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Development of bryozoan fouling on cultivated kelp (*Saccharina latissima*) in Norway

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Abstract Biofouling on cultivated kelp in open sea conditions is a challenge when fouling species such as the encrusting bryozoans *Membranipora membranacea* and *Electra pilosa* develop colonies that cover the surface of the kelp lamina. The bryozoan colonies make the flexible lamina brittle and susceptible to breakage and reduce the commercial value of the biomass for both human consumption and industrial applications. The development of the bryozoan fouling on cultivated *Saccharina latissima* in temperate coastal waters was studied at two locations in Norway from April to September. The time of settling and development of colonies of *M. membranacea* and *E. pilosa* were characterized. Sampling of bryozoan larvae abundance at the cultivation locations showed that the bryozoan colonies settled on the cultivated kelp in mid-June at both locations, followed by a rapid colony growth during late June and July. In August and September, the kelp was highly degraded by the bryozoan coverage and highly subjected to breakage of the lamina. *Membranipora membranacea* was the most prevailing of the two species. Although abundant at all cultivation depths, the results showed a decrease in bryozoan coverage with increasing depth. From a commercial point of view, *S. latissima* deployed in temperate Norwegian coastal waters in winter should be harvested in early June to avoid the negative impact from bryozoan fouling.

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Introduction

Currently, almost 100 % of the seaweed industry in Norway is based on the harvest of natural kelp beds. However, over the last few years, the interest for the cultivation of seaweed has increased, and several companies have got permits to cultivate seaweed. An attractive candidate for Norwegian seaweed cultivation is the brown kelp *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl, and G.W. Saunders, mainly because of its rapid growth and high content of polysaccharides, as well as being native and adapted to Norwegian coastal waters. The *S. latissima* sporophyte has a high growth rate from late winter to spring, whereafter the rate declines during the summer (Sjøtun 1993). Similar to other kelp species, the smooth, flexible, and wide lamina of *S. latissima* provide substrate and an excellent habitat for a variety of other organisms, both sessile and mobile (Bartsch et al. 2008; Christie et al. 2009). While this is an important ecosystem service in natural kelp beds, it causes a major challenge for the seaweed industry in terms of encrusting epifauna, which may lead to necrosis and subsequently loss of biomass (Fletcher 1995; Forbord et al. 2012; Peteiro and Freire 2013). For example, cultivating experiences with the kelp *Saccharina longicruris* in Canada have shown bryozoan colonization on the lamina and stipe, which reduced the lamina by 68 % (Gendron and Tamigneaux 2008), and the cultivation of *S. latissima* in Norway has shown best growth from February to June followed by heavily epigrowth during the summer (Forbord et al. 2012; Handå et al. 2013). It is therefore often advised to harvest the crops

before the onset of fouling to obtain the best product quality and to prevent loss of valuable biomass.

Encrusting fouling may damage the flexible nature of kelp, which could lead to canopy loss (Dixon et al. 1981). In a mechanical and histological study, the sporophytes of *S. longicruis* encrusted with the bryozoan *Membranipora membranacea* were shown to have increased lesions of the upper epidermal cells, which in turn led to a loss of strength and extensibility of the kelp blade (Krumhansl et al. 2011). Saunders and Metaxas have studied the impact of the introduced *M. membranacea* in the western North Atlantic, where the species is set in connection with a significant loss of kelp canopy in the Nova Scotia region (Saunders and Metaxas 2008) and shifts in population dynamics (Saunders and Metaxas 2009). Other negative impacts of the encrusting biofouling are inhibition of reproduction by preventing spore release (Saier and Chapman 2005), creating a barrier to nutrient uptake (Hurd et al. 2000), and inhibition of photosynthesis by blocking the surface area of the frond and reducing pigmentation (Hepburn et al. 2006). Reduction in the population of natural beds of *S. latissima* in Skagerrak, Norway, has also been linked to heavily fouling, with reduced access to light and disrupting the natural life cycle of the species (Andersen et al. 2011).

Colonies of the filter feeding bryozoans are one of the most conspicuous epifauna fouling on seaweeds (Ryland 1962). They arise from a bryozoan ancestrula cyphonaut larva that settles on the kelp substrate. Two common biofouling and kelp encrusting bryozoan species in the North-East Atlantic Ocean are *Membranipora membranacea* (Linnaeus) and *Electra pilosa* (Linnaeus), both from the class Gymnolaemata and Cheilostomata order (Hayward and Ryland 1995). The walls that enclose each individual zooid (zoecia) are lightly calcified, and together, the zooids create extensive, highly organized, mat-like colonies (Seed and O'Connor 1981).

