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Mesophotic Coral Ecosystems in the Eastern Tropical Pacific: The current state of knowledge and the spatial variability of their depth boundaries

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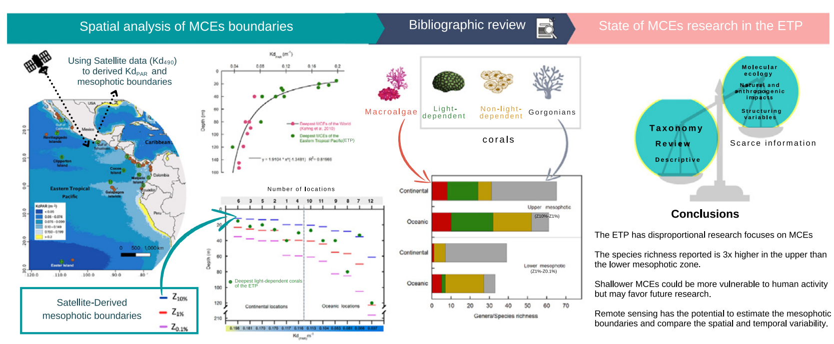
HIGHLIGHTS

- Review of MCE research in the ETP, using satellite-derived mesophotic boundaries.
- MCEs research is scarce and mainly focused on taxonomy and reviews.
- Species richness reported is 3x higher in the upper than the lower mesophotic zone.
- At coastal locations MCEs can occur as shallow as 13-15 m.
- Usefulness of satellite-derived Kd_{PAR} to identify the potential presence of MCEs.

GRAPHICAL ABSTRACT



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ABSTRACT

In the Eastern Tropical Pacific (ETP), Mesophotic Coral Ecosystems (MCEs) are limited by oceanographic conditions and are thought to be mostly absent. However, considering the currently discussed more flexible approach to define mesophotic boundaries, based on light availability, we performed a systematic search to assess their current state of knowledge. Using MODIS-Aqua satellite data (Kd_{490}), we calculated the mesophotic boundaries in the ETP, based on optical depths, and performed a bibliographic search of studies carried out at those depths, including those present in turbid waters with Kd_{PAR} values up to 0.2 m^{-1}. Seventy-seven papers on MCEs research were compiled in this review, recording a total of 138 species. The studies focus almost exclusively on taxonomy, ecosystem function, and reviews, indicating the need for future research regarding aspects, such as structuring environmental variables, molecular ecology, and natural resource management. Furthermore, remote sensing data show that there exists a high spatial variability of water transparency in the ETP, resulting in significant differences in Kd_{PAR} between oceanic and continental locations, mostly related to the occurrence of seasonal upwelling in the latter. Based on Kd_{PAR}, we estimated the mesophotic depth boundaries ($z_{10\%}$, $z_{1\%}$, $z_{0.1\%}$) for specific locations within the ETP and found that MCEs can potentially occur as shallow as 13-15 m in coastal regions. Also, we compared the calculated boundaries with the respective deepest records of light-dependent corals. With one exception, the presence of the corals was restricted to the upper mesophotic subzone ($z_{10\%}$-$z_{1\%}$), which agrees with reports for other regions, showing that light availability is one of the main drivers

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for the bathymetric distribution of MCEs and can be used as a first approach to identify their potential presence, though other local factors (*e.g.*, geomorphology, temperature, internal waves) should also be considered, as they can cause shifts in depth limits.

1. Introduction

Mesophotic ecosystems have attracted the attention of the scientific community over the last two decades, especially the Mesophotic Coral Ecosystems (MCEs), because of their potential to serve as a refuge for shallow coral communities affected by thermal stress (Bongaerts et al., 2010; Glynn, 1996). These shallow communities are degrading rapidly, mainly due to global climate change related impacts and disturbances caused by human activities, such as over-fishing, tourism, and coastal development (Hughes et al., 2017; Spalding and Brown, 2015).

According to the definition of the US National Oceanic and Atmospheric Administration (NOAA), MCEs are characterized by the presence of light-dependent corals and associated communities, composed of other corals, sponges, and algae. These ecosystems are typically found between 30 and 40 m and can extend down to 150 m in tropical and subtropical regions (Puglise et al., 2009). Although this definition has been widely accepted, there exists an ongoing discussion regarding the bathymetric boundaries of MCEs (Eyal et al., 2019; Laverick et al., 2020; Pyle and Copus, 2019; Tamir et al., 2019).

Commonly, the upper mesophotic boundary has been defined by fixed depths between 30 and 40 m, though this is more related to SCUBA diving limitations than to ecology (Laverick et al., 2016) and has been questioned, based on biological evidence of changes from shallow to MCEs communities at depths as shallow as 10 m and as deep as 50 m. Based on the former, the use of a biological definition of the upper mesophotic boundary rather than a fixed depth based on SCUBA limitations has been suggested (Laverick et al., 2017). Furthermore, a faunal transition has been reported at approximately 60 m and used as a division between an upper mesophotic subzone, a transition zone that includes shallow and mesophotic taxa, and the lower mesophotic subzone, characterized by taxa adapted to low-light environment (Kahng et al., 2019; Lesser et al., 2019, 2018). However, the fixed transition depth at 60 m fails to explicitly accommodate the environmental variation at specific locations (Laverick et al., 2017). Similarly, the lower mesophotic boundary is variable and defined by the deepest occurrence of light-dependent corals, which relates to the water quality at the locations and the associated light attenuation within the water column. Thus, the deepest records are found at locations with high optical water quality, suggesting that light availability, *i.e.* PAR (photosynthetically active radiation), represents one of the main factors defining MCEs' lower boundaries (Kahng et al., 2010). In this context, the diffuse light attenuation coefficient Kd_{PAR} is a parameter that characterizes the transparency of waters (Kirk, 2011) and hence, can be used to calculate optical depths of particular interest, such as the 10% and the 1% light level. These light levels are considered to be the midpoint and the bottom of the euphotic zone, respectively (Kirk, 2011). Thus, several recent studies proposed flexible depth limits to identify MCEs boundaries, defined by available light levels obtained from Kd_{PAR} for a given location ($z_{10\%}$, $z_{1\%}$, $z_{0.1\%}$), in combination with coral community data (Eyal et al., 2019; Kahng et al., 2010; Laverick et al., 2020; Lesser et al., 2018; Tamir et al., 2019). Moreover, a recent study provided a generalized light-driven model that can be used to predict mesophotic depth boundaries, through a combination of community-light relationships and underwater light field, defined by Kd_{PAR} values (Laverick et al., 2020). It also explains, why at some locations mesophotic species and communities have been recorded at depths as shallow as 10 m, as in these locations light attenuation within the water column is high.

On a global scale, studies of MCEs have been conducted mainly in the Atlantic region, Australia, the Red Sea, and Hawaii (Bongaerts et al., 2019; Eyal et al., 2021; Pyle and Copus, 2019). Of those, 57% have been conducted in the Caribbean since 1966 (Turner et al., 2017). Despite the increasing research efforts worldwide, many MCEs are still mostly unexplored, including those of the Eastern Tropical Pacific (ETP) (Baker et al., 2016). The latter is also related to the general assumption that MCEs are absent in the ETP, based on deep surveys in different locations within the ETP and due to the characteristically permanent shallow thermocline, with a commonly thin mixed layer located between 10 and 30 m (Fiedler and Lavín, 2017; Smith et al., 2017), that results in marked differences between shallow and mesophotic conditions due to declines in temperature and pH, as well as higher nutrient concentrations (Cortés, 2019). Reported coral reef communities of the ETP extend from Baja California Sur, Mexico, to the Gulf of Guayaquil in Ecuador and include the oceanic islands of Revillagigedo, Clipperton, Cocos, Galapagos, Malpelo, and the Easter Island (Glynn et al., 2017). These communities are exposed to mean sea surface temperatures ranging from 20 to 29 °C (Shea et al., 1992) and influenced by seasonal coastal upwelling due to intense winds bursts that prevail in the Gulfs of Tehuantepec, Papagayo, and Panama between November and April (Chapa-Balcorta et al., 2015; Kessler, 2006). The upwelling events affect water transparency and other oceanographic characteristics, such as temperature, salinity and pH, and transport nutrients from deeper areas to the sea surface, generating seasonal turbidity through algae blooms (García-Reyes and Largier, 2012).

