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Review

The cultivation of European kelp for bioenergy: Site and species selection



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ABSTRACT

Seaweeds are receiving increasing attention as third generation biofuels, which do not compete for land or freshwater with agricultural crops and have a high polysaccharide content. Seaweed growth is dependent on the presence of suitable physical and chemical conditions. The selection of cultivation sites with suitable characteristics is therefore essential for the successful establishment of European seaweed mariculture. The growth conditions of the site directly impact the biomass yield and composition of the crop, which in turn control the conversion efficiency of biomass to bioenergy. This review focuses on three European brown phaeophyte kelp species which may be suitable for large-scale offshore cultivation: *Laminaria digitata*, *Saccharina latissima* and *Sacchoriza polyschides*. It describes the known responses of each to a number of important physical and chemical parameters: temperature, salinity, water motion, nutrient concentrations, carbon dioxide/pH, light and ultra-violet radiation. It also reports density effects on their growth rate and what is known concerning the impact of disease and grazing. Conclusions are made on the conditions necessary for the optimal growth of each species for biofuel production. Where conditions are sub-optimal, this review has made recommendations for the most suitable species for a particular set of environmental conditions.

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1. Introduction

It is hoped that, as a third generation source of bioenergy, macroalgae will overcome the drawbacks inherent in the production of first generation biofuels from traditional first generation biomass. The main benefit is that macroalgae

cultivation does not require arable land or freshwater and so does not cause land use competition with food crops or indirect land use changes which can exacerbate climate change [1]. Furthermore, their high biological productivity and fast growth, high polysaccharide content and ability to reduce atmospheric carbon dioxide while oxygenating the surface ocean make macroalgae even more attractive for biofuel

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production [2–4]. Currently, the macroalgae industry is primarily focused on food products for human consumption, which account for 83–90% of the global value of seaweed [5], while a smaller share is held by the extraction of high value compounds, currently dominated by hydrocolloids which includes alginate, agar, and carrageenan [6]. The high polysaccharide content of macroalgae makes them very favourable for conversion into ethanol and biogas. To increase the profitability of this process, a biorefinery approach could be utilised, with conversion preceded by the extraction of high value products [7].

In Europe, the large scale cultivation of brown phaeophyte macroalgae, commonly known as kelp, has become a focus of research, in part due to their suitability as a biofuel source [3]. The methods for kelp cultivation were first developed for the species *Saccharina japonica* in 1950s China for human food consumption and to extract alginate, mannitol and iodine [8]. Single celled meiospores are first released from the sorus regions of fertile adults. These are then settled onto string or twine, which are then grown within seawater tanks in a ‘hatchery’ for two or more months until juvenile plantlets between 1 and 10 mm are present [9]. These are then out-planted and allowed to grow in coastal areas of the sea until they reach metres in length, within 4–8 months.

As sessile organisms, kelps must be tolerant of the physicochemical conditions of the seawater in which they are situated to be able to survive and grow. The seawater must be of a suitable temperature and salinity; adequate water movement must occur to deliver nutrients and carbon dioxide; sufficient light must be available to allow photosynthesis; and UV radiation should not be at damaging levels [10]. For optimal growth, all conditions must all be within a certain, usually narrow, range. Tolerance to these conditions varies between species with some able to grow well under conditions where another is excluded. An understanding of these tolerances is therefore essential to allow optimal site selection and so maximise the cultivation potential. Suboptimal conditions such as very low nutrients or very high light, can lead to physiological stress, reductions in growth rate, increase in tissue degradation or even death. Kelps are considered to have very high phenotypic plasticity allowing them to adapt to a wide range of fixed and changeable environmental conditions [11–13]. This requires them to undergo continuous physiological adjustment so as to preserve growth while withstanding biotic and abiotic stresses.

An additional consideration regarding site selection is that the growth environment is likely to impact their chemical and biochemical composition, which may in turn affect the quality and quantity of bioenergy produced from the biomass [14]. The composition of wild kelps are known to vary in response to seasonal and nutritional cues [15–17], however no-one has yet examined the composition of cultivated kelp and whether it matches the wild composition.

This review brings together information on the physicochemical conditions required by three candidate species for bioenergy production [14,17,18]. Two are true kelps of the order Laminariales, *Laminaria digitata* and *Saccharina latissima*, while the third is a “pseudo-kelp” of the order Tilopteridales, *Sacchoriza polyschides* which occupies a similar ecological

niche [19]. As is common practice, this review will refer to each of these species as kelp.

The offshore cultivation of *S. latissima* has been tested at various locations across Europe [20–22] and the North American coast [24]. In addition, to *S. latissima*, trial cultivation of *L. digitata*, *S. polyschides* and *Laminaria hyperborea* has also been attempted in Ireland and Scotland [25–27]. This review will refer to each of the main factors affecting kelp growth and the known species responses (summarised in Table 1). In addition it will discuss how the potentially negative impact of non-optimal growth conditions may be mitigated, where possible.

