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Competition for space limits the expansion of biogenic tubeworm reefs

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ABSTRACT: Competition for space is a critical driver of the distribution and dynamics of sessile marine organisms. This study investigated the competitive interactions between the honeycomb tubeworm *Sabellaria alveolata* and other sessile species, such as mussels, barnacles and articulated coralline algae, that dominate breakwaters along the Latium coast of the Northern Tyrrhenian Sea. We tested the hypothesis that removing dominant sessile organisms adjacent to *S. alveolata* patches would promote bioconstruction expansion. To test for the temporal generality of such a response, we performed 3 experimental trials differing in the timing of experimental removal of potential competitors of *S. alveolata*. In all trials, the percent cover of *S. alveolata*, estimated over about 1 yr, increased in cleared plots compared to unmanipulated control plots, where it was consistently almost null. The maximum expansion of sabellariid cover occurred where clearing preceded or coincided with the seasonal growth phase of *S. alveolata*. These findings highlight the role of competition in shaping the development of *S. alveolata* reefs and suggest its possible interplay with other temporally variable processes, such as natural life cycles and anthropogenic disturbances. They can also inform conservation strategies to preserve the ecosystem services provided by honeycomb worm reefs under increasing anthropogenic and natural environmental pressures.

KEY WORDS: Biogenic reef · Competition · Intertidal · Space occupancy · Temporal variation

1. INTRODUCTION

Competition is a primary biological driver of distribution patterns of marine organisms (Connell 1961, Hawkins & Hartnoll 1985, Keough et al. 1997, Edwards & Connell 2012). There is broad evidence, in particular, that species distribution ranges may shrink in the presence of other species with similar requirements (Endean et al. 1956, Angel et al. 2006, Godsoe et al. 2015). Competition for space is of overwhelming importance, especially for sessile organisms, and plays a fundamental role in the structure and dynamics of marine assemblages (Paine 1966, Schonbeck & Norton 1980, Firth & Crowe 2010, Lafferty & Suchanek 2016). Intertidal habitats, for example, are characterized by severe physical stress due to wave energy (Denny 1987, Gaylord 1999, Ventura et al. 2021) and extreme temperatures and desiccation (Raffaelli & Hawkins 1999, Denny & Wethey 2001). This makes the intertidal a very demanding environment, where space for settlement and growth is limiting for sessile organisms due to the monopolization of suitable spots by competitively dominant species (Worm & Karez 2002, Steinberg & Epifanio 2011). As a classic example, manipulative experiments showed that the competition between the barnacles *Chthamalus stellatus* and *Semibalanus balanoides* is a key factor shaping their vertical distribution on intertidal rocky shores. *S. balanoides* achieves a higher population density at low intertidal level, where it can

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outcompete *C. stellatus* by crowding or smothering. This interspecific competition restricts *C. stellatus* to the high shore, where the establishment of *S. balanoides* is prevented by its lower tolerance to heat and desiccation (Connell 1961). Similarly, on a Mediterranean rocky shore, the experimental removal of dominant sessile organisms, i.e. barnacles, turf-forming and encrusting algae, determined the expansion of the vertical range of distribution of the red alga *Rissoella verruculosa* and increased the local abundance of cyanobacteria and limpets (Benedetti-Cecchi et al. 1999).

Other strong competitors for space in intertidal environments are mussels, which can monopolize the substrate and drastically affect the structure of assemblages on several rocky shores worldwide (Paine & Levin 1981, Enderlein & Wahl 2004, Little et al. 2009, Erlandsson et al. 2011). Evidence of this has accumulated since the mid-1960s, when it was shown that the removal of the predatory sea star *Pisaster ochraceus* led to the shift from patches hosting diverse assemblages of algae and invertebrates to patches monopolized by mussels (Paine 1966). This underscores the effectiveness of removal experiments to assess the mechanisms that shape ecological communities (Díaz et al. 2003, Lilley & Schiel 2006). In such a context, the ecological importance of disturbance timing has also been widely reported (Peterson & Stevenson 1992, Addessi 1994, Hutchinson & Williams 2003, Kim et al. 2017) and related to its interaction with propagule supply (Sousa 2001, Bellgrove et al. 2004), recruitment seasonality (Underwood & Anderson 1994), dispersal patterns and fluctuations in the abundance of dominant species (Kim & DeWreede 1996, Foster et al. 2003), and climate change (Bernhardt & Leslie 2013).

