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On the presence of an unexpected meadow of *Penicillus capitatus* Lamarck (Bryopsidales: Chlorophyta) in Mallorca, Balearic Islands, Western Mediterranean

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Abstract

An unexpected meadow of the warm-water alga *Penicillus capitatus* was found thriving in sandy bottoms between 16 and 21 m depth in Mallorca, Balearic Islands. Plant densities and benthic coverage were very high when compared to most Mediterranean meadows of this species. As it is common in tropical meadows of this species, all the individuals were found in a *Penicillus* morphological state, whereas most Mediterranean individuals are always found in the filamentous (*Espera*) state. Due to the high biomass of the populations, the contribution to the primary productivity of the sandy bottoms it colonizes should be far from negligible. If the expansion of these species continues, the annual calcium carbonate production of the Balearic continental shelf will increase and previous estimated budgets will have to be reconsidered. Since no genetic analysis of the specimens have been performed so far, it is still early to know if the studied populations have been originated by native Mediterranean specimens or from a cryptic lineage of Western Atlantic or Macaronesian origin. Whatever the answer is, the current bloom of this population in an environment completely devoid of this species in the recent past, provides new evidence of the current tropicalization of the Mediterranean caused by global warming.

Keywords: Tropicalization; expansion; warming; biomass; calcium carbonate; Mediterranean.

Introduction

The genus *Penicillus* Lamarck includes nine species of green, calcified, filamentous thalli made by thin siphons that usually hold together to create a bulbous holdfast which produces an erect rigid stalk composed by closely interwoven siphons ended by a capitular tuft of free dichotomously branched siphons. The currently accepted nine species of the genus (Guiry & Guiry, 2023) are warm-water species that show a tropical to subtropical distribution, being present in the Atlantic, Indian and Pacific oceans as well as in the seas contiguous to these oceanic basins. *Penicillus capitatus* Lamarck is the type species for this genus which was thought to be endemic of the western Atlantic Ocean (Gepp & Gepp, 1911; Børgesen, 1913). However, a species described by Bornet (1892) from the western Mediterranean as *Penicillus mediterraneus* (Decaisne) Bornet resulted to be conspecific with *P. capitatus* (Huvé & Huvé, 1964; Friedmann *et al.*, 1977). Thus, it was believed that *P. capitatus* showed a disjunct distribution with most populations placed in the western Atlantic and some others, far less common, in the Mediterranean Sea (Meinesz, 1980) and adjacent

Atlantic waters (Gulf of Cádiz; Seoane-Camba, 1965). Later on, Audiffred & Prud'homme van Reine (2001) found *P. capitatus* in the offshore waters of Porto Santo, Madeira, which could act as a population bridge between the Western Atlantic and the Mediterranean and, more recently, extensive off-shore meadows of this species were described from La Palma, Canary Islands (Sangil *et al.*, 2010). So, at present, *P. capitatus* can be considered to be distributed in the tropical to subtropical waters of the Atlantic Ocean, the Gulf of Mexico, the Caribbean and the Mediterranean Sea.

Mediterranean populations of *P. capitatus* are mostly present as the “turf-like” filamentous form (*Espera* stage; Meinesz, 1980) lacking the typical paintbrush-shaped (*Penicillus*) form (composed of holdfast, stalk and capitulum), although the paintbrush form has also been recorded in late summer and autumn, but in very few places across the Mediterranean (Huvé & Huvé, 1964; Meinesz, 1972, 1980; Cinelli & Salghetti-Drioli, 1983; Ballesteros, 1992; Turna *et al.*, 2010; Bilecenoglu *et al.*, 2013; Boudouresque *et al.*, 2024). Depth distribution for Mediterranean *P. capitatus* populations ranges between 0.5 and 15 m (Boudouresque *et al.*, 2006; Rodríguez-Pri-

eto *et al.*, 2013), as is the case for Western Atlantic populations (Littler & Littler, 2000). In contrast, distributions are much deeper in the Canary Islands (20-50 m; Sangil *et al.*, 2010) and Madeira (50-110 m; Audiffred & Prud'homme van Reine, 1985). *P. capitatus* in the Mediterranean is found on dead *Posidonia oceanica* (matte) beds and shallow muddy bottoms colonized by *Cymodocea nodosa* or *Caulerpa prolifera* (Meinesz, 1980; Ballesteros, 1992; Boudouresque *et al.*, 2006; Turna *et al.*, 2010; Bilecenoglu *et al.*, 2013).

