



# Ecophysiological responses of *Fucus virsoides* (Phaeophyceae, Fucales) to past and present nutrient conditions in the northern Adriatic

Emmanuelle Descourvières<sup>1,2</sup> · Martina Mulas<sup>2,6</sup> · Sara Natale<sup>3</sup> · Raquel Sánchez de Pedro<sup>4</sup> · Alessandro Alboresi<sup>3</sup> · Cosimo Solidoro<sup>2,5</sup> · Vinko Bandelj<sup>2,5</sup> · Annalisa Falace<sup>1,2</sup>

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## Abstract

*Fucus virsoides* is a brown seaweed endemic to the Adriatic and the only species of its genus found in the Mediterranean. Historically widespread from the Venice lagoon (Italy) to Albania, this species has suffered a sharp decline and is currently threatened with extinction.

Over the past three decades, the northern Adriatic has seen a shift towards oligotrophy conditions, yet the ecophysiology of *F. virsoides* in response to nutrients changes has been poorly studied. Addressing this gap is crucial for understanding the extent to which these environmental changes may have contributed to the species' decline.

To test our hypothesis that nutrient changes might be the primary driver of *F. virsoides* decline, we conducted a two-week experiment exposing germlings and adults to six different nutrient conditions. These included three Redfield ratios recorded in the Gulf of Trieste in 1996, 2007 and 2017, reflecting the shift from eutrophic to oligotrophic conditions experienced by *F. virsoides* in the wild. Additionally, the adults were exposed to three supplementary eutrophic conditions (naturally and artificially fertilized).

Growth and physiological responses (measured via O<sub>2</sub> evolution and PAM fluorimetry) of *F. virsoides* to varying nutrient conditions were largely consistent, with only subtle effects observed. Our results highlight the species' acclimation potential, suggesting that short-term nutrient changes alone may not fully explain its decline. Understanding *F. virsoides* resilience to multiple environmental stressors is crucial for developing effective conservation strategies to preserve marine forests in the face of ongoing anthropogenic disturbances.

**Keywords** Mediterranean · Seaweeds · Metabolic rates · Photosynthetic performances

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Emmanuelle Descourvières and Martina Mulas authors contributed equally to this work.

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✉ Emmanuelle Descourvières  
emmanuelle.descourvieres@phd.units.it

- <sup>1</sup> Department Life Sciences, University of Trieste, Trieste, Italy
- <sup>2</sup> National Institute of Oceanography and Applied Geophysics – OGS, Trieste, Italy
- <sup>3</sup> Department of Biology, University of Padua, Padua, Italy
- <sup>4</sup> Departamento de Botánica y Fisiología Vegetal, Universidad de Málaga, Andalucía Tech, Campus de Teatinos, Málaga, Spain
- <sup>5</sup> National Biodiversity Future Center, Palermo, Italy
- <sup>6</sup> Present address: Department of Biology, University of Pisa, Pisa, Italy

## Introduction

Marine ecosystems are increasingly threatened by rapid climatic changes, exacerbated by human activities, which alter ecosystem structure and functioning and consequently affect the services they provide (Halpern et al. 2008; Pecl et al. 2017). Numerous studies on macroalgae have documented the cumulative impacts of these changes at both local and global scales (Smale and Wernberg 2013; Smale 2020). Key factors affecting macroalgae include temperature, salinity, photosynthetically active radiation (PAR), ultraviolet (UV) exposure, and nutrient availability, all of which significantly affect growth and productivity (Lüning 1990; Hurd et al. 2014; Perini and Bracken 2014).

In terms of nutrients dynamics, the Redfield ratio (C: N:P 106:16:1) serves as reference for many aquatic environments (Redfield et al. 1963), while a nitrogen (N) to

phosphorous (P) ratio of 30:1 is considered non-limiting for macroalgae and seagrasses (Atkinson and Smith 1983).

*Fucus virsoides* J. Agardh is the only endemic Mediterranean representative of the genus *Fucus* (Giaccone and Pignatti 1967; Munda 1973), which is otherwise distributed in colder temperate areas in the North Atlantic and North Pacific coasts, the Baltic Sea (Wahl et al. 2011) and at upwelling areas in the east Atlantic coasts and Strait of Gibraltar (Lourenço et al. 2016; Sánchez de Pedro et al. 2023a). Once considered almost ubiquitous from the lagoon of Venice to Albania (Linardić 1949; Kashta 1996; Mačić 2006), *F. virsoides*, restricted to the intertidal zone, has declined drastically and today only a few fragmented populations remain (Falace et al. 2010; Battelli 2016a; Gljušić et al. 2023; Descourvières et al. 2024a).

The ecological importance of *Fucus* spp. is well recognized, as they serve as primary producers and habitat-forming species, providing shelter, nursery and feeding grounds for a variety of associated species (Wahl et al. 2011). *Fucus* species are known for their ability to tolerate large fluctuations in environmental variables (Wahl et al. 2011; Ferreira et al. 2014), resulting in significant ecotypic and phenotypic differentiation even at local scale (Gylle 2011). From a ‘resistance–resilience’ perspective (Nimmo et al. 2015), their ecological success in fluctuating (i.e. intertidal zones) and disturbed environments (i.e. polluted sites) may be related to their broad ‘optimum’ performance range, in which physiological responses remain stable (resistance response), as well as their ability to recover their physiological functions (i.e. photosynthesis, nutrient uptake) following abiotic stress (Schagerl and Möstl 2011). However, the impact of a single stressor can exceed the natural physiological limits of *Fucus* species (e.g. Martínez et al. 2012; Falace et al. 2018a), leading to decline and local extinction (Nilsson et al. 2004; Nicastro et al. 2013; Sánchez de Pedro et al. 2023b).

In contrast to other congeneric species, such as *Fucus vesiculosus*, which have been extensively studied under various stressors (temperature, Graiff et al. 2015; temperature and salinity, Takolander et al. 2017; temperature and nutrients, Steen and Rueness 2004; Piñeiro-Corbeira et al. 2019), the literature on *F. virsoides* remains scarce (Zavodnik 1973; Kremer and Munda 1982). Recent studies have explored the responses of *F. virsoides* to eutrophication and pollutants such as glyphosate, a widely used fertilizer (Falace et al. 2018a; Feline et al. 2019; Gerdol et al. 2020). However, the causes of *F. virsoides* decline remain elusive (Falace et al. 2010; Orlando-Bonaca et al. 2013; Battelli 2016a; Descourvières et al. 2024a).

In its northern range, a decrease in P load of the Po River has been recorded since the late 1980s (Cozzi and Giani 2011; Giani et al. 2012), likely due to Italian legislation

reducing phosphates in detergents and thus nutrient load in wastewater (Totti et al. 2019). This P depletion (Solidoro et al. 2009; Grilli et al. 2020) has led to an increase in the N:P ratio in the northern Adriatic (Degobbis et al. 2000; Fanelli et al. 2022), which is now classified as oligotrophic (Mozetič et al. 2010). Phosphorus is crucial for nucleic acids, proteins, coenzymes and phospholipids and is essential for energy transfer through ATP, photosynthesis, respiration, and the priming of molecules for metabolic pathways (Douglas et al. 2014). In contrast, high nutrient levels (e.g. eutrophication) can trigger growth responses in environment where other conditions are suboptimal (e.g. salinity) (Nygård and Dring 2008). Increased nutrient loading may also promote competition with fast-growing macroalgae (e.g. *Ulva* spp.), sessile fauna and periphytic microorganisms, leading to the overgrowth of epibionts (Korpinen et al. 2010), impaired light penetration, phytoplankton blooms and altered vertical distribution of coastal macroalgae in the subtidal (Kautsky et al. 1986).

