



Growth and biofouling in kelp aquaculture (*Saccharina latissima*) : the effect of location and wave exposure

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Abstract

Seaweed aquaculture is receiving increasing attention for food and non-food applications in Europe, where it is still an emerging industry. The cultivation of seaweeds in the sea is attractive as it does not compete with agricultural crops for land and freshwater, whilst generating high yearly biomass yield. The selection of suitable cultivation sites in coastal waters is essential for the sustainable establishment and further development of seaweed aquaculture in Europe. Here, we investigate the effects of wave exposure and geographic location on growth and biofouling of kelp (*Saccharina latissima*), using a transplantation experiment along the Swedish west coast. Biofouling of kelp decreased with increased wave exposure, from 10 and 6% coverage at sheltered and moderately exposed locations, respectively, to 3% at exposed locations. Growth, measured as blade surface area, generally increased with decreased wave exposure, with approximately 40% less growth at exposed locations compared to sheltered or moderately exposed location. We identified that there is large spatial variation in growth and fouling of the seaweed biomass at the selected farm sites, with significant differences from the km-scale to the m-scale. In addition, exposure level affected the tissue composition, with a high carbon, but low nitrogen and water content at exposed locations compared to moderate and sheltered sites. Isotope signatures (i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) also differed between exposure levels. Together, these results indicate that wave exposure is an important factor to consider in site selection for both yield as well as quality of the seaweed biomass for future kelp farms.

Keywords Aquaculture · Biofouling · Biomass yield · Phaeophyta · *Saccharina latissima* · Seaweed farming · Wave exposure

Introduction

There is a growing interest in seaweed cultivation for food and non-food applications (Holdt and Kraan 2011). Current biomass production for food applications is mainly based on agriculture on land; however, crop yield trends are predicted to be insufficient to reach the double global crop production needed by 2050 to meet FAO projections for food demands (Ray et al.

2013). Contrary to land-based agriculture, there is no need for arable land, fresh water, fertilizers and pesticides for the cultivation of seaweed. Accordingly, seaweed cultivation is often considered as the most environmentally friendly form of aquaculture (Folke et al. 1998), with a number of ecosystem and bioremediation services offered by the seaweeds (Hasselström et al. 2018). As a result, seaweed aquaculture is gaining interest and is predicted to expand into regions where it has thus far largely been underdeveloped, such as Europe and North America (FAO 2018). Recent studies have shown that European temperate coastal regions offer excellent environmental conditions for the cultivation of different kelp species, not least the sugar kelp, *Saccharina latissima*, which is ubiquitously found at the rocky shores of the North Atlantic (Sanderson et al. 2012; Marinho et al. 2015; Peteiro et al. 2016; Stévant et al. 2017).

The cultivation period of kelp species, such as *S. latissima*, is primarily dictated by seasonal changes in seawater temperatures and biofouling (Førde et al. 2015; Rolin et al. 2017). In nutrient-rich areas of most temperate coastal regions in the northern hemisphere, the cultivation season generally starts

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when seawater temperature gets below 15 °C in September–November and lasts until rapid increase in biofouling caused by rising seawater temperatures (Saunders and Metaxas 2007; Scheibling and Gagnon 2009; Park and Hwang 2012; Freitas et al. 2016) dictates the harvest in April–June. In European temperate regions, the most productive periods, i.e. with highest daily growth rates, are in early Autumn and Spring, when daylight is abundant (Broch et al. 2019). Accordingly, previous studies have shown that early deployment in Autumn and delayed harvest in Spring can provide substantial yield (Broch et al. 2019, Visch et al. unpublished data) at the same time as it circumvents the problem of biofouling that occurs later in the Spring.

Biofouling is one of the major challenges and constraints in the development and growth of the seaweed aquaculture sector (Getachew et al. 2015; Lüning and Mortensen 2015; Stévant et al. 2017; Bannister et al. 2019). Effects of biofouling include the loss of commercial value (Park and Hwang 2012), decrease in productivity due to breaking fronds (Dixon et al. 1981; Krumhansl et al. 2011), and reduced growth due to limited nutrient uptake (Hurd et al. 2000) and restricted light availability (Cancino et al. 1987). Biofouling is well documented in natural kelp populations (Christie et al. 2003; Christie et al. 2009), in farmed kelp species (Handa et al. 2013; Peteiro and Freire 2013b; Førde et al. 2015; Marinho et al. 2015; Rolin et al. 2017), as well as various other cultured seaweed species (Buschmann and Gómez 1993; Fletcher 1995; Vairappan 2006). The timing of recruitment of fouling species on farmed kelps has shown to follow a distinct seasonal pattern with an accumulation of species towards the end of the cultivation period (Sogn Andersen et al. 2011; Park and Hwang 2012; Førde et al. 2015; Rolin et al. 2017). This pattern is predictable across years (Walls et al. 2017) and typically coincides with an increase in water temperature (Sogn Andersen et al. 2011; Bruhn et al. 2016; Matsson et al. 2019). However, biofouling on seaweeds can also vary profoundly within a relatively small geographic range, unrelated to seasonal changes (Matsson et al. 2019). One important factor causing this variation can be hydrodynamic forces (strong currents and wave action) as previous studies have reported different biofouling cover on seaweeds in sheltered, semi-exposed and exposed localities (Peteiro and Freire 2013b; Bruhn et al. 2016; Mols-Mortensen et al. 2017; Matsson et al. 2019). This indicates that wave exposure and/or water current might be important to consider for site selection in order to reduce biofouling.

