Resistance and recovery of benthic marine macrophyte communities to light reduction: Insights from carbon metabolism and dissolved organic carbon (DOC) fluxes, and implications for resilience

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ABSTRACT

A crucial factor in the long-term survival of benthic macrophyte communities under light-reduction stress is how they balance carbon metabolism during photosynthesis and respiration. In turn, the dissolved organic carbon (DOC) released by these communities, which can be highly light-dependent, stands as a source of carbon, fuelling marine communities and playing an important role in the ocean carbon sequestration. This is the first study to evaluate light-reduction stress and recovery in the seagrass *Zostera noltei* and the macroalga *Caulerpa prolifera*. Light reduction led to a significant decrease in the production of both communities from autotrophic to heterotrophic. Results indicated that most of the DOC released by vegetated coastal communities comes from photosynthetic activity, and that the net DOC fluxes can be greatly affected by shading events. Finally, both communities showed resilience underpinned by high recovery but low resistance capacity, with *C. prolifera* showing the highest resilience to unfavourable light conditions.

1. Introduction

Benthic macrophyte communities, including seagrass and macroalgal beds, are ecosystem engineers providing a large number of ecological functions and services, such as shoreline protection, suitable breeding habitats, and biodiversity hotspots (Campagne et al., 2015). Seagrass communities, due to their high productivity, are considered key elements for organic carbon (OC) sequestration in marine areas (i.e., blue carbon; Nellemann et al., 2009). Similar to seagrasses, benthic macroalgal communities have also recently been noted as an important contributor to carbon sequestration in marine sediments (Krause-Jensen and Duarte, 2016). The potential of natural ecosystems to act as carbon sinks has typically been linked to the huge OC pools buried in the sediments inhabited by rooted macrophytes, where a large amount of recalcitrant carbon (i.e., C with low biodegradability) is allocated into the belowground network (Kennedy et al., 2010). However, recent studies highlighted the importance of the recalcitrant fraction of the dissolved organic carbon (DOC) as an important carbon sink with potential to regulate climate (Jiao et al., 2010; Ridgwell and Arndt, 2015).

The DOC is one of the largest interchangeable organic carbon pools in the marine environment, being a cornerstone in the global carbon cycle (Hansell, 2013). Highly productive benthic vegetated habitats often act as source of DOC (i.e., positive net DOC flux) in marine environments, but can also act as DOC consumers (i.e., negative net DOC flux), especially under conditions of low-productivity (Barrón et al., 2014; Egea et al., 2019). The DOC export from benthic meadows (both, seagrasses and macroalgae) has recently received more attention because (1) it is a significant fraction of the net community production (NCP) of benthic habitats; (2) its labile fraction is a critical component of the carbon exchange among communities (Barrón et al., 2014; Egea et al., 2019) and (3) its recalcitrant fraction counteracts climate change (Duarte and Krause-Jensen, 2017; Egea et al., 2022; Jiménez-Ramos et al., 2022).

Benthic macrophytes, as photosynthetic organisms, depend on available light for growth, productivity, and survival (Hemminga and Duarte, 2000; Lee et al., 2007; Ralph et al., 2007). Although these communities experience annual seasonality in light levels in temperate areas (Egea et al., 2019; Vergara et al., 2012), light availability can be reduced further by turbid waters associated with dredging works and

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river plumes (Erftemeijer and Lewis, 2006), eutrophication-driven blooms of fast-growing photosynthetic organisms (Brun et al., 2002) and/or climate change-induced sea level rise (Watson et al., 1996). Global change may therefore result in a gradual shading of the bottoms of coastal ecosystems, but also in an increase in the frequency of events that dramatically decrease the amount of available light, followed by periods of light recovery (IPCC, 2014). A better knowledge of the mechanisms underlying macrophyte acclimation to environmental variability is key in understanding the long-term resilience of these communities in a changing world. Ecological resilience is considered as "the capacity of an ecosystem" to absorb repeated disturbances or shocks and adapt to change without fundamentally switching to an "alternative stable state" (Holling, 1973) and is a function of two components: resistance and recovery (Levin and Lubchenco, 2008; Unsworth et al., 2015). Resistance is the capacity of the system to be perturbed from its baseline state without that change becoming irreversible; ecosystems with greater resistance can withstand stronger forcing without apparent change (Carpenter et al., 2001). Recovery determines whether and how degradation is reversed and the time to return to equilibrium state (Folke et al., 2004). Unfortunately, studies on the resilience of macrophyte species and/or assessing simultaneously the response of different benthic macrophyte communities (i.e., seagrasses and macroalgal beds) to environmental perturbations are still poorly addressed (Egea et al., 2018a; Roca et al., 2016).

Seagrass and macroalgal communities play a similar role in coastal areas (Egea et al., 2019; Tuya et al., 2014), but they exhibit large differences in morphometric (e.g., length, width of leaves) and structural properties (including canopy height, density, and complexity of the rhizomatic-root system), which ultimately affect how these species behave under light reduction. The fact that seagrasses possess a large rhizomatous-radicular network makes them more sensitive to low-light conditions due to the respiratory demands of this heterotrophic biomass (Ralph et al., 2007; Short and Wyllie-Echeverria, 1996). In addition, they tend to inhabit hypoxic-to-anoxic and sulphide-rich sediments, forcing them to release oxygen from roots to minimize the risk of sulphide intrusions into plants (Frederiksen and Glud, 2006; Lamers et al., 2013). Despite belowground biomass of seagrasses initially making them more vulnerable to low-light conditions than macroalgal species, the mobilisation of resources from the rhizome-root system (Olivé et al., 2007; Terrados and Ros, 1995), provides a compensating mechanism that facilitates the recovery and regrowth of shoots when environmental conditions become favourable again (Govers et al., 2015; Sanmartí et al., 2021), which may also make seagrasses more resilient.

The responses of marine macrophytes to changes in light availability have been well documented photophysiologically and morphologically. Low-light conditions usually produce some physiological adjustments, such as an increase of the light-harvesting complex in photosystems and low light-saturation (I_k) or compensation (I_c) points (Pérez-Lloréns et al., 1996; Ralph et al., 2007). In addition, a reduction in shoot or assimilators density, leaf or frond width, number of leaves or fronds per shoot or assimilator, and growth rate are generally found under light limitation in seagrass and macroalgal species (Brun et al., 2006; Peralta et al., 2002, 2021; Schmid et al., 2021). However, most of these studies were conducted in situ (and the results could be affected, to some extent, by other environmental variables) or in mesocosms (outdoor or laboratory) using only macrophytes, excluding the interactions among the different components of the community. Therefore, whole-community mesocosm experiments are scarce, but necessary to improve scientific understanding of how low light harms these ecosystems. Moreover, a crucial factor in the long-term survival and growth of macrophytes to light reduction is how they balance photosynthetic carbon fixation and carbon consumption during respiration (Hemminga and Duarte, 2000), which ultimately constitutes the trophic status of the community (Barrón and Duarte, 2009; Mateo et al., 2006). Net community production (NCP) is used to define the trophic state of the system (i.e., autotrophic vs heterotrophic), which is critical for determining the

community carbon balance (Holmer, 2019). Light reduction can alter these balances and trigger drastic changes in the trophic status, weakening their resilience and capacity to act as carbon sinks (Egea et al., 2019, 2020; Ferguson et al., 2017). Likewise, DOC export from benthic macrophyte communities may be strongly influenced by light conditions (Barrón et al., 2014; Kaldy, 2012; Ziegler and Benner, 1999), but the effect of shading on these fluxes is still largely unknown.

The present study addresses how light attenuation can drive specific responses depending on the type of benthic macrophyte community and how the degree of recovery of these communities can be highly dependent on their dominant macrophyte species. Two different communities were chosen, one dominated by the temperate seagrass *Zostera noltei* and the other by the macroalgae *Caulerpa prolifera*. Responses ranging from individual (biomass, density, photosynthetic area and non-structural carbohydrates content) to community (production, DOC release, new vegetative units appearance) were studied in mesocosm experiments subjected for 42 days to three levels of light exposure (high, moderate and severe light deprivation), followed by another 42 days of recovery in order to gain insights into the differences between resistance and recovery phases.