Membranipora membranacea has a cyphonaut larval stage that may remain in the water column for several weeks or months before they settle on a substrate during the early spring to early summer (Ryland and Stebbing 1971). The triangular larva can be found in North Atlantic coastal plankton samples from February to November, with a peak between June and August (Ryland 1965). *Membranipora membranacea* prefers lamina of kelp as a substrate, especially species of *Laminaria* (Hayward and Ryland 1995). The cyphonaut larvae of *M. membranacea* are shown to be highly locomotive when exploring a suitable substrate and are able to move around in all directions, but normally possess an upstream motion (Abelson 1997). This ability may influence the positioning of settlement at the kelp frond, which is often at the base of the lamina (Ryland and Stebbing 1971), and thus upstream when the kelp is flowing with the current. The cyphonaut larvae of *E. pilosa* are mainly produced in late summer and remain present in the plankton throughout the year (Ryland 1965). The asexually produced colonies have a characteristic star-like shape and occur on almost any substratum (Hayward and Ryland 1995).

The objectives of the present study were to describe the development and the impact of bryozoan colonies on cultivated macroalgae *S. latissima* during the cultivation period by (1) taking regular sampling of cultivated *S. latissima* at two locations during the cultivation period in the sea and calculating the area coverage of bryozoan colonies at the different sampling dates; (2) taking measurements of coverage at different cultivation depths to investigate the depth dependencies of the bryozoan growth; and (3) taking regular plankton sampling and semi-quantitative analysis of cyphonaut larvae abundance during the cultivation period to investigate the effects of relative larvae abundance.

Materials and methods

The cultivation location and periods

The cultivation of *S. latissima* and plankton sampling for the detection of bryozoan larvae were carried out at two different locations in Norway, one in Mid-Norway and one close to a salmon farm in Western Norway (Fig. 1). The purposes for choosing the two different locations were to discover geographical differences in fouling during the growth season. The location for sampling in Mid-Norway was situated at Seaweed Energy Solutions AS (SES) cultivation site on the island of Frøya in Sør-Trøndelag county (Taraskjæra, 63° 42′ N, 08° 51′ E, Fig. 1). The SES location was semi-exposed, sheltered from southerly and westerly wind directions, but exposed to north-easterly wind directions. The average current speed (28 days) at 6-m depth from March 2012 was 9.4 cm s^{-1}, with the main current direction of 28° (north-east, measured by SES). The depth below the seaweed farm ranged from 30 to 50 m.

The location in Western Norway was at one of Marine Harvest Norway AS fish farms by the island of Reksta in Sogn og Fjordane county (Flåtegrunnen, 61° 34′ N, 04° 48′ E). The fish farm consisted of seven circular net pens in a single row east-westerly direction. Salmon were farmed in six of the net pens, and the seaweed was cultivated in an empty fish cage located at the eastern end of the farm. The main current direction at 5-m depth was measured by the Institute of Marine Research to be 90–110° (east) and 210–230° (southwest), depending on the tidal cycle, with a current speed of 2.4 cm s^{-1} in April 2013, and 8.6 cm s^{-1} in September 2013. The farm was situated above a steep slope, and the depth below the farm ranged from 75 to 200 m.

The sampling period at both locations lasted from April to September 2013 as this in earlier experiments was shown to be the ideal period for growth in Norway for *S. latissima* (Handå

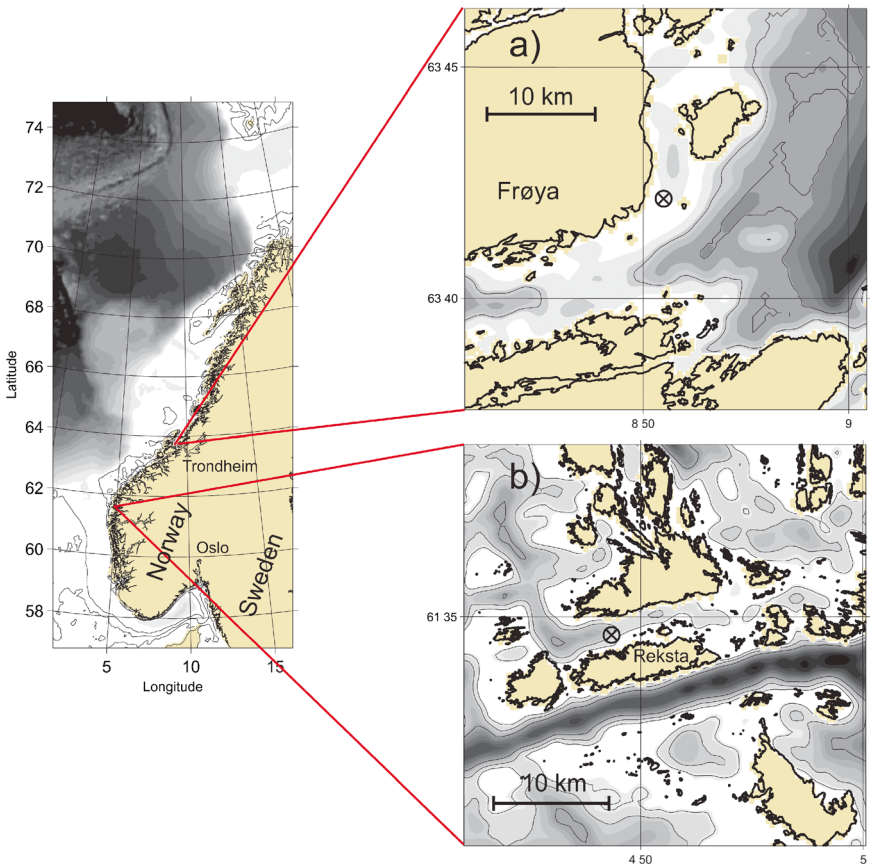

Fig. 1 Map of the two sampling locations at Frøya and Reksta in Norway

et al. 2013) and the period where most of the fouling occurs (Forbord et al. 2012). The sampling dates are summarized in Table 1 together with the total number individual samples of *S. latissima* and zooplankton samples for each sampling date.

