

Variation in biomass and biofouling of kelp, *Saccharina latissima*, cultivated in the Arctic, Norway

Sanna Matsson^{a,b,*}, Hartvig Christie^c, Reinhold Fiebler^a

^a Akvaplan-niva AS, Fram Centre, 9296 Tromsø, Norway

^b Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Breivika, 9037 Tromsø, Norway

^c Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway

ARTICLE INFO

Keywords:

Seaweed farming

Epibionts

Bryozoans

Biomass yield

Low trophic level aquaculture

ABSTRACT

In the present study, the kelp *Saccharina latissima* was cultivated at three sites in Troms, northern Norway (at 69–70°N). These sites, while close to each other geographically, were characterized by differences in exposure to waves and influence from oceanic water, and arranged in a gradient from semi-offshore through intermediate exposure to a more sheltered fjord with a stronger influence from freshwater run-off. The effect on kelp biomass and biofouling was studied from February to August in 2014. Large variation in biofouling cover was observed between sites. The site with highest exposure had the maximum kelp biomass, but also the highest cover of fouling organisms. The frond area covered by epibionts varied by a factor of 8 with lowest cover at the fjord site, intermediate cover at the inshore site and highest cover at the semi-offshore site. Species composition of the biofouling community also varied between sites, with the dominant taxa being hydroids at the most protected, and bryozoans at the most exposed site. The present study shows that both biomass yield and biofouling can vary profoundly within short geographical ranges and it thereby underlines the importance of thorough site selection for kelp cultivation in order to achieve maximum kelp biomass and minimum biofouling. It also reveals promising opportunities for kelp cultivation at higher latitudes.

1. Introduction

1.1. Macroalgae cultivation

Macroalgae cultivation, including brown, red and green algae, is gaining interest in Europe. This is due to a general need for ingredients in a number of products such as food, fish diets, cosmetics, pharmaceuticals, biofuel etc. (Skjermo et al., 2014). In Norway, as in the rest of Europe, macroalgal cultivation is at an early stage of development. The Norwegian coastline has a potential for macroalgae cultivation along the entire latitudinal gradient from 58 to 71°N, but cultivation activities in Norway have so far been located in southern and in mid Norway (Stévant et al., 2017). These activities have been classified as research and pilot-scale production, with some of the first commercial permits granted in 2014.

Sugar kelp, *Saccharina latissima* (L.) C.E. Lane, C. Mayes, Druehl, and G.W. Saunders, is distributed from Portugal to Spitsbergen (Araújo et al., 2016) and in the NW Atlantic. It is the favoured species for cultivation in both the North Atlantic region and Norway. This is due to its high growth rate and comparatively simple life cycle where sorus

induction, spore release and gametophyte growth can be controlled in the lab (Forbord et al., 2012; Marinho et al., 2015b; Marinho et al., 2015a), and it can easily be seeded and grown on rope or other convenient structures.

1.2. Biofouling

The kelp fronds provide an attractive substrate for a variety of epibionts, such as filamentous algae, bryozoans, hydroids, tunicates and herbivorous invertebrates (Andersen, 2013; Moy and Christie, 2012; Scheibling and Gagnon, 2009). The epibionts usually settle during late spring and early summer, coinciding with the time at which biomass and nutritional values of kelp are high (Marinho et al., 2015b; Marinho et al., 2015a). Epibionts may cause loss of kelp biomass (Scheibling and Gagnon, 2009; Skjermo et al., 2014) through increased drag and friction, decreased flexibility, mechanical damage (Krumhansl et al., 2011) and light retention (Andersen, 2013). Epibiont settlement can occur at different parts of the kelp and may vary by taxonomic group of biofouling organism (Wahl, 1989). Due to deterioration of kelp tissue, epibionts can make the biomass unsuitable for human consumption

* Corresponding author at: Akvaplan-niva AS, Fram Centre, 9296 Tromsø, Norway

E-mail address: sanna.matsson@akvaplan.niva.no (S. Matsson).

(Marinho et al., 2015a). The colonial encrusting bryozoan, *Membranipora membranacea* (L.) is one of the most common epibionts with detrimental effects on kelp fronds on both sides of the North Atlantic, on both wild kelps (Dixon et al., 1981; Saunders and Metaxas, 2009b; Scheibling and Gagnon, 2009) and cultivated kelps (Førde et al., 2015; Gendron et al., 2007; Marinho et al., 2015b). To ensure high quality of kelp biomass and to avoid biomass loss from the farm, the kelp is often harvested before the onset of colonisation by epibionts, reducing the growth season. Thus epibionts may cause a problem for the fledgling Norwegian kelp industry (Skjermo et al., 2014).

Mortality, possibly due to fouling, of wild stands of sugar kelp has been found mainly in southern and in mid Norway (Andersen et al., 2019). However, due to heavy grazing by sea urchins, sugar kelp beds are hardly found north of the Arctic Circle (Norderhaug and Christie, 2009). In recent years, monitoring programs have observed natural kelps without fouled laminas in Northern Norway (NIVA personal observations). Moy and Christie (2012) indicated that fouling showed a discontinuous pattern which seemed to be enhanced with decreasing wave exposure in natural sugar kelp beds. So far, the Norwegian experience with kelp farming, including damage caused by epibionts (Førde et al., 2015), has only been observed in areas south of the Arctic circle.

The objectives of this field study were to study the effect of site and cultivation depth on the (1) temporal variation of *S. latissima* biomass yield, (2) abundance and taxonomic composition of biofouling organisms, by examining the environmental parameters such as current strength, temperature, salinity and nitrate concentration. Lastly, (3) we wanted to quantify the magnitude of difference in biofouling levels between different areas on the kelp lamina.

2. Methods

2.1. Description of study sites

The experiment was carried out between February and August 2014 at three sites in Troms, Northern Norway (Fig. 1). The three sites were chosen to represent semi-offshore, inshore and fjord habitats. Currents and flow direction for the sites were collected prior to this study, following procedures in Norwegian standard NS 9415:2009 for analyses of aquaculture sites.

The fjord site was located in Ullsfjorden ($69^{\circ}40.452' N / 019^{\circ}46.043' E$), with a water depth of 90–95 m. This site is sheltered. Currents were measured at 6 m depth through 31 days from June to July 2010. The measurements show a moderate to high current velocity, averaging 11 cm s^{-1} , and a maximum of 42 cm s^{-1} . The flow direction was uniform throughout the water column from 5 m to 21 m with the main direction towards the northwest.

The inshore site was located on the island of Kvaløya ($69^{\circ}45.259' N / 019^{\circ}02.176' E$) near Tromsø, with a water depth of 15–20 m. This is a sheltered site, yet it has well-mixed water masses through tidal forcing. Current velocity was measured during 120 days at 12 m depth from March to July 2011, and is moderate, with an average of 3.4 cm s^{-1} , and a maximum of 22 cm s^{-1} . The main current direction was towards the northwest.

