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Restoration of soft-bottom habitats: assessing transplantation success and herbivore exclusion effects on two native seagrass species in the Eastern Mediterranean

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Abstract

Background Seagrass habitats are vital for maintaining marine biodiversity and ecosystem functions. In the Eastern Mediterranean Sea, *Posidonia oceanica* and *Cymodocea nodosa* are among the dominant seagrass species; however, these ecosystems are increasingly threatened by rising seawater temperatures, invasive herbivores, and anthropogenic pressures. Marine protected areas (MPAs) and active restoration practices have emerged as key strategies for their conservation. This study was conducted in the Gökova Bay MPA, South Aegean Sea, to evaluate the effectiveness of seagrass transplantation and the impact of invasive herbivores on restoration outcomes. Transplants were established within both open plot and exclusion cage systems to compare herbivory pressure and transplantation performance. Metrics, such as shoot density and leaf length were used to assess transplantation success, while visual surveys recorded evidence of grazing.

Results The results revealed species-specific responses: *P. oceanica* showed significant variability in shoot density under different experimental conditions, whereas *C. nodosa* consistently declined across all treatments. Cage systems had no significant effect on the biomass performance of *P. oceanica*, but negatively affected *C. nodosa*, leading to reduced shoot density.

Conclusions These findings highlight the importance of tailored restoration strategies that account for species-specific ecological responses and offer preliminary insights for improving habitat conservation efforts in the region.

Keywords Seagrass, Conservation, Transplantation, MPA, *Posidonia oceanica*, *Cymodocea nodosa*, Herbivore

Background

Marine ecosystems such as coral reefs, seagrass meadows, and coralligenous assemblages represent key structural habitats that support a wide range of ecological functions and services. Their structural complexity provides essential shelter, feeding, and breeding grounds for numerous aquatic species, contributing directly to high levels of marine biodiversity [29, 39]. In the Mediterranean Sea, seagrass meadows, macroalgal forests, and coralligenous formations are widely recognized as biological hotspots, harboring large biomass due to their functional importance and unique biogeographic heritage [10, 56,

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66]. Among these, seagrass meadows are globally considered one of the most ecologically and economically valuable habitats [16].

Despite increasing scientific attention, public awareness and conservation efforts remain limited to counter the rapid degradation of seagrass habitats. It is estimated that approximately 12000 km^2 of seagrass beds were lost globally between the 1980s and 1990s [72]. In the Mediterranean, this trend continues due to a multitude of stressors, including eutrophication, sedimentation, anchoring, illegal trawling, dredging, pollution, and climate change ([17, 50, 73] and references therein). Given the slow growth rates of many seagrass species, particularly endemic ones, natural recovery following disturbance may take decades or longer [44, 50].

The endemic species *P. oceanica* (Linnaeus) Delile forms extensive meadows along the Mediterranean coast (0–40 m depth), providing critical ecological services such as carbon sequestration, sediment stabilization, oxygen production, and nursery habitats for commercially important fish species [18, 32]. With horizontal rhizome growth of only 1 cm up to 14 cm/year, in average 6 cm per year, *P. oceanica* meadows are extremely slow to regenerate [21]. Their longevity, often exceeding centuries, underscores the importance of their preservation. Its ecological toleranceincludes a temperature range of 9–29.3 °C and even up to 30 °C in some parts of the Mediterranean [18, 48, 68, 82], and salinity down to 21.5–28.0 g/kg in the Marmara Sea [46] and higher than 39 g/kg in Mediterranean coasts of Türkiye, Spain and Sicily [35, 48, 75].

Due to the alarming rate of decline, *P. oceanica* meadows have been listed in Annex II of the Barcelona Convention's Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean (Protocol SPA, 1995), and as a priority habitat under the EU Habitats Directive (92/43/EEC; Habitat Type 1120). Turkish national legislation also includes protective measures under the Fisheries Circulars [4, 5], in alignment with international agreements.

Another widespread seagrass in the region, *C. nodosa* (Uchria) Ascherson, often forms mono- or mixed-species meadows with *P. oceanica* or *Nanozostera noltei* (Hornemann) Tomlinson & Poluszny 2001 [51]. Like *P. oceanica*, *C. nodosa* is also protected under the EU Habitats Directive and recognized by the OSPAR Convention due to its ecological significance [78].

Marine ecosystems are increasingly affected by both natural and anthropogenic drivers [30, 31]. Climate change in particular alters the physical and biogeochemical characteristics of marine environments, with rising sea temperatures, sea-level rise, and increased storm intensity all threatening the stability of seagrass habitats [57, 71]. In addition, eutrophication fosters excessive phytoplankton and macroalgal growth, which can shade and outcompete seagrasses [76]. There have already been declines of local *P. oceanica* meadows up to 40–60% in some places in the Mediterranean [77] and projections suggest that up to 75% of *P. oceanica* meadows may be lost by the mid-twenty-first century under worst-case climate scenarios, with complete disappearance possible by 2100 [25]. However, these predictions are opposed by some authors (such as Boudouresque et al. [17, 19]), with recent studies results showing recovery of *P. oceanica* meadows is possible after eliminating the cause of the impact but with slow growth rate total recuperation could take almost 100 years [40]. Moreover, most restoration studies to date have been experimental in nature rather than focused on large-scale recovery. As seagrass restoration ecology is still developing, there is a need to expand current knowledge and address critical gaps in *P. oceanica* restoration. Therefore, there is still hope/possibility that these dire predictions may be proved to be inaccurate.

Although global change is a pervasive pressure, human activities in coastal zones—including coastal development, pollution, and biological invasions—often act as more immediate threats [41]. These stressors can lead to ecosystem degradation, loss of native biodiversity, and increased vulnerability to invasive species [13, 83]. In particular, invasive herbivores in the Eastern Mediterranean such as *Paracentrotus lividus* Lamarck, 1816, introduced primarily via the Suez Canal, are known to alter food webs and directly consume seagrass species [24, 65, 85] as well as the native herbivors like *Sarpa salpa* Linnaeus, 1758 [14]. To address these challenges, a combination of passive and active conservation strategies is employed. Marine Protected Areas (MPAs) are among the most widely implemented passive measures aimed at reducing anthropogenic pressures and preserving biodiversity [49]. No-Take Zones (NTZs), which offer stricter protection by prohibiting extractive activities, are increasingly seen as more effective in enhancing resilience to climate impacts [64, 74]. However, passive approaches alone are often insufficient to reverse degradation.

