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Unveiling growth and carbon composition of macroalgae with different strategies under global change

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A B S T R A C T

Marine macroalgae ecosystems are increasingly recognized as potential contributors to carbon sequestration within blue carbon strategies. This study investigates how the carbon storage capacity of two macroalgal species with different living strategies, *Fucus vesiculosus* (k-strategy, slow-growing) and *Ulva lactuca* (r-strategy, fast-growing), respond to the individual or combined impacts of two drivers of global change, eutrophication and marine heatwaves. Differences in growth, biomass and carbon accumulation were assessed after 7 and 14 days in two experiments (field and laboratory) that tested different combinations of nutrient enrichment (increase nutrient/surface area of 1 g/cm^2 in the field experiment and a concentration of 10 ml/l of Provasoli solution in the laboratory) and warming (5 °C increase) treatments. Results revealed that nutrient addition treatments had significant effects, reducing carbon incorporation by up to 22.5 % in *F. vesiculosus* compared to control. This reduction was particularly evident in the field experiment, suggesting that eutrophication negatively impacts the carbon storage potential of this slow-growing species. However, *F. vesiculosus* demonstrated greater resilience in maintaining biomass stability, whereas *U. lactuca* exhibited reduced growth and carbon accumulation under natural conditions. These findings highlight species-specific differences in carbon assimilation and biomass composition among macroalgae, which can influence their potential contribution to carbon cycling and storage in marine ecosystems, shaped by their ecological and physiological traits, and emphasize the importance of nutrient management for optimizing blue carbon storage. This research contributes to our understanding of macroalgae's role in climate mitigation and underscores the need for targeted conservation strategies to enhance their ecosystem services.

1. Introduction

Achieving the goal set forth by the Paris Agreement and further reinforced by the United Nations Climate Change Conference (COP28), which entails limiting the global temperature increase to 1.5 °C, requires a worldwide reduction in CO_2 emissions and an increase in natural carbon sinks (IPCC, 2021; Seddon et al., 2021). The significant role that some marine vegetated ecosystems play as long-term carbon sinks is receiving growing attention, with the conservation and restoration of these ecosystems beginning to be considered as potential nature-based solutions to climate change, commonly known as blue carbon strategies (Duarte et al., 2013; Macreadie et al., 2019; Nellemann et al., 2009).

Until now, blue carbon research has primarily focused on marine vegetated coastal ecosystems growing in soft sediments (e.g., tidal marshes, mangrove forests, and seagrass beds). These ecosystems are highly productive (Duarte and Chiscano, 1999; Mateo et al., 1997; McLeod et al., 2011) and allocate a large fraction of their biomass in the soil compartment as roots and rhizomes (Duarte and Cebrián, 1996). In addition, these ecosystems exhibit high sedimentation rates (Rodriguez et al., 2020; Wilkinson et al., 2018) that contribute to high carbon burial rates and the formation of large organic carbon stocks in the soil compartment (Serrano et al., 2019) where the lack of oxygen prevent its remineralization and enhance its long-term storage (Mateo et al., 1997). However, non-accreting vegetated coastal ecosystems, dominated by large habitat-forming seaweeds, have traditionally not been considered as long-term blue carbon sinks (Filbee-Dexter and Wernberg, 2020; Krause-Jensen et al., 2018). Macroalgae forest rank among the most productive vegetated habitats globally (Duarte et al., 2022). However, most macroalgal communities lack belowground structures and grow in rocky environments, where on-site carbon burial is likely limited (Brenan et al., 2024). However, recent evidences suggest that seaweed habitats could contribute to long term storage of carbon through the export of biomass and burial in soft sediments beyond their own habitats, including coastal sediments (Erlania et al., 2023; Moreda et al., 2024), the deep ocean (Queirós et al., 2019) or adjacent blue carbon ecosystems (e.g., seagrass (Ortega et al., 2020)). Thus, their high

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productivity along with their substantial expanse and global distribution render macroalgal ecosystems as potentially larger carbon sinks than the traditional blue carbon ecosystems (Duarte et al., 2022; Filbee-Dexter and Wernberg, 2020). Moreover, while many studies emphasize the role of macroalgae in exporting biomass to adjacent soft sediment habitats for long-term carbon burial, recent evidence also demonstrates that certain macroalgae can sequester carbon in situ. For example, de los Santos et al. (2023) showed that in a temperate wetland seascape, rhizophytic macroalgal beds, alongside saltmarshes and seagrass meadows, exhibited significant sedimentary organic carbon and nitrogen sequestration along a vertical gradient. This finding suggests that macroalgae, such as *Caulerpa prolifera*, can effectively trap carbon within their own habitats, further reinforcing their reviewed role in climate mitigation (Krause-Jensen and Duarte, 2016; Yong et al., 2022).

Macroalgae are a very extensive and diverse group of species that show a broad range of structural and physiological features, that likely affect their potential as long-term carbon deposits. For instance, different survival strategies, which condition the biomass accumulation rate, the molecular composition of the algae biomass and, the biomass turn-over rate are likely to influence the carbon storage capacity across macroalgae species (Pessarrodona et al., 2022; Trevathan-Tackett et al., 2015). Assessing the potential role of macroalgae as carbon sinks requires understanding how differences among species determine their long-term carbon sequestration capacity (Fujita et al., 2023). For example, r-species (e.g., green algae as *Ulva* spp.) are fast growing species that can incorporate significant amounts of atmospheric carbon in their biomass in a relatively shorter-time period than k-species (e.g., brown algae such as *Fucus* spp.), which are a slower growing species (Pessarrodona et al., 2022). However, k-species usually exhibit larger biomass, extended longevity and slower turnover rate than r-species as their more recalcitrant organic matter prevent decomposition and the return of carbon to the atmosphere as CO_2 (Conover et al., 2016). On the other hand, global change pressures, such as increasing temperature and eutrophication, are exerting considerable pressure on macroalgae populations, with differentiated impacts between r-strategy and k-strategy species. Eutrophication (defined as the process by which water bodies become enriched with nutrients, often leading to excessive algal growth and altered ecosystem dynamics, Smith and Schindler, 2009) and marine heatwaves (periods of prolonged, unusually high sea surface temperatures, Hobday et al., 2016) have been shown to influence the carbon storage capacity of coastal vegetated ecosystems. In seagrass systems, for example, elevated temperatures have been linked to changes in carbon metabolism and dissolved organic carbon fluxes (Yamuza-Magdaleno et al., 2025), while increased nutrient loads accelerate the breakdown of refractory dissolved organic carbon (Zhang et al., 2025). By analogy, these studies suggest that similar global change drivers could significantly affect the carbon sequestration potential of macroalgal communities. Understanding these impacts is key to ultimately assess the potential of seaweeds as effective nature-based solutions for climate change.

