

ARTICLE

Coastal and Marine Ecology

Differential coping capacities underlie the overall resistance of temperate seagrasses to herbivory

J. Boada^{1,2} | T. M. Smith³ | A. M. Ricart⁴  | T. Alcoverro^{1,5} | M. Pérez⁶ |
 J. Romero⁶ | N. Sanmartí⁶  | Y. Ontoria⁶ | M. Pierrejen⁷ | R. Arthur⁵ |
 D. Alonso¹ | M. P. Adams^{8,9}  | F. Rossi¹⁰ 

¹Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Blanes, Spain

²Department of Integrated Marine Ecology, Stazione Zoologica Anton Dohrn, Naples, Italy

³Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Cairns, Queensland, Australia

⁴Institut de Ciències del Mar (ICM-CSIC), Barcelona, Spain

⁵Nature Conservation Foundation, Mysore, India

⁶Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain

⁷Département de Biologie, Université Laval, Québec, Canada

⁸School of Mathematical Sciences, Queensland University of Technology, Brisbane, Australia

⁹School of Chemical Engineering, The University of Queensland, St Lucia, Australia

¹⁰Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn–National Institute of Marine Biology, Ecology and Biotechnology, Genoa Marine Centre, Naples, Italy

Correspondence

J. Boada

Email: jboada@ceab.csic.es

Funding information

Spanish Ministry of Science, Innovation and Universities (MCIU), Grant/Award Numbers: CTM2017-86695-C3-1-R, CTM2017-86695-C3-3-R, PID2020-113745RB-100; Spanish National Research Council (CSIC); Australian Research Council, Grant/Award Number: DE200100683; TOTAL; Australian Government Endeavor Fellowship; Fondo Europeo de Desarrollo Regional (FEDER)

Handling Editor: Rochelle D. Seitz

Abstract

Grazing can impart long-lasting changes in vegetated ecosystems. How ecosystems respond to herbivory depends on the ecological and evolutionary histories of their foundational species. The overall ecosystem functioning and associated biodiversity depend on these responses but there is still little understanding on how the intensity and duration of herbivory interact and impact vegetated ecosystems. We experimentally tested in the field the responses of three seagrass species with distinct life history traits to increasing intensities of herbivory over time. Specifically, we assessed structural responses (i.e., canopy height and shoot density) to reflect the ecosystem state. Additionally, we used mechanistic models to assess induced and constitutive responses in the different seagrass species. Results show that seagrasses coped with herbivory differentially in relation to their life history traits. *Posidonia oceanica* (persistent species) was resistant and only registered declines in canopy height, whereas both canopy height and shoot density rapidly decreased for *Cymodocea nodosa* (intermediate-colonizing species) and *Zostera noltei* (colonizing species). Seagrasses also differed in the type of structural response, with the colonizing

J. Boada, T. M. Smith, and A. M. Ricart contributed equally to this study.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

species experiencing reductions in shoot density, and the persistent *P. oceanica* registering declines in canopy height. After months of exposure to cumulative herbivory, all three species showed signs of stability. Interestingly, none of the species disappeared completely even when exposed to extreme herbivory. Mechanistic models indicate that herbivory-induced responses are a potential explanation for these patterns. This study suggests that given the long evolutionary history of herbivory, some seagrasses may be remarkably well adapted to both intense and cumulative herbivory.

KEYWORDS

herbivory, life strategies, resilience, seagrasses, stressor duration, stressor intensity

INTRODUCTION

Herbivory is a major agent of change in both terrestrial and marine realms. Herbivore activity exerts a critical functional role on vegetated ecosystems and, in extreme cases, can cause the loss of its foundation species. When herbivores push vegetation to the edge of their physiological tolerance ranges and consumption exceeds production, they can trigger the collapse of the whole vegetated ecosystem which are alternate ecosystem states (Scheffer et al., 2001; Schmitz & Beckerman, 1997; Wernberg et al., 2016). Understanding how the different species respond to herbivory impact and which life history strategies are effective resistance mechanisms is necessary to comprehend the overall ecosystem stability and prevent diversity and productivity losses. In the marine environment, seagrasses and macroalgae can form large vegetated ecosystems, where herbivore-mediated transitions from vegetated to less-structured or unvegetated systems are generally caused by trophic imbalances related to the loss of top predators or by herbivore species range extensions (Estes et al., 2011; Schmitz & Beckerman, 1997; Vergés et al., 2014; Worm & Paine, 2016). These transitions can follow linear pathways or show abrupt trajectories of collapse that have significantly different implications for management and conservation. However, while the existence of nonlinear behaviors in macroalgal dynamics is largely demonstrated, very few studies have explored ecosystem transitions to degraded states in response to herbivores for seagrasses. Understanding and foreseeing the type of ecosystem state loss of seagrasses to impoverished habitats is critical to prevent shifts to undesired, unproductive ecosystem states.

Whether the impacts of herbivory on a foundation species result in abrupt changes or more continuous declines depends heavily on the specifics of the relationship between the plant and its herbivore. The responses of ecosystems to rampant herbivory pressure reflect the

ability of major habitat-forming species of primary producers to deal with this disturbance. As the oldest trophic interaction, plants and herbivores have shared a long coevolutionary history (Futuyma & Agrawal, 2009) that has shaped the contingent responses of plants to their herbivores. Both terrestrial and marine plants have a wide armory of mechanisms to deal with herbivory, either by staving off consumption (i.e., with structural and chemical deterrents), protecting vulnerable parts or life history stages of the plant (e.g., with protective architecture, modifying the timing of critical life history events, etc.), or with a host of compensatory mechanisms (e.g., modifying growth, translocation of resources between above- and below-ground parts, and between growth and reproduction, etc.) (Bennett & Wallsgrave, 1994; Hanley et al., 2007; Kant et al., 2015; Rosenthal & Kotanen, 1994). These mechanisms act as reinforcing feedback increasing plant resistance by delaying biomass loss. The relative success of these mechanisms in conferring resistance to the plant will vary with the herbivore species and the nature of the impact caused in the plant. Megaherbivores that consume the entire plant including below-ground structures, for instance, place very different demands on anti-herbivory strategies than species that eat just a few plant parts (selective folivores) (Kant et al., 2015). Similarly, whether herbivores target growing tips, older leaves or basal stalks could result in very different consequences for the plant survival or future performance in general (Vergés et al., 2011).

In unpacking the response of plant species to herbivory, it is important to consider both the intensity and the duration of the disturbance. While single and massive herbivory events can threaten plant survival, low levels of herbivory can add up to very significant costs for the plant when sustained over time (Ratajczak et al., 2017). In fact, the primary response to a massive herbivory event is driven by constitutive mechanical and/or chemical defense mechanisms (Wood et al., 2017), whereas the

response to long-term herbivory depends on induced mechanisms (Sanmartí et al., 2014; Vergés et al., 2008). However, constitutive and induced deterrent mechanisms may not be sufficient to ward off herbivore pressure ad infinitum, and there are natural limits to how much energy a plant can translocate to this purpose from their stored reserves. If foundation species had to rely merely on their defenses and available resources to weather disturbance, ecosystems would resist herbivory merely as a function of plant's stores, declining as these resources deplete. Another set of coevolutionary mechanisms of tolerance in response to herbivory (like compensatory growth) can confer resistance to herbivory (Lubchenco & Gaines, 1981; Strauss & Agrawal, 1999). These further induced responses could help plants cope with even longer periods of sustained herbivory and might be an important component of overall resistance in the face of press herbivore disturbances and eventually determine the response patterns of the ecosystem.

Seagrasses provide an ideal case study system to examine general hypotheses about how the resistance of vegetated ecosystems to herbivory differs among taxa, since seagrasses encompass widely differing life history strategies, from extremely slow-growing persistent species to fast-growing opportunistic colonizing species (Kilminster et al., 2015). Examples of large-scale seagrass decline to herbivory are linked to overgrazing by marine megaherbivores like turtles and dugongs (Fourqurean et al., 2010; Kelkar et al., 2013). Mesoherbivores, such as sea urchins, fishes, and seabirds can also have a significant impact, although overgrazing occurs over relatively small scales and seagrasses may recover relatively quickly after the disturbance (Eklöf et al., 2008). However, in determining the relative vulnerability of seagrasses, we still cannot foresee the course at which the loss of ecosystem state will occur in response to herbivory intensity and duration. This information will help forecast future scenarios and inform actions to properly manage these and other vegetated ecosystems and the services they provide.

