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How does seasonal seedling outplant influence sea-based *Ulva* aquaculture? Controlling performance and biochemical composition of a temperate seaweed crop

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ABSTRACT

Optimizing biomass yield and biochemical composition in sea-based cultivation of *Ulva fenestrata* requires balancing environmental conditions with cultivation timing. This study examined how outplant and harvest timing influence growth and biochemical traits in a temperate sea-based aquaculture system. Outplant timing had a pronounced effect on biomass yield, while biochemical composition was more strongly influenced by harvest timing and associated environmental factors. Seedlings deployed in autumn (September–November) achieved up to eight-fold higher biomass than those outplanted in late winter or spring (February–March). Despite low temperature and light during early winter, autumn outplants maintained slow but steady growth, indicating physiological resilience and effective nutrient utilization under suboptimal conditions. Biochemical composition – including crude protein, chlorophyll, carotenoids and total fatty acids – peaked during late winter to early spring harvests when ambient nitrate levels were highest. As temperature and light increased in spring, tissue nitrogen and polyunsaturated fatty acid contents declined, reflecting nitrogen limitation and temperature-driven lipid remodelling. This trade-off between maximizing biomass under warmer conditions and maintaining nutritional quality during cooler, nutrient-rich periods highlights the need for strategic cultivation management. We conclude that optimal production of *U. fenestrata* in temperate waters is achieved by autumn outplanting and harvest before the spring nutrient decline when aimed at food purposes. Continuous environmental monitoring, adaptive harvest timing and strain selection could further enhance both biomass yield and quality, supporting sustainable and high-value *Ulva* cultivation.

HIGHLIGHTS

- Autumn outplanting significantly enhances biomass accumulation in *Ulva fenestrata.*
- Harvest timing exerts stronger control on biochemical composition than deployment: peak protein, pigment and fatty acid levels coincide with high ambient nitrate while elevated temperature and irradiance reduce tissue nitrogen and PUFA content.
- Optimized production requires autumn seeding and pre-spring nutrient decline harvest.

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KEYWORDS Algae; blue economy; protein; seaweed; seedling

Introduction

The increasing focus on developing a more sustainable Blue Economy has driven research interest in marine macroalgae, including green, brown and red seaweeds (Kim *et al.*, 2017; FAO, 2018). These marine resources are recognized for their potential as sources of food, specific bioactive molecules and bio-based materials, making them a subject of interdisciplinary investigation (Barzkar *et al.*, 2019). Among them, green macroalgae stand out as their biomass holds promise for numerous industries, offering renewable sources of valuable compounds and materials (Hafting *et al.*, 2015) and are especially interesting to the rapidly developing vegetarian and vegan food industry (Hofmann *et al.*, 2025).

Green seaweeds of the genus *Ulva* represent one of the most ubiquitous groups of macroalgal species (Mantri *et al.*, 2020) and their high tolerance to environmental variables such as light, salinity and temperature enables them to thrive in a staggering variety of habitats, rarely seen in other algal genera (Rybak, 2018; Beer, 2023). Further, *Ulva* biomass recently gained attention and prominence in multiple economic sectors. *Ulva* biomass and its constituents have established roles in food production (Colombo *et al.*, 2006; Abreu *et al.*, 2014; Santos *et al.*, 2015), pharmaceuticals and cosmetics (Barzkar *et al.*, 2019), while also contributing to novel biomaterials (Wahlström *et al.*, 2020). Additionally, *Ulva* biomass has been explored for

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biofuel production. Altogether, underscoring its economic but also ecological significance (Abomohra *et al.*, 2018).

Several *Ulva* species stand out by exhibiting rapid growth rates and efficient assimilation of carbon, nitrogen and phosphorus, along with a remarkable ability to adjust to changing environmental conditions (Kang *et al.*, 2013; Hurd *et al.*, 2023). These traits do not only contribute to their physiological resilience but their potential for commercial cultivation is increasingly recognized as well (Bolton *et al.*, 2009; Califano *et al.*, 2020; Steinhagen *et al.*, 2021; Simon *et al.*, 2022; Lüning, 2023).

Although *Ulva* biomass is widely seen as a highly versatile and valuable marine resource with diverse applications across multiple industries, knowledge regarding its large-scale, yet sustainable production remains limited. This gap primarily arises from the challenges associated with life cycle control in many *Ulva* species, which hinder the development of reliable nurseries and seedling preparation – critical steps for cultivating seaweeds in sea-based systems such as in classical long-line farms often applied in e.g. kelp aquaculture (Bak *et al.*, 2020). Recent research has explored the potential of *Ulva* cultivation in sea-based and offshore environments (Carl *et al.*, 2014, 2016; Steinhagen *et al.*, 2021, 2022*a*, 2022*b*). Notably, for the northern hemisphere crop *U. fenestrata*, a fully integrated life-cycle aquaculture method has been successfully established, advancing to the industrial application scale (Steinhagen *et al.*, 2021, 2022*a*, 2022*b*). However, the commercial value of *Ulva* biomass is highly dependent on its biochemical composition, which has been shown to vary considerably under several intrinsic and extrinsic factors (Toth *et al.*, 2020; Fort *et al.*, 2021; Steinhagen *et al.*, 2022*a*, 2022*b*). Examples of such factors are applied species or strain, environmental conditions and potentially its associated microbiome (Rybak, 2018; Beer, 2023; van der Loos *et al.*, 2024, 2025). Among these, environmental growth conditions, including seasonal variations, are widely regarded as the primary drivers shaping the biochemical profile (Green & Fong, 2016). Light and nutrient availability, as well as temperature and salinity (Toth *et al.*, 2020; Olsson *et al.*, 2020*a*, 2020*b*; Moreira *et al.*, 2021; Steinhagen *et al.*, 2022*a*, 2022*b*), all affected both growth rates and the biochemical profile (including protein, fatty acid and carbohydrate content) of temperate *Ulva* (Toth *et al.*, 2020; Olsson *et al.*, 2020*a*; Stedt *et al.*, 2022*a*; Steinhagen *et al.*, 2022*a*, 2022b, 2022*b*). This highlights the importance of harvest timing in sea-based cultivation systems, as it directly impacts large-scale aquaculture viability and the ability to produce biomass with specific biochemical traits. With the increasing industrial application of full-life-cycle techniques in sea-based *Ulva* aquaculture, alongside growing research interest in optimizing cultivation methods, one critical aspect remains unexplored: the optimal timing for outplanting seedlings to sea-based infrastructure has not been systematically studied yet. The point at which nursery-grown *Ulva* seedlings are transferred to sea-based cultivation systems is likely to have a significant impact on growth performance, biomass yield and biochemical composition at harvest, as environmental factors such as temperature, light availability and nutrient levels fluctuate seasonally in temperate regions. This study aims to address this knowledge gap by examining the effects of different outplanting times from early autumn to late winter on the growth, selected biochemical properties and overall productivity of *Ulva* in a temperate sea-based aquaculture system.

