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Mesophotic zone as buffer for biodiversity protection: A promising opportunity to enhance MPA effectiveness

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ABSTRACT

Coastal areas conservation strategies often left deeper habitats, such as mesophotic ones, unprotected and exposed to anthropogenic activities. In this context, an approach for including the mesophotic zone inside protection plans is proposed, considering 27 Italian Marine Protected Areas (MPAs) as a model. MPAs were classified considering their bathymetries, exposure to marine heat waves (MHWs), mass mortality events (MMEs) and, using a local ecological knowledge (LEK) approach, the estimated resilience of certain sessile species after MMEs. Only 8 MPAs contained considerable mesophotic areas, with stronger MHWs mainly occurring in shallower MPAs, and MMEs mostly affecting coralligenous assemblages. Even with only a 10% response rate, the LEK approach provided useful information on the resilience of certain species, allowing us to suggest that the presence of nearby mesophotic areas can help shallower habitats facing climate change, thus making the "deep refugia" hypothesis, usually related to tropical habitats, applicable also for the Mediterranean Sea.

1. Introduction

Although 70% of the Earth is covered by oceans, more than 92.8% lack any level of protection and, still today, only 2.9% can be considered ''fully or highly protected against fishing impacts'' (http://mpatlas.org/, accessed July 02, 2024). Marine Protected Areas (MPAs) – defined as designated parts of the ocean where certain human activities are restricted for the long-term conservation of cultural heritage, marine resources, or ecosystem services (Duarte et al., 2020; Kriegl et al., 2021) – are considered as the "cornerstone" of global marine conservation and management, supporting the natural resilience of marine communities (Worm et al., 2006; Edgar et al., 2014; Mellin et al., 2016; Kriegl et al., 2021).

In the past, MPA zoning and siting have been heavily driven by socio-political dynamics, choosing boundaries based on logistics, public acceptance, or economical activities, and rarely prioritising the complexity of ecological processes taking place in the area (Roberts, 2000). In the last decade, this has changed turning into a more science-based process, with the planning and designing steps now focussing on the creation of ecologically coherent MPA networks, involving local communities and scientists in the process (Airame et al., 2003; O'Regan et al., 2021). Although MPAs have been identified as an efficient tool to limit the impact of certain human activities (e.g., fishing activities), they still do not provide any protection against climate change related threats, including invasive species, mucilage outbreaks, mass mortality events, and marine heat waves (Giakoumi et al., 2016; Garrabou et al., 2019, 2022a, 2022b; Montalbetti et al., 2023; Zentner et al., 2023). The everyday more present shadow of the climate crisis is calling for the development of climate-mitigation strategies, considering species resilience to climate change as a focal point for the establishment of appropriate buffers as part of the adaptive management (Simard et al., 2016; O'Regan et al., 2021).

Conservation initiatives have been traditionally focused on relatively shallow coastal areas, developing effective protection measures only for

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certain habitats, and neglecting deeper ones (Castellan et al., 2022a, 2022b). Thanks to the technological and methodological developments of underwater monitoring (Pulido Mantas et al., 2023), these habitats are now more accessible, feeding the growing interest of the scientific community (i.e., Rocha et al., 2018; Bongaerts and Smith, 2019; Cerrano et al., 2019; Pulido Mantas et al., 2022). In the Mediterranean Sea, the ecological importance of the mesophotic realm is widely recognized (Bramanti et al., 2017; Gori et al., 2017; Rossi et al., 2017; Cerrano et al., 2019; Micaroni et al., 2021; Castellan et al., 2022b), and, although less subjected to climate change, anomalously warm water events, also defined as Marine Heat Waves (MHWs), have increased in frequency and intensity (Marbà et al., 2015), reaching deeper waters, causing frequent and severe Mass Mortality Events (MMEs), and deeply affecting benthic communities (Garrabou et al., 2022b; Estaque et al., 2023).

In the mid ‘90s, the idea that deeper environments could represent a sort of refugium for species with shallow threatened populations was proposed for the first time, establishing the “Deep Reef Refugia’’ hypothesis (Glynn, 1996). However, this idea is still highly debated (Bongaerts et al., 2010; Rocha et al., 2018; Perkins et al., 2022) and its validity can differ between temperate and tropical areas, also depending on the considered taxon (Cerrano et al., 2019). Nevertheless, for the Mediterranean, some studies have demonstrated that, under certain conditions, deeper environments (such as mesophotic habitats) may serve as depth refuges from climate change effects (Giraldo-Ospina et al., 2020; Beauvieux et al., 2023; Bramanti et al., 2023). Indeed, deep populations can boost demographic resilience through vertical larval supply to damaged shallower populations (Pilczynska et al., 2016; Padrón et al., 2018; Takeyasu et al., 2023). Current MPAs are usually designed to protect shallower coastal habitats, leaving the mesophotic zone still highly exposed, often remaining at the MPAs’ edges (Appeldoorn et al., 2016; Etnoyer et al., 2016; Soares et al., 2019). As a point of fact, due to the edge-fishing effect occurring in the nearby areas of most MPAs in the world (Ohayon et al., 2021), not only we had left those habitats unprotected, but we had driven fishing impacts to them, compromising their integrity and potential natural mitigation processes against climate change.

In view of the expected expansion of existing MPAs, together with the establishment of new priority conservation areas aimed by the Agenda 30x30, it is urgent to develop an effective list of criteria that should be selected to address and tailor conservation efforts. In this context, and using Italian MPAs as a case study, the main aims of this research are to: (i) provide a comprehensive picture of the bathymetric ranges currently covered by Italian MPAs; (ii) assess their exposure to thermal stress by identifying and characterising MHW events over the past decades; (iii) explore the MME records inside each of the MPAs, paying special attention to the taxa and habitat affected; and (iv) explore if the nearby presence of mesophotic habitats may facilitate the resilience of the affected populations after mortality events.

2. Methods

2.1. Study areas

The network of 29 Italian MPAs updated in January 2024 is presented in Fig. 1. However, given the focus of the study regarding the possible influence of the mesophotic zone in recovery processes, two MPAs (Miramare and Torre Cerrano) were excluded due to their very shallow bathymetry. The list of 27 remaining MPAs considered for the analyses represents a pool of protected areas presenting different geomorphologies (i.e., islands, promontories, capes, shoals, and bays) and established from the mid ‘80s (Isola di Ustica, Isole Ciclopi and Capo Rizzuto) to the 2018 (Capo Milazzo and Capo Testa - Punta Falcone). Among their extensions, a different zonation (zone A, B and C) is present, being the no-entry, no-take zone (A) the only one presenting effective protection measures for mesophotic habitats. Nonetheless, given the general small area represented by the zone A and the availability and resolution of the data used for the bathymetry and the MHWs analyses (see following paragraphs), the entire extension of all MPAs was considered.

