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RESEARCH ARTICLE

Metabolic traits and thresholds to inform marine ecological conservation and restoration

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Abstract

1. The combined effects of anthropogenic pressures and climate change pose significant threats to key habitat-forming species, such as seagrasses. Understanding species' responses to environmental stressors and identifying their tolerance thresholds are essential for effective conservation and restoration efforts in coastal environments.
2. Through a mesocosm experiment, we assessed *Posidonia oceanica*'s metabolic responses under ecologically realistic conditions across three seasonal periods (February–March, June–July and October–November) when plants were naturally acclimated to different temperature regimes. Within each period, we tested plant responses to small temperature variations (ambient and two increasing steps of 2°C) crossed with four turbidity levels (0, 4, 16 and 34 mg/L), enabling the construction of ecologically realistic thermal performance curves.
3. Our findings reveal that turbidity may impair *P. oceanica* functioning, including decreased thermal performance and narrowed thermal tolerance window, impairing photosynthesis and potentially limiting growth. Metabolism increased with temperature up to a thermal optimum (T_{opt}) identified at 23°C for all turbidity and exposure time treatment levels. We demonstrate the relevance of stressor properties on *P. oceanica* responses, with individuals exposed to the more extreme treatment (high turbidity (34 mg/L) and increased exposure time (7 days)) presenting a reduced optimal thermal tolerance with respect to control.
4. *Synthesis and applications*. Integrating organismal responses to environmental stressors into monitoring protocols can provide early warning indicators of

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ecosystem health. This approach strengthens conservation and restoration initiatives, supporting policy decisions in the face of increasing coastal development and climate change.

KEYWORDS
anthropogenic stressors, climate change, conservation, ecosystem services, *Posidonia oceanica* seagrass, restoration, thermal tolerance, turbidity

1 | INTRODUCTION

Ecosystems worldwide are experiencing significant degradation, making their recovery and conservation a major challenge for the scientific community, managers and policymakers (Maes et al., 2024). Understanding ecosystem functions is crucial for maintaining the stability, productivity and resilience of ecosystems (Hooper et al., 2005). Functional traits of species, such as leaf area and root length in plants, play a key role in processes like carbon sequestration and soil stabilization that underpin ecosystem services essential for human well-being (Reich, 2014). Identifying functional thresholds in response to environmental changes is essential for ecologists, conservationists and natural habitat managers, particularly in coastal areas facing heightened pressures from anthropogenic stressors, including climate change (Hughes et al., 2017; Suding et al., 2004; Worm et al., 2006).

Traditionally, conservation and restoration strategies have focused on ecological thresholds—critical points that determine an ecosystem's ability to maintain its structure and function over time in the face of external disturbances (Hobbs & Norton, 2004; Isbell, 2022). These thresholds are particularly relevant for marine habitat-forming species (such as seagrasses and corals; Maes et al., 2024; NOAA, 2020), which act as primary producers and facilitate the growth, survival and reproduction of other species within the ecosystem (Orth et al., 2006; Waycott et al., 2009).

In this context, investigating the metabolic traits of habitat-forming species has become increasingly important to evaluate the effectiveness of conservation measures and predict restoration outcomes (Foley et al., 2017; NOAA, 2020). Key functional traits, such as respiration and oxygen production, provide valuable insights into the ecological performance and functionality of these species and serve as indicators of their success under varying environmental conditions (Brandl et al., 2023; Violle et al., 2012). Furthermore, these traits help identify critical thresholds for habitat resilience under multiple stressors. This is particularly important in coastal areas where multiple stressors interact, influencing the stability and persistence of habitat-forming species (Gunderson et al., 2016; Jackson et al., 2021). Integrating species' functional traits into conservation, management and restoration strategies is therefore essential to ensure that actions are both effective and ecologically sound.

Among marine habitat-forming species, the seagrass *Posidonia oceanica* (L.) Delile represents a critical case study in the Mediterranean Sea. This endemic species plays a crucial role in coastal ecosystems (Programme, 2020) by forming continuous meadows at depths from 0.5 to 50 m (depending on light availability). These meadows are key structuring habitats with significant socio-economic and ecological value, providing shelter for many species and contributing to a multitude of ecosystem services, including carbon sequestration, oxygen production, coastline erosion protection, water sanitization and nutrient recycling (Boudouresque et al., 2009, 2012; Campagne et al., 2015; Costanza et al., 1997; Danovaro & Boero, 2019; Scanu et al., 2022). Due to their ecological relevance, *P. oceanica* meadows are catalogued as a priority habitat for conservation by the EU (Salomidi et al., 2012); however, despite the species being listed as 'least concern' on the IUCN Red List (Pergent et al., 2016), recent studies have documented a significant decline in their performance—up to a 51% reduction in production over the past two decades—driven by rising sea surface temperatures, more frequent marine heatwaves and other anthropogenic stressors (Capello et al., 2014; Litsi-Mizan et al., 2023; Stipcich et al., 2022; Waycott et al., 2009).

Recent studies have shown that *P. oceanica* displays optimal growth between 17 and 20°C, with thermal stress occurring above 28°C (Rinaldi et al., 2023; Savva et al., 2018). The species' cover and density are significantly influenced by these seasonal temperature fluctuations, as its metabolic responses are strongly temperature-dependent (Weber et al., 2017). However, while some research has investigated stress responses in seagrasses, specific studies on the tolerance of *P. oceanica* to multiple, interacting environmental stressors remain scarce (Ceccherelli et al., 2018; Gunderson et al., 2016; Marín-Guirao et al., 2018). This gap in knowledge is particularly critical in understanding how thermal tolerance is modified by other anthropogenic pressures. Turbidity is one of the most significant anthropogenic stressors affecting marine primary producers, often exacerbated by human activities such as dredging and coastal development (Gacia & Duarte, 2001). Increased turbidity reduces light availability, inhibiting essential processes like photosynthesis, leaf gas exchange and nutrient uptake (Brodersen et al., 2017; Orth et al., 2006; Ruiz & Romero, 2003). Additionally, sediment deposition on seagrass leaves can create physical barriers to gas exchange and further exacerbate physiological stress. Extreme events exacerbated by climate change can further augment turbidity levels in coastal areas through increased frequency and intensity of storms, leading to prolonged periods of sediment resuspension (Fettweis et al., 2010). Importantly, turbidity and nutrient enrichment are closely linked, as nutrient runoff from coastal areas can increase eutrophic events, enhancing turbidity and sediment deposition, which stress seagrasses (Ceccherelli et al., 2018). These synergistic stressors significantly impair *P. oceanica* resilience, with nutrient enrichment exacerbating sediment burial effects and accelerating seagrass collapse, highlighting the interplay between light attenuation and eutrophication. The resilience of habitat-forming primary producers to these stressors, particularly in light of climate change-induced indirect effects such as altered salinity levels and changes in light availability (Mancuso et al., 2023), necessitates a comprehensive understanding of their ecological and biological responses, including physiological adjustments like osmotic regulation and morphological changes such as reduced growth and increased tissue necrosis. While different studies have examined the independent effects of temperature (Litsi-Mizan et al., 2023; Marín-Guirao et al., 2018; Rinaldi et al., 2023; Savva et al., 2018) and turbidity (González-Correa et al., 2008; Ruiz & Romero, 2001, 2003) on *P. oceanica*, their interactive effects remain poorly understood.