Here we characterize a *P. capitatus* meadow sampled in September 2021 in the MPA of Palma Bay (Mallorca, western Mediterranean). Previous surveys from 2001-2004 (Ballesteros & Cebrian, 2005) and 2011-2015 (Alós *et al.*, 2016) did not report any population or even a single specimen of *P. capitatus* in the whole MPA, pointing to a fast colonization and spread of this species. Our aim was to characterize the 2021 distribution of this *P. capitatus* meadow in order to obtain baseline data for future monitoring of the extension of this species. We examined depth distribution, bottom cover, density, and biomass. Also, we quantified the standing stock of calcium carbonate incorporated by *P. capitatus* since this species could largely modify the global carbonate production estimated for the upper part of the Balearic continental shelf (Canals & Ballesteros, 1996).

Materials and Methods

Presence of several specimens of *P. capitatus* was observed in September 2020 while monitoring for the spread of the invasive green alga *Halimeda incrassata* in the MPA of Palma Bay (Mallorca, Western Mediterranean) at depths of around 18 meters. Sampling was performed the following year, in September 2021, at the same geographical coordinates where the specimens were observed in 2020.

Sampling consisted of 5 different approaches: (1) Extension of the meadow was estimated by several punctual short dives at different depths (between 0 and 25 m), where the presence/absence of *P. capitatus* was reported. Results of this survey were translated to a GIS for estimating the year 2021 spread of *P. capitatus* inside the MPA. One sampling site per depth (16, 18 and 21 m) was afterwards selected in the central part of the area occupied by *P. capitatus*. (2) The presence of the different macrophyte species observed was annotated at each depth. (3) The percentage of sea bottom covered by *P. capitatus* and other species was estimated by deploying two 50-meters line transects per depth and measuring the length of each transect where the line was crossing over the following categories: *P. capitatus*, *C. nodosa*, bare sediment, *H. incrassata* and *Acetabularia calyculus*. (4) Density of individuals of *P. capitatus* inside the patches for each depth was estimated by deploying thirty 625 cm² quadrats and counting all specimens inside each quadrat. (5) Biomass was estimated by collecting all the individuals in three 400 cm² quadrats per depth. All individuals were carefully sorted and cleaned of sediment grains, dried at 60 °C

for 48 hours and weighed.

To determine the differences in the percentage of sea bottom cover by *P. capitatus* at different depths, a generalized linear mixed model (GLMM) was fitted using the “lme4” package (Bates *et al.*, 2015) in the R programming environment. This model accounted for the random effects of the different transects conducted, and considered the correlation among repeated observations within the same transects, thus addressing the hierarchical structure of the data and mitigating the lack of independence. Given the count nature of the collected data, the binomial distribution family was chosen for the GLMM. Furthermore, bootstrapping technique, employing the “boots” package (Canty & Ripley, 2022) in R, was utilized to estimate robust confidence intervals for the coefficients of the GLMM. This approach helped resolve issues related to the non-normal distribution of the coefficients and provided a reliable estimation of variability in the data. Differences in density (*Penicillus capitatus* thalli/ 625 cm²) and dry biomass (DB; g DB/ 400 cm²) across depth were tested for significance using a generalized linear model (GLM) fitted using the statistical software R (version 4.2.1) (R Core Team, 2022); given the nature of the collected data, the Gaussian distribution family was chosen for the GLM.

Samples were also collected for morphological identification. To quantify calcium carbonate content, 20 specimens were selected and brought to the laboratory. Special care was paid to the cleaning of these specimens in order to avoid any piece of sediment retained into the brush part of the thalli. Every specimen was dried at 60°C for 48 hours, weighed and homogenized with a pestle and a mortar, introduced in an Eppendorf vial and sent to the Scientific Technical Services of the University of A Coruña (SAI) for analysis. Carbonate content was estimated by using the Rietveld method (Rietveld, 2014). Mean carbonate content in percentage of dry biomass of *P. capitatus* was calculated as the average of the 20 specimens analysed.

