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Advances in Swedish Seaweed Aquaculture: Enhancing Biomass Production and Quality

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ABSTRACT

Seaweed aquaculture is rapidly growing globally and offers environmental benefits such as reducing eutrophication and increasing biodiversity. Sweden has a long coast with favorable conditions for seaweed cultivation, but the current industry remains small. Over the past decade, several innovative research projects have explored and developed techniques tailored toward sustainable seaweed aquaculture. This study synthesizes recent advances in Swedish seaweed aquaculture research, highlighting innovations that support biomass yield and quality. We conducted a systematic review of 130 studies from the Thomson Reuters Web of Science, focusing on Swedish seaweed aquaculture research, and ultimately included 21 relevant publications from 1984 to 2025. The main seaweed species cultivated in Sweden are the brown seaweed *Saccharina latissima* and the green seaweed *Ulva fenestrata*. Key strategies to enhance biomass productivity, quality, and sustainability include optimizing land-based juvenile preparation, careful selection of cultivation sites, and strategic timing of sea-based harvests. Innovative approaches like the utilization of nutrient-rich process waters from food production offer sustainable methods to boost yield and protein content, aligning seaweed cultivation with circular economy principles. Future development and optimization of cultivation protocols for other protein-rich seaweed species (e.g., *Palmaria palmata*) or species that tolerate lower salinity (e.g., *Fucus vesiculosus* or *U. intestinalis*) will be critical to maximize the potential of Swedish seaweed cultivation, ensuring its effective contribution to food security and environmental conservation. As commercial interest in seaweed continues to grow, findings summarized here provide a robust foundation for the expansion of seaweed aquaculture in Europe and beyond.

1 | Introduction

Seaweed aquaculture is rapidly growing on a global scale, and seaweed biomass has the lowest resource use per ton of produced edible protein compared to other crops and farmed animals [1]. Seaweed cultivation can also provide environmental benefits such as remediation of eutrophicated coastal waters [2] or food industry process waters [3], and the cultivated biomass can be used for a variety of applications including food, feed, and biomaterials [4]. Furthermore, the productivity of seaweed communities is high, especially in temperate and polar regions [5]. Some seaweed species, including members of the genera *Saccharina* and *Ulva*, can be grown at high production rates (e.g., [6, 7]) and contain commercially valuable compounds (e.g., proteins, vitamins, micronutrients, and specific carbohydrates) [7–13], making them a promising raw material for various industries.

Seaweed aquaculture is still very minor in Sweden, despite a long coast with clean and relatively pristine waters and a

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positive perception of seaweed aquaculture by the public [14]. The coastal conditions in Sweden are partly unique, with a small tidal range, relatively large spatial variations in salinity and temperature, and an extensive archipelago that provides shelter for seaweeds from the extreme forces of full wave exposure on more open coasts. These features provide challenges but also opportunities for large-scale seaweed farming. The large salinity gradient along the coastline from the north-eastern parts of the Baltic Sea to the north-western parts of the Skagerrak (≈2–30 PSU) results in a corresponding change in species richness of the marine flora. The seaweed diversity in the brackish Baltic Sea is relatively low, and the benthic flora is dominated by green seaweeds toward the Gulf of Bothnia, while the diversity is distinctively higher in the Skagerrak, where the benthic flora is dominated by red and brown seaweeds [15] (Figure 1). Several seaweed species in the Skagerrak are interesting from an aquaculture and industry perspective [16] including kelps (*Saccharina latissima*, *Laminaria digitata*, and *L. hyperborea*) and valuable green (*Ulva* spp.) and red species (*Gracilaria* spp., *Chondrus crispus*, *Porphyra* spp., and *Palmaria palmata*). Many of these species contain commercially interesting compounds, and some are cultivated in other parts of the world [17]. While kelps are absent from the Swedish east coast, some *Ulva* species (e.g., *U. intestinalis*) thrive in the lower salinities present in this region [18]. These species have biochemical profiles similar to cultivated *Ulva* crop species, such as *U. fenestrata* [19]. All these species hold great potential for the rapidly developing Swedish seaweed aquaculture sector. Interest in seaweed as food is growing in Sweden, and farmed species include *S. latissima*, *L. digitata*, *Ulva* spp., and *P. palmata* [20]. Seaweed is sold fresh or

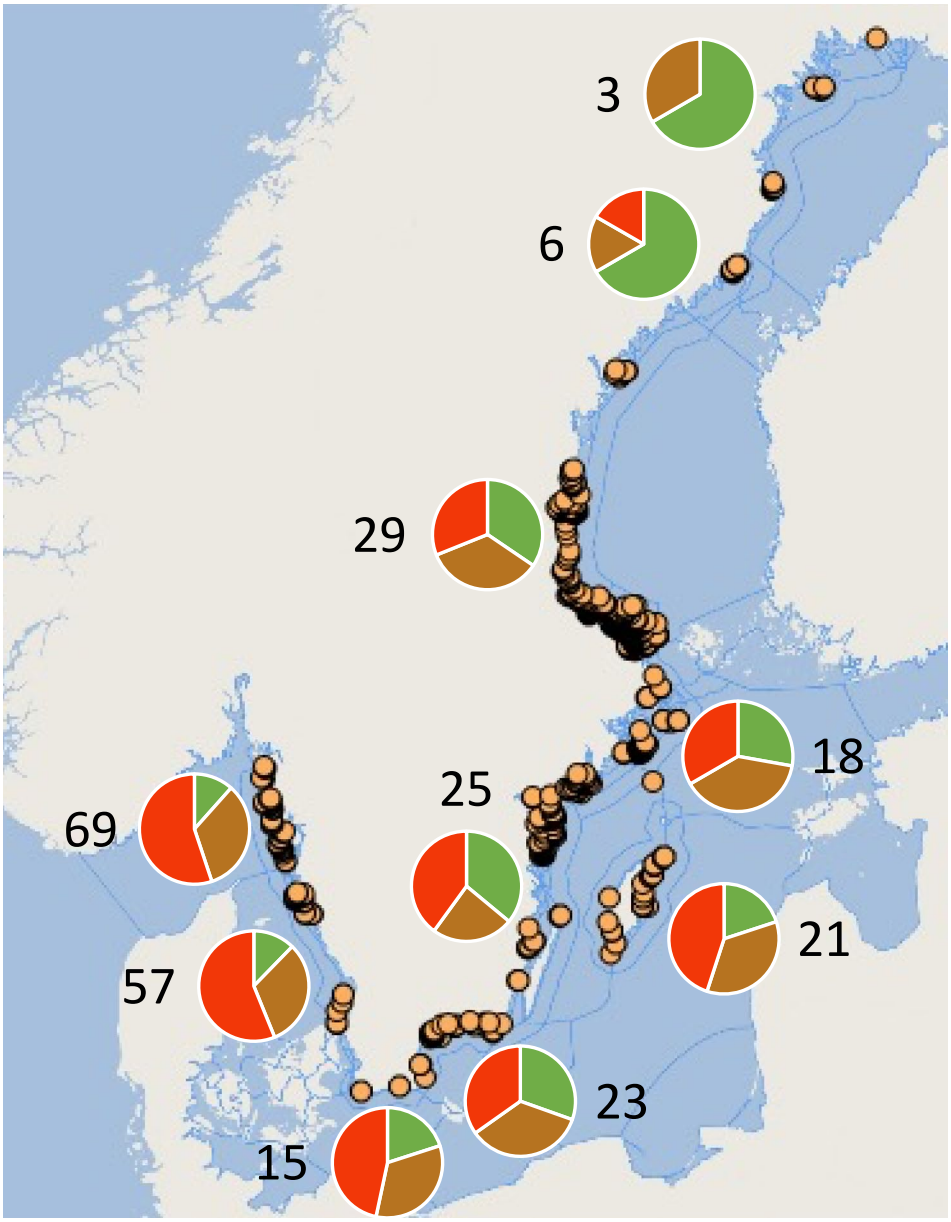


FIGURE 1 | Number of common seaweed taxa identified in different national monitoring programs 2020–2022 along the Swedish coastline. Pie charts show percentage of green, brown, and red seaweed taxa in different ocean basins. Yellow dots are sampling stations. Data retrieved from the Shark web database [15]. The true number of taxa is likely higher than those reported in monitoring programs, because rare and inconspicuous species may be overlooked. However, relative differences between ocean basins are probably correct.