Sample collection

The juvenile sporophytes deployed at Frøya were produced by inducing zoospores from sporophytes collected from wild populations near the deployment site according to the method

Table 1 Overview of sampling dates and number of seaweed and zooplankton samples at (a) Frøya and (b) Reksta location

(a) Sampling no.	Date	Total number of individual *S. latissima*			Total number of plankton samples
		3 m	8 m	15 m	
1	30.04.13	6	6	6	2
2	14.05.13	6	6	3	6
3	29.05.13	12	12	12	9
4	18.06.13	11	12	9	4
5	27.06.13	12	12	9	6
6	12.07.13	12	8	9	6
7	24.07.13	12	12	9	6
8	29.08.13	11	12	6	6
(b) Sampling no.	Date	Total number of individual *S. latissima*			Total number of zooplankton samples
		2 m	5 m	7 m	
1	11.04.13	12	12	12	0
2	10.06.13	12	12	12	6
3	07.08.13	12	12	12	6
4	12.09.13	6	7	5	6

used in Forbord et al. (2012). The juvenile sporophytes were deployed on frames hanging from longlines at depths of 3, 8, and 15 m. Three individuals were randomly chosen from each frame at depths of 3, 8, and 15 m (Table 1a). This was performed at four different frame stations whenever possible. The samples were kept cool in a portable cooler at 4 °C during transport to the laboratory by boat and car. Image analysis was performed within 24 h after collecting the seaweed.

The juvenile sporophytes used for the cultivation at the Reksta location were produced in November 2012 at the SINTEF Fisheries and Aquaculture seaweed laboratory by the same method used for the Frøya location. The seeded ropes with juvenile sporophytes were transported to and deployed at the Reksta location in February 2013. At this location, *S. latissima* sporophytes were cultivated on ropes hanging vertically from depths of 2 to 7 m from the floating collar of the empty fish cage, and seaweed samples were collected from depths of 2, 5, and 7 m on four different ropes. Three individual laminas from each depth were randomly chosen on each sampling date (Table 1b). The samples from April and June were stored at −20 °C for 11 and 20 days, respectively. The samples were thawed before image analysis. This method caused the lamina to be very soft and intractable but did not impair the bryozoan colonies or the image analysis. The samples from August and September were kept cool in a portable cooler and transported to the laboratory by boat or by car. The image analysis of these samples was performed within 24 h after collecting the seaweed.

Image analysis

The individual fronds were stretched out on a white background. An image of the whole lamina was taken on both sides of the frond to measure the total area of the lamina, using an Olympus E-500 digital camera (AF Olympus Zuiko digital 14–45 mm zoom lens, 1:3.5–5.6). Close-up images of the bryozoan colonies were taken by placing the frond on a fiber optic light table in order to easily see the outline of the colonies. The images were taken using a Nikon D200 digital camera (AF Micro Nikkor 60 mm 1:2.8). Whenever the fronds were too large for the light table, they were cut up to match the width of the light table. Segmented images were then taken of the whole lamina. The use of the light table made it possible to measure colonies on both sides of the lamina on the same image. Whenever the bryozoan cover was so heavy that it covered both sides, the measured area was multiplied by two to correct for the layer on both sides. The images were analyzed using the image processing program ImageJ 1.47v (Rasband 1997–2014) for the bryozoan area cover measurements. Due to the corrugated nature of the fronds, an average of the two sides multiplied by two was used to determine the total area.

To measure the area of the bryozoan colonies, a drawing tablet (Wacom Cintiq 12wx) was used to circle around every colony. The thallus was divided into three different areas (meristematic, mid and distal, Fig. 2) by the eye, and the size of the colonies measured within each area was calculated.

Plankton samples

The plankton samples were taken at the same dates and locations as the collecting of the seaweed. A standard plankton net with a 100-μm mesh and 30 cm in diameter was lowered to a depth of 15 m and vertically pulled up to the surface at a speed of approximately 1 m s^{-1}. The exact filtrated volume was not measured, but the volume was assumed to be approximately the same for each sampling due to consistency in sampling method. Six replicates were taken on each sampling date when possible (Table 1). On some of the sampling dates, bad weather caused interruption to the plankton sampling, and the sample size was thus smaller or lacking. The net samples were fixated with formaldehyde. On counting, the plankton samples were gently rinsed with tap water in a 100-μm mesh sieve to remove the formaldehyde, and thereafter, the samples were observed systematically in a Petri dish, under a stereomicroscope (Leica MZ 12.5, 0.8-10.0x). The number of cyphonaut larvae was counted both for the *M. membranacea* and *E. pilosa* in each sample.

