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# Seasonal Photosynthetic Acclimation as a Key Invasiveness Character in *Rugulopteryx okamurae* (Dictyotales, Ochrophyta)

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## ABSTRACT

The high variability of natural environments poses significant challenges to photosynthetic organisms, which must adapt to constant fluctuations. Mechanisms such as acclimation and adaptation are essential for mitigating stress and ensuring survival. *Rugulopteryx okamurae*, an invasive alien seaweed recently introduced into Mediterranean and Atlantic waters, displays a remarkable ecological success, forming dense monospecific populations throughout diverse environments. This persistence suggests highly efficient acclimation mechanisms, possibly driven by seasonal physiological performance. The aim of this study was to evaluate the seasonal physiological response of *R. okamurae* to seasonal environmental fluctuations within a *Posidonia oceanica* meadow in the Alboran Sea, to better understand the photosynthetic acclimation strategies underlying its invasiveness. Photosynthesis–irradiance curves, pigment concentrations and elemental composition were analysed in individuals sampled bimonthly from July 2021 to July 2022 at a −10 m depth. Results showed significant seasonal variation in physiological parameters, highlighting a consistent acclimation capacity and robust photosynthetic performance. Fluctuations in pigment content and photosynthetic variables reflected the species' ability to optimise metabolic activity in response to environmental changes. Light compensation and saturation parameters further indicated strong photoadaptive capacity, enabling the species to thrive under both low and high light conditions. Its tolerance to a broad range of environmental factors, combined with mechanisms that prevent photoinhibition, may explain its persistence across seasons and wide depth ranges in the Alboran Sea. Although further research along depth gradients is needed, these findings underscore the role of physiological plasticity in the ecological success of *R. okamurae* and highlight the value of field-based studies in understanding invasion processes of marine macrophytes.

## 1 | Introduction

The high variability of the natural environment poses significant challenges to photosynthetic organisms, which must grow and reproduce under constant fluctuations in both biotic and abiotic factors (Walters 2004). These continuous changes may induce stress in organisms, which develop mechanisms to mitigate an irreversible effect on their biological systems; among them, acclimation and adaptation are key contributors (Mitra et al. 2021). While adaptation involves long-term genetic changes that accumulate over successive generations, resulting in heritable modifications within a population (Hoffmann et al. 2003), acclimation—also known as phenotypic plasticity (Golo et al. 2024)—is a reversible physiological response that allows organisms to adjust their functions over their lifespan (Sinclair and Roberts 2005). This mechanism is especially important in marine environments, where factors such as salinity, temperature, pressure, dissolved oxygen levels and solar radiation can vary significantly over time (Smith 2009). In particular, seaweeds are primarily influenced by abiotic factors such as nutrient availability, temperature, and irradiance (Hurd et al. 2014). These organisms show a remarkable capacity for physiological and morphological adjustments, ensuring their survival under a wide range of marine conditions (Hanelt and Figueroa 2012; Quintano et al. 2019), particularly in terms of photosynthetic traits (Molina-Montenegro et al. 2012; Zanolla et al. 2015).

Both mechanisms of acclimation and adaptation are particularly important in determining the establishment and invasive behaviour of photosynthetic invasive organisms (Davidson et al. 2011). In this regard, acclimation allows these organisms to change, not only their physiological characteristics, but also their morphological and behavioural traits, enabling them to cope with changing environmental conditions (Richards et al. 2006; Smith 2009; Davidson et al. 2011; Gouvêa et al. 2022). Consequently, invasive alien species are capable of maintaining higher fitness in favourable environmental conditions, and even sustaining it under unfavourable ones, often giving them a competitive advantage over native species (Richards et al. 2006; Davidson et al. 2011; Gioria et al. 2023). For example, the widely distributed invasive seaweed in the Mediterranean Sea, *Caulerpa cylindracea* Sonder, demonstrates a remarkable strategy to maintain its population through low biomass under unfavourable conditions, but when conditions are optimal, the species grows rapidly due to its high seasonal acclimation, achieved by two mechanisms: increasing its photosynthetic efficiency in low-light conditions, thus maintaining its photosynthesis, and altering its maximum photosynthetic value without changing the photosynthetic efficiency (Raniello et al. 2004). Additionally, *Asparagopsis taxiformis* (Delile) Trevisan shows that its physiological response depends on the different thermal ecotypes, with the invasive lineage exhibiting phenotypic plasticity under thermal stress (Zanolla 2014; Zanolla et al. 2015).

On the other hand, some invasive seaweeds exhibit physiological responses that appear decoupled from environmental fluctuations, maintaining their physiological parameters stable across a wide range of conditions (Baer and Stengel 2010; Zanolla et al. 2015; Surget et al. 2017). For example, *Sargassum muticum* (Yendo) Fensholt has been shown to maintain its photosynthetic activity despite temperature fluctuations, preserving photosystem II function unaltered under different environmental conditions in invaded areas along the Irish coast, even without any morphological or developmental changes under different environmental conditions (Baer and Stengel 2010). These examples illustrate how wide physiological performance enables invasive seaweeds not only to adapt, but also to dominate new habitats, highlighting the importance of physiological responses in the context of invasiveness.

The introduction of *Rugulopteryx okamurae* (E. Y. Dawson) I. K. Hwang, W. J. Lee & H. S. Kim into Mediterranean and Atlantic waters has shown remarkable resilience to a variety of environmental conditions, allowing it to form dense monospecific populations throughout the year across its introduced distribution range (Altamirano et al. 2016, 2019; García-Gómez et al. 2018; Faria et al. 2021). This species can settle on both horizontal and vertical rocky substrates, and also grows epiphytically on soft and hard surfaces, colonising a wide bathymetric range and associated benthic communities (García-Gómez et al. 2018, 2021), from shallow eulittoral pools to depths exceeding 50 m (Altamirano et al. 2019). Moreover, *R. okamurae* can even survive in a pelagic form, unattached, in the bathyal zones of the Gulf of Cadiz, where large aggregations of thalli have been observed at depths of 1441 m, keeping an active photosynthesis after light exposure (Mateo-Ramírez et al. 2023).

