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Steinhagen, S., Johansson, I., Specht, J. et al (2025). Unlocking economic potential of the Ulva crop for low salinity environments: exploring the effect of salinity gradients on the performance and valuable compounds of Baltic Sea strains. Botanica Marina, 68(1): 65-82. http://dx.doi.org/10.1515/bot-2024-0079

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Research Article

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Unlocking economic potential of the *Ulva* crop for low salinity environments: exploring the effect of salinity gradients on the performance and valuable compounds of Baltic Sea strains

https://doi.org/10.1515/bot-2024-0079
Received September 24, 2024; accepted December 5, 2024; published online January 6, 2025

Abstract: The rising global significance of sea lettuce (*Ulva* spp.) in aquaculture stems from its versatility, rapid growth, and nutritional benefits. Cultivation expansion into lower salinity areas, like the Baltic Sea, is crucial for advancing aquaculture beyond traditional environments. This study investigated the impact of long-term (8 weeks) low salinity treatments on the biochemical content of eight *Ulva* strains – encompassing some of the most common *Ulva* crop species (*Ulva lacinulata*, *Ulva linza*, *Ulva intestinalis*, *Ulva fenestrata*) of the wider Baltic Sea area – from varying source salinities (30, 14, 9, 7). Most strains exhibited significantly higher growth rates and contents of crude protein under low salinity treatments, irrespective of where they came from (i.e. euhaline or mesohaline environments). However, effects on pigments and phenolic contents were strain-specific. *Ulva lancinulata* showed high resilience to salinity changes. Cultivating *Ulva* under low salinity conditions enhances its nutritional attributes and identifies the broader Baltic Sea as a viable cultivation environment. Nevertheless, careful selection of strains is crucial due to significant inter- and intraspecific differences. This research underscores the importance of tailored cultivation strategies for optimizing *Ulva* biomass production, particularly in the context of the expanding Blue Economy industry.

Keywords: adaptation; aquaculture; Blue Economy; crude protein

1 Introduction

Forecasts indicate that terrestrial crop yields may fall short of meeting global food demands by 2050 (Ray and Foley 2013). Simultaneously, projections suggest that agricultural expansion, including mariculture, could offer a viable solution to augment food production on a larger scale (Duarte et al. 2009). Seaweeds, particularly as a sustainable protein source, are gaining attention as a potential remedy to address these challenges (Hofmann et al. 2024; Juul et al. 2021, 2022; Kazir et al. 2019; Pliego-Cortés et al. 2020; Stedt et al. 2022a, b; Steinhagen et al. 2021, 2022a, b; Trigo et al. 2021). Unlike terrestrial crops, seaweeds provide a protein resource that does not compete for land use, thus potentially mitigating global pressures on agriculture and land resources (O'Brien et al. 2022; Spillias et al. 2023; Steinhagen et al. 2021). Their promising role in the ongoing protein-shift, i.e. the shift from red meat to more sustainable food protein sources, is underscored by the increasing interest in vegan proteins within the food industry in response to largely growing consumption trends (Alrosan et al. 2022).

The genus *Ulva*, commonly known as sea lettuce, comprises diverse green macroalgae which, because of their wide environmental tolerance, exhibit a cosmopolitan behavior, thriving in fully marine to freshwater environments (Bolton et al. 2016; Mantri et al. 2020; Steinhagen et al. 2023). In the context of European aquaculture, in addition to brown kelp species (e.g. *Alaria esculenta* and *Saccharina latissima*) and red seaweeds (*Porphyra* spp. and *Palmaria palmata*), green seaweeds of the genus *Ulva* currently emerge as one of the key macroalgal crop species (Hofmann

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et al. 2024). Its significance in aquaculture has been steadily increasing, marking a pivotal juncture in the exploration of sustainable marine cultivation practices.

Distinctive features contributing to *Ulva's* prominence are its ability to grow fast (Fort et al. 2019; Steinhagen et al. 2022a), adapt to diverse environmental conditions (Cardoso et al. 2023; Fort et al. 2019; Steinhagen et al. 2019a, b, 2023; Toth et al. 2020), and thrive under high stocking densities (Mata et al. 2010). Moreover, the biochemical compounds in *Ulva* are widely applicable in diverse economic sectors such as the food and feed industry (Holdt and Kraan 2011; Trigo et al. 2021), in functional foods, cosmeceuticals, nutraceuticals and pharmaceuticals (Ruslan et al. 2021), biofuels (Bikker et al. 2016; Bruhn et al. 2011), as soil ameliorates (Roberts and de Nys 2016), and in innovative biomaterials (Lakshmi et al. 2020; Wahlström et al. 2020). Three groups of such compounds are phenolics, carotenoids and chlorophylls, all which have been ascribed antioxidant activity (Pérez-Gálvez et al. 2020; Zeb 2020), but the pigments chlorophyll and carotenoids are also interesting as natural food colorants (Haryatfrehni et al. 2015; Martins et al. 2021a, b). The cultivation potential of *Ulva* is further emphasized by its ability to adapt to various cultivation methods such as offshore (Steinhagen et al. 2021, 2022b) or onshore aquaculture (Lüning 2023). Its versatility in cultivation techniques offers scalability and flexibility, providing valuable options for the aquaculture industry (Hofmann et al. 2024; Simon et al. 2022). In this context, the growing interest in *Ulva* aquaculture marks a significant stride toward sustainable and diversified marine cultivation practices. However, large-scale farming activities are mainly conducted in high salinity environments (Califano et al. 2020; Lawton et al. 2020; Simon et al. 2022; Steinhagen et al. 2021) widely neglecting the farm ground potential of diverse brackish water bodies of e.g. fjord systems, estuaries, inland salt streams, and the Baltic Sea. The need for investigations into new farm grounds, including brackish and low-salinity environments, gets reflected by the dynamic and robust growth of the European seaweed market, demonstrating an impressive annual expansion rate ranging between 7 and 10 % (Mendes et al. 2022).

Especially the brackish water bodies of the Baltic Sea, which are bordered by nine countries, are currently widely underused for macroalgal cultivation (Kotta et al. 2022; Weinberger et al. 2020) despite offering greatest potential for certain macroalgae to develop a Blue Economy in one of the world´s best researched waterbodies (Reusch et al. 2018). The wider Baltic Sea region is characterized by a strong salinity gradient which stretches from fully marine conditions in the Skagerrak (28–32) to almost freshwater in the Bothnian Bay (0–2) (Helcom 2018). The pronounced salinity gradient and prevailing substrata availability play pivotal roles in shaping the species biodiversity in the Baltic Sea (Reusch et al. 2018). Within this dynamic environment, *Ulva* species exhibit intriguing variations in their distribution patterns (Steinhagen et al. 2019a, 2023). Among them, *Ulva intestinalis* and *Ulva linza* demonstrate a remarkable adaptability to 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 in the Baltic Sea. Especially within the past years the aquaculture sector has developed a strong interest in various species and strains of *Ulva* due to their many beneficial traits such as high productivity, environmental tolerance (Bolton et al. 2016; Nardelli et al. 2019; Steinhagen et al. 2019a, b, 2021, 2023), and their efficient bioremediation of nutrients (Al-Hafedh et al. 2015; Sode et al. 2013) while simultaneously providing valuable biochemical compounds which can be applied in diverse economic sectors (Hofmann et al. 2024).

It is undisputed that adaptation and changes in environmental conditions and abiotic factors alter the performance, biochemical setup and therewith, the potential biomass value of *Ulva* (Cardoso et al. 2023; Nesterov et al. 2013; Olsson et al. 2020a, b; Stedt et al. 2022a, b; Steinhagen et al. 2021; Toth et al. 2020). It has been shown that changes in abiotic factors, such as the exposure of *Ulva* to short-term low-salinity treatments can have a significant effect on the performance and biochemical set up of the alga's biomass (Fort et al. 2024). To tailor properties such as the lipid profile (vital for potential food applications of *Ulva* biomass), 7 days of low salinity treatment were sufficient to optimize the lipid profile. Despite the negative impact of the low-salinity treatment on growth, it positively influenced the lipid profile of *Ulva*, thereby enhancing its suitability for customized applications in the food industry (Fort et al. 2024). However, environmental parameters do not exclusively determine the quality of *Ulva* biomass (Fort et al. 2024). Likewise, genetic factors play a substantial role in influencing the performance and metabolic content of *Ulva* (Fort et al. 2019) and natural variations are evident, both between *Ulva* species and among individuals of the same species under similar environmental conditions (Fort et al. 2019). Further, the interplay of different environmental conditions affects the biochemical profile in natural *Ulva* populations (Olsson et al. 2020b). This underlines that a comprehensive approach, considering both environmental and genetic factors as crucial components in future aquaculture and ecological studies, is needed.

