

Is *caulerpa cylindracea* sonders really one of the worst invaders of the Mediterranean Sea?

Abstract

A critical review of the Mediterranean distribution of the alien Chlorophyta *Caulerpa cylindracea* is conducted, focusing primarily on experimental field studies that have demonstrated its aggressiveness toward native populations and its ability to spread and establish itself in multiple substrates, and also it focuses on those experimental field studies, usually more recent, that have highlighted the spread of *C. cylindracea* as a consequence of factors that subjected the ecosystem to more or less reversible stress, which then allowed the invasion. Although this species is recognized for its broad tolerance to various environments, eutrophication, sufficient light radiation, and bare seabeds are conditions that favour or may be essential for its spread. It is highly likely that an ecosystem in biological equilibrium, with an intact food web, would not be subject to attacks by this species, except in sporadic and transient presences. Indeed, it is not clear whether the variations in the ecosystem are due to the alien species, to which they are usually attributed, or to other stress factors.

Keywords: *Caulerpa cylindracea*, non-native macroalgae, eutrophication, ecosystem decline, biological invasion

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A selection of the most important studies conducted on *Caulerpa cylindracea*

Caulerpa cylindracea Sonder (Chlorophyta, Bryopsidales), introduced in the early 1990s from the south-western coast of Australia,¹ has spread swiftly along Mediterranean coasts in 20 years.^{2,3} The taxonomic placement of this species is complex and controversial,⁴ previously named *C. racemosa* (Forsskål) and later *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman, Boudouresque, finally *C. cylindracea* Sonder.

Here, 44 studies on this species, conducted between 1998 and 2022 (Table 1), are examined, selected from 87 previously reviewed.

The selection excluded a large portion of studies that were limited to monitoring aimed only at establishing the presence and spread of the species in various areas, in the absence of a thorough examination of the ecosystem prior to the invasion, retaining 6. Five studies also concerned morphology and physiology, while those analysing toxins and other chemical components of the species were excluded from the evaluation, although cited where appropriate. Studies that demonstrated the species' aggressiveness and ability to invade substrates with field or laboratory experience were primarily selected, as were those that highlighted the ecosystem's weakness following stress and the impoverishment of native populations.

Table 1 Characterization of studies conducted on *C. cylindracea*, cited in the text from 1-49

year	ecosyst. already compromised	damage caused to the ecosystem	spread, areas	orig, phys. morphol.	exper.	MD	publ
2003	-			x		x	1
2005			mild climate			x	2
2005	-					x	3
2004				x		x	4
1998	unst. environ.			x		x	5
2002		pristine and e disturbed area				x	6
2002		turf penetration			x		7
2008		biodiv. loss*			x		8
2000		P. decline			x		9
2009				x	x		10
2001			fragments		x		11
2008			fragments				12
2005		**			x		13
2008		biodiv. loss*			x		14
2014				x		x	15
2011			dif. substr.			x	16
2011			bare bottom		x	x	17

Table 1 Continued...

2015		biodiv. loss*		x	18	
2016				x	19	
2020		trophicalteration***		x	x	20
2017		trophic alteration ***			x	21
2024		trophic alteration ***			x	22
2019		ecos. alteration	pioneer	x	x	23
2019		biol. homogen.	dif. substr.	x	x	24
2022			decline		x	25
		biol. homogen.		x		26
2019			widespread		x	27
2014	environment stress, eutrophication			x		28
2016	environment stress, eutrophication			x		29
2014	environ. stress			x		30
2010	environ. stress			x		31
2015			light limit.	x		32
2014	eutrophication			x		33
2015	eutrophication			x		34
2015	eutrophication			x		35
2017	eutrophication			x		36
2007	mechanic stress, T			x	x	37
2008	mechanic stress, T. natural environ.		widespread	x	x	38
2013			decline	x		39
	restor.					
2017	eutrophication			x		40
2022	P. decline			x		41
2021	environ. stress			x		42
2017		change passenger		x		43
2006			grazed	x		49

Ecosystem already compromised; damage caused to the ecosystem; spread, areas (propagation methods, diffusion substrates, widespread diffusion, regression and decline of the species, pioneer settlement, development constraints, eaten by animals); orig., phys., morphol.: studies on the origin, morphology and physiology of the species; exper: experimental study in situ or in lab; MD: monitoring and distribution study of the species in a coastal area; Publ.: references in the text.