Eutrophication may favour r-strategy algae species, characterised by rapid growth and reproduction in nutrient-rich environments (Teichberg et al., 2010). However, this process can lead to a decline in brown algae species (k-strategy), which prefer more stable environments and are less resilient (Straub et al., 2019). The latter are important in terms of biodiversity and as habitats for other marine species but are decreasing in some regions due to competition with fast-growing algae and the effects of climate change, such as sea temperature increase and higher frequency of extreme events (de Azevedo et al., 2023; Smith et al., 2023; Verdura et al., 2019). The shift from large species dominated macroalgae communities to small fast-growing species can potentially reduce the carbon storage capacity of the habitat (Hall et al., 2024). Besides, sea temperature increase affects the metabolic pathways of macroalgae. For instance, marine heatwaves can lead to community respiration rates increasing over gross primary productivity leading to a reduction in net community productivity, which could have significant consequences in carbon sequestration and storage capacity of macroalgae communities (Egea et al., 2023). In addition, eutrophication and warming may occur simultaneously in different regions leading to antagonistic or synergistic effects on macroalgae metabolism and net primary productivity, and, as a consequence, alter their carbon storage capacity (Brooks and Crowe, 2018).

In this study, we investigate the individual and combined effects of two global change pressures, marine heatwaves and eutrophication, on the growth (assessed through area and weight) and carbon assimilation capacity of two macroalgae species, representative of different life strategies: the common ephemeral seaweed capable of rapid growth *Ulva lactuca* (r-strategist) and the representative of one of the most common slow growing intertidal species (k-species) across the Northern Temperate Atlantic region *Fucus vesiculosus*. We carried out a field experiment and replicated it in a laboratory setting to control for factors that could not be managed in the field. The aim was to understand how these characteristics, associated with different survival strategies, influence the role of macroalgae as blue carbon sinks and the vulnerability of this ecosystem service to global change.

2. Methods

2.1. Studies location and species collection

The field experiment was conducted at the Malahide marina, on the east coast of Ireland (53°27′12″N, 06°9′5″W), from the 24th of August until the September 7, 2021. The marina is located in a sheltered area at the mouth of the Broadmeadow Estuary (Brooks et al., 2016). Laboratory experimentation was run at the IHCantabria Hydrobiology Laboratory (Spain) from 31st of January until February 14, 2022.

At Malahide, *F. vesiculosus* fronds were harvested from the lower intertidal rocks, during extreme low tides on August 24, 2021 (Fig. 1). Likewise, *U. lactuca* fronds were gathered on the same day and from the same pontoon where the experiment was set up. For the laboratory experiment, fronds of both species were collected on January 28, 2022 from the same site in the Ría de Boo (El Astillero, Cantabria, 43°24′25″N, 3°49′48″W) (Fig. 1). The Ría de Boo is an estuarine inlet influenced by tidal fluctuations. Fronds were gently cleaned of epiphytes after its collection.

In the field experiment, both sets of fronds were immersed in seawater for a period of less than 2 h before being affixed to their designated positions. For the laboratory experiment, algal material of each species was acclimated separately in aeration for 48h in a controlled chamber with a temperature of 16 °C, a light intensity of 100 μmol photons/m^2s and a long day photoperiod of 14:10 h (L:D), to reproduce Malahide Bay (Ireland) summer conditions.

2.2. Previous thermal exposition comparison

To assess whether macroalgae from both locations (Malahide and Cantabria) experienced similar thermal conditions prior to collection, we analysed sea surface temperature (SST) data from the three months preceding each sampling event. Specifically, we extracted SST values from May 24 to August 23, 2021, for Malahide and from October 15, 2021, to January 14, 2022, for Cantabria from OCLE database (de la Hoz et al., 2018). A two-sample *t*-test was performed to compare the mean temperatures at both sites. This analysis aimed to determine whether seasonal differences in collection dates could have influenced the physiological state of the algae before experimentation.

2.3. Experimental design and set up

The experimental design incorporated two factors: temperature, simulating marine heatwaves (MHWs), and eutrophication. The effect of MHWs was assessed by considering two temperature treatments: T0 (no increase in temperature) and T+ (elevated temperature). The

Fig. 1. Location of species collection at Malahide marina (Dublin, Ireland) in the left panel and at Boo ria (Cantabria, Spain) in the right panel.

temperature increase treatment was defined based on the definition of MHWs by Hobday et al. (2019, 2016), an increase in seawater temperatures over the seasonal 90th percentile, calculated over a span of at least 30 years for a minimum of 5 consecutive days. Sea surface temperature records spanning 1985 to 2015 were obtained from the OCLE database at the nearest point to Malahide marina (de la Hoz et al., 2018). Calculations were performed using the R package "heatwaveR" (Schlegel and Smit, 2018). The results guided the application of a 5°C increase to replicate a heatwave scenario, ultimately resulting in a control temperature of 16°C and a temperature treatment of 21°C.

The eutrophication factor was assessed through two nutrient treatments: no nutrient enrichment (N0) and nutrient enrichment (N+). The nutrient enrichment treatment was achieved by adding 0.022 g N/cm^2 and 0.014 g P/cm^2 in the field experiment and 0.14 ml N/L and 0.0225 mg P/L in the laboratory experiment.

This resulted in a total of four treatment groups: control (N0T0), nutrient enrichment (N+T0), temperature elevation (N0T+), and a combination of both (N+T+). To encompass the short and medium-term response to MHWs and eutrophication, two sampling periods were considered: 7 days (t7) and 14 days (t14) (i.e. half of the fronds were