Statistical analysis

All statistical analysis and graphs for the results were conducted using R, version 3.0.2 (R Core Team 2013) through RStudio, version 0.98.501 (RStudio 2012). The presence or absence of bryozoans was modeled in a binomial generalized linear mixed model (GLMM) with logit link function, where the nested dependencies between observations were fitted as a random intercept structure. All models were fitted with binomial error distribution using the lme4-packages in R (Bates et al. 2014). The random effect factor was chosen to be the ropes, as this would take variation dependencies within the stations into consideration. The variance dependencies were tested for depth, date, and site as fixed effect factors by comparing the alternative models using Akaike information criterion (AIC). Although likelihood ratio tests are not recommended for small to moderate sample sizes when using GLMMs (Bolker et al. 2009), as in this study, an ANOVA test was also performed.

Results

Time series of bryozoan growth on cultivated seaweed in Mid-Norway Early in the sampling period, from the end of April to the middle of June, no bryozoan colonies were

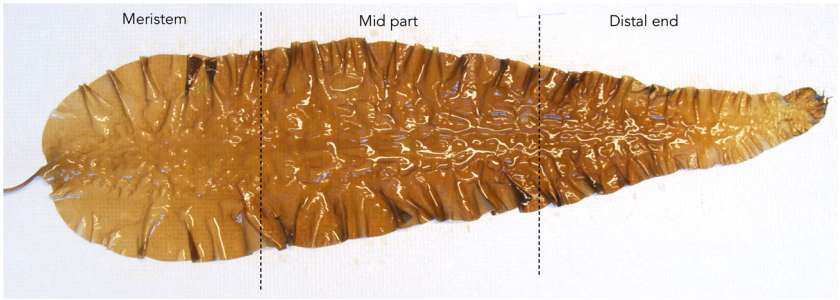

Fig. 2 Definition of the different area sections of the kelp lamina

observed on the cultivated seaweed at the Frøya location (Fig. 3). The first newly settled bryozoan colonies were observed on June 18 (Fig. 3). The colonies were abundant, but due to the small size of the colonies, the median percentage coverage of the lamina in June was only 0.7 %. The colonies then spread and grew rapidly during June and July (Fig. 3). In late July and in August, the fronds were heavily fouled with bryozoans, and the thallus started to degrade. Most of the seaweed individuals were by then not entirely intact. The bryozoan colonies that covered the lamina made it heavy, brittle, and easily breakable. *Membranipora membranacea* was the more abundant of the two species during the whole sampling period. The proportion of *E. pilosa* was higher early in the sampling season (11.67 % of the total bryozoan coverage in mid June), but then decreased as the bryozoan coverage increased in July (0.53 % in late July). The median total area (cm^2) of the lamina (Fig. 4) and thus the available substrate for bryozoan colonies decreased during the late sampling period and was in general smaller at increasing depths.

Bryozoan growth on seaweed cultivated in Western Norway At the Reksta location, bryozoan colonies were not observed at the first sampling in April (Fig. 5). Early settled colonies were present and abundant in the June sampling, although covering only 0.05 % of the thallus (median coverage) due to the small size of the colonies. In August, many of the fronds were degraded, and often, only the newly grown tissue at the meristem without bryozoans was left. This was also observed in September, when most of the sporophytes were either damaged or entirely missing, which resulted in a lack of samples from every depth on some of the ropes. *Membranipora membranacea* was the dominant species of the two during the whole sampling period also at this location. *E. pilosa* was present at the early sampling in mid June (0.83 % of the total bryozoan cover) but was not found at the later samplings when the total bryozoan cover increased. The total median size (cm^2) of the lamina of the sporophytes sampled at Reksta increased strongly from April to June but decreased in the late sampling season (Fig. 6). The difference in total area between the depths at Reksta was not as apparent as the Frøya sampling.

Missing distal ends As the bryozoan coverage increased, the *S. latissima* lamina became increasingly fragile and breakable. The bryozoans were present on every sampled individual at the late sampling. The fragile state of the kelp resulted in loss of the distal lamina (old tissue) end for several, but not all, of the sampled individuals at both sampling locations (Fig. 7). The samples taken in September at Reksta were all broken off, and the distal ends were missing. The new tissue at the meristem zone on the damaged lamina was less fouled than the rest of the lamina.

