The sugar kelp *Saccharina latissima* II: Recent Advances in farming and applications

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Abstract

The sugar kelp *Saccharina latissima* has received intense scientific attention over the last decades. In recent years, interest in cultivation of the species has strongly increased in the North Atlantic Ocean and the Eastern Pacific Ocean, driven by the great potential of *S. latissima* to be utilised for various industrial applications, including food, feed, and biomaterials. Accordingly, current research has focused on improving farming methods and technology, environmental impacts, and site selection. In addition, many studies have investigated the varying chemical composition of *S. latissima*, extraction of commercially interesting components, and the use of the biomass and its derived components in various applications. This review provides a comprehensive overview of farming and applications of *S. latissima* from the last 15 years. Additional insights on other research topics, such as ecology, physiology, biochemical and molecular biology of *S. latissima*, are given in the first review, "The sugar kelp *Saccharina latissima* I: recent advances in a changing climate" (Diehl et al. 2023).

Keywords: Aquaculture, Cultivation, Macroalgae, Seaweed, Nursery, Biorefinery

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Methodology

In this review, we aimed to synthesise recent findings on farming, technology and environmental and industrial applications of the kelp *Saccharina latissima*. Therefore, we reviewed 329 peer-reviewed research articles, book chapters, statutes and selected reports published between 2009 and June 2023. Earlier publications were only taken into account when necessary for the context. The review is organised in 11 main topics, including Seaweed in a traditional use (Section 1), *Saccharina latissima* as a target species in seaweed farming (Section 2), Cultivation strategies- Nursery (Section 3), Cultivation strategies- Sea Cultivation (Section 4), Technology development and upscaling (Section 5), Potential for carbon capture (Section 6), Environmental impacts and life cycle assessments (Section 7), Integrated Multi-Trophic Aquaculture (IMTA) (Section 8), Chemical composition of *Saccharina latissima* (Section 9), Biochemical extractions and methods (Section 10) and Applications of *Saccharina latissima* and derived components (Section 11). Finally, knowledge gaps and emerging issues are summarised in Section 12. The first part of the review (part I) focuses on the latest research on ecology, physiology, biochemical and molecular biology of *S. latissima*, "The sugar kelp *Saccharina latissima* I: Recent advances in research" (Diehl et al. 2023).

1. Seaweed in a traditional use

Seaweeds have traditionally been harvested from shorelines in most coastal communities worldwide for centuries and have played an important role in food, animal feed and fertiliser use. Around 26 countries still actively harvest seaweed from wild stocks, with around 1,1 million tonnes harvested annually (FAO 2021). As an example from Norway, *Laminaria hyperborea* and *Ascophyllum nodosum* harvested from wild stocks have been utilised in industry for more than five decades (Stévant et al. 2017b) and amounted to 163,000 tonnes of fresh weight in 2019 (FAO 2021). Primary applications include alginates or agricultural products like animal feed supplements and soil enhancers. The harvest of wild *L. hyperborea* remains controversial as the removal of and interference with natural habitats can affect local biodiversity, might negatively impact the abundance of gadoid fishes, and reduce the area of habitat preferred by foraging seabirds (Smale et al. 2013; Stévant et al. 2017b). Seaweed farming is a sustainable alternative to reduce further upscaling of the wild harvest industry but still expand the use of seaweed biomass for existing and new products and applications. The first attempts to cultivate the kelp *S. japonica*, a close relative to *S. latissima*, has its history from the 1930s-1940s in northern China, and the breakthrough came at the end of the 1950s with the horizontal long-line method (Su et al. 2017). Seaweed cultivation is mentioned as one of four alternative options to increase marine food production since the capture production of currently exploited marine fish stocks and other species has more or less reached its maximum and can only be slightly enhanced through better management (Van Der Meer et al. 2023).

2. *Saccharina latissima* as a target species in seaweed farming

There is a strong regional imbalance in seaweed production. In 2019, production in Asia contributed 97.4% of the worldwide seaweed production, reaching almost 35 million tonnes, while America and Europe had a share of 1.4 and 0.8%, respectively, and most came from wild harvest (Cai et al. 2021). Around 30-40% of the global seaweed production is consumed directly as food, and the most common seaweed taxa for cultivation are the brown algae *S. japonica* (kombu), *Undaria pinnatifida* (wakame) and *Sargassum fusiforme* (hiziki), together with the red algae *Eucheuma* spp. and *Kappaphycus alvarezii* (both for carrageenans), *Gracilaria* spp. (for agar) and *Porphyra/Pyropia* spp. (nori) (Buschmann and Camus 2019; Chopin and Tacon

2021). The industry sector uses the majority of seaweed biomass as polysaccharide additives and functional food ingredients, and the non-food sector as hydrocolloid products in nutraceuticals, pharmaceuticals, and cosmetics, and to a lesser extent as fertilisers, biofuels, bioplastics, and other industrial outputs (Naylor et al. 2021).

Although seaweed farming in the Western part of the world contributes to a minimal fraction of the world's production, this is an emerging industry fuelled by its potential contribution to climate change mitigation and an environmentally friendly bioeconomy (Van Den Burg et al. 2021b; Heidkamp et al. 2022). *Saccharina latissima* (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders 2006 (Lane et al. 2006) is one of the most economically and ecologically relevant species for cultivation in the Western world and is considered the fastest-growing species of cultivated kelp, with annual production capacities estimated at 75-200 tonnes wet weight per hectare at sea (Broch et al. 2013, 2019; Holdt and Edwards 2014). Due to various industrial applications and several other benefits, *S. latissima* has developed into one of the most important species in aquaculture (Fig. 1)

New consumer trends, market demands and opportunities for multiple uses of *S. latissima*, such as food (Slegers et al. 2021), bioactive components (Holdt and Kraan 2011), feed (Samarasinghe et al. 2021a), fertilisers (Marinho et al. 2016) and biofuels (Fernand et al. 2017) have strengthened the motivation for industrial macroalgal cultivation in Western countries. *S. latissima* has been cultivated in modest amounts during the last two decades in the North Atlantic Ocean, e.g., the United States (Kim et al. 2015), Canada (Campbell and Starko 2021), Spain (Freitas et al. 2016), Portugal (Azevedo et al. 2019), Faroe Island (Bak et al. 2019), Iceland (Stefaniak-Vidarsson et al. 2019), Norway (Forbord et al. 2020a), United Kingdom (Schultze-Jena et al. 2022), Ireland (Dolliver and O’Connor 2022), Denmark (Bruhn et al. 2016), Sweden (Hasselström et al. 2018), France (Monteiro et al. 2020), Germany (Buck et al. 2017), and in the Netherlands (Jiang et al. 2022a) as well as in the Eastern Pacific Ocean, e.g., Alaska (Raymond and Stekoll 2021; Stekoll et al. 2021). As an example, the cultivation of *S. latissima* was initiated almost 15 years ago in Norway with small-scale experiments (Forbord et al. 2012; Stévant et al. 2017b). The cultivation is currently in an early commercial phase, with 221 tonnes reported sold in 2022 (161 t *S. latissima* and 60 t *Alaria esculenta)* (Directorate of Fisheries 2023). Around 15 seaweed farmers along the Norwegian coast contributed to the production and primarily sold their biomass as a raw material to Europe's food and feed market.

3. Cultivation strategies - Nursery

Several cultivation protocols have been established for *S. latissima* over the last decade, providing detailed information necessary for performing cultivation experiments (Flavin et al. 2013; Redmond et al. 2014; Peteiro et al. 2016; Forbord et al. 2018; Theodorou et al. 2021). However, there is a need for further optimising production methods and protocols to achieve predictable biomass production of high quality and an economically viable business.

The cultivation process for *S. latissima* consists of two major stages: a nursery stage on land that provides conditions necessary for the development of microscopic gametophytes through their sexual phase and the subsequent development of juvenile sporophytes/seedlings for seeding on substrates suitable for deployment at sea; and a sea-farming stage that involves the on-growth of sporophytes until they reach a suitable size and quality for harvesting (see detailed life cycle in Fig. 2). Three main strategies exist to produce *S. latissima* seedlings before deployment at sea: seeding the growth substrate with either 1) zoospores, 2) gametophytes or 3) juvenile sporophytes. The settlement of spores or gametophytes (propagules) and their development into juvenile sporophytes in the nursery can be manipulated by light, nutrients, substrate surface conditioning and the addition of Germanium dioxide (GeO_2) to keep contamination by diatoms under control (Kerrison et al. 2016), as well as oscillatory water motions (Kregting et al. 2023). By manipulating the nursery conditions, the time required for spores to develop into juvenile sporophytes ready for deployment can be minimised, survivorship maximised, and costs associated with the land phase can be decreased. Seeding with spores requires fertile sporophytes with mature sori and is seasonal-dependent if these are collected in natural habitats. However, fertility can also be induced by removing the meristematic tissue, placing the sporophytes under an artificial day rhythm with a short-day regime, thus enabling access to spores independent of season (Forbord et al. 2012). Sporogenesis in *S. latissima* can also be induced efficiently out of season in total darkness (Boderskov et al. 2021).

Gametophytes, the microscopic, haploid life stage of *S. latissima*, can be kept in continuous cultures under red light for years, multiplied by periodical mechanical disruption of the filaments, renewal of the growth medium and then be available for seeding substrates or further development into juvenile sporophytes for direct seeding (Mols-Mortensen et al. 2017; Ebbing et al. 2020; Forbord et al. 2020b; Kerrison et al. 2020), or for breeding activity (Goecke et al. 2020, 2022; Augyte et al. 2020). This method is advantageous as incubation facilities can be shortened by several weeks or omitted completely by direct seeding using a binder to adhere the propagules to the substrate. A considerable amount of research has been undertaken over the recent years to understand the gametophyte biology, development and quality relating to several biotic and abiotic factors, such as age, density, seasonality, sex ratio, light, temperature, and nutrients (Nielsen et al. 2016a; Ebbing et al. 2020, 2021a, b; Raymond and Stekoll 2021; Boderskov et al. 2022). A bioreactor system that overcomes several implementation challenges for this controlled reproductive method, expanding the possibility of clonal gametophyte cultivation outside of expensive laboratory settings, has been validated (Ebbing et al. 2022). This system's three goals include maintaining clean gametophyte clonal cultures in non-sterile environments over prolonged periods, producing large numbers of juvenile sporophytes, and effective transportation of gametophytes and sporophytes.

Limited information exists on which seeding strategy yields the highest biomass at sea, and economic feasibility studies are necessary to guide seaweed farmers into choosing the right method for their business. The effect of using a binder for direct seeding and choosing suitable seeding substrates have been examined in a few studies over the past years (Kerrison et al. 2017, 2018b, 2019a, b). One study showed that the binder-seeding method using a commercial binder is an effective method of allowing textile substrates to be seeded for macroalgal cultivation (Kerrison et al. 2018a). Sporophyte seeding resulted in twice the final biomass yield compared with gametophyte seeding due to a two to three weeks developmental lag, while zoospore seeding without using a binder gave very poor results (Kerrison et al. 2018a). It is also shown that binder seeding can produce a similar or higher biomass yield during harvesting compared to the traditional twine-longline method. Morphological changes were observed, and the length distribution of the different experimental populations varied greatly due to differences in seeding density (Kerrison et al. 2020). They concluded that these differences are expected to impact the biochemical composition of the biomass and that the seeding method should be selected depending on the end use of the biomass. Another study tested two binder types (agar and κ-carrageenan) under two ecologically relevant flow regimes (5 and 15 cm s^{-1}) and a control condition (0 cm s^{-1}) in a laboratory flume (Visch et al. 2023). The results show no differences in results between the binder and non-binder treatments, and the results were also unaffected by the different flow velocities. In another study, a commercial binder was found to be more effective than any formulations of calcium alginate tested, but a detachment of 70-80% of the sporophytes was detected when keeping the seeded ropes under aeration compared to no water motion (Umanzor et al. 2020). These findings suggest that novel methods and further development of the binder-seeding method are highly recommended.

Three seeding methods (zoospore seeding on twine, gametophyte seeding on twine and direct seeding with gametophytes and juvenile sporophytes using a commercial binder) with different nursery periods were compared in a Norwegian case study by deploying *S. latissima* seedlings and comparing yields after 80 and 120 days on-growth at sea. The findings showed that seeding with zoospores pre-cultivated in the nursery for 42 days before deployment gave significantly longer fronds and a higher biomass yield at sea than any other seeding method (Forbord et al. 2020b). The seeding methods did not affect the biomass's protein content when harvested. A Danish study compared biomass yield and quality between direct seeding and traditional spore seeding on twine and two substrates, including three deployment times at three different cultivation sites (Boderskov et al. 2021). The main findings showed that the direct seeding method gave yields comparable to the traditional seeding method with spores at the most exposed site, whereas at the sheltered sites, the highest biomass yield was achieved using the traditional spore seeding method. The seeding method did not affect the biomass quality, but the quality differed significantly between sites. Another method of transplanting young fronds of *S. latissima* around 40 cm in length from indoor greenhouse tanks to sea has proved to be a technically and biologically viable method for obtaining good growth and productivity (Peteiro et al. 2014) but has not been further employed.

