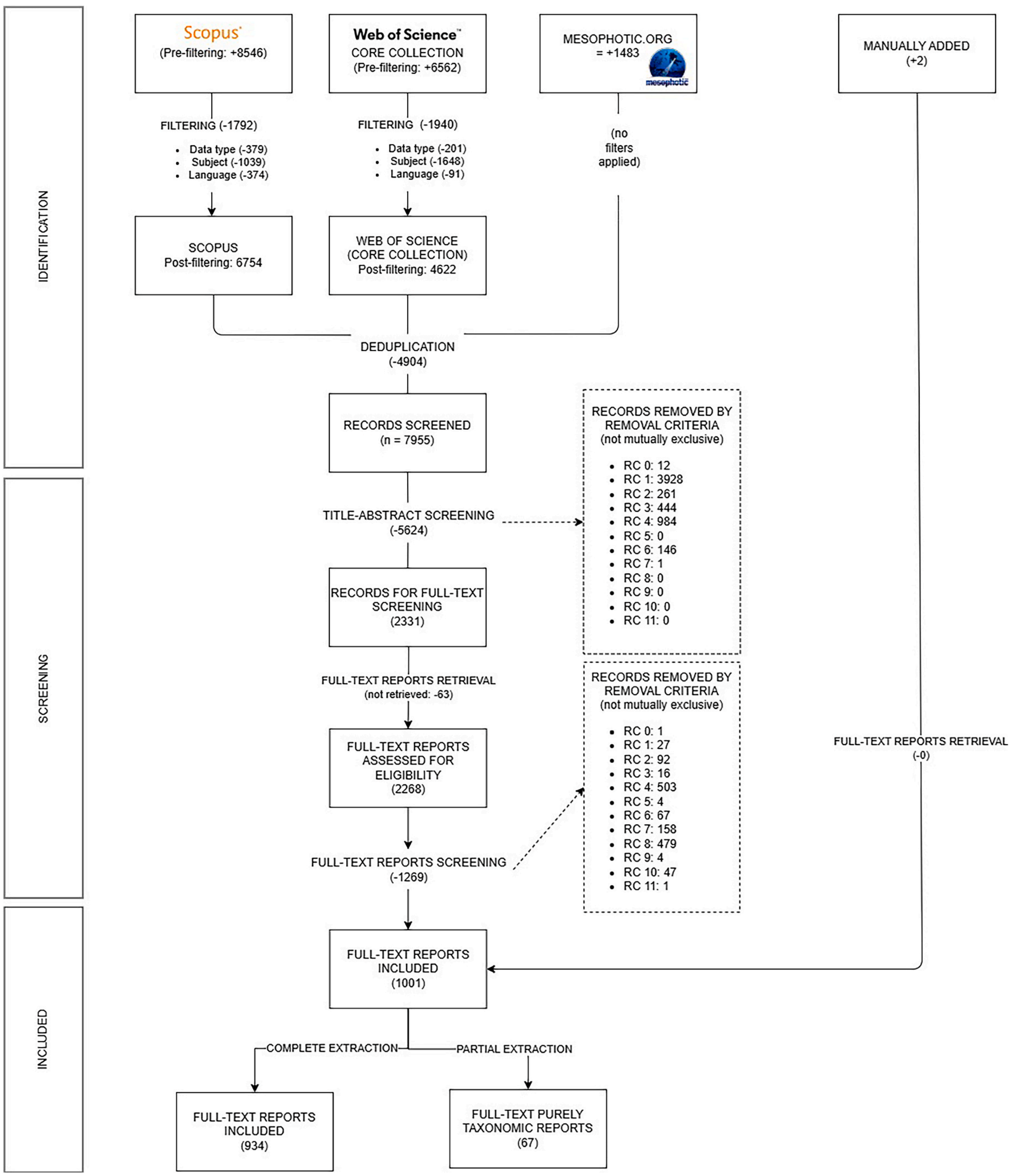

Fig. 1. Flowchart of the systematic bibliographic search and associated analyses step by step. RC = Removal Criterion. See Supplementary material 1 for a detailed explanation. Adapted from (Page et al., 2021). Removal criteria were not mutually exclusive, i.e. more than one removal criterion could be assigned to a single record.

ground-truthing. Alternatively, biologists and ecologists depended on "blind" sampling such as dredging, trawling, etc. or on the sporadic campaigns with submersibles or pioneer scientific divers (Pyle, 2019). Technological advancement in the field of underwater robotics and the consequent reduction in costs was certainly among the factors that boosted mesophotic research in the last two decades (Zapata-Ramírez et al., 2013; Armstrong et al., 2019).

In the context of climate change, a further incentive to mesophotic research was certainly given by the Deep Reef Refugia Hypothesis (DRRH), originally formulated by Glynn (1996) for MCEs, according to which mesophotic ecosystems may act as a refuge for the euphotic ones. However, the hypothesis has been revisited and there is no consensus over its validity in time and space, and it is likely site- and species-specific (Bongaerts and Smith, 2019). Moreover, with increasing literature on the topic, it is becoming more evident that mesophotic ecosystems can be affected by multiple threats (Smith et al., 2019; Wong et al., 2023), and may not act as a climate refugia for their shallow counterparts due to deep bleaching even down to 90 m (Frade et al., 2018; Eyal et al., 2022; Diaz et al., 2023) and mass mortality from heatwaves down to 45 m (Garrabou et al., 2022).

Due to technical constraints and scarce public awareness, mesophotic ecosystems have been mostly neglected and rarely included in conservation measures (Castellan et al., 2022; Bell et al., 2024). Their protection is urgent and different approaches were suggested, primarily

Table 1
Parameters extracted from articles during full-text screening. Parameters marked with an asterisk (*) were not collected for purely taxonomic studies, while parameters with a rhombus (◆) were not included in *a posteriori* quantitative analyses.

