Journal of Applied Phycology (2025) 37:1277–1287
https://doi.org/10.1007/s10811-025-03475-3

RESEARCH

Effect of temperature on growth and nitrate and phosphate uptake kinetics of juvenile *Saccharina latissima* sporophytes (Phaeophyceae)

Xiaowei Ding[1,2] · **Karline Soetaert**[1] · **Klaas Timmermans**[1]

Received: 7 January 2025 / Revised: 13 February 2025 / Accepted: 13 February 2025 / Published online: 4 March 2025

Abstract

Kelp forests play a vital role in marine ecosystems by contributing to nutrient cycling and providing habitat for marine organisms. However, the impacts of rising ocean temperatures threaten the survival and growth of kelp species, with implications for ecosystem resilience. The aim of this study was to assess the effect of temperature on growth and nutrient uptake kinetics of young *Saccharina latissima* sporophytes. Growth and uptake rates of nitrate (NO_3^-) and phosphate (PO_4^{3-}) were examined under 5 temperature treatments ranging from 7.6 °C to 24.5 °C. Our findings revealed that NO_3^- uptake significantly decreased when temperature was at or above 15.7 °C, while high temperatures had no effect on PO_4^{3-} uptake rates. Nitrate uptake significantly correlated with growth only at lower temperatures of 7.6 °C and 12.6 °C. In contrast, PO_4^{3-} uptake was significantly correlated with growth across all temperature treatments except the highest (24.5 °C). Interestingly, at high temperatures (20.9 °C and 24.5 °C), we observed NO_3^- release, while PO_4^{3-} uptake consistently showed positive values, suggesting distinct regulatory mechanisms for N (nitrogen) and P (phosphorus). These findings highlight potential disruptions in nutrient cycling under climate change and underscore the importance of optimizing nutrient availability in kelp aquaculture.

Keywords Kelp forests · Temperature · *Saccharina latissima* · Nitrate uptake · Phosphate uptake

Introduction

Global climate change presents an unprecedented threat to the kelp (Phaeophyceae, order Laminariales, brown seaweeds) forests, one of the largest habitats in the world. Kelps dominate shallow rocky shores in a wide range of geographic regions, from polar regions to subtropical areas (Wernberg et al. 2019; Jayathilake and Costello 2020). These natural kelp forests act as ecosystem engineers, not only supporting high biodiversity and primary production, but they also play crucial roles in bioremediation and carbon cycling, significantly providing benefits to marine ecology and economy (Teagle et al. 2017; Layton et al. 2020; Eger et al. 2023; Filbee-Dexter et al. 2024). The current decline of kelp forests in many regions has been directly linked to global climate change (Smale et al. 2013). Notably, in 2023, the North Atlantic recorded the highest sea surface temperature (SST) ever observed. Both marine heatwaves and the gradual increase in SST, are considered to threaten kelp forests(Hobday et al. 2016; Filbee-Dexter and Wernberg 2018; Arafeh-Dalmau et al. 2020; Smale 2020; McPherson et al. 2021; Intergovernmental Panel On Climate Change (IPCC) 2022; Diehl et al. 2024). The losses of habitat and productivity have caused the closure of fisheries, and the decline of ecosystem services (Wernberg et al. 2016; Rogers-Bennett and Catton 2019).

Temperature management critically regulates kelp metabolism across all life stages. The kelp life cycle alternates between haploid gametophytes and diploid sporophytes, with gametophytes producing juvenile sporophytes through sexual reproduction (Bell 1997). In cultivation, the early life stages (gametophytes and juvenile sporophytes) of kelp are maintained and induced under controlled conditions in land-based hatcheries before being transplanted to the sea for further development (Azevedo et al. 2016; Ebbing et al. 2021; Supratya and Martone 2024). Ensuring that sporophytes are

✉ Xiaowei Ding
xiaowei.ding@nioz.nl

1 Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute for Sea Research, PO Box 140, 4401, NT, Yerseke, the Netherlands

2 Centre for Isotope Research (CIO) - Oceans, Energy and Sustainability Research Institute 8 Groningen, Faculty of Science and Engineering, University of Groningen, PO Box 72, 9700 Groningen, AB, the Netherlands

exposed to optimal temperature conditions during the hatchery phase enhances growth potential throughout their development into mature kelp and improves yield (Raymond and Stekoll 2021). Early life history stages of kelp may be more sensitive to the effects of climate change than mature sporophytes (Coelho et al. 2000). Elevated temperatures have been demonstrated to significant reduce survival, growth and production in multiple kelp spices (e.g., *Nereocystis luetkeana*, *Ecklonia radiata* and *Saccharina latissima*) (Lee and Brinkhuis 1988; Mohring et al. 2013; Korabik et al. 2023). Juvenile sporophytes exhibit decreased respiration rates, photosynthesis efficiency, and growth performance under rising temperatures (Gao et al. 2013; Sato et al. 2021; Umanzor et al. 2021). Given these temperature-dependent physiological responses, understanding and maintaining optimal thermal conditions during early life stages is crucial for successful kelp aquaculture.

With rising temperatures, managing thermal stress in cultivation systems becomes extremely important for ensuring consistent productivity and reducing potential losses in kelp farms. *S. latissima* (sugar kelp) is an ideal species for studying the effects of temperature on the juvenile stages of kelp. *S. latissima*, the dominant kelp species in the Northern Hemisphere, is a perennial species that exhibits a strong seasonal growth pattern (Monteiro et al. 2021). Temperature is considered a primary environmental factor regulating the growth of macroalgae (Eggert 2012). Given its sensitivity to temperature as a cold-water species, *S. latissima*, serves as a valuable model for investigating the impact of temperature on kelp growth and related processes, such as growth and tissue integrity under elevated temperatures(Ding et al. 2025).

The growth of *S. latissima* depends on dissolved inorganic nitrogen (N) and phosphorus (P) (Lubsch and Timmermans 2019; Roleda and Hurd 2019). N is a key component of proteins, chlorophyll, and other cellular structures in seaweed(Raven 2015; Rimmer and Shorttle 2019). In contrast, P assimilation plays a different role in cellular functions, which is crucial for energy storage and transfer (e.g., as an important component in ATP). It has been reported that *S. latissima* can store nutrients internally as reserves for periods of low external nutrients available (Probyn and Chapman 1982; Lubsch and Timmermans 2019). This internal 'nutrient pool', most likely in vacuoles, allows individuals to take up excess nutrients when they are abundant and utilize these stores when needed (Lobban and Harrison 1994). This storage mechanism adds complexity to the impact of temperature on nutrient uptake kinetics, as both nutrients storage and immediate metabolic demands influence uptake rate under different temperatures.

Saccharina latissima exhibits optimal growth within the temperature range of 10–15 ˚C, temperatures above or below this range can slow down or stop growth or even cause tissue loss (Bolton and Lüning 1982; Andersen et al. 2013; Nepper-Davidsen et al. 2019; Ding et al. 2025). Existing studies have mainly investigated the effects of temperature and nutrient availability on kelp growth, focusing on how these factors influence visible growth and chemical compositions (Endo et al. 2017; Gao et al. 2017; Fales et al. 2023). Over extended periods of stable environmental conditions, growth rate in healthy macroalgae is proportional to nutrient uptake rates (Lobban and Harrison 1994). However, nutrient uptake does not always translate directly into growth, instead, it can result in transient nutrient storage within the organism (Lubsch and Timmermans 2019). The impact of temperature on macroalgal nutrient physiology has been studied (Fan et al. 2014; Gao et al. 2017; Lee and Kang 2020), but the relationship between nutrient uptake efficiency and growth performance of seaweed remains largely unexplored.