Given the oceanographic characteristics of the ETP, light-dependent corals in coastal regions are limited to shallow waters, which is why to date it is commonly assumed that MCEs are absent in this region. However, recent evidence regarding the definition of MCEs, based on light availability, suggests that in locations with low light levels due to high light attenuation, MCEs could be present as the so-called “shallow-water turbid reefs” (Laverick et al., 2020). Thus, in the present study, we performed a systematic bibliographic review of coral communities within the ETP and subsequently, in combination with site-specific determinations of Kd_{PAR} and derived optical depths, identified the studies that can be considered MCEs-related research for this region. Furthermore, from the obtained database, we extracted coral community data and assessed the current MCEs research status in the ETP.

We used the optical depths ($z_{10\%}$, $z_{1\%}$, $z_{0.1\%}$) as markers of the mesophotic boundaries, based on the evidence provided by previous studies. For example, in the Red Sea $z_{10\%}$ lies at 33 m (Kd = 0.07 m^{-1}), matching the fauna transition at 30 m reported by Eyal et al. (2019). In general, in the clear waters, where most MCEs studies were carried out, $z_{10\%}$ is close to 30-40 m and thus matches the fixed depth of the upper boundary zone according to NOAA. Similarly, the depth of $z_{1\%}$ is usually consistent with the general fauna breakpoint at 60 m, though Laverick et al. (2020) considered $z_{0.1\%}$ as the lower limit of the mesophotic zone because of the maximum depths records of light-dependent corals in some places (Kahng et al., 2010; Laverick et al., 2020). Therefore these optical depths represent a useful first approach to identify depth ranges for the potential occurrence of MCEs in regions, where information regarding geomorphology, community descriptions, and mesophotic indicator species are scarce or absent.

Specifically, the goals of this review were to answer the following questions:

Primary question:

- What is the status of knowledge of MCEs in the ETP, considering mesophotic boundaries based on light availability?

Secondary questions:

1. What are the mean values of Kd_{PAR} within the ETP and do they vary spatially and/or seasonally?
2. What are the corresponding mesophotic optical depths ($z_{10\%}$, $z_{1\%}$, $z_{0.1\%}$)?
3. What are the main research foci in mesophotic studies in the ETP?
4. Are there depth- and/or location-specific differences in the coral community composition, depending on mesophotic depth boundaries (upper and lower mesophotic zone)?
5. Do the maximum depth records of light-dependent corals show a good correlation with location-specific water transparency (Kd_{PAR}) and the derived optical mesophotic boundaries?

2. Methods

We performed a systematic review, using a search strategy adapted from other studies of systematic research (Laverick et al., 2016; Turner et al., 2017). Two independent and complementary search strings were carried out, followed by a remote sensing analysis for each string (Fig. 1).

The systematic search of scientific literature was performed using different digital databases (Web of Science, Google Scholar, mesophotic.org and Scielo). In the first search string, we searched for reports of diffuse attenuation coefficient (Kd_{PAR}) or similar parameters (Secchi, euphotic depth values) for the ETP, to calculate the optical depths of mesophotic boundaries for the region. For the second search string, we searched for studies with information about benthic coral communities (corals and macroalgae) in the ETP (see Supplementary Material for detailed description).

Only studies in English and Spanish were included, in which the search keywords appeared in the title, abstract or keywords, and grey literature and unavailable full texts were excluded. The studies were screened in a two-stage process, according to the following eligibility criteria (see also Fig. 1):

1) the title and the abstract were related to:
   a. the subject in question
   b. the study area was located in the ETP

2) for the full text:
   a) Studies contained precise information to respond to the secondary questions: *in situ* values of Kd and euphotic depths for the first set of secondary questions (1 and 2), and species/genera composition and depth for the next set of secondary questions (3 and 4).
   b) Articles that contained relevant information (*e.g.*, reports of species and depths) from other references were replaced by the original sources.

After applying the eligibility criteria, the full-text documents were evaluated for data extraction and quality assessment. The information was organized in a spreadsheet by location, primary research topics (descriptive, taxonomy, review, natural and anthropogenic impacts, life history, structuring variables, and ecosystem function), following those described by Turner et al. (2017). The information on corals and macroalgae was classified by country, depth, and continental or oceanic locations. The species were clustered into four artificial groups: macroalgae, light-dependent corals, gorgonians corals, and non-light-dependent corals (mostly asymbiotic scleractinians, with a few reports of black and soft corals). Subsequently, they were categorized by occurrence in either the upper ($z_{10\%}$-$z_{1\%}$) or lower mesophotic zone ($z_{1\%}$-$z_{0.1\%}$), based on site-specific Kd_{PAR} and derived mesophotic optical boundaries, obtained as described below.

2.1. Remote sensing approach to define mesophotic boundaries, based on optical depths

To estimate the apparent optical properties of the ETP, we used time-averaged maps and monthly time series of Kd_{490} from the NASA

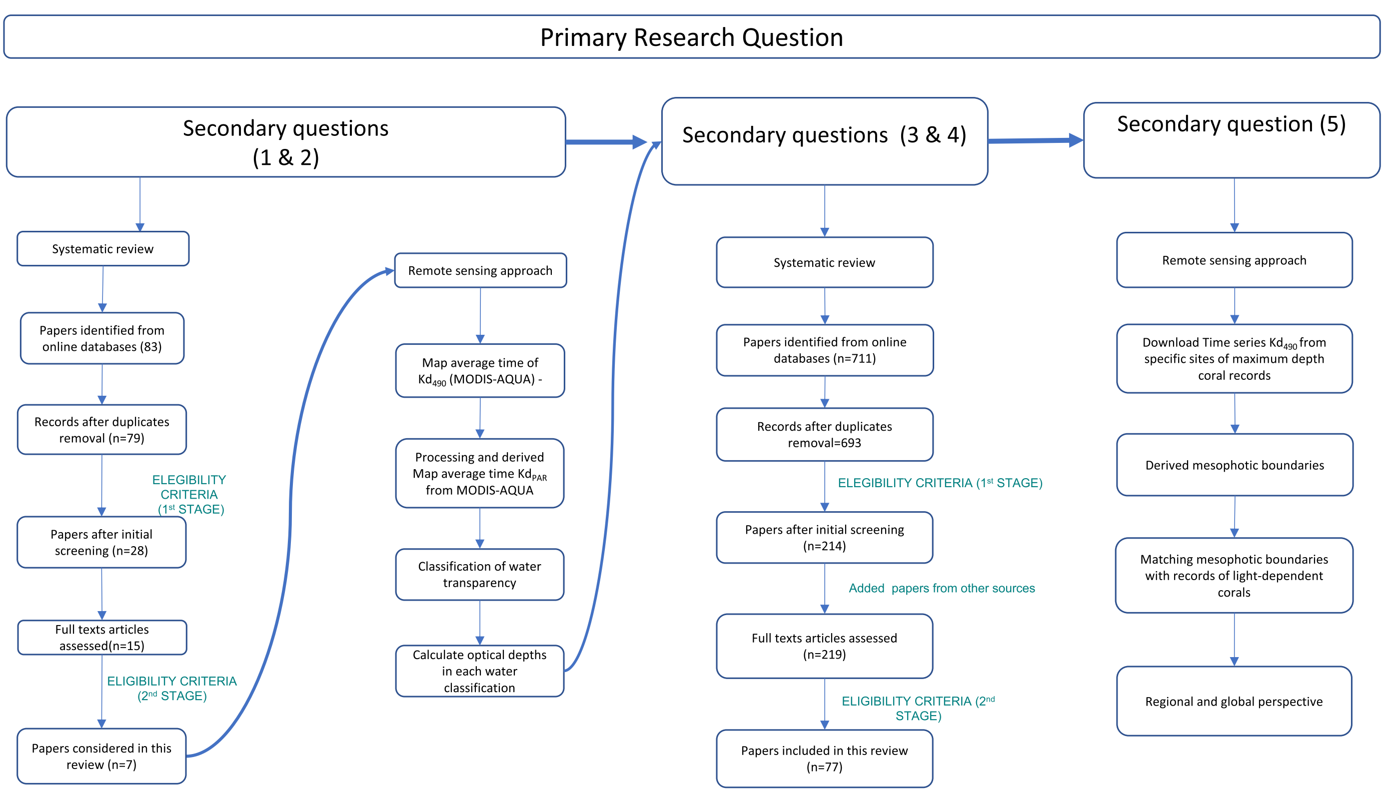

Fig. 1. Flowchart of the systematic bibliographic search and associated analyses.