Recent laboratory experiments have begun to reveal insights into the physiological behaviour of *R. okamurae*, maintaining high photosynthetic activity and nitrogen uptake under eutrophic conditions, particularly at elevated N:P ratios (Bonomi-Barufi et al. 2024). The species has also demonstrated its ability to sustain growth by efficiently assimilating organic nitrogen sources such as urea (Herrero et al. 2025). However, its seasonal physiological plasticity remains largely unexplored, with only a couple of field-based studies conducted on thalli collected near the Strait of Gibraltar (Figueroa et al. 2020; Muñoz et al. 2021).

One of the regions most affected by *R. okamurae* is the westernmost part of the Mediterranean Sea, namely the Alboran Sea. This area, considered as the origin of the invasion, is characterised by specific physical and chemical conditions due to its direct connection with the Atlantic Ocean (Ramírez et al. 2021). In terms of sea surface temperature (SST), the Alboran Sea experiences annual variations: in winter, temperatures average near 15°C, while in summer they reach around 23°C (Guijarro et al. 2015; Vargas-Yáñez et al. 2021). In terms of dissolved inorganic nutrients, the photic layer of this region is influenced by both stratification and upwelling events (Ramírez et al. 2021). During upwelling, nitrate concentrations typically range from 2 to 3 $\mu$M and phosphate from 0.15 to 0.2 $\mu$M, whereas under stratification conditions levels can drop below 0.25 and 0.06 $\mu$M, respectively (Ramírez et al. 2021). These pronounced environmental fluctuations in the Alboran Sea, coupled with the ability of *R. okamurae* to maintain large monospecific populations throughout the year in a wide range of environments (i.e., García-Gómez et al. 2021; Bellisimo et al. 2024; Rosas-Guerrero et al. 2025), suggest the presence of highly efficient acclimation mechanisms of the species in the invaded areas. However, such responses have not yet been characterised within *P. oceanica* meadows, where the species is also widely distributed (Junta de Andalucía 2019). Therefore, the aim of the following study is to determine the seasonal physiological response of *R. okamurae* in a *P. oceanica* meadow under the fluctuating environmental factors in the Alboran Sea, in order to better understand the acclimation mechanisms that may contribute to its invasiveness.

## 2 | Materials and Methods

### 2.1 | Sampling Procedure

Individuals of *R. okamurae* were collected on *P. oceanica* mattes located in a meadow of the Cambriles cliffs, Granada, Spain (36°44.0033′N, 3°20.6767′W), at a depth of 10 m. A description of the environmental conditions recorded during each sampling event at the study site is provided in Rosas-Guerrero et al. (2025). In brief, water temperature ranged seasonally from 14.8°C in January to 25.1°C in August, with relatively stable conditions in winter and higher variability in summer; photoperiod ranged from 10 to 14 h throughout the year; salinity remained stable within the range of 36.8 to 37.3; inorganic nutrient concentrations were generally low: nitrate ranged from below detection ($<0.2\,\mu$M) to 1.4 $\mu$M, ammonium from 0.5 to 1.6 $\mu$M, and both nitrite and phosphate remained below detection limits ($<0.2\,\mu$M; Rosas-Guerrero et al. 2025). Sampling was carried out by SCUBA diving at two-month intervals from July 2021 to July 2022 (July, September and November 2021, and January, March, May and July 2022). Individuals were carefully collected and placed in plastic bags in situ, avoiding damage to the meadow and preventing the dispersal of the invasive species. Samples were transported directly after collection to the laboratory of the University of Málaga, maintained in darkness and at a similar temperature to that recorded in the field. No acclimation treatment was applied to the thalli prior to the experimental measurements.

## 2.2 | Biological Variable Measurements

### 2.2.1 | Photosynthetic Parameters

Photosynthetic oxygen evolution rates were determined immediately after arrival at the laboratory from apical segments of three centimetres long ($n = 3$) from independent individuals at each sampling event. Measurements were performed in a liquid-phase incubation chamber with a Clark-type oxygen electrode (DW1/AD Hansatech Instruments) connected to an oxygen electrode system (Oxygraph+ Hansatech Instruments). The incubation temperature was maintained by a circulating cryothermostat (Frigiterm TFT-10J. P. Selecta) and adjusted to the in situ temperature recorded at the same time of sampling (July 2021: 17°C; September 2021: 23°C; November 2021, January and March 2022: 15°C; May 2022: 16°C; July 2022: 16°C). A series of 10 increasing irradiance levels (ranging from 0 to 950 $\mu$mol photons $m^{-2}\,s^{-1}$ PAR) were obtained with a white LED light source combined with neutral density filters. Irradiance was verified using a quantum photometer (LI-COR LI-250A) coupled to a spherical PAR sensor (US-SQS/L Walz). Each irradiance level was applied for 10 min until a steady-state photosynthetic rate was reached. Photosynthetic parameters were expressed as dry weight (DW; mg $O_2$ $g^{-1}$ DW $h^{-1}$), Chl *a* (mg $O_2$ $mg^{-1}$ Chl *a* $h^{-1}$) and thallus surface area (TS; mg $O_2$ $m^{-2}\,s^{-1}$). Photosynthetic parameters were derived from the photosynthesis-irradiance (P-I) curves according to the equation proposed by Platt et al. (1980), fitted with Kaleidagraph 4.0 software (Synergy Software). From these fits, the following photosynthetic parameters were estimated: the maximum net photosynthetic rate under light-saturated conditions ($PN_{max}$), photosynthetic efficiency ($\alpha$; calculated as the initial slope of the P-I curve under light-limited conditions) and the light compensation point ($I_c$). The light saturation parameter ($I_k$) was calculated as the ratio $PN_{max}/\alpha$ (Henley 1993). Dark respiration measurements were made by keeping the samples in darkness for the first 15 min.

### 2.2.2 | Pigment and Tissue Elemental Composition Analysis

Samples from *R. okamurae* were frozen and stored at −20°C upon arrival from the field for later analyses. For pigment extraction, thalli were immersed in N, N-dimethylformamide (DMF) and kept in the dark at 4°C for 24 h ($n=4$). The absorbance of the supernatant was then measured using an EON spectrophotometer (Biotek). The concentrations of Chl *a* were determined according to Wellburn (1994), while Chl *c* was estimated following the equation of Jeffrey and Humphrey (1975). Pigment content was expressed as both DW and TS basis. Thallus surface area was determined prior to drying, using fresh and hydrated samples carefully spread over acetate sheets to ensure complete extension of the fronds. Pictures of thallus surfaces were measured employing ImageJ 1.50i software (National Institutes of Health). Subsequently, these samples were dried at 60°C for 48 h to obtain their DW.