	PARAMETER	DESCRIPTION	VARIABLE TYPE AND STANDARD OR MODALITIES
Record	recordTitle	Title of the extracted record	Categorical unrestricted
	recordAuthors	Authors of the extracted record	Categorical unrestricted
	publicationYear	Year of the publication	Numerical
Study area	location	Location where fieldwork was conducted	Categorical unrestricted
	latitudinalRegion	Defined by Spalding et al. (2007)	Multi-label categorical restricted
	province	Marine province(s) defined by Spalding et al. (2007)	Multi-label categorical restricted
	ecoregion	Marine ecoregion(s) defined by Spalding et al. (2007)	Multi-label categorical restricted
	maximumSurveyedDepthInMeters	Maximum surveyed depth. If not explicit in text, it was derived from figures (e.g., using isobaths' ranges).	Numerical (Meters below the sea level)
	mininumSurveyedDepthInMeters	Minimum surveyed depth. If not explicit in text, it was derived from figures (e.g., using isobaths' ranges).	Numerical (Meters below the sea level)
	substrate	Substrate of the surveyed area. If all substrate categories were sampled, the study was assigned to "mixed"	Categorical: hard, soft, artificial, hard + artificial, soft + artificial, mixed
	habitat◆	Category or description of the habitat where fieldwork occurred	Multi-label categorical unrestricted
	protection	Whether in text was mentioned if the location was in protected areas (MPAs, Natural Parks, etc.) or other effective area-based conservation measures (OECMs), e.g., fishery restrictions.	Boolean (Yes/No)
Study aim	field	Research focus of the publication	Multi-label categorical restricted: Acoustics, Biodiversity and community structure, Conservation and management, Distribution and connectivity, Disturbance, Environmental drivers and spatio-temporal pattern, Mapping, Molecular ecology, Physiology, Taxonomy
	observationalORexperimental	Whether the publication was purely observational or it encompassed *in situ* manipulative experiment, e.g., transplants, species culling, etc.	Categorical: Observational, Experimental
	indicators	For the aim of this review, indicators included a) measured variables related to the biotic component of the ecosystem, and b) proxies of anthropogenic impact used for ecological status assessment. To ease *a posteriori* quantitative analyses, restricted modalities were defined, for example "photosynthetic rate" or "reproductive stage" were assigned to "physiological indicator".	Multi-label categorical restricted: full list of modalities, available at Supplementary Data 1, Table S5.
Taxonomic target	taxonomicTargetLevel	Whether the publications focus was on community assessment, towards a taxonomic group (e.g., a phylum/ order) or a single species. Publications with complex design had multiple values assigned. "Not applicable" was assigned for example to publications evaluating litter distribution. If there was no target groups/species/community, e.g., in publications assessing litter distribution, "Not applicable" was assigned.	Multi-label categorical: Community, Group, Single species, More than one species, Not applicable. "Group" was used to define any taxonomic level from genus to phylum. "More than one species" was used when a few species were targeted, but they were not phylogenetically closely related: e.g., *Corallium rubrum* (Linnaeus, 1758) (octocoral) and *Pseudosimnia carnea* (Poiret, 1789) (gastropod).
	detectedTaxonomicGroup	Taxonomic groups detected in studies at the community level (or combined) extracted from species list or in-text mentions. If there was no target groups/species/community, e.g., in publications assessing litter distribution, "Not applicable" was assigned. If there was no target groups/species/community, e. g., in publications assessing litter distribution, "Not applicable" was assigned.	Multi-level categorical unrestricted
	targetTaxa	If the study had a specific taxonomic target, irrespectively of the taxonomic level, e.g., Porifera if it was a sponge community assessment or *Corallium rubrum* if it was a transplantation study. If there was no target groups/species/ community, e.g., in publications assessing litter distribution, "Not applicable" was assigned.	Multi-level categorical unrestricted. Examples: a) *Paramuricea clavata* (Risso, 1827) and *Corallium rubrum* (Linnaeus, 1758) b) *Acropora spp.*
	environmentalPosition	Living location of the organism in relation to the sea floor. If there was no target groups/species/community, e.g., in publications assessing litter distribution, "Not applicable" was assigned.	Categorical: Epibenthic, Endobenthic, Hyperbenthic
	habit	Mobility capacity the organism(s) observed/targeted. If there was no target groups/species/community, e.g., in publications assessing litter distribution, "Not applicable" was assigned.	Categorical: Sessile, Vagile, Mixed (both sessile and vagile), Not applicable
Method	molecularAnalyses	Whether or not molecular techniques were used. If there was no target groups/species/community, e.g., in publications assessing litter distribution, "Not applicable" was assigned.	Boolean (Yes/No)
	samplingPlatform	System or device used to collect samples. In studies that relied on more than one platform, only the ones that were actually used at mesophotic depths (30–150 m) were included.	Multi-label categorical, restricted: acoustic (SSS, MBES, …), AUV (Autonomous Underwater Vehicle), BRUV (Baited Remote Underwater Video), CCR (Closed-Circuit Rebreather), dredges, drift camera, drop camera, fishery, grab sampler, HOV (Human-Occupied Vehicle), Open-

(continued on next page)

Table 1 (*continued*)

PARAMETER	DESCRIPTION	VARIABLE TYPE AND STANDARD OR MODALITIES
		circuit SCUBA, ROV (Remotely Operated Vehicle), SCUBA, TCS (Towed-Camera System), scientific trawl, other
collectedDataType	Type of data that were collected	Multi-label categorical restricted: video, photo, specimen, sediment, water, visual *in situ* measurement
samplingUnit*	Sampling unit, depending on the field and design of the study, could be spatial, e.g., transect, quadrat, …, or MaterialSample (e.g., specimen) or an experimental unit for manipulative studies. Multiple modalities could be assigned to this parameter, e.g., if photoquadrats were taken along videotransects, both quadrat and transect were extracted as samplingUnit.	Multi-label categorical restricted: see Supplementary Data 1, Table S7
design*,◆	Schematization of the study design, e.g., if multiple sites were sampled at multiple depths and the sampling units were transects, then the design was summarized as follow: site (depth(transect)),	unrestricted
visuallySurveyedSurface*,◆	Surface of the seafloor that was inspected with visual techniques	Categorical, restricted ranked: <1 m^2, 1–10 m^2, 10–100 m^2, …
temporalReplicates*	Whether or not temporal replicates were collected, for example in the context of monitoring programs or experimental setups	Boolean (Yes/No)
abioticVariables*	Abiotic variable included in the study	Multi-value categorical unrestricted
abioticVariablesCollection*	Whether the abiotic variables were collected *in situ, ex situ,* or both	Categorical: *in situ* (e.g. CTD) or *ex situ* (e.g. satellite data), *in*+ *ex situ*
visualDimensions*	For publications, whose data type included pictures or video, whether they did 2D analyses or also 3D reconstructions.	Multi-level categorical restricted: 2D, 3D, 2D+3D, notapp, nd
maxDepthROV	If applicable: maximum surveyed depth with a ROV	Numerical (Meters below the sea level)
minDepthROV	If applicable: minimum surveyed depth with a ROV	Numerical (Meters below the sea level)
maxDepthHOV	If applicable: maximum surveyed depth with a HOV	Numerical (Meters below the sea level)
minDepthHOV	If applicable: minimum surveyed depth with a HOV	Numerical (Meters below the sea level)
maxDepthSCUBA	If applicable: maximum surveyed depth by SCUBA divers	Numerical (Meters below the sea level)
minDephtSCUBA	If applicable: minimum surveyed depth by SCUBA divers (circuit undefined)	Numerical (Meters below the sea level)
maxDepthOpen	If applicable: maximum surveyed depth by SCUBA divers (circuit undefined)	Numerical (Meters below the sea level)
minDepthOpen	If applicable: minimum surveyed depth by open-circuit SCUBA divers	Numerical (Meters below the sea level)
maxDepthCCR	If applicable: maximum surveyed depth by closed-circuit rebreather divers	Numerical (Meters below the sea level)
minDepthCCR	If applicable: minimum surveyed depth by closed-circuit rebreather divers	Numerical (Meters below the sea level)

the adaptation of current MPA to effectively cover and conserve mesophotic ecosystems (Soares et al., 2020; Pulido Mantas et al., 2024).

1.2. Gaps and aims

Previous reviews covered different aspects of mesophotic ecosystems, such as their biodiversity (e.g.Lesser et al., 2018; Laverick et al., 2018), function (Slattery et al., 2024), conservation (Smith et al., 2019; Bell et al., 2024), and research trends (Radice et al., 2024; Banha et al., 2025). Nevertheless, most of them were either regional or limited to a latitudinal zone, with a strong imbalance towards Mesophotic Coral Ecosystems (MCEs); as a result, it is difficult to gain a global view of mesophotic research, even if in terms of collating literature a great advance was the creation of the Mesophotic.org repository (Bongaerts et al., 2019). Concerning the methodology, the only information that could be easily retrieved from the aggregated statistics (http://www.mesophotic.org/statistics) of the database is the research platform (e.g. ROV, submersible, etc.).