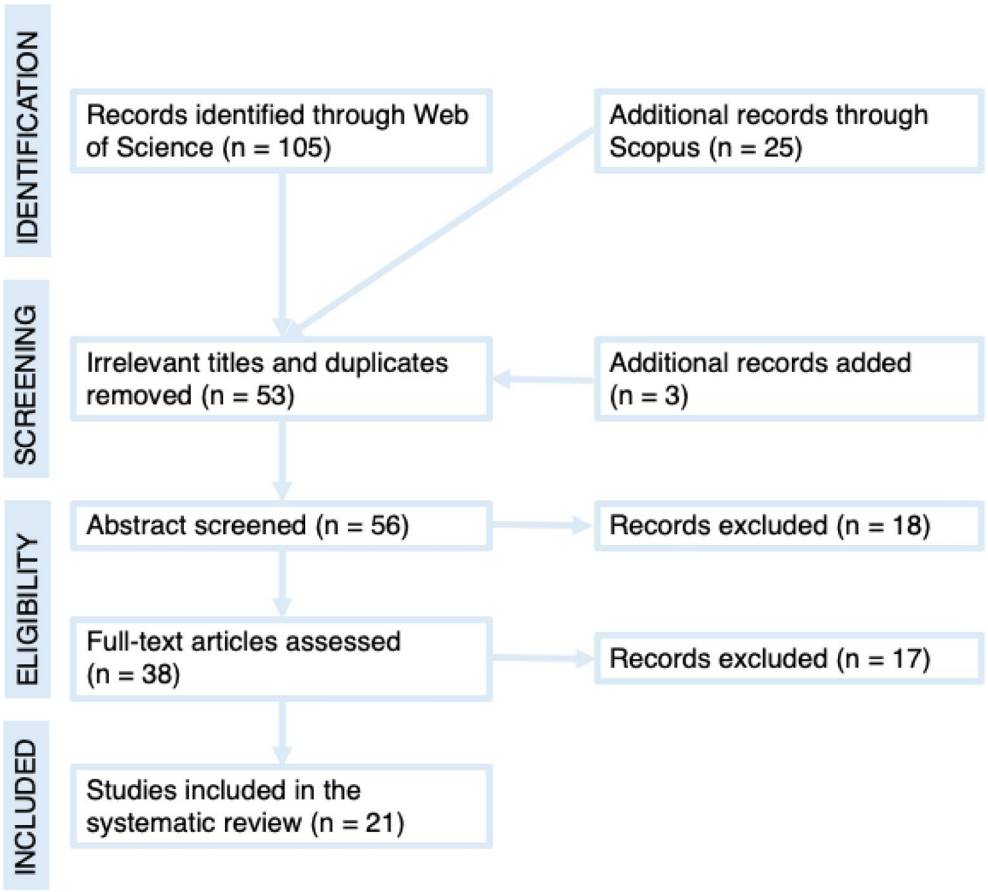


FIGURE 2 | PRISMA flowchart of the selection process of research articles studying development and optimization of yield and/or biochemical content of Swedish seaweed species.

processed through drying, blanching, freezing, or fermentation and is used in foods like spices, bread, pesto, snacks, soups, salads, pasta, and smoothies, as well as in food supplements [20].

Over the past decade, several national research projects have advanced Swedish seaweed aquaculture. These include SEAFARM (2013–2017), which explored the cultivation potential of *S. latissima* and *L. digitata*; AquaAgriKelp (2014–2018), which focused on upscaling kelp cultivation and established Sweden's first commercially operated kelp farm; and Sweaweed (2015–2020), which focused on the cultivation of *U. fenestrata*. Two projects, CirkAlg (2018–2021) and BlueGreen (2021–2025), focused on the potential of Swedish seaweed as a contributor to the "protein shift" by generating new circular cultivation techniques and biomass treatment methods. Currently, the projects SenseAlg (2022–2025) and Susweed (2023–2028) aim to promote the consumption of seaweeds through the development of new consumer products for the food market and through refined cultivation techniques for *U. fenestrata* and *P. palmata*. The aim of the present review is to present a summary of Swedish seaweed aquaculture research, focusing on the production of seaweed biomass and its quality and biochemical content.

2 | Methods

We used a systematic review approach to objectively search for relevant publications. The search terms were "Swed* AND (macroalg* OR seaweed*) AND (cultiv* OR aquacult*) AND (growth* OR yield* OR protein* OR qualit*)". The Thomson Reuters Web of Science was searched for all literature published before April 2024, and a total of 130 studies were retrieved. Criteria for including studies in the systematic review were that research (1) was performed in Sweden on native Swedish species, and (2) was aimed at optimizing seaweed biomass yield and/or quality during any stage of production. Studies that focused solely on down-stream processing of seaweed biomass (e.g., preservation, processing, extraction, or transformation of specific biomass components) were excluded from the review. After applying these criteria and screening the reference lists for additional relevant papers, 21 publications between 1984 and 2025 were retrieved for the systematic review (Figure 2). Data (mean values and standard error of the mean [SEM] or standard deviation [SD] for different treatments) were retrieved either directly from tables or from figures using the free software WebPlotDigitizer-4.2 [21] and are presented in Tables 1 and 2.

3 | Results

The retrieved publications mainly focused on the brown seaweed species *S. latissima* and the green seaweed species *U. fenestrata* and on raising seaweed juveniles and adults in both land- and seabased cultivation systems (Figure 3). The research topics included optimization of cultivation conditions, temporal and spatial factors influencing biomass yield

TABLE 1 | Data (mean ± SEM and % change) extracted from publications (Ref) investigating different sources of variation on yield and quality (Dependent variable) of cultivated *Saccharina latissima*.

Source of variation	Levels	Dependent variable	Mean	SEM	% change compared to	Ref
Binder treatments	Control	No of settled sporophytes cm^{-1}	47.55	3.58	71*	[22]
	Treatments		27.84	2.40	—	
Pre-cultivation time	2 weeks	Weight (g)	34.20	6.40	—	[23]
	4/6 weeks		57.20	5.20	67*	
Deployment time	September	Weight (g)	167.80	30.80	135*	
	October/November		71.30	6.30	—	
	September	Carbohydrates (mg g^{-1} dw)	675.50	52.50	10	
	October/November		616.50	39.80	—	
	September	Fatty acids (mg g^{-1} dw)	7.10	0.20	9	
	October/November		6.50	0.10	—	
	September	Proteins (mg g^{-1} dw)	31.10	5.10	—	
	October/November		47.50	6.50	53*	
Cultivation depth	2 m	Weight (g)	143.80	36.80	251*	
	4 m		40.92	11.64	—	
	2 m	Carbohydrates (mg g^{-1} dw)	717.00	65.00	29*	
	4 m		555.50	39.50	—	
	2 m	Fatty acids (mg g^{-1} dw)	6.90	0.20	1	
	4 m		6.80	0.20	—	
	2 m	Proteins (mg g^{-1} dw)	26.30	5.10	—	
	4 m		55.10	6.80	110*	
Area × exposure	North/Middle region	Size (g)	5.47	0.54	206*	[24]
	South region		1.79	0.21	—	
	Moderately exposed/ Sheltered area	Size (g)	4.82	0.45	72*	
	Exposed area		2.79	0.37	—	
	Exposed	Tissue carbon content (% dw)	31.64	0.40	5	
	Moderate/Sheltered		30.03	0.56	—	
	Exposed	Tissue nitrogen content (% dw)	0.99	0.07	−15*	
	Moderate/Sheltered		1.17	0.06	—	
	Moderate/Sheltered South	Biofouling (% area)	15.86	2.52	310*	
	Moderate/Sheltered Northern/middle exposed		3.87	0.93	—	
Nutrient addition	Control	Elongation (mm d^{-1})	17.95	1.34	—	[25]
	IMTA1		24.10	1.76	34*	
	IMTA2		27.51	3.35	53*	