The gregarious honeycomb polychaete *Sabellaria alveolata* builds extensive reefs in intertidal and shallow subtidal habitats with relatively high hydrodynamic energy and abundant suspended sediments in the Eastern Atlantic and the Mediterranean Sea (Naylor & Viles 2000, Dubois et al. 2002, Ingrosso et al. 2018, Sanfilippo et al. 2020; see also https://www.seanoe.org/data/00610/72164/). These reefs play a crucial ecological role stabilizing sediment, providing habitat for numerous species, and modulating coastal dynamics (Bertocci et al. 2017, Gravina et al. 2018, Jones et al. 2018, 2020, Bonifazi et al. 2019, Ventura et al. 2024), although being threatened by intensifying meteorological events (Tillin & Jackson 2018), harvesting of valuable associated species (Storari et al. 2024), and human trampling (Plicanti et al. 2016). As a result, *Sabellaria* reefs are categorized under Annex I of the EC Habitats Directive (European Council Directive 92/43 [https://eur-lex.europa.eu/eli/dir/1992/43/oj/eng] concerning the Conservation of Natural Habitats and of Wild Fauna and Flora) as a marine habitat that requires protection through the establishment of 'Special Areas of Conservation'.

Previous studies have discussed possible competition for space and food between *S. alveolata* and bivalves (Dubois et al. 2006) and have reported the ability of barnacles to encroach on the tubes of the honeycomb worm *Phragmatopoma californica* (Multer & Milliman 1967). In addition, stable isotope analyses suggested that differential food particle size selection from the water column may reduce competition between *S. alveolata* and other filter-feeding species, such as mussels and barnacles (Dubois & Colombo 2014, Jones et al. 2021). Nevertheless, there is a lack of experiments testing whether competition for space is a key limiting factor for the expansion of sabellariid reefs. To our knowledge, the only exception is a study that compared the occurrence of *S. alveolata* bioconstruction between boulders colonized by the invasive Pacific oyster *Magallana gigas* and bare boulders in Ireland. *S. alveolata* was primarily found on the underside of boulders and was greatly inhibited by the increasing cover of both living and dead oysters on the top side (Green & Crowe 2013). Filling these knowledge gaps would make an essential contribution to overcome the 'Data Deficient' classification attributed to sabellariid reefs in the IUCN Red List of Habitats (Gubbay et al. 2016).

In this study, we hypothesized that the development and expansion of *S. alveolata* patches would be hindered by the presence of sessile organisms that monopolize the rocky substrate at their external edges. Indeed, asexual reproduction is not known to occur in *S. alveolata* (Muir et al. 2020), consistent with the observation that clonality occurs in less than 1% of polychaetes (Wilson 1986). Therefore, apart from the growth of juvenile individuals in the early stages of development of new reefs, the most likely way of expansion of mature isolated patches is the settlement at their borders of drifting *S. alveolata* larvae and their subsequent development as formers of new tubes, a process that could be facilitated by the lack of competitors for space adjacent to the existing bioconstructed patch. This hypothesis was tested through the experimental removal of adjacent sessile organisms and the subsequent monitoring of the reef expansion towards the cleared areas. Moreover, the experiment was repeated 3 times to assess the temporal generality vs. context-dependancy of outcomes.

2. MATERIALS AND METHODS

2.1. Study area

The study was carried out at Marina di San Nicola, a sandy beach located along the northern Latium coast in the Northern Tyrrhenian Sea (12° 6′ 27.385″ E, 41° 55′ 55.647″ N). Despite intense terrigenous inputs from the nearby Tiber River, over the last decades this area has been subject to intense coastal erosion (Tortora 2020), which has been mitigated by the construction of breakwaters made of basalt and limestone blocks. Here, a recent study has mapped several emerged and submerged *Sabellaria alveolata* formations (Ventura et al. 2018), which are also common at other Latium locations, such as Ostia (about 30 km south of Marina di San Nicola), where they occupy, as extensive reefs or isolated concrections, a total area of approximately 275 000 km^2 along about 5 km of coastline (Bonifazi et al. 2019).