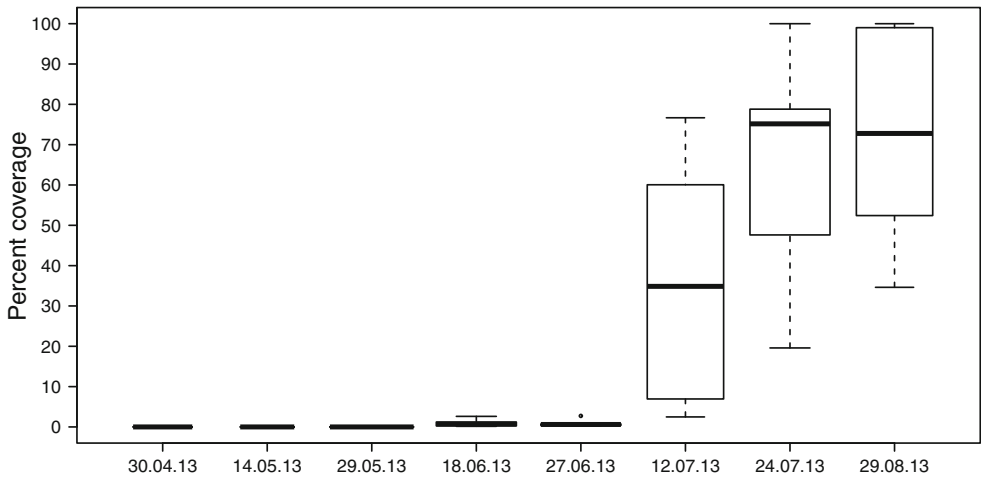

Fig. 3 The percentage coverage of bryozoan colonies on the lamina of *S. latissima* during the sampling period at the Frøya location. The boxplot shows the maximum and minimum values (*whiskers*), the lower and upper quartiles (*box*) and the median (*horizontal line*). The *width of the bars* is proportional to the sample size

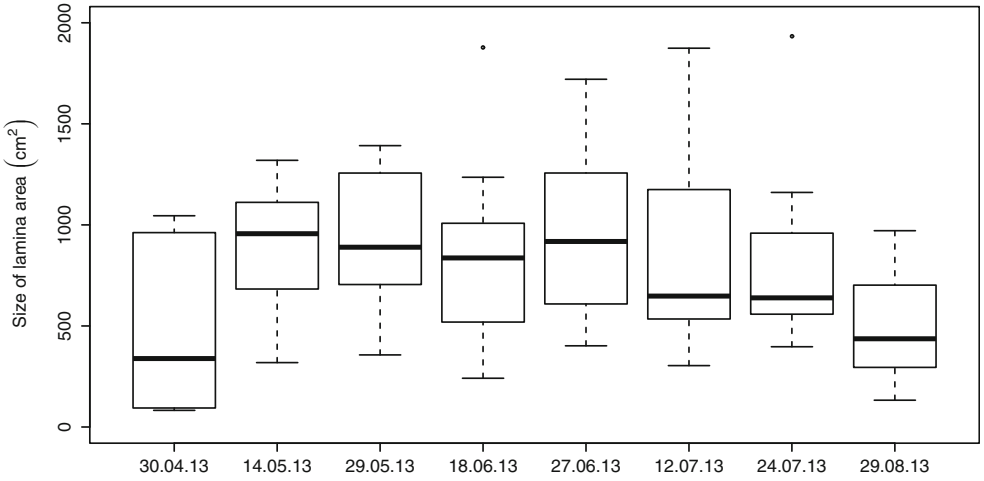

Fig. 4 Size of the total area of the sampled lamina of *S. latissima* at the different sampling dates at Frøya in cm^2. The boxplot shows the maximum and minimum values (*whiskers*), the lower and upper quartiles (*box*), and the median (*horizontal line*). The *width of the bars* is proportional to the sample size

Depth dependency The depth with most coverage differed for the different sampling dates at both locations (Fig. 8). At Frøya, the samples from a depth of 3 m were most overgrown with bryozoans at the beginning, but ended up at the last sampling day to have the least coverage (Fig. 8a). At 15 m, the cover was the lowest of the different depths for all sampling dates besides the last sampling. The difference between depths was greatest in the middle of July, where the 8-m samples had the most prominent bryozoan cover. From the statistical analysis based on AIC, the models were significantly improved when including depth as a fixed factor rather than having only a random intercept (Table 2) (Burnham and Anderson 2002). Altogether, there was a significant decrease in cover with increasing depth (likelihood ratio test: χ^2= 412.95, df=2, p value<0.001).

The development of bryozoan coverage at Reksta showed an increasing trend from June to August, except for the samples from a depth of 2 m, which still had a low cover in August (Fig. 8b). However, in September, the cover decreased for the samples from depths of 5 and 7 m, but increased for 2 m. The AIC comparison of the models including and excluding depth as a fixed factor from the Reksta location also significantly improved when the depth was included (Table 3) (Burnham and Anderson 2002). Overall, there was a significant decrease in coverage with increasing depth (likelihood ratio test: χ^2= 645.18, df=2, p value<0.001).