We conducted a controlled experiment to determine the effects of temperature on the nutrients (N and P) uptake kinetics and growth of young *S. latissima* sporophytes. The nutrient uptake rates and growth rates of sporophytes under different temperatures were measured over a 22-day experimental period. The results of this study could provide valuable insights into optimizing cultivation practices and predicting the impacts of global climate change on *S. latissima*.

Materials and methods

Experimental conditions

All experiments and analyses were carried out at the Royal Netherlands Institute for Sea Research (NIOZ) in Yerseke, the Netherlands. A total of 72 young sporophytes of *Saccharina latissima*, cultivated in a laboratory from parental plants collected from the field at NIOZ Texel, the Netherlands, were used in this study. The experiments were conducted from March/2023 to April/2023, ensuring that potential seasonal influence was considered. Those young sporophytes were selected with an initial surface area of 1.9 ± 0.6 cm^2. All the individuals were transferred to thirty-six 100-mL Erlenmeyer flasks with sterilized seawater from the Eastern Scheldt. The temperature treatments were achieved using 6 temperature-controlled 25-L incubators (Vevor, the Netherlands). For each temperature treatment, 6 flasks were placed in one incubator, each flask contained 2 individuals ($6 \times 2 = 12$ individuals per temperature treatment, Supplementary Fig 1). Each flask was treated as an experimental unit for statistical analysis purpose to provide sufficient replication within the experimental set-up. Aeration generated a gentle water flow, ensuring constant movements of the sporophytes and the water. During the acclimation period, the temperature was gradually adjusted from the initial temperature of 15 °C at a rate of 2 °C per day to prevent rapid temperature

shock, until the target temperatures of 5 °C, 9 °C, 13 °C, 17 °C, 21 °C, and 25 °C were reached. However, due to incomplete cooling in the incubators during experimental period, the 5°C treatment could not be maintained separately. Consequently, the 5°C and 9°C treatments were merged, leading to 5 final temperature conditions. The average temperatures maintained in the incubators were 7.6 ± 1.4°C (representing the merged 5°C and 9°C treatments), 8.4 ± 0.6°C, 12.6 ± 0.2°C, 15.7 ± 0.5°C, 20.9 ± 0.2°C, and 24.5 ± 0.1°C. Light (50 µmol of photons m^{-2} s^{-1} in a 12/12 day-night cycle), was provided by attached PURPL 18W white light LED panels. The light intensity of 50 µmol of photons m^{-2} s^{-1} was chosen to provide sufficient photosynthetic for *S. latissima* sporophytes while avoiding light-induced stress. Temperatures were monitored hourly by MX Temp and Light HOBO loggers (Onset, USA).

Survival / mortality

For the calculation of survival rate, the individuals were used as the unit of measurement. Mortality was recorded when any individual within a flask deceased. Sporophytes were considered deceased when no visible blade tissue remained attached to the stipe, indicating complete blade loss. The survival rate was calculated according to the following equation:

$$\text{Survival rate } (\%) = \left(\frac{\text{number of surviving individuals}}{\text{initial number of individuals}}\right) \times 100$$

Growth rate

All sporophytes were individually spread flat on a scaled sheet, and photographs were taken during every seawater medium exchange. SA (one side of the blade) analysis of the blade was carried out using the software ImageJ (National Institutes of Health, State of Maryland, USA). Growth rate (GR, in cm^2 day^{-1}) for each replicate was calculated as the total surface are of the 2 individuals within the flask, according to the following equation:

$$\text{GR} = \left(\text{SA}_2 - \text{SA}_1\right) \times \left(\text{t}_2 - \text{t}_1\right)^{-1}$$

where SA_1 is the initial surface area of both individuals within a flask at time t_1, and SA_2 is the surface area of both individuals within a flask at time t_2.

Seawater medium

Potassium-dihydrogen-phosphate (KH_2PO_4) and potassium nitrate (KNO_3) were added to sterilized seawater to enrich the medium to 93.9 ± 8.6 µmol L^{-1} NO_3^- and 9.6 ± 1.9 µmol L^{-1} PO_4^{3-}. The seawater was sterilized by autoclave, applying a pressure of 15–20 psi under 121°C, and running the cycle for 20 minutes to ensure sterilization. To ensure a continuous nutrient supply and prevent depletion effects, the seawater medium was refreshed every 2 or 3 days for a period of 22 days. During each exchange the seawater medium was filled up to 100 ± 0.5 mL.

Nutrient analysis

For each flask, a 4 mL water sample was filtered using a disposable 10-mL syringe (Terumo, Japan) 0.45 µm filter (Millipore SLHA 025 10, Germany) and stored in PICO vials at −20°C until analysis. NO_3^- and PO_4^{3-} concentration was measured by using QuAAtro (Seal Analytical, Germany) continuous flow analyzer in the NIOZ Yerseke nutrient laboratory. For NO_3^- concentration measurements, nitrate was first reduced to nitrite and measured at 540 nm after linked with α-naphtylenediamindihydrochoride (Searle 1984). PO_4^{3-} concentration was measured at 880 nm after the formation of antimony phosphomolybdate complex (Kirkwood 1996).

Nutrient uptake dynamics

The depletion method (Claassen and Barber 1974) was used to calculate the nutrient uptake rates by measuring the decrease in nutrient concentrations in the water over time. The nutrient uptake rate (µmol cm^{-2} day^{-1}) was normalized by surface area (SA, in cm^2) of 2 sporophytes and time (t, in days). Since each flask contained 2 individuals and nutrient measurements were taken per flask, the absolute nutrient uptake (µmol day^{-1}) was calculated as the total nutrient depletion from the medium per flask. The absolute nutrient uptake value was estimated to analyze its linear relationship with growth rate using the following equation:

$$\text{Uptake rate} = \left(\text{C}_1 - \text{C}_2\right) \times 0.1 \times \text{SA}^{-1} \times \left(\text{t}_2 - \text{t}_1\right)^{-1}$$
$$\text{Absolute uptake rate} = \left(\text{C}_1 - \text{C}_2\right) \times 0.1 \times \left(\text{t}_2 - \text{t}_1\right)^{-1}$$

where C_1 is the initial nutrient concentration at time t_1, C_2 is the nutrient concentration at time t_2, shortly before the next seawater medium exchange. *SA* is the total surface area (sum of the *SA* of the 2 sporophytes) at t_1. The number 0.1 indicates the volume of the medium, 0.1 L.

Statistics

Data analysis and figure generation were performed using R version 3.6.0 (R Core Team, 2023). One-way ANOVA was used to test whether temperature affects the GR and nutrient uptake rate of *S. latissima*. Post-hoc comparisons for the one-way ANOVA analyses were conducted using Tukey's

HSD test. Regression coefficients were employed to evaluate the relationship between GR and absolute nutrient uptake rate of replicates. Statistical significance was determined based on p-values, with significance levels defined as follows: $p > 0.05$ (not significant), $p < 0.05$ (* significant), $p < 0.01$ (** highly significant), and $p < 0.001$ (*** extremely significant). All data were presented as mean ± standard deviation (SD).

Result

Survival / mortality

All *S. latissima* individuals survived throughout the acclimation period in all temperature treatments except at 15.7 °C, where one individual died. During the experimental period, survival varied across temperature treatments (Fig. 1). Mortality was highest at 24.5 °C, where 50 % individuals died within 15 days, followed by 33 % at 15.7 °C. Only 8% individuals died at 20.9 °C, while 17% individuals died at 7.6 °C. Additionally, 100% individuals survived throughout the experimental period at a temperature of 12.6 °C.