Tissue elemental composition (carbon and nitrogen concentrations, as well as the C:N ratio; $n = 5$) was determined by applying the difference-by-ignition (DOI) method with a Perkin-Elmer 2400 elemental analyser (PerkinElmer). Samples were first dried at 60°C for 48 h and pulverised with a mixer mill MM400 (RETSCH).

## 3 | Statistical Analysis

Values of photosynthetic parameters, pigment content and the C:N ratio were analysed by one-way model ANOVAs ($p < 0.05$), with time as a fixed factor. Homoscedasticity and normality were assessed by Levene's and Shapiro-Wilk tests, respectively. When significance was detected, the Student–Newman–Keuls (SNK) test was used. Carbon and nitrogen concentrations were compared by the non-parametric Kruskal-Wallis test, and when significances were found, Dunn's test was applied ($p < 0.05$). All ANOVA and Kruskal-Wallis statistical analyses were performed in SigmaPlot 11.0 software (Systat Software Inc.).

The relationship between the measured biological variables (photosynthetic parameters, pigment content and tissue composition) and seasonal variations of the environmental factors (mean maximum and mean minimum temperatures, photoperiod, nitrate and ammonium concentrations; in Rosas-Guerrero et al. 2025) was tested using Pearson correlation. Additionally, forward stepwise analysis was performed to evaluate the potential effects of each environmental parameter from the coefficients of determination ($R^2$). All statistical analyses were conducted using SigmaPlot 11.0 software (Systat Software Inc.).

## 4 | Results

### 4.1 | Photosynthetic Parameters

The maximum net photosynthetic rate expressed as DW ranged from 10 to 16 mg $O_2$ $g^{-1}$ DW $h^{-1}$, peaking in May and July 2022 (Figure 1, Tables 1 and 2). In terms of TS, the values

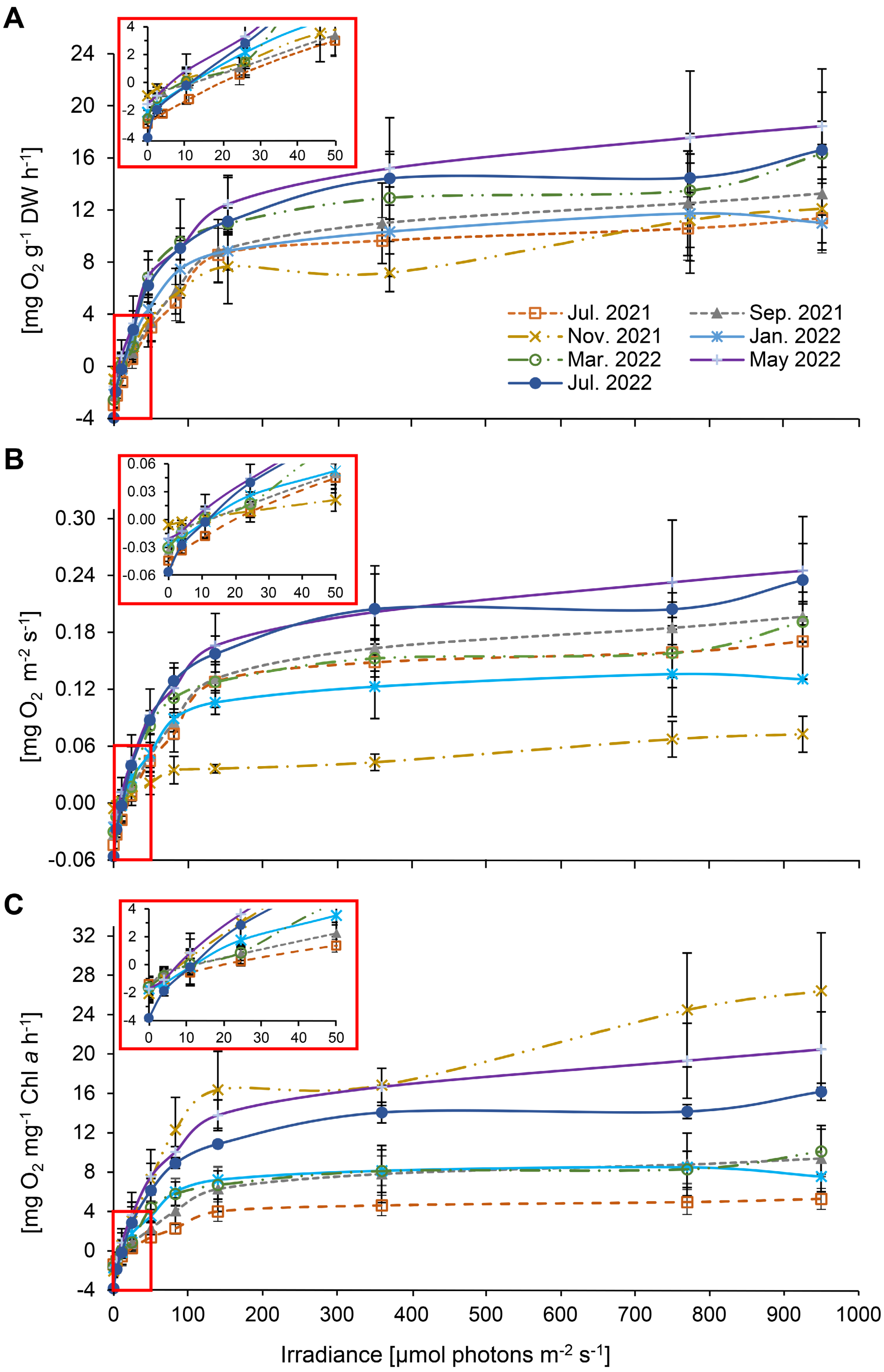

**FIGURE 1** | Photosynthesis-Irradiance curves (P-I curves) of *R. okamurae* individuals throughout the study period (July 2021–July 2022). P-I curves are expressed as dry weight (mg $O_2$ $g^{-1}$ DW $h^{-1}$) (A), thallus surface (mg $O_2$ $m^{-2} s^{-1}$) (B), and Chlorophyll *a* (mg $O_2$ $mg^{-1}$ Chl *a* $s^{-1}$) (C) basis. Data are expressed as mean ± SD ($n = 3$).