Our experiment focused on patches of *S. alveolata* bioconstructions developed on 3 breakwaters and alternating with adjacent rocky patches colonized by other sessile organisms, including mussels (*Mytilus galloprovincialis*), barnacles, mainly *Chthamalus stellatus*, and articulated coralline algae, such as *Ellisolandia elongata*, as the dominant species.

Breakwaters at the study site are tens of metres long and a few metres wide, positioned parallel to the shoreline and separated by about 100 m. Due to their similar orientation and proximity to the coast, it can be assumed that they are subject to comparable environmental conditions, including climatological, hydrological, sedimentary factors and accessibility to human visitors. Further information on the study system can be found in Storari et al. (2024).

2.2. Experimental design and collection of data

The study started in June 2022 and involved the repetition of 3 experimental trials differing in the time of clearing of potential competitors for space of *S. alveolata* (June 2022, October 2022, and April 2023 for Trial 1, Trial 2, and Trial 3, respectively). In each trial, 6 plots (30 × 30 cm each) were established at the external edge of bioconstructed patches distributed along the Marina di San Nicola breakwaters and marked at corners with epoxy putty for subsequent locating. Three plots were assigned at random to the removal treatment of sessile organisms, while the remaining 3 were left unmanipulated as controls (Fig. 1). Removal was done only at the beginning of each experimental trial using

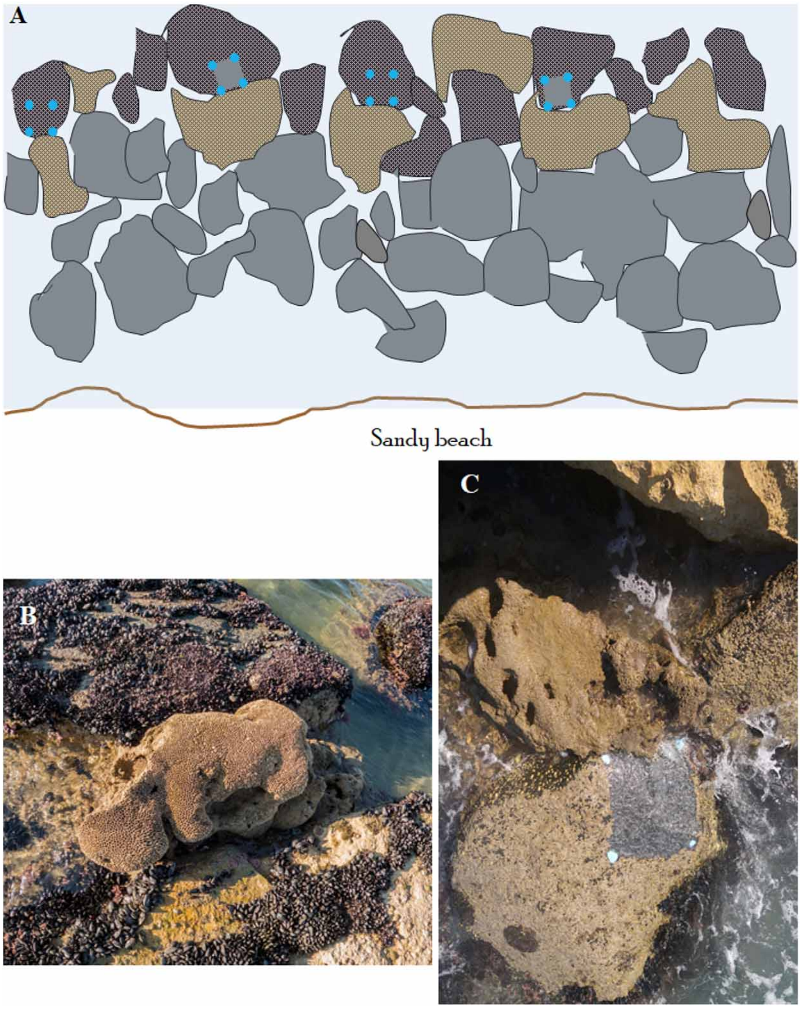

Fig. 1. (A) Schematization of a breakwater made of basalt/limestone blocks (grey) along the Marina di San Nicola sandy beach. *Sabellaria alveolata* patches (light brown) are interspersed among adjacent patches (dark brown) dominated by other sessile organisms (mainly mussels and encrusting coralline algae), within which experimental plots were marked at corners with epoxy putty (blue dots) and either assigned to the clearing treatment (grey squares) or left untouched as control. (B) Portion of breakwater showing a *S. alveolata* patch adjacent to areas dominated by mussels and articulated coralline algae. (C) Experimental plot (marked at corners with epoxy putty), originally dominated by barnacles such as the surrounding rock, cleared at the external border of a *S. alveolata* patch