Efforts to reduce biofouling by cultivating seaweeds at different exposure and/or water current might affect seaweed growth (i.e. yield and morphology) and chemical content of farmed seaweeds (Hurd 2000; Hepburn et al. 2007). It is often considered that growth in natural kelp populations is higher in moderately exposed environments than wave-exposed or sheltered habitats (Leigh et al. 1987; Kregting et al. 2016). With respect to farmed kelp, Peteiro and Freire (2013a) showed that

the biomass yield was higher at a moderately exposed location compared to a sheltered farm site, and Mols-Mortensen et al. (2017) found highest blade growth at a location with strong current compared to sheltered and wave-exposed sites. Furthermore, seaweeds grown in exposed water have higher carbon content due to increased carbon uptake and allocation to structural material (Kraemer and Chapman 1991b). Moreover, it is suggested that seaweed utilize different carbon sources (bicarbonate or carbon dioxide) depending on the wave exposure (Peterson and Fry 1987). Stable isotopes, such as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, can help determine the nutrient source (France 1995; Raven et al. 1995; Viana and Bode 2015). For example, tissue $\delta^{15}\text{N}$ and nutrient concentrations decreased from more sheltered estuarine sites to more exposed marine waters, suggesting larger dominance of anthropogenic nitrogen sources in the estuary (Deutsch and Voss 2006; Raimonet et al. 2013; Viana and Bode 2015). Except for high exposure, selection of localities with different exposure will be limited to near shore coastal areas where most seaweed cultivation is placed today. Environmental conditions in near shore waters can vary extensively, especially in fjord systems or archipelagos that are often used for cultivation purposes, affecting seaweed growth and the yield of farmed seaweeds (Kerrison et al. 2015; Kim et al. 2015; Bruhn et al. 2016).

The Swedish west coast experiences a strong north to south salinity gradient created by the inflow of brackish water from the Baltic Sea into fully saline marine water from the North Sea. In addition, the outflow of river runoff water resulting in drops in salinity locally complicates the selection farm sites with favourable growth conditions. Thus, site selection for optimising yield and quality (fouling coverage and chemical composition) of farmed seaweeds also need to take spatial variation into account.

The aim of this study was to assess quantitative and qualitative effects of wave exposure and spatial variation on cultivated kelp (*S. latissima*). Quantitative effects were assessed by growth measurements and qualitative effects by measuring biofouling coverage and analysing tissue content of water, carbon and nitrogen.

Material and methods

Sample preparation

Non-fertile *Saccharina latissima* individuals were collected at the Swedish west coast (58° 83' N, 10° 99' S). Fertile sorus tissue was induced during a 10-week culturing period in 10 °C, short-day photoperiod and removal of the basal blade meristem (15 cm above the base) (Pang and Lüning 2004; Forbord et al. 2012). The spores were released in autoclaved seawater (ASW) with half strength Provasoli's enriched seawater (PES) medium and the spore concentration was estimated using a haemocytometer. The spore solution was kept in

aerated glass flask (5 L) at 10 °C with a light intensity of approximately $70 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Medium was changed weekly until the first sporophytes were visible after approximately 2 weeks. The developing gametophytes/sporophytes were concentrated using a 20- μm filter, rinsed with ASW and fragmented using a blender for 10 s. The resulting solution was diluted according to the number of released spores and sprayed onto a 1.2-mm diameter nylon cultivation line. Further development of seedlings was done under laboratory conditions: long-day photoperiod (16 h light), filtered (0.2 μm) half-strength PES medium at 10 °C and a light intensity of approximately $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Two meters of seeded long line, with small seedlings of up to 1 cm, were transplanted at the experimental localities (Fig. 1).

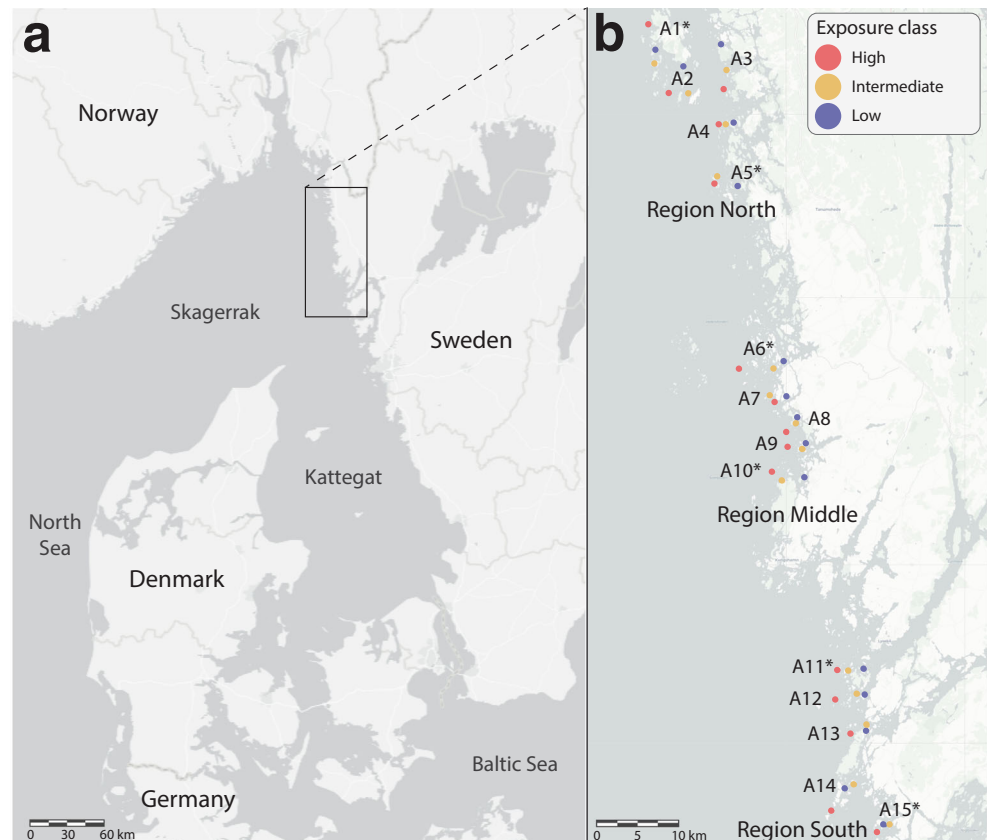
Experimental design and site description

