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# Temperate mesophotic ecosystems: gaps and perspectives of an emerging conservation challenge for the Mediterranean Sea

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## Abstract

Mesophotic habitats, hosting benthic assemblages totally unknown and unexpected in the early 2000s, are attracting an increasing interest from scientists. Realizing that many long living and habitat forming species are playing a unique pocket of biodiversity in the frame of climate crisis, it is important to recognize the potential of the mesophotic zone in conservation strategies. The mesophotic zone is characterized by environmental factors generally more stable than the shallow counterpart; therefore, it represents a refuge habitat to preserve species that, in shallow waters, may be involved in bleaching events, massive mortalities or other pathologies generally triggered by thermal anomalies. The definition of the mesophotic zone in the temperate seas is confused, creating possible misunderstandings and problems not only from a scientific point of view but also in communication and outreach strategies. Here, we review the scientific literature to build the best definition possible based on the maximum consensus coming from papers analysis. Moreover, the key roles of mesophotic habitats, including ecosystem engineers as animal forests, have been schematized to enhance the perception of the potential risks we are running in case of damage or loss of these habitats.

**Keywords:** *Twilight zone, ecosystem engineers, animal forests, exploration, scientific diving*

## Introduction

The distribution of living organisms on Earth is regulated by complex interactions between abiotic and biotic factors. In the marine environment, light is one of the main abiotic environmental factors influencing the distribution of benthic organisms along the continental shelf (Gattuso et al. 2006). The effects of this factor show different patterns at tropical, temperate and polar regions.

Generally, on the basis of the attenuation of the solar radiation along the water column, a zonation has been observed including i) the euphotic zone, where the Photosynthetically Active Radiation (PAR 400–700 nm) allows net photosynthesis; ii) the disphotic (or twilight) zone, where the light is not sufficient to support net photosynthesis but allows the perception of the organisms' shape (from the lower limit of the euphotic zone to 1000 m; Buesseler et al.

2007); iii) the aphotic zone, where the light is absent (Letelier et al. 2004).

However, since the 80's (e.g. Fricke & Knauer 1986; Schlichter et al. 1986), the expression "twilight zone" has been adopted to define a wide depth range taking in account the species living attached or close to the sea floor, the transition zone between the superficial benthic communities that depend on the photosynthesis, and the dark deep-sea ecosystems (Pyle 1996a, 1996b). This transition zone is only partially overlapped on its mesopelagic homonym, since it is located below the lower limit of the euphotic zone (i.e. photic depth, where PAR is 1% of the surface irradiance; Ryther 1956). Probably to avoid confusion between the two terminologies and, to stress the link with the concept of light availability/intensity, the expression "mesophotic zone" has been adopted since more than ten years (Ginsburg 2007; Reed & Pomponi 2008;

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Lesser et al. 2009). All the early studies on this depth range, included the pioneering ones in which neither twilight nor mesophotic terms were used, (e.g. Lang 1974; James & Ginsburg 1979; Reed 1985; Hanisak & Blair 1988), were related to tropical coral reefs, leading to the definition of Mesophotic Coral Ecosystems (MCEs; Fricke & Knauer 1986; Schlichter et al. 1986; Ginsburg 2007; Lesser et al. 2009; Hinderstein et al. 2010; Kahng et al. 2010). MCEs are defined as an extension of shallow coral reef communities from 30–40 m to the maximum depth at which zooxanthellate corals can live (Hinderstein et al. 2010), which can be sometimes deeper than the lower limit of euphotic zone, since other trophic processes are deemed able to compensate for the net loss of productivity at level of irradiance <1% (Lesser et al. 2009). The depth of this lower boundary changes by locations depending mainly on the transparency of the water and other physical factors that affect light penetration (Kahng et al. 2010), but the presence of zooxanthellate scleractinians has been documented at over 150 m of depth in tropical waters (e.g. Reed 1985; Maragos & Jokiel 1986; Fricke et al. 1987; Kahng & Maragos 2006), although zooxanthellae have been found down to 396 m inside antipatharians' polyps (Wagner et al. 2011). According to some authors (e.g. Kahng et al. 2014), the upper boundary has been chosen only by convention as the depth limit of the recreational SCUBA diving, while others authors (e.g. Hinderstein et al. 2010) consider a shift in the composition of the benthic assemblages as indicator (e.g. reduction of live coral cover, decrease of turf algal cover and increase of fleshy algal cover, increase of sponges and abiotic substratum; Liddell & Ohlhorst 1988; Garcia-Sais 2010).

Despite the study of the mesophotic zone has begun in tropical waters, in the recent years the investigation of the benthic communities inhabiting this depth range in temperate seas (i.e. Temperate Mesophotic Ecosystems – TMEs) is drawing the attention of the scientific community, both in the Mediterranean Sea (e.g. Cerrano et al. 2010, 2015; Bo et al. 2011; Bianchelli et al. 2013; Di Camillo et al. 2013; Chimienti et al. 2018a; Idan et al. 2018) and in Australian waters (e.g. Keesing et al. 2012; James et al. 2017). These areas host several assemblages structured by ecosystem engineers (*sensu* Jones et al. 1994) and/or habitat-forming species (Bertness & Callaway 1994; Etnoyer & Morgan 2005; Cerrano et al. 2006), many of which can be locally rare and/or threatened (Cerrano et al. 2015). However, in the Mediterranean Sea the definition of mesophotic zone needs to be clarified, being adopted for a wide range of depths and environmental factors (e.g. Cerrano et al. 2010; Bianchelli et al. 2013; Giusti et al. 2014;

Cau et al. 2015a; Grinyó et al. 2018b). For instance, there is a partial overlap with the definition of coralligenous habitats that could have led to possible confusion. The coralligenous, in fact, is defined as biogenic temperate reefs mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions (i.e. mesophotic conditions) between 20 and 120 m depth (Ballesteros 2006). Indeed, coralligenous is only one of the diversified habitats hosted by the Mediterranean mesophotic zone. On the other side, the typical aphotic cold-water coral reefs, thriving at the bathyal depths (Freiwald et al. 2009; Chimienti et al. 2018c), are considered as part of the mesophotic zone (e.g. Costantini & Abbiati 2016).

Here we analysed the peer-reviewed literature on the mesophotic zone at global scale, to gather information about the number of papers, their distribution and the methodologies selected for its investigation around the world. Then, we focused on the Mediterranean Sea, to underline the ecological importance of this peculiar transitional zone in temperate seas and to identify the main topics covered by the scientific community. Moreover, we suggest an unambiguous definition of mesophotic zone for the Mediterranean Sea, which will help the future studies to raise the veil on one of the less explored environments on the planet (Cerrano et al. 2010).

## Materials and methods

We conducted an extensive bibliographic search on the Elsevier's Scopus database ([www.scopus.com](http://www.scopus.com)), using the queries “twilight zone”, “mesophotic”, “twilight zone AND Mediterranean” and “mesophotic AND Mediterranean” in “Article title, Abstract, Keywords”, in all years and until the cut-off date 16 March 2019 (Appendix S1).

