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From waste to value: cultivating *Palmaria palmata* in liquid seafood side stream enhances its growth and nutritional composition

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ABSTRACT

The red seaweed *Palmaria palmata* is a promising candidate for sustainable food production due to its unique nutritional and sensory properties. Using side streams from the seafood industry to cultivate seaweed is an innovative circular approach to return otherwise lost nutrients back into the food chain. Our study investigates the use of herring production process water (HPPW) as a cultivation medium to improve the growth and nutritional quality of *P. palmata* in land-based systems. We identified the most favorable salinity and irradiance conditions (22.5PSU and 180 μmol photons m^{-2} s^{-1}) as well as the dilution level of HPPW (40 μM NH_4^+) to establish optimal cultivation conditions. When *P. palmata* was cultivated under these optimized conditions, it significantly improved growth rates, tissue nitrogen content, pigments, and total amino acid levels, including all essential amino acids in levels exceeding dietary recommendations. The toxic and potentially toxic elements arsenic, inorganic arsenic, mercury, lead, and cadmium did not limit the safe daily intake of the biomass, instead, iodine was the limiting factor restricting safe daily consumption of HPPW-cultivated *P. palmata* to 23 g dry weight. A portion of this size could make a valuable contribution to macro- and trace element intake, providing approximately 63 % of the recommended daily intake for potassium, 22 % for magnesium, and 17 % for copper. Together, these findings show that *P. palmata* has a strong potential as an alternative food source in sustainable food systems when cultivated under optimized land-based conditions and supplemented with repurposed liquid seafood industry side streams.

1. Introduction

Global food production places a significant strain on the environment by contributing to nearly half of all arable land use, consuming large volumes of freshwater, and accounting for over 25 % of all greenhouse gas emissions and nitrogen pollution [1,2]. At the same time, the growing global population continues to increase the demand for nutritious food [3]. In this context, seaweed aquaculture emerges as a promising alternative as seaweeds can be cultivated without using freshwater, fertilizer, or arable land while offering essential nutrients for human consumption [1,4–7]. Recently, the European Union recognized seaweeds as an essential source of alternative proteins, contributing to the development of sustainable food systems and global food security [8].

The red seaweed *Palmaria palmata* is a particularly promising species for human consumption thanks to its unique nutritional and sensory profile [6,9,10]. Red seaweeds generally have higher protein content than brown and green seaweeds [11]. In *P. palmata*, protein levels typically range between 7 and 19 % dry weight (dw), comprising high-quality protein with amino acid profiles often superior to many of its terrestrial counterparts [6,12–15]. Furthermore, *P. palmata* contains the light-harvesting pigments chlorophyll *a*, carotenoids, and phycobiliproteins [16]. These pigments offer potential health benefits for humans due to their antioxidant and anti-inflammatory properties [17,18]. Consequently, interest in these seaweed-derived compounds is growing from the pharmaceutical, cosmetic, and functional food industries.

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Seaweeds contain many essential minerals like iodine, potassium, iron, and zinc [9]. In many parts of the world, there is a deficiency of iodine, which is important for the human thyroid to function [6,19], and consuming seaweeds could help counteract this global health challenge [20]. However, high levels of iodine in some seaweeds could result in toxic health effects if overconsumed [20–22]. The risk of excess iodine intake is, however, lower for red seaweeds, with *P. palmaria* being reported to have over 100 times less iodine than some widely consumed kelp species [21,23]. Due to seaweeds' high capability to accumulate elements, there is also a concern for high levels of toxic elements (often including heavy metals) in the biomass [24,25]. The content of toxic elements is influenced by multiple factors, including age and morphology of the seaweeds, as well as environmental and cultivation conditions [26–28]. Consequently, when exploring seaweeds as a potential food source, it is essential to closely monitor potential toxic elements in the biomass [25]. Similar to toxic elements, the quality and composition of biochemicals in *P. palmata* are strongly influenced by the conditions under which it grows [14].

Cultivating seaweeds in land-based systems offers increased control over environmental abiotic factors like light, temperature, salinity, and nutrients [29–31]. Moreover, the perennial traits of *P. palmata*, together with its meristematic cells that support continuous vegetative growth, enable long-term tank cultivation and make year-round harvesting possible [14,32]. This could act as a complement to ocean-based tetraspore-reliant seeding practices, which so far have proven commercially challenging due to the species' complex life cycle [30,32].

The potential to improve the nutritional quality of seaweeds by manipulating growing conditions in land-based systems is a promising cultivation strategy. For example, increasing the nitrogen availability for seaweeds increases their protein content, as nitrogen is a major protein component [33–35]. A higher accumulation of phycobiliproteins in *P. palmata* has also been associated with increasing nutrient availability [36,37]. Achieving higher protein yields at the cultivation stage could contribute to more effective downstream applications in the food value chain and increase the competitiveness of *P. palmata* in the current protein market.

One promising approach to achieving this is systems like integrated multi-trophic aquaculture (IMTA), where seaweeds are typically co-cultivated with fed aquaculture species to utilize the nutrient-rich effluents from the farms [4,38]. This approach has also proven effective for *P. palmata* when cultivated in outlet water from fish farms [39–41]. Likely, other liquid side streams from the food industry could, in a similar way, be used for this purpose. For example, it is estimated that approximately $7m^3$ of water is used per ton of final product when producing marinated herring, from catch to final packaging [42,43]. In previous studies, we showed that these marinated herring production process waters can efficiently be used to boost growth rates by 342–505 % and crude protein content by 146–261 % of the green seaweed *Ulva fenestrata* compared with controls [44,45]. Since the process waters are rich in nutrients like nitrogen and phosphorus, with particularly high levels of ammonium (NH_4^+) [45], the preferred nitrogen source for *P. palmata* [14], we hypothesized that these waters can be effectively used for *P. palmata* cultivation. Repurposing the process waters as a cultivation medium for seaweeds helps bridge the food waste gap while simultaneously creating a new valuable product in the form of seaweed biomass [35,44,46–48].

The aim of this study was to investigate the potential of herring production process water (HPPW) to enhance the growth and nutritional quality of the red seaweed *P. palmata* for use as a safe and nutritious food source. To achieve this, we performed a set of experiments with the objectives to (i) find the optimal salinity and irradiance levels in land-based cultivation for growth and biochemical composition of *P. palmata*, (ii) find the optimal dilution level of HPPW for *P. palmata* cultivation, and (iii) investigate how the optimal salinity and irradiance levels, together with the optimal dilution level of HPPW, impact the growth and biochemical composition of *P. palmata*. We did this in three separate experiments, where the results from the first and second experiments facilitated the setup for the third experiment. We measured growth, tissue nitrogen content, amino acid composition, pigments (chlorophyll *a*, carotenoids, phycobiliproteins), and total elements in the cultivated biomass. Additionally, we investigated how the levels of some health-concerning toxic and potentially toxic elements and species, namely arsenic (As), inorganic arsenic (iAs), mercury (Hg), lead (Pb), and cadmium (Cd), as well as iodine (I), in the biomass were affected by cultivation in HPPW, and calculated the consumption limit for safe daily intakes. Based on this limit, we estimated the contribution of *P. palmata* cultivated with HPPW to the recommended daily intake (RDI) for some essential elements, namely calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), molybdenum (Mo), selenium (Se), and zinc (Zn).

2. Materials and methods

Palmaria palmata was collected by diving in the Koster archipelago on the Swedish west coast (N 58.838166, E 11.042859) on the 7th of February 2024 and brought to Tjärnö Marine Laboratory (TML, N 58.875759, E 11.146216). At TML, the *P. palmata* were cultivated by vegetative propagation in a greenhouse in aerated tanks following the seasonal variations in temperature and light on the west coast of Sweden. For the experiments, vegetative fronds from marginal proliferations on thalli of *P. palmata* were collected from a 1000 L aerated cultivation tank with a flow-through of filtered (0.2 μm) deep-seawater (40 m, 33PSU) at 18-22 L min^{-1}.

2.1. Effect of salinity and irradiance

Fronds of *P. palmata* (19.8 ± 5.3 cm^2, mean ± SD) were collected from the 1000 L tank on the 16th of July 2024 and divided between 2 L tanks at a density of 2.5 g fresh weight (fw) L^{-1}. In a fully crossed factorial design, the effect of salinity (7.5, 15, 22.5, and 33PSU) and irradiance (20, 80, and 180 μmol photons m^{-2} s^{-1}, light cycle: 16:8 h L:D, light source: Samsung LED24W, 6000 K, 3000 lm) was tested on the growth rate and biochemical composition of the *P. palmata*. Each treatment had eight replicates, resulting in 96 tanks. The different salinity levels were achieved by mixing deep-seawater (40 m, 33PSU) with fresh water in header tanks and then supplied to the different treatments, while irradiance was manipulated by shading the tanks with plastic netting until the desired irradiance was achieved. Aeration was provided from the bottom of the tanks to create water motion. All tanks were randomly placed in the cultivation area to avoid spatial bias. Salinity, temperature, and pH were measured daily using a multimeter (WTW Multi 3620 IDS, Xylem Analytics). The salinity in the different treatments was 7.5 ± 0.9, 15.2 ± 0.8, 22.5 ± 0.7, and 32.9 ± 0.3PSU, and the temperature and pH were 15.8 ± 0.7 °C and 7.93 ± 0.05 across the treatments (mean ± SD) during the experiment. The experiment lasted for three weeks, and on the last day, samples for growth, tissue nitrogen content, and pigments (chlorophyll *a*, carotenoids, phycobiliproteins) were collected.

2.2. Cultivation with herring production process water (HPPW)

In the next experiments, HPPW was tested as a cultivation medium for *P. palmata*. To find an optimal level of the HPPW for *P. palmata* cultivation, a dilution experiment was first performed.

The HPPW used in the experiment was collected in a food-grade state and originates from in-house storage of whole herring in 3 % sodium chloride at a primary industrial processor (Sweden Pelagic AB, Ellös, Sweden). Detailed information about the HPPW can be found in Stedt et al. [45]. After collection, the HPPW was filtered to remove coarse particles (>300 μm) and stored at −60 °C. The ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), and inorganic phosphorus/orthophosphate (PO_4^{3-}) content was analyzed for HPPW and deep-seawater using a

continuous segmented flow analyzer (QuAAtro 39 AutoAnalyzer, SEAL analytical Inc.) with detection limits at 0.04 μM for NH_4^+, 0.15 μM for NO_3^-, 0.05 μM for NO_2^-, and 0.07 μM for PO_4^{3-} (Table 1) after filtration through a 0.45 μm sterile syringe filter.

2.2.1. Effect of dilutions of HPPW

The HPPW was diluted with filtered (0.2 μm) deep-seawater (40 m, 33PSU) to nine different concentrations based on the ammonium (NH_4^+) concentration (0, 2.5, 5, 10, 20, 40, 80, 160, and 320 μM NH_4^+). Each treatment was replicated four times in 0.5 L tanks with one blade of *P. Palmaria* (11.2 ± 4.0 cm^2, mean ± SD) per tank (2.0 g fw L^{-1}) at 11 °C, under 12:12 h (L:D) light cycle, and at an irradiance of 50 μmol m^{-2} s^{-1} (light source: INDY66, LED60W, 4000 K, 6000 lm). Aeration was provided from the bottom of the tanks to create water motion. All tanks were randomly placed in the cultivation area to avoid spatial bias. The tanks were cleaned, and the HPPW was renewed every third day to avoid nutrient depletion and microbial spoilage. The experiment started on the 14th of November 2023 and lasted two weeks, after which samples for growth and tissue nitrogen content were collected.

2.2.2. Effect of nutrient additions

Fronds of *P. palmata* (15.8 ± 3.0 cm^2, mean ± SD) were collected from the 1000 L tank on the 1st of October 2024 and divided between 15 L tanks at a density of 2.5 g fw L^{-1}. Based on the optimal cultivation conditions from the previous experiments, the effect on growth rate and biochemical composition was tested at four different nutrient treatments (Table 2) at an irradiance of 180 μmol photons m^{-2} s^{-1} (light source: Samsung LED24W, 6000 K, 3000 lm), under 16:8 h (L:D) and a salinity of 22.5PSU. Each treatment had six replicates, resulting in 24 tanks. The salinity level was achieved by mixing deep-seawater (40 m, 33PSU) with fresh water in header tanks and then supplied to the different treatments at a constant flow of 0.6 L min^{-1}. Aeration was provided from the bottom of the tanks to create water motion. The treatments included tanks supplied with either (1) HPPW diluted to 40 μM NH_4^+ (HPPW), (2) pure nutrients normalized to the nutrient concentrations in HPPW (NE), (3) pulsed flow (PF), or continuous flow-through of seawater (CF) (Table 2). Every third day, HPPW or nutrient stock was added to the HPPW and NE tanks, and the water flow was turned off for 24 h to allow the *P. palmata* to utilize the media. The PF replicated this setting without adding any media, while the CF had a constant flow throughout the experiment. All tanks were randomly placed in the cultivation area to avoid spatial bias. Salinity and temperature were measured daily using a multimeter (WTW Multi 3620 IDS, Xylem Analytics). The salinity was 22.3 ± 0.9PSU, and the temperature and pH were 13.5 ± 1.0 °C and 8.04 ± 0.07 (mean ± SD) during the experiment. The experiment lasted for seven weeks. Samples for growth and tissue nitrogen content were collected every week, and the biomass was reset to the start density of 2.5 g fw L^{-1} during this collection. On the last day of the experiment, besides growth and tissue nitrogen content, samples for pigments (chlorophyll *a*, carotenoids, phycobiliproteins), amino acid content, total elements, inorganic arsenic, and iodine content were also collected. Additionally, water samples were collected from the deep-seawater, HPPW water, and undiluted HPPW water for analysis of total elements and iodine.

