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Research article

Indirect grazing-induced mechanisms contribute to the resilience of Mediterranean seagrass meadows to sea urchin herbivory

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Plant–herbivore interactions are often regulated by a series of direct and indirect buffer mechanisms (compensatory or defensive plant responses, population control, alternative resources) that can determine the relative stability of the system. In plant-dominated marine environments, these mechanisms are particularly important given how vulnerable these systems are to strong consumer pressure. Here, we evaluate the presence and, where possible, the strength, of five mechanisms that get activated under high herbivory pressure and are capable of dampening their effects in a seagrass meadow ecosystem: 1) seagrass compensatory growth, 2) increase in plant resistance, 3) availability of alternative resources, 4) predatory control and 5) density-dependent control. We assessed these mechanisms for the interaction between the Mediterranean seagrass *Posidonia oceanica* and the sea urchin *Paracentrotus lividus* through a short-term series of controlled field and laboratory experiments after simulated or natural herbivory events. Of the five mechanisms tested, we found that three mechanisms – availability of alternative resources, increased predation rate and reduction in sea urchin numbers – effectively dampened herbivory and worked as potential buffering mechanisms. In contrast, plant compensatory growth and resistance did not show clear responses. While compensatory growth and plant resistance are direct plant mechanism to tolerate the effects of herbivory, the rest are indirect mechanisms that begin with a modification of a plant trait (i.e. canopy height) that influences other species preference and/or behaviour, which in turn influences plant consumption. These adaptive behaviours may be a crucial and often overlooked factor in the remarkable resilience that Mediterranean seagrass ecosystems show to herbivory.

Keywords: behaviour, dampening mechanisms, herbivore, interaction, resilience, seagrass

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Introduction

Herbivores play a central role in processes, functions and services of vegetated ecosystems, shaping communities and promoting matter and energy transfer from producers to higher trophic levels (Hulme 1996, Augustine and McNaughton 1998, Duffy and Hay 2000, Maron and Crone 2006, Bakker et al. 2016a). Their role becomes particularly acute where large herbivores or major aggregations occur, both in terrestrial (Hobbs 1996, van de Koppel et al. 1997, van der Wal 2006, Lacher Jr. et al. 2019) and aquatic systems (Alcoverro and Mariani 2002, Christianen et al. 2014, Ling et al. 2015, Bakker et al. 2016b). While plant biomass is expected to decline linearly with herbivory pressure, the complexity of plant–herbivore interactions often leads to non-linear dynamics that often buffer the impact at the ecosystem level (Strauss and Agrawal 1999, Bergqvist et al. 2003, Nykänen and Koricheva 2004). This dampening effect is commonly driven by both plant responses and herbivore behaviour.

Plants can respond to herbivory with a range of strategies that are capable of reducing herbivory pressure (Karban and Baldwin 1997). These strategies include inbuilt structural responses (e.g. thorns or spines) and a series of induced responses that are triggered after an herbivory event. Induced responses can be further classified into resistance strategies, which tend to impair herbivore performance, hence reducing consumption; and tolerance strategies, which mitigate the negative effects of herbivory (Fritz and Simms 1992, Strauss and Agrawal 1999, Moran and Bjorndal 2005, Steele and Valentine 2015). Resistance strategies typically involve reducing leaf palatability by changing physico-chemical properties (e.g. increasing the amount of fibre in leaves) or by producing secondary metabolites (e.g. phenolics) that deter most herbivores (Coley 1983, Peeters 2002, Nykänen and Koricheva 2004). On the other hand, tolerance mechanisms allow plants to maintain or even enhance primary production (with compensatory or overcompensatory growth, respectively) after herbivore attack through nutrient or carbon translocation from belowground organs to leaves (McNaughton 1983, Tiffin 2000, Gadd et al. 2001). The ability of plants to deploy these mechanisms determines how susceptible they are to herbivore consumption. Marine seagrasses are typically well-adapted to herbivory and respond with a series of induced dampening responses (e.g. compensatory growth or chemical compounds) that reduce the impact of herbivory as offtake increases (Moran and Bjorndal 2005, Vergés et al. 2008, Steele and Valentine 2015).

Apart from mechanisms that emerge directly from plant responses, several indirect effects related to herbivore behaviour can potentially also serve as effective buffering mechanisms. For instance, intense herbivory can modify plant structural traits (e.g. canopy height) that in turn increase predation risk to the herbivores present in the habitat (Heck and Valentine 1995, Pagès et al. 2012). In this case, a substantial reduction in seagrass canopy height caused by herbivores serves to increase predation risk for other seagrass-dwelling herbivorous species, which, in turn, reduces herbivore pressure on the seagrass. The increase in predation risk linked to shorter canopies may also trigger another dampening mechanism by indirectly modifying movement behaviour and consumption of seagrass-dwelling herbivores (Pessarrodona et al. 2019, Pagès et al. 2021). As the canopy decreases, predation risk increases and seagrass-dwelling herbivores migrate, searching for new, more secure habitats, thus dampening the overall impact of herbivory. In some cases, these migrations occur in groups with several urchins creating devastating grazing fronts (Maciá and Lirman 1999, Rose et al. 1999, Alcoverro and Mariani 2002, Lauzon-Guay and Scheibling 2007). In fact, herbivore density has been observed to be often self-regulated by density-dependent mechanisms when resource scarcity causes herbivores to migrate (Bakker et al. 2016b). Finally, a release from herbivory pressure as a result of differential preference between plant resources can also serve as an indirect stabilising mechanism. Focused grazing on the dominant plant in the area can promote the growth of other plant species (Valdez et al. 2020), which can lead to herbivores shifting preference away from the dominant (Stephen and Krebs 1986, Belovsky 1997, Illius et al. 1999). These 'attractant-decoys' (sensu Atsatt and O'Dowd 1976) can decrease grazing impact on other plants within the system. This mechanism could operate in seagrass meadows, where, as canopy decreases through herbivory, sunlight can reach the bottom of the meadow and facilitate the growth of palatable rhizome epibionts (epiphytes, macroalgae or even other seagrass species) that are preferred by generalist herbivores (Prado et al. 2007a, Tomas et al. 2011, Marco-Méndez et al. 2012, 2017) thus alleviating herbivory pressure on the dominant seagrass. However, the existence of these mechanism will be often dependent on the specific plant–herbivore interaction as every herbivore will exploit resources in a different manner and every plant will have a set of different responses. Most of these buffering effects can only operate under certain contexts (e.g. predator presence is required for the success of predation risk mechanism), which strongly mediate the existence and strength of these mechanisms.

