

Communication



Double Trouble: Synergy between Habitat Loss and the Spread of the Alien Species *Caulerpa cylindracea* (Sonder) in Three Mediterranean Habitats

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Abstract: The role of habitat degradation on the spread of the alien green alga *Caulerpa cylindracea* is reported here by comparing observations achieved through a multi-year assessment on three Mediterraneans habitats, namely *Posidonia oceanica* meadows, *Phyllophora crispa* turf, and corallige-nous reefs. Due to the peculiarity of the study site, both natural-reference and impacted conditions were investigated. *C. cylindracea* occurred in all the studied habitats under impacted conditions. High susceptibility to the invasion characterized impacted *P. oceanica*, where *Caulerpa* cover reached 70.0% in summer months. *C. cylindracea* cover did not differ significantly among conditions in *P. crispa* turf, where values never exceeded 5.0%. Conversely, the invasive green algae was low in abundance and patchily distributed in coralligenous reefs. Our results confirmed that habitat loss enhances the spread of *C. cylindracea*, although with different magnitudes among habitats. Dead matte areas of *P. oceanica* represented the most vulnerable habitat among those analyzed, whereas coralligenous reefs were less susceptible to the invasion under both the studied conditions.

Keywords: invasive alien species (IAS); global change; Mediterranean Sea; *Posidonia oceanica* meadow; *Phyllophora crispa* turf; coralligenous reefs; human impact; habitat loss

1. Introduction

Human-mediated disturbances and climate changes act synergically and are rapidly altering the composition and functions of marine communities. Global climate changes strongly affect semi-enclosed basins, such as the Mediterranean Sea, where the habitat loss and the introduction of invasive alien species (IAS) represent the main threats that affect the biodiversity hosted [1,2]. As for alien species, the rate of new introductions was eight species per year during the 3 year period 2017–2019 [3], and 20 new records have been reported in 2021 [4]. Corridors between basins (such as the Suez Canal), shipping vectors and aquarium trades represent the primary introduction pathways of alien species [2]. To date, nearly 1000 alien species have been reported in the Mediterranean Sea, among which 660 species can be considered as already established [5]. The IUCN defines IAS as those species introduced accidentally or deliberately into a natural environment, where they become established, with serious negative consequences for their new environment, threatening native and endemic biodiversity [6].

The green macroalga *Caulerpa cylindracea* Sonder, 1845, is an endemic species from southwestern Australia that showed high development capacity throughout the central and western Mediterranean Sea at the end of the past century ([7] and references therein). The vectors and pathways of introduction within the Mediterranean basin remain uncertain. *C. cylindracea* is capable of rapid colonization of the seabed through conspicuous stolons,



Citation: Casoli, E.; Mancini, G.; Ventura, D.; Belluscio, A.; Ardizzone, G. Double Trouble: Synergy between Habitat Loss and the Spread of the Alien Species *Caulerpa cylindracea* (Sonder) in Three Mediterranean Habitats. *Water* **2021**, *13*, 1342. https://doi.org/10.3390/w13101342

Academic Editor: Lyudmila Kamburska

Received: 16 April 2021 Accepted: 10 May 2021 Published: 12 May 2021

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which modify the structure and reduce the diversity of the invaded benthic habitats [8-11]. It represents one of the most serious invasive species; in fact, it has been included in the "100's IASs of success" in the Mediterranean Sea [12]. Many experimental studies and field observations investigated the factors enhancing the spread of C. cylindracea [13,14] and its ability to compete with native species [15,16], especially in *P. oceanica* meadows and coralligenous reefs along the Italian coasts. The effects of human-related activities (e.g., habitat loss, increase in sedimentation rates, and nutrient load) facilitate the success of *C. cylindracea*, as outlined by the conceptual model proposed by Piazzi et al. [7], through the loss of the resistance of natural assemblages. As a consequence of this synergic disturbance, the structure of native assemblages significantly changes, moving to a permanent alternative stable state dominated by stress-tolerant species [17] that prevent the recovery of natural assemblages. The present study aims to assess the susceptibility of three different degraded Mediterranean habitats affected by degradation (*Posidonia oceanica* [L.] Delile, 1813 meadow, Phyllophora crispa [Hudson] P.S. Dixon, 1964 turf, and coralligenous reef) to the spread of the invasive species C. cylindracea. To this end, surveys were carried out at Giglio Island within the site where the Costa Concordia cruise ship sank in 2012. The operations performed to remove the wreck, and the wreck's presence itself caused confined habitat loss [18,19]. The remediation phase, which encompassed the removal of the main disturbances affecting the wreckage area (i.e., fine sediment and debris diffusion), ended in spring 2018. As a consequence of the remediation phase, bare portions of seafloor characterized the wreckage area where recolonization processes began. The area of interest near the Costa Concordia wreckage was used here as a natural-experimental seabed to assess if habitat depletion could facilitate the spread of C. cylindracea.