The different queries resulted respectively in: 633 publication since 1923 for “twilight zone”; 392 for “mesophotic” since 2007; 15 for “twilight zone AND Mediterranean” since 1995; 33 for “mesophotic AND Mediterranean” since 2009. The results were firstly screened (only title and abstract) to remove the papers not relevant to our target (i.e. benthic twilight or mesophotic zone). After our screening, we obtained 25 (~4%), 338 (~86%), 7 (~47%), and 29 (~88%) articles for each query, respectively from which we extracted the biogeographic region (i.e. “realm” following Spalding et al. (2007)) and the bathymetric limits of the mesophotic zone (or twilight zone) considered, if any (Table S1). Moreover, for the papers regarding the Mediterranean Sea also the sampling methods, the depth range of sampling and the target species were

recorded (Table S2). Depending on the typology of studies (e.g. descriptive; geomorphological; methodological; review; etc.), sometimes one or more of these categories is not available. The results of the two couples of queries “twilight zone” and “mesophotic”, “twilight zone AND Mediterranean” and “mesophotic AND Mediterranean” only partially overlap (respectively the 56% and the 71% of the result of the first query in each couple are exclusive of that query), and they were considered together in the data analyses. From the screening of the results of the research “mesophotic”, 3 articles regarding the Mediterranean Sea but not reporting the term “Mediterranean” in their titles, abstracts or keywords have been found. These papers have been pooled together with the others regarding the Mediterranean Sea.

## Results

Among the analysed articles, the first, found using the query “twilight zone”, dated back 1986, while the first one using “mesophotic” dated back 2008 (Figure 1). The number of articles containing in their titles, abstracts or keywords the expression “twilight zone” remains quite constant from 1986 (2) to 2018 (3), with a peak in 2017 (5), while there

is a clear increasing trend in the number of articles using the word “mesophotic” from 2008 (1) to 2018 (75), with 16 articles in less than three months in 2019. Adding the term “Mediterranean”, the first relevant paper dated back to 2008 for twilight zone and 2010 for mesophotic (Figure 1). Also in this case, for the first query the number of papers remained almost constant (never more than 2 papers per year, from 2008 to 2014), while it can be observed an increasing trend in number of papers for the second query, from 2008 (1) to 2018 (6), and the first three months of 2019 (4).

The most studied realm in the articles analysed was the Tropical Atlantic (44.2%), followed by Central Indo-Pacific (15.2%), Easter Indo-Pacific (11.3%), Temperate Northern Atlantic (10.8%), Western Indo-Pacific (5.9%), Temperate Northern Pacific (2.8%), Temperate Australasia (2%), Tropical Eastern Pacific (1.1%) and Temperate South America (0.6%). In the remaining 5.6% of the articles the location was not specified (mainly reviews or conceptual papers). No articles regarding the realms Arctic, Southern Ocean and Temperate Southern Africa have been found (Figure 2).

The analysis of the bathymetric limits considered in each article to delimit the mesophotic (or twilight)

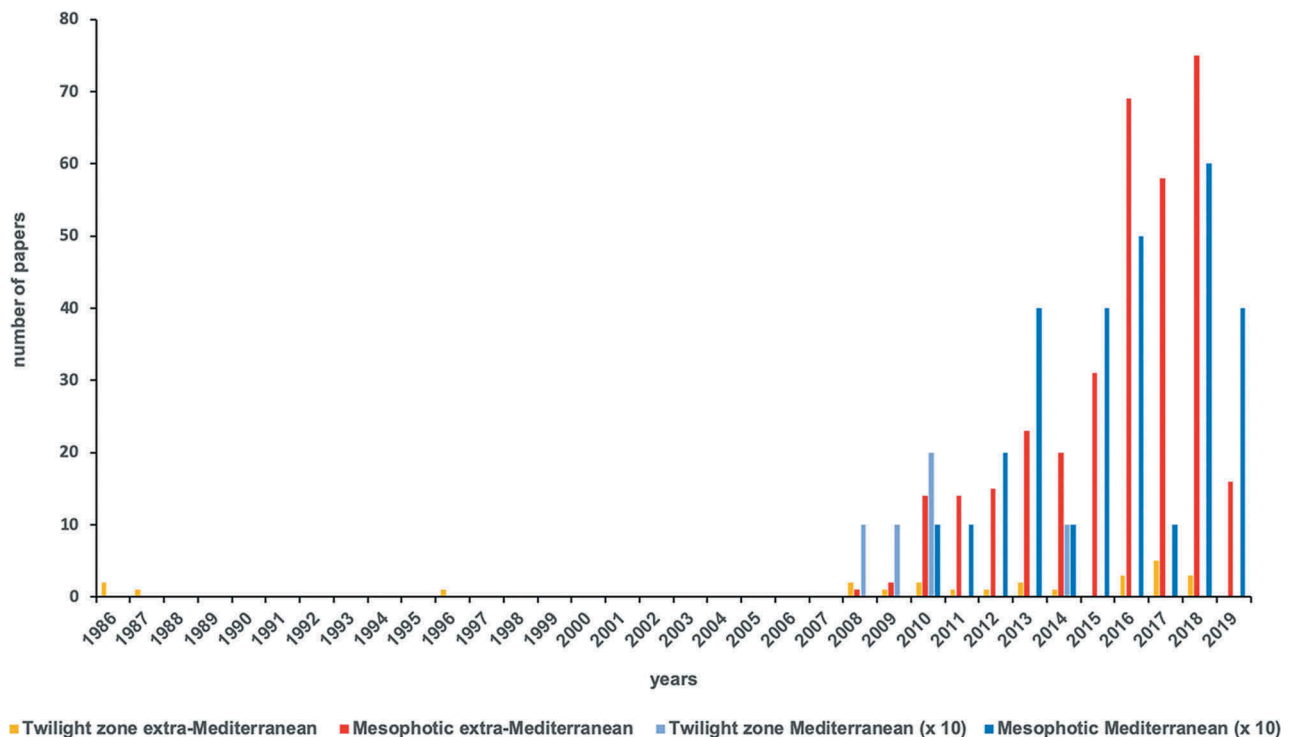


Figure 1. Temporal trend of the articles found asking for the queries “twilight zone”, “mesophotic”, “twilight zone AND Mediterranean”, “mesophotic AND Mediterranean” used in the bibliographic research on Elsevier’s Scopus database ([www.scopus.com](http://www.scopus.com)), in all years and until the cut-off date 16 March 2019.

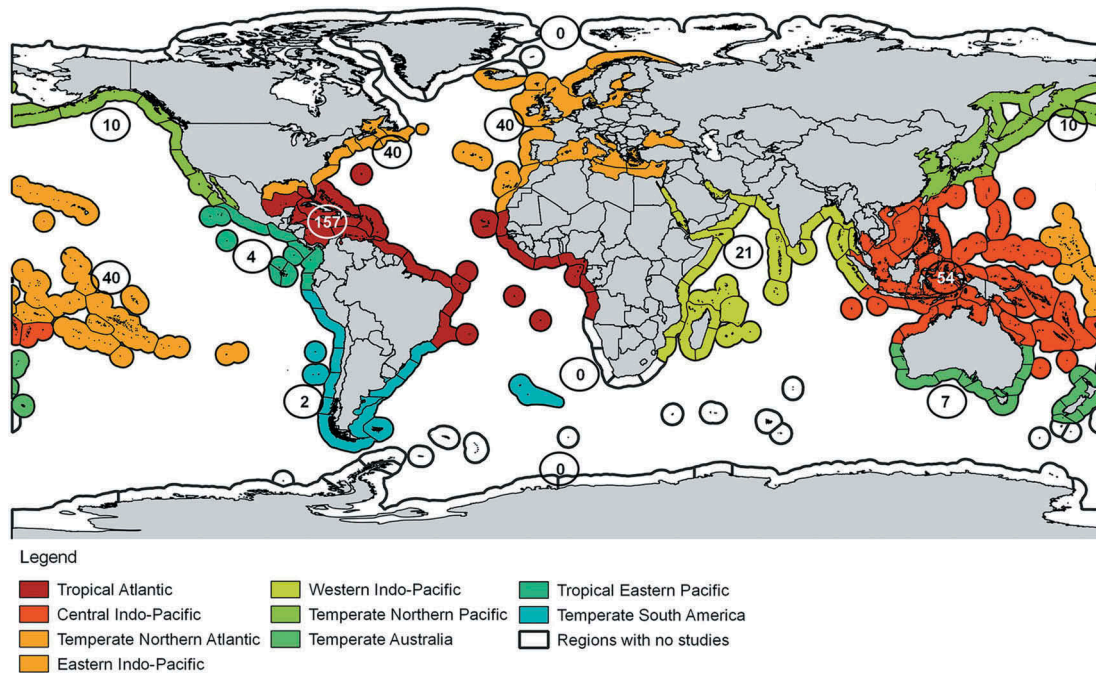


Figure 2. Geographic distribution of the papers selected by the bibliographic research based on the queries “twilight zone” and “mesophotic” (considering the realms of Spalding et al. 2007).