2. Temperature

Temperature has a direct effect on the metabolic rate of seaweeds and also their ability to successfully reproduce. This creates specific temperature range envelopes within which they can successfully grow, and so be cultivated. The kelps, are thought to have evolved in cold seas [28] and so are highly tolerant of the winter temperatures in Europe. *L. digitata* and *S. latissima* can tolerate temperatures of -1.5°C , while *S. polyschides* has a lower limit of $0-1^{\circ}\text{C}$ [29]. Nevertheless, growth at low temperature does affect the demography of natural kelp beds through a reduction in growth rate combined with increased longevity [30].

Many macroalgal species are particularly sensitive to high summer temperatures and the geographical ranges of kelp beds are often dictated by seasonal high temperature [31–33]. Kelps can tolerate and recover quickly from short-term (hour-day) increases of more than 10°C above their optimum [34,35]. Whereas, a persistent rise of only a few degrees above the optimum can destabilise proteins and uncouple metabolic pathways leading to cellular damage through the production of reactive oxygen species [31,36]. This increases their susceptibility to other stresses leading to reduced growth rate, fragmentation of the thallus or death [35,37].

Selective breeding has been successfully used to increase the temperature tolerance of commercially cultivated strains of *S. japonica* in SE Asia [38]. This has extended the growth season, increased the final quantity of biomass grown and allowed the expansion of mariculture into new coastal regions [38]. Similar selection could be utilised in European seaweeds to increase the latitudinal range over which they can be cultivated. Alternatively, moving the crop vertically into cooler water could also be used to prevent high temperature damage. On the Galician coast in NW Spain, such redeployment has been used to prevent high surface summer temperatures causing tissue damage in cultivated *S. latissima* [22].

Temperature is a key variable controlling the distribution of many kelps [32,33,39]. Climate change is projected to increase the average sea surface temperature by between 1 and 3°C over this century [40] and so is predicted to cause the northward retreat of kelps [41,42]. This will also be coupled to an increase in storminess and potential increases in nutrient loading during extreme weather events [43]. As discussed by Raybaud et al. [42], increasing temperature may have been a key determinant in declining natural populations of *L. digitata* in coastal Brittany, Normandy and the English Channel

Table 1 – Summarised response of three phaeophyte species to different environmental parameters, and, the ideal conditions for the cultivation of all species. Gray boxes indicate parameters in which the species is more tolerant than the others examined and so will be the preferred candidate for cultivation. Ecotypes may exist which survive in conditions where typical representative of each species cannot. Op: optimal condition, RG: reduced growth, D: death, CG: commonly grows, Ex: extends, S: survives, SS: severe stress. *This is largely based on natural occurrence as well as known light and UV tolerances and so the depth where maximum growth occurs cannot be determined.

Parameter	Macroalgal species			Ideal conditions
	<i>Laminaria digitata</i>	<i>Saccharina latissima</i>	<i>Sacchariza polyschides</i>	
Temperature (°C)	Op: 5–15. RG: 20–22. D: 22–24	Op: 5–15. RG: 17–21. D: 20–24.	Op: 5–17. RG: 20–23. D: 25, or 30d > 20 °C.	Op: 5–15. Not above: 18–20.
Salinity (PSS)	Op: 20–35. RG: 15–25. S: 5 for 5d.	Op: 24–35. RG: 15–21. SS: 5–11 for 3–4d.	Op: 25–35. RG: 20. D: <9.	Op: 30–35. Not below 25.
Water motion	Op: high flow. Also found in low flow.	Op: Low-moderate. Can grow well in strong current.	Op: Mod-High flow. Not found in very low flow.	Moderate to high (>25 cm s ⁻¹). Flow maintained throughout cultivation area.
Nutrients	Op: 10–40 μM NO ₃ ⁻	Op uptake: 30 μM NO ₃ or 10 μM.	No information.	NO ₃ ⁻ + NH ₄ ⁺ : ≥5 μM, PO ₄ ³⁻ : ≥0.3 μM. Additions may be beneficial.
Carbon dioxide/pH Depth of growth*	Normal. CG: 5 m. Ex: 40 m.	Normal. CG/Ex: 20 m. Op: 5–9 m.	Normal. CG: 15 m. Ex: 30 m.	pH 8–8.5. large deviations may lead to reduced growth or tissue damage. Submerged at 1–2 m, to a maximum of 4–5 m. Shallower if light penetration is low.
Optimal growth density	Unknown.	Unknown.	Unknown.	Unknown.

[44–46], *S. latissima* in Norway [47] and *S. polyschides* in Spain [48]. Selection for high temperature tolerant species may be useful for European mariculture in this century. However, such genetic selection should be considered carefully as there is the potential that it would lead to the transfer of genetic seedstock across Europe and its gene flow into natural populations. This could cause loss of genetic diversity in natural populations, making them more susceptible to other stresses. Another alternative is that selection may create a super-vital type, which becomes invasive, invading and replacing natural seaweed stands.

2.1. Known species responses

Adult *L. digitata* sporophytes are tolerant of the current temperature range in Northern European waters, showing an optimum growth at 5–15 °C with a reduction in growth rate by 50–75% at 20–22 °C [49]. In agreement with this, the microscopic gametophyte phase, shows reductions in growth rate at 20–21 °C with death occurring after 1 week at 22–24 °C [29,50]. The southernmost limit of the species in Europe is the south coast of Brittany [32], where summer temperature can reach 23–24 °C causing the death of adult plants [51].