Methods

Production and deployment of seedlings

Gametes were sourced from a clonal gametophytic strain of *U. fenestrata* maintained in long-term indoor tank cultivation at the Tjärnö Marine Laboratory, University of Gothenburg, Sweden (TML, 58°52′36.4″N, 11°6′42.84″ E). This clonal strain was originally derived through parthenogenetic propagation from a single gametophyte and has been continuously propagated via parthenogenesis to ensure genetic uniformity. Fertility was induced by mincing and rinsing matured parental tissue, following Steinhagen *et al.* (2021) and information on molecular identification of the parental biomass is detailed in Toth *et al.* (2020). A medium change in the morning, 5 days after fertility induction, triggered immediate gamete release in *U. fenestrata*. Gametes were immobilized by incubating in darkness at 15°C for 24 h, and their density was determined using a hemocytometer. A suspension of 10 000 gametes ml^{-1} seawater was evenly applied to a single twine (ø = 2–3 mm) coiled around a sterile PVC spool (n = 3) which had an absorbance of 7 AU (Fig. 1A). Spools were incubated for 6 weeks in 2 l aquaria with sterile filtered (0.2 µm + UV) nutrient-enriched seawater following Provasoli (1968). The seedling hatchery was maintained at 15°C in a light- and temperature-controlled cabinet (12:12 h L:D, 80–100 µmol m^{-2} s^{-1}, LuxaLight LED). To inhibit diatom growth, 1 mg l^{-1} GeO_2 was added, and the culture medium was refreshed weekly. After 6 weeks, juvenile thalli (0.5–1 cm) were acclimated to outdoor conditions by gradually lowering the temperature to the respective outdoor seawater temperature (max. 1.5°C per day, lowest outplant time 4.5°C) over one week in filtered (0.2 µm) seawater.

This seedling production cycle was repeated at seven time points, to facilitate the outplanting of 6-week-old seedlings with monthly intervals from September 2021 to March 2022 in the beginning of each month, depending on weather conditions.