zone showed that the most considered depth range is 40–120 m, followed by 30–120 m and 30–150 m (Figure 3(a)). A progressive smaller number of articles considered a deep lower limit (i.e. 170, 200, 220 m), while only few papers considered an upper limit shallower than 30 m.

For what concern the articles regarding the Mediterranean Sea, which is one of the six provinces that constitute the realm Temperate Northern Atlantic (Spalding et al. 2007), 47.8% of them were placed in the Western Mediterranean ecoregion, 20.8% in the Ionian Sea, 8.3% in the Levantine Sea, 6.3% in the Adriatic Sea, 4.2% both in the Aegean Sea and Tunisian Plateau, and 2.1% in the Alboran Sea (Figure 4). In the remaining 4.2% of the articles the location was not specified.

In this case, the analyses of the bathymetric limits considered showed a more differentiated scenario respect to the global one, with a plethora of depth ranges considered in defining the mesophotic zone. Also here, the most used range is 40–120 m, but with less dominance than at global level. Proportionally to the smaller number of papers, also wider ranges (e.g. 30–200 m; 40–150 m; 30–250 m) are often used. Moreover, there is significant proportion of papers that considered depth ranges with a lower limit deeper than the deepest used at global level (e.g. 250 m; 300 m; Figure 3(b)).

The most used sampling method in the Mediterranean Sea was SCUBA diving (38.9%

composed as follow: 8.2% air, 8.2% trimix, 8.2% rebreather, 4.1% commercial and 10.2% not specified), followed by ROVs (Remotely Operated Vehicles; 36.7%), multibeam echo sounder (10.2%), trawling (4.1%) and sub-bottom profiler (2%) (Figure 5). Some articles used remote methods, as literature review (4.1%), Web Ecological Knowledge (WEK; 2%) and niche modelling (2%). Just 67.6% of the articles used only one sampling method, while the remaining 32.4% used a combination of two or more of aforementioned methods. The analysis of the sampling methods used across the six Mediterranean ecoregions showed that the less studied areas (i.e. Aegean Sea, Alboran Sea, Tunisian Plateau, Levantine Sea) have been investigated only through remote techniques (i.e. niche modelling, literature review, WEK) and other indirect methods (i.e. ROVs and trawling), while SCUBA diving sampling has never been performed in these ecoregions (Figure 6).

In the Mediterranean province most of the studies were focalised on single taxa (67%), while the rest considered multi-taxa assemblages (37%) (Figure 7). Alcyonacea was the most studied taxon (43%), followed by Hydrozoa (8%), Antipatharia and Zoantharia (5% each), Phaeophyceae and Pennatulacea (3% each). Regarding assemblages, sponge grounds and habitat-forming corals accounted each for 11%, coralligenous for 5%, meiofauna and fish fauna for 3% each (Figure 7).



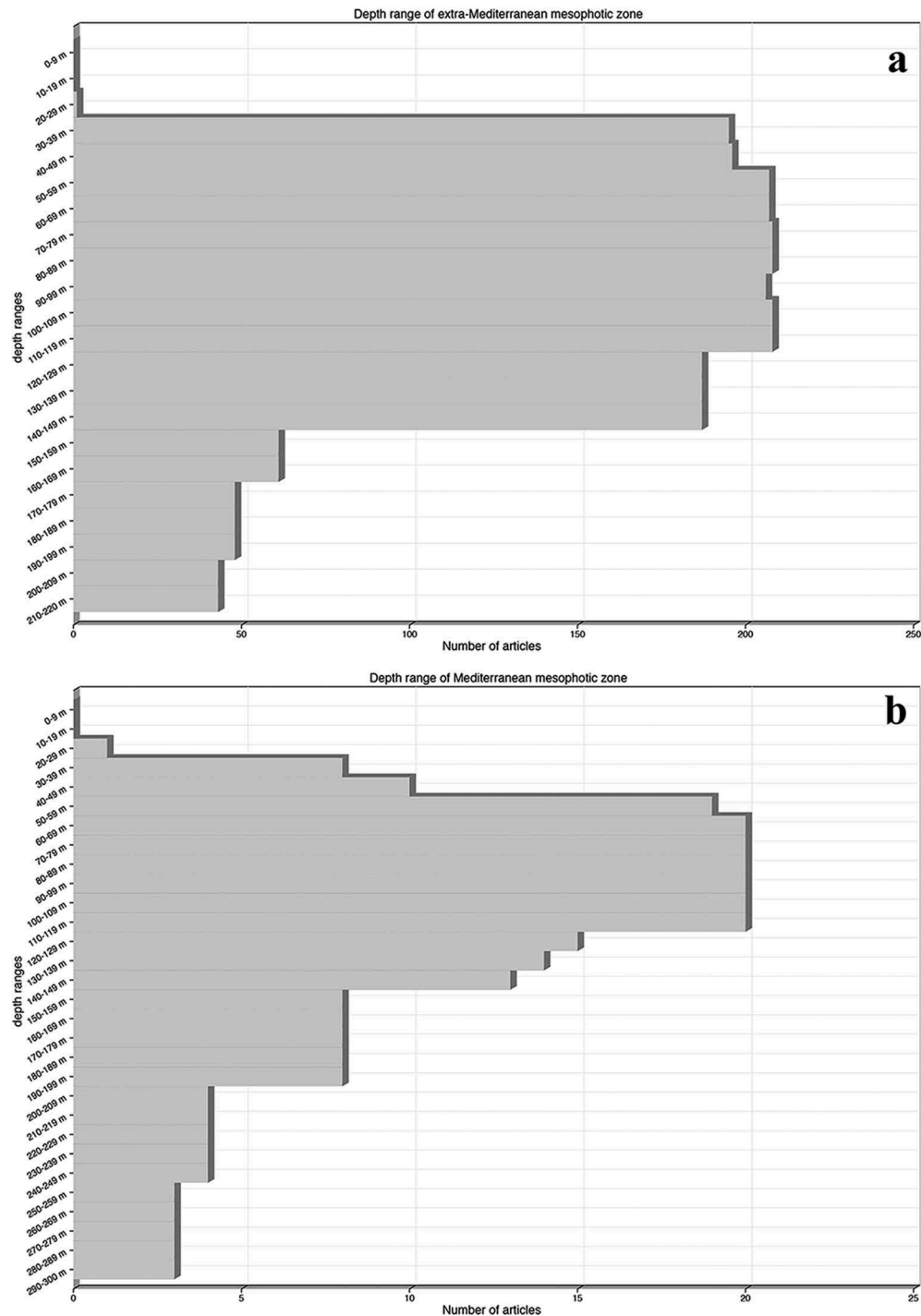


Figure 3. Depth ranges considered as mesophotic (or twilight) zone in the analysed papers: a) extra-Mediterranean Sea; b) Mediterranean Sea.