Seagrasses are one of the most important primary producers in coastal waters where overgrazing events are not rare (Heck and Valentine 2006). For instance, tropical seagrass ecosystems subject to intense herbivory by large herbivore aggregations or megaherbivores like sirenians, green turtles and sea urchins (Eklöf et al. 2008, Christianen et al. 2014, 2021, Nowicki et al. 2018, Carnell et al. 2020, Gangal et al. 2021) can undergo functional meadow extinctions. In temperate areas, in contrast, herbivory is mostly dominated by mesoherbivores such as gastropods or isopods where herbivory has a relatively minor role (Best and Stachowicz 2012, Carr and Boyer 2014). The enclosed Mediterranean is curious mix between a tropical and a temperate sea, with summer temperatures rising much higher than seas at a similar latitude. Despite having a large abundance of fish and sea urchin herbivores (Prado et al. 2008) seagrass meadows seem to be cope rather well (Prado et al. 2008, Planes et al. 2011) and only few cases of overgrazing have been observed, typically linked to environmental imbalances (e.g. excess nutrients, Ruíz et al. 2009). The relative resilience of temperate meadows to herbivory pressure may be linked to

the effectiveness of dampening mechanisms. Understanding these mechanisms is critical both to managing this resilience as well as to prepared for the ongoing expansion of new tropical herbivores in temperate systems (Vergés et al. 2014, 2016). We evaluated the presence and importance of a series of species-specific buffering mechanisms in *Posidonia oceanica* seagrass systems (Fig. 1). *Posidonia oceanica* systems are ideal to explore dampening mechanisms in response to herbivory, since the species appears to persist even when consumption/ defoliation rates temporarily exceed seagrass production (Tomas et al. 2005a, Prado et al. 2007b, Planes et al. 2011). We used a combination of short-term laboratory and controlled field experiments based on natural or simulated herbivory to test the hypotheses sketched in Fig. 1 and Table 1. In summary, we propose that an intense herbivory episode could trigger a series of direct and indirect (mediated by canopy height) responses that can buffer the impact of herbivores. These responses include: plant compensation responses (1), plant resistance responses (2), preferences for alternative resources (3) and herbivore population control via predation (4) or via migration/dislodgement (5).

Methods

Study system

Posidonia oceanica is a seagrass species endemic to the Mediterranean Sea. It provides habitat to a wide range of species (Francour 1997, Martínez-Crego et al. 2008) and is eaten by two main herbivores, the fish *Sarpa salpa* and the sea urchin *Paracentrotus lividus*. *Sarpa salpa* is a demersal fish that commonly forages in shoals of up to hundreds of individuals (Raventos et al. 2009, Buñuel et al. 2020). It is responsible for the bulk of the herbivory *P. oceanica* is subject to (up to 70% according to Prado et al. 2007b). Feeding by *P. lividus* constitutes the rest of the offtake. Between the fish and the urchin, these grazers can remove up to 50% of the annual primary production of *P. oceanica*, with some overgrazing events (consumption rates temporally exceeding primary productivity) having been reported in several areas (Verlaque and Nédelec 1983, Ruiz et al. 2001, Tomas et al. 2005a, Prado et al. 2007b, Planes et al. 2011). Apart from feeding on seagrass leaves, *P. lividus* uses the leaf canopy of *P. oceanica* rhizomes and shoots to shelter from predators (Farina et al. 2009, Pagès et al. 2012). In addition, both herbivores are generalists that feed on both seagrass and algae (Verlaque 1990, Boudouresque and Verlaque 2007), including the epiphytic algae living on *P. oceanica* leaves and rhizomes.