Biodiv. loss: biodiversity loss of the ecosystem; P. meadows: *Posidonia oceanica* meadows; trophic alteration: trophic alteration of the ecosystem; ecos. alteration: ecosystem alteration; biol. homogen.: tendency towards homogeneity of populations; environ. stress: stressful environment; eutroph.: eutrophication; mechanic stress, T.: environment subject to mechanical stress and increased temperature; natural environ. restor.: restoration occurred through a natural process; P. decline: decline of *Posidonia* meadow; dif. substr.: species adaptable to different substrates; unst. environ.: unstable environment; change passenger: species that contribute to the degradation of the ecosystem; fragments: propagation by fragments.

*It is uncertain whether the reduction in diversity is due to the invasive species or whether the species invaded following the reduction in diversity (disturbed area).

** No significant difference in taxa abundance between removal and control areas after one month.

*** Changes in trophism and the nature of the substrate may be caused by the alien species. However, it would be necessary to know whether the penetration occurred due to some ecosystem stress that weakened the resilience and defences

As in early studies, *C. cylindracea* was observed to spread in situation of environmental crisis and rarefaction of autochthonous populations, authors claimed that it was a stress-tolerant species and a possible indicator of environmental disturbance.⁵ Subsequently, it was deemed invasive and destructive to algae constituting turfs and to a lesser extent to taller species.⁶⁻⁸ Ceccherelli et al.⁹ indicated that where *C. cylindracea* was at the edge of *Posidonia oceanica* meadow, the vertical growth of the alga became sensitive to the combination of time, seagrass density and edge-meadow orientation. Also, the spread of the alga along the edge of the seagrass meadow became dependent on the characteristics of the area and that the growth of the alga inside the meadow was influenced by seagrass density. The susceptibility

of *P. oceanica* meadows to the invasive alga was related to the availability of newly formed sandy habitats (mattes erosion) and to dead mattes, since low invasion through the very dense edges of the seagrass meadows was observed, compared to the less dense ones. We would say today that if the meadow becomes rarefied it allows the intrusion of other species, including *C. cylindracea*.

Ruitton et al.² attributed the spread of *C. cylindracea* along the French coast, especially at depths between -10 and -35 m and on *P. oceanica* beds, to the mild climate, suitable substrates, the presence of dispersal vectors and the absence of effective biological control, factors that would have made the French Mediterranean coast particularly vulnerable to the spread of the alga.

Cebrian and Ballesteros¹⁰ argued that *C. cylindracea* poses a major threat to the diversity of coastal benthic ecosystems in the Mediterranean, interfering with native species and altering benthic assemblages. However, there was some consensus that dense cover of many established indigenous species can be a major factor in reducing the probability of successful invasion.⁹ Ceccherelli and Piazzini¹¹ tested the importance of thallus fragmentation in the recruitment of the invasive alga to the margins of a *P. oceanica* seagrass meadow. Although the results did not unveil the fate of the fragments lost from the seeded margins, whether they had deteriorated or settled elsewhere, away from the source. The Authors stated that “*this study indicates that drifting fragments of C. cylindracea can greatly contribute to the spread of the alga in the Mediterranean*” adducing characteristics of fragmentation that made the initial hypothesis possible.

In a critical review, Klein and Verlaque¹² concluded by saying that possible consequences of the *C. cylindracea* invasion included modifications of physical and chemical conditions (water movement, sediment deposition, substrate characteristics) and the underwater landscape, as well as profound modifications of benthic assemblages, and that *C. cylindracea* can be considered as a habitat modifier.