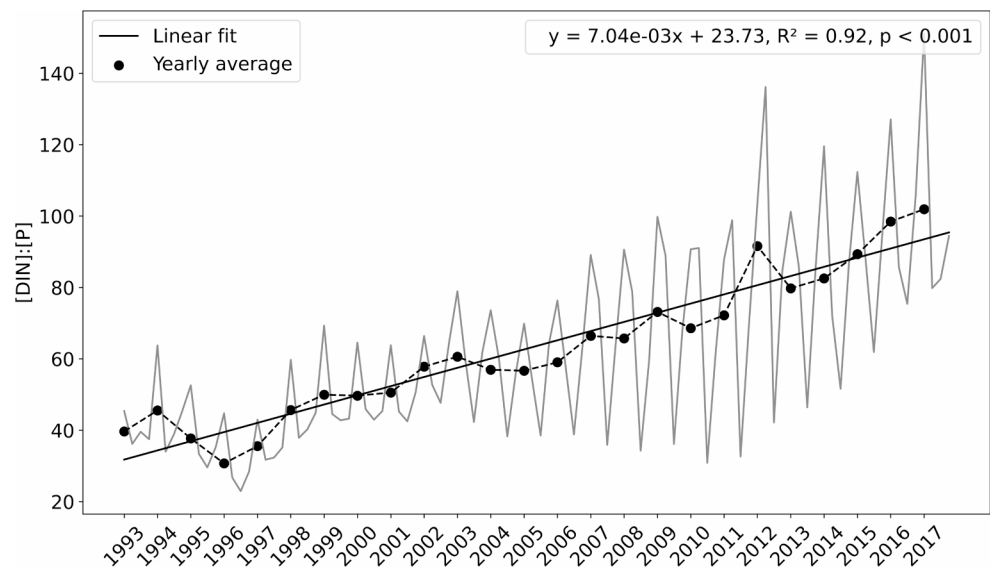
We hypothesized that the shift from eutrophy to oligotrophy in the northern Adriatic could be a driving factor in the decline of *F. virsoides* and that species’ responses may vary depending on its developmental stage. The aim of this study was to test this hypothesis under controlled laboratory conditions. We examined the effects of three dissolved inorganic nitrogen to phosphorus ratios ([DIN]: [P]) experienced by *F. virsoides* in the Gulf of Trieste (northern Adriatic) over the last 30 years on germlings and adult fronds. Additionally, we exposed adult fronds to three supplementary conditions (i.e. seawater collected at the sampling site, eutrophic and biofertilizer enriched). Our objectives were: (i) to assess differences in physiological performance and (ii) evaluate the morphological development of germlings and adult fronds to determine whether varying nutrient conditions could be blamed for the decline of *F. virsoides*.

## Materials and methods

### Analysis of the [DIN]: [P] ratio in the gulf of trieste

The long-term annual average concentrations of dissolved inorganic nitrogen [DIN] and [P] in the surface seawater of the Gulf of Trieste were assessed using the pre-processed datasets available on EMODnet: Mediterranean Sea – DIVA 4D 6-year seasonal analysis of Water body DIN 1990/2019 v2021 (<https://emodnet.ec.europa.eu/geonetwork/emodnet/api/records/3b85a714-cd1c-11e8-8664-8056f28224bb>) and Mediterranean Sea – DIVA 4D 6-year seasonal analysis of Water body phosphate 1968/2019 v2021 (<https://emodnet.ec.europa.eu/geonetwork/srv/api/records/158de2d6-ca8a-11e8-b0bc-8056f28224bb>). The downloaded dataset was

**Fig. 1** Long-term analysis of the seasonal [DIN]: [P] ratio in the Gulf of Trieste. The dots connected by dotted line represent the annual average values, while the black line represents the trend line with the corresponding equation ( $y$ ), R-squared ( $R^2$ ) and  $p$ -value ( $p$ ). Data were extracted from pre-processed datasets available on the EMODnet website (see the section “Analysis of the [DIN]: [P] ratio in the Gulf of Trieste” for more details)



**Table 1** Nutrient conditions used in the *Fucus virsoides* culture experiment derived from EMODnet and the literature<sup>a</sup> Values as reported by Gerdol et al. (2020); <sup>b</sup> Values as reported by Kaleb et al. (2023); <sup>c</sup> In addition to the N-NO<sub>3</sub>, C2 also included 20.75 μM N-NH<sub>4</sub>

Acronym	Culture Media	N-NO <sub>3</sub> (μM)	P-PO <sub>4</sub> (μM)	[DIN]: [P] ratio
R1	ASW + [DIN]: [P] ratio in 1996	3.18	0.12	31:1
R2	ASW + [DIN]: [P] ratio in 2007	3.58	0.05	66:1
R3	ASW + [DIN]: [P] ratio in 2017	2.46	0.03	102:1
C1	ASW + ARPA 2009–2014 <sup>a</sup>	25.99	0.05	577:1
C2	SW + AlgatronCifo <sup>®bc</sup>	0.86	0.02	1044:1
SW	SW at collection site <sup>b</sup>	1.25	0.02	121:1

formatted as a 6-year average for each season, covering the period from 1990 to 1995 to 2014–2019. Based on the calculated annual mean concentrations, we derived the corresponding annual [DIN]: [P] ratio. Data analysis was conducted using the Python programming language. From the results, we identified two extreme values of the annual mean [DIN]: [P] ratio: 31:1 in 1996 (R1) and 102:1 in 2017 (R3). Additionally, a median value of 66:1 from 2007 (R2) was selected to represent intermediate conditions. These three [DIN]: [P] ratios were chosen as the experimental conditions for testing the responses of both adults and germlings stages of *F. virsoides* (Fig. 1; Table 1). Historical data indicate that *F. virsoides* populations were abundant and widespread in the Gulf of Trieste during 1992–1993 (Lipizer et al. 1995). However, by 2009, Orlando-Bonaca et al. (2013) noted the absence of the species at several previously recorded sites, and by 2017, only the population of Marina Julia was reported (Falace et al. 2018a; Descourvières et al. 2024a). Given that the peak of growth of *F. virsoides* occurred under conditions similar to those in R1, this ratio was considered representative of non-limiting conditions for the species.