The semi-offshore site was located southeast of Helgøya ($70^{\circ}06.311' N / 019^{\circ}34.871' E$), with a water depth of 40–60 m. This site is relatively close to the open ocean (20 km) and is somewhat exposed to ocean swell but sheltered from wind-driven waves (Fig. 1a). Currents were measured in January and February 2012 at 5 m depth through 31 days. Current velocities were moderate to strong, with an average of 17 cm s^{-1} , and a maximum of 55 cm s^{-1} . Flow direction was uniform throughout the water column from 5 m to 21 m with the main direction towards the north and northwest. From examining ocean models, median temperature throughout the year was expected to be slightly higher than at the other two sites (Fig. 1b).

2.2. Seaweed material and experimental set-up

Fronds of adult sporophytes of *S. latissima* were collected in Grøtsund ($69^{\circ}45.259' N / 019^{\circ}02.176' E$) during the summer 2013. Sori were induced in culture as described by Forbord et al. (2012) and spore release was induced as described by Rød (2012). *S. latissima* were cultured using methods modified from those described in Edwards and Watson (2011). In the laboratory, the spores were sprayed onto nylon strings where young *S. latissima* sporophytes emerged within three to four weeks. The strings with densely grown sporophytes were spun around two horizontal polypropylene led ropes in $100 \times 50 \text{ cm}$ PVC-frames (2 m seeded ropes per frame). The sporophytes were approximately 10 mm in length when placed at the cultivation sites on 26–27 February, 2014. Three frames were employed at 3 m and at 8 m depth at each site, giving 18 frames and 36 m of seeded ropes in total (Fig. 2).

Once a month throughout the year 2014, salinity and temperature transects were collected at each of the three cultivation sites with a CTD, model SD 204. Water samples for nitrate concentration measurements were collected at 3 and 8 m depth with a Ruttner water sampler and analysed with an autoanalyser (Flow Solution IV System, I.O. Analytical) according to the Norwegian Standard 4745.

2.3. Biomass and biofouling analyses

Approximately once a month from deployment until final harvest, the kelp was monitored for biomass growth, weighted with a Rapala scale, and for epibiont cover. After 6 months in the sea, the frames were collected between 18 and 22 August 2014, and a minimum of three randomly chosen fronds per frame were analysed for epibionts, giving a minimum of 9 kelp fronds per depth and site. A modified version of the point-sampling-method described in Christie (1980) was used to estimate frond area covered by epibionts. A $15 \times 15 \text{ cm}$ grid system with 11 grid lines each vertically and horizontally was placed on top of the kelp fronds at each of three parts: distal, middle, and proximal (Fig. 3a), and each grid was photographed with a digital camera without magnification. The points below the intersection of the grid lines were analysed for presence/absence of epibionts. Where epibionts were present, the species were identified using the World Register of Marine Species (WoRMS, 2017). Ten specific points per grid were analysed in this fashion in a standardised pattern (Fig. 3b) starting in the uppermost left corner, moving diagonally down towards the right edge until the end of the grid or frond area, and then diagonally down the left and so on, thereby ensuring analyses of both edges and middle parts of each kelp frond. This was done on one side of the frond. The different epibiont species on the fronds differed in morphology and were easy to distinguish on the photographs.

The percentage biofouling cover was calculated by dividing 100% with number of points analysed, thereafter multiplying by the amount of points that covered any fouling. The percentage biofouling cover was visualised with boxplots separated into depths, species and blade regions as a function of site, with the remainder pooled.

2.4. Statistical analysis

The environmental parameters were presented through graphs made in Microsoft Excel. All other graphs and statistical analyses were conducted using R, version 3.5.1 (R Core Team, 2018) through RStudio version 1.1.456 (RStudio Team, 2016), using the package lme4 (Bates et al., 2015).

The kelp biomass was modelled by a linear mixed effects analysis of the relationship between biomass, depth and environmental parameters. As fixed effects, we used depth, and the environmental variables with significant impact on the biomass. For random effects, we had intercepts for site and date. Residual plots did not reveal any obvious deviations from homoscedasticity or normality.