2.3. Growth rate

The fresh weight of the *P. palmata* was measured in a standardized way by weighing it on a lab-scale (Fisherbrand RS232) after removing excess water with a salad spinner. The specific growth rate (SGR) was calculated according to the formula: $SGR = ((Ln(fw_t)-Ln(fw_0))/t)*100$, where fw_t is the fresh weight after t days, and fw_0 is the fresh weight at the start point. In the nutrient addition experiment, the average specific growth rate (ASGR) was calculated as the weekly recorded SGR averaged over the seven weeks among the replicates ($n = 6$). The samples were washed in filtered seawater, frozen, freeze-dried, and homogenized to a fine powder using a mortar and pestle, before further analysis of biochemical composition. The dried samples were weighed (dw), and a regression model between fw and dw showed $R^2 = 0.90$ ($n = 96$) for the salinity and irradiance experiment, and $R^2 = 0.95$ ($n = 168$) for the nutrient addition experiment, supporting fw as a viable measure of growth.

Table 2
Summary of nutrient addition and flow dynamics of the different treatments used in the nutrient addition experiment.

Treatment	Abbreviation	NH_4^+ (μM)	PO_4^{3-} (μM)	Seawater composition	Pulse 24 h
Diluted herring production process water	HPPW	40	153	Deep-seawater mixed with HPPW	Yes
Nutrient-enriched	NE	40	153	Deep-seawater enriched with NH_4Cl and KH_2PO_4	Yes
Pulse flow	PF	0.45	0.38	Deep-seawater	Yes
Continuous flow-through	CF	0.45	0.38	Deep-seawater	No

Refer to Table 1 for a detailed characterization of the deep-seawater.

2.4. Tissue nitrogen content and amino acid profile

For biochemical analyses, samples from the first two experiments consisted of homogenized whole fronds collected at the end of each experiment, while for the last experiment, surplus whole fronds beyond the weekly reset were collected. Total tissue nitrogen content was analyzed by combustion of the freeze-dried seaweed powder using a GSL elemental analyzer coupled to an isotope-ratio mass spectrometer (EA-IRMS, 20 - 22, Sercon Ltd., Crewe UK). In the nutrient addition experiment, the average tissue nitrogen content was calculated as the weekly measured content averaged over the seven weeks among the replicates (n = 6). Furthermore, specific nitrogen-to-protein conversion factors were determined by the ratio of total tissue nitrogen content and total amino acids on the last day.

Total amino acids (TAA) of *P. palmata* were analyzed following the protocol in Trigo et al. [49]. All measurements were made in triplicate. First, 100 mg of the freeze-dried seaweed powder and 4 mL of 6 M HCl were mixed in screw-cap glass tubes, after which the air in the tubes was replaced with nitrogen. The samples were hydrolyzed at 110 °C for 24 h using a heat block, and the samples were then filtered using a syringe filter (0.22 μm, PES; Fisher Scientific) and diluted with 0.2 M acetic acid. Hydrolysis blanks without samples, as well as quality control samples, were prepared in the same way. Two μL of each sample were run in a LC/MS (Agilent 1260-1290 Infinity LC System) with a Phenomenex column (Luna C18(2) 250 mm × 4.6 mm × 3 mm), coupled to an Agilent 6120 quadrupole in the SIM positive mode (Agilent Technologies). Separation at 0.7 mL min^{-1} for 40 min was performed using different ratios of mobile phase A (3 % methanol, 0.2 % formic acid and 0.01 % acetic acid) and mobile phase B (50 % methanol, 0.2 % formic acid and 0.01 %

Table 1
Characterization of the deep-seawater and undiluted herring production process water (mean ± SD, $n = 3$).

	Ammonium (μM NH_4^+)	Nitrate (μM NO_3^-)	Nitrite (μM NO_2^-)	Inorganic phosphorus (μM PO_4^{3-})
Deep-seawater	0.45 ± 0.03	3.55 ± 0.03	0.13 ± 0.02	0.38 ± 0.02
Herring production process water	3603.10 ± 368.40	nd	nd	13,745.00 ± 334.60

acetic acid). A mix of 18 amino acids (Amino Acid Standard H, Thermo Scientific) was used for the calibration curve. Methanol was used as a blank. Due to the use of acidic hydrolysis, (i) tryptophan and cysteine could not be recovered, and (ii) glutamine and asparagine were co-determined with glutamic and aspartic acid, respectively. MassHunter Quantitative Analysis software (version B.09.00, Agilent Technologies) was used to analyze the data.

2.5. Pigments (chlorophyll *a*, carotenoids, phycobiliproteins)

Determination of total content of chlorophyll *a*, and carotenoids, followed the protocol in Steinhagen et al. [50]. The content of chlorophyll *a* and carotenoids was extracted by placing 20 mg of freeze-dried and homogenized *P. palmata* tissue samples in 90 % acetone solution. The samples were placed in an ultrasonic bath for 10 min, followed by 50 min on a shaking table in darkness. The samples were then centrifuged for 10 min at 4000 rpm and 20 °C. The supernatants were collected, and using a spectrophotometer (Lambda XLS+, Perkin Elmer, Waltham, MA, United States), the absorbance was measured at the wavelengths 647, 664, 510, and 480 nm. The total content of chlorophyll *a* was calculated using the formula in Jeffrey and Humphrey [51], while carotenoids were calculated using the formula in Parsons et al. [52].

Determination of phycobiliproteins as R-phycoerythrin (R-PE) and R-phycocyanin (R-PC) followed the protocol in Sampath-Wiley and Neefus [53]. Briefly, 60 mg of freeze-dried and homogenized *P. palmata* tissue samples were stored at 1 °C for 45 min before starting the extraction. 0.1 M phosphate buffer (pH 7) was added at a 1 g biomass to 150 mL buffer ratio, followed by 65 min at 1 °C on a shaking table in darkness. The samples were then centrifuged for 20 min at 4000 rpm at 4 °C. The supernatants were collected, and using a spectrophotometer (Lambda XLS+, Perkin Elmer, Waltham, MA, United States) the absorbance was measured at the wavelengths 564, 618, and 730 nm. The R-PE and R-PC content was calculated using the formula in Sampath-Wiley and Neefus [53].

2.6. Total elements, inorganic arsenic, and iodine content

Total elements, including inorganic arsenic (iAs) and total iodine content, were analyzed from the water samples and freeze-dried and homogenized seaweed tissue samples by ALS Scandinavia AB (Luleå, Sweden). General precautions, detailed by Rodushkin et al. [54], were taken to avoid contamination of the samples. 0.5 g of sample was weighed into Teflon vials and mixed with 5 mL nitric acid and 0.02 mL hydrofluoric acid, both of Suprapur grade. A set of method blanks and test materials was prepared with each batch of samples. Vials were capped and put in a carousel placed in a microwave digestion system (Milestone, Sorisole, Italy), where a pre-programmed digestion cycle was initiated. Digests were then diluted to 10 mL with Milli-Q water (Millipore, Bedford, MA, USA), followed by additional dilution with 1.7 M nitric acid, resulting in a total digestion factor of approximately 500 m/v. All measurements of element concentrations were performed by double-focusing sector field ICP-MS ELEMENT XR (Thermo Scientific, Bremen, Germany) with methane added to the plasma [55]. Matrix effect correction was accomplished by internal standardization, where indium was added to all measurement solutions at a 2.5 μg L^{-1} concentration. Quantification was done by external calibration with synthetic, concentration-matched standards. For an in-depth description of the method, see Engström et al. [56].

The determination of iAs was performed according to the European Standard EN16802. The method uses extraction with dilute nitric acid and hydrogen peroxide in a hot water bath, followed by analysis with strong anion exchange HPLC-ICP-MS.

Iodine content was measured in a separate digest prepared by sintering [57] and analyzed by ICP-SFMS using ethylenediaminetetraacetic acid disodium salt dihydrate, Triton X-100, and an ammonia mixture to reduce carry-over in the introduction system and suppress the effect of oxidation state on the analyte intensity.

To assess safe consumption levels, the tolerable daily intake (TDI) for adults established by the European Food Safety Authority (EFSA) is used for elements and species of particular concern (As, iAs, Cd, Hg, Pb, and I) to calculate the maximum amount of freeze-dried *P. palmata* biomass that can safely be consumed. This is done using the formula: maximum intake = (TDI*i**bw)/C*i*, where TDI*i* is the tolerable upper daily intake for element *i* (μg d^{-1} bw) [58–62], bw is the referenced body weight for adults (63.3 kg) [63], and C*i* is the content of element *i* in the dried biomass (μg g^{-1} dw). Using a low reference body weight compared to the average weight for the European population (>75 kg) [64] results in conservative estimations for the European market. Additionally, the contribution of consuming the calculated safe consumption level of *P. palmata* cultivated with HPPW for some essential elements, namely calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), molybdenum (Mo), selenium (Se), and zinc (Zn) was assessed in relation to its recommended daily intake levels (RDI) [65].

2.7. Data analysis

All statistical analyses were performed in Rstudio (v. 2023.09.1 + 494). The data were visually checked for homogeneity and normality using diagnostic plots (density-, normality-, and QQ-plots). Furthermore, the data was checked for normality using the Shapiro-Wilk test and homogeneity using Levene's test.

In the salinity and irradiance experiment, SGR, tissue nitrogen- and pigment contents were analyzed using two-way ANOVA, with irradiance (3 levels) and salinity (3–4 levels) as fixed factors. Significant differences among means were compared using Tukey's HSD test.

In the dilution experiment, to describe the relationship between the SGR/tissue nitrogen content and the concentration of HPPW, a Michaelis-Menten curve was fitted to the data. V_{max} represents the maximum value of either SGR or tissue nitrogen content, and K_m represents the concentration of HPPW when SGR or tissue nitrogen content reaches half of the V_{max}.

In the nutrient addition experiment, all data were analyzed using one-way ANOVA with treatment (4 levels) as a fixed factor. Significant differences among means were compared using Tukey's HSD test.

3. Results

3.1. Effect of salinity and irradiance

3.1.1. Growth rate

Both salinity and irradiance had a significant effect on the SGR of *P. palmata*, and there was a significant interaction between the two factors ($p < 0.001$, Table 3A). The highest SGRs were achieved in the 180 μmol photons m^{-2} s^{-1} when cultivated in 22.5 and 33PSU, reaching 3.98 ± 0.31 % fw d^{-1} (mean ± SEM). Excluding the 7.5PSU treatment, SGR was almost 6 times higher at 180 μmol photons m^{-2} s^{-1} and 22.5PSU compared to 20 μmol photons m^{-2} s^{-1} and 33PSU (Tukey's HSD, $p < 0.001$, Fig. 1A). *P. palmata* cultivated under the 7.5PSU treatment exhibited negative SGRs across all irradiance levels, which was visible in their biomass as they lost color and were bleached. Due to biomass loss in the 7.5PSU treatments, these samples were excluded from the analysis of nitrogen and pigment content.

3.1.2. Tissue nitrogen content

The tissue nitrogen content ranged between 2.40 ± 0.06 and 3.16 ± 0.06 % dw (mean ± SEM, Fig. 1B). The two-way ANOVA showed a significant main effect of salinity ($p < 0.001$, Table 3B) and irradiance ($p < 0.001$, Table 3B) on tissue nitrogen content, but there was no significant interaction between them ($p = 0.66$, Table 3B). Tissue nitrogen content was significantly higher at salinity 15PSU (Tukey's HSD, $p = 0.03$), and 22.5PSU (Tukey's HSD, $p < 0.001$) compared to 33PSU, with

Table 3
Two-way ANOVA of (A) specific growth rate (% fw d^{-1}), (B) tissue nitrogen content (% dw), (C) chlorophyll *a* (mg g^{-1} dw), (D) carotenoids (mg g^{-1} dw), (E) phycoerythrin (mg g^{-1} dw), and (F) phycocyanin (mg g^{-1} dw) of *Palmaria palmata* cultivated under different levels of salinity and irradiance for three weeks. Significant *p*-values are indicated with italics. Data of means ± SEM are presented in Fig. 1A–E.

Source of variance	(A) Specific growth rate (% fw d^{-1})				(B) Tissue nitrogen content (% dw)				(C) Chlorophyll *a* (mg g^{-1} dw)			
	df	MS	F ratio	*p*	df	MS	F ratio	*p*	df	MS	F ratio	*p*
Salinity	3	49.01	223.99	*<0.001*	2	0.66	8.71	*<0.001*	2	0.20	10.39	*<0.001*
Irradiance	2	25.38	116.03	*<0.001*	2	1.14	15.09	*<0.001*	2	0.80	41.00	*<0.001*
Salinity × irradiance	6	3.16	14.44	*<0.001*	4	0.05	0.66	0.62	4	0.07	3.46	*0.01*
Residual	84	0.22			63	0.08			63	0.02		

Source of variance	(D) Carotenoids (mg g^{-1} dw)				(E) Phycoerythrin (mg g^{-1} dw)				(F) Phycocyanin (mg g^{-1} dw)			
	df	MS	F ratio	*p*	df	MS	F ratio	*p*	df	MS	F ratio	*p*
Salinity	2	0.02	6.13	*<0.01*	2	24.19	14.27	*<0.001*	2	1.74	19.57	*<0.001*
Irradiance	2	0.07	21.87	*<0.001*	2	0.58	0.34	0.71	2	0.001	0.02	0.99
Salinity × irradiance	4	0.008	2.65	*0.04*	4	0.66	0.39	0.81	4	0.04	0.45	0.76
Residual	63	0.003			63	1.70			63	0.09		

contents of 2.94 ± 0.06, 3.07 ± 0.07, and 2.74 ± 0.07 % dw (mean ± SEM), respectively (Fig. 1B). Similarly, tissue nitrogen content was significantly higher at irradiances of 20 µmol photons m^{-2} s^{-1} (Tukey's HSD, $p < 0.001$), and 80 µmol photons m^{-2} s^{-1} (Tukey's HSD, $p < 0.001$) compared to 180 µmol photons m^{-2} s^{-1}, with contents of 3.06 ± 0.05, 3.02 ± 0.05, and 2.67 ± 0.08 % dw (mean ± SEM), respectively (Fig. 1B).