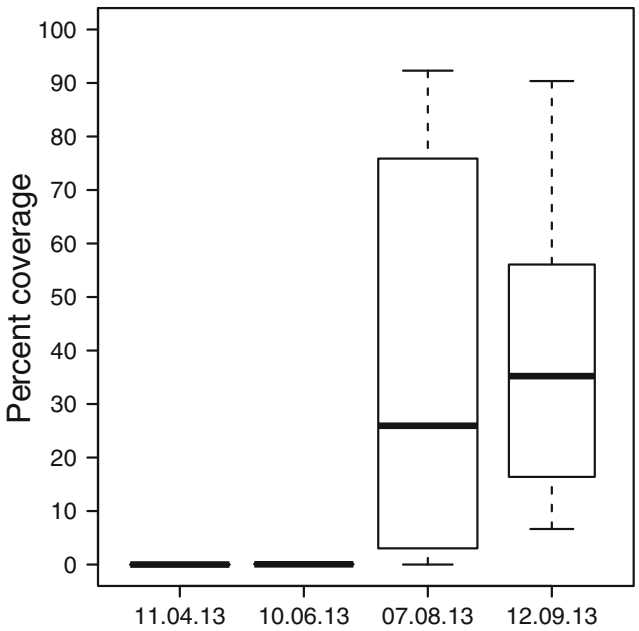

Fig. 5 The percentage coverage of bryozoans on the lamina of *S. latissima* during the sampling period at the Reksta location. The boxplot shows the maximum and minimum values (*whiskers*), the lower and upper quartiles (*box*), and the median (*horizontal line*). The *width of the bars* is proportional to the sample size

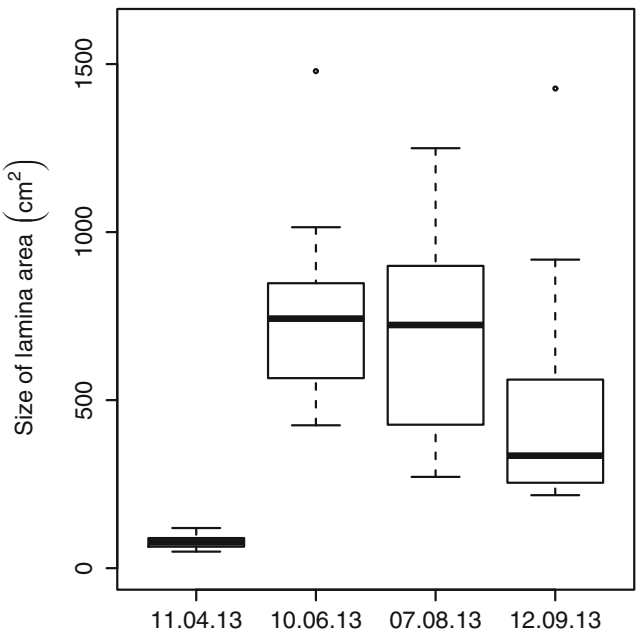

Fig. 6 Size of the total area of all the sampled lamina of *S. latissima* at Reksta in cm^2 on the different sampling dates. The boxplot shows the maximum and minimum values (*whiskers*), the lower and upper quartiles (*box*), and the median (*horizontal line*). The *width of the bars* is proportional to the sample size

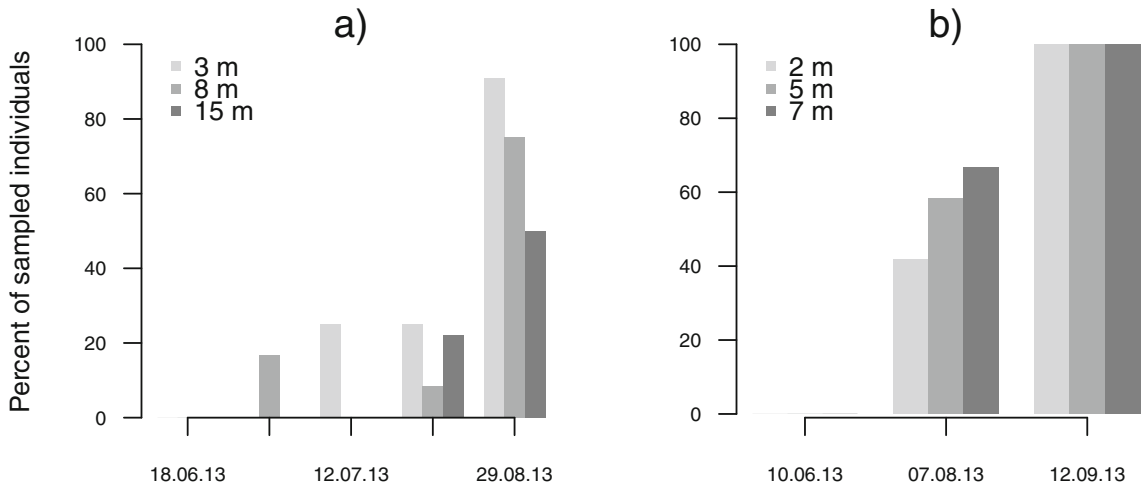

Fig. 7 Percentage of the sampled individual *S. latissima* with missing distal end at the **a** Frøya and **b** Reksta locations for each sampling date when bryozoans were observed on the lamina

Plankton sampling The semi-quantitative abundance of cyphonaut larvae for both *M. membranacea* and *E. pilosa* was registered at the Frøya location during the whole sampling period. The cyphonaut larvae were observed at all sampling dates from April to September (Fig. 9a). The relative abundance between the samples was, however, highest in late June for both species. This sample had an average of 49 (SD± 19.68) *Membranipora membranacea* larvae and 29 (SD± 14.38) *E. pilosa* larvae. The number of *E. pilosa* larvae was also relatively high in late August.