Here, we designed mesocosm experiments across three seasonal periods (winter, summer and autumn) to assess how turbidity affects the thermal tolerance of this endemic habitat-forming species under naturally occurring temperature conditions. We investigated how *P. oceanica*'s metabolic traits responded to varying levels of turbidity and temperature through measurement of respiration rate, gross and net primary production and photosynthetic activity (via chlorophyll-*a* fluorescence analysis). We hypothesize that elevated turbidity and increased temperature will interact to influence *P. oceanica's* metabolic rates, reducing photosynthetic activity and narrowing thermal tolerance breadth (Sokolova et al., 2012).

2 | MATERIALS AND METHODS

Our study was designed to assess *P. oceanica*'s responses under ecologically realistic environmental conditions. Rather than artificially imposing a wide temperature range at a single time point, we strategically conducted our experiments during three distinct seasonal periods that reflect the natural temperature variations in *P. oceanica*'s habitat. This task was achieved by segmenting a 12-month time period into three distinct experimental periods. Each period was tailored to mirror the natural temperature regimes characteristic of the species' habitat, based on temperature variation data from the sampling site off the coast of Civitavecchia in the northern Tyrrhenian Sea (Italy), and the observed species' realized thermal niche (Appendix S1: Figure S1). This region is subject to both natural seasonal fluctuations and anthropogenic pressures, including dredging activities that influence local turbidity levels, making it an ideal setting for examining the interaction of temperature and turbidity stressors. The first period (February–March, with temperatures ranging from 14 to 15°C) included the minimum temperatures usually experienced by *P. oceanica*. The second period (June–July, with temperatures ranging from 22 to 28°C) encompassed the highest temperatures experienced by the plant, while the third period (October–November, with temperatures ranging from 19 to 24°C) closely matched the potential optimum temperature range for *P. oceanica* (Appendix S1: Figure S1).

2.1 | Experimental treatments

The study included a total of 9 temperatures crossed with 4 turbidity levels.

Temperature: each of the three experimental periods included three temperature levels: the ambient seawater temperature at which *P. oceanica* was collected and two increasing steps of 2°C for a total of 9 tested temperatures over the study (first period = 15°C ambient, 17°C, 19°C; second period = 27°C ambient, 29°C, 31°C; third period = 21°C ambient, 23°C, 25°C).

Turbidity: to represent a broad spectrum of sediment concentrations, four progressive turbidity levels (0, 4, 16 and 34 mg/L) were selected, consistent with values reported for Civitavecchia's marine environment (Piazzolla et al., 2018). The upper limit (34 mg/L) was included to simulate conditions exceeding the 90th percentile of sediment concentration distributions observed in this area, aligning with national guidelines that encourage consideration of site-specific variability (ISPRA, 2016). Recognising that local measurements often capture typical conditions but may underestimate extreme events, we aimed to include higher turbidity levels to assess potential impacts on seagrass meadows. The sediment was collected at a depth of 50 m near the *P. oceanica* sampling site. In the laboratory, sediment was sieved retaining the fraction smaller than 63 μm (clay-silt), which was then placed at 450°C overnight to remove any biological contamination. The resulting sediments were predominately silt-sized, characteristic of dredge plumes (Piazzolla et al., 2018). Given that sediments at 50 m contain a significant amount of fine particles (<63 μm), which can easily be resuspended to shallower depths, the chosen turbidity levels likely represent conditions that seagrass meadows at 10 m may experience, especially in areas affected by coastal activities like dredging. Sediment was added to the tanks to obtain the four treatment levels of turbidity, and a circulating system was used to maintain constant turbidity levels. Turbidity levels were checked every day and adjusted as needed to maintain target concentrations.

2.2 | Sampling and laboratory setup

A total of 324 undamaged healthy *P. oceanica* orthotropic shoots, including rhizome and roots (108 shoots per period, 9 shoots per treatment combination), were collected in 2023 by SCUBA diving at a depth of 10 m, approximately 300 m off the coast of Civitavecchia (Lat: 42.076562, Long: 11.802896, Italy), in the northern Tyrrhenian Sea (no special authorisation was required for sampling). Shoots with similar leaf and rhizome length (mean ± SD: leaf length = 40.0 ± 11.7 cm, rhizome length = 9.2 ± 3.3 cm) were selected to reduce the effects of morphological variability between shoots of different ages (Ruocco et al., 2019; Tomasello et al., 2016).

Once collected, shoots were transported to the laboratory (about 15 min by boat) in coolers filled with ambient and aerated seawater. Plants were maintained under environmental conditions similar to those of the sampling site for 48 h prior to the experiment (Figure 1, Appendix S1: Figure S2, Table S1).

For each experimental period, the setup consisted of three temperature levels (the ambient seawater temperature and two increasing steps of 2°C) crossed with four levels of turbidity (0, 4, 16 and 34 mg/L), resulting in a total of 12 treatments in 12 cylindrical PVC tanks (30 L). After the acclimation, nine shoots of *P. oceanica* were randomly selected, labelled, attached to a PVC net and then placed within each experimental tank. Initially, all tanks were set to the ambient seawater temperature regardless of turbidity level. Subsequently, the temperature in selected tanks was increased at a rate of 1°C per hour until reaching the target level specified for the thermal treatments (e.g. Bosch-Belmar et al., 2022; Prusina et al., 2014). Once all tanks reached their respective target temperatures, they were left to acclimatize for 48 h. Metabolic measurements were then conducted after 2 days and repeated after 7 days of continuous exposure under the same conditions. Measurements for all treatments were conducted simultaneously within each period (i.e. across all 12 tanks at the same time), to ensure identical exposure duration before measurement. Measured leaves from each of the 9 shoots were independent and not reused between the 48-h and 7-day measurements.

