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Westernmost record of *Caulerpa taxifolia* var. *distichophylla* (Chlorophyta, Caulerpaceae) in the Mediterranean: a 20-year journey

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Abstract

The invasive alga *Caulerpa taxifolia* has been detected for the first time in the Cabo de Gata-Níjar Natural Park (Andalusia, southern Spain), after more than 30 years of active monitoring for invasive species. Morphological and phylogenetic analyses identified the taxon as *C. taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini 2013, a variety native to Australia and distinct from the aquarium strain introduced in Monaco in 1984. This variety is part of an independent invasion originating in the eastern Mediterranean, first reported in Syria in 2003, which since then has spread westward through the southern Mediterranean Sea. This record from Andalusia represents a significant westward range extension from previous occurrences in Tunisia (2015) and Sardinia, Italy (2016). In just two decades, the species has crossed the Mediterranean from the eastern to the westernmost coasts, demonstrating a remarkable capacity for long-distance dispersal and adaptation to a wide range of habitats. However, compared to the aquarium-released *C. taxifolia* strain, it differs in size, thermal tolerance, and potentially in reproductive traits and secondary metabolite profiles. These differences may determine its potential for spreading and its ecological impact during the ongoing invasion.

Keywords: alien species; Andalusia; *Caulerpa taxifolia* var. *distichophylla*; Mediterranean Sea.

Introduction

The genus *Caulerpa* is represented in the Mediterranean Sea by a single native species, *C. prolifera* (Forsskål) J.V. Lamouroux, and seven non-indigenous taxa (in alphabetical order): *C. chemnitzia* (Esper) J.V. Lamouroux, *C. cylindracea* Sonder, *C. mexicana* Sonder *ex* Kützing, *C. racemosa* f. *requienii* (Montagne) Weber Bosse, *C. scalpelliformis* (R. Brown *ex* Turner) C. Agardh, and *C. taxifolia* (M. Vahl) C. Agardh, *C. taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman and Procaccini (Verlaque *et al.*, 2015). Among them, *C. taxifolia* has been included in the list of the 100 "Worst Invasive" species in the Mediterranean Sea (Streftaris & Zenetos, 2006).

Caulerpa taxifolia, a tropical marine alga, was accidentally released from the aquariums of the Musée Océanographique in Monaco in 1984 (Meinesz & Hesse, 1991). Following its introduction, it has spread rapidly across the Mediterranean Sea, reaching the French coast, Italy (extending to Messina), and Spain (Balearic Islands) in 1992 (Pou *et al.*, 1993), Croatia in 1994 (Span *et al.*, 1998), with Tunisia in 2000 (Langar *et al.*, 2000) and Turkey (Turan *et al*., 2011).

The area covered by *C. taxifolia* increased dramatically, from just 1 hectare in 1989 (limited to France and Monaco) to over 13,000 hectares by 2000 across multiple Mediterranean countries (Meinesz *et al.*, 2001), causing a significant impact on native communities. However, after this phase of exponential expansion, its dispersal and colonisation capacity declined markedly, even leading to its disappearance in many of the previously invaded areas.

The invasive alga *Caulerpa taxifolia* var. *distichophylla*, native to the Pacific, was first recorded in the Mediterranean Sea along the Syrian coast in 2003. Ini-