Results

Penicillus capitatus was present in an area of 86 ha in Palma Bay MPA during September 2021 (Fig. 1), growing over sandy bottoms. Shoots of seagrass *C. nodosa* regularly appeared between the usually dense meadows of *P. capitatus*. *Dictyota linearis* was a regular epiphyte of seagrass leaves but was rarely attached to *P. capitatus*. *Halimeda incrassata* grew over the sediment intermixed with *P. capitatus* and *A. calyculus* was present only in the shallowest areas, attached to dead bivalve shells.

Depth distribution of the *P. capitatus* meadow in the MPA of Palma Bay ranged between ca. 16 and 21 m depth. Benthic cover values of *P. capitatus* patches increased from 16 to 18 meters depth and decreased afterwards, with highest cover values up to 30.5% at 18 m depth and down to 2.4% at 21 m depth. Pairwise comparisons indicate statistically significant differences between each depth pair (Fig. 2; Table 1). *P. capitatus* exhibited a

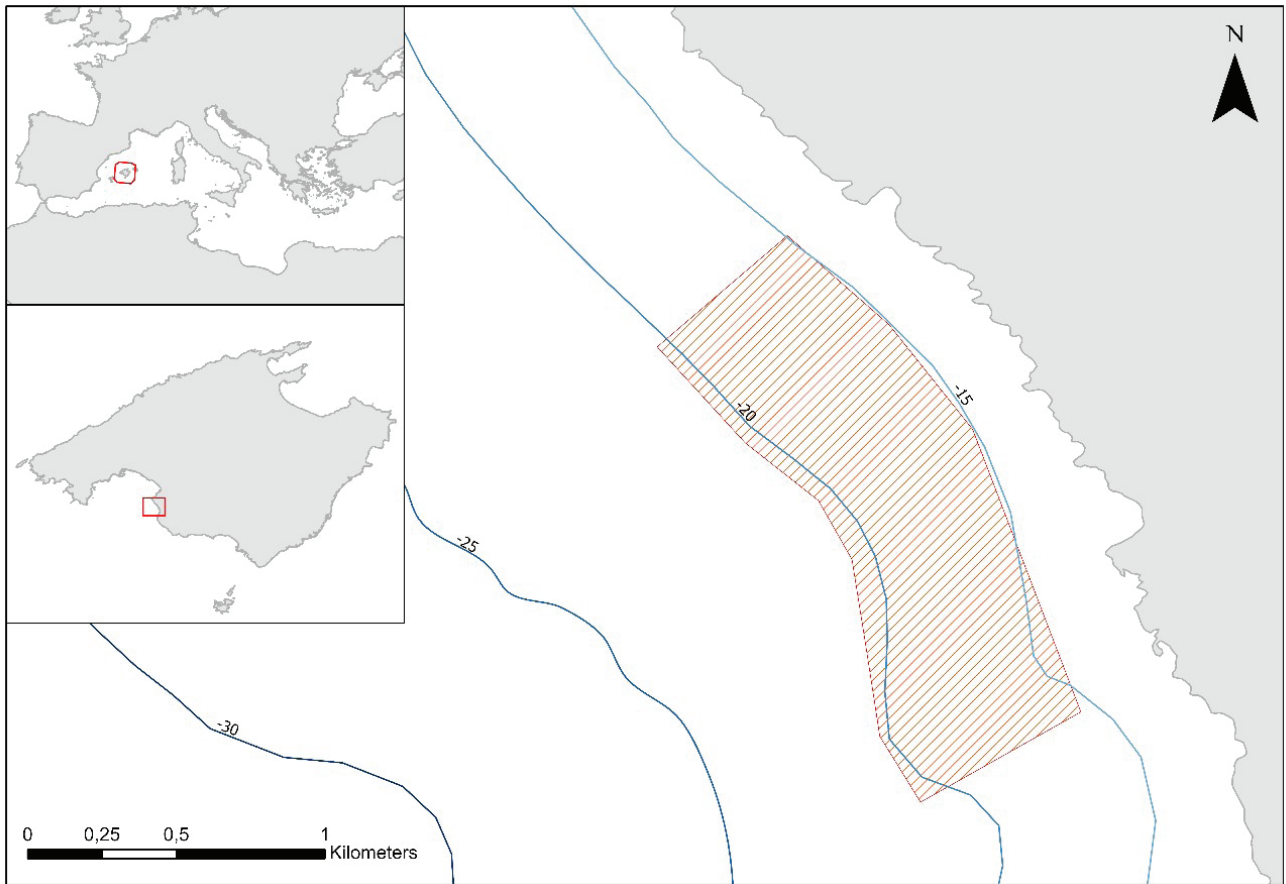


Fig. 1: Distribution (stripped area) of paintbrush-shaped thalli of *Penicillus capitatus* in Palma Bay MPA, September 2022.

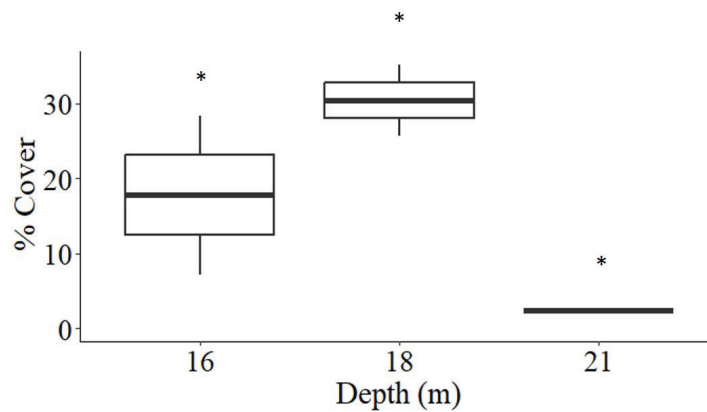


Fig. 2: Box plot of *Penicillus capitatus* bottom percentage cover at the three sampled depths (*significant differences).

Table 1. Results of the generalized linear mixed model (GLMM) comparing the percent coverage by *Penicillus capitatus* across depths.