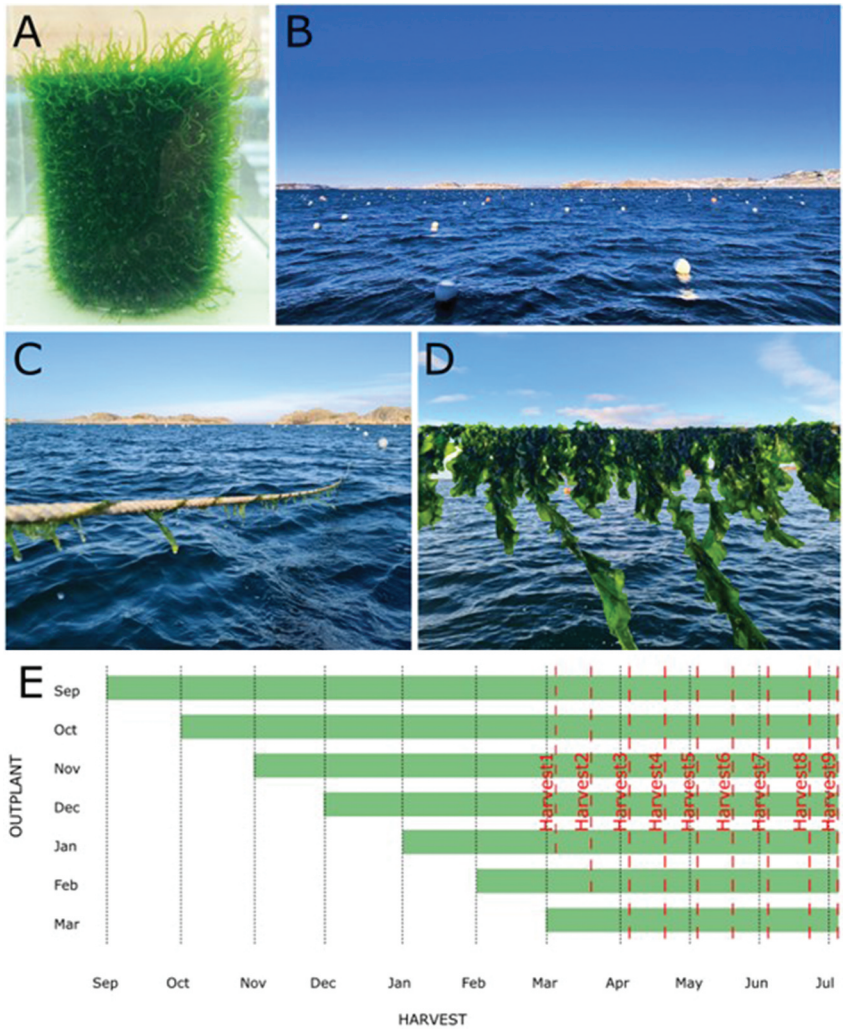

Fig. 1. Overview on the sea-based cultivation including various outplant and harvesting times of the crop *Ulva fenestrata*. **(A)** Seedlings attached to nylon twine wound on PVC spools in the nursery, prior to outplanting. **(B)** Cultivation site showing installed long-lines with described experiment deployed at the University of Gothenburg's sea farm in the Koster archipelago, Swedish west coast. **(C)** Long-line with attached seedlings immediately after installation in the sea farm. **(D)** Thalli of *U. fenestrata* grown under sea-based conditions. **(E)** Outplanting and harvesting schedule, illustrating seven monthly outplanting events (September–March) and nine bi-weekly harvests conducted from early March to early July.

The 2 ha (200 m × 200 m) seafarm, used for *Ulva* cultivation, was a rope-based structure (Steinhagen *et al.*, 2021) located in the Koster Archipelago on Sweden's west coast within the Skagerrak region (58°85.93′N, 11°06.82′E) (Fig. 1B). This species-rich marine area is characterized by rocky shores and experiences water level fluctuations of ± *C*2 m due to atmospheric pressure and wind-driven forces rather than tides (Johannesson, 1989). The farm site has a depth of approximately 10 m, with a seabed composed mainly of mud and sand.

The seeded cultivation twine was deployed at the seafarm on seven different outplant time points (Sept–Mar; n = 3, Fig. 1E), and coiled around 200 m fabric longlines, which were buoyed and anchored to the seafloor (Steinhagen *et al.*, 2021) (Fig. 1C). Seedlings grew (Fig. 1D) without further maintenance until harvest (Fig. 1E). The growth substrate was suspended at 1.5 m depth, with buoys placed every 10 m and a ~4 m spacing between parallel longlines. To assess the effect of outplant and harvest timing on *U. fenestrata* biomass yield, thallus length and biochemical composition (protein, fatty acids, pigments) were collected at nine time points with approximately 2-week intervals depending on prevailing weather conditions (sampling was postponed by a few days in the case of e.g. storm events): 2022-03-08; 2022-03-24; 2022-04-07; 2022-04-26; 2022-05-04; 2022-05-25; 2022-06-09; 2022-06-27; 2022-07-08) (Fig. 1E).

Biomass yield and thallus habitus

At each of the nine harvest time points, biomass yield was assessed by randomly sampling 1-m sections per replicate spool, totalling three replicates per outplant time. Fresh weight (fw) and dry weight (dw) per metre were measured using a Sartorius TE1502S balance (Göttingen, Germany) after excess water removal by spinning and lyophilization, respectively. Lyophilized biomass was ground to powder (pore size

<0.5 mm) and stored at −80°C for subsequent biochemical analysis. To evaluate thallus habitus, 10 randomly selected individuals per 1 m replicate (30 per outplant time) were photographed immediately post-harvest and analysed in ImageJ (Schneider *et al.*, 2012) for length. All data can be found in the appendix and only fw values are reported in detail within this study.

Biochemical composition

Crude protein content

Total nitrogen in *U. fenestrata* was measured using the Dumas combustion method (LECO Trumac analyser, LECO, USA). Approximately 50 mg of dried, homogenized algal material was combusted at high temperature in an oxygen-rich environment, and released nitrogen was quantified by thermal conductivity detection. Using the measured nitrogen amounts, crude protein content was calculated by applying a nitrogen-to-protein conversion factor of 5, following Angell *et al.* (2016).

Fatty acid content and composition

Fatty acids were analysed via GC-MS (Agilent 7890 A GC, 5975 C mass detector, Agilent Technologies, USA) using a VF-WAX column, following Harrysson *et al.* (2018). Approximately 25 mg of lyophilized *U. fenestrata* was extracted, trans-esterified with toluene (C17:0 as internal standard) and 10% acetyl chloride in methanol, then purified via ether partitioning. After evaporation and re-dissolution in isooctane, fatty acids were injected into the GC-MS system, quantified relative to the internal standard, and identified using GLC Reference Standard 463 (Nu-Chek Prep, USA) or the MS library. Results are expressed as milligram fatty acid per gram dw.

Pigment content (chlorophyll a, b, carotenoids)

Photosynthetic pigments were extracted from 60 mg of dried, homogenized *Ulva* material using 90% aqueous acetone. All steps were performed under exclusion of light. Samples were first sonicated in an ultrasonic bath for 10 min and subsequently placed on a shaker for 50 min to ensure complete pigment extraction. Following extraction, samples were centrifuged (4000 rpm), and the supernatant containing the extracted pigments was retained while the pellet was discarded. Pigment concentrations were determined spectrophotometrically, with chlorophyll *a* and *b* calculated using the equations of Jeffrey & Humphrey (1975) and total carotenoids according to Parsons (2013). Pigment concentrations are expressed as mg g^{-1} dry weight.