(Continues)

TABLE 1 | (Continued)

Source of variation	Levels	Dependent variable	Mean	SEM	% change compared to	Ref
	Control	Tissue nitrogen content (% dw)	0.70	0.10	—	
	IMTA1		1.70	0.50	143*	
	IMTA2		2.10	0.50	200*	
Nutrient addition	Control	Relative growth rate (mm d^{-1})	5.97	0.03		[26]
	Treated		5.90	0.04	−1	
	Control	Biofouling (abundance cm^{-2})	6.97	0.76	−43*	
	Treated		3.99	0.50	—	
	Control	Tissue nitrogen content (% dw)	2.82	0.11	8*	
	Treated		3.04	0.09	—	
Nutrient addition	Control	Weight (kg/m)	1.69	0.23	—	[27]
	Farm		2.49	0.20	47*	
Depth	1 m	Weight (kg/m)	2.85	0.28	114*	
	3 m		1.33	0.15	—	
	1 m	Tissue nitrogen content (% dw)	1.67	0.13	13*	
	3 m		1.48	0.10	—	
Nutrient × depth	Control 1 m	Epiphyte coverage (% area)	14.83	4.08	59*	
	Farm 1 m		6.12	2.24	—	
	Control 3 m	Epiphyte coverage (% area)	5.58	1.77	63*	
	Farm 3 m		2.04	1.36	—	
Exposure	Kärringön (exposed area)	Wet weight (g)	31.94	2.21	206*	[28]
	Other more sheltered areas		10.45	3.95	—	

*Denote statistically significant changes ($p < 0.05$).

and quality, and treatments aimed at a sustainable increase in nutrient availability (Figure 3). Protein and nitrogen content are correlated in seaweeds [37] and in all the reviewed papers, crude protein content was calculated from the tissue nitrogen content with a conversion factor of five [37].

3.1 | *Saccharina latissima* Aquaculture

Saccharina latissima (Linnaeus) C.E. Lane, C. Mayes, Druehl and G.W. Saunders 2006, is a cold-water kelp species that can be found along the Swedish west coast but is absent from the Baltic Sea due to its more marine salinity requirements [38]. It grows at relatively sheltered to exposed rocky shores where it can form extensive underwater forests that provide shelter and food for many associated organisms [39]. *Saccharina latissima* is commercially cultivated in several northern European countries (e.g., Faroe Islands, Denmark, Norway) [40–42]. Like other kelp species of the genus Laminariales, *S. latissima* has a haplodiplontic, heteromorphic lifecycle with microscopic, branched, uniseriate haploid gametophytes with apical growth and macroscopic, foliose, parenchymatous diploid sporophytes with intercalary growth [43].

3.1.1 | Seeding and Pre-Cultivation of Juveniles

The cultivation of *S. latissima* is divided into two phases: a land-based phase, where juvenile sporophytes are prepared, and a sea-based phase, where juveniles are transplanted to a sea-based cultivation site for growth into adults. The preparation of juvenile sporophytes involves various steps [22–24]. In Sweden, adult non-fertile sporophytes are collected from the field in summer or early autumn (June to August). Fertility is induced by cutting the laminas approximately 15–20 cm above the intercalary meristem, followed by incubation in half-strength Provasoli

TABLE 2 | Data (mean ± SEM and % change) extracted from publications (Ref) investigating different sources of variation on yield and quality (Dependent variables) of cultivated *Ulva fenestrata*.

Source of variation	Levels	Variable	Mean	SEM	% change compared to	Ref
Life-history phase	Recombinant gametophytes	Length (mm)	4.34	1.26	54*	[29]
	Clonal gametophytes		2.81	0.54	—	
	Recombinant gametophytes	Crude proteins (% dw)	22.67	0.67	22*	
	Clonal gametophytes		18.51	0.48	—	
	Recombinant gametophytes	Fatty acids (% dw)	2.27	0.06	3*	
	Clonal gametophytes		2.21	0.04	—	
	Recombinant gametophytes	Pigments (% dw)	0.34	0.02	19*	
	Clonal gametophytes		0.28	0.02	—	
	Recombinant gametophytes	Carbohydrates (% dw)	21.91	0.43	—	
	Clonal gametophytes		22.37	0.66	2	
Swarmer density	High	Yield (g dw m^{-1})	31.05	4.42	474*	[30]
	Low		5.41	2.19	—	
Harvest time	April	Yield (g dw m^{-1})	48.34	3.44	−80*	[31]
	Early May		115.17	3.51	−53*	
	Late May		243.13	3.89	—	
	Early June		194.79	5.29	−20	
	Mid June		136.49	5.01	−44*	
	April	Crude proteins (% dw)	20.55	0.66	—	
	Early May		7.12	0.30	−65*	
	Late May		7.12	0.35	−65*	
	Early June		5.83	0.35	−72*	
	Mid June		4.72	0.43	−77*	
Harvest time	April	Fatty acids (% dw)	20.56	0.72	—	
	Early May		3.89	0.94	−81*	
	Late May		7.44	0.88	−64*	
	Early June		6.67	1.37	−68*	
	Mid June		6.78	1.33	−67*	
Harvest time	April	Pigments (mg g^{-1})	40.9	0.32	—	
	Early May		36	0.93	−12*	
	Late May		32.1	0.48	−22*	
	Early June		28	0.58	−32*	
	Mid June		23.8	0.71	−42*	
	April	Carbohydrates (% dw)	32.10	1.27	−20*	
	Early May		33.43	0.94	−17*	
	Late May		29.45	2.03	−26*	
	Early June		38.73	1.67	−3	
	Mid June		40.06	0.77	—	

(Continues)

TABLE 2 | (Continued)

Source of variation	Levels	Variable	Mean	SEM	% change compared to	Ref
Irradiance	50 μmol photons $m^{-2} s^{-1}$	Growth rate (% day^{-1})	22.53	0.89	—	[32]
	100 μmol photons $m^{-2} s^{-1}$		26.08	0.76	16*	
	160 μmol photons $m^{-2} s^{-1}$		25.19	1.27	12*	
Temperature	13°C	Growth rate (% day^{-1})	25.95	0.38	11*	
	18°C		23.29	1.01	—	
Irradiance	50 μmol photons $m^{-2} s^{-1}$	Fatty acids (% dw)	1.43	0.05	—	
	100 μmol photons $m^{-2} s^{-1}$		1.29	0.03	−9*	
	160 μmol photons $m^{-2} s^{-1}$		1.21	0.05	−15*	
Temperature	13°C	Fatty acids (% dw)	1.20	0.03	−16*	
	18°C		1.43	0.02	—	
Nitrogen	< 5 μmol L^{-1} NO_3^-	Fatty acids (% dw)	1.32	0.02	—	
	150 μmol L^{-1} NO_3^-		1.73	0.05	31*	
	500 μmol L^{-1} NO_3^-		1.79	0.02	35*	
Irradiance	50 μmol photons $m^{-2} s^{-1}$	Crude proteins (% dw)	9.46	0.50	—	
	100 μmol photons $m^{-2} s^{-1}$		7.97	0.41	−16*	
	160 μmol photons $m^{-2} s^{-1}$		6.89	0.41	−27*	
Temperature	13°C	Crude proteins (% dw)	9.13	0.41	31*	
	18°C		6.97	0.33	—	
Nitrogen	< 5 μmol L^{-1} NO_3^-	Crude proteins (% dw)	5.15	0.17	—	
	150 μmol L^{-1} NO_3^-		15.06	0.54	193*	
	500 μmol L^{-1} NO_3^-		16.89	0.34	228*	
Irradiance	50 μmol photons $m^{-2} s^{-1}$	Phenolics (% dw)	0.13	0.00	—	
	100 μmol photons $m^{-2} s^{-1}$		0.13	0.00	−6	
	160 μmol photons $m^{-2} s^{-1}$		0.11	0.00	−19*	
Nitrogen	< 5 μmol L^{-1} NO_3^-	Phenolics (% dw)	0.15	0.01	—	
	150 μmol L^{-1} NO_3^-		0.23	0.01	51*	
	500 μmol L^{-1} NO_3^-		0.23	0.01	47*	
Temperature	13°C	Carbohydrates (% dw)	33.90	0.63	−10*	[33]
	18°C		37.69	0.65	—	
Nitrogen	< 5 μM NO_3^-	Carbohydrates (% dw)	31.44	1.42	—	
	150 μM NO_3^-		27.24	1.18	−13*	
	500 μM NO_3^-		26.71	1.88	−15*	
HPPWs	Seawater control (28 days)	Fresh weight (g)	6.17	0.20	—	[34]
	SAL (28 days)		27.26	0.70	342*	
	TUB (28 days)		37.11	1.99	502*	
	Seawater control (14 days)	Fresh weight (g)	9.80	0.98	—	
	SAL (14 days)		16.57	1.27	69*	
	TUB (14 days)		18.24	1.13	86*	