2.2. Bathymetric data collection and analysis

The bathymetric data were obtained from the EMODnet bathymetry portal (Thierry et al., 2019). The native resolution of this raster is 1/16 arc min., corresponding to a grid cell of around 115 m in latitude. To analyse the bathymetric range directly interesting the Italian MPAs, data were imported into QGIS software v. 3.12 (QGIS.org, 2022) and clipped by the extension of each MPA using the shapefiles defined by MAPAMED (2019), as a reference. Additionally, to explore bathymetries in the immediate vicinity of each MPA, a buffer of 0.5 km radius was created from the original MPA extensions and used in a second clipping process. The two outputs obtained from this two-step clipping process were exported as a GeoTiff for further analysis with the R software (R Core Team, 2022). Using the *raster* package (Hijmans and van Etten, 2012),

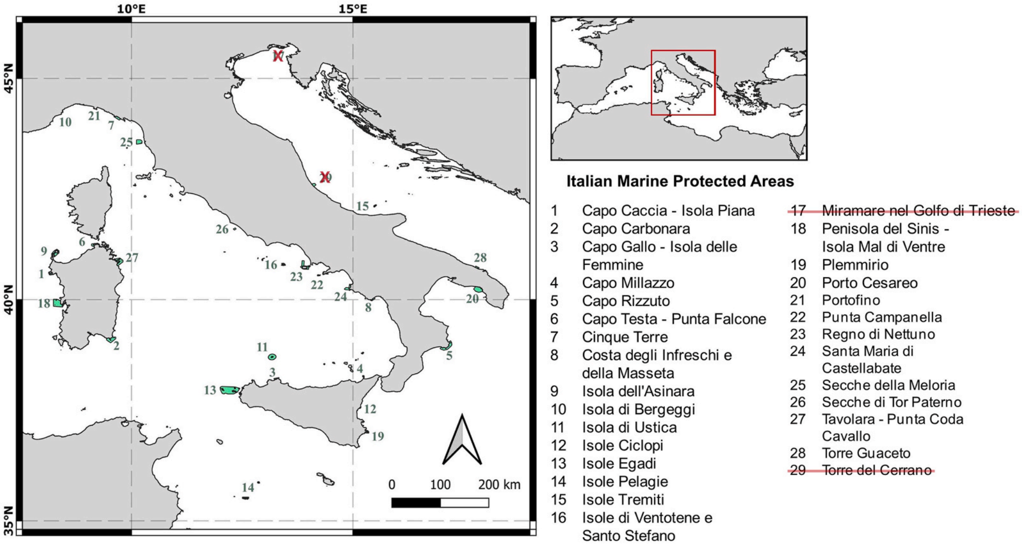

Fig. 1. Map of the location of the Italian Marine Protected Areas (MPAs). Barred MPAs are the ones excluded from the analyses due to their shallow bathymetry and the lack of coralligenous habitat.

the MPAs bathymetric frequencies were extracted and some terrain descriptors (e.g., maximum, minimum, and bathymetric standard deviation) were calculated. Furthermore, the mesophotic modelled distribution developed by Castellan et al. (2022b) was used to assess the potential inclusion of new mesophotic habitats within the MPAs and their nearby areas (0.5 km buffer). Overlaps between current MPAs' extension and the mesophotic zone were inspected and an MPA was considered to address a substantial mesophotic extension if at least a 40% of its current area included mesophotic characteristics. The same 40% extension criterion was applied to the surface added by the hypothetical 0.5 km buffer. The 40% here established is an arbitrary value based on our personal observations, which led us to consider as the minimum percentage able to play a positive ecological effect on the shallower areas damaged by thermal anomalies.

2.3. Detection and characterization of marine heat waves

MHWs are defined as events in which sea surface temperature (SST) exceeds an upper locally determined threshold (90th percentile relative to the long-term climatology) for at least five consecutive days at a certain location (Hobday et al., 2016). This threshold is defined by the local climatology, calculated using SSTs data within an 11-day window centred on the day from which the climatological mean and percentile are calculated (Hobday et al., 2016). MHWs were detected from the Copernicus Marine Environment Monitoring Service (CMEMS) Mediterranean Sea Surface Temperature (SST) (MED-REP-L4; Pisano et al., 2020, 2022). This consists of a daily dataset with a 0.05° horizontal resolution, covering the period from January 1st 1982 to a 1 or 2-day lag from the present date. For the current analysis, the SST series from 01-01-1982 to 31-12-2011 was considered to define the climatology, implementing the methodology developed in Hobday et al. (2016, 2018). MHWs were detected and described using the *m_mhw* Matlab toolbox (Zhao and Marin, 2019). MHW occurrences were assessed within each MPA extension for the period 1982–2023, and different descriptors were obtained to characterise the detected MHWs (event duration, frequency, intensity, and cumulative intensity). Additionally, each event was classified following the categories defined by Hobday et al. (2018), based on the number of times the temperature anomaly exceeds the distance between the local mean climatological temperature and the 90th percentile threshold: an anomaly 1–2 times higher than the distance was classified as *moderate*, 2–3 times higher as *strong*, 3–4 times higher as *severe*, and more than 4 times higher as *extreme*.

MHW descriptors were spatially averaged over each MPA and used as a variable to feed a Hierarchical Clustering on Principal Components analysis (HCPC; Josse, 2010), to identify groups of MPAs with similar exposure to MHW events. In the first place, a PCA was carried out to reduce the dimension of the data, considered as a preliminary denoising step which may lead to a more stable clustering. Subsequently, a hierarchical clustering was performed on the selected principal components using the Ward's criterion to group MPAs with similar MHWs descriptors. Finally, a dendrogram and a principal component map were produced with the *factoextra* package (Kassambara and Mundt, 2020) to visualise the clusters produced by the HCPC analysis in R software (R Core Team, 2022).

In addition, differences between the maximum intensity, mean intensity, cumulative intensity, and MHW durations were investigated among the groups identified by the HCPC using the nonparametric Kruskal-Wallis analysis of variance. If statistically significant differences were found, Dunn's post-hoc comparison was performed. All statistical analyses were conducted with a 95% confidence level, using the software PAST (PAleontological STatsistic; Hammer and Harper, 2001).