The individual and interactive effects of geographic location and wave exposure on length, width, surface area and wet weight of transplanted *S. latissima* were examined in 3 regions with 5 areas per region ($n_{\text{area}} = 15$). Each area contained three degrees of wave exposure, with two lines within each area wave exposure combination ($n_{\text{line}} = 90$). From each line, 10 individual seaweed blades ($n_{\text{individual}} = 900$) were collected for measurements (Fig. 1). The three regions were defined as “North”, “Middle”, and “South”, with a distance of approximately 20 km between

the nearest area from a different region. The lines were deployed approximately 20 m apart and contained 2 m seeded seaweed line that was anchored and buoyed to float so that the upper part of the line was submerged around 0.5 m below the water surface. The wave exposures were defined as follows: 500,000–800,000 m^2s^{-1} (exposed), 100,000–200,000 m^2s^{-1} (moderately exposed) and 10,000–30,000 m^2s^{-1} (sheltered). Data for wave exposure came from the simplified wave model method SWM (Isæus 2004), and the chosen groups of wave exposure were subsets of the classes “Exposed”, “Moderately exposed” and “Sheltered” in the wave exposure index as suggested by Isæus (2004). The experiment was conducted over a period between January and June 2018 (147–172 days).

At the Swedish west coast, natural kelp (*S. latissima*) populations are present at the rocky shores from a depth of about 1 m. The tidal ranges are small (<0.3 m), but differences between high and low water levels up to 2 m still occur due to changes in atmospheric pressure and wind (Johannesson 1989). The mean surface water (0–10 m deep) salinity during cultivation months of the last decade (2008–2018) at the experimental sites varied between 27.6 ± 3.5 psu (mean \pm sd, $n = 333$), 28.3 ± 5.2 psu (mean \pm sd, $n = 588$), and 25.7 ± 3.6 psu (mean \pm sd, $n = 485$) in the northern, middle and southern experimental regions respectively (SMHI 2019). This is primarily influenced by the inflow of saline marine water from the North Sea and low saline water from the

Fig. 1 Geographical location and study design. The study area (a), the study design with the locations of the 15 experimental areas — each area exposure combination contains two lines ($n = 90$) — within three regions and three wave exposure classes (b). Asterisks denote the locations with temperature loggers



Baltic Sea into the Skagerrak (Fig. 1a). Drops in salinities are locally due to nutrient-rich river run off, primarily in late spring/early summer. Historic nutrient concentrations in the seawater (i.e. total nitrogen, $\text{NO}_2 + \text{NO}_3$, NH_4 , total phosphorus and PO_4) at the three experimental regions during the experimental period indicates relatively small variability between regions, but slightly higher concentrations of dissolved N and P the middle region compared to the northern and southern region (SMHI 2019; Table S1). In addition, the experimental regions consist primarily of rocky shores with many islands and skerries, creating variation of hydrodynamic forces on relatively small geographic scales without altering the chemistry of the seawater. Data from the STRÅNG model system (Landelius et al. 2001) show that the mean light irradiance during the experiment was $1320 \pm 1159 \text{ Wh m}^{-2}$ (mean \pm sd, $n = 7568$), with an irradiance of $2799 \pm 824 \text{ Wh m}^{-2}$ (mean \pm sd, $n = 1408$) in the final month of the experiment (Fig. S1). Seawater surface temperature ($^\circ\text{C}$) was measured throughout the experimental period at selected areas within the experimental regions (Fig. 1) using Onset HOBO Pendant UA-002-64 loggers. The water temperature was $< 15 \text{ }^\circ\text{C}$ until the middle of May, after that a sharp increase was noted up to approx. $20 \text{ }^\circ\text{C}$ (Fig. S2).

Growth and biofouling measurements

From each 2-m seeded seaweed line, 10 individual seaweed blades were haphazardly selected at 20-cm intervals starting at the water surface. Data was collected on wet weight (WW), length (L), width (W), surface area (SA), fouling coverage (F) and composition of fouling taxa. The size and fouling measurements (i.e. L, W, SA and F) were analysed using ImageJ software. The contribution of fouling species was related to total blade surface area, and biofouling species were grouped according to taxa.

Tissue composition

The same samples ($n = 10$) used for growth and fouling analysis were analysed for variation in water content (%), which was calculated by comparing tissue dry weight after freeze-drying with the tissue wet weight directly after harvest. The variation in chemical composition of total carbon, nitrogen, and C:N ratio of blade tissue related to wave exposure was analysed for a subset of seaweeds ($n = 18$) within the middle region. These samples were also analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, in order to investigate the accessibility of carbon and the source of nitrogen (i.e. from a marine or terrestrial origin) that were assimilated by the seaweed in their respective exposure class. Freeze-dried blade samples were ground into a fine powder with a mortar, and samples of approximately 10 mg samples were analysed using an elemental analyser coupled to

an isotope ratio mass spectrometer (SerCon GSL and 20–22 IR;MS; SerCon Ltd., UK).

