

Research Article

Invasion alert: rapid range expansion of *Caulerpa taxifolia* var. *distichophylla* in Maltese waters (central Mediterranean)

Therese Ellul, Julian Evans* and Patrick J. Schembri

Department of Biology, University of Malta, Msida MSD2080, Malta

Author e-mails: therese.ellul.11@um.edu.mt (TE), julian.evans@um.edu.mt (JE), patrick.j.schembri@um.edu.mt (PJS)

*Corresponding author

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Abstract

The alien alga *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman and Procaccini was first discovered in Malta in June 2013 and had spread to three sites spanning some 8 km by 2014. A monitoring programme in combination with a citizen science reporting initiative revealed a dramatic expansion in the distribution of this species, which was found at 23 sites over a 45 km stretch of coastline in 2016 and at four additional sites in 2017 (including three sites where it was previously absent in 2016). The alga is now distributed along the entire northeastern coasts of the Maltese Islands, as well as in northwestern and southeastern Malta, with mean frond densities of 91–972 fronds/m² and mean total frond lengths (including the rachis) of 12.3–41.8 mm. It was found at depths down to 40 m, predominantly on rocky substrata intermixed with other macroalgae (especially when the rocky substratum had a thick layer of sediment covering it) or on heterogeneous bottoms, including at the borders of *Posidonia oceanica* patches, but not within dense meadows of this seagrass. The remarkably rapid spread of *C. taxifolia* var. *distichophylla* and its ability to colonise several different habitats indicate that this alga should be regarded as invasive in Maltese waters.

Key words: alien species, Caulerpaceae, citizen science, Malta, non-indigenous species, phenotypic plasticity

Introduction

The genus *Caulerpa* is represented in the Mediterranean by one native species, *C. prolifera* (Forsskål) J.V. Lamouroux, and seven non-indigenous taxa: *C. chemnitzia* (Esper) J.V. Lamouroux; *C. cylindracea* Sonder; *C. mexicana* Sonder ex Kützinger; *C. scalpelliformis* (R. Brown ex Turner) C. Agardh; *C. taxifolia* (M. Vahl) C. Agardh; *C. taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman and Procaccini; and *C. racemosa* var. *lamourouxii* f. *requienii* (Montagne) Weber-van Bosse; Verlaque et al. (2015). Of these, *C. chemnitzia*, *C. mexicana*, and *C. scalpelliformis* were first recorded between 1926 and 1939, and are potentially invasive in the Mediterranean, while *C. racemosa* var. *lamourouxii* f. *requienii* was first recorded in 1951 and has no reported ecological impacts. The other three non-native species of *Caulerpa* were introduced more recently and are considered to be invasive in the Mediterranean (Verlaque et al. 2015).

Caulerpa taxifolia was first recorded from Monaco in 1984, and quickly became one of the most notorious marine alien species in the Mediterranean, being nicknamed the “killer alga” by the media due to its rapid spread and impacts on seagrass habitats (Meinesz 1999), and has been listed as one of the top 100 worst non-indigenous species in the world by the IUCN Invasive Species Specialist Group (Lowe et al. 2000). Despite records from southeastern Sicily and Tunisia, *C. taxifolia* has not been reported from the Maltese Islands (Evans et al. 2015). *Caulerpa cylindracea* received less public attention, but is even more invasive than the “killer alga”, spreading further and faster, and having similar environmental impacts to *C. taxifolia* (Klein and Verlaque 2008). It was first recorded from Libya in 1990, and quickly spread throughout the entire Mediterranean basin; in the process, *C. cylindracea* became the first alien species of *Caulerpa* to be recorded from Maltese waters (Borg et al. 1997). Both *C. taxifolia* and *C. cylindracea* are included in the list of the 100 worst alien species of the Mediterranean Sea (Streftaris and Zenetos 2006), and a recent quantification of impacts by Mediterranean marine alien species ranked them amongst the top four species in terms of their overall impact score (Katsanevakis et al. 2016).