tially, it was misidentified as a dwarf form of *C. mexicana* or *C. taxifolia* (RAC/SPA–UNEP/MAP, 2003; Bitar *et al.*, 2010, 2017). After that, a population detected in the Gulf of Iskenderun (Turkey) in 2006 was analysed in detail, revealing that it had thinner thalli compared to the more robust *C. taxifolia* released from the aquariums already present in the region. Its morphology closely resembled that of the Australian species *C. distichophylla* (Sonder, 1845), but due to insufficient molecular distinction, it was initially classified as *C. taxifolia* (Famà *et al*., 2002; Cevik *et al.*, 2007). Subsequent molecular studies revealed genetic differences, leading to the designation of *C. taxifolia* var. *distichophylla*, characterised by narrow, elongated thalli and fine rhizoids (Jongma *et al.*, 2013). The variety was reported in the south of Sicily (Punta Bracetto and Marina di Ragusa) in 2007 (Jongma *et al.*, 2013), and later in northern Sicily (Sant'Ambrogio) in 2013 (Musco *et al.*, 2014). Its spread has been rapid throughout the central and eastern Mediterranean basins, reaching Cyprus in 2009 (Çiçek *et al.*, 2013), Rhodes (Greece) in 2010 (Aplikioti *et al.*, 2016), Malta in 2013 (Schembri *et al.*, 2015), Tunisia in 2015 (Chartosia *et al.*, 2018), Calabria and Sardinia (Italy) in 2016 (Di Martino *et al.*, 2018), Lebanon in 2016 (Bitar *et al.*, 2017), and Libya in 2017 (Shakman *et al.*, 2017). In Sicily, due to the extensive proliferation recorded in recent years (Picciotto *et al.*, 2016; Mannino & Balistreri, 2017; Mannino *et al.*, 2019), it is now considered fully naturalised. Recently, it has also expanded along the Turkish Aegean coast (Mutlu *et al.*, 2025), reaching the Marmara Sea in 2022 (Taşkın *et al.*, 2023; Zenetos *et al.*, 2025). In contrast to the strain of *C. taxifolia* from the Monaco aquarium, the variety *distichophylla* is currently in an expansion phase. Since its initial detection in 2003 on the easternmost coasts of the Mediterranean, it has shown a continuous pattern of westward spread.

The region of Andalusia (southern Spain) is located at the southwestern limit of the Mediterranean Sea. Owing to its considerable distance from the Suez Canal, the primary entry source of exotic marine species into the Mediterranean Sea, the region remained relatively unaffected by invasive algae for years. In response to growing concern caused by the rapid expansion of *C. taxifolia* in the western Mediterranean, early detection efforts were carried out between 1994 and 1996 along the Andalusian coastline, particularly focusing on the coast of Almería and Alborán Island. These surveys, funded by the European LIFE Programme, did not detect any presence of *C. taxifolia* in the area (Ballesteros *et al.*, 1996; Moreno, 2009, 2010). However, this situation has changed in recent decades with the arrival and establishment of several non-indigenous macroalgae with highly invasive potential in the region, such as *Asparagopsis taxiformis* (Báez *et al.*, 2001), *Caulerpa cylindracea* (Moreno, 2010), and *Rugulopteryx okamurae* (Altamirano *et al.*, 2016), which have been included with *C. taxifolia* in the Spanish Catalogue of Invasive Alien Species (Royal Decree 630/2013 and subsequent updates). Despite this increasing trend of macroalgal invasions, *C. taxifolia* var. *distichophylla* has only been recorded in the eastern Mediterranean Sea, with its westernmost occurrence reported in the Sardinia Channel. In this study, we provide the first evidence of its recent expansion to the westernmost part of the Mediterranean Sea, along with a detailed analysis of its distribution and habitat preferences.

Material and Methods

Sampling sites

The study was conducted in the coastal waters of Almería, Granada and Málaga (Alborán Sea, Andalusia). This area is strongly influenced by Atlantic waters, resulting in relatively cooler and eutrophic conditions that support high algal productivity and diverse macroalgal communities. The monitoring and assessment of seagrass habitats along the coast of Andalusia was carried out in June and July 2023 by the Spanish Institute of Oceanography of the Spanish National Research Council (IEO-CSIC) in the context of the Marine Strategy Framework Directive (MSFD). A total of 46 linear km of seabed were recorded using georeferenced underwater video, 74 ground-truth points were surveyed, and 49 stations were sampled via scuba diving, covering approximately 300 km of coastline from Terreros (Almería) to Nerja (Málaga). On 5 July, 2023, a putative specimen of *Caulerpa taxifolia* var. *distichophylla* was collected at Punta de la Media Naranja (Cabo de Gata-Níjar Natural Park, Almería), with its presence also detected at two nearby sites (<250 m).

Additional sampling was conducted for monitoring of seagrass meadows and exotic species in Andalusia under the Sustainable Management Programme for the Andalusian Marine Environment (Department of Sustainability and Environment, Junta de Andalucía). Several scuba dives were performed from 18 July, 2023 to 6 August, 2024 to assess the distribution and abundance of the invasive taxa. A total area of 2 km^2 between Punta de la Media Naranja and El Plomo was prospected and 10 locations with a putative *Caulerpa taxifolia* var. *distichophylla* were detected. For each site, the geographic coordinates, depth, type of substrate, abundance and any other relevant characteristics such as pigmentation and size were recorded (Table 1).