Experimental design

Compensatory growth and increase in plant resistance
To assess if substantial biomass loss induces compensatory growth and/or deterrence mechanisms in *P. oceanica*, we conducted a field experiment where we simulated an intense grazing event. We established eight treatment (1 m²) and six control plots (two plots were lost during the experiment) in a seagrass meadow in Cala Canyelles (41°42′13.5″N, 2°53′04″E; all at approximately 5 m depth). We excluded
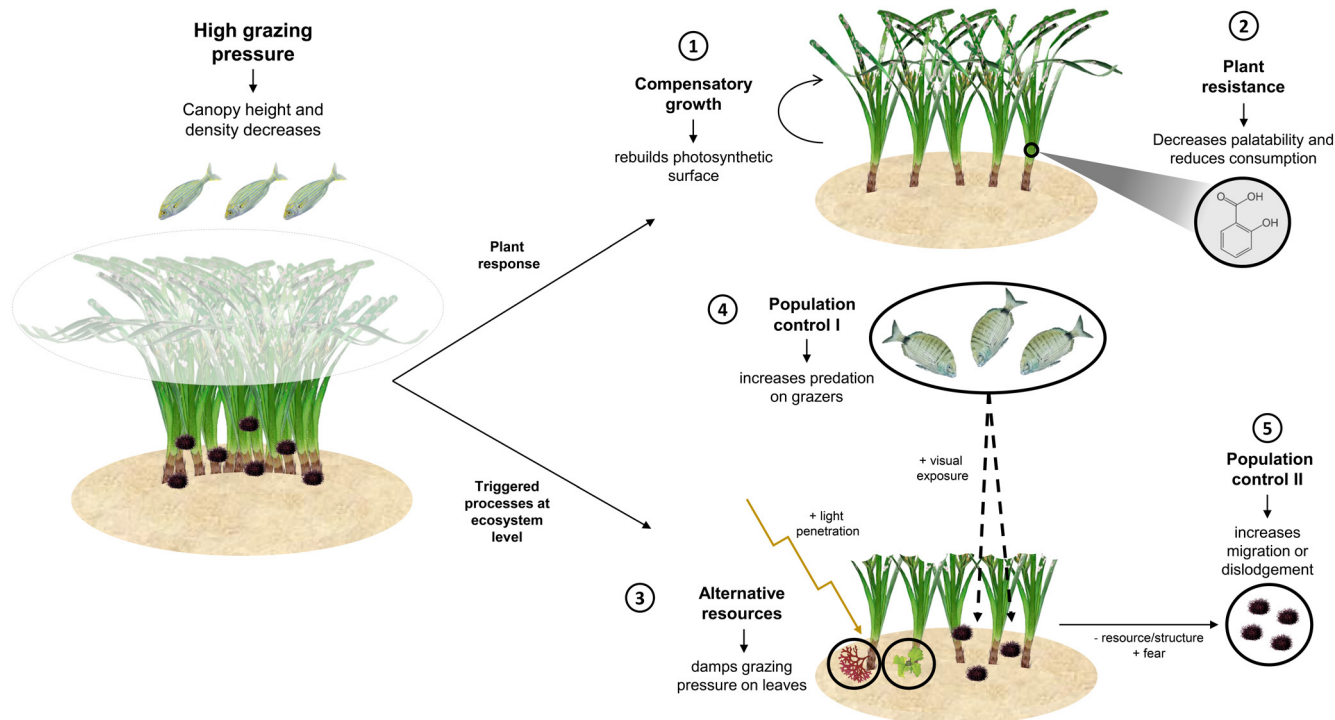

Figure 1. Schematic representation of dampening mechanisms of *P. oceanica* systems resulting from an intense grazing episode. Dashed semi-transparent oval represents the amount of canopy lost to grazing.

Table 1. List of the different dampening mechanisms of *P. oceanica* systems induced by simulated grazing tested in this study.

Mechanism	Proposed machanism (after an intense grazing episode)	Mechanism-inducing process
1) Compensatory growth	Grazing induces increased leaf growth on *P. oceanica*, allowing the recovery of lost photosynthetic surface	Direct
2) Increase in plant resistance	*Posidonia oceanica* reduces its palatability to herbivores by accumulating secondary metabolites or increasing physical resistance, thus decreasing additional biomass loss	Direct
3) Availability of alternative resources (change of preference from seagrasses to algae)	Canopy reduction caused by grazing improves light climate in the rhizomes, stimulating growth of epiphytic algae. Herbivores shift their feeding behaviour, preferring the more palatable algae, thus decreasing grazing pressure on the seagrass	Indirect
4) Increased predation rate on sea urchins	Canopy reduction caused by grazing reduces sea urchin shelter against predation and increases predation rates, resulting in a reduction of sea urchin abundance and grazing pressure	Indirect
5) Density-dependent reduction in sea urchin number	Canopy loss enhances competition for resources and decreases protection for dense sea urchin aggregations, which results in a reduction of sea urchin number and grazing pressure	Indirect

sea urchins from all plots and any stray individuals were removed in our periodic monitoring of the plots (every five days, approximately); through the course of the experiment there were very few instances of sea urchin intrusions. We left control plots (C) untouched, while in the treatment plots (T), we clipped all seagrass shoots to 50% of their initial canopy height, equivalent to an intense grazing event. To measure canopy height, we extended the leaves to their maximum height, and ignoring the tallest 20% of leaves, measured from the sediment to the height of the top of the remaining shoots using a 1-m ruler (Short et al. 2001). In order to minimize the error, five measurements of the initial canopy height were taken for each plot. Clipping was performed following methodologies developed in Verges et al. (2008). The experiment lasted one month, and we clipped shoots twice during that time: at the start of the experiment and 15 days later, in order to maximize the effects of intense herbivory. We clipped the plots a second time to maintain seagrass at 50% of its initial canopy height. The experiment was performed from May to June 2019, when natural fish grazing is still low (Prado et al. 2007b), so we could test the effects of the experimental grazing without additional impacts. We also removed all *P. lividus* from the plots and surrounding area to exclude sea urchin herbivory and removed all cut leaves from the area to prevent any interference with the experiment.

To measure shoot growth, we used a modified Zieman's method (Pérez and Romero 1994) on 15 random shoots per plot. For each shoot, we pierced all leaves just above the ligule (the junction between the leaf blade and the leaf base) at the start of the experiment. After ten days of the first clipping, we collected all pierced shoots in control and treatment plots and brought them to the laboratory, where we measured growth (cm day^{-1}). Given that *P. oceanica* shoots within each plot are likely to be connected via rhizomes, shoot growth was averaged for all shoots within each plot. Compensatory growth was assessed by comparing shoot growth rate in clipped relative to control plots.