This study aimed to assess the cultivation potential of four Northern Hemisphere *Ulva* species, *U. fenestrata* Postels

et Ruprecht, *U. lacinulata* (Kuetzing) Wittrock, *U. intestinalis* Linnaeus, and *U. linza* Linnaeus, originating from diverse locations in the wider Baltic Sea area, under varying salinity regimes. The research explored the impact of changing salinities on the biochemical composition of biomass at both inter- and intraspecific levels. Specifically, the study investigated the effects of salinity variations on crude protein, chlorophylls *a and b*, carotenoids, and phenolic acid content, as well as on the alga's growth rate. The underlying theory posited variations in biomass composition or growth rate of the different *Ulva* species and strains, contingent upon their natural origin and their response to diverse salinity conditions. Hence, the aim of the study was to assess the species' and strains' ability to thrive across varying salinity conditions which might position them as potential key players in sustainable aquaculture practices rapidly evolving in the Baltic Sea area.

2 Materials and methods

2.1 Algal source material and taxonomic identification

Individuals of *Ulva fenestrata* originated from long-term indoor tank cultivation at Tjärnö Marine Laboratory, Sweden (TML, 58°52′33.7″ N 11°08′44.9″ E; Figure 1). Various populations of *U. lacinulata*, *U. intestinalis*, and *U. linza* were collected from different salinity conditions across the range to be found between the Atlantic and the inner parts of the Baltic Sea (Figure 1). Taxonomic identification of the *Ulva* strains was based on molecular identification of the *tufA* marker gene and followed the procedure as described by Toth et al. (2020). Collection data, including the salinity at the collection site, and information on molecular identity including GenBank reference numbers can be found in Table 1. During collection, populations were pre-identified using morphological characteristics defined in previous studies (Steinhagen et al. 2019a, 2023). The collected samples were transferred in plastic bags with seawater from the collection site and transported to the lab within 24 h. In the lab, they were stored in a controlled temperature room (12 °C; 90–110 µmol m^{-2} s^{-1}; light:dark regime of 16:8 h) in 14-L aquaria containing seawater (filtered [0.2 µm], deep-sea [40 m]) adjusted to the salinity of the sampling site using tap water, with permanent aeration, and supplemented with Provasoli Enriched Seawater (PES; Provasoli 1968). Acclimatization to these conditions was conducted for a minimum of one week prior to subsequent experiments. On this background, and based on previous experience, we assumed that the overall biological set up of the different strains was similar at the start of the experiment. The seaweeds were rinsed in 0.2-µm filtered seawater before the start of the experiments and samples were taken before the experiments ('t0') for subsequent biochemical analysis. Per population, three randomly selected individuals were subsequently identified by molecular techniques to assess their taxonomic species affiliation. Resulting sequences were uploaded to GenBank and are publicly available (see Table 1).

2.2 Experimental setup and growth measurements

After a minimum of one week acclimation in the controlled temperature room (12 °C), the collected strains (one strain of *U. fenestrata* and *U. lancinulata* from salinity 30, four strains of *U. intestinalis* from salinities 30, 14, 9 and 7 and two strains of U. *linza* from salinities 14 and 9) were subjected to five salinity treatments of 5, 10, 15, 20 and 30 in biological replicates (n = 3) for a total of 8 weeks. The excess water of the biomass was removed by spinning the seaweeds in a salad spinner and 10 g fresh weight (FW) were submersed in 1-L aquaria supplied with sterile filtered seawater (0.2 µm + UV, 9 L h^{-1}) at salinities of 5, 10, 15, 20, and 30 (natural seawater [33] diluted with sterile distilled water; n = 3) and an average irradiance of 80–100 µmol m^{-2} s^{-1} under a 16:8 h L:D light regime (light source: OSRAM Lumilux Cool daylight L 58W/865) with permanent aeration. Growth medium PES was added once per week following the concentration specifications of Provasoli (1968) and was connected with a weekly performed water change. To prevent diatom growth, 1 mg L^{-1} GeO_2 was added to all treatments. GeO_2 was found to negatively affect diatom growth whereas it was reported to not have any effect on *Ulva* growth (Rautenberger 2024). In combination with the weekly water change, each culture was weighed (Sartorius TE1502S, Göttingen, Germany), after removing the excess water with a salad spinner as described above, to determine growth rates. Afterwards, the biomass was re-adjusted to 10 g in any of the containers by removing excess biomass. Salinity and pH (WTW MultiLine 3420, Xylem Analytics, Weilheim, Germany) remained stable throughout the experiment in all treatments and no additional adjustments were necessary. Final measurements took place on the 8th week of the experiment. After the biomass had been weighed, samples were frozen and stored at −60 °C until lyophilized and homogenized into a fine powder by grinding the biomass with pestle and mortar for subsequent crude protein, pigment and phenolic content analysis.

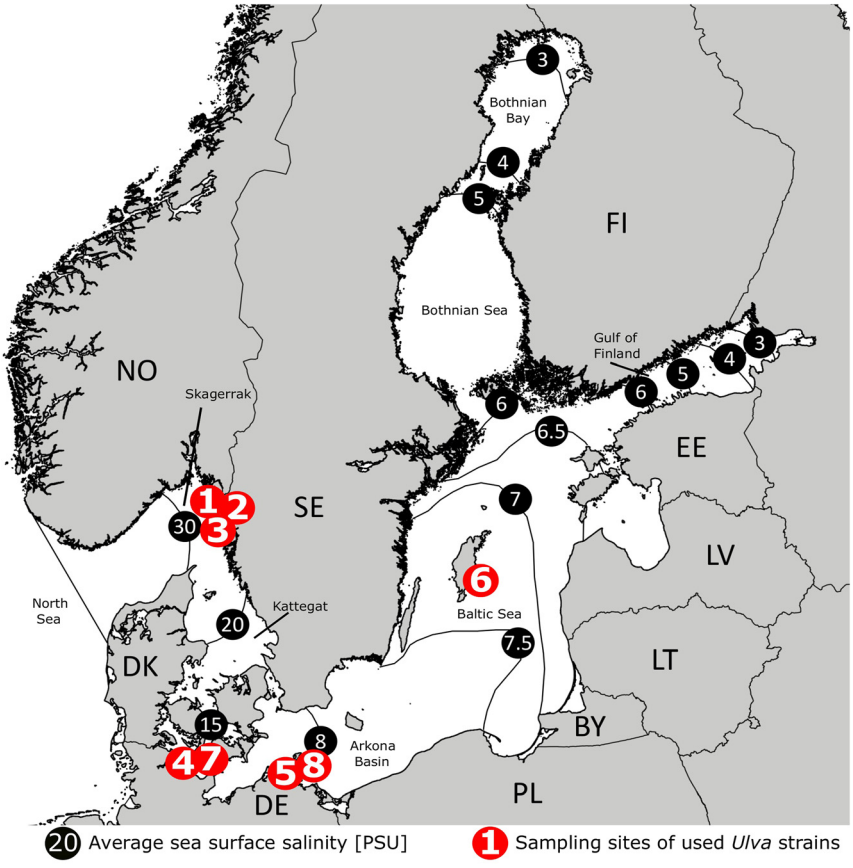


Figure 1: Map of sampling sites (1–8, red circles) of *Ulva* strains used in the present study collected in 2023 across the Atlantic-Baltic sea gradient and used in the salinity experiments. Average sea surface salinity (black circles) is indicated.

Table 1: List of *Ulva* strains collected in 2023 across the Atlantic-Baltic Sea gradient and used in the salinity experiments.