Statistical analysis

All analyses were conducted using R software (R Core Team 2018). Effects on growth (WW, L, W, and SA), fouling coverage and water content of blade tissue for exposure (fixed factor, 3 levels), region (fixed factor, 3 levels), area within region (random factor, 5 levels, varying intercept) and line within area (random factor, 2 levels, varying intercept) were statistically analysed with mixed model analysis of variance (ANOVA) using the *lmer* function from the lme4 package (Bates et al. 2014). Means from duplicate samples of total carbon and nitrogen, C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were statistically analysed with ANOVA using the *lm* function (R Core Team 2018) using exposure (3 levels) as fixed factor. Differences in biofouling species composition were analysed using descriptive statistics, as the abundant double zero's among samples restricted statistical testing.

Prior to all statistical analyses, data was graphically analysed and the best suited normalizing transformation was estimated using the *bestNormalize* package (Peterson 2017). Multiple comparisons of significant different fixed factors were performed with a Student-Newman-Keuls (SNK) post hoc test ($\alpha = 0.05$), using the *SNK.test* function in the *agricolae* package (version 1.3-1). Marginal R_m^2 and the conditional R_c^2 were used to estimate the amount of variance explained by the fixed effects only and the combined fixed and random effects of the models, respectively (Nakagawa and Schielzeth 2013).

Results

Blade biofouling

The biofouling of the seaweed blades was interactively affected by exposure and region (Table 1). The overall pattern indicated less fouling with increasing exposure (Fig. 2b), with significantly lower fouling cover at exposed localities in each region and except for the north region also significantly lower fouling cover for the moderately exposed localities compared to the sheltered localities (Table 1; *post hoc* test §3). From a total of 729 blade samples, biofouling was absent in 79 individuals (i.e. 10.8%), of which 66 were found at exposed, 9 at moderate and 4 at sheltered locations. The mean biofouling coverage for the exposed, moderately exposed and sheltered localities was $2.8 \pm 0.3\%$ (mean \pm se, $n = 152$), $6.2 \pm 0.2\%$ (mean \pm se, $n = 282$) and $10.1 \pm 0.6\%$ (mean \pm se, $n = 295$), respectively. The blade biofouling was also affected by region, with significantly higher fouling coverage for sheltered

Table 1 Mixed model analysis of variance (ANOVA) table to assess different effects in (square root transformed) surface area (cm²) and (arcsinh square root transformed) individual blade fouling (%), and water content (%) from exposure, region, area and line. *ndf* and *ddf* indicate the calculated df in the nominator and denominator respectively, SNK is the

post hoc test, σ^2 is the variance, LRT is the likelihood ratio test, the marginal R^2 (R_m^2) is the variance explained by the fixed effects, and the conditional R^2 (R_c^2) is the variance explained by both fixed and random effects

Source of variation	Surface area				Fouling				Water content			
	<i>ndf</i> , <i>ddf</i>	<i>F</i> value	<i>p</i>	SNK	<i>ndf</i> , <i>ddf</i>	<i>F</i> value	<i>p</i>	SNK	<i>ndf</i> , <i>ddf</i>	<i>F</i> value	<i>p</i>	SNK
Fixed effects												
Exposure (<i>E</i>)	2, 18.5	13.69	< 0.001	§1	2, 21.3	48.11	< 0.001		2, 22.2	7.32	0.004	§4
Region (<i>R</i>)	2, 12.5	32.95	< 0.001	§2	2, 12.4	2.34	0.136		2, 12.6	8.38	0.005	§5
Exposure × Region	4, 18.5	0.90	0.482		4, 21.3	8.95	< 0.001	§3	4, 22.1	1.77	0.171	
Random effects	$\sigma^2 \pm sd$	LRT	p		$\sigma^2 \pm sd$	LRT	p		$\sigma^2 \pm sd$	LRT	p	
Area (<i>R</i>)	0.77 ± 0.88	6.05	0.014		0.023 ± 0.153	3.31	0.069		0.45 ± 0.67	0.58	0.446	
Area (<i>R</i>) × <i>E</i>	0.43 ± 0.66	2.41	0.121		0.009 ± 0.093	0.28	0.592		2.41 ± 1.55	27.89	< 0.001	
Line (area (<i>R</i>) × <i>E</i>)	0.63 ± 0.79	45.28	< 0.001		0.048 ± 0.219	26.49	< 0.001		0.04 ± 0.19	0.06	0.809	
Residuals	2.19 ± 1.48				0.205 ± 0.453				5.30 ± 2.30			
R_m^2/R_c^2	0.59/0.78				0.35/0.53				0.29/0.54			

Significant differences (*p* < 0.05) are denoted in italic

Surface area and fouling: number of obs.: *n*=729, groups: Area(*R*) = 15, Area(*R*) × *E* = 43, Line(Area(*R*)) × *E* = 81.

Water content: number of obs.: *n*=697, groups: Area(*R*) = 15, Area(*R*) × *E* = 43, Line(Area(*R*)) × *E* = 81.

§1: $E_{\text{exposed}} < E_{\text{moderate}} = E_{\text{sheltered}}$

§2: $R_{\text{south}} < R_{\text{north}} < R_{\text{middle}}$

§3: $E_{\text{exposed}}: R_{\text{south}} < R_{\text{middle}} < R_{\text{north}}$

$E_{\text{moderate}}: R_{\text{middle}} < R_{\text{north}} < R_{\text{south}}$

$E_{\text{sheltered}}: R_{\text{middle}} \leq R_{\text{north}} < R_{\text{south}}$

$R_{\text{north}}: E_{\text{exposed}} < E_{\text{moderate}} \leq E_{\text{sheltered}}$

$R_{\text{middle}}: E_{\text{exposed}} < E_{\text{moderate}} < E_{\text{sheltered}}$

$R_{\text{south}}: E_{\text{exposed}} < E_{\text{moderate}} < E_{\text{sheltered}}$

§4: $E_{\text{exposed}} < E_{\text{moderate}} < E_{\text{low}}$

§5: $R_{\text{south}} < R_{\text{north}} < R_{\text{middle}}$

and moderately exposed localities at the southern region (16.6 ± 1.0% (mean ± se, *n* = 177)) compared to the northern (5.3 ± 0.3% (mean ± se, *n* = 200)) and the middle (3.7 ± 0.2% (mean ± se, *n* = 200)) region (Table 1; *post hoc* test §3). For exposed localities, the highest fouling coverage was in the northern region (4.3 ± 0.7% (mean ± se, *n* = 59)), followed by the middle region (2.0 ± 0.4% (mean ± se, *n* = 41)), and then by the southern region (1.6 ± 0.5% (mean ± se, *n* = 52)). Additionally, the fouling cover varied significantly among lines while variability was much lower among the area.