	Df	Sum Sq	Mean Sq	F	p-value
Depth	3	96.81	48.41	48.40	0.01
Pairwise comparisons	Depth 16 m	Depth 18 m	Depth 21 m		
Depth 16 m		<0.001	<0.001		
Depth 18 m	<0.001		<0.01		
Depth 21 m	<0.001				

patchy distribution at 16 m and 18 m depth, being inter-mixed with sandy bottoms, while at 21 m depth thalli of *P. capitatus* were not aggregated in clumps but solitary and were co-inhabiting with thalli of *H. incrassata* (Fig. 3). We detected a significant difference of inside-patch densities between 16 and 21 m depth ($p < 0.01$) and between 18 and 21 m depth ($p < 0.001$) (Table 2), with highest values of 63.2 ± 21.6 ind./625 cm² (i.e. around 1000 ind. m⁻²) at 18 m depth, intermediate values of 36.9 ± 32.5 ind./625 cm² at 16 m depth, and lowest values of 8.9 ± 3.7 ind./625 cm² at 21 m depth (Fig. 4). Biomass inside *P. capitatus* patches ranged between 7.1 ± 1.2 and 1.0 ± 0.3 g

DB/400 cm², corresponding to 177.5-25.0 g DB m⁻² (Fig. 5), and being significantly different amongst 16 and 18 m depth with respect to 21 m depth ($p < 0.001$, Table 3).

The average carbonate content of *P. capitatus* specimens was 87.8% of dry biomass. Combining data from percentage cover of the sea bottom, average biomass, and mean carbonate content, the estimates of total calcium carbonate incorporated by *P. capitatus* amount to 27.7 g at 16 m depth, 44.7 g at 18 m depth and 0.5 g at 21 m depth.

