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RESEARCH ARTICLE

Green gold rush in the Baltic Sea: Investigating sea lettuce's performance by distribution mapping of valuable compounds in a fluctuating environment

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Abstract

The growing prominence of *Ulva* in aquaculture is driven by its adaptability, rapid growth, nutritional advantages, and diverse biochemical composition. These green macroalgae have gained increasing attention for cultivation in lower salinity areas, expanding aquaculture beyond traditional euhaline environments. Our study investigated the distribution of economically valuable compounds in the most prominent *Ulva* crop species of the wider Baltic Sea region. We included 249 populations across the full Atlantic-Baltic Sea transect (>3000 km) and took into account prevailing fluctuating abiotic factors like salinity and nutrient regimes during the vegetation peak season. We revealed an overall trend of increasing crude protein content with increasing salinity in species with occurrence along the whole Atlantic-Baltic Sea transect (*U. intestinalis*: slope = 0.29; *U. linza*: slope = 0.09) and those only present in higher salinity regions (*U. compressa*: slope = 0.36; *U. fenestrata*: slope = 0.18) and confirmed an increase of pigments with increasing nitrogen tissue levels for most species (*U. compressa*: $r_{\text{pigments}} = 0.43$; *U. fenestrata*: $r_{\text{pigments}} = 0.01$; *U. intestinalis*: $r_{\text{pigments}} = 0.13$; *U. linza*: $r_{\text{pigments}} = 0.21$). With this mapping of the resource availability of valuable compounds in natural *Ulva* biomass of the Baltic Sea region, we have contributed to the understanding of the potential of *Ulva* species as key players in sustainable aquaculture practices evolving in the Baltic Sea region. Further, we have underscored the necessity of habitat-dependent crop selection and the importance of horticulture methodology for establishing *Ulva* as a viable future crop in the wider Baltic Sea.

KEYWORDS
aquaculture, Baltic Sea, blue economy, low salinity crop, protein, *Ulva*

INTRODUCTION

The projected global population of 9.9 billion by 2050 is anticipated to escalate the agricultural food gap and resource scarcity due to climate change-induced constraints on natural resources such as freshwater and farmland (Population Reference Bureau, 2020). Consequently, global attention has shifted toward oceans

Abbreviations: ANOVA, analysis of variance; CL, confidence level; *df*, degrees of freedom; DIN, dissolved inorganic nitrogen; *SD*, Standard deviation.

Sophie Steinhagen and Elena Schrofner-Brunner shared first authorship and contributed equally to the study.

as crucial components in addressing this resource gap (Food and Agricultural Organization of the United Nations & Fisheries Department, 2000). The rising interest in macroalgae cultivation, observed across Europe, signifies the growing acknowledgement of algae aquaculture as an ecologically sustainable approach to enhance renewable resource production while safeguarding natural algae stocks. Macroalgae cultivation offers advantages over terrestrial crop systems, requiring no arable land and minimizing freshwater, pesticide, and fertilizer usage (Duarte et al., 2017). Under optimal conditions, macroalgae exhibit faster growth rates and higher biomass production per unit area per year compared with fast-growing terrestrial crops (Stévant et al., 2017). Furthermore, macroalgae cultivation proves advantageous in mitigating greenhouse gas emissions by substituting items with higher carbon footprints and showcasing versatility in various industrial applications (Troell et al., 2023). Despite these benefits, macroalgae production in Europe contributes only to 0.1% of global production, with approximately 35 million tons of macroalgae wet weight produced worldwide (Food and Agricultural Organization of the United Nations & Fisheries Department, 2000). Nevertheless, the sector is experiencing constant growth, surpassing 35 million tons in aquaculture production in 2022 (FAO, 2022), emphasizing its increasing significance.

In Europe, the primary focus of macroalgae cultivation has centered on a limited selection of species. *Saccharina latissima* (commonly known as sugar kelp) is among the most frequently sea-based cultivated macroalgae (Lüning & Mortensen, 2015). However, emerging initiatives are focusing on the urgent need to diversify the sector by targeting more food-favorable algae with beneficial nutritional content (Trigo et al., 2021), such as green macroalgae like sea lettuce (*Ulva fenestrata*; Steinhagen et al., 2021; Steinhagen, Larsson, et al., 2022; Steinhagen, Enge, et al., 2022) and dulse (*Palmaria palmata*; Grote, 2019; Schmedes & Nielsen, 2020), which are central to the rapidly developing European Blue Economy. The necessity for novel green protein sources is further underscored by the rising interest in vegan and vegetarian food sources, driving research toward sustainable alternatives like sea lettuce (Trigo et al., 2021).

Likewise, the opening of new farm grounds in, for example, low salinity ecosystems such as estuaries and the world's largest brackish waterbody, the Baltic Sea (including Skagerrak and Kattegat), which is bordered by nine countries but still widely underused for macroalgae cultivation, has become of the utmost interest. Currently, commercial macroalgae cultivation is mainly concentrated in smaller systems with higher salinity areas (Weinberger et al., 2020).

The cultivation of macroalgae in the Baltic Sea represents an emerging frontier in marine resource utilization, offering potential contributions to sustainable food production and environmental stewardship. The wider Baltic Sea region is characterized by a strong salinity gradient that stretches from fully marine conditions in the Skagerrak

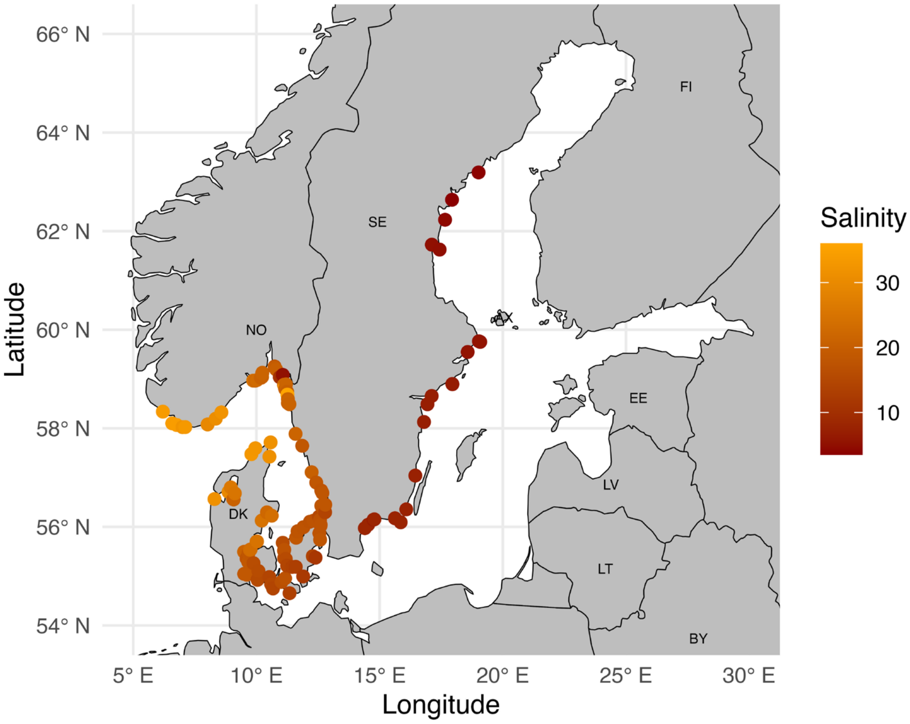

FIGURE 1 Overview map delineating the 122 sampling sites wherein *Ulva* populations were systematically collected across the Atlantic–Baltic Sea transect as part of this study. Displayed are respective prevailing salinity regimes measured during sampling events at the single sites (see color code).