Fouling species

Four major biofouling taxa were observed to contribute to biofouling of the transplanted blade of *S. latissima*: bryozoans (*Membranipora membranacea* and *Electra pilosa*), hydroids (mainly *Obelia geniculata*), tube-building amphipods (mainly *Jassa falcata*) and tunicates (*Ciona intestinalis*). There was also a considerable amount of debris (denoted “undefined”) contributing to the total fouling cover. In terms of blade coverage (%), amphipods were most dominant (7.7 ± 0.6%), followed by

bryozoans (4.7 ± 0.4%), hydroids (2.7 ± 0.3), undefined (1.7 ± 0.1) and tunicates (1.2 ± 0.1) (mean ± se) (Fig. 3). In addition, species composition varied between regions and exposure (Table S2). For example, tunicates were found to be most abundant in the northern and middle region at sheltered and moderately exposure while they were totally absent at the exposed locations. The fouling composition at exposed locations consisted predominately of bryozoans and hydroids, whilst biofouling of blades cultured at sheltered and moderately exposed locations in the northern and middle regions were found to be more species diverse. Fouling in the southern region consisted mainly of tube-building amphipods, covering most of the blade.

Seaweed growth

Across all samples blade growth, expressed as surface area, increased with 85.5 ± 2.0 cm² (mean ± se, *n* = 729) during the experimental period. Both exposure and region had a significant effect on the blade surface area (Table 1; Fig. 2a), as well as on all other measures of growth (i.e. wet weight, length and width; see Table S3 and Fig. S3). The highest growth was

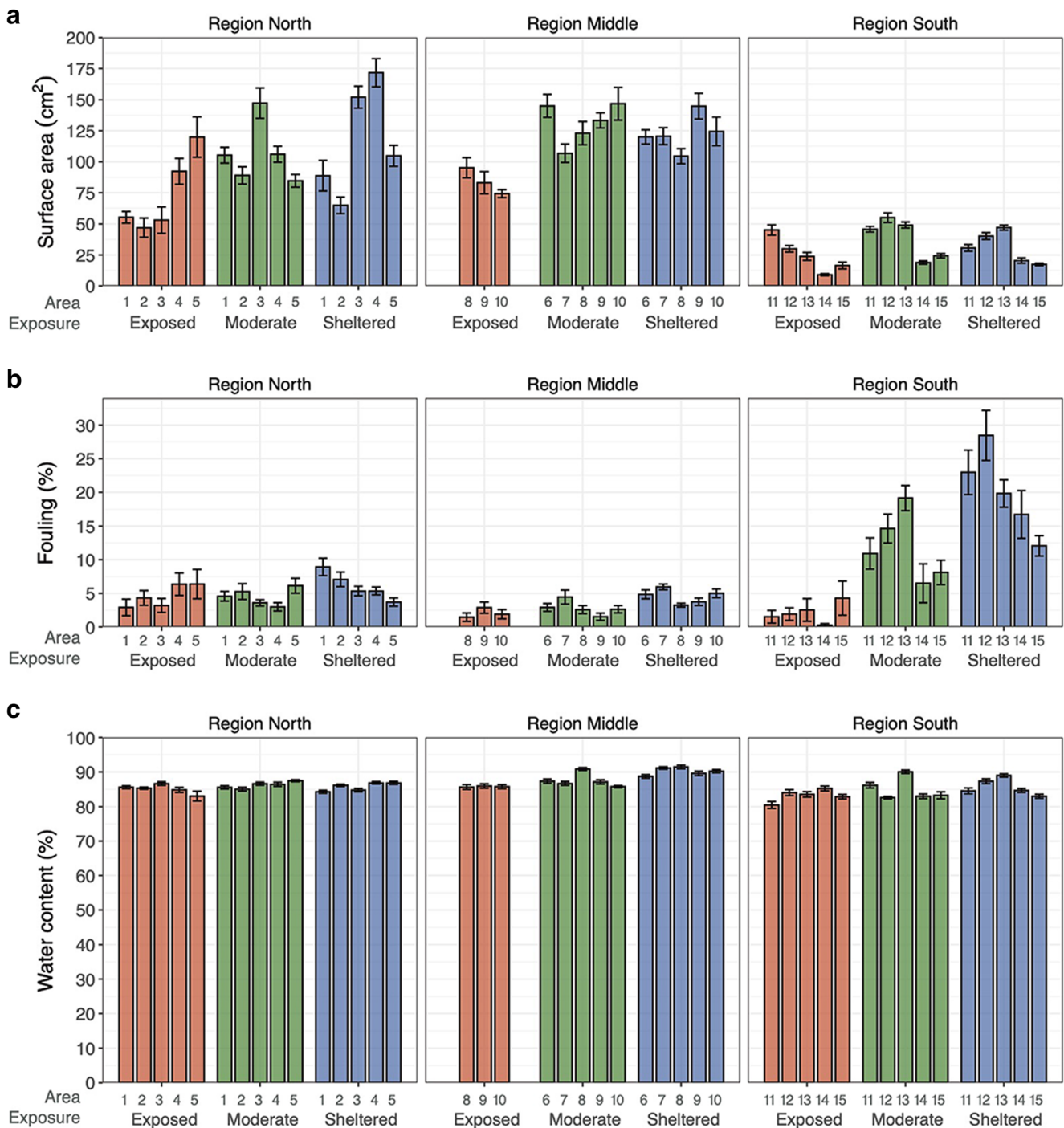


Fig. 2 Growth, fouling, and water content. The mean increase in **a** surface area, **b** mean blade fouling and **c** mean water content of area within region and exposure. Error bars show SEM, $n = 20$