ranged from 0.08 to 0.20 mg $O_2$ $m^{-2} s^{-1}$, with the lowest value recorded in November 2021 and the highest in September and July 2022 (Figure 1, Tables 1 and 2). When values were expressed on a Chl *a* basis, the maximum net photosynthetic rate exhibited the highest value in November, which was up to 86% higher than in July 2021 (Figure 1, Tables 1 and 2). The highest $\alpha$ values, when expressed on a DW basis, were recorded between January and July 2022, showing an increase by half compared to the other months (Tables 1 and S1). When expressed in terms of TS, $\alpha$ values were considerably higher in March and July 2022 than in November 2021 (Tables 1 and S1). Photosynthetic efficiency values, expressed on a Chl *a* basis, were substantially greater in November, May, and July 2022 than in July 2021 and September (Tables 1 and S1). Dark respiration rates, expressed on a DW and TS basis, were at their maximum in July 2021 and 2022, while the lowest value was

**TABLE 1** | Photosynthetic parameters of *R. okamurae* estimated from P-I curves throughout the study period (July 2021–July 2022).

| Parameter | July 21 | September 21 | November 21 | January 22 | March 22 | May 22 | July 22 |
|---|---|---|---|---|---|---|---|
| $PN_{max}$ | | | | | | | |
| DW | $10.79^{b} \pm 2.90$ | $10.70^{b} \pm 0.24$ | $9.45^{b} \pm 0.25$ | $10.56^{b} \pm 1.34$ | $12.37^{b} \pm 1.48$ | $15.04^{a} \pm 0.74$ | $15.88^{a} \pm 0.70$ |
| TS | $17.63^{a} \pm 1.83$ | $19.68^{a} \pm 1.77$ | $7.52^{b} \pm 2.37$ | $14.05^{a} \pm 3.10$ | $17.18^{a} \pm 2.03$ | $19.46^{a} \pm 2.37$ | $19.97^{a} \pm 2.20$ |
| Chl *a* | $4.18^{e} \pm 0.67$ | $10.71^{d} \pm 1.77$ | $28.00^{a} \pm 1.08$ | $9.05^{d} \pm 1.1$ | $9.71^{d} \pm 1.1$ | $18.06^{b} \pm 3.24$ | $14.94^{c} \pm 0.11$ |
| $\alpha$ | | | | | | | |
| DW | $0.12^{b} \pm 0.03$ | $0.10^{b} \pm 0.005$ | $0.08^{b} \pm 0.01$ | $0.18^{a} \pm 0.01$ | $0.22^{a} \pm 0.03$ | $0.21^{a} \pm 0.04$ | $0.21^{a} \pm 0.01$ |
| TS | $0.20^{c} \pm 0.02$ | $0.17^{c} \pm 0.02$ | $0.07^{d} \pm 0.02$ | $0.19^{c} \pm 0.01$ | $0.27^{ab} \pm 0.04$ | $0.23^{bc} \pm 0.05$ | $0.29^{a} \pm 0.03$ |
| Chl *a* | $0.03 \pm 0.01^{c}$ | $0.04 \pm 0.01^{c}$ | $0.17 \pm 0.01^{a}$ | $0.12 \pm 0.02^{b}$ | $0.11 \pm 0.02^{b}$ | $0.19 \pm 0.01^{a}$ | $0.21 \pm 0.01^{a}$ |
| DR | | | | | | | |
| DW | $3.50^{ab} \pm 0.52$ | $2.01^{bc} \pm 0.23$ | $1.31^{c} \pm 0.10$ | $2.06^{bc} \pm 0.10$ | $2.28^{bc} \pm 0.19$ | $2.84^{bc} \pm 0.42$ | $4.42^{a} \pm 1.47$ |
| TS | $4.58^{a} \pm 0.23$ | $3.42^{bc} \pm 0.18$ | $0.64^{e} \pm 0.27$ | $2.72^{cd} \pm 0.18$ | $3.14^{c} \pm 0.12$ | $2.27^{d} \pm 0.41$ | $4.03^{ab} \pm 0.76$ |
| $I_c$ | $19.20^{a} \pm 2.64$ | $14.62^{bc} \pm 1.95$ | $12.54^{bc} \pm 0.39$ | $13.25^{bc} \pm 2.55$ | $13.07^{bc} \pm 1.88$ | $8.29^{c} \pm 3.11$ | $12.17^{b} \pm 1.48$ |
| $I_k$ | $74.97^{c} \pm 1.67$ | $114.89^{a} \pm 2.11$ | $109.23^{a} \pm 12.54$ | $55.70^{d} \pm 7.20$ | $70.46^{c} \pm 9.10$ | $87.90^{b} \pm 3.73$ | $67.31^{c} \pm 5.98$ |

*Note:* Data are expressed as mean ± SD ($n = 3$). Different letters denote significant differences among months ($p < 0.05$). Maximum net photosynthetic rate ($PN_{max}$), photosynthetic efficiency ($\alpha$) and dark respiration (DR) are expressed as dry weight (DW: Mg $O_2$ $g^{-1}$ DW $h^{-1}$) and thallus surface (TS: Mg $O_2$ $m^{-2}s^{-1} \cdot 10^{-2}$), and $PN_{max}$ and $\alpha$ are also expressed as chlorophyll *a* (Chl *a*: Mg $O_2$ $mg^{-1}$ Chl *a* $h^{-1}$). Light compensation point ($I_c$) and light saturation parameter ($I_k$) are expressed as μmol photons $m^{-2}s^{-1}$.

observed in November (Tables 1 and S1). The light compensation point decreased significantly from 19 ± 2 μmol photons $m^{-2}s^{-1}$ in July 2021 to 8 ± 3 μmol photons $m^{-2}s^{-1}$ in May 2022 (Tables 1 and S1). The light saturation parameter was significantly higher in September and November 2021 (113 ± 7 μmol photons $m^{-2}s^{-1}$), but decreased by half in January 2022 (Figure 1, Tables 1 and S1). No photoinhibition was detected when photosynthetic parameters were expressed in any values (Figure 1).