Physiological experiments suggest that *S. latissima* is more temperature sensitive than *L. digitata* [35] although the southernmost limit of this species in Europe is northern Portugal. It grows well between 5 and 17 °C [52–54] and displays a phenotypic plasticity well-tuned to maintain carbon and nitrogen metabolism in seawater temperatures as high as 20 °C [55]. At the high end of this temperature range, net photosynthesis declines and acclimation effort increases, involving the upregulation of many temperature responsive genes [31,56]. Tissue loss or death is commonly reported for this species above 17–20 °C [57,58]. Temperature ecotypes may exist which have adapted to high seasonal temperature exposure: populations from Helgoland, can tolerate temperatures of 18–20 °C [59], while populations in New York, USA can survive at >20 °C, albeit with substantially reduced growth [58]. It should be noted that the existence of temperature ecotypes is yet to be supported by gametophyte culturing studies [60].

Juvenile *S. polyschides* grow well when the temperature is between 5 and 17 °C, but development is slowed or prevented at between 20 and 23 °C, with death at 25 °C [61,62]. In natural populations, the southernmost limit is Cape Jubi, Morocco and it is also found in certain regions of the Mediterranean [32]. It is thought that extended (30 consecutive day) periods of >20 °C on the Spanish Iberian Peninsula exclude the establishment of *S. polyschides* [48]. The authors are not aware of any laboratory experiments examining the temperature tolerance of adult plants of this species.

2.2. Recommendations

Mariculture sites should be chosen where, for much of the year, temperature is within the range 5–15 °C. Ideally, the summer temperature should not exceed 18–20 °C for more than a few days. With this in mind, predicted future increases in sea surface temperature due to climate change should be considered. In regions where the maximum

summer temperature exceeds 18 °C, *S. polyschides* would be the best choice for mariculture, while *L. digitata* and *S. latissima* are recommended for use only where temperature does not exceed 18 °C. Growing a high temperature ecotype or selection of a stock with a high temperature tolerance could be used to expand the geographical range for mariculture in the future, or to maintain it in the face of climate change. Offshore sites where water temperature is cooler than at the coast may also be highly suitable but this may have implications in terms of reduced level of nutrients leading to lower levels of biomass [63].

3. Salinity

Macroalgae balance the external osmotic pressure of seawater with their internal osmotic pressure to prevent unwanted movement of water. This is achieved by altering the inorganic and organic constituents of their cells [64]. In many brown macroalgae, intracellular mannitol concentrations are present in osmotically significant amounts and as a direct function of salinity [65] with 5–45% of dry weight in *S. latissima* [14,66,67]. Mannitol is a source of fermentable carbohydrate for ethanol production and so high concentrations may be favoured in a crop [14]. A salinity of 33–35 psu on the practical salinity scale commonly results in optimal growth, while areas of reduced salinity such as at river mouths, are amenable to the survival of fewer, tolerant species.

3.1. Known species responses

L. digitata can be classed as semi-euryhaline as it is tolerant to some variation in salinity. Over a range of 20–35 psu, no change in their growth rate or photosynthetic ability is observed [68], whilst, natural populations occur in fjords where the salinity is between 15 and 25 psu [69]. Furthermore, they can tolerate a five day exposure to 5 psu, with only a 50% reduction in photosynthetic performance [68].

S. latissima can also be classed semi-euryhaline, but appears more sensitive than *L. digitata*. No reduction in growth rates is observed between 24 and 35 psu [52,57] and there may even be an increase [57]. Below 24 psu, a stress response can be observed: a 20–25% reduction in growth rate at 21 psu [57] and a 20–30% reduction in photosynthetic performance at 15–20 psu [68]. Natural populations do occur at this tipping point, such as those in the White Sea where salinity is 24–26 psu [70] and in Danish fjords where salinity is 22–24 psu [71]. These may represent locally adapted ecotypes [70]. Young *S. latissima* sporophytes can survive a four day exposure to 11 psu although significant stress is observed [23], while exposure of only a few days to 5 or 6 psu, results in either a 95% reduction in photosynthetic performance and significant pigment loss, or death [23,68].

In comparison to the others, little is known about *S. polyschides*. The available information suggests that it is stenohaline and so sensitive to reduced salinity, as it does not naturally occur where salinity is below 33–35 psu [72]. A salinity below 20 psu reduces growth, while a salinity of 9 irreversibly inhibits growth leading to death [72].

3.2. Recommendations

Sites selected for seaweed mariculture should ideally have salinity between 30 and 35 psu and not suffer from significant seasonal or sporadic reductions in salinity below this. Sudden reductions in salinity due to freshwater runoff in nearshore locations, such as fjords, sea lochs and coastal bays, can severely inhibit or kill local stenohaline macroalgae species, which can only tolerate a narrow range of salinities. These locations should be avoided for the mariculture of these types of kelp. Offshore locations that are less affected by coastal fluctuations in salinity may be highly suitable for all species, provided other conditions are favourable. Where a site has fluctuating salinity, the tolerant species *L. digitata* and *S. latissima* should be cultivated in preference to *S. polyschides*.