2.4. Mass mortality events records

To obtain the most updated list of MME occurrences inside Italian MPAs, our approach considered three different sources: (i) firstly, all the publicly available records present in the Mass Mortality Events database (MME-T-MEDNet; Garrabou et al., 2019) were collected; (ii) secondly, we benefited from the review effort performed by Garrabou et al. (2022b); (iii) in addition, we considered the records coming from the Med-MME Review Collaborative Exercise, a review effort involving a network of more than 30 research institutions from different countries in the gathering and harmonisation of all available Mediterranean MMEs related information (Garrabou et al., unpublished; Carlot et al., unpublished). Special attention was paid during the analysis to the geographical and depth distribution of the records, together with the taxa and habitat affected by the MME.

2.5. Assessment of demographic resilience of species affected by mass mortality events

Although the documentation of Mediterranean MMEs has exponentially increased in number and details over the past decades, the information regarding the resilience of marine populations affected by these events is still scattered and scarce (Bonhomme et al., 2003; Cerrano et al., 2005; Garrabou et al., 2019; Medrano et al., 2019; Garrabou et al., 2022b). Because of this deficiency and to obtain a general overview of certain populations' resilience inside the Italian MPAs, we decided to implement a Local Ecological Knowledge (LEK) approach (Ruddle and Davis, 2013; Bastari et al., 2017). In this case, our targeted stakeholders were diving centres and associations working inside Italian MPAs. An initial list of 675 diving centres and associations was obtained from a web-scraping tool for the whole Italy. Only the ones at a maximum distance of 50 km from an MPA were selected for this survey, leaving us a total of 350 diving centres and associations to contact. A tailored questionnaire was produced using Google Forms and distributed to the diving centres via email. At the beginning of the questionnaire form, a glossary was provided containing all necessary definitions to correctly fill the survey, including pictures of the targeted species to avoid potential confusions or misidentifications (Supplementary Material, File S1). After this preliminary section, a series of questions allowed to collect information regarding: (i) the MPA in which they perform their activity (if applicable), (ii) if they have witnessed any MMEs over the past decades, (iii) which organism/s was/were affected (if applicable), (iii) their perception about the resilience of the affected populations (see Supplementary Material, File S1 for details).

As for population resilience, we followed the concept of demographic resilience established by Capdevilla et al. (2020), defined as the ability of populations to resist and recover from alterations in their demographic structure. We therefore asked to the diving community about its perception about affected populations returning to similar densities to the ones present before the MME(s), simplified in the LEK-questionnaire using the term "recovery". Although the questionnaire included the possibility to add any group of affected organisms, when reporting a MME or any degree of recruitment success, we decided to provide already the organisms detected as the most affected ones in the collected MME records of section 2.4.

Additionally, the questionnaire offered the possibility to upload photos (up to five pictures) of recorded MMEs. When feasible, the data collected have been verified with local researchers working in the area.

3. Results

3.1. Italian MPAs and nearby areas bathymetric assessment

At present, more than 50% of the Italian MPAs mainly focus their extension on bottoms shallower than 100 m (Fig. 2), with Secche della Meloria presenting the shallower maximum depth (46 m), followed by Torre Guaceto (56 m), and Capo Caccia and Porto Cesareo (58 m). Conversely, 6 MPAs (Isole Pelagie, Plemmirio, Isole Egadi, Regno di Nettuno, Capo Carbonara and Isola di Ustica) include depths from 337 m (Isole Pelagie) down to 1523 m (Isola di Ustica). Only 8 out of the 27

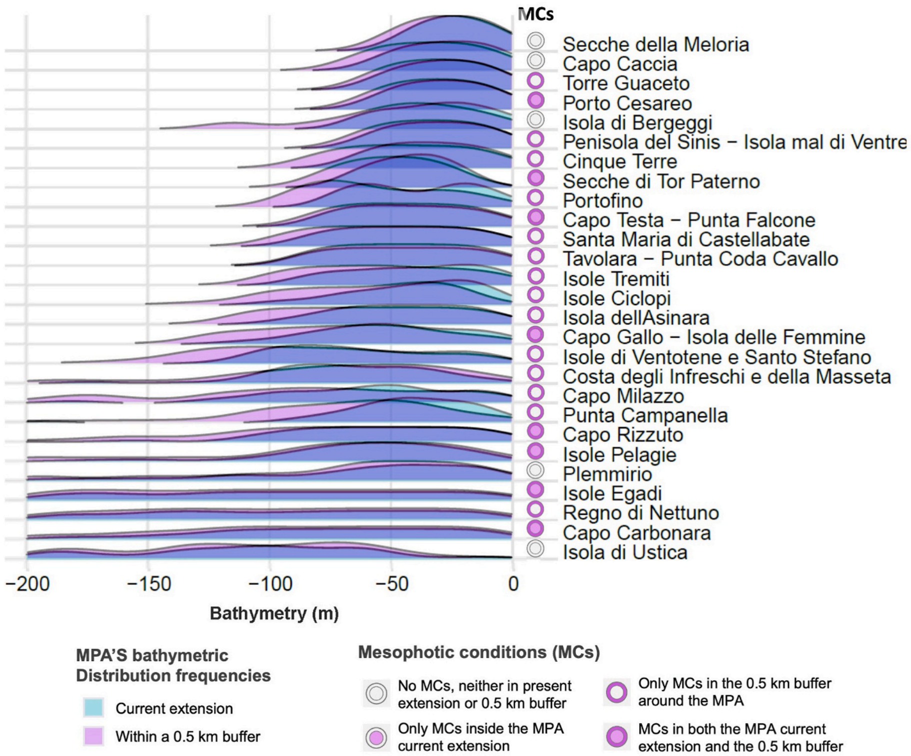

Fig. 2. Density plot showing bathymetric distribution frequencies of Italian marine protected areas (MPAs) within their current extension (light blue) overlapped with frequencies considering a hypothetical extension of 0.5 km radius (purple). Please note that the bullet-ring points in the Mesophotic Conditions (MCs) column provide information about the inclusion of seabed under MCs over ≥40% within the MPA present extension and within a buffered area of 0.5 km radius of its current extension, based on Castellan et al. (2022b) estimations.