Environmental variables

Hydrographic data on water temperature, salinity, ammonium NH4-N, nitrate NO3-N and total phosphorus TOT-P of monthly samplings between September 2021 and July 2022 were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) SHARK database at the station Kosterfjorden NR16 (58°52.10′N, 11°06.20′E) which is in close proximity (~2 km) to the sea farm. Data from 0 and 2 m depth were averaged for the sampling dates. Hours of daylight were calculated as hours between sunrise and sunset at the respective sampling.

Statistics and data analyses

All statistical analyses were performed in RStudio version 2025.05.0 R (R Core Team, 2020). Data on biomass yield and biochemical composition were modelled using a linear mixed effect model (lmer()-function in lme4 package; Bates *et al.*, 2015) with outplant time and sampling date as categorical, fixed factors with interactions and a random intercept for each spool to account for repeated measures of the spools during sampling. The anova()-function (type III) from the lmerTest package was used to test for the effects of outplant time, sampling date and their interaction using the Kenward–Roger method to approximate the degrees of freedom for the denominator of the F-test. Multiple comparisons of the models´ estimated marginal means for outplants within sampling dates and sampling dates within outplants were performed using the emmeans-function (emmeans package; Lenth, 2014) with Tukey's adjustment of p-values. The cld-function (multcomp package; Hothorn *et al.*, 2008) was used to generate a group display of the multiple comparisons. Data on fw, protein, total chlorophyll and total carotenoid content was square root transformed prior to analysis to normalize model residuals and improve model fit.

Results

The Supplementary table S1 contains a comprehensive table of all measured variables.

Environmental variables

As expected for temperate regions water temperature, light availability and nutrient concentrations in the seawater showed a seasonal pattern (Fig. 2, Supplementary table S2). The water temperatures at the first outplant time in September were with 17°C relatively high but gradually decreased reaching values of 4–5°C from January to early April. Water

temperatures rapidly increased from 5°C in early April to 18°C in early July (Fig. 2A). The concentrations of nitrate in the seawater were ≥ 0.1 µM at the first outplant in September and gradually increased during autumn and winter reaching maximal values of 7.6 µM in early March. During spring the concentrations drastically decreased to 3.1 µM in early April and to values ≥ 0.1 µM from early May and onwards. Ammonium concentrations were generally low and below 0.3 µM with a peak in October to November (1.2–1.6 µM) and one in January (0.7 µM). Total phosphorus concentrations ranged from 0.3–0.9 µM showing highest values of 0.7–0.9 µM between January and early April and lowest values of 0.3–0.4 µM from May to July (Supplementary table 2B).

Biomass yield

There was a significant interaction between outplants and sampling dates on the fresh weight biomass (Table 1), indicating that the effect of outplant differed depending on the sampling date (Fig. 3A). At the first sampling in early March biomass yields followed the order of the outplanting (=cultivation time) decreasing from 214 g fw m^{-1} for the September outplant to 25 g fw m^{-1} for the January outplant (Fig. 3A). While there were no significant differences in biomass between the September–December outplants during the first three samplings from early March to early April, the biomass of the January outplants was significantly lower compared with the September–November outplants (Fig. 3A, Supplementary table S3). The amount of biomass, except for some minor fluctuations, gradually increased until June for all outplants after which they started to decrease (Fig. 3A). Maximum yields were obtained in early June for the January–March outplants and in late June for the September–December outplants (Fig. 3A). The biomasses of the February and March outplants were consistently and significantly lower compared with all other outplants and reached maximum values of only 229 and 349 g fw m^{-1}, respectively (Fig. 3A, Supplementary table S3). From late April the November outplant consistently produced highest biomasses reaching a maximum value of 3063 g fw m^{-1}, but only at the last two samplings in late June and early July its biomass was significantly higher compared with every single other outplant (Supplementary table S3). However, a clear bell-shaped pattern with biomass values Sep < Oct < Nov > Dec > Jan > Feb > Mar could be observed in the sampling period from late April to the last sampling in July (Fig. 3A). The biomass yields as dry weight followed as expected the same pattern as the biomass yields as fresh weight (Supplementary fig. S1, table S4).

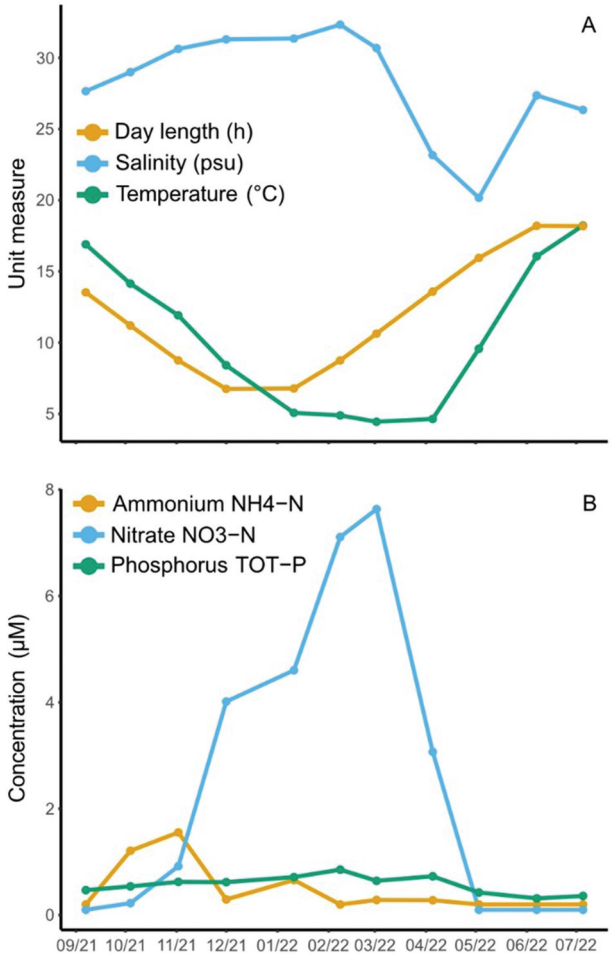

Fig. 2. Environmental variables from first outplant in September 2021 until last sampling in July 2022 at SMHI monitoring station Kosterfjord NR16 located in close proximity to the cultivation location in the Koster archipelago, Sweden.