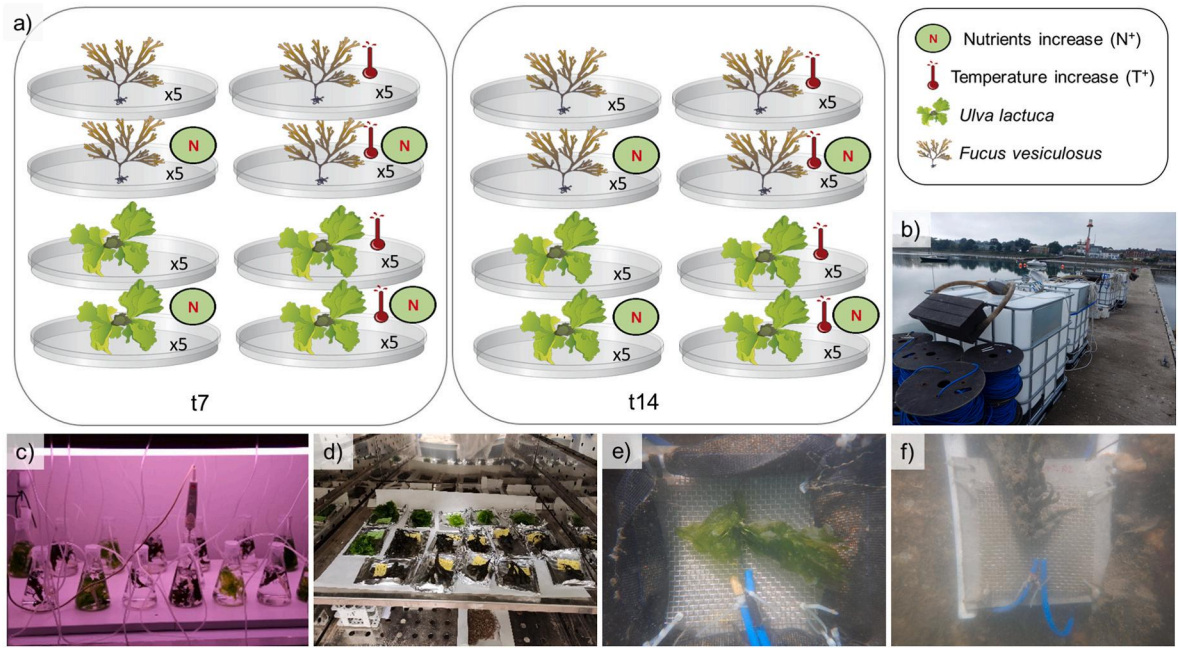

Fig. 2. a) Schematic overview of experiments set up. b) Heating system at Malahide marina. c) Set up of flasks in the IHCantabria laboratory and the sounding line in the middle. d) Samples at the oven. e) *Ulva lactuca* plate under water at Malahide marina with nutrients and temperature treatment. f) *Fucus vesiculosus* plate under water at Malahide marina with temperature treatment. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

exposed for 7 days (t7) and the other half for 14 days (t14) to treatments) (Fig. 2). In the field experiment, 40 samples were exposed in each period, while in the laboratory experiment, 32 samples were used per period. In both experiments, the total number of samples was evenly divided among treatments, ensuring that each treatment had the same number of replicates.

At Malahide, a total of 80 plates were employed (4 treatments x 2 species x 5 replicates x 2 sampling periods). Increased temperature was achieved using the programmable system developed by Browne et al. (2016). This system involved four 1000-litre water tanks and 40 separate lengths of 100-m polyethylene tubing. The polyethylene tubing sections were interconnected via a manifold to 12 V bilge pumps, which continuously delivered heated seawater to the designated treatments along the pontoon at 4.88±0.5 L/h. The seawater temperature within the tanks was raised using pool heaters (Elecro engineering Nano 3 KW mono) housed in weather-proof enclosures attached to the tank sides. A water circulation mechanism was established by linking the heaters to a 25 mm tubing connected to a submerged bilge pump in the tank. Seawater was pumped across the heating element and then returned to the tank. The employed pool heaters featured internal thermostats to uphold the specified treatment temperatures, according to previous studies (Brooks and Crowe, 2018). Nutrient enrichment was administered following the procedure outlined by Brooks and Crowe (2018). Polyethylene mesh diffuser bags (measuring 800 × 50 mm) with a mesh-size of 1 mm^2 were employed to enclose nutrient pellets. These pellets were slow-release fertiliser pellets coated with a composition of 17 % nitrogen (NO_3^- and NH_4^+), 11 % phosphate (P_2O_5), and 10 % potassium (K_2O). By utilizing cable ties, the bags were subdivided into four distinct sections, each measuring 200 × 50 mm. Consequently, each section contained 80 g of pellets, ensuring a nutrient-to-surface area ratio of 1 g^{-1} cm^2. These nutrient bags were fastened to the backing plates within individual plots using cable ties. Notably, nutrient levels were not gauged within the plots, as Brooks and Crowe (2018) have already demonstrated the relative differentiation of this treatment in comparison to the controls. Subsequently, each frond was individually fastened onto sections of mesh using gardening ties. These mesh sections were affixed to concrete backing plates measuring 250 × 250 mm using cable ties. These backing plates were suspended from the wooden buffer timbers of the breakwater at Malahide at a depth of 75 cm from the plate's centre. Plates were positioned at random intervals of at least 1.5 m along the breakwater to ensure independence, as outlined by Browne et al. (2016), and were randomly assigned to the respective stressor treatments. During the field experiment, we observed the loss of five *U. lactuca* samples. Yet, three replicates for each treatment remained, making statistical analysis viable.

For laboratory experimentation, flasks of 250 ml were distributed into two controlled chambers to simulate temperature treatments. Temperature was recorded every minute during the whole experiment to ensure conditions were maintained (Supplementary material 1). Nutrients enriched treatment was achieved by using Provasoli solution (Provasoli, 1963); meanwhile for control flasks half-strength of Provasoli solution was used as media (Starr and Zeikus, 1993). The Provasoli solution is a nutrient-enriched medium originally developed to support the growth of marine and freshwater microalgae, providing essential vitamins, trace elements, and organic compounds necessary for optimal physiological functions (Provasoli, 1963). As a result, in the control 10 ml of Provasoli solution were added by litre of filtered seawater; and 20 ml of Provasoli solution by litre of filtered seawater in the enriched treatment. Media was changed every 7 days. In each chamber, flasks were randomly assigned to stressor treatments and maintained constantly aerated through a plastic tube connected to a pump. To avoid evaporation flasks were covered with laboratory film. Light intensity was kept around 100 μmol photons/m^2s and a long day photoperiod of 14:10h (L:D). A total of 64 culture flasks were used (five replicates for *F. vesiculosus* and three for *U. lactuca* due to algal material limitations), with additional samples collected for wet-to-dry weight conversion and organic carbon content analysis (Ale et al., 2011).

Moreover, we sampled 5 additional fronds from each species and site for obtaining an average percentage of initial organic carbon by DW (OC %DW) per species and location.

Additional photos and schemas concerning experimental set up can be found in the Supplementary material 2.

2.4. Samples processing

Wet weight (WW) of each frond was measured at the beginning of the experiment (t0) and after the conclusion of the experiment (t7 and t14). Prior to weighing, epiphytes that had developed on the fronds throughout the experiment were removed and the material was gently blotted with tissue for 5 s to eliminate excess water. At the conclusion of the experiment, biomass as dry weight (DW, g) of each frond was measured after drying in an oven at 70 °C for 24 h. A conversion factor obtained from the average ratio WW: DW of each frond at sampling day was used to estimate fronds DW at t0. The area of the frond (at the beginning and at the end of the experiment) was measured using photographs (Ale et al., 2011), applying the ImageJ software (Schneider et al., 2012).