## Discussion

Despite its recognized potential importance, the functional role of Mediterranean mesophotic zone is still little studied (Cerrano et al. 2010), not only with respect to shallower or deeper ecosystems, but also

with respect to MCEs (e.g. Kahng et al. 2014; Loya et al. 2016; Turner et al. 2017). The vast majority of the studies about mesophotic, in fact, regarded tropical latitudes (77.7%), and only a small portion (16.7%) the temperate seas. From our review only 37 articles have reported explicitly the terms

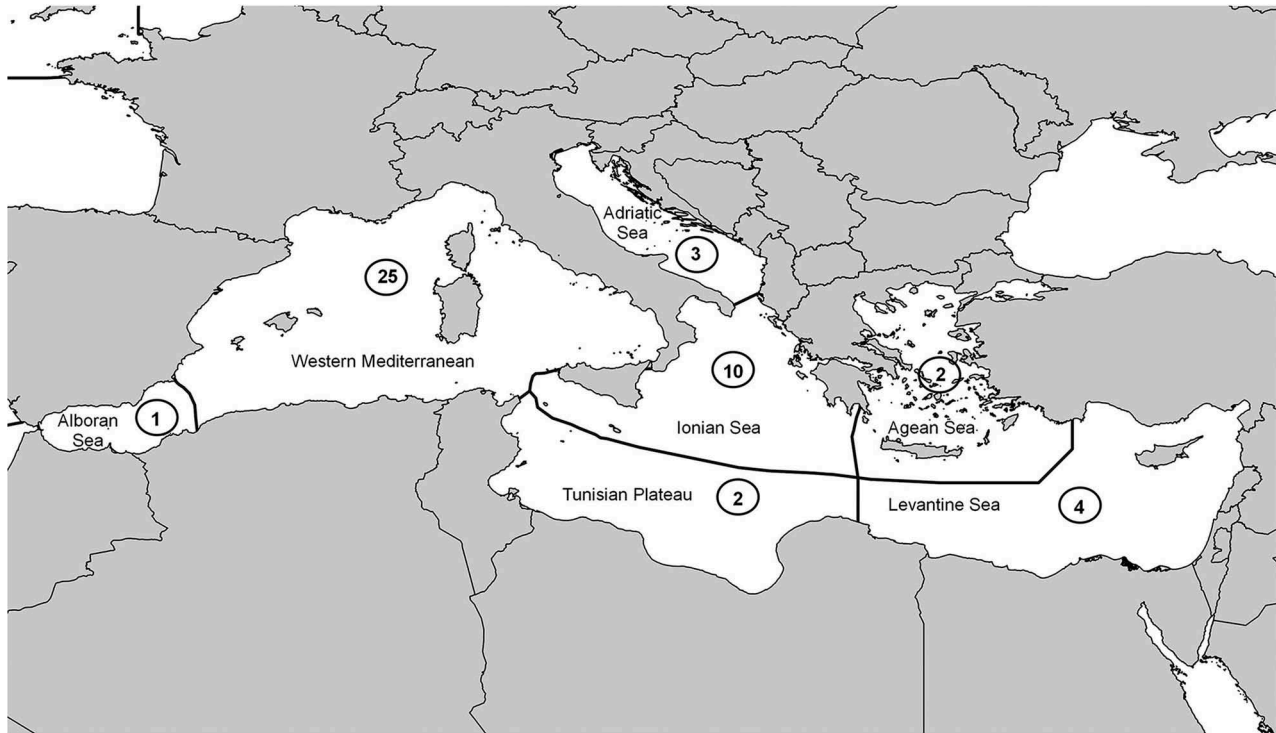


Figure 4. Geographic distribution of the study sites of the publications resulted from the bibliographic research using the queries “twilight zone AND Mediterranean” and “mesophotic AND Mediterranean” (considering the ecoregions of Spalding et al. 2007).

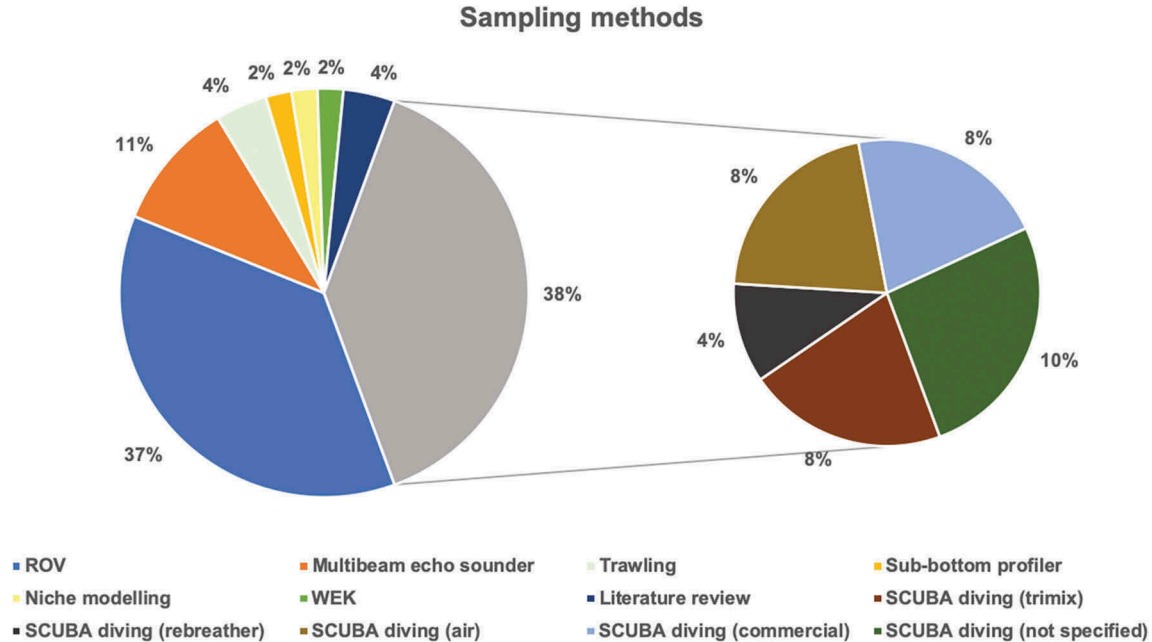


Figure 5. The proportion of the different sampling methods used in the papers resulted from the bibliographic research using the queries “twilight zone AND Mediterranean” and “mesophotic AND Mediterranean”.