To assess how biomass loss influenced plant defensive strategies, we used a palatability experiment with the assumption that herbivory-induced defences would manifest as reduced palatability by herbivores. We conducted herbivore consumption experiments in laboratory conditions, using plant tissues collected from control and treatment plots established in the field (see previous paragraph) as food for the main invertebrate herbivore, the sea urchin *P. lividus*. Before the experiment we collected sea urchins of a similar size (4–6 cm without spines) from a bay close to the laboratory and placed them in water tanks for a 3-day adaptation period without food. Then, we placed a total of 60 *P. lividus* individuals in 15 aerated flow-through aquaria (55.5 × 40.5 × 25 cm), divided into four compartments (60 compartments in total). Each urchin was randomly allocated to a compartment together with one random seagrass rhizome fragment with 3–4 shoots (30 from control plots and 30 from clipped plots after one month, 60 fragments in total). Within a shoot leaves displaying lateral bite marks or leaves with less than 15 cm were discarded, while the rest were clipped to a standard length of 15 cm and their epiphytes carefully removed with a plastic ruler so as not to damage the leaf. In each shoot we counted the total number of leaves and measured the width of each leaf in order to calculate the initial area per replicate. The total leaf area offered to grazers was greater than 60 cm^2 in all cases (the maximum leaf consumption observed during previous pilot experiments), ensuring that sea urchins could feed ad libitum. Additional *P. oceanica* fragments were placed in pairs in aquaria (30 × 17.5 × 15 cm) without herbivores to assess natural changes in leaf area for further corrections. We also recorded sea urchin size, which was later used as a covariate in our linear models. At the end of the experiment (five days later), fragments were removed and leaves were separated from the shoot. At the end of the experiment (five days later), fragments were removed, leaves were separated from the shoot and photographed to calculate consumption comparing leaf area to the initial values. We used ImageJ ver. 1.52p to measure areas.

Availability of alternative resources influencing consumption

To test if the occurrence of epiphytic algae on *P. oceanica* rhizomes influenced *P. oceanica* leaf consumption by *P. lividus*, we performed a laboratory feeding experiment. In June 2018, we collected 40 *P. oceanica* fragments (containing 2–5 shoots) with abundant epiphytic macroalgal cover on rhizomes from a meadow in Llançà (42°23′0.5″N, 3°9′31″E; ca 5 m depth), and transported them to the laboratory. The algal community comprised both brown and red algae, dominated by *Padina pavonica*, *Peyssonnelia* spp. and *Dictyota* spp. We used half of these samples in consumption experiments as treatments (T, rhizomes with algae), and removed all epiphytic algae from the rhizomes of the other half to be used as controls (C, clean rhizomes). We only used shoots without lateral bite marks and cut the apex of the leaves to a standard length of 15 cm and carefully removed epiphytes from leaves using a plastic ruler so as not to damage the leaf. In each shoot we counted the total number of leaves. We also collected sea urchins of a similar size (4–6 cm without spines) in a bay close to the laboratory and placed the sea urchins in tanks for a three-day adaptation period without food before the start of the experiment. We used 20 aerated flow-through aquaria (30 × 17.5 × 15 cm), divided into two compartments separated with a plastic mesh, to which we randomly allocated a total of 40 *P. lividus* individuals (one individual per compartment). In each compartment we placed either a control seagrass fragment (rhizomes without epiphytes) or a treatment seagrass fragment (rhizome with epiphytes; leading to a total number of 20 control and 20 treatment conditions). Since we were interested in the amount of *P. oceanica* leaf consumption as a function of the presence of algal biomass on the rhizomes (not in the algal area consumed), we used rhizomes covered with abundant macroalgal epiphytes (ad libitum) but we do not measure its area. Also, we made sure that the amount of seagrass leaf was not limiting as well (ad libitum), but similar among replicates (3–4 shoots per rhizome, 3–5 leaves per shoot and 15 cm length) to standardise initial leaf area. Within a shoot, leaves displaying lateral bite marks or leaves with less than 15 cm were discarded. In each shoot we counted the total number of leaves and measured the width of each leaf in order to calculate the initial area per replicate. We also recorded sea urchin size, which was later used as a covariate in our linear models. After two days, all fragments were removed, and leaves were separated from the shoot. We photographed each leaf and calculated individual final leaf area using ImageJ. The area consumed was the difference between the initial and the final length.

Herbivore population control I: increased predation rate

To assess if a reduction in canopy height increased urchin predation risk, we used an existing data set (Pagès et al. 2012) to re-evaluate if the observed indirect interaction constituted a dampening mechanism. We restricted our analysis to adult and young adult sea urchins that contribute the bulk of herbivory (Pessarrodona et al. 2019). The data was obtained from a natural experiment in a *P. oceanica* meadow in the Medes Islands marine protected area (42°02′51″N, 3°13′22.3″E, NW; ca 5 m depth) where the main predators, the fish species