## 4.2 | Pigment Content

Chlorophyll *a* and *c*, expressed on a DW basis, did not differ significantly over sampling time (Figure 2, Table S1). However, when Chl *a* and Chl *c* were expressed as TS, as well as the Chl *c*:Chl *a* ratio expressed as DW and TS, significant differences were observed throughout the study period (Figures 2 and 3, Table S1). In terms of TS, the concentration of Chl *a* was lower in January and March 2022, being 25% inferior to the concentration in July (Figure 3A, Table S1). A similar pattern was observed for Chl *c* content, with a 25% decrease in January compared to the other sampling months (Figure 3B, Table S1). The ratio of Chl *c*:Chl *a* reached its highest value in May 2022, which was 25% higher than the ratio recorded in September (expressed as DW) and 36% higher than in January (expressed as TS; Figures 2C and 3C, Table S1).

## 4.3 | Analysis of Tissue Elemental Concentration

Nitrogen and carbon concentrations of the samples, as well as the C:N ratio, exhibited significant temporal variations (Figure 4, Table S1). Carbon concentration showed the highest value in July 2021 and July 2022, averaging 36% DW, and decreased to 26% DW in September and November 2021 (Figure 4, Table S1). Conversely, nitrogen concentration peaked in January 2022, nearly doubling the values observed in July 2021 (Figure 4, Table S1). The C:N ratio reached its maximum in July 2021, which was twice as high as the lowest values in November 2021 (Figure 4, Table S1).

## 4.4 | Relationship of Biological Variables and Environmental Factors

Light compensation point, light saturation parameter, carbon and nitrogen concentration of the tissue elemental composition, $\alpha$, $PN_{max}$, and pigment content expressed on a DW basis, as well as Chl *c* expressed on a TS basis, showed no significant correlations with any of the environmental factors analysed ($p > 0.05$; Table 2).

By contrast, $PN_{max}$ and Chl *a* expressed as TS basis, $PN_{max}$ expressed as Chl *a*, DR expressed as DW and TS, and C:N ratio were positively correlated with any of the measured abiotic factors (Table 2). According to the forward stepwise regression analysis, the $PN_{max}$ expressed as TS basis was positively correlated with photoperiod (60%) and ammonium concentration (35%), whereas $PN_{max}$ expressed as Chl *a* basis was correlated with nitrate concentration (51%; Table 3). Seasonal variations in DR expressed as DW basis were explained by photoperiod (71%), while DR expressed as TS basis was correlated with photoperiod and nitrate concentration, which together explained 37% and 46% of its seasonal variation, respectively (Table 3). The Chl *a* content expressed as TS was positively correlated with mean

**TABLE 2** | Correlation matrix and Pearson correlation coefficients ($R$) between biological variables and environmental factors measured throughout the study period (July 2021–July 2022).

| Parameter | Max $T$ | Min $T$ | LH | $NO_3^-$ | $NH_4^+$ |
|---|---|---|---|---|---|
| $PN_{max}$ | | | | | |
| DW | 0.24 | 0.19 | 0.59 | −0.32 | −0.46 |
| TS | 0.51 | 0.68 | 0.73* | 0.68 | 0.59* |
| Chl *a* | −0.01 | −0.25 | −0.31 | 0.72* | 0.54 |
| $\alpha$ | | | | | |
| DW | −0.25 | −0.17 | 0.31 | −0.49 | −0.51 |
| TS | 0.14 | 0.28 | 0.61 | −0.66 | −0.54 |
| Chl *a* | −0.08 | −0.30 | −0.01 | 0.30 | 0.10 |
| DR | | | | | |
| DW | 0.57 | 0.48 | 0.84* | −0.27 | −0.19 |
| TS | 0.42 | 0.58 | 0.23* | 0.68* | −0.49 |
| $I_c$ | 0.18 | 0.24 | 0.07 | −0.12 | 0.20 |
| $I_k$ | 0.39 | 0.38 | −0.10 | 0.47 | 0.37 |
| Pigment content ($mg\,g^{-1}$ DW) | | | | | |
| Chl *a* | 0.01 | −0.20 | −0.12 | 0.17 | 0.09 |
| Chl *c* | 0.38 | 0.14 | −0.15 | 0.44 | 0.55 |
| Chl *c*:Chl *a* | 0.15 | 0.07 | 0.63 | 0.40 | 0.30 |
| Pigment content ($mg\,cm^{-2}$) | | | | | |
| Chl *a* | 0.72* | 0.54 | 0.16* | 0.34 | 0.36 |
| Chl *c* | 0.59 | 0.42 | 0.0001 | 0.41 | 0.52 |
| Chl *c*:Chl *a* | 0.10 | −0.01 | 0.60 | 0.42 | 0.33 |
| C concentration | −0.16 | −0.15 | 0.36 | −0.45 | −0.28 |
| N concentration | −0.69 | −0.56 | −0.61 | −0.40 | −0.42 |
| C:N | 0.39 | 0.29 | 0.67* | 0.06 | 0.19 |

*Note:* Asterisks represent significant correlation coefficients ($p < 0.05$). Maximum net photosynthetic rate ($PN_{max}$); dry weight (DW); thallus surface (TS); Chlorophyll *a* (Chl *a*); photosynthetic efficiency ($\alpha$); dark respiration (DR); light compensation point ($I_c$); light saturation parameter ($I_k$); carbon concentration (C concentration); nitrogen concentration (N concentration); carbon: nitrogen ratio (C:N); maximum average temperature (Max $T$); minimum average temperature (Min $T$); photoperiod (LH); nitrate concentration ($NO_3^-$); ammonium concentration ($NH_4^+$).

maximum temperature and photoperiod, which explained 52% and 26% of its seasonal variation, respectively (Table 3). The C:N ratio was positively correlated with photoperiod, accounting for 45% of its seasonal variation (Table 3).

## 5 | Discussion

*Rugulopteryx okamurae* currently invading a *P. oceanica* meadow located at the Cambriles cliffs, exhibited remarkable physiological plasticity, acclimating its photosynthetic performance and pigment content in response to varying environmental conditions (see Rosas-Guerrero et al. (2025) for a summary of environmental conditions). Such plasticity likely contributes to its invasiveness, allowing it to survive and thrive under a wide range of environmental conditions.