## Sampling

*Fucus virsoides* samples were collected in the Gulf of Trieste at Marina Julia (45°46′37.7 “N, 13°32′02.6 “E) during

low tide (ca. 1m above Chart Datum) in May–July 2023. In this area (northern Adriatic), the mean recorded tidal amplitude reaches its peak up to ca. 90 cm compared to the average 20–30 cm recorded in the rest of the Adriatic and the Mediterranean (Battelli 2016b). To minimize the impact on the population, only apical fronds were collected rather than whole individuals. To ensure that different individuals were sampled, fronds were collected at least 10 cm apart. Approximately 150 fronds with mature receptacles and around 100 sterile fronds (ca. 5 cm long) were gathered and transported under dark, cold conditions to the Phycological Laboratory of the University of Trieste (Italy) within one hour. The samples were then cleaned of epiphytes, sand and pebbles using artificial seawater (ASW) and tweezers. For the germling experiment, fertile fronds were stored at 4°C for 24 h to induce the release of gametes (Falace et al. 2018b; Kaleb et al. 2022).

All fronds were photographed and weighed (fresh weight, FW) using an analytical scale ( $\pm 0.1$  mg) (Sartorius, Göttingen, Germany). The fronds were then dark-adapted in Petri dishes for 20 min (Kaleb et al. 2023) before measuring the maximal quantum efficiency of photosystem II ( $F_v/F_m$ ) using a PAM Imaging Fluorometer Open FluorCam (Photon Systems Instruments©, Czech Republic). Initial basal fluorescence ( $F_0$ ) was measured, followed by the application of a saturating light pulse to induce and measure the

maximum fluorescence ( $F_m$ ).  $F_v/F_m$  was then calculated using the equation of Maxwell and Johnson (2000). Only samples with  $F_v/F_m \geq 0.6$ , indicative of a healthy ecophysiological state (e.g. Schagerl and Möstl 2011; Martínez et al. 2012), were selected for the experiments.

## Experimental setup

Cultures of germlings and fronds of *F. virsoides* were maintained under controlled conditions at  $15 \pm 0.5$  °C, with a light intensity of  $125 \pm 30$   $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , salinity of 35, and a photoperiod of 15:9 h light-dark cycle similar to field condition. Light was provided by white LED lamps (ADDLIVE LED, Dongguan, China) and measured using a LI-COR190/R photometer (LICOR-Biosciences, Lincoln, NE, USA).

Culture media were prepared with ASW (ca. 30–40 L per conditions) using Instant Ocean® Salt (Aquarium Systems, Sarrebourg, France) following the protocols of Nielsen and Nielsen (2012). Temperature and salinity were monitored daily using a digital thermometer (ThermoPro, Shenzhen, China) and a portable refractometer RSM/ATC (Exacta and Optech, San Prospero, Modena, Italy), respectively.

The effects of the three specific [DIN]: [P] ratios (R1, R2 and R3) were tested on both adult fronds and germlings. Each nutrient condition was replicated in three 1-liter tanks, containing five clay tiles for the germlings culture and seven fronds for the adults culture (Fig. 2), resulting in a total of 45 clay tiles and 63 fronds. The fronds were needle-punched

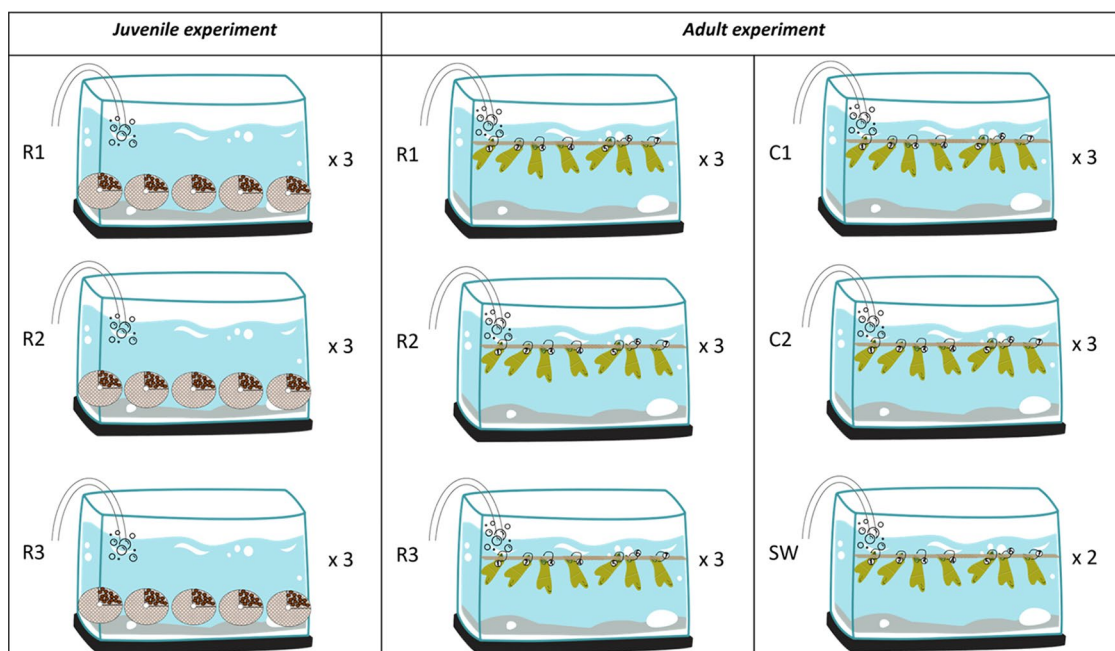
at their base, labelled with plastic beads, and suspended in the tanks using nylon strings.

In addition to the three [DIN]: [P] conditions, adult fronds were exposed to three additional nutrient conditions (Table 1):

- C1: representing higher annual mean values recorded in the Gulf of Trieste by the Regional Environmental Protection Agency – Friuli Venezia Giulia (ARPA FVG, 2009–2014) (Gerdol et al. 2020).
- C2: enriched with the biofertilizer AlгатronCifo® (Cifo S.p.A. San Giorgio di Piano, Bologna, Italy) which has been shown to enhance photophysiological and growth performance in other Fucales (e.g. *Gongolaria barbata*, Kaleb et al. 2023; *Ericaria amentacea*, Malfatti et al. 2023).
- SW: filtered seawater collected at the sampling site in Marina Julia.

R1 was used as control condition for a three-day acclimation period, as it was considered optimal for *F. virsoides* based on historical data from the 1990s when it was widespread and abundant in the Gulf of Trieste.

Culture media R1, R2, R3 and C1 were prepared by adding sodium nitrate ( $\text{NaNO}_3$ , SigmaAldrich), and potassium phosphate ( $\text{KH}_2\text{PO}_4$ , SigmaAldrich) to ASW. Nitrites ( $\text{NO}_2^-$ ) were not included due to their typically low concentrations compared to nitrates in the North Adriatic Sea (Degobis and Gilmartin 1981). Both nutrients were dissolved in



**Fig. 2** Experimental design for the different nutrient conditions in the germling and adult experiment. R1 = [DIN]: [P] ratio in 1996, R2 = [DIN]: [P] ratio in 2007, R3 = [DIN]: [P] ratio in 2017, C1 = higher

annual mean values registered in the Gulf of Trieste, C2 = biofertilizer additive AlгатronCifo® and SW = filtered seawater collected at the sampling site



distilled water and then added to the ASW batches. Instant Ocean contains trace amounts of  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  (ca. 0.5  $\mu\text{M}$   $\text{NO}_3^-$  and ca. 0.3  $\mu\text{M}$   $\text{PO}_4^{3-}$ ); however, since the same amount of salt was added to each condition involving ASW, these trace amounts and other micronutrients present in the filtered SW were not included in the nutrient listings. For the C2 and SW conditions, seawater was collected from the sampling site and filtered through 0.22  $\mu\text{m}$  Durapore membrane filters (Merck Millipore Ltd). The C2 condition was prepared by adding 4.5  $\text{mL L}^{-1}$  of AlgaTronCifo<sup>®</sup> to the seawater, as in Kaleb et al. (2023).