The biofouling cover was modelled by a binomial generalized linear

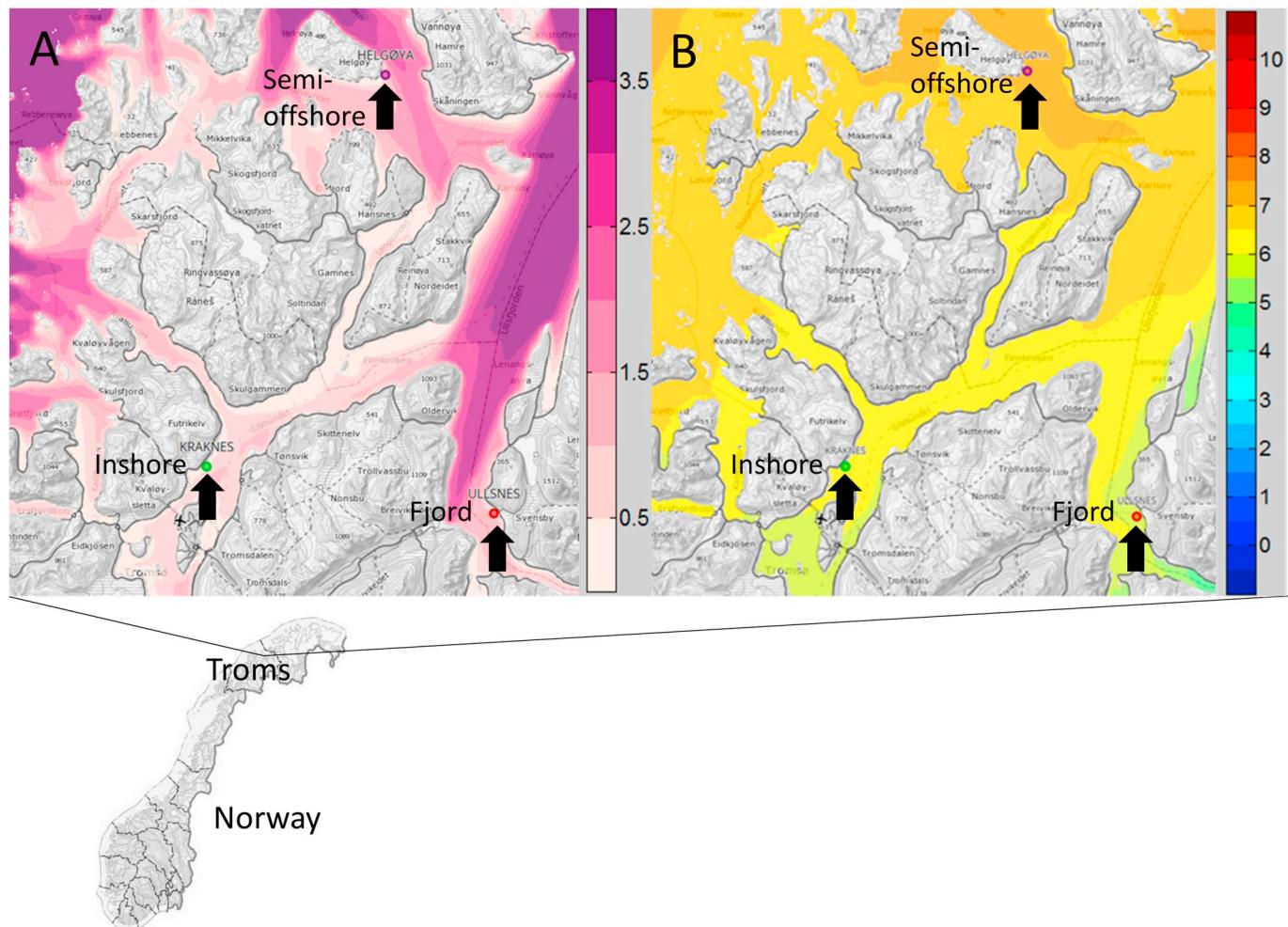


Fig. 1. Map of the three cultivation sites for *Saccharina latissima* in northern Norway with black arrows indicating the site and illustrating, A) modelled extreme wave heights in metres, B) the 50 percentile of modelled water temperature throughout the year in degrees Celsius.

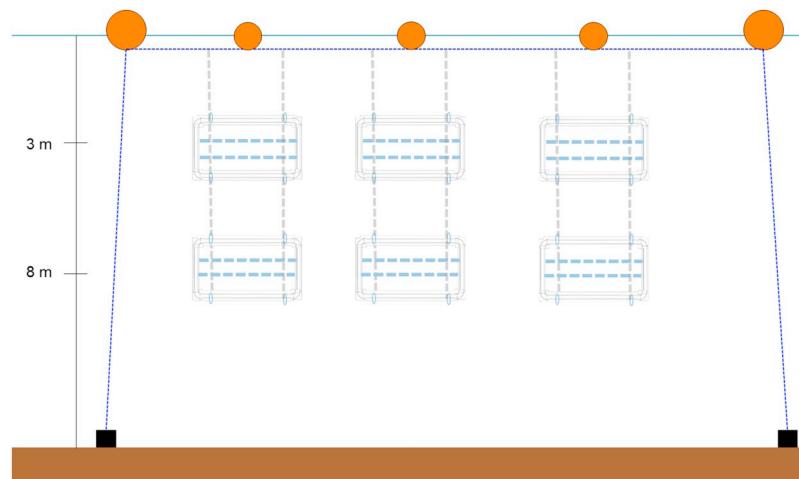


Fig. 2. Experimental set-up with PVC-frames at 3 m and 8 m and three replicates at each depth. Each frame (grey rectangles) consisted of two sets of ropes (stippled lines) with *S. latissima* sporophytes, in total 2 m of rope per frame. Circles denote buoys, black squares are anchors attached to the bottom substrate, and the blue solid lines show the anchoring and horizontal carrying ropes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mixed model (GLMM) (Bates et al., 2015), with logit link function, analysing the relationship between biofouling cover, depth, blade age and environmental parameters. As fixed effects, blade age, and the environmental variables with significant impact on the biofouling cover were selected. Fixed factors without significant impact on the dependent variable were omitted from the model. For random effects, we had intercepts for frames nested in site. Interpretation of residual plots

where conducted with the DHARMA package (Hartig, 2018), as residual interpretation for GLMMs often are problematic. These did not reveal any apparent deviations from homoscedasticity or normality. *P*-values were achieved by likelihood ratio tests of the full model with the effect in question against the models without the effect in question. R2 values for the GLMMs was calculated using the package r2glmm (Jaeger, 2017) with the Nakagawa and Schielzeth approach applied.

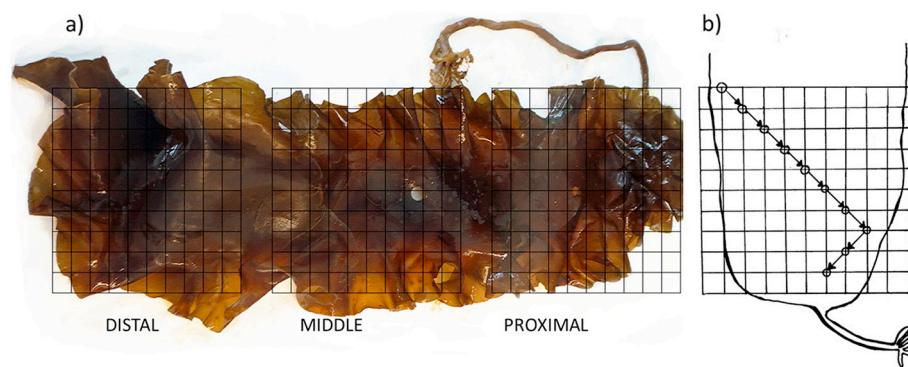


Fig. 3. a) The system of grids used for biofouling analysis of *Saccharina latissima*. The frond was divided into three parts: the distal, middle and proximal region. b) Standardised pattern for point-sampling analyses of biofouling.

3. Results

3.1. Environmental conditions

The temperature slowly increased at all sites and both depths until June, and then increased more rapidly until August (Fig. 4). The semi-offshore site had a slightly higher temperature compared to the inshore site (averaging $+0.4 \pm 0.2^\circ\text{C}$ at 3 m depth and $+0.25 \pm 0.2$ at 8 m) and the fjord site (averaging $+0.8 \pm 0.2$ at 3 depth and $+0.7 \pm 0.2^\circ\text{C}$ at 8 m). The salinity was quite constant at both depths throughout the five first months of the study (Fig. 4), but after July the readings at the semi-offshore site increased, while they dropped at the fjord site. The ambient nitrate levels were overall slightly higher at the semi-offshore site, and lowest at the fjord site (Fig. 5). The nitrate levels dropped rapidly at the end of April, coinciding with the spring bloom. The drop occurred faster, and earlier at the fjord site compared to the two other sites, as was expected due to less mixing of the water masses. The nitrate values were similar between the two depths studied.

3.2. Kelp biomass

The kelp biomass initially increased slowly from February to May (Fig. 6), and thereafter increased rapidly until August. In August, biofouling added to the total biomass, especially on the semi-offshore site with the highest amount of biofouling cover. The highest weight pre-fouling was 15.0 ± 0.3 kg per meter of rope at 3 m at the semi-offshore site on 15 July. The inshore site had the lowest biomass growth from June onwards. The inshore site experienced impact from a storm in May that caused some loss of biomass. This is visualised by the flat portions of the curves for the inshore site.

