Latin American Journal of Aquatic Research, 53(4): 703-711, 2025
DOI: 10.3856/vol53-issue4-fulltext-3279

Short Communication

Marine animal forests in temperate mesophotic ecosystems of Central Chile

Ana N. Campoy[1], Florencia Ponce-Toro[2], Rodrigo Alarcón-Ireland[3,4] Judith Camps-Castellà[5,6] & Miriam Fernández[2,3,4]
[1]Department of Ecology and Geology, Faculty of Sciences, University of Malaga, Málaga, Spain
[2]Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
[3]Millennium Nucleus for the Ecology and Conservation of Temperate Mesophotic Reef Ecosystems (NUTME), Las Cruces, Chile
[4]Estación Costera de Investigaciones Marinas (ECIM), Pontificia Universidad Católica Las Cruces, Chile
[5]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia Universitat de Barcelona, Barcelona, Spain
[6]Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción Concepción, Chile
Corresponding author: Ana N. Campoy (anavcampoy@gmail.com)

ABSTRACT. Marine animal forests (MAFs) play a crucial role in enhancing biodiversity and ecosystem functionality in marine environments. However, MAFs are poorly known in some ecosystems. This study focuses on one of the least known ecosystems, temperate mesophotic ecosystems (TMEs), by characterizing and quantifying branching invertebrates, particularly corals and sponges, that form MAFs in Central Chile. Utilizing towed underwater video surveys, we identified and quantified three key taxa, the octocorals *Leptogorgia chilensis* and Plexauridae, and the sponges *Axinella* spp., across various depths and locations along the central Chilean coast. In addition, we report the presence of black corals (Antipatharia) in the study area. Our findings expand the known geographical and bathymetric ranges of these taxa, thereby contributing to the limited understanding of habitat-forming species in TMEs within this region. Considering the ecological value of MAFs, this study emphasizes the critical need to advance in understanding their role in hosting biodiversity and fostering ecological interactions, particularly in less-studied ecosystems, and provides a foundation for effective management and conservation initiatives.

Keywords: habitat-forming species; corals; sponges; video surveys; Chile

Marine animal forests (MAFs) are defined as three-dimensional structures formed by benthic animals acting as autogenic ecosystem engineers, which provide new ecological niches and colonization surfaces for other organisms, resulting in enhanced diversity and increased provision of functions and services (Rossi 2013, Orejas et al. 2022). They are vital for numerous species, providing food, shelter, and breeding grounds within them, often serving as critical nursery habitats for various mobile species throughout their lifecycle (Cerrano et al. 2009, Rossi 2013). Furthermore, MAFs enhance benthic-pelagic coupling, function as significant carbon and nutrient sinks, influence current flow velocity, and facilitate the reten-

Associate Editor: Laura Schejter

tion of particles. Some of these processes contribute to coastal protection and erosion mitigation (Rossi 2013, Försterra et al. 2017, Ponti et al. 2017, Rossi et al. 2017).

Corals, sponges, bryozoans, and ascidians primarily engineer MAFs. Notably, the role of these structuring species in mesophotic reefs is particularly noteworthy. These light-dependent ecosystems are found in the twilight zone, commonly between 30 and 150 m depth, exhibiting a community composition and structure that vary markedly between (sub) tropical areas (mesophotic coral ecosystems, e.g. Kahng et al. 2017, Loya et al. 2019, Bongaerts 2022) and temperate seas (temperate mesophotic ecosystems - TMEs, e.g. Cerrano et al. 2019, Bell et al. 2022). Notably, while kelp and algae decrease in prevalence with depth, benthic invertebrates such as sponges, gorgonians, brachiopods, and anemones exhibit increased prevalence in TMEs compared to shallower ecosystems, suggesting the critical ecological role of MAFs within these environments (Bell et al. 2022, Campoy et al. 2023).