Growth rate

The mean size of *S. latissima* replicates at the beginning of the experimental period was 1.82 ± 0.46 cm^2, with GRs showing some fluctuations, but averaging approximately 0.26 cm^2 day^{-1} throughout the experimental period at temperatures below or equal to 12.6 °C (Fig. 2). At 15.7 °C and above, the GRs were negative at the beginning of the experiment. In the 15.7 °C treatment, GRs increased to positive values, then stabilized over time. In the 20.9 °C treatment, GRs were initially negative and later stabilized near 0%, fluctuating slightly between positive and negative values throughout the experiment. Negative GRs were observed throughout the entire experimental period in the 24.5 °C treatment.

ANOVA showed that the GR of sporophytes was significantly influenced by temperature (ANOVA, $F_{(1,307)} = 128.8$, $p < 0.001$, Supplementary Table 1). Tukey's HSD test showed that the 5 temperature treatments could be divided into 2 distinct groups: a lower-temperature group (7.6°C, 12.6°C) and a higher-temperature group (15.7°C, 20.9°C, 24.5°C). A statistically significant difference in GR was observed between the lower-temperature and higher-temperature groups (Tukey's HSD, $p < 0.001$), with no significant differences within each group. The lower-temperature group had a higher mean GR of 0.26 ± 0.27 cm^2 day^{-1} (Fig. 3). GR in this group ranged from −0.35 to 1.44 cm^2 day^{-1}; at the end of the 22 days, the sporophytes had tripled in size. In contrast, the higher-temperature group exhibited a lower, negative mean GR of −0.01 ± 0.13 cm^2 day^{-1}.GR in this group ranged from −0.47 to 0.39 cm^2 day^{-1}. Larger SDs in lower-temperature group indicate higher data variability compared with the higher-temperature group.

Nutrient uptake kinetics

The NO_3^- and PO_4^{3-} uptake rates of *S. latissima* exhibited a distinct pattern across the different temperature treatments (Fig. 4). As with the GR, NO_3^- and PO_4^{3-} uptake rates could be separated into 2 discernible clusters: a lower-temperature group (7.6°C, 12.6°C) and a higher-temperature group (15.7°C, 20.9°C, 24.5°C). The NO_3^- and PO_4^{3-} uptake rates in the lower-temperature group remained positive throughout the experimental period. In the higher-temperature group, conversely, the NO_3^- uptake rates initially dropped to negative values, followed by a subsequent increase. In

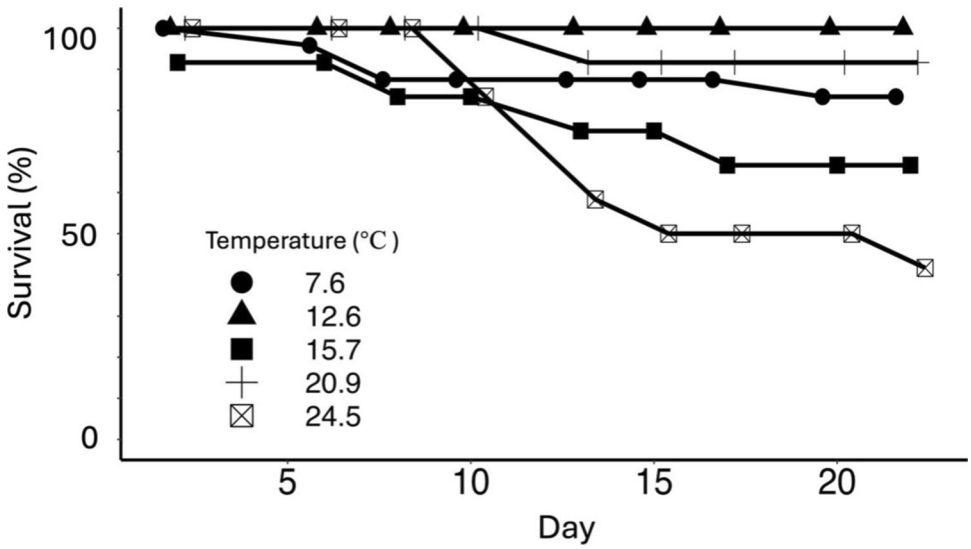

Fig. 1 Percent survival (%) of *S. latissima* sporophytes (n = 12 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C; n = 24 in treatments of 7.6°C) exposed to 5 temperature treatments in the 22-day experiment

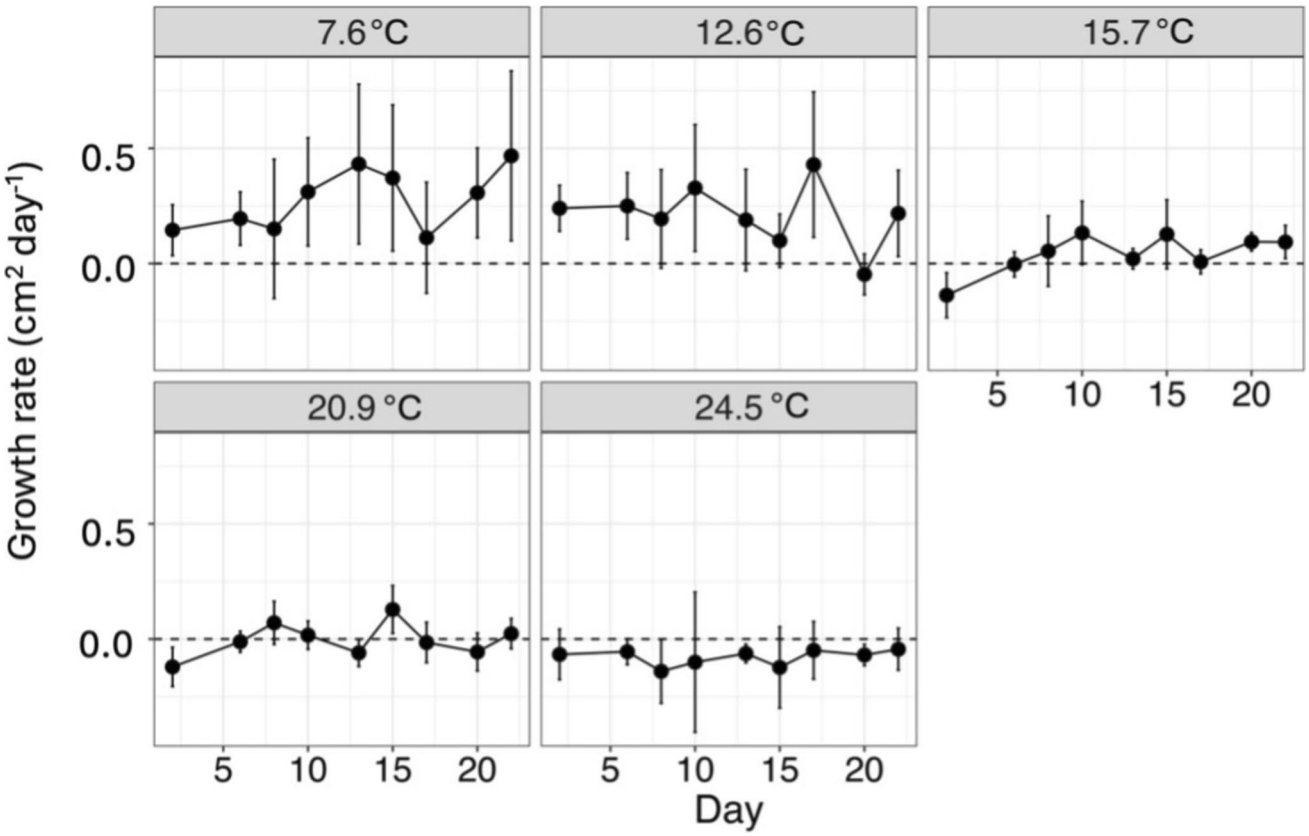

Fig. 2 Growth rate (cm^2 day^{-1}) of *S. latissima* over time (x-axis, days) under different temperature treatments (n = 6 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C ; n = 12 in treatments of 7.6°C). The horizontal dashed lines indicate a GR of 0 cm^2 day^{-1}