Organic carbon percentage (OC%DW) was measured at the end of the experiment from each frond (three subsamples each) using a Shimadzu TOC-LCPH model analyser with the SSM-5000A solid unit. Organic carbon content per frond was estimated as grams (g) of organic carbon from OC concentration and frond biomass applying the formula:

$$OCcontent = \frac{OC\%DW}{100} * DW$$

Organic carbon stock per surface area (OC_{stock}, g OC cm^{-2}) per frond was estimated from frond area and carbon content, applying the formula:

$$OC_{stock} = OCcontent / Area$$

2.5. Statistical analysis

Prior to assessing differences among treatments and the control, a paired *t*-test analysis was conducted to determine whether significant changes occurred within individuals over time. Specifically, for each combination of site, species, and treatment, we compared the values of biomass, area, OC content, and OC stock between t0 and the subsequent measurement (either t7 or t14) using a paired *t*-test.

The impact of the treatments on the growth and carbon incorporation in the fronds was assessed comparing the frond biomass, area, OC content, and OC stock by surface area between the initial date (t0) the collection date (t7 or t14). This was done applying a repeated measures analysis of variance (ANOVA), which allows to compare means across multiple conditions or time points within the same subjects, accounting for within-subject variability and reducing error variance associated with individual differences. Specifically, for each species (*F. vesiculosus* and *U. lactuca*) and site (field and laboratory), we assessed differences in fronds biomass (g), area (cm^2), organic carbon content (OC content, g), and organic carbon stock (OCstock, g OC cm^{-2}) across treatments (N + T0, N0T+, and N + T+) relative to the control (N0T0) considering time (t0 and either t7 or t14) as a random factor in the analysis. When ANOVA assumptions of normality and homogeneity of variance were met, we applied a repeated measures ANOVA, which includes Treatment and Time as fixed factors and individual samples as a random factor. A post hoc Tukey test was performed to identify significant differences between treatments. If assumptions were violated, we used the non-parametric Aligned Rank Transform (ART) approach (Wobbrock et al., 2011) to account for the repeated measures structure. In this case, statistical significance was determined using the Wald F test with Kenward-Roger adjusted degrees of freedom (Kenward and Roger, 1997; Wobbrock et al., 2011).

All statistical analyses were conducted using R Studio software (v4.3.1; R Core Team, 2023). Further methodological details are available in Supplementary Material 3.

3. Results

For both species biomass and organic carbon content increased along the experiment (i.e. showed higher values on sampling days (t7, t14) compared to the initial day (t0) in the controls (Supplementary Material 3, Figs. S2, S3, S10, S11, S18, S19, S26 and S27 for t7 and Figs. S6, S7, S14, S15, S30 and S31 for t14), suggesting that no stress related to the handling of the fronds occurred along the experiments, except the marginal decrease observed for *U. lactuca* in the field by t14 (Supplementary Material 3, Figs. S22 and S23).

For the samples collected to determine the initial organic carbon percentage, which correspond to the five additional fronds per species and site mentioned in the Methods section, the initial OC percentage (t0) was 31.85 % for *F. vesiculosus* and 24.63 % for *U. lactuca*. While for the laboratory experiment in Cantabria, this initial OC percentage (t0) was 23.42 % for *F. vesiculosus* and 32.73 % for *U. lactuca*.

For ease of interpretation, the results shown here focus on the measurements obtained at the end of the exposure period (t14), presented as the differences between the values on t14 and the initial day (t0) for biomass and organic carbon content. For Area and OC_{stock} and all times plots (t0, t7, t14) the reader can check Table 1, Table 2 and figures in Supplementary Material 3.

3.1. Previous thermal exposition comparison

The comparison of SST between Malahide and Cantabria for the three months preceding the respective sampling dates revealed no significant differences ($p = 0.808$). This result suggests that macroalgae from both locations were exposed to similar temperature regimes before collection, minimizing potential biases related to seasonal thermal variability.

3.2. Fucus vesiculosus

For *F. vesiculosus*, changes in biomass and OC content along the experiment were significant for all treatments in the field experiment; meanwhile in the laboratory only control and the nutrient enrichment treatment showed significant differences between t0 and t14 (Fig. 4).

In the field experiment, the highest increase in biomass was recorded in the control treatment (N0T0), with an average DW increase of 1.11 g (from 1.56 g at t0 to 2.34 g at t14). Treatments involving nutrient enrichment resulted in significantly lower biomass accumulation compared to the control (N+T0: $p < 0.0001$, N+T+: $p = 0.0002$), with similar trends observed at t7 (N+T0: $p < 0.0001$, N+T+: $p = 0.0018$, Table 1 and Supplementary Material 3, Section 3.2).

In the laboratory experiment, the highest increase in biomass was observed in the N+T0 treatment (+0.245 g DW, from 0.874 g at t0 to 1.12 g at t14), whereas the lowest biomass values were recorded in the N+T+ treatment (−0.035 g DW, from 1.32 g at t0 to 1.28 g at t14). However, no significant differences were detected among treatments (Fig. 3b).

Regarding OC content, a general increase was observed across all treatments over time. In the field experiment, the highest values at t14 were recorded in the control treatment (N0T0, 0.7681 g, Fig. 3c). Nutrient-enriched treatments showed significantly lower values than the control (N+T0: $p < 0.0001$, N+T+: $p < 0.0001$), with significant differences also detected at t7 (N+T0: $p = 0.0417$, Table 1 and Supplementary Material 3, Section 3.3).

In the laboratory experiment, the N+T+ treatment at t14 exhibited the highest increase in OC content (0.071 g OC, from 0.308 g OC at t0 to 0.379 g OC at t14, $p = 0.019$, Fig. 3d). At t7, both temperature-related treatments differed significantly from the control (N0T+: $p = 0.047$, N+T+: $p = 0.002$, Table 1 and Supplementary Material 3, Section 5.3).

3.3. Ulva lactuca

The pattern observed in *U. lactuca* regarding changes in biomass and OC content along the experiment differs between the field and laboratory experiments and across treatments within the field experiment. Yet changes in biomass and OC content along the experiment were not significant within treatments in none of the experiments. (Fig. 4).

In the field experiment, both the control (N0T0) and combined stress treatment (N+T+) showed a decline in biomass from t0 to t14 (N0T0: 0.057 g DW, N+T+: 0.123 g DW). The highest increase in biomass was recorded in the N+T0 treatment (+0.206 g DW, from 0.594 g at t0 to 0.8 g at t14, Fig. 4a). However, no significant differences were detected among treatments (Table 2).