(Continues)

TABLE 2 | (Continued)

Source of variation	Levels	Variable	Mean	SEM	% change compared to	Ref
	Seawater control (28 days)	Crude proteins (% dw)	12.90	0.24	—	
	SAL (28 days)		33.39	0.81	159*	
	TUB (28 days)		31.77	0.48	146*	
	Seawater control (14 days)	Crude proteins (% dw)	8.39	0.32	—	
	SAL (14 days)		29.84	0.48	256*	
	TUB (14 days)		30.24	0.24	261*	
HPPWs	Control	Fresh weight (g)	164	7.33	—	[35]
	SAL		230	1.33	40*	
	TUB		214	4.00	30*	
	Control	Crude proteins (% dw)	2.88	0.10	—	
	SAL		12.02	0.50	320*	
	TUB		16.94	0.35	488*	
HPPWs	Control (PES)	Fresh weight (g)	614.79	1.21	—	[36]
	TUB		600.82	4.25	2*	
	Start	Crude proteins (% dw)	21.80	0.17	—	
	Control (PES)		26.80	0.29	23*	
	TUB		37.40	1.04	72*	

*Denote statistically significant changes ($p < 0.05$).

medium (PES) [44] at 10°C under white light (≈100 μmol photons $m^{-2} s^{-1}$) and short-day (8 h light:16 h dark) conditions. After 5–10 weeks, fertile sorus tissue is dissected and kept overnight in damp paper towels at 10°C to induce zoospore release. After emersion in seawater, released zoospores develop into gametophytes that can be grown vegetatively for > 6 months if they are kept in aerated flasks at 12°C under red light and long-day (16 h light: 8 h dark) conditions [22–24]. Furthermore, gametophytes can be cryopreserved for long-term storage using different combinations of cooling methods and cryoprotectants [45]. Gamete release and fertilization are induced by transferring the gametophytes to white light (35–70 μmol photons $m^{-2} s^{-1}$) and long-day (16 h light: 8 h dark) conditions. The resulting juvenile sporophytes are seeded for out-planting to the sea-based cultivation site by allowing zoospores/gametophytes to attach and mature for several weeks or months on thin twine in tank cultures [22–24].

The preparation of juveniles is energy and labor intensive, and it is desirable from an economic point of view to minimize the time juveniles spend in the tank cultures. To simplify the seeding process, spores, gametophytes, or juvenile sporophytes can be applied to ropes using different binder treatments [46]. Binders (usually a hydrocolloid) allow in situ adhesion of the microscopic gametophytes and embryonic sporophytes (or a mix of both) onto substrates and allow for direct transfer to the sea-based cultivation without pre-cultivation in land-based tank cultures. Visch et al. [22] applied two different binder treatments (agar and *k*-carrageenan) and application procedures (gametophytes added on top of binder or mixed with binder) to investigate if this procedure is suitable for Swedish *S. latissima*. The binder treatments decreased the number of surviving sporophytes irrespective of application method [22] (Table 1). At a flow speed of 0.5 cm s^{-1}, 71% more juvenile sporophytes were found in the controls without binder treatment, indicating that the tested binder treatments were not effective for Swedish *S. latissima* [22] (Table 1). However, these results should be interpreted with caution as they derive from a single study.

Another way to reduce the cost associated with the juvenile preparation is to decrease the juvenile pre-cultivation time. Thomas et al. [23] investigated the effect of juvenile pre-cultivation time and timing of deployment on adult *S. latissima* sporophyte size and biochemical content at harvest. Juveniles were developed from spores and pre-cultivated for 2, 4, or 6 weeks in land-based tanks and were deployed either in September, October, or November at the same sea-based farm site. All seaweeds were harvested at the end of May. Adult sporophytes pre-cultivated for 4 and 6 weeks were 67% larger in terms of wet weight compared to sporophytes pre-cultivated for 2 weeks [23] (Table 1). Furthermore, sporophytes deployed in early autumn (September) were 135% heavier and had 10% higher total carbohydrate and 9% higher fatty acid content compared to sporophytes deployed in October and November [23] (Table 1). However, the protein content was 53% higher in sporophytes deployed late in November compared to September [23]. These results indicate that a land-based pre-cultivation period of juveniles for at least 4 weeks is needed for optimal yield and that deployment timing is important for both the yield and biochemical content of the adult *S. latissima* sporophytes. However, size at harvest and biochemical content varied on different spatial scales, from replicate cultivation ropes to different cultivation

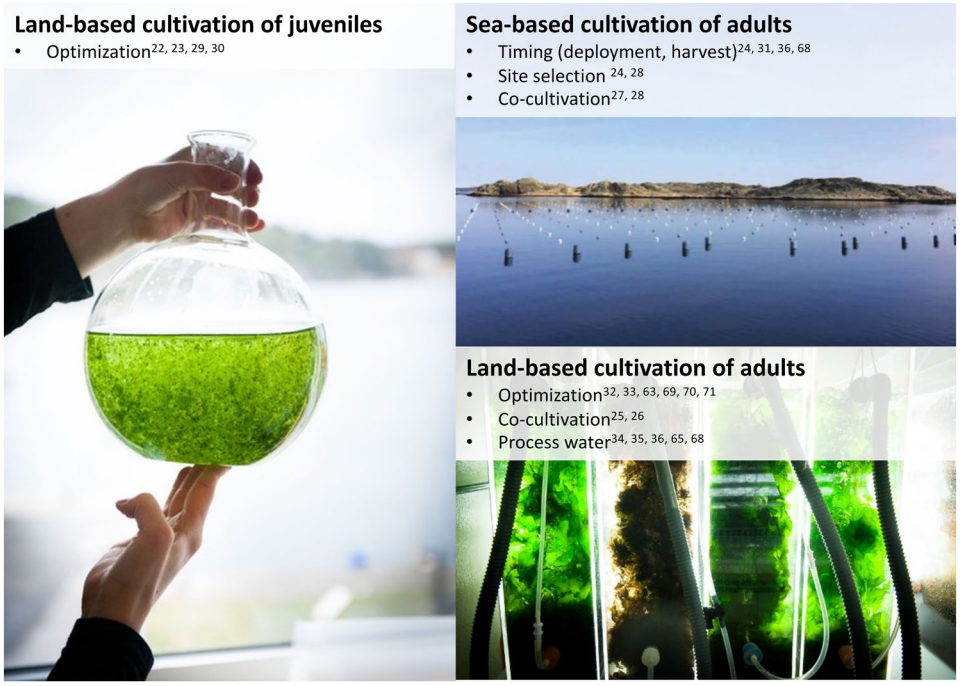


FIGURE 3 | Subject overview and publications included in the systematic review. (a) Laboratory culture of *Ulva fenestrata* juveniles, (b) Sea-based seaweed cultivation site in the Koster Archipelago, Sweden (58°51′33.4″ N 11°4′3.9″ E), and (c) Tank cultures of *U. fenestrata*. Reference numbers are the same as in reference list. Photos: Karin Björk, Göran Nylund, and Gunnar Cervin.

sites [23], indicating that site selection is also important in *S. latissima* aquaculture.