In the Linear Mixed-Effects Model of kelp biomass as a function of the fixed factors depth and environmental factors, currents and nitrate

were omitted due to non-significant contributions shown in the analysis. The AIC comparison of the models including and excluding the fixed factors in question, significantly improved the model (Table 1). Model comparisons showed that depth had the highest impact on kelp biomass (likelihood ratio test: $\chi^2 = 57.924$, df = 1, p value < .001), thereafter temperature (likelihood ratio test: $\chi^2 = 25.813$, df = 1, p value < .001), and salinity (likelihood ratio test: $\chi^2 = 6.611$, df = 1, p value < .05) impacted the seaweed biomass in declining degree.

Model comparisons with currents did not show any impact (likelihood ratio test: $\chi^2 = 0.450$, df = 1, p value = .502), neither did nitrate (likelihood ratio test: $\chi^2 = 0.257$, df = 1, p value = .613).

3.3. Biofouling

No epibionts were observed at any of the sites between February and late June. The first colonies of epibionts were observed in field, but not analysed, at all sites in mid-July. The semi-offshore site had the highest fouling with a coverage of $61.0 \pm 6.5\%$ (mean of 3 frames \pm SE) at 3 m depth and $59.0 \pm 9.5\%$ at 8 m depth (Fig. 7a). The fjord site had $15.7 \pm 2.7\%$ at 3 m depth and $7.0 \pm 4.7\%$ at 8 m. The inshore site had $14.8 \pm 4.2\%$ at 3 m depth and $13.3 \pm 0.87\%$ at 8 m.

Three major biofouling taxa (Fig. 8) were identified on the fronds of *S. latissima*: the bryozoan, *Membranipora membranacea* (Linnaeus, 1767); the hydroid, *Obelia geniculata* (Linnaeus, 1758); and a filamentous brown alga, *Ectocarpus* sp. In addition, the blue mussel, *Mytilus edulis*, and the gastropod *Lacuna vincta* were occasionally observed on the kelp fronds, but as these organisms did not cover any of the points sampled in the image processing they were omitted from the analysis. The composition of species covering the fronds varied between the three sites (Fig. 7b). The frond community at the fjord site was dominated by the hydroid *O. geniculata*, followed by *Ectocarpus* sp. and only $0.67 \pm 0.16\%$ of the fronds were covered by *M. membranacea*. At the

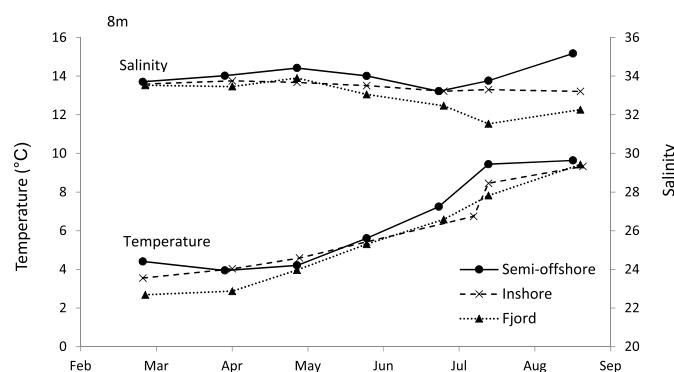
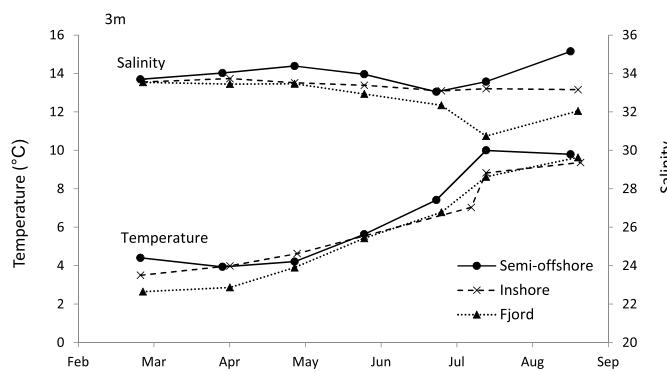


Fig. 4. Temperature and salinity measured at 3 and 8 m depth at the semi-offshore site (marked with ●), the inshore site (marked with X), and the fjord site (marked with ▲).

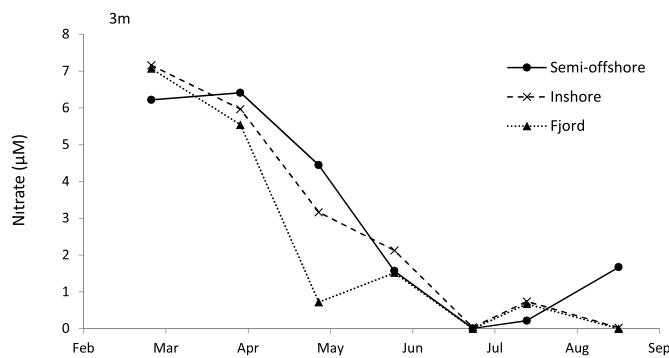


Fig. 5. Nitrate concentration measured at 3 and 8 m depth at the semi-offshore site (marked with ●), the inshore site (marked with X), and the fjord site (marked with ▲).

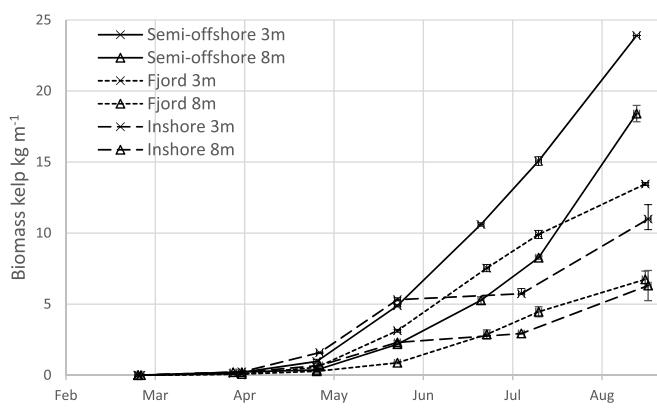
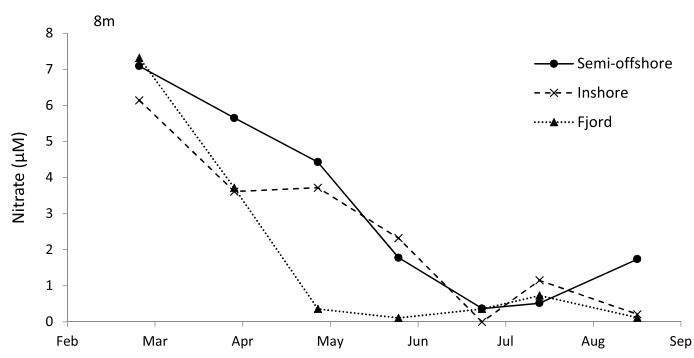


Fig. 6. Kelp biomass in kg per meter of rope on each sampling date. All three sites are shown at 3 m (marked with X) and 8 m depth (marked with Δ). The error bars show the standard error.

inshore site the frond community consisted of *O. geniculata* and some *M. membranacea*. The frond community at the semi-offshore site was dominated by *M. membranacea* and had no registered *O. geniculata* and very little *Ectocarpus* sp.