2. Material and methods

2.1. Collection of benthic macrophyte communities

Dense, monospecific meadows of the seagrass *Zostera noltei* Hornemann and the rhizophyte *Caulerpa prolifera* (Forsskål) J. V. Lamouroux were selected at a depth of 1–2 m (low tide) in submerged meadows at Cadiz Bay (southern Spain, 36°29′19.79″N; 6°15′53.05″E). Eighteen whole-benthic community samples (26 × 26 cm, nine for *Z. noltei* and nine for *C. prolifera*), at least 10 m apart, were randomly selected and carefully collected with a shovel to a sediment depth of 5–7 cm (to keep the sediment intact, as well as above- and belowground biomass), gently transferred to aquaria (26 × 26 × 36 cm; 20 l) and transported to the laboratory within 1 h of collection. Although each community was dominated by different benthic macrophyte species (i.e., *Z. noltei* or *C. prolifera*), the samples were actually an assemblage of various biological components, such as *epi*phytes, other macroalgae, fauna (epi and endo), and sediment microbes. Once in laboratory, all aquaria were acclimated for 5 days in aerated and filtered (0.45 μm) natural bay seawater under sub-saturating light (ca. 250 μmol photons m^{-2} s^{-1}) with a 16:8 h light:dark cycle at 20 °C before conducting the experiment.

2.2. Experimental design

The experiment was conducted in an open-water indoor mesocosm system inside a climate-controlled room (EMR 300-500 LXPD) set at 20 °C at the Faculty of Marine and Environmental Sciences (University of Cadiz) for 12 weeks. This time span is long enough to detect any treatment-driven changes in morphological and population traits of these fast-growing species (e.g., Egea et al., 2018b; Peralta et al., 2002). The mesocosm set-up consisted of 18 aquaria (26 × 26 × 36 cm; 20 l) randomly distributed among three light doses (i.e., CL - control light, ML - medium light and LL - low light treatments; Table 1), with six aquaria per treatment (three each for *Z. noltei* and *C. prolifera*, respectively) providing independent replicates for each community and treatment (Fig. 1).

Lighting was provided by lamps with 12 cool fluorescent tubes (T5 High Output Blau Aquaristic aquarium color extreme fluorescents) on a 16:8 h light:dark cycle. The two reduced light- treatments (i.e., ML and LL) were achieved by turning off some of the fluorescent tubes until the required light dose was reached. Dense black tarp screens were used to isolate the three light treatments from each other, preventing light scattering. This design allowed each single aquaria to be subjected to a homogenous light environment. In addition, to recreate the natural conditions of sunrise and sunset, the switching on and off, respectively,

Table 1

Daily integrated photon irradiance distribution in each community and treatment at (a) the water surface and (b) the middle canopy height (ca. 7 cm in *Zostera noltei* and ca. 4.5 cm in *Caulerpa prolifera*) for resistance (i.e., light reduction) and recovery experimental phases. SI: surface irradiance. Data are expressed as mean $\pm$ SE ($n = 630$).

(a) Daily integrated photon irradiance at the water surface

Experimental phase	Resistance		Recovery	
Treatment	Light (mol photon m^{-2} d^{-1})	% SI	Light (mol photon m^{-2} d^{-1})	% SI
Control light (CL)	17.9 $\pm$ 0.6[a]	100	18.1 $\pm$ 0.1[a]	100
Medium light (ML)	8.6 $\pm$ 0.4[b]	48	17.8 $\pm$ 0.3[a]	98
Low light (LL)	3.1 $\pm$ 0.2[c]	17	18.1 $\pm$ 0.1[a]	100

(b) Daily integrated photon irradiance at the middle canopy height

Experimental phase	Resistance		Recovery	
	Light (mol photon m^{-2} d^{-1})	% SI	Light (mol photon m^{-2} d^{-1})	% SI
Zostera noltei				
Control light (CL)	10.7 $\pm$ 1.2[a]	59	11.2 $\pm$ 0.1[a]	62
Medium light (ML)	7.3 $\pm$ 0.4[b]	41	14.6 $\pm$ 0.2[a]	81
Low light (LL)	2.4 $\pm$ 0.1[c]	14	16.5 $\pm$ 0.1[a]	91
Caulerpa prolifera				
Control light (CL)	11.8 $\pm$ 0.3[a]	66	11.6 $\pm$ 0.1[a]	64
Medium light (ML)	8.2 $\pm$ 0.4[b]	45	13 $\pm$ 0.2[a]	72
Low light (LL)	2.8 $\pm$ 0.2[c]	16	13.4 $\pm$ 0.1[a]	74

of the fluorescent tubes were programmed gradually two by two with 30 min intervals (until reaching the maximum irradiance of each treatment). This also avoided light-stress in the community due to sudden changes in irradiance. Every day, light (lumens m^{-2}) and temperature (°C) were monitored in each of the aquaria (two-minutes recording intervals for 10 min) when lights were on with two HOBO data loggers (UA-002-64) placed both at the water surface and at the mid-canopy height (ca. 7 cm in *Z. noltei* and ca. 4.5 cm in *C. prolifera*). Light intensity was converted from HOBO values in Lux (lumens m^{-2}) to µmol photons m^{-2} s^{-1} according to a previous calibration with a LiCOR light sensor (LI-1400, LI-COR Biosciences, United States) under laboratory conditions.

The aquaria were aerated to homogenize the water and reduce the diffusive boundary layer. The water in each aquarium was renewed by individual water pumps at a rate of 2.5 l d^{-1}, propelling pre-filtered (0.45 µm) seawater from a reservoir tank (250 l). Water from the reservoir tank was renewed every 4 days with freshly natural seawater collected from the bay (35 salinity and low levels of ammonium (ca. 0.7 µM), nitrate and phosphate (1–2 µM)). Seawater quality was monitored in each aquarium by analysing nutrients (every 15 days) and salinity (Crison conductivity meter CM35) (every 2–3 days). Epiphytes growing on the aquaria walls were removed and aquaria were randomly reallocated to minimize any spatial heterogeneity each time the water was renewed. In addition, all detached leaves were removed from each aquarium and weighed (fresh mass).

The experimental period consisted of two phases. In the first, the effect of light reduction was evaluated for 42 days (resistance phase). Three sampling events were established on days 3, 15 and 42 from the beginning of the experiment to evaluate the short- and medium-term effects of light reduction. Subsequently, the second phase was initiated, in which all aquaria that underwent 42 days of light reduction were returned to full light conditions (i.e., all lamps in the light-reduction treatments were turned on). This phase (recovery phase) also lasted 42 days and two sampling events were chosen on days 63 and
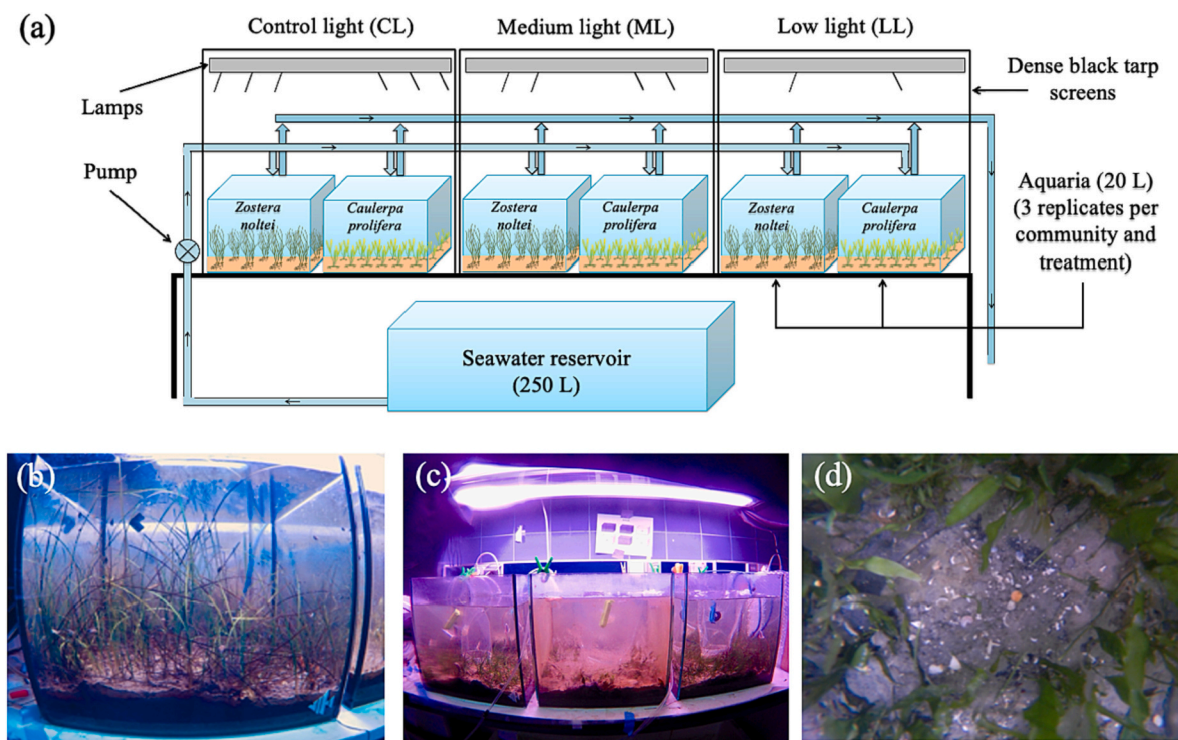
Fig. 1. (a) Simplified diagram of the experimental design. (b) A representative aquarium with the community dominated by *Zostera noltei*. (c) One treatment and the incubators used to assess the community carbon metabolisms (see detailed description in Section 2.3). (d) Gap formed at the end of the resistance phase in one representative aquaria with the community dominated by *Caulerpa prolifera* (see detailed description in Section 2.3).