Morphological identification

Specimens were morphologically identified in the laboratory based on diagnostic traits (stolon, fronds, pinnules, rhizoidal pillars, midrib) following the criteria used by Jongma *et al.*, (2013). Morphological characterisations were conducted on 10 individuals from each site. Furthermore, the thalli were photographed both *in situ* and in the laboratory. Six herbarium voucher specimens were deposited at the Research Centre for Scientific Collections of the University of Almería (CECOUAL), with collection numbers: HUAL-ALGA259 to HUAL-ALGA264.

Table 1. Records of *Caulerpa taxifolia* var. *distichophylla* in the Cabo de Gata-Níjar Natural Park (Andalusia, Spain).

Site	Date	Coordinates*	Depth (m)	Substrata	Abundance	Observations	Source
Punta de la Media Naranja	2023-07-05	36.93280º N 01.91555º W	10	*C. nodosa*	Scarce	First observation and samples	IEO-CSIC
Punta de la Media Naranja	2023-07-05	36.93182º N 01.91557º W	14	*C. nodosa*	Scarce	Record	IEO-CSIC
Punta de la Media Naranja	2023-07-05	36.93137º N 01.91535º W	18	*C. nodosa*	Scarce	Record	IEO-CSIC
Punta de la Media Naranja	2023-07-18	36.93559º N 01.92257º W	6	*C. nodosa*	Frequent	Samples and photographs	SMPAME (JA)
Punta de la Media Naranja	2023-07-18	36.93304º N 01.91552º W	7	*C. nodosa*	Scarce	Record	SMPAME (JA)
Agua Amarga	2023-07-18	36.93789º N 01.93381º W	3	*P. oceanica* & *C. nodosa*	Frequent	Also dead matte. Samples and photographs	SMPAME (JA)
El Plomo	2023-07-18	36.92446º N 01.95063º W	6	*P. oceanica*	Scarce	Record	SMPAME (JA)
Agua Amarga (POSIMED St.)	2023-11-29	36.93615º N 01.93082º W	12	*C. nodosa*	Scarce	Photographs	SMPAME (JA)
Agua Amarga	2024-03-17	36.93882º N 01.93348º W	3	*C. nodosa*	Scarce	Molecular analysis and photographs	SMPAME (JA)
Punta de la Media Naranja	2024-08-06	36.93333º N 01.91458º W	9.5	*C. nodosa*	Frequent	Photographs	SMPAME (JA)
Punta de la Media Naranja	2024-08-06	36.93306º N 01.91478º W	10	*C. nodosa*	Abundant	Samples and photographs	SMPAME (JA)
Punta de la Media Naranja	2024-08-06	36.93290º N 01.91507º W	10.5	*C. nodosa*	Frequent	Samples and photographs	SMPAME (JA)
Punta de la Media Naranja	2024-08-06	36.93253º N 01.91557º W	11.5	*C. nodosa*	Abundant	Samples and photographs	SMPAME (JA)
Agua Amarga (POSIMED St.)	2024-12-11	36.93615º N 01.93082º W	12	*C. nodosa*	Absent		SMPAME (JA)

* ETRS89 Datum. IEO-CSIC: Instituto Español de Oceanografía- Centro Superior de Investigaciones Científicas. SMPAME (JA): Sustainable Management Programme for the Andalusian Marine Environment (Junta de Andalucía)

Molecular identification

Specimens were also identified through molecular analyses of the rDNA 18S-5.8S-28S region, conducted at the Andalusian Institute of Agricultural and Fisheries Research and Training (IFAPA) (Department of Agriculture, Fisheries, Water and Rural Development, Regional Government of Andalusia) at El Puerto de Santa María (Cádiz). Two algal samples collected from Agua Amarga, 17 March, 2024 (Table 1) were homogenized using a TissueRuptor® tissue homogenizer (Qiagen) in five vol of lysis buffer from the NucleoSpin™ Tissue Mini Kit (Macherey-Nagel). Thereafter, total genomic DNA was extracted following the manufacturer's protocol. DNA concentration was determined using a Nanodrop™ ND-8000, and quality was assessed via agarose gel electrophoresis.