Caulerpa taxifolia var. *distichophylla* is the most recent *Caulerpa* to have been introduced in the Mediterranean. Morphological and molecular studies have shown that this is distinct from the *Caulerpa taxifolia* of “killer alga” fame, and represents a different strain that was independently introduced into the Mediterranean (Jongma et al. 2013). It was first found in Syria in 2003 (misidentified as a dwarf form of *C. mexicana*; see Bitar et al. 2017), with subsequent records from Turkey (as *C. taxifolia*; Cevik et al. 2007), Sicily (Cormaci and Furnari 2009; Meinesz et al. 2010), Cyprus (Çiçek et al. 2013; Tsiamis et al. 2014), Malta (Schembri et al. 2015), Rhodes, Greece (Aplikioti et al. 2016), Lebanon (Bitar et al. 2017), Libya (Shakman et al. 2017), Tunisia and Sardinia (Di Martino et al. 2018). The first central Mediterranean records of *C. taxifolia* var. *distichophylla*, from the southeastern Sicilian coasts in May 2007, occurred less than four years after the first finding of this species in the Levantine basin. Such a rapid expansion mirrors the distributional spread previously seen in *C. taxifolia* and *C. cylindracea*, giving rise to concerns about potential impacts from the new invader. In fact, *C. taxifolia* var. *distichophylla* can be considered as invasive in Sicily, where it is extending its range, having now reached the northern coasts (Musco et al. 2014; Picciotto et al. 2016), and it has also had significant ecological impacts on the ecosystems it has colonised. In particular, the alga has been shown to monopolize space in certain habitats and to cause changes in the community structure of the associated macro- and meiofauna (Musco et al. 2015). It has also affected fishing activities by clogging nets, and therefore has pest status (Musco et al. 2014).

In Malta, *C. taxifolia* var. *distichophylla* was first discovered in June 2013 when a few fronds were identified in a sample taken as part of a benthic

survey; subsequent surveys at the same site in winter did not locate any specimens. The alga reappeared at this site in June 2014, this time occupying a much larger area and with a higher frond density. In July 2014, it was recorded from a second site, about 7.4 km distant from the first, but only in two small patches (Schembri et al. 2015). This pattern suggests that *C. taxifolia* var. *distichophylla* was in its initial stages of colonisation in 2013–2014. Evans et al. (2015) reported finding it at a third site, and hence considered it to have become established in Maltese waters. Given its ability to spread rapidly, and potential for having ecological impacts, Schembri et al. (2015) highlighted the need for careful monitoring of this species. Within this context, a surveying programme was initiated in 2016 to document changes in the distribution and to assess the abundance of *C. taxifolia* var. *distichophylla* in Maltese waters, hence providing ecological data to support management actions.

Materials and methods

Monitoring was undertaken between 2016 and 2017 during the summer months since Schembri et al. (2015) reported that *C. taxifolia* var. *distichophylla* fronds regressed in winter but reappeared in summer. The surveys were made through a two-pronged approach. First, a series of 29 monitoring sites were established along the accessible shores of the Maltese Islands. The sites were distributed around the three main islands, but with a higher density along the northeastern shores since the southwestern coasts are dominated by inaccessible cliff shores. The infralittoral zone (down to a maximum of 40 m depth) at these sites was surveyed via snorkelling and SCUBA diving to search for the alien alga. An average duration of 35 minutes was spent searching a given site, in each case covering an area of approximately 1,800 m². In sites where the alga was not found within the above time period, a further intense searching effort was undertaken in small 16 m² patches, looking closely at the substratum and searching amongst erect or decumbent algae and seagrasses, since *C. taxifolia* var. *distichophylla* can be difficult to spot when growing sparsely amongst taller algae.

Whenever *C. taxifolia* var. *distichophylla* was present at a site, the depth (m) at which the alga occurred, presence or absence of other species of *Caulerpa* in the vicinity, and the habitat were recorded. The abundance of the alien alga was then estimated by taking 12 replicate frond density counts within a 5 × 5 m area containing the alga, using a 0.25 × 0.25 m quadrat. Approximately 30 entire fronds of *C. taxifolia* var. *distichophylla*, or all fronds present if they amounted to less than 30 in total, were then collected at random from the general area, placed in labelled sample bottles with seawater, and transferred to the laboratory.

The fronds were submerged in a few mm of water and photographed from directly above against a white background together with a scale.