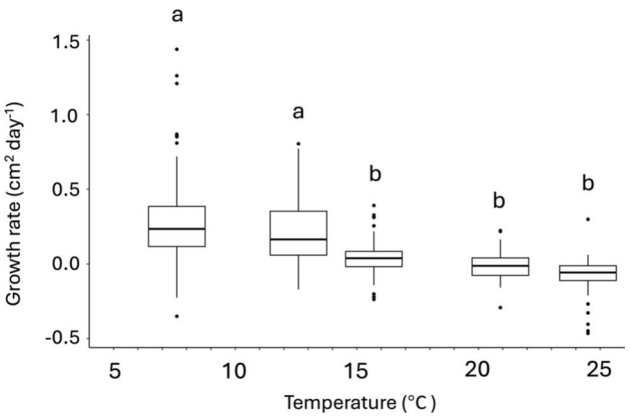

Fig. 3 Overall growth rate (y-axis, cm^2 day^{-1}) of *S. latissima* under different temperatures (x-axis, °C) (n = 6 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C; n = 12 in treatments of 7.6°C). The boxes show the lower and the upper quartile, the horizontal line in the middle of each box indicates the median value of GR. Different letters on the top of bars indicate the significant differences (Tukey's HSD test, P < 0.05) among the temperature treatments

contrast, the PO_4^{3-} uptake rates exhibited an initial increase followed by a decrease, remaining mostly positive across all temperature treatments. While NO_3^- and PO_4^{3-} uptake rates fluctuated similarly in the lower-temperature group, this was not the case in the higher-temperature group. After 5 days, NO_3^- uptake rates decreased below 0, while PO_4^{3-} uptake rates simultaneously exhibited a rise in the higher-temperature group.

Temperature significantly influenced the NO_3^- uptake rates (ANOVA, $F_{(1,307)} = 85.54$, $p < 0.001$, Supplementary Table 2), but not the PO_4^{3-} uptake rate (ANOVA, $F_{(1,307)} = 3.82$, $p = 0.05$, Supplementary Table 3). Similar to the relationship between GR and temperature, the NO_3^- uptake rates in the higher-temperature group (15.7°C, 20.9°C, 24.5°C) were lower than those in the lower-temperature group (7.6°C, 12.6°C), and increasing temperature had no significant effect on NO_3^- uptake rates within either group. In the lower-temperature group, the mean NO_3^- uptake rate was 0.4 ± 0.3 µmol cm^{-2} day^{-1} (Fig. 5). The mean NO_3^- uptake rate in the higher-temperature group was −0.2 ± 0.8 µmol cm^{-2} day^{-1}. The mean PO_4^{3-} uptake rates were positive under all temperature treatments, with a mean value of 0.06 ± 0.06 µmol cm^{-2} day^{-1}, the highest PO_4^{3-} uptake rate was observed at 7.6 °C (0.07 ± 0.04 µmol cm^{-2} day^{-1}), and the lowest at 24.5 °C (0.05 ± 0.12 µmol cm^{-2} day^{-1}).

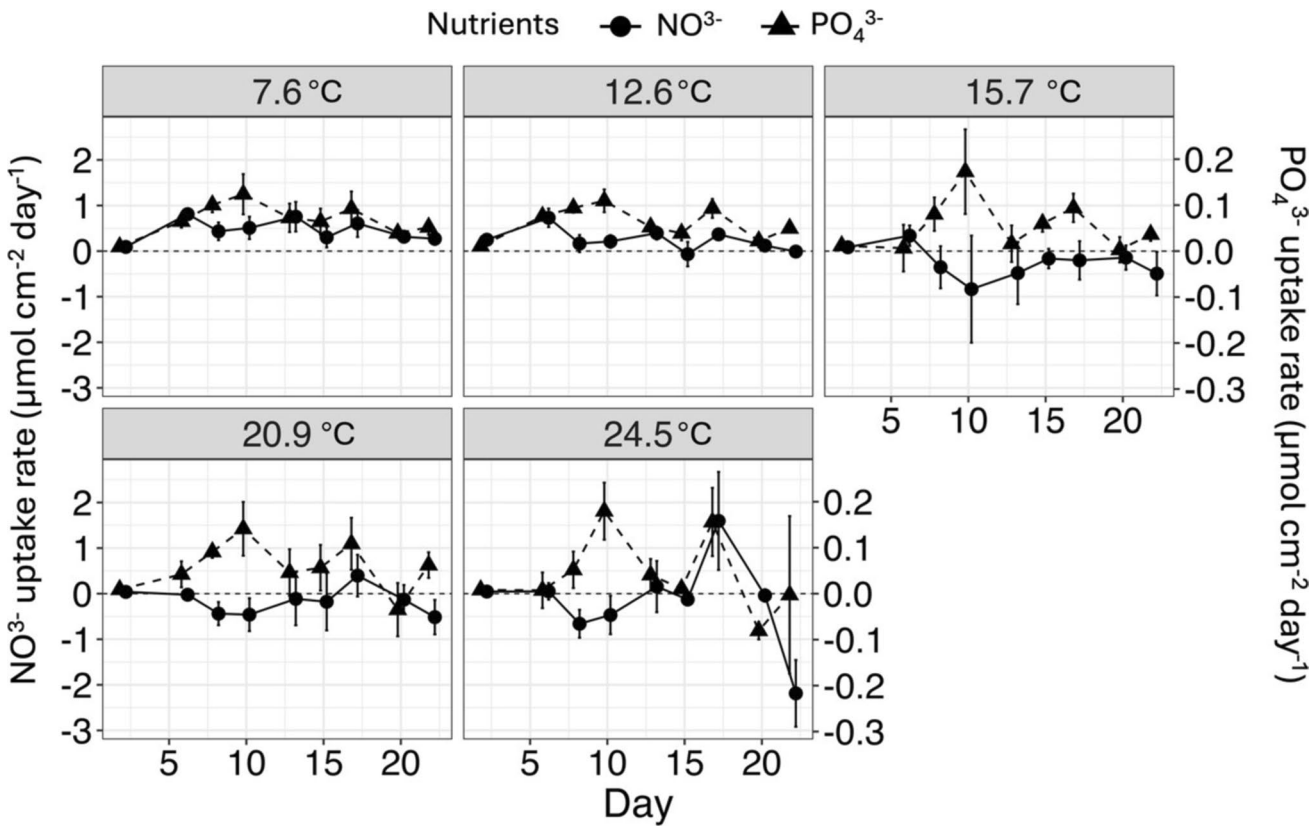

Fig. 4 NO_3^- and PO_4^{3-} uptake rate (y-axis, µmol cm^{-2} day^{-1}) of *S. latissima* (n = 6 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C ; n = 12 in treatments of 7.6°C) exposed to different temperatures over time (x-axis, days). The horizontal dashed lines indicate a NO_3^- or PO_4^{3-} uptake rate of 0 µmol cm^{-2} day^{-1}

Relationships between GR and absolute nutrient uptake rates

The relationship between GR and absolute NO_3^- uptake rate of *S. latissima* blades showed that GRs and NO_3^- uptake rates were not correlated in the higher-temperature group (15.7°C, 20.9°C, 24.5°C) (Fig. 6). Significant positive correlations were observed in the 7.6 °C temperature treatment (linear regression, $R^2 = 0.17$, $F_{(1,105)} = 21.9$, $p < 0.001$) and the 12.6 °C temperature treatment (linear regression, $R^2 = 0.20$, $F_{(1,52)} = 12.6$, $p = 0.001$). When *S. latissima* was exposed to higher temperatures of 20.9 °C and 24.5 °C, a negative absolute NO_3^- uptake rate (=nutrient release) was observed, akin to the negative growth rate of the blades.