Here, a systematic global literature review was carried out to highlight current gaps and emerging trends in the study of mesophotic ecosystems. The focus was narrowed to studies that relied partially or completely on visual-based techniques (such as divers, ROVs, etc.), considering their increasing availability for surveying mesophotic ecosystems and the fact that they are potentially less destructive. This systematic review complements available literature, especially Radice et al. (2024); Banha et al. (2025), analyzing not only spatial, temporal, and taxonomic trends, but also compiling more granular information related to fieldwork methodologies and sampling design. This data will help identify methodological limitations in current literature and provide information indispensable for the development of standardized fieldwork protocols and reporting schemes. This will produce more comparable results and more reliable data to support effective conservation measures.

2. Methods

A systematic literature review was carried out according to the PRISMA protocol (Page et al., 2021), its steps were illustrated in the flow diagram, Fig. 1, and the PRISMA Eco-Evo Checklist (O'Dea et al., 2021) can be accessed in the supplementary data(Supplementary Data 1, Table S1). The databases Web of Science, SCOPUS, and Mesophotic.org were accessed at the end of November 2023. While all publications from the latter automatically passed to the deduplication phase since it is a dedicated database, for SCOPUS and Web of Science, the search was refined using a query and limited to title, abstract, and keywords. After more than twenty scoping exercises with different word combinations, search terms were grouped into 6 blocks, and the query was built using the following syntax: *((depth) OR (habitat)) OR (platform AND domain AND (field OR taxa))*. This was the final string:

("twilight zone*" OR mesophotic* OR "deep reef*" OR circalittoral OR "sponge garden*" OR "sponge ground*" OR coralligenous OR maerl OR "rhodolith bed*" OR "roche* du large*") OR (("remote* operated vehicle*" OR rov OR rovs OR auv OR auvs OR "autonomous underwater vehicle*" OR "towed camera*" OR "drop camera*" OR "baited remote underwater video*" OR bruv OR bruvs OR trimix OR rebreather* OR submersible*) AND ((sponge* OR coral* OR rhodolith* OR cnidar* OR

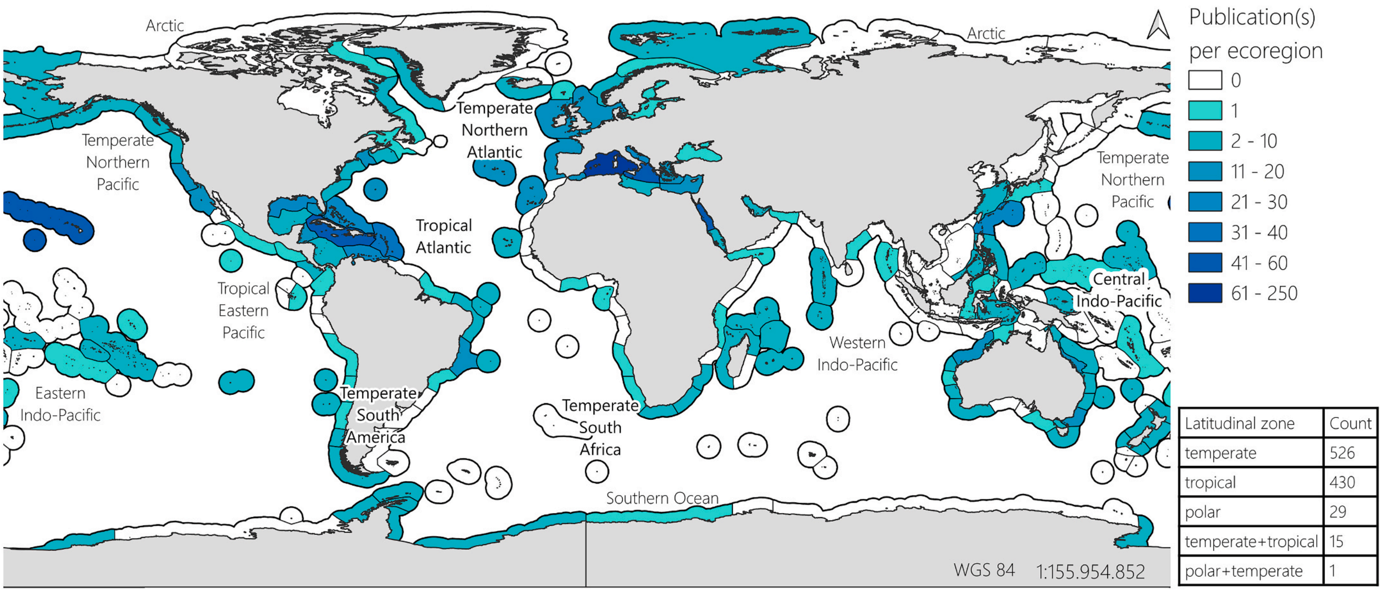

Fig. 2. Geographical distribution of the records included in the review per Marine Ecoregions of the world as defined by Spalding et al. (2007). Marine realms names indicated on map. Right: table with the number of publications per latitudinal region.

bryozoa* OR porifera OR fish* OR alga* OR benth* OR demersal) OR (geolog* OR ecolog* OR oceanograph*)) AND (marine OR sea* OR ocean*))

Further database-specific filters (e.g., only English) were set, see Supplementary materials for a detailed explanation and considerations on the scoping methodology (Supplementary Data 1, Tables S2 and S3).

2.1. Deduplication and screening

All publications stored in the Mesophotic.org database were passed to title-abstract screening. The dataset that resulted merging records from SCOPUS, Web of Science and Mesophotic.org was subjected to deduplication in R using the RefDeduR package (Shen et al., 2022) and adapting the deduplication pipeline of the package tutorial, see online repository for the script.

Screening was a two-step process: 1) title-abstract and 2) full-text screening. Based on the content, studies were removed if conducted outside of the 30–150 depth range and if no visual platform was used. Considering the focus on the benthic realm the results were circumscribed further by removing records targeting fish with no quantitative data on other benthic organisms and no habitat characterization. A full account of the exclusion criteria is listed in Supplementary materials 1 (Table S4) and a full list of removed records is available in Multimedia component 6. More than one removal criterion was assigned if applicable, i.e. removal criteria were not mutually exclusive.

2.2. Data collection and analysis

The information extracted from each publication that passed full-text screening was organized in the parameters listed in Table 1. For exclusively taxonomic papers with new species description, some parameters were not extracted (marked with an asterisk) because information related to the field methodology was usually lacking or partial. When needed to collect data of interest for this systematic review, especially species list and sampling sites characterization, reports' supplementary materials were accessed. To analyze the spatial distribution of the publications, the marine hierarchical classification proposed by Spalding et al. (2007) was used, consequently all publications depending on the survey location(s) were attributed to one or more environment (polar/temperate/tropical), realm, province, and finally ecoregion. For a more exhaustive analysis of the most common visual sampling platforms, minimum depth, and maximum depth at which they were used were extracted. Missing values for each parameter were marked as ND (Not Defined). Quantitative analyses for the different parameters collected were conducted on a clean subset after removal of missing data, whose percentage is presented in Table S6 (Supplementary Data 1). All analyses and visualization were run using R version (R Core Team, 2025), except for the map which was made with QGIS (QGIS Development Team, 2025). All the analyses on the global dataset (Multimedia component 2) presented in the result section were also run separately for each latitudinal region (tropical in Multimedia component 3, temperate in Multimedia component 4, polar in Multimedia component 5). All data and scripts are available in an online repository (https://github.com/CCampanini/Campanini_et_al-Peering_into_the_twilight_mesophotic_systematic_literature_review).