A study conducted in Sardinia (Italy) aimed at establishing differences in the zoobenthos community, one month apart, in an area covered by *C. cylindracea* and in an area where the species had been removed, did not show significant variations, but this was not enough to suspend the preconceived judgement, in this case, of species with invasive characteristics that cause profound changes in host communities.¹³

In a 2008 study comparing epiphytism on the rhizomes of two *P. oceanica* meadows, one infested with *C. cylindracea* and the other intact, it was found that the average number of taxa per rhizome had decreased sixfold in the former compared to the latter, with the decline occurring mainly in Ochrophyta and encrusting algae, which decreased by 11.6 and 13.3 times, respectively. According to the authors, these results provided ‘additional information on the extremely invasive behaviour of *C. cylindracea* in the Mediterranean Sea’.¹⁴ In 2009, the species was reported at a depth of 30 metres along the coast of Almeria (Spain).¹⁵

In a study involving extensive monitoring, the authors reported rapid spread of *C. cylindracea* in the Murcia region (Spain), which appeared to pose a potential threat to native benthic communities.¹⁶ Similarly, along the coasts of the Gulf of Salerno (Campania, Italy) a vast settlement of *C. cylindracea* was observed on a soft bottom mostly devoid of vegetation, on which an alteration of the zoobenthic populations was hypothesized.¹⁷

In a study conducted in Lipsi, a Greek island in the Aegean Sea, in four bays with increasing intensity of invasion by *C. cylindracea*, a significant correlation emerged between the increase in the abundance of *C. cylindracea* and the height of the fronds and the thickness of the stolons, and a significant negative correlation between the increase in the abundance of *C. cylindracea* and the richness and diversity of native macroalgae species.¹⁸ However, the study photographed a situation that was already underway, and there is no reason to believe that the development of *C. cylindracea* was not the cause of what was attributed to it, but rather the consequence of a factor that made that particular substrate permeable to invasion.

Other studies have also considered the possible interference of the species in the benthos communities. Alomar et al.¹⁹ argued that the spread of *C. cylindracea* in Mediterranean coastal habitats is of concern, leading to differences in community structure. In a

subsequent study, a correlation was found between *C. cylindracea* and Amphipoda, Caridea and Tanaidacea, even when this Chlorophyta was not dominant.²⁰ This species was indicated as a potential modifier of macrozoobenthic communities, creating an extension of trophic and edaphic communities. But is coincidence sufficient to establish that the mere presence of the species favoured those species of zoobenthos? Could there have been other factors that were not as obvious as the alien species? Factors that could have also made the introduction and spread of Chlorophyta possible?

In some studies, conducted along the Calabrian coast (Southern Italy) to verify the spread of *C. cylindracea*, widespread distribution on different substrates was observed. Although no specific study was conducted, the authors argued that ‘the main effects of *Caulerpa cylindracea* colonisation have led to a gradual decline in crustacean species, while herbaceous species have increased in abundance, altering the native structure of macroalgal associations’.²¹ Furthermore, alarm was expressed that “the rapid and increasing spread of the species could influence the structure of Mediterranean biota or, alternatively, lead to the creation of new ecological niches over time”.²² However, it is not known for certain whether the species took over due to stress on the coastal ecosystem or thanks to its impetuosity. When the development of this alien species is observed, it is assumed that it took over by force.

Similarly, a study conducted in the Favignana Marine Protected Area (Sicily) concluded that *C. cylindracea* can have negative effects on the habitat in which it settles in two different ways: a) by influencing the structure of the native algal community, which has low diversity, and b) by favouring the settlement of other alien species.²³ Marine protected areas are not, by definition, free from critical issues. In fact, this study established that a high sedimentation rate plays a decisive role in the structure of communities, and *C. cylindracea* appears to be favoured as a pioneer species.

In a study conducted in the Portofino Marine Protected Area (Liguria, Italy), where *C. cylindracea* was observed for the first time, it was defined as “one of the worst invaders of the Mediterranean Sea” due to its great adaptability to a wide range of environmental conditions and its ability to expand into different habitats, reducing the dissimilarity between recipient communities, a sort of biotic homogenisation.²⁴ Subsequently, again in the same marine protected area of Portofino, a reduction in coverage at all depths by the alien species was verified in 2019, but it is still referred to as “the worst invasive species in the Mediterranean Sea”.²⁵ The same hypothesis of a tendency towards biological homogenization had also been reached on the basis of experimental results from another study.²⁶

A study conducted along the coast of the marine protected area of the Tremiti Islands in the Adriatic Sea has revealed a widespread invasion of the species at depths of between -5m and -25m, on algal turf and especially on bare bottoms.²⁷