In the laboratory experiment, all treatments showed an increase in biomass over time, with the highest increase observed in N+T0 (+0.399 g DW, from 0.57 g at t0 to 0.969 g at t14, Fig. 4b). No significant differences were found among treatments at t14, although at t7, the N+T0 treatment differed significantly from the control ($p = 0.002$, Table 2 and Supplementary Material 3, Section 7.2).

Regarding OC content, in the field experiment, the highest increase at t14 was recorded in the N+T0 treatment (+0.055 g OC, from 0.146 g OC at t0 to 0.202 g OC, Fig. 4c), which showed significant effects in t7 (N+T0, -0.04 g OC, from 0.1 g at t0 to 0.06 g at t7, $p = 0.0015$, Table 2). On the other hand, the control and N+T+ treatments showed a decrease in OC content (N0T0: 0.006 g OC, N+T+: 0.031 g OC).

In the laboratory experiment, all treatments showed an increase in OC content over time, with the highest values recorded in the control treatment (N0T0, +0.098 g OC, from 0.1185 g OC at t0 to 0.248 g OC at t14, Fig. 4d), followed by N+T0 (+0.075 g OC, from 0.187 g OC at t0 to 0.261 g OC at t14, Fig. 4d). While no significant differences were detected at t14, the N+T0 treatment differed significantly from the control at t7 ($p = 0.002$, Table 2 and Supplementary Material 3, Section 7.3).

4. Discussion

Our results highlight the relevance of eutrophication as a key stressor for slow-growing species such as *Fucus vesiculosus*, affecting their growth and carbon accumulation capacity. While we initially hypothesized that the combination of eutrophication and marine heatwaves would

Table 1
Fucus vesiculosus p-values results from repeated measures ANOVA comparing treatments against the control (Tukey post hoc test applied for multiple comparisons) or Aligned Rank Transform approach (Wald F test post hoc test applied for multiple comparisons) for the field and laboratory experiments in t7 and t14.

	Field				Laboratory			
	t7		t14		t7		t14	
	Biomass	OC content	Biomass	OC content	Biomass	OC content	Biomass	OC content
N+T0	<0.0001*	0.0417*	<0.0001*	<0.0001*	0.7385	0.1231	0.2324	0.1967
N0T+	0.4007	0.8987	0.9781	0.9966	0.5185	0.047*	0.9987	0.9938
N+T+	0.0018*	0.2126	0.0002*	<0.0001*	0.3090	0.002*	0.2445	0.019*

The asterisk (*) indicates statistical significance ($p < 0.05$).

Table 2
Ulva lactuca p-values results from repeated measures ANOVA comparing treatments against the control (Tukey post hoc test applied for multiple comparisons) or Aligned Rank Transform approach (Wald F test post hoc test applied for multiple comparisons) for the field and laboratory experiments in t7 and t14.

	Field				Laboratory			
	t7		t14		t7		t14	
	Biomass	OC content	Biomass	OC content	Biomass	OC content	Biomass	OC content
N+T0	0.002*	0.0015*	0.7864	0.9878	–	0.1312	0.9379	0.9982
N0T+	0.2642	0.2376	0.6763	0.4113	–	0.1068	0.5386	0.3035
N+T+	0.5218	0.3823	0.4061	0.5349	–	0.1951	0.9972	0.8388

The asterisk (*) indicates statistical significance ($p < 0.05$).

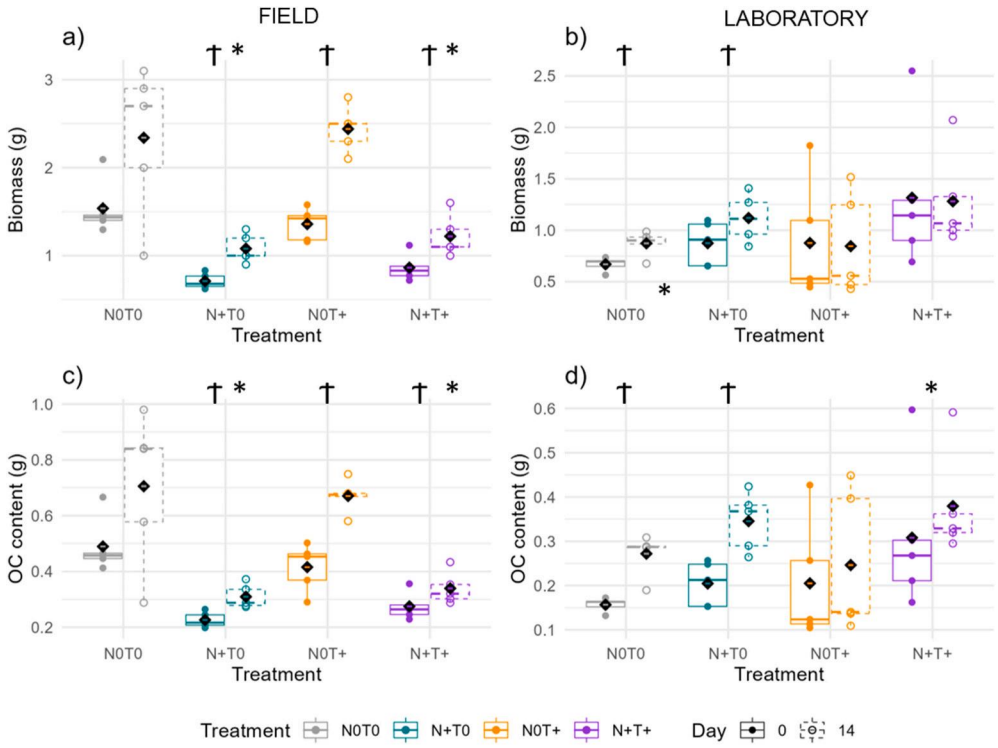

Fig. 3. Boxplot of *Fucus vesiculosus* biomass (g) and organic carbon content (g) on day 0 and day 14 in the field (a, c) and in the laboratory (b, d) experiments. Mean values are shown as black dots. Samples from day 0 are represented with a solid line, while those from day 14 are represented with a dashed line. Cross symbols (†) indicate significant differences between day 0 and day 14 within each treatment ($p < 0.05$). Asterisks (*) indicate statistical significance ($p < 0.05$) between treatments and the control (N0T0). The horizontal axis shows the treatments: N0T0 (control, grey), N+T0 (nutrient addition, green), N0T+ (warming, orange), and N+T+ (nutrient addition + warming, purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

exacerbate these effects, our results did not show significant differences in biomass or organic carbon accumulation between 14-day marine heatwaves treatments and eutrophication alone. Contrary to our expectations, neither *F. vesiculosus* nor *Ulva lactuca* exhibited significant effects on their biomass or organic carbon accumulation when exposed to 14-day marine heatwaves.