Active restoration methods—including transplantation, translocation, and physical habitat modifications—have gained prominence as complementary tools for ecosystem recovery [37]. While many seagrass transplantation efforts have shown promise, success rates vary widely depending on species, technique, environmental conditions, and human pressures [19, 28, 36, 67]. In the Mediterranean, restoration trials with *P. oceanica* date back to the 1970s but have often yielded inconsistent outcomes due to factors such as wave exposure, disease, and herbivory [27, 69].

Understanding site-specific stressors is critical for the success of restoration. The Eastern Mediterranean, and in particular Gökova Bay, faces unique challenges due to the proliferation of invasive herbivores such as *Siganus rivulatus* and *S. luridus*, which now account for the majority of herbivorous fish biomass in the region [52]. On top of these fishes herbivors like *S. salpa* [14] and invertabrates like sea urchin *P. lividus* [24] are also known grazers that are also present in the area. These species have been directly linked to the overgrazing of macroalgae and seagrasses in different parts of the Mediterranean, resulting in barren seafloor patches and reduced seagrass cover ([19, 70] and references within).

Gökova Bay, a biodiversity hotspot and Special Environmental Protected Area (SEPA), hosts six NTZs that provide a rare opportunity to evaluate restoration techniques in a controlled setting with minimal anthropogenic interference [79]. Since their designation in 2010, these NTZs have shown promising outcomes in terms of fish biomass recovery and habitat improvement [45].

This study aims to assess the effectiveness of caging as a protective measure in seagrass transplantation efforts, focusing on the differential responses of *P. oceanica* and *C. nodosa* in the presence of invasive herbivores. By conducting experiments within a no-take marine reserve, the research isolates ecological factors influencing transplantation success and offers insight into scalable, evidence-based restoration strategies in degraded soft-bottom habitats.

Materials and methods

Study site

The study was conducted in Gökova Bay, located on the southwestern coast of Türkiye, in the Eastern Mediterranean Sea (Fig. 1). Gökova Bay is a designated Special Environmental Protection Area (SEPA) and a biodiversity hotspot that has been under increasing ecological pressure due to the proliferation of alien herbivorous fish species, particularly *S. luridus* and *S. rivulatus* (Giakoumi et al., 2019). These invasive species have established large populations and now represent a significant portion of the herbivorous fish biomass in the region.

Seagrasses such as *P. oceanica* and *C. nodosa* are part of these herbivores diet, making them highly vulnerable to grazing. To assess the effects of herbivory on transplant success, we employed protective caging systems over the transplanted seagrass units. In parallel, uncaged plots were also established to enable direct comparison and evaluate the extent to which grazing pressure influences transplantation success. This experimental design allowed us to isolate the impact of herbivory from other environmental variables in the restoration process.

Survey design

The experimental design was conducted on soft-bottom habitats suitable for both seagrass species, *P. oceanica* and *C. nodosa,* in Gökova Bay. The main aim was to assess transplant success under varying environmental and biotic pressures, grazing by invasive herbivorous species. Three experimental stations were selected for *P. oceanica*, two located within the MPA and one outside its boundaries. These stations were treated as fixed spatial plots representing differing environmental contexts (MAP vs. non-MPA in this case). Regarding *C. nodosa*, the experiment was conducted at a single station.

At each station, two (cage) x three (treatment) factorial design were applied (Fig. 2). Three habitat types were tested; (i) natural seagrass meadow, (ii) unvegetated bare sediment (control), (iii) Transplanted shoots on bare sediment (as potential former seagrass habitat). In addition, each treatment was applied under two grazing conditions; (i) caged plots (herbivore exclusion), (ii) open plots (grazing access for invasive allien species). Each combination was replicated three times (biological replicates), totalling nine cages and nine open plots per station. Replicates were located within two and half meters to minimize spatial autocorrelation.

Posidonia oceanica experiment

Transplantation experiments for *P. oceanica* were conducted in July 2017 for 2 years long at three stations (Fig. 1). Two of these stations (#1 and #2) were located within the boundaries of the Marine Protected Area (MPA), while the third station (#3) was situated outside the MPA. The distances between the stations were approximately 300 m (Stations 1–2), 2400 m (Stations 2–3), and 1530 m (Stations 1–3), respectively.

Each experimental unit measured 1 × 1 m (with 0.5 height of cages), and cages were construced using 12 polyethylene sticks covered with plastic mesh with a one cm^2 mesh size to exclude larger grazers (Fig. 3a)., while open plots had no mesh (Fig. 3b). All cages and plots were securely anchored to the sediment using iron stakes (50 cm in length, 12 mm in diameter), driven into the substrate with a hammer to ensure structural stability under field conditions.

Donor shoots were collected from the similar depth range as the experimental stations (8–10 m). Using a hand shovel, shoots with intact rhizomes and surrounding sediment were carefully uprooted and transferred underwater in bags. Within each experimental unit, approximately 30 shoots (arranged in three rows of about 10 shoots each) were transplanted into 15 cm-deep holes along a 70 cm iron rod. Zip ties were used to secure the shoots and enhance anchorage.