3.1.3. Pigment content

The chlorophyll *a* content ranged between 0.67 ± 0.06 and 1.30 ± 0.03 mg g^{-1} dw (mean ± SEM), and the carotenoid content ranged between 0.19 ± 0.03 and 0.38 ± 0.01 mg g^{-1} dw (mean ± SEM) (Fig. 1C–D). For both chlorophyll *a* and carotenoid content, there was a significant interaction between salinity and irradiance ($p < 0.001$, Table 3C–D). The chlorophyll *a* and carotenoid content were favored by 80 µmol photons m^{-2} s^{-1}, with two times higher contents at 80 µmol photons m^{-2} s^{-1} and 22.5PSU compared to at 180 µmol photons m^{-2} s^{-1} and 15PSU (Tukey's HSD, $p < 0.01$, Fig. 1C–D).

Among the measured phycobiliproteins, R-PE constituted 76–78 % and R-PC constituted 22–24 % of the total content (Fig. 1E). For both R-PE and R-PC, only salinity had a significant effect on its content ($p < 0.001$, Table 3E–F), with *P. palmata* cultivated in 22.5 and 33PSU having significantly higher contents compared to when cultivated at 15PSU (Tukey's HSD, $p < 0.001$). R-PE content was 80 and 86 % higher at 22.5PSU (3.76 ± 0.26 mg g^{-1} dw), and 33PSU (3.89 ± 0.3 mg g^{-1} dw) compared to 15PSU (2.09 ± 0.21 mg g^{-1} dw, mean ± SEM). Similarly, R-PC content was 70 and 75 % higher at 22.5PSU (1.09 ± 0.06 mg g^{-1} dw) and 33PSU (1.12 ± 0.06 mg g^{-1} dw) compared to 15PSU (0.64 + 0.05 mg g^{-1} dw, mean ± SEM).

3.2. Cultivation with herring production process water (HPPW)

3.2.1. Effect of dilutions of HPPW

For both SGR and tissue nitrogen content, there was a direct positive response of adding the HPPW at the lower concentrations (Fig. 2A–B). The effect stagnated already at low levels of HPPW-derived NH_4^+, which is indicated by the K_m for both SGR (2.88 µM NH_4^+) and tissue nitrogen content (0.85 µM NH_4^+). However, there was no negative effect of adding higher concentrations of HPPW. Based on the fitted Michaelis-Menten curve, the maximum SGR and tissue nitrogen content (V_{max}) were 2.06 % fw d^{-1} and 4.53 % dw, respectively. Based on these results and the low variance within the HPPW-dilution providing 40 µM NH_4^+, this concentration was chosen as the optimal cultivation dilution for further experiments.

3.2.2. Effect of nutrient additions

3.2.2.1. Growth rate. There was a significant effect of treatment on the ASGR after seven weeks of cultivation ($p < 0.001$, Table 4A). Cultivating *P. palmaria* with added HPPW and NE resulted in 70 % higher ASGR compared to CF and PF (Tukey's HSD, $p < 0.001$, Fig. 3A), reaching 5.09 ± 0.08 and 5.19 ± 0.11 % fw d^{-1} with HPPW and NE, respectively, compared to 2.90 ± 0.2 in CF and 3.04 ± 0.26 % fw d^{-1} in PF (mean ± SEM). The *P. palmata* cultivated with HPPW showed notable morphological changes after five weeks, with fronds curling and developing a more leathery and tough texture (Fig. 4).

3.2.2.2. Tissue nitrogen content and amino acid profile. There was a significant effect of treatment on the average tissue nitrogen content after seven weeks of cultivation ($p < 0.001$, Table 4B). By cultivating the *P. palmata* with HPPW the average tissue nitrogen content reached 4.04 ± 0.19 % dw (mean ± SEM), which was 54–76 % higher than in NE (2.62 ± 0.06 % dw), CF (2.59 ± 0.07 % dw), and PF (2.30 ± 0.05 % dw) (Tukey's HSD, $p > 0.001$, Fig. 3B).

The amino acid profiles of *P. palmata* after cultivation in the four different treatments are presented in Table 5. For reference, the recommended AA profile based on required EAA by WHO/FAO/UNU [66], and EAA profiles of other protein-rich foodstuffs are presented. Similar to the tissue nitrogen content, there was a significant effect of treatment on the TAA ($p < 0.001$, Table 4C). By cultivating the *P. palmata* with HPPW, the TAA content reached 13.61 ± 0.33 % dw (mean ± SEM), which was 48–77 % higher than in NE (9.17 ± 0.15 % dw), CF (7.96 ± 0.27 % dw), and PF (7.68 ± 0.34 % dw) (Tukey's HSD, $p > 0.001$, Table 5). Furthermore, there was a significant effect on the TEAA profile by the different treatments ($p < 0.001$, Table 4D–E). Due to the increase of nonessential amino acids like proline and glutamic acid, cultivating *P. palmata* in the HPPW resulted in a significantly lower ratio of TEAA compared to the other treatments (Tukey's HSD, $p < 0.001$, Table 5). However, total content of TEAA in the HPPW cultivated biomass was 50.41 ± 1.08 mg g^{-1} dw (mean ± SEM), which was significantly higher compared to 34.15 ± 1.30, 35.86 ± 1.12, and 38.76 ± 0.64 mg g^{-1} dw (mean SEM) in the PF, CF, and NE treatments, respectively (Tukey's HSD, $p < 0.001$, Table 5). Independent of treatment, all *P. palmata* surpassed the EAA profile set by WHO/FAO/UNU [66]. Based on amino acid analyses, the specific nitrogen-to-protein conversion factor for the *P. palmata* in this experiment ranged between 3.52 and 3.71 (Table 5).

3.2.2.3. Pigments. The content of chlorophyll *a*, carotenoids, R-PE, and R-PC in *P. palmata* cultivated in the four different treatments is displayed in Fig. 3C. There was a significant effect of treatment on chlorophyll *a*, carotenoids, R-PE, and P-PC ($p < 0.05$, Table 4F-I). The chlorophyll *a*

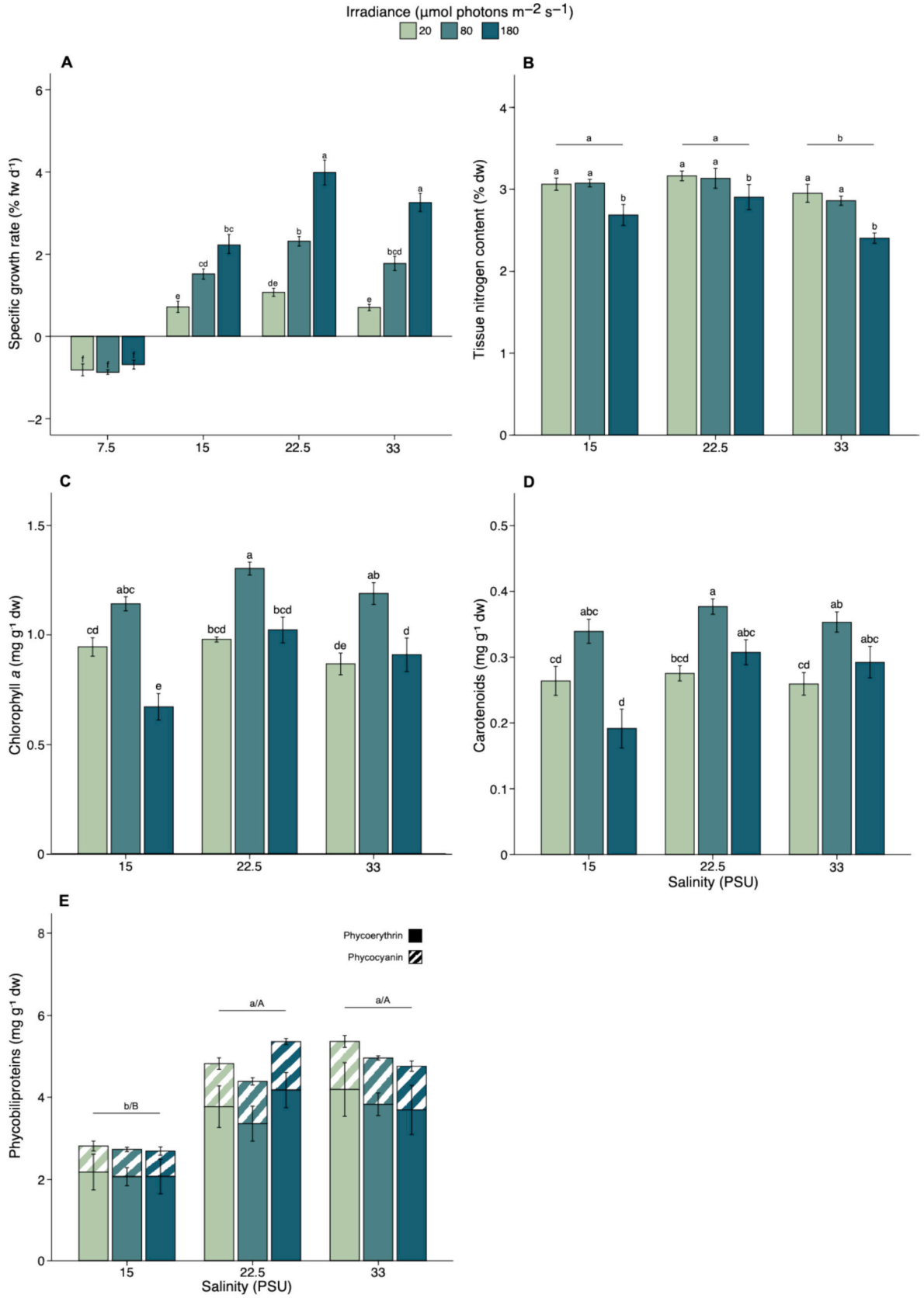


Fig. 1. (A) Specific growth rate (% fw d^{-1}), (B) tissue nitrogen content (% dw), (C) chlorophyll *a* (mg g^{-1} dw), (D) carotenoids (mg g^{-1} dw), and (E) phycobiliproteins (mg g^{-1}) as R-phycoerythrin (R-PE) and R-phycocyanin (R-PC) in *Palmaria palmata* cultivated under a fully crossed combination of irradiance and salinity levels (mean ± SEM, $n = 8$). Letters above bars show significant differences between means based on Tukey's HSD test ($p < 0.01$). For phycobiliproteins, lowercase letters indicate significant differences for R-PE, while capital letters indicate significant differences for R-PC.

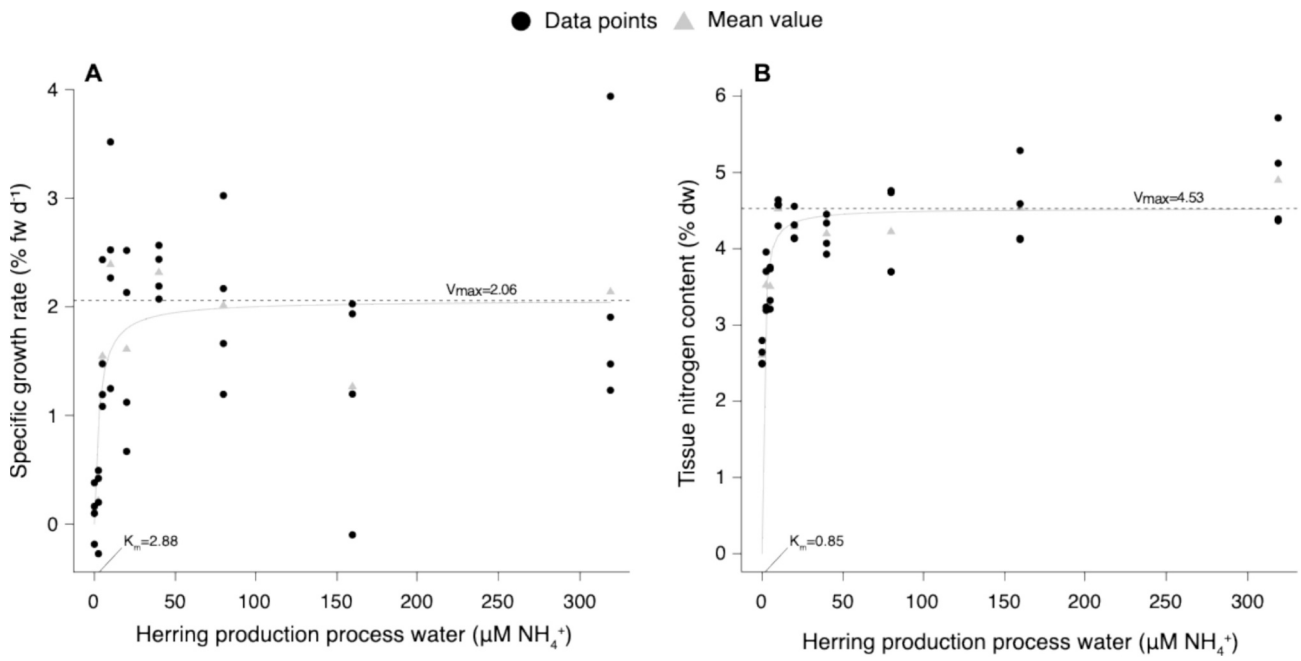


Fig. 2. (A) Specific growth rate (% fw d^{-1}), and (B) tissue nitrogen content (% dw) of *Palmaria palmata* as a function of the herring production process water (HPPW) concentration (µM ammonium). A Michaelis-Menten curve is fitted to the data with V_{max} representing the maximum value of the measured parameter and K_m representing the concentration of HPPW when the measured parameters reach half of the V_{max}.

Table 4
One-way ANOVA of (A) average specific growth rate (% fw d^{-1}), (B) average tissue nitrogen content (% dw), (C) total amino acids (% dw), (D) total essential amino acids (g 100 g amino $acids^{-1}$), (E) total essential amino acids (mg g^{-1} dw), (F) chlorophyll *a* (mg g^{-1} dw), (G) carotenoids (mg g^{-1} dw), (H) phycoerythrin (mg g^{-1} dw), and (I) phycocyanin (mg g^{-1} dw) of *Palmaria palmata* cultivated in four different treatments for seven weeks. Significant *p*-values are indicated with italics. Data of means ± SEM are presented in Fig. 3A–C and Table 5.