To avoid possible nutrient limitation, culture media were renewed every three days in the germlings tanks and every two days in the adult tanks. To control the variation of light intensity with position under the lamp, tanks and tiles within the tanks were randomly repositioned under the lamps when culture media was refreshed.

## Germlings culture

After 24 h in dark and cold conditions, the receptacles were placed in six 300 mL beakers filled with R1 solution and left undisturbed for an additional 24 h under laboratory conditions (see previous section) until the gamete release and fertilization occurred. The receptacles were then carefully removed, and concentrated zygote solution was prepared by removing ca. 250 mL of R1 from each beaker. An area of  $3.2 \pm 0.22 \text{ cm}^2$  on 45 clay tiles was inoculated by pipetting the zygote solution. The tiles were acclimatized for 24 h, after which five tiles per tank were randomly assigned (T0). The following measurements were conducted (Table 2):

- *Morphometry*: One tile for each tank was used for morphometric analysis, where 10 embryos were randomly selected and photographed under an inverted microscope

(Leica, DM IL LED) using a Canon PowerShot G9. This procedure was repeated after 3 (T1), 6 (T2), 9 (T3), and 12 days (T4). The following variables were measured using ImageJ<sup>®</sup> software (Schneider et al. 2012): embryo length and width, rhizoid length, hyaline hair length and number (measured from T2 to T4).

- *Embryo density and survival rate*: The number of embryos per tile was determined from images of 4 tiles per tank, taken with a digital camera (Olympus Tough TG-7) at T0 and T4. The tiles were positioned on a plasticized grid paper, which served as a reference for germling coverage in the images. The survival rate (%) was then manually calculated using ImageJ<sup>®</sup> software.
- *Photosynthetic efficiency*:  $F_v/F_m$  was measured on the surface of the germlings-covered tiles at T2, T3 and T4 using a PAM Imaging Fluorometer Open FluorCam as previously described (Malfatti et al. 2023).

## Adults culture

Fronds were acclimatized in R1 solution for three days before being randomly assigned to tanks (T0). Measurements were conducted as follows (Table 3):

- *Photosynthetic performance*: Rapid Light Curves (RLCs) measurements were performed on three randomly selected fronds per tank with the PAM Imaging Fluorometer Open FluorCam at day 0 (T0), 4 (T1), 8 (T2), and 12 days (T3). RLCs consisted of eight actinic light steps (18, 101, 188, 277, 451, 622, 1118, 1588  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ), each lasting 60 s. A saturating light pulse of 4040  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  was applied at the end of each step to determine the minimum ( $F_0$ ) and maximum fluorescence ( $F_m$ ). Each RLC lasted

**Table 2** Data collected on germlings

Time	Sample size	Variable
T0 = random assignment of the tiles to the different nutrient concentrations	4 tiles per tank	density
T1 = 3 days	10 embryos per tank	embryos length and width rhizoids length
T2 = 6 days	10 embryos per tank	embryos length and width rhizoids length hyaline hairs length and number
T3 = 9 days	4 tiles per tank 10 embryos per tank	$F_v/F_m$ embryos length and width rhizoids length hyaline hairs length and number
T4 = 12 days	4 tiles per tank 10 embryos per tank	$F_v/F_m$ embryos length and width rhizoids length hyaline hairs length and number
	4 tiles per tank	density
	4 tiles per tank	$F_v/F_m$

**Table 3** Data collected on adult fronds. \*Asterisks indicate the time intervals of the metabolic rates measurements, one day later than the other measurements

Time	Sample size	Variable	Unit
T0 = random assignment of fronds to the different nutrient concentrations	3 fronds per tank 63 fronds	RLCs Length	- mm
T0* = 1 days	3 fronds per tank	Metabolic rates	$\mu\text{mol O}_2 \cdot \text{gFW}^{-1} \cdot \text{h}^{-1}$
T1 = 4 days	3 fronds per tank	RLCs	-
T1* = 5 days	3 fronds per tank	Metabolic rates	$\mu\text{mol O}_2 \cdot \text{gFW}^{-1} \cdot \text{h}^{-1}$
T2 = 8 days	3 fronds per tank	RLCs	-
T2* = 9 days	3 fronds per tank	Metabolic rates	$\mu\text{mol O}_2 \cdot \text{gFW}^{-1} \cdot \text{h}^{-1}$
T3 = 12 days	3 fronds per tank 63 fronds	RLCs Length	- mm
T3* = 13 days	3 fronds per tank	Metabolic rates	$\mu\text{mol O}_2 \cdot \text{gFW}^{-1} \cdot \text{h}^{-1}$

approximately 8 min and recorded the fluorescence yield (F), the maximum fluorescence yield of a light-adapted frond ( $F'_m$ ), the effective quantum yield of PSII ( $\phi_{\text{PSII}}$ ), and the electron transport rate (ETR). Following Ralph and Gademann (2005), the initial slope of the RLC before the onset of saturation ( $\alpha$ ), the minimum saturating irradiance ( $E_k$ ) and the maximum relative electron transport rate ( $r\text{ETR}_{\text{max}}$ ) were determined by fitting the RLC to a curve as function of PAR irradiance (SigmaPlot v. 12.0, Systat Software Inc.) using the equation of Platt et al. (1980). For each light step, non-photochemical quenching (NPQ) was calculated as the ratio of the difference between  $F_m$  and  $F'_m$  to  $F'_m$ , and fitted as function of PAR irradiance to obtain the maximum non-photochemical quenching ( $\text{NPQ}_{\text{max}}$ ), representing maximum thermal energy dissipation, according to Serôdio and Lavaud (2011).