platform Giovanni: Goddard Earth Sciences Data and Information Services Center (https://giovanni.gsfc.nasa.gov/). The Kd_{490} products of Giovanni were converted to Kd_{PAR}, using the following equation (Morel et al., 2007):

$$Kd_{PAR} = 0.0864 + 0.884\, Kd_{490} - 0.00137\, [Kd_{490}]^{-1}$$

Using the QGIS software (QGIS, 2021), a time average map of Kd_{PAR} (Jan 2018-Dec 2020) was employed to regionalize the water transparency in the ETP, which were categorized into five water types, based on Kd_{PAR} ranges, and were subsequently used to extract the respective regional benthic community data. Also, for each category or Kd_{PAR} interval (Kd_1-Kd_2), the depths of the upper and lower mesophotic light intervals were calculated, which for the purposes of this study were defined as $z_{10\%}$ to $z_{1\%}$ and $z_{1\%}$ to $z_{0.1\%}$, respectively:

$$Kd_{PAR}\ \text{interval} = (Kd_1 - Kd_2)$$

$$\text{Upper mesophotic light interval} = (z_{10\%} - z_{1\%})$$

$$z_{10\%} = 2.3/Kd2$$

$$z_{1\%} = \frac{4.6}{(Kd1 + Kd2)/2}$$

$$\text{Lower mesophotic light interval} = ((z_{1\%} + 1) - z_{0.1\%})$$

$$z_{0.1\%} = 6.9/Kd1$$

Furthermore, based on the available maximum depth records of light-dependent corals for specific continental and oceanic locations, found in the bibliographic search, the Kd_{490} time series (Aqua-MODIS (https://giovanni.gsfc.nasa.gov/) for those locations were downloaded (Jan 2018-Dec 2020) to compare the Kd_{PAR}-derived lower mesophotic boundary with those records. Here, continental locations are considered those on the continental shelf, including islands separated from the shelf by shallow and narrow arms of the sea. Oceanic locations are represented by oceanic islands that arise from the bottom of the sea as a result of the volcanic activity of the seabed, without connections to continental landmasses, and generally located far from the continent and separated by large depths (Fernández-Palacios and Morici, 2004).

The Kd_{490} time series were transformed to Kd_{PAR} as described above, and the values were averaged for each location to obtain the corresponding site-specific optical depths ($z_{10\%}$, $z_{1\%}$, $z_{0.1\%}$), according to Kirk (2011). In addition, to verify the accuracy of the satellite-derived data, we compared reported *in situ* Kd_{PAR} or Kd_{490} values with those obtained from the MODIS-AQUA satellite data for the same location and, if available, the same date.

2.2. Statistical analysis

Using R software we performed a non-parametric Kruskal-Wallis test to determine significant differences in Kd_{PAR} between the locations in the ETP, which was then followed by pairwise comparisons using Wilcoxon rank sum test. Furthermore, using STATISTICA 7.0 we evaluated the relationship between deepest coral records and light attenuation (Kd_{PAR}). For this, the parameters were logarithmically transformed to normalize their distribution and subsequently fitted to an exponential function.

3. Results

3.1. The state of MCEs research in the ETP

Seventy-seven MCEs-related papers were compiled in this study, covering the region of Loreto, in Baja California Sur, Mexico, to Easter Island in Chile. The earliest study was published in 1975, with a considerable increase in research efforts since 2000 (Fig. 2). Of all available studies, 49% were carried out in the continental zone, while 61% were performed in oceanic regions, with eight studies covering both continental and oceanic locations.

Some of the studies reviewed in this work were carried out in two or more countries in the ETP, most of them in Costa Rica (20 papers), followed by Mexico and Panama (Fig. 3A). In remote locations, like Easter and Clipperton Island, only a few research studies are available (five or six studies).

Regarding the research focus of studies on MCEs in the ETP, ecosystem functions have been studied in seven countries, while reviews are available for most countries. Most MCEs-related studies in the ETP available for continental locations focused on taxonomy, reviews, and natural and anthropogenic impacts, with 34%, 15%, and 15%, respectively. Meanwhile, the research foci at oceanic locations were mostly reviews (34%), as well as ecosystem functions (21%) and descriptive ecology (16%), while only 4% of the studies were focused on biotic variables that structure the community along a depth gradient (Fig. 3B).

3.2. Spatial Kd_{PAR} variability in the ETP and the implications for mesophotic boundaries

In this review, we identified 51 locations along ETP, where research on mesophotic environments have been carried out, mostly concentrated in turbid continental waters (Kd_{PAR} = 0.1-0.2 m^{-1}) in the north of Mexico, Costa Rica, and Panama (Fig. 4).

The water transparency was found to be highly variable within the ETP, being highest in the southern, oceanic region of the ETP, close to Easter Island ($Kd_{PAR} < 0.05\ m^{-1}$), and lowest along the coasts of Peru and Chile ($Kd_{PAR} > 0.2\ m^{-1}$) and some areas of the Gulfs of California, Panama, Papagayo, and Tehuantepec (Fig. 4). In the majority of the oceanic region, where islands like Clipperton, Cocos, and Revillagigedo are located, the Kd_{PAR} presents values between 0.05 and 0.1 m^{-1}. On the other hand, most of the continental coastal zone within the ETP, as well as the Galapagos and Malpelo Islands present mean Kd_{PAR} values between 0.10 and 0.2 m^{-1} (Fig. 4).

Reports of *in situ* Kd measurements within the ETP are scarce, limited to Mexico, Panama, and Easter Island. However, their comparison with Kd values, obtained from satellite data, showed that there was general consistency between the two approaches (Table S1).

When comparing the Kd_{PAR} values of locations in the ETP, for which deepest records of light-dependent corals are available (see Fig. 4), significant differences between oceanic islands and continental areas were found (Fig. S1). Thus, considering the variability in water transparency within the ETP, we divided the region of the ETP in five different categories of water types, based on their Kd_{PAR} range (Table 1). Here, the

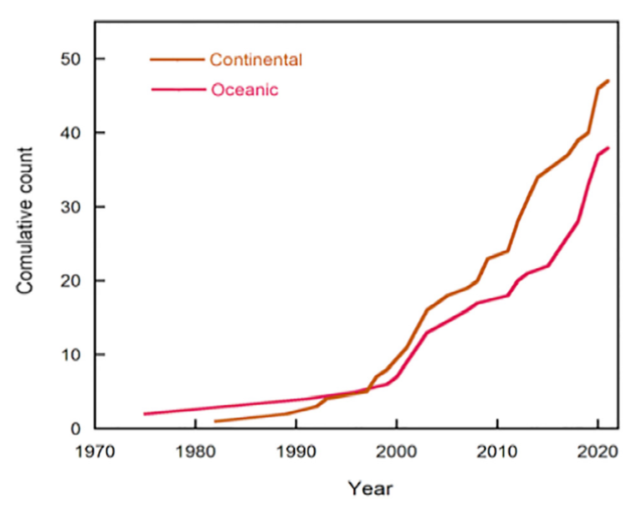

Fig. 2. Cumulative number of scientific publications over time, divided in studies at continental and oceanic locations.