(28–32) to an almost freshwater state in the Bothnian Bay (2–0; Figure 1; Helsinki Commission, 2023). The pronounced salinity gradient and the prevailing substrate availability structure the species biodiversity in the Baltic Sea (Reusch et al., 2018). Despite the decrease in macroalgae biodiversity with decreasing salinity, certain species stretch their distribution almost across the complete Baltic Sea (Schories et al., 2009; Steinhagen et al., 2023; Weinberger et al., 2020). The most prominent macroalgae representatives with a ubiquitous distribution in the Baltic Sea, ones that furthermore also maintain economic relevance, are *Fucus* spp., *Ulva* spp., and *Furcellaria lumbricalis* (Johannesson et al., 2011; Steinhagen et al., 2023; Weinberger et al., 2020). However, in the Baltic Sea's main waterbody (with a salinity <8), the establishment of commercial large-scale macroalgae farming faces a significant constraint, as viable cultivation of developed euhaline macroalgae crop strains has primarily occurred in the Skagerrak and Kattegat (Steinhagen et al., 2021; Weinberger et al., 2020). Due to non-established crop strains and missing cultivation practices of meso- and oligohaline macroalgae species, there are currently no large-scale commercial macroalgae cultivators in, for example, the Baltic Sea proper (Weinberger et al., 2020). Previous studies have, however, addressed the great potential of sea lettuce cultivation across the fluctuating waterbodies of the Baltic Sea (Kotta et al., 2022). Notably, *Ulva* species have exhibited intriguing variations in their distribution patterns within this dynamic environment (Steinhagen et al., 2019a, 2023), and among them, *Ulva intestinalis* and *Ulva linza* stand out as noteworthy examples, demonstrating remarkable adaptability by thriving across the entire salinity gradient of the Baltic Sea (Steinhagen et al., 2023). This unique ecological resilience (Björk et al., 2004; Kotta et al., 2022; Rybak, 2018; Steinhagen et al., 2019b) makes them particularly intriguing candidates for further exploration in the context of future aquaculture endeavors; however, a vast knowledge gap consists in the mapping of, for example, high-value biochemical compounds, which are known to be vastly altered by changing abiotic factors and, hence, environments (Fort et al., 2024; Olsson, Raikova, et al., 2020; Olsson, Toth, et al., 2020; Steinhagen, Enge, et al., 2022; Steinhagen, Larsson, et al., 2022; Toth et al., 2020).

Our study aimed to investigate the natural set-up of a selection of economically valuable compounds (protein and pigments: chlorophylls *a* and *b*, carotenoids) of the most prominent *Ulva* crop species (*U. fenestrata*, *U. compressa*, *U. intestinalis*, and *U. linza*) along their natural distribution range in the fluctuating environment of the Atlantic–Baltic Sea transect. The research explored the impact of changing salinities, nutrient regimes, and species identity on the biochemical composition of biomass at both inter- and intraspecific levels. Therefore, a large-scale field sampling across >3000 km of coastline covering the full Atlantic–Baltic Sea gradient, including three Scandinavian countries (Norway, Sweden, Denmark), was carried out. Efforts were tailored to the above-named natural *Ulva* populations in order to systematically map the distribution of naturally occurring resources, which positions *Ulva* species as potential key players in sustainable future aquaculture practices rapidly evolving in the Baltic Sea area.

MATERIALS AND METHODS

Study area, *Ulva* source material, sample preparation, and taxonomic identification

All data and code used in this study are available from the public data storage platform Dryad and can be accessed by the following link: https://doi.org/10.5061/dryad.xd2547drk. Samples of various populations of *Ulva fenestrata* ($n=29$), *U. compressa* ($n=34$), *U. intestinalis* ($n=87$), and *U. linza* ($n=99$) used in the present study were collected along their natural distribution ranges in the full salinity gradient of the Baltic Sea and adjacent areas such as the Kattegat, Skagerrak, and the eastern North Sea (Figure 1; see also Steinhagen et al., 2023). In total, 122 sampling sites (Figure 1)—45 in Sweden, 54 in Denmark, and 23 in Norway—were visited during 2020 during the vegetation peak season in summer (June–August; see also Tables S1 and S2). The salinity was measured with a WTW portable conductivity meter (Xylem Analytics, Germany) at the respective sites where *Ulva* populations were collected. The collection range, which was based on the species' respective range margins and distribution limits, is presented in Figures 1 and 2 (*Ulva fenestrata* 12–34.3, *U. compressa* 15–33.7, *U. intestinalis* 3.5–36, and *U. linza* 3.5–31.3; see also Table S1). In addition, both water temperature (°C) and oxygen levels ($\text{mg} \cdot \text{L}^{-1}$) were measured at most of the sites (Table S2), and 50-mL water samples at each collection point were retrieved by sterile filtrating with a syringe and 0.2-μm filter adaptors (Sarstedt, Germany) and collected in sterile 50-mL tubes (Sarstedt, Germany). The water samples were immediately frozen (−20°C) in a portable freezer and kept frozen in the lab until dissolved inorganic nitrogen (DIN [NH_4, NO_2, NO_3]) and phosphate (PO_4) were measured using an automated wet chemistry analyzer (San^{++}, Skalar Analytical B.V., Breda/Netherlands). Sampling encompassed diverse habitats across the broader Baltic Sea region, including rock pools, harbors, marine national parks, estuaries, fjords, drain channels, and both exposed and sheltered coastal areas. Various substrates (organic and inorganic, natural and artificial) hosting attached thalli were considered, and drift populations were also sampled. Collection of algae up to a depth of approximately 1.5 m below mean sea level in the supra- and midlittoral zones was achieved using waders. Additionally, snorkeling was employed for sampling in the mid- and infralittoral zones at selected sites. At each site, representative specimens