Species	Collection location	Coordinates	*Site in map* (Figure 1)	Date	Original salinity	Sample ID	GenBank ID
U. fenestrata	Cultivation, Tjärnö Marine Lab, Sweden	58°52′33.7″ N 11°08′44.9″ E	1	n.a. (long-term cultivation >10 years)	30	Fen30	MN240309, MN240310, MN240311
U. lacinulata	Båleröd, Strömstad, Sweden	58°53′24.5″N 11°11′48.7″E	2	April 2023	30	Lac30	PP354974
U. intestinalis	Lindholmen, Strömstad, Sweden	58°53′22.0″N 11°07′12.7″E	3	April 2023	30	Int30	PP354975
U. intestinalis	Bülk, Strande, Germany	54°27′13.3″N 10°11′50.4″E	4	April 2023	14	Int14	PP354976
U. intestinalis	Deviner Bucht, Stralsund, Germany	54°16′07.5″N 13°08′38.5″E	5	April 2023	9	Int9	PP354977
U. intestinalis	Närshamn, Gotland, Sweden	57°13′30.9″N 18°39′43.6″E	6	April 2023	7	Int7	PP354978
U. linza	Friedrichsort, Kiel, Germany	54°23′37.0″N 10°11′21.5″E	7	April 2023	14	Lin14	PP354979
U. linza	Sassnitz, Rügen, Germany	54°30′46.9″N 13°38′46.6″E	8	April 2023	9	Lin9	PP354980

2.3 Growth rate and crude protein content

To calculate average growth rate (AGR), the weekly recorded change in fresh weight was averaged over the eight measurement time points among the replicates (n = 3). Analyses of nitrogen content were performed according to the Dumas method on the biomass of the final sample point using an LECO Nitrogen Analyzer (TruMac N, LECO

Corporation, USA). EDTA Calibration Sample (LECO Corporation, USA) was used as standard. Subsequently, the crude protein content was estimated based on the nitrogen-to-protein conversion factor of five for seaweeds (Angell et al. 2016).

2.4 Pigment (chlorophylls *a* and *b*, carotenoids) and phenolic content

Pigment and phenolic contents were determined at the end of the experiment on all treatments and replicates (n = 3) from lyophilized and homogenized tissue material. Extractions followed the detailed protocol available in Steinhagen et al. (2021).

Total contents of chlorophylls *a and b* and carotenoids in the 90 % aq. acetone extract were assessed spectrophotometrically (Lambda XLS+, Perkin Elmer, Waltham, MA, United States) using the formula and wavelength given in Jeffrey and Humphrey (1975) for chlorophyll and Parsons et al. (1984) for total carotenoids. Total phenolic content was spectrophotometrically determined at 765 nm (Lambda XLS+, Perkin Elmer, Waltham, MA, United States) using the colorimetrical Folin-Ciocalteu phenol assay and gallic acid (Sigma-Aldrich, St. Louis, MO, United States) as a standard. The total phenolic content was expressed as % of dw.

2.5 Statistical analyses

Data on growth, crude protein, pigment, and phenolic content of all samples were statistically analyzed in JMP (JMP®, Version 15, SAS Institute Inc., Cary, NC, USA). The effect of salinity treatment on AGR, crude protein, Chla, Chlb, carotenoids and phenolic content was analyzed for each strain using one-way ANOVA with the different salinity treatments (5, 10, 15, 20, 30) as a five level, fixed factor. Significant differences among means were compared using Tukey's HSD test. All data were visuallyed for homogeneity and normality with diagnostic plots (density-, normality- and QQ-plots).

3 Results

3.1 Average growth rate (AGR) and crude protein content

After 8 weeks of exposure to different salinities, the AGR significantly ($p < 0.05$) differed among the salinity treatments in four (Fen30, Int30, Int9, Lin14) out of the eight tested *Ulva* strains (Table 2 and Figure 2) whereas no significant differences among salinities were observed in Lac30, Int14, Int7, Lin9. In Fen30, the AGR in the lowest salinity treatment, 5, was higher than in the other salinities (Figure 2A), and reached 17.7 %. In Int30, the highest salinity treatment (30) resulted in a lower AGR than the other salinity treatments (Table 2 and Figure 2C). Further, with decreasing salinity the AGR generally increased and algae grown at a salinity of five displayed an AGR of 15.7 % which was significantly higher than for algae grown at salinities of 15 and 20 (Table 2 and Figure 2C). Similarly, strain Int9 exposed to the lower salinity treatments (5 and 10) had higher AGRs compared to higher salinities (Table 2 and Figure 2E), and strain Lin14 also had a higher AGR (14.8 %) at five than at higher salinities (Table 2 and Figure 2G).

There was a significant difference in crude protein content, explained by differences in salinity levels, in five (Fen30, Int30, Int7, Lin14, Lin9) out of the eight strains (Table 2 and Figure 3). Furthermore, the crude protein content in most of the strains and treatments was notably higher after 8 weeks than at the start (t0) of the experiments (Figure 3A, C–H) although a decrease of crude protein content during the experiments was observed for strain Lac30 (Figure 3B). In Fen30 we detected significantly higher crude protein content in salinities of 5 (27.97 %) and 10 (27.28 %) compared to the higher salinity treatments of 15, 20 and 30 (<25.7 %) (Table 2 and Figure 3A). In Int30, the lowest crude protein content (22.13 %) was observed at highest (30) salinity treatment. The highest crude protein content for Int30 (26.87 %) was found at salinity 10 (Table 2 and Figure 3C). With decreasing salinity, the crude protein content of strain Int7 increased and algae treated with a salinity of five displayed the highest tissue crude protein concentration of 33.67 %, which also was the highest crude protein value measured within this study (Table 2 and Figure 3F). Similar observations were made for strains Lin14 and Lin9 in which crude protein content increased with decreasing salinity and the highest values were recorded at salinity 5 (Table 2, Figure 3G and H).

Overall, the trend of higher AGR and crude protein content in low salinity treatments was seen between species as well as at an intraspecific level and is widely displayed among the tested species and strains (Table 2, Figures 2 and 3). Significant results documented this phenomenon in at least half of the investigated strains, whereas a clear trend was observed in the full data set (Figures 2 and 3). Strain Lac30 was the most resilient to the salinity treatments and showed no significant differences in AGR or crude protein content (Table 2, Figure 2B, 3B).

Table 2: One-way ANOVA of A) average growth rate (AGR) (g), and B) crude protein (% DW), C) chlorophyll *a* (µg mg^{-1}), D) chlorophyll *b* (µg mg^{-1}), E) carotenoids (µg mg^{-1}), and F) phenolic content (µg mg^{-1}) of *Ulva* spp. after 8 weeks of culture at salinities of 5, 10, 15, 20, 30.

A) Average growth rate (g)						B) Crude protein (% DW)					
Sample ID	**Source of variance**	**DF**	**MS**	***F***	***p***	**Sample ID**	**Source of variance**	**DF**	**MS**	***F***	***p***
Fen30	AGR	4	0.260	4.293	***0.028***	Fen30	Protein	4	5.404	9.356	***0.002***
Lac30	AGR	4	0.095	0.824	0.539	Lac30	Protein	4	1.32	2.9	0.078
Int30	AGR	4	0.333	8.108	***0.004***	Int30	Protein	4	11.16	8.39	***0.003***
Int14	AGR	4	0.159	3.052	0.069	Int14	Protein	4	3.188	1.871	0.199
Int9	AGR	4	0.183	6.13	***0.009***	Int9	Protein	4	4.484	2.544	0.113
Int7	AGR	4	0.044	3.16	0.064	Int7	Protein	4	19.32	67.29	***0.0001***
Lin14	AGR	4	0.174	5.578	***0.013***	Lin14	Protein	4	19.73	26.11	***0.0001***
Lin9	AGR	4	0.027	3.006	0.072	Lin9	Protein	4	8.014	14.84	***0.0003***
C) Chlorophyll *a* (µg mg^{-1})						**D) Chlorophyll *b* (µg mg^{-1})**					
Sample ID	**Source of variance**	**DF**	**MS**	***F***	***p***	**Sample ID**	**Source of variance**	**DF**	**MS**	***F***	***p***
Fen30	Chla	4	0.003	0.28	0.884	Fen30	Chlb	4	0.315	15.45	***0.0003***
Lac30	Chla	4	0.041	5.35	***0.014***	Lac30	Chlb	4	0.015	1.954	0.1779
Int30	Chla	4	0.043	12.26	***0.001***	Int30	Chlb	4	0.123	11.8	***0.0008***
Int14	Chla	4	0.134	11.27	***0.001***	Int14	Chlb	4	0.02	0.843	0.5287
Int9	Chla	3	0.008	6.241	***0.017***	Int9	Chlb	3	0.276	8.391	***0.0075***
Int7	Chla	2	0.052	3.324	0.107	Int7	Chlb	2	0.109	1.498	0.2999
Lin14	Chla	4	0.008	0.467	0.759	Lin14	Chlb	4	0.015	0.727	0.5932
Lin9	Chla	4	0.077	3.484	***0.049***	Lin9	Chlb	4	0.068	2.585	0.1017
E) Carotenoids (µg mg^{-1})						**F) Phenolic content (µg mg^{-1})**					
Sample ID	**Source of variance**	**DF**	**MS**	***F***	***p***	**Sample ID**	**Source of variance**	**DF**	**MS**	***F***	***p***
Fen30	Carot	4	0.07	3.443	0.051	Fen30	Phenolic	4	0.002	0.936	0.482
Lac30	Carot	4	0.044	5.692	***0.012***	Lac30	Phenolic	4	0.001	0.782	0.562
Int30	Carot	4	0.134	27.18	***0.0001***	Int30	Phenolic	4	0.006	22.84	***0.0001***
Int14	Carot	4	0.06	4.176	***0.03***	Int14	Phenolic	4	0.002	3.041	0.07
Int9	Carot	3	0.064	9.595	***0.005***	Int9	Phenolic	3	0.002	7.954	***0.009***
Int7	Carot	2	0.059	7.902	***0.021***	Int7*	Phenolic	–	–	–	–
Lin14	Carot	4	0.03	1.31	0.331	Lin14	Phenolic	4	0.002	4.935	***0.019***
Lin9	Carot	4	0.164	3.919	***0.036***	Lin9	Phenolic	4	0.002	2.604	0.1