Bryozoan cyphonaut larvae were also found in all samples at Reksta (Fig. 9b), but the relative abundance was not as high as in some of the samples from Frøya. Note that the samples were not taken at Reksta in late June and July, when the peak in abundance at Frøya occurred. The number of *M. membranacea* larvae was relatively stable for all the samplings, but *E. pilosa* showed an increase in relative abundance during August and September.

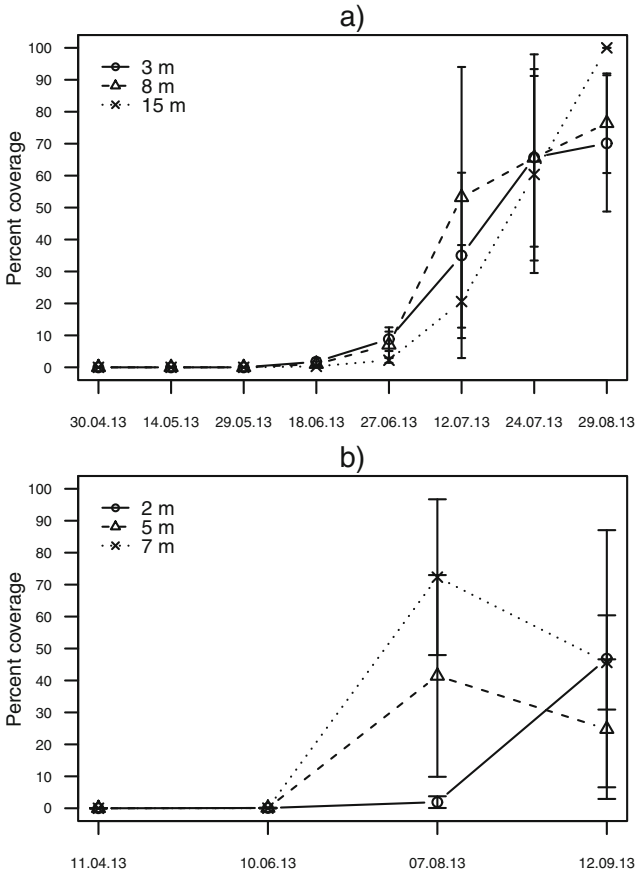

Fig. 8 Mean percentage coverage at depths of 3, 8, and 15 m on each sampling date at Frøya (**a** *upper panel*), and mean percentage coverage at depths of 2, 5, and 7 m on each sampling date at Reksta (**b** *lower panel*). The *error bars* show the standard deviation (*n*=Table 1)

Discussion

Development of bryozoan cover The observed result with increased bryozoan settlement from the end of June is in agreement with earlier experiences from other seaweed cultivation experiments in Norway (Forbord et al. 2012; Handå et al. 2013). The time of observation of the first settled colonies (week 24) was the same for both sampling locations. A rapid increase in cover followed during late June and July. The increase in bryozoan cover percentage tended to decrease during the late season. A reason for the reduced ratio may have been caused by the breakage and loss of the heavily covered distal

Table 2 AIC model comparison with and without depth as fixed factor for the Frøya location

Rank	Formula	K (parameters)	AIC	ΔAIC
1	Respons ~ Depth + (1|Rope)	3	43377.54	0
2	Respons ~ 1 + (1|Rope)	1	43786.49	408.95

Table 3 AIC model comparison with and without depth as fixed factor for the Reksta location

Rank	Formula	K (parameters)	AIC	ΔAIC
1	Respons ~ Depth + (1|Rope)	3	10015.61	0
2	Respons ~ 1 + (1|Rope)	1	10656.79	641.18

ends, while the less covered newly grown tissue at the meristem was left, resulting in an overall decrease in percent cover.

The total median bryozoan cover was in general higher at Frøya than Reksta. Environmental conditions such as temperature and wave action have been shown to affect the population dynamics of the different sites (Saunders and Metaxas 2008), but the environmental data necessary to explore this interaction were not gathered as it was beyond the scope of this particular study. Another reason for the site difference may have been differences in the total biomass or density of the kelp cultivated at the site. The amount of cultivated seaweed was higher at Frøya than at Reksta, which could have led to higher densities of bryozoan colonies due to spawning and recruitment from the already settled colonies in the close vicinity, as well as from other natural occurrences (Yoshioka 1982).

Available space for settlement and growth is one of the limiting factors in algal epifauna (Seed and O'Connor 1981).