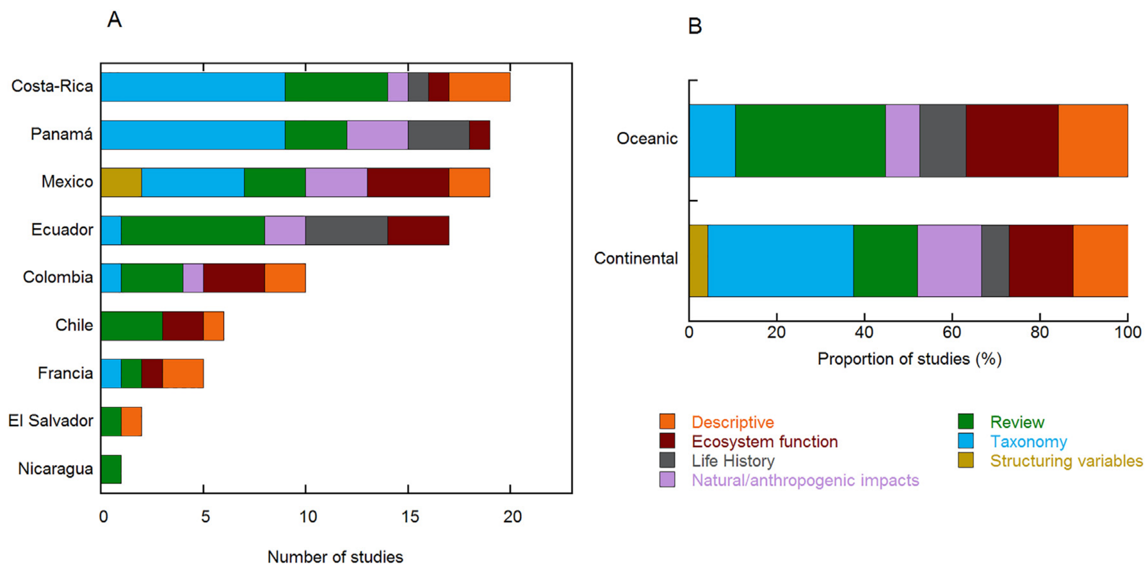

Fig. 3. Overview of MCEs-related studies in the ETP. Number of studies with specific research foci for (A) different countries of the ETP and (B) as relative proportion for oceanic and continental locations.

oceanic region, where Easter Island is located, represents the highest water transparency (Hyperclear), followed by the oceanic region of the ETP (Clear 1 and 2). In contrast, the continental regions exhibit lower water transparency, with the highest Kd_{PAR} values registered for coastal regions under the influence of seasonal upwelling and the derived optical depths for these regions ($Kd_{PAR} > 0.1$ m^{-1}; Table 1) indicate the beginning of the mesophotic zone ($z_{10\%}$) at depths as shallow as 13-15 m.

The found spatial variability in seawater apparent optical properties within the ETP seemed to be the result of substantial differences at a seasonal scale that were more pronounced at continental locations, which experienced periods of high values ($Kd_{PAR} > 0.1$ m^{-1}) from November to May, corresponding to the coastal upwelling season, and low values (Kd_{PAR} ~ 0.1 m^{-1}) between June and October (Table S2; Fig. S2).

3.3. Benthic community composition in the upper and lower mesophotic zone

Based on the definition of mesophotic depth boundaries, derived from site-specific water transparency (see Table 1), we identified 51 locations within the ETP, where research on mesophotic environments has been carried out (Fig. 4). In these studies, a total of 138 species were recorded in mesophotic environments of the ETP, 21 of them

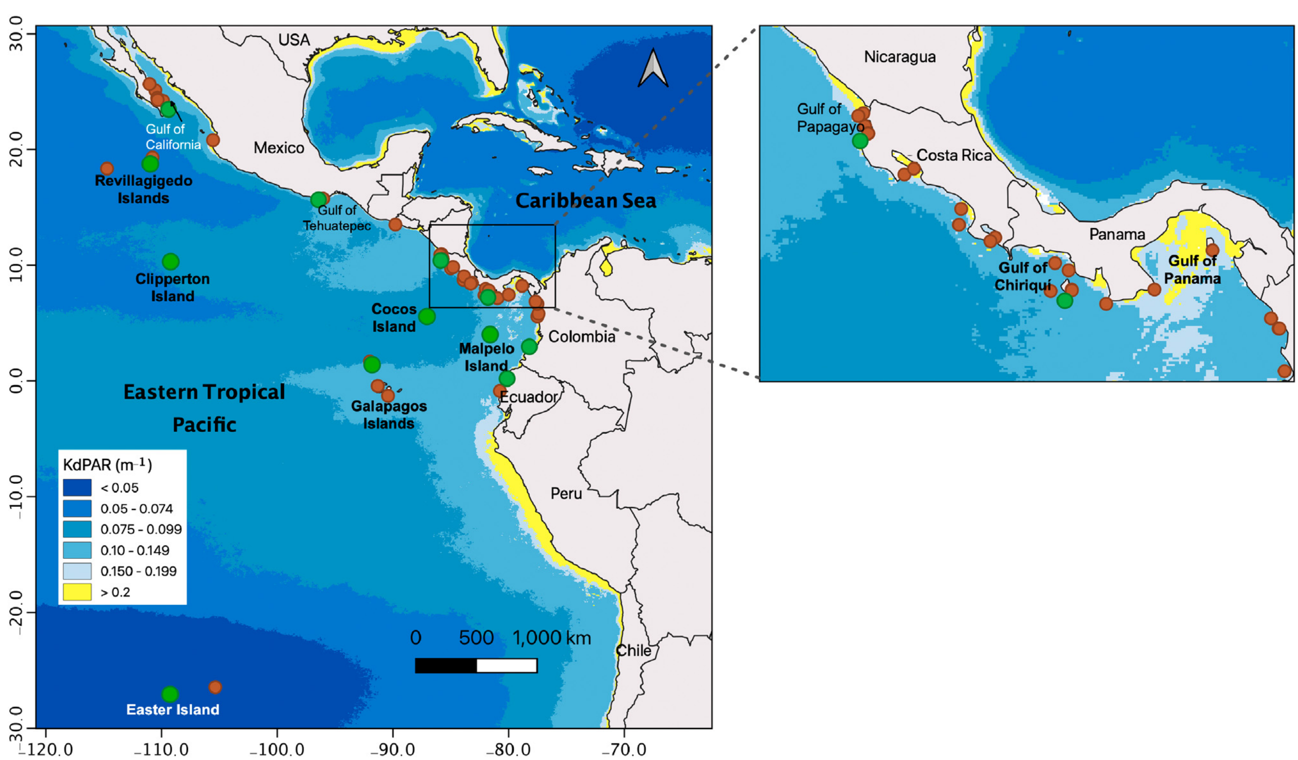

Fig. 4. Spatial variability of satellite-derived Kd_{PAR} in the ETP, shown in the time average map of Kd_{PAR} downwelling irradiance (Jan 2018 to Dec 2020) (monthly 4 km resolution; MODIS-Aqua L3m_Kd490 v2018). Locations with MCEs-related studies are indicated by brown circles and those where deepest light-dependent corals records are available by green circles.

Table 1
Water classification in the ETP, according to Kd_{PAR} ranges (see Fig. 4) and the derived mesophotic boundaries, based on optical depths.