84 from the start of the experiment to assess the recovery of the communities.

2.3. Sample collection

The net DOC flux (i.e., the rate of change in DOC concentration between final and initial sample) was determined at each sampling event (i.e., $t = 3d$, $t = 15d$, $t = 42d$, $t = 63d$ and $t = 84d$) for each aquarium. Three water samples per aquarium were taken from the surface using a 50 ml (polyethylene) acid-washed syringe at 3 different times: i) just before light off (S1), ii) right after the next light on (S2), and iii) 6 h after the light on (S3). Therefore, dark and light periods were considered for DOC flux (Barrón and Duarte, 2009; Egea et al., 2019). To transform each aquarium into a closed system during the sampling period for DOC, water renewal and aquarium aeration were halted. To measure DOC exchange between the aquaria and the atmosphere, a control assay was performed prior to the start of the experiment (i.e., aquarium filled with natural seawater from the bay, but without communities) to subtract the atmosphere-water DOC exchange effect, which was negligible.

Community carbon metabolism was assessed using benthic chambers (or incubators), which were randomly placed in each aquarium (one incubator per aquaria) the day after DOC sampling event (but assigned the same codes as DOC fluxes throughout the manuscript, i.e., $t = 3$-84d, respectively). Incubators (0.7 ± 0.02 l) were similar to those in previous studies (Barrón and Duarte, 2009; Egea et al., 2018b): a rigid polyvinyl chloride cylinder (8 cm in diameter) sunk to a depth of about 5 cm into the sediment and a gas-tight polyethylene plastic bag fitted to each cylinder enclosing the macrophytes. Light penetration measured inside the incubators was ca. 99.15 ± 0.01 % of incident light outside the bag. Water samples from the incubators were withdrawn through the sampling port using a 50 ml (polyethylene) acid-washed syringe coinciding with the three DOC sampling periods mentioned above (S1, S2 and S3). This is the usual time span used for this methodology (e.g., Barrón and Duarte, 2009; Egea et al., 2019) because it is long enough to determine changes in dissolved oxygen (DO) while avoiding oxygen oversaturation in the incubators. Nevertheless, it is possible that the NCP may be underestimated to some extent due to the isolation of the communities within the incubators, which would indicate that the community could be more autotrophic than our previous findings suggest (Egea et al., 2019; Olivé et al., 2016).

At the end of the light treatments (i.e., the resistance phase; $t = 42d$), biomass samples were collected from the middle of each aquarium using a 10-cm diameter core. The resulting gap was filled with new in situ pre-washed sandy sediment (from the field sampling place) previously sieved (1 mm) to remove fauna and large particles. The spread of macrophytes over the refilled gaps was then monitored during the recovery phase by taking photographs every seven days. New vegetative units (NVU, i.e., shoots or assimilators) within the gap area were counted by treating the images with the ImageJ2 software (Rueden et al., 2017). Accumulative NVUs values during five weeks were normalized by aboveground dry weight (g DW m^{-2}) at the end of the resistance phase (i.e., $t = 42d$) and expressed per m^{-1} of meadow edge (using the length of the circumference produced by the gap as meadow edge). The relative mean lengths of NVUs were also measured as a proxy of meadow growth rate. Finally, at the end of the recovery phase (i.e., $t = 84d$), all macrophyte biomass (including belowground biomass) was collected. The following morphometric attributes were estimated from biomass samples at $t = 42d$ and $t = 84d$, as well as from an initial pool of plants: above (AG-) and belowground (BG-) biomass (dry mass at 60 °C), standing stock density (n° shoot or assimilator·m^{-2} sediment surface) and the shoot/assimilator area (cm^2 of shoot or assimilator·shoot^{-1} or assimilator^{-1}). In this work, AG-biomass of *C. prolifera* refers to assimilators (those that arise directly from the stolon) whereas the BG biomass is the subterranean network of cylindrical stolons with a number of rhizoid clusters (sensu Vergara et al., 2012). For *Z. noltei*, AG-biomass was considered as the shoots whereas BG-biomass was considered as

the rhizome-roots complex (Brun et al., 2003). A fraction of the macrophyte biomasses collected at the end of both phases was used to measure non-structural carbohydrates (NSC; i.e., sucrose and starch in AG- and BG-tissues) using the resorcinol-anthrone assays following Brun et al. (2002).

2.4. Carbon community metabolism and DOC analysis

Water samples for determination of dissolved oxygen (DO) concentration were fixed immediately after collection in each incubator, kept in darkness and refrigerated, and analysed by a spectrophotometric modification of the Winkler titration method (Pai et al., 1993; Roland et al., 1999). Hourly community respiration rates (CR^h) were estimated as the difference in DO concentrations between S2 and S1 samplings divided by the time span between them. Hourly net community production rates (NCP^h) were estimated from the difference in DO concentrations between S3 and S2 samplings divided by the time span between the two samplings. Hourly gross primary production rates (GPP^h) were calculated as the sum of the hourly rates of CR^h and NCP^h. Finally, daily rates of gross primary production (GPP) were calculated using the photoperiod, whereas daily rates of community respiration (CR) were calculated by extrapolating the CR^h to 24 h. Daily net community production rates (NCP) were calculated as the difference between GPP and CR. For detailed information on the calculations and equations used, see Egea et al. (2019). Oxygen metabolic rates were converted to carbon units assuming photosynthetic (PQ = moles O$_2$: moles CO$_2$) and respiratory quotients (RQ) of 1, a widely value used for benthic macrophyte communities (e.g., Egea et al., 2019; Tuya et al., 2014), representing carbohydrate degradation.

DOC samples were filtered through pre–combusted (450 °C for 4 h) Whatman GF/F filters (0.7 μm) and were kept with 0.08 ml of H$_3$PO$_4$ (diluted 30 %) at 4 °C in acid–washed material (20 ml glass vials encapsulated with silicone-PTFE caps) until further analyses. DOC concentrations were obtained by catalytic oxidation at high temperature (720 °C) and chemiluminescence using a Shimadzu TOC-VCPH analyzer. Certified reference material for DOC (Low and Deep), provided by D. A. Hansell and W. Chen (University of Miami), was used to evaluate the accuracy of the estimates. Hourly DOC export rates during dark period were estimated as the difference in DOC concentrations between the S2 and S1 samplings divided by the time elapsed between them. Hourly DOC export rates during light period were estimated as the difference in DOC concentrations between the S3 and S2 samplings divided by the time elapsed between both samplings. Finally, net DOC flux was calculated by summing the DOC flux during the light period multiplied by the hours of light and the DOC flux during the dark period multiplied by the hours of darkness. For detailed information on the calculations and equations used, see Egea et al. (2019). Thus, when net DOC flux was positive, the community was considered to act as a net DOC producer (i.e., source). However, when net DOC flux was negative, the community was considered to act as a net DOC consumer (i.e., sink).

2.5. Data and statistical analysis

Data are presented as mean $\pm$ SE. The effects of light reduction on each response variable were tested using generalised linear models (GLMs). For each response variable, we selected a particular family error structure and link function to reach the assumptions of linearity, homogeneity of variances, and no overdispersion, which were checked by visual inspection of residuals and Q-Q plots (Harrison et al., 2018) after modelling. Levene's test for equality of variances was used to verify this assumption. Community metabolism; AG-biomass and shoot leaf area for *Zostera noltei*; BG-biomass and assimilator area for *Caulerpa prolifera*; and the number and length of new vegetative units (NVU) were modelled using Gaussian distribution with identity link. DOC fluxes; BG-biomass for *Z. noltei* and AG-biomass and assimilator density for *C. prolifera*; and non-structural carbohydrates content were modelled

using Gamma distribution with inverse link. We performed post-hoc comparisons between combinations of treatments and sampling events using estimated marginal means with a Bonferroni correction ("emmeans" R package, Lenth et al., 2019). The estimated marginal means allow pairwise comparisons between groups using a reference grid consisting of combinations of factor levels, with each covariate set to its mean value. For each response variable, we calculated a 95 % confidence interval. Additionally, we performed pairwise comparisons of estimated marginal means between all factor levels using Tukey-adjusted comparisons, setting alpha at 0.05. We performed two different types of comparisons using emmeans: 1) comparisons among sampling events for a given treatment, and 2) comparisons of treatments within a given sampling event. This allowed us to test hypotheses related

to significance differences among treatments that are independent of sampling events as well as significance differences among sampling events that are independent of treatments. Assumptions of normality and homocedasticity were assessed by examining the residuals of all linear models. Statistical analyses were computed using R 4.0.2 statistical software (R Development Core Team 2020).