The tanks had a conical–cylindrical shape at the base to reduce sediment deposition on any horizontal surfaces (Figure 1). Tanks were filled with 1.2 μm (Whatman GF/C) filtered seawater, which was kept circulating by a magnetic drive, centrifugal pump that collected water from the top of the tank and forced flow up from the centre point of the inverted pyramid at the base to maintain constant turbidity levels. Light was provided by custom-built LED arrays suspended above each tank. Each lamp consisted of 6 rows of blue LEDs (400–540 nm) and 5 rows of green LEDs (520–565 nm) to reproduce the spectral distribution characteristic of 10 m depth. A control unit regulated both photoperiod and light intensity throughout the day to simulate natural conditions. Light was highly homogenous, with a mean irradiance corresponding to 50, 80 and 92 μmol quanta $m^{-2} s^{-1}$ (measured just underneath the seawater surface of each tank using a Apogee SQ-520 full-spectrum quantum sensor) for the first, second and third periods, respectively (Madonia et al., 2021). These light intensities were estimated through a mathematical model capable of estimating the Photosynthetically Active Radiation (PAR) at the sea surface and along the water column as a function of the time and geographic location (Marcelli et al., 2005; Piermattei et al., 2006). The model used as input the in situ vertical profiles of downward spectral irradiance measured in the sampling area off the coast of Civitavecchia, where *Posidonia oceanica* shoots were collected, using a Satlantic OCR-507 multispectral radiometer. These field-derived measurements informed the light conditions applied in the mesocosm experiments.

Seawater within each aquarium was aerated and monitored daily for temperature (±0.1°C), pH (±0.01, WTW Multi 3420) and salinity (±0.1). Water was completely replaced every 3 days. Salinity level was kept constant at 35 psu by supplying osmotic water as needed. Water temperature within tanks was continuously monitored using HOBO Pendant loggers and maintained at treatment conditions using thermostatic controllers.

2.3 | Metabolic measurements

2.3.1 | Respiration and net photosynthesis

For each treatment level, we estimated oxygen production and consumption in nine individual leaves of *P. oceanica* experimental

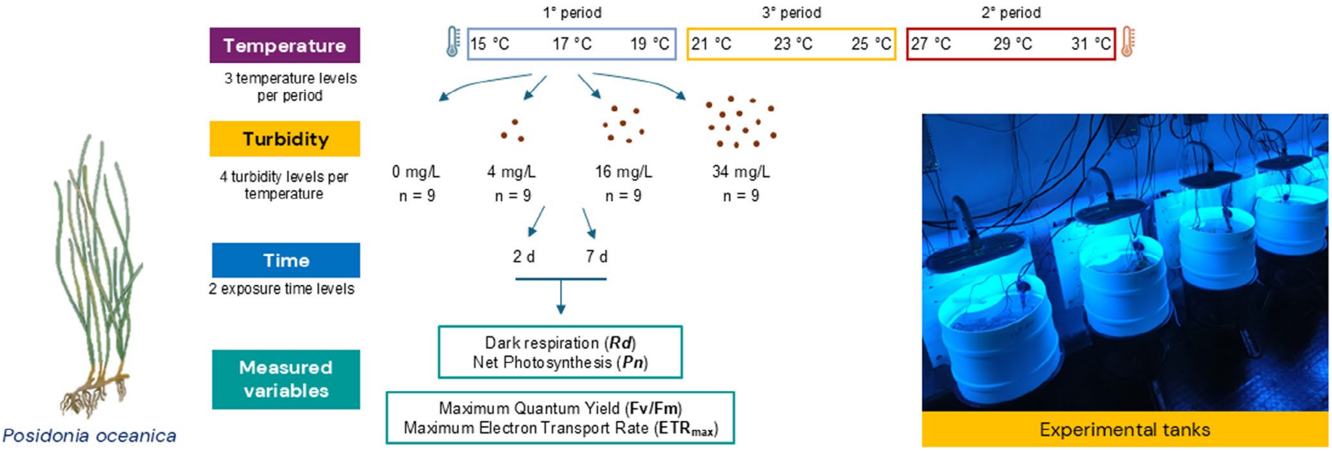

FIGURE 1 Experimental design. Illustration of experimental treatments. After collection, samples were randomly distributed among the experimental tanks and acclimated following the environmental conditions of the considered period (first period: Temperature of 15°C, salinity of 35 psu, light intensity of ~50 μmol quanta $m^{-2} s^{-1}$ and a photoperiod of 10:14 h light: Dark cycle. Second period: Temperature of 27°C, salinity of 35 psu, light intensity of ~80 μmol quanta $m^{-2} s^{-1}$ and a photoperiod of 10:14 h light: Dark cycle. Third period: Temperature of 21°C, salinity of 35 psu, light intensity of ~92 μmol quanta $m^{-2} s^{-1}$ and a photoperiod of 10:14 h light: Dark cycle).

shoots. Each individual was placed in a separate respirometric chamber (270 mL) filled with filtered (Whatman GF/F 0.7 µm) air-saturated seawater. As controls, three respirometric chambers were filled only with filtered seawater. The seawater within each chamber was consistently stirred using a magnet bar and an individual stirring device. Subsequently, the respirometric chambers were placed in temperature-controlled water baths (Grant Optima TX150), and the concentration of dissolved oxygen was measured using three optical oxygen meters (PyroScience Firesting O_2). Each meter was equipped with four optodes and a temperature compensation probe. Before each incubation, the oxygen electrodes were calibrated using the manufacturer's 1-point method (100% air-saturated water).

The dissolved oxygen concentration was then monitored under dark conditions every second for at least 90 min after the slope of the dissolved oxygen versus time had stabilized. Afterwards, the light was turned on, and the oxygen concentration was measured for another 90 min. The respirometric chambers were calibrated to replicate the light spectrum and intensity of the experimental treatment tanks, ensuring consistency with the conditions experienced by *Posidonia oceanica* under the different treatment levels.

Dark respiration (*Rd*) and net photosynthesis (*Pn*) rates were measured under dark and light conditions, respectively, and were calculated using the following equations (Rosewarne et al., 2016; Svendsen et al., 2016):

$$Rd_{(mg\ O_2\ gr^{-1} h^{-1})} = \frac{V_{\mathfrak{R}}}{g}|\beta| \tag{1}$$

$$Pn_{(mg\ O_2\ gr^{-1} h^{-1})} = \frac{V_{\mathfrak{R}}}{g}\beta \tag{2}$$

where V_R is the effective seawater volume (L) of the respirometric chamber, *g* is the dry weight (DW, 48 h at 60°C) as expressed in grams of *P. oceanica* and β is the slope of the regression line between oxygen concentrations and incubation time. While *Rd* represents dark respiration occurring when there is no light, *Pn* captures the net effect of photosynthesis and respiration during light conditions. It represents the balance between the oxygen produced through photosynthesis and the oxygen consumed through respiration during that time. Net primary production (NPP) was calculated by subtracting *Rd* from *Pn* (NPP = *Pn* − *Rd*) (Falkowski & Raven, 2007). Therefore, NPP represents the net primary production after accounting for both light and dark respiration, providing an estimate of the actual organic carbon accumulation by *P. oceanica* over time (Falkowski & Raven, 2007).