But other factors were then taken into consideration. Manipulative experiments conducted on sedimentation rates and nutrient concentrations, demonstrated that changes in the structure of macroalgal assemblages caused by these stressors can facilitate the spread of *C. cylindracea*, suggesting the importance of maintaining good water quality and natural habitat structure to contain biological invasions.^{28,29}

Some studies observed that, although *C. cylindracea* can establish itself in both degraded and uncontaminated environments, its ability to become a dominant component of macroalgal associations seems greater in the former. This statement stems from a study of

a *P. oceanica* meadow that was suitably manipulated to simulate mechanical disturbances of varying intensity. Sixteen months after the start of the experiment, no *C. cylindracea* was found within the meadow, while at the edges its presence and abundance depended on the intensity of the disturbance, being greater where the rhizomes had been damaged.³⁰ However, relatively high densities of *C. cymodocea* at the edges of *P. oceanica* meadows and within gaps in fragmented meadows were also observed in a previous study.³¹ Marin-Guirao et al.³² observed in a field experiment that a limiting factor to the penetration of *C. cylindracea* into *P. oceanica* meadows was the strong light limitation, therefore light seemed to play a key role in the diffusion of this species.

In a manipulative field experiment conducted over a period of one year, in a rocky subtidal area where *C. cylindracea* had been transplanted into both nutrient-enriched and control macroalgal assemblages, the results showed the penetration and biomass of allochthonous Chlorophyta in the previously nutrient-treated assemblages were greater than in the control assemblages, indicating that communities stressed by nutrient pollution are more vulnerable to invasion.³³

Gennaro et al.³⁴ showed in a field experiment in a subtidal area that *C. cylindracea* had a particularly high nitrogen requirement, while a P-limiting nutritional status was detected in both *C. cylindracea* and two concomitant species, the allochthonous Rhodophyta *Laurencia chondrioides* and the native Chlorophyta *Flabellia petiolata*. According to the authors, the absence of inhibition under hypertrophic conditions and in the presence of high ammonia levels, together with strong absorption and rapid reallocation of nutrients within the thallus, are probably the main advantages over other concomitant species, which could explain part of the success of *C. cylindracea* in the Mediterranean Sea.

The predisposition to eutrophication was also tested by Bulleri and Piazzì,³⁵ establishing that both the intensity and the importance of *C. cylindracea* competition on the cover of resident communities increased following nutrient enrichment.

It was then observed that *C. cylindracea* took over from *Cystoseira brachycarpa* and the associated macroalgal community if eutrophication conditions were induced.³⁶

In the coastal stretch at Santa Liberata bay (Tyrrhenia Sea, Italy), a back reef area of *Posidonia oceanica* (L.) Delile had a habitat characterized by distinctive mixed meadow communities of macroalgae (algal turfs of the photophilic infralittoral) and seagrasses (*Nanozostera noltei* and *Cymodocea nodosa*), since 2003 the mixed meadow suddenly disappeared. Between 2004 and 2005, *C. cylindracea* spread shoreward from the barrier reef of *P. oceanica*, on substrate of *P. oceanica* dead matte, replacing algal turf.³⁷ *C. cylindracea* biomass showed an increase of two orders of magnitude between July 2005 and July 2006,³⁸ confirming the considerable substrate-covering capacity and rapid development shown by this species in other parts of the Mediterranean Sea and also its aggressiveness on shallow sheltered bottoms with dead mattes. But the crisis of *N. noltei* and *C. nodosa* meadows and algal turfs preceded the *C. cylindracea* spread. During 2003, the area had undergone severe thermal stress that coincided with a large increase in tourist influx and subsequent intense bottom trampling. The seagrass beds of the seagrasses *N. noltei* and *C. nodosa* and the algal turfs of the photophilic infralittoral had disappeared within two years, and within 2006 only *C. cylindracea* dominated over *P. oceanica* dead matte with thin algal turf.³⁸