In this study, we evaluate the resistance of three temperate seagrass species with different life histories to a gradient of herbivore density through time to assess the seagrass responses to intensity and the duration of this source of stress. Specifically, we use (1) an in situ experimental approach to identify the trajectories of change in response to sea urchin herbivory in colonizing, persistent and intermediate range seagrass species, and (2) a modeling approach to propose a framework for how constitutive and induced mechanisms may determine the differences in resistance between these seagrasses to different intensity and duration of sea urchin herbivory. We hypothesize that based on their species traits, colonizing

and intermediate seagrass species will have significantly lower capacities to cope with herbivory than persistent species. The firsts, will therefore experience a faster decrease in canopy height and shoot density and would approach a functional shift, understood as a shift in the seagrass ecosystem state of sufficient magnitude to cascade to other organization levels, earlier (Figure 1).

METHODS

Study sites and experimental design

We conducted a set of field experiments in the Mediterranean Sea where three seagrass species that differ in their life history traits: the long-lived persistent species *Posidonia oceanica*, the intermediate species (between colonizing and opportunistic) species *Cymodocea nodosa*, and the colonizing species *Zostera noltei* (classification sensu Kilminster et al., 2015, hereafter persistent, intermediate, and colonizing). The Mediterranean Sea is a biodiversity hotspot (Coll et al., 2010), enclosed between Europe, Africa, and Asia naturally connected to the Atlantic Ocean through the Strait of Gibraltar and anthropogenically connected to the Red Sea through the Suez Canal. All three species are common in shallow sandy coastal habitats of the Mediterranean, where they form generally monospecific seagrass meadows. We chose three coastal areas where these species form healthy meadows in the NW Mediterranean Sea, one for each species, and established herbivore stocking experiments with increasing densities of the purple sea urchin *Paracentrotus lividus* (~5 cm test diameter). *P. lividus* is a model herbivore species that feeds on all three seagrasses. It is one of their major consumers and one of the most important grazers in the Mediterranean (Boudouresque & Verlaque, 2001; Jiménez-Ramos et al., 2018; Prado et al., 2007). Sea urchin densities were: H0 (control), 5, 8, 12, 16, 20, 26, 32, and 36 sea urchins m⁻². The upper range varied for *Z. noltei* (up to 20 urchins m⁻²) to maintain a similar impact given the smaller seagrass biomass per square meter for this species. Tides in the Western Mediterranean Sea rarely exceed increases of 0.3 m with typical variations in the study region between 10 and 30 cm. The experimental design was conceived to adapt to this condition. We designed different sea urchin enclosures for each seagrass species to both fit the requirements of the study site, exclude other potential herbivores and to avoid causing any interference with other organisms in general, such as perching birds, for example that may result in potential bias or confounding factors to the sea urchin herbivory impact. For the *Z. noltei* and *C. nodosa* experiment we used standard

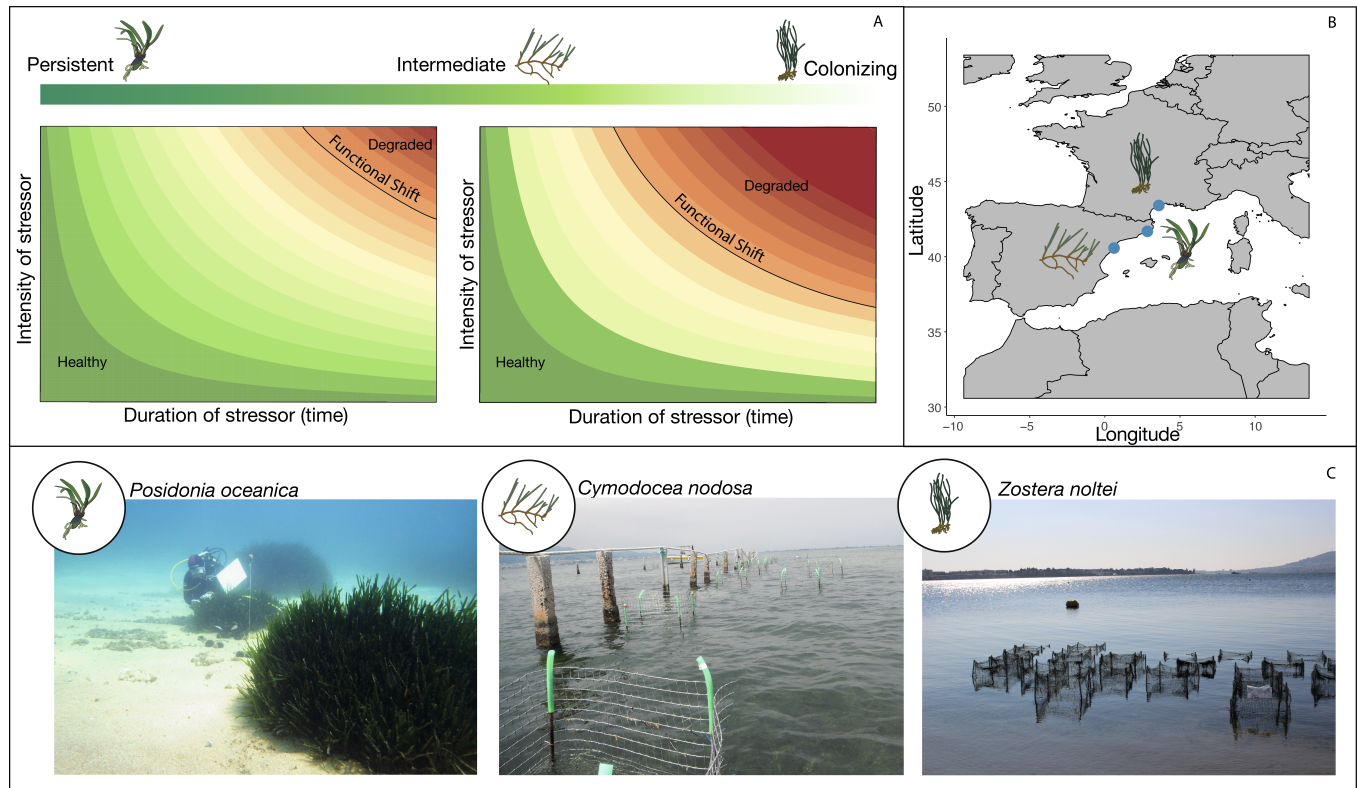


FIGURE 1 (A) Conceptual model describing the hypothesized change of ecosystem state (seagrass structure) at different intensity and duration of a given stressor (e.g., herbivory). Green-scale colors indicate healthy ecosystem states, while reds/browns indicate degraded ecosystem states. We hypothesize that colonizing and opportunistic species will experience a significant loss of structure triggering a functional shift earlier (right panel) than persistent seagrass species (left panel) both for the intensity and duration of herbivory stress. (B) Map of the study locations in the NW Mediterranean and the species used in each of them. (C) Photos of the experimental design and methodology used for each seagrass species in the different locations (Photo credits: A. Martínez-Ricart, N. Sanmartí and F. Rossi).

large open cages (0.75 m × 0.75 m; Figure 1), large enough to avoid any caging effects on sea urchin herbivory. Similar cages have been used in other experiments in the study region to exclude herbivores, proofing to be good installations for the proposed objectives (Boada et al., 2017; Gera et al., 2013). During the experiment, all the cages emerged sufficiently from seawater to avoid the entrance of other herbivores in the plots. For *P. oceanica*, cages were not used for logistical reasons and given the contextual conditions of the open sea study site. The hydrodynamic regime in the study area and the depth of the experimental location made inefficient to install and maintain exclusion cages over a long period of time. Instead, we used seagrass patches completely isolated by sand which provided physical barrier to urchin movement (Alcoverro & Mariani, 2002). All experiments started in spring 2016 and lasted 4, 5, and 6 months for *C. nodosa*, *Z. noltei*, and *P. oceanica*, respectively. The duration of the experiments varied between species in order to achieve a similar impact as a function of their species-specific traits (at least 50% of their above-ground biomass reduced).

We selected shallow seagrass meadows, where the depth and hydrodynamics depended on the characteristics of the species and their habitats: 1 meter and sheltered meadows for both *Z. noltei* and *C. nodosa* and 7 meters and exposed for *P. oceanica*. All seagrass areas selected for the experimental setup were initially free of sea urchins and with very few fish herbivory marks to avoid any interference with this experiment. The presence of other seagrass herbivores in the area is very low mainly due to the habitat fragmentation, and its effects are therefore negligible.