2.3.2 | Chlorophyll-*a* fluorescence

At the end of the incubation measurements, the photosynthetic activity of each individual of *P. oceanica* was assessed by measuring in vivo chlorophyll-*a* fluorescence of photosystem II (PSII) with a portable pulse amplitude modulation fluorometer (Junior-PAM, Waltz). For each sample, a Rapid Light Curve (RLC) was performed to evaluate differences in the photosynthetic capacity of *P. oceanica* at different irradiance levels. To ensure reliable measurements, RLC was performed immediately after *P. oceanica* was adapted to light (coming from NPP measurements) conditions to prevent the plant from dark-adapting (Beer et al., 2014). RLCs were obtained by calculating the electron transport rate (ETR) through PSII for nine incremental quantum flux densities of Photosynthetically Active Radiation (PAR) (0, 66, 90, 125, 190, 285, 420, 625, 845 µmol photons $m^{-2} s^{-1}$) for 20 s. The ETR was calculated as:

$$\mathrm{ETR}_{(\mu\mathrm{mol\ electrons\ m^{-2}\ s^{-1}})} = \Phi\mathrm{PSII} \times \mathrm{PAR} \times \mathrm{AF} \times 0.5$$

were ΦPSII is the effective quantum yield of PSII calculated according to (Genty et al., 1989) as ΦPSII = (*Fm*′-*Ft*)/Fm, obtained by applying a saturating light pulse at each irradiance level; PAR is the incident irradiance of PAR; AF is the absorption factor, which is the fraction of PAR absorbed by the leaves. It was calculated by covering a quantum sensor with the leaves of *P. oceanica* and calculating the fraction of PAR absorbed by the leaves as AF = (incident PAR − transmitted PAR)/incident PAR (Beer et al., 2014). Finally, the factor 0.5 represents the distribution of photons between photosystems II and I, assuming that 4 of the 8 electrons required to assimilate 1 CO_2 molecule are supplied by PSII (Beer et al., 2014). Maximum electron transport rate (ETR_{max}), an estimator of photosynthetic production, was obtained from the tangential function reported by Eilers and Peeters (Eilers & Peeters, 1988).

Maximum quantum yield (F_v/F_m) was determined on 15-min dark-adapted samples; this time was previously estimated to be adequate for *P. oceanica* to oxidize the reaction centres of photosystem II. As reported for other seagrasses, the age of *P. oceanica* leaves can affect fluorescence parameters (Enríquez et al., 2002). Therefore, fluorescence was measured three times for each individual of *P. oceanica*, starting from 4 cm from the base of the leaf. The average of these three replicates was considered in the following analysis. Then, we measured the minimum (basal) fluorescence (F_o) and the maximum fluorescence (F_m) after a saturation pulse (9000 mmol photon $m^{-2} s^{-1}$, 800 ms) of actinic light and estimated the maximum quantum yield as $F_v/F_m = (F_m - F_o)/F_m$ (Murchie & Lawson, 2013). F_v/F_m ratio represents the maximum potential yield and it is usually used as a measure of stress that affects components of photosystem II, such as the D1 protein (Beer et al., 2014).

2.4 | Data analysis

For each treatment level investigated, the performance of *P. oceanica* was modelled by a continuous nonlinear reaction norm (i.e. Thermal Performance Curve—TPC) using the rTPC pipeline (Padfield et al., 2021) in the R (v. 4.4.2) software environment. The best nonlinear least squares (NLLS) regression model was chosen from the 27 provided in the 'rTPC' package (v. 1.0.2). Of the 27 models tested, 6 were removed because they failed to fit data (see Supporting Information for further details). The selection of the best model was based on the AICc criterion (Angilletta, 2006), and models within a delta of 2 AICc were retained. Among the selected models, the final choice was made based on the model that best fitted the response of *P. oceanica* across all turbidity levels. After identifying the best-predicted model, model assumptions were visually assessed using the 'test.nlsResiduals' function of the 'nlstools' package (Baty et al., 2015). Additionally, this function conducted formal tests to assess the normality of residuals and autocorrelation. A square-root transformation was applied to meet model assumptions. Subsequently, a bootstrapping procedure was employed by resampling the data to estimate model prediction and parameter confidence intervals. TPC parameters, such as optimal temperature (T_{opt}), thermal performance breadth (T_{br}) and rate at optimum temperature (μmax) were estimated for each selected model and used to mechanistically describe the seagrass variation in thermal sensitivities and turbidity. In particular, T_{br} was calculated as the range of temperatures where the curve's rate is above 69% of the maximum value (Caretto et al., 2015; Matzelle et al., 2015).

3 | RESULTS

Temperature and turbidity significantly influenced the physiological performance of *P. oceanica*, with a general decline in performance observed as turbidity and exposure time increased. These effects were accompanied by contractions in the thermal tolerance ranges, highlighting the species' sensitivity to these environmental stressors.

3.1 | Respiration and net photosynthesis

We observed that intermediate (16 mg/L) and high (34 mg/L) levels of turbidity caused a strong decrease of 40% to 50% in the thermal performances of *P. oceanica*. Across the range of temperatures investigated (15–31°C), the net photosynthetic rates (*Pn*) of *P. oceanica* followed a temperature-dependent relationship with typical nonlinear responses across all levels of turbidity and time investigated (Figure 2a,b). Overall, *Pn* increased with temperature up to a thermal optimum (T_{opt}) identified at 23°C for all turbidity levels and times (Figure 2a,b; Appendix S1: Table S2). Increasing turbidity caused a decrease in *Pn* performance (μ_{max}) and a narrowing of the thermal tolerance window (T_{br}; Figure 2, Appendix S1: Table S2). After 2 days of treatment, the highest turbidity treatment (34 mg/L) exerted larger effects on the *Pn* of *P. oceanica*, with values that were markedly lower compared to the other treatments. After 7 days, we observed an overall reduction in the breath (T_{br}) of the TPC across all turbidity levels and an overall increase in *Pn* values (Figure 3, Appendix S1: Table S2). Moreover, there was an overlap of TPCs between turbidity levels of 0 and 4 mg/L that presented significantly higher performance values compared to the 16 and 34 mg/L treatments which instead tended to cluster around each other (Figure 2, Appendix S1: Table S2).

In contrast to net photosynthetic rates, dark respiration rates (*Rd*) increased up to 31°C with no identification of an optimum temperature (Figure 2c,d). Moreover, there were no visible effects of increased turbidity on *Rd*, except for the fact that after 2 days we observed lower *Rd* values at 15–19°C under the turbidity levels of 16 and 34 mg/L compared to the other turbidity treatments (Figure 2c,d).

Net Primary Production (NPP) of *P. oceanica* showed a similar trend of *Pn*, with NPP increasing with temperature up to an optimum (T_{opt} = 23°C) and a decrease in performance (μ_{max}) caused by increasing turbidity levels (Figure 2e,f; Appendix S1: Table S2). However, in contrast to *Pn*, the thermal performance breadth (T_{br}) of NPP increased at high turbidity levels (Figure 3, Appendix S1: Table S2).