4.1. Growth and organic carbon accumulation responses

Results support the crucial role of macroalgae in carbon incorporation and biomass dynamics, as both species considered increased their organic carbon content in their biomass under control conditions, except *U. lactuca* in the field experiment, which is a first step to contribute to on-site carbon sequestration (Duarte et al., 2022). As their actual contribution to medium-term carbon sequestration would depend on additional processes, such as export, burial, and resistance to remineralization. Though, each species responds differently to the treatments and the level of control of the conditions (laboratory vs field). *F. vesiculosus* and *U. lactuca* ability to incorporate organic carbon in their biomass is influenced by various factors, including the species and its unique physiology, as well as environmental conditions. The ability of macroalgae to store carbon varies among species due to differences in cellular composition, growth strategies, and physiological adaptations (Hall et al., 2022). These structural and biochemical traits influence their potential for long-term carbon sequestration, as observed in the distinct carbon storage mechanisms of *F. vesiculosus* and *U. lactuca*. *F. vesiculosus* exhibited greater increases in organic carbon content over time compared to *U. lactuca*, which aligns with its distinct physiology and lower turnover rate. The cell walls of *F. vesiculosus* contain fucoidans, a type of polysaccharide primarily composed of fucose, with minor contributions from other monosaccharides, including glucose. The presence of glucose might play a role in facilitating the diffusion of CO_2 within the cell wall, which could enhance the efficiency of carbon fixation by allowing CO_2 to reach the carboxylation sites in the chloroplasts more quickly, and this mechanism may contribute to the remarkable sequestration of carbon in fucoidans (Hagen et al., 2023; Raven, 1997). On the other side, the cell walls of *U. lactuca* are primarily composed of cellulose, a rigid polymer made of β-1,4-linked D-glucose. Despite being

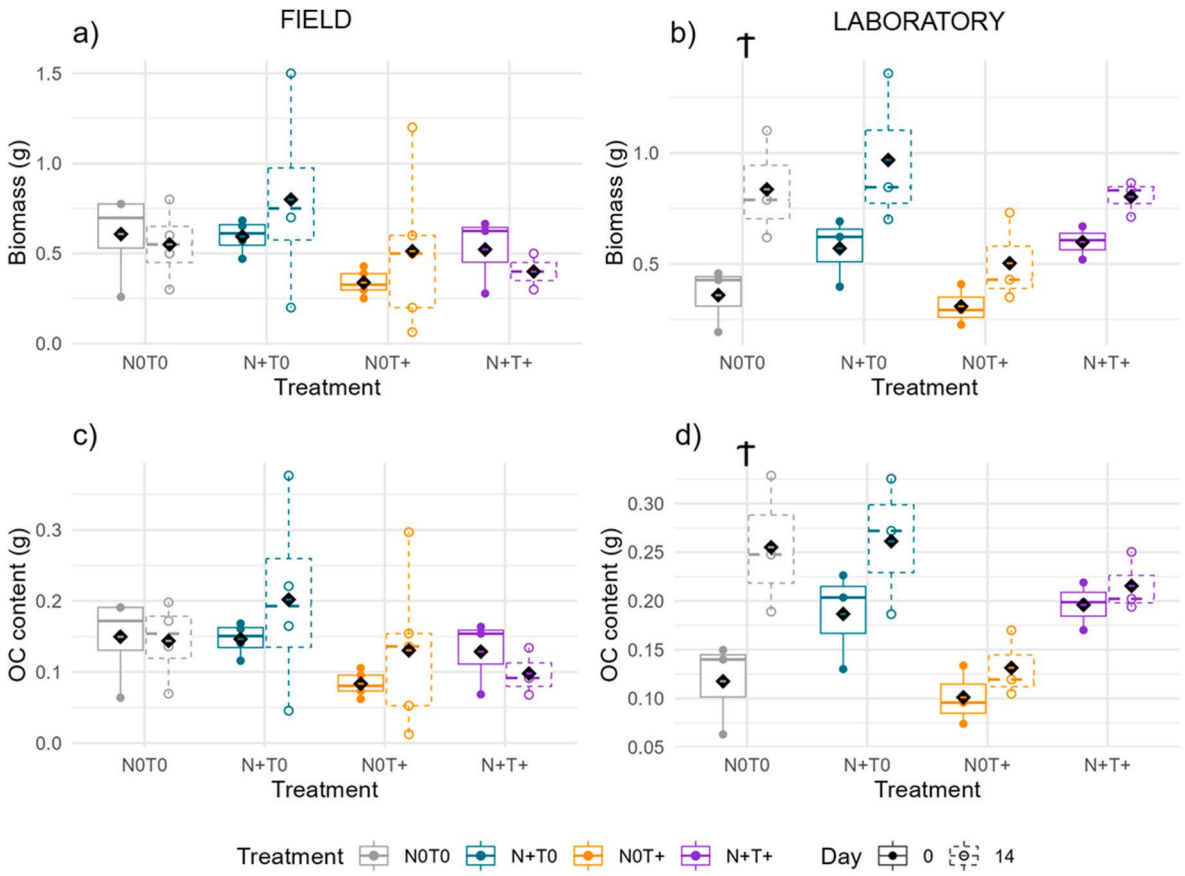

Fig. 4. Boxplot of *Ulva lactuca* biomass (g) and organic carbon content (g) on day 0 and day 14 in the field (a, c) and in the laboratory (b, d) experiments. Mean values are shown as black dots. Samples from day 0 are represented with a solid line, while those from day 14 are represented with a dashed line. Cross symbols (†) indicate significant differences between day 0 and day 14 within each treatment ($p < 0.05$). Asterisks (*) indicate statistical significance ($p < 0.05$) between treatments and the control (N0T0). The horizontal axis shows the treatments: N0T0 (control, grey), N+T0 (nutrient addition, green), N0T+ (warming, orange), and N+T+ (nutrient addition + warming, purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

glucose-based, the highly ordered and crystalline structure of cellulose differs from the sulfated polysaccharides found in *F. vesiculosus*, which may influence CO_2 diffusion through the cell wall (Ponce and Stortz, 2020). While the statistical analysis did not indicate significant effects of the treatments on *U. lactuca*, noticeable trends in biomass and organic carbon accumulation were observed, particularly in the laboratory experiment under nutrient addition. The lack of statistical significance does not imply the absence of biological effects, but rather may reflect the limited sample size of the experiment. These trends suggest that nutrient enrichment might enhance *U. lactuca* growth and carbon incorporation potential, but further studies with increased replication and longer exposure times are necessary to confirm these patterns.