P. oceanica experimental setup

The *P. oceanica* experiment was conducted in Fenals (41°41.3' N, 02°49.7' E). Fenals is an exposed coastal marine location in Northern Catalonia where *P. oceanica* creates a discontinuous meadow of 1–5 m² isolated seagrass patches in a sandy matrix mosaic at depths of 7–8 m (see Figure 1C) that provided a physical barrier to urchin movement (Alcoverro & Mariani, 2002; Farina et al., 2017;

Hovel & Fonseca, 2005). Twenty-four small ($\sim 1 \text{ m}^2$) isolated patches were selected at least 5 m away from the nearest patch. Treatments were randomly allocated with sea urchin additions at densities of 0 (control), 5, 8, 12, 16, 20, 26, and 32 urchins m^{-2} ($n = 3$ patches per treatment).

C. nodosa experimental setup

The *C. nodosa* experiment was conducted in Alfacs Bay ($40^\circ 35' \text{ N}$, $0^\circ 41' \text{ E}$), a large sheltered estuarine bay at the Ebro River delta. Alfacs Bay is dominated by extensive *C. nodosa* meadows distributed along the edges of the bay, mostly at depths shallower than 2 m (Hovel & Fonseca, 2005). In Alfacs Bay *C. nodosa* forms continuous meadows and, therefore, cages were used to maintain urchin densities during the experiment. Twenty-four $0.75 \times 0.75 \text{ m}$ cages were established in a continuous *C. nodosa* meadow, at least 2 m apart from each other (see Figure 1C). The cages were open in the upper part (0.5 m high) and made of plastic mesh ($3 \times 3 \text{ cm}$ mesh size) to prevent other mesoherbivores entering the cages. Grazers smaller than the mesh size include mainly amphipod species which cause negligible impact to the seagrass compared with sea urchins which are the main herbivores in the location (Pérez & Romero, 1994). Cages were randomly distributed to densities of 0 (control), 5, 8, 12, 16, 20, 26, and 32 sea urchins m^{-2} ($n = 3$ cages per treatment).

Z. noltei experimental setup

The *Z. noltei* experiment was conducted in the Thau Lagoon on the French Mediterranean coast ($43^\circ 23' 56.2'' \text{ N}$, $03^\circ 37' 46.6'' \text{ E}$). Thau Lagoon covers an area of 75 km^2 and has an average depth of 4.5 m. Twenty-five $0.75 \text{ m} \times 0.75 \text{ m}$ cages were established at least 2 m apart from one another in a shallow ($< 1 \text{ m}$) continuous *Z. noltei* meadow. In this case, cages were similar to those used for *C. nodosa* ($3 \times 3 \text{ cm}$ mesh size) and rose 0.5 m above sea level preventing other mesoherbivores to enter the cages (see Figure 1C). Cages were randomly allocated to have 0 (control), 5, 8, 12, or 20 sea urchins m^{-2} ($n = 5$ cages per treatment). As in the Alfacs Bay, grazers smaller than the mesh size include mainly amphipod species which cause negligible impact to the seagrass compared with urchins which are the main herbivores in the location.

Sampling strategy

We measured the ecological state of the seagrass meadows in terms of its habitat structure (canopy height

and shoot density) before adding the sea urchins to the experimental units, and periodically after adding them. In *P. oceanica*, we randomly recorded 25 in situ measurements of canopy height (length of the longest leaf at that point) in each patch. To assess mean shoot densities per patch, we averaged the total number of seagrass shoots from three $20 \times 20 \text{ cm}$ quadrats. We periodically repeated the measurements of canopy height after 29, 47, 68, 83, 104, 124, and 191 days and shoot density after 29, 83, and 191 days (~ 6 months, at the end of the experiment). In *C. nodosa*, we recorded 35 measurements of canopy height and we counted the number of shoots within each plot (cage) to later calculate shoot densities, which was monitored every 2 weeks for 4 months. Similarly, in *Z. noltei* cages, we monitored canopy height monthly, by recording 10 measurements of canopy height and shoot densities every 1–2 weeks for 5 months. In this case, we measured shoot densities by placing $0.5 \times 0.5 \text{ m}$ (subdivided in $0.1 \times 0.1 \text{ m}$ grid) quadrats within cages and counted the number of shoots within 5 randomly allocated grid squares. For all experiments, we carefully surveyed the number of urchins in each sampling event to ensure that there were no losses or gains to each plot (cage/patch) due to escapes/intrusions or natural mortality. We replenished all plots with new urchins or removed them when necessary, during each monitoring occasion. In the *P. oceanica* experiment, where no cages were installed, the average sea urchin loss between sampling times was lower than 15%.

Data treatment and statistical analyses

After visually exploring the data, we observed clear non-linearities in some of the trajectories of change of the ecosystem structure (see Appendix S1). We used generalized linear mixed models (GLMM) to test the effect of herbivore density (intensity) and duration (as explanatory variables) on each ecosystem structure variable (i.e., canopy height and shoot density response variables). Effects of seasonality are visible in all the studied trends (see Figure 2; Appendix S2), therefore, we standardized the two ecosystem structure variables (i.e., canopy height and shoot density) to remove these effects. To do so, values of each experimental plot or patch for each species were divided by the initial values before sea urchins were added (i.e., proportion of change in respect to T_0) and then divided by the averaged values in the control plots (i.e., 0 urchins) at each time point. Finally, to illustrate the effect of both intensity and duration of herbivory at the ecosystem scale we used the maximum value of each ecosystem variable found during the experiments and reported each ecosystem state variable as a percentage of maximum values. Detailed raw and transformed data visualizations

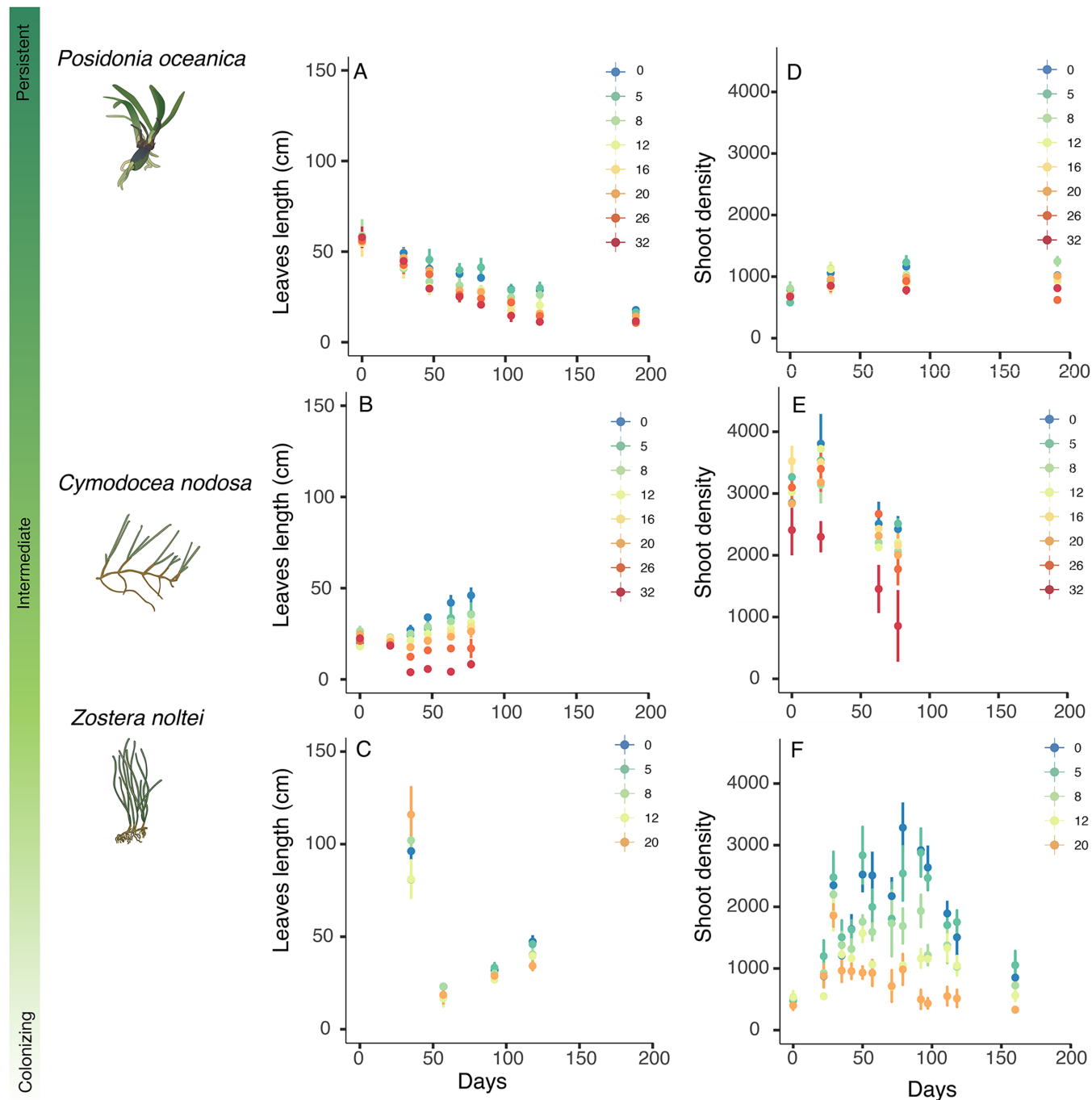


FIGURE 2 Change in the ecosystem structure (mean \pm SE) of the three seagrass species studied from the beginning to the end of the experiment. (A, B, and C) The change in canopy height (i.e., length of leaves) for *P. oceanica*, *C. nodosa* and *Z. noltei*, respectively. (D, E, and F) The change in shoot density (in shoots per square meter) for *P. oceanica*, *C. nodosa*, and *Z. noltei*, respectively. Different colors represent the different urchin densities. Note that the final time is not the same for all the experiments and that only 5 of the 8 density treatments were conducted in *Zostera noltei* experiments.