Overall, a performance reduction of 40% for *Pn* (0.5 O_2 mg gr^{-1} DW h^{-1}) and 20% for NPP (0.2 O_2 mg gr^{-1} DW h^{-1}) was observed from the control to the highest turbidity level (34 mg/L), along with a narrowing of the optimal tolerance window of 3–4°C. Particularly, *P. oceanica* exposed to the more extreme treatment (high turbidity (34 mg/L) and increased exposure time (7 days)) presented a reduced optimal thermal tolerance range from 22 to 24°C, with respect to control (19.5 to 26.5°C).

3.2 | Chlorophyll-*a* fluorescence

The analysis of ETR_{max} showed a similar trend to what was observed for the physiological responses previously reported, with similar optimum temperatures (T_{opt} ~ 23°C) and with an overall effect of increasing turbidity that causes a reduction in the photosynthetic performance of *P. oceanica* and a contraction of the species' tolerance range (Figure 4).

The analysis of maximum photosynthetic efficiency (Fv/Fm) showed how the increase in temperature caused a decrease in *P. oceanica* photosynthetic performances, as evidenced by reduced Fv/Fm values. This decrease was accentuated with increasing exposure time and was not dependent on turbidity (Figure 5). Moreover, after 7 days of treatment exposure, it was possible to identify an optimum temperature of 19°C (Figure 5, Appendix S1: Table S3).

4 | DISCUSSION

Our mesocosm experiment underscored the critical role of stressor properties in influencing *P. oceanica*'s responses to turbidity and temperature. Intermediate (16 mg/L) and high (34 mg/L) turbidity levels significantly affected the seagrass' photosynthetic performance. Prolonged exposure to these stressors further diminished the species' functioning, leading to a narrowing of its thermal tolerance window by 3–4°C. These findings highlight the vulnerability of *P. oceanica* to combined environmental stressors, emphasizing the urgent need to integrate an understanding of how organisms respond to multi-stressor interactions into conservation and restoration frameworks.

Recent studies have underscored the increasing impact of water turbidity, exacerbated by land use changes in coastal areas, on

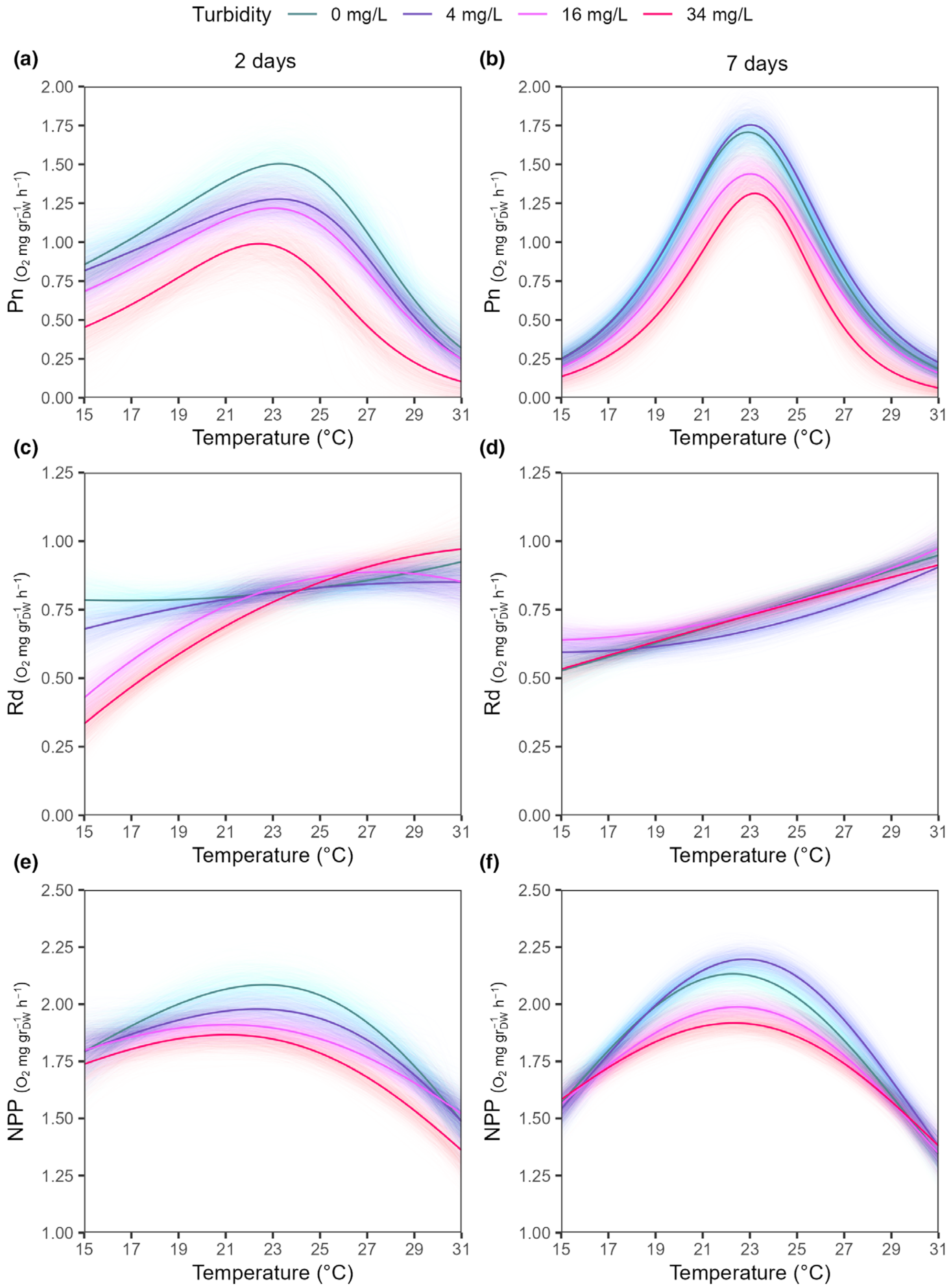

FIGURE 2 Net Photosynthesis (Pn, *a* = at 2 days, d = at 7 days), Dark Respiration (Rd, b = at 2 days, e = at 7 days) and Net Primary Production (NPP, c = at 2 days, f = at 7 days) of *Posidonia oceanica* after 2 and 7 days of treatment exposure. Thermal performance curves of *P. oceanica* exposed to increasing turbidity levels (0–34 mg/L). Solid lines represent the average fitted values ($n=9$ for each temperature) according to the selected model (Pawar for Pn and NPP; quadratic for Rd). Shaded lines are bootstrapped predictions showing ±95% CI based on 999 iterations. Data were square-root (Pn and Rd) and square-root +3 (NPP) transformed.

primary producers functioning, identifying it as a critical environmental stressor (Zweifler et al., 2021). These responses can be primarily explained through direct and indirect physiological mechanisms. Light attenuation caused by higher turbidity directly reduces photon availability at PSII reaction centers, as indicated by our ETR_{max} measurements and consistent with recent findings on Mediterranean seagrasses (Bité et al., 2007; Marín-Guirao et al., 2018; Ruiz & Romero, 2003). This photosynthetic impairment has been quantified through chlorophyll fluorescence measurements, with ETR_{max} reductions of up to 50% observed under high turbidity conditions (Ralph et al., 2007; Silva & Santos, 2004). Additionally, sediment particles accumulating on leaves can create a physical barrier potentially impeding gas exchange with the surrounding water (Brodersen et al., 2017). Sediment may also alter nutrient dynamics and impair habitat structure, ultimately contributing to the decline of *P. oceanica* meadows, especially close to urban areas (Ruiz & Romero, 2003).