Crude protein content

There was a significant interaction between outplants and sampling dates on the crude protein content (Table 1), indicating that the effect of outplant differed depending on the sampling date. With values between 21–25% (dw) the September–January outplants showed high protein contents from early March until early April (Fig. 3B). There were no significant differences among these outplants within the sampling dates during this period, except on the first sampling date where the protein content of the January outplant was significantly lower than the content of the September outplant (Fig. 3B, Supplementary table S5). At its first sampling in early April, the February outplant had a protein content of 18% (dw), which was significantly lower compared with the September–November outplants (Fig. 3B, Supplementary table S5). At the end of April, the protein content significantly decreased to values of 6–13% (dw) in all outplants, with no significant

Table 1. Analyses of variance for the fixed effects outplant, sampling and their interaction on the biomass and biochemical composition of *Ulva fenestrata*. Shown are numerator degrees of freedom (df1), denominator degrees of freedom (df2) estimated using the Kenward–Roger approximation, F-values and associated p-values for the fixed effects in the linear mixed model. Statistical tests were performed on the square root-transformed scale of the model for fresh weight, protein, chlorophyll and carotenoids content.

	Fresh weight				Protein				Total fatty acids			
Fixed effect	df1	df2	F-value	p-value	df1	df2	F-value	p-value	df1	df2	F-value	p-value
Outplant	6	14	259.4	<0.001***	6	14	98.4	<0.001***	6	14	7.8	<0.001***
Sampling	8	102	179.4	<0.001***	8	102	1099.7	<0.001***	8	102	202.5	<0.001***
Outplant:Sampling	43	102	3.1	<0.001***	43	102	7.9	<0.001***	43	102	3.7	<0.001***
	Total PUFAs				**Total chlorophyll**				**Total carotenoids**			
Fixed effect	df1	df2	F-value	p-value	df1	df2	F-value	p-value	df1	df2	F-value	p-value
Outplant	6	14	21.5	<0.001***	6	14	59.4	<0.001***	6	14	36.9	<0.001***
Sampling	8	102	499.7	<0.001***	8	102	539.0	<0.001***	8	102	589.9	<0.001***
Outplant:Sampling	43	102	6.2	<0.001***	43	102	4.6	<0.001***	43	102	6.9	<0.001***