are presented in Appendix S1. We used general additive models (GAM) to visualize and predict the combined effect of herbivore density (intensity) and duration (as explanatory variables) on each structural variable of interest. All statistical analyses were performed in R (R Development Core Team, 2013) using *visreg* and *mgcv* packages (Breheny & Burchett, 2017; Wood, 2011).

Modeling responses

Field data revealed strong differences in the seagrass species response to prolonged herbivory, with the persistent species essentially being more able to maintain shoot density and experiencing non-critical reductions in the canopy height, and colonizing and intermediate

species being severely affected. Also, at the end of the experiments, we found signs of stabilization or partial recovery of the seagrass structure. In order to explore the mechanism behind these trends in the three species, we developed a simple consumer-resource model that included species-specific constitutive responses (structural defenses and growth) and herbivory-induced responses (compensatory growth or herbivore-induced defenses) (Sanmartí et al., 2014; Vergés et al., 2008).

Given that plants responded to herbivory impact with changes in mainly one of the structural variables (i.e., canopy height or shoot density) we used the term biomass to refer to plant structure. In the model, overall plant growth (in units of biomass production per area per time) follows the net effect of three different processes: logistic growth, linear intrinsic mortality, and herbivory via a Holling Type II functional response.

$$\frac{dX}{dt} = bX \left(1 - \frac{X}{N} \right) - mX - \frac{aY}{1 + a\tau X} X.$$

Here, X represents the seagrass ecosystem state (in units of biomass per area), b is the biomass production rate at low biomass (in units of inverse time), N is the carrying capacity (that is, the maximum biomass possible per unit area in the absence of other processes), m is the intrinsic mortality rate (in units of inverse time), a is the encounter rate between herbivores and plants (in units of area per biomass per time), τ represents the handling time (a characteristic timescale indicating how quickly urchins consume seagrass biomass; see Appendix S2).

In this model, the effect of constitutive traits in providing resistance against herbivory is explored by (1) changing values of biomass production by growth (b) according to the different seagrass species, and (2) modifying the constitutive chemical or mechanical defenses by altering the handling time τ . The more defenses, the longer it will take an herbivore to consume a given seagrass biomass. The effect of herbivory-induced mechanisms is tested in a similar way. Compensatory growth after a prolonged perturbation is simulated by increasing values of biomass production (b) at a given time partway through the model simulation. Similarly, to test the effect of induced defenses, we increased values of handling time (τ) as time increases. The model was parametrized using arbitrary units relative to species traits data (see Table 2) and previous knowledge on the species. More details of the model and its parameter values can be found in Boada et al. (2017) and Appendix S3, respectively.

RESULTS

Seagrass responses to intensity and duration of herbivory

The three seagrass species responded differently to both intensity and duration of herbivory. The most impacted species was *C. nodosa* that at the highest urchin density showed a decline in canopy height and shoot density of up to 90% and 42%, respectively, with respect to controls in the first 2 months (from an average of ~42 cm and ~2500 shoot m^{-2} to ~4 cm and ~1459 shoots m^{-2} , Figure 2B,E; Appendix S1). In striking contrast, *P. oceanica* was highly resistant to herbivory, reducing by only 35% of its canopy height and 21% of its shoot density at even the highest intensities of urchins, over the entire duration of the experiment (from ~18 to ~12 cm of leaves length and from ~1022 to ~814 shoots m^{-2} ; Figure 2A,D; Appendix S1). *Z. noltei* showed an intermediate response, with losses attributable to herbivory no greater than 30% in the canopy height but up to 61% of its shoot density (from ~853 to ~332 shoots m^{-2} , Figure 2C,F; Appendix S1). Interestingly, *P. oceanica* and *C. nodosa*, were primarily affected at its canopy height (i.e., leaf length reduction) while the density of shoots was less affected by the effect of herbivory in general and varying in the different plots following similar patterns in time and there were only small differences between treatments with low and high herbivory impacts (Figure 2B,E). In contrast, *Z. noltei* shoot density changed most significantly (i.e., shoot mortality) while canopy remained relatively intact (Figure 2C,F).

The type of seagrass response changed with increasing intensity and duration and among species (Figure 3, Table 1). Initially, all three species showed signs of decreasing structural complexity (either canopy height or shoot density) with increasing herbivore abundance (intensity). However, with increasing duration, *C. nodosa* showed a clear nonlinear decline in the ecosystem state after ~20 days (Figure 3E; Appendix S1). Nonlinearities were less evident for *P. oceanica* and *Z. noltei* even with increasing duration although the loss of *Z. noltei* shoot density followed a steeper path than the loss of canopy height in *P. oceanica* (Figure 3B,H; Appendix S1). The seagrass *P. oceanica* dealt best with sea urchin herbivory, experiencing more or less linear declines on its canopy height with increasing urchin densities but with no signs of imminent collapse even after sustained (8 months) high rates of herbivory. In contrast, the other two seagrasses showed their ecosystems states clearly damaged in time at mid to high herbivory intensities (Figure 3).

Interestingly, heat maps based on GAM predictions of how the ecosystem state progressed with the duration of the experiment, showed clear differences on the