- **Relative Growth Rate (RGR):** The FW of all fronds was recorded at T0 and T3. RGR was calculated as the difference between the logarithms of the final and initial FW divided by the time interval (Lüning 1990).
- **Metabolic rates:** To minimize stress to the fronds, metabolic rates were recorded one-day after the photosynthetic performance measurements, referred to as T0\*, T1\*, T2\*, T3\*. Oxygen evolution was measured by incubating individual fronds in 20 mL gas-tight glass vials equipped with sensor spots (three fronds per tank, one per vial) alongside a control vial containing only the tank medium to account for possible microbial activity. Once incubated, the fronds were put back into the tank and left to acclimate again to the laboratory conditions. Dissolved oxygen (DO) was recorded through contactless optical fibers, with the oxygen curve recorded in real-time using a 4-channel optical  $\text{O}_2$  readout device (FireSting-O2; FSO2-C4, PyroScience GmbH, Aachen, Germany) at one-minute interval, with data stored in the Pyroscience Workbench software. The incubation lasted approximately 15–20 min and was conducted under both light and dark conditions to measure net production (NP) and respiration rate (R), respectively. The incubation

time was defined appropriate after some preliminary tests combining biomass, vials volume and time, so to prevent any photorespiration process happening in the light incubation (Ouissè et al. 2014). While light incubations did not require a specific acclimation time because conducted at laboratory conditions, prior respiration measurement, fronds acclimation was ensured by starting at least one hour after the lamps switched off. To prevent the boundary layer formation at the beginning and at the end of the incubation, the vials were carefully shaken, stirring the water inside during the experiment and before recording the values. DO measurements were automatically adjusted for temperature changes using the Tsub21 temperature sensor (PyroScience GmbH, Aachen, Germany), which was inserted into the culture medium within the tank and connected to the readout device. At the end of each incubation cycle, each frond was photographed and weighed (FW) to express metabolic rates as  $\mu\text{mol O}_2 \cdot \text{gFW}^{-1} \cdot \text{h}^{-1}$ . Net production and respiration were calculated as the difference between the final and initial values. Assuming a constant respiration rate throughout the daily cycle, gross primary productivity (GPP) was calculated as follows:  $\text{GPP} = \text{NP} + \text{R}$  (Guy-Haim et al. 2016).

## Statistical analysis

Statistical tests were performed in RStudio (R Core Team 2023). Germling morphometric measurements and density were analyzed by a Split-Plot ANOVA with 'Tank' as the within-subjects identifier (9 levels), 'Time' as the within-subjects factor (4 or 3 levels), and 'Nutrient' as the between-subjects factor (3 levels) using the 'anova\_test' function from the 'rstatix' package (Kassambara 2023). When these were significant, we proceeded with pairwise comparison analysis with Bonferroni adjustment using the 't-tests' function from 'rstatix'. Linear mixed-effects models were used to account for the nesting design with the function 'lmer' from the package 'lme4' (Bates et al. 2020) and Type II or

III Wald Chi-Square tests were applied to assess the significance of the fixed effects. For the analysis of photosynthetic performances and metabolic rates, the factors ‘Nutrient’ (3 or 6 levels) and ‘Time’ (3 or 4 levels) were treated as fixed effects, while ‘Tank’ was included as a random effect (9 or 17 levels). For the RGR, the factor ‘Nutrient’ (6 levels) was treated as a fixed effect and ‘Tank’ as a random effect (17 levels). Estimated marginal means analysis with pairwise comparison test with Tukey adjustment was then performed using the ‘emmeans’ package (Lenth et al. 2023) when necessary.

## Results

Morphometric measurements of germlings significantly increased over time, but no significant differences were observed between treatments (Tables S1, S2). However, at T4, the mean length of hyaline hairs in the R1 condition was ca. 52  $\mu\text{m}$  smaller than in R2 and R3 ( $284.76 \pm 45.42 \mu\text{m}$ ,  $337.92 \pm 58.97 \mu\text{m}$  and  $335.28 \pm 7.49 \mu\text{m}$ , respectively). Germling density decreased significantly and uniformly over time across all conditions (Split-plot ANOVA,  $F_{2,6} = 59.85$ ,  $p < 0.01$ ), while no significant differences in germling survival were observed (Linear mixed model,  $\text{Chi}^2_2 = 0.03$ ,  $p = 0.98$ ) (Fig. S1).

$F_v/F_m$  ratio was similar across different nutrient conditions (Linear mixed model,  $\text{Chi}^2_2 = 0.09$ ,  $p = 0.96$ ), but significant differences were observed over time and in the interaction between nutrient conditions and time ( $\text{Chi}^2_2 = 76.71$ ,  $p < 0.01$  and  $\text{Chi}^2_4 = 10.73$ ,  $p < 0.05$ , respectively). A slight decrease in  $F_v/F_m$  was observed over time in all nutrient conditions, with mean values ranging from  $0.68 \pm 0.01$  ( $\pm$ SD) at T2 to  $0.63 \pm 0.03$  ( $\pm$ SD) at T4.

In adult fronds,  $F_v/F_m$  decreased slightly over time (Linear mixed model,  $\text{Chi}^2_3 = 55.25$ ,  $p < 0.01$ ), but not uniformly across nutrient conditions ( $\text{Chi}^2_{15} = 52.76$ ,  $p < 0.01$ ) (Table S3). Notably,  $F_v/F_m$  values at T3 remained consistently above 0.6 in C1 and SW, whereas these values decreased to 0.56–0.58 in R1, R2, R3 and C2 (Fig. 3a, Table S4). Similar to  $F_v/F_m$ ,  $r\text{ETR}_{\text{max}}$  also showed significant differences over time (Linear mixed model,  $\text{Chi}^2_3 = 54.51$ ,  $p < 0.01$ ) and in the interaction of the factors ( $\text{Chi}^2_{15} = 67.85$ ,  $p < 0.01$ ) (Table S3). However, similar  $r\text{ETR}_{\text{max}}$  values of ca. 83  $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$  were found at both T0 and T3 (Fig. 3b, Table S4). Differences were also observed for  $\alpha$  and  $E_k$  in both factors and their interaction (Table S3). In particular, samples cultured in R1, R2 and R3 exhibited lower  $\alpha$  values than those in C1, C2 and SW (Fig. 3c, Table S5) and higher  $E_k$  values compared to C1 (Fig. 3d, Table S5). A similar trend to  $r\text{ETR}_{\text{max}}$  was observed for  $\text{NPQ}_{\text{max}}$  (Fig. S2, S3).  $\text{NPQ}_{\text{max}}$  only showed significant differences when the