Morphometric measurements were then made from the images using the “Measurement Tool” in ImageJ v.1.41 (Schneider et al. 2012). Following Jongma et al. (2013), the following measurements were taken (in mm accurate to 0.01 mm): stolon diameter; rhizoidal pillar length; rachis length; frond length; frond width; pinnule length; pinnule width; and interpinnular distance. Replicate measurements of pinnule length ($n = 10$), pinnule width ($n = 10$) and interpinnular distance ($n = 5$) were made for each frond; these were not taken from the base or tip of the fronds since pinnules in these areas are generally smaller than those from the central region. No morphometric measurements of fronds which appeared damaged, or which exhibited a tristichous pinnule arrangement or primary, secondary and tertiary ramification, were made.

The second approach to monitoring the spread of *C. taxifolia* var. *distichophylla* in Maltese waters involved the initiation of a citizen-scientist reporting programme for this species. A request for sightings was issued, targeting snorkelers and recreational divers. To this end, a poster with representative photographs of the alga and details on how to report the species was prepared and distributed to local dive schools and dive clubs, as well as shared online through social media. When a report was received indicating the presence of *C. taxifolia* var. *distichophylla* at a site that had not yet been surveyed, the sighting was confirmed through field surveys within the area reported, except in cases where the reports could be verified through the identification of the species from *in situ* photographs taken by the person reporting the alga.

Monitoring at pre-selected sites was undertaken between June and September 2016. Seven sites where *C. taxifolia* var. *distichophylla* was absent in summer 2016, and which seemed to lie outside the distribution extent of this species in Maltese waters at the time, were surveyed again between June and September 2017 to check if the algae had spread to these sites in the interim period, while an additional site was also surveyed in summer 2017. The citizen science programme was initiated in July 2015, and we record here all sightings reported to us up to the end of December 2017.

Results

Caulerpa taxifolia var. *distichophylla* was recorded from 16 of the 29 monitoring sites surveyed in summer 2016, while reports from citizen scientists came from seven additional sites that had not been surveyed; the presence of the alga was subsequently verified at six of these sites, resulting in a total of 22 verified records and one unverified sighting by December 2016. These records covered practically all the northern, northeastern and eastern coasts of the archipelago, stretching over an along-coast distance of some 45 km in total. In contrast, the alien alga was absent from sites located on the western and southwestern sections of Malta and Gozo islands

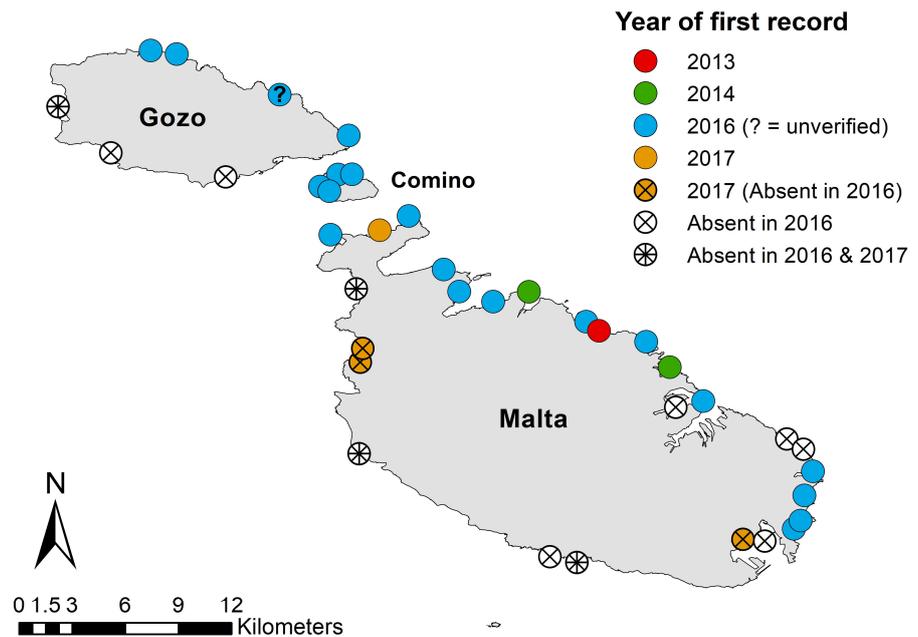


Figure 1. Map of the Maltese Islands showing locations in which *Caulerpa taxifolia* var. *distichophylla* has been recorded, colour-coded according to the year of first sighting, and sites where this species was not found in surveys made in summer 2016 and 2017.