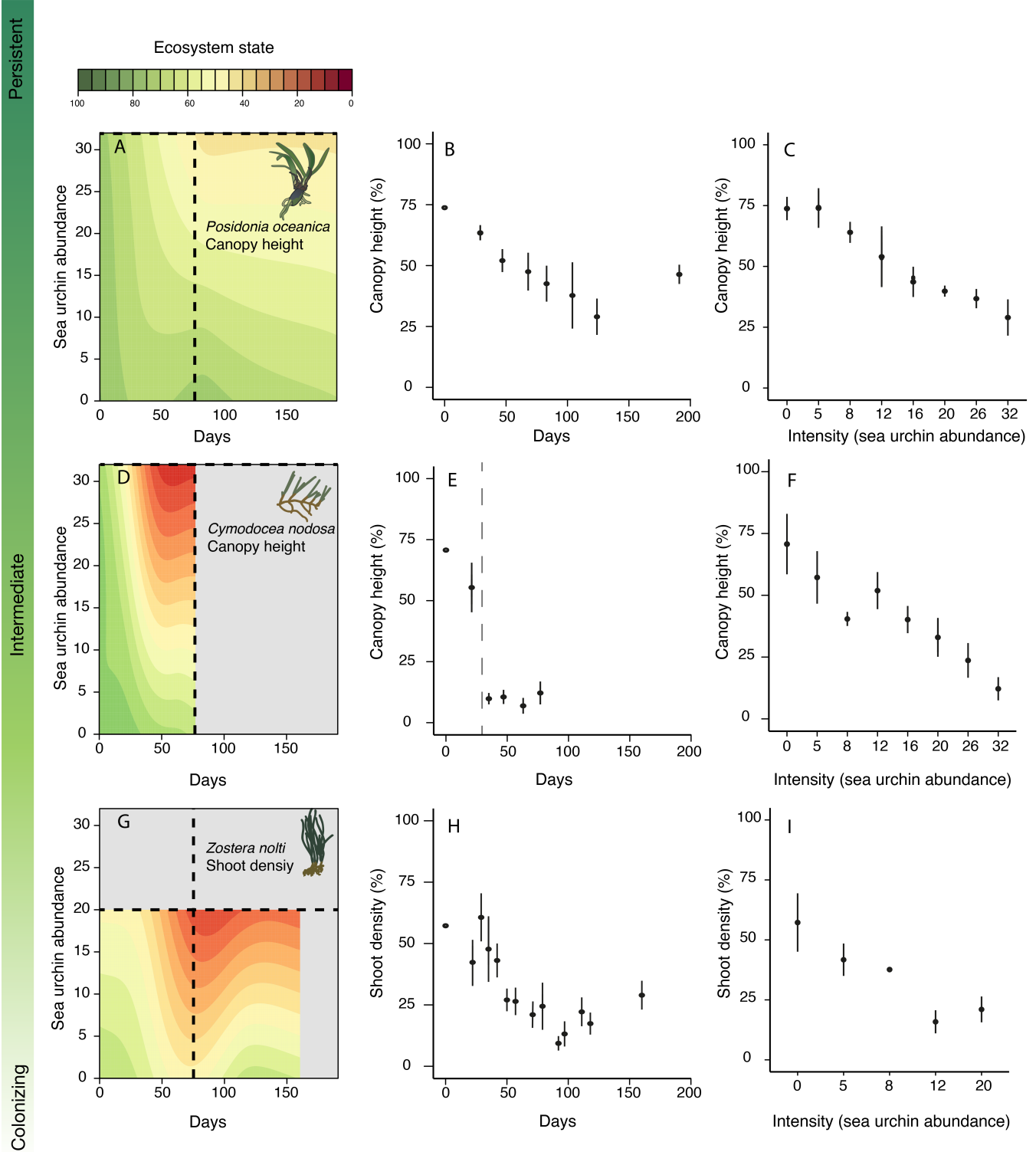


FIGURE 3 Changes in the ecosystem state of the most responsive variable (i.e., canopy height for *P. oceanica* and *C. nodosa* and shoot density for *Z. noltei*). (A, D, G) Ecosystem state predictions using visreg based on general additive models results for the whole gradient of intensities and duration in the experiment. The horizontal and vertical dashed lines indicate the time and intensity represented in the rest of the graphs. (B, E, H) The changes in the ecosystem state at the highest herbivory intensity for each species (i.e., 32 individuals m^{-2} for *P. oceanica* and *C. nodosa* and 20 individuals m^{-2} for *Z. noltei*). The vertical dashed line in (E) indicates the position of the threshold found for *C. nodosa*. (C, F, I) Similar changes in the ecosystem state at ~70 days after the beginning of the experiment at increasing urchin densities which is the maximum comparable time among species.

TABLE 1 Summary of statistical results for the standardized data.

Species	Structural response variable	Model	Explanatory variable	Significance
<i>Posidonia oceanica</i>	Canopy	GLM family Poisson with random factors	Duration	0.25
			Intensity	0.60
	Shoot density	LM with random factors	Duration	0.22
			Intensity	0.04
<i>Cymodocea nodosa</i>	Canopy	LM with random factors	Duration	<0.01
			Intensity	<0.01
	Shoot density	LM with random factors	Duration	<0.01
			Intensity	0.01
<i>Zostera noltei</i>	Canopy	GLM family Poisson with random factors	Duration	0.88
			Intensity	0.78
	Shoot density	GLM family Poisson with random factors	Duration	0.04
			Intensity	0.35

Note: The table details the statistical models for species and structural response variable and the significance of the two explanatory variables (i.e., duration as per time in days and intensity as per sea urchin density). Duration, time in days; intensity, sea urchin density. Bold Indicates significant values. Abbreviations: GLM, generalized linear mixed; LM, linear mixed.

TABLE 2 Biological traits susceptible to influence the resistance of seagrass species to herbivory.

Parameters by mechanism of resistance to herbivory	<i>Posidonia oceanica</i>	<i>Cymodocea nodosa</i>	<i>Zostera noltei</i>
Growth			
Carbohydrates in rhizome (%)	10.0	8.5	4.8
No. leaves × shoot	4.5	3.3	2.8
Leaf surface area (cm ²)	174.0	4.1	4.5
Above-Ground Biomass (g DM m ⁻²)	291.2	230.0	64.1
Below-Ground Biomass (g DM m ⁻²)	4196	198.0	64.2
Shoot elongation (g DM shoot day ⁻¹ m ⁻²)	1.9	1.9	0.8
Max. compensatory growth (% increase)	60.0	25.0	NA
Consumption (in leaves)			
Defenses			
Structural defenses			
Rhizome diameter (mm)	9.7	1.6	1.8
Leaf sheath size (mm)	36.0	100.0	39.0
Leaf thickness (mm)	0.4	0.2	0.1
Breaking force (Newtons)	23.4	6.8	1.1
Palatability			
C:N ratio (leaves)	25.0	15.0	17.1
Phenolic compounds (%)	5.0	2.3	2.3
Nitrogen content in leaves (%)	1.9	2.2	2.2

Note: Values of species traits in this table have been collected from the bibliography (see Appendix S3). These values represent average values for traits of the three species from locations representative to this study. Traits without values have not been measured in representative locations (compensatory growth). Abbreviation: DM, dry mass; NA, not available.

responses between species as pointed above. This indicates a species-specific capacity of structural resistance. Additionally, trends show that the ecosystem potentially

improved for the three species indicating the potential existence of herbivory-induced responses (Figure 3A,D,G; Appendix S1).

Mechanistic model projections

To evaluate the effect of species traits in constitutive and herbivory-induced responses in conferring resistance to seagrasses, model predictions were made for two different hypotheses about how seagrass response trajectory is affected by herbivory: (1) seagrass defense or compensation to herbivory is unchanging in time and is based only on predetermined traits of the seagrass (“constitutive responses”) and (2) seagrass responds to herbivory by increasing its defenses (“herbivory-induced responses”), the latter occurring via some combination of compensatory growth, increased chemical defense or increased mechanical defense.

Constitutive resistance model

Changes in seagrass biomass production (via growth), predicted a differential resistance to herbivory impact. Species that produce less biomass per unit ground area (that is available to consumption) are more susceptible to herbivory than those with higher production through growth (Figure 4A; Appendix S2). Similarly, species with more defenses, that is, that are less attractive to herbivores, would resist higher herbivory intensities compared with those with limited or no defenses (Appendix S2). Model output predictions were plausible when compared with observations in the field (Figure 4A,B).

Herbivory-induced responses models

When induced mechanisms are introduced as plant responses in the model, ecosystem state trajectories change influencing the overall resistance. Specifically, when we considered an increased biomass production by growth of the plant (delayed with time-compensatory growth) as a response to prolonged herbivory impact, the model predicted either a delay in ecosystem collapse or a recovery of the ecosystem state depending on the magnitude of the response (Figure 4C; Appendix S2). Similar results were obtained in simulations that considered an herbivory-mediated induction of defenses (increase in handling time, Appendix S2). These projections suggest a plausible explanation for observations in the field which followed similar trends to model predictions (Figure 4D).

DISCUSSION

Herbivory is a key structuring agent in both terrestrial and marine environments, and can impact the health

and functioning of ecosystems dominated by vegetation. While macroalgal communities show great sensibility to herbivory intensity (Boada et al., 2017; Vergés et al., 2014), we experimentally showed that seagrasses can be highly tolerant to herbivory. Moreover, our modeling approach explained that variations in constitutive and induced species traits and responses inherently determine the differential tolerance of seagrasses to instant and sustained herbivory. Therefore, the manner that ecosystems cope with this impact depends on both the nature of grazing impact (intensity and duration) and the plant anti-herbivore responses.

Species present a variety of strategies to cope with herbivory resulting from their differential life histories. The three seagrasses studied, differed significantly in their ability to resist sea urchin herbivory with morphological and physiological traits of each species being key to explaining the differences observed (Table 2; Appendix S3). The long-lived, fast-growing *P. oceanica* was the most resistant to both intensity and duration of herbivory. While no caging was used in the *P. oceanica* experiment, escape/mortality rates from controlled plots was rather low (less than 15% average) and therefore underestimation of herbivory in the experiment is highly unlikely considering the maximum sea urchin consumption found in a parallel experiment (see Buñuel et al., 2023). The large, strong leaves of *P. oceanica* combined with large energy stores and chemical deterrents enables the species to withstand high intensity of sea urchin grazing over long periods. In fact, this species has been observed to sustain combined fish and sea urchin high herbivory rates that can consume up to 80% of their primary production (Prado et al., 2007, 2008). In contrast, at high herbivory intensities *C. nodosa* clearly showed an abrupt reduction in ecosystem state (i.e., canopy height) and *Z. noltei* showed a linear but drastic decline in shoot density. These two species have much smaller leaves, lower below-ground energy stores, and are more palatable, making them more susceptible to ecosystem shifts (Table 2).