“mesophotic” or “twilight zone” related to Mediterranean Sea in their titles, abstracts or keywords since 2008, up today, though with an increasing annual trend in the last years. Even inside the

Mediterranean basin, the studies resulted not equally distributed among the ecoregions (Spalding et al. 2007), with a strong bias toward the Western Mediterranean (50%) and the Ionian Sea (20.8%)

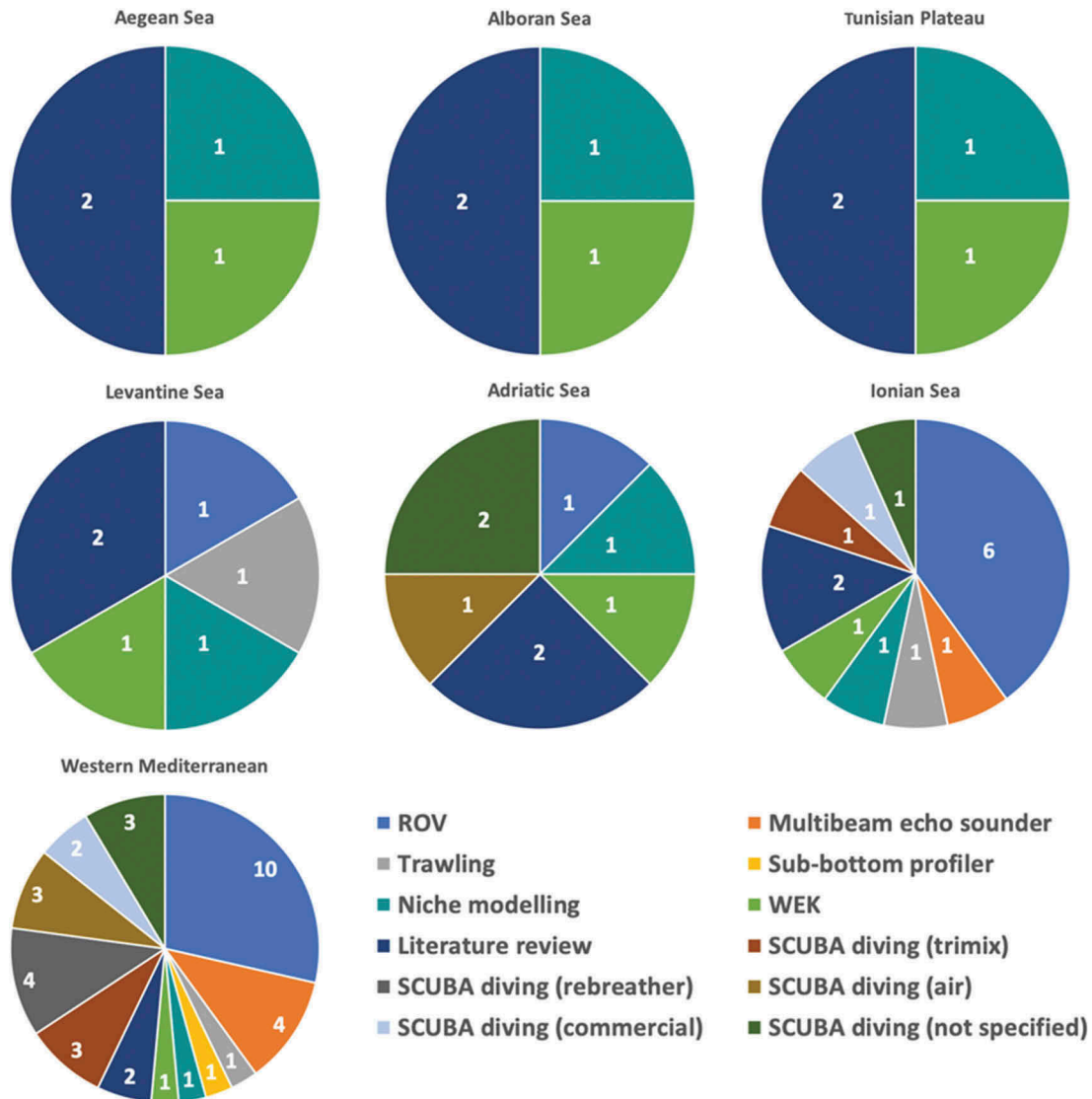


Figure 6. The proportion of the different sampling methods used in each ecoregion of the Mediterranean Sea (considering the ecoregions of Spalding et al. 2007).

and only few articles regarding the other Mediterranean ecoregions. One of the future priorities will be to assess the spatial distribution of the TMEs in the Mediterranean Sea, especially in those ecoregions less known, through multibeam mapping and niche modelling approaches, integrating the results of the few studies available until now (Giusti et al. 2014; Boavida et al. 2016). Notwithstanding, beside these remote methods and others indirect sampling techniques (i.e. ROVs, trawling, dredging, etc.), the improvement of our knowledge about the mesophotic zone cannot disregard to the direct exploration and manipulation through advanced SCUBA diving (e.g. trimix, rebreather) (Sherman et al. 2013; Jessup 2014). Unfortunately, in this work also a strong bias

in the sampling methodologies towards indirect techniques (61.1%) with respect to direct ones (38.9%) has been found. Moreover, this bias is particularly strong in the less studied areas, like Aegean Sea, Alboran Sea, Tunisian Plateau and Levantine Sea, where direct exploration of the mesophotic depths through SCUBA diving has never performed. This bias became even stronger taking in consideration some articles on the Mediterranean mesophotic zone that were not detected from our research, in which authors used ROVs (Orejas et al. 2009, 2017; Ambroso et al. 2013; Porporato et al. 2014; Angiolillo et al. 2015; Coppari et al. 2016; Grinyó et al. 2016, 2018a; Dominguez-Carrió 2018; Chimienti et al. 2019b) or trawls and dredges



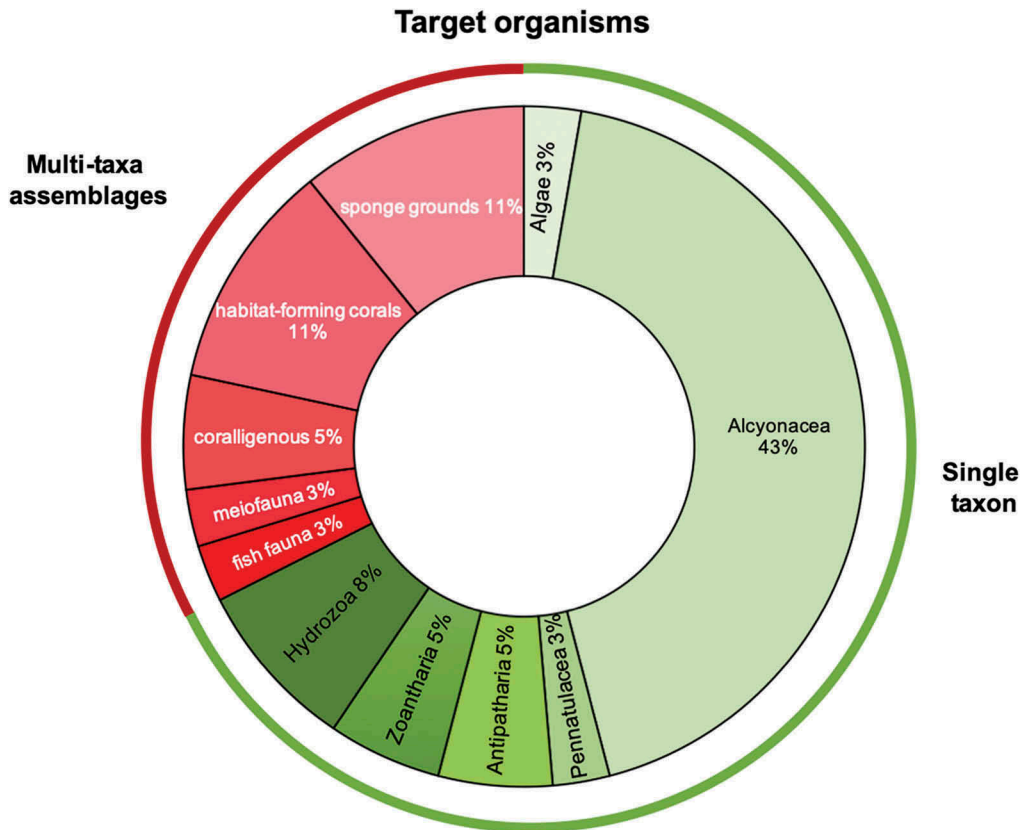


Figure 7. Proportion of the target taxa or multi-taxa assemblages investigated in the publications resulted from the bibliographic research using the queries “twilight zone AND Mediterranean” and “mesophotic AND Mediterranean”.