There is a significant gap in our knowledge of MAF biodiversity along the southeastern Pacific coast of South America. In Chile, the role of structuring invertebrates has received less attention than that of macroalgae from shallow-water habitats (e.g. Almanza & Buschmann 2013, Vásquez et al. 2014). While research efforts have expanded significantly over the past two decades, they have been unevenly distributed across this vast territory. Biodiversity surveys conducted between 1998 and 2016 in the south Chilean fjord region have uncovered diverse assemblages dominated by habitat-forming species such as the scleractinian *Desmophyllum dianthus*, the hydrocoral *Errina antarctica*, the octocorals *Thouarella* spp., *Acanthogorgia* spp., and *Primnoella chilensis*, or the black coral *Lillipathes* sp. (Häussermann 2006, Häussermann & Försterra 2007, Försterra et al. 2017). Other taxa also form habitats along the Chilean Patagonia, e.g. different mussels and the brachiopod *Magellania venosa* form banks, aggregations of the barnacle *Austromegabalanus psittacus,* or sponge fields (Försterra et al. 2017). North of the fjord region, knowledge of MAFs along the Chilean coast is limited. Recent research has begun to shed light on the TMEs of Central Chile, revealing a notable abundance of sponges and octocorals, while also underscoring the need for further investigation into these vital ecosystems (Campoy et al. 2023). Structuring species recognized in this study included the gorgonian *Leptogorgia chilensis* found at depths of 25-57 m, and the branching sponges *Axinella* spp. at 32-58 m depth. *L. chilensis* was also previously reported in Algarrobo at 33°21.6'S (Breedy & Guzmán 2007, Camps-Castellà et al. 2023). Camps-Castellà et al. (2024) describe dense gorgonian gardens of another *Leptogorgia* species in shallow waters (5-30 m) of Caleta Pichicuy (32°21'S). Another octocoral, *Phycogorgia fucata*, has been described from southern (36°16.2'-39°57'S) at depths of 5-45 m (Breedy et al. 2021). Sparse studies of the bycatch of demersal fisheries have also revealed previously unnoticed structuring of corals in continental Chile (e.g. Araya et al. 2018). On the other hand, marine sponges remain largely unexplored in Chile despite some research efforts (Desqueyroux & Moyano 1987, Azevedo et al. 2009). It is important to note that most of the studies on this taxonomic group have also focused on the Chilean Patagonia region (Willenz et al. 2009, Hajdu et al. 2013, Bertolino et al. 2019). As of 2020, a total of 187 species had been described, with only 73 identified north of the fjord region (Bertolino et al. 2020). In general, the characterization and current status of MAFs in Chile are limited, despite increasing anthropogenic impacts in their distributional area.

Comprehensive research to map MAFs is essential for accurately assessing their roles in ecosystem services and informing effective management and conservation strategies (Rossi 2013, Braga-Henriques et al. 2022). This study is focused on branching or tree-like invertebrates with the potential to form MAFs. Specifically, it presents, describes, and quantifies them along the Central Chilean coast, a region with a high concentration of human activity. To achieve this, this work builds upon previously collected and reported data by Campoy et al. (2023).

Towed underwater video (TUV) surveys were conducted to describe and quantify the mesophotic community along the Central Chilean coast. The TUV methodology consisted of a camera system (SeaViewer 6000 HD Sea Drop) equipped with 21 LED lights and two parallel lasers for a reference scale (11 cm) suspended beneath a drifting vessel by a 150 m live-feed cable. As the vessel moved forward at an average speed of 1.4 m s^{-1}, the camera recorded video while maintaining a distance of 0.5-1 m from the seafloor. The timing and location were collected and stored simultaneously by a GPS device (Garmin GPS Map Sounder Model 420s) at 30-s intervals. TUV transects were conducted at four sites along the Central Chilean coast from October 2018 to January 2019 (Campoy et al. 2023). The four sites, spanning approximately 400 km, were, from north to south, Los Vilos (~31°52.8'S),

Algarrobo (~33°21'S), El Quisco (~33°24'S), and Las Cruces (~33°29.4'S). Following a rocky substrate, multiple transects were conducted from depths of 4.7 to 95.5 m. More details on the sampling and the methodology are reported in Campoy et al. (2023).