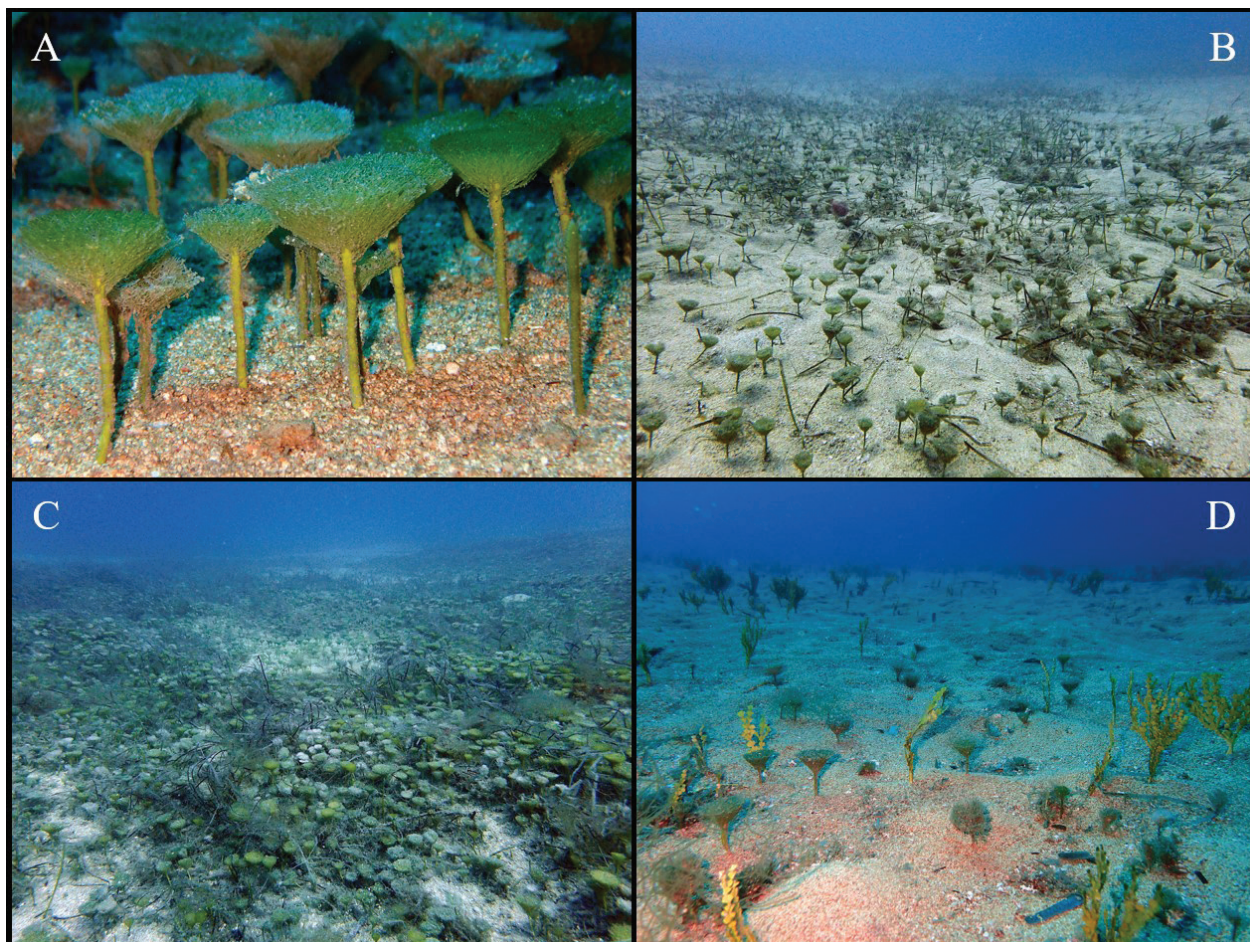


Fig. 3: A: Paintbrush-shape thalli of *Penicillus capitatus* growing in sandy bottoms at Palma Bay MPA.; B: Aspect of *P. capitatus* beds growing at 16 m depth; C: Aspect of *P. capitatus* beds growing at 18 m depth; D: Aspect of *P. capitatus* growing at 21 m depth together with *Halimeda incrassata*.