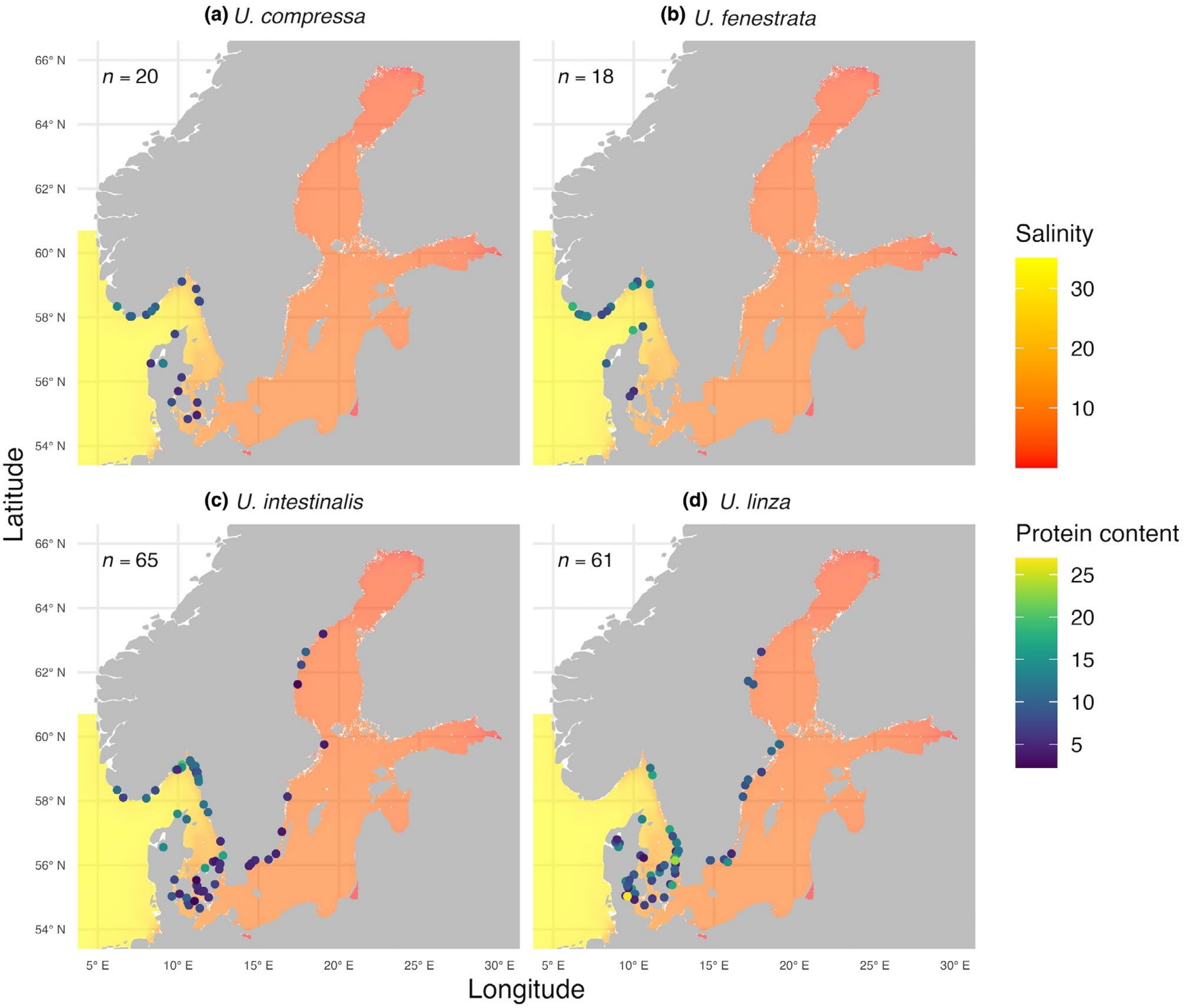

FIGURE 2 (a–d) Maps of sampling sites separated by algae species showing the geographical distribution of the different *Ulva* species *U. compressa* (a), *U. fenestrata* (b), *U. intestinalis* (c) and *U. linza* (d). The color of each point corresponds to the mean crude protein content per sampling site. Salinity shows mean Sea Surface Salinity during the sampling period between August and June 2020 (Copernicus Marine Service).

of each population were collected, ranging from the supralittoral to the sublittoral. For DNA barcoding of all populations, clean and epiphyte-free tissue samples (~1 cm^2) of representative individuals were collected, and molecular procedures, phylogenetic analyses, and respective sequencing data are readily available in Steinhagen et al. (2023). Therefore, all populations used in this study have been barcoded, and molecular identification followed distinct protocols and the latest taxonomic advancements (Steinhagen et al., 2023; Tran et al., 2022). During sampling, excess water was removed by a salad spinner, and all samples were stored in a portable freezer (−20°C) until transfer to −80°C in the laboratory. Subsequently, the samples were freeze-dried, lyophilized, and homogenized by milling (particle size <0.5 mm) to a homogeneous powder and stored at −80°C before analysis.

Protein content

Analyses of nitrogen content were performed by the combustion method using a LECO Nitrogen Analyzer (TruMac N, LECO Corporation, United States), applying EDTA Calibration Sample (LECO Corporation, United States). Subsequently, the crude protein content was estimated based on the nitrogen-to-protein conversion factor of 5 for seaweeds (Angell et al., 2016) which has been validated to be suitable for *Ulva* previously (Stedt et al., 2022).

Pigment (chlorophyll *a* and *b*, carotenoids) content

The chlorophyll *a*, chlorophyll *b*, and carotenoid contents in all samples were determined through a 90%

aqueous acetone extraction, followed by spectrophotometric analysis using the formulas and wavelengths outlined in Jeffrey and Humphrey (1975) for chlorophyll and Parsons et al. (1984) for total carotenoids. The extraction process adhered to the comprehensive protocol provided in Steinhagen et al. (2021).

Statistical and data analyses

All statistical analyses and visualizations were performed in R version 4.3.3 (R Core Team, 2024). Data were curated and visualized using the tidyverse, ggplot2, terra, MASS, and ncdf4 packages (Hijmans, 2023; Pierce, 2024; Venables & Ripley, 2002; Wickham, 2016; Wickham et al., 2019). Furthermore, data were derived from the seawater salinity model (https://doi.org/10.48670/moi-00013 ; https://doi.org/10.48670/moi-00059) available from the Copernicus Marine Service (https://marine.copernicus.eu/) representing the geographic extent and the sampling time of the study, for which two different datasets (daily measurements, 01/06/2020 to 31/08/2020) were used to cover both the Baltic Sea and the Atlantic-European North-West Shelf. In R, the two raster groups were merged, and the mean salinity for each pixel was calculated using the terra package. For better cartographic representation, crude protein content was pooled (i.e., mean) for sampling sites with more than one replicate per species.

To evaluate the respective effect of salinity and seawater nitrogen content on the crude protein content of seaweed tissue, we applied a linear model. Although sampling at all sites was performed in the same season (summer), the date of sampling, equivalent to the time of year, was controlled for in our model. Since all sampling took place between June and August 2020, we were able to assume a linear relationship between sampling date and salinity and seawater nitrogen content, respectively. Moreover, the dependencies of both salinity and seawater nitrogen content on the geographical position were included by adding both variables to our models (Models S1–S3). The linear models' assumptions were evaluated using Q-Q plots and robust linear regressions to assess the effect of outliers (R package MASS). The models were also tested with the interaction of salinity and seawater nitrogen content; however, the interaction was removed when not significant. For a detailed overview of the models applied, see the Appendix S1 (Models S1 and S2).