Campoy et al. (2023) described and quantified the benthic community using quadrats placed along the TUV transects. While this methodology provided a comprehensive overview of the community within the sampled area, the quadrats did not include a vast area, and thus, a) some structuring species may have gone unnoticed, and b) the distribution of the described species may be biased. To account for these limitations, we reanalysed the TUVs and quantified all the habitat-forming invertebrates that could be recognized. We focused on branching or tree-like species for a double reason: a) they have the potential to form MAFs, especially relevant in TMEs where other habitat-forming species as macroalgae are absent, b) they are clearly distinguished in the TUVs, while other morphologies like encrusting or massive, are difficult to identify, and c) the number of colonies can be quantified irrespective of the camera angle.

The first step in examining the TUVs was to select the sections of the videos that could be analysed. Since the GPS divided the videos into approximately 30-s intervals (with timing and location data), we first deleted those intervals for which the visibility prevented us from recognizing the target species which occurred in various situations: a) due to natural visibility conditions, b) when the camera was not pointing to the sea bottom due to the manual control, c) when the light was insufficient, and the image became too dark at greater depths, and d) when the lasers could not be distinguished. In addition, we deleted intervals for which more than 50% of the recording was on sandy substrate since the target species inhabit reefs. This process resulted in a total of 516 video intervals, with a duration range of 2-37 s (29.5 ± 3.09 s; mean ± standard deviation, SD), 1-42 m length (12.77 ± 5.57 m), 0.22-4.88 m width (2.26 ± 0.87 m), and a calculated 0.59-110.26 m^2 area (30.43 ± 20.01 m^2) (see Data availability). Using this data, we created distribution maps in QGIS (QGIS Development Team, 2017) and generated distribution graphs with R software (R Core Team 2022) using the ggplot2 library (Wickham 2016).

From the TUV surveys, three taxa were recognised and quantified: two octocorals and sponges of the genus *Axinella* (here identified as *Axinella* spp.). Among the octocorals, one species was recognized as *L. chilensis* (Fig. 1a,d), while the other was identified as belonging to the family Plexauridae (Fig. 1b,e-f). *L. chilensis* is easily distinguishable due to its larger sizes (>30 cm in length and width), presenting a lanky and bushy appearance with long, slender, light pink branches that are dichotomously divided in a single plane (Breedy & Guzmán 2007, Camps-Castellà et al. 2023). Plexauridae colonies are much smaller than *L. chilensis*, with varying colours from reddish to purple, with branching (not always present) in multiple planes and generally thicker branches. It is prone to confusion with another species of the genus *Leptogorgia*, also present in Central Chile (Camps-Castellà et al. 2024); however, Plexauridae is less bushy, often presenting a single branch (Fig. 1b,f). The branching sponges were identified as *Axinella* spp., as they are clearly distinguished by their bright to pale yellow colouration, branching more commonly in a single plane, with or without a central branch (Fig. 1a,g-i). Observed morphological variation suggests the presence of more than one species of Plexauridae and *Axinella* in the study area. The three taxa were found growing in flat to vertical rocky substrates. Not all branching invertebrates could be identified in the videos, although some of them were forming dense MAFs.

The density of *Axinella* spp. varied from 0 to 5.66 ind m^{-2}, being the taxon with the highest density. *L. chilensis* reached maximum densities of 2.29 ind m^{-2}, while Plexauridae was recorded more sparsely, with less than 1 ind m^{-2}. *Axinella* spp. and *L. chilensis* appeared broadly distributed in the studied area, in contrast, Plexauridae only appeared in Los Vilos and Las Cruces (Table 1).

Axinella spp. were recorded in a depth range of 30.9 to 82.1 m. The maximum density occurred at 57.1 m in El Quisco (Fig. 2). All video intervals with more than 50 ind were also registered in El Quisco.