3. Results

After the first search in SCOPUS and Web of Science and adding all records in Mesophotic.org, 12859 articles were found. The deduplication process, including automated and manual check of putative duplicates, resulted in the removal of 4904 duplicates. 7955 passed to title-abstract screening, of which only 2331 passed to full-text screening. Finally, 1001 were included in this review after the full-text reading (Fig. 1), of which 67 taxonomic studies underwent partial extraction (Table 1). Notably, 503 publications outside of the pre-set depth range (30–150 m) could be removed only through full-text screening because the depth range was not specified in the abstract.

3.1. Investigation effort and technique in time and space

Overall, the research effort was evidently unbalanced in its geographical distribution. Most publications were limited to a single latitudinal region with the highest number carried out in the temperate ecosystems (526, ~53%) followed by the tropics (430, ~43%) (see Fig. 2). Considering realms, the gap in terms of number of records ranged from 492 in the Temperate Northern Atlantic (~49%), followed by Tropical Atlantic (237, ~24%), to realms with no more than 10 studies. Impressively, a quarter of the screened studies were carried out in a single ecoregion, the Western Mediterranean Sea, while around 44% of all ecoregions had no records, and 16% had only a single study.

Around 61% of the studies targeted exclusively natural hard

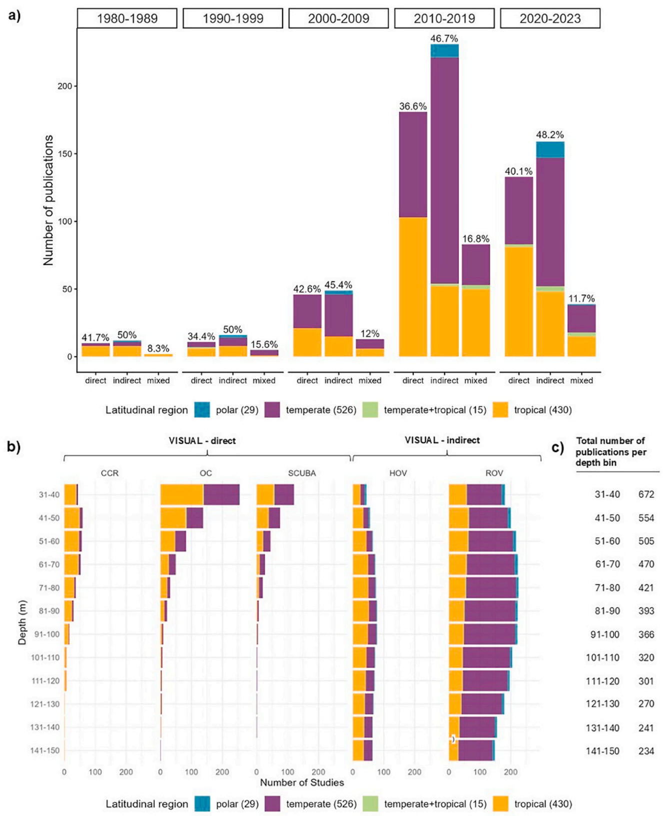

Fig. 3. a) Bar chart showing the number of publications by decades, by technique and by environment. The last quadrant includes studies from 2020 to 2023 only. The only study performed both in temperate and polar zone is not shown in the plots (temperate + polar). b) Bar plot with the number of publications per 10-m-depth interval for the most common visual platforms (CCR = close-circuit rebreather, OC = open-circuit scuba diving, HOV = Human-occupied vehicle, ROV = Remotely Operated Vehicle). Studies encompassing more than one depth interval were counted in each bin. c) Total number of publications per depth interval (all platforms included). The only study performed both in temperate and polar zone is not shown in the plots (temperate + polar).

substrates, only 5.1% soft bottoms and 27.7% included both (Multimedia component 1, Fig. S1). When artificial substrates were included (~6%), it was mainly to assess the impact of underwater structures (e.g., oil & gas platforms) or their potential as artificial reefs. Of the publications targeting or including hard bottoms, 346 referred to MCEs and 161 to coralligenous ecosystems, and 99 either rhodoliths or maerl beds.

The authors refer that field work was conducted completely (165, 16.5%) or partially (108, 10.8%) inside protected areas or areas where some sort of regulations were in place, e.g., fishery restrictions. However, this information was lacking for 656/1001 studies and included mainly in studies for which the authors considered it relevant for the experimental design, e.g., in conservation studies.

Visual-based exploration of mesophotic ecosystems was limited to four publications (not included in Fig. 3a) before 1980 and a first burst occurred in the early thousands. However, the most striking increase in the number of publications was recorded from 2010, more than 4 times higher than the previous decade (495 vs 108) (Fig. 3a). This trend is expected to be confirmed considering that from 2020 to 2023, the number of publications was already 332 at the time of the screening. Overall, during the last 3 decades, half of the studies have relied on indirect techniques (divers not involved), slightly more than direct-based, while mixed-are limited to a smaller share. Despite this, direct techniques were still preferred in tropical ecosystems. All studies performed in polar mesophotic ecosystems (30) adopted indirect techniques and, except for 6, were published in the last two decades. The number of studies steadily decreased with depth (Fig. 3c), with a third of the studies not going deeper than 60 m and this decrease is more accentuated for tropical regions (SM3). While for most of the publications, a single platform (e.g., ROV, scuba) was adopted (~73%), ~21% studies had two and the remaining ~6% three or more (Supplementary Data 1, Table S8). Starting from 2000, the two most widely used platforms were ROVs and open circuit scuba diving, despite the latter being mainly restricted to the upper mesophotic (Fig. 3b). Studies that did not specify the type of circuit were assigned to "scuba" and they have a similar maximum depth pattern as open-circuit scuba (OC). In studies relying partially or entirely on direct techniques, CCRs were preferred for higher depths. CCRs and HOVs were adopted predominantly in tropical context (80/91 and 86/128, respectively). By contrast, ROVs were far more popular in temperate regions.

3.2. Field and indicators

Overall, most publications could be assigned to more than one field and in around 85% of the publications more than one ecological indicator were gathered. Almost half of the studies were assigned to "Biodiversity and community structure" (415) (Fig. 4). "Diversity", here encompassing both records of presence and community diversity, was

Fig. 4. Heatmap with the most common indicators collected divided per most common field. Assigned fields were not mutually exclusive. Numbers in brackets represent the total number of publications per each field/indicator. ALDFGs = Abandoned, Lost or otherwise Discarded Fishing Gear.