MPAs already include substantial mesophotic areas (≥40%) within their actual extension (light purple bullet in MCs column, Fig. 2). Considering the applied hypothetical buffer extension of 0.5 km, this number rises up to 22 MPAs potentially including mesophotic habitats (dark purple ring in MCs column, Fig. 2). A peculiar case is represented by 5 MPAs (Secche della Meloria, Capo Caccia, Isola di Bergeggi, Plemmirio and Isola di Ustica) that, even though they already include mesophotic areas inside their current boundaries or within their hypothetic buffer, it does not reach the threshold of the 40% of their total extension set by this study (Fig. 2).

3.2. *MHW's exposure assessment*

A total of 3136 MHWs were identified and characterised within the extension of the selected Italian MPAs for the 1982–2023 period (Table S1, Fig. S1). Italian MPAs boundaries recorded a yearly average of 16 ± 12 days under MHW conditions for the considered period. The MPAs presenting the highest number of MHWs were Porto Cesareo (128), Santa Maria di Castellabate (128), Regno di Nettuno (127), Tavolara – Punta Coda Cavallo (126), and Secche della Meloria, Portofino and Torre Guaceto (124 each), while Isole Pelagie (103), Cinque Terre (107) and Capo Carbonara (108) presented the lowest (Fig. 3a). However, considering the categories established by Hobday et al. (2018), most of events were classified as moderate in all MPAs. Considering strong events only, Capo Rizzuto (35), Isola di Ustica (33), Tavolara – Punta Coda Cavallo (33), Isola dell'Asinara (32), Isola di Bergeggi (32) and Torre Guaceto (32) were the MPAs displaying the highest count (Fig. 3a). Of the 35 severe events recorded, 20 occurred between 2022 and 2023, being Cinque Terre (4), Capo Testa – Punta Falcone (3), Isola di Ventotene e Santo Stefano (3), Isole Egadi (3) and Isole Tremiti (3) the MPAs accounting for the higher number of severe events (Fig. 3a).

The HCPC analysis performed on the MHW metrics identified 3 groups of MPAs (Fig. 3b). The blue cluster grouped together the 15 MPAs presenting the MHWs with the lower average cumulative intensity and average duration (28.1 ± 0.9 °C · days, and 15.7 ± 0.9 days, respectively). Conversely, the dark red cluster grouped the 4 MPAs showing both the higher average cumulative intensity and average duration (34.3 ± 0.9 °C and 20 ± 2 days, respectively). Then, the grey cluster, grouped together the 8 MPAs undergoing MHWs with intermediate average intensity values (1.8 ± 0.2 °C). For further analyses of the differences identified among the MPAs groups, a Kruskall-Wallis test was performed for all MHW metrics. A significant difference among groups was found for all metrics ($p < 0.05$). Dunn's post-hoc tests showed significant differences ($p < 0.05$): (i) among all groups for the average intensity; (ii) between the dark red and the other two groups for event's duration; (iii) between the blue and the other two groups for the cumulative intensity; (iv) between grey and the other two groups for the maximum intensity.

3.3. *Mass mortality event records within Italian MPAs extension*

Between 1961 and 2020, a total of 277 MMEs was recorded inside the extensions of Italian MPAs (Fig. 4a). These records came from 19 different MPAs, being Portofino (59), Regno di Nettuno (58), Cinque Terre (41) and Tavolara - Punta Coda Cavallo (40), the ones contributing the most to the database. A clear increase in the number of records can be observed from 2000 with an exponential growth after 2015 (Fig. 4a). MMEs were mostly recorded in coralligenous assemblages (98), dim-light sublittoral bottoms (32), hard substrates (29), well-lit sublittoral hard bottoms (24) and seagrasses (17) (Fig. 4b). While regarding the taxonomic groups interested by mortalities, Cnidaria was the most affected (140), followed by Rhodophyta (22) and Mollusca (19) (Fig. 4c).