The 18S-5.8S-28S region was amplified in two separate PCR reactions using the primer pairs 18S-ITS1F-new/TW13 (Omelchenko *et al.*, 2019; Fang *et al.*, 2023) and AB28/T13N (De Clerck *et al.*, 2006). Each PCR reaction was performed in a final volume of 12.5 µl, containing 40 ng of template DNA, 300 nM of each specific forward and reverse primer, and 6.25 µl of Platinum Multiplex PCR Master Mix (2x, Thermo Fisher Scientific). The thermal cycling conditions included an initial denaturation at 94 °C for 4 min, followed by 30 cycles of 94 °C for 40 seconds, annealing at 46 °C for 1 min, and

extension at 72 °C for 2 min, with a final step at 72 °C for 6 min. PCR products were cloned into a TOPO-TA vector and subsequently sequenced using the BigDye® Terminator v3.1 kit (Life Technologies) when necessary. Sequences obtained were assembled using SeqMan v8.2 (DNASTAR) and analysed for similarity using BLAST (blastn) at NCBI. The final sequences were deposited in GenBank/EMBL/DDBJ under accession numbers PV037361 and PV037362.

Phylogenetic analyses were conducted using the maximum likelihood method in IQ-TREE 2 v2.1.2 (Trifinopoulos *et al.*, 2016), with 1,000 ultrafast bootstrap replications and a minimum correlation threshold of 0.99 as the convergence criterion. The TPM2+F+G4 substitution models were selected based on the Bayesian information criterion (BIC) score. Phylogenetic trees were visualised with FigTree1.4.4 with *Caulerpa serrulata* designated as the outgroup. The accession numbers of the species included in the phylogenetic analysis were as follows: *Caulerpa taxifolia* var. *distichophylla,* LN559619, LN559620, EF190263; *Caulerpa taxifolia,* AF316358, AJ299754, AF316355, AY034869, AJ299772, AJ299757, AJ316268, AJ316269; *Caulerpa sertularioides,* JQ745715; *Caulerpa racemosa*, AJ297652, AJ297653, JQ745722; *Caulerpa mexicana*, JQ745720; *Caulerpa scalpelliformis*, JQ745714; *Caulerpa serrulata*, JQ745711.

Results

Distribution, morphological and molecular identification

Specimens morphologically consistent with *Caulerpa taxifolia* var. *distichophylla* were found at 13 locations within the Cabo de Gata-Níjar Natural Park (Almería, southern Spain) along approximately 4 km of coastline between Punta de la Media Naranja and El Plomo (Table 1; Fig. S1). The macroalgae showed highly variable abundances in the invaded sites, ranging from a presence that is especially abundant at the edges of *Cymodocea nodosa* meadows and in the understorey of these formations, where it is generally hidden by the leaves of this angiosperm, to small colonies comprising a few isolated individuals. No monospecific patches have been observed in the area. No clear pattern associated with depth was observed, with a presence between 3 and 18 metres. The species identified in this study predominantly colonise *C. nodosa* meadows, occurring both within the meadows and along their edges. Additionally, the alga was observed at the edges of *Posidonia oceanica* meadows and on *P. oceanica* dead matte, but it was not detected within the meadows themselves or on loose sandy substrates.

All collected specimens were characterised by a generally thin and delicate thallus. The stolons were cylindrical and thin, approximately 1 mm in diameter, very light whitish-green in colour (Fig. 1A), with thin and