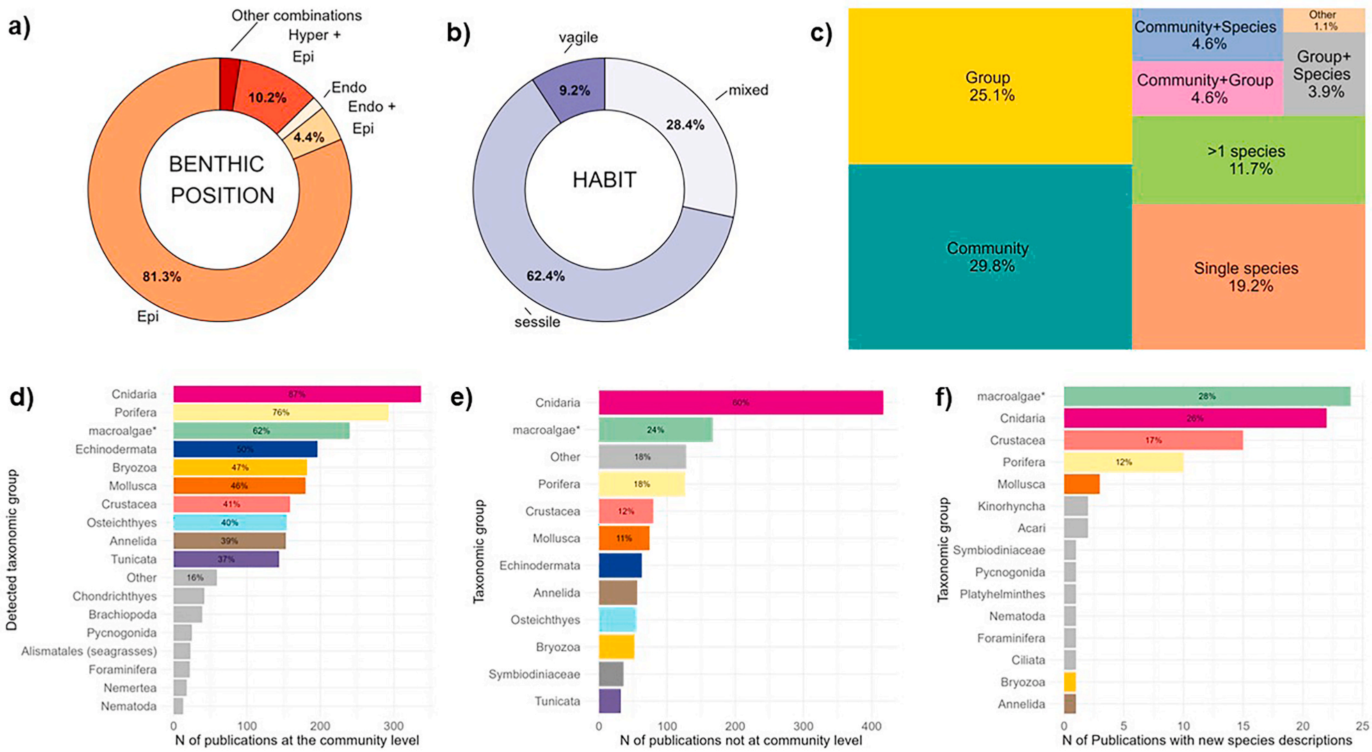

Fig. 5. a) Donut chart showing the proportion of publications by benthic position (Epi = epibenthos, Hyper = hyperbenthos, Endo = endobenthos). b) Donut chart showing the proportion of publications by habit of the taxonomic target. c) Treemap with the proportion of publications(%) by targeted taxonomic level (Group = any taxonomic group superior to the genus level. Species = one or a few target species. d) Bar chart with publications per detected taxa in community-level studies (Community, Community + Group, and Community + Species). e) Bar chart with publications at group level by targeted taxonomic group. f) Bar chart with taxonomic publications with new species/genus description by taxonomic group. (* algae is the only taxonomic group adopted in the analyses which is not considered monophyletic).

the most collected indicator (Supplementary Data 1, Fig. S2). However, it must be considered that abundance in terms of number of individuals/colonies, density, or cover are all proxies aimed at quantifying the target taxon/taxonomic group. At the individual level, size was measured in around 20% of the studies (218) (Fig. 4), either *in situ* or from collected samples or videos/photos. By contrast, due to the challenge in its direct measurement, biomass (~7%) was often estimated *a posteriori* using length-weight conversions. Even if they were not the main aim of the study, proxies of impacts were often assessed, for example the presence of either ghost nets or litter (~6.4%). Health, usually in terms of colony necrosis or disease prevalence, was included in ~9% (92) of the publications and, in all but 14 studies, it was assessed exclusively on Cnidaria, especially Octocorallia (34/92), Scleractinia (23/92), and Antipatharia (6/92). Of the records that included trophic indicators (~6%) or functional groups (2%), not all were collected *in situ* in the context of the study, but in many cases, especially for studies adopting a trait-based approach, trophic guilds were assigned *a posteriori* for the analyses. If we exclude purely taxonomic studies, most of the records (810/934) did not present molecular analyses and, if present, they were mainly studies assessing genetic connectivity or Symbiodiniaceae diversity among populations/along a depth gradient. Indeed, of the ~50 records (~5%) directly referring to the Deep Reef Refugium Hypothesis in their goals, >40% assessed populations connectivity using molecular techniques. Publications that included *in situ* manipulative experiments were scarce (10%), mainly consisted of often (reciprocal) transplantations at different depths, and only 6 were in the field of restoration (Multimedia component 2).

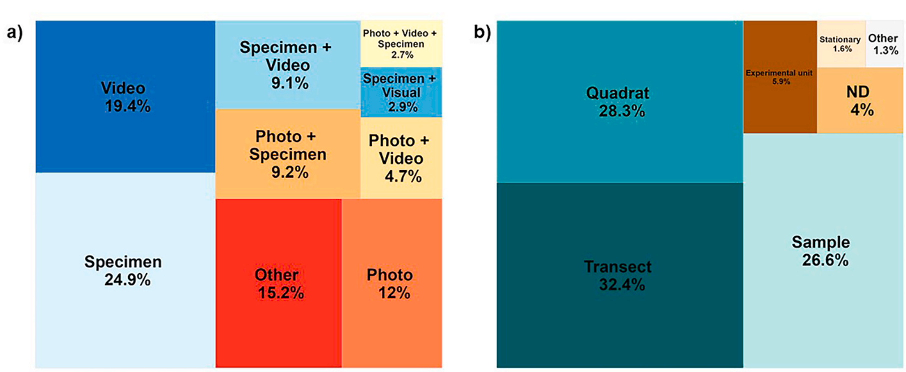

Fig. 6. Treemap with annotated percentage value of a) data type with combination and b) simplified sampling unit. (ND = not defined).

3.3. Target organisms

Publications included in this review focused prevalently on epibenthic organisms (>80%) (Fig. 5a). More than 60% targeted exclusively sessile organism(s), while only around 9% exclusively vagile organism(s) (Fig. 5b). More than a third of the publications were at the community level (29.8%), followed by group (25.1%), here intended as any taxonomic group higher than the genus level (phylum, order, family, etc.) (Fig. 5c). The most common taxonomic groups reported in studies at the community level and not at the community level are shown in Fig. 5d and e, respectively. When publications focused on a single or a few species, the top target was the red coral *Corallium rubrum* (Linnaeus, 1758) (32), followed by the red gorgonian *Paramuricea clavata* (Risso, 1827) (27), and the scleractinian *Montastraea cavernosa* (Linnaeus, 1767) (27). New taxa were described in 77 of the 1001 studies included for this review and consisted mainly of algae (28%), cnidarians (26%), and crustaceans (17%) (Fig. 5f). Most taxonomic publications could be clustered by research groups/authors specializing in a given taxonomic group. Since only visual-based studies were included in this review, these new discoveries derived from the intentional collection of voucher specimens mainly with ROVs, HOVs, or technical divers. More than half of the newly discovered taxa were described based solely on morphological characteristics. For an in-depth analysis of target organisms distinguishing among latitudinal regions, see Multimedia component 3, Multimedia component 4, and Multimedia component 5.