Table 2. Results of the generalized linear model (GLM) comparing the density (*Penicillus capitatus* thalli/ 625 cm²) of *Penicillus capitatus* across depths.

	Estimate	Std.Error	T value	p-value
Depth 16 m	2.71	0.58	5.05	<0.001
Depth 18 m	0.98	0.73	1.32	0.18
Depth 21 m	-2.19	0.73	-3.00	<0.002
Pairwise comparisons	Depth 16 m	Depth 18 m	Depth 21 m	
Depth 16 m		0.38	<0.01	
Depth 18 m	0.38		<0.001	
Depth 21 m	<0.01	<0.001		

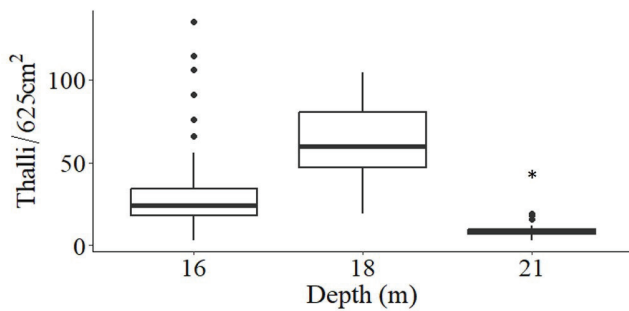


Fig. 4: Box plot of *Penicillus capitatus* density (*Penicillus capitatus* thalli/ 625 cm²) at the three sampled depths (*significant differences).

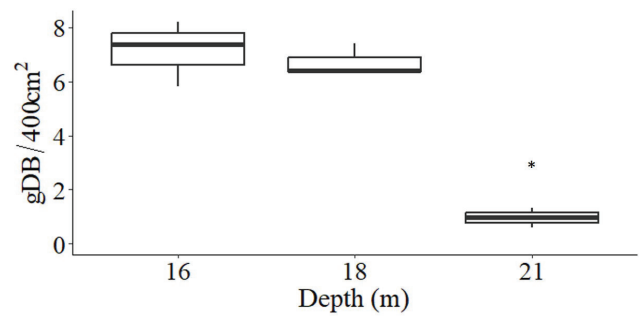


Fig. 5: Box plot of *Penicillus capitatus* dry biomass (DB) at the three sampled depths (*significant differences).

Table 3. Results of the generalized linear model (GLM) comparing the dry biomass (g DB/400 cm²) of *Penicillus capitatus* across depths.

	Estimate	Std.Error	T value	p-value
Depth 16 m	0.02	0.01	1.44	0.2
Depth 18 m	0.003	0.01	0.18	0.86
Depth 21 m	1.04	0.26	3.87	0.008
Pairwise comparisons	Depth 16 m	Depth 18 m	Depth 21 m	
Depth 16 m		0.98		<0.001
Depth 18 m	0.98			<0.001
Depth 21 m	<0.001	<0.001		

Discussion

The abundance of *P. capitatus* in the MPA of Palma Bay is still anecdotal since it occupies a very small part (3.7%) of the total area of the MPA, and this may be due in part to the fact that most of the MPA is comprised of healthy seagrass meadows of *P. oceanica* (Ballesteros & Cebrian, 2005), which *P. capitatus*, at least thus far, does not colonize. The northwest and southwest lateral limits of the current distribution of *P. capitatus* may be defined by the change in landscape, where sandy bottoms are replaced by *P. oceanica* meadows. This is not the same for the upper and lower depth limits, where seagrass meadows are absent. Thus, both the shallowest limit, now situated just above 16 m depth, and the deepest limit, now around 21-22 m depth, could change if the colonization progresses. While 22 meters depth was the deepest limit reported until now for *P. capitatus* in the Mediterranean Sea (Boudouresque *et al.*, 2006; Rodríguez-Prieto *et al.*, 2013; Turna *et al.* 2010), populations of this species from Macaronesian islands (Madeira, La Palma) reach much deeper environments (20 – 100 m; Sangil *et al.*, 2010, Audiffred & Prud'homme van Reine, 1985), suggesting that further expansion is possible.