(Maldonado 1992; Calcinaï et al. 2013). The main reasons for this intensive use of the ROVs (34.7% of the collected articles), despite its intrinsic high costs, are the remoteness or the inherent characteristics of some study sites that make the use of SCUBA difficult (e.g. Bo et al. 2009, 2011; Salvati et al. 2010), and the wide bathymetric ranges of many studies, in which mesophotic zone is only the upper portion (e.g. Orejas et al. 2009; Giusti et al. 2012; Ambroso et al. 2013; Tecchio et al. 2013; Angiolillo et al. 2015; Dominguez-Carrió 2018; Grinyó et al. 2018a). Furthermore, diving at mesophotic depths, especially below 60 m depth, requires advanced training and specific equipment, which strongly limit the number of researchers having the opportunity to develop this kind of exploration. To partially fill this gap, SCUBA diving sampling in the mesophotic zone is often performed by non-scientific divers (Costantini et al. 2013; Priori et al. 2013, 2015; Cannas et al. 2015; Benedetti et al. 2016; Costantini & Abbiati 2016; Corriero et al. 2019), while rarely scientific divers were present underwater (Cerrano et al. 2010, 2015; Di Camillo et al. 2013; Vezzulli et al. 2013). Conversely, many SCUBA diving studies on MCEs

were performed directly by researchers (e.g. Brokovich et al. 2008, 2010; Sherman et al. 2009; Garcia-Sais 2010; Bongaerts et al. 2013; Bejarano et al. 2014; Pyle & Kosaki 2016; Pyle et al. 2016), which sometimes were specifically trained for advanced scientific diving by their host organizations (e.g. Sherman et al. 2013). Given the unparalleled possibility of scientific divers to make detailed observations, careful collections of samples and *in-situ* experiments respect to indirect sampling methods (Sherman et al. 2013), the idea to encourage and promote the use of advanced scientific diving in the study of Mediterranean mesophotic zone cannot be discarded.

From our review emerged clearly the inherent complexity of the Mediterranean mesophotic zone, which lacks a unifying concept like those of the mesophotic coral ecosystems. The Mediterranean mesophotic zone encompasses: i) various geomorphological zone and/or features (Gori et al. 2017), like deep coastal areas (e.g. Cerrano et al. 2010; Angiolillo et al. 2012; Ledoux et al. 2015; Fava et al. 2016; Capdevila et al. 2018; Idan et al. 2018; Ponti et al. 2018; Chimienti et al. 2018b; Corriero et al. 2019), continental shelf (e.g. Bo et al. 2009; Salvati et al. 2010; Bianchelli

et al. 2013; Giusti et al. 2014; Priori et al. 2015), shelf edge (e.g. Cannas et al. 2015; Cau et al. 2015b; Benedetti et al. 2016; Cánovas-Molina et al. 2016; Costantini & Abbiati 2016; Grinyó et al. 2016; Galil et al. 2019; Paletta et al. 2019) and seamounts (Bo et al. 2011); ii) different seabed typologies, like rocky bottoms (e.g. Bo et al. 2011; Angiolillo et al. 2012; Giusti et al. 2012), coastal detritic bottoms (e.g. Cerrano et al. 2010, 2015; Di Camillo et al. 2013), sandy bottoms (Bastari et al. 2018; Chimienti et al. 2018b), coralligenous outcrops (Fava et al. 2016; Ponti et al. 2018; Pica et al. 2018) and maërl beds (Grinyó et al. 2016); iii) various kind of communities, like arborescent coral (i.e. anthozoans) forests (e.g. Bo et al. 2009, 2011; Cerrano et al. 2010, 2015; Angiolillo et al. 2012; Bianchelli et al. 2013; Di Camillo et al. 2013; Cau et al. 2015a; Grinyó et al. 2016; Rossi et al. 2017), stylasterid forests (Salvati et al. 2010), mesophotic coral (i.e. scleractinians) reefs (Corriero et al. 2019), sea pen fields (Chimienti et al. 2018b), sponge grounds (Idan et al. 2018) and even macroalgal forests (Capdevila et al. 2018). To solve this complexity we suggest to refer to all communities living in the bathymetric range called mesophotic zone as Temperate Mesophotic Ecosystems (TMEs), regardless of the geomorphological zones or seabed typologies.

Another important issue emerging from our bibliographic analysis is the absence of a univocal identification of this bathymetric range. Both the upper and the lower limit, in fact, result more variable in the articles regarding the Mediterranean Sea respect to those about the tropical mesophotic zone. Following the definitions given in the articles, the extension of Mediterranean mesophotic zone is wider, with the shallowest upper limit (i.e. 20 m) and the deepest lower one (i.e. 300 m) respectively shallower and deeper than the limits extrapolated from the articles regarding the rest of the world (i.e. 30 and 220 m). The definition of the lower limit in the tropical seas, which represents the location of the vast majority of the studies outside the Mediterranean Sea, is linked to the concept of MCEs, characterized by the presence of zooxanthellate reef-building scleractinians and than limited to depths where they can live (Lesser et al. 2009; Kahng et al. 2014). Given the exiguous number of zooxanthellate organisms in the Mediterranean Sea and their limited depth distribution (see Forcioli et al. 2011; Gori et al. 2012; Casado-Amezúa et al. 2014; Caroselli et al. 2015 for anthozoans; Rosell & Uriz 1992 for sponges), this approach cannot be followed. Therefore, we propose as lower limit of the Mediterranean mesophotic zone the deepest

extent of benthic primary producers, delineated by the compensation irradiance (i.e. absolute irradiance) for growth ( $E_{\text{growth}}$ ), “the irradiance at which gross primary production balances the carbon losses (respiration, herbivory, exudation of dissolved organic carbon, and reproduction) for a particular organism” (Gattuso et al. 2006). In this way, the limit varies according to transparency of water (e.g. Duarte 1991 for seagrasses). Until now the deepest benthic primary producers were found at 268 m in the Bahamas (macrophytes; Littler et al. 1985) and at 285 m off North Carolina (microphytobenthos; Cahoon 1986), while in the Mediterranean Sea the deep-water kelp *Laminaria rodriguezii* Bornet was recorded at 260 m in the Adriatic Sea (Ercegović 1960), even if below 180–200 m algae are present as scattered specimens and not as algal assemblage (Pérès & Picard 1964; Pérès 1982). Instead, as upper limit we propose the depth at which arrives the 1% of the surface irradiance (i.e. photic depth; Ryther 1956), traditionally considered the lower limit of the euphotic zone (Letelier et al. 2004) and the limit of the infralittoral zone, where the euphotic zone intersects the seabed (Pérès & Picard 1964; Pérès 1982; EuSeaMap 2012). Other authors proposed the limit of 3% of surface irradiance (Enrichetti et al. 2019), making it coincide with the upper limit of coralligenous (Ballesteros 2006), but we believe that this threshold is too high, and it locates the upper part of the mesophotic zone well inside the euphotic zone triggering some possible confusion.

With the limits proposed in this paper, the mesophotic zone acquires a clear conceptual position between the euphotic and the aphotic zone, and a variable bathymetric position, depending on the transparency of the water.