The species displayed a robust physiological response to the environmental conditions in the study area. The $PN_{max}$ of *R. okamurae* measured in this study was consistent with those reported for populations from nearby areas of the Strait of Gibraltar (Muñoz et al. 2021). However, when values were compared with the native species of the family Dictyotaceae present in the study area, *R. okamurae* exhibited values considerably higher than the species *Dictyota dichotoma* (Hudson) J. V. Lamouroux (4–11 $mg\ O_2\ g^{-1}\ DW\ h^{-1}$) and *D. implexa* (Desfontaines) J. V. Lamouroux (4–8 $mg\ O_2\ g^{-1}\ DW\ h^{-1}$; Peckol and Ramus 1992), indicating superior photosynthetic performance and a high capacity to cope with the fluctuating environmental conditions. Furthermore, the values of *R. okamurae* also exceeded those reported for other invasive alien seaweeds in the region, such as *C. cylindracea* Sonder (Robledo and Freile-Pelegrín 2005) and *A. taxiformis* (Delile)

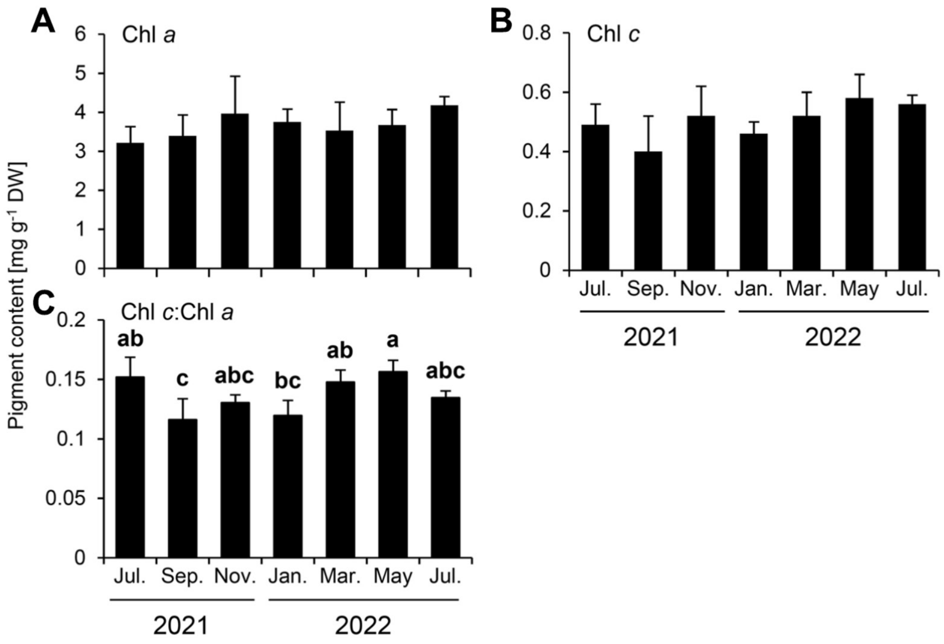

**FIGURE 2** | Pigment content of *R. okamurae* samples throughout study period (July 2021–July 2022) expressed as dry weight basis (mg g$^{-1}$ DW). Data are expressed as mean ± SD ($n = 5$). Different letters denote significant differences among months following ANOVA results ($p < 0.05$).

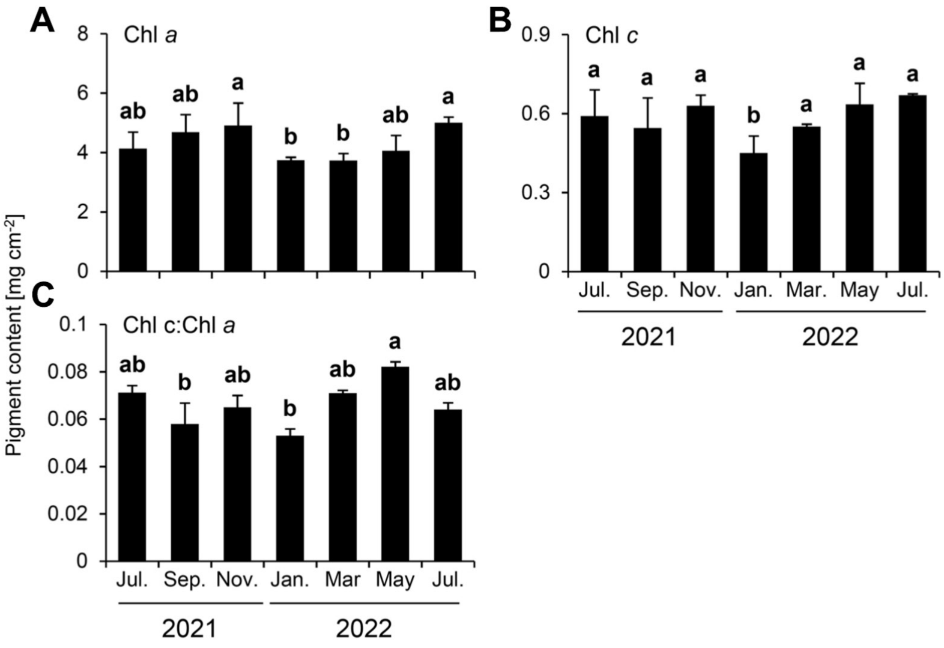

**FIGURE 3** | Pigment content of *R. okamurae* samples throughout study period (July 2021–July 2022) expressed as thallus surface basis (mg cm$^{-2}$). Data are expressed as mean ± SD ($n = 5$). Different letters denote significant differences among months following ANOVA results ($p < 0.05$).

Trevisan (Zanolla 2014), further highlighting its competitive advantage in this area.

This physiological dominance over the native species of the genus *Dictyota* has also been observed at light saturation points (Peckol and Ramus 1992; Plus et al. 2005), where the species exhibited $I_k$ values comparable to those of native upper-intertidal species such as *Ulva* spp. and *Jania rubens* (Linnaeous) J. V. Lamoroux (Saroussi and Beer 2007). In this study, *R. okamurae* maintained its photosynthetic activity at irradiances exceeding 1000 μmol photons m$^{-2}$ s$^{-1}$ without exhibiting a photoinhibitory response, indicating a high tolerance to intense light conditions. This absence of a photoinhibition response at such high irradiances may be attributed to the concentration of carotenoids, which play a key role in photoprotection against excessive light exposure (Stengel et al. 2011; Hanelt and Figueroa 2012; Celis-Plá et al. 2017).