There was a clear trend for increased blade area fouled towards the older, distal parts of the kelp fronds (Fig. 7c). The largest differences of biofouling cover on proximal and distal regions were seen at the inshore and fjord sites, where the inshore site had $27.0 \pm 3.2\%$ at the distal ends and $6.3 \pm 2.6\%$ at the proximal parts, and the fjord site had $21.1 \pm 4.5\%$ at the distal and $4.0 \pm 2.1\%$ at the proximal parts. Total biofouling was modelled with GLMM as a function of the fixed factors temperature, blade age and temperature. Salinity and depth were omitted due to non-significant contributions. An AIC comparison of the full model, with reduced models excluding factors in question, showed a significant difference between models (Table 2). Model comparisons showed that temperature (likelihood ratio test: $\chi^2 = 13.292$, df = 1, p value < .001), blade age (likelihood ratio test: $\chi^2 = 124.83$, df = 2, p value < .001), and currents (likelihood ratio test: $\chi^2 = 8.89$, df = 1, p value < .01), had a significant impact on total biofouling. Whereas, depth (likelihood ratio test: $\chi^2 = 0.0069$, df = 1, p value = .934), and salinity (likelihood ratio test: $\chi^2 = 0.45$, df = 1, p value = .5039), did



not. R^2 showed that temperature had the highest influence on total biofouling of the fixed factors.

4. Discussion

4.1. Kelp biomass

Saccharina latissima was successfully cultivated at all three sites. Before the onset of heavy fouling we registered at 3 m depth an average biomass yield per meter rope of 5.7 kg at the inshore site, 11.0 kg at the fjord site, and 15.1 kg at the semi-offshore site. In comparison, Druehl et al. (1988) registered 8 kg m^{-1} cultivation rope, Bruhn et al. (2016) 0.51 kg m^{-1} , and Peteiro and Freire (2013b) registered 16 kg m^{-1} .

Our results show that elevated sea temperatures, cultivation at shallower waters (3 versus 8 m), and increased salinity had a positive correlation with higher kelp biomass in Arctic waters, while currents and nitrate did not have any significant impact on the kelp biomass in our field study. Mols-Mortensen et al. (2017) conducted a similar field study at the Faroe Islands. They did not find a relationship between current exposure and *S. latissima* biomass yield either. Gerard (1982) found that current speeds of 2.5 cm s^{-1} were sufficient to saturate the nutrient uptake of the macroalgae *Macrocystis pyrifera*. Thus current speeds are within the measured values at all our sites.

4.2. Effects of environmental variables on biofouling

The biofouling model showed that temperature had the highest influence on total cover of biofouling. There are many other studies (Saunders and Metaxas, 2007, 2009a; Saunders et al., 2010; Scheibling and Gagnon, 2009) showing the correlation between elevated sea temperatures with a higher degree of fouling by *M. membranacea*. A model developed by Saunders et al. (2010) predicted that a temperature difference of 1°C and 2°C will increase the coverage by *M. membranacea* on wild kelp beds by a factor of 9 and 62, respectively. At the semi-offshore site in this study, the average daily temperature was 0.8°C higher than at the fjord site, but the coverage by *M. membranacea* at the semi-offshore site was 64 times as high as at the fjord site. Hence the temperature could have had some impact, but is most likely not the only causative factor involved in increased epibionts at the semi-offshore site. At the same time, this study only measured ambient

Table 1

AIC model comparison and associated R^2 values for the effect on kelp biomass with and without depth, salinity and temperature as fixed factors.

Rank	Formula	K (parameters)	AIC	ΔAIC	R2
1	$\log(\text{Biomass} + 1) \sim \text{Depth} + \text{Salinity} + \text{Temp} + (1 \text{Date}) + (1 \text{Site})$	7	44.39	0.0	0.853
2	$\log(\text{Biomass} + 1) \sim \text{Depth} + \text{Temp} + (1 \text{Date}) + (1 \text{Site})$	6	48.69	4.3	0.874
3	$\log(\text{Biomass} + 1) \sim \text{Depth} + \text{Salinity} + (1 \text{Date}) + (1 \text{Site})$	6	67.89	23.5	0.058
4	$\log(\text{Biomass} + 1) \sim \text{Salinity} + \text{Temp} + (1 \text{Date}) + (1 \text{Site})$	6	100.00	55.6	0.859