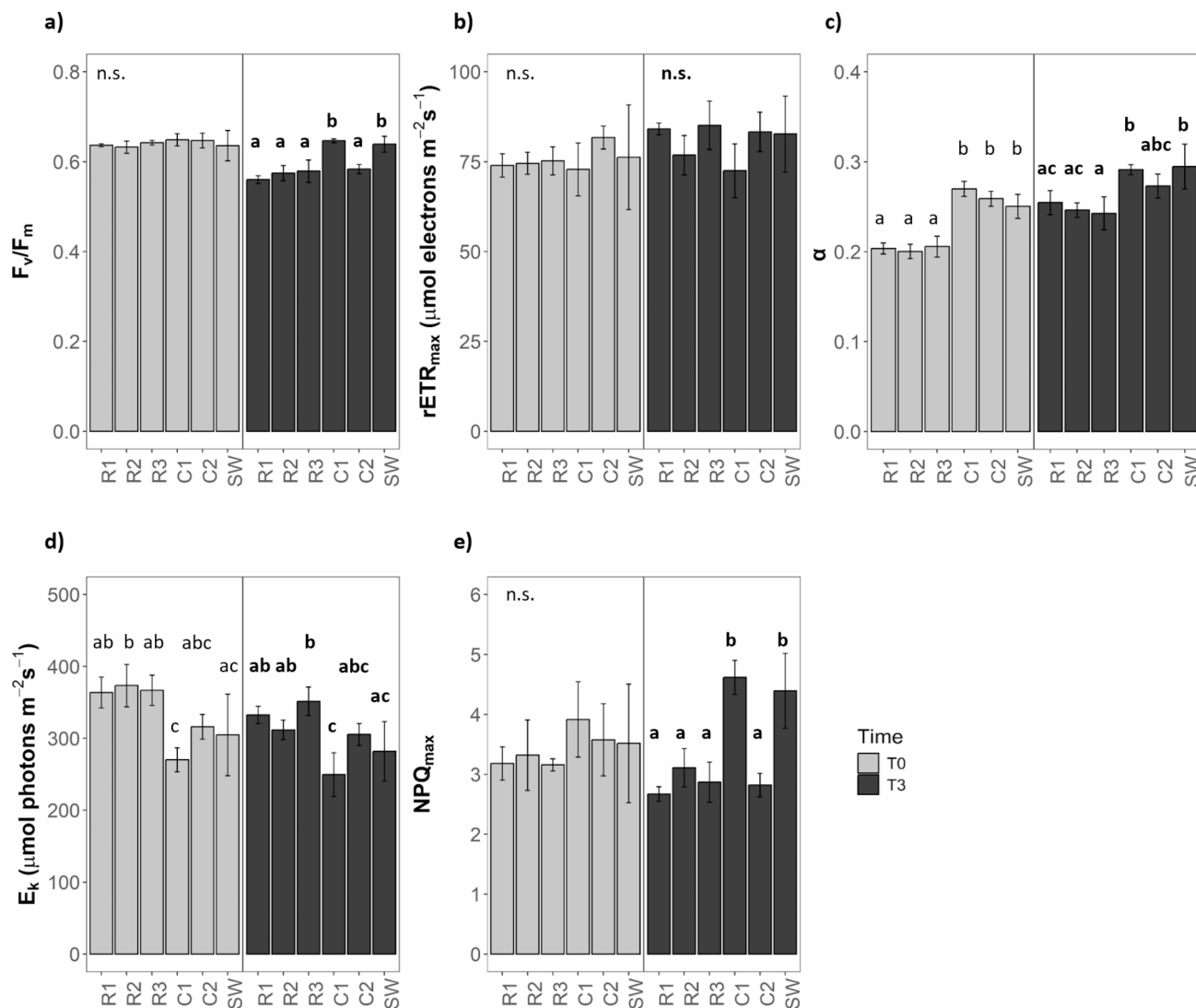
interaction of the two factors was considered (Linear mixed model,  $\text{Chi}^2_{15} = 27.66$ ,  $p < 0.01$ , Table S3). At the end of the experiment, higher  $\text{NPQ}_{\text{max}}$  values were observed in C1 and SW compared to R1, R2, R3 and C2 (Fig. 3e, S5).

The average RGR ranged from  $1.54 \pm 0.28$  in C2 to  $2.71 \pm 1.32\% \text{ d}^{-1}$  in R3. The RGR in C2 was ca. 1% lower than in R2, R3, C1 and SW, and R3 showed a slightly higher RGR than R1 (Linear mixed model,  $\text{Chi}^2_{15} = 29.16$ ,  $p < 0.01$ ) (Fig. 4, Table S6).

Metabolic rates, net oxygen production (NP) and respiration (R), remained consistent over time (Linear mixed model,  $\text{Chi}^2_3 = 3.37$ ,  $p = 0.34$ ,  $\text{Chi}^2_3 = 6.94$ ,  $p = 0.07$ , respectively) (Fig. 5, Table S7). Nonetheless significant differences were observed between treatments ( $\text{Chi}^2_5 = 19.38$ ,  $p < 0.01$  and  $\text{Chi}^2_5 = 59.68$ ,  $p < 0.001$ ) and in the interaction between time and treatment. Notably, samples in the R3 exhibited the highest R values at T0\*. Additionally, NP was similar across the six nutrient conditions, except for R1, which was significantly lower than R2 and R3 (Table S8). By the final measurement (T3\*), R values were similar across all conditions, while R2 showed a higher NP than C2. The calculated gross primary productivity (GPP) values were initially (T0\*) higher in R3 compared to the other conditions, with R2 significantly higher than C1 and C2 after two weeks (T3\*).

## Discussion

This study provides new insights into the ecophysiology (i.e. growth, photosynthesis, oxygen production and respiration) of *Fucus virsoides*. Although the decline of *F. virsoides* is mainly associated with pollution, habitat fragmentation and climate change (e.g. Boero et al. 2008; Orlando-Bonaca et al. 2013; Gerdol et al. 2020; Descourvières et al. 2024a), the exact cause-effect relationships have not yet been assessed and the reasons for this loss are still unclear. The occurrence of remnant populations is often restricted to areas close to freshwater inputs (Gerdol et al. 2020), this may be due to *F. virsoides* finding shelter in nutrient enriched areas as a consequence of the remarkable changes in trophic conditions in the northern Adriatic. Based on these assumptions, these changes were therefore hypothesized as a possible driver for the species’ decline. In addition, according to Wahl et al. (2011), different responses were expected at different developmental stages, with greater effects on early life stages, as in other Fucales (Coelho et al. 2000; Kraufvelin et al. 2012; Falace et al. 2021), and especially within the first two weeks of development (Tarakhovskaya et al. 2017). Factors influencing germling physiology and growth include storm and wave action (Norton et al. 1981; Vadas et al. 1990; Serão et al. 1996), temperature (Falace et al. 2021; Sánchez



**Fig. 3** (a)  $F_v/F_m$ , (b)  $rETR_{max}$ , (c)  $\alpha$  and (d)  $E_k$  and (e)  $NPQ_{max}$  measured in adult fronds of *Fucus virsoides* under different nutrient conditions on day 0 (T0) in grey and day 12 (T3) in black. R1 = [DIN]: [P] ratio in 1996, R2 = [DIN]: [P] ratio in 1996, R3 = [DIN]: [P] ratio in 2017, C1 = higher annual mean values recorded in the Gulf

of Trieste, C2 = biofertilizer additive AlгатronCifo® and SW = filtered seawater collected at the sampling site. Data are presented as mean values ( $n = 3$ )  $\pm$  SD. Different regular and bold letters indicate statistically significant differences between nutrient conditions at T0 and T3, respectively ( $p < 0.05$ ); n.s. = not statistically significant