Additionally, the species also maintained its light compensation point at 13 μmol photons m$^{-2}$ s$^{-1}$ for most of the year, a characteristic indicative of well-adapted species to low light conditions (Hanelt and Figueroa 2012). This finding

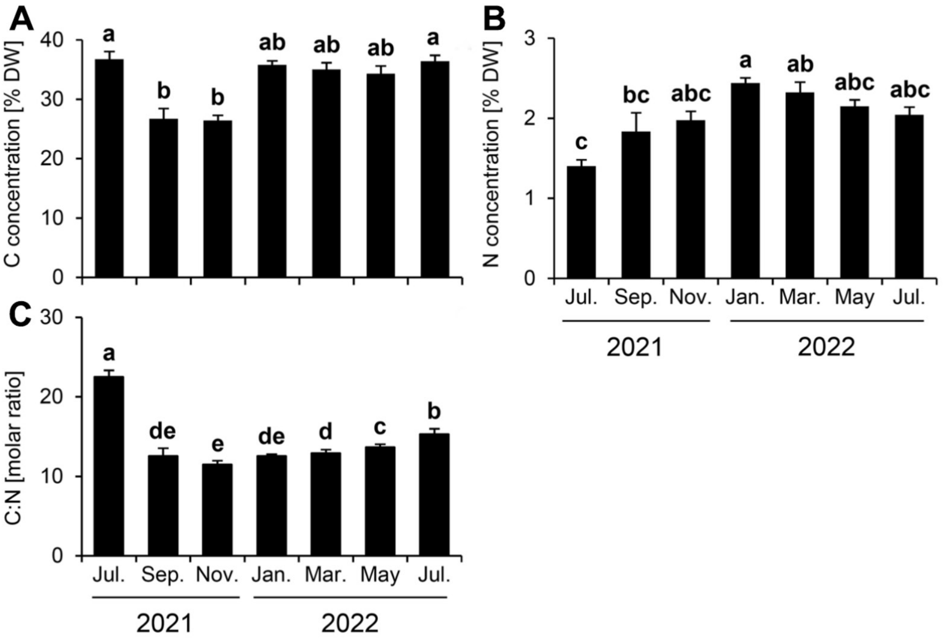

**FIGURE 4** | Tissue elemental composition of *R. okamurae* individuals throughout the study period (July 2021–July 2022). (A) Carbon concentration, (B) nitrogen concentration, (C) and C:N ratio. Data are expressed as mean ± SD ($n = 5$). Different letters denote significant differences among months following ANOVA results ($p < 0.05$).

**TABLE 3** | Contribution (%) of each abiotic factor to the total variance of any dependent biological variable calculated ($r \cdot 100$) from the coefficients of determination obtained by the forward stepwise analysis.

| Parameter | Max *T* | Min *T* | LH | $NO_3^-$ | $NH_4^+$ |
|---|---|---|---|---|---|
| $PN_{max}$ TS | — | — | 60.4 | — | 35.0 |
| $PN_{max}$ Chl *a* | — | — | — | 51.3 | — |
| DR DW | — | — | 70.8 | — | — |
| DR TS | — | — | 36.8 | 45.9 | — |
| Chl *a* TS | 52.0 | — | 25.9 | — | — |
| C:N | — | — | 45.2 | — | — |

*Note:* Maximum net photosynthetic rate ($PN_{max}$); thallus surface (TS); chlorophyll *a* (Chl *a*); dark respiration (DR); dry weight (DW); carbon: nitrogen ratio (C:N); maximum average temperature (Max *T*); minimum average temperature (Min *T*); photoperiod (LH); nitrate concentration ($NO_3^-$); ammonium concentration ($NH_4^+$).

highlights an adaptive mechanism that allows *R. okamurae* to thrive in environments with limited light availability (Eggert and Wiencke 2000; Hanelt and Figueroa 2012) while still achieving high maximum photosynthesis rates. The capacity of *R. okamurae* to tolerate low light conditions could be particularly advantageous for its survival within this *P. oceanica* meadow, where light availability at the seafloor is significantly reduced possibly by both the canopy of *P. oceanica* and intraspecific competition, driven by high population densities in late summer and autumn and increased biomass in spring and early summer (Rosas-Guerrero et al. 2025). In this context, Bernardeau-Esteller et al. (2015) reported that, the low light levels within the *P. oceanica* canopy can exceed the photoacclimation capacity of the invasive *C. cylindracea*, thereby constraining its photosynthetic performance. However, the sustained photosynthetic activity of *R. okamurae* under these similar light-limiting conditions suggests a greater photoacclimation capacity, enhancing the ability to adjust to shaded environments and enabling it to thrive beneath the canopy of *P. oceanica* habitats.

*Rugulopteryx okamurae* not only maintains high photosynthetic rates and a broad tolerance to light conditions but also adjusts its physiological performance in response to the environmental fluctuations in the study area. In this context, $PN_{max}$ fluctuated by up to 63% between the highest and the lowest value. For comparison, the *A. taxiformis* population in nearby areas exhibited a broader seasonal range, with $PN_{max}$ values ranging from 1 to 8 mg $O_2$ $g^{-1}$ DW $h^{-1}$, exhibiting a 75% fluctuation (Zanolla 2014). This comparatively narrower seasonal variation in *R. okamurae* suggests a greater stability in its photosynthesis under changing environmental conditions, reflecting an acclimation capacity that may be more robust than other invasive seaweeds in the Alboran Sea.

Moreover, the peak in photosynthetic rates observed during May and July 2022 could be linked to the species' vegetative and reproductive phenology, as this period corresponds to its highest capacity for biomass (Rosas-Guerrero et al. 2025) and reproductive structures within the thallus (pers. obs.). Additionally, the fact that *R. okamurae* populations are primarily maintained through clonal reproduction, ensures the persistence of this photosynthetic performance over time, further supporting its ability to adapt and acclimate to the specific environmental conditions (Altamirano et al. 2016, 2017).