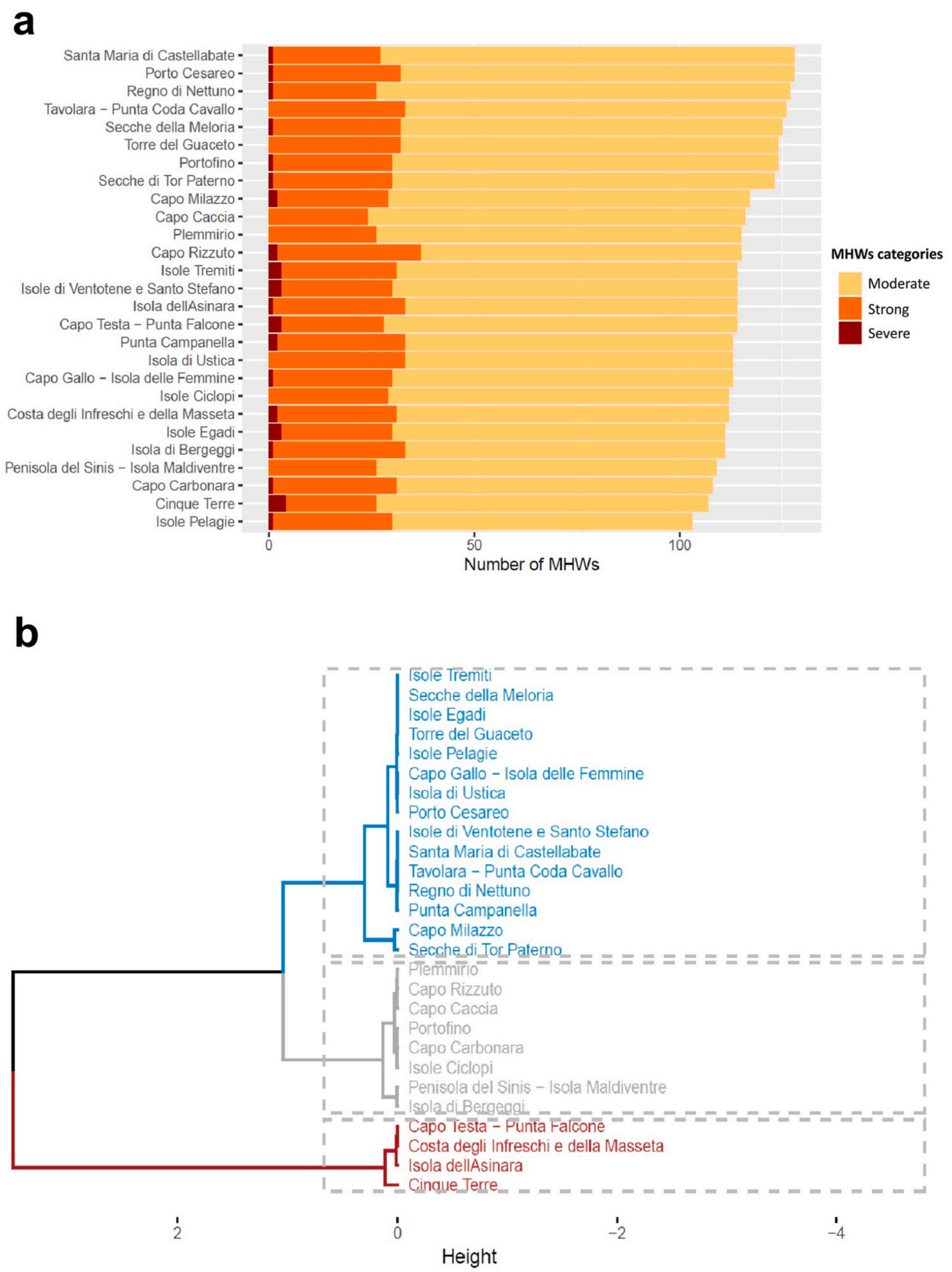

Fig. 3. (a) Total number of marine heat waves (MHWs) per marine protected area for the analysed period (1982–2023). The bars are coloured depending on the MHW categories defined by Hobday et al. (2018). (b) Dendrogram showing groups with similar MHW descriptors' values resulted from the Hierarchical Clustering on Principal Components analysis based on the MHW metrics.

3.4. Demographic resilience, a local ecological knowledge approach

Of the 350 diving centres and associations contacted, 41 replied to the survey, of which, 9 did not carry out their activity within the extension of an MPA. Therefore, a total of 32 answers were considered for the analyses. Three diving centres claimed not to have witnessed any MME over the past decades. The remaining ones provided us with information about 19 MPAs (Table S2), thus leaving 7 MPAs (Capo Rizzuto, Cinque Terre, Isole di Ventotene e Santo Stefano, Penisola del Sinis - Isola Mal di Ventre, Santa Maria de Castellabate, Secche della Meloria, and Capo Milazzo) out of the LEK analyses. To the best of our knowledge, the LEK approach provided the first testimonies of MMEs in three Italian MPAs: Capo Testa - Punta Falcone (in 2003, 2008, 2018 and 2021), Capo Gallo - Isola delle Femmine (in 2021) and Plemmirio (in 1998 and 2020), all of them affecting gorgonian populations. Most of the MMEs and resilience information reported were on cnidarians (especially gorgonian species) and bivalves (in specific *Pinna nobilis*), while only a few records were obtained for the other investigated taxa (Fig. 5 and TableS2). In terms of demographic resilience, for *P. nobilis* just a single resilience event was reported Isola di Bergeggi MPA (Fig. 5). Considering cnidarians, a different situation was recorded depending on the sub-class: hard corals (i.e., *Cladocora caespitosa* and *Astroides calycularis*) presented a single positive resilience record, while gorgonian species (i.e., *Eunicella singularis*, *Eunicella cavolini*, *Paramuricea clavata*) presented a higher demographic resilience, with a total of 12 records (Fig. 5 and TableS2).

4. Discussion

In the entire Mediterranean basin, more than 1200 MPAs (all

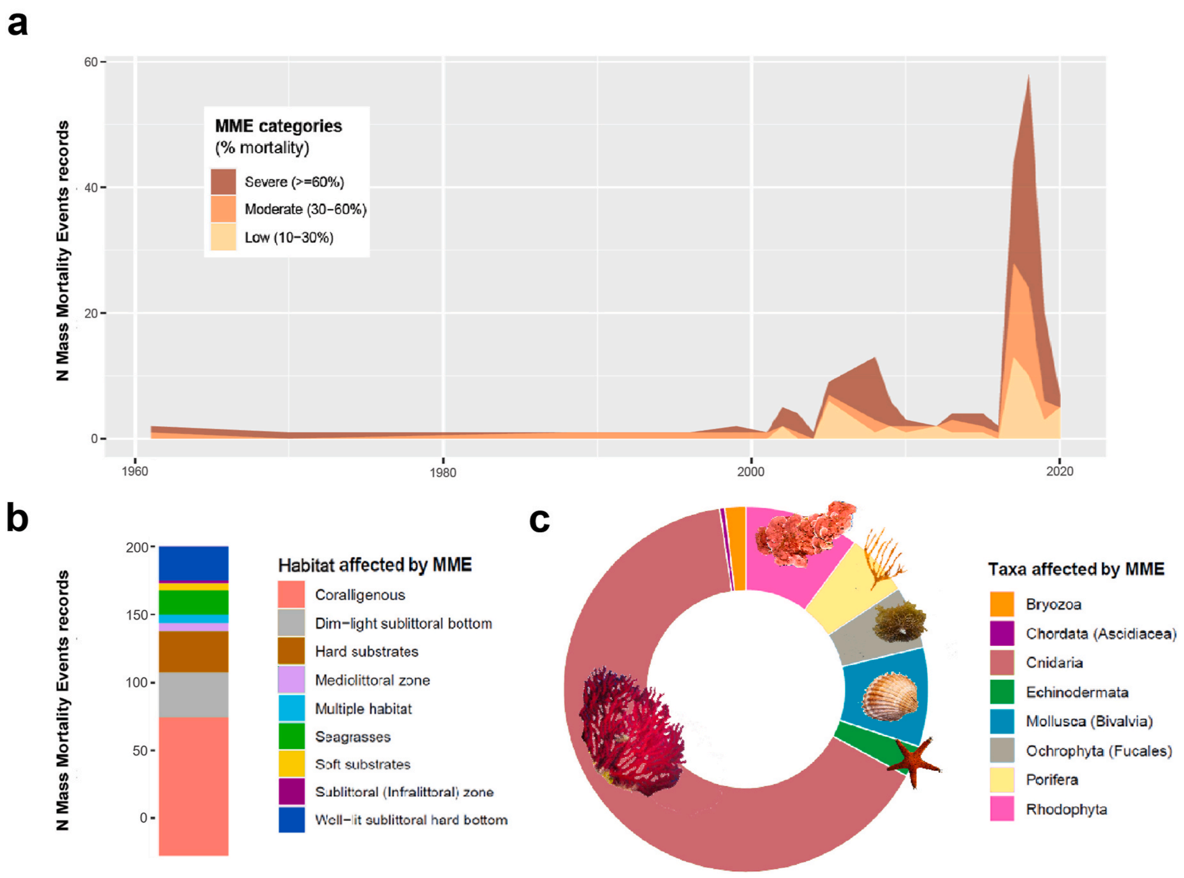

Fig. 4. Mass mortality event (MME) records occurred inside Italian marine protected areas: (a) number of records through the past decades depending on its severity; (b) habitats affected and (c) main taxa affected by those mortalities.