3. Results

3.1. Light measurements

Daily integrated photon irradiance at the water surface (i.e., SI - surface irradiance) for the CL treatment was ~18 mol photon $m^{-2} d^{-1}$ in
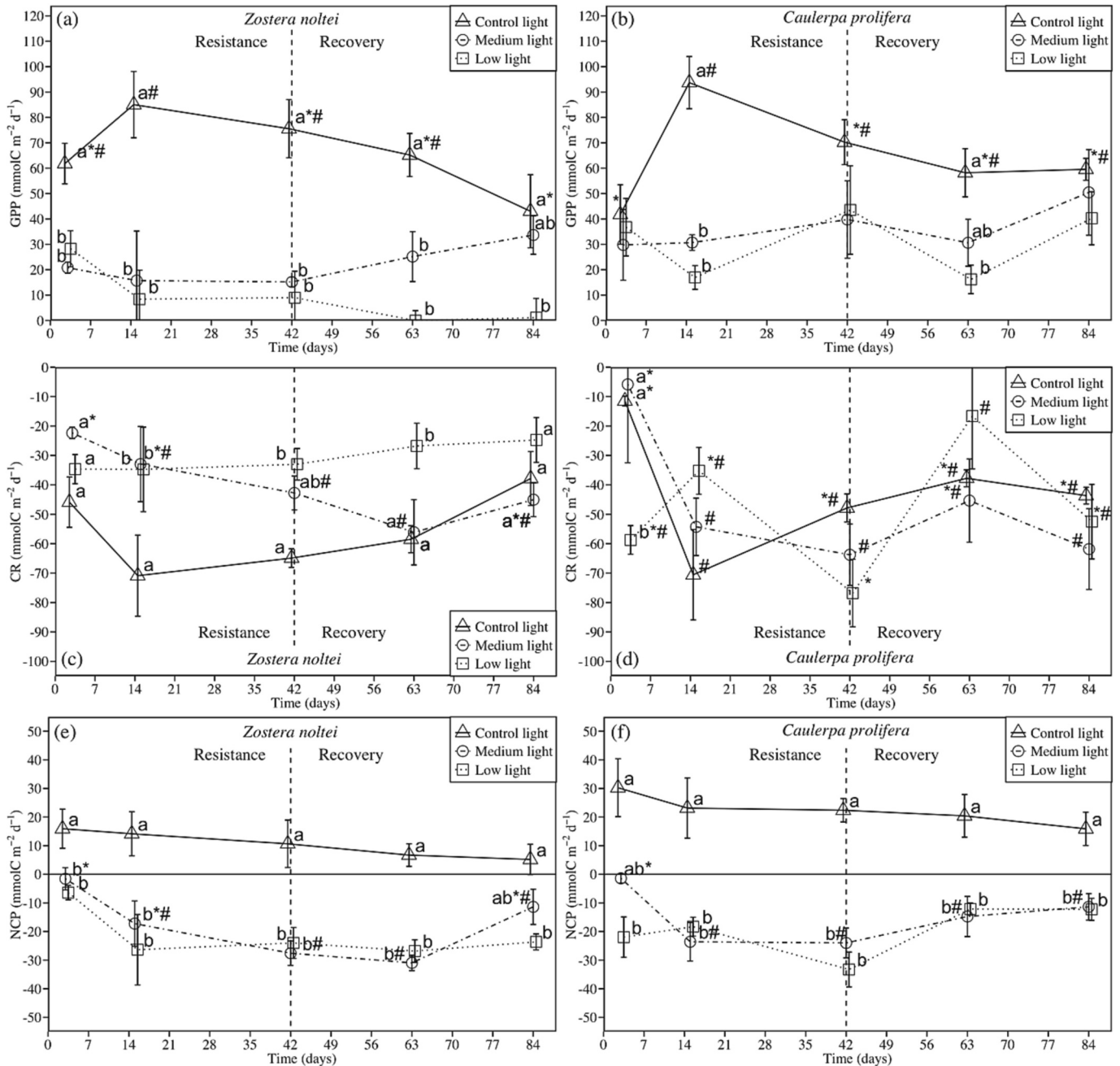
Fig. 2. Effect of light reduction (resistance and recovery phases) on Community Gross Primary Production (GPP) (a, b); Community Respiration (CR) (c, d) and Net Community Production (NCP) (e, f) in communities dominated by *Zostera noltei* (left) and *Caulerpa prolifera* (right). Dotted vertical line separates the resistance and recovery phases. Different letters indicate significant differences among treatments that are independent of sampling events, while different symbols indicate differences among sampling events that are independent of treatments. Data are expressed as mean ± SE (*n* = 3).

both experimental phases (i.e., resistance and recovery) and communities (i.e., dominated by *Zostera noltei* and *Caulerpa prolifera*), whereas light values decreased to 8.6 and 3.1 mol photon m^{-2} d^{-1} (48 % and 17 % SI, respectively) for the ML and LL treatments, respectively. Daily integrated photon irradiance in the middle of the canopies were lower than at the water surface and varied depending on the community (Table 1). During the recovery phase, light reaching the canopy center was higher in ML and LL than in CL in both communities (Table 1).

3.2. Effects on the community metabolism

Under control light (CL, 100 % SI), GPP and CR values increased in both communities during the first half of the resistance phase (i.e., t = 3-15d), decreasing toward the second half (i.e., t = 15-30d) and during the recovery phase until reaching values close to those recorded at the beginning of the experimental period. NCP values remained constant throughout the entire experimental period for both communities (Fig. 2). Under the two reduced light treatments (i.e., ML and LL), GPP decreased sharply from the beginning of the resistance phase (i.e., *t* = 3d) in *Zostera noltei* community and from the second half of the resistance phase (i.e., *t* = 15d) for *Caulerpa prolifera* one. GPP values of in *Z. noltei* community from ML showed a smooth but continuous increase during the recovery phase. These values were significantly lower in ML relative to CL at the beginning of the recovery phase but became similar to CL at the end. However, under LL treatment, GPP continued to decrease during the recovery phase (Fig. 2a). In contrast, GPP in *C. prolifera* community from the two reduced light treatments showed similar values throughout the experimental phase (Fig. 2b). A stark decrease in CR (compared to CL) was also observed under the two reduced light treatments for *Z. noltei*, becoming significant in the second half (i.e., *t* = 15-30d) of the resistance phase. These differences became non-significant in the recovery phase in ML, which showed values similar to those of CL. No clear patterns were observed in CR for *C. prolifera* (Fig. 2c, d). Finally, NCP in both communities grown under reduced light showed a sharp decrease (compared to CL) from the start of the resistance phase showing similar values through the experimental phase. The only exception was the *Z. noltei* community from ML that showed a significant increase at the end of the recovery phase reaching

similar values to those from CL (Fig. 2e; Table 2).

3.3. Effects on DOC fluxes

Similar net DOC fluxes were observed in both communities under CL, which remained constant throughout the experimental period (Fig. 3; Table 2). Light reduction triggered a decrease in net DOC fluxes in *Zostera noltei* community, reaching significant differences in LL (compared to CL) from the third experimental day, where net DOC fluxes became negative. Similarly, light reduction in *Caulerpa prolifera* community resulted in a reduction of net DOC fluxes from the third experimental day, especially in ML treatment, but without significant differences. From the 15th experimental day, an increase in net DOC release was observed in both communities under LL, which was significant for *C. prolifera*, whereas net DOC released in ML remained close to its respective CL values. During the recovery phase, net DOC release decreased in both communities from LL to reach values similar to their respective CL at the end of the experimental period. Likewise, the net DOC released in ML of both communities increased slightly to values similar to those of their respective CL. DOC fluxes in light were higher (*p* < 0.05) than in darkness in both communities throughout the experimental period. Moreover, DOC fluxes during daylight hours were typically positive in both communities, whereas DOC fluxes during night hours where mostly negative in *Z. noltei* and mostly positive in *C. prolifera* (Fig. 3; Table 2).