For nursery operations that do not have access to flow-through deep water with high concentrations of essential nutrients year-through (Forbord et al. 2012), frequent water exchange and nutrient addition are necessary for fast and efficient seedling production (Boderskov et al. 2021). For a seaweed producer to be organic certified, conventional fertilisers cannot be used in the nursery, so six potential organic certified nitrogen (N) sources, all with N concentrations up to 150 µM (degassed manure, protamylasse, three commercial liquid fertilisers and mussel excreted ammonium) have been investigated to see how they affect the growth and early stage development of *S. latissima* juvenile sporophytes (Boderskov et al. 2022). Results showed that spore germination was generally unaffected by either N source or concentration, but impaired gametogenesis and slower growth were found for all N sources and at concentrations higher than 100 µM N. Further development is needed before the organic nutrient sources can substitute conventional fertilisers in an efficient commercial nursery (Boderskov et al. 2022). Several experiments have examined new stimulants to enhance *S. latissima* growth in the nursery. Preliminary results indicate that a marine plant extract powder (AMPEP, Acadian Seaplants, Ltd.) may enhance the growth capacity of *S. latissima* when exposed to suboptimal temperatures, allowing them to overcome heat stress more effectively while maintaining growth (Umanzor et al. 2019). A more recent study investigated the potential of Kelpak® (a seaweed extract from *Ecklonia maxima*) as a useful biostimulant to enhance juvenile sporophyte growth of *S. latissima* while in the nursery. It also provides insights into practical applications to enhance the species' thermal tolerance before deployment at sea, which could result in a competitive advantage compared to non-treated individuals (Umanzor et al. 2020).

For the future of seaweed aquaculture, in order to meet the expanding industry's raw material needs, nursery production should increase alongside ocean cultivation. An extensive literature review has been undertaken to quantify the *S. latissima* nursery production costs and identify the potential barriers to cost-effective scaling (Coleman et al. 2022). The most important research priorities identified for optimising the nursery were to reduce the sporophyte grow-out duration, increase the labour capacity, develop energy-efficient flowthrough systems, and minimise the facility size by optimising equipment used in production.

4. Cultivation strategies - Sea cultivation

There is a great need for cultivation management strategies that produce specific crop characteristics, optimise yield, widen the harvesting window, and lower the investment- and operational costs. Site selection is one of the biggest challenges and a critical issue when setting up a new seaweed farm and upscaling possibilities. The response of *S. latissima* to several important physical and chemical parameters that will vary between sites, like temperature, salinity, water motion, nutrient concentrations, carbon dioxide/pH, light and ultraviolet radiation, have a significant impact on the cultivated biomass (Kerrison et al. 2015). Numerous studies with *S. latissima* have shown extreme variation in growth, quality and chemical composition between different locations (Peteiro and Freire 2013; Nielsen et al. 2014; Bruhn et al. 2016; Mols-Mortensen et al. 2017; Matsson et al. 2019; Forbord et al. 2020a; Boderskov et al. 2021; Wang et al. 2022; Thomas et al. 2022). The same applies to the deployment time and depth (Peteiro and Freire 2009; Handå et al. 2013; Sharma et al. 2018; Matsson et al. 2021).

Models can be an important tool to quantify kelp growth during different seasons and environmental conditions (Broch and Slagstad 2012; Venolia et al. 2020) and are particularly interesting to use for open ocean and offshore conditions, which are largely untested (Strong-Wright and Taylor 2022). Offshore cultivation can solve conflicts with other uses of coastal areas, such as fishing, aquaculture, and recreational activities. Also, farms can preferably be located with other compatible activities, such as wind energy production, to optimise costs and operation. Earlier experiments and projects working with offshore and Multi-Use Aquaculture (combining various uses at one site) with cultivated *S. latissima* have been summarised in an earlier review (Buck et al. 2017).

The cultivation potential of *S. latissima* has been evaluated as a function of latitude and near- and offshore position along the Norwegian coast using a coupled 3D biophysical model system (Broch et al. 2019). The model results were compared with growth data from kelp cultivation experiments. The model demonstrated a higher production potential offshore than in inshore regions, mainly due to limitations in nutrient availability. The results also indicated a latitudinal effect on the timing of peak growth, similar to the results found in cultivation experiments along the Norwegian coast (Forbord et al. 2020a). It is also found that *S. latissima* grows well under offshore conditions at the species' southern distribution limit in northern Portugal in the first half of the year (Azevedo et al. 2019), while at the Swedish west coast growth generally increased with decreased wave exposure, with approximately 40% less growth at exposed locations compared to sheltered or moderately exposed locations (Visch et al. 2020b). The hydrodynamic conditions under offshore cultivation have been found to change the morphological features of cultivated *S. latissima* (Peteiro and Freire 2011) and affect the frond surface shape (Zhu et al. 2021a). Even though offshore seaweed farming can give higher yields than coastal locations, installations of offshore structures can be challenging and expensive. An offshore long-line macroalgal cultivation rig was developed and tested in the Faroe Islands in 2010 and found appropriate for cultivation in exposed and deep water locations (water depth > 50 m), and the economic risk related to lost cultivation structures is deemed to be low (Bak et al. 2018, 2020). Detailed numerical models based on high-fidelity datasets of engineering parameters are essential when *S. latissima* farms move into more exposed and offshore conditions, and the aim is to produce high volumes of biomass (Fredriksson et al. 2023).

Removing the distal end of long fronds can offer biological benefits such as increased sunlight and nutrients for the remaining thalli and increased overall growth (Grebe et al. 2021b). The high cost of seeding material and deployment was reduced by testing multiple partial harvesting in the Faroe Islands where only the fronds were cut off, leaving haptera, stipes and 5-15 cm of the fronds (a method also known as coppicing). This cutting length was used to preserve the meristematic zone to allow re-growth. Four non-destructive harvests were conducted during a two-year growth period without re-seeding the lines (Bak et al. 2018). In Denmark, it was found that the use of coppicing enabled multiple harvests of *S. latissima*, but the quality of the biomass was reduced in the second year (Boderskov et al. 2023). In the Shetland Islands, *S. latissima* has been identified as a potential candidate for regrowth and multiple harvests within a single growing season, but the growth period is limited by the biofouling that occurs in late summer (Rolin et al. 2017).

Fouling by epibionts on *S. latissima* fronds is a challenge for seaweed farmers and usually occurs from spring to autumn, depending on location, latitude, and inter-annual variation. Epibionts, and in particular encrusting bryozoan, grow as colonies that cover the frond surface and form a barrier inhibiting nutrient and light absorption (Andersen et al. 2019) and often cause loss of biomass due to increased drag and friction and decreased flexibility (Krumhansl et al. 2011). Other common epibionts on *S. latissima* are hydroids, crustaceans, bivalves, sponges, tunicates, snails, benthic diatoms, and filamentous algae (Krumhansl et al. 2011; Forbord et al. 2020a; Corrigan et al. 2023) and bacterial colonies (Liu et al. 2022; Burgunter-Delamare et al. 2023). Biofouling makes seaweed biomass less appealing for human consumption and affects the commercial value of the yield. To avoid biomass loss and reduced value, kelp is usually harvested before the onset of epibionts (Marinho et al. 2015b; Førde et al. 2016; Matsson et al. 2021). Harvesting at different times for different usage of *S. latissima* biomass could be a viable option, or if the seaweed is left unharvested, the epibionts can contribute to local biodiversity and fisheries enhancement and additional ecosystem services, including biofiltration and nutrient regulation (Corrigan et al. 2023). Site selection can be an essential tool for controlling the biofouling on seaweed fronds. A study in northern Norway showed that biomass yield and biofouling can vary significantly within short geographical ranges, underlying the importance of thorough site selection for *S. latissima* cultivation, to achieve maximum kelp biomass and minimum biofouling (Matsson et al. 2019). It has been investigated that the onset of biofouling follows a latitudinal pattern with delayed onset in northern locations (Forbord et al. 2020a). Biofouling on *S. latissima* is also found to decrease with increased wave exposure (Peteiro and Freire 2013; Visch et al. 2020b), at freshwater-influenced sites (Forbord et al. 2020a), with increasing depth (Førde et al. 2016), at lower seawater temperature (Wang et al. 2022) and higher nutrient levels (Wang et al. 2022). A complete absence of epiphytic animals throughout the year has been found for tank-grown *S. latissima*, probably mainly due to the mechanical prevention of larval settlement in tank tumble culture (Lüning and Mortensen 2015).

Developing cultivars for improved traits like low affinity for biofouling, high biomass production and increased content of valuable compounds could be of great importance for the future seaweed industry. Local genetic material and technologies to prevent hybridisation between cultivated and wild populations are important elements in seaweed's responsible and sustainable utilisation. The use of local strains is highly recommended in several Scandinavian countries, and breeding is not yet recommended as a tool to obtain the wanted traits of *S. latissima* (Hasselström et al. 2018; Barbier et al. 2019; Goecke et al. 2020). Investigations in Norway have shown that the natural population of *S. latissima* is separated into three distinct genetic groups corresponding to distinct geographical ecoregions along the coast (Evankow et al. 2019), and it is suggested that the Norwegian Coastal Current strongly influences genetic connectivity between populations on the coast (Ribeiro et al. 2022). Microsatellite analysis of 14 populations sampled across the northern part of the Irish Sea indicated four distinct genetic clusters (Mooney et al. 2018). Results from Denmark showed that the *S. latissima* populations were structured into two clusters corresponding to brackish versus marine sites; also, gene flow was reduced between clusters and populations within clusters (Nielsen et al. 2016b). In Maine, it is found that populations are finely structured across small spatial scales due to a strong influence of the Eastern Maine Coastal Current, as well as geographic isolation associated with major bays (Breton et al. 2018). Future management and farming efforts in this area should maintain genetic diversity and assess the cultural potential of local populations. One should prevent the translocating of *S. latissima* between ecoregions to maintain a healthy coastal ecosystem and natural population genetic diversity. An initial simple and low-cost breeding strategy based on recurrent mixed hybridisation and phenotypic selection within local populations is proposed for *S. latissima* and other kelp species (Goecke et al. 2020). Crossing of different *Saccharina* species can also serve as a novel strategy to meet the expanding demands of the *S. latissima* farming industry. Findings suggest that *S. latissima* crossed with the skinny kelp S. *angustissima* provides improved yield compared to pure *S. latissima* crosses (Li et al. 2022). This work is part of a selective breeding program for regional strains of *S. latissima* to improve the competitiveness of kelp farming in the United States (Augyte et al. 2021; Umanzor et al. 2021). The capacity to conserve genetic diversity for breeding programs aimed at developing seed stock for onward cultivation is a key feature, and cryopreservation can be a useful preservation method for male and female *S. latissima* gametophytes. It can also be an attractive option for long-term preservation (Visch et al. 2019).

5. Technology development and upscaling

Seaweed can enhance flavour and enrich food with dietary fibres, antioxidants, iodine and other minerals and vitamins (Roleda et al. 2018; Sappati et al. 2019). The amount of seaweed currently cultivated in the Western world to produce such products is sufficient, but if the market is aiming for other uses, e.g., feed ingredients, fertilisers and biofuels, the production needs to be massively upscaled. Industrial, cost-effective cultivation requires novel technology applied to the whole production line, targeting mechanisation and automation of the seedling production, deployment at sea and harvesting operations. The solutions used in the Western world today are time- and resource-demanding, yielding low volumes. A strategy for increasing the area yield of cultivated *S. latissima* can be to optimise the cultivation infrastructure by using a net system instead of a multi-layer single-line system or to increase the cultivation line density in the upper water column (Boderskov et al. 2023). Improving existing technology and designing new solutions to seed and deploy long-lines effectively, with minimum workload, is getting a lot of attention and will help reduce labour- and production costs (Verdegem et al. 2023). The design of aquaculture systems also requires understanding the drag forces on cultivated *S. latissima* (Lei et al. 2021). An example of recently developed technology for *S. latissima* farming is a mobile, inexpensive, easy-to-deploy system that was developed and tested for exposed sea conditions in Maine and gave a high yield (12.7 kg m^{-1}) over an 8-month fall-winter growth period (St-Gelais et al. 2022). As a second example, a design study in Norway came up with a module-based solution for industrial seaweed cultivation, with specific solutions for spinning seeded twine onto long lines and a robotic module for interaction with a submerged farm at deployment and harvest (Solvang et al. 2021).

Production cost for *S. latissima* biomass is still very high, and for biofuel purposes, estimation showed that costs were higher per dry tonne at farm scales of 1000 hectares or more in waters up to 200 km from shore (US$200-$300 per tonne dry) compared to production in farms closer to shore with optimal growth conditions ($100 per tonne dry), the latter situation making seaweed economically competitive with land-based biofuel feedstocks (Kite-Powell et al. 2022). Using economic modelling, a study from the North Sea concluded that offshore *S. latissima* production was not yet economically feasible (Van Den Burg et al. 2016). Several opportunities to improve the economic feasibility of a North Sea seaweed value chain were identified, like technical innovation and systems enabling multiple harvests per year and further development of the biorefinery concept and a more defined end-marked.