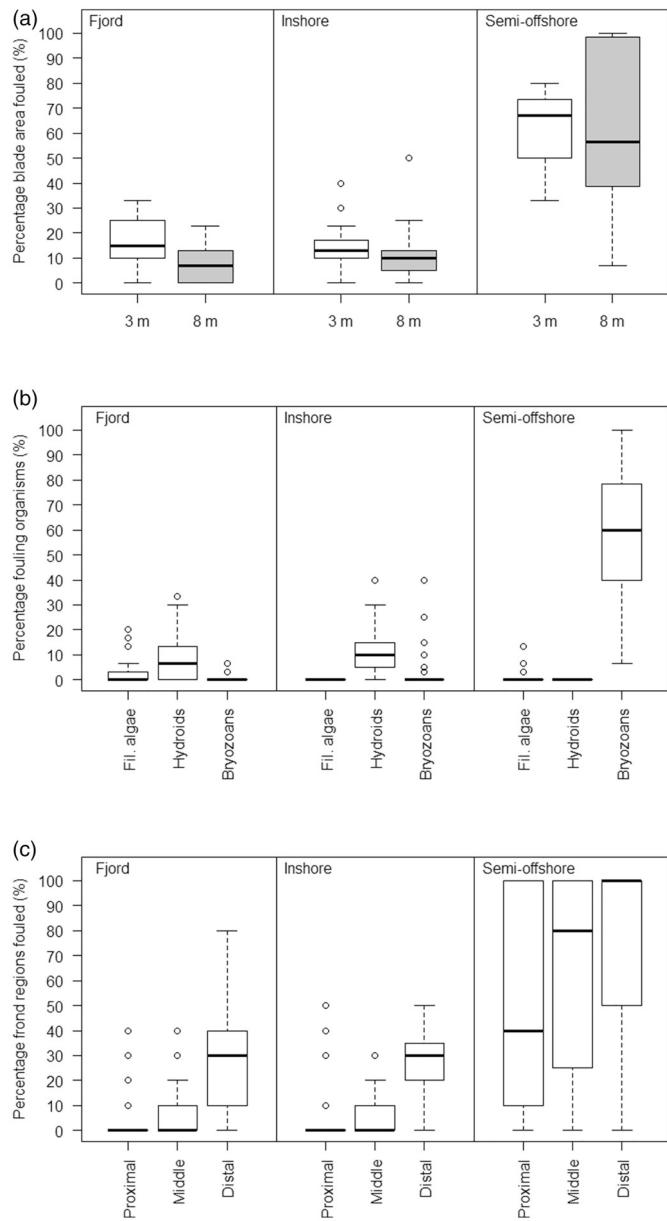


Fig. 7. a–c) Epibionts on *S. latissima* at three sites (fjord, inshore and semi-offshore) studied in late August 2014; a) Percentage of whole kelp fronds covered by epibionts at two depths, 3 and 8 m. b) Percentage of whole kelp fronds covered by epibionts, separated by taxon. c) Percentage of epibionts on the kelp fronds divided into three parts: proximal (younger tissue)-, middle- and distal (older tissue) regions. The box plots show the median percentages (the horizontal lines within the boxes), the 25th and the 75th percentiles (top and bottom of the boxes) and the interquartile range of 3/2 (whiskers) separating the main body of the data from the outlying values (points). In b–c) the two depths are pooled.

temperatures between February and August, whereas the life cycles of the epibionts are affected by the physical environment throughout the year.

Salinity did not have any significant impact on the cover by biofouling. The impact of varying salinity on *M. membranacea* is not well studied, but it is a eurohaline species that can be found at salinity levels as low as 20 psu in fjords (personal observation Christie).

The semi-offshore site, which was most exposed to currents, had significantly higher biofouling cover in comparison with the two more sheltered sites. The same site also had the highest kelp biomass. This difference was significant despite all sites being located within a

distance of 50 km from each other.

The biofouling model showed that increased currents had a significantly positive relationship with higher biofouling cover. In contrast, Peteiro and Freire (2013a) found more biofouling on cultivated *S. latissima* and *Undaria pinnatifida* on a less current-exposed site compared to a higher current-exposed site in Spain. Also, Mols-Mortensen et al. (2017) observed more heavily fouled individuals on *S. latissima* cultivated at wave exposed and sheltered sites than at a site exposed to high current velocities at the Faroe Islands in 2015. Among wild sugar kelp in Norway, Moy and Christie (2012) found more fouling at the sheltered sites. In natural kelp beds, the interaction between kelps, waves and bottom-substrate may act differently than in kelps cultivated in the water column without the possibilities to interact with a bottom-substrate. A field study on the bryozoan *Membranipora serrilamella* (Arkema, 2009), a closely related specie of *M. membranacea* (Schwaninger, 2008), showed that sites with intermediate ambient flow speed ($10\text{--}12 \text{ cm s}^{-1}$) gave the highest feeding success, and that both flow speeds $< 5 \text{ cm s}^{-1}$ and $> 20 \text{ cm s}^{-1}$ had the lowest feeding success. The feeding success was positively correlated with percent cover. In this perspective, the conditions in the fjord site would offer the best feeding base to *M. membranacea*, but only a few colonies of this specie were registered at this site.

In this study we did not find a correlation between biofouling cover and depth, but we saw a non-significant trend of less biofouling at 8 m compared to 3 m. Earlier studies on depth dependencies indicated decreased fouling on cultivated kelp with increasing water depth from 1 to 15 m (Førde et al., 2015) while on wild kelp fouling increased with depth (Saunders and Metaxas, 2007).

4.3. Species composition of frond community

S. latissima was colonized by the bryozoan *M. membranacea*, the hydroid *O. geniculata* and filamentous brown algae as the major fouling organisms, with prevalence and abundances varying between the three study sites. The method used in this study registered only sessile organisms. The sessile species fouling the kelp fronds may have different impacts on the kelp (Hepburn et al., 2006). *M. membranacea*, which has a sheet-like growth, forms a barrier for nutrients and light between the kelp and the surrounding water (Andersen, 2013). The hard calcium carbonate skeleton reduces flexibility and increases brittleness on the kelp fronds, potentially causing substantial loss of algal biomass up to 100% (Krumhansl et al., 2011; Skjermo et al., 2014). Epibionts with an erect growth form, such as *O. geniculata*, are less likely to have such severe effects (Hepburn et al., 2006). *O. geniculata* is also protected by a calcium carbonate shell, but the stoloniferous growth form usually provides no barrier for nutrient uptake on the host (Hepburn et al., 2006). The filamentous brown algae were mostly found on the edge of the kelp fronds, associated with low coverage. Therefore, it is expected that filamentous brown algae here only had a slight impact on the availability of light and nutrients for the kelp. A high occurrence of bryozoans at the semi-offshore site may have had a high impact on the kelp biomass, whereas the relatively high occurrence of hydroids in the fjord site may not have had the same detrimental effect, possibly allowing for an extended cultivation season in aquaculture systems. The fragile state of the bryozoan covered kelp individuals at the semi-offshore site, as well as the storm event at the inshore site, resulted in some loss of the distal ends from several individuals. This may have affected the amount of filamentous algae at these sites.

The amount of species found on the kelp blades in this study were lower than in some other studies. Walls et al. (2016) found 32 species (both sessile and mobile species) inhabiting cultivated *Alaria esculenta* in Ireland. Sogn Andersen et al. (2011) observed blue mussels, sponges, filamentous algae, bryozoans (both *M. membranacea* and *Electra pilosa*) and a high number of the vase tunicate *Ciona intestinalis* on wild *S. latissima* in Skagerak, Norway. Rolin et al. (2017) found three main epibionts on cultivated *S. latissima* in the Shetland Islands, and in their



Fig. 8. The three main taxa of epibionts found at the three locations studied in northern Norway. Yellow arrows (left picture) shows examples of the bryozoan *Membranipora membranacea*, green arrow (middle) show filamentous algae, *Ectocarpus* sp., and red arrow (right picture) point at colonies of the hydroid, *Obelia geniculata*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study the kelp was highly fouled by bryozoans, but they also had a high occurrence of tunicates.

4.4. Total biofouling on frond area

The highest abundances of biofouling organisms was found on the distal ends of the blades. As the proximal regions are the growth zone of kelps, and the distal ends have the oldest tissue, the variation in biofouling cover are most likely an effect of accumulation and growth of epibionts over time (Jennings and Steinberg, 1997). The place of fouling may be relevant for regrowth potential. If the main occurrence of fouling occurs at the distal tips these can be removed, either naturally or through cutting, enabling new, clean kelp tissue to grow (Rolin et al., 2017). In this study, two of the locations, the fjord and the inshore site, had very little occurrence of biofouling on the meristematic region. Further studies may reveal whether cutting of the older blade parts would result in regrowth of clean biomass.