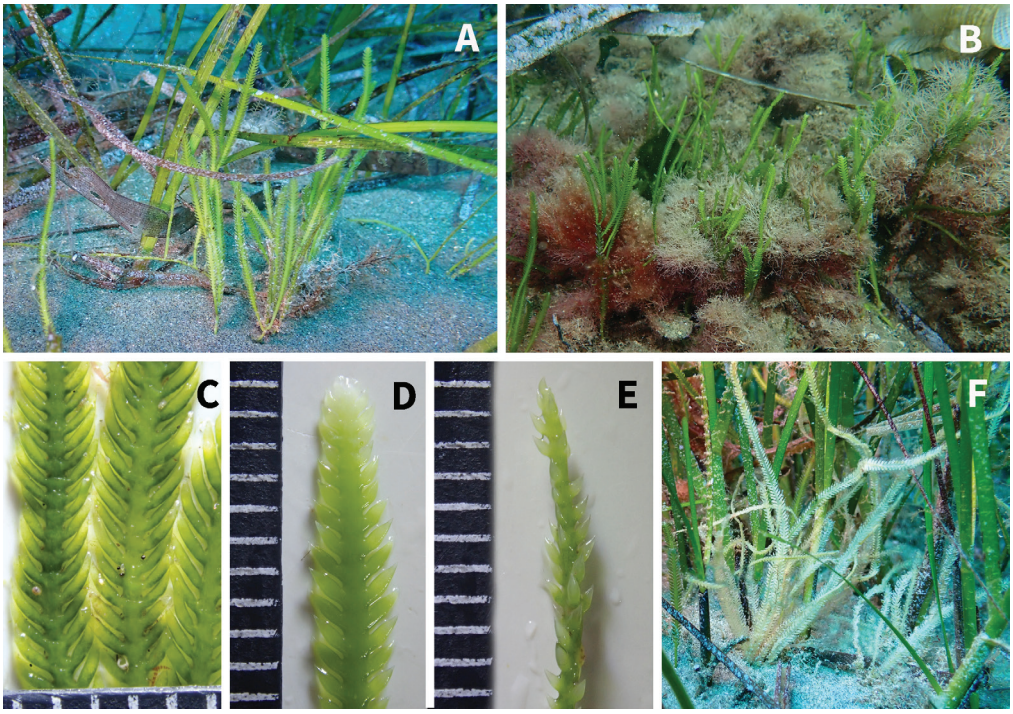

Fig. 1: *Caulerpa taxifolia* var. *distichophylla* from Cabo de Gata-Níjar Natural Park (Andalusia, Spain). A: Specimen within a *Cymodocea nodosa* meadow (-9.5 m; 6 August, 2024). B: Specimens in a gap of a *Posidonia oceanica* meadow (-3 m; 18 July, 2023). C: Middle portion of distichous fronds (-3 m; 17 March, 2024). D: Detail of the upper portion of a distichous frond (-3 m; 18 July, 2023). E: Detail of the upper portion of an irregular frond (-3 m; 18 July, 2023). F: Depigmented specimen in a dense *Cymodocea nodosa* meadow (-9.5 m; 6 August, 2024). In C, D and E, each interval in the scale bar corresponds to 1 mm. Photographs by Agustin Barrajón (A, F) and Diego Moreno (B, C, D, E)/ Sustainable Management Programme for the Andalusian Marine Environment/ Junta de Andalucía).

branched rhizoidal pillars. The fronds were green, generally simple and more rarely divided (Fig. 1B), with lengths ranging from 3 to 10 cm (maximum 12 cm), and 2-3 mm wide (Fig. 1C). Along the stolon, the fronds were often grouped in sets of 3-10 fronds (Fig. 1B). The rachis was cylindrical, less than 1 mm in diameter, with numerous flattened pinnules on each side, very close to each other, with a wider shape in the centre, and pointed and somewhat curved at the end (Fig. 1D). The pinnules were generally all located on the same plane with respect to the rachis, giving the frond a characteristic distichous appearance (Fig. 1D), although occasionally thalli with pinnules arranged irregularly around the rachis were also observed (Fig. 1E). Numerous depigmented thalli were observed in August 2024 within a dense *C. nodosa* meadows at Punta de la Media Naranja, between depths of 10 and 11 metres (Fig. 1F). However, most thalli exhibited the characteristic light green pigmentation.

The nucleotide sequences of the analysed samples were 1090 and 1093 bp in length and showed a 100% match with previously published sequences classified as *C. taxifolia* var. *distichophylla* at NCBI/EMBL/DDBJ. Phylogenetic analysis confirmed that our samples clustered in a group highly supported by a bootstrap value of 94 with *C. taxifolia* var. *distichophylla* specimens (Fig. 2).

Discussion

Morphological and molecular analyses confirmed the presence of *Caulerpa taxifolia* var. *distichophylla* for the first time in 13 sites of the Cabo de Gata-Níjar Natural Park (Almería, southern Spain). This finding provides new evidence of the species' westward expansion, with the nearest known population located over 1000 km away in the Sardinia Channel. The species is now established from the easternmost to the westernmost coasts of the Mediterranean Sea. Nucleotide sequences of rDNA grouped the Almería samples within a strongly supported clade that includes specimens of *C. taxifolia* var. *distichophylla* from Sicily (Jongma *et al.*, 2013), Greece and Cyprus (Aplikioti *et al.*, 2016). Furthermore, the thalli observed in the samples studied are morphologically similar to those described in other Mediterranean populations of this species. The fronds of the specimens inhabiting *C. nodosa* meadows reached lengths of 10–12 cm. In Sicily, established populations show frond lengths ranging from 8–10 cm on sand (sparse fronds), up to 15 cm in sheltered and shaded breakwaters, and 20–35 cm in *P. oceanica* meadows, in areas shaded by the seagrass canopy (Musco et *al.*, 2014). In contrast, the fronds of the aquarium strain of *C. taxifolia* in Cap Martin (France) can exceed 60 cm (Meinesz & Hesse, 1991),