To produce large quantities of *S. latissima*, large-scale open ocean cultivation is the only viable solution. On the other hand, advantages of land-based cultivation include better control of the cultivation system, easy access to the produced biomass regardless of season or the weather conditions, and increased potential to be used for bioremediation for land-based fed aquaculture. In such systems, it is easy to manipulate key resources, such as light intensity and nutrient loading, with combinations that do not usually occur in the sea and, thus, have higher control over biomass yield, chemical composition, and epiphytes (Lüning and Mortensen 2015; Boderskov et al. 2016; Azevedo et al. 2016; Jevne et al. 2020). If the emerging market of functional products from seaweed for human consumption is considered, which requires traceability and security of supply, land-based cultivation can be essential for this production, allowing the highest levels of control (Hafting et al. 2012).

6. Potential for carbon capture

Carbon sequestration by coastal vegetation has drawn significant attention over the last two decades, especially after the conception of "Blue Carbon" released by a UN report in 2009 (Nellemann and Corcoran 2009; Macreadie et al. 2021). Besides mangroves, salt marshes and seagrass meadows, as the recognised "blue carbon" contributors, there is an ongoing evaluation and debate about the role of macroalgae in carbon sequestration (Macreadie et al. 2019; Troell et al. 2023; Filbee-Dexter et al. 2023). Specifically, the well-recognized definition of carbon sequestration is the CO_2 removal from the atmosphere and secure carbon storage for at least 100 years (GESAMP et al. 2019; Hurd et al. 2022; Troell et al. 2023). However, while macroalgae constitute the most productive coastal ecosystems, their contribution to long-term carbon storage remains hard to trace and calculate. The time-span of carbon storage by macroalgae is questioned because macroalgae themselves are relatively short-lived, and their biomass enters the trophic network (e.g., consumption via food, feed and fuels) in a large proportion, which does not directly contribute to long-term sequestration (Hughes et al. 2012; Troell et al. 2023). Hence, the carbon assimilated by macroalgae in their biomass is generally considered carbon storage in a broader sense and lasts over various timescales (Hurd et al. 2022). However, multiple studies have illustrated that macroalgae likely contribute to long-term carbon storage via three well-established sequestration pathways, including the carbon burial in sediments, the transport of macroalgal carbon into the deep sea, and the secretion of compounds in the form of recalcitrant dissolved organic carbon (RDOC), which can be stored in seawater for hundreds or even thousands of years (Li et al. 2022; Pessarrodona et al. 2023). According to simulation results from coastal and oceanic hydrodynamic models, particulate organic matter (POM) from kelp aquaculture may be transported from a few hundred metres up to a hundred kilometres away from the release site, depending on the sinking rates, time of release, and the location properties (sheltered, exposed or offshore). The depth at which POM settles on the sea floor likewise depends on the properties of the POM and the bathymetry of the receiving sites (Broch et al. 2022). A rough estimate suggests that about 173 TgC yr^{-1} (range: 61-268 TgC yr^{-1}) could be sequestered by macroalgae globally, which is higher than the amount buried in angiosperm-dominated coastal habitats (Duarte et al. 2005; Krause-Jensen and Duarte 2016).

Furthermore, about 88% of this carbon sequestration is contributed by organic carbon transported to the deep sea, and the rest is via burial in coastal sediments, resulting in a small proportion of local carbon sequestration (Krause-Jensen and Duarte 2016). To date, efforts to establish a framework for accounting carbon flows in macroalgae are ongoing and face various challenges. Here, we summarise the research progress of *S. latissima* related to its potential for long-term carbon storage. Although limited by methodology and definition updates, the current works may not address the fluxes directly leading to long-term carbon storage but provide a baseline for further research.

The amount of biomass released to the environment was quantified to evaluate the potential carbon sequestration rates of *S. latissima* in a kelp farm off Northern Ireland (Dolliver and O'Connor 2022). This investigation showed that about 41% of the net primary productivity (NPP) of cultivated *S. latissima* was lost because of tissue loss before harvest. About 4% of the carbon in fronds falling off the rope can be attributed to sequestration in sediments on the continental shelf, while 10% can be attributed to sequestration in the deep sea (Krause-Jensen and Duarte 2016). Hence, an average carbon sequestration of 7.4 kg was generated per 100 m longline during the cultivation period (Dolliver and O'Connor 2022). An additional 43% of NPP may have been lost by long-term erosion and exudation of organic carbon, though it is a coarse estimate and needs further verification. Still, when this estimated carbon sequestration rate of *S. latissima* meets the agroforestry schemes funded by several governments, it largely promotes the sustainable development of the *S. latissim*a aquaculture industry that could, in turn, be used as carbon credits. Another experiment conducted in Long Island Sound and the Bronx River Estuary, USA, revealed via monitoring the tissue C content that cultivated *S. latissima* could capture carbon into biomass from 1100 to 1800 kg C ha^{-1} (Kim et al. 2015). Besides, the harvest time plays an important role in carbon sequestration of *S. latissima* (Fieler et al. 2021). The late harvest in August can increase biomass losses by up to 49% of the annual production, which exports more carbon and increases the potential for long-term carbon sequestration. Therefore, the operational management of *S. latissima* cultivation could be adjusted based on the specific objective, either by harvesting early for high-quantity and quality food or late for higher carbon exportation. By conducting the total carbon footprint accounting, including both carbon capture by *S. latissima* biomass and the embodied carbon footprints of system inputs, four *S. latissima* cultivation systems built in Denmark are regarded as carbon-negative, contributing to greenhouse gas emission reduction of 174-1160 kg CO_{2eq} ha^{-1} year^{-1} (Zhang et al. 2022). In Greenland, wild floating macroalgal biomass was mostly retained within the Nuup Kangerlua Fjord, with unknown carbon sequestration potential. Only 6.92 t C yr^{-1} of the biomass was exported beyond the fjord (Ager et al. 2023). In sediment cores collected on the northwest coast of Norway at depths between 200-500 m, a qPCR approach was applied to detect and quantify the kelp species present in the sediments. *S. latissima* was much less common than *L. hyperborea*, and when present, its quantities were lower (Frigstad et al. 2021). The contribution of the two kelps for the total carbon captured in the sediments was 10-32%.

The climate benefits of seaweed aquaculture might be further enhanced by mechanically sinking the biomass into the deep sea for carbon sequestration. However, this solution may lead to unknown consequences on the marine ecosystem (Duarte et al. 2021) and must be further investigated by long-term research projects and large-scale demonstrations to provide evidence of permanent and additional climate benefits (Hasselström and Thomas 2022; DeAngelo et al. 2023; Wu et al. 2023). A kelp aquaculture bio-techno-economic model in which large quantities of *S. latissima* would be farmed at an offshore site, transported to a deep water "sink site", and then deposited below the sequestration horizon has been developed to quantify the baseline costs and identify potential optimising strategies for kelp carbon dioxide removal (CDR) (Coleman et al. 2022). According to the model, the spatial sequestration rate and unit costs of kelp CDR would be 0.6 tCO_{2eq} and \$17,048 tCO_{2eq}^{-1}, respectively, with an "additionality" rate (AR) of 39%. AR describes the extent to which a carbon credit results in a reduction in emissions or removal of carbon that would not otherwise have happened. Following parameter optimisation, expenses decreased to \$1,257 $tCO_{2eq}^{-1,}$ and AR rose to 91%. Carbon fluxes during the macroalgae open ocean mariculture and sinking (MOS) process were computed by integrating a macroalgae model into an Earth system model (Wu et al. 2023). Carbon captured and exported by MOS is 270 PgC, with artificial upwelling (AU) adding to 447 PgC. Due to feedback in the Earth system, the oceanic carbon stores only increase by 171.8 PgC (283.9 PgC with AU) in the idealised scenarios. Currently, ambiguities in monitoring, reporting, and verification (MRV), high production costs, and energy-intensive processes may restrict the effective kelp CDR (Coleman et al. 2022). To achieve the full benefit of *S. latissima* cultivation as a climate solution, MRV standards and improved methods for assessing carbon uptake and permanence need to be developed thoroughly (Rose and Hemery 2023).

Another solution for using *S. latissima* for CDR is biochar production. Biochar is a sustainable carbonaceous material with applications in diverse areas, including improving soil organic content. Applying biochar to soil improves soil quality and is deemed a negative emission technology through carbon sequestration (Deng et al. 2020).

In a critical review of the life cycle climate impact in seaweed value chains to support carbon accounting and blue carbon financing, it is stated that climate benefits can only be claimed by tracking carbon flows across whole life cycles and over time since climate effects depend on the specific production setup, product choice and the fate of the product on the market (Hasselström and Thomas 2022). It is also suggested that financing macroalgal-based CDR projects should be directed only to setups that lead to additional and permanent carbon storage.

7. Environmental impacts and life cycle assessments

If adequately managed, seaweed cultivation can provide critical ecosystem services while contributing to developing marine resources currently underexploited in the Western world. However, there is a lack of knowledge on balancing the potential environmental risks associated with seaweed farming with the benefits to ensure the carrying capacity of the receiving environments, especially when considering expanding the industry. A recent review on this topic addressed several ecosystem changes that may be associated with a developing seaweed aquaculture industry (Campbell et al. 2019). Absorption of light, nutrients, carbon and kinetic energy, addition of artificial material and noise, release of dissolved and particulate matter, habitat for diseases, parasites and non-native species, release of reproductive material and artificial habitat creation are described as the key drivers of environmental changes, assuming standard practice and siting. The facilitation of disease, alteration of population genetics and broader alterations to the local physiochemical environment were identified as the environmental changes of greatest concern (Campbell et al. 2019). Aquaculture of *S. latissima* has been found to have limited environmental effects on the coastal environment, especially compared to other forms of aquaculture, such as fish and bivalve farming (Visch et al. 2020a). No changes were observed in benthic oxygen flux, dissolved nutrient concentrations, and benthic mobile fauna between farm and control sites; however, the farmed crop may provide habitat to mobile faunal species (Visch et al. 2020a). A *S. latissima* farm in Central Norway holds lower taxa abundance and richness and lower biodiversity than the wild kelp forests studied, but the farmed kelp hosted many associated species with communities different from what was found in the water column. The kelp farm can, thus, before harvest, serve as a "hanging garden" and attract pelagic fish (Bekkby et al. 2023). Another study, using a holistic qualitative assessment of ecosystem services, suggests that supporting, regulating, and provisioning services are mainly positively or non-affected by *S. latissima* cultivation, while some of the cultural services (recreation and aesthetic values) are likely negatively affected (Hasselström et al. 2018). The same study concluded that since many of the negative impacts on ecosystem services are local and many of the positive impacts are regional or even global, decision-makers should particularly consider the distribution of benefits and costs when framing policies for this sector in Europe and elsewhere. It is poorly understood how seaweed farms affect the local hydrodynamic environment, especially turbulence, which is essential for nutrient transport and availability. Using results from a controlled flume experiment with mimic seaweed thalli, it was concluded that expanding seaweed culture brings a dual-risk of seabed erosion and low nutrient diffusion (Zhu et al. 2021c). *S. latissima* farms may, though, serve as a form of nature-based coastal protection and have the potential to attenuate waves if numerous long lines of densely grown kelp are installed perpendicular to the direction of wave propagation (Zhu et al. 2021b).

A recent study investigating benthic degradation of kelp detritus in a defaunated mesocosm was carried out. Kelp fragments were deposited on the sediment surface (oxic degradation) or just below the oxic surface sediment layer (anoxic degradation). The results showed a high initial O_2 consumption followed by an exponential decrease in O_2 uptake over time and a linear increase in degradation rates with the amount of kelp added for both methods (Boldreel et al. 2023). This study underscores the importance of further investigating microbial degradation dynamics and its key variables for *in situ* conditions for assessing the environmental implications of seaweed farming.