Water type	Locations	Interval Kd_{PAR} (m^{-1})	Upper mesophotic zone $z_{10\%}$-$z_{1\%}$ (m)	Lower mesophotic zone ($z_{1\%}$ + 1)-$z_{0.1\%}$ (m)
Hyperclear	Easter and Salas y Gomez Is.	0.03-0.05	45-115	116-230
Clear 1	Revillagigedo Is.	0.05–0.074	30-74	75-140
Clear 2	Clipperton and Cocos Is.	0.075-0.099	25-50	51-90
Turbid 1	Malpelo and Galapagos Is. and continental locations	0.10 - 0.149	15-35	36-70
Turbid 2	Continental locations	0.15 - 0.199	13-25	26-45

were only identified at the genera level: 19 taxa of macroalgae, 28 species of light-dependent corals, 63 species of gorgonians, and 28 species of non-light-dependent corals (scleractinians corals, black corals, soft corals). In general, the species richness in the here specified upper mesophotic zone was higher and decreased in the lower mesophotic zone in both continental and oceanic locations (Fig. 5A). Also, the number of macroalgal genera in the upper mesophotic zone was similar in the two types of locations, while the species richness of light-dependent corals was higher in oceanic, compared to the continental locations. In contrast, gorgonians showed a higher number (4×) of species in continental locations. Likewise, in the lower mesophotic zone, more gorgonian species were reported for continental locations, while light-dependent corals were absent, with available records only for Clipperton Island represented in the water type Clear 2 (Fig. 5).

There was a notable difference in species richness among the different water types. Regions with higher light attenuation (Turbid 1 and 2), such as the continental areas and Galapagos and Malpelo Island, present a higher species richness, while for the more remote islands with clearer waters ($Kd_{PAR} < 0.1$ m^{-1}), the species richness was considerably lower, especially in Revillagigedo (Clear 1) and Easter Island (Hyperclear) (Fig. 5B).

In general our revision resulted in reports of eight genera of light-dependent corals and 15 macroalgal genera in the upper mesophotic zone, while in the lower mesophotic zone, four genera of macroalgae have been registered, and only at Clipperton Island, light-dependent corals of the genus *Pavona* have been reported (Table S3).

3.4. Coral depth records and mesophotic boundaries

The importance of light availability in determining the lower limits of the mesophotic zone was shown by the strong exponential relationship between Kd_{PAR} and reported deepest coral records found in the present study and those reported previously for other regions by Kahng et al. (2010) (Fig. 6).

Similarly, the comparison of the mesophotic depth boundaries ($z_{10\%}$, $z_{1\%}$, $z_{0.1\%}$), derived from the mean Kd_{PAR} (Jan 2018-Dec 2020) at the different locations, with the deepest records of light-dependent corals also showed that as light attenuation decreased, the reported depth distribution of light-dependent corals increased in both continental locations and oceanic islands (Fig. 7A). The maximum depth for light-dependent coral distribution on the continental shelf has been reported between 15 and 40 m, with the deepest record for Cabo Pulmo, located in Baja California Sur, Mexico. This deepest record, together with those reported for Culebra Bay in Costa Rica and Puerto Angel, Mexico (Perez-Castro, pers. obs.), was consistent with $z_{1\%}$ calculated with the site-specific Kd_{PAR}. This pattern was also found for the oceanic locations Wenman Island in Galapagos, and Easter Island (Fig. 7A). The latter location registered the deepest light-dependent coral occurrence of the Eastern Pacific at 120 m, which agrees with their extremely low Kd_{PAR} values (Fig. 2, Table 1). The second deepest record was found at 80 m at Clipperton Island, but in this case, this depth corresponded to an optical depth of ~$z_{0.1\%}$. On the other hand, the deepest occurrence of light-dependent corals for Socorro, Malpelo, and Gorgona Islands were recorded at depths that are closer to $z_{10\%}$.

When comparing our findings with data reported for tropical and subtropical regions, it seems that in contrast to the MCEs in the ETP, in those regions light-dependent corals are able to extend to depths close to $z_{0.1\%}$, with some exceptions, *e.g.* Bermuda, Curacao and West Florida Shelf, were their bathymetric light limit is closer to those found in the ETP (Fig. 7B).

4. Discussion

4.1. The current state of MCEs research in the ETP

Studies on MCEs have increased considerably over the last decade, from 200 to more than 600 studies, though these include only a few studies in the ETP (Bongaerts et al., 2019). However, considering the theoretical mesophotic boundaries based on light availability, as defined

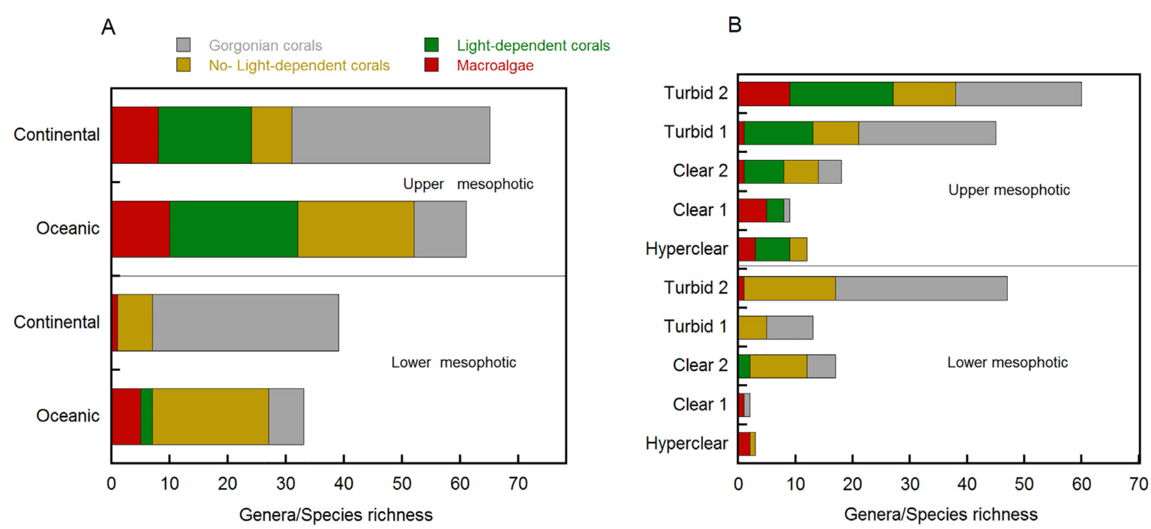

Fig. 5. Species richness of different benthic groups in the upper and lower mesophotic zone at A) continental and oceanic locations, and B) in different water types (see Table 1).

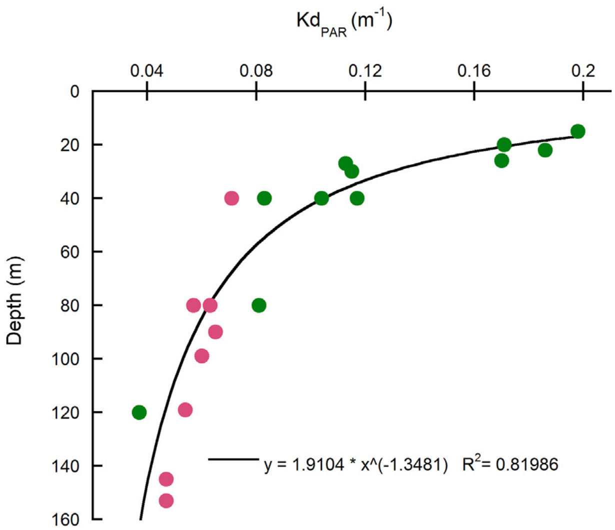

Fig. 6. Exponential relationship between the maximum depth distribution of light-dependent corals with light attenuation coefficient (Kd_{PAR}) (green circles- present study, pink circles- data reported in Kahng et al. (2010), including different locations in the Caribbean, the Red Sea, and Hawaii).

in the present study, we were able to account for a total of 77 MCEs-related studies in the ETP. Nevertheless, this region is greatly understudied, compared to the Tropical Western Atlantic and the Indo-Pacific, which account for 444 and 245 mesophotic studies, respectively (Eyal et al., 2021). This difference could be related to the general assumption that MCEs should be absent in most of the ETP, based on NOAA's definition of a fixed depth of the upper mesophotic boundary, since the oceanographic conditions of the ETP are limiting the development of light-dependent coral communities below 30 m in most locations. As a result, less than ten studies from the ETP contain the term "mesophotic" to date. Likewise, the relatively few studies in the ETP could be associated to the limited research infrastructure in the mostly developing countries of this region. From those, 33 studies have been conducted in continental areas, while 26 have been carried out at oceanic locations. This difference might be related to the lack of resources and potential difficulties regarding access to the remote islands.