The results of this review depict a scenario showing a growing interest by the scientific community in the exploration of the mesophotic zone. This interest is mainly due to the greater accessibility given by the improving technologies, both for direct (trimix, rebreather) and indirect (ROV) exploration, and to the research opportunity that this highly stable habitat offers respect the shallower ones. A possible definition of stability of an ecosystem considers its propensity of returning to its functioning regime after a change in its biotic components and/or abiotic components. A still open question is how the stability of an ecosystem is related to its complexity, as roughly measured by the ecosystems' diversity in species and their interactions (Loreau & de Mazancourt 2013; D'Alelio et al. 2016). In the marine environment little attention has been devoted to the key role of stability in triggering

speciation processes. The geological and biological stability of a landscape, its level of isolation, and the absence of human disturbance are the main factors explaining high level of endemism in several areas of the world (e.g. New Zealand).

At the end of Last Glacial Maximum (i.e. 19000 BP) the mean sea level in the Mediterranean Sea was around 120 m lower than the current one, while at the beginning of the Holocene (i.e. 11,700 BP) it ranged from -40 m to -68 m (Lambeck & Purcell 2005; Benjamin et al. 2017). This means that the deeper part of the mesophotic zone (i.e. lower mesophotic, deeper than 60 m; Slattery et al. 2011; Loya et al. 2016) has never been exposed to air in the last almost twelve thousand years. Therefore, mesophotic habitats are characterized by greater stability respect to shallower ones across glacial sea level changes (Slattery et al. 2011) regarding the main environmental parameters, hosting biocoenoses that had never been completely erased but only changed matching sea level variations (Di Camillo et al. 2013; Grinyó et al. 2016) across ice ages (Slattery et al. 2011). Such stability, together with the generally lower productivity of the deeper habitats that limits food supply favouring longer lifespans (Larson 2001), and the reduced competition with fast-growing autotroph (Zabala & Ballesteros 1989), fostered the development of slow-growing and long-living species, especially sponges and anthozoans (Montero-Serra et al. 2018). For instance, the Mediterranean black coral *Leiopathes glaberrima* (Esper, 1788) shows an incredible longevity, reaching 2000 years (Bo et al. 2015), while a close tropical relative of the gold coral *Savalia savaglia* (Bertoloni, 1819), the Hawaiian gold coral *Kulamanamana haumeae* Sinniger, Ocaña & Baco, 2013, can reach >2700 years (Roark et al. 2009). Both *L. glaberrima* and *S. savaglia* are two important habitat forming species in the Mediterranean mesophotic zone (e.g. Cerrano et al. 2010; Bo et al. 2015 and references therein). Moreover, since the rise in sea-level aforementioned (Benjamin et al. 2017), this zone hosts biogenic buildings made by coralline algae (i.e. coralligenous; Ballesteros 2006; Ingrosso et al. 2018) developed thousands of years ago at shallower depths (e.g. from 3000 to 7000 years BP in the Western Mediterranean, Bertolino et al. 2014 and Sartoretto et al. 1996 respectively; 12,000–14,000 years BP in the Eastern Mediterranean, Georgiadis et al. 2009). Stability and longevity can allow to some organisms living in this zone, such as gorgonian (e.g. Grinyó et al. 2016) and arborescent coral (e.g. Bo et al. 2009; Cerrano et al. 2010), to reach large sizes (Gori et al. 2011; Grinyó et al. 2016), enhancing their effects as ecosystem engineers and habitat-forming species (Werner & Gilliam 1984), shaping

the so-called animal forests (Cerrano et al. 2010; Rossi et al. 2017).

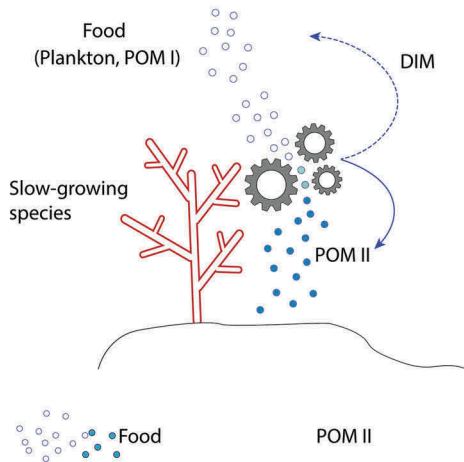
The increase of biodiversity, stability and longevity amplifies the net of ecological interactions (Finke & Denno 2004; Edwards et al. 2010; Estes et al. 2013), which, in turn, can influence the nature and magnitude of eco-evolutionary feedbacks and contribute to the stability of the ecosystem itself (Strauss 2014).

Furthermore, the mesophotic zone is a key transition zone between shallow and deep environments (Cerrano et al. 2010, 2015; Di Camillo et al. 2013), where species with shallower and deeper distributions can meet (e.g. Brokovich et al. 2008; Santín et al. 2018; Grinyó et al. 2018a) determining a “mid-domain effect” (Colwell & Lees 2000; Colwell et al. 2004). Because of these peculiar features, the Mediterranean mesophotic zone supports high levels of habitat complexity and biodiversity (e.g. Bo et al. 2009, 2011; Cerrano et al. 2010, 2015; Grinyó et al. 2016; Idan et al. 2018; Corriero et al. 2019). It hosts several species that are elsewhere rare or threatened, like fucoid algae *Cystoseira zosterooides* (Turner) C. Agardh 1821 (Capdevila et al. 2018), the Mediterranean kelp (*L. rodriguezii*), the gold coral *S. savaglia* and the purple gorgonian *Paramuricea clavata* (Risso, 1826) (Cerrano et al. 2010), the black corals *L. glaberrima* and *Antipathes dichotoma* (Pallas, 1766), the red coral *Corallium rubrum* (Linnaeus, 1758) and the large hydrozoan *Lytocarpia myriophyllum* (Cerrano et al. 2015). These species, with many others, are able to form algal (Barberá et al. 2012; Joher et al. 2012; Capdevila et al. 2018) and animal forests (Rossi et al. 2017). Given the light attenuation with depth, forests created by benthic sessile animals are more common and abundant in the mesophotic zone respect to those formed by macroalgae (Cau et al. 2015a). Here the animal forests are dominated by gorgonians and black corals, together with other cnidarians, sponges, bryozoans, crinoids, brachiopods and ascidians, both on hard and soft bottoms, all acting as ecosystem engineers (see Gori et al. 2017 for an extensive review). For these reasons, the mesophotic assemblages need to be considered with a multiscale approach, organisms select habitat at multiple hierarchical levels and at different spatial and/or temporal scales within each level. Scale is the lens that focuses ecological relationships (McGarigal et al. 2016). The presence of this long living assemblages play a key role not only in the benthic-pelagic coupling (BPC) through the alteration of the water movement and the retention of particles (Figure 8(a)), but in the regulation of competitive and cooperative processes at the base of any coevolutionary processes where eggs, larvae, juveniles and adults can

# TEMPERATE MESOPHOTIC ECOSYSTEMS

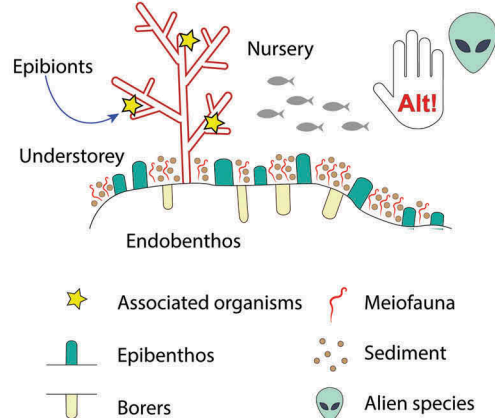
## a BPC and trap effect

Suspended particulate matter can be captured and transformed or simply trapped on the sea floor