Potential correlations between salinity and pigments, as well as water nitrogen content and pigments, were evaluated using a Spearman's rank correlation (interactions and corrr packages; Kuhn et al., 2022; Long, 2019). To test the effect of salinity and water nitrogen content on pigments, respectively, analyses of variance (ANOVA) were performed using linear models.

Mean pigment contents were compared while correcting for the effects of salinity and seawater nitrogen content as well as sampling date, using estimated marginal means (emmeans package, Lenth, 2024). Subsequently, pairwise comparisons were calculated with the Tukey adjustment (95% confidence level).

Data for the Secchi depth and, hence, light attenuation of seawater (https://doi.org/10.48670/moi-00281) for the study period and area (global data, daily measurements), provided by Copernicus Marine Service, was used to determine light regimes and their potential effects on pigment composition and crude protein content at the different sampling locations. However, since light properties are aligned with latitude and other environmental covariates, a correlation without accounting for this multicollinearity might lead to spurious results. Therefore, we added the light data as Secchi disk depth to a linear model with seawater salinity and seawater nitrogen content (Model S3). The apparent effect of the sampling date in this model might be explained by the fact that light data was unavailable for all sampling locations due to a reduced overlap in data points based on valid coordinates, resulting in a dataset with fewer sampling dates. This means that because *Ulva* populations accessed within this study had a preferred habitat in the intertidal zone, Secchi depth data was not available for several of the examined natural populations that were mainly located <1 m offshore.

RESULTS

The cartographic representations provided in Figure 2a–d illustrate the disparate distribution patterns observed among the four examined *Ulva* species (*U. compressa*, *U. fenestrata*, *U. intestinalis*, and *U. linza*) across the surveyed area. Notably, *U. compressa* and *U. fenestrata* exhibited a distribution within the Skagerrak and Kattegat, extending toward the western reaches of the Öresund region. However, they were absent within the entirety of the inner Baltic Sea during the observational period, which agrees with previous studies of this region (Steinhagen et al., 2019a, 2023). Conversely, *U. intestinalis* and *U. linza* had distribution ranges encompassing the full Atlantic–Baltic Sea transect. This delineation underscores the discernible variances in habitat preferences and ecological niches among the *Ulva* taxa. Furthermore, our dataset highlighted the significant influence of environmental factors, such as the prevailing salinity gradient and respective nitrogen availability, on the number of valuable compounds present within *Ulva* biomass. Species and habitat-specific patterns on the respective compounds are explained in detail below.

TABLE 1 Mean, standard deviation, and minimum and maximum values for crude protein content (in % dw), salinity and seawater nitrogen content for all species of *Ulva* across all sites.

	Variable	Mean	*SD*	Min	Max
U. compressa	Protein content	8.18	2.92	3.22	16.1
	Salinity	23.6	6.55	15	33.7
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	2.19	2.55	0.593	9.00
U. fenestrata	Protein content	12.6	4.19	5.35	20.0
	Salinity	28.5	5.97	12	34.3
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	2.65	2.61	0.692	9.00
U. intestinalis	Protein content	8.02	3.94	2.23	19.9
	Salinity	16.6	7.72	3.5	36
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	2.08	2.13	0.557	14.1
U. linza	Protein content	10.2	4.86	2.39	27.0
	Salinity	15.3	6.69	3.5	31.3
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	1.99	2.47	0.282	14.0

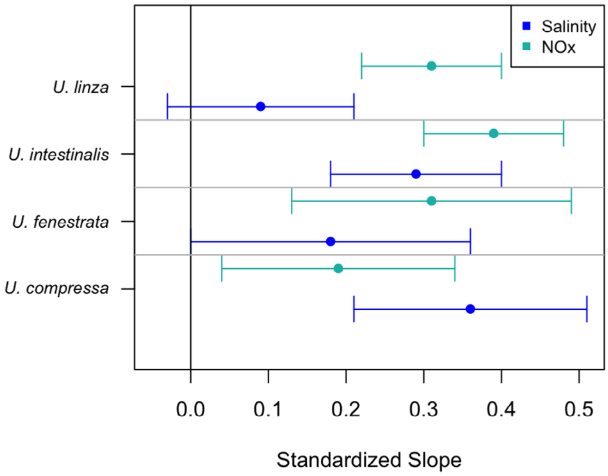

FIGURE 3 Forest plot displaying effect sizes for dissolved inorganic nitrogen (DIN) content and salinity with regard to crude protein content (Table 1), divided by species. Dots display standardized slopes, and error bars show lower and upper standard errors. The vertical reference line at zero indicates the point on the *x*-axis equal to no effect.

Crude protein content

Distinct distribution patterns of mean crude protein concentrations among the different investigated *Ulva* spp. were observed (Figure 2a-d). The cartographic representations in Figure 1 elucidated the mean crude protein concentrations across distinct sampling sites, employing a chromatic scheme to signify variations. Overall, there was a discernible trend within all investigated species toward exhibiting higher crude protein levels when proceeding from the Baltic Sea toward the Atlantic. In habitats characterized by more marine or euhaline conditions, wherein all four species potentially coexist, alterations in crude protein content did not transpire uniformly across the species spectrum. Rather, disparities appeared to be species-specific (Table 1). For instance, upon comparing *U. compressa* and *U. intestinalis*, it became evident that declines in crude protein content materialized earlier in the former as opposed to the latter when transitioning from the Atlantic Ocean to the Baltic Sea (Figure 2a,c). This implies that in regions where the protein content remains high in *U. intestinalis*, it is already declining in *U. compressa*. Further, we can show that the environmental variables tested had an overall stronger effect on crude protein content in *U. intestinalis* compared to *U. compressa* (Figures 3 and 4a,c).

In detail, crude protein content increased with rising salinity levels in *Ulva compressa* (slope = 0.36, $p = 0.023$, Table 2, Figure 3), whereas seawater nitrogen did not have a significant effect (slope = 0.19, $p = 0.218$). In *U. fenestrata*, neither salinity (slope = 0.18, $p = 0.328$) nor seawater nitrogen content (slope = 0.31, $p = 0.094$) impacted crude protein content significantly, but weak positive effects could be observed in both variables. However, neither of the two species was located in low salinities (i.e., the Baltic Sea) during this study. Crude protein content increased with rising salinity (slope = 0.29, $p = 0.014$) as well as seawater nitrogen levels (slope = 0.39, $p = <0.001$) in *U. intestinalis*. The same was observed for increasing seawater nitrogen content in *U. linza* (slope = 0.31, $p = 0.001$), but here again, salinity had no effect (slope = 0.09, $p = 0.463$). No interaction was observed between salinity and seawater nitrogen for any of the studied species.