2. Materials and Methods

Underwater Visual Census (UVC campaigns) aided by photographic samplings were carried out by scientific SCUBA divers at Giglio Island (central Tyrrhenian Sea, Italy) from December 2018 to December 2020 every 6 months. The investigated seabed encompassed three types of benthic habitats from 5 to 40 m depth characterized by the presence of P. oceanica (POSID), P. crispa turf (PHYLL), and coralligenous reefs (CORAL) located both inside the area of Costa Concordia shipwreck removal operation (impacted condition) and at one control site located a few hundred meters far from the impacted area (used as the natural-reference condition) (Figure 1). Both sites share the same geomorphological features: they are characterized by monzogranite rocky ridges, developing from a few meters up to 60-80 m depth along W-E direction, surrounded by P. oceanica meadows, which covers the sandy seabed up to 30 m depth. Below 15 m depth, two main habitats can be recognized on the rocky seabed: P. crispa turf and coralligenous reef. Both P. oceanica meadows (POSID) and coralligenous reefs (CORAL) are protected by EU regulation, and their ecological status should be maintained and improved according to the Marine Strategy Framework Directive [20]. On the other hand, P. crispa turf (PHYLL) has been poorly investigated and remains largely unknown in terms of biodiversity hosted and functioning within the Mediterranean basin.

Six photographs of 1 m² standard surface were randomly taken at each of the threehabitats in the impacted and reference condition areas at 6 monhtly intervals. Photographs were collected at the same stations in December and July during the period 2018–2020: sampling stations were distributed between 15–25 m depth in POSID, 20–30 m depth in PHYLL, and 25–35 m depth in CORAL. The photographs were analyzed using open source image processing software ImageJ to identify the presence and quantify the percentage cover of *C. cylindracea*.



Figure 1. Map showing the spatial location of the sampling stations within the study area. Sampling stations at the impacted site are indicated in red, whereas sampling stations at the control site are highlighted in green. The blue line defines the boundary of the restricted area defined during Costa Concordia wreck removal and the following remediation phases.

For each habitat, a nested multifactorial analysis of variance (ANOVA) was carried out: *C. cylindracea* percentage cover was used as a dependent variable. Data were logtransformed [log(x + 1)] to respect the assumption of normal distribution and homogeneity of variance. Two independent factors were selected: type of condition (two levels: impacted and natural-reference) and sampling events (five levels: December 2018, July 2019, December 2019, July 2020, and December 2020). Data were analyzed in the R platform version 4.0.2.

The investigated habitats are characterized by high seascape complexity (Figure 2). *P. oceanica* forms dense meadows settling on matte, a biogenic substratum formed by the dense twist of seagrass portions roots, rhizomes, and sediment. The regression of meadows causes the persistence of the biogenic originated matte substratum, which is commonly recognized as dead matte. *P. crispa* is a semi-schiaphilic red alga that grows on flat bottoms forming turfs or mats due to its vegetative growth and sediment deposition [21]. Coralligenous reefs represent one of the most diffuse biogenic concretions in the Mediterranean Sea; encrusting algae (belonging to the Orders Corallinales and Peyssonneliales) growing in dim light conditions represent the primary builders contributing to the growth of the framework. In the shallow water of the study area (up to 50 m depth), coralligenous reefs mainly develop on vertical cliffs.



Figure 2. Habitats at the reference site: (a) *P. oceanica* meadow at 20 m depth, (b) *P. crispa turf* at 30 m depth, and (c) coralligenous reef at 30 m depth (Photographs by E. Casoli).

3. Results

C. cylindracea was reported in all the three habitats under impacted condition andshowed different percentage covers among the three investigated habitats. Maximum values were associated with impacted POSID (Figure 3a), where up to 70.0% in cover was reported in July 2020, while the natural POSID condition registered a maximum of just about 10.0% cover in July 2019. Low abundance was reported in both impacted and control PHYLL, not exceeding 5.0% over the study period (Figure 3b). *C. cylindracea* colonization on impacted CORAL started in December 2019 and not before; in the natural-reference site, it was reported exclusively in July 2020, accounting for only 0.03%. As proven by the wide standard deviation bars, not all the replicate samples were characterized by *C. cylindracea* presence, which reflected a patchy distribution pattern on CORAL possibly of the greater depth (Figure 3c). Wide seasonal variations in *C. cylindracea* cover were consistent among the three investigated habitats, with the maximum development in summer.