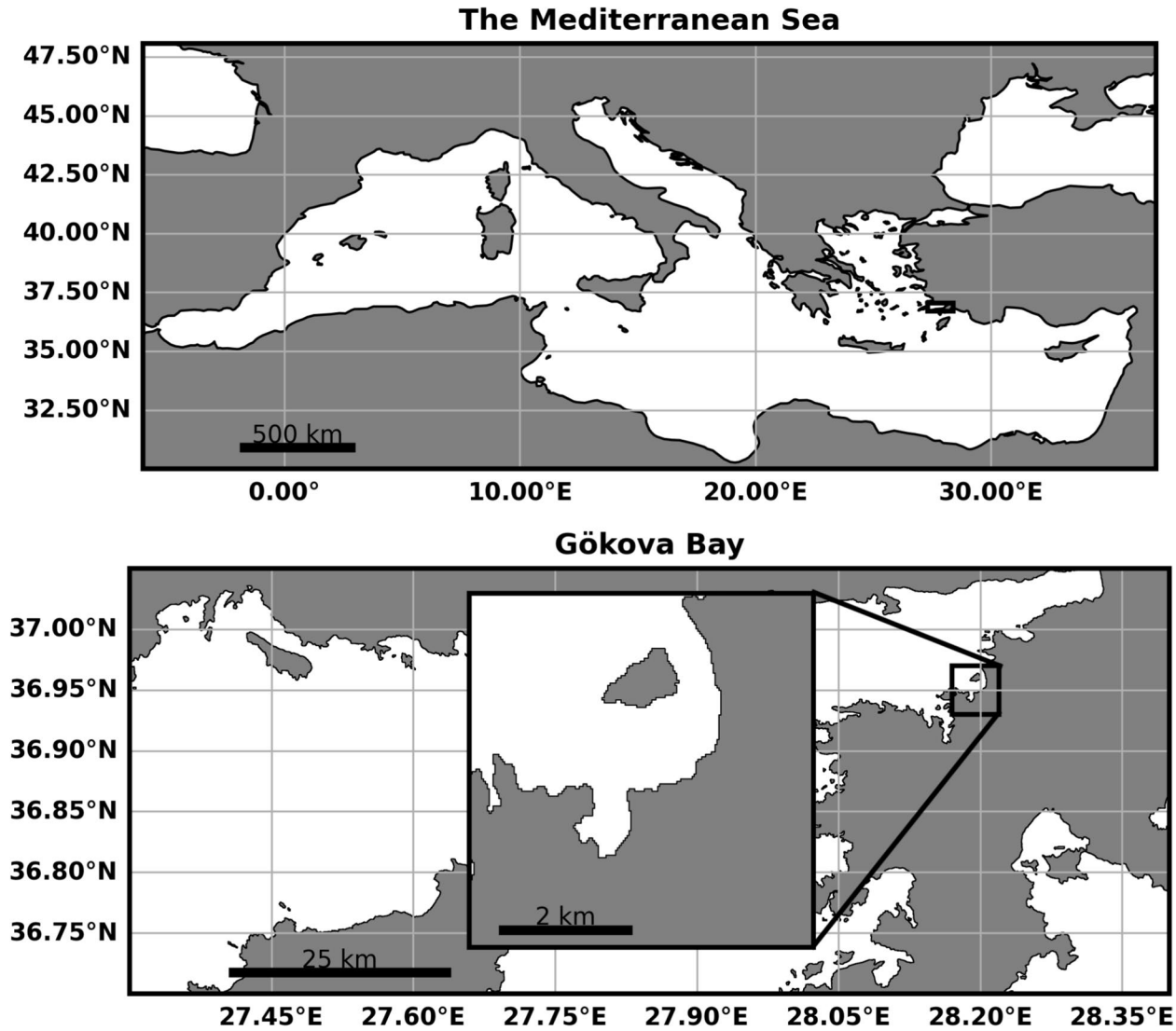

Fig. 1 Gökova Bay as the study area and the location of the stations. The top panel shows the location of Gökova Bay within the Mediterranean Sea, while the bottom panel presents a detailed view of the study area in the bay

To ensure minimal stress on the transplants, all operations were performed underwater during SCUBA dives, following best practices outlined in Sanchez-Lizaso et al. [67]. No cleaning of epiphytes or sediment was conducted on the leaves or rhizomes prior to transplantation. Consequently, no selection was made regarding rhizome length or shoot type (apical or non-apical). Cages were cleaned biweekly to prevent fouling and shading.

To monitor transplantation success and grazing effects, key parameters; (i)shoot density (shoots m^{-2}) via three 25×25 cm quadrats per treatment, (ii) leaf length and width (ten randomly selected leaves per replicate), and (iii) grazing marks (presence/absence of bites on ten leaves per replicate) were recorded annually. Annual changes in density and leaf morphology were recorded and classified into binary categories (positive or negative change) for trend.

Cymodosea nodosa experiment

Transplantation experiment of *C. nodosa* was conducted in July 2018 only at Station #1 and followed the same overall design; (i) natural meadow, (ii) bare sediment, and (iii) transplanted shoots—each under caged and open plot conditions (Fig. 4). The dimensions and materials of the cages and plots were identical to *P. oceanica* experiments, ensuring consistency.

The transplantation procedure for *C. nodosa* differed slightly from the *P. oceanica* protocol. Transplants (20–35