found at moderately exposed locations ($95.64 \pm 3.1 \text{ cm}^2$ (mean \pm se, $n = 282$)) and sheltered locations ($91.4 \pm 3.4 \text{ cm}^2$ (mean \pm se, $n = 295$)), while growth at exposed locations was significantly lower ($55.3 \pm 3.0 \text{ cm}^2$ (mean \pm se, $n = 152$)) (Table 1; *post hoc* test §1). This resembled a difference of approximately 40% in surface area (cm^2) between both sheltered and moderately exposed locations compared to exposed

locations. The regional difference consisted of lowest growth in the southern region ($32.2 \pm 1.1 \text{ cm}^2$ (mean \pm se, $n = 229$)), followed by the northern region ($101.0 \pm 3.2 \text{ cm}^2$ (mean \pm se, $n = 259$)) and the middle region ($119.4 \pm 2.7 \text{ cm}^2$ (mean \pm se, $n = 241$)) (Table 1; *post hoc* test §2). Additionally, the growth of blade surface area was found to vary significantly between areas and among lines (Table 1).

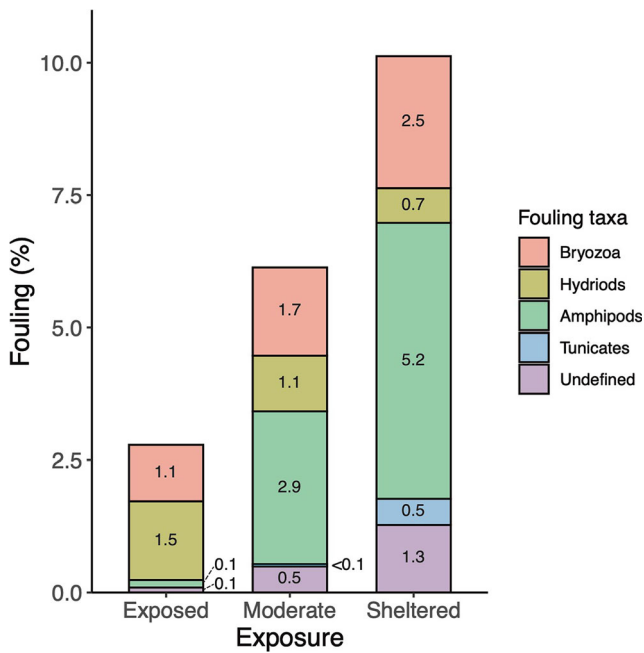


Fig. 3 Mean fouling coverage by taxa on *S. latissima* blades from three exposure levels (exposed, moderate, sheltered). Data are means from blades from all regions, and values indicate fouling contribution (% of the blade) by fouling taxa

Tissue composition

The water content was significantly affected by exposure with decreasing levels when exposure increased (Table 1; *post hoc* test §4). In addition, region had a significant effect on the water content with highest levels in the middle region, followed by the northern region, while the lowest water content was observed at the southern region (Table 1; *post hoc* test §5). This pattern corresponded to the observed differences of growth in blade surface area (i.e. middle > north > south). The variability among areas was ten times higher than among lines, although the variance contribution for neither of the factors was statistically significant. With respect to the chemical content in the seaweed tissue (Table 2), we found a near significant effect of exposure on the carbon content in the tissue ($p = 0.053$) with a higher mean at more exposed locations compared to the moderate and sheltered sites (Fig. 4a). Tissue nitrogen content significantly differed between exposure, with a higher content at sheltered locations compared to exposed sites (Fig. 4b). Consequently, a significantly higher C:N ratio was found at exposed locations compared to moderate and sheltered sites (Table 2 and Fig. 4c). $\delta^{13}\text{C}$ was also significantly different between exposures, with a lower value at exposed compared to moderate and sheltered sites (Table 2, Fig. 4d). Additionally, $\delta^{15}\text{N}$ was significantly higher at sheltered compared to exposed and moderate locations (Table 2, Fig. 4e).

Table 2 Chemical content. Summary of analysis of variance (ANOVA) of the mean carbon and nitrogen content (% dry weight), the C/N ratio and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ nitrogen content (% dry weight) of a random subset from the three exposure classes within the middle region

Source of variation	Carbon		Nitrogen		C/N ratio		$\delta^{13}\text{C}$ carbon		$\delta^{15}\text{N}$ nitrogen											
	df	MS	F value	p	MS	F value	p	MS	F value	p										
Exposure	2	13.35	3.13	0.053	0.21	3.36	0.043	§1	291.07	4.11	0.023	§2	15.35	12.68	< 0.001	§3	5.78	44.3	< 0.001	§4
Residuals	47	4.27			2.70		70.86		1.23								0.13			

Significant differences ($p < 0.05$) are denoted in *italic*

- §1 exposed \leq moderate \leq sheltered
- §2 sheltered = moderate < exposed
- §3 exposed < moderate < sheltered
- §4 exposed = moderate < sheltered