3.4. Sampling design

Overall, in more than half of the studies either photo or videos were collected (Fig. 6a). In spite of the focus on visual-based techniques, around a quarter of the records still relied solely on the collections of specimens. For around 45% of the studies, more than one type of data was collected with the more common combination being photo and specimen (9.2%) (Fig. 6a). In Fig. 6b, the sampling unit's categories are simplified, e.g. line-intercept transects or circular transects, were merged into the broader category “transect”, for a full account, see Supplementary Data 1, Table S5. The most widely adopted unit of sampling were transect (32.4%) followed by quadrats (28.3%) (Fig. 6b); in 209 of the 316 studies relying on quadrats, the latter were either collected along a transect or were extracted *a posteriori* as “digital quadrats” from video recordings, selecting random frames or at constant distance/time interval. By contrast, only 18 of the 934 records in this review specifically mentioned surveying either permanent quadrats or transects. When large surfaces (>100000 m^2) were surveyed, it was mainly for mapping purposes and thanks to longer dive time allowed by indirect platforms. Even in studies surveying large areas for biodiversity and/or community structure, quantitative analysis often relied on small subsamples (e.g., selected frames from videos) with the analyzed area differing by one or more order of magnitude from the total area surveyed.

Virtually, no study clearly referred to widely adopted monitoring protocols. Temporal replicates at different time scales were included in around a quarter of the studies (244/934), often in the context of manipulative experiments (68/244) or before-after impact studies. By contrast, long-term monitoring projects and data-series (>1 year) were limited to less than 10 publications. Around 60% of the studies did not include environmental parameters, and when present they were mainly collected *in situ*; the most common was temperature (~22%), followed by sediment composition, and salinity.

4. Discussion

4.1. Investigation effort and technique in time and space

The rise in the number of publications was quantified for MCEs in Turner et al. (2017) and Turner et al. (2019), and for TMEs, i.e. Temperate Mesophotic Ecosystems, in Cerrano et al. (2019); here, we confirm this trend for visual surveys at both latitudes. Nonetheless, the spatial distribution of studies is still evidently uneven as previously observed for MCEs (Kahng et al., 2017) and both MCEs and TMEs (Radice et al., 2024). This review complements previous results with the few records conducted in polar mesophotic ecosystems, highlighting that even less is known of these habitats, especially sub-ice ones, due to the additional challenges that their exploration entails. Although the costs of studying mesophotic habitats are decreasing respect to the past, research on deeper habitats still demands high effort in terms of both technical and financial resources with high-income countries leading the way as occurring for deep-sea ecosystems (Bell et al., 2023). The completely inhomogeneous coverage of mesophotic depths is further exacerbated by the concentration of the research effort in a few ecoregions, sometime even in a few locations. When multiple studies were carried out at the same location, this could be explained by: a) the implementation of long-term monitoring (e.g. Caribbean Research and Management of Biodiversity, CARMABI, Curaçao), b) conservation interest (Portofino MPA in Italy, or Cap de Creus MPA in Spain), and/or c) proximity to a research facility (e.g. Inter-University Institute for Marine Sciences IUI, in Eilat, Israel).

Even if the lack of a standard classification impeded quantitative analyses, it resulted evident that the more popular habitats were mesophotic coral ecosystems mainly at tropical latitudes and the coralligenous assemblage at temperate, followed by rhodolith beds; the latter spans in both temperate and tropical environments and their prominence in literature emerged also in the topic modelling analysis by Bahia et al. (2025). The possible reasons for the scarce representation of soft bottoms in this review, focused on studies that included visual-based techniques, are a) that their investigation is still very often performed with non-visual and destructive techniques such as trawling, dredging, etc. which in turn allow the characterization of the infauna, b) sediment resuspension increases water turbidity thus reducing the effectiveness of visual-based techniques on soft bottoms, and c) they are often considered less charismatic habitats with reduced tourism attractiveness.

Nevertheless, as the spatial scale of the investigation of the mesophotic realm increases not only new species, but new-to-science biotopes/facies will likely be described, possibly spotlighting the role of often overlooked taxa as habitat-formers at mesophotic depths. This occurred for example with the discovery of a monospecific brachiopod biotope of *Megerlia truncata* (Linnaeus, 1767) (Angeletti et al., 2020), a sabellid forest of *Bispira riccardi* Giangrande, Putignano & Enrichetti, In Enrichetti, Baldrighi, Bavestrello, Betti, Canese, Costa, Del Pasqua, Giangrande, Langeneck, Misic, Putignano, Toma & Bo, 2022; Enrichetti et al. (2022), and bryozoans bottoms (Holz et al., 2020).

Likely, the reason for the increase in publications in the last decades does not reflect an increased interest only but stems directly from technological advances and the consequent increased availability of platforms at a relatively low price. The popularization of close-circuits rebreathers outside of the military or commercial diving markets that occurred in the nineties opened the way to the exploration of lower mesophotic depths. Indeed, the fact that CCRs were not previously available and that studies marked as “scuba” have a similar maximum depth distribution as open-circuit studies, supports the hypothesis that they were actually mainly open-circuit studies. At even higher depth (>120 m), ROVs followed by submersibles, are definitely the most common platforms thanks to their versatility. With respect to other indirect but visual techniques such as towed-camera systems or drop cameras, both platforms may come with robotic arms allowing for *in situ* manipulation and sampling. Indeed, in one third of the studies that adopted no other platform than ROVs, they were not used exclusively for collecting videos/photos, but for specimen collection as well. Studies not providing any quantitative data of the benthic community other than fish were excluded from this review and this explains the scarce representation of BRUVs among the sampling platforms. For an in-depth analysis of pros and cons of each platform, refer to Armstrong et al. (2019).

4.2. Field and indicators

Logistics is a constraint that prevents the wide realization of manipulative experiments at mesophotic depths and when set, they were mainly performed in the upper mesophotic relying on divers. Thus, most studies were purely observational. Studies where the main objective was mapping were often coupled with acoustics techniques as visual characterization often served to ground-truth preliminary acoustics surveys. It is not surprising that when photo/videos were collected, data on community composition and structure were coupled with the collection of data on visible impact, for example the presence of either ghost nets or litter was assessed in ~7% of the studies. A large-scale field assessment of MCEs raised concerns as anthropogenic debris was found to be more abundant at mesophotic depths than in shallow reefs (Pinheiro et al., 2023). Indeed, a growing number of publications demonstrated the ongoing changes and stressors affecting mesophotic ecosystems (Soares et al., 2019; Micaroni et al., 2021; Wong et al., 2023; Bell et al., 2024; McWhorter et al., 2024). In a global assessment per depth realm, Jacquemont et al. (2024) denounced the mismatch between fishing pressure and protection status; among the realms mostly within exclusive economic zones (EEZs), lower mesophotic (60–150 m), together with rariphotic realm, were found to be the least protected in spite of suffering from high fishing pressure. As a consequence, considering their importance as much as their vulnerability, mesophotic ecosystems should be considered high conservation priority areas to reach international targets such as the “30x30” target (Convention on Biological Diversity, 2022). Most studies in this review specified the protection status of the location(s) only when relevant for the design, so the number of studies that were actually performed inside protected or fishery-restricted areas was likely higher. However, even when regulations are in place, their effectiveness is often limited (Relano and Pauly, 2023).