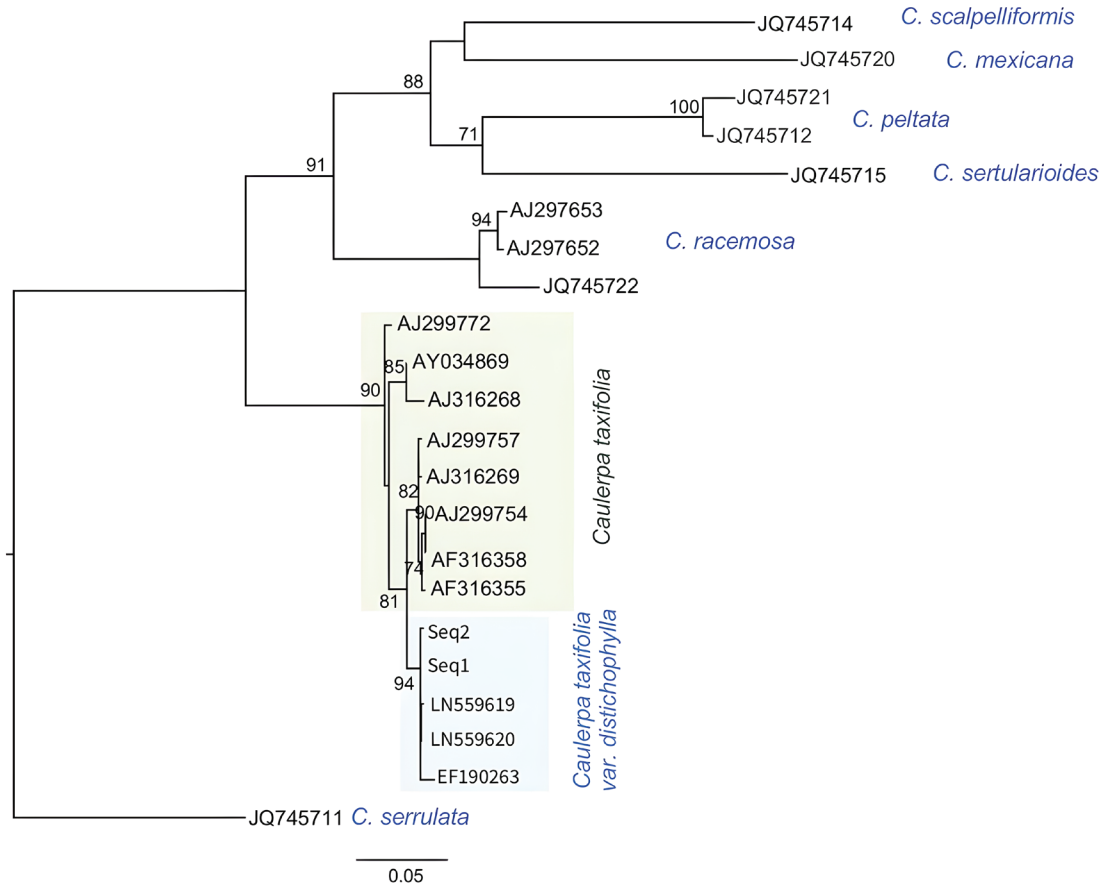

Fig. 2: Phylogenetic tree of *Caulerpa* species using the Maximum Likelihood method. Sequences from this study are labelled as Seq1 and Seq2. Accession numbers for each species are provided. Clades corresponding to *C. taxifolia* var. *distichophylla* and *C. taxifolia* are shaded in blue and green, respectively. Bootstrap values higher than 70 are shown in each node.

reaching up to 80 cm in autumn (Boudouresque *et al.*, 1995). The modest size observed in Almería may reflect an early stage of colonization, with potential for increasing growth as populations become more established. One plausible vector for the arrival of this invasive species is maritime traffic, particularly large commercial vessels operating in the vicinity. The nearby port of Carboneras (<6 km), which hosts intensive industrial activity including a cement plant and a thermal power station, could be a potential point of introduction.