3.1.2 | Spatial Selection of Optimal Cultivation Sites

Selecting suitable cultivation sites is essential for optimizing *S. latissima* yield at harvest. Environmental factors such as light and nutrient availability, salinity, temperature, and wave exposure impact sporophyte growth and vary across spatial scales. Thomas et al. [23] found that the cultivation depth (2 m vs. 4 m) significantly affects sporophyte size at harvest. Sporophytes grown at 2 m were 251% heavier compared with sporophytes grown at 4 m [23] (Table 1), likely due to greater light availability at 2 m. While the total fatty acid content remained consistent between depths, sporophytes at 2 m had a 29% higher total carbohydrate content, whereas those at 4 m showed 110% higher total protein content [23] (Table 1).

Visch et al. [24] further investigated the variation in growth, carbon and nitrogen content, and biofouling of *S. latissima* at different spatial scales and three levels of wave exposure along the ~400 km Swedish west coast [24]. Despite similar average nutrient concentrations, irradiance, salinity, and temperature across regions, significant growth variations were observed at all spatial scales, from duplicate ropes 20 m apart to regions separated by 20 km. Overall, the sporophytes growing in the north/middle region were 206% larger than seaweeds growing in the south region, and sporophytes growing in moderately exposed/sheltered areas were 72% larger compared to seaweeds growing in the exposed areas [24] (Table 1). The carbon content was 5% higher, and nitrogen content was 15% lower, in seaweeds grown in exposed compared to moderately exposed/sheltered sites. Furthermore, biofouling was 310% higher in the moderately exposed/sheltered sites in the southernmost region compared to the northern/middle region and the exposed sites [24] (Table 1).

3.1.3 | Added Nutrients—Co-Cultivation With Bivalves

Integrated multi-trophic aquaculture (IMTA) combines species from different trophic levels to utilize excess nutrients and prevent environmental degradation [47, 48]. Extractive species such as bivalves and seaweeds are often included in these systems to scavenge particulate and dissolved nutrients from fed aquaculture such as finfish or crustaceans [49, 50]. Even without a fed species, integrating seaweeds with bivalves can help mitigate local nutrient loading [27] and increase seaweed quality as bivalves emit their own metabolic wastes [51] and potentially reduce fouling organisms due to their filtering capacity [26, 27].

The effect of added nutrients on *S. latissima* growth was tested in outdoor tanks, using both artificial nutrients and blue mussel (*Mytilus edulis*) effluents [25]. Artificial nutrient concentration and composition were chosen to mimic effluents from finfish farms (IMTA1, on average 2.73, 3.2, and 0.07 $\mu mol\,L^{-1}$ ammonium, nitrate, and phosphate respectively), and mussels were added to study the combined effect of nutrients released from an IMTA setting with fish and bivalves (IMTA2, on average 3.11, 2.66, and 0.13 $\mu mol\,L^{-1}$ ammonium, nitrate, and phosphate, respectively). The relatively modest nutrient addition compared to controls (on average 1.14, 0.36, and 0.08 $\mu mol\,L^{-1}$ ammonium, nitrate, and phosphate, respectively) resulted in 34%–53% more growth in terms of elongation and 143%–200%

higher total nitrogen content in one-year-old *S. latissima* sporophytes [25] (Table 1). In contrast, no significant growth difference was observed when co-cultivating *S. latissima* sporophytes with bivalves only (blue mussels and oysters, *Magallana gigas*) in a similar tank-cultivation experiment (Table 1) [26]. The relative nutrient increase in the bivalve treatments was lower (on average 4.4 and 0.64, 5.5 and 0.73, and 4.9 and 0.72 $\mu mol\,L^{-1}$ ammonium and phosphate in control, blue mussel, and oyster treatments respectively) compared to the treatment effect in the study by Rugiu et al. [25]. However, bivalve treatments decreased biofouling by 43% and increased the nitrogen content by 8% in treated sporophytes compared to controls that received seawater only [26] (Table 1).

The experiments described above were both done in outdoor tank systems and may have overestimated the effect of bivalves on seaweeds as there is no nutrient dilution from waves or currents. In a field setting, nutrients from finfish farms are typically diluted to background concentrations within 200 m from the farm [52, 53]. Furthermore, the capacity of the bivalves to remove biofouling propagules may also be overestimated because most of the water passes through the bivalve "filter." Hargrave et al. [27] investigated integrated co-cultivation by deploying *S. latissima* at 1 and 3 m depth in a commercial-scale blue mussel farm on the Swedish west-coast [27]. They found a 47% higher yield of kelp cultivated near the mussel farms compared to control sites 500 m upstream of the farm sites, and the kelp at 1 m depth grew 114% more compared to 3 m [27] (Table 1). The kelp nitrogen content was not affected by proximity to farms, but seaweeds at 1 m depth had 13% higher nitrogen content compared to those at 3 m [27]. Furthermore, biofouling on kelp lamina was reduced by 59% and 63% at 1 and 3 m depth near the farms [27] (Table 1). As biofouling and nutrient limitation are commonly discussed as problems in seaweed aquaculture [54], these results indicate additional benefits of co-cultivation of kelp and blue mussels beyond nutrient addition.

Co-cultivation can be challenging when species have different environmental requirements and optima for growth. For example, blue mussels need a high availability of phytoplankton and can tolerate a wide range of temperatures and salinities [55]. Kelps, on the other hand, prefer areas rich in dissolved nutrients, with less resuspended material and sufficient light availability and are usually not as tolerant to fluctuating temperature and salinity conditions [56, 57]. Visch et al. [28] investigated spatial growth differences and nutrient mitigation capacity of *S. latissima* and blue mussels at scales ranging from 500 m to more than 50 km in a Swedish fjord system. They found that optimum conditions for *S. latissima* and blue mussel growth differ, with kelp growth 206% higher at the outer, relatively exposed areas, while inner, relatively sheltered areas favored blue mussel growth [28] (Table 1). These results clearly show the importance of careful site selection when considering co-cultivating different species together in an IMTA setting, compared to monocultures.

3.2 | *Ulva fenestrata* Aquaculture

Ulva fenestrata Postels and Ruprecht 1840, is a marine species found along the Swedish Skagerrak coast down to the Danish straits but is absent from the Baltic Sea [58]. It grows to a depth of about 0.5 m attached to stones or as epiphytes on other seaweeds. *Ulva fenestrata* has a haplodiplontic, isomorphic lifecycle with identical macroscopic gametophyte and sporophyte generations [43]. The haploid gametophytes are either recombinant and originate from haploid zoids or clonal and originate from unmated gametes [59]. Swarmer (gametes and zoids) formation and release are controlled by different inhibitors and can be induced if these are removed [59]. Foliose members of *Ulva*, such as *U. fenestrata*, show potential as free-floating cultures in tanks, bioreactors, basins, or ponds [32, 60–62].

3.2.1 | Pre-Cultivation of Juveniles—Seeding Density, Temperature, and Nutrient Availability

Ulva fenestrata can be cultivated by vegetative propagation in land-based tank cultures or on seeded long-lines in the open ocean. In the latter case, cultivation techniques resemble those of *S. latissima* in that both a land-based seeding and pre-cultivation phase and a sea-based growth phase are needed. To optimize conditions in the pre-cultivation phase, the early ontogenetic development of gametes and unmated zoids cultivated at different densities (500, 5000, and 10,000 swarmers mL^{-1}) and exposed to different temperatures (10°C and 15°C) and nutrient conditions (PES or 3xPES medium) [44] were studied [29]. Furthermore, the biochemical profiles of the resulting recombinant and clonal gametophytes were compared after 12 weeks of pre-cultivation in tank cultures. Swarmer density and temperature had relatively small effects on the growth and biochemical content of juvenile *U. fenestrata*, but nutrient addition was needed for normal development in all treatments. Recombinant gametophytes had faster ontogenetic development, a 54% higher growth rate in terms of length, and contained 22% more crude proteins, 3% more fatty acids, and 19% more pigments compared to clonal gametophytes [29] (Table 2). Carbohydrate content was similar among the different life-history phases, with clonal gametophytes having, on average, a 2% higher carbohydrate content [29] (Table 2).