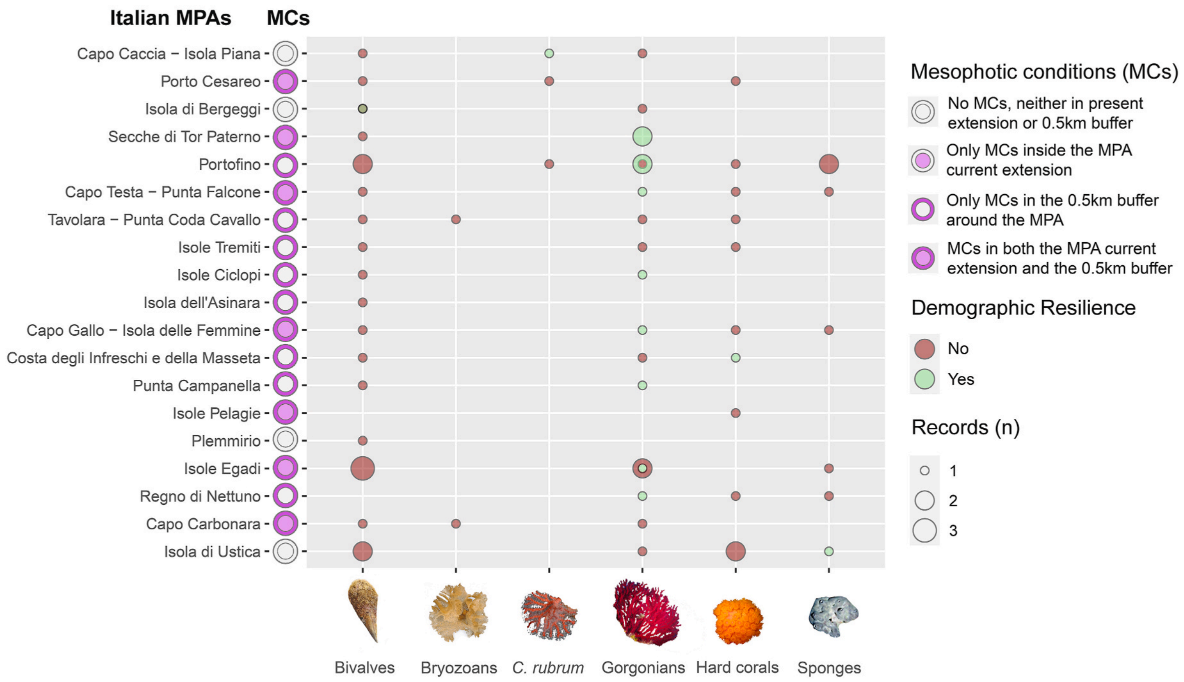

Fig. 5. Summary of demographic resilience assessed through the local ecological knowledge approach per marine protected area (MPA) for the main groups affected by mass mortality events. Please note that here is presented again the bullet-ring points providing information about the inclusion of seabed under mesophotic conditions (MCs) over ≥40% within the MPA present extension and within a buffered area of 0.5 km radius of its current extension.

designations combined) have been established so far, covering up to 8.33% of its total area, with only 4.11% being effectively protected (MedPAN, SPA/RAC, WWF, Prince Albert II of Monaco Foundation, 2022). However, due to the prioritisation towards shallow coastal areas for the implementation of protection measures conducted in the past, most mesophotic habitats are still unprotected and exposed to intensive human activities (i.e., fishing activities; Ohayon et al., 2021).

In the context of the current international marine policies (e.g., EU Biodiversity Strategy, 2030 and the Agenda 30x30 targets), a redesign, enlargement and/or implementation of new MPAs is expected in the following years; still criteria to prioritise and select those areas are under discussion. Using the current network of Italian MPAs as a model and based on the potential refugia effect played by temperate mesophotic habitats (Cerrano et al., 2019), we propose a new approach to support the identification of priority conservation areas including mesophotic environments within their boundaries. The exercise here performed, using a homogenous enlargement of only 0.5 km of the current MPAs extensions, identified 22 potential candidates that would increase their mesophotic representativity, 14 of which do not currently include a considerable seafloor extension (≥40% of current extension) under mesophotic conditions. This lack of protection is not limited to the Mediterranean Sea: a recent global scale analysis highlighted how mesophotic ecosystems in temperate areas are poorly represented in MPAs planning, especially when it comes to fully protected areas (Bell et al., 2024). The proposed exploratory exercise could be replicated not only in other temperate areas but also extended to other climate regions, helping in identifying potential priority conservation areas for the implementation of climatic mitigation strategies.

Even though the scientific community repeatedly highlighted the need to create tailored habitat-based protection measures for the Mediterranean mesophotic (e.g., Cerrano et al., 2019; Castellan et al., 2022a; Pulido Mantas et al., 2022; Bramanti et al., 2023; Enrichetti et al., 2023), this is the first time that a pseudo-quantitative assessment has been conducted at national level. This approach provides new insights for future conservation efforts, but it strongly relies on the resolution of the bathymetric and SSTs data, as well as on the intrinsic uncertainty of habitat modelling (Barry and Elith, 2006). Therefore, for local scale applications, higher resolution data and ground truthing are required to effectively inform local stakeholders and decision-makers in drawing or re-shaping MPAs boundaries, thus increasing their awareness about the crucial importance to preserve these habitats.

Seabed geomorphology, bathymetry, and hydrodynamic conditions may drive not only the development of mesophotic habitats, but also the occurrence, intensity, and duration of thermal anomalies and potentially related MMEs (Juza et al., 2022). Indeed, MPAs characterised by average shallow depths were found among the ones presenting the higher number of overall MHWs or among the ones suffering from severe events (Fig. 3). However, MPAs covering deeper bathymetric ranges, such as Capo Carbonara, Regno di Nettuno and Isole Egadi, were also found highly affected by MHWs. Even though our analyses were based on satellite SSTs, studies conducted in these areas highlighted a compelling warming trend along the water column, down to 3500 m depth (Fuda et al., 2002), suggesting that some of the MHWs identified in surface waters reached deeper layers as well.