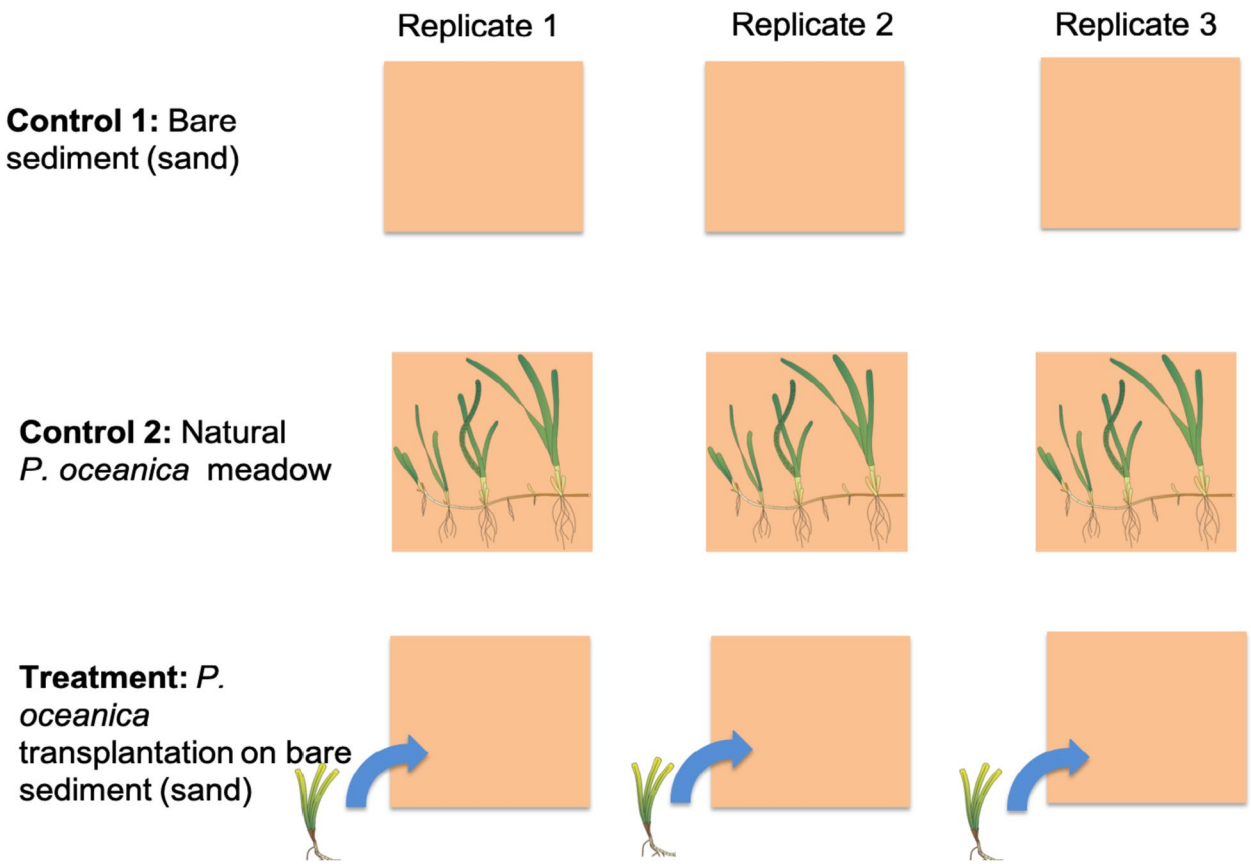

Fig. 2 The design of the *P. oceanica* experiment (Experiment conducted with cages and plots)

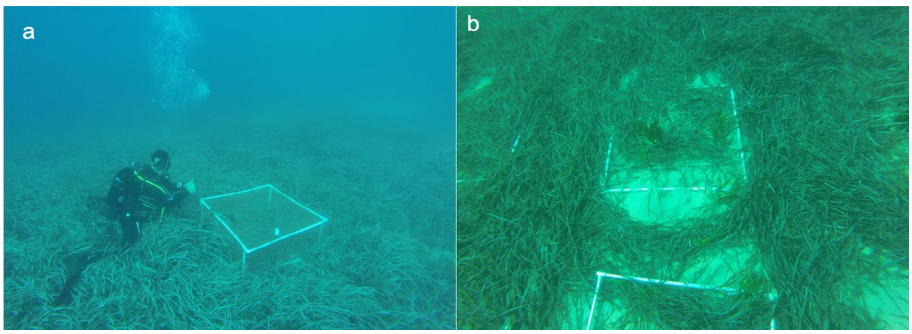

Fig. 3 Cages and plots used for both *P. oceanica* and *C. nodosa* experiments **a** Cage settlement on natural *P. oceanica* meadow; **b** Plot settlement on natural *P. oceanica* meadow)

shoots per unit) were sourced from depth of 11–14 m. Because roots of *C. nodosa* are more delicate, small seedling containers, commonly used for plant transplantation, were used instead of rods for stabilization.

Biweekly cage cleaning and annual monitoring were exactly the same with the *P. oceanica* protocol, with identicalparamteres recorded (shoot density, leaf size and width, grazing marks).

Statistical analysis

Stations were not included as fixed or random factors in the statistical models. However, potential environmental differences were monitored such as light availability, depth, and substrate type throughout the experiment. Regular cleaning and other standardization measures were conducted to reduce variability, and no consistent or significant differences across stations were detected.

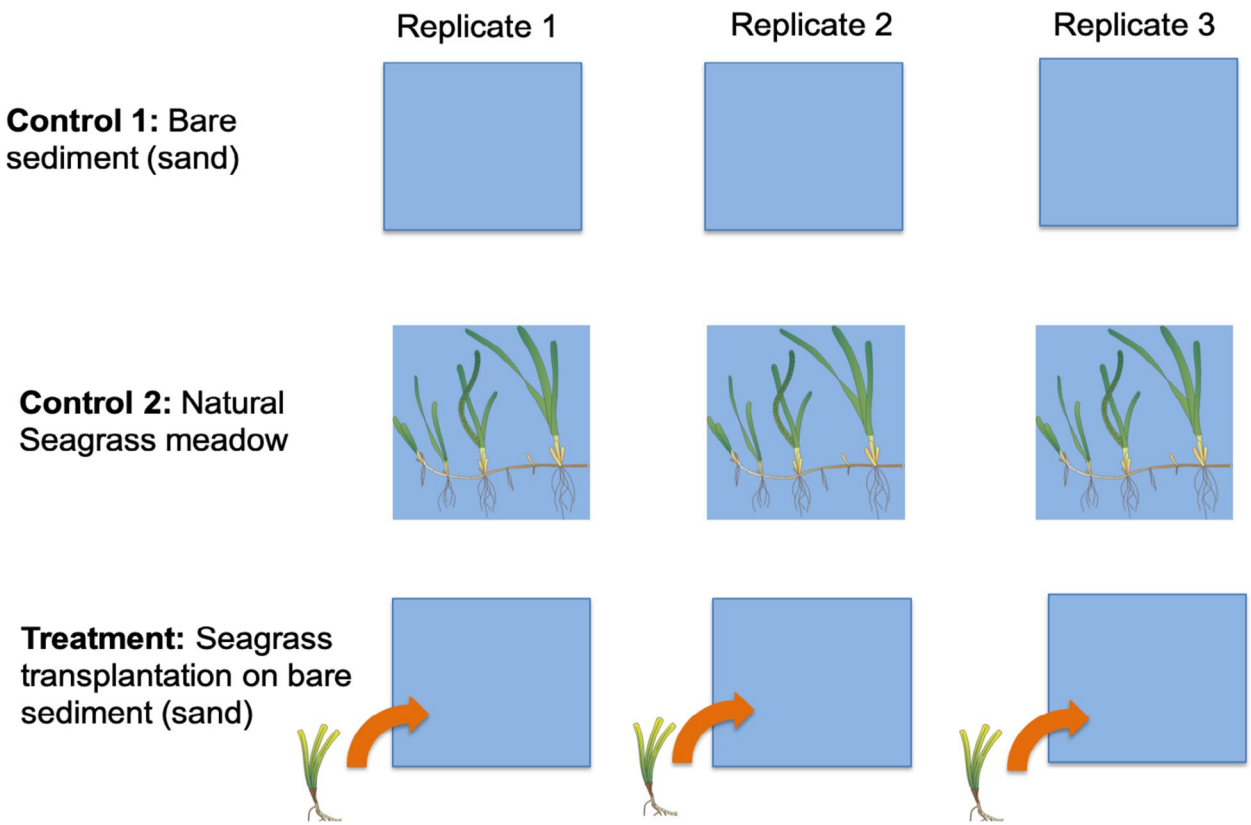

Fig. 4 The design of *C. nodosa* experiment (Experiment conducted with cages and without cages (plots))

Therefore, station identity was not included as a separate factor in the analysis.