Significant *p*-values are indicated in bold and italics. Treatment means are shown in Figure 2. Asterisk (*) indicates data insufficiency to e.g. mortality.

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

There were no clear overall trends in pigment content nor in phenolic content in response to the salinity treatments (Table 2 and Figure 4).

3.2.1 Chlorophyll *a* (Chla)

There was a significant difference in chlorophyll *a* content observed in five (Lac30, Int30, Int14, Int9, Lin9) out of eight strains (Table 2 and Figure 4). In Lac30, the lowest salinity (5) resulted in significantly lower average Chla content (1.12 µg mg^{-1}) than the other salinity treatments (Table 2 and Figure 4B). Strain Int30 showed highest values in salinities 10 and 15 and the lowest value in 30 (Table 2 and Figure 4C). Strain Int14 had significantly higher Chla content in salinities of 20 and 30 compared to the other salinity treatments (Table 2 and Figure 4D). Strain Int9 showed a higher Chla content at 20 than at 5 and 10 (Table 2 and Figure 4E). Data on the highest salinity (30) treatment for this strain were not included in the statistical analysis because mortality reduced the number of replicates. The lowest Chla content in strain Lin9 was observed at salinity 15 whereas higher values were observed at both 5 and 30 (Table 2 and Figure 4H).

3.2.2 Chlorophyll *b* (Chlb)

There were significant differences in chlorophyll *b* content in only three (Fen30, Int30, Int9) of the eight strains (Table 2 and Figure 4).

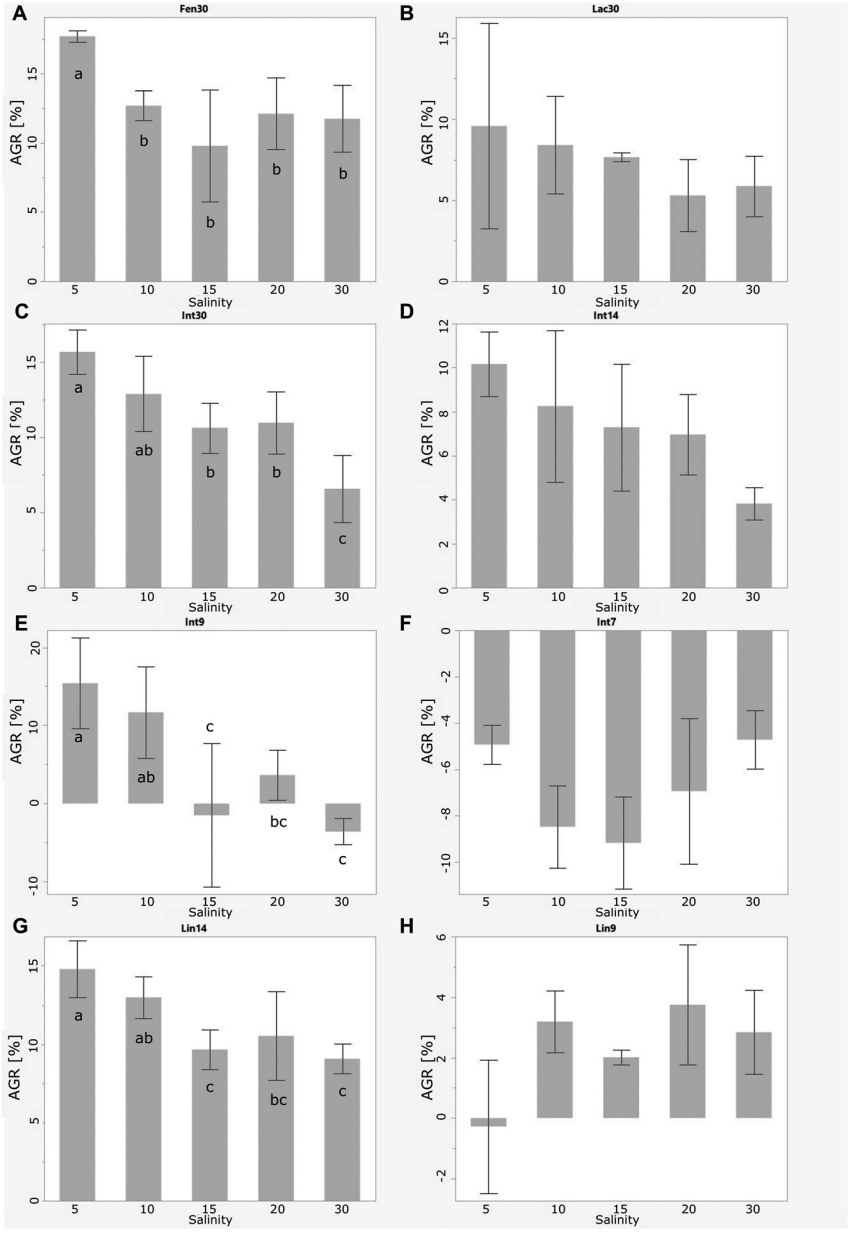


Figure 2: Effect of salinity treatments on the average growth rate (AGR; % change in FW) of different *Ulva* strains: (A) Fen30, (B) Lac30, (C) Int30, (D) Int14, (E) Int9, (F) Int7, (G) Lin14, and (H) Lin9 (see Table 1 for strain abbreviations) after 8 weeks of culture at salinities of 5, 10, 15, 20, and 30 (n = 3). Error bars show standard deviations and means labelled with different lower-case letters are significantly different at p = 0.05, based on Tukey's HSD test. Where no letters are shown, there were no significant differences for that strain.

In Fen30, the highest salinity (30) resulted in lower Chlb content than the other salinity treatments (Table 2 and Figure 4A). In Int30, the Chlb contents in salinities 10 and 15 were higher than in 5, 20 and 30 (Table 2 and Figure 4C), whereas strain Int9 had higher Chlb contents in salinities of 15 and 20 than in 5 and 10 (Table 2 and Figure 4E). Again, the highest salinity (30) treatment was not included in the statistical analysis for this strain due to lack of replicates.