4. Water motion and flow rate

The presence of water motion is an important criteria for a kelp farm site [73]. In stagnant or slowing moving water, a large boundary layer develops around the macroalgal thalli. This limits the supply of carbon dioxide required for photosynthesis [74] and so reduces their ability to absorb nutrients from the water [75], leading to reduced growth rates [76,77]. With increasing water motion, the diffusive boundary layer becomes thinner and is further reduced by thallus pitching and flapping [78,79]. The rates of photosynthesis and nutrient uptake increase in correlation to the current velocity until these metabolic processes become saturated [77,80,81]. This occurs with current velocities of approximately 0.1 m s⁻¹, with anything less defined as low water motion [81]. Anything above 0.25 m s⁻¹ can be considered as high water motion [82]. In large macroalgal stands, reductions in water flow due to drag can cause stagnation of water towards the stand centre, leading to sub-optimal conditions and lower growth rates [33].

Fast flow may also reduce the settlement and abundance of epiphytes, grazers and sediment which could smother or degrade the macroalgae, reducing growth rate [41]. Nevertheless, moderate wave exposure may lead to increased invertebrate abundance [83]. Very high water motion may however, be counterproductive, increasing the dislodgement of fully-grown adults [77]. On exposed coasts, kelps can be exposed to wind-wave induced orbital water velocities as high as 2–3 m s⁻¹ [84]. Macroalgae grown in such high water motion, invest more energy into the development of large hold-fasts to attach more firmly to the substrate [85,86], at the cost of reduced growth size and productivity [76].

Flow rate also has a considerable effect on the blade and stipe morphology of kelps. In sheltered conditions the thallus becomes wide and thin, and in some species corrugated i.e. *S. latissima*. It is thought that the increased surface area enables maximal photon capture and gas/nutrient exchange, while thallus undulations may increase turbulence [11,77,87–89]. In exposed conditions the thallus becomes narrow and thick with a robust stipe [77]. This makes the thallus more hydrodynamic and reduces its drag which is reasoned to prevent breakage or dislodgement of the adult sporophyte [11,88]. However, thallus reconfiguration in *Ecklonia radiata* under high

flows, show that total thallus area and not morphology is the main determinant of drag [84]. When adult kelp grow in close proximity, they tend to collapse together into a ‘streamlined bundle’ reducing the drag on each individual thallus and so reducing dislodgement [87,90,91].

4.1. Known species responses

While *L. digitata* is most commonly found in locations with high water motion, it may also be present in more sheltered locations [39,92]. High flow can increase the biomass density at which it grows by four times in comparison to lower flow areas [93].

S. latissima prefers low to moderate water motion areas and is usually absent in locations with high motion or surf [52,92,94]. Nevertheless, *S. latissima* has been successfully cultured in high motion with currents up to 1.53 m s^{-1} [73]. This suggests that their exclusion from high water motion locations may be due to other factors, such as being out-competed for space by a species more adapted to this environment.

S. polyschides prefers moderate to high water motion and will often not grow in very sheltered areas [39,92].

4.2. Recommendations

Ideally, mariculture sites should have moderate to high water motion where flow is usually $>0.1\text{--}0.25 \text{ m s}^{-1}$. This will maintain supplies of CO_2 and nutrients to the macroalgae and maximise both their growth rate and growth density. All three species are likely to grow well in high water motion areas. In locations with lower flow, it is expected that *L. digitata* and *S. latissima* will grow more successfully than *S. polyschides*. For kelp bioenergy to be a viable industry, large cultivation areas will be needed, producing a chemically uniform crop. To achieve this at each location, the density of culturing and the orientation of offshore cultivation structures must be carefully considered so that sufficient water flow is present, throughout the cultivation area, to maintain peak growth of the seaweed.

5. Nutrients

Kelps maintain growth throughout the year by accumulating luxurious nutrient reserves in times of plenty to sustain them during nutrient limitation, particularly during summer [95]. Such nutrient reserves also increase tolerance to high temperatures, possibly by increasing the production of heat shock proteins [96]. Growth in the summer can become limited if insufficient reserves of nutrients are available [97–99] as photosynthetic rates slow when nutrients are scarce [100]. Additions of $15 \mu\text{mol L}^{-1}$ nitrate and $3 \mu\text{mol L}^{-1}$ phosphate has been shown to boost the growth rates of both *L. digitata* and *S. latissima* during summer nutrient limitation [98]. In the Australian kelp *E. radiata*, it has been found that minor increases in nutrient concentration in field-based mesocosms from 1.25 nmol L^{-1} ammonium and 0.08 nmol L^{-1} phosphate to 1.91 nmol L^{-1} and 0.10 nmol L^{-1} respectively, lead to a four times increase in biomass accumulation [101].

Areas with high nutrient loading will sustain rapid macroalgal growth during the summer [97]. Even where nutrient loading is lower, high flow increases the nutrient uptake rate of macroalgae by refreshing the boundary layer [75] and so maximal growth rates can be sustained. Extended cultivation of hatchery juveniles in high nutrient media has been demonstrated to lead to increased final size and allow earlier harvesting in the East Asian kelp *Undaria pinnatifida* [102]. Fertilisation may increase the growth rate and yield of large-scale kelp cultivation. In which case, ammonium would be the preferable nitrogen source as it is taken up in preference to nitrate [103,104]. Nonetheless, an assessment of the benefits and potential environmental ramifications of such fertilisation must be fully investigated before such action is taken. Recently, nutrient additions for macroalgal cultivation in coastal China have contributed to regular large-scale algal bloom events in the Yellow Sea [105]. Cultivation in coastal areas with upwellings of nutrient rich deep water or where eutrophication is an issue may allow natural fertilisation.