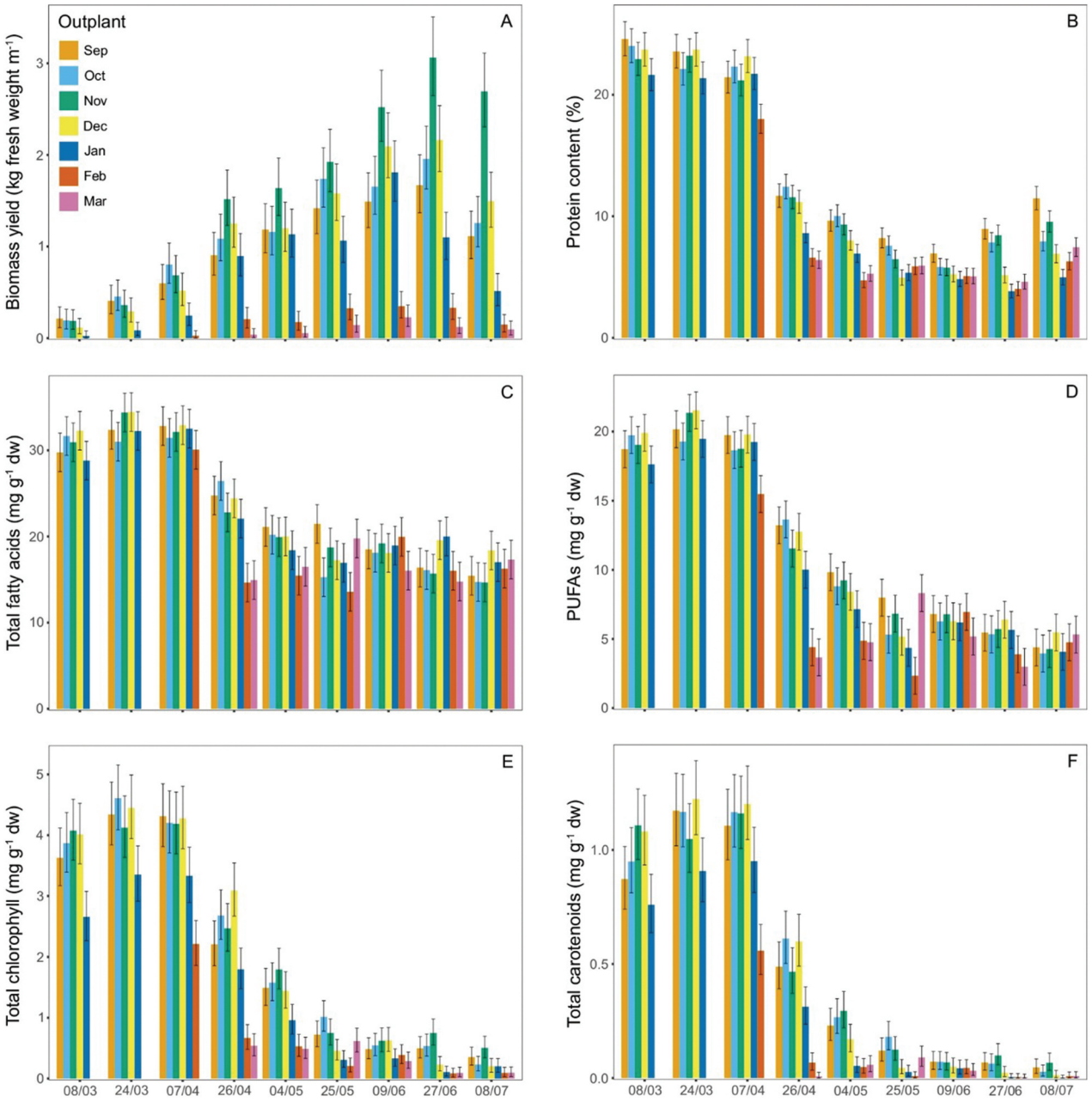

Fig. 3. Temporal variation in biomass yield and biochemical composition of *Ulva fenestrata* with regards to outplant time (Sept–Mar, marked in colours) at each sampling date. Error bars represent 95% confidence intervals (n = 3).

differences between the September–December outplant but significant lower values in the January–March outplants (Fig. 3B, Supplementary table S5). The protein content continued to decrease during the sampling season. The September–November outplants reached their minimum values of 6–7% (dw) in early June while the December outplant reached its minimum value of 5% already in late May. The January–March outplants reached their minimum values of 4–5% (dw) first in late June (Fig. 3B). Protein contents slightly recovered towards the end of the sampling period. By the latest sampling in July. all outplants apart from the January outplant showed a significant increase in their protein content to values between 6–12% (dw) compared with their respective minimum values (Fig. 3B, Supplementary table S5). In general, the September–November outplants maintained the highest protein contents after the drastic decrease in late April, but the differences compared with the December–March outplants were only significant in late June (Fig. 3B, Supplementary table S5).

Total fatty acid and polyunsaturated fatty acid (PUFA) content

There was a significant interaction between outplants and sampling dates on the total fatty acid and polyunsaturated fatty acids (PUFA) content (Table 1), indicating that the effect of outplant differed depending on the sampling date. The total fatty acid content was highest during the first three samplings from early March to early April reaching values of 28.8–34.5 mg g^{-1} dw (Fig. 3C). There were no significant differences in fatty acid content among outplants within sampling dates nor among sampling dates within outplants during this period (Fig. 3C, Supplementary table S6). By the end of April, the fatty acid content significantly decreased for the September–February outplants (Fig. 3C). At this sampling the February and March outplants had values of 14.6–14.9 mg g^{-1} dw, a significant lower content than the September–January outplants (22.1–26.4 mg^{-1} dw) (Fig. 3C, Supplementary table S6). From early May to July, the fatty acid content fluctuated between 13.6–21.5 mg g^{-1} dw and did not show any clear patterns among the outplants within sampling dates nor among the sampling dates within outplants (Fig. 3C).

The content of PUFAs was also highest during the first three sampling events from early March to early April reaching values of 17.6–21.5 mg g^{-1} dw in the September–January outplants corresponding to 59–63% of the total fatty acids (Fig. 3D). There were no significant differences in PUFA content among outplants within sampling dates nor among sampling dates within outplants during this period (Fig. 3D, Supplementary table S7). An exception was the February outplant, which showed a significantly lower content (15.5 mg g^{-1} dw) than the September–January outplants at its first sampling in early April. The PUFA content decreased significantly in late April in all outplants (Fig. 3D, Supplementary table S7). At this sampling, the February and March outplants showed significantly lower PUFA content (3.7–4.4 mg g^{-1} dw, 43–44% of total fatty acids) compared with the September–January outplants (10.0–13.6 mg g^{-1} DW, 39–51% of total fatty acids) (Fig. 3D, Supplementary table S7). The PUFA content in the February and March outplants were fluctuating over the sampling period from late April to early July and did not show a general pattern (Fig. 3D). In the September–January outplants the PUFA content, except for some fluctuations in the late May sampling, continuously declined during the sampling period reaching values between 3.9–5.5 mg g^{-1} dw, corresponding to 24–30% of the total fatty acids. At none of the sampling dates could any significant differences in the PUFA content be detected among the September–December outplants (Fig. 3D, Supplementary table S7).

Pigment content

There was a significant interaction between outplants and sampling dates on the total chlorophyll and carotenoid content (Table 1), indicating that the effect of outplant differed depending on the sampling date. The total chlorophyll content (Chl *a* + Chl *b*) was highest during the first three samplings from early March to early April (Fig. 3E). During this period, the September–December outplants reached maximal values of 4.2–4.8 mg g^{-1} dw. The January outplant showed lower chlorophyll contents with a maximum value of 3.4 mg g^{-1} dw, which were significantly lower compared with the contents in the September–December outplants at the first sampling in early March, but not in the early April sampling (Fig. 3E, Supplementary table S8). At its first sampling in early April, the February outplant had a chlorophyll content of 2.2 mg g^{-1} dw which was significantly lower compared with the September–January outplants (Fig. 3E, Supplementary table S8). In late April, the September–February outplants showed a significant decrease in the chlorophyll content (Fig. 3E, Supplementary table S8). The October–December outplants had significantly higher values (2.5–3.1 mg g^{-1} dw) compared with the January–March outplants (0.5–1.8 mg g^{-1} dw) at this sampling date (Fig. 3E, Supplementary table S8). The observed decrease continued with some fluctuations for all outplants reaching values of

0.1–0.5 mg g^{-1} dw at the last sampling in July (Fig. 3E). The January–March outplants had in general the lowest chlorophyll contents at each sampling date except for the late May sampling (Fig. 3E).