4.5. Latitudinal differences

In *S. latissima* cultivated at the southwest coast of Norway in Lysefjord ($59^{\circ} 0' N$, $6^{\circ} 16' E$) in 2012 (Lüning and Mortensen, 2015) epibionts were first recorded in early May. By 31 May approximately 50% of the blade area was fouled, and by 22 August the majority of the blades had disappeared. On *S. latissima* cultivated in central Norway at Frøya ($63^{\circ} 42' N$, $8^{\circ} 51' E$) and Reksta ($61^{\circ} 34' N$, $4^{\circ} 48' E$) in 2013 the first epibionts were observed in mid-June, followed by a rapid increase of biofouling (Førde et al., 2015). At the end of July the biofouling covered around 75%, and in the end of August many of the blades were degraded and lost. Based on this observation, the authors suggest that cultivation of *S. latissima* is impractical during July and August in that part of Norway. In Galicia ($43^{\circ} 22' N$, $8^{\circ} 15' W$ and $43^{\circ} 25' N$, $8^{\circ} 16' W$), Spain, Peteiro and Freire (2013a) estimated the kelp blades of *U. pinnatifida* and *S. latissima* to be 33–53% covered by fouling, depending on site and kelp species, as early as on the 26 April. At present, common

practice is to harvest farmed sugar kelp in central Norway before the end of May for the food market (Seaweed farming industry, personal communication), to avoid any biofouling. The consequence of this is that farmers cannot utilize the favourable light conditions with related biomass gain that would be possible during June, July and August.

However, we hardly observed any fouling before August at either of the sites, suggesting that harvesting of kelp biomass with little or no epibionts can be successful during the late summer growth period in the High North, particularly at the fjord and inshore sites in this study. North of the Arctic Circle, farmers can therefore take advantage of the summer season with 24 h daylight at these high latitudes. Yet the current study also shows a large variation in fouling on kelp at sites which are located < 50 km apart from each other. Both when it comes to biomass yield and biofouling, our results emphasize the importance of thorough site selection and pre-testing using small scale farms, before establishing large scale kelp farming operations.

5. Conclusions

All sites in this study had promising biomass yields, showing that cultivation of *S. latissima* is favourable in Northern Norway. Biomass was positively correlated with elevated sea temperatures, higher salinity and rather shallow depths. The variation of spatial patterns in abundance and in taxonomic groups of epibionts, fouling cultivated *S. latissima*, was surprisingly large between sites within the same geographical region. Such variation in fouling can affect the period for harvesting of cultivated kelp by several month, depending on end-use. The highest coverage of fouling organisms was found on the oldest parts of the kelp blades, and there was no significant difference in biofouling with regard to coverage between the two cultivation depths. It is of large interest to further investigate factors influencing the life cycle of epibionts, in particular the highly destructive *M. membranacea*. With regard to differences in productivity caused by extended growth periods and destructive effects from fouling, our study gives evidence for the importance of thorough site selection for kelp farms, even for sites in

Table 2

AIC model comparison and associated R² values for total biofouling with and without the fixed factors; temperature, currents and blade age.

Rank	Formula	K (parameters)	AIC	ΔAIC	R2
1	Total biofouling~Temperature + Currents + Bladeage + (1 Site/Frame)	7	1692.47	0.00	0.154
2	Total biofouling~Temperature + Bladeage + (1 Site/Frame)	6	1699.35	6.88	0.128
3	Total biofouling~Currents + Bladeage + (1 Site/Frame)	6	1703.75	11.28	0.101
4	Total biofouling~Temperature + Currents + (1 Site/Frame)	5	1813.27	120.80	0.129

the same geographical region.

Ongoing studies indicate that our results also can be applied to other regions, showing that fouling, both in abundance and species composition, has large spatial variation and fundamentally effects the productivity of kelp farms.

Acknowledgements

The authors would like to thank Professor Bodil Bluhm and Professor Malcolm Jobling for constructive comments to the manuscript, Professor Nigel Gilles Yoccoz and Dr. Martin Biuw for valuable input on the statistical work. Lerøy Aurora is thanked for deploying the rigs. We would also like to thank the anonymous reviewer who contributed with valuable and constructive input, improving this manuscript substantially. This research was supported by projects from Troms County (RDA12/234 “Pilotstudie på bioenergy fra tare”) and from the Research Council of Norway (MACROSEA, No. 254883/E40).

Conflicts of interest

None.