The mariculture of animals, such as fish and mussels, release dissolved nutrients into the surrounding water [106]. The association of macroalgal mariculture with either animal mariculture as part of integrated multi-trophic aquaculture (IMTA) can therefore lead to increased growth rate of the macroalgae, while removing these excess nutrients [21]. However, recent experimentation in Denmark did not show any benefit in terms of growth, N, P or amino acid content of *S. latissima* cultured in proximity to fish and mussel aquaculture [107,108]. This has yet to be attempted at a large scale.

It is unknown whether limitation of other nutrients will have a significant impact on macroalgal growth on offshore structures. Iron is an essential element for photosynthesis, commonly limiting microalgae growth in open ocean regions [109]. It is currently unknown whether the offshore mariculture of seaweeds would benefit from iron fertilisation.

5.1. Known species responses

In juvenile sporophytes of *L. digitata*, $>10 \mu\text{mol L}^{-1}$ of nitrate is required to maximise growth rate [110]. Nitrate reductase activity is light stimulated in *L. digitata* leading to greater assimilation during the day than night [111]. It has been shown in *S. latissima* that $10 \mu\text{mol L}^{-1}$ of nitrate is required to maximise growth rate and leads to internal storage for later use [112]. Its growth has been shown to be enhanced by IMTA alongside fish or mussel biomass [106,113], although this was not found in another study [108]. No studies have been conducted on *S. polyschides*.

5.2. Recommendations

Little information exists on the optimal nutrient requirements of each species. Locations with elevated nutrient levels due to coastal eutrophication, nearby animal mariculture or upwelling, may be particularly conducive to the mariculture of seaweeds. In locations where nutrient levels are low, high flow rates are preferable as this increases nutrient uptake. Offshore locations may be very suitable for this reason. During summer when nutrient concentrations are low, the addition of fertiliser may increase growth rates, although the possible

environmental and physiological impacts and effectiveness of such an action requires further investigation. For instance, increased nutrient availability in summer may cause a downregulation of carbohydrate storage by increasing protein synthesis [114]. This may affect the value of the harvest as a biofuel for fermentation to ethanol or butanol by reducing the biomass energy density, alternatively, this decrease in C:N ratio may improve the suitability of the biomass for anaerobic digestion.

6. pH and carbon dioxide concentration

As carbon dioxide is consumed by photosynthesis, the pH of seawater increases from the background level of 8.1. This effect can be considerable where the algal biomass is high and water flow is restricted [115,116]. Macroalgae, including kelps are known to convert the abundant bicarbonate in seawater to CO₂ allowing photosynthesis to continue even at high pH where CO₂ is scarce [117]. Both *L. digitata* and *S. latissima* have similar compensation points at pH 9.6–9.8 [118] indicating the presence of an effective carbon concentrating mechanism (CCM). Since *S. polyschides* grows in a similar ecological niche it may be assumed that it has a similar CCM.

Ocean acidification has so far led to a decline in the average pH of the surface ocean from 8.2 to 8.1 [119]. This is set to continue over the current century and is predicted to decline a further 0.3–0.4 units by the year 2100 [40]. While broadly speaking, non-calcifying autotrophs are predicted to benefit due to the increased CO₂ availability [120], no clear conclusion can be made about the response of kelps, since macroalgal responses appear to be highly species-specific [121]. One experiment has shown *S. latissima* has decreased growth at lower pH [122], a second showed no change in growth rate in *U. pinnatifida* [101], while others suggests that large leathery macroalgae, appear to cope well in areas of naturally low pH [123,124].

6.1. Recommendations

Mariculture areas should ideally have a normal pH of around 8.1 with a summer maximum of less than pH 8.5. The flow of water through the cultivation area must be maintained so that CO₂ is constantly replenished to maintain growth. Some ocean acidification may benefit macroalgal mariculture by increasing the supply of CO₂; however, it may also decrease the growth rate of sensitive species. *S. latissima* may be sensitive to future decreases in pH due to ocean acidification; however this needs to be confirmed through further experimentation. There is also some evidence that CO₂ enrichment can alter the overall chemical composition of macroalgae [121] and this will impact directly on bioenergy production from the biomass.

7. Photosynthetically active radiation (PAR)

The availability of light is highly spatio-temporally variable and its oversupply can be a major threat to macroalgal survival [125]. If too much light is absorbed by kelp, the excess

energy can inhibit photosynthesis [104] and may lead to cellular damage and death of the organism. This sets an upper depth limit for many species. Conversely, sufficient PAR must be supplied to sustain growth, so setting a lower depth limit. In very clear waters, some kelps can grow down to 30–40 m [19,32] while in waters carrying suspended sediment, light penetration declines quickly, leading to a shallow limit of less than a metre. Depth and water transparency have been shown to both be key to predicting the spatial distribution of *L. digitata* beds in Brittany [41,42].