The data from all three stations were combined and focused on treatment-level effects. Since each treatment was replicated equally within each station, this design accounted for spatial variation without increasing model complexity. By following this approach, pseudo-replication risk was reduced while maintaining statistical power.

Including three spatially separated stations also served as a safeguard against unexpected events at individual sites, such as illegal fishing or anchoring damage outside marine protected areas. This setup helped improve the ecological reliability of the results while keeping the statistical design clear.

Initial conditions and annual measurements were recorded to evaluate how treatments responded over time under consistent environmental and human-related conditions. All values were compiled by year, and descriptive statistics were calculated for each replicate and station to summarize biological variation. Then Analysis of Variance (ANOVA) were used to test for treatment differences within each year (three levels for *P. oceanica*, two for *C. nodosa*) and to assess patterns across all years based on shoot density (shoots m^{-2}) and leaf length (cm).

To verify the assumptions of ANOVA, the Shapiro–Wilk test [63] was used to check normality and Bartlett's test to assess variance homogeneity [11]. When these assumptions were met, Tukey's Honestly Significant Difference (HSD) test was applied for post-hoc comparisons [84].

Annual changes were classified in biomass as positive (coded as 1) when net growth exceeded initial values. This classification provided a simplified but meaningful way to track trends, especially considering the natural variability in seagrass dynamics. Although replication was adequate, the dataset size remained moderate, and biological variation was sometimes high. For this reason, a trend-based comparison was preferred using binary classification instead of relying solely on parametric models. This method helped avoid overfitting and allowed clearer interpretation, especially when data loss or uncertainty occurred.

Grazing activity was evaluated as a binary variable, assigning 1 when bite marks were observed. Chi-square tests [1] was used to compare grazing differences among treatments and applied pairwise comparisons of Pearson residuals using the "chisq.posthoc.test" package in R [34].

All statistical analyses were performed in R using the "Stat" package [62]. SApproach was designed to ensure robust and interpretable results while addressing ecological variability and limitations in the dataset.

Results

Shoot density

Shoot density is a key descriptor for assessing ecosystem health as it provides insights into the status of seagrass meadows [58]. At the start of the experiment, shoot densities ranged from 160 to 400 shoots m^{-2} for *P. oceanica* and 256–576 shoots m^{-2} for *C. nodosa* in the natural plots. For the transplanted plants, densities ranged from 352 to 448 shoots m^{-2} for *P. oceanica* and 400–560 shoots m^{-2} for *C. nodosa*. By the end of the experiment after 2 years, shoot densities ranged from 192 to 448 shoots m^{-2} for *P. oceanica* and 112–400 shoots m^{-2} for *C. nodosa* in the natural plots, while for transplanted plants, densities were 336–448 shoots m^{-2} for *P. oceanica* and 256–0 shoots m^{-2} for *C. nodosa* (Table SM1, Supplementary Material). According to the UNEP/MAP-RAC/SPA Monitoring Protocol (2011), the health status of *P. oceanica* habitats at a depth of 11 m was initially classified as "moderate in density" in the natural plot. By the end of the experiment, no significant changes were observed.

The comparison of shoot densities for *P. oceanica* revealed that the caged natural plots initially exhibited significantly lower densities than other experimental settings (ANOVA, $p < 0.01$). However, there were no significant differences in shoot density between the experimental settings in the subsequent years. For *C. nodosa*, there were no initial differences; however, during the monitoring year, the experimental settings showed significantly lower densities than the natural plot (ANOVA, $p < 0.01$).

Interannual comparisons indicated that only the caged natural plots exhibited significant increases in shoot density in the 1st year (ANOVA $p < 0.01$). Conversely, no significant changes in shoot density were observed in other settings for *P. oceanica*. In contrast, for *C. nodosa*, while the natural plot's density remained stable throughout the experiment, other settings showed significant decreases in shoot density (ANOVA $p < 0.01$). Transplanted plants in cages experienced the most dramatic reductions in shoot density (ANOVA $p < 0.01$).

Analysis on the changes in shoot density for *P. oceanica* showed significant differences among most experimental settings ($\chi^2 = 106.71$; df = 3; $p < 0.01$). Specifically, unlike transplanted grasses, the caged natural plots showed a positive trend in shoot density. Notably, negative changes in density in the transplanted plot without a cage occurred at a significantly higher percentage than in their caged counterparts ($\chi^2 = 106.71$; df = 3; $p < 0.01$, Table SM1, Supplementary Material). For *C. nodosa*, all settings exhibited negative changes in shoot density. The natural plot without a cage showed a significantly lower percentage of negative density changes as compared to the other settings, all of which exhibited negative density changes in all replicates ($\chi^2 = 9.81$; df = 3; $p < 0.05$, Table SM1, Supplementary Material).

Leaf length

At the beginning of the experiment, leaf length ranged between 14 and 60 cm for *P. oceanica* and 8–26 cm for *C. nodosa* in the natural plots. For the transplanted plants, leaf lengths ranged between 14 and 51 cm for *P. oceanica* and 4–31 cm for *C. nodosa*. By the end of the experiment, leaf lengths ranged between 12 and 68 cm for *P. oceanica* and 7–31 cm for *C. nodosa* in the natural plots, and 0–43 cm for *P. oceanica* and 0–19 cm for *C. nodosa* in the transplanted plants. Descriptive statistics for each experimental year are summarized in Table SM2 in Supplementary Material and shown in Fig. 5.

Comparisons of leaf length for *P. oceanica* among the experimental settings revealed that the natural population had significantly longer leaves in the 1st year of the experiments. This significant difference persisted until the end of the experiment. In addition, a significant difference was observed between transplanted plants with and without cages, with caged plants exhibiting longer leaves (ANOVA, $p < 0.01$, Table 1). For *C. nodosa*, no significant differences in leaf length were found among experimental settings at the start of the experiment. By the end of the experiment, significant decreases were observed in the transplanted plants, while natural plant plots remained unchanged (ANOVA, $p < 0.01$, Table 1).