Moreover, our revision shows that most of MCEs research in the ETP has been so far focused on taxonomy and reviews, while studies on other topics, which are well-studied in other regions, such as community structure, molecular ecology (Bongaerts et al., 2019), are extremely scarce.

4.2. Spatial Kd_{PAR} variability in the ETP and the implications for mesophotic boundaries

The ETP presents a wide range of water transparency (Kd_{PAR}) and thus, this region represents an excellent case study to assess the accurateness of using mesophotic boundaries, based on light availability, and the presence of light-dependent corals.

The oceanic region is the most likely place where MCEs could develop in the ETP, falling into the water type categories Hyperclear, Clear 1, and Clear 2. These three water types present Kd_{PAR} values within the range of most of the locations at which MCEs studies have been carried out (0.045 to 0.08 m^{-1}) (Kahng et al., 2010; Laverick et al., 2017; Lesser et al., 2018; Tamir et al., 2019). However, our work shows that at locations within the ETP that are influenced by seasonal upwelling events and thus exhibit higher mean Kd_{PAR} values (0.1-0.2 m^{-1}), the upper boundary of the mesophotic zone is located at shallow depths (13-15 m), with the deepest records of light-dependent corals reported between the optical depths of $z_{10\%}$ and $z_{0.1\%}$. This agrees with the suggestion of Laverick et al. (2020) of considering turbid coral reefs, such as occurring at the coastal regions of the ETP, as MCEs.

Based on the present study, at some locations in the ETP corals can be referred to as mesophotic when occurring at depths just below 10 m, due to the oceanographic conditions in the region (seasonal upwelling events) that make it possible to find relatively shallow refugia in this region. Smith et al. (2017) distinguished in the ETP some potential zones for depth-refugia, mostly at oceanic islands, including some places in continental areas, like the Gulf of Chiriquí, where a depth refugia of *Millepora intricata* was found at 25 m.

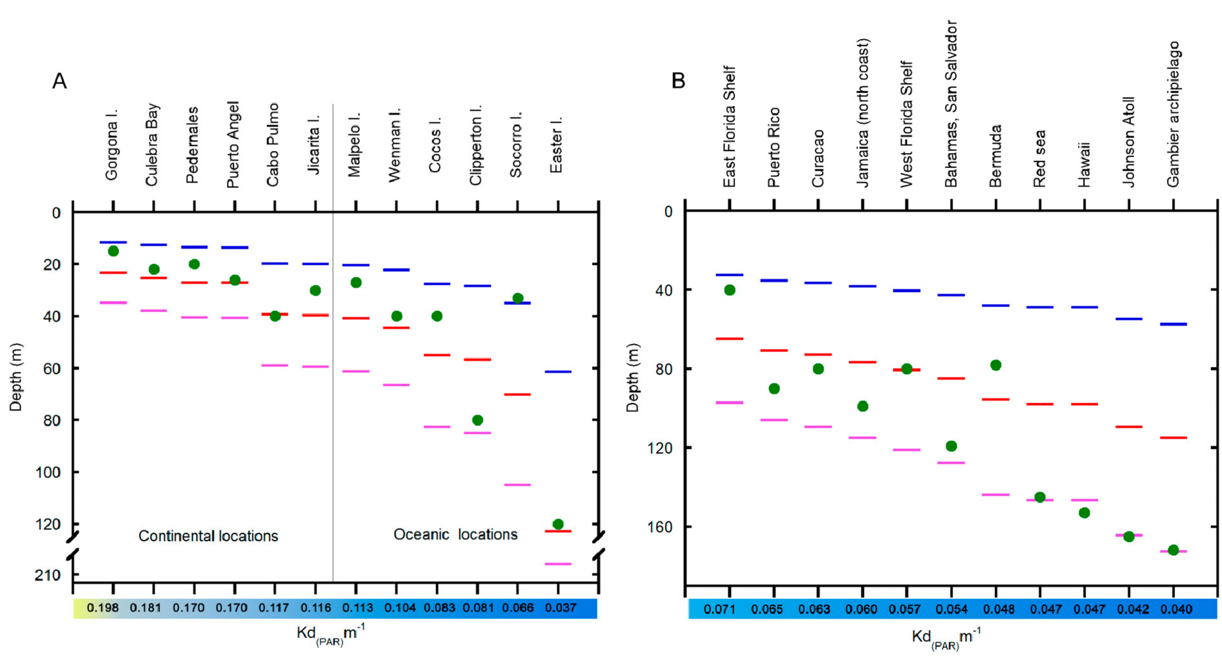

Fig. 7. A) Theoretical mesophotic light boundaries derived from Kd_{PAR} ($z_{10\%}$ blue line, $z_{1\%}$ red line, $z_{0.1\%}$ purple line) and the respective maximum depth records of light-dependent corals (green circles) in different location of the ETP, and B) Kd_{PAR} values and associated light-dependent coral depth records reported by Kahng et al. (2010). Mesophotic boundaries at Johnson Atoll (coral records from Kahng et al., 2010) and Gambier Archipelago (Rouzé et al., 2021) were derived from Kd_{PAR} values, obtained from MODIS-AQUA.

Even using the most common Kd_{PAR} range for MCEs, the difference in the Kd_{PAR} values of those clear waters is large, resulting in enormous differences in the depth of the lower mesophotic boundaries. For example, the deepest record of light-dependent corals is currently at 172 m at Gambier archipelago (Rouzé et al., 2021), which present a $Kd_{PAR} = 0.04$ m^{-1}, while in Clipperton Island, with a Kd_{PAR} of 0.081 m^{-1}, the maximum coral record is at 80 m, but in both cases this depth represents the $z_{0.1\%}$ (Fig. 7). Similarly, when comparing Easter Island, a location with hyperclear waters ($Kd_{PAR} = 0.037$ m^{-1}), with Galapagos or Cabo Pulmo ($Kd_{PAR} \sim 0.11$ m^{-1}) or with Curacao in the Caribbean, the deepest records of light-dependent corals correspond to the same optical depth ($z_{1\%}$).

Considering that the maximum depth of light-dependent corals is the conditional factor of the lower limit of MCEs, in the ETP, these ecosystems are limited to the upper mesophotic zone ($z_{10\%}$ -$z_{1\%}$), unlike to other tropical regions where they can be found down to the $z_{0.1\%}$ light level. Our results suggest that these notable differences may be due to the influence of seasonal upwelling that causes significant shifts in light availability and hence, associated optical depths (Table S2), likely limiting light-dependent corals to shallower depths (above $z_{1\%}$), in order to avoid light limitation during upwelling events. Moreover, seasonal upwelling is accompanied by low temperatures and low pH, variables that can affect the survival and growth of scleractinians corals.

Also, even though there exists a strong correlation between maximum coral records and light attenuation (Fig. 6), in some places corals can be limited to depths closer to $z_{10\%}$, due to the influence of other environmental factors, such as a seasonally changing thermocline and internal waves, as reported in Revillagigedo and Cocos Islands (Carter et al., 2020). The generally shallow thermocline, which at Cocos Island lies at 50 m depth, has been reported to produce a pronounced difference between benthic communities above and below the thermocline, possibly as a result of drastic changes in light availability due to the accumulation of particulate matter in this layer (Cortés, 2019).