(Figure 1). In 2017, *C. taxifolia* var. *distichophylla* was recorded from four additional sites, including three sites (two in northwest Malta and one in southeast Malta) where it was previously absent in 2016. On the other hand, surveys made in eastern Gozo and southwestern Malta indicated the alga was still absent along these coasts (Figure 1; Supplementary material Table S1).

Caulerpa taxifolia var. *distichophylla* was recorded from an overall wide depth range. In the 16 monitoring sites where it was found, the sightings were made at depths of 1.7–28.4 m; however, one of the reports received through the citizen science programme and which was subsequently confirmed by surveying the area, was from a depth of 40 m. The alga was predominantly recorded from rocky substrata, intermixed with other macroalgae, especially when the rocky substratum had a thick layer of sediment covering it, and from areas with a mixed heterogeneous bottom that included a small-scale mosaic of rocky, sandy and occasional small dead matte patches, often with shoots of the seagrass *Posidonia oceanica* in the vicinity. It was frequently found at the borders of *P. oceanica* patches, but not within dense meadows of this seagrass. *Caulerpa taxifolia* var. *distichophylla* was also recorded from a sandy bottom next to a seagrass bed, but on only one occasion.

The mean abundance and mean total frond length of *C. taxifolia* var. *distichophylla* recorded from each of the 16 monitoring sites surveyed in detail are shown in Figures 2 and 3. No obvious spatial pattern in values for these two parameters is evident, although the sites in Comino island tended to have comparatively high frond densities and lengths. Mean frond

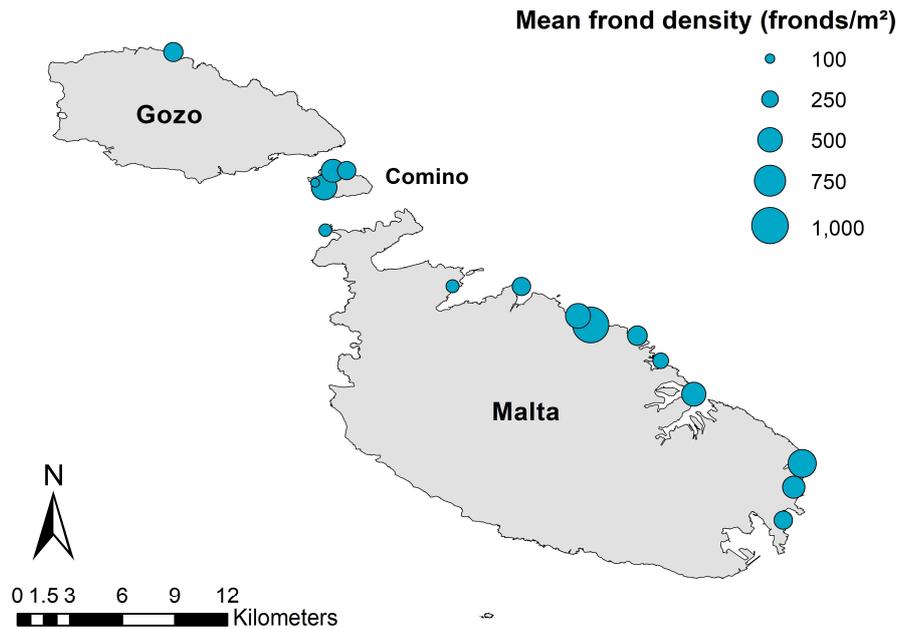


Figure 2. Map of the Maltese Islands showing mean frond density of *Caulerpa taxifolia* var. *distichophylla* recorded at 16 sites surveyed in summer 2016.