Life cycle assessments (LCA) have been performed to evaluate the overall environmental sustainability of *S. latissima* cultivation and supply chains to support emerging seaweed farming activities along the European Atlantic coast. In a comparative environmental LCA of nursery, cultivation, and biomass preservation (hang-drying outdoors, heated air-cabinet drying, ensiling, and freezing) of *S. latissima* at a pilot farm in Sweden, more carbon was found to be captured by photosynthesis during growth than was emitted by the cultivation and preservation of kelp (Thomas et al. 2021). The energy-intensive preservation methods (freezing and air-cabinet drying) and the cultivation infrastructure were found to have the largest share of emissions in the supply chain. Despite the small scale of European seaweed aquaculture, *S. latissima* production is relatively resource-efficient compared to microalgae and some terrestrial plants (such as sugar beets, maize, and potatoes), according to a study from France and Ireland (Taelman et al. 2015). There is also a great potential to reduce the footprint of seaweed cultivation when less transport and electricity are used and biomass productivity increases. As energy is expected to be increasingly generated by renewable sources, it is anticipated that the footprint of seaweed production will be even smaller in the future (Taelman et al. 2015). An LCA has also been performed to calculate the environmental performance and evaluate possible improvements of the entire value chain from the production of *S. latissima* seedings to extracted protein (Koesling et al. 2021). The current production of *S. latissima* protein was found to have a global warming potential that is four times higher than that of soy protein from Brazil. To produce a seaweed protein with a lower environmental impact than soy protein, the dry matter content in *S. latissima* biomass used for extraction must be 20%, and the protein content between 19.2% and 24.3% of the dry matter in the two best scenarios modelled. The source of drying energy is also a significant variable to consider for improving the environmental impact of seaweed protein production (Koesling et al. 2021). In another study assessing the feasibility of an integrated biorefinery approach to valorise *S. latissima*, LCA of the supercritical CO_2 extraction of fucoxanthin shows that the drying process of the kelp biomass and the energy used to compress the CO_2 are the elements with the highest ecological impact in this process, suggesting routes for reducing the environmental footprint (McElroy et al. 2023). Similar results are identified performing an LCA of a seaweed-based biorefinery concept with *S. latissima* to produce food, materials and energy where they found that the biorefinery has the potential to be sustainable. However, several improvements are necessary before it is competitive with land-based systems (Nilsson et al. 2022). For *S. latissima* cultivation, fuel use and drying of kelp biomass were the main environmental hot spots, and for the alginate extraction process, the yield and purification after extraction were the most critical steps (Nilsson et al. 2022). The environmental impacts of the production of a bioplastic film at an experimental pilot scale have been assessed using LCA. The results show that the main hotspot is film fabrication, the last step in the production, mainly due to the glycerol used in this process (Ayala et al. 2023). Looking further into the environmental impact and nutritional value of food products, an LCA analysis concludes that including *S. latissima* in future vegetarian burgers or as salt replacement can positively affect the environmental impacts of these food products (Slegers et al. 2021). The environmental impact can be reduced by increasing yields, materials' lifespan, and transport efficiency. In particular, the study points towards one hotspot in cultivating seaweeds, which is the transport vessel that contributes significantly to the global warming potential (Slegers et al. 2021).

8. Integrated Multi-Trophic Aquaculture (IMTA) and bioremediation

Cultivation of *S. latissima* may serve as a biomitigation measure, extracting nutrients and critical elements from coastal systems. Macroalgae has been described as having a high potential for biosorption of many heavy metals (Zeraatkar et al. 2016), the order of the Laminariales being one of the most influential groups (Davis et al. 2003). Their abundance of cell wall matrix polysaccharides and extracellular polymers allow for a natural ion-exchange (Davis et al. 2003). The potential of bioremediation of heavy metals holds both advantages and disadvantages for farming *S. latissima*, and it might offer a cheap and efficient method to remove heavy metals from the surrounding waters, cleaning the ocean without negative ecological impacts (Zeraatkar et al. 2016).

S. latissima has the ability to remove excessive nutrients from eutrophic waters and/or reduce nutrient input into the ecosystem by fish farming in an Integrated Multi-Trophic Aquaculture (IMTA) system, where extractive species from lower trophic levels are co-cultured to utilise waste nutrients from fed species (Troell et al. 2009; Broch et al. 2013; Reid et al. 2013; Wang et al. 2014; Umanzor and Stephens 2023). Enhanced growth and yields of *S. latissima* are found when grown adjacent to salmon farm cages compared to control locations (Sanderson et al. 2012; Handå et al. 2013; Marinho et al. 2015c; Fossberg et al. 2018) confirming that this cultivation strategy can be a part of the future solution for both effective biomass production and co-use of limited coastal space. It is also found that cultivating *S. latissima* in nutrient enrichment mimicking IMTA settings will increase the biomass quality with potentially higher market value (Rugiu et al. 2021). The nitrogen content of *S. latissima* biomass grown close to the fish cages is also greater than those grown at reference sites away from the cages, indicating a higher protein content (Sanderson et al. 2012; Fossberg et al. 2018). The results from a hydrodynamic-ecological model suggest that one hectare of cultivated *S. latissima* in the vicinity of a fish farm (producing 5000 t salmon in a production cycle) can potentially remove about 0.36 t ammonium (NH_4^+) with a cultivation period from August to June, or 0.15 t NH_4^+ with a cultivation period from February to June (Broch et al. 2013). Another IMTA model with *S. latissima* and salmon estimated that a 25 ha kelp farm could take up 1.6 t of the 13.5 t of dissolved inorganic nitrogen released from the salmon between February-June (Fossberg et al. 2018). An area of approximately 220 ha would be needed to cultivate enough *S. latissima* to fix an equivalent of the nitrogen released by the fish and achieve an even mass balance (Fossberg et al. 2018). Estimations from a cultivation experiment with a monoculture of *S. latissima* in the Western Gulf of Maine, USA, found that harvesting a hypothetical hectare of *S. latissima* after 6-7 months of cultivation would have the potential to remove 0.02-0.2 t N ha^{-1}, depending on the density of long-lines (Grebe et al. 2021a).

Promising results have also been seen when cultivating *S. latissima* with other species than salmon, e.g., mussels and oysters (Jiang et al. 2022b; Lavaud et al. 2023). Compared to natural populations, *S. latissima* from mussel-integrated culture systems was found to have almost twice as much protein content, giving greater added value to the species, both as potential food and feed (Freitas et al. 2016). A study also showed that bivalves can benefit from co-cultivation, where *S. latissima* serves as a biogenic buffer against present and future ocean acidification, and *S. latissima* can benefit from the increased CO_2 (Young et al. 2022). By co-cultivating *S. latissima* in tank systems with bivalves, a significant reduction of fouling epiphytes on seaweed fronds of around 50% by bivalve filtration was observed, and a significant elevation of NH_4^+ and phosphate (PO_4^{3-}) by bivalves and alterations in kelp tissue quality were also detected (Hargrave et al. 2022).

Public acceptance of IMTA is a challenge, given the present management approach of aquaculture companies and the regulatory environment in most of the Western world. An assessment of the financial performance of a salmon monoculture versus an IMTA operation with salmon, blue mussel, and *S. latissima* in Canada using a discounted cash-flow analysis showed that IMTA operation was more profitable, even when no price premium was included for its products (Carras et al. 2020). However, multiple challenges related to the financial and environmental performance of IMTA and the increased operational complexity must be solved. The positive effects of IMTA are well documented, but the knowledge concerning economics related to these operations is still more or less in its infancy (Knowler et al. 2020).

9. Chemical composition of *Saccharina latissima*

Saccharina latissima is rich in carbohydrates (namely laminarin, alginate, cellulose, fucoidan, and the sugar alcohol mannitol) and ash, where sodium, potassium, calcium, magnesium, chlorine, bromine, iodine, phosphorus and sulphur are the most prevalent elements (Kreissig et al. 2021). *S. latissima* is also a source of protein and contains all essential amino acids (EAAs) and non-essential amino acids (NEAAs) (Sharma et al. 2018) and additionally contains a low lipid fraction (Marinho et al. 2015a). The chemical composition of *S. latissima* varies significantly due to abiotic factors, such as temperature, salinity, nutrients, irradiance, currents, depth, season and latitude. To a certain degree, the choice of cultivation site, deployment, and harvest time can be used to tailor the chemical composition for targeting commercially attractive components (Schiener et al. 2015; Marinho et al. 2015b; Sharma et al. 2018).

Numerous studies have described the chemical composition of *S. latissima*, and how this varies with cultivation period and location, as shown for amino acids and proteins (Marinho et al. 2015b; Bruhn et al. 2016; Mols-Mortensen et al. 2017; Sharma et al. 2018; Bak et al. 2019; Forbord et al. 2020a, b; Monteiro et al. 2021), carbohydrates (Vilg et al. 2015; Manns et al. 2017; Bruhn et al. 2017; Sharma et al. 2018; Samarasinghe et al. 2021b; Konstantin et al. 2023), lipids (Marinho et al. 2015a; Vilg et al. 2015; Barbosa et al. 2020; Monteiro et al. 2021; Samarasinghe et al. 2021b), micro elements including iodine and other minerals, pigments, sterols, vitamins and antioxidants (Schiener et al. 2015; Lüning and Mortensen 2015; Bruhn et al. 2016; Fernandes et al. 2016; Roleda et al. 2018; Marinho et al. 2019; Kreissig et al. 2021; De Jong et al. 2021; Wang et al. 2022), but also for toxic elements like arsenic, cadmium, lead, and mercury (Bruhn et al. 2016; Roleda et al. 2019; Pétursdóttir et al. 2019; Kreissig et al. 2021; Blikra et al. 2021; Samarasinghe et al. 2021b). **Table 1** shows the seasonal variation of ash, iodine, arsenic, cadmium, mannitol, uronic acid, fucose, glucose, protein, total amino acids, total lipids, total phenolic content and selected pigments on dry weight (DW) basis for *S. latissima*, listed as a value range from the 19 studies reviewed. For additional information on the chemical composition of *S. latissima*, read sections 2 and 4 in the review: "The sugar kelp *Saccharina latissima* I: recent advances in research" (Diehl et al. 2023).

10. Biochemical extractions and methods

Several chemical components can be extracted from *Saccharina latissima* and used for various applications, including human and animal nutrition, biomedical applications, biomaterials, fuel, and fertiliser. Due to the high content of carbohydrates, extraction of commercially valuable polysaccharides has been widely studied, but extraction of other valuable components, including protein, lipids, pigments and phenolic components, was also investigated.

Carbohydrates/Polysaccharides

Saccharina latissima contains several polysaccharides of commercial interest, some of which are water-soluble (fucoidan, laminarin and mannitol (sugar alcohol)), and others are insoluble (alginate and cellulose). One of the most commercially relevant polysaccharides is alginate. Alginate production in Europe is primarily based on wild-harvested brown kelp, mainly *Laminaria hyperborea* and *L. digitata*. With a growing global demand for hydrocolloids and the development of new alginate-based applications, cultivated *S. latissima* can be an important future source of alginates (Nøkling-Eide et al. 2023a). Here, the sequential extraction of additional high-value products will be an important driver to ensure an economically and environmentally feasible value chain, coupled with the development of markets for these added-value products (Birgersson et al. 2023). Depending on the target products, *S. latissima* can be pre-treated by different physical and chemical methods to enhance the yields and quality of extracted products. Formaldehyde or non-polar organic solvents are commonly used to remove phlorotannins, pigments and lipids (Bilan et al. 2010). The biomass can also be pre-treated with warm water to reduce the content of minerals and other soluble compounds prior to extraction of water-insoluble compounds or deionised water for increased solubility of proteins through an osmotic shock (Schiener et al. 2017). Of note, preservation and storage conditions for the biomass can have significant impacts on the yields and quality of extracted products, e.g., by chemical and enzymatic depolymerisation of biopolymers (Albers et al. 2021; Nøkling-Eide et al. 2023b).

Extraction of alginate from *S. latissima* follows the conventional approach of pre-treating with dilute acid to convert alginate to its acid form and remove cross-linking calcium ions, followed by an alkali treatment to solubilise alginate and allow separation from the residual biomass. Alginate from *S. latissima* has been shown to have a guluronic acid fraction (F_G) of 0.45-0.51 (Haug 1964; Nøkling-Eide et al. 2023a) and molecular weight average (M_w) above 600 kDa, depending on the extraction conditions (Nøkling-Eide et al. 2023b). One study evaluating the effects of different extraction conditions showed that high yields of alginate are obtained from *S. latissima* under mild conditions and short extraction times, but also that the yield was improved by increasing the pH from 8 to 9 during alkaline extraction (Nøkling-Eide et al. 2023b). Sodium carbonate (Na_2CO_3) and sodium bicarbonate ($NaHCO_3$) are conventionally used for alkaline extraction of alginate, whereas other calcium-chelating salts such as sodium citrate have been explored towards achieving a high yield and molecular weight of alginates under less alkaline conditions (Sterner and Edlund 2016).

Residual material after alginate extraction is enriched in cellulose, which can be extracted using strong alkali such as sodium/potassium hydroxide at high temperatures and a bleaching treatment with hydrogen peroxide or sodium chlorite. A few studies have characterised cellulose structure from *S. latissima* and shown variations in crystallinity and allomorph distribution (cellulose Iα and Iβ), presumably due to different extraction conditions. A cellulose yield of 15-17% of the residues' DW in fresh and acid-preserved *S. latissima*, where the crystallinity index (CI) was determined at 51% with an Iα content of 64% based on x-ray diffraction (XRD) and Fourier-transform infrared (FTIR) analysis, respectively, was obtained in one study (Nøkling-Eide et al. 2023b). Similar CI values were found in another study, whereas their extracted cellulose was mainly in the Iβ form (Bogolitsyn et al. 2022a). In another study, a yield of 26% cellulose was obtained due to a more extensive alginate extraction from the residues and a significantly higher crystallinity index of 91% (Cebrián-Lloret et al. 2022).

Fucoidans, laminarin and mannitol, can be retrieved from aqueous extracts of *S. latissima*. The yield of fucoidan has been shown to improve with increasing temperature and decreasing pH (Hahn et al. 2012), whereas excessively harsh extraction conditions (very high temperature and very low pH) can depolymerise fucoidan and compromise the quality of subsequently extracted products, such as alginates. Here, ranges of 50-70°C and pH 3.5-5.5 have been proposed to ensure high fucoidan yields while maintaining a high molecular weight of both fucoidan and alginate (Birgersson et al. 2023). Enzymatic-assisted extraction by adding cellulase and alginate lyase has been shown to avoid successfully depolymerisation and obtain pure fucoidans without the need for further purification steps (Nguyen et al. 2020; Rhein-Knudsen et al. 2023). Depending on the harvest location, laminarins can be co-extracted with fucoidans from biomass harvested in late spring/early summer. Separation of laminarin from fucoidan and subsequent fractionation/concentration based on molecular size can be done through cross-flow filtration or charge through ion-exchange chromatography (Sterner and Gröndahl 2021). Laminarins can be precipitated from a solution using >60% ethanol or acetone, leaving mannitol in the supernatant (Sterner and Edlund 2016).