In August 2011, *C. cylindracea* showed a decrease in cover, returning to 2005 levels, while *N. noltei* increased. Phytobenthos

still consisted mainly of a thin compact mat, dominated by the dense texture of *Jania rubens* and *Cladophora* spp., with a prevalence of the latter, from which emerged sparse *N. noltei* leaves and tufts of *Padina pavonica* and *Dictyota dichotoma*, that sometimes developed into extensive patches.³⁹ In that study, the conclusion was that “the invasive potential and danger of *C. cylindracea* is expressed when environmental conditions permit, as in the case of biocoenoses impoverished for different reasons”. In later years, it was observed (Lenzi, unpubl. data) the total disappearance from the back reef area of *C. cylindracea* and the return of the macroalgal turfs of the photophilic infralittoral, but not a complete return to the origins of *N. noltei* and *C. nodosa* seagrass beds, the causes of which are likely to be attributed to disturbance by bathers’ trampling, which to a good extent continued. Bathing involves a sediment organic matter decrease, which occurred entirely by chance when this particular small stretch of coast became more frequented.³⁷

Uyà et al.,⁴⁰ in a study conducted in pools on intertidal rock, confirmed significant development under eutrophication conditions. According to Houngnandan et al.,⁴¹ the development and spread of *C. cylindracea* follows the decline and regression of *P. oceanica* meadows.

Bouiadjra et al.,⁴² in an experiment in situ, claimed that the invasive alga *C. cylindracea* tended to colonise disturbed ecosystems, reflecting a reduction in native algal diversity.

But the hypothesis has also been put forward, after field experience, that some non-native species, including *C. cylindracea*, may be stronger competitors than the native ones, despite their low abundance, and that the non-native species can act as “passenger of change” and may promote the persistence of alternative degradation states.⁴³

Some reports claim *C. cylindracea* can be dangerous for its grazers because the caulerpenyne in the thalli may cause alteration of the fish behavior.^{44,45} However, amount of the sesquiterpene contained in *C. cylindracea* is significantly lower than that contained in both *C. taxifolia*⁴⁶ - another “terrible invasive”, which has not been much talked about since desperate alarms in the 1990s - and *C. prolifera*, non-native species well naturalized in the Mediterranean Sea,⁴⁷ which has never been reported for caulerpenyne toxicity, although present.⁴⁸

Furthermore, these concerns contrast with an older study which found that certain fish species, including *Boops boops* and *Sarpa salpa*, and the Mediterranean sea urchins *Paracentrotus lividus* and *Sphaerechinus granularis*, were able to graze on *C. cylindracea* without suffering damage, although, according to the authors, they were unable to sufficiently counteract the growth of the Chlorophyta during the grazing period, which was limited to late summer and autumn.⁴⁹

Table 1 summarises the characteristics that the various studies on *C. cylindracea* cited have highlighted: if it has damaged the ecosystem and in what way, if it found an ecosystem that was already altered, if the ecosystem has recovered on its own, if the study was essentially a monitoring of the spread of the species, if experiments were conducted in the field or in the laboratory, if the study focused on the origin of the invasive species, its physiology and morphology, etc.

Final considerations

From the literature consulted, the initial alarm seems to have been about the danger posed by alien species in general, and this species in particular due to its rapid growth and adaptability to any substrate. Subsequently, on the one hand, this approach has continued, almost

at a rapid pace, mostly simply monitoring the presence, spread, and development of the species; on the other, some research has begun to clarify the role of eutrophication, rarefaction and regression of meadows, and critical ecosystem issues.

The phenomenon of macroalgal blooms has been known for many decades; today, it is a global phenomenon, affecting most of the world's coasts.^{50,51} Species capable of producing high vegetative growth can be either native or non-native. Many native species have exhibited an opportunistic behaviour, with unpredictable range expansions and significant biomass increases that we had never observed before.⁵²⁻⁵⁴ This is just as can happen with non-native species, some of which remain marginal or disappear after a few years, while others exhibit a highly opportunistic and invasive nature. In all cases of macroalgal blooms, eutrophication-related phenomena have sometimes been combined with other ecosystem alterations caused by global warming, acidification, and other environmental changes.