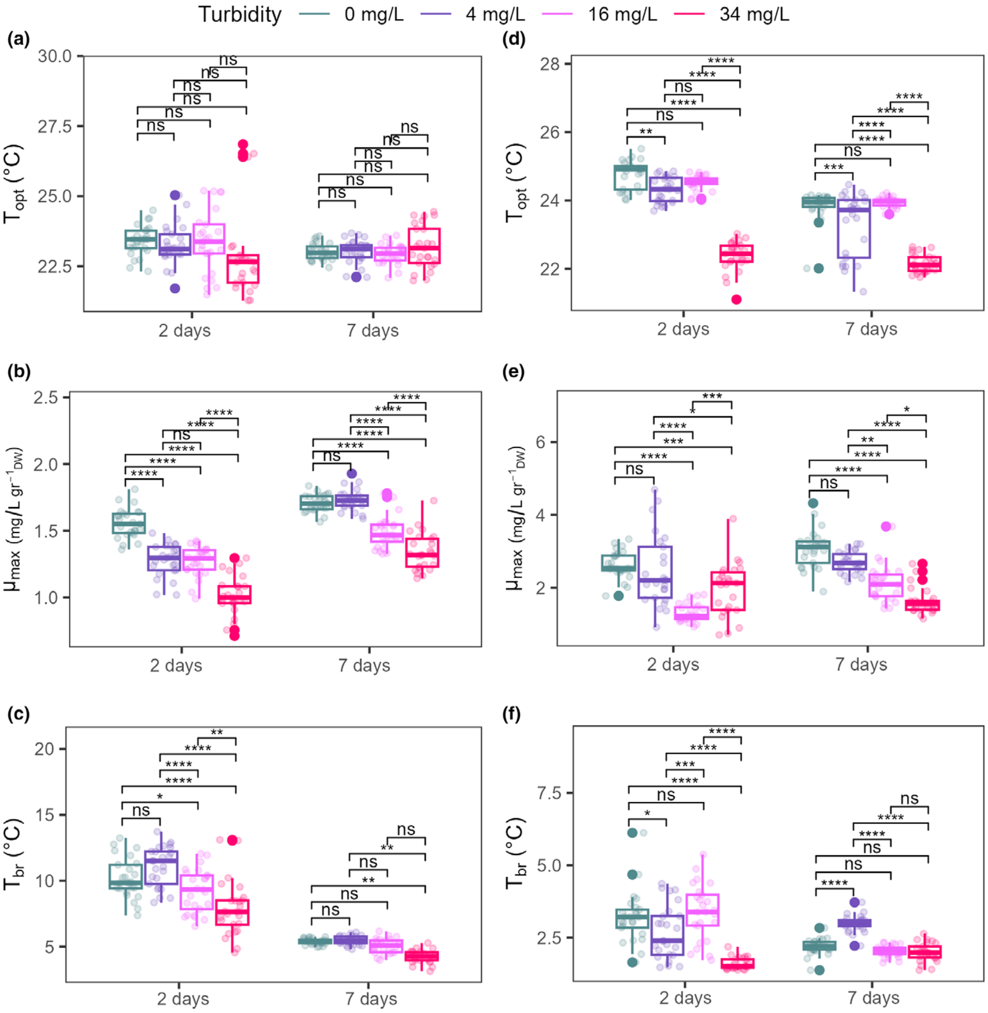

FIGURE 3 Thermal performance parameters for Net Photosynthesis (*Pn*, a–c) and Net Primary Production (NPP, d–f) of *Posidonia oceanica* after 2 and 7 days. T_{opt}, optimum temperature; μ_{max} = maximum rate; T_{br} = thermal performance breadth estimated at 69%. Colour-coded boxes represent turbidity levels: Blue (0 mg/L), purple (4 mg/L), violet (16 mg/L) and red (34 mg/L). Significance levels were adjusted using the Bonferroni correction ($p < 0.0001$ ****, $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $p \geq 0.05$ ns).

Such declines may lead to biodiversity loss and reduced ecological productivity within seagrass ecosystems (Orth et al., 2006). Turbidity values equal to or greater than 16 mg/L significantly impaired *P. oceanica* performance, particularly through reduced photosynthetic capacity over time. This emphasizes the dual influence of stressor intensity (increasing sediment concentrations) and duration (2 or 7 days of treatment). Prolonged exposure may amplify the negative effects on photosynthetic capacity and overall plant health, suggesting that chronic turbidity events could have far-reaching implications for the resilience of *P. oceanica* meadows (Serrano et al., 2011). Over time, this sustained stress may not only impair individual plant functioning but also compromise the structural integrity and ecosystem services provided by these seagrass habitats.

Temperature emerges as a primary driver of seagrass metabolic processes, underscoring the need to assess how stressors interact with natural temperature fluctuations to better predict species persistence under global warming scenarios (Sokolova et al., 2012; Staudt et al., 2013). Our findings align with and extend recent studies on *P. oceanica*'s thermal physiology, in which similar optimal temperatures (22–24°C) were found (Rinaldi et al., 2023; Savva et al., 2018), but our results provide new insights by demonstrating how turbidity can constrain the thermal tolerance window of the species, which can impair its growth dynamics and photosynthetic processes (Gacia & Duarte, 2001; Ruiz & Romero, 2003). This constraint is particularly relevant given the warming trend in the Mediterranean Sea (Garrabou et al., 2022; Pastor et al., 2020), as it suggests turbidity could exacerbate temperature stress effects.