Proteins

Generally, brown algae contain lower amounts of protein than red and green algae, but when cultivated at a large scale, *S. latissima* can still be a significant future source of protein for food and feed (Aasen et al. 2022), and protein content up to 16% on DW basis has been reported (Bruhn et al. 2016). Various traditional methods for protein determination exist: the Kjeldahl Method (nitrogen determination and multiplying the nitrogen content with a convention factor of 6.25 to calculate the protein), the Lowry Method (colorimetric assay), the Bradford Method (colorimetric assay) (indirect method), and direct analyses of total amino acids (Mæhre et al. 2018). A review of 236 studies of protein extraction from red, green, and brown algae (including 40 measurements on *Laminaria/Saccharina*) showed that direct protein determination was used in 42% of the studies and the Kjeldahl Method in 52% of all studies (Angell et al. 2016). The commonly used conversion factor of 6.25 originates from a presumption that protein contains 16% nitrogen, which is typical in animal protein. However, algae additionally have nitrogen bound in components like pigments, nucleic acids, free amino acids, and inorganic nitrogen compounds (Jones 1931; Mariotti et al. 2008), which leads to an overestimation of the protein content when the Kjeldahl method is used (Mæhre et al. 2018). Based on these studies, the conversion factor has more recently been proposed to be around 5 for brown algae in general (Mariotti et al. 2008; Angell et al. 2016) and around 4 for *S. latissima* (Forbord et al. 2020a). However, direct analysis of the total amount of amino acids is the most accurate method for calculating protein content in *S. latissima* (Bak et al. 2019).

Recent studies have evaluated new methods for rapid and accurate determination of protein content in *S. latissima.* Near-infrared and Fourier transform infrared spectroscopy are efficient and accurate alternatives to the traditional methods for determining the protein content in *S. latissima* (Niemi et al. 2023). The pH-shift method has been demonstrated as an efficient way of extracting protein from *S. latissima* (Harrysson et al. 2018). The protein extraction yield has been shown to increase with increasing pH (up to pH 12) and by applying an osmotic shock with fresh water, where increasing the volume of water relative to biomass resulted in increased protein yields per dry-weight seaweed (Vilg et al. 2015). Applying polysaccharide-degrading enzymes has also increased the yield of extracted proteins (Aasen et al. 2022). The chosen method for stabilising *S. latissima* also affects the extraction yield, where one study observed significantly higher protein yield from freeze-dried, oven-dried and -20°C frozen *S. latissima* than from sun-dried, -80°C frozen and ensiled raw material (Abdollahi et al. 2019). It has also been studied how blanching of *S. latissima* before pH-shift protein extraction affects the yield, where blanching at 45°C did not compromise total protein yield (Trigo et al. 2023). Cultivation of *S. latissima* and three species of green algae in process water from various food production was studied to see if cultivation in nutrient-rich water would potentially increase the protein content of the seaweed. For the green algae, more than a 60% increase in growth rate and protein content up to four times the amount of the seawater control was demonstrated. *S. latissima* had a negative growth rate in all processing waters; therefore, this is not a successful method for protein enrichment of *S. latissima* (Stedt et al. 2022).

Lipids

Saccharina latissima contains low levels of lipids, ranging from 0.62% to 3.90% of the dry weight (DW), depending on harvest time and location (Marinho et al. 2015a; Vilg et al. 2015; Foseid et al. 2020; Monteiro et al. 2021). However, the lipid fraction has a high ratio of polyunsaturated fatty acids (PUFAs) and essential fatty acids (18:2 n-6, 18:3 n-3, 20:4 n-6, and 20:5 n-3), which potentially confers health benefits in nutritional applications despite the low quantity (Monteiro et al. 2020; Afonso et al. 2021). Lipid extraction from *S. latissima* is commonly performed by the traditional Bligh and Dyer-method, mixing the biomass in an aqueous methanol and chloroform solution (Marinho et al. 2015a; Monteiro et al. 2020). However, an alternative extraction method initially developed for microalgae (Cavonius et al. 2014), using transesterification with Potassium hydroxide (KOH), is an efficient alternative for fatty acids extraction from *S. latissima* (Vilg et al. 2015). Analysis of lipid extracts from *S. latissima* by Hydrophilic Interaction Liquid Chromatography-Mass Spectrometry (HILIC-LC-MS) identified 197 molecular species of polar lipids: 57 glycolipids, 120 phospholipids, 12 arsenolipids and eight betaine lipids (Rey et al. 2019).

Pigments and phenolic compounds

Pigments and phenolic compounds, including phlorotannins, are conventionally extracted from brown algae using a variety of combinations of solvents. One study found the optimal conditions (pH, temperature, time) for fucoxanthin extraction from *Fucus vesiculosus* with acetone, and the same protocol was used on other brown seaweeds, including *S. latissima*. For *S. latissima*, the extracts from fronds, holdfast and stipes were analysed separately, showing fucoxanthin concentrations of approximately 500, 150 and 150 μg g^{-1} of the dry weight (DW), respectively (Shannon and Abu-Ghannam 2017).

The seasonal changes in antioxidant components in *S. latissima* have been studied by extracting pigments using methanol with butylated hydroxytoluene in a sonication bath, followed by separation with High-Performance Liquid Chromatography (HPLC). A seasonal variation of the most prevalent pigments was found, with extraction yields of 222 to 665 μg g^{-1} and 170 to 655 μg g^{-1} of the DW of fucoxanthin and chlorophyll *a*, respectively (Marinho et al. 2019). Another study showed that fucoxanthin and chlorophyll could be extracted and separated in a single step in an aqueous solution, resulting in high chlorophyll and fucoxanthin extraction yields (Martins et al. 2021). Seasonal changes in pigment content have further been correlated with nutrient accessibility for biomass (Boderskov et al. 2016). A pigment-rich fraction from *S. latissima* was obtained by extraction with supercritical CO_2. A two-level factorial design was applied and showed that the pigment yields were primarily dependent on pressure (and hence CO_2 density) and not on temperature during extraction, and that total pigment yields were further improved (up to 0.4% of DW) using ethanol as a co-solvent (McElroy et al. 2023).

The phenolic content of *S. latissima* is 0.1-0.5% of DW (Zhang and Thomsen 2019), which is low compared with other species of brown algae such as *Ascophyllum nodosum* (Schiener et al. 2017), and thus few studies have focused on developing methodology for extraction of phenolic compounds specifically from *S. latissima*. The Folin-Ciocalteu (FC) assay is conventionally used to quantify total phenolic content (TPC) in extracts but is not specific for phlorotannins and requires complementary methods such as NMR, HPLC and mass spectrometry for more accurate quantification and characterization of phlorotannins in brown algae.

Polyphenols, or phlorotannins in brown algae, are conventionally obtained with a single liquid-solid extraction step using polar aprotic and protic solvents such as acetonitrile, acetone, ethanol and methanol in water (Schiener et al. 2015; Vilg et al. 2015; Sharma et al. 2018; Sardari et al. 2021). Extraction yields are positively correlated with the polarity of the solvent, as one study demonstrated higher phenolic content in methanol extracts compared with ethyl acetate (Marinho et al. 2019).
S. latissima extracts may give deceivingly high TPC values from the FC assay due to a high co-extracted protein and mannitol content. One study applied a solid-phase extraction by HPLC on lyophilized ethanol extracts to address this, achieving a tenfold concentration of phlorotannins from *S. latissima* compared with ethanol alone (Sardari et al. 2021).

Phlorotannins have been proposed to exist in two forms, soluble and membrane-bound, depending on their location in the brown algal cells and which may have different structures and bioactivities. Soluble phlorotannins have been extracted using two-solvent methods with sequential application of methanol and chloroform or dichloromethane, followed by ethyl acetate. The solid algal residues were in the same study treated with alkali to extract membrane-bound phlorotannins (Liu et al. 2017).

11. Applications of *Saccharina latissima* and derived components

Saccharina latissima contains several components of commercial value, including alginate, mannitol, laminarin, fucoidan, iodine, pigments, phenolics and lipids, which can be utilised for various industrial applications for food, feed, fertiliser, biofuels, cosmetics, pharmaceuticals, and nutraceuticals (Holdt and Kraan 2011; Stengel et al. 2011; Kraan 2013). Due to its nutritional composition, *S. latissima* is already used commercially in food applications and is a potential functional food ingredient (Neto et al. 2018; Rey et al. 2019). Many components show a diversity of bioactivities, which can potentially improve human health. *In vitro* and animal studies have, for example, reported antioxidant, antiviral, anticancer and anticoagulant effects of compounds derived from *S. latissima* (Hafting et al. 2015; Afonso et al. 2021).

Food and feed

Saccharina latissima can be used as an ingredient in human and animal nutrition, to add nutritional compounds and flavour, or as a texturising agent. *S. latissima* can also be a functional food ingredient, conferring antioxidants and immunomodulatory properties (Neto et al. 2018; Afonso et al. 2021). *S. latissima* is already used commercially in plant-based burgers and minces, pasta, pesto, spice - and salt mixes (Van Den Burg et al. 2021a; Mendes et al. 2022). Moreover, it has been shown that inclusion of cultivated seaweed in such products can have a positive environmental impact on diets (Stefaniak-Vidarsson et al. 2019; Slegers et al. 2021). A sensory study indicated that consumers rated *S. latissima* as the saltiest, sourest, and bitterest compared to *L. digitata* and *Alaria esculenta* (Chapman et al. 2015). *S. latissima* is commonly processed for food applications by freezing, blanching or drying. However, more research efforts recently focused on fermentation as an alternative processing method for cultivated kelps, both because it is a less energy-intensive processing method compared to freezing and drying and because it can change the sensorial properties and chemical composition (Chapman et al. 2015; Mouritsen 2017; Stévant et al. 2017a; Bruhn et al. 2019; Akomea-Frempong et al. 2021; Sørensen et al. 2021; Yen et al. 2022).

S. latissima contains a high amount of iodine (I) compared to other seaweed species. The exact content varies greatly and has been reported in ranges from 2.8 to 6.6 g I kg^{-1} DW (Stévant et al. 2017a; Nielsen et al. 2020; Afonso et al. 2021). *S. latissima* can be used as a plant-based iodine source, especially suited for vegetarian and vegan diets, which are often iodine deficient (Groufh-Jacobsen et al. 2020). However, the daily recommended intake (DRI) of iodine is 150 µg in Europe and USA. The upper intake level (UL) is 600 µg and 1100 µg in Europe and the US, respectively (Trumbo et al. 2001). The UL for I limits the amount of *S. latissima* used in food applications (Bouga and Combet 2015) to less than 1 g day^{-1} (Afonso et al. 2021). In comparison, *A. esculenta*, another kelp species that is cultivated commercially and used for food applications in Europe (Mendes et al. 2022), contains 0.2 g I kg^{-1} DW (Stévant et al. 2018b), which allows for higher inclusion levels in food products without exceeding UL for iodine.

The choice of post-harvest processing and stabilisation method will influence the biochemical composition of *S. latissima and* the quality and shelf-life (Standal et al. 2023). By soaking or blanching in warm water after harvest, the water-soluble iodine can be reduced by more than 80% compared to freshly harvested *S. latissima*, which allows higher inclusion levels of *S. latissima* in food products (Stévant et al. 2017b; Nielsen et al. 2020). Furthermore, there are indications that blanching increases the consumer acceptance of *S. latissima* in food (Akomea-Frempong et al. 2021). However, the blanching treatment also reduced the content of other water-soluble components, including minerals, polyphenols, and fucoxanthin, and will therefore influence the total nutritional content and potentially functional properties of *S. latissima* (Stévant et al. 2017a). In order to limit the loss of nutrients and flavour, it is beneficial to blanche *S. latissima* in seawater instead of freshwater (Krook et al. 2023). Other preservation methods such as freezing, sun-drying, oven-drying and ensiling of *S. latissima* after harvest have also been shown to affect the composition of the seaweed significantly. Of these, oven-drying overnight at 40°C and freezing at -20°C were shown to have the smallest effect on the composition (Albers et al. 2021). The effects of drying have been investigated in more detail, where one study compared convective air-drying at 25, 40, and 70°C and freeze-drying of *S. latissima*. Here, it was found that freeze-drying resulted in significantly lower iodine contents compared to air-drying at all three temperatures, but the overall nutritional value, flavour and aroma were similar for all drying methods. The swelling capacity (the capability to absorb water) was lower for air-dried than freeze-dried samples, and a difference in mouthfeel was observed in the sensory evaluation (Stévant et al. 2018a). Another study compared the effects of sun drying, freeze drying, and heat pump-based drying systems at different air temperatures and relative levels of air humidity (30, 50, and 70°C and 25 and 50% humidity) on the physicochemical properties, phenolic activity, and antioxidant capacity of *S. latissima*. The results showed that all drying methods significantly decreased total phenolic and vitamin C content and antioxidant activity compared to fresh *S. latissima*. The best method for maintaining functional properties and nutritional components was drying at temperatures below 50°C and low humidity (Sappati et al. 2017, 2019). A recent study has examined the effect of high-pressure processing (HPP) of *S. latissima* on the chemical composition, colour, texture and microbial stability. HPP was efficient for retaining the nutritional content and colour, but significantly reduced the hardness and compression of *S. latissima.* Due to the low initial microbial load, the microbial stability and shelf life were difficult to assess (Jönsson et al. 2023). Instead of directly consuming *S. latissima* and derived components, *S. latissima* can also potentially be used to improve the shelf-life and taste of other foodstuff, as shown for Atlantic salmon fillet stored with wet *S. latissima* (Kirkholt et al. 2019).