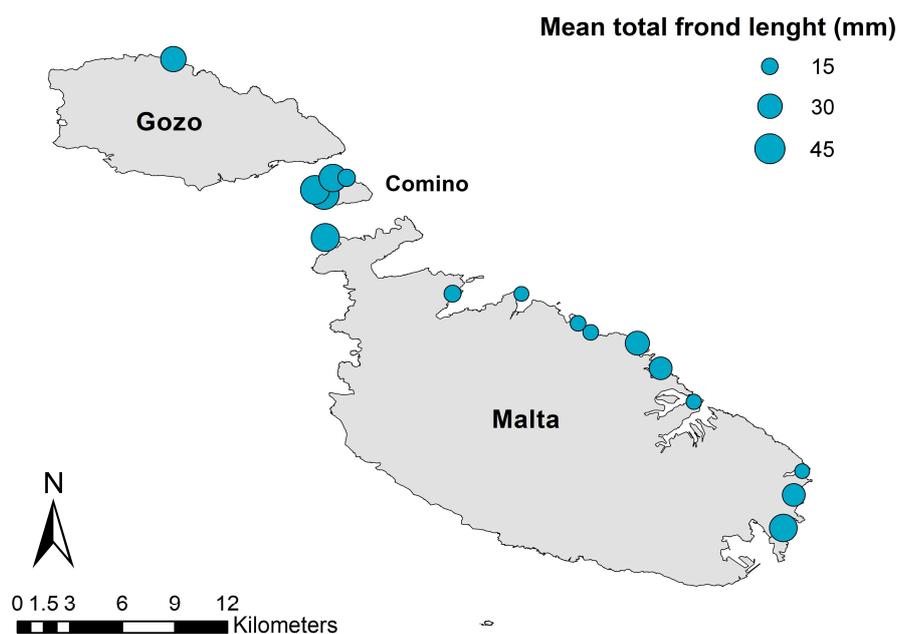


Figure 3. Map of the Maltese Islands showing mean total frond length of *Caulerpa taxifolia* var. *distichophylla* recorded at 16 sites surveyed in summer 2016.

density ranged between 91–972 fronds/m², while mean total frond length (including the rachis) ranged between 12.3–41.8 mm. There was a moderate, but not statistically significant, negative correlation between frond density and length (Pearson correlation: $r = -0.40$; $p = 0.125$). *Caulerpa cylindracea* co-occurred with *C. taxifolia* var. *distichophylla* in seven of the 16 sites, but had no effect on the frond density of the latter species (T-test: $t = -0.25$; $p = 0.804$). The smallest and largest mean values of

Table 1. Morphometric measurements for *Caulerpa taxifolia* var. *distichophylla* recorded in summer 2016, including the minimum and maximum mean values recorded from any one site, and the overall grand mean value recorded across all 16 sites surveyed. All measures are in mm.

Parameter	Minimum	Maximum	Grand Mean
Stolon diameter	0.19 (\pm 0.04 SD)	0.74 (\pm 1.65 SD)	0.47 (\pm 0.12 SD)
Rhizoidal pillar length	2.71 (\pm 0.41 SD)	11.27 (\pm 6.55 SD)	6.67 (\pm 2.59 SD)
Rachis length	2.07 (\pm 0.78 SD)	10.00 (\pm 4.95 SD)	5.37 (\pm 2.51 SD)
Frond length (excluding rachis)	8.16 (\pm 3.04 SD)	33.15 (\pm 12.76 SD)	19.96 (\pm 9.00 SD)
Total frond length	12.30 (\pm 6.42 SD)	41.81 (\pm 25.41 SD)	25.33 (\pm 11.14 SD)
Frond width	0.98 (\pm 0.20 SD)	2.47 (\pm 0.89 SD)	1.92 (\pm 0.38 SD)
Pinnule length	0.40 (\pm 0.10 SD)	1.07 (\pm 0.41 SD)	0.80 (\pm 0.16 SD)
Pinnule width	0.13 (\pm 0.05 SD)	0.38 (\pm 0.26 SD)	0.24 (\pm 0.07 SD)
Interpinnular distance	0.09 (\pm 0.04 SD)	0.20 (\pm 0.07 SD)	0.13 (\pm 0.03 SD)

the measured morphometric parameters recorded from any one site, together with the overall grand mean recorded across all sites, are given in Table 1. For most parameters, the range of mean values per site was quite wide, with the largest mean value being up to five times larger than the smallest mean value. Nonetheless, all morphometric measures fell within the range previously reported for populations in Sicily and Malta (Jongma et al. 2013; Schembri et al. 2015). All data recorded from the individual sites, including the depth range and microhabitats in which the alien alga was recorded, the mean frond density, and the mean values for every morphometric measure, are provided as supplementary material (Table S2).