The response of *U. lactuca* to nutrient enrichment was weaker than expected for an r-strategist species, which typically thrives under eutrophic conditions (Teichberg et al., 2010). Several factors could explain this pattern. Firstly, excessive nutrient availability, particularly imbalanced N:P ratios, can lead to physiological stress and reduced growth efficiency (Gao et al., 2017; Pedersen et al., 2010). It is important to note that phosphorus was not directly measured in this study, preventing us from evaluating the exact N:P ratio in either the field or laboratory experiments. Secondly, field conditions introduced uncontrolled factors, such as herbivory and turbidity, which may have counteracted the potential benefits of nutrient enrichment. In particular, increased grazing pressure, as suggested by field observations (Supplementary Material 4), could have limited *U. lactuca* biomass accumulation in the field experiment (Geertz-Hansen et al., 1993). Thirdly, temperature-nutrient interactions may have played a role, as warming can increase respiration rates and weaken *U. lactuca* tissue structure, potentially offsetting growth benefits from nutrient addition (Zeroual et al., 2020). Lastly, differences between laboratory and field conditions suggest that *U. lactuca* can optimise nutrient uptake in controlled environments but is more vulnerable to environmental fluctuations in natural settings (Chen et al., 2019). These findings highlight that *U. lactuca* response to eutrophication is influenced by multiple interacting factors, which should be explored in future studies considering longer exposure times and varying environmental conditions.

Contrary to what was observed for *U. lactuca*, for *F. vesiculosus*, the treatments involving nutrient addition (alone and in combination with warming) reduced the capacity to accumulate biomass and organic carbon, only significant in the field experiment. This result suggests that a positive impact in photosynthetic activity and on carbon assimilation under eutrophication suggested in previous studies (Brooks and Crowe, 2018) might depend on different factors, such as species and seasonality. For instance, *Caulerpa prolifera* has shown lower production under nutrient enrichment during summer compared to winter conditions (Egea et al., 2020). Additionally, it is important to consider whether *F. vesiculosus* is a nitrophilic species or if the donor meadow is already nutrient-saturated. Some studies suggest that *F. vesiculosus* has a moderate response to nutrient enrichment and its capacity for additional nutrient uptake can be limited when background levels are already high (Pedersen et al., 2010). Moreover, increased nutrient availability appears to reduce the concentration of phlorotannins in *F. vesiculosus*, altering the carbon and nutrient balance in tissues, which suggests that nutrient enrichment decreases investment in chemical defenses (Hemmi

et al., 2005; Hemmi and Jormalainen, 2002). This reduction in defensive compounds makes *F. vesiculosus* more susceptible to herbivory, particularly in its apical sections, where changes in primary metabolism under high-nutrient conditions increase palatability (Hemmi et al., 2004).

It is important to note that eutrophication encompasses not only increased nutrient loading but also a reduction in light availability due to enhanced microalgal blooms (Smith and Schindler, 2009). The results presented here focus solely on the effects of nutrient enrichment; however, the concurrent decrease in light penetration in eutrophic environments could further alter macroalgal growth and carbon sequestration. Light limitation has been shown to reduce photosynthetic efficiency (Ralph et al., 2007) and may exacerbate the negative effects of eutrophication by decreasing carbon assimilation rates (Duarte, 1995). For *U. lactuca*, which thrives in high-light environments, prolonged shading from phytoplankton blooms could suppress its growth and limit its ability to act as a carbon sink (Lee and Kang, 2025). Conversely, *F. vesiculosus*, which is adapted to intertidal habitats with fluctuating light conditions, may be more resilient to temporary reductions in irradiance but could still experience long-term declines in productivity under chronic light limitation (Andersen et al., 2013).

In addition to nutrient enrichment, the increase in water temperature can accelerate metabolism and increase the respiration, often resulting in faster growth but with decreased tissue quality (Harley et al., 2012). In the case of *U. lactuca*, it has been observed that under stressful conditions tissues become thinner and less resilient, making them more susceptible to degradation and physical damage (Zeroual et al., 2020). Studies have also found that elevated temperatures can negatively affect cell wall composition of *F. vesiculosus*, making it less robust against decomposition by microorganisms as its ability to induce chemical defenses (phlorotannins) was strongly reduced (Kinnby et al., 2021). This contributes to greater vulnerability to degradation. In this experiment, the heatwave treatments did not significantly impact biomass and organic carbon content, following time-increment patterns similar to those of the controls. When nutrients addition is combined with water warming, the resulting effects are very similar to only nutrients treatment, which suggest a dominant role of this stressor (Folt et al., 1999). Previous works have established how the effects of stressors can shift due to changes in their length (from antagonistic to additive, dominant or synergistic), therefore detailed experimentation is required to accurately characterize its effects (Brooks et al., 2023; Mack et al., 2022).

4.2. Ecological implications of species-specific responses

In general, *F. vesiculosus* seems to adapt better to changing environments, showing increases in biomass and percentage of carbon content across all treatments with time, although getting lower values than the control. This may be due to its more complex structure, as well as its intertidal nature, which confers greater resilience to increased nutrient inputs and warming waters (Gao et al., 2017). However, following this same pattern, in the field the values are higher than in the laboratory, suggesting that *F. vesiculosus* benefits from variables such as greater agitation and changing conditions.

Compared to *F. vesiculosus*, *U. lactuca* exhibited lower increases in biomass and organic carbon content over time in the field, reaching negative values for the combination of stressors, than in the laboratory. This suggests that under favourable environmental conditions, due to its opportunistic nature, *U. lactuca* is a relevant competitor (Chen et al., 2019; Fortes and Lüning, 1980). In contrast, uncontrolled factors in the field experiment, such as turbidity or herbivory, amplify the stress associated with the treatments, resulting in a slower response from *U. lactuca*. Additionally, the tissue formed under these conditions is likely of lower quality and therefore more susceptible to degradation.

4.3. Methodological limitations and future research directions

Although our SST analysis indicates that macroalgae from Malahide and Cantabria were exposed to comparable thermal conditions in the months prior to collection, other sources of variation may have contributed to the differences observed between field and laboratory experiments. One key aspect to consider is the genetic differentiation between populations, which can result in distinct physiological traits and adaptive responses, even under similar environmental conditions. Local adaptation in macroalgae has been widely documented (Hu et al., 2023), suggesting that individuals from different populations may exhibit inherent differences in their metabolism, growth rates, or stress tolerance. Additionally, seasonal physiological states may influence macroalgal performance. Even if the water temperatures were similar before collection, the photoperiod, nutrient availability, and metabolic activity differed between the two sites due to seasonal variations, which could have affected the physiological condition of the algae at the time of collection (Fortes and Lüning, 1980; Gao et al., 2017). For example, macroalgae collected in winter tend to have lower metabolic activity compared to those collected in summer (Pedersen and Borum, 1997), which may influence their response to experimental conditions. Furthermore, differences between field and laboratory results could also be attributed to environmental factors that were not controlled in the field, such as grazing pressure. Herbivory is a well-documented factor affecting macroalgal growth and survival, and it is often exacerbated by eutrophication (Geertz-Hansen et al., 1993). The photographs in Supplementary Material 4 suggest that grazing may have influenced the outcomes of the field experiment, potentially contributing to differences observed between field and laboratory conditions. However, the low biomass per unit area in this experiment may not have been sufficient to effectively counterbalance grazing pressure, meaning that herbivory could have disproportionately impacted the results.