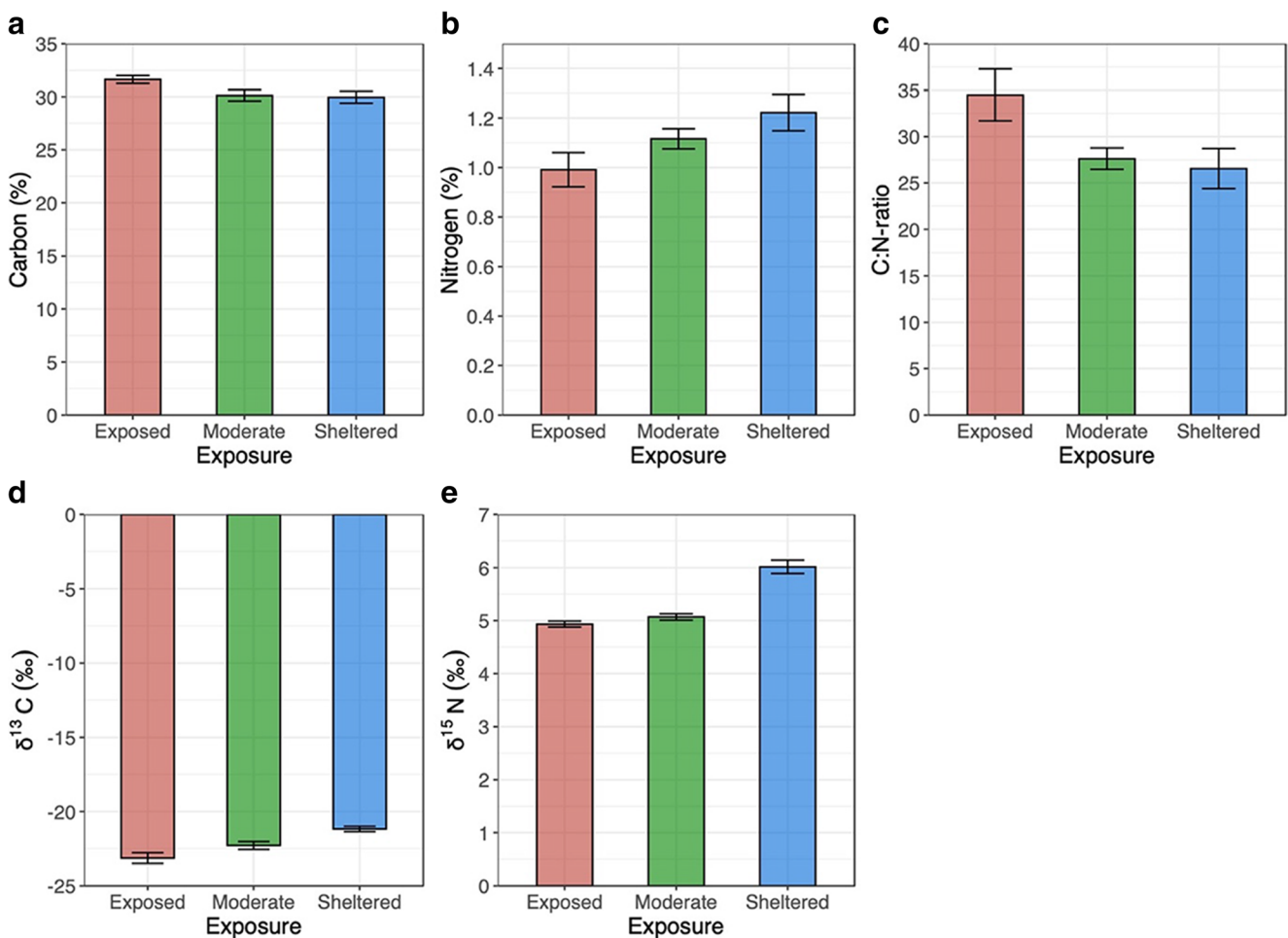


Fig. 4 Chemical content. **a** Mean carbon and **b** nitrogen content (% dry weight), **c** C:N ratio, **d** $\delta^{13}\text{C}$ and **e** $\delta^{15}\text{N}$ of a subset of blades from three exposure classes within the middle region. Samples were analysed in duplicate, and error bars show SEM ($n = 18$)

Discussion

In this study, cultivation of *S. latissima* was successful within all levels of exposure and tested regions along the northern part of the Swedish west coast. Wave exposure was found to affect biofouling, with less fouling at higher wave exposure. The exposure level also affected the tissue composition, with a high carbon but low nitrogen and water content at exposed locations compared to moderate and sheltered sites. In addition, there was relatively large spatial variation, from m-scale to tens of km-scale, in the growth of *S. latissima*. Overall, growth significantly increased with decreased wave exposure.

Biofouling has been identified previously as a key constraint for many seaweed farms worldwide (Fletcher 1995; Lüning and Mortensen 2015; Kim et al. 2017). Here, we found that biofouling occurred at all exposure levels, but that it was significantly lower at more exposed locations, which corroborates previous findings (Sogn Andersen et al. 2011; Peteiro and Freire 2013a). However, Matsson et al. (2019) found a reversed pattern, with a higher fouling coverage of the blade at more exposed sites compared to the inshore and fjord location in northern

Norway, and Bruhn et al. (2016) found that fouling did not correspond to estimated degree of exposure within a Danish estuary. In addition, one of the most popular location for seaweed cultivation in Korea (Wando region) experiences significant problems with biofouling (Park and Hwang 2012), despite relatively high current velocities (approx. 50 cm s^{-1}) compared to exposed locations where biofouling in European kelp farms has been examined (Peteiro and Freire 2013b; Førde et al. 2015; Mols-Mortensen et al. 2017; Matsson et al. 2019). Although we purposefully used single dropper lines in the present experiment that allowed us to explore various exposure classes at a greater geographic scale, the results may have been influenced by the size and density of the cultivation as wave exposure and/or current velocities are likely to alter within a large-scale farm and change during the cultivation period as the biomass increases (Shi et al. 2011).