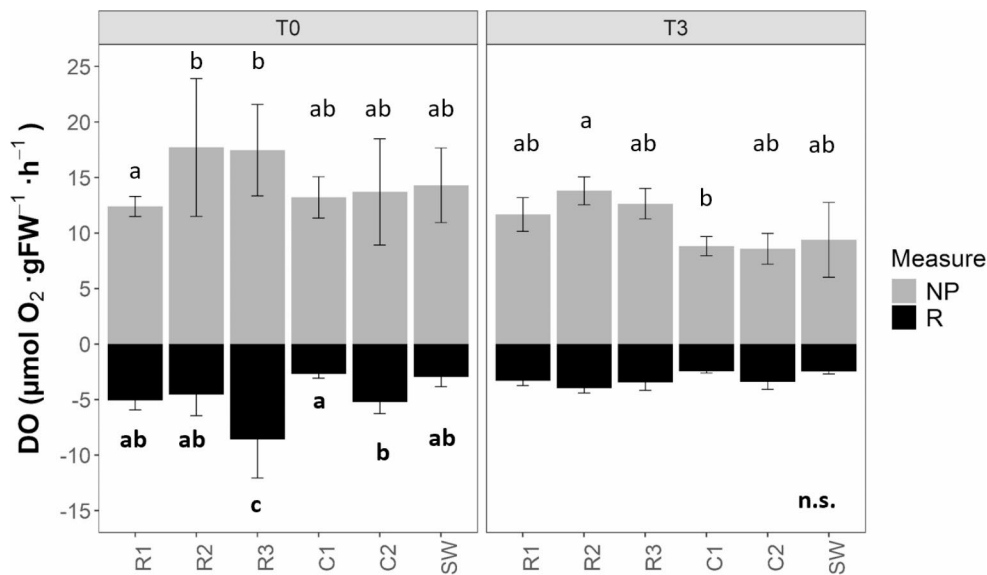
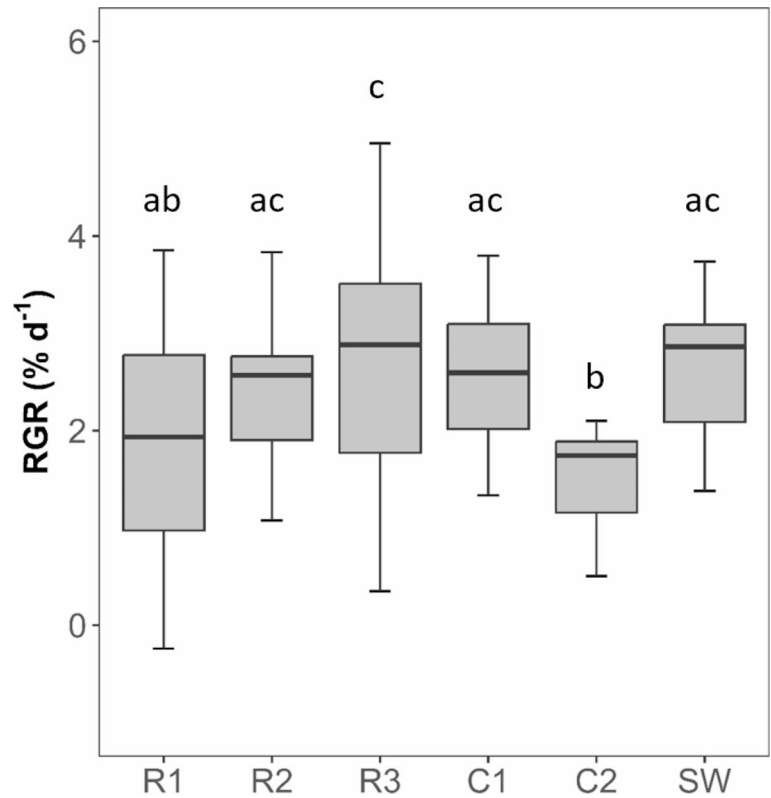
de Pedro et al. 2022, 2023a), light intensity (Creed et al. 1996), UV exposure (Schoenwaelder et al. 2003), eutrophication (Bergström et al. 2003), trace metals (Andersson and Kautsky 1996), pollutants (Creed et al. 1996, 1997) and acidification (Al-Janabi et al. 2016). However, in our study, we observed only subtle differences in the physiological responses of both early life stages and adults under varying nutrient conditions, ranging from eutrophic to oligotrophic environments. Despite the limited significant changes in physiological traits of *F. virsoides*, we recorded consistent growth over time across all conditions, suggesting that none of the conditions were severely limiting to the species' development and/or function. For germlings, significant

differences were only observed over time, while in adults, some differences were also noted across treatments.

For instance, the  $NPQ_{max}$  values of adults fronds cultured in C2, R1, R2 and R3 media were approximately half ( $2.82 \pm 0.58$ ,  $2.67 \pm 0.69$ ,  $3.11 \pm 1.09$  and  $2.87 \pm 0.62$ , respectively) of those cultured in C1 and SW. Lower  $NPQ_{max}$  values indicate reduced photoprotective activity, suggesting that the conditions can be interpreted as non-stressful or indicative of allostasis and that photosynthetic efficiency is likely to be higher under these conditions. Kaleb et al. (2023) observed that nitrogen enrichment through the addition of Alгатron could enhance the biosynthesis of light-harvesting centers or, as Gerard (2008) noted, increase the density of



**Fig. 4** Median values, 25th and 75th percentiles of relative growth rates expressed in terms of fresh weight (RGR%) of adult fronds of *Fucus virsoides* exposed to the different nutrient conditions. R1 = [DIN]: [P] ratio in 1996, R2 = [DIN]: [P] ratio in 1996, R3 = [DIN]: [P] ratio in 2017, C1 = higher annual mean values recorded in the Gulf of Trieste, C2 = biofertilizer additive AlгатronCifo® and SW = filtered seawater collected at the sampling site. Data are presented as mean values ( $n=3$ )  $\pm$  SD. Different letters indicate statistically significant differences among nutrient conditions and times ( $p < 0.05$ )



**Fig. 5** Metabolic oxygen evolution rates measured on adult fronds of *Fucus virsoides* under light (net production: NP) and dark conditions (respiration: R) incubations on day 1 (T0\*) and 13 (T3\*). R1 = [DIN]: [P] ratio in 1996, R2 = [DIN]: [P] ratio in 1996, R3 = [DIN]: [P] ratio in 2017, C1 = higher annual mean values recorded in the Gulf of Tri-

este, C2 = biofertilizer additive AlгатronCifo® and SW = filtered seawater collected at the sampling site. Data are mean values ( $n=3$ )  $\pm$  SD. DO: dissolved oxygen. Different regular and bold letters indicate statistically significant differences between nutrient conditions in NP and R, respectively ( $p < 0.05$ ); n.s. = not statistically significant

PSII centers. However, the lower  $F_v/F_m$  values (0.56–0.58) and RGR ( $1.54 \pm 0.28\% d^{-1}$ ) measured in the ammonium-rich biofertilizer condition (C2, AlгатronCifo®) compared to the other treatments suggest that these samples may have experienced some nutrient limitation. This indicate that the

concentrations of this algal extract may be suboptimal for *F. virsoides*. In addition, significant P-limitation is expected in C2, as indicated by the [DIN]: [P] ratio of 1044:1. Some previous studies in the Fucales restoration context recorded enhancement of physiological performance, fertility (Kaleb

et al. 2023), growth, survival and microbial biofilm communities (Malfatti et al. 2023) when the species were treated with AlgaTron addition. Because of its valorization potential, a further consideration of this biofertilizer could lead towards new actions aiming at restoring the species within the area, as already tested (Kaleb et al. 2022). However, our results along with observations from restoration trials conducted in our laboratory (unpublished data) convey that AlgaTron is not suitable for *F. virsoides*.