Beyond merely enduring the stress, all three species, albeit to differing degrees, showed signs of stabilization or even recovery after prolonged herbivory. The stabilization into a new steady state of reduced biomass, that the plants seem to reach after sustained herbivory and/or the recovery of the structure, guarantees the long-term plant survival. Traits related to the resistance of herbivory such as the lack of palatability, the compensatory growth, or the structural defenses seem to be more predominant in *P. oceanica* compared with the other two species. In contrast, traits more related to the recovery, such as fast new shoots regrowth, fast rhizome growth, or high production of local seeds, seem to be more common in

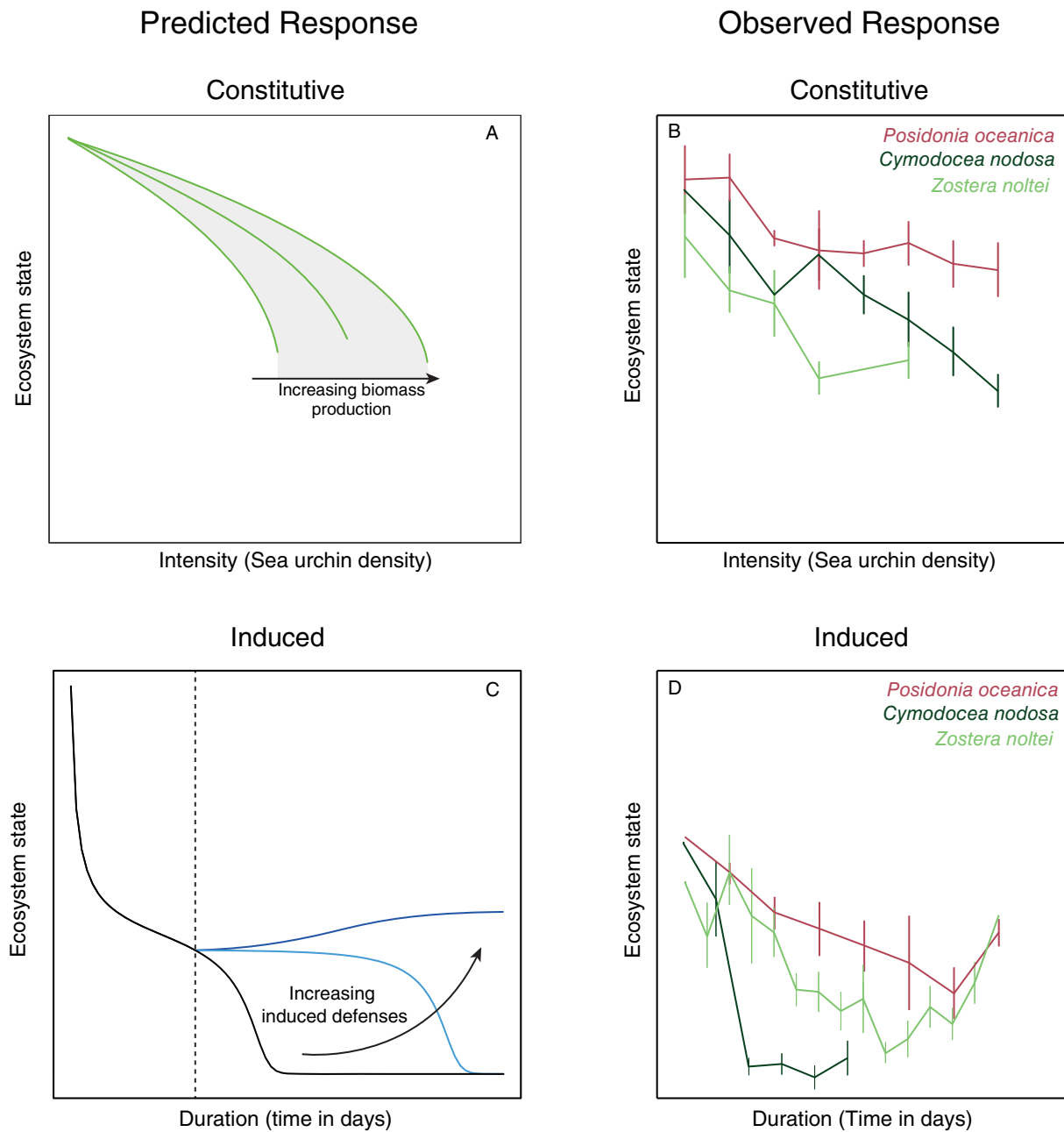


FIGURE 4 Model projections and summary of the experimental results of the ecosystem state to herbivory intensity and duration. (A) Predicted change in the ecosystem state in scenarios of increasing biomass production through growth (b , seagrass production rate). The higher the produced biomass per unit time, the more resistant to herbivory. (B) Ecosystem state change found experimentally for each species according to urchin densities. (C) Projections of change in the ecosystem state along time. After a short time delay (black dashed line), potential responses of the seagrass growth to herbivory are explored. Black: No response, light blue: Intermediate response and dark blue: High response (recovery). (D) Experimental results for each species along time. Arrows and shadowed areas in (A) and (C) indicate the range of possibilities according to levels of induced mechanisms.

species that invest in recovery. Our results show that the activation of induced responses when the stress is sustained over time is one of the plausible explanations. In fact, even after complete defoliation, *C. nodosa* had the capacity to regrow shortly after the stress was completely removed (visual observations at the end of the experiment).

While we are unable to determine the specific mechanisms in play and differentiate between paths to full recovery or maintenance in new structurally depleted steady states, the induced responses we documented could be due either to a compensatory growth mechanism or to the production of additional chemical deterrents that reduced the amount of herbivory over time.

Several studies confirm the existence of these induced responses that can explain this behavior (Sanmartí et al., 2014; Vergés et al., 2008). Interestingly, these trends can be explained by our model projections that show a similar behavior when constitutive and induced responses are included in the model and represent a very similar behavior as well as that observed in the field. While our experiment endured sufficiently to capture seasonal effects, examination of a continued time series of seagrass morphological responses beyond the duration of our experiment would be needed to confirm the initial signs of recovery suggested by our data.

Sea urchin densities used in the experiment represent the maximum encountered in natural ecosystems (Boada et al., 2018; Planes et al., 2011), and results indicate that they do not represent as much of a challenge for the persistence of temperate seagrasses. In fact, massive herbivory events concentrated and continuous in time are common in temperate seagrasses, especially on *P. oceanica* leaves related to fish and sea urchin herbivory (Buñuel et al., 2020; Pagès et al., 2012). *P. oceanica* resistance seems to be tightly associated to the preservation of the plants below-ground biomass and the strength and palatability of the leaves and, therefore, to the type of damage herbivores produce to plants in their foraging activities. *P. oceanica* also has a series of mechanisms in order to preserve the nutrients in the canopy like leaf nutrient relocation to the new growing leaves that can help to compensate for the biomass lost (Prado et al., 2008). In fact, recovery time between seagrasses that lost only the above-ground biomass, like *C. nodosa* in this experiment, a highly palatable species, compared with above- and below-ground biomass show tremendous differences (Sanmartí et al., 2021). The induced responses of increased growth, impose an energetic tax which the plant has to bear either by tapping into below-ground reserves or by reallocating resources away from reproduction (Heck & Valentine, 1995). These fitness costs will potentially lead to population reductions and an eventual functional loss. However, some seagrass species have disturbance-mitigating traits that only express under conditions of high stress. For instance, while vegetative growth is the dominant form of spread, seagrasses like *P. oceanica* use flowering and fruiting as an in extremis measure to deal with heat stress (Diaz-Almela et al., 2007). It is hypothesized that this may be an effective escape strategy, at once spreading the genet and helping the plant escape stressful conditions.