The carotenoid content followed the same pattern as the chlorophyll content (Fig. 3F). The total carotenoid content was highest between early March to early April reaching maximum values 1.16–1.20 mg g^{-1} dw in the September–December outplants and there were no significant differences neither among the outplants within sampling date nor among sampling dates within outplants (Fig. 3F, Supplementary table S9). The January outplant showed slightly lower carotenoid contents with a maximum value of 0.95 mg g^{-1} dw, which were significantly lower compared with the contents in the November and December outplants at the first sampling in early March and the December outplant in the late March sampling (Fig. 3F, Supplementary table S9). At its first sampling in early April the February outplant had a significantly lower carotenoid content (0.55 mg g^{-1} dw) compared with the September–January outplants (Fig. 3F, Supplementary table S2). The carotenoid content significantly decreased in late April to values below 0.61 mg g^{-1} dw in the September–February outplants (Fig. 3F, Supplementary table S9). At this date, the carotenoid content was significantly lower (0.01–0.07 mg g^{-1} DW) in the February and March outplants compared with the September–January outplants (Fig. 3F, Supplementary table S9). The carotenoid content continued to decrease with some fluctuations in all outplants reaching values from <0.01 to 0.07 mg g^{-1} dw. In general, the September–November outplants maintained the highest carotenoid contents after the drastic decrease in late April, but these differences were only occasionally significant compared with the other outplants (Fig. 3F, Supplementary table S9).

Discussion

Our study demonstrates that both the timing of seedling outplant and seasonal environmental fluctuations substantially influence biomass yield and biochemical composition in sea-based *Ulva fenestrata* aquaculture. While environmental conditions such as temperature, light and nutrient availability are recognized drivers of growth and chemical composition in seaweeds, our results highlight the critical role of the outplanting schedule in determining cultivation outcomes in terms of biomass yield and biochemical composition.

Effects of outplant timing

The timing of seedling transfer from nursery systems to sea-based cultivation had a pronounced impact on biomass yield, particularly during later stages of cultivation. Seedlings deployed in autumn (September–December) consistently outperformed those deployed in late winter and spring (February and March) in terms of biomass accumulation throughout the growing season.

At the first sampling, biomass yields reflected the outplanting dates (=cultivation time) ranging from 25 g m^{-1} for the January outplant to eight times more biomass for the September outplants indicating that seedlings deployed in autumn continued to grow, albeit slowly, despite decreasing light and temperature conditions which are known to limit photosynthetic efficiency and metabolic activity in *Ulva* spp. This suggests a level of physiological resilience of the northern hemisphere crop *Ulva fenestrata* that enabled the seedlings to capitalize on available resources in the form of dissolved inorganic nutrients despite the adverse conditions. However, no statistically significant differences were detected among the September–December outplants at the first samplings implying the biomass differences as a result of differing cultivation times may have been neutralized by uniformly poor environmental conditions during the early winter months.

As environmental conditions improved in spring (e.g. rising temperature and light), the effect of outplant timing became increasingly apparent resulting in a bell shape pattern of biomass production peaking in the November outplant and being drastically lower in the February and March outplants. These results indicate that even though growth is slow during the autumn and winter months, it is still extremely important for attaining high biomass yields in sea-based cultivations since late outplants could not compensate for this initial growth in this study and priming period.

The effect of outplant timing on the biochemical composition was less pronounced compared with the effect on biomass yields. However, crude protein, total fatty acids, PUFA, chlorophyll and carotenoid contents in the late outplants (January–March) were either comparable or often reduced compared with the autumn outplants (September–November), indicating again the importance of the autumn and winter cultivation period.

Therefore, while outplanting in winter (December–March) is technically feasible, it resulted in reduced final yields both in terms of biomass and biochemicals and may not be optimal for biomass production in temperate sea-based cultivation systems.

Effects of harvest time on biomass yield and biochemical composition

Our data underscore the importance of harvest timing in determining both the biomass yields and quality of *Ulva* biomass. The biochemical composition of

Ulva was more strongly influenced by harvest time and associated environmental conditions than by outplant timing which supports the findings by Steinhagen *et al.* (2021). This further reflects the well-established sensitivity of seaweed biochemistry to external factors, especially nutrient availability and light (Naldi & Wheeler, 1999).

During the winter months, water column nutrient concentrations – especially nitrate – are relatively high, allowing seeded *Ulva* to accumulate nitrogen in the form of chlorophyll and primarily protein, the latter which constitutes the largest nitrogen pool in the tissue (Naldi & Wheeler, 1999). This storage strategy is particularly effective in periods of suppressed growth, enabling the seaweed to build a biochemical N-reserve and explains the primarily high crude protein and chlorophyll contents in *Ulva* tissue during the late winter and early spring harvests. In our study, protein content peaked in late winter to early spring, coinciding with high ambient nutrient levels. Additionally, total fatty acids and PUFA as well as carotenoid content has been demonstrated to be positively associated with nitrogen availability in *Ulva* spp. (Kumari *et al.*, 2014; Van Alstyne, 2018) and is reflected in the high contents during late winter and early spring in *U. fenestrata*. Besides nutrient availability, temperature strongly influences PUFA composition in *Ulva* spp., with lower temperatures generally promoting higher PUFA-proportions to maintain membrane fluidity. This trend has been reported across green macroalgae, including *Ulva*, where cold-adapted thalli exhibit elevated PUFA levels compared with those grown under warmer conditions (Roleda *et al.*, 2021; Kumari *et al.*, 2014). Further, the pattern of nitrogen storage in *Ulva* is consistent with previous findings that *Ulva* can store sufficient internal nitrogen for approximately 10 days of growth in the absence of external inputs (Lubsch & Timmermans, 2018) and supports a recurring mechanism, documented by previous studies (Steinhagen *et al.*, 2021, 2022*b*).