The sandy bottoms that are currently being colonized by *P. capitatus* were almost devoid of any other macroalgae twenty years ago (Ballesteros & Cebrian, 2005). Bare sand was the most prominent feature of the seascape, although some running shoots of the seagrass *C. nodosa* were present, never forming a true meadow. *Dictyota linearis* was also present as a seagrass epiphyte and *A. calyculus* was a rare species growing over dead bivalve shells

(Ballesteros & Cebrian, 2005). This seascape suddenly changed in 2011, when most of these sandy bottoms were colonized by the invasive tropical alga *H. incrassata* (Alós *et al.*, 2016). Now, these same bottoms have been colonized by *P. capitatus*, which has replaced *H. incrassata* as the most common macrophyte at depths between 16 and 18 m (Fig. 2). The colonization of sandy bottoms is striking, given that the usual habitats where both the *Espera* and the *Penicillus* stages of *P. capitatus* grow in the Mediterranean Sea are dead seagrass meadows of *P. oceanica* or muddy bottoms in very sheltered environments (Meinesz, 1980; Ballesteros, 1992; Boudouresque *et al.*, 2006; Rodríguez-Prieto *et al.*, 2013). However, growth on a sandy substrate was observed by Turna *et al.* (2010) in Turkey.

Western Atlantic populations of *P. capitatus* typically colonize sheltered and shallow lagoons intermixed with seagrasses (*Halophila*, *Syringodium*, *Thalassia*) and other macroalgae of the genus *Halimeda*, *Rhizocephalus*, *Caulerpa*, *Udotea* and *Padina*, amongst others (Bach, 1979; Wefer, 1980; Biber & Irlandi, 2006; Bedinger *et al.*, 2013). However, *P. capitatus* offshore meadows from the Canary Islands grow over volcanic sandy bottoms in mixed stands with the seagrass *Halophila decipiens* and green algae *Caulerpa prolifera* and *Caulerpa cylindracea* (Sangil *et al.*, 2010), but not co-occurring with *H. incrassata*, even though this species is also invasive in the same geographical area and in similar bottoms where *P. capitatus* grows (Sangil *et al.*, 2018).

Another interesting feature of the *P. capitatus* meadow studied is the percent cover. Both at 16 and 18 m depth *P. capitatus* grows in patches, often surrounded by

bare sand, while at 21 m these aggregations do not exist and the specimens are more uniformly distributed over the sea bottom (Figs 2, 3). In deep waters, the percentage cover is very low but at 16 and 18 m depth it ranges between 18 and 31%, a figure much lower than the 75% reported for the Canary Islands populations (Sangil *et al.*, 2010). Since sampling was performed only one year after the sighting of the first individuals, it is possible that the population is still expanding, so these values are very preliminary and likely to increase.

Biomass of *P. capitatus* inside the patches reached 177.5 g DB m⁻², but when balanced with the bottom percent cover of the patches, it comes out to 31.5 g DB m⁻² at 16 m depth, 50.9 g DB m⁻² at 18 m depth and 0.6 g DB m⁻² at 21 m depth at the seascape level. Unfortunately, we have not found biomass data from other populations in the literature and no comparisons are possible for this parameter. In contrast, some density data is available for the Mediterranean, with figures of 1 to 10 specimens m⁻² (Turna *et al.*, 2010; Bilecenoglu *et al.*, 2013) to 450 specimens m⁻² (Cinelli & Salghetti-Drioli, 1983). The Canary Islands population reaches densities of 1.245 specimens m⁻² (Sangil *et al.*, 2010). Inside-patch densities from the Palma Bay MPA populations ranged between 1.012 specimens m⁻² (at 18 m depth) and 142 specimens m⁻² (at 21 m depth), which makes the Palma Bay populations the densest recorded in the Mediterranean and almost comparable to the Canary Islands populations.