References

- Andersen, G.S., 2013. Growth, survival and reproduction in the kelp *Saccharina latissima*: Seasonal patterns and epiphytism. Dissertation. Department of biosciences, University of Oslo, Oslo.
- Andersen, G.S., Christie, H., Moy, F.E., 2019. In a squeeze: Epibiosis may affect the distribution of kelp forests, *Ecology and evolution* 9 (5), 2883. <https://doi.org/10.1002/ece3.4967>.
- Araújo, R., Assis, J., Aguilar, R., Airoldi, L., Bárbara, I., Bartsch, I., Derrien-Courtel, S., 2016. Status, trends and drivers of kelp forests in Europe: an expert assessment. *Biodivers. Conserv.* 25 (7), 1319–1348.
- Arkema, K.K., 2009. Flow-mediated feeding in the field: consequences for the performance and abundance of a sessile marine invertebrate. *Mar. Ecol. Prog. Ser.* 388, 207–220.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bruhn, A., Torring, D.B., Thomsen, M., Canal-Vergés, P., Nielsen, M.M., Rasmussen, M.B., ... Petersen, J.K., 2016. Impact of environmental conditions on biomass yield, quality, and bio-mitigation capacity of *Saccharina latissima*. *Aquacult. Environ. Interact.* 8, 619–636.
- Christie, H., 1980. Methods for ecological monitoring: biological interactions in a rocky subtidal community. *Helgoländer Meeresun.* 33 (1), 473.
- Dixon, J., Schroeter, S.C., Kastendiek, J., 1981. Effects of the encrusting bryozoan, *Membranipora membranacea*, on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). *J. Phycol.* 17 (4), 341–345.
- Druehl, L., Baird, R., Lindwall, A., Lloyd, K., Pakula, S., 1988. Longline cultivation of some Laminariaceae in British Columbia, Canada. *Aquac. Res.* 19 (3), 253–263.
- Edwards, M., Watson, L., 2011. Aquaculture explained no. 26 "Cultivating Laminaria digitata".
- Forbord, S., Skjermo, J., Arff, J., Handå, A., Reitan, K.I., Bjerregaard, R., Lüning, K., 2012. Development of *Saccharina latissima* (Phaeophyceae) kelp hatcheries with year-round production of zoospores and juvenile sporophytes on culture ropes for kelp aquaculture. *J. Appl. Phycol.* 24 (3), 393–399.
- Forde, H., Forbord, S., Handå, A., Fossberg, J., Arff, J., Johnsen, G., Reitan, K.I., 2015. Development of bryozoan fouling on cultivated kelp (*Saccharina latissima*) in Norway. *J. Appl. Phycol.* 28 (2), 1225–1234.
- Gendron, L., Gauthier, P., Savard, G., 2007. Expériences préliminaires de culture de l'algue brune *Laminaria longicurvis* en laboratoire et en mer au large de Paspébiac (Québec) en 2006: Direction régionale des sciences, pêches et océans Canada. Institut Maurice-Lamontagne.
- Gerard, V., 1982. In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 69 (1), 51–54.
- Hartig, F., 2018. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. Retrieved from. <https://CRAN.R-project.org/package=DHARMA>.
- Hepburn, C.D., Hurd, C.L., Frew, R.D., 2006. Colony structure and seasonal differences in light and nitrogen modify the impact of sessile epifauna on the giant kelp *Macrocystis pyrifera* (L.) C Agardh. *Hydrobiologia* 560 (1), 373–384.
- Jaeger, B., 2017. r2glmm: Computes R Squared for Mixed (Multilevel) Models: R Package Version 0.1.2. Retrieved from. <https://CRAN.R-project.org/package=r2glmm>.
- Jennings, J., Steinberg, P., 1997. Phlorotannins versus other factors affecting epiphyte abundance on the kelp *Ecklonia radiata*. *Oecologia* 109 (3), 461–473.
- Krumhansl, K.A., Lee, J.M., Scheibling, R.E., 2011. Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. *J. Exp. Mar. Biol. Ecol.* 407 (1), 12–18.
- Lüning, K., Mortensen, L., 2015. European aquaculture of sugar kelp (*Saccharina latissima*) for food industries: iodine content and epiphytic animals as major problems. *Bot. Mar.* 58 (6), 449–455.
- Marinho, G.S., Holdt, S.L., Birkeland, M.J., Angelidaki, I., 2015a. Commercial cultivation and bioremediation potential of sugar kelp, *Saccharina latissima*, in Danish waters. *J. Appl. Phycol.* 1–11.
- Marinho, G.S., Holdt, S.L., Angelidaki, I., 2015b. Seasonal variations in the amino acid profile and protein nutritional value of *Saccharina latissima* cultivated in a commercial IMTA system. *J. Appl. Phycol.* 27 (5), 1991–2000.
- Mols-Mortensen, A., Ortind, E.A.G., Jacobsen, C., Holdt, S.L., 2017. Variation in growth, yield and protein concentration in *Saccharina latissima* (Laminariales, Phaeophyceae) cultivated with different wave and current exposures in the Faroe Islands. *J. Appl. Phycol.* 29 (5), 2277–2286. <https://doi.org/10.1007/s10811-017-1169-4>.
- Moy, F.E., Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Mar. Biol. Res.* 8 (4), 309–321.
- Norderhaug, K.M., Christie, H.C., 2009. Sea urchin grazing and kelp re-vegetation in the NE Atlantic. *Mar. Biol. Res.* 5 (6), 515–528.
- Peteiro, C., Freire, Ó., 2013a. Epiphytism on blades of the edible kelps *Undaria pinnatifida* and *Saccharina latissima* farmed under different abiotic conditions. *J. World Aquacult. Soc.* 44 (5), 706–715.
- Peteiro, C., Freire, Ó., 2013b. Biomass yield and morphological features of the seaweed *Saccharina latissima* cultivated at two different sites in a coastal bay in the Atlantic coast of Spain. *J. Appl. Phycol.* 25 (1), 205–213.
- R Core Team, 2018. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria Retrieved from. <https://www.R-project.org/>.
- Rød, K.K., 2012. Sori disinfection in cultivation of *Saccharina latissima*: Evaluation of chemical treatments against diatom contamination.
- Rolin, C., Inkster, R., Laing, J., McEvoy, L., 2017. Regrowth and biofouling in two species of cultivated kelp in the Shetland Islands, UK. *J. Appl. Phycol.* 1–11.
- RStudio Team, 2016. RStudio: Integrated Development for R. RStudio, Inc, Boston, MA Retrieved from. <http://www.rstudio.com/>.
- Saunders, M., Metaxas, A., 2007. Temperature explains settlement patterns of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 344, 95–106.
- Saunders, M., Metaxas, A., 2009a. Effects of temperature, size, and food on the growth of *Membranipora membranacea* in laboratory and field studies. *Mar. Biol.* 156 (11), 2267–2276.
- Saunders, M., Metaxas, A., 2009b. Population dynamics of a nonindigenous epiphytic bryozoan *Membranipora membranacea* in the western North Atlantic: effects of kelp substrate. *Aquat. Biol.* 8 (1), 83–94.
- Saunders, M., Metaxas, A., Filgueira, R., 2010. Implications of warming temperatures for population outbreaks of a nonindigenous species (*Membranipora membranacea*, Bryozoa) in rocky subtidal ecosystems. *Limnol. Oceanogr.* 55 (4), 1627–1642.
- Scheibling, R.E., Gagnon, P., 2009. Temperature-mediated outbreak dynamics of the invasive bryozoan *Membranipora membranacea* in Nova Scotian kelp beds. *Mar. Ecol. Prog. Ser.* 390, 1–13.
- Schwaninger, H.R., 2008. Global mitochondrial DNA phylogeography and biogeographic history of the antitropically and longitudinally disjunct marine bryozoan *Membranipora membranacea* L. (Cheilostomata): another cryptic marine sibling species complex? *Mol. Phylogenet. Evol.* 49 (3), 893–908.
- Skjermo, J., Aasen, I.M., Arff, J., Broch, O.J., Carvajal, A., Christie, H., Rustad, T., 2014. A new Norwegian bioeconomy based on cultivation and processing of seaweeds: opportunities and R&D needs. SINTEF Report A 25981 (46pp).
- Sogn Andersen, G., Steen, H., Christie, H., Fredriksen, S., Moy, F.E., 2011. Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway: implications for forest recovery. *J. Mar. Biol.* 2011.
- Stévant, P., Rebours, C., Chapman, A., 2017. Seaweed aquaculture in Norway: recent industrial developments and future perspectives. *Aquac. Int.* 1–18.
- Wahl, M., 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar. Ecol. Prog. Ser.* 58, 175–189.
- Walls, A., Kennedy, R., Fitzgerald, R., Blight, A., Johnson, M., Edwards, M., 2016. Potential novel habitat created by holdfasts from cultivated *Laminaria digitata*: assessing the macroinvertebrate assemblages. *Aquacult. Environ. Interact.* 8, 157–169.
- WoRMS, E.B., 2017. World Record of Marine Species. Retrieved from. <http://www.marinespecies.org/>.