In the few studies where biomass was assessed, it was mostly estimated indirectly from size using allometric conversions and mainly for fish; indeed such equations are more likely to be available in literature for species of commercial interests. Remarkably, only five publications included the monetary estimation of ecosystem services from visual analyses, of which two examined the correlation between the aesthetic value of coralligenous ecosystems and their attractiveness for tourism (Tribot et al., 2016; Langlois et al., 2021). In spite of the benefits provided by mesophotic ecosystems to humans, the dearth of quantitative ecosystem services assessments hinders their accounting in management and policymaking (Holstein et al., 2019).

4.3. Target organisms

Cnidarians were both the more common detected taxonomic groups in community level studies and the most popular phylum for target organisms. This is likely to reflect their role as habitat-formers in different mesophotic ecosystems from tropical coral reefs (Bell et al., 2019; Slattery and Lesser, 2021) to temperate marine animal forests (Angiolillo et al., 2017). Almost 1 out of 10 of the studies included in this review lead to the description of at least one new species. This proportion emphasizes the potential of new discoveries. Moreover, the share of taxonomic studies is likely underestimated because the effort in the description of new mesophotic species is biased towards bony fishes (Radice et al., 2024; Banha et al., 2025), which were excluded for the aim of this review.

Interestingly, there is a partial mismatch between the representation of the taxonomic group detected in studies focusing on the community level and the target taxon/taxa of studies at the group or species level. Cnidarians, sponges, and algae were surely well represented at all levels from community to species-level studies. That was not the case for other taxonomic groups like Echinodermata and Bryozoa that did not have many dedicated studies even if they were reported in more than 40% of community-level studies and were conspicuous and visible contributors to the overall community composition. This pattern, especially for bryozoans, is likely derived from the availability of taxonomists focusing on a given group rather than from prioritization for biological/ecological reasons.

Apart from specimen collection for taxonomy, Reimer et al. (2019) advocates for the incorporation in monitoring programs of the so-called “minor taxa”, mostly neglected and difficult to detect, for example by integrating high-definition images or photoquadrats along ROV tracks/diver transects. Another possible solution from the Marine Sampling Field Manuals for Monitoring Australia's Commonwealth Waters (Monk et al., 2020) is the “dual transect approach”, which consists in a first rapid survey of the transect area to assess the presence of highly mobile taxa followed by survey at slow speed to detect smaller and cryptic organisms.

4.4. Sampling design

In more than 50% of the publications, either photos or videos or both were collected for quantitative analysis, often coupled with specimen collection (~20%). However, in most cases the impact was still limited because visual-based techniques can guide selective sampling of target species and/or specimen collection was not systematic but consisted of voucher specimens for taxonomy and/or molecular analyses. Despite photos or even samples are irreplaceable for some purposes, e.g. fine-scale and detailed community description, the collection of videos as raw data is gaining popularity promoted by the spread of quality, mass-produced, high-definition (HD) cameras (e.g. GoPro©) (Bicknell et al., 2016). Apart from the fact that they constitute a non-destructive sampling method, they carry many advantages: a) they can be stored and re-analyzed in time, b) they can be analyzed for different purposes and lead to multiple publications, for example coupling community description with ecosystem services (Doxa et al., 2016; Tribot et al., 2016; Langlois et al., 2021) or litter impact assessment (e.g. Consoli et al., 2018, 2021), and c) they can be obtained as opportunistic footage. The latter was very often the case of studies assessing the artificial structures, e.g. oil and gas platforms, where photos/videos from routine industrial monitoring were analyzed by researchers for ecological studies (Rouse et al., 2019; Redford et al., 2021; Torquato et al., 2021; Bull et al., 2023). Even if many publications in this review adopted dedicated software for video/image analyses (e.g. BiiGle, PhotoQuad, etc.); however, this step still represents a limiting factor because it is considerably time-consuming (Gomes-Pereira et al., 2016). Indeed, in almost all large-scale surveying studies, only a small subset of the surface was actually used for quantitative analysis. One notable exception was a scallop stock assessment for which extensive survey design using a drop camera system and covering around 70000 km^2 was set in place (Stokesbury and Bethoney, 2020). A definitive push towards visual-based research and large-scale image collection will be favored by the development of automated and semi-automated image annotation (Rubbens et al., 2023); indeed, in the last few years new algorithms are being trained for different conditions and environments, and in the future they will likely cover more habitats found at mesophotic depths. Even if less than 2% studies relied on 3D reconstructions, probably due to bottom time limitations at mesophotic depths for direct methods and high navigation skills for indirect methods, this number is likely to increase according to an observed trend in the monitoring of marine environments (Pulido Mantas et al., 2023).

Only a few studies resulted from long-term monitoring programs and are based on a data series that encompasses more than a year and often resulted in multiple publications (e.g. Bak and Nieuwland, 1995; Calnan et al., 2008; Nugues and Bak, 2008; de Bakker et al., 2016, 2017; Ferraro et al., 2017; Bethoney and Stokesbury, 2018; Rosellon-Druker and Stokesbury, 2019; Tran et al., 2022). The lack of baseline data hampers the possibility to test hypotheses on mesophotic ecosystem's structure and functioning and the disentanglement of population fluctuations and anthropogenic impacts (Micaroni et al., 2021). Current knowledge of ecosystems at mesophotic depths is so limited that many studies and discoveries result either from ‘incidental data’, i.e. via opportunistic sampling with no structured design or taxonomic scope, or ‘elementary inventory’ *sensu* Guralnick et al. (2018). The latter consists of a single survey, with a limited spatiotemporal scope, e.g. in this review mainly exploratory transects whose aim did not go beyond mapping/habitat characterization. Techniques to explore mesophotic depth were either adapted from shallow-water ones or relying on the ones typically used for deep sea explorations (Locker et al., 2010). Indeed, while the research of shallow ecosystems has a long history and monitoring protocols are more widely adopted, given the current status of research in mesophotic and even deeper environments, standards are far from being established. It is worth mentioning exceptions, indeed many publications stemmed from standardized surveys under the Australian Government's Integrated Marine Observing System (IMOS) (Lara-Lopez et al., 2016), a national collaborative research infrastructure in the form of a sustained *in-situ* ocean observing system. Another collaborative effort at national level involving 70 experts from 30 Australian institutions (Przeslawski et al., 2019), prompted the development of standardized field manuals, each dedicated to a different sampling platform (Przeslawski and Foster, 2018, accessible at https://marine-sampling-field-manual.github.io/). Researchers in Australia can benefit also from a standardized classification for aggregation, annotation and automated processing of underwater imagery, the “Collaborative and Automated Tools for Analysis of Marine Imagery” (CATAMI) (Althaus et al., 2015), which has already been applied in hundreds of publications, many of which included in this review.