a chisel mounted on a battery drill. For each trial, the abundance of sessile and mobile species in experimental plots was sampled before clearing (Time 0 [T0]) to guarantee that assemblages in plots assigned to the treatment and those assigned to the control did not differ at the beginning of the experiment. The cover of *S. alveolata* in the same plots was subsequently estimated (Trial 1: July 2022, October 2022, April 2023, and June 2023; Trial 2: April 2023, June 2023, and December 2023; Trial 3: June 2023, December 2023, March 2023, and July 2024). Ideally, each trial should have been sampled at the same intervals of time after the respective clearing, but this was impossible due to adverse weather conditions that prevented to visit the site at the appropriate times. The percent cover of bioconstruction was assessed visually in the field using a quadrat of 20 × 20 cm, placed in the centre of each plot to avoid edge effects, divided into 25 sub-quadrats of 4 × 4 cm each. Following the widely used procedure by Dethier et al. (1993) for estimating the percentage cover of sessile organisms, including intact sabellariid formations (e.g. Plicanti et al. 2016), we assigned to each sub-quadrat a score from 0 (no bioconstruction present) to 4 (bioconstruction occupying the entire sub-quadrat). Scores were summed across all the 25 sub-quadrats to finally obtain *S. alveolata* cover values in each plot expressed as percentages.

2.3. Data analysis

To confirm that plots assigned at random to the unmanipulated control and to the clearing treatment were comparable at the start of the experiment, data collected at T0 were analysed with 2-way PERMANOVA (permutational multivariate analysis of variance; Anderson 2001) based on Bray-Curtis dissimilarities and 9999 permutations. This analysis included the crossed factors Condition (fixed, 2 levels, i.e. treatment vs. control) and Trial (random, 3 levels), with 3 replicates. No T0 analyses were done on *S. alveolata* cover since all experimental plots were established at the external edge of bioconstructed patches.

The percentage cover of *S. alveolata* bioconstruction estimated during the experiment was analysed through linear mixed-effects models (LMEMs; Singer & Willett 2003). To test for changes in the temporal trends of this variable in response to the removal of adjacent sessile organisms in each trial, the factors Time, Treatment and Trial were included in the fixed part of the model, while 'Time | Plot ID' was included in the random part in order to model variation in intercepts and slopes among plots, thereby accounting for repeated sampling. To test for treatment effect at the end of the experiment, Time was centered over the last sampling date. The analysis was done using the 'lmer' function of the 'lme4' R package (Bates et al. 2015), and results were summarized as ANOVA output. Model assumptions were checked with the 'DHARMa' R package (Hartig 2024), and data were log-transformed to meet them (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/meps15038_supp.pdf). Temporal trends of *S. alveolata* cover in each trial were represented as predicted values according to the adopted LMEM, using the 'plot_model' function of the 'sjPlot' R package (Lüdecke 2024). All analyses were performed in R v4.4.2 ((R Core Team 2024).).

3. RESULTS

At the beginning of the experiment (T0), the plots assigned to each combination of Condition (control vs. clearing treatment) and Trial hosted comparable assemblages (Table 1).

Consistently across experimental trials, the temporal trend of *Sabellaria alveolata* cover differed between treated and control plots (Table 2). In each trial, an expansion of *S. alveolata* into cleared plots was already evident at the first time of sampling, while it was absent or almost absent throughout the experiment in unmanipulated plots. More specifically, fitted data indicated that the difference between treated and control plots was approximately constant throughout the experiment in Trial 1, while it became more pronounced over time in both Trial 2 and Trial 3 (Fig. 2).