In the present work, no significant effects have been observed due to MHWs after 14 days of exposure, but it should be explored longer-term degradation and recovery patterns of macroalgae beyond the current 14-day exposure (Kristensen, 1994). Assessing the resilience of these species over prolonged periods is crucial for understanding their ecosystem services roles. Despite not having shown significant effects, it would be interesting to assess the effects on species considering the cumulative effects of multiple heatwaves, with varying intensities and durations (Smith et al., 2024).

Equally important is a detailed analysis of carbon pathways (including fixation, remineralization, and grazing), both at the source and across coastal shelves. This comprehensive approach is essential to fully understand macroalgae's role in carbon sequestration across their entire life cycle (Hall et al., 2022; Krause-Jensen and Duarte, 2016; Lian et al., 2023; Queirós et al., 2019), as a significant portion of macroalgal organic carbon production is exported to other ecosystems and deep ocean layers, where it can be stored for extended periods (Christianson et al., 2022; Hill et al., 2015; Krause-Jensen et al., 2018; Krause-Jensen and Duarte, 2016; Moreda et al., 2024; Watanabe et al., 2020). Moreover, while individual frond data provide valuable insights, it's imperative to consider the broader biological context. Investigating macroalgae within more ecologically realistic settings, such as multi-species assemblages, could offer a clearer understanding of species interactions and their collective resilience to climate stressors (Brooks and Crowe, 2018; Hu et al., 2023). Additionally, recent research underscores the role of marine flora in long-term carbon sequestration not only through particulate organic carbon (POC) burial but also via the export of dissolved organic carbon (DOC). Jiménez-Ramos et al. (2022) demonstrated that seagrass meadows can act as significant sources of both labile and recalcitrant DOC, with the presence of invasive macroalgae altering DOC fluxes and potentially reducing carbon export. Similarly, Zhang et al. (2023) found that the biodegradation of *Saccharina japonica* results in the transformation of labile DOC into refractory DOC, which resists microbial degradation and can persist for extended timescales in marine systems. These findings highlight the importance of considering DOC export dynamics when evaluating the carbon sequestration potential of macroalgae, particularly under

climate change scenarios that may influence DOC production and transformation processes. Future studies should aim to quantify the relative contributions of macroalgal-derived DOC to oceanic carbon storage and its interactions with microbial communities.

4.4. Summary of key findings and implications

This study demonstrates that in 14 days, the fronds of *F. vesiculosus* and *U. lactuca* not only grow and accumulate organic carbon but also show differential responses to nutrient enrichment and warming, with the response to these stressors differing between two species that employ very different strategies. Specifically, the fast-growing species *U. lactuca* appears to have lower metabolic plasticity than the slow-growing species *F. vesiculosus*, whose more complex structure provides greater resilience to stressors. Furthermore, this work underscores the critical role of nutrient supply in ecosystems that export a substantial portion of their production (Duarte and Cebrián, 1996), as the needs to consider the effects derived of the combination of stressors (Ban et al., 2014; Birk et al., 2020; Orr et al., 2020).

Results reinforce the crucial role of nutrient discharge management in preserving macroalgal ecosystems' carbon sequestration potential. Our work shows that eutrophication, even over short timescales, can significantly alter biomass accumulation and organic carbon incorporation, particularly in slow-growing species like *F. vesiculosus*. Given that many macroalgal ecosystems act as exporters of carbon to adjacent habitats, effective nutrient management policies are necessary to prevent degradation of these carbon stocks and maximize their role in blue carbon strategies. Integrated coastal management approaches that regulate nutrient runoff from agriculture, wastewater, and industrial sources should be prioritized to mitigate the combined impacts of eutrophication and climate change on marine vegetation.

These findings underscore the importance of adopting a holistic and species-specific perspective when considering macroalgae's role in the blue carbon balance. This approach is crucial for making informed management decisions, especially considering ecosystems service they provide. Accurate knowledge of macroalgal responses to environmental stressors is key to guiding their conservation and adaptation strategies, which is likely to be more cost-effective than restoration efforts.

5. Conclusions

Eutrophication, both alone and in combination with marine heatwaves, emerged as a significant stressor reducing the growth and carbon incorporation potential of slow-growing species like *Fucus vesiculosus*. Our findings suggest that while *F. vesiculosus* retains carbon more efficiently under stress conditions, *Ulva lactuca*'s contribution to medium-term sequestration may be limited due to its rapid turnover rate and susceptibility to degradation. Interestingly, despite being an r-strategist species, *U. lactuca* exhibited a weaker-than-expected response to nutrient enrichment, suggesting that factors such as grazing pressure or nutrient imbalances may limit its capacity to take advantage of eutrophic conditions.

Unexpectedly, results revealed that neither *F. vesiculosus* nor *U. lactuca* displayed notable changes in biomass or organic carbon accumulation following exposure to 14-day marine heatwaves. This could be because the experiments were relatively short; as discussed earlier, one of the impacts of warming is that algae produce weaker tissues, which decompose more easily. Such effects may not be detectable in a 14-day experiment.

These results underscore the critical role of nutrient availability, highlighting the need to effectively manage anthropogenic nutrient sources to mitigate their impact on marine ecosystems. Furthermore, our findings indicate that *F. vesiculosus* demonstrates greater resilience to environmental fluctuations compared to *U. lactuca*, likely due to its more complex structure and slower turnover rate. This suggests that slow-growing macroalgae may be better adapted to persist under shifting environmental conditions, whereas fast-growing species like *U. lactuca* may be more vulnerable to fluctuating stressors.

CRediT authorship contribution statement

Camino F. de la Hoz: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Paul R. Brooks:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Jennifer Coughlan:** Writing – review & editing, Methodology, Investigation. **Inés Mazarrasa:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Elvira Ramos:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Samuel Sainz-Villegas:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Araceli Puente:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Jose A. Juanes:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Tasman P. Crowe:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107128.

Data availability

The processed data and the codes to run the analyses are available in the Supplementary Material 2.

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