Source of variance	(A) Average specific growth rate (% fw d^{-1})				(B) Average tissue nitrogen content (% dw)				(C) Total amino acids (% dw)			
	df	MS	F ratio	*p*	df	MS	F ratio	*p*	df	MS	F ratio	*p*
Treatment	3	9.41	33.79	*<0.001*	3	3.68	77.83	*<0.001*	3	45.35	96.52	*<0.001*
Residual	20	0.28			20	0.05			20	0.47		

Source of variance	(D) Total essential amino acids (g 100 g amino $acids^{-1}$)				(E) Total essential amino acids (mg g^{-1} dw)				(F) Chlorophyll *a* (mg g^{-1} dw)			
	df	MS	F ratio	*p*	df	MS	F ratio	*p*	df	MS	F ratio	*p*
Treatment	3	80.92	197.9	*<0.001*	3	322.10	47.54	*<0.001*	3	0.11	3.83	*0.03*
Residual	20	0.41			20	6.8			20	0.03		

Source of variance	(G) Carotenoids (mg g^{-1} dw)				(H) Phycoerythrin (mg g^{-1} dw)				(I) Phycocyanin (mg g^{-1} dw)			
	df	MS	F ratio	*p*	df	MS	F ratio	*P*	df	MS	F ratio	*p*
Treatment	3	0.025	4.61	*0.01*	3	2.51	3.67	*0.03*	3	0.19	6.21	*<0.01*
Residual	20	0.006			20	0.68			20	0.03		

content was 1.12 ± 0.11 mg g^{-1} dw (mean ± SEM) in *P. palmata* cultivated with the HPPW, which was 40 % higher than 0.80 ± 0.035 mg g^{-1} dw (mean ± SEM) in the CF (Tukey's HSD, $p = 0.02$, Fig. 3C). Furthermore, the carotenoid content followed the same pattern with 0.42 ± 0.05 mg g^{-1} dw (mean ± SEM) when cultivated with HPPW, which was 56 % higher compared to 0.27 ± 0.02 mg g^{-1} dw (mean ± SEM) in CF (Tukey's HSD, $p = 0.01$, Fig. 3C). For R-PE, the content was 48 % higher in *P. palmaria* cultivated with HPPW compared to in PF (Tukey's HSD, $p = 0.03$), reaching 4.43 ± 0.37 mg g^{-1} dw (mean ± SEM) and 2.99 ± 0.36 mg g^{-1} dw (mean ± SEM), respectively. The R-PC content was 39 and 53 % higher with HPPW compared to in CF and PF, respectively (Tukey's HSD, $p < 0.05$, Fig. 3C), reaching 1.10 ± 0.08 mg g^{-1} dw with HPPW, 0.79 ± 0.05 mg g^{-1} dw in CF, and 0.72 ± 0.08 mg g^{-1} dw (mean ± SEM) in PF.

3.2.2.4. Total elements, inorganic arsenic, and iodine content. The results from the analysis of total elements in the *P. palmata* biomass and water samples are presented in the supplementary appendix Table A.1. For the toxic and potentially toxic elements, As, iAs, Cd, Hg, Pb, and I, the content in the biomass was lower with NE and HPPW compared to CF and PF, with the exception of Cd (Table 6). The proportion of iAs relative to total As varied between the treatments; in CF and PF, iAs made up approximately 11 % of total As, whereas in NE and HPPW, it accounted for only 1.2–2 %. Nevertheless, iodine content was the limiting element for daily consumption of *P. palmaria* biomass for all treatments, with tolerable daily intakes ranging from 7 g dw d^{-1} in CF to 24 g dw d^{-1} in

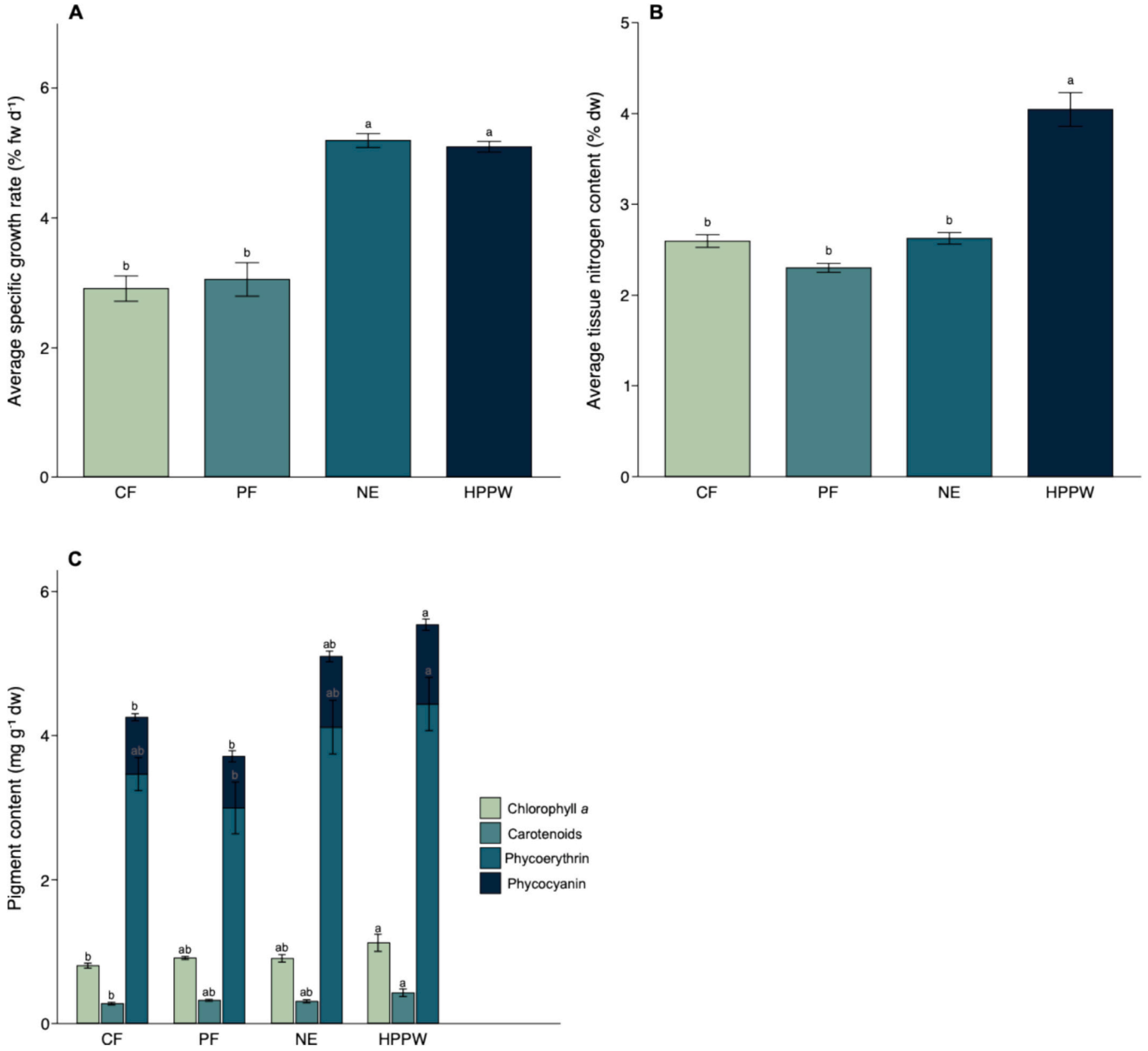


Fig. 3. (A) Average specific growth rate (% fw d^{-1}), (B) average tissue nitrogen content (% dw), and (C) pigment content (mg g^{-1} dw) in *Palmaria palmata* cultivated in the four different treatments continuous flow-through (CF), pulse flow (PF), nutrient-enriched (NE), and herring production process water (HPPW) (mean ± SEM, $n = 6$). For a full explanation of the different treatments, see Table 2. Letters above bars show significant differences between means based on Tukey's HSD test ($p < 0.05$).

NE (Table 6). When set in relation to the contribution of essential elements, a portion of 23 g dw *P. palmata* cultivated with HPPW would contribute to approximately 63 % of the RDI for K, 22 % for Mg, 17 % for Cu, 9 % for Se and Mo, as well as 3–5 % for Zn, Fe, Ca, and Mn (Table 7). Thus, *P. palmaria* could be considered a source of the three former elements (>15 % RDI).

4. Discussion

In this study, we show that the growth rate and nutritional quality of *P. palmata* can be significantly enhanced by optimizing its cultivation conditions. Adding herring production process water (HPPW) into the cultivation medium shows high potential, further improving both the growth rate and biochemical composition of the *P. palmata*. This was verified by multiple findings, including (i) significantly higher growth rate, (ii) significantly higher pigment content, (iii) significantly higher levels of total nitrogen and total amino acids, the latter including all essential amino acids in quantities exceeding dietary requirements, and (iv) an increase in the safe daily consumption from 7 g dw to 23 g dw, corresponding to 160 g fw (limited by iodine), in *P. palmata* grown with HPPW. Combined, the results show that *P. palmata* is a promising candidate for sustainable cultivation with HPPW, supporting the use of currently discarded liquid food side streams by turning them into a valuable nutrient-rich resource for seaweed cultivation. Strategies like this can help contribute to the development of circular and resource-efficient food production systems.

4.1. Effect of salinity and irradiance

This experiment showed that both salinity and irradiance

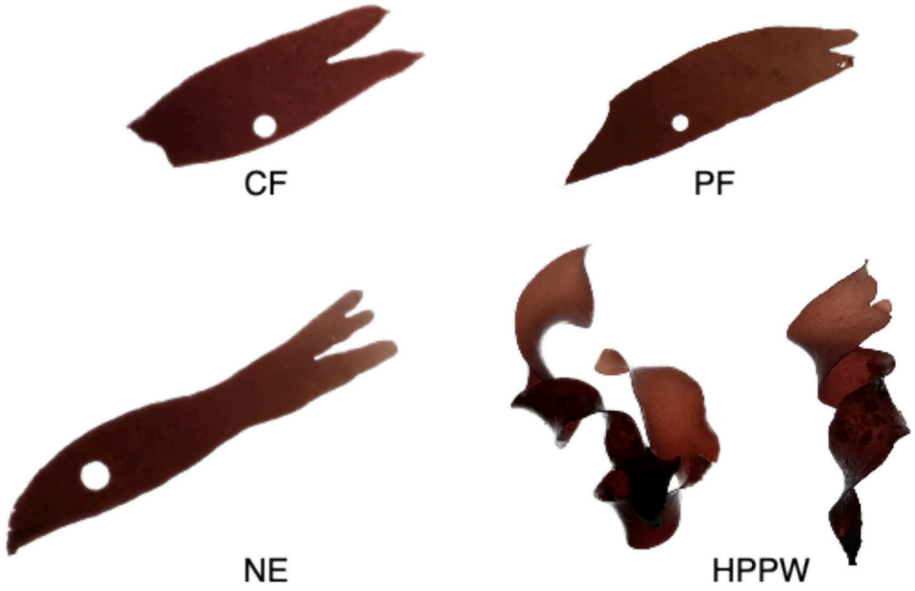


Fig. 4. Representative photos of *P. palmata* cultivated in the four different treatments: continuous flow-through (CF), pulse flow (PF), nutrient-enriched (NE), and herring production process water (HPPW).

interactively influence the growth rate of *P. palmata*. Although the individuals of *P. palmata* in this study naturally grow in environments with salinities around 33PSU, both in the wild and in our long-term stock cultures, they managed to grow effectively at two out of three reduced salinities in this experiment. At the lowest salinity level (7.5PSU), all *P. palmata* exhibited a negative growth rate independent of irradiance level, indicating that such a low salinity level is a significant negative stressor for the seaweed. However, *P. palmata* maintained positive growth at 15PSU, with optimal growth rates at 22.5PSU under high irradiance levels (180 μmol photons m^{-2} s^{-1}), which is notably lower than 30-32PSU, the salinity in which it naturally grows [69]. Furthermore, tissue nitrogen content was highest at 15 and 22.5PSU, while *P. palmata* in the highest irradiance level (180 μmol photons m^{-2} s^{-1}) resulted in the lowest tissue nitrogen contents, which is likely a reflection of a dilution effect, where rapid biomass growth uses internal storage of nitrogen [70].

Previous research supports the findings, showing higher growth rates in *P. palmata* under reduced salinity levels [30,71]. Similarly, low salinities have been shown to positively affect the growth and biochemical composition of other seaweeds, like the green seaweed *Ulva* spp. [72,73]. Seaweeds have been shown to rapidly take up nutrients in low salinity environments for growth [34], and in *Ulva,* elevated protein content under such conditions has been hypothesized to stem from its higher uptake of nitrogen for osmoregulation and increased levels of osmoregulatory amino acids [73]. It is possible that *P. palmata* exhibits similar mechanisms, though this would necessitate further research. Despite being collected from somewhat stable salinity conditions at deeper waters (10-12 m depth), this population of *P. palmaria* demonstrated an adaptability to variable environmental conditions, increasing its potential to expand the cultivation to both high and low salinity environments.

Similar to our results, higher irradiances have been shown to stimulate tissue growth but result in a reduction in tissue nitrogen content [30,74,75], consistent with the dilution effect described above [70]. Furthermore, the pigment analysis showed that chlorophyll *a* and carotenoids were highest at the moderate irradiance level of 80 μmol photons m^{-2} s^{-1}. These pigments are used for light harvesting in photosynthesis, while carotenoids are also used for photoprotection under high light conditions [16]. The moderate irradiance level likely provides the optimal balance, as lower irradiance (20 μmol photons m^{-2} s^{-1}) may be limited by energy availability, and the higher irradiance (180 μmol photons m^{-2} s^{-1}) is at the maximum photosynthetic activity, both thereby reducing the demand for these pigments [37]. This reflects the natural seasonal variations of these pigments, with pigment levels typically lowest in summer due to high irradiance and increased sun hours [37,76].