Chlorophyll *a* and *b*, carotenoids

All four species exhibited similar pigment concentration ranges (chlorophylls *a* and *b* and carotenoids;

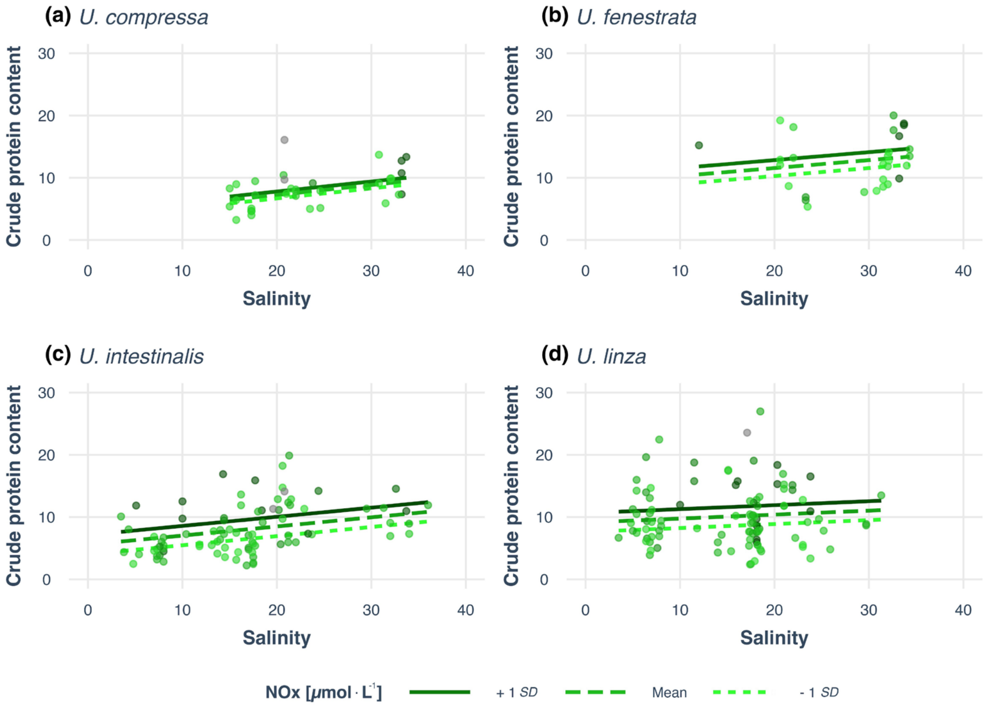

FIGURE 4 Response of crude protein content (% dw) to seawater nitrogen content and salinity in the four *Ulva* species *U. compressa* (a), *U. fenestrata* (b), *U. intestinalis* (c), and *U. linza* (d). Solid and dashed green lines resemble the response of crude protein content to the respective prevailing nitrogen level (low to high) at a set measured salinity, with mean Nox being represented by a medium green dashed line, +1 standard deviation of seawater nitrogen content (i.e., high nitrogen levels) by a dark green solid line and –1 standard deviation of seawater nitrogen content (i.e., low nitrogen levels) by a light green dashed line.

TABLE 2 Summary table for each linear model using crude protein content as the response variable.

	Variable	Standardized slope	*SE*	*t*-Value	*p*
U. compressa	Sampling day	–0.21	0.13	–1.55	0.132
	Salinity	0.36	0.15	2.41	0.023*
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	0.19	0.15	1.26	0.218
	Model fit: $R^2 = 0.425$, adj. $R^2 = 0.363$, $F(3, 28) = 6.889$				
U. fenestrata	Sampling day	–0.37	0.18	–2.05	0.051
	Salinity	0.18	0.18	1.00	0.328
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	0.31	0.18	1.74	0.094
	Model fit: $R^2 = 0.241$, adj. $R^2 = 0.150$, $F(3, 25) = 2.645$				
U. intestinalis	Sampling day	–0.20	0.12	–1.69	0.094
	Salinity	0.29	0.11	2.50	0.014*
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	0.39	0.09	4.38	<0.001***
	Model fit: $R^2 = 0.354$, adj. $R^2 = 0.330$, $F(3, 80) = 14.62$				
U. linza	Sampling day	0.18	0.12	1.52	0.13
	Salinity	0.09	0.12	0.74	0.46
	NOx [µmol · L^{-1}] (Coeff. 1.0000)	0.31	0.09	3.30	0.001**
	Model fit: $R^2 = 0.114$, adj. $R^2 = 0.085$, $F(3, 94) = 4.02$				