The relationship between GR and absolute PO_4^{3-} uptake rate under different temperature treatments exhibited clear differences (Fig. 7). Significant positive correlations were observed in the temperature treatments from 7.6 to 20.9 °C (linear regression, 7.6 °C, $R^2 = 0.04$, $F_{(1,105)} = 4.6$, $p = 0.035$; 20.9 °C, $R^2 = 0.09$, $F_{(1,52)} = 4.9$, $p = 0.032$), moreover, the most pronounced correlations were observed in the 12.6 °C and 15.7 °C treatments (linear regression, 12.6 °C, $R^2 = 0.25$, $F_{(1,52)} = 17.2$, $p < 0.001$; 15.7 °C, $R^2 = 0.26$, $F_{(1,49)} = 17.5$, $p < 0.001$). The majority of individuals in the higher-temperature group (15.7°C, 20.9°C, 24.5°C) exhibited positive absolute PO_4^{3-} uptake rates, despite some individuals showing negative growth rates.

Discussion

This study was performed to explore the relationship between nutrient (NO_3^- and PO_4^{3-}) uptake and growth in *S. latissima*, and how these parameters separately and jointly were affected by temperature. The results revealed that both blade growth rate and NO_3^- uptake of *S. latissima* were highly linked to temperature to which it was exposed, while PO_4^{3-} uptake remained unrelated to temperature exposure across all treatments. Interestingly, NO_3^- uptake significantly correlated with growth at 7.6 °C and 12.6 °C, while PO_4^{3-} uptake correlated with growth at all temperatures except 24.5 °C. These findings provide important insights into the thermal limits of *S. latissima*.

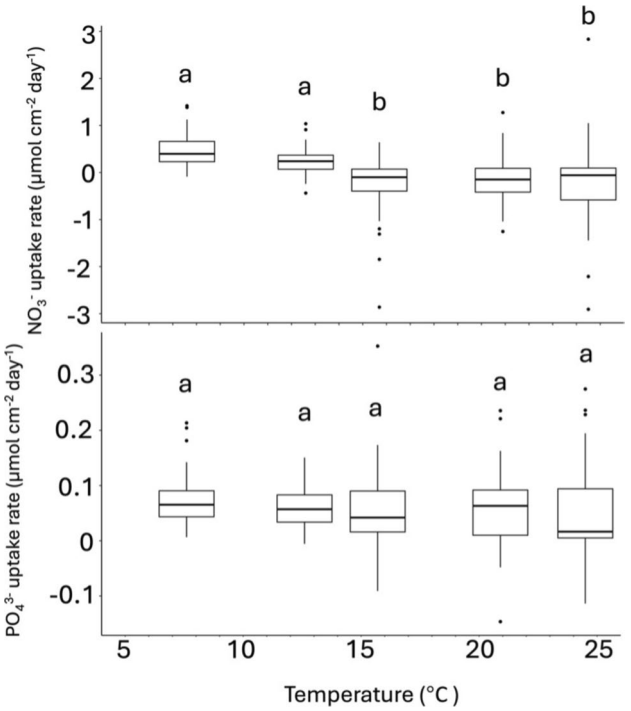

Fig. 5 NO_3^- and PO_4^{3-} uptake rate (y-axis, μmol cm^{-2} day^{-1}) of *S. latissima* (n = 6 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C ; n = 12 in treatments of 7.6°C) exposed to different temperatures (x-axis, °C). The boxes show the lower and the upper quartile, the horizontal line in the middle of each box indicates the median value of NO_3^- or PO_4^{3-} uptake rate. The letters on the top of bars indicate the significant differences (Tukey's HSD test, $P < 0.05$)

Survival / mortality

Numerous studies have investigated the effects of temperature on growth, with temperatures between 10 and 15 °C reported as the optimal range for *S. latissima* growth, temperatures of 23–24 °C as lethal (Bolton and Lüning 1982; Andersen et al. 2013; Nepper-Davidsen et al. 2019). In line with these findings, we found that 50% of *S. latissima* individuals died after exposure to 24.5 °C for 2 weeks (Fig.1). At 24.5°C, blade erosion resulted in negative growth rates, which, in turn, contributed to the subsequent mortality of individuals. In contrast, all the individuals survived throughout the experimental period only at 12.6 °C, which suggests that this temperature may be favorable for *S. latissima*. These findings highlight the clear temperature limits for *S. latissima* growth and survival, emphasizing its vulnerability to rising temperatures.

In our experiment, there was a remarkable difference in mortality rates at 15.7 °C and 20.9°C, with lower mortality rates at the 20.9 °C exposure. One potential explanation for this finding is that sub-lethal temperatures may cause physiological stress over prolonged exposure. However, temperatures closer to the upper limit of sub-lethal temperature range (20.9°C) could have triggered a different response. This result suggests that the effects of sub-lethal temperature-induced stress and acclimation capacity of seaweed may be complex that are not readily predictable. Additionally, it is important to consider other experimental conditions, such as individual variability, that may have contributed to the observed differences in survival probabilities. We have considered these explanations in interpreting our results and further exploration of how seaweed acclimates under sub-lethal temperature in future studies is necessary.

Growth

Although we found no significant difference in growth in the lower temperature treatments (7.6 °C, 12.6 °C), the significant decrease in growth at 15.7 °C and higher temperatures (Fig.3), is consistent with the observations of the limit of optimal temperature range of 10–15 °C. More frequent negative growth was found after exposure to 20.9° C and 24.5°C, indicating a net loss of blade area. This aligns with our observation of increased tissue loss in *S. latissima* blades at higher temperatures (Ding et al. 2025). Elevated temperatures (above 18 °C) have been shown to damage the cellular structure of *S. latissima* tissues (Simonson et al. 2015), potentially making the seaweed more vulnerable to additional stressors such as unfavorable light conditions, waves, and low water quality (Wernberg et al. 2010; Krumhansl et al. 2011; Krumhansl and Scheibling 2012). This increase susceptibility to stressors may indirectly contribute to the temperature-driven inhibition of seaweed growth.

Nutrient uptake kinetics

Our study demonstrated that temperature significantly influenced the uptake rate of NO_3^- by *S. latissima* (Fig.5). *Saccharina latissima* has been shown to store NO_3^- internally during the winter (mean SST of 7.02 ± 0.48 °C) at levels above those needed for recovery or growth, this supports our results that the highest NO_3^- uptake rate was observed at 7.6 °C (Chapman et al. 1978; Mathis et al. 2015). The decreased NO_3^- uptake rate under higher temperatures is consistent with previous studies indicating that temperatures higher than the optimal limit can negatively influence the metabolic activities in *S. latissima* (Andersen et al. 2013; Nepper-Davidsen et al. 2019). Elevated temperature can decrease the enzyme activity involved in nutrient absorption, such as nitrate reductase, which has been reported to have an optimal temperature of 10 °C in *S. latissima* (Davison and Davison 1987; Young et al. 2007). This may explain why we observed a decrease in growth rates and nutrient uptake efficiency in *S. latissima* individuals at 15.7 °C, 20.9°C and 24.5°C.