Table 1. Results of PERMANOVA comparing assemblages among plots assigned to each combination of experimental Condition (unmanipulated control vs. clearing) and Trial before treatment application (Time 0)

Source of variation	df	MS	pseudo-*F*	p	Denominator	Unique permutations
Condition	1	1663.5	0.81	0.544	Condition × Trial	9962
Trial	2	2353.6	1.15	0.322	Residual	9920
Condition × Trial	2	2049.9	1.00	0.423	Residual	9929
Residual	12	2053.0				

Table 2. Results of linear mixed-effects models (LMEM) assessing the effect of the removal of adjacent organisms on the percentage cover of *Sabellaria alveolata* bioconstruction in each of 3 experimental trials. Results are reported as ANOVA output. *F*-tests were performed using the Satterthwaite's method. df_N: df numerator; df_D: df denominator. $^{**}p < 0.01$, $^{***}p < 0.001$

	MS	df_N	df_D	*F*	p
Time	6.59	1	35.27	14.72	***
Treatment	7.56	1	18.76	16.89	***
Trial	0.34	2	18.73	0.76	>0.48
Time × Treatment	4.49	1	35.27	10.02	**
Time × Trial	0.44	2	35.09	0.98	>0.38
Treatment × Trial	0.19	2	18.73	0.42	>0.66
Time × Treatment ×Trial	0.64	2	35.09	1.44	>0.25
Transformation	$\ln(x + 1)$				

4. DISCUSSION

This study provides one of the first experimental tests of competition for space between the tube worms *Sabellaria alveolata* and other sessile organisms. In line with the initial hypothesis, removing adjacent potential competitors promoted the expansion of *S. alveolata* bioconstructions. Moreover, this response was consistent across experimental trials, although relatively more marked in Trial 2 and Trial 3.

Direct evidence of competition between sessile species and *S. alveolata* was shown in a previous Irish study focusing on the invasive Pacific oyster *Magallana gigas* (Green & Crowe 2013). Our results generally agree with their findings, further supporting competition for space as a process limiting the enlargement of tube-worm reefs. In the Irish study, however, *S. alveolata* was completely excluded from areas occupied by living or dead *M. gigas*. In our study, removing potential native competitors allowed the expansion of *S. alveolata* bioconstructions towards the adjacent plots, but biogenic tubes were also found in control plots, although with very low abundance. These dissimilar competitive dynamics might be attributed to differences in species-specific traits and in the scale of the assessed impact of competitors. The invasive *M. gigas* is characterized by rapid growth, high fecundity and extreme tolerance to a wide range of environmental conditions (Ruesink et al. 2005), likely representing a stronger competitor for space than the present native Mediterranean species. These, in turn, having co-evolved with *S. alveolata*, would possess traits that allow for some degree of coexistence with the tube-forming species, as observed in invasive and native plants (Huang et al. 2018). Moreover, Green & Crowe (2013) examined the broad-scale impact of the climate-driven range expansion of *M. gigas*, which is likely toproduce dramatic and widespread environmental alterations (e.g. Rius et al. 2014). By contrast, we focused on local-scale competitive interactions between *S. alveolata* and algal and invertebrate sessile species within their natural range, a type of interaction that is likely to result in milder and more spatially limited impacts (Gioria & Osborne 2014).

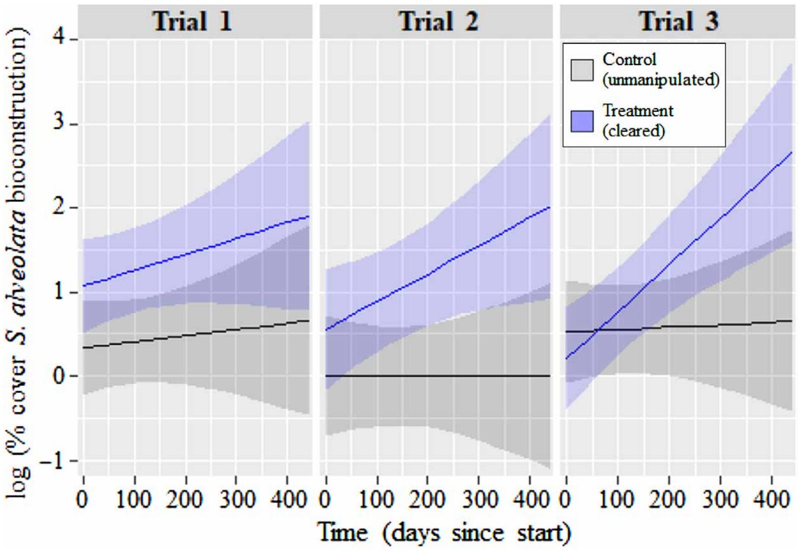

Fig. 2. Temporal trends of linear mixed-effects model (LMEM)-predicted values of *Sabellaria alveolata* bioconstruction cover (log scale) in control (unmanipulated) and treated (competitors cleared) plots in experimental Trial 1 (clearing in June 2022), Trial 2 (clearing in October 2022), and Trial 3 (clearing in April 2023). Ribbons around the fitted lines represent 95% confidence intervals