3.2.3 Carotenoids

In six (Lac30, Int30, Int14, Int9, Int7, Lin9) out of eight experiments significant differences were observed in carotenoid content in response to the applied salinity regimes (Table 2 and Figure 4). Specimens of Lac30 treated with the lowest salinity (5) had a lower carotenoid content than all other salinity treatments (Table 2 and Figure 4B). In strain Int30, the lowest value was detected at the highest salinity (30) and the highest carotenoid contents were at 10 and 15 (Table 2 and Figure 4C). The differences were less pronounced in strain Int14 but the highest carotenoid contents were found at salinities 20 and 30 (Table 2 and Figure 4D). Salinities 15 and 20 resulted in a higher carotenoid content for strain Int9 than salinities of 5 and 10 (Table 2 and Figure 4E) but, again, the highest salinity (30) treatment could not be included in the analysis due to lack

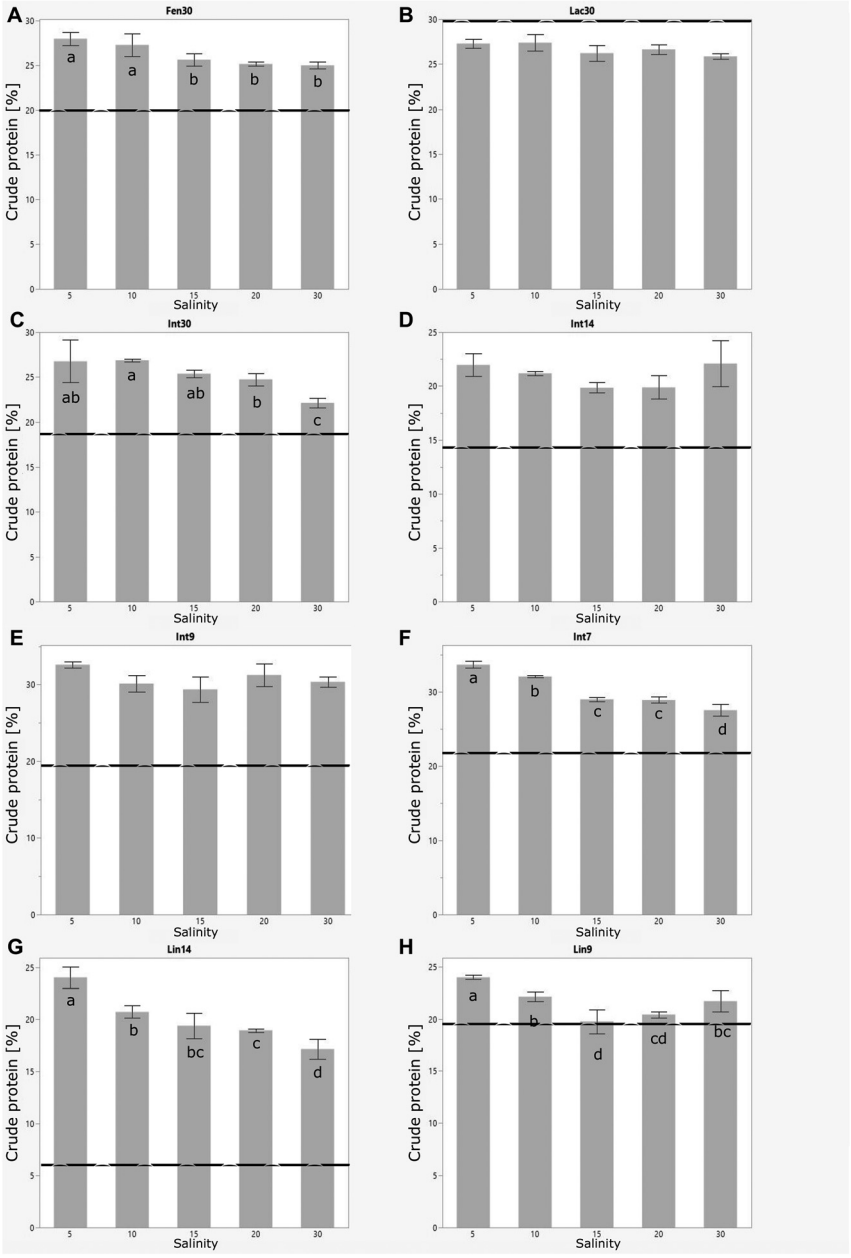


Figure 3: Effect of salinity treatments on the crude protein content (% DW; dashed line indicates protein content at t0) of different *Ulva* strains: (A) Fen30, (B) Lac30, (C) Int30, (D) Int14, (E) Int9, (F) Int7, (G) Lin14, and (H) Lin9 (see Table 1 for strain abbreviations) after 8 weeks of culture at salinities of 5, 10, 15, 20, and 30 (n = 3). Other details as Figure 2.

of replicates. Strain Int7 grown at salinity 20 had a higher carotenoid content than at 5 and 30 (Table 2 and Figure 4F) but there was mortality in the 10 and 15 salinity treatments and these results could not be included in the analyses. In strain Lin9, the carotenoid content at salinities of 5, 10 and 30 was higher than that at 15 and 20 (Table 2 and Figure 4H).

3.2.4 Total phenolic content

We detected significant differences in total phenolic content among the different salinity treatments in three (Int30, Int9, Lin14) out of the seven strains tested and analysed (Table 2 and Figure 5). Statistical analyses were not performed for strain Int7, because high mortality within the strain meant that there was insufficient sample replication.

In strain Int30, higher phenolic content was observed at salinities 10 and 15 than at other salinities, and the lowest phenolic content was at salinity 5 (Table 2 and Figure 5C). There were significant differences in the phenolic content of strain Int9 among the salinity treatments and the highest content was found at salinity 15 (Table 2 and Figure 4E), although the results for the highest salinity (30) treatment could not be analysed due to lack of replicates. For strain Lin14, the phenolic content at salinity 30 was lower than at all other salinities (Table 2 and Figure 5F).

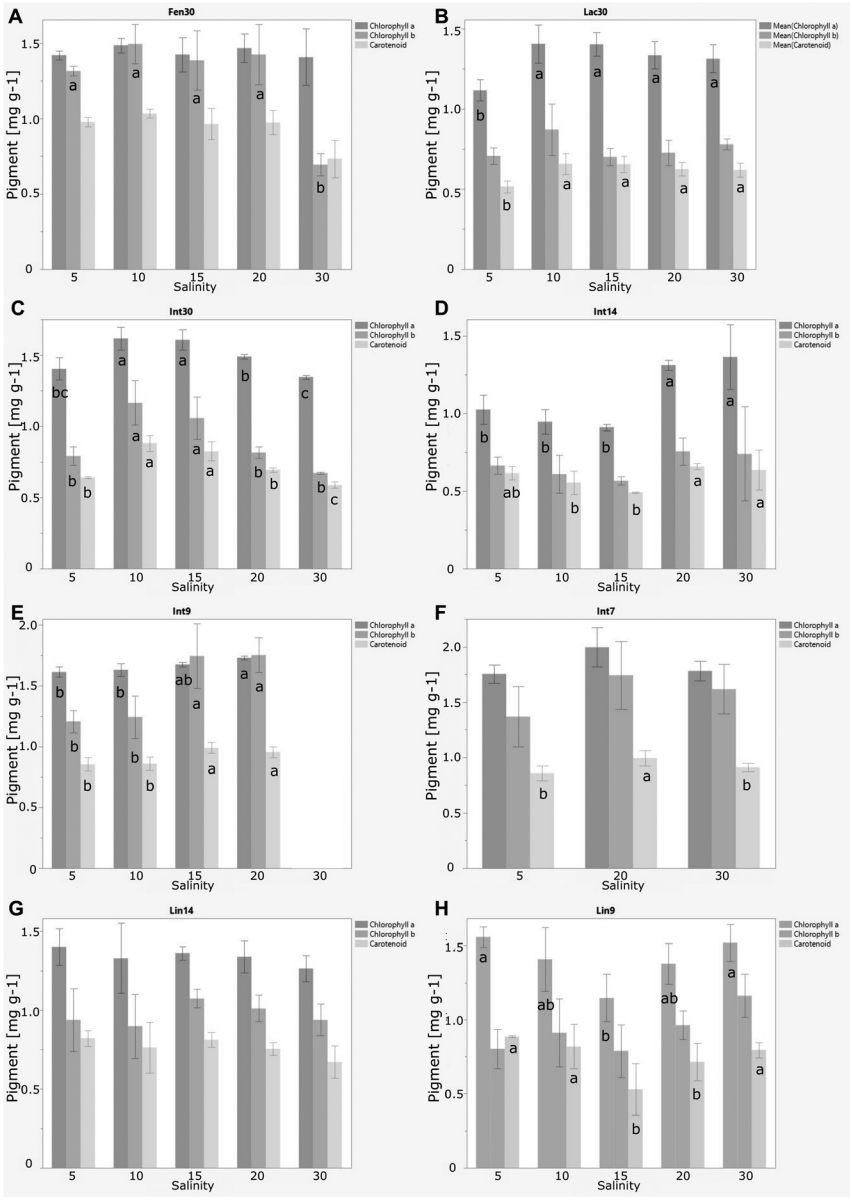


Figure 4: Effect of salinity treatments on the chlorophyll *a* (µg mg^{-1}), chlorophyll *b* (µg mg^{-1}), and carotenoid (µg mg^{-1}) content of different *Ulva* strains: (A) Fen30, (B) Lac30, (C) Int30, (D) Int14, (E) Int9, (F) Int7, (G) Lin14, and (H) Lin9 (see Table 1 for strain abbreviations) after 8 weeks of culture at salinities of 5, 10, 15, 20, and 30 (n = 3). Other details as Figure 2.