Coris julis and *Diplodus sargus*, are very abundant (García Rubies and Zabala 1990) and predation on sea urchins is very high (Boada et al. 2015a). Instead of using clipping to simulate grazing, the study used the heterogeneous canopy height naturally caused by *S. salpa* through its patchy grazing behaviour, which produces small-scale variability in meadow canopy height (Tomas et al. 2005a). This kind of grazing is often determined by shoaling behaviour of the fish and nutrient content of the seagrass (Tomas et al. 2005b, Prado et al. 2010, Gera et al. 2013, Buñuel et al. 2020). They selected three different canopy height treatments based on the intensity of fish grazing: 'mowed' (7 ± 1 cm), hereafter 'high grazing', 'short' (26 ± 2 cm), hereafter 'moderate grazing', and 'long' (47 ± 3 cm), hereafter 'control'. Nine plots (1.5 × 1.5 m) per treatment were chosen and for each experimental plot, 10 sea urchins of the same size class were pierced through the test with a hypodermic needle, threaded with monofilament line (nylon, 30 cm length) and tied to metal pegs (see Methods in Boada et al. 2015b). Each tethered urchin was uniquely identified with a number and placed randomly inside the plot, after verifying that the plot was free of the main benthic predator, the gastropod *Hexaplex trunculus*. Mortality owing to the tethering manipulation itself was 2.5% (similar to rates found in other studies, Sala and Zabala 1996). These individuals were removed from any further analysis. Urchins were monitored every day to be able to carefully attribute mortality to predation. In addition to the treatment plots inside the meadow, three more plots were established on a bare sand patch as a time control, with the urchins totally exposed, to determine the endpoint of the experiment. Complete urchin predation in the sand patch took place within five days, after which pegs from treatment and control plots were removed and the remaining sea urchins counted (for more methodological details see Pagès et al. 2012).

Herbivore population control II: reduction in sea urchin numbers

To evaluate changes in sea urchin density over time caused by reductions in canopy height and/or density-dependence, we manipulated the number of urchins in a set of seagrass patches in the field. All urchins used in this experiment belong to the same size class (4–5 cm, test diameter without spines). We monitored sea urchin densities in patches for six months during which canopy height changed from 20 to 60 cm. Specifically, in May 2016 we selected 21 isolated patches of *P. oceanica* in a sand matrix, separated at least 5 m from each other in Fenals (41°41′33.1″N, 2°50′0.5″E, ca 6 m depth). The meadow is characterised by very low predation on sea urchins (Boada et al. 2015a), which minimized predator interference. We randomly assigned one of seven urchin densities used as treatments (i.e. 5, 8, 12, 16, 20, 26 and 32 individuals·m^{-2}) to each patch, and established three replicates for each treatment. To do so, we measured patch size and adjusted the number of urchins within each patch to match the assigned density. We also measured the initial canopy height and shoot density of each patch. From the start of the experiment to October 2016, we periodically

visited all patches (seven times) and measured the variation in the number of sea urchin individuals, in canopy height and in shoot density. At each visit, urchins were added or removed to match the initial density conditions assigned to that patch.

Statistical analysis

All categorical relationships were analysed using linear and general linear models (GLM and betareg packages) in R, with the inclusion of random effects as grouping factors whenever necessary, as suggested by the Akaike information criterion (AIC and AICc, AICcmodavg package) (Zuur et al. 2010). The accurate distribution for each model was found using Fitdistr package. All models were graphically, using Q–Q and residuals plots (mcheck() function), and numerically checked, using Shapiro–Wilk and Brown–Forsythe tests (*shapiro.test()* and *bf.test()* functions), for normality and homoscedasticity. Also, we checked for overdispersion for each model using the *P_disp function()* from msme() package.

For the compensatory growth experiment, we used a linear model to test if the fixed factor 'Simulated herbivory' (two levels: control and high herbivory) influenced the response variable 'growth rate'.

For the plant resistance experiment, we tested if the response variable 'Leaf consumption' was influenced by the fixed factor 'Simulated herbivory' (two levels: control and high herbivory) and the random factor 'Urchin size' using a GLM model with a Gamma distribution. As suggested by AIC and AICc, the continuous variable 'Urchin size' was dropped from the analysis.

To test if epiphytic algae occurrence on *P. oceanica* rhizomes buffered herbivory pressure by *P. lividus*, we evaluated if the response variable 'Leaf consumption' was influenced by the predictor variables 'Algal presence' (two levels: control and rhizome algae), the covariate 'Urchin size', as well as their interaction, using a GLM model with a Gamma distribution.

For the predation risk experiment, we assessed the effects of the predictor variable 'canopy height' (three levels: control, moderate herbivory and high herbivory) on the response variable 'percentage of sea urchins eaten', as a proxy of sea urchin predation rate, using a GLM model with a Beta distribution.

Finally, we evaluated if the response variable '% of urchin number reduction' was influenced by 'Urchin density' (seven levels: 5, 8, 12, 16, 20, 26, 32) and 'Canopy height' as predictor variable, using a GLM model with a Beta distribution.

Results

Compensatory growth and plant resistance

Despite losing 50% of its photosynthetic surface, *Posidonia oceanica* maintained similar growth rates at high simulated herbivory compared to controls (Fig. 2a, $p = 0.199$, $F = 1.844$, $df = 1$). In addition, simulated herbivory did not enhance plant resistance to herbivores; instead, the trend observed suggests that sea urchins fed more readily on shoots exposed to high intensity clipping (Fig. 2b), although there was no significant evidence of this trend ($p = 0.354$, $\chi^2 = 0.856$, $df = 1$).

Availability of alternative resources influencing consumption

The occurrence of epiphytic algal on *P. oceanica* rhizomes significantly reduced consumption on seagrass leaves by sea urchins ($p = 0.008$, $\chi^2 = 6.926$, $df = 1$). *Posidonia oceanica* shoots with epiphytic algae on their rhizomes had four times lower leaf consumption rates than control shoots (without algae covering their rhizomes, Fig. 2c). The interaction also came out significant ($p = 0.01$, $\chi^2 = 6.69$, $df = 1$), although no bias in urchin distribution between treatments was found.

Population control I: increase in predation rate

Results from the predation risk experiment conducted in the Medes Island marine protected area (high predation area) showed that canopy height strongly influenced urchin survival ($p = 1.13 \times 10^{-5}$, $\chi^2 = 76.164$, $df = 2$). The percentage of sea urchins preyed on differed significantly between treatments and was much higher in the plots with high herbivory conditions than in plots with moderate grazing, and control plots (high canopy, no/very low herbivory) (Fig. 2d). Specifically, the percentage of urchin predation was four times higher in the plots subjected to high herbivory than in controls.