Interannual comparisons showed that leaf lengths for *P. oceanica* in all experimental settings significantly decreased in the first monitoring year, followed by a sudden increase in the 2nd year (ANOVA, $p < 0.01$, Table SM2, Supplementary Material). However, transplanted plants did not show significant increases in the second monitoring year. For *C. nodosa*, leaf lengths in the natural experimental settings exhibited no significant differences between the initial and 1st year. In contrast, transplanted plants showed significantly Shorter leaves in the first monitoring year as compared to the 1st year of the experiments (ANOVA, $p < 0.01$, Table 1).

Analysis of changes in leaf length for *P. oceanica* indicated significant differences between most experimental settings ($\chi^2 = 109.03$; df = 3; $p < 0.01$). Overall, transplanted plants with cages showed significantly more negative changes in leaf length than other settings ($\chi^2 = 109.03$; df = 3; $p < 0.01$), while natural caged plants and transplanted plants without cages did not show significant differences. In contrast, natural plots exhibited

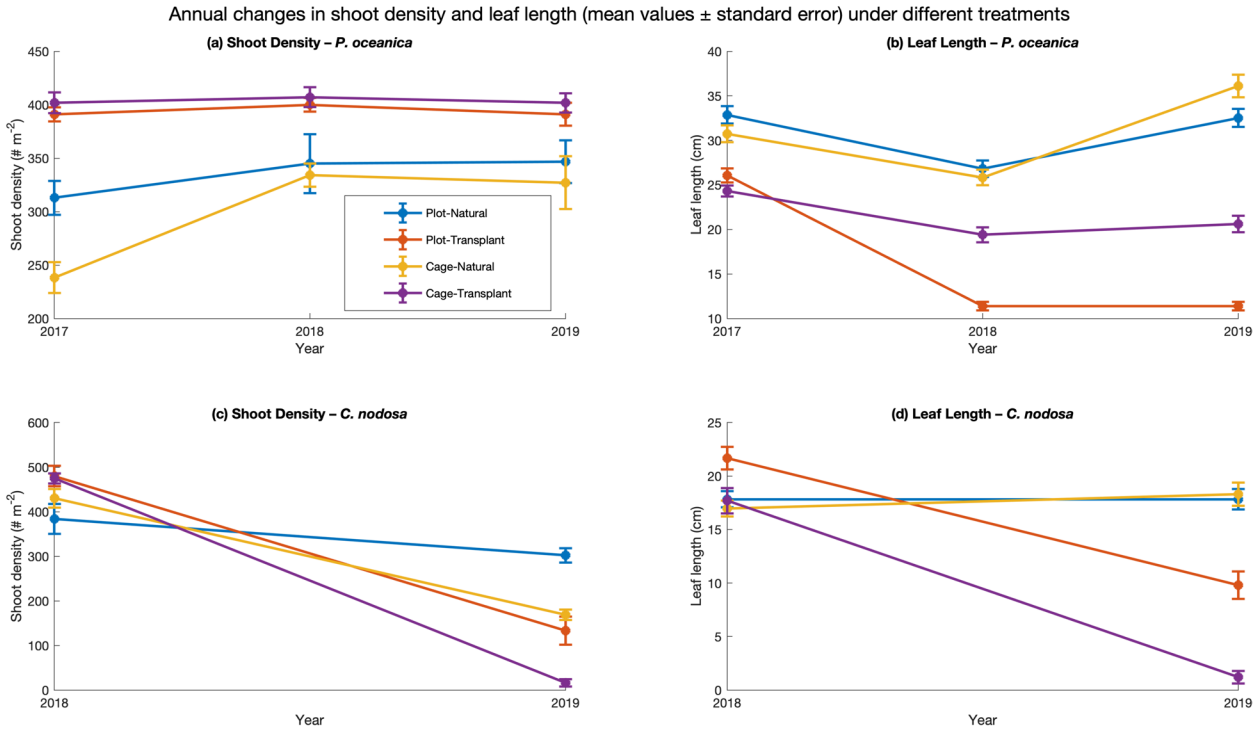

Fig. 5 Annual changes in shoot density and leaf length (mean values ± standard error) of *P. oceanica* and *C. nodosa* under different treatments over the years 2017–2019. Panels **a** and **b** show shoot density and leaf length for *P. oceanica* (data from 2017 to 2019), while panels **c** and **d** show shoot density and leaf length for *C. nodosa* (data from 2018 to 2019, as this species was monitored from 2018 onwards). Treatments include Plot-Natural, Plot-Transplant, Cage-Natural, and Cage-Transplant. Error bars represent the standard error of the mean

Table 1 Analysis of variance (ANOVA) results for shoot density and leaf length of *P. oceanica* and *C. nodosa* across different treatments and years. Four treatment groups were analyzed: Natural Open, Natural Caged, Transplant Open, and Transplant Caged. Data for P. oceanica cover 3 years (2017–2019), while the data for C. nodosa cover 2 years (2018–2019). Degrees of freedom reflect the number of treatments multiplied by the number of years minus one

Source of variation	Variable	df	MS	*F*	*p*
P. oceanica (4 treatments × 3 years)	Shoot density (m^{-2})	11	23239	11.02	6.70E-13
	Leaf length (cm)	11	6869	99.05	2.00E-16
C. nodosa (4 treatments × 2 years)	Shoot density (m^{-2})	7	273262	65.31	2E-16
	Leaf length (cm)	7	1293	45.04	2.00E-16

a significantly higher positive change in leaf length compared to other settings ($\chi^2 = 109.03$; df = 3; $p < 0.01$). For *C. nodosa*, there were significant differences in leaf length changes between natural and transplanted plant plots ($\chi^2 = 31.68$; df = 3; $p < 0.01$). Specifically, while more than 50% of natural plants showed a positive change, over 90% of transplanted plants exhibited a negative change in leaf length (Table SM1 in Supplementary Material, Fig. 6).

Grazing impact

Observations of grazing impact on *P. oceanica* leaves indicated a higher grazing percentage in caged settings. The highest grazing rates were observed in natural plants with cages ($\chi^2 = 142.42$; df = 3; $p < 0.01$, Table SM1, Supplementary Material). No significant differences were observed between natural and transplanted plants (Table SM1, Supplementary Material). For *C. nodosa*, high grazing impact was recorded across all experimental settings, ranging from 80 to 100% of grazing occurrence (Table SM1, Supplementary Material), with no significant differences between the settings ($\chi^2 = 7.64$; df = 3; $p < 0.05$, Table 1).