In a separate experiment, clonal *U. fenestrata* gametophytes were seeded on twine at different densities (500, and 10,000 swarmers mL^{-1}) and exposed to different temperatures (10°C and 15°C) and nutrient conditions (PES or 3xPES) for 6 weeks in the land-based pre-cultivation phase [30]. The differently treated juvenile gametophytes were then transplanted to a sea-based cultivation site and allowed to grow for 6 months (October to April). At harvest, the yield of adult *U. fenestrata* seeded at a high swarmer density was 474% higher compared to the yield of seaweeds seeded at a low density [30] (Table 2), possibly due to a better resistance to fouling and over-growth. However, nutrient addition and temperature during the pre-cultivation phase had only minor effects on the yield of adult *U. fenestrata* grown in the sea. Furthermore, all the applied treatments during the pre-cultivation phase had only minor effects on the biochemical content of the adult *U. fenestrata* gametophytes [30]. The biochemical contents were in the ranges of 16.6%–20.7% dry weight (dw) for crude proteins, 3.2%–3.6% dw for total fatty acids, 25.7%–29.7% dw for total carbohydrates, 2.5%–3.8% dw for total pigments, and 0.2%–0.3% dw for total phenolics [30]. These results show that nutrient addition

is needed for the normal development of *U. fenestrata* in the pre-cultivation phase and that seeding with a high swarmer density results in a higher yield at harvest. However, the environmental conditions (temperature and nutrients) during the pre-cultivation phase have minor effects on the yield and quality of the adult seaweeds.

3.2.2 | Timing of Harvest

Biomass yield and quality were further investigated in a large-scale (2 ha) cultivation experiment where *U. fenestrata* was harvested at different time points [31]. Juveniles were seeded at high density (10,000 swarmers mL^{-1}), pre-cultivated for 6 weeks at 15°C with nutrient addition (normal strength PES medium) [44], and transplanted to the farm site in the autumn (October). Biomass yield, biofouling, and biochemical content were determined at different harvest dates (starting early April and continuing to mid-June). Harvest time affected most of the measured variables. The biomass yield was highest in late May; between 25% and403% higher than the earlier or later harvest dates [31] (Table 2). Biomass quality in terms of crude protein, fatty acid, and pigment (Chl *a* and *b*) content was between 189%–335%, 176%–429%, and 14%–72% higher in early April compared to later harvest dates [31] (Table 2). Total carbohydrates increased slightly at the end of the harvest season (mid-June) and were between 3% and 36% higher than the earlier harvest dates [31] (Table 2). This study clearly showed that there is a trade-off between biomass quality and yield (i.e., higher quality early but higher yield later in the season) and that the timing of harvest of *U. fenestrata* is highly dependent on the downstream application of the biomass (e.g., food or biomaterials).

3.2.3 | Optimizing Biomass Yield and Quality in Tank Cultures

The advantage with indoor tank cultivation is that environmental factors such as light, temperature, nutrients, and CO_2 can be manipulated to maximize yield or content of desired biochemicals (such as proteins, lipids or carbohydrates) [32, 33]. Different environmental factors contributing to the growth and quality of *U. fenestrata* were tested in a series of multifactorial experiments manipulating levels of irradiance, temperature, nutrients (nitrate and phosphate), and CO_2 [32, 33]. The seaweeds had a 16% higher growth rate in ≥ 100 μmol photons $m^{-2} s^{-1}$ compared with 50 μmol photons $m^{-2} s^{-1}$, and an 11% higher growth rate in 11°C compared with 18°C [62] (Table 2). Surprisingly, neither the addition of nutrients (150 or 500 μmol L^{-1} nitrate and/or 50 μmol L^{-1} phosphate) nor CO_2 (2500 ppm) increased the yield of *U. fenestrata*, possibly due to induction of fertility and swarmer release [32]. Corroborating these results, the growth of *U. fenestrata* was not affected by nutrient addition (PES or 3xPES medium), but fertility was 29% higher in the nutrient treatments compared to the control [63]. However, there was a trade-off in terms of biomass growth and quality, as high and medium irradiance resulted in 9% and 15% lower fatty acid, 16% and 27% lower crude protein, and 6% and 19% lower phenolic content, respectively, compared with low irradiance [32]. Low temperature, on the other hand, resulted in 16% lower fatty acid, 31% higher crude protein content, and 10% lower total carbohydrate content compared to high temperature [32, 33] (Table 2). The addition of nutrients (especially 150 and 500 μmol L^{-1} nitrate) increased biomass quality in terms of crude proteins by 193 and 228%, fatty acids by 31% and 35%, and phenolic content by 51% and 47%, and decreased the total carbohydrate content by 13% and 15% [32, 33] (Table 2).

For seaweeds to become tenable alternative protein sources, cultivation conditions need to be optimized to maximize protein content. Early harvest and addition of nutrients will increase the likelihood of a biomass with high protein content [32, 33], but the protein content of seaweeds is commonly lower than in traditionally farmed crops, such as soybeans (with a crude protein content of 35%–40% dw) [64]. One way of increasing the protein content is to cultivate seaweeds in nutrient-rich process water from food industries [3]. In a screening experiment, the growth rate and crude protein content of three green seaweed species (*U. fenestrata, U. intestinalis*, and *Chaetomorpha linum*) were compared after 8 days of cultivation in two dilutions (providing 20 and 200 μmol L^{-1} ammonium) of 8 different process waters [65]. The process waters originated from salmon aquaculture, production of peeled shrimps, marinated herring, and oat-based products, and two controls were included (seawater with ambient nutrient concentrations and seawater enriched with NH_4Cl) [65]. Growth rates of the green seaweeds were up to 62%, 63%, and 18% higher (17.3%, 8.2%, and 9.5% d^{-1}), and crude protein content was up to 131%, 256%, and 283% higher (23.2%, 21.9%, and 25.1% dw) in *U. fenestrata*, *U. intestinalis*, and *C. linum*, respectively when cultivated in the food production process waters, compared to seawater controls [65]. Growth rates were on average 20% higher in the presence of 20 μmol L^{-1} compared to 200 μmol L^{-1} ammonium (8.5% vs. 7.1% d^{-1}), which indicates that high ammonium concentrations can be inhibitory for seaweed growth [66].

Ulva fenestrata was further tested as a candidate species in a circular production system where nutrients in herring production process waters (HPPWs) were used to produce sustainable protein-rich biomass [34–36, 65]. The effect of two types of HPPWs on *U. fenestrata* growth and crude protein content was tested in two tank cultivation experiments [34]. The process waters included saturated salt brine from maturation of herring fillets (SAL) and tub water from in-house pre-processing storage of whole herring in 3% NaCl (TUB). The HPPWs were diluted to contain 25 μmol L^{-1} ammonium, and seawater was used as a control. The first experiment lasted for 28 days, and there was a 342% and 505% higher biomass yield in the SAL and TUB treatments, respectively, compared with controls, clearly showing that *U. fenestrata grows* successfully in both HPPWs. In the second experiment that lasted for 14 days, the yield was 69% and 86% higher in the HPPWs compared to controls [34] (Table 2). Furthermore, the crude protein content increased to ≈30% dw in the HPPW-treated *U. fenestrata* (a 146%–261% increase compared to the controls), while there was no significant difference between the HPPWs [34] (Table 2). These results show that although *U. fenestrata* grows successfully in both HPPWs, the TUB water yielded the highest biomass. Furthermore, the crude protein content in *U. fenestrata* can be boosted almost to the level of soybeans after only 14 days of cultivation [34]. Stedt et al. [34] also measured the amino acid (AA) composition and heavy metal content of the seaweeds and found that most of the AAs were present at least two to three times higher in the

HPPW-treated seaweeds compared to controls. To receive all required essential AAs from *U. fenestrata*, a person would need to eat around 230 g dw per day, which can be compared to 170 g dw of soybean [64]. Furthermore, the heavy metal content in the biomass was below the maximum allowed concentrations in foodstuff set by the commission of the European communities [67, 68].