The similarly low values recorded for R1, R2 and R3 conditions suggest that there is no consistent pattern in these responses as higher values were observed in conditions such as SW and in the most eutrophic condition, C1. Therefore, these results should not be overgeneralized, and future studies should investigate whether higher concentration of AlgaTron could enhance both growth and photosynthetic efficiency in this species. Additionally, the potential role of high ammonium concentration in lowering pH and thus altering nutrient bioavailability should be further explored (Ravaglioli et al. 2017; Prisa 2021).

We also quantified the primary production of *F. virsoides*, adding further valuable information on this species. The mean GPP value determined in the laboratory was ca.  $14 \mu\text{mol O}_2 \cdot \text{gFW}^{-1} \text{h}^{-1}$ , while a single field measurement conducted in August 2023 yielded a mean value of ca.  $44.5 \mu\text{mol O}_2 \cdot \text{gFW}^{-1} \text{h}^{-1}$ . The R values under both conditions were ca.  $-5 \mu\text{mol O}_2 \cdot \text{gFW}^{-1} \text{h}^{-1}$ . However, these two measurements were not directly comparable due to differences in irradiance and temperature between the laboratory and field conditions, which were 125 vs. ca.  $800 \mu\text{mol photons} \cdot \text{m}^{-2} \text{s}^{-1}$  and 15 vs.  $27^\circ\text{C}$ , respectively.

Earlier studies on this topic date back to the 1970s (Zavodnik 1973; Kremer and Munda 1982). Zavodnik (1973) performed both field and laboratory measurements, reporting values of ca. 27 and  $5.4 \mu\text{mol O}_2 \cdot \text{gFW}^{-1} \text{h}^{-1}$  and R values of ca. -17 and  $-4.5 \mu\text{mol O}_2 \cdot \text{gFW}^{-1} \text{h}^{-1}$  for in-situ and *ex-situ* conditions, respectively. Similar data were obtained by Viñepla et al. (2006), who tested *Fucus spiralis* in southern Spain (Tarifa) under different irradiances; when exposed to ca.  $120 \mu\text{mol photons} \cdot \text{m}^{-2} \text{s}^{-1}$ , they recorded a productivity of ca.  $13 \mu\text{mol O}_2 \cdot \text{gFW}^{-1} \text{h}^{-1}$ . The consistent results across different studies highlight the wide adaptability of the *Fucus* genus. The higher GPP values recorded in the field both by this study and Zavodnik (1973) can be attributed to the maximum saturation of intertidal macroalgae at 400–600  $\mu\text{mol photons} \cdot \text{m}^{-2} \text{s}^{-1}$  (Lüning 1981). This also suggests a potential limitation in our study when assessing metabolic rates and photosynthetic activities at irradiance levels below the maximum saturation ones. Nonetheless, these findings provide a solid foundation for follow-up experiments that could explore these physiological responses under varying

PAR conditions, which might influence other aspects such as faster desiccation (Descourvières et al. 2024b).

The lack of significant physiological differences under the nutritional conditions tested may be attributed to the evolutionary history and biogeographical distribution of *F. virsoides*. As the only Mediterranean representative of the genus, it may have descended from a common ancestor with *F. spiralis* (Serrão et al. 1999) and subsequently became isolated in the Adriatic during the last glaciation. Nonetheless, given its geographical distribution from the Venice lagoon to Albania, the term ‘glacial relict’ may be misleading.

Unlike other genera adapted to more stable environments (e.g. the Baltic Sea), *F. virsoides* is well adapted to a wide range of natural environmental conditions, as evidenced by its latitudinal distribution. An analysis of annual nutrient concentrations within the three sub-basins (Artegiani et al. 1997) in the surface waters from 1993 to 2017 revealed considerable temporal and spatial variability (Fig. S4, data obtained from available datasets in EMODnet). The northern sub-basin exhibited the largest range of DIN concentrations (from 1.60 to  $4.72 \mu\text{M}$ ), while the southern sub-basin had the widest range of DIP concentrations (from 0.03 to  $0.14 \mu\text{M}$ ).

Although further species-specific research on *F. virsoides* is required to address gaps in knowledge regarding nutrient uptake, storage strategies and its general ecophysiology. Other *Fucus* species demonstrate remarkable nutrient adaptive strategies which may be shared by this Mediterranean representative. For instance, *Fucus serratus* can thrive in low external P-concentrations by employing high nutrient storage as well as non-saturating or biphasic kinetics (Gordillo et al. 2002). Generally, *Fucus* spp. have a high capacity for nutrients accumulation, reflecting the water trophic status (Wahl et al. 2011), making them effective bioindicators (García-Seoane et al. 2021). Moreover, Munda and Veber (1996) reported that *F. virsoides* could increase its P-content by 8 to 37 times without hindering growth, except under high concentration of heavy metals (Kremer and Munda 1982).

These findings, along with our results, suggest that the interactive effect of non-climatic stressors (Gunderson et al. 2016) such as nutrients availability in combination with other factors like temperature (Colvard and Helmuth 2017; Gouvea et al. 2017; Umanzor et al. 2021; Fales et al. 2023) and/or salinity (Nygård and Dring 2008), could contribute to the decline of this species, as observed in other Fucales. This highlights the importance of understanding how multiple stressors interact (Kunze et al. 2021) and how factors often considered detrimental may instead enhance performance in some aspects, such as productivity (Connell et al. 2013). It has been suggested that higher nutrient availability could improve the resilience of *Fucus* species to abiotic and/

or biotic stressors (e.g. Colvard and Helmuth 2017; Felline et al. 2019; Gerdol et al. 2020). For instance, extreme events such as heatwaves and cold spells, which are occurring with increasing frequency and unpredictability might trigger unforeseen responses, necessitating further investigations into thermal limits (e.g. thermal tolerance curves). Declines in *Fucus* populations have also been documented in other regions; for example, *Fucus guiryi* has declined in the southern Canary Islands due to a 'site effect' associated with increased wind speed, air temperature and sea surface temperature (SST) (Álvarez-Canali et al. 2019). Similarly, *F. vesiculosus* has experienced a range contraction, disappearing along the Moroccan coast to southern Portugal, likely due to the rising SST, and the spatial fragmentation and isolation of its populations (Nicastro et al. 2013).

Further species-specific experiments are needed to explore the effects of nutrient conditions, ideally at 'the omics' level, to better understand the ecophysiology of this endangered species and its responses to interaction with other factors (e.g. marine heat waves, UV exposure). This research will be critical for developing effective conservation and reforestation strategies. The potential disappearance of this species could have profound implications, including the loss of ecosystem functions and biodiversity associated with it, as well as socio-economic impacts due to the bioactive compounds it provides (Jerković et al. 2021).

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04523-1>.

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**Author contributions** AF, ED, MM, and VB conceived the project. ED and MM collected the data and conducted the experiments. SN, MM and ED analyzed the data. MM, ED, SN, and AF wrote the first draft. All the authors contributed to interpreting the results, writing and approved the submission.

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**Data availability** Data will be made available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors declare that they have no financial or non-financial competing interests to disclose.

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