Species abundance and biofouling taxa recorded in this study were both within the same range (between 3 and 32 species) and species composition compared to previous findings from other kelp farms (Kim et al. 2017; Rolin et al. 2017; Walls et al. 2017; Bannister et al. 2019; Matsson et al. 2019).

Fouling taxa overlapped between region and exposure, but the species composition (i.e. the number of taxa) decreased with increased exposure. Similar to Matsson et al. (2019), hydroids and bryozoans were predominantly found at exposed locations. Biofouling of tunicates (*C. intestinalis*) was also observed at kelp farms in waters surrounding the Shetland Islands and Skagerrak (Sogn Andersen et al. 2011; Rolin et al. 2017); however, its presence was not related to the level of exposure. Here, we found that fouling of *C. intestinalis* was limited to sheltered and moderately exposed environments. The tube dwelling amphipod (*J. falcata*) was the dominant fouling species at low and intermediate exposure levels in the southern region. It is an important fouling organism that forms dense mats or “nests” made of debris that started at the culture line close to the base of the blade, from where it expanded towards the distal part. This pattern differed from the other fouling taxa found in the present study that mainly started at the distal part of the blade (Visch, pers. observation). The temperature during the experimental period in spring and early summer of 2016 was relatively warm in northern Europe (SMHI 2016a, 2016b) (Fig. S2), which may have affected the biofouling and its succession on the seaweed blades as it is known to coincide with increasing seawater temperature (Sogn Andersen et al. 2011; Bruhn et al. 2016; Matsson et al. 2019). Consequently, future predictability of timing of the harvest may be altered, as the frequency and duration of marine heat waves are expected to increase (Oliver et al. 2018).

Growth, expressed as blade surface area, was found to be lower at exposed locations compared to sheltered and moderately exposed locations. Previous studies investigating yield of kelp farms in relation to exposure have focused on different exposure types (e.g. sheltered, current velocity or wave exposure); therefore, results have been ambiguous and general conclusions have been difficult to draw. For example, high-exposed environments are where found to generate lower yields (Sanderson et al. 2012), or higher yields at wave-exposed and sheltered sites compared to current-exposed locations (Mols-Mortensen et al. 2017). Others, however, found a positive relationship between current velocity and yield (Peteiro and Freire 2011, 2013a), or no relationship between yield and degree of exposure (Bruhn et al. 2016; Matsson et al. 2019). In natural kelp populations, exposure has shown to affect productivity, with higher growth in moderately exposed environments compared to sheltered or wave-exposed habitats (Leigh et al. 1987; Kregting et al. 2016). The present study, showing less growth at higher wave exposure, provided a strong test of the effect of wave exposure that most likely were only minorly confounded with current exposure as it was conducted in waters with very weak tidal currents (tidal range < 0.3 m).

Morphological and biomechanical responses of seaweeds to different hydrodynamic regimes are well documented in natural communities, with generally narrow/thick blades in exposed habitats and wide/thin blades in sheltered habitats (Hurd et al. 1996;

Hurd 2000; Koehl et al. 2008; Bekkby et al. 2014). The narrower blades found at kelp farms in exposed sites found in the present study, and in a study by Mols-Mortensen et al. (2017), substantiate this pattern. Furthermore, effects of wave exposure on tissue carbon content was previously found to be related to an increase in carbon uptake that is allocated to structural cell wall material (Kraemer and Chapman 1991a, b). It is hypothesised that differences in growth rate due to water motion may be related to trade-offs between blade growth and an increase in tissue strength (Kregting et al. 2016). This is corroborated by the chemical analysis and growth rates observed in the present study showing a higher carbon content in exposed locations, but a greater yield at moderately exposed cultivation sites. Based on the expected preferential uptake of ^{12}C in seaweeds (Keeley and Sandquist 1992), the observed difference in $\delta^{13}\text{C}$ could be explained by differences in accessibility of carbon at the different exposure levels, with less access of carbon in the sheltered localities. Overall, tissue nitrogen content was relatively low compared to previous findings for cultured kelp (Sanderson et al. 2012; Handa et al. 2013; Wang et al. 2014). This could be the result of a delayed harvest date (i.e. June) in the present study, compared to normal harvesting period in April/May in the region (Handa et al. 2013). Exposure also had a strong impact on the nitrogen content in the tissue, with elevated concentrations at sheltered locations. This could however be confounded by higher concentrations of dissolved inorganic nitrogen at sheltered sites unrelated to exposure level, as they were located closer to the shore where higher seawater nitrogen concentrations can be expected from an influx of nutrients from land. Although the dissolved nutrients were not directly measured, the elevated tissue $\delta^{15}\text{N}$ at the sheltered sites suggest a larger dominance of anthropogenic nitrogen compared to more moderately and exposed locations (Deutsch and Voss 2006; Raimonet et al. 2013; Viana and Bode 2015).

Increasingly, there is the need to study and understand the potential effects of cultivation site on the quality and quantity of the biomass in seaweed aquaculture. In a recent study, between 475 and 544 km² of sea area within the Swedish exclusive economic zone (EEZ) along the west coast was identified as suitable for seaweed cultivation, without conflicting with socio-economic activities (Thomas et al. 2019). Here, we identified effects of wave exposure on biofouling, growth and chemical content that will be informative for identifying new kelp farm locations within this area. A particular priority for consideration should be the large km-scale geographic variation in biomass yield and blade fouling. In conclusion, our findings together with previous studies can facilitate site selection in seaweed aquaculture, thereby improving the yield as well as the quality of farmed seaweed biomass.

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