The bathymetric range of *Caulerpa taxifolia* var. *distichophylla* in Almería (3-18 m) is consistent with previous records from Turkey, Cyprus, Malta, and Italy (0-20 m) (Cevik *et al.*, 2007; Çiçek *et al.*, 2013; Schembri *et al.*, 2015; Mannino & Balistreri, 2017; Mannino *et al.*, 2019). However, deeper occurrences have also been reported in the eastern Mediterranean Sea, reaching depths of 28 m in Malta (Ellul *et al.*, 2019), 48 m in Cyprus and Lebanon (Aplikioti *et al.*, 2016; Bitar *et al.*, 2017), and up to 100 m in Greece (Aplikioti *et al.*, 2016). In comparison, *C. taxifolia* has been observed from shallow waters to depths of 100 m in Monaco (Belsher & Meinesz, 1995), and *C. cylindracea* typically ranges from 0 to 70 m (Klein & Verlaque, 2008). The shallow distribution of the Almería populations suggests a preference for warmer habitats, possibly due to thermal constraints, but further studies are necessary to confirm this hypothesis. In this study, *C. taxifolia* var. *distichophylla* was mainly found in *C. nodosa* meadows with lower occurrences near *P. oceanica* edges, dead matte, and occasionally near *C. cylindracea*. In contrast, in Sicily, where the species is widespread, it shows high coverage (>50%) in *P. oceanica*, especially on dead matte and meadow edges, with lower abundance in *C. nodosa* (<10%). It has also been observed on sand, rocks, artificial substrates, and mooring lines in Sicily (Musco *et al.*, 2014). Across the Mediterranean, the species has been recorded on a wide variety of substrates (e.g. mud, sand, gravel, rock, biogenic hard bottoms, shipwrecks) and habitats, including bioconstructions (e.g., *Sabellaria* spp.), macroalgal communities (*Cystoseira* spp., *Codium bursa*, *Caulerpa* spp., *Penicillus capitatus*), and seagrass meadows (*C. nodosa*, *P. oceanica, Halophila stipulacea*) (Mannino *et al.*, 2019). This ecological plasticity, coupled with the availability of suitable habitats (e.g., *C. nodosa* and *P. oceanica* meadows and some areas of dead matte) suggests a high potential for further spread in Almería unless constrained by other environmental factors (e.g., temperature).

The aquarium-derived strain of *Caulerpa taxifolia* expanded along the cooler northern Mediterranean coasts in the late 20th century—from Monaco, France, Italy, Croatia, and Spain (Balearic Islands)—but remained rare in warmer southern regions, with the exception of Tunisia (Meinesz *et al.*, 2001; 2010). Its spread is limited by a lower thermal tolerance (lethal temperature below 7 °C) (Boudouresque *et al.*, 1995). In contrast, *C. taxifolia* var. *distichophylla* has primarily colonized warmer regions of the eastern and southern Mediterranean Sea, including Syria, Lebanon, Cyprus, southern Turkey, Greece, Libya, Malta, Tunisia, Sicily, Calabria, and southern Sardinia (Mannino *et al.*, 2019). Its distribution appears to be constrained by the temperature of the 15 °C February isotherm, which may explain its absence from colder northern coasts (Jongma *et al.,* 2013). Recent westward records in Tunisia (2015) (Chartosia *et al.*, 2018) and southern Sardinia (2016) (Di Martino *et al.*, 2018) remain within thermally mild zones. Similarly, in Panarea (north of Sicily, Italy), its presence is restricted to hydrothermal vent areas characterized by warmer waters, where it coexists with *C. cylindracea* and *H. stipulacea* (Gaglioti & Gambi, 2018). These patterns suggest that the biogeographic range of this variety is largely determined by thermal limitations, although the reproductive potential and other ecological traits probably also constrain its distribution.