The potential for kelps to be used as feed for farm animals has been evaluated (Makkar et al. 2016). Due to a low protein content (up to 16% protein DW^{-1}, Bruhn et al. 2016) compared to other widely used feed ingredients like soybean meal (48% protein DW^{-1}) and fish meal (68.7% protein DW^{-1}) (Angell et al. 2016), enrichment of the protein fraction and/or co-extraction with other high-value ingredients will presumably be required for commercially viable processing (Emblemsvåg et al. 2020; Aasen et al. 2022). *S. latissima* is a good source of microelements, including I, Cu, Fe, Mn, and Se. However, the high content of total As, which is reported in the range from 20 to 90 mg kg^{-1} DW (Schiener et al. 2015; Bruhn et al. 2016; Kreissig et al. 2021), is potentially a limiting factor for the use of *S. latissima* in feed, which has a limit of 40 mg kg DW^{-1} total As for "seaweed meal and feed materials derived from seaweed" (COMMISSION REGULATION (EU) 2019/1869 (EU 2019)). It should be noted that the vast majority (>99%) of As in *S. latissima* is organic, which is less of a health concern compared with inorganic As (Trumbo et al. 2001; Pétursdóttir et al. 2019; Blikra et al. 2021). Although high inclusion levels of whole *S. latissima* in animal feed might be problematic, it can still be an interesting functional feed ingredient that provides laminarin, fucoidan and essential fatty acids (Samarasinghe et al. 2021b).

By biorefining *S. latissima*, the nutritional values can be increased, thus making it more suitable as an animal feed supplement (Schiener et al. 2017). Bioactive components derived from *S. latissima*, such as laminarin and fucoidan, can be functional feed ingredients with potentially positive health effects in animal nutrition (Øverland et al. 2019). Another critical aspect of cultivated seaweed to become commercially viable as an animal feed ingredient is developing cost-efficient preservation methods (Yen et al. 2022), such as ensiling (Novoa-Garrido et al. 2020). One *in vitro* study showed that *S. latissima* could be mixed with other feed ingredients (including corn, wheat and soybean meal) into multinutrient blocks for feeding ruminants (Marcos et al. 2023).

Several animal feeding trials have studied the effect of including *S. latissima* (whole or extracts) in the diet of ruminants (Samarasinghe et al. 2021a; Grabež et al. 2022, 2023; Qin et al. 2023), monogastric animals (Gahan et al. 2009; McDonnell et al. 2010; Krogdahl et al. 2021; Juul et al. 2022; Fjære et al. 2022) and fish (Ferreira et al. 2020; Granby et al. 2020). In a feeding trial with Norwegian lambs, the effect of replacing 5% of the control diet with dry *S. latissima* in the finishing diet was studied. A significant increase in iodine and arsenic was found in raw meat and dry-cured leg, as well as a significant selenium increase in raw meat. A sensory panel tasted the dry-cured leg to evaluate odour and taste, which showed no effect of including *S. latissima* on the sensory properties of the dry-cured leg (raw meat was not evaluated) (Grabež et al. 2022). In another study, rainbow trout were fed diets with 1, 2 and 4% dry *S. latissima*, with varying effects: 4% inclusion level decreased the body weight, and 1 and 2% inclusion had no negative effect on the final weight of the trout. 2% inclusion led to a significant downregulation of an oxidative stress marker, which implies that *S. latissima* can mitigate oxidative stress. The lipid metabolism was altered, causing a decrease in fatty acids in the trout fillet without compromising the concentrations of EPA and DHA (Ferreira et al. 2020). The effect of including laminarin, fucoidan, or a mix of the two (extracted from *Laminaria* spp.) in the diet for weaning piglets was studied. The result showed that piglets fed diets with laminarin gained more weight and had reduced diarrhoea and faecal *Escherichia coli* populations compared to the control diet and diet with fucoidan, indicating that laminarin improved gut health in weaning piglets (McDonnell et al. 2010). A rat study showed low digestibility of protein from *S. latissima*; however, the rats were fed whole *S. latissima*, and the digestibility was presumed to improve by using protein-enriched *S. latissima* extracts, potentially in combination with other high-quality protein sources (Juul et al. 2022). Information about the bioavailability of protein from *S. latissima* is scarce, but a study of protein release in an in vitro digestion model showed a protein release of 52.7% after 120 min of duodenal digestion (Vasconcelos et al. 2023).

Food and feed safety

S. latissima is accepted in the Novel Food Catalog (Regulation (EU) 2017/2470, (EU 2017)), meaning it is authorised for human consumption in the EU. The General Food Law (Regulation (EC) No 178/2002, (EU 2002a)) regulates the food safety of all EU food products, including seaweed products. Similarly, food safety in the United States is regulated by The U.S. Food and Drug Administration (FDA) (Kim et al. 2019). The FDA is giving any substance considered safe for human consumption the status GRAS = Generally Recognized As Safe. In Europe, the Commission Regulation (EC) No 1881/2006 (EU 2006) regulates maximum levels of heavy metals and other toxic substances in food, but no specific maximum levels exist for seaweed in food. One exception is France, which has recommended limit values for Cd, I and As in seaweed of 0.5, 2000 and 3 mg kg^{-1} DW, respectively (Mabeau and Fleurence 1993; Stévant et al. 2017a). Values of As, Cd, Cr, Pb and Hg in *S. latissima* are reported in some studies being above the maximum level for other foodstuffs (the maximum level for Cd is 0.2 and 1 mg kg^{-1} of fresh weight for leafy vegetables and bivalve molluscs, respectively; Maulvault et al. 2015; Stévant et al. 2017a; Banach et al. 2020). When comparing the metal content (As, Cd, Cr, Hg, Pb) in *S. latissima* from 2012-2014 in Long Island Sound and New York, it was found that all metals except Pb were below most existing maximum levels (Kim et al. 2019). However, the study also described a strong temporal variation, suggesting that regular monitoring of heavy metal content of cultivated seaweeds is necessary. The temporal and spatial variation of heavy metal content for *S. latissima* were confirmed in a Danish study (Boderskov et al. 2021); thereby, As and Cd concentrations exceeded the current regulations in some regions and sampling periods. High concentrations of As and Cd in *S. latissima* were also found in Danish, Icelandic and Norwegian regions, which might limit the commercial use of *S. latissima* (Nielsen et al. 2016b; Samarasinghe et al. 2021b; Yen et al. 2022). Nevertheless, high metal concentrations were shown to be reduced by treating cultivated *S. latissima* with high temperatures and fermenting them with lactic acid bacteria (Na: -15%; Cd: -35%, Hg: -37%; Bruhn et al. 2019).

The Commission Recommendation (EU) 2018/464 (EU 2018) recommended monitoring metals and iodine in seaweed, halophytes and products based on seaweed. Data was collected in 2018, 2019 and 2020, and it is expected that the EU Commission will evaluate options for risk management of heavy metals and iodine in seaweed food products within the next few years (Lähteenmäki-Uutela et al. 2021; Hogstad et al. 2023). Specific regulations for the use of macroalgae in food supplements exist, and the Commission Regulation (EC) No 1881/2006 (EU 2006) sets maximum levels for cadmium (3.0 mg kg^{-1} DW) and mercury (0.1 mg kg^{-1} DW) in food supplements with seaweed (Rahikainen et al. 2020). Feed safety is controlled by specific regulations, and various algae-based feed products are accepted for use in the EU, as listed in Commission Regulation (EU) No 68/2013 (EU 2013). Maximum levels of toxic components, including heavy metals, are listed in Directive 2002/32/EC (EU 2002b). Specific limits exist for As (40 mg kg^{-1} DW and 2 mg kg^{-1} DW for total and inorganic, respectively) in seaweed-based feed (Rahikainen et al. 2020).

There is a risk that the marine allergens from crustaceans, molluscs and fish can be transferred to *S. latissima* due to their co-existence, both in the wild and especially in Integrated Multi-Trophic Aquaculture (IMTA) systems, when *S. latissima* is grown near other species. In a recent study where *S. latissima* was farmed in three different Norwegian IMTA farms, the crustacean allergen *tropomyosin* was above the detection limit, corresponding to 0.2 mg kg^{-1} DW per sample at all three locations. Levels of up to 1 mg kg^{-1} DW were detected; however, this is not considered a critical consumption level (Mildenberger et al. 2022).

Microbial safety is another essential aspect of *S. latissima* for human and animal consumption. The six pathogens *Listeria monocytogenes*, *Salmonella enterica*, *Staphylococcus aureus*, pathogenic *Escherichia coli*, *Vibrio vulnificus* and *Vibrio parahaemolyticus* were inoculated on freshly harvested *S. latissima* from Maine, USA, and the pathogen load was evaluated under three storage temperatures (4, 10 and 20°C) and two drying methods (air- and freeze drying). The results showed reduced pathogen load after storage for all conditions except for storage at 20°C (Vorse et al. 2023). The ability of extracts from dry *S. latissima* to inhibit the growth of *Staphylococcus aureus* was also demonstrated in another study from Main (Cusson et al. 2021). The microbial safety of fresh and heat-treated cultivated *S. latissima* from Norway was analysed, and all samples had low total plate counts (1 to 3 log colony-forming unit; cfug^{-1}), and none of the pathogenic bacteria examined (enterococci, coliforms, *Vibrios* and *Listeria* monocytogenes) were detected (Blikra et al. 2019). Another study on cultivated *S. latissima* from Scotland from two different harvest years (2019 and 2020) found that the microbial load varied significantly between the two seasons, which highlights the need for a better understanding of microbial safety of cultivated seaweed and its variation based on external environmental factors, genetic variation, and handling/storage post-harvest (Lytou et al. 2021).

Biomedical compounds

Components from *S. latissima* show promise for utilisation in biomedical applications. For instance, its sulphated polysaccharides (fucoidans) have demonstrated a wide range of bioactivities, including anticancer, immune-stimulating, anti-inflammatory, antiviral, antithrombotic, anticoagulant, and antioxidant effects (Holdt and Kraan 2011; Fitton 2011; Wijesinghe and Jeon 2012; Ehrig and Alban 2014; Venkatesan et al. 2015; Gomez-Zavaglia et al. 2019). Other components with potential medical use are laminarin, alginate, mannitol, polyphenols and some pigments (Venkatesan et al. 2015; Stévant et al. 2017a; Zargarzadeh et al. 2020; Karuppusamy et al. 2022). Several studies compare the bioactivities of these components from various brown algae species, including *S. latissima* (Jiao et al. 2011; Wijesinghe and Jeon 2012; Brown et al. 2014; Ganesan et al. 2019; Gabbia and De Martin 2020; Bi et al. 2022; Karuppusamy et al. 2022), whereas the following studies focused solely on *S. latissima* and its derived components. *S. latissima* cultivated in France was screened for potential impact on obesity, diabetes, arterial pressure, and antioxidant content for use as a functional food ingredient. Water, ethanol, and acetone extracts were prepared and evaluated for their ability to inhibit enzymes that affect blood sugar (α-glucosidase), digestion (lipase), and blood pressure (angiotensin-converting enzyme (ACE)). The results showed modest ability to inhibit α-glucosidase and lipase. A more promising result was seen on ACE inhibition, indicating a potential positive impact on blood pressure (Neto et al. 2018). Another study using cultivated *S. latissima* from the US showed that inclusion of *S. latissima* in the diet of mice could potentially inhibit obesity by preventing obesity-associated metabolic disturbances and Non-alcoholic steatohepatitis (NASH) (Kim et al. 2021). A recent study looked at the effect of alginate, laminarins and two fractions of fucose-containing sulphated polysaccharides (FCSPs) extracted from *S. latissima* cultivated in Scotland on immunostimulatory and hypocholesterolemic activity in an *in vitro* model. One FCSP contained mainly uronic acid and fucose, and the other FCSP fucose and galactose. Both FCSPs had immunostimulatory effects on B lymphocytes. Only the FCSPs that contained uronic acid showed a significant hypocholesterolemic effect. No effect was observed from laminarin and alginate. This study supported the potential of fucoidans to be a health-promoting functional ingredient (Moreira et al. 2023). Another study compared FCSPs extracted from *S. latissima* (wild harvest from the Kiel Fjord, Baltic Sea and Faroe Islands, North Atlantic Ocean) to commercially available FCSPs from *Fucus vesiculosus*. The results demonstrated that FCSPs have antitumor, antimetastatic and antiangiogenic activity and may be used for tumour therapy. The results showed a stronger effect of FCSPs from *S. latissima* than *F. vesiculosus* (Schneider et al. 2015). Inhibition of the neutrophil elastase enzyme has been a proposed anti-cancer activity of fucoidan and similar sulphated polysaccharides. One study prepared fucoidan extracts from various sources of *S. latissima* with different compositions/structures and found that elastase inhibition and anticoagulating properties increased with the fucose content and sulfation degree of the polysaccharide extracts (Ehrig and Alban 2014). Fucoidans from *S. latissima* have also been demonstrated to inhibit inflammatory cytokine expression, complement activation, growth factor signalling, and oxidative damage associated with age-related macular degeneration (Dörschmann et al. 2019, 2023).