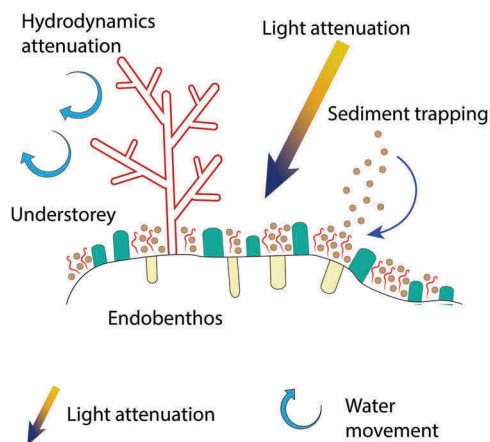
## b Biodiversity enhancement

Long-living organisms, creating stability, offer the unique opportunity to coevolutionary processes to be tested and selected, facilitating the survivor of fragile species



## c Effects on edaphic factors

The physical presence of habitat-forming species reduces water speed triggering sediment stability and limiting resuspension process



## d Absence: assemblage disgregation

The loss of habitat formers leads to a continuous friction of water and sediments on the sea floor leading to a reduction of the community complexity

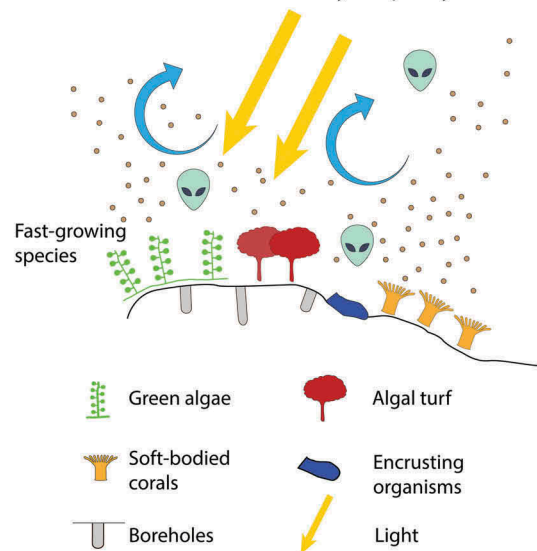


Figure 8. Schematic representation of the effects of presence and loss of Temperate Mesophotic Ecosystems (TMEs). (a–c) A healthy TME (green circles) has a three-dimensional architecture hosting five main levels of benthic organisms (long-living animal forests, epibionts, juveniles of vagile species, communities of the understorey and the endobenthos). This ecosystem regulates edaphic factors driving the development of sciaphilous communities (d) Unhealthy TME (red circles) shows loss of mesophotic forests, leading to a bi-dimensional ecosystem, dominated by fast-growing species tolerant to light exposure and sediment rain.



develop different level of interaction (Baillon et al. 2012) (Figure 8(b)). Regarding environmental variables, animal forests create a sort of buffer zone, limiting resuspension processes and shadowing the understorey (Figure 8(c)). The loss of ecosystem engineers affects the animal forests triggering a gradual—but irreversible—process of habitat degradation, opening corridors to alien species (Ponti et al. 2018) and leading towards a bi-dimensional, less complex ecosystem (Figure 8(d)).

Mesophotic assemblages facilitate organic matter accumulation, enhancing meiofaunal abundance and diversity in the surrounding sediments (Cerrano et al. 2010, 2015). Thus, mesophotic animal forests provide habitat, refuge, shelter and food for peculiar species (Gori et al. 2017) and represent feeding grounds, spawning and nursery areas for both demersal and pelagic species also with high economic value (e.g. fishes, crustaceans, cephalopods, etc.) (Marliave et al. 2009; Orejas et al. 2009; Baillon et al. 2012; Rossi 2013; Paoli et al. 2017). These characteristics make the mesophotic animal forests worth to be recognized as Vulnerable Marine Ecosystems (VMEs; criteria include rarity of species or habitat, fragility, structural complexity, life histories that limit the capacity of recovery, FAO 2009) and Essential Fish Habitats (EFHs; “habitats identified as essential to the ecological and biological requirements for critical life histories stages of exploited fish species” STECF 2006) as already done for deeper counterparts (Rogers & Gianni 2010; Fabri et al. 2014; Colloca et al. 2015; Sion et al. 2019; Tugores et al. 2019; Chimienti et al. 2019a). Moreover, even if it is now recognized that, at global level, actual pristine conditions are virtually inexistent (Pinnegar & Engelhard 2007; Erlandson & Rick 2010; Ingrassia et al. 2016), semi-pristine animal forests could still thrive in some remote sites (e.g. Bo et al. 2011) or where accidentally fishing activities have been limited (Bo et al. 2014, 2015; Mastrototaro et al. 2017) due to legal restrictions or complex geomorphologies. Such communities, experiencing conditions of minimal human pressure, could represent ecological baselines to which compare the status of disturbed ecosystems (Clark et al. 2001; Roberts 2003; Lotze & Worm 2009) fundamental to assess their long-term changes (Borja et al. 2012). In this sense, the mesophotic zone could be also a useful tool to fight the “shifting baseline syndrome” (i.e. the gradual sliding of the baselines for marine ecosystems towards more degraded state; Pauly 1995), providing us a glimpse of the aspects and structures of undisturbed communities and allowing us to use real, and

not altered, nearly-pristine conditions as baselines (Jackson et al. 2001; Hobday 2011). Owing to the depth, mesophotic ecosystems are less exposed to the variability of environmental parameters and to thermal anomalies and related mass-mortality events that have been affected the Mediterranean Sea in the last two decades (Cerrano et al. 2000; Garrabou et al. 2009). Thus, their role as possible *refugia* against climate change (i.e. “habitats that component of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions”; Keppel et al. 2012) has been hypothesized, eventually fostering the recovery of shallow populations through the supply of propagules (Bongaerts et al. 2010). This hypothesis is highly controversial and has been investigated both in tropical areas (mainly on coral reefs; e.g. Bongaerts et al. 2010; Slattery et al. 2011; Van Oppen et al. 2011; Holstein et al. 2015, 2016), and Mediterranean Sea (Costantini et al. 2010, 2011, 2013, 2016). Overall, the vertical connectivity between deep and shallow coral reefs seems to be strongly species-specific and site-specific (Van Oppen et al. 2011; Bongaerts et al. 2017), as well as limited due to specific life traits (Bongaerts et al. 2010), although the potential of MCEs to serve as refugia has been demonstrated (Holstein et al. 2015, 2016). For the Mediterranean Sea, limited vertical connectivity between mesophotic and shallow population of *C. rubrum* (Costantini et al. 2010, 2011, 2013) and of white gorgonian *Eunicella singularis* (Esper, 1791) (Costantini et al. 2016) has been found, suggesting that the climate refugia hypothesis could be not feasible for the Mediterranean mesophotic zone. Notwithstanding, since Assis et al. (2016) have been demonstrated that past deep refugia during warmer period have been crucial for the survival of temperate marine forests (comprised the Mediterranean ones), and given the recognized paramount role of climate refugia in conservation planning and climate change management (Groves et al. 2012; Keppel & Wardell-Johnson 2012; Keppel et al. 2015), the potential as refugia of the Mediterranean mesophotic zone cannot be discarded at a long term scale (e.g. considering the sea level variations during glacial periods), and further studies are needed to clarify this aspect.

Conservation biologists should ask high attention towards highly stable regions hosting the greatest depth and breadth of the tree of life. Not only biodiversity *per se* must be protected but also the areas where the speciation processes can develop, saving the pocket areas where phylogenetic pathways can evolve (Losos 2017).



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