3.4. Effect on morphometric variables

Biomass, density, and shoot/assimilator photosynthetic area changed throughout the experimental period in both communities, showing a sharp decrease (*p* < 0.05) during the resistance phase, and a slight increase (often statistically significant) during the recovery phase (Fig. 4; Table 2). At the end of the resistance phase (i.e., *t* = 42d), ML treatment resulted into a significant decrease in AG-biomass (−67 % and −71 % for *Zostera noltei* and *Caulerpa prolifera*, respectively) and BG-biomass (−46 % and −38 % for *Z. noltei* and *C. prolifera*, respectively). This decrease was more acute under LL treatment (−85 % and −88 % for AG-biomass and −62 % and −69 % for BG-biomass, in *Z. noltei* and

Table 2
Results of GLM analysis to test the significance of treatments, time (i.e., sampling events) and their interactions on responses variables. GPP: Community Gross Primary Production; CR: Community Respiration; NCP: Net Community Production; DOC: Dissolved Organic Carbon; AG: Aboveground; BG: Belowground; Accum: Accumulated; NVU: New Vegetative Unit. Symbols indicate significant differences at α < 0.05 (*); α < 0.01 (**); α < 0.001 (***). Expanded statistical tables are presented in Supplementary material.

Response variable	Factors	*Z. noltei*	*C. prolifera*	Response variable	Factors	*Z. noltei*	*C. prolifera*
GPP	Treatment	<0.001***	<0.001***	Shoot density	Treatment	0.002**	0.004**
	Time	0.118	0.002**		Time	<0.001***	<0.001***
	Treatment & time	0.043*	0.028*		Treatment & time	<0.001***	0.026*
CR	Treatment	0.005**	0.052	Shoot leaf area	Treatment	<0.001***	0.018*
	Time	0.012*	0.002**		Time	<0.001***	0.004**
	Treatment & time	0.015*	0.014*		Treatment & time	<0.001***	0.084
NCP	Treatment	0.014*	<0.001***	Sucrose AG	Treatment	1.000	0.010*
	Time	0.648	0.029*		Time	0.018*	0.001**
	Treatment & time	0.099	0.150		Treatment & time	0.011*	0.017*
DOC fluxes	Treatment	0.612	0.088	Sucrose BG	Treatment	0.012*	1.000
	Time	0.026*	0.029*		Time	<0.001***	0.875
	Treatment & time	0.015*	0.200		Treatment & time	0.001**	0.011*
DOC at light hours	Treatment	0.337	0.074	Starch AG	Treatment	0.136	0.044*
	Time	0.011*	0.007*		Time	0.018*	0.595
	Treatment & time	0.036*	0.204		Treatment & time	0.223	0.034*
DOC at night hours	Treatment	0.362	0.184	Starch BG	Treatment	0.684	0.037*
	Time	0.300	0.045*		Time	0.195	0.014*
	Treatment & time	0.144	0.075		Treatment & time	0.740	0.032*
AG biomass	Treatment	0.035*	<0.001***	Accum. shoot appearance	Treatment	1.000	1.000
	Time	0.008*	0.024*		Time	0.019*	0.014*
	Treatment & time	0.17	<0.001***		Treatment & time	0.002**	0.003**
BG biomass	Treatment	0.013*	0.028*	NVU length	Treatment	1.000	1.000
	Time	0.354	0.06		Time	<0.001***	<0.001***
	Treatment & time	0.020*	0.007*		Treatment & time	0.069	0.04*
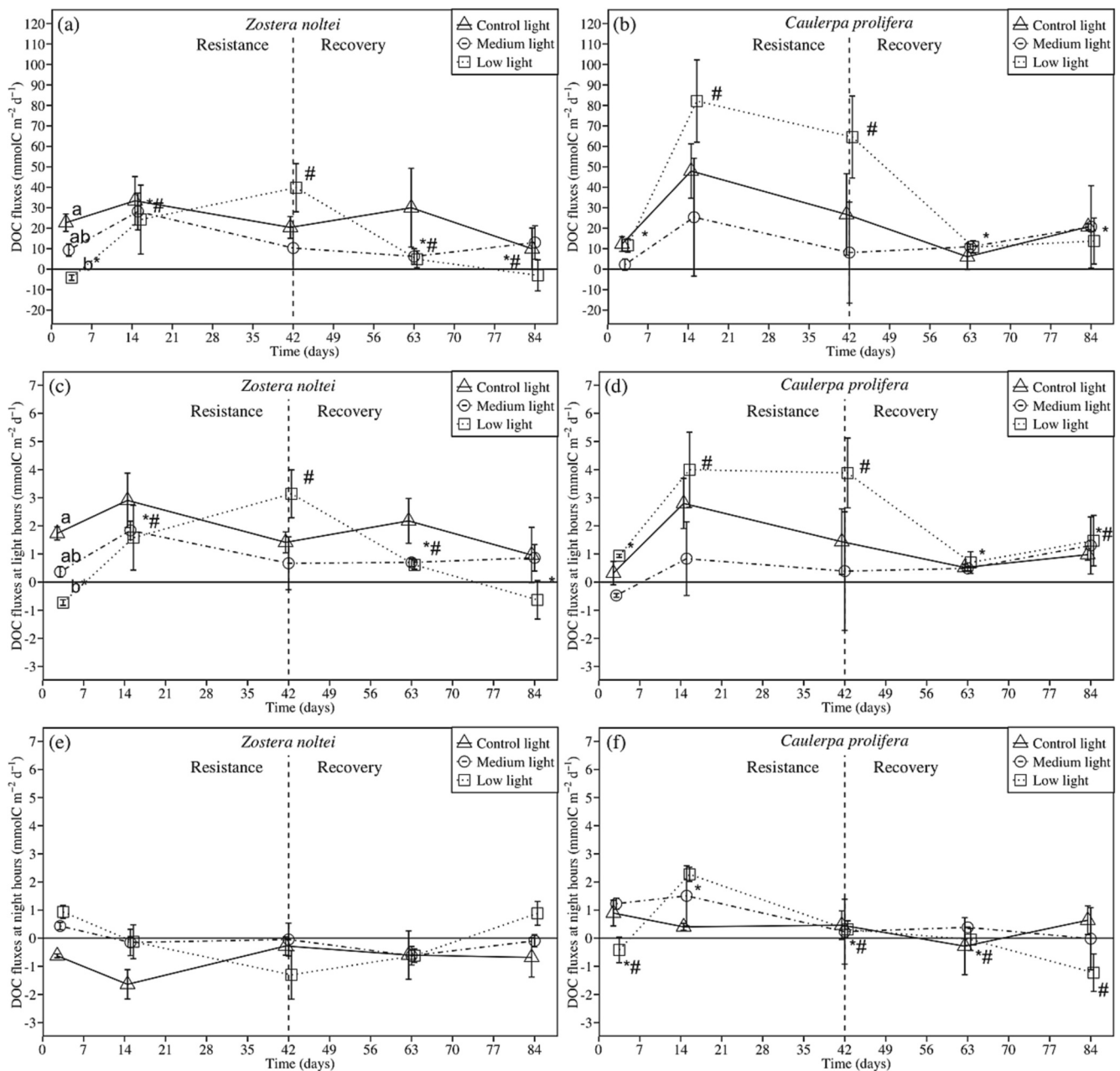
Fig. 3. Effect of light reduction (resistance and recovery phases) on the net daily Dissolved Organic Carbon (DOC) fluxes (a, b); DOC fluxes at light hours (c, d) and DOC fluxes at night hours (e, f) in communities dominated by *Zostera noltei* (left) and *Caulerpa prolifera* (right) (figure details as in Fig. 2).

C. prolifera, respectively) (Fig. 4a, b). Similarly, shoot or assimilator density showed a significant decrease under ML (−65 % and −41 % for *Z. noltei* and *C. prolifera*, respectively) and especially under the LL treatment (−86 % and −88 % for *Z. noltei* and *C. prolifera*, respectively) (Fig. 4c, d). Finally, photosynthetic area decreased in both communities under ML (−71 % and −60 % for *Z. noltei* and *C. prolifera*, respectively) and especially under LL for *Z. noltei* (−86 %) (Fig. 4e, f). During the recovery phase, *Z. noltei* showed signs of recovery in ML for AG-biomass and shoot leaf area (+32 % and +104 % with respect to the end of the resistance phase), while *C. prolifera* showed sign of recovery in ML for AG-, BG-biomasses and assimilator area (+50 %, +8 %, and +23 % with respect to the end of resistance phase). For both species, these values were significantly lower in ML compared with CL at the beginning of the recovery phase, but became similar to CL at the end. In LL treatment, no signs of recovery were found for *Z. noltei*, while in *C. prolifera* there was a trend toward improvement in AG-, BG-biomass, assimilator density and

assimilator area (+16 %, +57 %, +181 % and +14 % respect the end of resistance phase), but without reaching statistical significance (Fig. 4; Table 2).