4 Discussion

Our study shows that low-salinity and brackish water environments hold great potential for the cultivation of various *Ulva* species and strains by simultaneously increasing high-value biochemicals which might be suitable both in future on-shore as well as sea-based cultivation systems. Applying long-term salinity treatments as a tool for strain selection and biomass optimization, we were able to document that optimization of certain functional traits and nutritional properties could be achieved. Notably, besides *Ulva* species originating from mesohaline water bodies (5–18) also strains originating from fully marine conditions (>30) showed significant positive response towards long-term low-salinity treatments on certain compounds – and in several cases also on total biomass yields. We incorporated diverse genotypes from various species and strains originating in the broader Baltic Sea region (including the Skagerrak), expanding our perspective to encompass strains and species from varied salinity environments. This approach enhanced our comprehension of the collective impact of prolonged salinity treatments and hence long cultivation periods in low salinity environments on *Ulva*.

Notably, previous studies have highlighted that certain *Ulva* species exhibit subtle morphological differences due to significant genetic variations, leading to pronounced

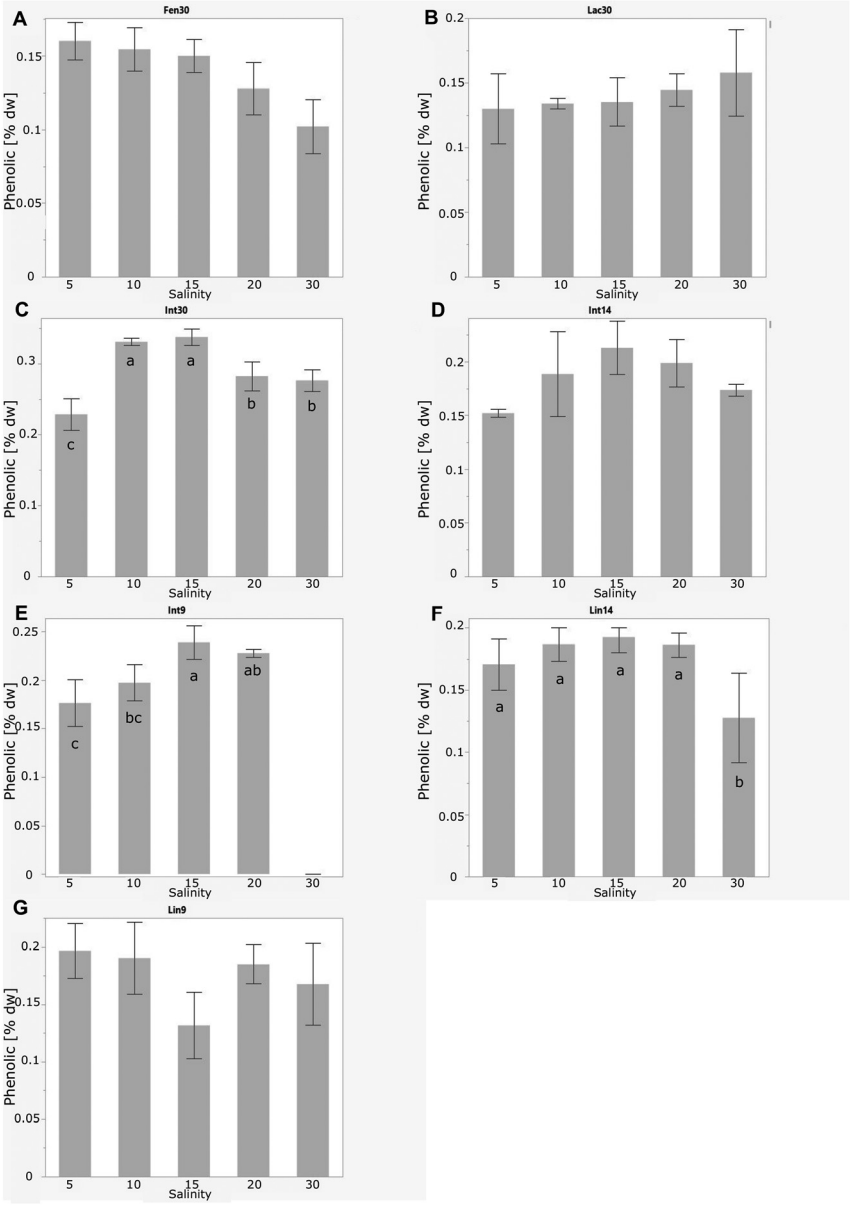


Figure 5: Effect of salinity treatments on the phenolic (µg mg^{-1}) content of different *Ulva* strains: (A) Fen30, (B) Lac30, (C) Int30, (D) Int14, (E) Int9, (F) Lin14, and (G) Lin9 (see Table 1 for strain abbreviations) after 8 weeks of culture at salinities of 5, 10, 15, 20, and 30 (n = 3). Other details as Figure 2.

variations in growth rate and metabolic composition (Fort et al. 2024). Under standard euhaline conditions it was observed that *Ulva* species display distinct differences in growth patterns, fatty acids, and lipid profiles, with short-term salinity treatment exerting a pronounced Genotype × Environment interaction (Fort et al. 2024). In addition to interspecific variation in performance and biochemical composition, intraspecific factors such as the life-history phase have been identified to significantly define the performance of *Ulva* (Steinhagen et al. 2022a). Together with our study, this highlights the necessity of precise species selection for economically viable mass cultivation of *Ulva* as a commercially viable food source, emphasizing the importance of understanding the cellular, molecular, and metabolic changes triggered by treatments of varying abiotic factors.

Additionally, it is pertinent to emphasize the significance of exploring brackish environments, given that the majority of algal aquaculture predominantly occurs in fully marine conditions. Therefore, our study provides crucial insights into algal aquaculture in the Baltic Sea and its establishment as a novel farm ground. Further, whereas on-shore facilities such as recirculating aquaculture systems (Cardoso et al. 2023) provide highest quality control, maintenance costs are high. Using selected strains adapted to low-salinity, as shown in our study, could reduce production costs and improve the economic feasibility by minimizing e.g. the environmental impact of water

disposal by lowering salt concentration and desalination expenses in nursery and on-shore facilities (Cardoso et al. 2023).

Although our study underlines and confirms inter-as well as intraspecific differences in valuable biochemicals with nutrient, pigment and antioxidant functions depending on salinity regimes, we furthermore point out that, overall, a similar trend of the effect of low-salinity long-term treatments on certain variables (e.g. the protein content) was observed across the investigated strains. The single effects will be discussed in detail below whereas limitations and future perspectives are discussed in detail within the next section.

4.1 Average growth rate

Generally, in most of the investigated species and strains we found a positive AGR in all tested salinity regimes. Notably, deleterious impacts of low salinity on growth in foliose *Ulva* species has been previously documented in different studies (Angell et al. 2016; Fort et al. 2024; Lu et al. 2006). Especially in mesohaline environments below salinities of 15, a significant decrease in growth rate was observed in various foliose *Ulva* species (*U. australis*, *U. lacinulata*, *U. lactuca*, *U. ohnoi*), suggesting a similar inhibitory mechanism in growth by low-salinity treatments in euhaline species (Angell et al. 2016; Fort et al. 2024; Lu et al. 2006). Our experiment, using long-term salinity exposure, however, documented that various genotypes, originating from an environments over a wide salinity range, such as the Baltic Sea (Reusch et al. 2018), performed significantly better in the lowest salinity treatment (5) than at higher salinity levels – independent of the strain's original salinity (euhaline or mesohaline). It should be mentioned that detrimental effects of salinity treatments <10 were observed in only two (Int7; Lin9) out of the eight tested strains, such effects were not found to be species specific and the overall performance of strains was generally very low compared to the other strains. Nevertheless, such data underlines that genotype specific differences towards changing abiotic factors need to be distinctively monitored and that rather large screenings of many different strains are favorable to find best performing genotypes in dependence of the cultivation environment. As discussed in previous studies, varying growth rates likely have metabolic implications (Fort et al. 2024) and could be causal for variations in the nutritional content of *Ulva* biomass. Therefore, intricate connections between low salinity and its effects on growth necessitate further comprehensive investigation of the physiology and metabolic pathways to find causative mechanisms for the differences observed. It can however be summarized that genotypes originating from the wider Baltic Sea area seem to be capable to tolerate changing salinities whereas especially the low salinity treatments seem suitable for growth optimization and can contribute to the optimization of industrial cultivation protocols.