L. chilensis was found at depths ranging from 32 to 76.2 m, and its maximum density was observed at 60 m in Algarrobo (Fig. 3).

Plexauridae exhibited the more extensive depth range and the deeper records, ranging from 34.9 to 97.3 m, although the pattern was skewed towards shallower depths. Thus, its maximum density occurred at 39.5 m in Los Vilos (Fig. 4). Although they appear in 24 video intervals in Los Vilos, they always exhibit very low densities.

L. chilensis and *Axinella* spp. had a wide distribution across sites. The density of these species was positively correlated, with a Pearson correlation coefficient of 0.66 ($P < 0.001$). By contrast, the correlation of these species with Plexauridae was lower than 0.1 (-0.4 with *L. chilensis*, and 0.01 with *Axinella* spp.).

Figure 1. a-c) Video frames (species indicated by an arrow), and d-i) photographs showing the four taxa of this study. a) *Leptogorgia chilensis* and *Axinella* sp., El Quisco, 50.3 m, b) Plexauridae, Los Vilos, 39.5 m, c) Antipatharia, Los Vilos, 61.3 m, d) *L. chilensis*, Algarrobo, 30 m, e) Plexauridae, Los Molles, 40 m, f) Plexauridae, Pichicuy, 45 m, g-i) *Axinella* spp., Los Molles, 35-38 m. Photographs by Alejandro Pérez-Matus (d), Diego Gatica (e, g-i), and Judith Camps-Castellà (f).

In addition to the identification of these three taxa, five colonies of black corals (order Antipatharia) were distinguished in five different video intervals of Los Vilos (31.87-31.88°S), between 64.1 and 80.7 m depth (see Data availability). A black skeleton and an arborescent shape distinguished these specimens (Fig. 1c).

As a result of these findings, this study expands the reported geographic ranges of *L. chilensis*, *Axinella* spp., Plexauridae, and Antipatharia. Notably, two of these taxa (Plexauridae and Anthipatharia) were overlooked using the benthic survey methodology outlined by Campoy et al. (2023), likely due to their focus on the general benthic community and the use of quadrats, which required a perpendicular view of hard substrates as a strict prerequisite for estimating percent cover.

Recent reviews of Chilean corals (Delgado 2009, Addamo et al. 2022) did not document *L. chilensis*. However, it was previously included in a revision of this genus, where the species originally cited in Algarrobo (Philippi 1866) was re-described using a specimen from California (Breedy & Guzmán 2007). Subsequently, Camps-Castellà et al. (2023) suggested that the Chilean specimens might represent a distinct species from those in California. They reported its distribution in Chile between 32 and 33°S at depths of 30-45 m. More recently, Campoy et al. (2023) documented the species between 31.8 and 33.7°S at depths of 25.2-57 m. This study reveals that the depth

Table 1. Density (ind m^{-2}) of each taxon on each site and across sites. Values indicate density range (minimum-maximum) and mean density ± standard deviation in parentheses. Maximum density is shown in bold. The total mean is the mean of the sites where the species appeared.

	Las Cruces	El Quisco	Algarrobo	Los Vilos	Total
Axinella spp.	0-1.04 (0.09 ± 0.19)	0-**5.66** (0.57 ± 1.35)	0-5.19 (0.15 ± 0.59)	0-1.70 (0.04 ± 0.20)	0-5.66 (0.15 ± 0.61)
Leptogorgia chilensis	0-0.36 (0.04 ± 0.07)	0-1.49 (0.20 ± 0.36)	0-**2.29** (0.10 ± 0.30)	0-0.08 (0.00 ± 0.01)	0-2.29 (0.07 ± 0.22)
Plexauridae	0-0.03 (0.00 ± 0.00)	-	-	0-**0.87** (0.03 ± 0.11)	0-0.87 (0.02 ± 0.33)