In shallow waters that are exposed to high irradiance levels, red seaweeds often lose some of their red pigmentation, as it is not needed for effective light harvesting under such conditions [12,77,78]. Surprisingly, in this experiment, phycobiliprotein content was unaffected by the irradiance level. Furthermore, although phycobiliproteins are known to correlate with tissue nitrogen content due to their function as nitrogen reserves [77,79,80], no such correlation was observed in this experiment. It was only salinity that significantly influenced phycobiliprotein content, where *P. palmata* grown in 22.5 and 33PSU had 70–86 % higher content compared to those grown in 15PSU. This is consistent with previous studies of red seaweeds such as *Gracilaria corticate* and *Gelidium coulteri*, where accumulation of phycobiliproteins occurred between 25-35PSU, while lower salinity levels resulted in reduced pigment content [80,81].

Combined, the results from the first experiment show that the interaction of 22.5PSU and 180 μmol photons m^{-2} s^{-1} produced the highest growth rates, resulting in 40–80 % higher total nitrogen and 27–90 % total pigment yields, compared to the other cultivation conditions. Based on these findings, this cultivation setup was chosen to investigate whether the addition of nutrient pulses in the form of HPPW can further increase the biochemical composition of the biomass while maintaining high growth rates [30,46].

4.2. *Effect of nutrient additions and implications for food production*

Based on the results from the dilution experiment, a dilution level of 40 μM NH_4^+ was selected for cultivation of *P. palmata* in HPPW. Both SGR and tissue nitrogen content showed rapid positive responses to increasing concentrations of HPPW, but the effect stagnated already at relatively low HPPW levels. While there were no negative effects at higher HPPW levels, levels contributing with 40 μM NH_4^+ provided the lowest variance for both growth and tissue nitrogen content. This finding aligns with previous studies demonstrating that *P. palmata* can grow under elevated nitrogen conditions of 2000 μM NH_4^+ [82], 1200 μM NO_3^- [30], 300 μM NH_4^+ [46], and 300/12 μM NH_4^+/NO_3^- [40]. However, despite high uptake and accumulation of NH_4^+, Morgan and

Table 5
Amino acid profiles in g 100 g amino acids^{-1} (and in mg g^{-1} in brackets) of dried biomass of *Palmaria palmata* from the four different treatments continuous flow-through (CF), pulse flow (PF), nutrient-enriched (NE), and herring production process water (HPPW) (mean ± SEM, $n = 6$). Essential amino acids (EAA) are indicated by bold font, and significant differences between treatments for TAA and TEAA are denoted by superscript letters. For reference, recommended amino acid profiles of required EAA by WHO/FAO/UNU [66] are presented. For direct comparisons with the *P. palmata* biomass in this study, the EAAs of some protein-rich foodstuffs are cited from Friedman [67] and Tessari et al. [68].

Amino acid	Amino acid profile, g 100 g amino acids^{-1} (mg g^{-1} dw)										
	CF	PF	NE	HPPW	WHO/FAO/UNU requirements	Beef[b]	Egg white[b]	Soy protein[b]	Pea[c]	Quinoa[c]	Sea bass[c]
Glycine	4.59 ± 0.02 (3.64 ± 0.14)	4.59 ± 0.02 (3.49 ± 0.16)	4.59 ± 0.05 (4.16 ± 0.07)	4.19 ± 0.05 (5.69 ± 0.11)							
Alanine	6.78 ± 0.08 (5.38 ± 0.19)	6.94 ± 0.07 (5.28 ± 0.28)	7.03 ± 0.04 (6.37 ± 0.12)	7.22 ± 0.09 (9.84 ± 0.32)							
Serine	6.03 ± 0.18 (4.79 ± 0.24)	6.03 ± 0.08 (4.59 ± 0.23)	6.39 ± 0.1 (5.79 ± 0.13)	5.46 ± 0.05 (7.43 ± 0.19)							
Proline	5.78 ± 0.19 (4.57 ± 0.18)	6.08 ± 0.22 (4.64 ± 0.35)	8.29 ± 0.23 (7.52 ± 0.29)	10.83 ± 0.29 (14.7 ± 0.46)							
Valine	**5.48 ± 0.08 (4.34 ± 0.13)**	**5.34 ± 0.03 (4.06 ± 0.18)**	**5.19 ± 0.05 (4.70 ± 0.10)**	**4.51 ± 0.03 (6.14 ± 0.14)**	3.9	4.54	6.78	4.91	4.11	4.90	4.90
Threonine	**5.41 ± 0.09 (4.29 ± 0.14)**	**5.40 ± 0.04 (4.11 ± 0.18)**	**5.31 ± 0.06 (4.81 ± 0.09)**	**4.68 ± 0.03 (6.36 ± 0.14)**	2.3	4.21	4.68	3.84	5.64	4.33	4.54
Isoleucine	**4.35 ± 0.07 (3.44 ± 0.09)**	**4.33 ± 0.06 (3.29 ± 0.12)**	**4.29 ± 0.05 (3.89 ± 0.08)**	**3.5 ± 0.03 (4.76 ± 0.10)**	3.0	4.18	5.28	4.71	3.65	4.12	4.29
Leucine	**7.63 ± 0.09 (6.04 ± 0.19)**	**7.51 ± 0.05 (5.71 ± 0.26)**	**7.51 ± 0.10 (6.81 ± 016)**	**6.35 ± 0.06 (8.64 ± 0.18)**	5.90	7.75	8.76	8.51	6.22	7.14	7.77
Aspartic acid[a]	10.45 ± 0.19 (8.31 ± 0.39)	10.23 ± 0.22 (7.85 ± 0.50)	10.68 ± 0.16 (9.68 ± 0.25)	11.95 ± 0.21 (16.2 ± 0.32)							
Lysine	**6.97 ± 0.19 (5.56 ± 0.33)**	**6.77 ± 0.11 (5.14 ± 0.25)**	**6.22 ± 0.10 (5.63 ± 0.09)**	**6.06 ± 0.06 (8.25 ± 0.25)**	4.50	7.94	6.98	6.34	6.33	5.23	9.49
Glutamic acid[a]	16.17 ± 0.20 (12.8 ± 0.41)	16.79 ± 0.28 (12.7 ± 0.41)	16.33 ± 0.18 (14.8 ± 0.17)	18.66 ± 0.34 (25.4 ± 1.04)							
Methionine	**3.03 ± 0.05 (2.39 ± 0.06)**	**3.05 ± 0.05 (2.32 ± 0.09)**	**2.92 ± 0.02 (2.64 ± 0.05)**	**2.36 ± 0.03 (3.20 ± 0.06)**	1.6	3.27	6.64	6.81	1.73	2.88	4.21
Histidine	**1.96 ± 0.05 (1.56 ± 0.03)**	**1.98 ± 0.06 (1.51 ± 0.03)**	**1.65 ± 0.04 (1.51 ± 0.02)**	**1.78 ± 0.04 (2.42 ± 0.05)**	1.5	3.20	2.25	2.54	1.55	2.44	2.59
Phenylalanine + tyrosine	**10.40 ± 0.19 (8.24 ± 0.20)**	**10.60 ± 0.22 (8.01 ± 0.23)**	**9.68 ± 0.08 (8.77 ± 0.11)**	**7.82 ± 0.07 (10.6 ± 0.24)**	3.80	7.02	9.08	9.68	6.27	7.87	7.19
Arginine	5.27 ± 0.09 (4.19 ± 0.19)	5.30 ± 0.06 (4.04 ± 0.21)	5.12 ± 0.04 (4.63 ± 0.07)	4.64 ± 0.02 (6.31 ± 0.15)							
TAA (% dw)	7.96 ± 0.27c	7.68 ± 0.34c	9.17 ± 0.15b	13.61 ± 0.33a							
TEAA	45.10 ± 0.24a (35.86 ± 1.12b)	44.55 ± 0.33a (34.15 ± 1.30b)	42.27 ± 0.23b (38.76 ± 0.64b)	37.05 ± 0.22c (50.41 ± 1.08a)		42.11	50.45	47.34	35.49	38.91	44.98
tissue nitrogen content (% dw)	2.29 ± 0.12	2.10 ± 0.15	2.48 ± 0.06	3.80 ± 0.15							
nitrogen-to-protein conversion factor	3.52 ± 0.24	3.71 ± 0.21	3.71 ± 0.09	3.60 ± 0.12							

TAA total amino acids, TEAA total essential amino acids.
[a] Glutamine and asparagine were co-determined with glutamic and aspartic acid, respectively.
[b] Friedman [67].
[c] Tessari et al. [68].

Simpson [82] reported that the high concentration of NH_4^+ was "somewhat toxic" at these levels, while Grote [40] showed that there were some negative effects such as bleached tissue and reduced growth rates after three weeks in concentrations of 500 uM/12 uM NH_4^+/NO_3^+. This, combined with the estimated maximum SGR of 2.06 % fw d^{-1} and tissue nitrogen content of 4.53 % dw in this study, justified the selection of using the HPPW dilution providing 40 μM NH_4^+.

When *P. palmata* was cultivated with the HPPW and the nutrient-enriched control in the following experiment, it resulted in 70 % higher growth rates compared to the seawater controls. There was a rapid increase in growth rate already after two weeks in the media (Fig. A.1A), which then stagnated and remained stable over the seven

Table 6
Content of toxic and potentially toxic elements (As, iAs, Cd, Hg, Pb, and I) in dried biomass of *Palmaria palmata* from the four different treatments: continuous flow-through (CF), pulse flow (PF), nutrient-enriched (NE), and HPPW (mean ± SEM, n = 6). The tolerable upper daily intake (TDI) for adults set by the European Food Safety Authority [59,61,62] is referenced based on a body weight for adults at 63.3 kg [63]. TDI is used to calculate the maximum possible *P. palmata* biomass intake per day.

Element	Content in biomass (μg g^{-1} dw)				TDI (μg d^{-1})	Max. seaweed biomass intake (g dw d^{-1})			
	CF	PF	NE	HPPW		CF	PF	NE	HPPW
Total arsenic (As)	6.12 ± 0.13	5.91 ± 0.28	3.12 ± 0.12	4.06 ± 0.09	Not established				
Inorganic arsenic (iAs)	0.64 ± 0.048	0.70 ± 0.14	0.07 ± 0.02	0.05 ± 0.01	8.30	13	12	119	166
Cadmium (Cd)	0.14 ± 0.02	0.13 ± 0.01	0.07 ± 0.01	0.05 ± 0.002	22.61	162	174	323	452
Mercury (Hg)	0.0058 ± 0.0004	0.0048 ± 0.0003	0.0047 ± 0.0005	0.0076 ± 0.0010	36.17	6236	7535	7697	4759
Lead (Pb)[a]	0.122 ± 0.009	0.098 ± 0.008	0.065 ± 0.005	0.061 ± 0.004	22.78	187	232	350	373
Iodine (I)	85.05 ± 10.20	54.50 ± 4.30	24.68 ± 4.14	26.47 ± 3.91	600	7	11	24	23

[a] EFSA does not provide reference values for inorganic arsenic and lead; instead, the lowest dietary exposure (0.13 and 0.36 μg kg body $weight^{-1}$, respectively) in average adult consumers in Europe is used as a reference [58,60] for conservative values.

Table 7
Recommended daily intake (RDI) of selected essential elements (Ca, Cu, Fe, K, Mg, Mn, Mo, Se, and Zn) as set by the Swedish Food Agency [65], and the contribution to the RDI from consuming 23 g of dry weight (dw) of *P. palmata* cultivated with herring production process water (HPPW). For comprehensive details on total elements, see Table A.1.

	RDI (mg)	mg from 23 g dw	% of RDI from 23 g dw
Ca	950[a]	27.07	3
Cu	0.9[b]	0.15	17[d]
Fe	9[b]	0.37	4
K	3500[a]	2206	63[d]
Mg	350[b]	75.51	22[d]
Mn	3[c]	0.14	5
Mo	0.065[c]	0.006	9
Se	0.09	0.008	9
Zn	12.7[b]	0.34	3

[a] adults aged 25 and older. No RDI is established for K and Se, instead, the adequate intake (AI) is used.
[b] men aged 17 and older.
[c] adults aged 18 and older.
[d] qualify for a nutrition claim (RDI > 15 %).

weeks of the experiment. The increase in growth rate observed in HPPW and nutrient-enriched controls at around 5 % fw d^{-1} is in agreement with previous studies using nutrient-enriched media for *P. palmata.* For example, Corey et al. [39] showed that *P. palmata* integrated with Atlantic halibut in a land-based aquaculture system grew by 1.1 % d^{-1} compared to 0.8 % d^{-1} in the controls, while Schmedes and Nielsen [30] observed a max SGR of 3.9 % d^{-1} at 120 μM NO_3^- and 6.86 % d^{-1} at 1200 μM NO_3^-. It is, however, important to consider the size and developmental stage of *P. palmata* used in the different experiments, as Corey et al. [39] uses larger, mature fronds that tend to grow more slowly than the smaller tissue fragments used in Schmedes and Nielsen [30].

Interestingly, *P. palmata* cultivated with HPPW developed morphological changes after five weeks, with fronds becoming curled, leathery, and tougher in texture (Fig. 4). Corey et al. [83] described comparable morphological changes in high nitrogen concentrations (300 μM NO_3^-) and hypothesized that the ruffling may lead to an increase in surface area available for nutrient uptake. Similar changes in morphology have also been observed for *Prasiola stipitata* when growing in nitrogen-rich environments such as rocks defecated by sea-birds (S. Steinhagen, pers. com, 2025). However, in our experiment, *P. palmata* cultivated in the nutrient-enriched control did not exhibit such morphological changes, suggesting a unique effect of the HPPW. Another possible explanation is that the HPPW contains or increases the growth of morphogenesis and growth-promoting bacteria associated with the seaweed [84,85]. Seaweeds are dependent on symbiotic bacterial communities on their surfaces and rhizoids for their development and functioning. For example, in some *Ulva* species, the morphology is strongly influenced by the presence of specific bacteria. Depending on the associated bacteria, their structure can be either flat and two-cell layered or tubular and single-cell layered [86,87]. An increase in functioning microbiota on the *P. palmata* could also help explain the higher nitrogen and amino acid content in biomass cultivated in the HPPW, discussed below. Further research should characterize the bacterial communities of *P. palmata* under different cultivation conditions, as this may have important effects on biomass production and quality in aquaculture.