Population control II: reduction in sea urchin densities

Sea urchin loss from *P. oceanica* patches decreased exponentially with increasing seagrass canopy height ($p = 1.14 \times 10^{-9}$, $\chi^2 = 37.06$, $df = 1$); and as expected, sea urchin loss increased with sea urchin density ($p = 5.93 \times 10^{-5}$, $\chi^2 = 16.124$, $df = 1$) (Fig. 3, Table 2).

Discussion

While many marine plant communities are highly susceptible to intense herbivore pressure, *Posidonia oceanica* meadows show remarkable resilience to intense grazing events. Our work shows that this resilience is due, at least in part, to a range of indirect dampening mechanisms, largely related to changes in plant–herbivore interactions, that could buffer the system during intense herbivory episodes. We found evidence for three indirect mechanisms that diminished herbivore damage and contributed to *P. oceanica* resilience to herbivory. In contrast the two direct plant responses, compensatory growth and plant resistance, were not as effective. The three indirect mechanisms all began with a modification
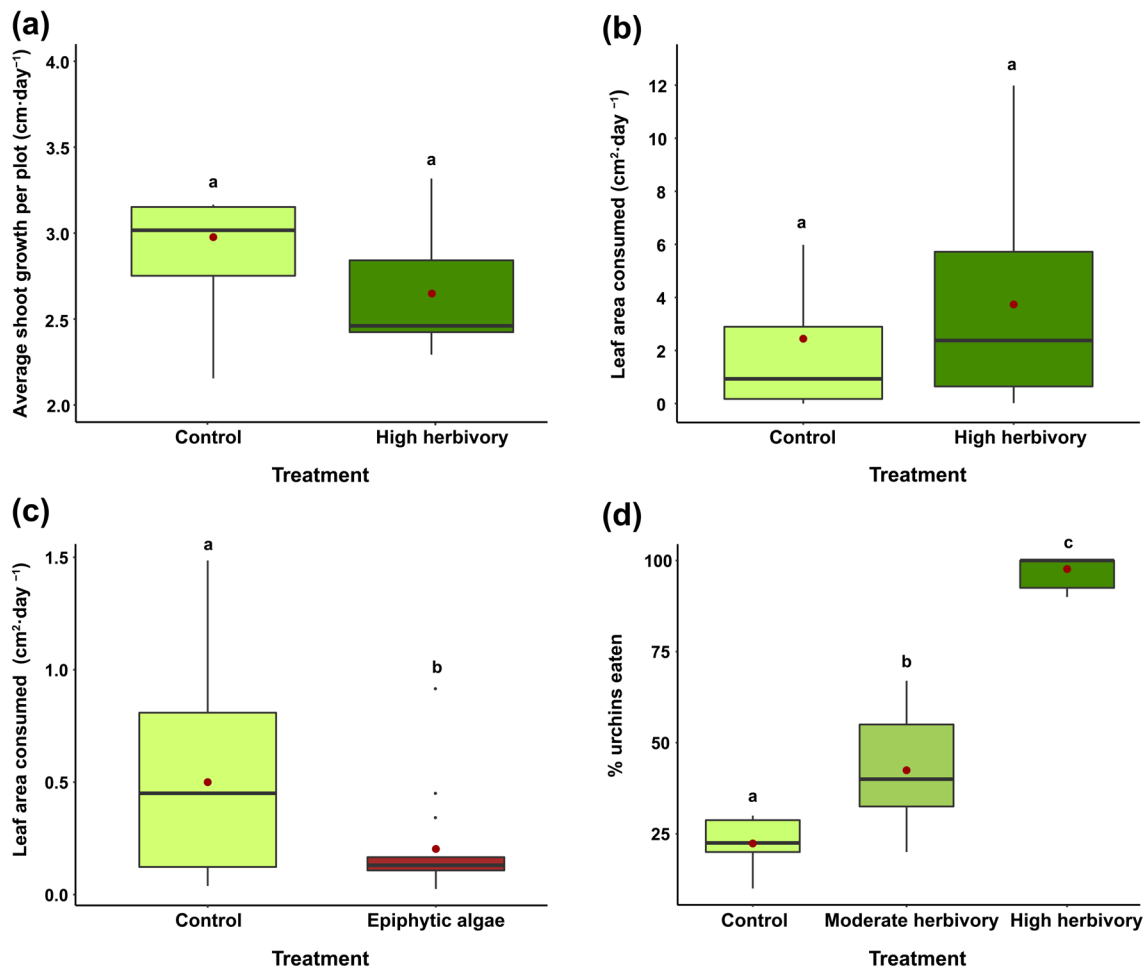
Figure 2. Dampening mechanisms of *P. oceanica* system in response to discrete levels of herbivory. (a) Compensatory growth mechanism (average shoot growth rate per plot for control and high-simulated herbivory treatment), (b) plant resistance mechanism (leaf area consumed by sea urchins for control and shoots subjected to high simulated herbivory), (c) availability of alternative resources influencing consumption (leaf area consumption per day by sea urchins for control shoots and shoots with epiphytic algae on their rhizomes) and (d) predation rate (percentage of sea urchin individuals eaten by fish predators in each of the treatments with differing herbivory levels). In the boxplot, the black line represents the median and boxes are Q1 and Q3 (interquartile range). Vertical lines show values beyond the interquartile range and red dots show the mean. Letters indicate significant differences among treatments (Table 2).

of a plant trait (i.e. canopy height) and reduced herbivore occurrence and/or its feeding behaviour. In addition, we argue that contextual drivers were crucial for the occurrence and effectiveness of the mechanisms observed. In addition, our results highlight the importance of indirect mechanisms that reduce herbivore populations and feeding behaviour that could be key in explaining how plants persist under intense herbivory.