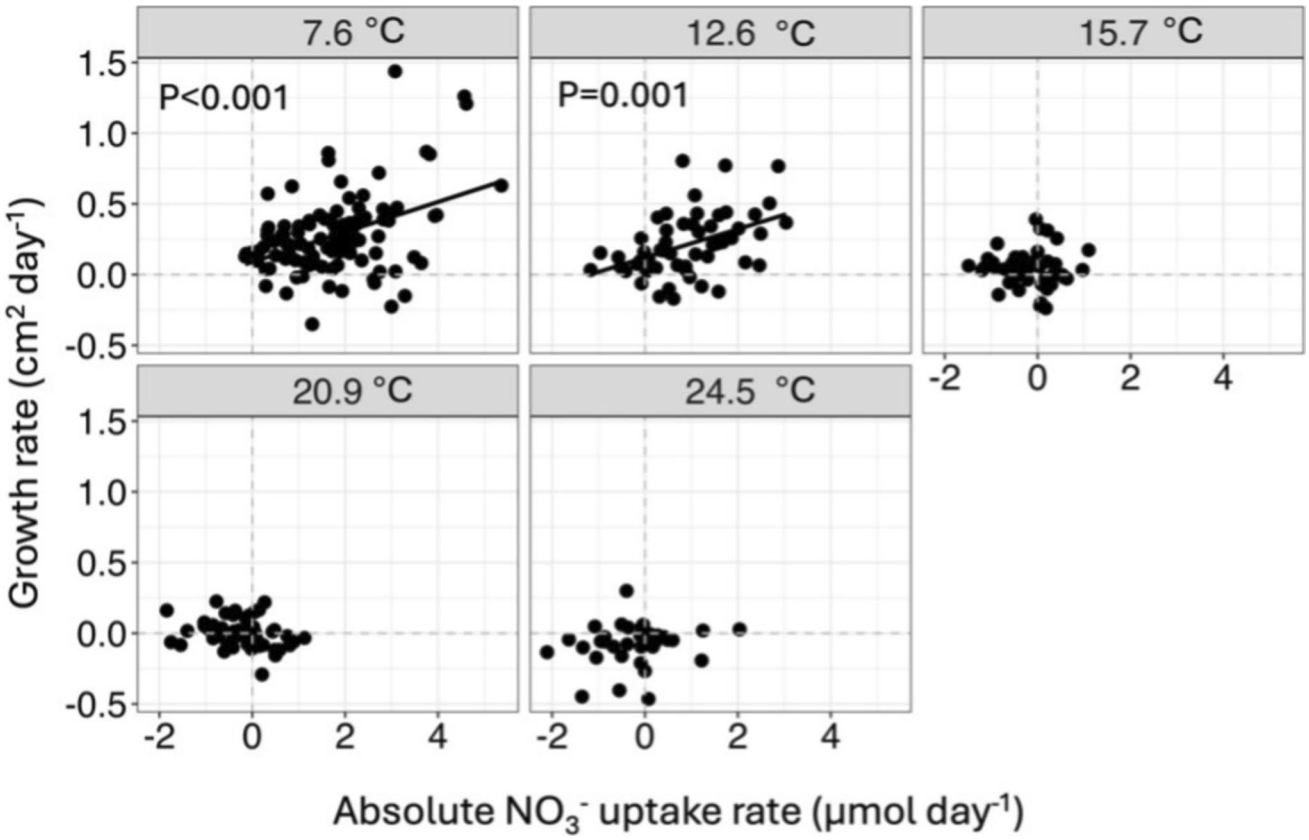

Fig. 6 The relationship between the growth rate (y-axis, $cm^2\ day^{-1}$) and absolute NO_3^- uptake rate (x-axis, µmol day^{-1}) of *S. latissima* (n = 6 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C ; n = 12 in treatments of 7.6°C) exposed to different temperatures. The solid lines show the linear relationship between the data points. The dashed lines indicate the 0 value of GR or NO_3^- uptake rate. The individual dots represent all the data points from all individuals at different time points throughout the 22-day experimental period. Statistics of the fitted lines: 7.6 °C, $R^2 = 0.17$, $F_{(1,105)} = 21.9$, $p < 0.001$; 12.6 °C, $R^2 = 0.20$, $F_{(1,52)} = 12.6$, $p = 0.001$

Interestingly, there was no significant effect of temperature on PO_4^{3-} uptake rate, suggesting distinct regulatory mechanisms governing nitrogen (N) and phosphorus (P) assimilation in *S. latissima*. A possible explanation is that N assimilation is often tightly linked to growth and metabolic processes (Raven 2015; Rimmer and Shorttle 2019). In contrast, P assimilation may not be as directly linked to short-term uptake responses to temperature as N. Thus, while N uptake is closely tied to rapid metabolic adjustments in response to temperature changes, P uptake seems to be governed by a more stable, perhaps longer-term regulatory mechanism. While our study provides the insights into the temperature-dependent uptake of N and P in *S. latissima*, we acknowledge that the regulatory mechanisms of N and P uptake behind these processers remain unclear. Further research is needed to investigate the specific factors governing N and P assimilation in this species, which will not only enhance our understanding of nutrient processing under heat stress but also contribute to ecological insights into how *S. latissima* may adapt to future environmental changes.

Relationship between growth and nutrient uptake

As temperature increased, the decoupling of NO_3^- uptake from growth indicates that *S. latissima* mobilized internal stores of NO_3^-. In contrast, the linear relationship between PO_4^{3-} uptake and growth rate in *S. latissima* was largely unaffected by temperature, showing a significant correlation at all temperatures treatments except at 24.5 °C (Fig.7). This indicates that phosphate uptake might rely on a temperature-independent pathway or a mechanism with high efficiency across a wide temperature range.

The negative nitrate uptake at higher temperatures of 20.9 °C and 24.5 °C, implies release of NO_3^- from the blades, contributing to the nutrient discharge back into the environment. Exposure to higher temperatures may have compromised membrane integrity in *S. latissima* cells, leading to tissues erosion (Ding et al. 2025) and the release of stored dissolved nutrients from the internal stocks. The release of nutrients could also have broader implications for marine ecosystems, influencing nutrient availability for other organisms and altering local biogeochemical processes.