Discussion

Although numerous studies on the conservation and monitoring of seagrasses have been conducted, this topic remains relatively underexplored in the eastern Mediterranean, particularly along Turkish coasts. A recent review by Akcalı et al. [2] highlighted significant data gaps regarding the distribution of *P. oceanica* along Turkish coasts. On the other hand, a status evaluation

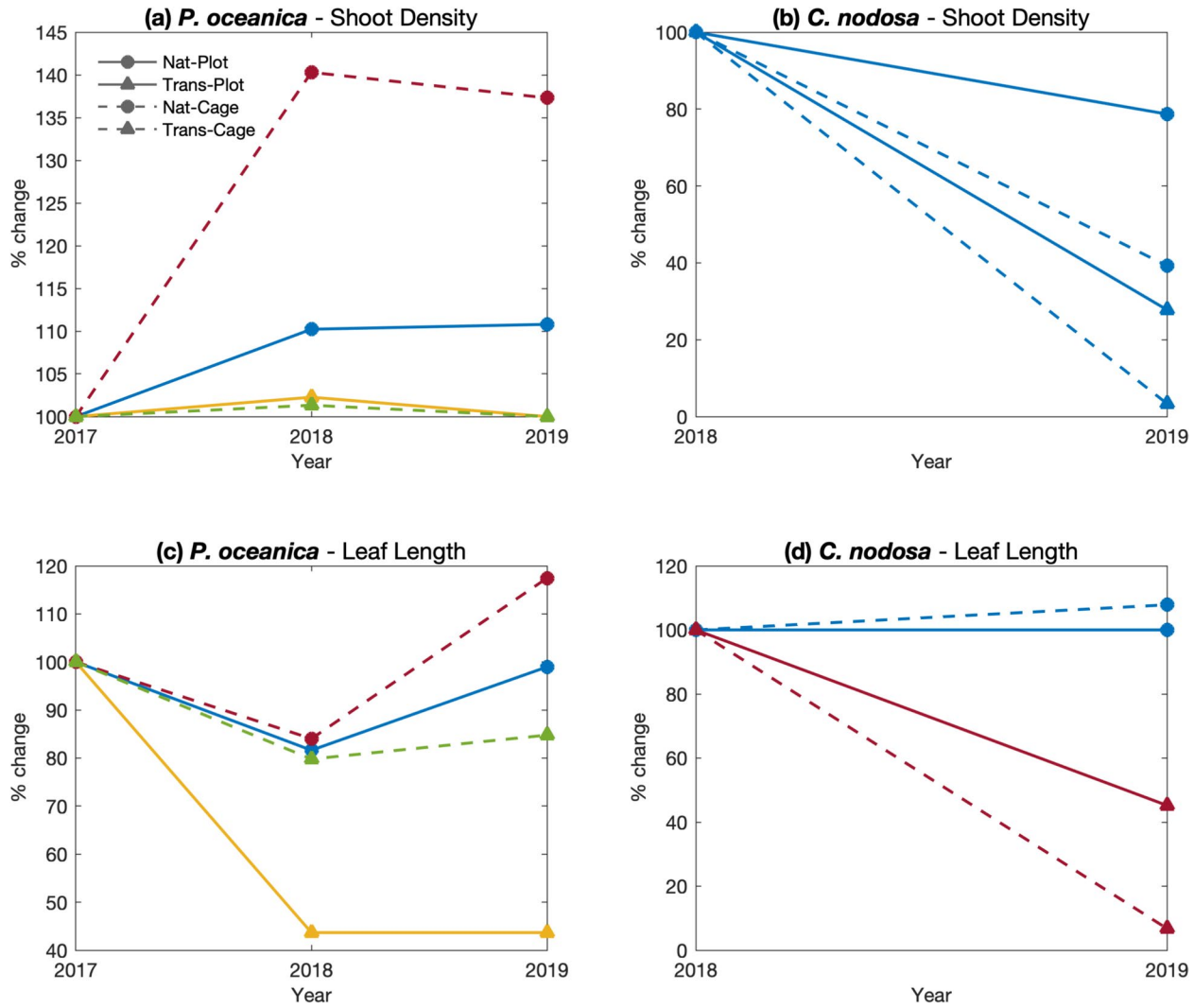

Fig. 6 Percent change in shoot density and leaf length for *P. oceanica* and *C. nodosa* under four experimental treatments (Natural-Plot, Transplant-Plot, Natural-Cage, Transplant-Cage) from 2017 to 2019, relative to 2017 baseline (100%) for *P. oceanica* and 2018 baseline (100%) for *C. nodosa* due to missing 2017 data. Subplots show: **a** *P. oceanica* shoot density, **b** *C. nodosa* shoot density, **c** *P. oceanica* leaf length, and **d** *C. nodosa* leaf length. Treatments are represented by line styles and markers: solid line with circles (Natural-Plot), solid line with triangles (Transplant-Plot), dashed line with circles (Natural-Cage), and dashed line with triangles (Transplant-Cage). Colors indicate statistically homogeneous groups based on Tukey HSD tests ($p < 0.05$): blue for groups a, d, j, k; yellow for a,b, d,e; red for b, e, l; and green for c, f (see Table SM1 for details, Supplementary Material). The legend in subplot **a** uses gray lines and markers to denote treatments without color information

of *P. oceanica* in the Turkish Aegean Sea concluded that the shoot density characteristics of *P. oceanica* are generally within normal or above-normal ranges, according to the density scale proposed by Dural [33], which corresponds to "moderate" and "good" in the UNEP/MAP-RAC/SPA Monitoring Protocol [80]. The results of this study from Gökova Bay showed "normal" shoot density ranges. Notably, the density of natural *P. oceanica* with a cage started below normal (238 ± 14 shoots m^{-2}), but increased to a normal range after 1 year, and this trend continued into the 2nd year. This suggests that caging, for a certain amount of time, may effectively enhance *P. oceanica* meadow density to normal levels, according to Dural's [33] scale.

However, this was not the case for *C. nodosa* in our study. While the species' previous ecological condition and distribution are largely unknown in the study area, the poor results of transplantation and caging experiments suggest a potential dramatic decline in *C. nodosa* meadows over the next few decades due to the hydrodynamic impacts of cage deployment. Based on the available literature, the current status of *C. nodosa* in Gökova

Bay appears better than populations in the western Mediterranean [78] and northern Aegean Sea [3], and similar to those in the central Mediterranean [47] in terms of shoot density. However, a dramatic decline in *C. nodosa* meadows in the Mediterranean was reported two decades ago [78], driven by factors such as invasive marine plant species [22], hydrodynamic stress [47], and anthropogenic impacts.