Although we have estimated the calcium carbonate standing stock of *P. capitatus*, we do not know the renovation rate of its thalli in Palma Bay MPA. However, if we consider that only one generation of paintbrush thalli is produced per year as suggested by Meinesz (1975), the standing stock should equal the carbonate production per year, with figures ranging from 0.5 g m⁻² at 21 m to 44.7 g m⁻² at 18 m. These values are of the same order of magnitude than those reported by Wefer (1980) in Harrington Sound (Western Atlantic) (30 g m⁻² year⁻¹) for *Penicillus* beds, but are one order of magnitude lower than meadows of *H. incrassata* with or without *Penicillus* (van Tussenbroek & van Dijk, 2007; Hatt & Collado-Vives, 2019) in the Caribbean and the Gulf of Mexico. Regarding the calcium carbonate production of the different habitats in the Balearic Islands continental shelf (Canals & Ballesteros, 1997), these *Penicillus* populations still show a low carbonate production when compared with rocky bottoms or maërl beds, but the presence of *Penicillus* increases by almost two orders of magnitude the calcium carbonate produced by sandy bottoms devoid of vegetation (Canals & Ballesteros, 1997). Since sandy bottoms cover a big percentage of the total area of the infralittoral zone, the amount of calcium carbonate produced by *Penicillus* would strongly increase the total carbonate budget of the Balearic continental shelf if its abundance expands at the current rates.

The sudden spread of *P. capitatus* in the sandy bottoms of Palma Bay MPA is surprising, not only because of the dense populations it makes and the complete dominance of the paintbrush-shaped thalli, but also because sandy bottoms are not the normal habitats where Mediter-

anean *P. capitatus* is present. Due to the contrasting ecological differences between these new populations and the normal Mediterranean populations of *P. capitatus*, one may question if they belong to the same taxonomical entity. Morphological features of the specimens in these new populations fit completely within the description of *P. capitatus* and no major morphological differences have been detected between normal Mediterranean specimens and those collected in the sandy bottoms of Palma Bay MPA [see, for example descriptions in Littler & Littler (2000) and Rodríguez-Prieto *et al.* (2013)]. However, this morphological match does not mean that we are unequivocally dealing with the same entity, but perhaps with cryptic lineages or even species. Similar situations have already been described in the Mediterranean. For example, *Asparagopsis taxiformis* was a native species in the southeastern Mediterranean Sea but an Indopacific strain has been colonizing the eastern, central and western Mediterranean (Andreakis *et al.*, 2009; Nahor *et al.*, 2022) since 1993 (Ballesteros & Rodríguez-Prieto, 1996). In the case of *P. capitatus*, it is possible that a cryptic Western Atlantic lineage has been expanding first to Macaronesia (Audiffred *et al.*, 1985; Sangil *et al.*, 2010) and later arriving to the Western Mediterranean, a hypothesis that can be tested by conducting genetic analyses. An alternative hypothesis is that, being *P. capitatus* a warm-water species, the current increase in seawater temperature recently witnessed in the Mediterranean Sea has increased its ability to proliferate at densities and with a morphological form that were exceptional in the past (Boudourisque *et al.*, 2024), also allowing it to thrive in environments not reported before. A similar hypothesis seems to be proven valid for the zooxanthellate coral *Oculina patagonica*, once considered invasive in the Mediterranean Sea (Zibrowius, 1974; Fine *et al.*, 2001) but currently considered native (Leydet & Hellberg, 2015) and undergoing geographical and bathymetric expansion due to warming (Serrano *et al.*, 2013; Martínez *et al.*, 2021).

In short, we have characterized a remarkable meadow of *P. capitatus* in the Mediterranean Sea growing at unusual depths and habitats and constituted by specimens with the uncommon paintbrush morphological shape. Extension rate and seasonal data on the morphological cycle are still necessary to precisely quantify the importance of these new populations as contributors to primary productivity and the carbonate budget of the Balearic Islands continental shelf. Nevertheless, the extensive beds of *P. capitatus* discovered in Palma Bay adds to other evidences of warm-affinity species invasions and extensions in the Mediterranean Sea (Francour *et al.*, 1994; Parravicini *et al.*, 2015), and is a clear reminder of the current tropicalization trend of the Mediterranean basin biota caused by global warming (Bianchi & Morri, 2003).

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