Biomaterials

Polysaccharides extracted from *S. latissima* can be used in a variety of biomaterials. Notably, alginates form ionic cross-links in the presence of divalent ions, which can be exploited to form hydrogels, fibres, films and other composite materials. Cellulose fibres, including micro- and nanocrystalline and fibrillar derivatives, can have properties similar to other cellulose sources and, thus, a vast array of material applications (Birgersson et al. 2023).

Alginate fibres from *S. latissima* have been prepared through wet spinning, extruding highly concentrated alginate solutions into a calcium chloride bath followed by winding the fibres on a rotating drum and drying (Silva et al. 2023). Out of four evaluated brown algal species, the *S. latissima* alginate extract exhibited superior spinnability, forming 100-140 µm fibres with better tensile properties compared with reference materials gum arabic, starch film, polyhydroxybutyrate, and carboxymethyl cellulose.

Minimally processed protein-cellulose complexes (PCC) have been generated from *S. latissima* by extracting lipid- and water-soluble compounds and alginate from the biomass before freeze-drying the residual materials to form PCCs. These porous materials demonstrate good adsorptive properties for potential applications in pharmacy and environmental remediation (Bogolitsyn et al. 2022a). In these studies, complexes from *S. latissima* showed a higher adsorption capacity for ionic dyes than similar materials derived from *L. digitata*, presumed due to a higher protein content and/or higher ratio of cellulose in phase Iα in *S. latissima* (Bogolitsyn et al. 2022b). Composite films of *S. latissima* have been prepared by dissolving the dried algae in trifluoroacetic acid and blending with microcrystalline cellulose for use in biomaterials for wound healing. Here, it was found that films prepared with *S. latissima* were more ductile than films with cellulose alone, had more potent antioxidant activity than similar films prepared from red and green algae, and showed anti-inflammatory properties in fibroblast cell cultures (Guzman-Puyol et al. 2017).

After alginate extraction, residual fractions of *S. latissima* have been used to produce cellulosic films for potential use in food packaging applications. It was found that treatment of the residues with strong alkali resulted in a purer cellulose matrix and improved transparency and mechanical properties of the films compared with less refined fractions containing residual alginate, proteins, and other compounds. The less refined films did, however, exhibit lower water permeability due to interactions between the residual compounds (Cebrián-Lloret et al. 2022). It is economically advantageous to extract alginate and cellulose directly from fresh seaweed without energy- and cost-demanding pre-processing like freezing or drying. Stabilisation of fresh *S. latissima* with formic acid at low temperatures before extraction has been shown to preserve the alginate and cellulose quality for further use for biomaterials and other applications (Nøkling-Eide et al. 2023a).

Biofuel, biochemicals and fertiliser

The storage carbohydrates laminarin and mannitol accumulate in *S. latissima* during spring and summer, constituting up to 15 and 25% of the DW, respectively (Schiener et al. 2015). Laminarin and mannitol can be fermented for biofuel production, offering a sustainable alternative to fossil fuels (Adams et al. 2009; López-Contreras et al. 2014; D'Este et al. 2017; Lamb et al. 2018). The structural polysaccharides alginate and cellulose are fermentable with certain microbial strains and enzymatic hydrolysis, adding up to 65-70% carbohydrates of the DW. Preservation with sulphuric and formic acid has shown to be an efficient method for preserving mannitol and laminarin in *S. latissima*, intended for use as feedstock for biofuel production (Sandbakken et al. 2018). One recent study demonstrated the use of enzymatically hydrolysed *S. latissima* as a substrate for producing acetone, butanol, and ethanol (ABE), however, with low efficiency and long fermentation lag time. There is a need for further optimisation to make ABE production from cultivated *S. latissima* economically feasible (Schultze-Jena et al. 2022). One possibility is to improve the biofuel yield from *S. latissima* by using a cascading circular bioenergy system for the production of biochar, syngas and bio-oil through incorporated pyrolysis, which has been shown to increase the biomethane yield from *S. latissima* by 16% with optimal biochar addition (Deng et al. 2020). Another option is to ferment *S. latissima* together with other inexpensive feedstock. One recent study evaluated the co-fermentation of *S. latissima* hydrolysate together with candy-factory waste and digestate from a biogas plant by various lactic acid bacteria, resulting in a successful production of lactic acid (Papadopoulou et al. 2023). Another study showed that adding up to 50% of *S. latissima* under anaerobic digestion of municipal wastewater sludge optimised the digestion conditions (Ometto et al. 2018). Co-fermentation of *S. latissima* with wheat straw increased biogas yield (Vivekanand et al. 2012). Hydrothermal treatment of *S. latissima* before fermentation has proven to be an efficient method for producing biohydrogen and biomethane biogases (Vivekanand et al. 2012; Lin et al. 2019). Hydrothermal liquefaction (HTL) of *S. latissima* at high temperatures (585°C min^{-1}) also caused increased production of bio-oil (Bach et al. 2014).

Mannitol-rich extracts from *S. latissima* have also been shown to be a useful substrate for growing *Bacillus methanolicus* to produce valuable chemicals, like the amino acid derivative *cadaverine* (Hakvåg et al. 2020).

Wild-harvested seaweed has been used as a fertiliser in coastal areas for centuries due to its high mineral content and the ability to improve porosity, thereby increasing the water and air penetration of the soil (Craigie 2011). The potential of cultivated *S. latissima* to reduce eutrophication by circular nutritional management was studied in a comparative Life Cycle Assessment (LCA), comparing three seaweed biomass management scenarios, including using it as a fertiliser. Using *S. latissima* as a fertiliser showed the lowest environmental impact (Seghetta et al. 2016b). The use of *S. latissima* for fertiliser production has better potential when produced together with other components (e.g., protein and bioethanol) in a biorefinery set-up (Seghetta et al. 2016a).

Another type of soil enrichment/treatment is biochar. Biochar is produced by converting biomass to a carbon-rich black material via several thermochemical methods, such as pyrolysis, hydrothermal carbonization, and torrefaction (Farghali et al. 2023)**.** Due to their specific properties (Osman et al. 2022), biochar can be used in several fields like agronomy and animal farming, soil remediation and water treatment, energy storage, biogas production, or carbon sequestration (Sun et al. 2022; Farghali et al. 2023). Biochar can be produced from various commercially cultivated seaweeds (including *Saccharina* sp.; (Roberts et al. 2015)), and because the nutrients contained in macroalgae are preserved and concentrated in biochar (Farghali et al. 2023)**,** it holds the potential to be a cost-effective fertiliser (Sun et al. 2022)**.** Biochar produced from brown seaweed species has lower concentrations of potassium and sulphur and higher pH and carbon and hydrogen content than those produced from red seaweed species (Roberts et al. 2015). However, seaweed biochar is consistently different from biochar produced from lignocellulosic sources (Adams et al. 2020), having low carbon content but high concentrations of exchangeable nutrients (in particular N, P, K, Ca, and Mg; Roberts et al. 2015; Sun et al. 2022). Preliminary work/results with biochar/pellets from different macroalgae, including *S. latissima* sampled on mussel lines, show possible limitations of algal biochar

(Adams et al. 2020), as high proportions of sodium are retained in the macroalgae char and may have a negative effect through increasing soil salinity (Adams et al. 2020). A few studies on biochar produced from *S. japonica* showed that it could be used for pollutant removal, like heavy metal (Poo et al. 2018) or industrial dye (Boakye et al. 2019; Sewu et al. 2021), with higher efficiency than conventional woody biochar or carbonaceous adsorbents. Creating biochar with unique mixes of seaweed and lignocellulosic sources could be a way to fertilise specific soil types in agronomy (Roberts et al. 2015).

***Saccharina latissima* as feedstock in biorefineries**

As described above, *S. latissima* can be used for multiple applications (food, feed, biomedical applications, biomaterials, fuel, fertiliser, etc.). However, it might be economically favourable to extract various components from *S. latissima* and use them for different applications and markets. The feasibility of using *S. latissima* as feedstock for biorefineries has been studied extensively over the last decade (López-Contreras et al. 2014; Marinho et al. 2016; Schiener et al. 2016; Zhang and Thomsen 2019, 2021; Larsen et al. 2021; McElroy et al. 2023) and has shown potential for increasing the value of cultivated *S. latissima*. A biorefinery approach, in combination with a thorough understanding of the effect of seasonal variation of the composition, is a likely way forward for creating revenue from sustainably and economically cultivated *S. latissima* (Seghetta et al. 2016a; Zhang and Thomsen 2019; Adams et al. 2020; Chauton et al. 2021; Nilsson et al. 2022).

12. Knowledge gaps and concluding remarks

Industrial cost-effective cultivation requires novel technology with a high degree of mechanisation and automation along the entire production chain comprising production in nursery, deployment, on-growth at sea, monitoring, harvesting and stabilisation/processing. To allow transition from "low-tech" (labour-intensive) to "high-tech" (cost-effective) cultivation, technology transfer from the successful marine and maritime industries to seaweed farming should be prioritised. In order to optimise biomass yields, more knowledge is needed on the abiotic and biotic factors that control growth and biofouling on farmed *S. latissima*, and site selection is crucial. Developing cultivars for improved traits like high biomass production, increased content of valuable compounds and low affinity for biofouling could be of great importance for the future industry and are of current interest.

The harvest season for *S. latissima* is condensed to a 6-8-week period in spring/early summer for most of the near coastal cultivation locations where the species is cultivated nowadays. Later in the season, when water temperature increases, epiphytes grow on the kelp fronds, making it less suitable for human consumption, which is the main market today. *S. latissima* is an easily perishable raw material that must be stabilised quickly after harvesting. Freezing and drying are the main stabilisation/processing methods used today, but there is a need to develop less energy-intensive and more cost-efficient processing methods to lower production costs and enable rapid processing of large amounts. Acid preservation and fermentation are promising methods currently being evaluated for various markets. For seaweeds, including *S. latissima*, to become a more mainstream food in Western countries, there is a need to continue to develop tasty food products. Moreover, to unlock markets like feed and biomedical applications, there is a need for further documentation of health effects.

For future cultivation measures, it would be beneficial to understand the genetic diversity and population structure of *S. latissima* in order to obtain information on optimal management and conservation, and to identify genetic resources. As farmers attempt to improve yields and to ensure that *S. latissima* farms withstand climate change, more research into using genetic tools will be necessary. Research into how priming (Scheschonk et al. 2023) can improve *S. latissima* resilience to stress and eventually prolong the growing season; studies on which breeding techniques (Goecke et al. 2020) are more effective in *S. latissima* are all likely to increase and provide valuable tools for cultivation and restoration.

In the near future, the ecological impacts of *S. latissima* farming and how this could contribute to climate change mitigation and adaptation will need to be further explored. A recent review on the effects of kelp aquaculture on biodiversity revealed a general lack of data on the topic (Forbes et al. 2022). They warn that kelp farming might not be the ideal solution to increase ecosystem services provided by marine forests. Similarly, while seaweed farming is being advocated as a solution to fight climate change (Duarte et al. 2017), several authors have been critical of oversimplifications of this role and call for more research before large productions are encouraged (Hasselström and Thomas 2022; Troell et al. 2023).

The expected increase in *S. latissima* farms and capacity over the next decades raises societal challenges. Namely, the competition for space with other maritime activities might arise, for example, with fisheries and wind turbines, the latter also expected to proliferate. Acceptance by local communities will depend on this competition but also on the number of jobs created and the impact on the landscape (lower than the one created by wind turbines, for example). On a governance level, sustainable *S. latissima* farming is an excellent economic activity to address pressing global issues, such as climate change and marine biodiversity loss. However, the extent of its application will depend on regional and local marine spatial planning plans, legislation and overall public acceptance.

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Figure legends

Fig. 1 Impacts of *Saccharina latissima* farming. Abiotic factors of the environment (e.g., temperature, irradiance) influence the physiology, biochemistry and performance of *S. latissima* (see more in Review I, Diehl et al. 2023). This affects the concentration of chemical compounds in the sporophytes (e.g., vitamins, carbohydrates), which determines the use of *S. latissima* (e.g., for food, feed, biomaterial). Further, the presence of *S. latissima* farms impacts the environment (e.g., by altering the water hydrodynamics, creating habitat for associated species). The use of *S. latissima* farms is also promoting further sectors (e.g., fisheries, carbon uptake).