From the literature consulted, the initial alarm appears to have been about the danger posed by alien species in general, and *C. cylindracea* in particular, due to its rapid growth and adaptability to any substrate. Subsequently, on the one hand, this approach has continued, almost at a rapid pace, mostly limited to monitoring the presence, spread, and development of the species, which has continued to be labelled a dangerous invasive species. On the other hand, some research has begun to clarify the role of eutrophication, grassland rarefaction and regression, and ecosystem problems.

C. cylindracea undoubtedly displays a high degree of adaptability, however, in all cases where environmental conditions are reported in in situ experiments, the species has shown a strong affinity for high nutrient concentrations. This environmental criticality harms native populations and favours opportunistic algae, including *C. cylindracea*, which can develop extensive blooms. Therefore, it is highly likely that, in all cases, algal blooms of widespread opportunistic species occur because ecosystems are already compromised. And this goes well beyond attributing the causes to globalization and intensified trade, or to the ways in which invasive species propagate. It is therefore important to consider these phenomena, that of *C. cylindracea* and other bloom-forming species, from a different perspective, one that takes into account ecosystem restoration, wherever possible.

Another consideration concerns the eradication of invasive alien species. This is considered to be relatively ineffective^{55,56} or to have spatially limited effects,⁵⁷ requiring considerable effort and high costs, often with very modest results. Furthermore, if included in national regulations, at the urging of scientists, it would become a narrow-minded practice, considering that some alien species can improve a degraded ecosystem.⁵⁸

Eno et al.⁵⁹ argued that no marine alien species has ever been directly eradicated from British waters, while some have become extinct due to external factors, such as the direct cause of ecosystem stress that allowed alien species to establish themselves.

Conversely, Tamburello et al.⁶⁰ in a meta-analysis to test whether and how the direction and magnitude of alien macroalgal effects on resident communities and species vary with cumulative levels of human impact, found that: 1) the magnitude of the negative effects of algae on community evenness tended to increase with levels of human impact; 2) communities in urban and pristine sites did not differ in the case of invasion, but did so when *C. cylindracea* was removed; 3) more negative impacts can be expected in less stressful environments. The authors suggest that implementing strategies to control the establishment of non-native algae should be considered

a priority to preserve biodiversity in relatively pristine areas, while controlling invaders in degraded sites may be warranted to reduce their role as sources of propagation.

Although an eradication operation should be conducted once its feasibility and sustainability have been established, the problem of the ecosystem's permeability to further attacks remains, so I would add that it is also temporally limited. A compromised ecosystem that has allowed the intrusion and spread of a non-native species is likely in a state of reduced resilience, and this remediation operation, even assuming it could be perfectly successful, cannot be sufficient to restore it, nor would it allow native species to recover, unless the critical conditions that allowed the invasive species to thrive are eliminated.

The small Tyrrhenian Sea Bay invaded by *C. cylindracea* had previously been affected by an anomalous rise in temperatures in 2003, which had affected the photophilous infralittoral biocoenosis, penalizing native species and favouring *C. cylindracea*. However, the latter subsequently declined until it disappeared as soon as the pre-stress environmental conditions returned, and within a few years the climax was re-established. This sequence of events demonstrated the area's good resilience, evidently only temporarily compromised by an exceptional heat wave. This may demonstrate that ecosystems, if not severely compromised, are capable of returning to their natural balance as soon as the causes that led to the degradation are significantly reduced or eliminated.

There is no significant evidence that *C. cylindracea* has prevailed over a healthy ecosystem, altering its structure and food webs. *C. cylindracea* has so far been excluded from *P. oceanica* meadows, and as for the "pristine" habitats where it has been observed, there is no certainty that they are truly pristine. The temperature of the Mediterranean Sea has increased by 1°C in the last 25 years.⁶¹ Warming coastal waters may compromise the health of seagrass meadows and other coastal ecosystems, causing their depletion and allowing alien algae to take over. And this will not be caused solely by their aggressiveness. Much emphasis has been placed on the invasion of alien species, much more than on cosmopolitan or opportunistic native species, which develop and create just as much trouble. We tend to attribute aggressiveness and dangerousness to various alien species as if they were intrinsic properties, external to the ecosystem context. Versatility, resistance, broad tolerance, and nitrophilia are not intrinsically negative attributes; they become so in degraded environments.

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Conflicts of interest

We declare that there is no conflict of interest of any kind.

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