Abiotic parameters, both *in* and *ex situ,* were rarely gathered and even less included in the analyses since many studies were purely descriptive. Considering the feasibility of its collection even using recreational diving computers, and the context on ongoing climate change, it is not surprising that the more common environmental parameter to be collected was temperature. However, the *in-situ* collection of environmental variables should be promoted since satellite data are less reliable with increasing depth. Moreover, environmental variables are necessary to examine drivers of mesophotic ecosystem variability, test ecological hypotheses, and guide conservation measures. For example, de la Maza et al. (2024) in an oceanographic study analyzed interannual temperature variation along the South Eastern Pacific by coupling long-term temperature data from both *in situ* and *ex situ* observations and their results challenge the potential role of mesophotic as climatic refugia at temperate latitudes. However, purely oceanographic or biological studies are not enough to fully test such hypothesis and interdisciplinary research relating environmental and biological variability is urgent.

4.5. Review limitations and recommendations

Following either a light- or community-based definition, mesophotic boundaries would vary depending on the habitat and/or environmental conditions. However, for the aim of this systematic global review, conventional depths of 30 and 150 m were set to define an unambiguous eligibility criterion. While having fixed parameters is convenient, many studies performed in mesophotic conditions were probably excluded, especially in temperate environments where it is likely that mesophotic conditions could be found beyond the selected depth range, even at shallower depths. However, it must be noted that mesophotic abiotic conditions alone, i.e. low-light conditions and poor visibility, at shallow reef (<30 m) may not determine a community composition that typically occurs at mesophotic depths (Harris et al., 2021).Of the 2331 articles selected for full-screening, 1006 were putatively included reading the abstract because they possibly used terms that are often associated to mesophotic environments (e.g., "coralligenous" or "deep reef") without using the term "mesophotic" and without specifying the depth interval. These records were thus included for full-text screening to adopt a conservative approach, but 503 did not pass it because they were performed outside of the targeted depth range. A possible improvement which would have fastened the screening process and that has already been implemented in the Mesophotic.org database, would be the addition of a depth range filter in marine journals/databases. In order to facilitate literature searches, systematic reviews, and meta-analyses, machine-readable metadata compilation could be required during the submission process or metadata extraction tools could be implemented (Stocker et al., 2025).

Considering the focus of this review of field methods, it suffered from the huge discrepancy in the level of details that are usually provided in the method section dedicated to laboratory and informatic protocols/pipelines as opposed to field procedures; the latter were often scant or incomplete and often basic information, such as depth interval or platform, could not be retrieved by checking the supplementary materials or derived from other parameters. For example, when not explicitly reported, it was impossible to extract the surveyed area from more than half of the records. For example, in many studies done with ROVs/AUVs (i.e., Autonomous underwater vehicles), one or more of the following parameters were lacking: dive time, covered distance, navigation speed, and/or field of view. Another example, for surveys employing divers, many times it was impossible to determine whether they were using open-circuit or close-circuit SCUBA, let alone information on the gas mixture (e.g., air, trimix, helitrox, etc.). More rigorous methods and even the definition of reporting standards could be defined and recommended at the publication stage for field studies. Only a subset of data was extracted for this review from pure taxonomic studies as they almost systematically lack information related to the methods, and even to the ecological context as denounced by Di Camillo et al. (2018). A similar limitation affects studies at community level, indeed quantitative comparisons are mined by the unavailability of raw data, e.g. species lists, either in text or supplementary materials (Costello et al., 2013; Di Camillo et al., 2018; Roveta et al., 2022). This lack leads to a loss of potential information of species distribution and species-habitat association in an era when records species lists with coordinates could be easily integrated in existing databases, e.g. GBIF (GBIF: The Global Biodiversity Information Facility, 2025; https://www.gbif.org) and OBIS (OBIS. Intergovernmental Oceanographic Commission of UNESCO, 2025, https://obis.org/).

There are only a few standard habitat classifications at regional/national level, e.g. the European Union Nature Information System (EUNIS) (Davies et al., 2004), but even in studies where mapping was one of the main goals, they were almost never mentioned/applied. The lack of a common standardized nomenclature system for habitats, facies, and associations for the mesophotic zone at global level hampers the collection and homogenization of data for its quantitative analysis, hence the observation of geographical/temporal patterns, etc. A global habitat classifications scheme with a hierarchical structure could serve for this purpose by aggregating habitats to a coarse level for generalization and comparisons among studies (Strong et al., 2019), while lower levels could be used to refine the habitat characterization. Maintaining hierarchy leaves space for further updates and extensions of existing classifications to match ecosystem-specific requirements; for instance, Davies et al. (2017) proposed the integration of new low biotope-related levels for cold-water coral habitats into the EUNIS scheme. Despite the challenges posed by the development of a common classification at a global scale, a similar tool was already implemented for terrestrial environments with the creation of the Land Cover Classification System (LCCS) developed by the FAO (Di Gregorio, 2005). A similar effort not for habitats but to describe marine geomorphologies at a global scale was achieved through a collaborative initiative, namely the International Seabed Geomorphology Mapping Working Group (ISGM), that developed a classification and supporting tools (Nanson et al., 2026). Ultimately, the information obtained by applying a similar global framework for marine habitats could then be used in policymaking and to draw attention to overlooked habitats.

5. Conclusions

The attested potential of mesophotic ecosystems for new discoveries at multiple levels, from new useful molecules to species and biotopes, has sparked a growing interest in their investigation. Nonetheless, the lack of baseline ecological data and the skewed research effort towards a few locations and taxa can possibly lead to wrong conclusions and perception biases.

To improve our knowledge and tailor conservation measures, broader exploration campaigns should be launched coupling acoustics techniques (e.g. side-scan sonar and multibeam echosounder) to survey large areas and guide the selection of smaller priority areas for ground-truthing. Notwithstanding, it is clear that the main barrier preventing large-sale implementation of mesophotic ecosystem exploration derives from technical constraints and corresponding costs.

Furthermore, this review points out the need for better reporting of field methods and habitat-specific and regional standardized protocols, which are essential for comparison in space and time and to enforce habitat-based protection measures.

The vast majority of the mesophotic realm is not encompassed inside marine protected areas or areas where other effective conservation measures were in place. Considering the recognized multiple pressures to which they are exposed, the conservation of mesophotic ecosystems should be prioritized in protection plans.

The exploration of mesophotic depths should be considered essential to guide marine spatial planning. This goal will hopefully be achieved thanks to the increasing availability and accessibility of technologies, and the development of promising complementary tools. We barely possess knowledge of a few points in space and time, feeble lights scattered in the dark vastness of the mesophotic zone, and it is time to expand our vision.

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CRediT authorship contribution statement

Claudia Campanini: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Martina Coppari:** Writing – review & editing. **Cristina Gioia Di Camillo:** Writing – review & editing. **Chiara Gregorin:** Writing – review & editing. **Teo Marrocco:** Writing – review & editing. **Torcuato Pulido Mantas:** Writing – review & editing. **Camilla Roveta:** Writing – review & editing. **Carlo Cerrano:** Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108212.

Data availability

All data and code are available in an online repository (https://github.com/CCampanini/Campanini_et_al-Peering_into_the_twilight_mesophotic_systematic_literature_review).

Systematic literature review of visual -based investigation of worldwide mesophotic (Original data) (Campanini_et_al-Peering_into_the_twilight_mesophotic_systematic_literature_review)

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