Macroalgae grown in either high or low light environments employ different light use strategies to either reduce or increase the absorption of light to optimise their growth [126]. For example, this may be acclimation based on their phenotypic range, such as has been reported in *L. digitata*, or there may be adaptation resulting in light ecotypes, as has been found in *S. latissima* [127]. The meiospore and juvenile sporophyte stages of kelp can both be very sensitive to high light, and require less PAR to sustain their growth.

7.1. Known species responses

L. digitata grows in the shallow subtidal and is regularly exposed to full sunlight on low neap tides. Therefore, it is expected to be more tolerant of high light conditions than other species. It is commonly only found down to 5 m [92], but can extend down to 40 m [32]. This species displays a high level of phenotypic plasticity allowing it to acclimate to this wide range of light conditions [126]. Growth of juvenile sporophytes is maximised at 20–30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with photosynthesis apparatus saturated at 2–3 times this value [128]. Adult sporophytes become light saturated at around 150–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [129].

S. latissima commonly grows down to 20 m [32,92], usually deeper than *L. digitata* [129]. Its optimum depth for growth has been reported as 9–12 m in Maine, USA [130], 5 m in mid-Norway [131] or only 1.5–3 m in Scotland [132]. Young sporophytes appear to have similar light requirements and tolerance as *L. digitata* [128], whilst adults are light saturated at around 215 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and have their maximum photosynthetic rate at 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [133]. One or 2 h of light at 500–700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ leads to significant dynamic photo-inhibition and photodamage, with young sporophytes being more susceptible than adults [37,134]. High light exposure can therefore lead to the death of thallus tissue and the loss of biomass.

S. polyschides commonly grows down to 15 m [92], replacing *L. digitata* where beds have been disturbed [42] but can extend down to 35 m [19]. No information is available of the light requirements and tolerances of this species.

7.2. Recommendations

Cultivation substrates should be deployed at a minimum depth of 1–2 m and a maximum depth of 5–7 m in the clearest waters. In areas with lower light penetration or when growing kelp at higher densities, the shallower depths stated will most likely be necessary. Juvenile sporophytes should be protected from high light during transportation, and may also benefit from initial deployment at a greater depth. Both *L. digitata* and

S. polyschides may be more tolerant of growing at shallow depths (1 m) than *S. latissima*. The depth distributions of *L. digitata* and *S. polyschides* may suggest that they have a lower light requirement, and so may grow better than *S. latissima* at depths of 5–7 m.

8. Ultra-violet radiation (UV)

Near the seawater surface, macroalgae are exposed to levels of UVA + B radiation that are known to have damaging effects on many aquatic organisms [135]. UV radiation damages proteins and leads to radical oxygen formation [136]. The upper depth limit of the Laminariales is thought to be dictated by their UV sensitivity [137]. The early lifestages of many macroalgae (meiospore, gametophyte and juvenile sporophyte) are sensitive to UV [138]. An hour exposure, reduces the germination of meiospores and photosynthetic efficiency rate of gametophytes and juvenile sporophytes in both *L. digitata* and *S. latissima* [139], with *S. latissima* the more sensitive [139,140]. Similar reductions in germination due to UV exposure have been reported in other kelps [141].

8.1. Known species responses

L. digitata is very tolerant of UV [139]; as a shallow sub-tidal species, it is naturally exposed to higher UV radiation than the other lower sub-tidal species, and so seems to have evolved a certain resilience [140].

S. latissima is also tolerant of UV, but less so than *L. digitata* [139]. Other research on this species has shown that damage caused by UV may be ameliorated or prevented if sufficient nitrogen stores are available [142]. Interestingly, some UV exposure boosts the growth of this species, possibly due to absorption spectra overlap with the blue light stimulated ionic carbon acquisition mechanism seen in some brown algae including *S. latissima* [122].

It is unknown how *S. polyschides* responds to UV, although it is predicted that its tolerance will be similar to that of *S. latissima*.

8.2. Recommendations

To avoid cellular damage from UV radiation, macroalgae should be deployed at a minimum depth of 1–2 m. The meiospore and juvenile stages of the sporophyte may require additional protection from UV exposure.

9. Growth density and achievable biomass

Density dependent growth has been observed in macroalgae [143–145] and will have a controlling influence on both the final biomass attained and its chemical composition. Spacing individual macroalgae far apart results in improved survival, and maximises their growth rate, but when averaged over the cultivation area, the overall biomass yield per square metre of sea area will be low. At higher growth densities, intraspecific competition occurs due to resource limitation, in particular

with respect to light and nutrients [93,146]. This reduces the survival rate and growth rate of individuals in the population [143–145] but may increase the overall biomass yield. At very high densities, the biomass yield may also be reduced as all individuals only grow to a much smaller size due to resource limitation. Since the growth density is known to affect the kelp morphology, with more elongate forms present at higher densities [147], this may also affect the chemical composition of the kelp although this has yet to be studied. The optimal growth density for highest achievable biomass yield for species of kelp is currently unknown.