The two previous studies [34, 65] clearly showed that the growth and crude protein content of *U. fenestrata* (and other green seaweed species) can be boosted in small-scale tank cultures. Sea-based cultivation, on the other hand, offers a practical and cost-efficient method of producing high quantities of biomass on a large commercial scale [30], but the growth and biomass quality are seasonally dependent [31]. Maximizing yield by harvesting late in the season results in biomass with low crude protein content [69]. Therefore, Stedt et al. [35] investigated if cultivation in HPPWs can be used as a short-term, post-harvest treatment to boost the crude protein content of *U. fenestrata* harvested from a sea-based cultivation at an optimal time in terms of yield, but sub-optimal in terms of protein content. *U. fenestrata* individuals collected from the sea-based cultivation at the end of May and with a crude protein content of 3.67% ± 0.22% dw (mean ± SEM), were transferred to either TUB or SAL process water [35]. After 14 days, the biomass yield increased by 40.2% and 30.5% in the HPPW treated seaweeds compared with the controls (Table 2). Even though the crude protein content did not reach the levels found in the previous studies [34, 65], the crude protein content in the HPPW treated seaweeds increased with a significant 320% and 488% (to 12% and 17% dw) in SAL and TUB water, respectively [35] (Table 2).

In a follow up experiment, Steinhagen et al. [36] used *U. fenestrata* harvested at its natural peak protein content at the end of February to test if a post-harvest treatment with HPPWs could optimize the yield and protein content of the seaweeds even further. When seaweed biomass with a crude protein content of 21.83% ± 1.25% dw (mean ± SD) was exposed to TUB water for 14 days, the biomass grew by 22.9 ± 0.3(mean ± SD). Furthermore, the crude protein content increased by a significant 72% compared to the crude protein content at harvest to a level of 37.4% ± 1.8% dw (mean ± SD) [36] (Table 2). These studies clearly show that HPPWs can be used as a sustainable nutrient source for *U. fenestrata* and that the crude protein content in the seaweeds can be boosted to the levels of soybeans (35%–40% dw) [64] after only 14 days of cultivation [34–36]. This is the highest crude protein content reported for a commercially grown *Ulva* biomass [36] and the described methodology can be applied by farmers as a value-adding post-treatment to the seaweed crop. Furthermore, a sensory analysis of the biomass was performed where a test panel assessed the biomass appearance, odor, taste, flavor, and texture [36]. Seaweeds cultivated in HPPWs had a more intense odor and green color compared to control seaweeds, indicating that protein content is positively correlated to color intensity.

3.2.4 | Relationship Between Protein Content and Color

Quantification of protein content in seaweed tissues usually involves methods that require laboratory procedures and are both time consuming and expensive. For farmers to estimate the protein content of the crop, there is a need for alternative methods that are cheap, fast, and preferably can be performed in the field. The relationship between nitrogen content and color of *U. fenestrata* was studied in seaweeds sampled from the sea-based cultivation [70]. Seaweeds were sampled weekly for 15 weeks starting in the beginning of March and covering the full harvest season [70]. Color was determined by analyzing photographs of the seaweeds for the three band colors red, green, and brown (RGB-values). The nitrogen content ranged from 0.54% to 5.22% dw during the sampling period. Regression models showed that color image analysis accurately estimated the nitrogen content both for fresh seaweed tissue ($R^2 = 0.944$) and for dried powder ($R^2 = 0.827$) [71]. Based on these models, the authors developed a web-based application that automatically estimates the nitrogen content of *U. fenestrata* from uploaded images (https://www.seaweed-nitrogen.com). Furthermore, a color guide based on the Pantone color system was developed [70]. Using the web-based application and color guide will allow seaweed farmers to assess the nitrogen (and hence crude protein) content of their crop fast and effectively without the need for expensive chemical analyses.

3.3 | Cultivation of Swedish Seaweeds Under Brackish Conditions

Saccharina latissima and *U. fenestrata* are both fully marine species that are not present on the Swedish east coast. However, the Baltic Sea has high nutrient concentrations that offer ample opportunities for seaweed cultivation. The systematic review approach used in the present study only found three papers investigating the growth of seaweeds originating from the Baltic Sea [71–73]. Haglund and Pedersén [71] tested a spray cultivation technique for cultivating Swedish seaweed species (*Furcellaria lumbricalis, C. crispus, Ahnfeltia plicata, F. vesiculosus* and *U. lactuca*) using either brackish water (7 PSU) or brackish water with the addition of NaCl (15–20 PSU). The objective was to investigate if it is possible to utilize parts of the Swedish east coast to cultivate seaweeds from marine conditions. The spray cultivation facility was set up in a greenhouse off the northeastern coast of Gotland on the Swedish east coast. Seaweeds were kept on layered nets, and water was sprayed over the top-most layer and allowed to drip through the lower layers (flowrate between 10 and 17 $L\,m^{-2}\,min^{-1}$). Seaweeds were cultivated between 2 and 17 weeks depending on the species [71]. The morphology of the species affected their suitability for cultivation on nets in spray culture. The Baltic form of *F. lumbricalis* was too soft and was regarded as unsuitable for spray cultivation, but the marine form of *F. lumbricalis*, as well as *C. crispus* and *F. vesiculosus*, were regarded as suitable species. *Fucus vesiculosus* had the highest growth rate of 0.9% day^{-1} after 8 weeks of cultivation. *Ulva lactuca* also had a high growth rate (2.5% day^{-1} after 8 weeks of cultivation) but was not suitable for spray cultivation due to fragmentation of the thallus after reproductive events [71]. *Chondrus crispus* had a lower growth rate (0.5% day^{-1} over 17 weeks), possibly due to bleaching at high temperatures [71].

The growth rate of *F. vesiculosus* originating from the northern Baltic Sea (natural salinity of 5 PSU) was investigated in aquaria cultures with artificial seawater under different levels of salinity (5, 10, 20, 35, 45 PSU), dissolved organic carbon (DIC, 1 and

2 mmol L^{-1}), and nutrients (0.05 and 0.2 μmol L^{-1} ammonium, 3 and 12 μmol L^{-1} nitrate, and 0.185 and 0.75 μmol L^{-1} phosphate) for 5 weeks [72]. Controls were cultivated in natural seawater from the Baltic Sea. *Fucus vesiculosus* had the highest relative growth rate (2.1%–2.2% day^{-1} or 202% higher than controls) under high DIC and nutrient concentrations in 10–20 PSU [72]. Although the study was not aimed at optimizing seaweed aquaculture, the results show that *F. vesiculosus* from the Baltic Sea could be kept in tank cultivation to achieve a relatively high growth rate under brackish conditions, and that it may be an interesting species for further development of seaweed cultivation in the Baltic Sea. Furthermore, Steinhagen and co-workers [73] investigated the impact of long-term (8 weeks) cultivation in different salinities (ranging between 5 to 30 PSU) on the growth rate and crude protein content of 8 *Ulva* strains from varying source salinities (7–30 PSU). Most strains exhibited higher growth rates and crude protein content when grown in low salinity, irrespective of the salinity of the source populations.

4 | Discussion

Swedish seaweed aquaculture aiming to optimize biomass yield and quality has a short history but has been developing rapidly during the last decade. Two species, the kelp *S. latissima* and the green seaweed *U. fenestrata*, have received most attention with successful cultivation in both sea-based (*S. latissima*, *U. fenestrata*) and land-based (*U. fenestrata*) cultivation systems. To achieve a sustainable and economically viable seaweed aquaculture industry, integration of multiple biological, environmental, and operational factors is essential. This approach should consider species-specific growth requirements, genetic variability, and interactions within the cultivation environment. Additionally, understanding the impact of abiotic factors such as light, temperature, nutrient availability, and water chemistry is crucial. Integrating these aspects with advanced cultivation techniques and management practices can ensure the optimization of biomass yield and quality while maintaining ecological balance and economic feasibility.