Our simulated herbivory study suggests that the response of *P. oceanica* when subjected to intense simulated herbivory was based more on tolerance than on resistance, although these strategies are not mutually exclusive. Similar tradeoffs have been documented in many plant species (Coley et al. 1985, Herms and Mattson 1992, Mauricio and Rausher 1997). Plants from intensively clipped plots grew at similar rates despite having much less biomass than shoots in control plots, while their unchanged palatability hinted at a lack of

inducible defences (at least not effective enough to deter *P. lividus*). Although we did not detect compensatory growth responses in this study, *P. oceanica*'s capacity to display compensatory growth has been well documented in other studies (Cebrián et al. 1998, Vergés et al. 2008, but see Hernán et al. 2019) and represents a buffering mechanism that presumably allows fully functional seagrass meadows to persist with moderate to high grazing. This response is probably linked to the substantial amount of belowground tissue that allows the plant to translocate nutrients from the rhizomes to the leaves (Valentine and Heck 2021). However, there is a threshold to compensatory growth mechanism beyond which plants cannot compensate anymore (Vergés et al. 2008). It is possible that the limited response we recorded in the experiment represents a point beyond the plant's ability compensate. On the other hand, our consumption experiment documented a possible preference of grazers for leaves that had already
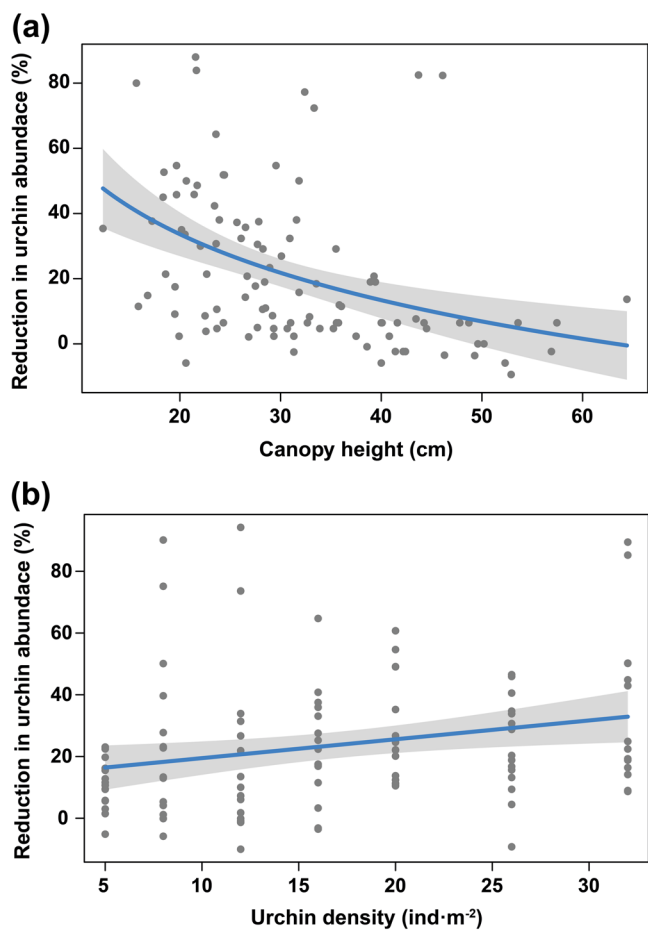
(a)

(b)

Figure 3. Model results of reduction of *P. lividus* individuals in *P. oceanica* meadows where predation is very low with (a) canopy height and (b) urchin density using Visreg package from R. Blue solid lines indicate the best predicted relationship using original scale (not log-transformed data as used in statistical analysis) and the grey band corresponds the 95% confidence interval.

been grazed (albeit without statistical significance), a trend already observed in earlier work at certain simulated grazing conditions (Vergés et al. 2007, Hernán et al. 2019). If these patterns were confirmed, it would imply a non-linear negative effect whereby herbivores preferentially feed on already grazed leaves. This has been observed in the grazing behaviour of large herbivores, such as moose, wildebeests, geese, turtles, dugongs and fishes, where herbivores prefer already grazed

leaves, leading to the formation of grazing plots (McNaughton 1976, Black et al. 1992, Preen 1995, Bergqvist et al. 2003, Aragones et al. 2006, Buñuel et al. 2020, Scott et al. 2020, Christianen et al. 2021). Grazing halos (or mowed patches) have been reported in *P. oceanica* meadows subject to heavy grazing by fish (Tomas et al. 2005a), indicating that there is some support for this observation.

While mechanisms resulting from direct responses of plants to herbivory pressure are relatively well explored in the literature, we found a raft of subtler indirect interactions that emerged as canopy height decreased with increasing herbivory. For a start, in meadows with heavily grazed, shorter canopies, sunlight can penetrate to the rhizome layer, promoting the growth of erect epiphytic algae (Boudouresque 1974, Piazzi et al. 2002). Our results suggest that the increased abundance of this alternative food resource can alleviate grazing pressure of *P. lividus* on seagrass leaves, likely constituting a buffering mechanisms that reduces grazing impact on *P. oceanica*. This mechanism is caused by a release from herbivory pressure as a result of differential preference which indirectly facilitates the less preferred species (Kelkar et al. 2013). This matches the observed preference of the two main herbivores, *P. lividus* and (young) *Sarpa salpa* for algae (Havelange et al. 1997, Boudouresque and Verlaque 2007). Additionally, a substantial reduction of sea urchin densities was observed in two independent experiments in meadows with shorter canopies. Inside the MPA (where predation rates on sea urchins were typically high (García Rubies and Zabala 1990, Pessarrodona et al. 2019), we found that predation pressure on sea urchins was 4–5 times higher in plots with short canopies (direct consumptive effects). Thus, the dual use of *P. oceanica* by *P. lividus* – as sheltering habitat and as resource – becomes an obvious mechanism of seagrass stability that likely prevents potential overgrazing events by sea urchins (Maxwell et al. 2017), provided the system harbours an abundant predator community. We also observed a similar reduction in urchin numbers in the experiment performed in a low predation area (Boada et al. 2015a), in crowded seagrass patches with low canopy heights. We can attribute this urchin reduction to either of three mechanisms linked to reduced canopy: direct predation (as previously discussed), dislodgement by currents or storms due to lower physical protection (Pagès et al. 2013), and migration linked to intraspecific competition for scarce resources or perceived vulnerability (Tomas et al.