This study reveals that HPPW has a strong positive effect on the measured biochemical composition of *P. palmata*. HPPW elevated the tissue nitrogen content by 54–76 %, to an average of 4.04 % dw, compared to the other treatments. This effect was visible already after the first week (Fig. A.1B). Previous studies have shown that the typical tissue nitrogen content of *P. palmata* ranges from 1.5 to 4.04 %, with high levels achieved in nutrient-rich media [14]. For example, Idowu et al. [36] found that cultivation in F/2 media increases the tissue nitrogen content to 3.18–4.15 % dw compared to 1.10–1.21 % dw in controls. The buildup of nitrogen in the biomass from cultivation in HPPW also resulted in biomass with a higher content of TAA. However, the specific nitrogen-to-protein conversion factor for the *P. palmata* in this experiment ranged between 3.52 and 3.71, indicating that a proportion of the nitrogen is non-protein nitrogen and thus used for things other than protein synthesis [33,88]. Using the conventional conversion factor of 6.25, or the more recent adapted factor of 5, for seaweeds [33] would therefore overestimate the protein content in this study, which is in line with previous studies [88,89]. Part of the explanation for the lower conversion factor in this study may be attributed to the analytical method used for AA quantification, in which e.g. tryptophan, cysteine, and methionine are either destroyed or partially destroyed during the acid hydrolysis, leading to underestimation of the nitrogen-to-protein conversion factor. Furthermore, the nitrogen content of amino acids varies considerably, making the specific amino acid composition of the seaweed biomass a key factor influencing the conversion factor [33,90,91]. In addition, seaweed biomass contains nitrogen compounds other than proteins, such as nucleic acids and amines [88,91,92]. Nonetheless, the results show that the biomass of *P. palmata*, regardless of cultivation medium, possesses a high-quality amino acid profile comparable to that of high-protein sources such as beef, fish, and soy protein [67,68], and containing all the EAA in levels exceeding the requirements set by the WHO/FAO/UNU [66]. Additionally, the *P. palmata* biomass cultivated in HPPW was rich in the umami-enhancing amino acids glutamic acid and aspartic acid, indicating its potential value for use in food applications [93].

For the measured pigments, the results from this experiment showed that chlorophyll *a* (1.12 mg g^{-1} dw), carotenoid (0.42 mg g^{-1} dw), and phycobiliprotein (R-PE: 4.43 mg g^{-1} dw, R-PC: 1.10 mg g^{-1} dw) content increased when cultivated with the HPPW compared to in seawater controls. The increase in chlorophyll content is consistent with nitrogen being a significant component of the chlorophyll molecule [94,95].

Regarding the upregulation of phycobiliproteins, it aligns with their function as nitrogen storage compounds in red seaweeds [77,79,80]. While this relationship between pigments and elevated nitrogen levels [34] was not evident in the first experiment, it became visible under nutrient-rich cultivation conditions. There is a growing interest in these seaweed-derived pigments due to their potential antioxidant and anti-inflammatory properties with a role in human health [17,18]. As a result, this has evoked increased attention from the pharmaceutical, cosmetic, and functional food industries [17,18]. Other promising applications of the monitored seaweed-derived pigments are as food colorants [96] and in different biomedical applications and clinical diagnostics [97]. Consequently, enhancing pigment content in *P. palmata* through cultivation with nutrient-rich media like HPPW offers a valuable strategy to increase the functional and economic potential of the biomass.

It is well known that seaweeds can accumulate toxic elements from their environment [25], which may be a concern for their use in food applications. Of specific concern is iAs as it is the cancerogenic form of As, while Cd, Pb, and Hg can have severe effects on the kidney function, nervous system, or increase the risk of cancer [25,27,98]. Furthermore, while iodine is an essential micronutrient for human health, excess intake may lead to negative effects [20,21]. In this experiment, the contents of these toxic and potentially toxic elements were generally lower in *P. palmata* biomass cultivated with the HPPW compared to in the seawater controls. Notably, the proportion of iAs to As in *P. palmata* cultivated in the seawater controls was around ten-fold higher than in nutrient-enriched and HPPW treatments. However, all levels of the measured toxic elements were below previously reported values for *P. palmata*, showing that it is important to consider geographic, seasonal, and cultivation variations, as these factors seem to influence the content of the biomass significantly [6,10,27,99].

Although the reason for the lower levels of toxic and potentially toxic elements in the *P. palmata* cultivated with HPPW and nutrient-enriched media is only speculative at this point, one hypothesis is that increased growth rates lead to a dilution effect of the toxic elements. This is supported by a negative correlation between SGR and toxic element concentration (Fig. A.2), and similar patterns have also been observed for rapidly growing tree leaves [100]. Another possible explanation involves changes in the biochemical composition of the biomass, where increased levels of proteins and macrominerals (Table A.1) may reduce the relative proportion of negatively charged sulfated polysaccharides. Furthermore, since binding efficiency is influenced by the degree of sulfation, a reduction in sulfated groups could lead to a decreased metal uptake [101,102]. Regardless, cultivation in nutrient-enriched media results in a reduced accumulation of toxic and potentially toxic elements in the biomass, and the cause of this effect is an area that is worth investigating further.

For all treatments, iodine was the limiting factor for tolerable daily intake. The maximum daily consumption of *P. palmata* based on iodine content was 23 g dw for *P. palmata* grown in HPPW, corresponding to 160 g dw per week. Converted to fresh weight, it would mean 160 g and 1130 g on a daily or weekly intake, respectively. When compared to the average daily seaweed biomass intake in Japan (4.0 g dw), China (5.2 g dw), or South Korea (8.5 g dw) [103], the potential health risk for excess iodine intake appears relatively low. Furthermore, these estimations are based on the EFSA reference body weight for adults (63.3 kg) [63], a conservative estimate that likely underestimates the average European body weight, while also assuming that all iodine and toxic elements are bioavailable. Due to the enhanced growth and raised content of protein and phytonutrients of *P. palmata* when cultivated in HPPW, the contribution of essential elements when consuming the safe intake portion of 23 g dw was assessed. Beyond providing 3-4 g of protein, this amount would contribute to a substantial fraction of the RDI for K, Mg, and Cu, while also making a meaningful contribution to the intake of other essential elements. For example, compared to commonly consumed vegetables such as fresh spinach, which are often cited for their high macro- and trace element content, dried *P. palmata* contains approximately 13 times more K, 3 times more Se, 1.4–1.6 times more Ca and Zn, while offering comparable levels of Fe [104]. These findings suggest that seaweeds may become an important dietary source of macro- and trace elements. It is essential to further investigate how post-harvest processing methods like blanching, washing, and boiling affect the content and bioavailability of these elements [22,105,106], while also investigating the impact of protein extraction processes [107,108]. In relation to blanching, there has been significantly more focus to date on the brown kelp species than on the red species, such as *P. palmata*.

5. Conclusion

This study demonstrates that the growth and nutritional content of *P. palmata* can be significantly boosted by adding discarded food side streams to the cultivation settings. Thus, supporting the sustainable and circular transformation of discarded food side streams into valuable nutrient-rich resources for seaweed cultivation. Optimal growth rates were achieved at 22.5PSU and 180 μmol photons m^{-2} s^{-1}, and adding HPPW further boosted the growth rate, tissue nitrogen content, and provided amino acid content exceeding dietary requirements for all essential amino acids. *P. palmata* cultivated with HPPW also showed elevated pigment content and reduced concentration of toxic and potentially toxic elements, including inorganic arsenic, cadmium, and lead. While iodine limits the safe daily intake to 23 g dw (160 g fw) in HPPW cultivated biomass, this level is well above the average seaweed consumption in Asia, and could serve as a valuable dietary source of macro- and micronutrients. The findings of this study support recent recommendations for developing the European seaweed sector with cultivation protocols for underutilized, protein-rich seaweeds and the reuse of nutrient-rich food process waters as a strategy to enhance biomass productivity and circularity in food production [109]. From a food perspective, the observed morphological change under HPPW cultivation and its implications on texture, sensory qualities, and nutrient bioavailability warrant further investigation. Finally, given the seasonal variability in growth, protein-, and elemental content of *P. palmaria*, future studies should assess year-round cultivation in the proposed settings.

CRediT authorship contribution statement

Kristoffer Stedt: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Moa Skagerlind:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Klara Helgesson:** Writing – review & editing, Investigation. **Ilia Rodushkin:** Writing – review & editing, Investigation. **Ingrid Undeland:** Writing – review & editing, Resources, Funding acquisition. **Gunilla B. Toth:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Henrik Pavia:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT (GPT-4.0, OpenAI) in order to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. All authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.algal.2025.104371.

Data availability

Data will be made available on request.

References

[1] J.A. Gephart, P.J.G. Henriksson, R.W.R. Parker, A. Shepon, K.D. Gorospe, K. Bergman, G. Eshel, C.D. Golden, B.S. Halpern, S. Hornborg, M. Jonell, M. Metian, K. Mifflin, R. Newton, P. Tyedmers, W. Zhang, F. Ziegler, M. Troell, Environmental performance of blue foods, Nature 597 (7876) (2021) 360–365, https://doi.org/10.1038/s41586-021-03889-2.

[2] J. Poore, T. Nemecek, Reducing food's environmental impacts through producers and consumers, Science 360 (6392) (2018) 987–992, https://doi.org/10.1126/science.aaq0216.

[3] T.W. Hertel, The challenges of sustainably feeding a growing planet, Food Secur. 7 (2) (2015) 185–198, https://doi.org/10.1007/s12571-015-0440-2.

[4] T. Chopin, A.H. Buschmann, C. Halling, M. Troell, N. Kautsky, A. Neori, G. P. Kraemer, J.A. Zertuche-González, C. Yarish, C. Neefus, Integrating seaweeds into marine aquaculture systems: a key towards sustainability, J. Phycol. 37 (6) (2001) 975–986, https://doi.org/10.1046/j.1529-8817.2001.01137.x.

[5] S.L. Holdt, S. Kraan, Bioactive compounds in seaweed: functional food applications and legislation, J. Appl. Phycol. 23 (3) (2011) 543–597, https://doi.org/10.1007/s10811-010-9632-5.

[6] H.K. Mæhre, M.K. Malde, K.E. Eilertsen, E.O. Elvevoll, Characterization of protein, lipid and mineral contents in common Norwegian seaweeds and evaluation of their potential as food and feed, J. Sci. Food Agric. 94 (15) (2014) 3281–3290, https://doi.org/10.1002/jsfa.6681.

[7] S. Spillias, H. Valin, M. Batka, F. Sperling, P. Havlík, D. Leclère, R.S. Cottrell, K. R. O'Brien, E. McDonald-Madden, Reducing global land-use pressures with seaweed farming, Nat. Sustain. (2023), https://doi.org/10.1038/s41893-022-01043-y.

[8] European Commission, A farm to fork strategy for a fair, healthy and environmentally-friendly food system. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Brussels. COM(2020): 381. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52020DC0381, 2020.

[9] M. Jönsson, A. Merkel, C. Fredriksson, E.N. Karlsson, K. Wendin, Nutritional, physicochemical, and sensory characterization of four common Northern European seaweed species intended for food, Algal Res. 75 (2023) 103258, https://doi.org/10.1016/j.algal.2023.103258.

[10] O.G. Mouritsen, C. Dawczynski, L. Duelund, G. Jahreis, W. Vetter, M. Schröder, On the human consumption of the red seaweed dulse (*Palmaria palmata* (L.) Weber & Mohr), J. Appl. Phycol. 25 (6) (2013) 1777–1791, https://doi.org/10.1007/s10811-013-0014-7.

[11] J. Fleurence, Chapter 5 - seaweeds as food, in: J. Fleurence, I. Levine (Eds.), Seaweed in Health and Disease Prevention, Academic press, San Diego, 2016, pp. 149–167, https://doi.org/10.1016/B978-0-12-802772-1.00005-1.

[12] K.C. Morgan, J.L. Wright, F. Simpson, Review of chemical constituents of the red alga *Palmaria palmata* (dulse), Econ. Bot. 34 (1) (1980) 27–50, https://doi.org/10.1007/BF02859553.

[13] P. Rawiwan, Y. Peng, I.G.P.B. Paramayuda, S.Y. Quek, Red seaweed: a promising alternative protein source for global food sustainability, Trends Food Sci. Technol. 123 (2022) 37–56, https://doi.org/10.1016/j.tifs.2022.03.003.

[14] P. Stévant, P.S. Schmedes, L. Le Gall, S. Wegeberg, J. Dumay, C. Rebours, Concise review of the red macroalga dulse, *Palmaria palmata* (L.) Weber & Mohr, J. Appl. Phycol. (2023), https://doi.org/10.1007/s10811-022-02899-5.

[15] S.M. Tibbetts, J.E. Milley, S.P. Lall, Nutritional quality of some wild and cultivated seaweeds: nutrient composition, total phenolic content and in vitro digestibility, J. Appl. Phycol. 28 (6) (2016) 3575–3585, https://doi.org/10.1007/s10811-016-0863-y.

[16] C.L. Hurd, C.S. Lobban, K. Bischof, P.J. Harrison, Light and photosynthesis, in: C. L. Hurd, C.S. Lobban, K. Bischof, P.J. Harrison (Eds.), Seaweed Ecology and Physiology, 2 edn, Cambridge University Press, Cambridge, 2014, pp. 238–293, https://doi.org/10.1017/CBO9781139192637.007.

[17] C. Jiménez-González, A.M.T. Agrasar, F. Mallo, M.L. Rúa, C. Fuciños, Red seaweed proteins: valuable marine-origin compounds with encouraging applications, Algal Res. 75 (2023) 103262, https://doi.org/10.1016/j.algal.2023.103262.

[18] S. Sekar, M. Chandramohan, Phycobiliproteins as a commodity: trends in applied research, patents and commercialization, J. Appl. Phycol. 20 (2) (2008) 113–136, https://doi.org/10.1007/s10811-007-9188-1.

[19] P.P.A. Smyth, Iodine, seaweed, and the thyroid, Eur. Thyroid J. 10 (2) (2021) 101–108, https://doi.org/10.1159/000512971.