3.5. Effects on non-structural carbohydrates content

Non-structural carbohydrates (NSC) content was species-specific and was affected by light reduction. Sucrose was the main NSC in *Zostera noltei*, especially in belowground tissues. In contrast, starch was the main NSC in *Caulerpa prolifera*, which showed similar NSC content in both aboveground and belowground parts. Light reduction triggered a decrease in sucrose content in above and belowground parts of *Z. noltei*, whereas no pattern was found in its starch content. Similarly, light reduction caused a decrease in above and belowground starch content in *C. prolifera*, especially in LL, where statistical significance was found, whereas no pattern was observed in its sucrose content. During the
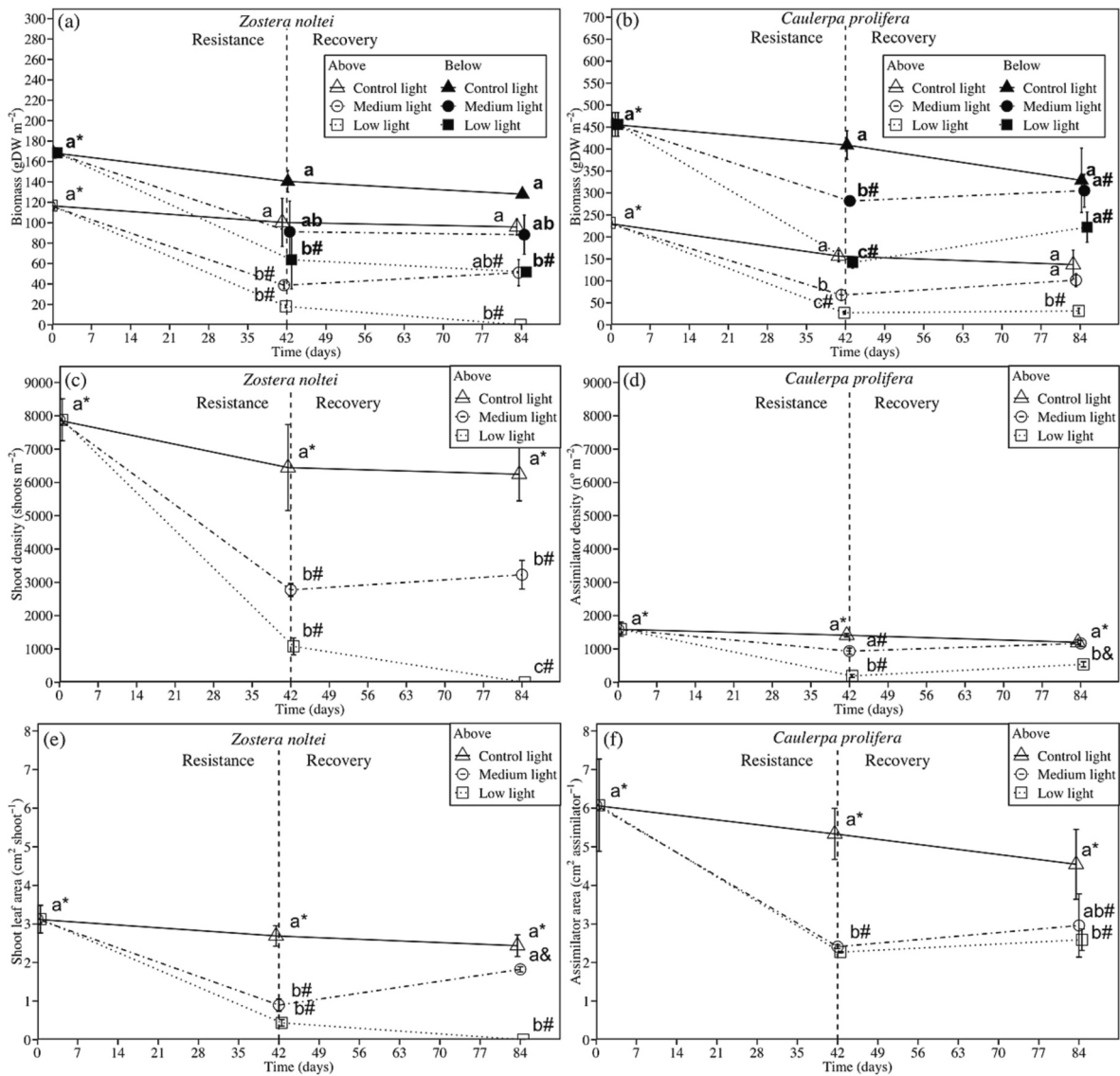
Fig. 4. Effect of light reduction (resistance and recovery phases) on (a, b) biomass, (c, d) vegetative units density and (e, f) vegetative unit area in the community dominated by *Zostera noltei* (left) and *Caulerpa prolifera* (right). Open symbols represent aboveground tissues and closed symbols represent belowground tissues (figure details as in Fig. 2). Plain font letters and symbols for differences in aboveground tissues and bold font letters and symbols for differences in belowground tissues. Note difference in Y-axis scale in panels a and b.

recovery phase, the main NSC of each macrophyte species increased until reaching values similar to those of their respective CL at the end of experimental phase (Fig. 5; Table 2).

3.6. Effects on meadow growth and spread

The number and length of new vegetative units (NVU, i.e., shoots or assimilators) that appeared within the gap area during the recovery phase were similar between both macrophyte species in the CL treatment (Fig. 6; Table 2). Overall, light reduction resulted in a significant decrease in the number of NVUs, but when normalized by aboveground dry weight (g DW m^{-2}) at the end of the resistance phase (i.e., $t = 42$d), those treatments showed greater accumulative shoot or assimilator appearance than controls.

4. Discussion

4.1. Effect of light reduction on benthic macrophyte production

Light at the water surface in control light (CL, 100 % SI) treatments during the two phases of the experimental period (i.e., resistance and recovery) was in the range of the values measured in situ for both communities (Egea et al., 2019). This value is below the light-saturating intensity for *Zostera noltei* (Peralta et al., 2002) and close to the light saturation point for *Caulerpa prolifera* (Vergara et al., 2012). Daily integrated photon irradiance was significantly lower in the light-reduced treatments at half the canopy height (41–45 % SI in ML and 14–16 % SI in LL), resulting in a high-moderate (in ML) and severe (in LL) light deprivation for both macrophyte species (Peralta et al., 2002; Vergara et al., 2012).

Both communities were autotrophic in the CL treatments as they had a positive daily rate of net community production (NCP), suggesting their potential contribution to net carbon storage, in agreement with previous reports (e.g., Duarte et al., 2010; Egea et al., 2019; Tuya et al.,
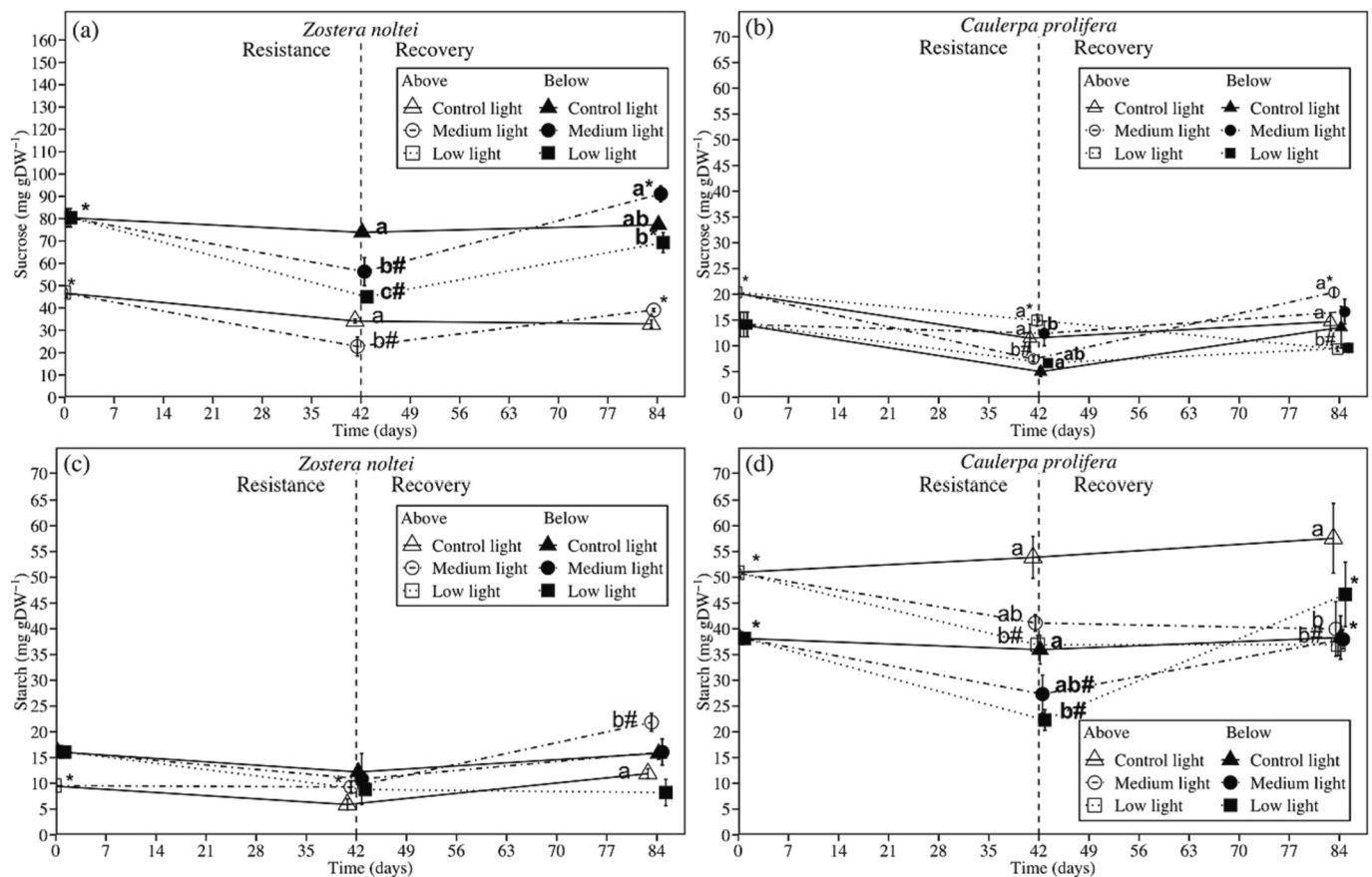
Fig. 5. Effect of exposure (i.e., light reduction) and recovery periods on (a, b) sucrose and (c, d) starch in communities dominated by *Zostera noltei* (left) and *Caulerpa prolifera* (right) during the experimental period. Open symbols represent aboveground tissues and closed symbols represent belowground tissues (figure details as in Fig. S1). Plain font letters and symbols for differences in aboveground tissues and bold font letters and symbols for differences in belowground tissues. Note difference in Y-axis scale in panels a and b.