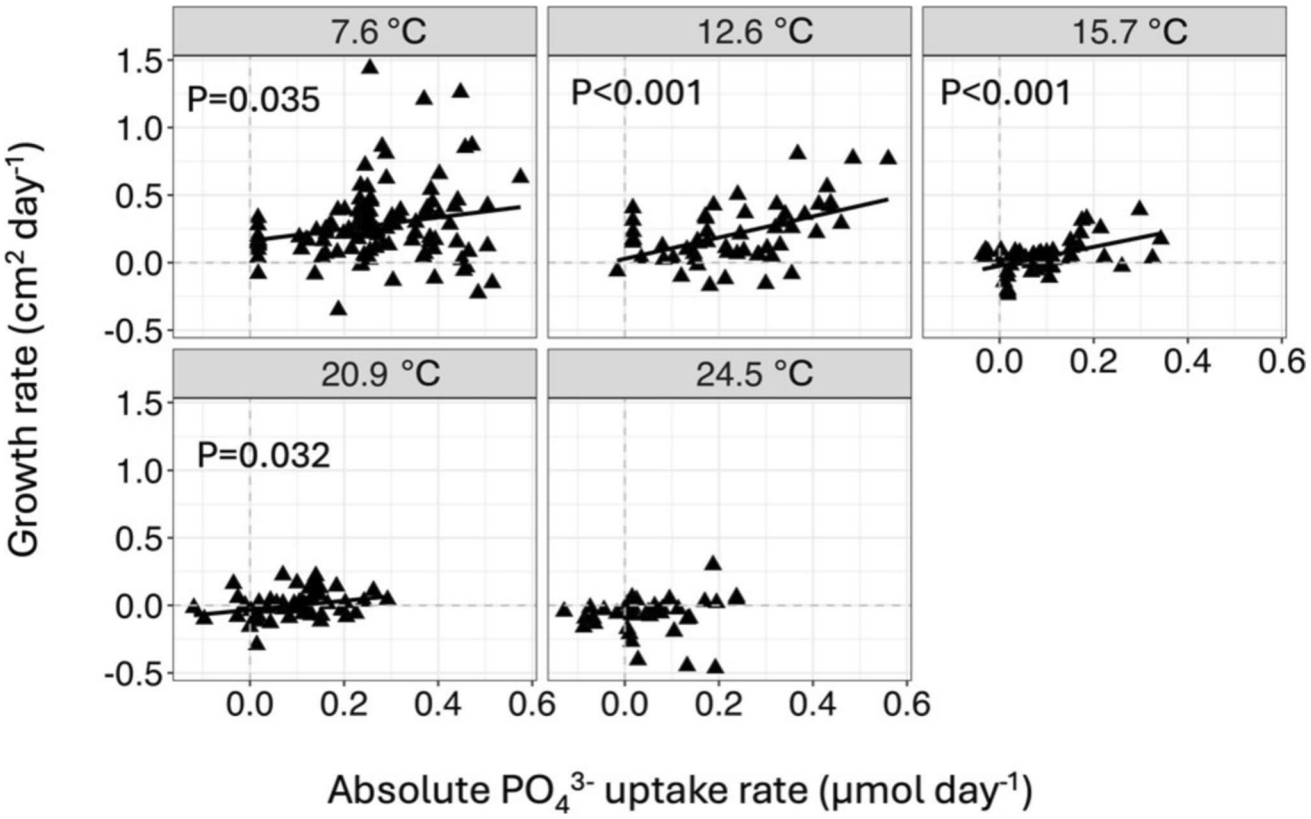

Fig. 7 The relationship between the growth rate (y-axis, $cm^2\ day^{-1}$) and absolute PO_4^{3-} uptake rate (x-axis, µmol day^{-1}) of *S. latissima* (n = 6 in treatments of 12.6 °C, 15.7 °C, 20.9°C and 24.5°C ; n = 12 in treatments of 7.6°C) exposed to different temperatures. The solid lines show the linear relationship between the data points. The dashed lines indicate the 0 value of GR or PO_4^{3-} uptake rate. The individual dots represent all the data points from all individuals at different time points throughout the 22-day experimental period. Statistics of the fitted lines: 7.6 °C, $R^2 = 0.04$, $F_{(1,105)} = 4.6$, p = 0.035; 12.6 °C, $R^2 = 0.25$, $F_{(1,52)} = 17.2$, $p < 0.001$; 15.7 °C, $R^2 = 0.26$, $F_{(1,49)} = 17.5$, $p < 0.001$; 20.9 °C, $R^2 = 0.09$, $F_{(1,52)} = 4.9$, $p = 0.032$

While *S. latissima* stores N in vacuoles as NO_3^- , P is stored in the form of polyphosphate (Yang et al. 2017; Forbord et al. 2021). Unfortunately, the ammoniumheptamolydate method used in our nutrient analysis only detects orthophosphate and cannot directly measure polyphosphate (Kirkwood 1996), so we cannot rule out that the macroalgae did not leak these components, although this may seem unlikely as PO_4^{3-} uptake remained positive.

Our study provides insights into the physiological responses of *S. latissima* to rising temperatures and their implications for both natural ecosystems and aquaculture. We found that elevated temperatures may negatively impact nutrient uptake and cellular integrity in *S. latissima*. These findings indicate that kelp may have difficulty maintaining growth and metabolic functions under ocean warming, leading to reduced biomass and weakened ecosystem services. Additionally, impaired nutrient uptake at high temperatures may disrupt coastal nutrient cycling, potentially contributing to eutrophication or nutrient imbalances. In the context of aquaculture, high temperatures, particularly at the end of the growing season (e.g., May-June), may limit *S. latissima* cultivation by reducing nutrient assimilation efficiency. Thus, these insights are valuable for both improving the sustainability of kelp aquaculture and advancing our understanding of coastal ocean nutrient cycling under temperature stress.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s10811-025-03475-3.

Acknowledgements We are grateful for Matyas Jedlicka (NIOZ intern) who helped during measurements and sampling. The technical support from Peter van Breugel (NIOZ) made the experiments possible. Xiaowei Ding also acknowledges financial support from the China Scholarship Council.

Authors' contribution Xiaowei Ding: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing-original draft, Review & Editing.
Karline Soetaert: Review & Editing.
Klaas Timmermans: Conceptualization, Review & Editing.

Funding This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Data availability Data and photos obtained during the experiment are available upon request.

Declarations

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.

References

Andersen GS, Pedersen MF, Nielsen SL (2013) Temperature acclimation and heat tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). J Phycol 49:689–700

Arafeh-Dalmau N, Schoeman DS, Montaño-Moctezuma G, Micheli F, Rogers-Bennett L, Olguin-Jacobson C, Possingham HP (2020) Marine heat waves threaten kelp forests. Science 367:635–635

Azevedo IC, Marinho GS, Silva DM, Sousa-Pinto I (2016) Pilot scale land-based cultivation of *Saccharina latissima* Linnaeus at southern European climate conditions: growth and nutrient uptake at high temperatures. Aquaculture 459:166–172

Bell G (1997) The evolution of the life cycle of brown seaweeds. Biol J Linn Soc 60:21–38

Bolton JJ, Lüning K (1982) Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. Mar Biol 66:89–94

Chapman ARO, Markham JW, Lüning K (1978) Effects of nitrate concentration on the growth and physiology of *Laminaria saccharina* (Phaeophyta) in culture. J Phycol 14:195–198

Claassen N, Barber SA (1974) A method for characterizing the relation between nutrient concentration and flux into roots of intact plants. Plant Physiol 54:564–568

Coelho SM, Rijstenbil JW, Brown MT (2000) Impacts of anthropogenic stresses on the early development stages of seaweeds. J Aquat Ecosyst Stress Recov 7:317–333

Davison IR, Davison JO (1987) The effect of growth temperature on enzyme activities in the brown alga *Laminaria saccharina*. Br Phycol J 22:77–87

Diehl N, Li H, Scheschonk L, Burgunter-Delamare B, Niedzwiedz S, Forbord S, Sæther M, Bischof K, Monteiro C (2024) The sugar kelp *Saccharina latissima* I: recent advances in a changing climate. Ann Bot 133:183–212

Ding X, Brussaard CPD, Timmermans KR (2025) Effects of elevated temperature on erosion of *Saccharina latissima* (Laminariales, sugar kelp) blades. J Exp Mar Biol Ecol 582:152071

Ebbing APJ, Pierik R, Fivash GS, van de Loosdrecht NCJ, Bouma TJ, Kromkamp JC, Timmermans K (2021) The role of seasonality in reproduction of multiannual delayed gametophytes of *Saccharina latissima*. J Phycol 57:1580–1589

Eger AM, Marzinelli EM, Beas-Luna R et al (2023) The value of ecosystem services in global marine kelp forests. Nat Commun 14:1894

Eggert A (2012) Seaweed responses to temperature. In: Wiencke C, Bischof K (eds) Seaweed Biology. Springer, Berlin, pp 47–66

Endo H, Suehiro K, Gao X, Agatsuma Y (2017) Interactive effects of elevated summer temperature, nutrient availability, and irradiance on growth and chemical compositions of juvenile kelp, *Eisenia bicyclis*. Phycol Res 65:118–126

Fales RJ, Weigel BL, Carrington E, Berry HD, Dethier MN (2023) Interactive effects of temperature and nitrogen on the physiology of kelps (*Nereocystis luetkeana* and *Saccharina latissima*). Front Mar Sci 10:1281104