Unpacking the capacities of a system to cope with both the intensity and the duration of herbivory stress is critical to predict major changes in ecosystem configuration. Intensity and duration constitute two separate axes

of stress, and ecosystems may vary in how they respond on each of them. Here we found that, while intensity responses may rely completely on constitutive traits, some physiological plastic responses may develop only as a result of intermediate to long duration stressors. Despite several important trait-mediated differences in their responses, foundational seagrass species in the Mediterranean showed signs of being highly resistant to both the intensity and duration of herbivory. Whether temperate seagrasses are equally resistant to all forms of herbivory as they are to urchin grazing is a key question. In tropical and temperate seagrass systems, large urchin fronts have been known to devastate large meadows as they advance (Alcoverro & Mariani, 2002; Carnell et al., 2020; Rose et al., 1999). This does not seem to be a mechanism that operated in our study system as Mediterranean Sea urchins generally do not group in this type of front in seagrass meadows. In the Mediterranean, herbivory by the native fish *Sarpa salpa* can be intense in patches, severely reducing seagrass canopies when feeding in large shoals (Buñuel et al., 2020) but never as devastating as the megaherbivores what can decimate seagrass meadows. Additionally, as temperate waters warm, an assemblage of newly arriving tropical herbivorous fish are expanding their ranges of distribution in many coastal areas (Hyndes et al., 2016; Vergés et al., 2014). It is unclear if seagrass meadows will be as resistant to the prolonged impact of these new voracious herbivores that has already caused the collapse of large macroalgal forests.

Declines in ecosystem state were generally not abrupt, which seems to be positive for the recovery of the system, especially because we did not find signs of hysteresis. The exception was *C. nodosa* which underwent an abrupt decline to extremely low levels of canopy height. Encouragingly though, all three species did, in time appear to show signs of physiological responses to cope with herbivory allowing ecosystem states to endure or potentially improve slightly after a sustained stress. In the last two decades, theoretical and managerial interests have rightly focused on understanding nonlinear catastrophic shifts in ecosystems. This comes in the wake of dramatic declines of nearshore benthic communities like coral reefs and kelp beds (Fung et al., 2011; Ling et al., 2015), as well as terrestrial ecosystems (Estes et al., 2011). They present vexing problems for management, since their hysteretic nature does not guarantee a quick recovery once the stress has abated. Given the long evolutionary history of plant-herbivore interactions, seagrass species will likely be able to cope with even high intensities of herbivory for prolonged periods of time, at least with the current set of herbivores and conditions.

AUTHOR CONTRIBUTIONS

All authors contributed to conceiving the idea of the study and developed the final study design. T. M. Smith, T. Alcoverro, A. M. Ricart, R. Arthur, and J. Boada performed the *P. oceanica* experiment, M. Pérez, J. Romero, N. Sanmartí, Y. Ontoria, A. M. Ricart, and T. M. Smith performed the *C. nodosa* experiment and F. Rossi and M. Pierrejen performed the *Z. noltei* experiment. J. Boada, A. M. Ricart, and T. M. Smith performed the statistical analysis and designed the final figures with contribution of all authors. D. Alonso, M. P. Adams and J. Boada described the mathematical models. J. Boada, T. M. Smith, and A. M. Ricart wrote the manuscript with significant contribution of all authors.

ACKNOWLEDGMENTS

This study is part of the research project CTM2017-86695-C3-1-R and CTM2017-86695-C3-3-R UMBRAL funded by the Spanish Ministry of Science, Innovation and Universities (MCIU) and Spanish National Research Council (CSIC) (2014–2016) attributed to F. Rossi by the TOTAL foundation. J. Boada acknowledges the support received from the Spanish Ministry of Science and Innovation under the RyC fellowship (RYC2021-033650-I) and PID2022-140652NA-I00 MITnPOINT funded by the MCIN/AIEI/10.13039/501100011033 and Fondo Europeo de Desarrollo Regional (FEDER). T. M. Smith was funded by the Australian Government Endeavor Fellowship program. The Spanish National Research Council supported RA's visitorship with the MoU between CEAB-NCF. M. P. Adams's contribution was funded by an Australian Research Council Discovery Early Career Researcher Award DE200100683.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Boada et al., 2024) are available from Zenodo: <https://doi.org/10.5281/zenodo.13902850>.

ORCID

A. M. Ricart  <https://orcid.org/0000-0001-7769-1661>
 N. Sanmartí  <https://orcid.org/0000-0001-8503-1006>
 M. P. Adams  <https://orcid.org/0000-0003-4875-0225>
 F. Rossi  <https://orcid.org/0000-0003-1928-9193>

REFERENCES

Alcoverro, T., and S. Mariani. 2002. "Effects of Sea Urchin Grazing on Seagrass (*Thalassodendron ciliatum*) Beds of a Kenyan Lagoon." *Marine Ecology Progress Series* 226: 255–263.

- Bennett, R. N., and R. M. Wallsgrove. 1994. "Secondary Metabolites in Plant Defence Mechanisms." *New Phytologist* 127: 617–633.
- Boada, J., A. M. Ricart, T. Smith, T. Alcoverro, J. Romero, M. Pérez, Y. Ontoria, N. Sanmartí, M. Pierrejen, M. Adams, F. Rossi, & D. Alonso (2024). Differential coping capacities underlie the overall resistance of temperate seagrasses to herbivory [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.13902850>
- Boada, J., R. Arthur, D. Alonso, J. F. Pagès, A. Pessarrodona, S. Oliva, G. Ceccherelli, L. Piazzini, J. Romero, and T. Alcoverro. 2017. "Immanent Conditions Determine Imminent Collapses: Nutrient Regimes Define the Resilience of Macroalgal Communities." *Proceedings of the Royal Society B: Biological Sciences* 284: 20162814.
- Boada, J., S. Farina, R. Arthur, J. Romero, P. Prado, and T. Alcoverro. 2018. "Herbivore Control in Connected Seascapes: Habitat Determines when Population Regulation Occurs in the Life History of a Key Herbivore." *Oikos* 127: 1195–1204. <https://doi.org/10.1111/oik.05060>.
- Boudouresque, C.-F., and M. Verlaque. 2001. "Chapter 13 Ecology of *Paracentrotus lividus*." *Developments in Aquaculture and Fisheries Science* 37: 243–285. [https://doi.org/10.1016/S0167-9309\(07\)80077-9](https://doi.org/10.1016/S0167-9309(07)80077-9)
- Breheeny, P., and W. Burchett. 2017. "Visualization of Regression Models Using Visreg." *The R Journal* 9(2): 56–71.
- Buñuel, X., T. Alcoverro, J. Boada, L. Zinkunegi, T. M. Smith, A. Barrera, M. Casas, et al. 2023. "Indirect Grazing-Induced Mechanisms Contribute to the Resilience of Mediterranean Seagrass Meadows to Sea Urchin Herbivory." *Oikos* 2023: e09520. <https://doi.org/10.1111/oik.09520>.
- Buñuel, X., T. Alcoverro, J. F. Pagès, J. Romero, J. M. Ruiz, and R. Arthur. 2020. "The Dominant Seagrass Herbivore *Sarpa salpa* Shifts its Shoaling and Feeding Strategies as They Grow." *Scientific Reports* 10: 10622.
- Carnell, P. E., D. Ierodiaconou, T. B. Atwood, and P. I. Macreadie. 2020. "Overgrazing of Seagrass by Sea Urchins Diminishes Blue Carbon Stocks." *Ecosystems* 23: 1–12. <https://doi.org/10.1007/s10021-020-00479-7>.
- Coll, M., C. Piroddi, J. Steenbeek, K. Kaschner, F. B. R. Lasram, J. Aguzzi, E. Ballesteros, et al. 2010. "The Biodiversity of the Mediterranean Sea: Estimates, Patterns and Threats." *PLoS One* 5(8): e11842. <https://doi.org/10.1371/journal.pone.0011842>.
- Diaz-Almela, E., N. Marbà, and C. M. Duarte. 2007. "Consequences of Mediterranean Warming Events in Seagrass (*Posidonia oceanica*) Flowering Records." *Global Change Biology* 13: 224–235.
- Eklöf, J. S., M. de la Torre-Castro, M. Gullström, J. Uku, N. Muthiga, T. Lyimo, and S. O. Bandeira. 2008. "Sea Urchin Overgrazing of Seagrasses: A Review of Current Knowledge on Causes, Consequences, and Management." *Estuarine, Coastal and Shelf Science* 79: 569–580.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333: 301–6.
- Farina, S., A. Oltra, J. Boada, F. Bartumeus, J. Romero, and T. Alcoverro. 2017. "Generation and Maintenance of Predation Hotspots of a Functionally Important Herbivore in a Patchy Habitat Mosaic." *Functional Ecology* 66: 1–10.