4.2 Crude protein

A notable shift in dietary patterns is observed, with a discernible move away from red meat consumption towards green and blue protein sources and this transition aligns with burgeoning concerns over environmental sustainability and the ecological footprint associated with livestock farming (Eckl et al. 2021; Wickramasinghe et al. 2021). Seaweeds, as marine macrophytes, present a possible compelling alternative as blue-green protein sources, offering an interesting nutrient profile while minimizing environmental impact (Juul et al. 2024; Samarathunga et al. 2023; Stedt et al. 2022a,b). Additionally, the increasing trend towards vegetarianism and veganism as well as the consumption trends of alternative protein sources predicted to increase by 9 % annually until 2054 (Probst et al. 2015), underscore the urgency of exploring novel vegan protein sources beyond over-exploited terrestrial options (Juul et al. 2024; Van den Boom et al. 2023; Wickramasinghe et al. 2021). Seaweed's capacity to thrive in marine environments, coupled with their possibilities to attain protein contents similar to soy (Stedt et al. 2022a), positions them as promising candidates in a more diversified future food protein portfolio. Enhancing the downstream applications of seaweed proteins is paramount, and the refinement of novel protein extraction methodologies holds promise in achieving this objective (Juul et al. 2021, 2022; Trigo et al. 2021, 2024). By extracting the proteins, their purity, digestibility, taste and functionality can be enhanced (e.g. Trigo et al. 2021), expanding the potential applications of seaweed proteins in various products. However, it is imperative to underscore that the ultimate efficacy of downstream applications significantly hinges upon optimizing and increasing the intrinsic protein content within the seaweed biomass itself. Elevating protein content at the source ensures a more abundant and sustainable raw material for extraction, thus amplifying the overall efficiency and economic viability of seaweed protein utilization.

Our study has documented that salinity-induced alterations in crude protein content occur in *Ulva* spp., revealing a consistent trend of increased crude protein contents with decreasing salinity independent of species and strain origin. Across eight experiments, including different species and strains, five strains had their highest average crude protein content at the lowest salinity level of five.

Furthermore, it is noteworthy that the crude protein contents measured in the examined strains of this study were generally higher – especially in specific strains exposed to lower salinity treatments – when compared to previously reported protein values documented in both natural (4.8–8.2 %; Olsson et al. 2020a) and cultivated (4.67–20.79 %; Steinhagen et al. 2021, 2022a, b) *Ulva* biomass within the wider Baltic Sea region. Further, in seven out of eight experiments the crude protein content was higher in all salinity treatments than at the starting point. Our measured crude protein values, generally falling within the upper range reported for *Ulva* (Hofmann et al. 2024; Holdt and Kraan 2011), provide additional support for the impact of salinity treatments to be used in biochemical engineering endeavors for protein-enriched *Ulva* biomass. Moreover, our results suggest the viability of cultivating *Ulva* in low salinity environments, including fjords, estuaries, and the Baltic Sea. This expands the potential cultivation sites to brackish-water inland streams, and utilizing low-salinity environments in on-shore facilities may offer a cost-effective strategy for *Ulva* cultivation (Cardoso et al. 2023), particularly noteworthy as most current commercial *Ulva* farming is predominantly conducted in fully marine habitats (e.g. Bolton et al. 2009; Califano et al. 2020; Ghaderiardakani et al. 2019; Steinhagen et al. 2021). This approach furthermore has the potential to expand the cultivation of *Ulva* for *in-situ* bioremediation and nutrient capture in low salinity environments and further enables the reuse of nutrient-rich side streams from agriculture and industry (Sode et al. 2013; Stedt et al. 2022a,b).

A plausible rationale for the observed higher crude protein content at lower salinity levels may stem from the potentially increased nitrogen uptake rates exhibited by these species in environments with reduced salinity compared to higher salinity conditions. While scant research has delved into the impact of salinity on nutrient uptake in seaweeds (Roleda and Hurd 2019), conclusive attribution of our results to salinity-induced changes in uptake rates remains challenging. Nevertheless, Wu et al. (2018) noted a significant increase in nitrate uptake rates in *U. prolifera* at 5–15 compared to 20–50, concomitant with a decrease in tissue nitrogen content as salinity rose. In another study, Cohen and Fong (2004) hypothesized that the salinity tolerance of *U. intestinalis* could be linked to its adept nitrate uptake for osmoregulation. Substantiating this as an explanation for the observed crude protein content pattern would however necessitate further causal driven investigations.

Unexpectedly, no discernible parallels are evident between the patterns observed for crude protein and pigment content. While prior research has noted color variations in *Ulva* thalli in response to changes in biomass nitrogen content (Robertson-Andersson et al. 2009), a recent study by Stedt et al. (2022c) demonstrated the accurate estimation of nitrogen content in euhaline *U. fenestrata* through color image analysis. The absence of a clear relationship between protein content and pigment content in the strains tested here was unexpected.

4.3 Pigments and total phenolic compounds

Pigments and phenolics play crucial roles in the biology of seaweeds, contributing to various physiological functions and ecological adaptations. Pigments, such as chlorophylls, carotenoids, and phycobilins, are essential for photosynthesis, and hence for converting light energy into chemical energy (Harrison and Hurd 2001; Ramus et al. 1976) – therefore directly affecting the biochemical set-up of a seaweed. Carotenoids, on the other hand, aid in photoprotection by dissipating excess light energy and scavenging reactive oxygen species (Eismann et al. 2020). Phenolics, a group of secondary metabolites, serve multiple functions in seaweeds, including defense against herbivores, protection against UV radiation, and modulation of cell wall properties (Cotas et al. 2020; Farvin and Jacobsen 2013). These compounds possess antioxidant properties, helping to mitigate oxidative stress induced by environmental factors (Cotas et al. 2020). The intricate interplay of photosynthetic pigments and phenolics in seaweeds underscores their adaptive strategies towards changing biotic and abiotic factors and ecological significance. Increasing interest from economic sectors has arisen for seaweed derived pigments and phenolics as they find application in e.g. the pharmaceutical, cosmetic, and functional food industries.

Our study documented that, in terms of pigment and phenolic content, no discernible trend analogous to that observed for crude protein content or growth is evident. There was an absence of a definitive correlation between pigments and salinity that reflects across the investigated species and strains, with no consistent pattern of increase or decrease noted.

In the salinity regimes of 5–10, Chla content ranged from 0.94 to 1.75 μg mg^{-1} and Chlb content varied between 0.60 and 1.55 μg mg^{-1}, falling within the anticipated range based on previous findings (Holdt and Kraan 2011; Steinhagen et al. 2021, 2022a, b). The carotenoid content ranged from 0.51 to 0.99 μg mg^{-1} and was therefore within the expected range of carotenoids in *Ulva* spp. (Steinhagen et al. 2021, 2022a, b).

Although, significant differences were observed between different salinity treatments, the overall effect was rather small and values observed for pigments and phenolics at

both inter- and intraspecific levels resemble previous findings and no distinct detrimental effects of varying salinity towards the pigment and phenolic composition of tested genotypes were observed. It requires further investigation if the photosynthetic apparatus and associated pigments of Baltic Sea strains are generally better adapted to salinity fluctuations, as previous studies have reported that e.g. in *Ulva prolifera*, photosynthetic rates decreased at low salinity, together with increased signs of oxidative stress (Luo and Liu 2011; Xiao et al. 2016). Further, *U. australis* exposed to short-term low salinity treatments accumulated higher amounts of photosynthetic pigments (Kakinuma et al. 2006). It should however be mentioned that our experiments were performed over a course of 8 weeks, whereas most previous work has investigated short-term effects of low-salinity treatments in *Ulva* (Fort et al. 2024; Kakinuma et al. 2006; Luo and Liu 2011; Xiao et al. 2016). It remains to be determined what effect the time of exposure has and whether euhaline *Ulva* strains might adjust as well over a longer course of treatment exposure.