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

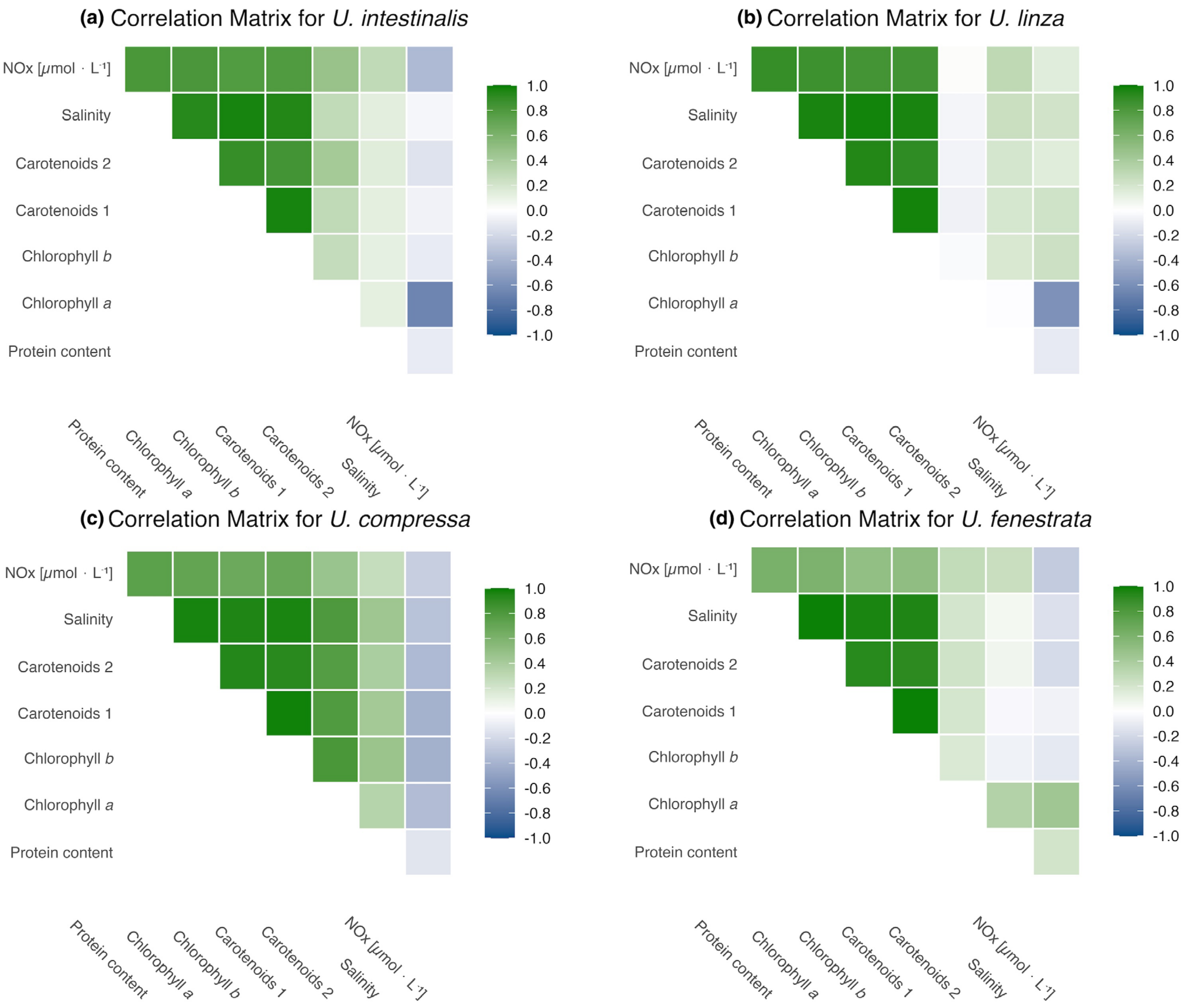

FIGURE 5 Correlation plots showing Spearman correlations (color) between crude protein content, pigment content, seawater salinity at the sampling site, seawater nitrogen content at the sampling site and day of sampling for *U. intestinalis* (a), *U. linza* (b), *U. compressa* (c), and *U. fenestrata* (d). Darker shades of green (positive) and blue (negative), respectively, indicate stronger correlations.

Figure S1). Considering that all pigments were positively correlated with each other within each species (Figure 5a-d), differences among individual pigments between species appear to vary with species-specific responses to seawater nitrogen and salinity levels, similar to crude protein content (Figure S1, Table 3).

In more detail, the effects of measured variables on the different pigment contents within a sample were determined to be similar across species (Figure 5a-d). Hence, chlorophyll *a*, chlorophyll *b*, and carotenoids are hereafter referred to as *pigments* and are not split into single compounds. We measured the highest pigment contents in *Ulva linza*, whereas *U. compressa* displayed the lowest pigment amounts measured across the species (Figure S1). However, the pigment content of *Ulva compressa* ($r_{\text{chlorophyll } a}$: 0.446, $r_{\text{chlorophyll } b}$: 0.387, $r_{\text{carotenoids}}$: 0.423 and 0.465) was highly associated with geography-dependent fluctuations in seawater nitrogen content, as depicted in Figure 5c. In *U. fenestrata* ($r_{\text{chlorophyll } a}$: 0.056, $r_{\text{chlorophyll } b}$: 0.069, $r_{\text{carotenoids}}$: −0.033 and −0.069), in constrast, pigment composition was not correlated strongly to measured seawater nutrient levels. In both *U. intestinalis* ($r_{\text{chlorophyll } a}$: 0.130, $r_{\text{chlorophyll } b}$: 0.145, $r_{\text{carotenoids}}$: 0.122 and 0.114) and *U. linza* ($r_{\text{chlorophyll } a}$: 0.251, $r_{\text{chlorophyll } b}$: 0.199, $r_{\text{carotenoids}}$: 0.189 and 0.182), a weak positive association was observed. A strong positive correlation of pigment content with salinity was observed in *U. compressa* ($r_{\text{chlorophyll } a}$: 0.804, $r_{\text{chlorophyll } b}$: 0.772, $r_{\text{carotenoids}}$: 0.793 and 0.817), but none was detected in *U. linza* ($r_{\text{chlorophyll } a}$: −0.051, $r_{\text{chlorophyll } b}$: −0.062, $r_{\text{carotenoids}}$: −0.073 and −0.028). Intermediate effects were observed in *U. intestinalis* ($r_{\text{chlorophyll } a}$: 0.288, $r_{\text{chlorophyll } b}$: 0.418, $r_{\text{carotenoids}}$: 0.290 and 0.271) and *U. fenestrata* ($r_{\text{chlorophyll } a}$: 0.205, $r_{\text{chlorophyll } b}$: 0.221, $r_{\text{carotenoids}}$: 0.196 and 0.172). Crude

TABLE 3 Model summary of each linear regression model, including comparisons of means (*df* = degrees of freedom; CL = confidence level, 95% confidence interval).

Pigment	Species	Emmean	Std. error	*df*	Lower CL	Upper CL
Chlorophyll *a*	*U. compressa*	0.428	0.1072	206	0.217	0.639
	U. fenestrata	0.595	0.1678	206	0.264	0.925
	U. intestinalis	0.718	0.0537	206	0.612	0.824
	U. linza	0.901	0.0552	206	0.792	1.010
Chlorophyll *b*	*U. compressa*	0.206	0.0798	206	0.0482	0.363
	U. fenestrata	0.328	0.1250	206	0.0819	0.575
	U. intestinalis	0.352	0.0400	206	0.2735	0.431
	U. linza	0.455	0.0411	206	0.3739	0.536
Carotenoids 1	*U. compressa*	0.174	0.0382	204	0.0991	0.250
	U. fenestrata	0.203	0.0598	204	0.0848	0.321
	U. intestinalis	0.260	0.0193	204	0.2216	0.298
	U. linza	0.321	0.0200	204	0.2817	0.361
Carotenoids 2	*U. compressa*	0.196	0.0532	204	0.0913	0.301
	U. fenestrata	0.271	0.0833	204	0.1064	0.435
	U. intestinalis	0.322	0.0269	204	0.2687	0.375
	U. linza	0.408	0.0279	204	0.3531	0.463

Note: Means of pigment content corrected for salinity and nitrogen differences by species (see Model S2).

protein content was highly correlated with pigment concentration, suggesting higher protein levels in darker seaweeds (Figure 5d). This is in line with earlier reporting from Stedt et al. (2022) and Nissen et al. (2024).

A correlation between seawater salinity and Secchi disk depth was detected (Figure S2), aligning with the findings of previous studies. The study of Opdal et al. (2023) revealed higher rates of light attenuation due to freshwater browning in low salinity settings such as the Baltic Sea, with salinity levels, therefore, being used as a measure of light attenuation. This relationship between seawater salinity and light attenuation makes it difficult to determine whether the observed effect of salinity on crude protein content and pigmentation was actually brought about by salinity itself and not light, even if the latter alone had no effect (Table S3).