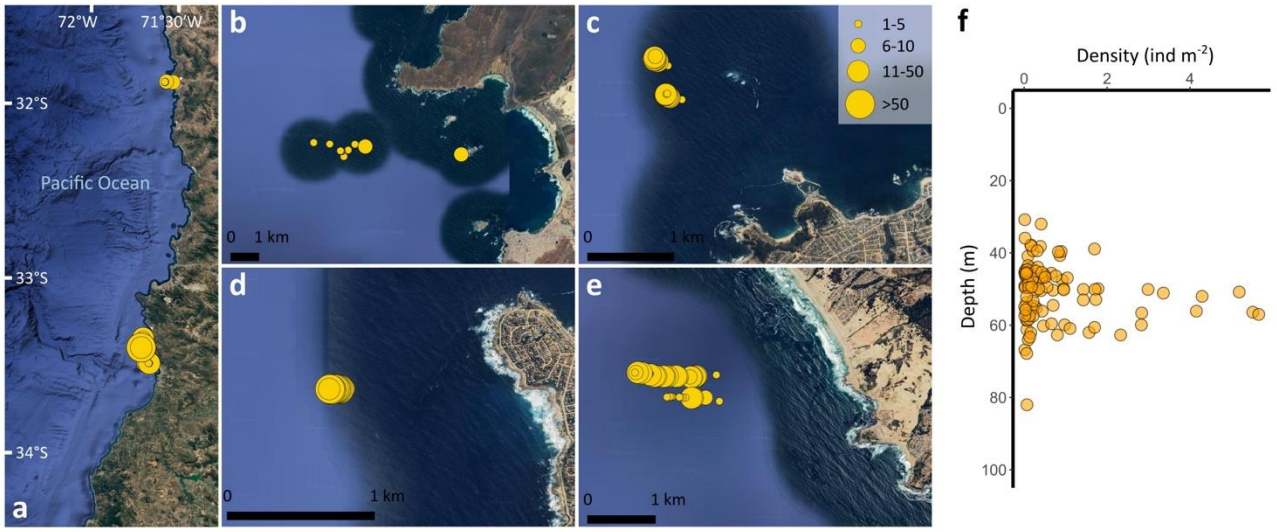

Figure 2. Distribution of *Axinella* spp. The number of individuals on each video interval is proportional to the size of the circles, as the legend shows in the top right. a) General overview of the study area, b) detailed view of Los Vilos, c) detailed view of Algarrobo, d) detailed view of El Quisco, e) detailed view of Las Cruces, and f) density distribution in depth across sites.

range of *L. chilensis* can extend to a maximum of 76.2 m.

Delgado (2009) and Addamo et al. (2022) document various genera within the family Plexauridae. However, most have recently been reassigned to the families Paramuriceidae and Gorgoniidae (McFadden et al. 2024). Among these, *Muriceides* (Paramuriceidae), *Psammogorgia* (Gorgoniidae), and *Swiftia* (Plexauridae) are potentially present in our study area (Delgado 2009, Addamo et al. 2022). The species we have encountered do not bear resemblance to any of these genera, and due to limitations in our image resolution, further identification is not feasible at this point. To progress, collecting samples and conducting morphological and genetic analysis is essential. Nonetheless, this marks the first record of Plexauridae at 33°S (Las Cruces). Given its presence at the northern site (31.8°S, Los Vilos), it is conceivable that its distribution also includes intermediate locations.

Antipathes, *Chrysopathes*, *Leiopathes*, and *Lillipathes* (Antipatharia) have been reported in our study area (Delgado 2009, Addamo et al. 2022), but all records are from depths greater than our target depth (>100 m). Gorny et al. (2018) reported the first shallow-water record of a black coral in continental Chile. They distinguished two morphological species, namely Antipatharia sp. 1 and 2, at 107 and 70 m, respectively, in the Coquimbo Region (29°S). Since there have been no subsequent findings at these depths, our five black corals represent the second record of shallow-water black corals for continental Chile. Given the proximity of the records (31°54'S), they could belong to the same