Discussion

The initial arrival of *C. taxifolia* var. *distichophylla* in Maltese waters was attributed to recreational and/or commercial shipping, particularly given the heavy maritime traffic linking Malta with southeastern Sicily (Schembri et al. 2015). Since the alga is small and can easily be obscured by taller growing species, Schembri et al. (2015) suggested that it may have been present in Malta earlier than the first sighting in 2013 but noted that it was still at an early colonisation phase. The present results show that a dramatic change in the distribution on this species occurred over just two years, expanding to 23 sites over a 45 km stretch of coastline in 2016, compared to just three sites spanning some 8 km in 2014. Such a rapid spread indicates that *C. taxifolia* var. *distichophylla* is most likely colonising new sites through propagation by fragmentation. This has major management implications; as any physical intervention in an attempt to control the species is likely to lead to its fragmentation, this would simply facilitate further spread of the species.

There has been speculation that winter temperatures of less than 15 °C can limit the northern and western expansion of *C. taxifolia* var. *distichophylla* in the Mediterranean, which initially suggested that the alga was at its limit of thermal tolerance in Malta and southern Sicily, where seawater temperatures can drop to around 15 °C in winter (Jongma et al. 2013). This could explain why in Malta, fronds seem to regress in winter

(Schembri et al. 2015). Such disappearance of fronds in winter may serve to limit the impact of *C. taxifolia* var. *distichophylla* on native assemblages. Nonetheless, this alga has now spread to northern Sicily (Musco et al. 2014; Picciotto et al. 2016) and south Sardinia (Di Martino et al. 2018) indicating that it can survive at temperatures below 15 °C. Whether this means that *C. taxifolia* var. *distichophylla* in the central Mediterranean may eventually acclimate and persist without experiencing significant reduction in frond densities during colder months can only be ascertained through regular seasonal monitoring.

The present work has confirmed that *C. taxifolia* var. *distichophylla* is not only established but also rapidly expanding its population in Maltese waters. Such an exponential growth is typical of species regarded as being invasive; once an alien species reaches high abundances, it can threaten the diversity or abundance of native species and the ecological stability of the impacted ecosystem. *Caulerpa taxifolia* var. *distichophylla* is already invasive in some parts of southern Sicily, where it has become the dominant algae on dead seagrass mat, often monopolizing space availability in this habitat (Musco et al. 2014). It is also resulting in changes to faunal communities: macrofaunal assemblages from *Posidonia oceanica* meadows were found to support a higher proportion of molluscs and polychaetes and less crustaceans when partially or severely invaded by the alien alga, compared to uninvaded control sites, while changes in meiofaunal communities also occurred in severely invaded meadows (Musco et al. 2015). Similarly, Cevik et al. (2012) have reported changes in soft bottom invertebrate diversity, with a decrease in polychaete species but an increase in mollusc and crustacean richness, as a result of *C. taxifolia* var. *distichophylla* colonisation, although in this case the presence of the alien alga led to an overall increase in species diversity.

The habitats in which *C. taxifolia* var. *distichophylla* was found in Maltese waters are very similar to those reported from elsewhere in the Mediterranean (e.g. Musco et al. 2014; Di Martino et al. 2018). In Sicily, Musco et al. (2014) reported that the alien alga formed dense mats that carpeted the bottom, but this situation has not been observed in Malta where *C. taxifolia* var. *distichophylla* fronds were generally found in between other algae and never became dominant or monopolized space. Interestingly, during the present work the highest frond density was recorded from Bahar ic-Caghaq—the site where the alien alga was first discovered in 2013—and the present values represent a threefold increase in frond density compared to that reported for 2014 (Schembri et al. 2015), suggesting that *C. taxifolia* var. *distichophylla* could become more dominant over time.

Although we do not have data on the impacts of *C. taxifolia* var. *distichophylla* on native species in Maltese waters, it clearly shares

characteristics with other species of *Caulerpa*, including *C. cylindracea* which is considered invasive in Malta and which can modify the floristic component of its habitats (Sciberras and Schembri 2007). Considering that *C. taxifolia* var. *distichophylla* has shown a remarkably rapid spread and has successfully colonised several habitats in Malta (analogous to the situation previously observed with *C. cylindracea*), and taking into account that even moderate invasion levels have been observed to impact benthic assemblages in Sicily (Musco et al. 2015), it is clear that this alga should be regarded as invasive in Maltese waters.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Geo-referenced distribution data for *Caulerpa taxifolia* var. *distichophylla* in Maltese waters.

Table S2. Monitoring data (depth, habitat characteristics, frond density, morphometric measures) for *Caulerpa taxifolia* var. *distichophylla* in Maltese waters.

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