[20] I. Aakre, D. Doblaug Solli, M. Wik Markhus, H. K. Mæhre, L. Dahl, S. Henjum, J. Alexander, P.-A. Korneliussen, L. Madsen, M. Kjellevold, Commercially available kelp and seaweed products – valuable iodine source or risk of excess intake? Food Nutr. Res. 65 (2021) https://doi.org/10.29219/fnr.v65.7584.

[21] M.J. Blikra, I. Aakre, J. Rigutto-Farebrother, Consequences of acute and long-term excessive iodine intake: a literature review focusing on seaweed as a potential dietary iodine source, Compr. Rev. Food Sci. Food Saf. 23 (6) (2024) e70037, https://doi.org/10.1111/1541-4337.70037.

[22] J.P. Trigo, K. Stedt, A.E.M. Schmidt, B. Kollander, U. Edlund, G. Nylund, H. Pavia, M. Abdollahi, I. Undeland, Mild blanching prior to pH-shift processing of *Saccharina latissima* retains protein extraction yields and amino acid levels of extracts while minimizing iodine content, Food Chem. 404 (2023) 134576, https://doi.org/10.1016/j.foodchem.2022.134576.

[23] J. Darias-Rosales, C. Rubio, Á.J. Gutiérrez, S. Paz, A. Hardisson, Risk assessment of iodine intake from the consumption of red seaweeds (*Palmaria palmata* and *Chondrus crispus*), Environ. Sci. Pollut. Res. 27 (36) (2020) 45737–45741, https://doi.org/10.1007/s11356-020-10478-9.

[24] V. Besada, J.M. Andrade, F. Schultze, J.J. González, Heavy metals in edible seaweeds commercialised for human consumption, J. Mar. Syst. 75 (1) (2009) 305–313, https://doi.org/10.1016/j.jmarsys.2008.10.010.

[25] N. Prashant, M. Sangwan, P. Singh, P. Das, U. Srivastava, F. Bast, Anti-nutritional factors and heavy metals in edible seaweeds: challenges, health implications, and strategies for safer consumption, J. Food Compos. Anal. 140 (2025) 107283, https://doi.org/10.1016/j.jfca.2025.107283.

[26] C. Ortiz-Calderon, H.C. Silva, D.B. Vásquez, Metal removal by seaweed biomass, in: T. Jaya Shankar (Ed.), Biomass Volume Estimation and Valorization for Energy, IntechOpen, Rijeka, 2017, https://doi.org/10.5772/65682 (Ch. 16).

[27] M.Y. Roleda, H. Marfaing, N. Desnica, R. Jónsdóttir, J. Skjermo, C. Rebours, U. Nitschke, Variations in polyphenol and heavy metal contents of wild-harvested and cultivated seaweed bulk biomass: health risk assessment and implication for food applications, Food Control 95 (2019) 121–134, https://doi.org/10.1016/j.foodcont.2018.07.031.

[28] K. Véliz, P. Toledo, M. Araya, M.F. Gómez, V. Villalobos, F. Tala, Chemical composition and heavy metal content of Chilean seaweeds: potential applications of seaweed meal as food and feed ingredients, Food Chem. 398 (2023) 133866, https://doi.org/10.1016/j.foodchem.2022.133866.

[29] J.T. Hafting, A.T. Critchley, M.L. Cornish, S.A. Hubley, A.F. Archibald, On-land cultivation of functional seaweed products for human usage, J. Appl. Phycol. 24 (3) (2012) 385–392, https://doi.org/10.1007/s10811-011-9720-1.

[30] P.S. Schmedes, M.M. Nielsen, Productivity and growth rate in *Palmaria palmata* affected by salinity, irradiance, and nutrient availability—the use of nutrient pulses and interventional cultivation, J. Appl. Phycol. 32 (6) (2020) 4099–4111, https://doi.org/10.1007/s10811-020-02248-4.

[31] G.B. Toth, H. Harrysson, N. Wahlstrom, J. Olsson, A. Oerbekke, S. Steinhagen, A. Kinnby, J. White, E. Albers, U. Edlund, I. Undeland, H. Pavia, Effects of irradiance, temperature, nutrients, and pCO(2) on the growth and biochemical composition of cultivated *Ulva fenestrata*, J. Appl. Phycol. 32 (2020) 3243–3254, https://doi.org/10.1007/s10811-020-02155-8.

[32] P. Liboureau, D.M. Pampanin, Effects of vegetative propagation on protein content and bioactivity of the red seaweed *Palmaria palmata*, Food Chem. 455 (2024) 139929, https://doi.org/10.1016/j.foodchem.2024.139929.

[33] A.R. Angell, L. Mata, R. de Nys, N.A. Paul, The protein content of seaweeds: a universal nitrogen-to-protein conversion factor of five, J. Appl. Phycol. 28 (1) (2016) 511–524, https://doi.org/10.1007/s10811-015-0650-1.

[34] M.Y. Roleda, C.L. Hurd, Seaweed nutrient physiology: application of concepts to aquaculture and bioremediation, Phycologia 58 (5) (2019) 552–562, https://doi.org/10.1080/00318884.2019.1622920.

[35] K. Stedt, H. Pavia, G.B. Toth, Cultivation in wastewater increases growth and nitrogen content of seaweeds: a meta-analysis, Algal Res. 61 (2022) 102573, https://doi.org/10.1016/j.algal.2021.102573.

[36] A.T. Idowu, M. Amigo-Benavent, M. Santos-Hernández, S. Whelan, M.D. Edwards, R.J. FitzGerald, Impact of growth conditions on the nitrogen, protein, colour and

amino acid profiles of the cultured macroalga, *Palmaria palmata*, J. Appl. Phycol. 35 (5) (2023) 2397–2411, https://doi.org/10.1007/s10811-023-03057-1.
[37] F. Lalegerie, V. Stiger-Pouvreau, S. Connan, Temporal variation in pigment and mycosporine-like amino acid composition of the red macroalga *Palmaria palmata* from Brittany (France): hypothesis on the MAA biosynthesis pathway under high irradiance, J. Appl. Phycol. 32 (4) (2020) 2641–2656, https://doi.org/10.1007/s10811-020-02075-7.
[38] A. Neori, T. Chopin, M. Troell, A.H. Buschmann, G.P. Kraemer, C. Halling, M. Shpigel, C. Yarish, Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture, Aquaculture 231 (1) (2004) 361–391, https://doi.org/10.1016/j.aquaculture.2003.11.015.
[39] P. Corey, J.K. Kim, J. Duston, D.J. Garbary, Growth and nutrient uptake by *Palmaria palmata* integrated with Atlantic halibut in a land-based aquaculture system, Algae 29 (1) (2014) 35–45, https://doi.org/10.4490/algae.2014.29.1.035.
[40] B. Grote, Bioremediation of aquaculture wastewater: evaluating the prospects of the red alga *Palmaria palmata* (Rhodophyta) for nitrogen uptake, J. Appl. Phycol. 28 (5) (2016) 3075–3082, https://doi.org/10.1007/s10811-016-0848-x.
[41] J.C. Sanderson, M.J. Dring, K. Davidson, M.S. Kelly, Culture, yield and bioremediation potential of *Palmaria palmata* (Linnaeus) Weber & Mohr and *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders adjacent to fish farm cages in northwest Scotland, Aquaculture 354-355 (2012) 128–135, https://doi.org/10.1016/j.aquaculture.2012.03.019.
[42] C.P. Baron, C. Østerberg, C. Kemp, E. Rós Brink, G. Olafsdottir, S. Folmer, N. Gringer, C. Eriksson, T. Svendsen, I. Undeland, PIPE Pelagic Industry Processing Effluents Innovative and Sustainable Solutions, 2015, p. 128, in: https://www.nordicinnovation.org/2016/pipe-pelagic-industry-processing-effluents-innovative-and-sustainable-solutions (Oslo).
[43] B. Forghani, T.C. Svendsen, A. Pratap-Singh, C. Jacobsen, I. Undeland, Biomass recovery from herring brines: exploring quality and functionality of protein and n-3 polyunsaturated fatty acids, Food Chem. 484 (2025) 144403, https://doi.org/10.1016/j.foodchem.2025.144403.
[44] K. Stedt, O. Gustavsson, B. Kollander, I. Undeland, G.B. Toth, H. Pavia, Cultivation of *Ulva fenestrata* using herring production process waters increases biomass yield and protein content, Front. Mar. Sci. 9 (2022), https://doi.org/10.3389/fmars.2022.988523.
[45] K. Stedt, J.P. Trigo, S. Steinhagen, G.M. Nylund, B. Forghani, H. Pavia, I. Undeland, Cultivation of seaweeds in food production process waters: evaluation of growth and crude protein content, Algal Res. 63 (2022) 102647, https://doi.org/10.1016/j.algal.2022.102647.
[46] P. Corey, J.K. Kim, J. Duston, D.J. Garbary, B. Prithiviraj, Bioremediation potential of *Palmaria palmata* and *Chondrus crispus* (Basin Head): effect of nitrate and ammonium ratio as nitrogen source on nutrient removal, J. Appl. Phycol. 25 (5) (2013) 1349–1358, https://doi.org/10.1007/s10811-013-9977-7.
[47] A. Schieber, Side streams of plant food processing as a source of valuable compounds: selected examples, Annu. Rev. Food Sci. Technol. 8 (1) (2017) 97–112, https://doi.org/10.1146/annurev-food-030216-030135.
[48] S. Steinhagen, K. Stedt, J.P. Trigo, I. Undeland, H. Pavia, A step towards closing the food-waste gap in novel protein sources: post-harvest protein boost of the seaweed crop *Ulva* by herring production tub water, Futur. Foods 9 (2024) 100347, https://doi.org/10.1016/j.fufo.2024.100347.
[49] J.P. Trigo, N. Engström, S. Steinhagen, L. Juul, H. Harrysson, G.B. Toth, H. Pavia, N. Scheers, I. Undeland, In vitro digestibility and Caco-2 cell bioavailability of sea lettuce (*Ulva fenestrata*) proteins extracted using pH-shift processing, Food Chem. 356 (2021) 129683, https://doi.org/10.1016/j.foodchem.2021.129683.
[50] S. Steinhagen, S. Enge, K. Larsson, J. Olsson, G.M. Nylund, E. Albers, H. Pavia, I. Undeland, G.B. Toth, Sustainable large-scale aquaculture of the northern hemisphere sea lettuce, *Ulva fenestrata*, in an off-shore seafarm, J. Mar. Sci. Eng. 9 (6) (2021) 615, https://doi.org/10.3390/jmse9060615.
[51] S.W. Jeffrey, G.F. Humphrey, New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton, Biochem. Physiol. Pflanz. 167 (2) (1975) 191–194, https://doi.org/10.1016/S0015-3796(17)30778-3.
[52] T.R. Parsons, Y. Maita, C.M. Lallli, A manual for Chemical and Biological Methods for Seawater Analysis, Pergamon Press, Oxford, UK, 1984, https://doi.org/10.1016/C2009-0-07774-5.
[53] P. Sampath-Wiley, C.D. Neefus, An improved method for estimating R-phycoerythrin and R-phycocyanin contents from crude aqueous extracts of *Porphyra* (Bangiales, Rhodophyta), J. Appl. Phycol. 19 (2) (2007) 123–129, https://doi.org/10.1007/s10811-006-9118-7.
[54] I. Rodushkin, E. Engström, D.C. Baxter, Sources of contamination and remedial strategies in the multi-elemental trace analysis laboratory, Anal. Bioanal. Chem. 396 (1) (2010) 365–377, https://doi.org/10.1007/s00216-009-3087-z.
[55] I. Rodushkin, P. Nordlund, E. Engström, D.C. Baxter, Improved multi-elemental analyses by inductively coupled plasma-sector field mass spectrometry through methane addition to the plasma, J. Anal. At. Spectrom. 20 (11) (2005) 1250–1255, https://doi.org/10.1039/B507886E.
[56] E. Engström, A. Stenberg, S. Senioukh, R. Edelbro, D.C. Baxter, I. Rodushkin, Multi-elemental characterization of soft biological tissues by inductively coupled plasma–sector field mass spectrometry, Anal. Chim. Acta 521 (2) (2004) 123–135, https://doi.org/10.1016/j.aca.2004.06.030.
[57] H. Österlund, I. Rodushkin, K. Ylinenjärvi, D.C. Baxter, Determination of total chlorine and bromine in solid wastes by sintering and inductively coupled plasma-sector field mass spectrometry, Waste Manag. 29 (4) (2009) 1258–1264, https://doi.org/10.1016/j.wasman.2008.07.017.
[58] EFSA, Cadmium in food - scientific opinion of the panel on contaminants in the food chain, EFSA J. 7 (3) (2009) 980, https://doi.org/10.2903/j.efsa.2009.980.
[59] EFSA, Scientific opinion of arsenic in food - panel on contaminants in the food chain, EFSA J. 7 (10) (2009) 1351, https://doi.org/10.2903/j.efsa.2009.1351.
[60] EFSA, Scientific opinion on lead in food - panel on contaminants in the food chain, EFSA J. 8 (4) (2010) 1570, https://doi.org/10.2903/j.efsa.2010.1570.
[61] EFSA, Scientific opinion on the risk for public health related to the presence of mercury and methylmercury in food - panel on contaminants in the food chain, EFSA J. 10 (12) (2012) 2985, https://doi.org/10.2903/j.efsa.2012.2985.
[62] EFSA, Overview on Tolerable Upper Intake Levels as Derived by the Scientific Committee on Food (SCF) and the EFSA Panel on Dietetic Products, Nutrition and Allergies (NDA), 2024.
[63] EFSA, Dietary reference values for nutrients summary report, EFSA Support. Publ. 14 (12) (2017) e15121E, https://doi.org/10.2903/sp.efsa.2017.e15121.
[64] worlddata.info, Average sizes of men and women. https://www.worlddata.info/average-bodyheight.php, 2025. (Accessed 4 July 2025).
[65] Swedish Food Agency, Salt och mineraler. https://www.livsmedelsverket.se/livsmedel-och-innehall/naringsamne/salt-och-mineraler1/, 2025. (Accessed 4 July 2025).
[66] WHO/FAO/UNU, Protein and amino acid requirements in human nutrition, in: Geneva, Switzerland. WHO Technical Report Series 935. Report of Joint WHO/FAO/UNU Expert Consultation xi, 2007. https://iris.who.int/items/78c03092-bcc2-40f5-90d1-60641ecdf6ea (265p).
[67] M. Friedman, Nutritional value of proteins from different food sources. A review, J. Agric. Food Chem. 44 (1) (1996) 6–29, https://doi.org/10.1021/jf9400167.
[68] P. Tessari, A. Lante, G. Mosca, Essential amino acids: master regulators of nutrition and environmental footprint? Sci. Rep. 6 (1) (2016) 26074 https://doi.org/10.1038/srep26074.
[69] The Swedish Meterological and Hydrological Institute, Svenskt HavsARKIV (SHARK). https://shark.smhi.se/hamta-data/, 2025 (Kosterfjorden stationsnamn 16, 2018-2024).
[70] P.J. Harrison, C.L. Hurd, Nutrient physiology of seaweeds: application of concepts to aquaculture, Cah. Biol. Mar. 42 (1–2) (2001) 71–82.
[71] P.S. Schmedes, M.M. Nielsen, J.K. Petersen, Improved Palmaria palmata hatchery methods for tetraspore release, even settlement and high seedling survival using strong water agitation and macerated propagules, Algal Res. 40 (2019) 101494, https://doi.org/10.1016/j.algal.2019.101494.
[72] A. Fort, J.P. Monteiro, C. Simon, M. Rosário Domingues, R. Sulpice, Short term decreases in salinity, combined with the right choice of species, can allow for a more nutritious sea lettuce lipid profile, Food Chem. 437 (2024) 137865, https://doi.org/10.1016/j.foodchem.2023.137865.
[73] S. Steinhagen, I. Johansson, J. Specht, S. Enge, K. Larsson, I. Undeland, G.B. Toth, 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, Bot. Mar. (2025), https://doi.org/10.1515/bot-2024-0079.
[74] B. Lafeuille, É. Tamigneaux, M.P.R. Rodriguez, K. Berger, V. Provencher, L. Beaulieu, Indoor tank cultivation of *Palmaria palmata* from Atlantic Canada: effects of light and nitrogen enrichment on specific growth rate, chemical composition and in vitro bioactivities, J. Appl. Phycol. 37 (2) (2025) 1123–1137, https://doi.org/10.1007/s10811-025-03483-3.
[75] J.A. Manríquez-Hernández, J. Duston, D.J. Garbary, Effect of irradiance on bioremediation capacity of the red algae *Chondrus crispus* and *Palmaria palmata*, Aquac. Int. 24 (1) (2016) 39–55, https://doi.org/10.1007/s10499-015-9907-6.
[76] P. Sampath-Wiley, C.D. Neefus, L.S. Jahnke, Seasonal effects of sun exposure and emersion on intertidal seaweed physiology: fluctuations in antioxidant contents, photosynthetic pigments and photosynthetic efficiency in the red alga Porphyra umbilicalis Kützing (Rhodophyta, Bangiales), J. Exp. Mar. Biol. Ecol. 361 (2) (2008) 83–91, https://doi.org/10.1016/j.jembe.2008.05.001.
[77] H. Mizuta, Y. Shirakura, H. Yasui, Relationship betweenn phycoerythrin and nitrogen content in *Gloiopeltis furcata* and *Porphyra yezoensis*, Algae Kor. Soc. Phycol. 17 (2) (2002) 89–93, https://doi.org/10.4490/algae.2002.17.2.089.
[78] S. Sagert, H. Schubert, Acclimation of *Palmaria palmata* (Rhodophyta) to light intensity: comparison between artificial and natural light fields, J. Phycol. 36 (6) (2000) 1119–1128, https://doi.org/10.1046/j.1529-8817.2000.99156.x.
[79] M.J. García-Sánchez, J.A. Fernández, F.X. Niell, Biochemical and physiological responses of *Gracilaria tenuistipitata* uuder two different nitrogen treatments, Physiol. Plant. 88 (4) (1993) 631–637, https://doi.org/10.1111/j.1399-3054.1993.tb01382.x.
[80] M. Kumar, P. Kumari, V. Gupta, C.R.K. Reddy, B. Jha, Biochemical responses of red alga *Gracilaria corticata* (Gracilariales, Rhodophyta) to salinity induced oxidative stress, J. Exp. Mar. Biol. Ecol. 391 (1) (2010) 27–34, https://doi.org/10.1016/j.jembe.2010.06.001.
[81] B.A. Macler, Salinity effects on photosynthesis, carbon allocation, and nitrogen assimilation in the red alga, *Gelidium coulteri*, Plant Physiol. 88 (3) (1988) 690–694, https://doi.org/10.1104/pp.88.3.690.
[82] K.C. Morgan, F.J. Simpson, Cultivation of *Palmaria* (Rhodymenia) *palmata* - effect of high-concentrations of nitrate and ammonium on growth and nitrogen uptake, Aquat. Bot. 11 (2) (1981) 167–171, https://doi.org/10.1016/0304-3770(81)90057-7.
[83] P. Corey, J.K. Kim, D.J. Garbary, B. Prithiviraj, J. Duston, Bioremediation potential of *Chondrus crispus* (Basin Head) and *Palmaria palmata*: effect of temperature and high nitrate on nutrient removal, J. Appl. Phycol. 24 (3) (2012) 441–448, https://doi.org/10.1007/s10811-011-9734-8.
[84] M. Gemin, A. Peña-Rodríguez, E. Quiroz-Guzmán, P. Magallón-Servín, D. Barajas-Sandoval, R. Elizondo-González, Growth-promoting bacteria for the green