Table 2. Results of the ANOVA analysis for dampening mechanisms of *P. oceanica* between treatments.

Source of variation	Shoot growth rate				Herbivore deterrence			Predation risk		
	df	MS	F	p-v	df	χ^2	p-v	df	χ^2	p-v
Treatment	1	0.49	1.844	0.199	1	0.856	0.354	2	76.164	**1.13×10^{-5}**
Error	13	3.217								
Source of variation	Availability of alternative resource					Urchin number reduction			
	df	χ^2	p-v	Source of variation		df	χ^2	p-v
Treatment	1	6.926	**0.008**	Canopy height		1	37.06	**1.14×10^{-9}**
Urchin size	1	0.057	0.81	Urchin density		1	16.124	**5.93×10^{-5}**
Treatment × Urchin size	1	6.69	**0.01**					

2005c, 2006, Pinna et al. 2012, Marco-Méndez et al. 2015, Pessarrodona et al. 2019). Whatever the underlying mechanism, the reduction in urchin numbers with declining canopies protects seagrass from runaway consumption.

The capacity of direct and indirect mechanisms to increase the resilience of seagrass ecosystems is highly context dependent. There is ample evidence that plant–herbivore interaction dynamics can be regulated by the plant community (Barbosa et al. 2009, Underwood et al. 2014, Riolo et al. 2015), nutrient conditions (Burghardt 2016, Van Nuland et al. 2016, Boada et al. 2017) and predation risk (Flagel et al. 2016, Pessarrodona et al. 2019). For example, as mentioned earlier, predator abundance is critical in determining the relevance of dampening mechanisms mediated by predation, given that sea urchin populations cannot be controlled from the top down without a healthy population of fish predators (Eklöf et al. 2008). This mechanism might be particularly strong in MPAs, where fish populations are protected, but not operational in overfished areas. Similarly, the relevance of alternative preference mechanisms will depend on contextual factors that influence the abundance, diversity and growth of epiphytic algae on seagrass rhizomes, such as irradiance or nutrient availability (Piazzi et al. 2002, Balata et al. 2008, Nesti et al. 2009). This is clearly important for seagrass species that have large and long-lived rhizomes (i.e. *Posidonia* spp.; *Thalassia* spp.) that can have large macroalgal epiphytes, and that have very thick canopies. For short lived species with small rhizomes, epiphytes may not constitute a significant alternative. Even compensatory growth can be highly context dependent. For instance, Cebrián et al. (1998) found disparate compensatory responses among a variety of seagrass species after a simulated herbivory episode. The kind of compensatory responses can differ between species, with some for instance, choosing to invest in the production of new shoots instead of leaf compensatory growth (Valentine et al. 1997, 2000). In addition, the importance of each mechanism will be linked to the specific characteristics of the herbivore, such as body size, preferences or grouping behaviour (Scott et al. 2018, Crawley 2019). Mesoherbivores often feed on specific parts of the plant while megaherbivores tend to graze indiscriminately, resulting in different impacts at physiological and population dynamics levels. The overall resilience of meadows is likely dependent on how these context-specific conditions influence buffering mechanisms to intense herbivory.

Herbivory is a central process both in aquatic and terrestrial vegetated ecosystems (Bakker et al. 2016b, Scott et al. 2018, Pausas and Bond 2019, 2020, Valentine and Heck 2021). Our study provides a holistic insight into the many direct and indirect dampening mechanisms that can explain the persistence of *P. oceanica* under even intense grazing pressure. The fish *S. sarpa* and the urchin *P. lividus* are the only voracious herbivores in the north-western Mediterranean, feeding interchangeably on macroalgae and *P. oceanica* meadows (Verlaque 1990, Havelange et al. 1997, Boudouresque and Verlaque 2007). However, the Mediterranean is changing, as exotic invaders and climate change modify the functioning of this enclosed sea. A steady stream of novel herbivore species are rapidly expanding from the eastern Mediterranean, where they have already established (Castriota and Andaloro 2008, Daniel et al. 2009). In addition, as temperatures rise, existing trophic interactions are also likely to be modified with climate change (Pagès et al. 2018, Buñuel et al. 2021). How *Posidonia oceanica* will respond to these new pressures is still an open question, but its resilience to herbivory is most likely going to be dependent on the continued effectiveness of the mechanisms we describe. What is clear is that the presence of indirect mechanisms is critical to fully predict how ecosystems respond to herbivory. Indirect interactions are not the most evident, and are often overlooked when describing overall ecosystem behaviours. As our work shows though, these subtle mechanisms may be the key to ecosystem resilience.

Author contributions

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Data availability statement

Data are available from the Figshare Digital Repository: https://figshare.com/s/68692a773ee49219cf45 (Buñuel et al. 2023).

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