Seagrass restoration typically involves actively altering the ecological state, from sparse vegetation or bare soils to densely vegetated plots [54], with transplantation of vegetative material often being the primary restoration strategy [8, 9, 55]. By itself, seagrass conservation is generally considered more passive, including monitoring and establishing Marine Protected Areas (MPAs) to aid recovery. Although it has been suggested that seagrass conservation costs less than active restoration [53], the success or failure of restoration efforts is context-dependent [59]. Cages are frequently used to protect transplanted seagrasses from herbivory [8], but it is not a permanent solution rather than a temperary one, just aiding to the success of the transplants. It should be kept in mind that a hollistic approach should be taken for higher transplantation and restoration success, such as managing herbivor pressure through targeted fisheries or suchas along side limiting anchoring damage etc. The transplantation of *P. oceanica* in the eastern Mediterranean was successful, with shoot density showing excellent results in the first 2 years of the experiment. More than 80% success was achieved under cages, and 40% in open transplanted grasses (Fig. 2). Thus, transplantation may be a viable option for restoration efforts in No-Take Zones (NTZs). However, the transplantation of *C. nodosa* failed to achieve successful restoration or conservation outcomes. Caging negatively impacted both transplanted *C. nodosa* and the density of natural plants. On the contrary, a recent study's cage experiments prevented grazing affect by fish *S. salpa* [19]. This suggests that alternative prevention methods for *C. nodosa* should be tested against different grazers than *S. salda* in the eastern Mediterranean.

Herbivory has long been recognized as a major factor influencing seagrass and seaweed populations [60]. Invasive herbivorous fish species such as *S. rivulatus* and *S. luridus* compete with native species like *S. salpa* and *Sparisoma cretense* [38]. Celebi et al. [23] documented the effects of invasive gastropod species (e.g., *Conomurex persicus*) on grazing. Despite higher predation rates of *S. salpa* on *P. oceanica* [7], juvenile *Siganus* species are also known to graze *P. oceanica* meadows extensively [43], which contributes to significant reductions in seagrass canopies [20, 42]. In our study, cages, contrary to expectations, increased grazing rates on *P. oceanica*. This may be due to the fact that the cage systems provided shelter for juvenile fish, including juvenile herbivores, thus increasing their grazing pressure on the leaves. The characteristic semicircular bite marks observed on the leaves support the hypothesis that fish, rather than sea urchins or mollusks, were responsible for the grazing [61].

Interestingly, higher grazing pressure was observed on the leaves of natural *P. oceanica* populations compared to transplanted plants, possibly due to the denser leaf cover in natural populations, which provides both a food source and shelter from predators. Regarding *C. nodosa*, grazing pressure remained high in all experimental settings, with no significant difference between caged and transplanted plants.

MPAs that are well-enforced have shown positive effects on marine ecosystems by mitigating human activities [81]. In well-enforced MPAs, the composition of fish biomass differs, with apex predators and carnivorous fish making up a larger proportion of the biomass compared to non-protected areas [66]. The present study, conducted in one of the Mediterranean's largest well-enforced MPAs, provides valuable insights into the conservation and restoration of seagrass meadows in the face of invasive species and anthropogenic impacts. It suggests that well-enforced MPAs are important sanctuaries for seagrasses, where herbivore pressure can be reduced and restoration efforts may be more successful.

Conclusions

The evaluation of multiple experimental settings highlighted that caging had a limited effect on *P. oceanica* biomass performance. Two important conclusions can be drawn from the caging experiments; (i) Cage systems may help improve abnormal shoot density ranges in *P. oceanica*. Although the applicability of caging on a larger scale (for a certain period of time) remains debatable, this finding encourages further studies to understand the factors that impact the growth dynamics of this species. (ii) Caging can significantly decelerate leaf shortening in transplanted *P. oceanica* seedlings over time, making it a potential strategy for the sustainable transplantation of *P. oceanica*. However, herbivory emerged as a critical factor shaping restoration outcomes. Contrary to expectations, caging often increased grazing pressure, likely by providing shelter for juvenile herbivorous fish, which contributed to more intense seagrass consumption—particularly in natural *P. oceanica* plots. In the case of *C. nodosa*, high grazing intensity was observed across all treatments, with no significant mitigation effect from caging. These findings emphasize that invasive herbivores may undermine both conservation and restoration efforts, and that species specific effective grazing management should be an integral part of future restoration strategies, especially in

the eastern Mediterranean. In contrast, caging had negative effects on *C. nodosa*, not only reducing shoot densities but also decreasing leaf lengths. Therefore, the use of cages in *C. nodosa* restoration efforts in the eastern Mediterranean is not recommended.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12302-025-01201-x.

Supplementary material 1. Table SM1. Summary of positive and negative changes in shoot density, leaf length, and grazing activity for *P. oceanica* and *C. nodosa* under four experimental treatments (Natural, Transplant, Plot, Cage). Each cell presents the number of observations (# of marks) and corresponding percentage (%) within a category. Positive change indicates annual net growth exceeding initial values; negative change represents zero or declining growth. Grazing activity is classified as positive or negative based on the presence or absence of bite marks. Percentages are calculated as (# of marks in category / total observation in treatment) × 100. Subscript letters (e.g., a, b, c) denote statistically homogeneous groups within each variable, based on Tukey HSD post-hoc tests at the 0.05 significance level. Table SM2. Descriptive properties of abundance and growth datasets in each year from the initialization of the experiment (2017 for *P. oceanica*; 2018 for *C. nodosa*) to the last monitoring (2019).

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During the preparation of this manuscript, the authors used the large language models solely to improve the clarity, grammar, and formal tone of the English text. The model was not involved in the design, analysis, or interpretation of the research. The authors carefully reviewed all content after generation and take full responsibility for the final version of the manuscript.

Author contributions
Conceptualization: IT, EGTB, FB; methodology: IT, EGTB, FB; field experiments: IT, VA, BA; data analysis: FB; writing draft and original versions: IT, EGTB, FB; review-editing: IT, EGTB, FB.

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Data availability
No datasets were generated or analysed during the current study.

Declarations

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Not applicable.

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The authors declare no competing interests.

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