Likewise, shallower MPAs were the ones mostly interested by MMEs, mainly affecting organisms belonging to coralligenous assemblages. The coralligenous (i.e., unique landscapes built by calcareous algae frameworks growing in dim-light conditions; Ballesteros, 2006) is considered the most representative Mediterranean mesophotic habitat (Castellan et al., 2022a; Garrabou et al., 2022b). Despite listed as natural habitats of community interest by the EU Habitats Directive (92/43/EEC, code 1170), with an *ad hoc* action plan developed for its safekeeping (UNEP-MAP-RAC, SPA, 2008), no standardized and effective conservation measures have been implemented so far (Gómez-Gras et al., 2021; Pulido Mantas et al., 2022). Over the past two decades, with the increase in frequency and severity of extreme climatic events and related MMEs, the conservation status of shallow coralligenous assemblages (35–50 m depth) is in decline, while their deeper counterpart still remains poorly explored and widely unprotected (Holbrook et al., 2019; Garrabou et al., 2022b; Bramanti et al., 2023), mainly due to the logistical challenges (e.g., fundings, bottom time constrains, sampling effort) in reaching such depths (Navarro-Barranco et al., 2023). Nowadays, the development of technical diving and the rise of low-cost remotely operated vehicles is leading to an increase in accessibility, exploration and monitoring of mesophotic habitats (Armstrong et al., 2019; Pulido Mantas et al., 2023), potentially contributing to a better understanding of their ecological role in the coming years.

Among all organisms affected by MMEs, gorgonian octocorals and Corallinaceae, both representatives of coralligenous assemblages, were identified as the most susceptible taxa, supporting previous studies (Garrabou et al., 2019, 2022b; Estaque et al., 2023). Considered as key-stone species for their high structural complexity and long lifespans, the rapid decline of gorgonian populations is expected to lead to strong disruptions in carbon capture and sequestration potential, sedimentation, larval settlement dynamics, benthic-pelagic coupling, nutrient cycling, nursery effect, and a dramatic simplification of the system food web (Gili and Coma, 1998; Ponti et al., 2014; Cerrano et al., 2019; Gómez-Gras et al., 2021).

The LEK survey received only around 10% of response, suggesting that the mortalities and the recoveries are not easy to be detected also among frequent divers, thus calling for alternative or parallel engagement strategies for future survey efforts. The organization of preliminary online/*in situ*-seminars on the topic or the creation of small clips illustrating the problem at hand before handling the survey, as well as considering the gamification of the survey (e.g., using game-like elements, such as competition and rewards to motivate people) might help on considerably rising the response rate in the future (Deutskens et al., 2004; Triantoro et al., 2020; Sutton, 2021).

Nonetheless, the part of the diving community who responded to the online survey, perceived octocoral populations as the ones showing the higher demographic resilience after MMEs. In particular, most of perceptions of a positive demographic resilience were recorded in those MPAs with nearby mesophotic areas. These results may suggest a potential benefit coming from the presence of deeper populations for certain species, recalling what is defined as the "refugia effect" (Glynn, 1996). Although the refugia hypothesis described for tropical coral reefs cannot be considered a general rule for all taxa, it provides a glimpse of hope also in temperate areas for certain organisms (i.e., gorgonians), suggesting the existence of a potential reservoir of biodiversity in deeper waters (Cerrano et al., 2019; Bramanti et al., 2023). Some studies already proved the importance of mesophotic refugia for many habitat-formers, such as scleractinians (Goodbody-Gringley et al., 2021; Hoarau et al., 2021), octocorals (Pilczynska et al., 2016; Padrón et al., 2018; Bramanti et al., 2023), hydrocorals (Hoarau et al., 2021) or sponges (Beazley et al., 2021; Idan et al., 2020). However, by focussing our efforts mainly on coastal shallow waters over the past century, we put at stake the integrity of deeper habitats, jeopardising a natural buffer that could have helped shallower populations to cope with the current and future climate conditions.

Together with coralligenous, seagrass meadows (mainly of *Posidonia oceanica*) suffered from the effect of MHWs, especially related to MMEs of the noble pen shell *Pinna nobilis*. Being a long-living sessile filter-feeder, this species plays a key ecological role by removing high quantity of detritus from the water, contributing to water clarity, while, presenting a hard shell, it provides a hard substrate within soft-bottom ecosystems (Cabanellas-Reboredo et al., 2019). In the last decade, MMEs of *P. nobilis* (up to 100% of mortality rates) have been related to various pathogens outbreaks (i.e., the protozoan *Haplosporidium pinnae*, and bacteria *Mycobacterium* and *Vibrio* spp.) caused by the high-water temperatures (Cabanellas-Reboredo et al., 2019; Carella et al., 2020; Scarpa et al., 2021). The LEK assessment well described this phenomenon, recording 22 MMEs spread in 17 MPAs around Italy. Within the

Western Mediterranean ecoregion, *P. nobilis* showed a generalised disruption in recruitment, putting the recovery of its populations in a dramatic scenario (Kersting et al., 2020). Among all the analysed MPAs, the demographic resilience of this species was, in fact, recorded only on one occasion, suggesting that its fate is uncertain also at Italian scale.

Considering the assessment of MMEs and demographic resilience occurrences, the higher interest for charismatics habitats (i.e., *Posidonia* meadows and coralligenous assemblages) and species (i.e., gorgonians and *P. nobilis*) have surely biased the current knowledge and general picture we obtained on these phenomena. We, therefore, suggest that a greater effort in the monitoring of MMEs should be addressed towards less monitored habitats (e.g., soft bottoms) as well as less charismatic taxa (e.g., sponges and bryozoans) known to be sensitive to such events and to be crucial in the ecosystem functioning. The implementation of citizen science initiatives by diving centres with the engagement of trained volunteer divers may help to overcome this issue, thus playing a fundamental role in the monitoring and potential conservation strategies (Garrabou et al., 2022a; Figuerola-Ferrando et al., 2023; Coppari et al., 2024).