2014). Light reduction led to a significant decrease in NCP in both communities from the onset of the resistance phase (i.e., $t = 3d$) shifting the system from autotrophic to heterotrophic (Fig. 2). Surprisingly, non-significant differences were found in either gross primary production (GPP) or NCP during the resistance phase between ML and LL treatments in either community, despite the observed effects on some population attributes (e.g., biomass, vegetative unit density and area; Fig. 4). This result is probably due to the observed reduction in self-shading within the canopy that would result in higher understory light levels (Table 1), allowing greater light absorption and yielding higher productivity per biomass unit in the LL treatments (Hemminga and Duarte, 2000). The shift of the community from being autotrophic to heterotrophic has important consequences since the photosynthetically fixed carbon cannot meet the requirements of community respiration. This shift results in an imbalance in community carbon metabolism that requires allochthonous organic carbon subsidies and leads these communities to act as CO_2 source and O_2 sink (Duarte et al., 2010). This may result in 'cascading effects', weaken all the ecological services they provide, including their capacity to act as carbon sinks and essential role for coastal biodiversity (Ferguson et al., 2017). Furthermore, decreased GPP under low-light conditions can trigger noteworthy consequences for macrophytes themselves, as this reduction in carbon input can negatively affect the synthesis of carbon skeletons that could be used directly for growth or stored, supporting seagrasses during other unfavourable conditions (Brun et al., 2002, 2008).

4.2. Effect of light reduction in community dissolved organic carbon (DOC) fluxes

A substantial and similar amount of autochthonous DOC was generated by both vegetated communities in the CL treatments according to their high productivity, which is in agreement with previous studies (Barrón and Duarte, 2009; Egea et al., 2019). Interestingly, the light reduction produced opposite responses depending on severity of light reduction (i.e., ML or LL treatments) (Fig. 3). Overall, ML resulted in a decrease in net DOC release in both communities. In contrast, under LL there was an initial decrease in net DOC release (especially in *Zostera noltei*), followed by a significant increase (from day 15 in *Caulerpa prolifera* and from day 42 in *Z. noltei*). Several mechanisms could explain these results. For instance, at the beginning, the decrease in GPP (due to light reduction) would lessen net DOC fluxes due to the strong dependence between net DOC fluxes and carbon metabolism reported in these communities (Barrón et al., 2014; Egea et al., 2019). Furthermore, given that the low-light conditions were quite long-lasting, it is likely that there was also a stimulation of organic matter (OM) remineralization, which could be enhanced by increased OM inputs from dead tissues (especially under LL), enhancing DOC fluxes. This process was especially important in *C. prolifera* community as this species usually thrives in fine-grained sediments with high OM content (i.e., muddy sediments; Belando et al., 2021; Holmer et al., 2009). On the other hand, our results also showed that both communities displayed a higher net DOC release during sunlight hours than in darkness, when the communities in general act as DOC consumer in *Z. noltei* and as DOC producer in *C. prolifera* (Fig. 3). Thus, our results suggest that DOC release from vegetated
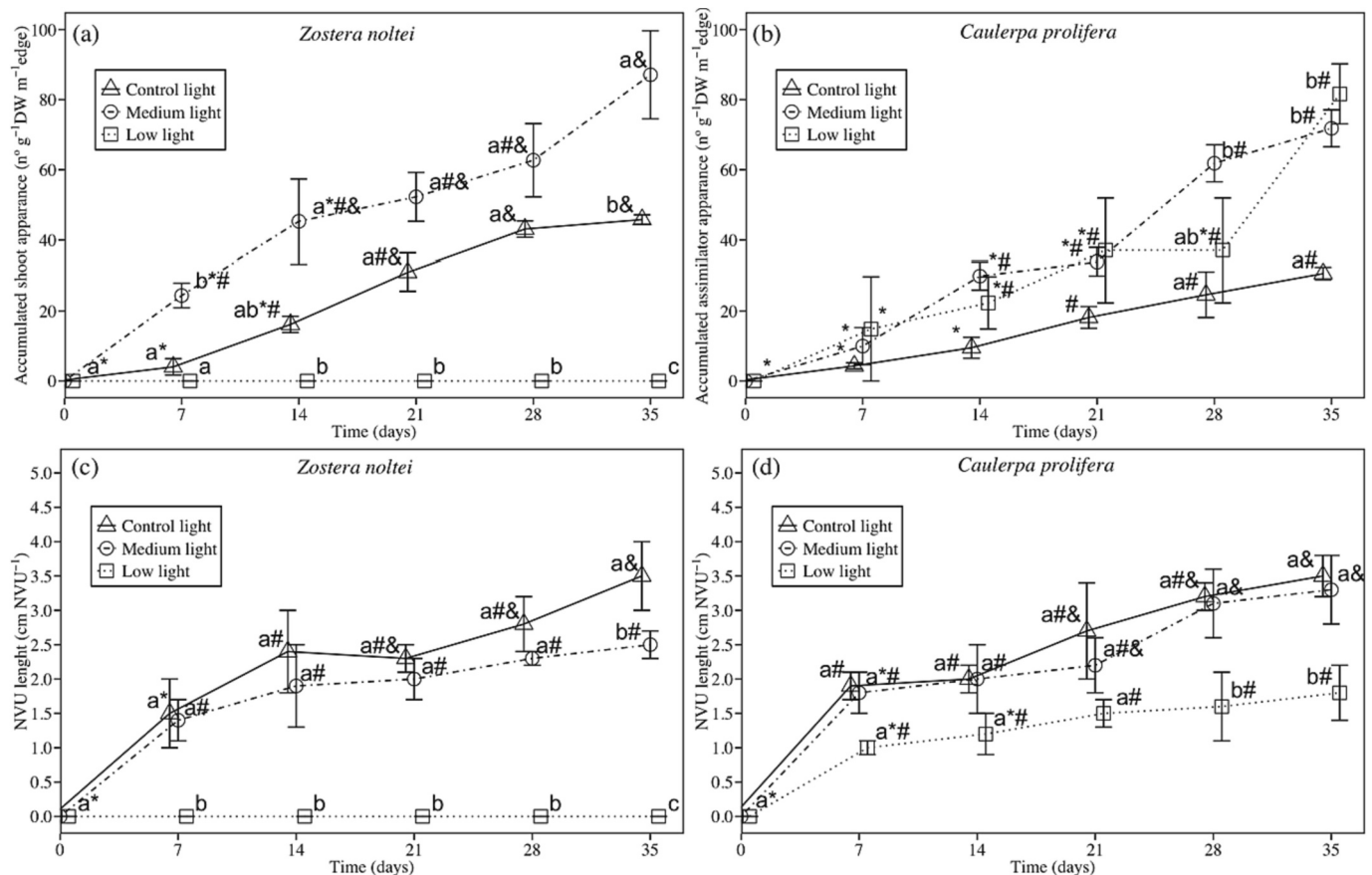
Fig. 6. Accumulative number (a, b) and relative mean lengths (c, d) of new vegetative units (NVUs, i.e., shoots or assimilators) appearing within the gap area in the community dominated by *Zostera noltei* (left) and *Caulerpa prolifera* (right) during the recovery phase (figure details as in Fig. 2).

coastal communities is highly dependent on light. However, light-independent mechanisms may also affect the DOC release rate, such as nutrient assimilation (Egea et al., 2020; Mueller et al., 2016), temperature (Egea et al., 2022) and DOC produced during the degradation of OM by sediment bacteria (Gómez-Consarnau et al., 2019).