DISCUSSION

The economic value of bioresources is intricately linked to their biochemical composition. Our study has shown that the most common *Ulva* crop species (*U. fenestrata*, *U. compressa*, *U. intestinalis*, and *U. linza*) of the Atlantic-Baltic Sea region exhibit valuable compounds to serve the growing Blue Economy—especially the food and feed industries. Distinct gradients of valuable compounds have been revealed for certain species within the region dependent on prevailing abiotic factors. This suggests the necessity of choosing crop species based on the desired farming region and the great opportunity of, for example, optimizing cultivation parameters in the Atlantic-Baltic Sea transect. We confirmed this with four lines of evidence, including: (1) an overall trend of increasing crude protein content with increasing salinity was detected in the investigated natural *Ulva* populations across the Atlantic-Baltic Sea transect; (2) an increase of pigments with increasing nitrogen tissue level was measured within the seaweed biomass; (3) *Ulva* spp. collected in the Baltic Sea were distinctively less pigmented than those collected in higher salinity regions (Skagerrak, Atlantic); and (4) in environments with varying levels of marine or euhaline conditions, where all four species can coexist, changes in biochemical content occurred unevenly among the species.

The Baltic Sea region, with its relative wealth in underused seaweed resources, has previously been described as an important future driver of the growing Blue Economy in the region (Kotta et al., 2022; Steinhagen et al., 2021; Weinberger et al., 2020). It was emphasized that the high production potential of macroalgae farms in the Baltic Sea, with widespread potential farm locations across the different ecosystems that present distinct production hotspots for various farmed species, could contribute significantly to the reduction of eutrophication symptoms in the region while simultaneously driving the Blue Economy and supporting livelihoods (Kotta et al., 2022). Our study supports that several different *Ulva* species have great potential to be used in aquaculture endeavors, whereas the species-specific distribution and range margins in the area (see also Steinhagen et al., 2019a, 2023) suggest different crop species should be used across the region. This study has revealed that the biochemical set-up of the investigated *Ulva* spp., decisive for the further use of the biomass, varies within the fluctuating environments of the Atlantic–Baltic Sea transect. The dependency on abiotic factors of *Ulva*'s performance and biochemical set-up is known to strongly alter the biomass (Toth et al., 2020). Our study has shown that in the Baltic Sea, salinity and nitrogen regimes define the crude protein and pigment content in natural *Ulva* populations.

Notably, the crude protein and pigment content of natural *Ulva* populations was generally observed to decrease with decreasing salinities, which was a trend in all four tested species of our study while showing profound significance in *U. compressa* and *U. intestinalis*. However, under controlled laboratory conditions applying sufficient nitrogen resources, positive effects of short- and long-term salinity treatments on both strain performance and increased desired biochemical composition have been reported (Fort et al., 2024). Furthermore, previous studies have highlighted that adult thalli of *U. linza* experienced synergistic effects of high nutrients and low salinity on photosynthesis that facilitated rapid growth in brackish environments (Kang et al., 2014). Similar results were confirmed by us in an earlier experiment, using diverse Baltic Sea strains in long-term low salinity cultivations under laboratory conditions, showing that the crude protein content can be significantly increased and engineered by salinity treatment selection (Steinhagen et al., 2025). Consequently, such results achieved under controlled conditions (Fort et al., 2024) diverge from the effect of low salinities in natural populations. However, the intricate interplay of seasonal differences in dissolved inorganic nitrogen (DIN) availability and, hence, the distinct synergistic physiological effects of prevailing low salinity environments needs further investigation in natural *Ulva* populations as well as in sea-based cultivated *Ulva* biomass. This is because the here presented data collection was only performed at vegetation peak during summer—a season where it is known that most DIN species are fixed within the vegetation and widely inaccessible in the water column. Further, in classical sea-based *Ulva* aquaculture settings of the Northern Hemisphere, seedlings are transferred to their respective farm sites after vegetation maxima in late autumn (Steinhagen et al., 2021; Steinhagen, Larsson, et al., 2022), when DIN is abundant throughout the water column, supporting the seedlings to accumulate nitrogen over the winter months. Our present study investigated natural crude protein levels of different *Ulva* populations, and it remains to be investigated if these differentiate from those of cultivated seaweeds in which seedlings have been pre-conditioned and received an advantageous outplant over autumn and winter, hence minimizing the competition for DIN in spring. Additionally, although our results are representative of summer conditions, a comprehensive understanding of the interplay between abiotic factors such as irradiance as well as natural salinity and temperature fluctuations and their effects on the biochemical composition of the biomass would benefit from a more detailed temporal analysis across different seasons.

Given the notable shift in dietary patterns toward green protein sources, driven by environmental sustainability concerns over livestock farming (Eckl et al., 2021; Wickramasinghe et al., 2021), it is of paramount importance to increase the protein contents within seaweed biomass and in novel aquaculture crop species as well as to select favorable farm sites (Steinhagen et al., 2021; Steinhagen, Enge, et al., 2022; Steinhagen, Larsson, et al., 2022). The mapping of naturally occurring crude protein levels (2.23%–27% dry weight) in different *Ulva* spp. revealed a generally suitable protein content for the investigated early summer season in the area. Previous studies have shown a decrease in crude protein content in cultivated seaweeds during early summer with levels <5% dry weight (dw; Steinhagen, Larsson, et al., 2022), whereas the present study has revealed significantly higher crude protein levels in several investigated strains from oligohaline to euhaline environments, suggesting not only the necessity of suitable farm ground selection but also the intricate interplay of strain-specific differences for subsequent horticulture methodology in *Ulva*. The increasing trend toward vegetarianism and veganism, coupled with projections of a 14% compound annual growth rate (CAGR) regarding alternative protein consumption between 2020 and 2035 (Morach et al., 2021; Probst et al., 2015), underscores the urgency to explore novel green protein sources beyond terrestrial plants (van den Boom et al., 2023; Wickramasinghe et al., 2021). Here algae can play a significant role. Our study supports the possibility of screening natural *Ulva* populations for best-performing strains in the wider Baltic Sea region. Enhancing the downstream applications and up concentration of seaweed proteins is crucial, with novel extraction methodologies holding promise for improving, for example, protein purity, digestibility, and functionality (Juul et al., 2021, 2022; Trigo et al., 2021, 2024). However, it is imperative to emphasize that the efficacy of downstream up concentration critically depends on optimizing and increasing the intrinsic protein content within seaweed biomass. Elevating protein content at the source ensures a more abundant and sustainable raw material for extraction, thereby enhancing the overall efficiency and economic viability of seaweed protein utilization.