Regarding the phenolic content, no discernible salinity-dependent trend was evident, indicating variability in phenolic acid content responses across *Ulva* species and strains. The phenolic content in the lower salinity range falls between 0.13 and 0.33 % of dry weight, aligning with previously reported values (Steinhagen et al. 2021, 2022a, b; Toth et al. 2020). Although this study did not observe values surpassing the expected range, it does not preclude the potential extraction of phenolics from *Ulva* biomass cultivated in low-salinity environments, hinting at potential economic value. It should however be mentioned that phenolic compounds are often regarded as anti-nutritional factors due to their ability to interfere with nutrient absorption and digestion (Bora 2014). These compounds can form complexes with proteins, carbohydrates, and minerals, reducing their bioavailability (Bora 2014). Further emphasis needs to be put into the downstream application of *Ulva* biomass used in food and feed stuffs. However, overall, our observed pigment and phenolic values in Baltic Sea strains of *Ulva* suggest commercial viability, indicating that the lower salinity environment prevalent in the wider Baltic Sea does not impede the exploitation of such compounds for potential commercial applications.

It is noteworthy to emphasize that, apart from specific photosynthetic pigments, the salinity treatments did not have a significant effect on the investigated variables in *U. lacinulata* (Figure 2B, 3B) suggesting that this is a resilient species with relative stability in response to changing abiotic factors such as salinity. Previous studies have underscored this phenomenon of stable performance in *U. lacinulata*, indicating similar reactions among different genotypes originating from various regions across Europe (see also Cardoso et al. 2023; Fort et al. 2024). Despite being frequently employed as a commercial crop species (Bachoo et al. 2023; Califano et al. 2020), *U. lacinulata* exhibits a proclivity for sudden biomass disintegration events, necessitating meticulous monitoring for its cultivation in aquaculture settings.

5 Limitations and future perspective

This study provides valuable insights into the aquaculture of *Ulva* spp. in low salinity environments, highlighting several promising areas for future research. One area is improving our understanding of the relationship between fresh weight (FW) and dry weight (DW) ratios in *Ulva* biomass, especially in studies such as the present one in which different salinities might influence osmolyte activity, cell water content, or excess water. Although, FW measurements were used for long-term monitoring in this study, further research could explore the specific contributions of different water sources to mass variability. A particular focus could be placed on the influence of surface-bound excess water as well as intracellular water content, which we hypothesize could be a major source of variation. Investigating these factors in controlled aquaculture settings may provide deeper insights into how environmental conditions impact water retention and biomass growth. While FW assessments were essential for continuous monitoring in this study and allowed for an extended experimental phase of 8 weeks, future work could incorporate DW-based assessments in short-term experiments to obtain more precise data on biomass accumulation under varying salinity conditions. This approach would provide a more detailed understanding of *Ulva*'s growth dynamics and resilience in low salinity environments, paving the way for optimized cultivation practices.

Another promising area for future research is the refinement of protein content estimation methods for *Ulva* under various environments. Our study utilized nitrogen-based calculations, yet it is well established that the use of a universal conversion factor can lead to inaccurate protein estimates (Shuuluka et al. 2013), especially given the variability across seaweed species (Biancarosa et al. 2017). To exclude an overestimation of the crude protein content with the traditional conversion factor of 6.5 (Biancarosa et al. 2017) as well as with the more moderate conversion factor of 5.45 (Shuuluka et al. 2013), however, we applied the updated nitrogen to protein conversion factor 5 (Angell et al. 2016), which is in better agreement with nitrogen to protein conversions in *Ulva* species (Stedt et al. 2022c). However, future

studies could additionally employ amino acid profiling to achieve more accurate and species-specific protein content data and profiles. This would provide valuable information on the nutritional and biochemical properties of *Ulva* biomass originating from different environments, particularly under varying salinity conditions. Moreover, research into the nitrate storage capacity of *Ulva*, particularly in response to salinity fluctuations, could shed light on the relationship between stored nitrate and protein synthesis. *Ulva* species are known to store nitrate as an osmolyte in vacuoles, but this stored nitrate might not always be assimilated into proteins or amino acids (Lartigue et al. 2003; Xing et al. 2021). Exploring these nitrate dynamics could help clarify whether changes in measured protein content reflect actual increases in protein levels and detect potential shifts in nitrate storage. Further investigations should also focus on osmolyte production, especially the role of amino acids such as proline in response to salinity stress (Xing et al. 2021). Previous observations suggest that osmolyte production can significantly increase in response to environmental stressors such as temperature, with increases up to tenfold (Ghaderiardakani et al. 2022). Extending this research to salinity stress could reveal important biochemical adaptations that support *Ulva* cultivation in low-salinity aquaculture systems. Understanding these adaptive responses is essential for optimizing growth conditions and improving the overall yield and biochemical profile of seaweed biomass.

To achieve a more comprehensive understanding of the intra- and interspecific variation in *Ulva* species, it is essential to screen a broader array of strains from both local and non-local populations. Our research has shown that *Ulva intestinalis* and *Ulva linza*, which naturally occur in the low-salinity waters of the Baltic Sea, exhibit strong potential as future crop strains due to their adaptability and resilience in such environments. However, it is equally important to investigate the cultivation potential of *Ulva* species that are not typically found in low-salinity ecosystems, such as those from marine environments. These species may still perform well under controlled conditions in on-shore cultivation systems, where salinity and other growth parameters can be optimized. By broadening the scope of species and strains tested, we can better identify candidates for sustainable seaweed production across diverse environments, both in natural habitats and engineered aquaculture systems.

Hence, the observations presented in this study serve as preliminary indications and highlight potential trends that warrant further investigation. However, these findings offer only a snapshot of a complex system and should not be generalized across all contexts. Specific to aquaculture, environmental and operational factors can vary significantly, suggesting that these results may differ under natural farming conditions in the Baltic Sea region. Therefore, additional large-scale studies, particularly those conducted in actual aquaculture settings, are essential to validate these initial results and understand their broader applicability.

6 Conclusions

The establishment of new farm grounds for expanding seaweed aquaculture, particularly within low salinity and brackish water ecosystems, is imperative for advancing sustainable aquaculture practices, and fostering the development of novel crop species. The world's largest brackish water body, the Baltic Sea, with its unique environmental conditions and abundant resources, emerges as a particularly valuable waterbody, offering substantial potential for future farming endeavors in nine bordering countries, which has not yet reached full potential. This study reports on the use of long-term low-salinity treatments to modify the average growth rate, crude protein, pigment, and phenolic content of eight genotypes of different *Ulva* species originating from the wider Baltic Sea area. Interestingly, our study points out that the biomass concentrations of targeted valuable compounds can be significantly altered with salinity treatments and that especially low-salinity (<10) treatments seem favorable for strains originating from the wider Baltic Sea area to increase desired biochemicals such as crude protein as well as growth rates. The distinct alteration and effect sizes were however found to remain genotype dependent, which underlines the necessity for detailed screenings of future aquaculture strains.

Acknowledgments: The authors want to thank the FORMAS-funded projects 'A manual for the use of sustainable marine resources' (Grant no. 2022–00331) and BlueGreen (Grant no. 2021-02340) as well as the ULTFARMS project (Grant no. 101093888), funded by the European Union, for financial support. Additionally, the authors thank the COST Action CA20106 "Tomorrow's wheat of the sea': *Ulva*, a model for an innovative mariculture", supported by COST (European Cooperation in Science and Technology, www.cost.eu) for their support of the here presented work. Further, we thank Katharina Romoth (Leibnitz Institute for Baltic Sea Research Warnemünde), Eva Strothotte and Tim Staufenberger (both FuE-Zentrum FH Kiel GmbH) for support during sample provision.

Research ethics: Not applicable.

Informed consent: Not applicable.

Author contributions: The authors have accepted responsibility for the entire content of this manuscript and

approved its submission. Conceptualisation: SST and IJ; data curation: SST and IJ; formal analysis: SST, IJ, KL, and SE; funding acquisition and supervision: SST, IU, and GT; writing original draft: SST and IJ; writing – review and editing: SST, IJ, KL, SE, IU and GT.

Use of Large Language Models, AI and Machine Learning Tools: Not applicable.

Conflict of interest: The authors declare that they have no conflicts of interest regarding this article.

Research funding: This study was supported by the Swedish Government Research Council FORMAS ('A manual for the use of sustainable marine resources', grant no. 2022-00331; BlueGreen grant no. 2021-02340). Furthermore, this project received financial support from the ULTFARMS project funded by the European Union (grant no. 101093888).

Data availability: Not applicable.

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