Fig. 2 Life cycle of *Saccharina latissima*. The life cycle of *S. latissima* can be split into a diploid (blue) and a haploid (yellow) phase. Adult sporophytes (2n) release zoospores, which grow into female or male gametophytes (1n). Female gametophytes release eggs (1n); male gametophytes release gametes (1n). Egg and gametes will fuse to zygotes (2n), which grow into sporophytes (2n). Photographs show how the different farming steps are implemented in the life cycle of *S. latissima*. Photos: Seaweed solutions and SINTEF Ocean. Modified after Diehl et al. 2023.

Table legend

Tab 1: Seasonal variation of selected components in *Saccharina latissima*. DW = dry weight.

Figure 1:

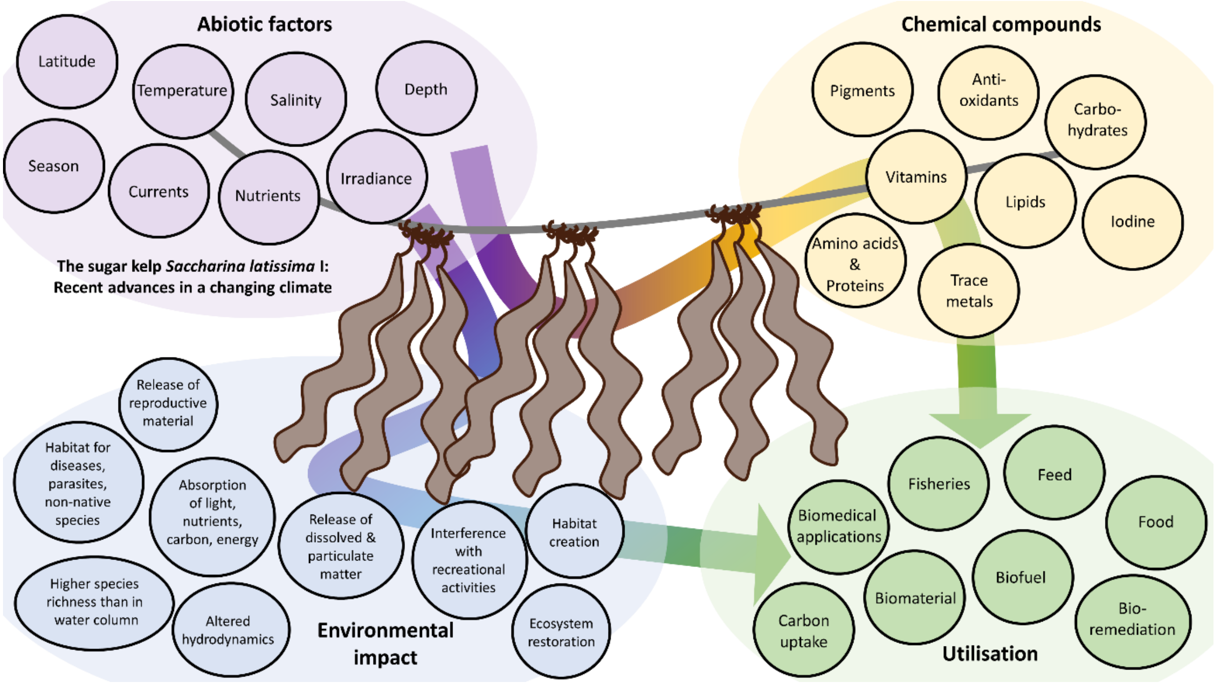
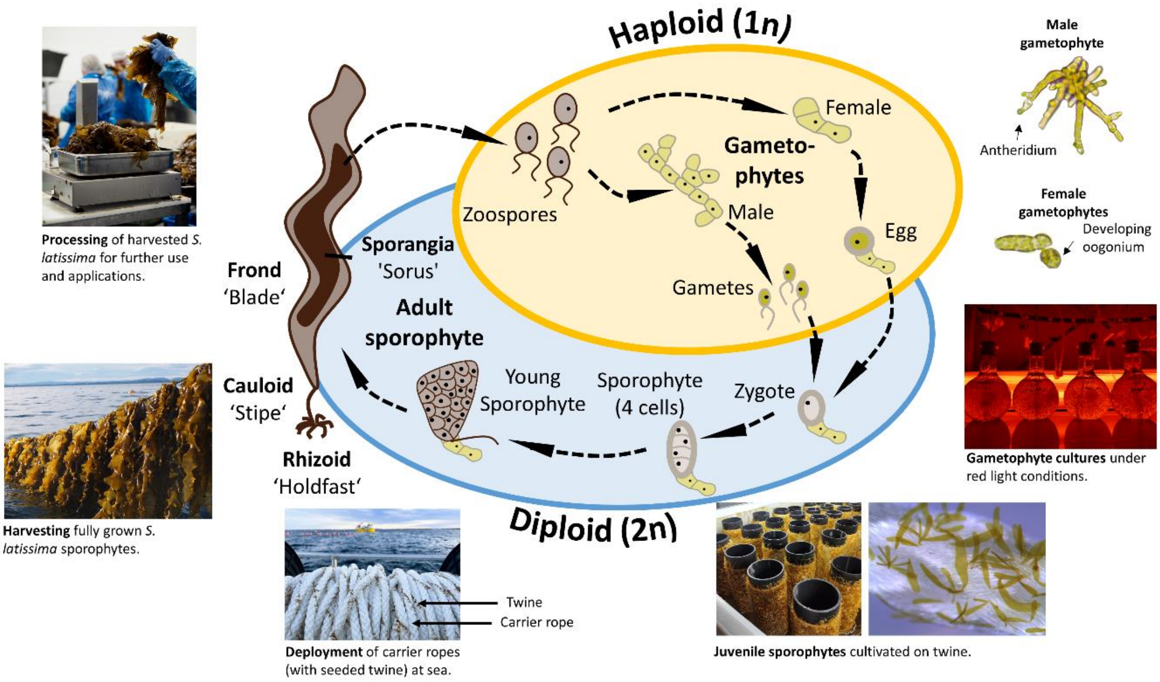


Figure 2:



Processing of harvested *S. latissima* for further use and applications.

Harvesting fully grown *S. latissima* sporophytes.

Deployment of carrier ropes (with seeded twine) at sea.

Juvenile sporophytes cultivated on twine.

Gametophyte cultures under red light conditions.

Table 1:

Component	Value	Harvest month	Source (W=wild, C=cultivated), Country, Reference
Ash (g kg^{-1} DW)	315-402	January	C Denmark (Marinho et al. 2015b); C Faroe Islands (Bak et al. 2019)
	274-444	May	C Norway (Sharma et al. 2018); C Faroe Islands (Bak et al. 2019)
	170-291	June	W Russia (Konstantin et al. 2023); C Norway (Sharma et al. 2018)
	130-199	July	W Russia (Konstantin et al. 2023); C Denmark (Marinho et al. 2015b)
	120-389	August	W Russia (Konstantin et al. 2023); C Norway (Sharma et al. 2018)
Iodine (I; mg kg^{-1} DW)	3985	March	W Scotland (Schiener et al. 2015)
	2067-3600	May	C Denmark (Samarasinghe et al. 2021b); W Scotland (Schiener et al. 2015); C Norway (Sharma et al. 2018)
	1655-7933	June	C Norway (Lüning and Mortensen 2015); C Norway (Sharma et al. 2018); C Norway (Wang et al. 2022)
	3499	July	W Scotland (Schiener et al. 2015)
	1600-2000	August	C Norway (Sharma et al. 2018)
Arsenic (As; mg kg^{-1} DW)	64	March	W Scotland (Schiener et al. 2015)
	22	April	C Denmark (Bruhn et al. 2016)
	43-73	May	C Denmark (Samarasinghe et al. 2021b); C Norway (Sharma et al. 2018); W Scotland (Schiener et al. 2015)
	32-76	June	C Norway (Sharma et al. 2018); C Norway (Wang et al. 2022)
	88	July	W Scotland (Schiener et al. 2015)
	23-30	August	C Norway (Sharma et al. 2018)
Cadmium (Cd; mg kg^{-1} DW)	1.2	April	C Denmark (Bruhn et al. 2016)
	0.8-0.9	May	C Denmark (Samarasinghe et al. 2021b); C Norway (Sharma et al. 2018)
	0.6-2.2	June	C Norway (Sharma et al. 2018); C Norway (Wang et al. 2022)

	1.7-2.0	August	C Norway (Sharma et al. 2018)
Mannitol (g kg^{-1} DW)	120-128	May	C+W Denmark (Manns et al. 2017); C Norway (Sharma et al. 2018)
	89-128	June	W Sweden (Vilg et al. 2015); W Russia (Konstantin et al. 2023); C Norway (Sharma et al. 2018)
	40-175	July	W Russia (Konstantin et al. 2023); C+W Denmark (Manns et al. 2017)
	45-130	August	C Norway (Sharma et al. 2018); W Sweden (Vilg et al. 2015); W Russia (Konstantin et al. 2023)
Uronic acids* (g kg^{-1} DW)	130-290	May	C+W Denmark (Manns et al. 2017); C Norway (Sharma et al. 2018)
	138-340	June	C Norway (Sharma et al. 2018); C+W Denmark (Manns et al. 2017); W Russia (Konstantin et al. 2023)
	340-350	July	W Russia (Konstantin et al. 2023)
	64-370	August	C Norway (Sharma et al. 2018); W Russia (Konstantin et al. 2023)
Fucose (g kg^{-1} DW)	7-27	May	C Denmark (Samarasinghe et al. 2021b); C Norway (Sharma et al. 2018)
	15-25	June	W Sweden (Vilg et al. 2015); C Norway (Sharma et al. 2018)
	5-14	August	W Sweden (Vilg et al. 2015); C Norway (Sharma et al. 2018)
Glucose (g kg^{-1} DW)	60-131	May	C+W Denmark (Manns et al. 2017); C Norway (Sharma et al. 2018)
	77-143	June	W Sweden (Vilg et al. 2015); C Norway (Sharma et al. 2018)
	60-130	July	C+W Denmark (Manns et al. 2017)
	52-93	August	C Norway (Sharma et al. 2018); W Sweden (Vilg et al. 2015)
Protein (g kg^{-1} DW)	59-165	April	C Faroe Islands (Bak et al. 2019); C Norway (Monteiro et al. 2021); C Faroe Islands (Mols-Mortensen et al. 2017); C Denmark (Bruhn et al. 2016)
	13-73	May	C Denmark (Marinho et al. 2015b); C Norway (Forbord et al. 2020b)
	29-89	June	C Faroe Islands (Bak et al. 2019); W Sweden (Vilg et al. 2015); C Norway (Forbord et al. 2020b); C Norway (Monteiro et al. 2021)

	13-40	July	C Denmark (Marinho et al. 2015b); C Faroe Islands (Mols-Mortensen et al. 2017)
	97	August	W Sweden (Vilg et al. 2015)
Total amino acids (g kg^{-1} DW)	155	April	C Faroe Islands (Mols-Mortensen et al. 2017)
	15-144	May	C Denmark (Marinho et al. 2015b); C Faroe Islands (Mols-Mortensen et al. 2017); C Norway (Sharma et al. 2018)
	59-121	June	C Faroe Islands (Mols-Mortensen et al. 2017); C Norway (Sharma et al. 2018)
	20-88	July	C Denmark (Marinho et al. 2015b); C Faroe Islands (Mols-Mortensen et al. 2017)
	218	August	C Norway (Sharma et al. 2018)
Total lipids (g kg^{-1} DW)	13	April	C Norway (Monteiro et al. 2021)
	2-7	May	C Portugal (Barbosa et al. 2020); C Denmark (Samarasinghe et al. 2021b)
	3-8	June	W Sweden (Vilg et al. 2015); C Norway (Monteiro et al. 2021)
	8	July	C Denmark (Marinho et al. 2015a)
	2	August	W Sweden (Vilg et al. 2015)
Total phenolic content (g kg^{-1} DW)	2	March	W Scotland (Schiener et al. 2015)
	1-5	May	C Norway (Sharma et al. 2018); W Scotland (Schiener et al. 2015)
	1-10	June	C Norway (Sharma et al. 2018); W Sweden (Vilg et al. 2015)
	7	July	W Scotland (Schiener et al. 2015)
	1-6	August	C Norway (Sharma et al. 2018); W Denmark (D’Este et al. 2017); W Sweden (Vilg et al. 2015)
Chlorophyll *a* (g kg^{-1} DW)	1-2	April	C Denmark (Bruhn et al. 2016)
	0.3	May	C Denmark (Marinho et al. 2019)
	0.3	June	W Sweden (Vilg et al. 2015)
	0.3	August	W Sweden (Vilg et al. 2015)

Fucoxanthin (g kg^{-1} DW)	0.6-1.1	April	C Denmark (Bruhn et al. 2016)
	0.4	May	C Denmark (Marinho et al. 2019)
	0.03	July	C Portugal (Fernandes et al. 2016)
β-Carotene (g kg^{-1} DW)	0.01-0.03	April	C Denmark (Bruhn et al. 2016)
	0,009	May	C Denmark (Marinho et al. 2019)

*Includes data on both total uronic acids and total alginate