4.3. Benthic community composition

The transition from shallow to mesophotic reefs does not occur at a specific depth, but rather depends on location-specific factors, such as water clarity, temperature, substrate type, water currents, geomorphology, among others (Costa et al., 2015). However, light is the primary factor in controlling the bathymetric structure of photosynthetic communities (Lesser et al., 2009; Tamir et al., 2019), as also shown here by the strong correlation between Kd_{PAR} and deepest light-dependent coral records (Fig. 6).

The species richness compiled in this systematic review reflects an acceptable notion of the components of MCEs. The species composition of mesophotic environments in the ETP presents differences between the upper mesophotic and the lower mesophotic zone, with a general reduction in the species richness of autotrophs in the lower mesophotic zone. In the continental locations and some oceanic islands with upwelling events, light-dependent corals can be found between 15 m and 40 m corresponding to the upper mesophotic light interval ($z_{10\%}$-$z_{1\%}$), while the lower mesophotic light interval ($z_{1\%}$-$z_{0.1\%}$) is dominated by crustose coralline algae (CCA), gorgonians and non-light-dependent corals. The oceanic and continental locations present a similar community composition in the upper mesophotic zone, while in the lower mesophotic there are more macroalgal species and non-light-dependent corals in oceanic locations. Furthermore, only at Clipperton Island light-dependent corals of the genera *Pavona* were found along the entire mesophotic zone down to ~$z_{0.1\%}$. The species richness of the MCEs was considerably higher in turbid waters, in comparison with clear waters, where it was 27% lower in both upper mesophotic and lower mesophotic zones, though this considerable reduction may be related to the lower sampling effort in the most remote areas of the ETP.

4.4. Advantages and disadvantages of Kd_{PAR}-derived satellite data

To improve, the estimations of the depth of the euphotic zone ($z_{10\%}$ and $z_{1\%}$), semi-analytical models have been developed and improved (Lee et al., 2007; Son and Wang, 2015). These models have been applied in different regions of the world and suggest an average percentage error in a linear scale of 13% (Lee et al., 2007). Such small errors suggest a closure between the two independent measurements and determinations and indirectly validate the semi-analytical derivation of inherent optical properties (IOPs) from remote sensing reflectance (Rrs) (Lee et al., 2007). However, to ensure its reliable applications to a broad range of water types, more tests and validations with a wider dynamic range are certainly desired (Lee et al., 2007). It is important to mention that $z_{1\%}$ (or $z_{10\%}$) measurements with IOPs from Rrs is much more rigorously than Secchi depth or even those derived from chlorophyll-a concentrations. Though, specific local conditions, such as the above-mentioned shallow thermocline for Cocos Island and the associated accumulation of particulate matter, might cause a change in Kd_{PAR}, not reflected in the remote-sensing-derived values.

The derived IOPs from MODIS-Aqua satellite could present a gap in a specific place for some months, especially when the selected area is close to the minimum resolution (4 km). This was one of the reasons that we used an average of three years of Kd values for a specify location. Though, the scarce data available regarding the apparent *in situ* optical properties of the water column and the underwater light environment in the ETP showed a good consistency with our estimations using IOPs for the same place and date from MODIS-Aqua (Table S1).

5. Conclusions

Studies on mesophotic ecosystems are very scarce in the ETP, compared to other regions of the world. The available information indicates that the species richness is higher at the continental shelf, compared to oceanic islands, but in both regions, it is higher in the upper than the lower mesophotic zone. The MCEs are generally located in the upper mesophotic zone (down to $z_{1\%}$), while CCA, gorgonians, and other non-light-dependent corals dominate the lower mesophotic zone. This study covers an important gap of knowledge of MCEs around the world (see Eyal et al., 2021). However, the disproportion of studies towards those focused on taxonomy highlights the need for future studies focused on structuring environmental variables, molecular ecology, anthropogenic impacts, and natural resource management, as suggested by Turner et al. (2019, 2017). The latter is especially important in continental areas, where proximity to human activities directly impacts these ecosystems. As our study shows, MCEs are relatively shallow in the ETP, which may favor future investigations in the region and further the global understanding of these important ecosystems.

Our approach of using mesophotic boundaries derived from apparent optical properties of the water column (Kd_{PAR}), shows clearly that they can vary considerably at a spatial scale. This evidence, together with the reported maximum depth distributions of light-dependent corals, supports the suggestion put forward recently in several studies regarding the need for a definition of MCEs based on regional/local seawater optical properties, in combination with coral community data, instead of using a fixed depth limit (Eyal et al., 2019; Kahng et al., 2010; Laverick et al., 2020; Lesser et al., 2018; Tamir et al., 2019). In addition, we found an important temporal variability that has not yet been considered in the mesophotic boundaries, but was suggested by Laverick et al. (2020) as an important element for obtaining more accurate models.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150576.

References

Baker, E.K., Puglise, K.A., Harris, P.T., 2016. Mesophotic coral ecosystems. A lifeboat for coral reefs? The United Nations Environment Programme and GRID-Arendal, pp. 1–100

Bongaerts, P., Ridgway, T., Sampayo, E.M., Hoegh-Guldberg, O., 2010. Assessing the "deep reef refugia" hypothesis: focus on Caribbean reefs. Coral Reefs 29, 1–19. https://doi.org/10.1007/s00338-009-0581-x.

Bongaerts, P., Perez-Rosales, G., Radice, V.Z., Eyal, G., Gori, A., Gress, E., Hammerman, N.M., Hernandez-Agreda, A., Laverick, J., Muir, P., Pinheiro, H., Pyle, R.L., Rocha, L., Turner, J.A., Booker, R., 2019. Mesophotic.org: a repository for scientific information on mesophotic ecosystems. Background & summary. Database : The Journal of Biological Databases and Curation https://doi.org/10.1093/database/baz140.

Carter, A.L., Wilson, A.M.W., Bello, M., Hoyos-Padilla, E.M., Inall, M.E., Ketchum, J.T., Schurer, A., Tudhope, A.W., 2020. Assessing opportunities to support coral reef climate change refugia in MPAs: a case study at the Revillagigedo Archipelago. Mar. Policy 112. https://doi.org/10.1016/j.marpol.2019.103769.

Chapa-Balcorta, C., Hernández-Ayón, M., Durazo-Arvizu, R., Siqueiros-Valencia, A., 2015. Flujos de carbono en el golfo de tehuantepec posterior a eventos tehuanos. Estado Actual Del Conocimiento Del Ciclo Del Carbono y Sus Interacciones En México: Síntesis a. 2015, pp. 501–507.

Cortés, J., 2019. Isla del Coco, Costa Rica, Eastern Tropical Pacific, pp. 465–475 https://doi.org/10.1007/978-3-319-92735-0_26.

Costa, B., Kendall, M.S., Parrish, F.A., Rooney, J., Boland, R.C., Chow, M., Lecky, J., Montgomery, A., Spalding, H., 2015. Identifying suitable locations for mesophotic hard corals offshore of Maui, Hawai'i. PLoS ONE 10, 1–24. https://doi.org/10.1371/journal.pone.0130285.

Eyal, G., Tamir, R., Kramer, N., Eyal-Shaham, L., Loya, Y., 2019. The Red Sea: Israel, pp. 199–214 https://doi.org/10.1007/978-3-319-92735-0_11.

Eyal, G., Laverick, J.H., Bongaerts, P., Levy, O., Pandolfi, J.M., 2021. Mesophotic coral ecosystems of the great barrier reef are understudied and underexplored. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.622856.

Fernández-Palacios, J.M., Morici, C., 2004. Island ecology. Ecología Insular/Island Ecology. Asociación Española de Ecología Terrestre-Cabildo Insular de La Palma, Madrid.

Fiedler, P.C., Lavín, M.F., 2017. Oceanographic conditions of the eastern 3 tropical Pacific. Coral Reefs of the Eastern Tropical Pacific, Coral Reefs of the World. 8. https://doi.org/10.1007/978-94-017-7499-4_3.