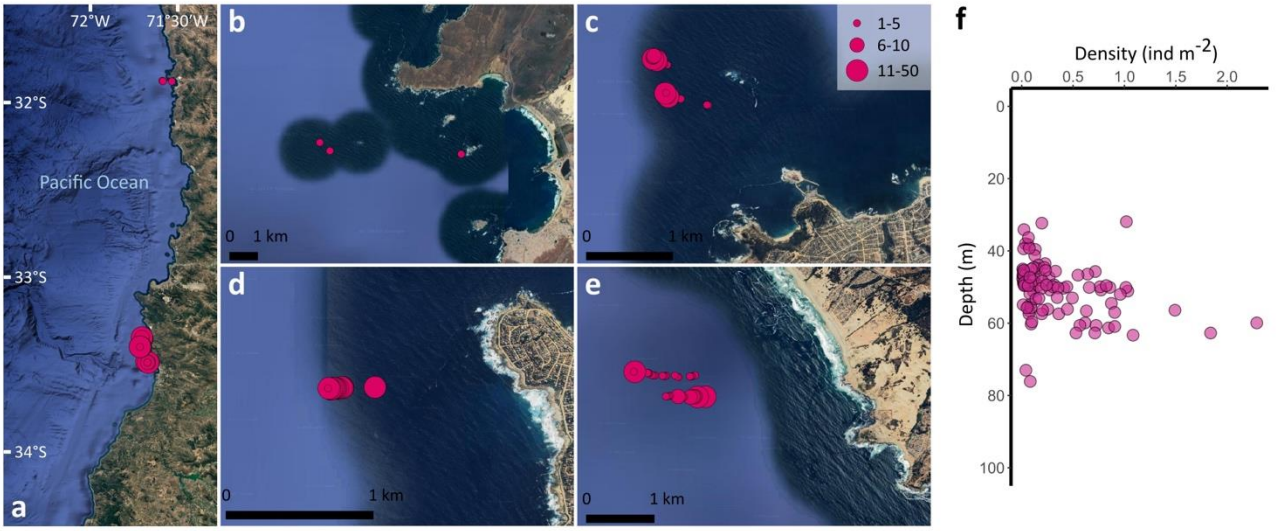

Figure 3. Distribution of *Leptogorgia chilensis*. The number of individuals on each video interval is proportional to the size of the circles as the legend shows in the top right. a) General overview of the study area, b) detailed view of Los Vilos, c) detailed view of Algarrobo, d) detailed view of El Quisco, e) detailed view of Las Cruces, and f) density distribution in depth across sites.

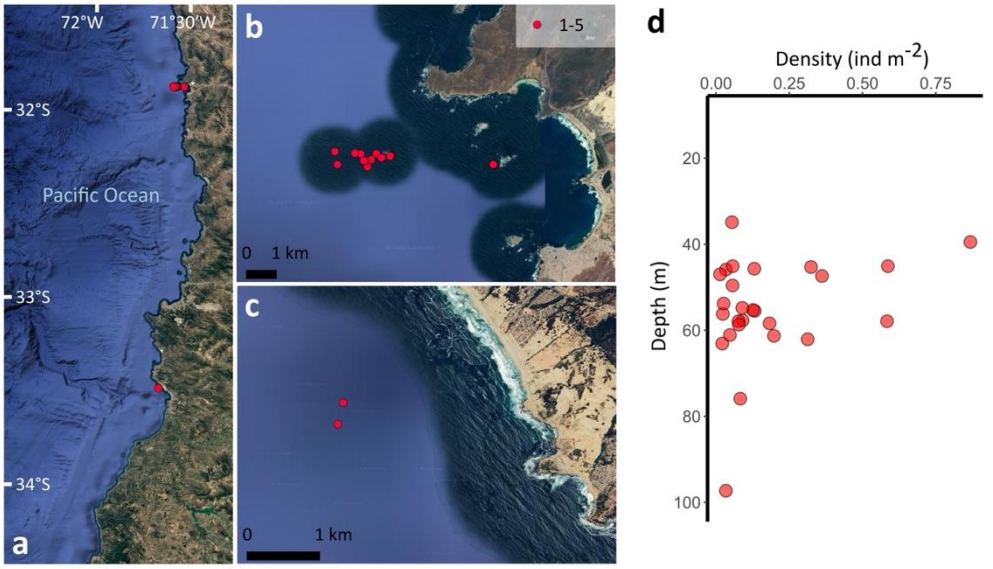

Figure 4. Distribution of Plexauridae. a) A general overview of the study area, b) a detailed view of Los Vilos, c) a detailed view of Las Cruces, and d) density distribution in depth across sites.