seaweed *Ulva clathrata*, Aquac. Res. 50 (12) (2019) 3741–3748, https://doi.org/10.1111/are.14336.
[85] L.M. van der Loos, B.K. Eriksson, J.F. Salles, The macroalgal holobiont in a changing sea, Trends Microbiol. 27 (7) (2019) 635–650, https://doi.org/10.1016/j.tim.2019.03.002.
[86] M. Spoerner, T. Wichard, T. Bachhuber, J. Stratmann, W. Oertel, Growth and thallus morphogenesis of *Ulva mutabilis* (Chlorophyta) depends on a combination of two bacterial species excreting regulatory factors, J. Phycol. 48 (6) (2012) 1433–1447, https://doi.org/10.1111/j.1529-8817.2012.01231.x.
[87] L.M. van der Loos, S. D'Hondt, A. Willems, O. De Clerck, Characterizing algal microbiomes using long-read nanopore sequencing, Algal Res. 59 (2021) 102456, https://doi.org/10.1016/j.algal.2021.102456.
[88] I. Biancarosa, M. Espe, C. Bruckner, S. Heesch, N. Liland, R. Waagbø, B. Torstensen, E. Lock, Amino acid composition, protein content, and nitrogen-to-protein conversion factors of 21 seaweed species from Norwegian waters, J. Appl. Phycol. 29 (2) (2017) 1001–1009, https://doi.org/10.1007/s10811-016-0984-3.
[89] M. Bjarnadóttir, B.V. Aðalbjörnsson, A. Nilsson, R. Slizyte, M.Y. Roleda, G.Ó. Hreggviðsson, Ó.H. Friðjónsson, R. Jónsdóttir, *Palmaria palmata* as an alternative protein source: enzymatic protein extraction, amino acid composition, and nitrogen-to-protein conversion factor, J. Appl. Phycol. 30 (3) (2018) 2061–2070, https://doi.org/10.1007/s10811-017-1351-8.
[90] S.O. Lourenço, E. Barbarino, J.C. De-Paula, LodS Pereira, U.M.L. Marquez, Amino acid composition, protein content and calculation of nitrogen-to-protein conversion factors for 19 tropical seaweeds, Phycol. Res. 50 (3) (2002) 233–241, https://doi.org/10.1046/j.1440-1835.2002.00278.x.
[91] F. Mariotti, D. Tome, P.P. Mirand, Converting nitrogen into protein - beyond 6.25 and Jones' factors, Crit. Rev. Food Sci. Nutr. 48 (2) (2008) 177–184, https://doi.org/10.1080/10408390701279749.
[92] D. Shuuluka, J.J. Bolton, R.J. Anderson, Protein content, amino acid composition and nitrogen-to-protein conversion factors of *Ulva rigida* and *Ulva capensis* from natural populations and *Ulva lactuca* from an aquaculture system, in South Africa, J. Appl. Phycol. 25 (2) (2013) 677–685, https://doi.org/10.1007/s10811-012-9902-5.
[93] V. Figueroa, A. Bunger, J. Ortiz, J.M. Aguilera, Sensory descriptors for three edible Chilean seaweeds and their relations to umami components and instrumental texture, J. Appl. Phycol. (2022), https://doi.org/10.1007/s10811-022-02848-2.
[94] D.V. Robertson-Andersson, D.T. Wilson, J.J. Bolton, R.J. Anderson, G. W. Maneveldt, Rapid assessment of tissue nitrogen in cultivated *Gracilaria gracilis* (Rhodophyta) and *Ulva lactuca* (Chlorophyta), Afr. J. Aquat. Sci. 34 (2) (2009) 169–172, https://doi.org/10.2989/ajas.2009.34.2.7.894.
[95] K. Stedt, G.B. Toth, J. Davegård, H. Pavia, S. Steinhagen, Determination of nitrogen content in *Ulva fenestrata* by color image analysis – a rapid and cost-efficient method to estimate nitrogen content in seaweeds, Front. Mar. Sci. 9 (2022), https://doi.org/10.3389/fmars.2022.1081870.
[96] A.N.A. Aryee, D. Agyei, T.O. Akanbi, Recovery and utilization of seaweed pigments in food processing, Curr. Opin. Food Sci. 19 (2018) 113–119, https://doi.org/10.1016/j.cofs.2018.03.013.
[97] E. Manirafasha, T. Ndikubwimana, X. Zeng, Y. Lu, K. Jing, Phycobiliprotein: potential microalgae derived pharmaceutical and biological reagent, Biochem. Eng. J. 109 (2016) 282–296, https://doi.org/10.1016/j.bej.2016.01.025.
[98] A. Duinker, M. Kleppe, E. Fjære, I. Biancarosa, H.E. Heldal, L. Dahl, B.T. Lunestad, Knowledge Update on Macroalgae Food and Safety: Based on Data Generated in the Period 2014–2019 by the Institute of Marine Research, Ministry of Trade, Industry and Fisheries, Norway, 2020, https://doi.org/10.13140/RG.2.2.20134.14407.
[99] I. Maribu, K. Elvevold, K.E. Eilertsen, M.J. Blikra, Seasonal variation in the nutritional composition and potentially toxic elements of the red macroalga *Palmaria palmata* in the Arctic, Food Res. Int. 212 (2025) 116477, https://doi.org/10.1016/j.foodres.2025.116477.
[100] I. Rodushkin, N. Pallavicini, E. Engström, D. Sörlin, B. Öhlander, J. Ingri, D. C. Baxter, Assessment of the natural variability of B, Cd, Cu, Fe, Pb, Sr, Tl and Zn concentrations and isotopic compositions in leaves, needles and mushrooms using single sample digestion and two-column matrix separation, J. Anal. At. Spectrom. 31 (1) (2016) 220–233, https://doi.org/10.1039/C5JA00274E.
[101] K.C. Güven, A. K., T. Yurdun, Selectivity of heavy metal binding by algal polysaccharides, Toxicol. Environ. Chem. 47 (1–2) (1995) 65–70, https://doi.org/10.1080/02772249509358127.
[102] G. Jiao, G. Yu, J. Zhang, H.S. Ewart, Chemical structures and bioactivities of sulfated polysaccharides from marine algae, Mar. Drugs 9 (2) (2011) 196–223.
[103] Q. Chen, X.-D. Pan, B.-F. Huang, J.-L. Han, Distribution of metals and metalloids in dried seaweeds and health risk to population in southeastern China, Sci. Rep. 8 (1) (2018) 3578, https://doi.org/10.1038/s41598-018-21732-z.
[104] Swedish Food Agency, Näringsinnehåll Spenat. https://soknaringsinnehall.livsmedelsverket.se/Home/FoodDetails/4941, 2025. (Accessed 4 July 2025).
[105] M.J. Blikra, X. Wang, J. Philip, S. Dagbjørn, *Saccharina latissima* cultivated in northern Norway: reduction of potentially toxic elements during processing in relation to cultivation depth, Foods 10 (6) (2021) 1–18, https://doi.org/10.3390/foods10061290.
[106] P. Stévant, H. Marfaing, A. Duinker, J. Fleurence, T. Rustad, I. Sandbakken, A. Chapman, Biomass soaking treatments to reduce potentially undesirable compounds in the edible seaweeds sugar kelp (*Saccharina latissima*) and winged kelp (*Alaria esculenta*) and health risk estimation for human consumption, J. Appl. Phycol. 30 (3) (2018) 2047–2060, https://doi.org/10.1007/s10811-017-1343-8.
[107] I. Maribu, M.J. Blikra, K.E. Eilertsen, K. Elvevold, Protein enrichment of the red macroalga *Palmaria palmata* using pulsed electric field and enzymatic processing, J. Appl. Phycol. 36 (2024) 3665–3673, https://doi.org/10.1007/s10811-024-03338-3.
[108] J.P. Trigo, S. Steinhagen, K. Stedt, A. Krona, S. Verhagen, H. Pavia, M. Abdollahi, I. Undeland, A new method for protein extraction from sea lettuce (*Ulva fenestrata*) via surfactants and alkaline aqueous solutions, Food Chem. 464 (2025) 141839, https://doi.org/10.1016/j.foodchem.2024.141839.
[109] G.B. Toth, M. Hargrave, K. Stedt, S. Steinhagen, W. Visch, H. Pavia, Advances in Swedish seaweed aquaculture: enhancing biomass production and quality, Rev. Aquac. 17 (3) (2025) e70031, https://doi.org/10.1111/raq.70031.