The interaction between turbidity and temperature likely operates through metabolic compensation: as temperature rises, a greater photosynthetic capacity would typically be required to offset increased respiratory demands. However, light limitation caused by turbidity can hinder this compensatory mechanism, preventing *P. oceanica* from maintaining metabolic balance under such conditions (Marín-Guirao et al., 2018). Our work is the first to quantify this interaction, showing that high turbidity (>16 mg/L) can reduce *P. oceanica* thermal tolerance window by up to 4°C. The identified

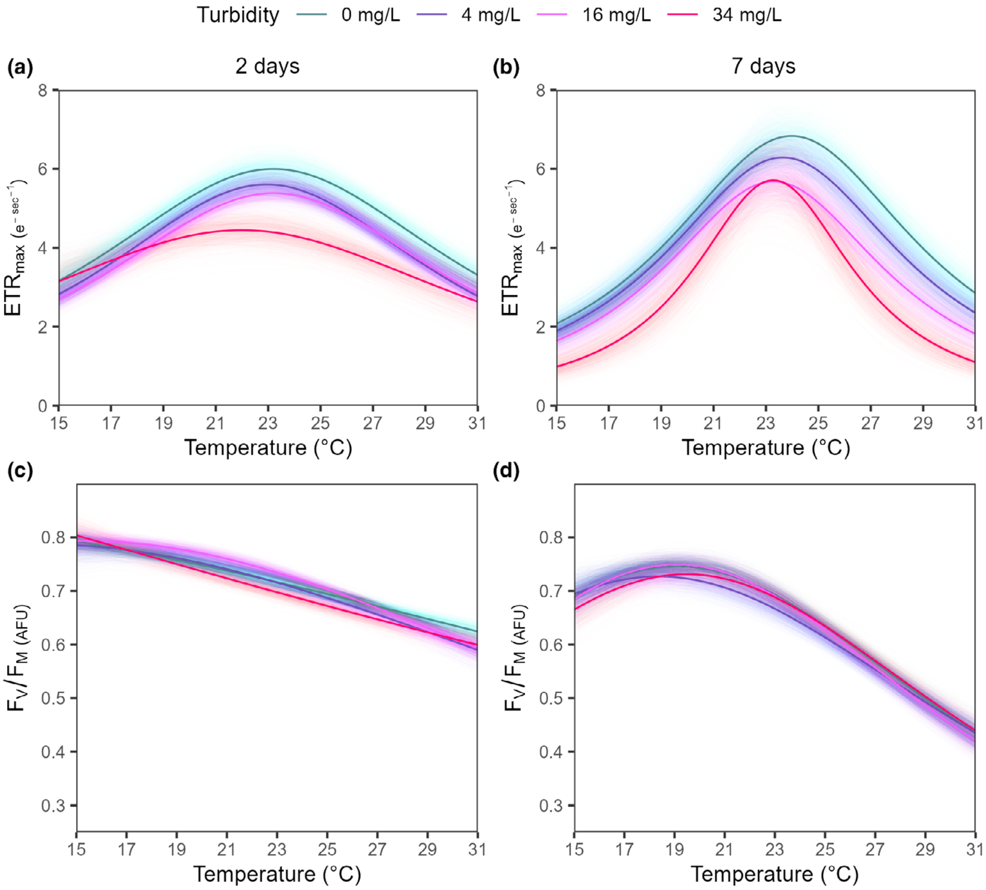

FIGURE 4 Maximum Electron Transport Rate (ETRmax, a = at 2 days, b = at 7 days) and Maximum Quantum Yield (FV/FM, c = at 2 days, d = at 7 days) of Posidonia oceanica after 2 and 7 days of treatment exposure. Thermal performance curves of P. oceanica exposed to increasing turbidity levels (0–34 mg/L). Solid lines represent the average fitted values ($n = 9$ for each temperature) according to the selected model (Flinn). Shaded lines are bootstrapped predictions showing ±95% CI based on 999 iterations. ETRmax data were square-root transformed.

turbidity threshold aligns with recent Mediterranean-wide assessments of water quality impacts on seagrass health (Fernández-Torquemada et al., 2020) and provides a clear management target. Moreover, the observed narrowing of *P. oceanica's* optimal tolerance window may compromise its persistence and adaptive capacity under present and projected warming scenarios. With a reduced thermal margin, *P. oceanica* operates closer to its physiological limits, meaning that even small increases in water temperature can overwhelm its compensatory mechanisms, resulting in carbon imbalances, reduced growth and higher mortality rates. This increased vulnerability undermines the resilience and adaptive potential of *P. oceanica* meadows, rising the risk of irreversible ecosystem degradation under future climate conditions.

Our findings extend previous work on isolated effects of temperature (Rinaldi et al., 2023; Savva et al., 2018) and turbidity (Ruiz & Romero, 2003) by providing insights into their combined effects on seagrass physiology. High turbidity narrowed the thermal tolerance window of *P. oceanica* by 4°C, consistent with studies showing that environmental stressors can constrain species thermal tolerance (Pazzaglia et al., 2020; Wang et al., 2022). While Pazzaglia et al. linked nutrient stress to reduced thermal tolerance under eutrophic conditions, our results show that turbidity creates similar constraints through different mechanisms. These findings suggest that projections of warming impacts may underestimate seagrasses vulnerability in turbid coastal waters (Wang et al., 2022). Our approach of measuring metabolic traits across seasonal temperature variations provides a more ecologically relevant assessment than traditional single-season experiments, better reflecting natural habitat conditions. The interactive effects we documented indicate that turbidity not only directly impacts seagrass through light limitation, as shown by Ruiz and Romero (2003), but also fundamentally alters their capacity to respond to thermal stress. It is a finding that bridges previous research on isolated stressor effects with more ecologically realistic multi-stressor scenarios.

Integrating scientific insights into practical conservation plans while considering complex environmental interactions can significantly enhance the precision and effectiveness of management strategies (Hendriks et al., 2017). Trait-based approaches have significant practical applications in ecological conservation and restoration. Particularly, eco-physiological traits are increasingly valued as indicators of organismal performance and ultimately fitness, offering faster and equally reliable assessments compared to traditional

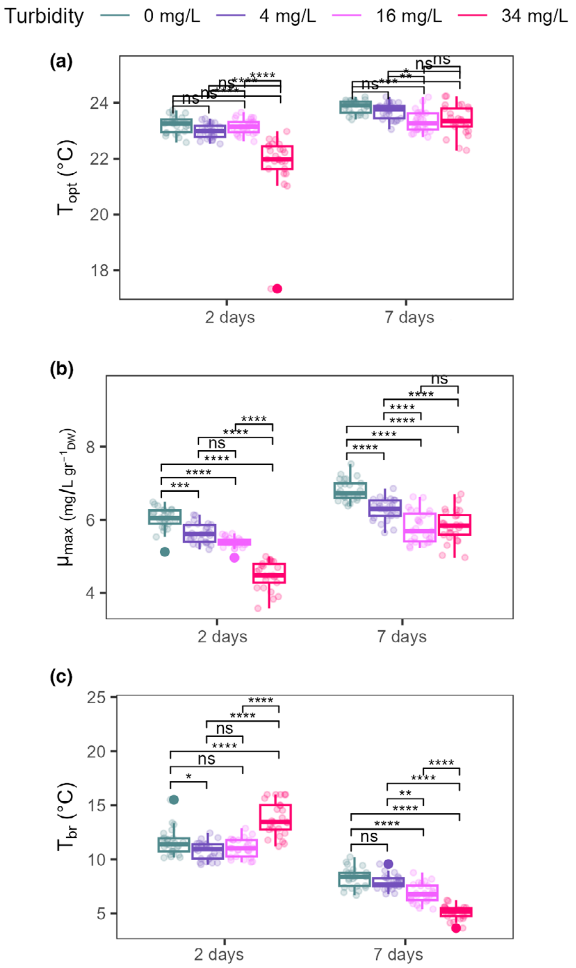

FIGURE 5 Thermal performance parameters for Electron Transport Rate (ETRmax) of Posidonia oceanica after 2 and 7 days. (a) Topt, optimum temperature; (b) µmax = maximum rate; (c) Tbr = Thermal performance breadth estimated at 69%. Colour-coded boxes represent turbidity levels: Blue (0 mg/L), purple (4 mg/L), violet (16 mg/L) and red (34 mg/L). Significance levels were adjusted using the Bonferroni correction ($p < 0.0001$ ****, $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $p \geq 0.05$ ns).