Depigmented fronds observed in some *C. taxifolia* var. *distichophylla* samples from Almería may indicate a reproductive process, potentially linked to gamete release. However, their uniformly whitish appearance contrasts with the partial depigmentation observed in fertile thalli of other *Caulerpa* species (e.g., *C. taxifolia*, *C. cylindracea*, *C. chemnitzia*) (Panayotidis & Žuljević, 2001; Phillips 2009; Caronni *et al.*, 2021). Unlike the aquarium-derived strain of *C. taxifolia*, which shows no evidence of sexual reproduction in the Mediterranean, likely due to its hybrid origin (Meinesz, 1992; Boudouresque *et al.*, 1995), the sexual reproductive capacity of *C. taxifolia* var. *distichophylla* remains unknown. The decline in *C. taxifolia* expansion since the early 2000s across the Mediterranean Sea may be partially explained by the lack of sexual reproduction and the emergence of algal disease, possibly caused by pathogenic agents (Meinesz *et al.*, 2010; Žuljević *et al.*, 2019; Kleitou *et al.*, 2025). Therefore, investigating the reproductive strategy of *C. taxifolia* var. *distichophylla* is critical to assess its potential for long-term persistence and expansion.

Although no ecological impacts have been observed yet in Almería, the presence of *C. taxifolia* var. *distichophylla* raises concerns due to its invasive potential. Its size and morphology, distinct from the aquarium-derived *C. taxifolia,* may result in different ecological interactions (Musco *et al.*, 2014). While the impacts of *C. taxifolia* on benthic communities and seagrass meadows are well documented (Boudouresque *et al.*, 1995), the effects of *C. taxifolia* var. *distichophylla* remain poorly understood. Preliminary studies suggest possible impacts on polychaete assemblages in muddy sand (Cevik *et al.*, 2012) and *P. oceanica* dead matte (Musco *et al.*, 2014). The absence of caulerpine in native populations of this variety (Schwede *et al.*, 1986) could imply lower toxicity compared to other *Caulerpa* species (Lemée *et al*., 1996), potentially reducing its biotic impact. However, its ability to monopolize space, accumulate as wrack, and cause socioeconomic impacts such as interference with fishing activities (Musco *et al.*, 2014) reinforce the importance of ongoing monitoring in the western Mediterranean Sea. Additionally, seasonal variability may modulate its ecological impact. In Malta, fronds seem to regress during winter (Schembri *et al.*, 2015), potentially reducing ecological impacts on native assemblages (Ellul *et al.*, 2019).

A similar seasonal pattern has been observed in Almería (southeastern Spain), where the species is abundant in summer but becomes scarce or absent in November. This suggests temperature-dependent dynamics, but long-term systematic monitoring is required to confirm seasonal trends and their ecological significance.

The future expansion of *C. taxifolia* var. *distichophylla* in southeastern Spain remains uncertain. In contrast to *C. taxifolia* in the Mediterranean Sea, *C. cylindracea* has exhibited a continuous and rapid spread since its first detection in Almería in 2008 (Moreno, 2010), reaching multiple locations in Andalusia within a few years (Junta de Andalucía, 2010, 2013, 2014; Arroyo *et al.*, 2015). After more than 15 years of presence in Andalusia, and despite its wide distribution from the shallow photophilous algae communities to depths exceeding 30 m, *C. cylindracea* has shown limited impact on well-structured *P. oceanica* meadows. It predominantly colonises sandy patches within meadows, dead matte, and maerl beds at depths from 20 to over 30 m (Carreto *et al.*, 2021). Similar patterns have been described around the Balearic Islands (Cebrian & Ballesteros, 2009). Interestingly, recent data indicate a decline or disappearance of *C. cylindracea* in some previously dense populations (Junta de Andalucía, 2024). The available evidence suggests that *C. taxifolia* var. *distichophylla* may expand along southeastern Spain and further north, especially under continued sea surface warming, which may benefit this thermophilic, invasive taxon. However, its potential expansion into the Alborán Sea could be constrained by the Almería-Oran front, a well-known biogeographic barrier for many species (Real *et al.*, 2021), and by the influence of colder Atlantic waters. Ongoing monitoring will be key to tracking these dynamics.

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Supplementary Data

The following supplementary information is available online for the article:

S1: Distribution map of *Caulerpa taxifolia* var. *distichophylla* in the Mediterranean Sea (red dots, bibliography records) and in Andalusia, Spain (yellow dots, present study). A: First records in the eastern Mediterranean basin and distribution of the species in the Mediterranean Sea. B: Location of Agua Amarga (Andalusia, Spain). C: New records of the species (yellow star, first observation) between Punta de la Media Naranja and El Plomo (Cabo de Gata-Níjar Natural Park, Andalusia).