4.1 | *Saccharina latissima* Aquaculture

Optimizing both the land- and sea-based cultivation phases is important for the economic viability of S. *latissima* aquaculture. Reducing time in the land-based phase using direct seeding with binders without compromising sporophyte quality, and selecting optimal deployment and harvest times, as well as cultivation sites, based on environmental variables can enhance productivity and profitability. However, for Swedish *S. latissima*, direct seeding with binders was not successful [22]. A land-based pre-cultivation period of at least 4 weeks was optimal, leading to significantly larger sporophytes compared to shorter periods [23]. These results corroborate findings for both Norwegian and Danish *S. latissima* [74, 75]. In Norway, biomass yield was lowest for sporophytes seeded with a binder and directly transferred to the cultivation site and highest for sporophytes seeded as spores and transferred after a 42-day-long land-based hatchery phase [74]. In Denmark, sporophytes directly seeded with binders generally performed poorly compared to those seeded using traditional methods, except at one exposed site deployed in November, where no significant differences between the treatments were observed [75]. The timing of deployment also affected the yield or size of Swedish [43], Norwegian [76–78], and Danish [75] *S. latissima*, with earlier deployments generally resulting in larger sporophytes compared to later deployments. The quality of the biomass was affected by both deployment and harvest time at several locations including Sweden [23], Norway [76–80], and Denmark [75], but not in the Faroe Islands [81]. These results probably reflect the seasonal changes in environmental variables of Scandinavian coastal waters, compared to the relatively stable Atlantic conditions of the Faroe Islands [81].

In addition to seasonal variability, several Scandinavian studies show a large spatial variation in sea-based cultivation conditions for *S. latissima* [23, 24, 75, 76, 79, 80, 82–84]. In general, sporophytes grow best at shallow depths [23, 76, 79, 80, 84], medium to high exposure [24, 75, 83], low temperature ([84], but see [80]), high salinity [83, 84], and high nutrient levels [82, 84]. Furthermore, higher nutrient levels close to fish or bivalve aquaculture increase *S. latissima* growth in IMTA systems [27, 76]. Additionally, the integration of kelp cultivation with bivalve farming provides benefits such as biofouling reduction [27], suggesting that the filtration capacity of bivalves can indirectly benefit kelp aquaculture by reducing fouling organisms. Together, these findings highlight the importance of careful site selection and the consideration of environmental variables for successful *S. latissima* cultivation.

4.2 | *Ulva* spp. Aquaculture

In contrast to *Saccharina latissima* aquaculture, cultivation of *Ulva* spp. has received less attention but is still an important species in the European aquaculture sector [85]. This is also reflected in the number of studies published for Northern European cultivation of *Ulva* spp. Morphological characteristics alone have proven inadequate for reliably identifying species within the genus *Ulva* [18]. Therefore, species names reported in previous studies that did not employ molecular markers for identification should be interpreted with caution. To our knowledge, optimization of the land-based pre-cultivation phase, as well as sea-based cultivation on long-lines, has only been studied in Swedish *Ulva fenestrata*. The results from this review showed that swarmer density and temperature had relatively minor impacts on the growth and biochemical content of *U. fenestrata* juveniles during the land-based pre-cultivation phase, while nutrient addition was essential for normal development [29]. On the other hand, high swarmer density in the pre-cultivation phase significantly boosted yield during the sea-based cultivation phase [30], emphasizing the importance of initial seeding density. However, nutrient addition and temperature had minimal effects on adult yield and biochemical content [30], suggesting that the pre-cultivation phase primarily sets the stage for growth, while environmental conditions during the sea-based phase play a crucial role in the final yield and quality of the crop. Interestingly, recombinant *U. fenestrata* gametophytes exhibited superior growth and biochemical profiles compared to clonal gametophytes, highlighting potential benefits of using recombinant gametophytes in land-based cultivation. On the other hand, clonal gametophytes do not require a fertilization procedure for propagation and may therefore be easier to handle

from an aquaculture perspective. As for *S. latissima*, the timing of harvest in sea-based cultivation of *U. fenestrata* is critical for optimizing biomass yield and quality, as there is a trade-off with higher yields obtained later in the season and higher quality (proteins, fatty acids, and pigments) observed in earlier harvests [31]. This trade-off necessitates strategic planning based on the intended use of the biomass. For instance, early harvest may be preferable for food applications requiring high nutritional content, while later harvests might be better suited for bulk biomass production for biomaterials.

Indoor tank cultivation offers precise control over environmental conditions, allowing for optimization of growth and biochemical content. High irradiance and low temperature were found to be optimal for growth in Swedish *U. fenestrata*, though these conditions resulted in lower biochemical quality in terms of fatty acids, proteins, and phenolic content [56]. Conversely, nutrient addition, particularly nitrate, significantly enhanced protein, fatty acid, and phenolic content, albeit at the expense of carbohydrate content [33, 57]. In accordance with these results, Bruhn and coworkers [86] found a positive correlation between irradiance and biomass production, tissue C:N ratio and monosaccharide content in Danish *U. lactuca*. This suggests that targeted manipulation of cultivation conditions can produce biomass tailored to specific nutritional or industrial requirements.

The potential of using nutrient-rich process waters from food industries to boost the growth and protein content of *U. fenestrata* has been explored with promising results [34–36, 65, 69, 87]. Process waters from herring production significantly increased yield and protein content, bringing *U. fenestrata*'s protein content levels close to those of soybeans [36], while promoting sustainability by recycling industrial by-products. Furthermore, Danish *U. lactuca* also increased growth rate, as well as amino acid and or protein content when grown in liquid manure [87] and reject water from digested water sludge [69]. The successful growth and protein enhancement of *Ulva* spp. when cultured in process waters demonstrates a viable method for integrating seaweed cultivation into circular economy models. To facilitate the practical application of these findings, a relationship between protein content and color in *U. fenestrata* was established. Nitrogen content, a proxy for protein, correlates strongly with the seaweed's color [70]. This led to the development of a web-based application and a color guide using the Pantone system, enabling farmers to estimate protein content rapidly and accurately without extensive laboratory analyses. This innovation could significantly streamline the monitoring and optimization of seaweed crops in commercial settings.

5 | Conclusion

Swedish seaweed aquaculture has progressed notably over the past decade, with focused research efforts on *Saccharina latissima* and *Ulva fenestrata* laying a strong foundation for optimizing biomass yield and quality. This review highlights how success in seaweed cultivation hinges on integrating species-specific biology with environmental, genetic, and operational insights. For *S. latissima*, refining the land-based phase, selecting optimal deployment and harvest windows, and leveraging spatial variability have proven critical to maximizing yield and product quality. Similarly, *U. fenestrata* cultivation has demonstrated that pre-cultivation seeding density, harvest timing, and environmental control—particularly in land-based systems—are key drivers of both productivity and biochemical composition. Innovative strategies such as the use of recombinant gametophytes, integration with bivalve aquaculture, and reuse of nutrient-rich process waters underscore the potential of Swedish seaweed farming to contribute to both sustainability and circular economy models. Tools like the color-based protein estimation guide further bridge research and practice, offering scalable solutions for commercial application. Looking forward, future development should focus on expanding species diversity, improving strain selection through molecular tools, and scaling up integrated multi-trophic and land-based systems. As global interest in seaweed continues to grow, the Swedish case offers valuable insights for cultivating seaweeds in temperate, non-traditional regions. Continued investment in research, innovation, and interdisciplinary collaboration will be essential to fully unlock the ecological and economic potential of seaweed aquaculture.

Author Contributions

Gunilla B. Toth: conceptualization, data curation, funding acquisition, project administration, visualization, writing – original draft, writing – review and editing, methodology, supervision. **Matthew Hargrave:** conceptualization, investigation, writing – review and editing. **Kristoffer Stedt:** conceptualization, investigation, writing – review and editing. **Sophie Steinhagen:** conceptualization, investigation, writing – review and editing. **Wouter Visch:** conceptualization, investigation, writing – review and editing. **Henrik Pavia:** conceptualization, funding acquisition, writing – review and editing, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing are not applicable to this article as no new data were created or analyzed in this study.

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