traits. These traits have been effectively used to predict species distributions and assess ecological risks, as demonstrated in recent studies, underscoring their growing relevance as essential management tools (Bosch-Belmar et al., 2021, 2022; Marchessaux et al., 2022). The specific thresholds we identified (turbidity <16 mg/L, optimal temperature range 19.5–26.5°C) provide quantitative guidelines for both conservation planning and coastal management (NOAA, 2020), informing regulations on turbidity levels during human activities (e.g. dredging, coastal development, etc.), guiding, for example, conservation actions or restoration site selection and informing the timing of restoration efforts. Measured metabolic indicators (*Pn*, NPP, ETR_{max}) complement traditional monitoring metrics and can support long-term monitoring and early-warning systems by detecting stress before visible meadow damage occurs (Moreno-Marín et al., 2018). As direct measures of performance linked to fitness (Andersson et al., 2022), these traits offer a proactive management tool when integrated into real-time monitoring networks using cost-effective technologies like IoT sensor systems (dos Santos Alvalá et al., 2019). The application of metabolic traits in this context remains limited, likely due to the specialized knowledge, instruments and techniques required for their measurement. However, their direct link to organismal functioning and rapid, measurable response makes them a promising tool for conservation, with demonstrated applicability in several case studies.

Our findings hold relevant implications for the ecosystem services provided by *P. oceanica*, particularly regarding its ability to sustain net primary production (NPP) under stress conditions. Elevated turbidity levels directly impair oxygen production, translating into a reduced growth rate (Larkum et al., 2006). This, in turn, may lead to phenological, morphological and ecological effects, including shoot shortening, reduced leaf per individual, diminished structural complexity and slower meadow spread. These changes ultimately influence ecosystem stability by altering sediment dynamics, nutrient recycling and coastal erosion protection with potential consequences for human well-being (Campagne et al., 2015; Costanza et al., 1997). By concentrating on metabolic responses, restoration strategies can be refined with precise thresholds, such as specific turbidity and temperature limits, to optimise intervention timing and improve seagrass recovery outcomes.

Our study provides valuable insights, but certain aspects should be carefully considered when integrating and applying these findings. While our seasonal sampling approach effectively captured natural temperature variations, the 7-day exposure period may not fully reflect the species potential long-term acclimation, as suggested by recent extended-duration studies (Egea et al., 2018). Although different seagrass species have shown a high degree of adaptation to thermal stressful events such as heat waves (Nguyen et al., 2020; Pazzaglia et al., 2022), it remains unclear whether the species can develop similar adaptive responses to pulse turbidity events or the interaction of multiple stressors. Therefore, future studies investigating these types of adaptations (i.e. at the epigenetic level) are needed. Additionally, mesocosm conditions cannot fully replicate the complexity of field environments where multiple stressors (e.g. salinity, nutrients, hydrodynamics) may influence responses (Egea et al., 2018; Moreno-Marín et al., 2018). Further field validation of these thresholds is recommended, particularly across different meadow depths and geographical regions.

5 | CONCLUSIONS

Our research demonstrates critical implications for seagrass conservation and restoration strategies. Establishing quantitative thresholds for turbidity related to temperature can guide site selection and preservation of habitat of seagrasses like *P. oceanica* (Gacia & Duarte, 2001; Ruiz & Romero, 2003). The integration of metabolic traits into monitoring protocols, beyond traditional metrics like coverage and density, provides earlier detection of stress and a more comprehensive assessment of restoration success (Purvaja et al., 2020;

Stipcich et al., 2022). Metabolic indicators like net primary production (NPP) and photosynthetic efficiency (ETRmax) may serve as sensitive metrics for ongoing habitat monitoring, offering an advantage over traditional density-based metrics. Operationalizing these thresholds within coastal management policies could enhance resilience against climate-induced stressors (Li et al., 2010).

The demonstrated interaction between turbidity and temperature is particularly relevant for the Mediterranean Sea, classified as 'rapidly warming' (Pastor et al., 2020). Our findings suggest that managing local water quality could help build resilience against climate change impacts (Pörtner & Farrell, 2008). This research supports an integrated approach to conservation, combining physiological thresholds with practical management guidelines to preserve these valuable habitats and their ecosystem services in the face of increasing environmental pressures.

AUTHOR CONTRIBUTIONS

Mar Bosch-Belmar, Francesco Paolo Mancuso and Gianluca Sarà: idea conception and experimental design; Viviana Piermattei and Marco Marcelli: design, development and testing of the experimental components (tanks and light systems); Mar Bosch-Belmar, Francesco Paolo Mancuso, Mario Francesco Tantillo, Martina Russi, Daniele Piazzolla and Alice Madonia: data acquisition; Mar Bosch-Belmar and Francesco Paolo Mancuso: data curation, analysis and visualization; Mar Bosch-Belmar, Francesco Paolo Mancuso and Gianluca Sarà: writing the original draft; Mar Bosch-Belmar, Francesco Paolo Mancuso and Gianluca Sarà and Marco Marcelli: review and editing; Viviana Piermattei, Marco Marcelli and Gianluca Sarà: funding acquisition.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.qfttdz0sv (Bosch-Belmar et al., 2025).

STATEMENT ON INCLUSION

Our study brings together authors with diverse scientific backgrounds. Sample collection was made according to the local marine conservation policy. Whenever possible, our research was discussed with local stakeholders to seek feedback on the questions to be tackled and the approach to be considered.

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SUPPORTING INFORMATION

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

Figure S1. Realised thermal niche of *Posidonia oceanica* in the Mediterranean Sea.

Figure S2. Detailed experimental design for *P. oceanica*.

Table S1. Average environmental conditions of the sampling site through the three periods.

Table S2. Thermal performance parameters for Net Photosynthesis (*Pn*) and Net Primary Production (NPP) of *P. oceanica* after 2 and 7 days.

Table S3. Thermal performance parameters for maximum Electron Transport Rate (ETR_{max}) of *P. oceanica* after 2 and 7 days.

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