García-Reyes, M., Largier, J.L., 2012. Seasonality of coastal upwelling off central and northern California: new insights, including temporal and spatial variability. J. Geophys. Res. Oceans 117. https://doi.org/10.1029/2011JC007629.

Glynn, P.W., 1996. Coral reef bleaching: facts, hypotheses and implications. Glob. Chang. Biol. 2, 495–509.

Glynn, P.W., Alvarado, J.J., Banks, S., Cortés, J., Feingold, J.S., Jiménez, C., Maragos, J.E., Martínez, P., Maté, J.L., Moanga, D.A., Navarrete, S., Reyes-bonilla, H., Riegl, B., Rivera, F., Vargas-ángel, B., Wieters, E.A., Zapata, F.A., 2017. Eastern Pacific coral reef provinces, coral community structure and composition: an overview. In: Glynn, P., Manzello, D., Enochs, I. (Eds.), Coral Reefs of the Eastern Tropical Pacific. Coral Reefs of the World. Springer, Dordrecht, pp. 107–176 https://doi.org/10.1007/978-94-017-7499-4.

Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas, J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., van Nes, E.H., Scheffer, M., 2017. Coral reefs in the anthropocene. Nature https://doi.org/10.1038/nature22901.

Kahng, S.E., Garcia-Sais, J.R., Spalding, H.L., Brokovich, E., Wagner, D., Weil, E., Hinderstein, L., Toonen, R.J., 2010. Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29, 255–275. https://doi.org/10.1007/s00338-010-0593-6.

Kahng, S.E., Akkaynak, D., Shlesinger, T., Hochberg, E.J., Wiedenmann, J., Tamir, R., Tchernov, D., 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral. Ecosystems, 801–828 https://doi.org/10.1007/978-3-319-92735-0_42.

Kessler, W.S., 2006. The circulation of the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 181–217. https://doi.org/10.1016/j.pocean.2006.03.009.

Kirk, J.T.O., 2011. Light and Photosynthesis in Aquatic Ecosystems. third edition. Cambridge University Press, New York, New York, USA.

Laverick, J.H., Dominic, A., Andradi-Brown, D.A., Exton, D.A., Bongaerts, P., Bridge, T.C.L., Lesser, M.P., Pyle, R.L., Slattery, M., Wagner, D., Rogers, A.D., 2016. To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? Environ. Evid. 5, 16. https://doi.org/10.1186/s13750-016-0068-5.

Laverick, J.H., Andradi-Brown, D.A., Rogers, A.D., 2017. Using light-dependent scleractinia to define the upper boundary of mesophotic coral ecosystems on the reefs of Utila, Honduras. PLoS ONE 12, 8–17. https://doi.org/10.1371/journal.pone.0183075.

Laverick, J.H., Tamir, R., Eyal, G., Loya, Y., 2020. A generalized light-driven model of community transitions along coral reef depth gradients. Glob. Ecol. Biogeogr. 29, 1554–1564. https://doi.org/10.1111/geb.13140.

Lee, Z.P., Weidemann, A., Kindle, J., Arnone, R., Carder, K.L., Davis, C., 2007. Euphotic zone depth: its derivation and implication to ocean-color remote sensing. J. Geophys. Res. Oceans 112. https://doi.org/10.1029/2006JC003802.

Lesser, M.P., Slattery, M., Leichter, J.J., 2009. Ecology of mesophotic coral reefs. J. Exp. Mar. Biol. Ecol. 375, 1–8. https://doi.org/10.1016/j.jembe.2009.05.009.

Lesser, M.P., Slattery, M., Mobley, C.D., 2018. Biodiversity and functional ecology of mesophotic coral reefs. Annu. Rev. Ecol. Evol. Syst. 49–71.

Lesser, M.P., Slattery, M., Laverick, J.H., Macartney, K.J., Bridge, T.C., 2019. Global community breaks at 60 m on mesophotic coral reefs. Glob. Ecol. Biogeogr. 28, 1403–1416. https://doi.org/10.1111/geb.12940.

Morel, A., Gentili, B., Claustre, H., Babin, M., Bricaud, A., Ras, J., Tièche, F., 2007. Optical properties of the "clearest" natural waters. Limnol. Oceanogr. 52, 217–229. https://doi.org/10.4319/lo.2007.52.1.0217.

Puglise, K.A., Hinderstein, L., Marr, J.C.A., Dowgiallo, M.J., Martinez, F.A., 2009. Mesophotic Coral Ecosystems Research Strategy: International Workshop to Prioritize Research and Management Needs for MesophotIc Coral Ecosystems. NOAA National Centers for Coastal Ocean Science, p. 24.

Pyle, R.L., Copus, J.M., 2019. Mesophotic coral ecosystems: introduction and overview. Mesophotic Coral Ecosystems. Springer, Cham, pp. 3–27.

QGIS, 2021. QGIS Geographic Information System. QGIS Association. http://www.qgis.org.

Rouzé, H., Galand, P.E., Medina, M., Bongaerts, P., Pichon, M., Pérez-Rosales, G., Torda, G., Moya, A., Bardout, G., Périé-Bardout, E., Marivint, E., Lagarrigue, G., Leblond, J., Gazzola, F., Pujolle, S., Mollon, N., Mittau, A., Fauchet, J., Paulme, N., Pete, R., Peyrusse, K., Ferucci, A., Magnan, A., Horlaville, M., Breton, C., Gouin, M., Markocic, T., Jubert, I., Herrmann, P., Raina, J.B., Hédouin, L., 2021. Symbiotic associations of the deepest recorded photosynthetic scleractinian coral (172 m depth). ISME J. 15, 1564–1568. https://doi.org/10.1038/s41396-020-00857-y.

Shea, D.J., Trenberth, K.E., Reynolds, R.W., 1992. A global Monthly Sea surface temperature climatology. J. Clim. 5. https://doi.org/10.1175/1520-0442(1992)005<0987:AGMSST>2.0.CO;2.

Smith, T.B., Maté, J.L., Gyory, J., 2017. Thermal refuges and refugia for stony corals in the eastern tropical Pacific. In: Glynn, P.W., Manzello, D.P., Enochs, I.C. (Eds.), Coral Reefs of the Eastern Tropical Pacific. Coral Reefs of the World. Springer, Dordrecht, pp. 501–515 https://doi.org/10.1007/978-94-017-7499-4.

Son, S.H., Wang, M., 2015. Diffuse attenuation coefficient of the photosynthetically available radiation Kd(PAR) for global open ocean and coastal waters. Remote Sens. Environ. 159, 250–258. https://doi.org/10.1016/j.rse.2014.12.011.

Spalding, M.D., Brown, B.E., 2015. Warm-water coral reefs and climate change. Science https://doi.org/10.1126/science.aad0349.

Tamir, R., Eyal, G., Kramer, N., Laverick, J.H., Loya, Y., 2019. Light environment drives the shallow-to-mesophotic coral community transition. Ecosphere 10. https://doi.org/10.1002/ecs2.2839.

Turner, J.A., Babcock, R.C., Hovey, R., Kendrick, G.A., 2017. Deep thinking: a systematic review of mesophotic coral ecosystems. ICES J. Mar. Sci. 74, 2309–2320. https://doi.org/10.1093/icesjms/fsx085.

Turner, J.A., Andradi-Brown, D.A., Gori, A., Bongaerts, P., Burdett, H.L., Ferrier-Pagès, C., Voolstra, C.R., Weinstein, D.K., Bridge, T.C.L., Costantini, F., Gress, E., Laverick, J., Loya, Y., Goodbody-Gringley, G., Rossi, S., Taylor, M.L., Viladrich, N., Voss, J.D., Williams, J., Woodall, L.C., Eyal, G., 2019. Key Questions for Research and Conservation of Mesophotic Coral Ecosystems and Temperate Mesophotic Ecosystems. In: Loya, Y., Puglise, K., Bridge, T. (Eds.), Mesophotic Coral Ecosystems https://doi.org/10.1007/978-3-319-92735-0_52.