In the natural environment, the attainable density of many large brown macroalgae ranges from 6 to 37 kg m⁻² of wet biomass [143]. This standing density is significantly reduced when conditions are limiting such as light with increasing depth, or CO₂ and nutrients supply in sheltered conditions [93,146]. Many natural European kelp communities have densities ranging from 5 to 10 kg m⁻² of wet material [148–150]. *L. digitata* and *S. latissima* communities have been reported up to 12.5 kg m⁻² of wet material [45,93] while communities of the related species *L. hyperborea* in wave exposed sites reach 18 kg m⁻² of wet material, with productivity of 12.5 kg m⁻² yr⁻¹ of wet material [151]. If 12.5 kg m⁻² of wet material is achieved by offshore mariculture within a single growth season, this would equate to a production of 125 tonne ha⁻¹ yr⁻¹ of wet material. We estimate the seaweed productivity of this cultivation would be 6.1 tonne ha⁻¹ yr⁻¹ of carbon. This is based on a mean Laminariales water content of 85% and a seasonal maximum carbon content of approximately 30–35% in the dried material, [14,152].

To date, the majority of productivity data from the cultivation of kelps is reported as kg m⁻¹ of longline; with *S. latissima* achieving up to 28.4 kg m⁻¹ yr⁻¹ of wet material, *L. digitata* 8.0 kg m⁻¹ yr⁻¹ of wet material and *S. japonica* 34.0 kg m⁻¹ yr⁻¹ of wet material [25,153–155]. Studies rarely report the number of longlines or how far apart they were placed, meaning productivity per hectare cannot be calculated. An exception is Zhang et al. [156], who reported productivity for *S. japonica* as 29–35 tonne ha⁻¹ of dried material over five years of study, within a 0.67–300 ha cultivation area. This translates into a productivity of 8.4–10.2 tonne ha⁻¹ yr⁻¹ of carbon, bearing in mind that this dried material still contains approximately 10% water [157]. On a far smaller scale, European *S. latissima* has been shown to achieve 20.3 kg m⁻² of wet material on a 5 m diameter offshore ring in the North Sea [20], while 4 kg m⁻² of wet material was achieved on nine parallel 40 m longlines in coastal Spain [158]. However, extrapolations from small areas to large scale cultivation is likely to overestimate the productivity, as flow is known to decrease towards the centre of dense macroalgal stands [159,160], which can directly influence the achievable biomass of seaweeds [93] by reducing the supply of nutrients and CO₂ [77]. More research is needed to inform mariculturists/growers of the expected yields for large-scale cultivation areas. There is little information available on the chemical composition of cultivated kelps [107,108], only their wild harvested counterparts [14,17]. There is a need assess how the type of mariculture affects the chemical composition of the biomass including the importance of the time of harvesting to ensure

optimum chemical profile and the impact this will have on bioenergy production.

10. Disease and grazing losses

Little is currently known about diseases in kelp, or seaweeds in general, although various causative agents have been implicated [161]. Problematic diseases/syndromes have been identified in large scale cultivation of kelp over the last half century [162] and their occurrence has increased as cultivation has intensified, with a 4–5% yield loss now reported in Korean cultivation [161]. The bacteria *Pseudoalteromonas* spp. and *Alteromonas* spp. are known to be responsible for some disease [163], but in numerous cases, the agent has not been identified. The prevalence of endophytic infection is known to be high in wild kelp populations [164], and so there are concerns that a) pathogens may be transplanted with seaweed stocks, infecting nearby natural seaweed beds and b) as physicochemical stress is often a trigger for outbreaks in cultivated kelp [162], climate change impacts such as rising seawater temperatures may in the future lead to more severe disease impacts.

The main grazers of natural kelp forests are benthic invertebrates such as sea urchins, snails, abalone and small crustaceans. Natural kelp beds can be decimated by a outbreaks of these grazers, although these may be prevented by top-down pressure from predators such as carnivorous fish or otters [165,166]. During kelp cultivation, the growth substrates are suspended mid-water and so are not accessible to sessile benthic invertebrates, however, their planktonic larval stages can settle, leading to significant grazing as the organisms develop. In the UK, numerous 1–5 mm *Lacuna vincta* snails are found on cultivated thalli of *S. latissima* during early summer (pers. obs.). If the crop remains in the water for the remainder of the summer, these gastropods can cause extensive tissue loss. In other locations, the overgrowth of the cultivated thalli by epiphytes such as bryozoans, mussels and other seaweed, causes degradation and tissue loss in the crop during late spring or early summer ([107], Pers. Obs.). Because of site-specific differences in grazing and epiphytic overgrowth, the timing of harvest (peak seaweed biomass with as little damage from epiphytes and invertebrate grazers) will vary with location and species. Many fish species also graze on wild kelp, but are considered to only have a minor influence on standing biomass. Similarly, during kelp cultivation experiments in Spain, fish grazing was considered to only cause a small decrease in overall yield [167].

10.1. Recommendations

High macroalgal densities should be tested. Although this may produce smaller individuals on average, it is likely to result in greater overall biomass yield within a given mariculture area. Experimentation in the field is needed to determine the optimal seeding density. As mentioned earlier, water flow must be maintained throughout the mariculture area, as this will allow the macroalgae to attain a higher final biomass yield m^{-2} . This should be coupled to measurements of the

chemical composition of the biomass. Outbreaks of disease can cause significant losses of biomass from cultivated kelp systems in Asia, with the likelihood of such outbreaks increasing as cultivation intensifies. By suspending growth substrates in mid-water, damage from benthic invertebrate grazing is avoided. However, in late spring and early summer the development of settled larvae of grazers and other epiphytes can cause thallus deterioration. This event often controls the timing of the harvest.