A phenomenon observed in our study that supported previous observations (Stedt et al., 2022) was the increase in color intensity of the biomass—measured as pigment (chl *a*, chl *b*, carotenoids) concentrations—with increasing crude protein levels. Biomass collected from populations of the inner Baltic Sea was distinctively less colored, exhibiting a paler green appearance compared with *Ulva* populations collected in the Atlantic and Skagerrak. Further, the mutual interdependence among investigated pigments was evident, as respective increases or decreases were simultaneously observed among the here investigated pigments. Chlorophylls are essential for capturing light energy, and carotenoids play a role in photoprotection by both dissipating excess light energy and scavenging reactive oxygen species (Eismann et al., 2020) as well as by harvesting light under certain circumstances (Liguori et al., 2017). These compounds possess antioxidant properties, mitigating oxidative stress induced by environmental factors (Cotas et al., 2020) and making them interesting bioactive compounds. Seaweed-derived pigments are increasingly sought by, for example, pharmaceutical, cosmetic, and functional food industries, due to their diverse applications (Eismann et al., 2020). Light quality is a critical determinant influencing algae growth and the biochemical composition of biomass (Amaro et al., 2024), particularly of pigments such as carotenoids, as has been demonstrated with laboratory-cultivated *Ulva* (Toth et al., 2020). Toth et al. (2020) investigated the effects of various environmental variables on *U. fenestrata* in cultivation. It was observed that specimens of *U. fenestrata* displayed higher protein contents in low irradiance settings, in contrast to the observations made on natural populations in this study. Toth et al. (2020) explained this pattern as more energy being used for photoprotection rather than protein production under high light conditions (see also Mhatre et al., 2019). Compared to the current study, previous studies have focused on laboratory conditions in fully controlled environments, mainly under euhaline conditions and have not combined low irradiance with low salinity treatments, both of which might affect results. In a similar study by Steinhagen et al. (2025), *Ulva* was exposed to different salinity treatments in laboratory conditions. Although light settings remained constant throughout treatments, the seaweeds showed higher protein content in low salinity treatments. However, the set-up used by Steinhagen et al. (2025) was designed to omit nutrient depletion at any point during the study, in contrast to the natural conditions populations used in the present study were exposed to. However, the present results align with findings made by Volpe et al. (2024), who stated that different ecotypes of diatoms occur in regions with different salinity and, hence, light properties, allowing the assumption for a similar case in species of *Ulva*, with those in the salinity-rich Skagerrak Sea being pressured into adapting to light stress by their comparatively fluctuating environment (see also Steinhagen et al., 2025). The potential presence of various ecotypes with different light tolerance adaptations should be investigated further.

Although the biomass presented in this study was collected within the same season and the collection date did not exhibit any interaction with the biochemical parameters measured, future research should prioritize a detailed analysis of irradiance conditions, particularly across different seasons, examining the adaptability of respective populations. Furthermore, the available light attenuation data represented the average daily light conditions, often not sufficiently mirroring the actual light conditions at a given sampling date and time. Finally, sampling took place above the Secchi disk depth of a certain location in most cases, confirming the importance of including in situ light data sampling in future studies.

Their role as green tide-forming species might explain why some of the four *Ulva* species did not thrive under low nitrogen conditions in the Skagerrak–Baltic Sea transect and highlights their opportunistic behavior when it comes to positive alterations in nutrient availability (Bermejo et al., 2022; Fort et al., 2020). Although the apparent indifference of *U. fenestrata* to elevated nutrient levels in our study mirrors the absence of this species in green tides, *U. compressa*, in particular, has often exhibited remarkable growth in euhaline and eutrophic conditions (Kang et al., 2014), which would make it a suitable candidate for land-based aquaculture systems. It should, however, be mentioned that the usage of green tide-prone strains in aquaculture settings demands strict controls so that escapes to the wild do not jeopardize natural populations and so as to protect sensitive marine and brackish water environments.

Ulva intestinalis and *U. linza* have emerged as highly sought-after prospective crop species within the Baltic, while *U. fenestrata* and *U. compressa* are primarily cultivated in environments characterized by elevated salinity, albeit with more established populations. Hence, based on the natural distribution of the *Ulva* species in the Baltic Sea (see also Steinhagen et al., 2023), our study has emphasized *U. intestinalis* and *U. linza* as suitable crop strains for the wider Baltic Sea region and especially for the lower salinity water bodies of the Baltic Sea. Previous studies have already revealed the species' strong adaptation potential to fluctuating abiotic factors (Björk et al., 2004; Steinhagen et al., 2019b), and model-driven studies have suggested the suitability of *U. intestinalis* for the seaweed aquaculture sector in the region (Kotta et al., 2022). Although we confirmed such results within our study, it should be mentioned that even though *U. intestinalis* has proven suitable to becoming a thriving crop system in the Baltic Sea, full life-cycle aquaculture technology still needs to be developed for these species in order to rely on more than natural stocks and, especially, drive sea-based cultivation techniques.

CONCLUSIONS

The establishment of novel farm sites for facilitating the expansion of seaweed aquaculture, particularly in low salinity and brackish water environments, is essential for the advancement of sustainable agricultural practices and the cultivation of new crop species. The Baltic Sea, the world's largest brackish water body, characterized by its distinctive environmental parameters and abundant resources, has emerged as a particularly valuable region for such endeavors. Our study has underscored the intricate relationship between the economic value of bioresources and their biochemical composition, particularly in the context of the growing Blue Economy. We have demonstrated that common *Ulva* species in the Atlantic–Baltic Sea region harbor valuable protein and pigment resources, especially interesting for the food and feed industries. The observed gradients of these compounds across species and the different environments of the Atlantic–Baltic Sea transect highlight the importance of selecting species for cultivation based on regional abiotic factors. This study provides compelling evidence, which includes the correlation between crude protein content and salinity, the relationship between pigment levels and nitrogen availability, and the distinctiveness of Baltic Sea *Ulva* populations. Our findings support the notion that the Baltic Sea holds significant potential for seaweed aquaculture, with different *Ulva* species showing adaptability to varying environmental conditions. Moving forward, prioritizing species selection and cultivation techniques tailored to regional conditions will be crucial for maximizing the economic and ecological benefits of seaweed aquaculture in the Baltic Sea and beyond.

AUTHOR CONTRIBUTIONS

Sophie Steinhagen: Conceptualization (lead); data curation (lead); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (lead); project administration (lead); resources (lead); software (equal); supervision (lead); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Elena Schrofner-Brunner:** Data curation (equal); formal analysis (equal); investigation (equal); software (lead); validation (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Benedikt Schrofner-Brunner:** Formal analysis (supporting); software (supporting); visualization (supporting); writing – review and editing (equal). **Karin Larsson:** Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (equal). **Ingrid Undeland:** Funding acquisition (equal); methodology (equal); resources (equal); writing – review and editing (equal).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species abundances (specimen count) throughout the different measured seawater salinity regimes. Salinity classes were taken from the Venice salinity classes (Venice System, 1959).

Table S2. Water temperatures (in°C) at the different sampling sites of each collected species.

Table S3. Summary table for the linear model including light data using crude protein content as the response variable.

Figure S1. Boxplots showing pigment concentration ranges for each pigment (chlorophyll *a*, chlorophyll *b*, and carotenoids) and species (*Ulva compressa*, *U. fenestrata*, *U. intestinalis* and *U. linza*). Between species, chlorophyll *a* and *b* as well as carotenoid contents of *U. compressa* and *U. linza* were significantly different. In all species, concentrations of all pigments were not significantly different when comparing *U. fenestrata* and *U. intestinalis* with either *U. compressa* or *U. linza*.

Figure S2. Correlation plot displaying the relationship between seawater salinity and Secchi disk depth (log-transformed for better visibility).

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