By May, however, rising temperatures and light levels accelerated growth, while ambient nitrate concentrations dropped from maximal levels in March to minimal levels. As a result, tissue nitrogen – and by extension, crude protein content – and chlorophyll as well as total fatty acids, PUFAs and carotenoids declined rapidly in the *Ulva* biomass. This nitrogen limitation also led to reductions in chlorophyll, carotenoids, total fatty acids, especially PUFAs. Specifically, under nitrogen-enriched conditions, *Ulva* species exhibited higher PUFA content, particularly C18 and C20 PUFAs, which are essential for membrane structure and function (Kumari *et al.*, 2014). Conversely, nitrogen deprivation resulted in a shift towards increased saturated and monounsaturated fatty acids, with a corresponding decrease in PUFA levels.

This trade-off between high biomass yield and high biochemical quality presents a cultivation challenge: maximizing biomass and maintaining high protein content are mutually exclusive goals under natural sea-based conditions in temperate regions. Therefore, harvest timing must be strategically chosen based on the intended application of the biomass (e.g. as a protein-enriched ingredient for food and feed vs. bulk biomass for bioenergy or materials), as has been previously shown by Steinhagen *et al.* (2021, 2022*b*). In addition, post-harvest enrichment strategies – such as supplementation with nutrient-rich aqueous side-streams from food production (Stedt *et al.*, 2022*b*; Steinhagen *et al.*, 2024) – represent a promising approach to enhance protein content and thereby sustain the value of *Ulva* biomass for high-quality food applications.

Implications for cultivation optimization

Our findings suggest that for high-quality biomass as rich as possible in protein or other nitrogen-based compounds, harvest should occur before nitrate concentrations begin to decline in spring and outplant times should be chosen between September–November to reach highest possible biomass. This pattern was also shown for the other constituents measured in this study. Continuous monitoring of water nutrients could support real-time decision-making to optimize harvest timing. Further, an optical approach for estimating tissue nitrogen content in the crop *U. fenestrata*, based on thallus colour analysis, as demonstrated by Stedt *et al.* (2022*c*), offers a practical, non-destructive method that could help farmers determine the optimal harvest time based on real-time crop nutritional status. Alternatively, a post-harvest nutritional boost – such as the controlled nutrient enrichment strategies demonstrated by Stedt *et al.* (2022*a*, 2022*b*) and Steinhagen *et al.* (2024) – could be explored to enhance protein content in both high-biomass, late-harvested crops as well as early harvested protein-rich biomass.

Additionally, our results show that PUFA content in *Ulva fenestrata* decreased with rising sea temperatures, a pattern that aligns with findings in other macroalgae and marine organisms. This trend can be explained by homeoviscous adaptation, a physiological mechanism by which organisms modify membrane lipid composition to maintain membrane fluidity under varying temperatures (Hazel, 1995). At lower temperatures, organisms increase the proportion of PUFAs to preserve membrane function, while higher temperatures typically trigger a shift towards more SFAs, which are less prone to oxidative degradation and more stable under thermal stress (Harwood, 1998; Schmid *et al.*, 2018).

In *Ulva* species, temperature has been shown to significantly influence lipid composition, including reductions in omega-3 and omega-6 PUFAs during warmer periods (Mhatre *et al.*, 2025). Since PUFAs are nutritionally valuable – particularly in feed and food applications – maintaining a high PUFA content is desirable for certain markets. This reinforces the importance of integrating environmental monitoring into cultivation strategies to time harvests when PUFA content is at its peak, typically during cooler months. However, it also suggests a trade-off between maximizing biomass (which occurs under higher temperatures), and preserving nutritional quality, particularly fatty acids. Future research could investigate cultivar or strain selection or explore controlled post-harvest enrichment strategies to decouple this trade-off. Based on the present findings; however, tuning harvest when protein levels peak would be of larger nutritional significance than adjusting it based on PUFA. The latter are still on the very low side for inducing e.g. cardiovascular health benefits. The most generous EFSA health claim, on supporting normal heart function, requires 250 mg EPA plus DHA/day. Here, EPA contributed approximately 1–2% of the total fatty acids. However, *Ulva* biomass can still be a contributing source, combined with other sources of long-chained n-3 PUFA.

Finally, we recognize that spatial and interannual variability in environmental conditions, particularly sea surface temperature, light regimes and nutrient availability may influence the optimal timing of both outplant and harvest. While our findings provide general guidance – favouring autumn outplants and late winter to early spring harvests for high protein content – year-to-year monitoring and adaptive management especially under the prevailing effects of climate change remain essential.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Supplementary data

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at https://doi.org/10.1080/09670262.2026.2659224

Supplementary table S1: Data_Sea farm 2021-2022

Supplementary table S2: Environmental variables

Supplementary tables S3-S9: Group classifications of pairwise comparisons

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