species reported by Gorny et al. (2018). Like theirs, the specimens identified here were characterized by their dark skeleton and branching morphology. Although the image quality is severely deficient, the appearance and branching pattern closely resemble those of Antipatharia sp. 2, i.e. bushy and arborescent. The presence of black corals in this area suggests a well-preserved environment since these organisms are highly long-lived and slow-growing (Gori et al. 2017).

L. chilensis and *Axinella* spp. were found together on several occasions, forming multispecies MAFs, which suggests that these species share similar ecological or environmental preferences. *Axinella* spp. were previously reported at depths of 32-57.9 m (Campoy et al. 2023), whereas in this study, they were observed at depths ranging from 28.85 to 78.58 m. In Chile, the only species of the genus *Axinella* described outside the Patagonia region is *A. crinita* (Bertolino et al. 2020).

The species observed in this study could correspond to this species, but some observed individuals might also represent a different (probably undescribed) species. To address this question, an in-depth study is necessary, including an examination of the spicule morphology of these specimens.

The primary contribution of this study is to draw attention to the often-overlooked or under-mapped MAFs in Central Chile. Due to their shape and size, tree-like corals and sponges are particularly vulnerable to demersal fishing, as they remain easily entangled in nets and longlines (Gori et al. 2017). They are commonly encountered as bycatch on fishing lines (e.g. Araya et al. 2018). MAFs associated with TMEs may be particularly vulnerable, as these reefs are target areas for conger fisheries (*pers. obs.*). Furthermore, it appears that benthic fishing for piure (*Pyura chilensis*), which involves removing entire rocks including the attached gorgonians, also harms these corals in shallow waters (*pers. obs.*).

The vulnerability of certain MAFs to fishing activities is internationally recognized under the designation of Vulnerable Marine Ecosystems (UNGA Resolution 61/105, FAO 2009). Specifically, MAFs must be unique, rare, fragile, or difficult to recover after damage to qualify as Vulnerable Marine Ecosystems (Orejas et al. 2022). However, insufficient information is available to assess the health status of these ecosystems in Chile. Therefore, increased efforts are needed to: 1) address the significant gaps in taxonomic knowledge surrounding these species to establish reliable diversity baselines, 2) map Chilean MAFs in general, and particularly areas exhibiting high densities of these species or that qualify as Vulnerable Marine Ecosystems to prioritize their protection, and 3) deepening our ecological understanding of these species, including the connectivity and resilience of their populations.

Credit author contribution

A.N. Campoy: conceptualization, validation, supervision, formal analysis, writing-original draft; F. Ponce-Toro: methodology, data curation, review, and editing; R. Alarcón-Ireland: conceptualization, methodology, review, and editing; J. Camps-Castella: methodology, review and editing; M. Fernández: conceptualization, funding acquisition, project administration, supervision, review, and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

Data availability

The distribution data that support the findings of this study are available at [https://github.com/anavcampoy/MAFsCentralChile].

ACKNOWLEDGMENTS

We acknowledge Katherine Espinoza and Carlos Molinet for their advice on using the towed underwater video cameras. We especially thank Ainara Aguilar for her collaboration on field trips. This research was partially funded by the Núcleo Milenio NUTME, grant No. ICM_NCN19_056. We thank the NUTME team, especially Vladimir Garmendia, Evie A. Wieters, and Alejandro Pérez-Matus, for their support.

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Received: June 3, 2024; Accepted: July 29, 2025