11. Discussion

The physicochemical conditions of the inshore or offshore area selected for seaweed cultivation and the orientation and spatial arrangement of cultivation structures will be critically important to the successful growth of a harvestable crop. By selecting a site, and planning its arrangement/design based on the optimal conditions for growth of the target species, maximum yield of biomass should be obtained. This review summarises the known responses of three brown macroalgal species (*L. digitata*, *S. latissima* and *S. polyschides*) to a range of physicochemical properties of seawater, the known effects of growth density and their productivity during cultivation. The information can be used to guide mariculturists on the selection of suitable European coastal areas for their cultivation or the evaluation of existing sites. This technique has already been applied to coastal regions of Japan for *S. japonica* cultivation and North America for the genera *Saccharina* and *Laminaria* [168–170].

Each of the three species examined are suitable for cultivation in European coastal waters, however none can be cultivated across all coastal environments due to their individual physicochemical tolerances (Table 1). *S. polyschides* can tolerate the highest water temperatures so may be cultivated across the entire European latitudinal range, however, it has the greatest sensitivity to salinity fluctuations and may not attach and grow well in areas of low current flow. *S. latissima* is less tolerant of high water temperature and so is restricted to Northern Europe. It can tolerate some salinity fluctuations, but may be more vulnerable to tissue damage by high light conditions. *L. digitata* is even more temperature sensitive than *S. latissima*, but is tolerant of a wider salinity range and can grow over a wider light range than the other species. This information may be used to select suitable species for particular coastal habitats and latitudes. All three species appear to prefer moderate to high water motion and have similar nutrient and carbon dioxide requirements.

While the physicochemical parameters of seawater fluctuate daily with a natural rhythm of pH, light, UV etc., the extreme deviations from typical conditions can severely inhibit or kill cultivated macroalgae; such as clear sunny days when PAR and UV are very high; during summer when water temperatures reach their maximum; or reductions in salinity due to land runoff after intense rain. The extremes of a particular site should be known before cultivation begins so that appropriate steps can be taken to prevent the loss of a crop, these may include: selection of a tolerant species, seasonal or constant deployment at a greater depth, selecting the

outplanting and harvesting times and/or choosing a more suitable location.

While nearshore waters offer ease of access to a cultivation site, they can vary considerably in their physicochemical conditions. This creates a complex spatial mosaic of environments with differing ranges of parameters. For example salinity, temperature and light penetration gradients and fluctuations in proximity to estuaries, or shallow embayments where slow water refreshment results in large fluctuations in temperature and large pH shifts due to naturally occurring macrophyte beds [116,171]. In addition to this, competition with other users (i.e. recreational uses, shipping lanes and marine structures) and the visual impact of cultivation sites, would constrain locations where nearshore large-scale cultivation would be accepted [169]. Further offshore, the conditions in the photic zone are more constant over larger geographical regions making them a more suitable location for the establishment of this industry. Notwithstanding this, the high wave energy environment would necessitate careful engineering of the cultivation structures and could potentially lead to detachment and loss of the crop [73].

12. Kelp cultivation knowledge gaps

While many articles have been published on the physicochemical tolerances of the described species, many knowledge gaps still exist regarding their use in cultivation:

1. The physicochemical conditions of the cultivation site will influence the chemical composition of the kelp biomass and ultimately bioenergy production from the biomass. This is likely to include the type of bioenergy conversion used to process the biomass.
2. Scant information is available on the tolerances of *S. polyschides*. This is because unlike the other two species, it has not been targeted by many groups as a species suitable for macroalgal cultivation research due to its high water content of 91–92% [172]. This may however be an oversight as its wide temperature tolerance and large growth size achieved within a single season, provide some benefits over other species.
3. The authors found very little published information regarding the effects of density on the growth of these species and nothing regarding how the proximity of cultivation structures will affect growth and final yield within a defined growth area. This information is necessary so that maximum biomass ha^{-1} that can be achieved to maximise the economic viability of large scale cultivation is identified and compared across geographical locations, systems and species.
4. Existing information is scarce on how pH will impact the growth rate of these species. It is possible that pH conditions outside of the norm may be detrimental to the survival or growth of cultivated macroalgae.
5. Little is known about the exact nutrient requirements for each species. Nutrient additions may be beneficial to the growth of cultivated macroalgae and its success as an economically industry. However, caution must be taken as the effectiveness of such applications is currently

unknown and there exists a high potential for environmental damage from eutrophication of the regions downstream of the cultivation site.

6. Finally, despite widespread cultivation of kelp in many Asian countries, little information is yet available on their diseases. Knowledge in this area may prevent future outbreaks.

13. Conclusion

Available literature was reviewed describing the tolerances of *L. digitata*, *S. latissima*, and *S. polyschides* to a range of physicochemical conditions. Optimal ranges of each parameter have been suggested, which in combination, should allow successful growth of each species. Furthermore, the conditions have been identified in which each species are most tolerant. In areas where the conditions are outside of the ideal optimal ranges, particular species should be grown in preference based on these individual tolerances.

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