Consequently, our results indicate that most of the DOC released by coastal vegetated communities depends on photosynthetic activity and that net DOC fluxes can be strongly affected by disturbances such as shading episodes. The magnitude and direction (i.e., toward more net DOC producer or consumer) of such changes depend on multiple factors, including the duration and/or the extent of shading episodes. These changes have important ecological implications as DOC from vegetated coastal communities constitutes an important source of carbon in the trophic web (i.e., labile DOC; Egea et al., 2019; Romera-Castillo et al., 2011), fuelling both the same and adjacent communities. Moreover, another fraction of the DOC released by seagrass and macroalgal communities shows low bioavailability (i.e., recalcitrant DOC), representing another pathway for blue carbon sequestration (Egea et al., 2022; Jiménez-Ramos et al., 2022; Krause-Jensen and Duarte, 2016).

4.3. Resistance, recovery and resilience strategy

The large decrease in biomass and density evidenced a high sensitivity of both macrophyte species to prolonged shading (Fig. 4). Reductions of AG-biomass and/or canopy density under dim light are usually reported for *Zostera noltei* and other seagrass species (Ralph et al., 2007) as an adaptive mechanism to maximize understorey available light by reducing self-shading (Collier et al., 2012; Table 1 in this study). However, our results revealed harmful effects similar to those reported previously (e.g., Brun et al., 2008; de los Santos et al.,

2010). Regarding *Caulerpa prolifera*, the high sensitivity to low-light contrasts with most previous studies on *Caulerpa* spp., that highlighted these macroalgae as shade-adapted with a low photoprotective capacity (Ukabi et al., 2013; Zubia et al., 2020). However, some populations of *C. prolifera*, such as those used in our work, also exhibited high light-saturation values (up to 750 µmol photons m^{-2} s^{-1}; Vergara et al., 2012). This indicates that this species can adapt its photosynthetic parameters to moderate/high rather than low light conditions, which means a certain degree of sensitivity to long-term shading conditions. This was observed in other species of this genus such as *C. taxifolia*, which may grow worse under very low light and/or long-term shading conditions (Burfeind and Udy, 2009). Overall, our results indicated that, although *C. prolifera* is usually adapted to thrive under to low-light conditions, if these conditions are severe and long-lasting, their populations can undergo a significant loss of biomass, shifting the community from autotrophic to heterotrophic. Therefore, our results highlighted a low resistance to severe and/or prolonged light reduction for both communities, which may hinder the community's capacity to recover despite restored light level conditions. This low resistance likely arises from their limited total biomass and non-structural carbohydrate (NSC) reserves compared to other macrophyte species with higher biomass and/or slower growth rates (Larkum et al., 2018; O'Brien et al., 2018).

Our results indicated that both species had low resistance but a quite large recovery capacity, even after suffering severe biomass and density reduction, probably due to better light penetration within the canopy under such conditions (see Table 1). However, the rate and magnitude of recovery were community-specific. For example, *Caulerpa prolifera* evidenced signs of recovery in the LL treatment but not *Zostera noltei*, attesting to widespread plant death and meadow loss. This implies that

the duration of low-light conditions in LL exceeded the resistance capacity of *Z. noltei*. In relation to morphometric variables, *Z. noltei* showed signs of recovery under ML as AG-biomass and shoot leaf area increased reaching values similar to those of CL, but others such as BG-biomass and density remained low (Fig. 4). On the contrary, a significant morphological recovery in *C. prolifera* was observed under ML (including AG-, BG-biomasses and assimilator area), but partially under LL, since the increase in these variables did not reach statistical significance. Signs of recovery were also observed at the physiological level, as the main NSC contents for each macrophyte (i.e., sucrose for *Z. noltei* and starch for *C. prolifera*) reached and/or exceeded those of the CL at the end of the recovery phase (Fig. 5). Finally, the spreading capacities of these meadows were evaluated in control and reduced-light treatments during the recovery phase (Fig. 6). Both macrophytes showed similar rates of shoot or assimilator appearance and a similar NVU growth rate in CL treatments. In general, treatments under light reduction showed higher accumulative shoot or assimilator appearance than controls, indicating a higher potential for recovery and growth, probably due to better light penetration within the canopy. Therefore, both communities showed a resilience ability underpinned by high recovery but low resistance capacity, with *C. prolifera* evidencing a higher resilience ability under the unfavourable light conditions tested in this work.

4.4. Ecological implications

Our results suggest that if shading events are more frequent in the future, as predicted under climate change, both communities could be severely damaged, especially that of *Zostera noltei*, which could even be completely lost under extreme conditions. The low resistance of both macrophyte communities reported in our work contrasts with the rather high recovery capacity, especially for *Caulerpa prolifera*, which showed a great spreading capacity during the recovery phase. This could, to some extent, alter the balance between these species favouring *C. prolifera* in areas where both species cohabit as noted in previous studies (Antón et al., 2011; Tuya et al., 2013). Our results indicate that these changes in the equilibrium between species would not necessarily lead to altered balances in carbon uptake and DOC release in the area, since both communities show comparable values. However, it should be noted that carbon fate often follows different pathways in seagrasses and macroalgae, and then the ecosystem structure and functioning can be deeply disrupted (e.g., Egea et al., 2019, 2020), as well as nutrient cycling (Human et al., 2015), and faunal abundance and diversity (Jiménez-Ramos et al., 2021; Tuya et al., 2014). On the other hand, dead macrophyte biomass removed by hydrodynamic processes may be an important source of DOC to coastal areas, which should be further assessed in future research. This study provides additional arguments to the growing need to protect and conserve seagrass meadows as valuable ecosystems to counteract climate change under the IPCC framework. Future research should investigate on how worsening light conditions, acting together with other environmental or anthropogenic stressors, can affect the carbon dynamics of vegetated coastal ecosystems to improve our understanding of how these threatened ecosystems can help to mitigate the effects of climate change. On the other hand, in the same way as done in other sympatric species (e.g., van Treeck et al., 2020; Vitasse et al., 2019), more research comparing resistance and recovery among cohabiting-foundational species is needed. In this regard, we emphasize that it would be necessary to deepen not only in the differences in sensitivity between these sympatric species to global change, but also to develop a better selection of species for conservation issues, and to improve the objective evaluation of the success of restoration projects.

5. Conclusions

The simulated light reduction produced a significant decrease in NCP in both communities, shifting the system from autotrophic to heterotrophic, weakening all the ecological services they provide us, including their capacity to act as carbon sinks, as well as probably making these macrophytes more vulnerable to other unfavourable conditions. Importantly, our results confirmed that most of the DOC released from vegetated coastal communities rely on photosynthetic activity and that net DOC fluxes from these communities are strongly affected by shading events. The magnitude and direction (i.e., toward net DOC producer or consumer) of these changes depend on multiple factors, including the time span and/or magnitude of shading events. Finally, this study revealed that the resistance and recovery capacity under severe and/or prolonged light reduction varied greatly depending on the species, ultimately affecting carbon metabolism and the spread and growth of these populations. Both communities showed resilience underpinned by high recovery but low resistance capacity, even after suffering a severe reduction in biomass and density, probably due to the improvement of light penetration within the canopy under these light-limiting preconditions.

CRediT authorship contribution statement

Rocío Jiménez-Ramos: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Fernando G. Brun:** Conceptualization, Funding acquisition, Project administration, Investigation, Writing – review & editing. **José L. Pérez-Lloréns:** Conceptualization, Funding acquisition, Project administration, Investigation, Writing – review & editing. **Juan J. Vergara:** Conceptualization, Investigation, Writing – review & editing. **Fátima Delgado-Cabezas:** Investigation, Methodology, Writing – review & editing. **Noelia Sena-Soria:** Investigation, Methodology, Writing – review & editing. **Luis G. Egea:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.114630.

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