Fan X, Xu D, Wang Y, Zhang X, Co S, Mou S, Ye N (2014) The effect of nutrient concentrations, nutrient ratios and temperature on photosynthesis and nutrient uptake by *Ulva prolifera*: implications for the explosion in green tides. J Appl Phycol 26:537–544

Filbee-Dexter K, Wernberg T (2018) Rise of turfs: a new battlefront for globally declining kelp forests. BioScience 68:64–76

Filbee-Dexter K, Pessarrodona A, Pedersen MF, Wernberg T, Duarte CM, Assis J, Bekkby T, Burrows MT, Carlson DF, Gattuso J-P, Gundersen H, Hancke K, Krumhansl KA, Kuwae T, Middelburg JJ, Moore PJ, Queirós AM, Smale DA, Sousa-Pinto I, Suzuki N, Krause-Jensen D (2024) Carbon export from seaweed forests to deep ocean sinks. Nat Geosci 17:552–559

Forbord S, Etter SA, Broch OJ, Dahlen VR, Olsen Y (2021) Initial short-term nitrate uptake in juvenile, cultivated *Saccharina latissima* (Phaeophyceae) of variable nutritional state. Aquat Bot 168:103306

Gao X, Endo H, Taniguchi K, Agatsuma Y (2013) Combined effects of seawater temperature and nutrient condition on growth and survival of juvenile sporophytes of the kelp *Undaria pinnatifida* (Laminariales; Phaeophyta) cultivated in northern Honshu, Japan. J Appl Phycol 25:269–275

Gao X, Endo H, Nagaki M, Agatsuma Y (2017) Interactive effects of nutrient availability and temperature on growth and survival of different size classes of *Saccharina japonica* (Laminariales, Phaeophyceae). Phycologia 56:253–260

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver ECJ, Benthuysen JA, Burrows MT, Donat MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227–238

Intergovernmental Panel On Climate Change (IPCC) (2022) The ocean and cryosphere in a changing climate: special report of the intergovernmental panel on climate change, 1st edn. Cambridge University Press, Cambridge

Jayathilake DRM, Costello MJ (2020) A modelled global distribution of the kelp biome. Biol Conserv 252:108815

Kirkwood JG (1996) The general theory of irreversible processes in solutions of macromolecules. J Polym Sci B 34:597–610

Korabik AR, Winquist T, Grosholz ED, Hollarsmith JA (2023) Examining the reproductive success of bull kelp (*Nereocystis luetkeana*, Phaeophyceae, Laminariales) in climate change conditions. J Phycol 59:989–1004

Krumhansl K, Scheibling R (2012) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–302

Krumhansl KA, Lee JM, Scheibling RE (2011) Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. J Exp Mar Biol Ecol 407:12–18

Layton C, Coleman MA, Marzinelli EM, Steinberg PD, Swearer SE, Vergés A, Wernberg T, Johnson CR (2020) Kelp forest restoration in Australia. Front Mar Sci 7:74

Lee JA, Brinkhuis BH (1988) Seasonal light and temperature interaction effects on development of *Laminaria saccharina* (Phaeophyta) gametophytes and juvenile sporophytes. J Phycol 24:181–191

Lee JE, Kang JW (2020) The interactive effects of elevated temperature and nutrient concentrations on the physiological responses of *Ulva linza* Linnaeus (Ulvales, Chlorophyta). J Appl Phycol 32:2459–2467

Lobban CS, Harrison PJ (1994) Seaweed ecology and physiology. Cambridge University Press, Cambridge, p 384

Lubsch A, Timmermans KR (2019) Uptake kinetics and storage capacity of dissolved inorganic phosphorus and corresponding dissolved inorganic nitrate uptake in *Saccharina latissima* and *Laminaria digitata* (Phaeophyceae). J Phycol 55:637–650

Mathis M, Elizalde A, Mikolajewicz U, Pohlmann T (2015) Variability patterns of the general circulation and sea water temperature in the North Sea. Prog Oceanogr 135:91–112

McPherson ML, Finger DJI, Houskeeper HF, Bell TW, Carr MH, Rogers-Bennett L, Kudela RM (2021) Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. Commun Biol 4:298

Mohring MB, Kendrick GA, Wernberg T, Rule MJ, Vanderklift MA (2013) Environmental influences on kelp performance across the reproductive period: an ecological trade-off between gametophyte survival and growth? PLoS ONE 8:e65310

Monteiro C, Li H, Diehl N, Collén J, Heinrich S, Bishof K, Bartsch I (2021) Modulation of physiological performance by temperature and salinity in the sugar kelp *Saccharina latissima*. Phycol Res 69:48–57

Nepper-Davidsen J, Andersen D, Pedersen M (2019) Exposure to simulated heatwave scenarios causes long-term reductions in performance in *Saccharina latissima*. Mar Ecol Prog Ser 630:25–39

Probyn TA, Chapman ARO (1982) Nitrogen uptake characteristics of *Chordaria flagelliformi*s (Phaeophyta) in batch mode and continuous mode experiments. Mar Biol 71:129–133

Raven JA (2015) Interactions between nitrogen and phosphorus metabolism. In: Plaxton WC, Lambers H (eds) Annual Plant Reviews, vol. 48. Wiley Blackwell, Chichester, pp 187–214

Raymond AET, Stekoll MS (2021) Conditions for staggering and delaying outplantings of the kelps *Saccharina latissima* and *Alaria marginata* for mariculture. J World Aquac Soc 52:1135–1157

Rimmer PB, Shorttle O (2019) Origin of Life's building blocks in carbon- and nitrogen-rich surface hydrothermal vents. Life 9:12

Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Sci Rep 9:15050

Roleda MY, Hurd CL (2019) Seaweed nutrient physiology: application of concepts to aquaculture and bioremediation. Phycologia 58:552–562

Sato Y, Nagoe H, Nishihara GN, Terada R (2021) The photosynthetic response of cultivated juvenile and mature *Undaria pinnatifida* (Laminariales) sporophytes to light and temperature. J Appl Phycol 33:3437–3448

Searle PL (1984) The Berthelot or indophenol reaction and its use in the analytical chemistry of nitrogen. A review. Analyst 109:549–568

Simonson E, Scheibling R, Metaxas A (2015) Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. Mar Ecol Prog Ser 537:89–104

Smale DA (2020) Impacts of ocean warming on kelp forest ecosystems. New Phytol 225:1447–1454

Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins S (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. Ecol Evol 3:4016–4038

Supratya VP, Martone PT (2024) Kelps on demand: closed-system protocols for culturing large bull kelp sporophytes for research and restoration. J Phycol 60:73–82

Teagle H, Hawkins SJ, Moore PJ, Smale DA (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. J Exp Mar Biol Ecol 492:81–98

Umanzor S, Sandoval-Gil J, Sánchez-Barredo M, Ladah LB, Ramírez-García MM, Zertuche-González JA (2021) Short-term stress responses and recovery of giant kelp (*Macrocystis pyrifera*, Laminariales, Phaeophyceae) juvenile sporophytes to a simulated marine heatwave and nitrate scarcity. J Phycol 57:1604–1618

Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol Lett 13:685–694

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–172

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the world's kelp forests. In: Sheppard C (ed) World seas: an environmental evaluation, 2nd edn. Academic Press, London, pp 57–78

Yang SY, Huang TK, Kuo HF, Chiou TJ (2017) Role of vacuoles in phosphorus storage and remobilization. J Exp Bot 68:3045–3055

Young EB, Dring MJ, Savidge G, Birkett DA, Berges JA (2007) Seasonal variations in nitrate reductase activity and internal N pools in intertidal brown algae are correlated with ambient nitrate concentrations. Plant Cell Environ 30:764–774