The present study also tested whether the response of *S. alveolata* could be generalized independently of the timing of removal of potential competitors, or was context-dependent. Accordingly, the clearing times in each experimental trial were not chosen *a priori* to test the role of any specific process that could be responsible for the effects of disturbance timing. They were established to span a relatively large period over which abiotic and biological processes were likely to vary. Nevertheless, the relatively small differences among trials in the temporal trends of *S. alveolata* expansion could be retrospectively, and cautiously, interpreted in the context of the possible effects of temporally variable anthropogenic pressures and the phases of the natural cycle of *S. alveolata* formations. *S. alveolata* reefs exhibit distinct seasonal patterns of growth (progradation) and regression (retrogradation) (Gruet 1986, Dubois et al. 2005, Gravina et al. 2018, Bonifazi et al. 2019, Curd et al. 2019, Borghese et al. 2022). In the Mediterranean Sea, the progradation phase typically begins in March, when environmental conditions become favourable and stimulate reef-building activity. During this period, worms actively construct new tubes, leading to reef expansion and enhanced diversity of associated fauna (Bonifazi et al. 2019, Borghese et al. 2022). Conversely, the retrogradation phase usually starts in late summer and is marked by reef deterioration and fragmentation during the subsequent stormy months (Bonifazi et al. 2019, Lisco et al. 2020, Borghese et al. 2022). This natural cycle is likely to interact with anthropogenic disturbances that are variable in intensity and timing. Human trampling, for instance, is more intense during tourist season peaks and can cause significant sabellariid reef damage persisting for some months after the disturbance (Plicanti et al. 2016). Thus, it is predictable that the overlap between the retrogradation phase and the tourist season would reduce the positive effect of the loss of *S. alveolata* competitors, especially in easily accessible areas such as our study site. By contrast, the progradation phase conciding with reduced human disturbance would be the most favourable condition to promote reef development. Within this framework, the less pronounced response of *S. alveolata* observed in Trial 1 could be explained by its performance from June until the following June, which captured just the final part of the bioconstruction growth phase, the potential impact of summer tourist activity, and the entire retrogradation phase. Conversely, Trial 3, starting in April, coincided with the early progradation phase, which could explain the more pronounced and temporally increasing positive response of *S. alveolata* to the clearing treatment as a result of the natural development phase of the bioconstruction, boosted by reduced competition. Trial 2 started within the advanced retrogradation phase (October) but continued through the subsequent growth phase, which could explain the similar trend observed in this experimental repetition compared to Trial 3.

In conclusion, this work provides insights into competitive interactions as drivers of patterns of growth and space occupancy of *S. alveolata* patches in the context of concomitant variability of temporally variable natural and anthropogenic processes. It suggests, in particular, the need for capturing the effect of the retrogradation and progradation phases when assessing the ecological responses of tube-worm reefs (see also Bonifazi et al. 2019). In this respect, future studies should specifically examine how such phases would interact with competition for space in modulating sabellariid reef expansion. This would require establishing multiple experimental trials differing in the time of the clearing treatment within each phase. This would provide a formal test of the issues we have speculatively discussed in the present study. The resulting information could be combined with that from long-term surveys suited to capture interannual variations in *S. alveolata* bioconstruction dynamics and identify relevant scales of variation of target organisms. This could guide effective conservation and management strategies that consider both direct anthropogenic impacts and the broader ecological context (e.g. Benedetti-Cecchi et al. 2003, 2018, Plicanti et al. 2016, Bertocci et al. 2017). A multifaceted approach combining long-term monitoring suited to assess reef health and identify emerging threats (Gravina et al. 2018) and enforced legal limitation of access to vulnerable areas appears as the best strategy to conserve such valuable habitats under ongoing climate change and increasing coastal development, in line with the objectives of the European Habitats Directive (Domy et al. 2023). It would also greatly contribute to resolve the 'Data Deficient' classification attributed by IUCN to worm reefs.

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