- Fourqurean, J., S. Manuel, K. Coates, W. Kenworthy, and S. Smith. 2010. "Effects of Excluding Sea Turtle Herbivores from a Seagrass Bed: Overgrazing May Have Led to Loss of Seagrass Meadows in Bermuda." *Marine Ecology Progress Series* 419: 223–232.
- Fung, T., R. M. Seymour, and C. R. Johnson. 2011. "Alternative Stable States and Phase Shifts in Coral Reefs under Anthropogenic Stress." *Ecology* 92: 967–982.
- Futuyma, D. J., and A. A. Agrawal. 2009. "Macroevolution and the Biological Diversity of Plants and Herbivores." *Proceedings of the National Academy of Sciences of the United States of America* 106: 18054–61.
- Gera, A., J. F. Pagès, J. Romero, and T. Alcoverro. 2013. "Combined Effects of Fragmentation and Herbivory on *Posidonia oceanica* Seagrass Ecosystems." *Journal of Ecology* 101: 1053–61.
- Hanley, M. E., B. B. Lamont, M. M. Fairbanks, and C. M. Rafferty. 2007. "Plant Structural Traits and their Role in Anti-Herbivore Defence." *Perspectives in Plant Ecology, Evolution and Systematics* 8: 157–178.
- Heck, K. L., and J. F. Valentine. 1995. "Sea Urchin Herbivory: Evidence for Long-Lasting Effects in Subtropical Seagrass Meadows." *Journal of Ecology* 189: 205–217.
- Hovel, K. A., and M. S. Fonseca. 2005. "Influence of Seagrass Landscape Structure on the Juvenile Blue Crab Habitat-Survival Function." *Marine Ecology Progress Series* 300: 179–191.
- Hyndes, G. A., K. L. Heck, A. Vergés, E. S. Harvey, G. A. Kendrick, P. S. Lavery, K. McMahon, et al. 2016. "Accelerating Tropicalization and the Transformation of Temperate Seagrass Meadows." *BioScience* 66: 938–948.
- Jiménez-Ramos, R., F. G. Brun, L. G. Egea, and J. J. Vergara. 2018. "Food Choice Effects on Herbivory: Intra-Specific Seagrass Palatability and Inter-Specific Macrophyte Palatability in Seagrass Communities." *Estuarine, Coastal and Shelf Science* 204: 31–39.
- Kant, M. R., W. Jonckheere, B. Knegt, F. Lemos, J. Liu, B. C. J. Schimmel, C. A. Villarroel, et al. 2015. "Mechanisms and Ecological Consequences of Plant Defence Induction and Suppression in Herbivore Communities." *Annals of Botany* 115: 1015–51.
- Kelkar, N., R. Arthur, N. Marbà, and T. Alcoverro. 2013. "Greener Pastures? High-Density Feeding Aggregations of Green Turtles Precipitate Species Shifts in Seagrass Meadows." *Journal of Ecology* 101: 1158–68.
- Kilminster, K., K. McMahon, M. Waycott, G. A. Kendrick, P. Scanes, L. McKenzie, K. R. O'Brien, et al. 2015. "Unravelling Complexity in Seagrass Systems for Management: Australia as a Microcosm." *Science of the Total Environment* 534: 1–13.
- Ling, S. D., R. E. Scheibling, A. Rassweiler, C. Johnson, N. Shears, S. D. Connell, A. K. Salomon, et al. 2015. "Global Regime Shift Dynamics of Catastrophic Sea Urchin Overgrazing." *Philosophical Transactions of the Royal Society B: Biological Sciences* 370: 20130269.
- Lubchenco, J., and S. D. Gaines. 1981. "A Unified Approach to Marine Plant-Herbivore Interactions. I. Populations and Communities." *Annual Review of Ecology, Evolution, and Systematics* 12: 405–437.
- Pagès, J. F., S. Farina, A. Gera, R. Arthur, J. Romero, and T. Alcoverro. 2012. "Indirect Interactions in Seagrasses: Fish Herbivores Increase Predation Risk to Sea Urchins by Modifying Plant Traits." *Functional Ecology* 26: 1015–23.
- Pérez, M., and J. Romero. 1994. "Growth Dynamics, Production, and Nutrient Status of the Seagrass *Cymodocea nodosa* in a Mediterranean Semi-Estuarine Environment." *Marine Ecology* 15: 51–64.
- Planes, S., N. Raventos, B. Ferrari, and T. Alcoverro. 2011. "Fish Herbivory Leads to Shifts in Seagrass *Posidonia oceanica* Investments in Sexual Reproduction." *Marine Ecology Progress Series* 431: 205–213.
- Prado, P., S. Farina, F. Tomas, J. Romero, and T. Alcoverro. 2008. "Marine Protection and Meadow Size Alter Fish Herbivory in Seagrass Ecosystems." *Marine Ecology Progress Series* 371: 11–21.
- Prado, P., F. Tomas, T. Alcoverro, and J. Romero. 2007. "Extensive Direct Measurements of *Posidonia oceanica* Defoliation Confirm the Importance of Herbivory in Temperate Seagrass Meadows." *Marine Ecology Progress Series* 340: 63–71.
- Ratajczak, Z., P. D'Odorico, S. L. Collins, B. T. Bestelmeyer, F. Isbell, and J. B. Nippert. 2017. "The Interactive Effects of Press/Pulse Intensity and Duration on Regime Shifts at Multiple Scales." *Ecological Monographs* 87: 198–218.
- Rose, D., J. W. Fourqurean, P. E. Whitfield, M. O. Hall, J. F. Valentine, E. J. Prager, W. G. Lyons, J. H. Hunt, W. K. Kenworthy, and W. C. Sharp. 1999. "Overgrazing of a Large Seagrass Bed by the Sea Urchin *Lytechinus Variegatus* in Outer Florida Bay." *Marine Ecology Progress Series* 190: 211–222.
- Rosenthal, J. P., and P. M. Kotanen. 1994. "Terrestrial Plant Tolerance to Herbivory." *Trends in Ecology & Evolution* 9: 145–48.
- Sanmartí, N., A. M. Ricart, Y. Ontoria, M. Pérez, and J. Romero. 2021. "Recovery of a Fast-Growing Seagrass from Small-Scale Mechanical Disturbances: Effects of Intensity, Size and Seasonal Timing." *Marine Pollution Bulletin* 162: 111873.
- Sanmartí, N., L. Saiz, I. Llagostera, M. Pérez, and J. Romero. 2014. "Tolerance Responses to Simulated Herbivory in the Seagrass *Cymodocea nodosa*." *Marine Ecology Progress Series* 517: 159–169.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. "Catastrophic Shifts in Ecosystems." *Nature* 413: 591–96.
- Schmitz, O., and A. Beckerman. 1997. "Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions." *Ecology* 78: 1388–99.
- Strauss, S. Y., and A. A. Agrawal. 1999. "The Ecology and Evolution of Plant Tolerance to Herbivory." *Trends in Ecology & Evolution* 14: 179–185.
- Team, R. C. R. 2013. *A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical computing. <http://www.R-project.org/>.
- Vergés, A., T. Alcoverro, and J. Romero. 2011. "Plant Defences and the Role of Epibiosis in Mediating within-Plant Feeding Choices of Seagrass Consumers." *Oecologia* 166: 381–390.
- Vergés, A., M. Pérez, T. Alcoverro, and J. Romero. 2008. "Compensation and Resistance to Herbivory in Seagrasses: Induced Responses to Simulated Consumption by Fish." *Oecologia* 155: 751–760.

- Vergés, A., P. D. Steinber, M. E. Hay, A. G. B. Poore, A. H. Campbell, E. Ballesteros, K. L. Heck, et al. 2014. “The Tropicalization of Temperate Marine Ecosystems: Climate-Mediated Changes in Herbivory and Community Phase Shifts.” *Proceedings of the Royal Society B: Biological Sciences* 281: 20140846.
- Wernberg, T., S. Bennett, R. C. Babcock, T. de Bettignies, K. Cure, M. Depczynski, F. Dufois, et al. 2016. “Climate-Driven Regime Shift of a Temperate Marine Ecosystem.” *Science* 353: 169–172.
- Wood, K. A., M. T. O’Hare, C. McDonald, K. R. Searle, F. Daunt, and R. A. Stillman. 2017. “Herbivore Regulation of Plant Abundance in Aquatic Ecosystems.” *Biological Reviews* 92: 1128–41.
- Wood, S. N. 2011. “Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models.” *Journal of the Royal Statistical Society Series B* 73(1): 3–36.
- Worm, B., and R. T. Paine. 2016. “Humans as a Hyperkeystone Species.” *Trends in Ecology & Evolution* 31: 1–8.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Boada, J., T. M. Smith, A. M. Ricart, T. Alcoverro, M. Pérez, J. Romero, N. Sanmartí, et al. 2024. “Differential Coping Capacities Underlie the Overall Resistance of Temperate Seagrasses to Herbivory.” *Ecosphere* 15(12): e70075. <https://doi.org/10.1002/ecs2.70075>