When considering photosynthetic rates expressed as Chl *a* basis, the maximum values for $PN_{max}$ and $\alpha$ were recorded in November, indicating that the photosynthetic apparatus was more efficient during this period compared to other sampling times. Although $PN_{max}$ showed a correlation with nitrate concentrations, it is likely that intraspecific competition also played a significant role. The high population density observed in November—exceeding 3000 individuals $m^{-2}$, with sizes not exceeding 6 cm (Rosas-Guerrero et al. 2025)—suggests that individuals may have developed acclimation mechanisms to optimise the use of available resources and ensure survival. This intraspecific competition can also modulate the concentration of pigment contents, which increases as biomass and individual densities rise from early spring to late autumn (Rosas-Guerrero et al. 2025). During these periods, greater competition for resources, particularly light, may drive the need for higher pigment concentrations. By contrast, when the population density was considerably lower in winter, intraspecific competition was reduced, and consequently, individuals did not require high pigment concentrations or elevated photosynthetic rates, reflecting a reduced physiological demand and a mechanism to optimise available resources for survival. A similar pattern has been documented in *Ecklonia cava* Kjellman, where young individuals increase their pigment content to compensate for shading caused by adults, thus optimising their photosynthetic capacity in response to intense intraspecific competition (Altamirano et al. 2003). This dynamic suggests that reduced competition and increased access to light during winter may influence the acclimation of *R. okamurae* physiological response within the population. This acclimation is supported by the observed decrease in the Chl *a*:Chl *c* ratio, which is often associated with shading and enhanced photosynthetic responses under low light conditions (Wheeler 1980; Campbell et al. 1999).

Additionally, although morphological variation in *R. okamurae* was not specifically analysed in this study, changes in morphology could significantly influence the observed fluctuations in pigment content patterns. The species exhibits two distinct morphotypes throughout the year: a thicker form in winter and a thinner one in summer (Salido and Altamirano 2020). The thinner morphotype, which possesses a reduced width of thallus surface area, but not necessarily a smaller overall size, may require higher chlorophyll concentrations per unit surface to enhance light capture efficiency. This may represent a compensatory mechanism to counterbalance its lower light-harvesting surface area per unit volume.

However, when pigment content was expressed as DW basis, values remained within the ranges reported for other *Dictyota* species (Bogaert et al. 2020) and closely aligned with those reported for *R. okamurae* by Bonomi-Barufi et al. (2024), without showing temporal variation. This discrepancy in pigment content, when expressed as TS or DW basis, may be attributed to the morphological differences previously discussed, given that the relationship between morphology and volume remains unclear. It may also be attributed to the anatomical characteristics of the species, specifically considering that pigments are concentrated in the cells of the monolayered cortex, while cells of the thick monolayered medulla are devoid of pigments (Hwang et al. 2009; Verlaque et al. 2009). Thus, the thallus surface area plays a crucial role in determining pigment concentration densities. As a result, for a given biomass, individuals of the thicker winter morphotype possess a larger thallus surface area, which may mask the true temporal fluctuations in pigment content when measurements are made as TS basis. As there is not a clear relationship between these photosynthetic parameters and the different morphotypes, further studies under controlled conditions would be essential to assess the intrinsic differences between morphotypes and to identify the environmental factors that optimise the physiological responses of each morphotype.

Despite the decrease in Chl *a* synthesis during the winter months, *R. okamurae* exhibited remarkable photosynthetic activity throughout the study period, maintaining its C:N ratio above 12, which is within the typical range for seaweeds (Plus et al. 2005). *Although* nitrogen content dropped below 2% in July 2021, indicating potential nitrogen limitation (Hanisak 1979) and resulting in a notably high C:N ratio, overall values remained consistent with previous analyses of *R. okamurae* (Córdoba-Granados et al. 2024). This suggests that nitrogen availability is generally not a limiting factor for *the species at this particular site. In this context*, Herrero et al. (2025) reported that *R. okamurae* was able to use urea as a nitrogen source, an important trait to sustain growth in low inorganic nitrogen environments. This is also crucial for pigment synthesis (Dean and Hurd 2007), further demonstrating its adaptation to survive and tolerate the low concentrations of inorganic nitrogen typical of the Alboran Sea during stratification events (nitrate ~1 $\mu$M, nitrite $< 0.2\,\mu$M and ammonium between 1.5 and 0.5 $\mu$M; Ramírez et al. 2021). This ability not only explains its capacity for pigment synthesis under nitrogen limitation but also supports the species' rapid development of high individuals' densities and biomass production (Rosas-Guerrero et al. 2025), as evidenced by the values of dark respiration. In this sense, dark respiration, an indicator of metabolic and growth activity of macroalgal species (Weykam et al. 1996), was particularly high during the summer, which may be associated with *R. okamurae* ability to increase its growth rate, reaching up to 18 cm in a short period of time (Rosas-Guerrero et al. 2025) and its production of large numbers of propagules and spores (Salido and Altamirano 2020).

Overall, the seasonal changes in physiological parameters, combined with robust photosynthetic performance, likely enhance the species' ability to optimise metabolic functions in response to biotic and abiotic environmental factors. Light compensation and saturation parameters underscore its photoadaptive capacity. These traits likely contribute to the species' persistence and establishment across seasonal cycles and throughout a wide light range. This suggests its potential for horizontal and bathymetric expansion. However, further research along depth gradients is required to confirm this ability. Overall, this physiological plasticity enables *R. okamurae* to rapidly acclimatise and occupy the seafloor with high abundances, displacing both native and other invasive species, thereby reinforcing its ecological success and underscoring its invasiveness.

## Author Contributions

Jesús Rosas-Guerrero contributed to the methodology, conducted the investigation, curated the data, performed the formal analysis, wrote the original draft, and participated in the review and editing of the manuscript. Raquel Carmona contributed to the methodology, participated in the investigation, and contributed to the review and editing of the manuscript. María Altamirano conceptualised the study and defined the objectives, contributed to the methodology, supervised the project,

participated in the formal analysis and in the review and editing of the manuscript, and acquired the funding.

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## Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** One-way ANOVA for photosynthetic parameters of maximum net photosynthetic rate ($PN_{max}$), photosynthetic efficiency ($\alpha$), dark respiration (DR), light compensation point ($I_c$) and light saturation parameter ($I_k$) expressed as dry weight (DW), thallus surface (TS) and chlorophyll *a* (Chl *a*) basis; pigment content of Chl *a*, Chl *c*, and Chl *c*: Chl *a*, expressed as DW and TS basis; and carbon: nitrogen ratio (C:N). Kruskall-Wallis for tissue elemental composition of carbon and nitrogen concentration. Asterisks represent significant differences ($p < 0.05$).