Overall, our results seem to suggest that areas characterised by the vicinity of mesophotic conditions may show a better demographic resilience for certain taxa (i.e., gorgonians) compared to areas surrounded by shallower bathymetries or with respect to remote islands (e.g., Isola di Ustica and Isole Pelagie; Fig. 6). Remote islands generally suffer from genetic isolation due to a limited larval supply given by the lack of connection with the mainland, as reported in the MacArthur and Wilson's hypothesis (1967) for terrestrial ecology, and recovery of biodiversity is generally limited. Previous studies demonstrated that a physical connection with the mainland, such as seamount chains, can play a critical role in marine species connectivity and population dynamics, providing stepping stones for island colonisation (Pinheiro et al., 2017; Hirschfeld et al., 2023). The climate crisis is altering benthic communities, but long-term effects can be different depending on the local geomorphology and hydrodynamic conditions (Fig. 6). It is urgent to define the main key-species connectivity dynamics and, thus, the refugia potential of mesophotic habitats on a coherent MPA network to select stepping-stone climatic oases that could ensure long-term conservation efforts, in line with present and future international marine policies (Podda and Porporato, 2023).

5. Conclusions

During the past few years various climate mitigation strategies have been proposed for the design of more resilient MPA networks (Gross et al., 2016; Simard et al., 2016; Bates et al., 2019; Jacquemont et al., 2022; Zentner et al., 2023), highlighting genetic connectivity as a critical attribute for the definition of effective networks (Smith et al., 2023). The approach proposed in this study may help to focus the monitoring and conservation efforts of MPA managers on specific areas, and it may guide local, regional and national stakeholders supporting an evidence-based planning of new protected areas and helping in the consolidation of a more coherent MPA network. Nonetheless, if this strategy will be applied in the future, some challenges and opportunities could arise concerning both a conservation and a socio-economic perspective (Ban and Klein, 2009). For example.

(i) The extension and/or the creation of new protected areas may entail a rise of the costs in terms of personnel, monitoring/operational efforts and management (Ban and Klein, 2009);

(ii) Considering that one of the main tasks of an MPA is the monitoring of the habitats included inside its boundaries (Gross et al., 2016), the need of trained technical scientific divers and/or remotely operated vehicles (ROVs) is required due to the depths at which mesophotic habitats develop. Due to the high cost of mixed-gas diving and of ROV operations, the involvement of local diving centres and trained volunteers with the proper skills can represent a great opportunity to reduce operational costs, also triggering citizen science initiatives (Coppari et al., 2024);

(iii) The implementation of the most effective communication strategies to inform the local stakeholders (e.g., commercial, artisanal and recreational fishermen) that might be affected by the change of MPA boundaries and protection measures. This can increase the local community awareness on the crucial role played by mesophotic habitats in sustaining commercial fish stocks, thus ensuring the long-term effectivity of the new/enlarged MPAs.

Even though the response rate obtained through the LEK approach is a limitation for the present study, the insights gathered from divers' perspectives and expert opinion partially address the scientific gap

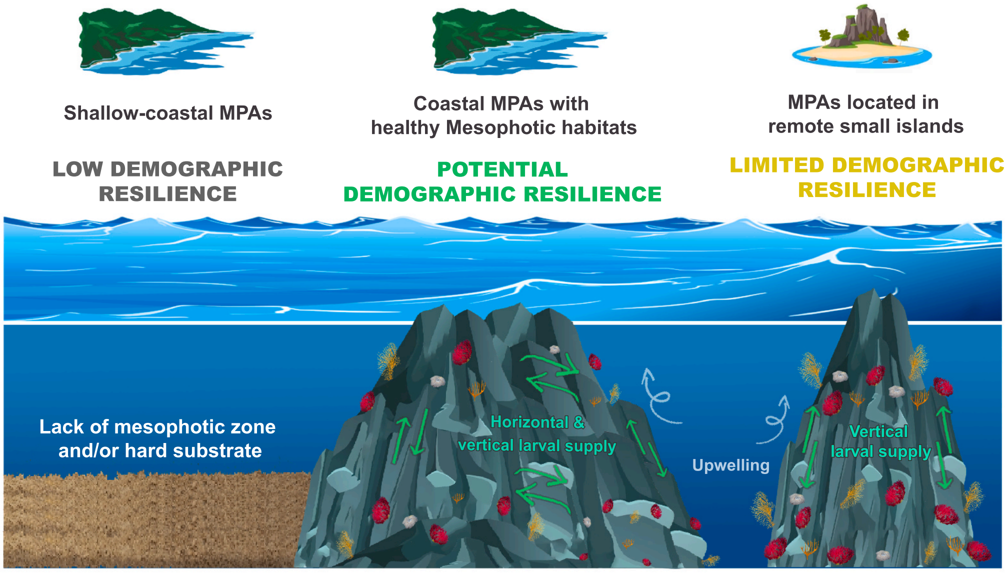

Fig. 6. Conceptual representation of the mesophotic potential enhancement of demographic resilience, considering the MacArthur and Wilson (1967) and the more recent works of Pinheiro et al. (2017) and Hirschfeld et al. (2023).

related to the potential of habitat resilience in the Mediterranean Sea. This information can be helpful in identifying indicators for testing the hypothesis that the mesophotic zone may play a role in the resilience of shallower habitats, depending on the local geomorphology and the level of protection within MPAs. To conclude, the EU Biodiversity Strategy 2030 states that the Member States pledge to protect 30% of the EU's land and 30% of its marine areas by 2030, of which 10% must be strictly protected, and we here highlight the urgency to start including the mesophotic zone in the criteria for future Marine Spatial Planning efforts to identify areas to be strictly protected.

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Declaration of generative AI

During the preparation of this manuscript, the authors did not use any generative AI and/or AI-assisted technologies in the writing process.

CRediT authorship contribution statement

Torcuato Pulido Mantas: Writing – original draft, Formal analysis, Conceptualization. **Camilla Roveta:** Writing – original draft, Formal analysis, Conceptualization. **Barbara Calcinai:** Writing – review & editing. **Claudia Campanini:** Writing – review & editing. **Martina Coppari:** Writing – review & editing. **Pierpaolo Falco:** Writing – review & editing. **Cristina Gioia Di Camillo:** Writing – review & editing. **Joaquim Garrabou:** Writing – review & editing, Conceptualization. **Man Chun Lee:** Writing – original draft, Formal analysis, Conceptualization. **Francesco Memmola:** Formal analysis. **Carlo Cerrano:** Writing – review & editing, Conceptualization.

Declaration of competing interest

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106676.

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