The results of the ANOVA (Table 1) performed on POSID data revealed significant *p*-values for both the factors and their interaction, indicating differences in *C. cylindracea* percentage cover according to the type of condition over time. As for PHYLL, ANOVA did not report significant differences according to condition and the interaction between condition and time; on the other hand, *C. cylindracea* differed significantly over time. The output of the ANOVA carried out on CORAL data revealed no significant differences across the investigated factors and their interaction; as mentioned before, this pattern could be due to the large variability of the data collected on CORAL.



Figure 3. Mean percentage cover ($\% \pm SD$) of the IAS *C. cylindracea* during each sampling event in the investigated habitats: POSID (**a**), PHYLL (**b**), and CORAL (**c**). Colors refer to impacted (red) and natural-reference conditions (green).

Table 1. Results of the nested multifactorial analysis of variance (ANOVA) on *C. cylindracea* percentage cover for the three investigated habitats. The bold type highlights significant values.

P. oceanica meadow					
Source of variation	Df	SS	MS	F-value	<i>p</i> -value
Condition	1	25.47	25.46	38.97	<0.001
Time	4	37.49	9.37	14.34	< 0.001
Condition \times Time	4	8.50	2.12	3.25	0.02
Residuals	50	32.67	0.65		
		P. crispa turi	f		
Source of variation	Df	SS	MS	F-value	<i>p</i> -value
Condition	1	0.18	0.18	2.87	0.09
Time	4	2.65	0.66	10.53	< 0.001
Condition \times Time	4	0.09	0.02	0.38	0.82
Residuals	50	3.14	0.06		
		Coralligenous	reef		
Source of variation	Df	SS	MS	F-value	<i>p</i> -value
Condition	1	0.62	0.62	2.14	0.15
Time	4	0.85	0.21	0.73	0.57
Condition \times Time	4	0.77	0.19	0.66	0.62
Residuals	50	14.59	0.29		

4. Discussion

The study confirms how habitat loss, as a consequence of human-related activities, promotes the spread of *C. cylindracea*, which acts as pioneer species rapidly colonizing the impacted seabed. A gradual susceptibility to invasion for the three investigated habitats is reported, leading to a different percentage cover of *C. cylindracea* even in natural-reference conditions, highlighting that habitat features may favor the settlement and diffusion of this species.

Degraded (dead *matte*) areas of *P. oceanica* represent excellent substrata for the spread of *C. cylindracea* and are the most vulnerable habitat among those analyzed in the present study. It is likely that the factors responsible for the observed pattern are linked to seagrass regression, high irradiance, the topography of the matte, and sediment accumulation. The dense canopy of natural *P. oceanica* meadow limits *C. cylindracea* photosynthesis and growth, reducing light irradiance at rhizome level through shading [22]; in the case of seagrass disappearance due to human disturbance, the increase in light irradiance and reduction of competition with the native species allow a successful settlement and the following widespread colonization of *C. cylindracea* [23,24]. Furthermore, the dead *matte* features, in terms of topography, porosity, and capability of trapping sediment, promote the anchoring of the *Caulerpa* rhizoids and increase the "invasion" rates. The *C. cylindracea* abundance rapidly increased between years in dead *Posidonia* matte, showing a fast completion of the three initial phases (i.e., arrival, settlement, and expansion) recognized in the non-indigenous species invasion [25].

The percentages cover here reported in *P. crispa* turf are consistent with previous observations carried out under both natural and disturbed conditions [26], although no significant differences emerged from the analysis. As mentioned before for *Posidonia*, the presence of a dense canopy formed by seaweeds (in this particular case by the *P. Crispa* thalli and its associated assemblage) inhibits the spread of the *C. cylindracea* [27]. Nevertheless, the occurrence of the IAS thalli under natural-reference conditions may be favored by the sediment accumulation rates that concern the gently sloped/flat bottoms, such as those colonized by the *P. crispa* turf [21,28]. *C. cylindracea* did not show high percentage coverage at the impacted condition, as we hypothesized; however, *C. cylindracea* characterized the first phase of substrate recolonization even without the invasive mode. The presence of bare surfaces (i.e., not colonized) did not favor the "rooting" of *Caulerpa* stolons; moreover, the juvenile assemblages that developed in the first succession phases after the seabed cleaning were not dominated by filamentous algal turf, which has been recognized as a morphofunctional group of macroalgae that significantly influence the spread of *C. cylindracea* [29].

The coralligenous reef was the habitat that was least susceptible to C. cylindracea invasion under both conditions. The spread of the invasive green algae in a single portion of the reef exclusively, the only one not facing north, accounted for the wide data fluctuation. The combined effect of substrate inclination (coralligenous reef characterized vertical walls in the study area), greater depth (25-35 m), and orientation may prevent the spread of *C. cylindracea* due to energetic costs for photoacclimation under high shading conditions [30,31]. In fact, *Caulerpa* thalli have been mostly reported colonizing coralligenous reefs in shallower waters or developing on horizontal coralligenous concretions [30,32,33], whereas other sciaphilous IASs, such as the filamentous Rhodophyta Acrothamnion preissii (Sonder) Wollaston and Womersleyella setacea (Hollenberg) R.E.Norris, 1992, have commonly reported forming dense turfs at higher depths [34,35]. On the contrary, the cavities created by the accretion of encrusting Rhodophyta increase the complexity of coralligenous concretions, favoring the spreading and anchoring of the *Caulerpa* stolons [36]. Our results contrast with recent observations carried out within a Marine Protected Area (Capo Carbonara MPA) in the southern Tyrrhenian Sea, where coralligenous reefs were among the habitats most exposed to C. cylindracea and further non-indigenous species settlement [37].

A strong seasonal variation, with a maximum development in summer and regression in winter, was highlighted in all the investigated habitats: this is consistent with what has been previously described for shallow habitats [8,38]. Conversely, our findings did not confirm the maintenance of biomass during winter in deeper habitats [31]: seasonal variation in *C. cylindracea* percentage cover differed with results provided by Piazzi et al. as well [37]. Both photoperiod and temperature are the main factors responsible for the observed pattern, considering the southern origin of the IAS.

The integration of biological sampling with acoustic underwater techniques, such as high-resolution multibeam echosounder (MBES) and Side Scan Sonar (SSS), together with the methods applied in this study (Underwater Visual Censusand image analysis) could provide more accurate spatial information [39,40] for fine-scale mapping of benthic habitats. Further, the output from acoustic campaigns (DTMs, slope, rugosity, and orientation grids) could be also a valuable tool to remotely assess the suitable grounds for the spread of *C. cylindracea*, as well as other IASs. Future studies should adopt a multi-purpose approach, coupling both geomorphological and biological observations, to investigate patterns and factors leading to the diffusion of IASs within the Mediterranean Sea.

5. Conclusions

The present study highlights the importance of habitat integrity for the IAS diffusion and the connection between habitat features and susceptibility to invasion. Decrease in the diversity of natural assemblages, topography, sedimentation rate, light irradiance, and orientation are critical factors driving the colonization of *C. cylindracea* [7], being primarily responsible for the pattern observed in this study. Although the scientific literature has covered several biological and ecological aspects of C. cylindracea spread over the Mediterranean Sea, this work adds further information for a scarcely investigated and still poorly known habitat, namely P. crispa turf. In this regard, further studies should focus on other alien species and their role in preventing habitat resilience after human impacts, especially in poorly investigated habitats. This study highlights the urgent need for achieving the United Nations Sustainable Development Goals (UNSDGs), with a particular emphasis on the SDG 14-Life Below Water. In light of the multitude of disturbances threatening both the Mediterranean and worldwide benthic ecosystems, an increase in sustainable management and protection actions is mandatory to face synergic pressures and avoid significant impacts. Furthermore, the development of active restoration actions strengthens the resilience of the natural communities at impacted sites, thereby contrasting the diffusion of IASs. Ad hoc national and supranational plans, such as the new EU Biodiversity Strategy for 2030 adopted in May 2020 in the post-COVID-19 context, should contain all the actions mentioned above to achieve healthy and productive ecosystems.

Author Contributions: Conceptualization, E.C.; methodology, E.C., D.V., G.M., A.B.; formal analysis, E.C., D.V., G.M.; investigation, E.C., D.V., G.M.; writing—original draft preparation, E.C., D.V., G.M.; writing—review and editing, E.C., A.B., G.A.; supervision, G.A. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study is available on request from the corresponding author.

Acknowledgments: We wish to thank Max Shark, Fulvia Farina, Lorenzo Donnini, and Sara Cardone for help and assistance during field samplings.

Conflicts of Interest: All the authors, as scientists of the Sapienza University of Rome and CIBM, were commissioned by the Costa Crociere S.p.A. to assess the environmental risks of engineering operations and to monitor and restore the environmental conditions in the impacted areas in order to protect marine habitats during the salvage of the Concordia wreck and the following phases.

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