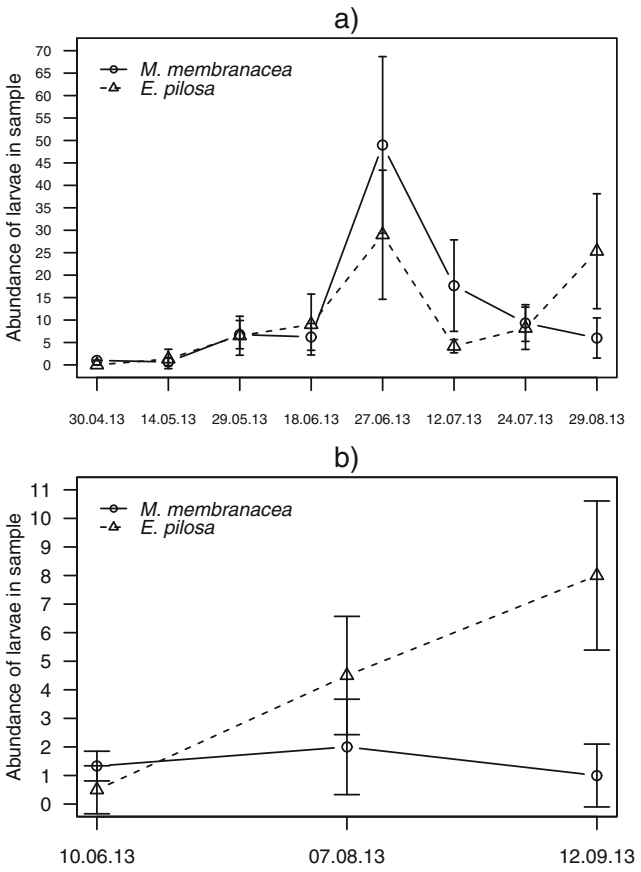

Fig. 9 Average abundance of cyphonaut larvae of *M. membranacea* and *E. pilosa* found in plankton samples during the sampling period at Frøya (**a** *upper panel*) and Reksta (**b** *lower panel*). The *error bars* show the standard deviation (n=Table 1)

Bryozoan species composition The species composition in this study shows that the main bryozoan species grows on cultivated *S. latissima* is *M. membranacea*. This may be due to the species' preferences in selecting a substrate. A collection of observations presented by Ryland (1962) showed that *M. membranacea* is more selective when it comes to substrate and prefers macroalgae as a substrate and especially the Laminarian species. *E. pilosa* tends to be less selective when choosing a substrate and occurs both on algae and hard substrates like rocks and shells. Thus, *E. pilosa* could be more easily outcompeted by *M. membranacea* due to its preferences. According to the zooplankton samples, cyphonaut larvae of *E. pilosa* were definitively present, but according to the species composition on the cultivated kelp, *M. membranacea* was more adapted to growth on the seaweed.

Another reason for the dominance of *M. membranacea* on the kelp could have been due to the greater success of *M. membranacea* in the competition between the two species. Seed and O'Connor (1981) postulated that of the common bryozoans in Britain, *E. pilosa* tends to be overgrown by other species. Similar results were seen in interactions between *M. membranacea* and *E. pilosa* in a study from Canada (Yorke and Metaxas 2011), where *E. pilosa* showed a slower growth rate than *M. membranacea*. Overgrowing of colonies was also observed on Frøya and Reksta, creating double layers of bryozoan cover. This was regarded as the same as one-layer coverage when this observation was recorded, and the area of the dominant/overlapping species was calculated. The higher abundance of *M. membranacea* out of the two species may thus be a combination of its preferences in selecting a substrate, a higher growth rate, and the ability to grow over *E. pilosa*.

Depth dependencies The statistical analysis of the data showed significantly less cover with increased depth. However, bryozoans fouled the sampled sporophytes at all depths in various amounts in this study. Although the statistical analysis showed a significant decrease in cover with increasing depth, the depth with the most coverage differed during the sampling period. For instance, in August, the seaweed samples from a depth of 15 m at Frøya had the highest coverage (mean=100 %, SD±0.001). One reason could be that the seaweed cultivated at greater depths are more sheltered from wave action and turbulence than the seaweed grown closer to the surface, thus experiencing less breakage of the lamina and loss of the distal end, which in total gave higher cover. The length of cultivated kelp has been shown to grow faster at intermediate depths of around

5 m and less at 8 m (Handå et al. 2013). If the growth of the bryozoan colonies is greater or equal to the growth of new tissue, the lamina may be fully covered and inhibit further growth. Although the growth rate was not measured in this study, it could explain the high percentage coverage at depths below 8 m. The total area of the lamina collected at 15 m at Frøya was in general less than the seaweed grown at a depth of 3 m, and the bryozoans would have a greater chance to overgrow the smaller than the larger lamina during the same time span. The 15-m samples also had less loss of distal ends than the other depths.

For the Reksta location, bryozoan cover on samples from a depth of 2 m was relatively low in August (mean=1.92 %, SD ±1.83) compared to 5 and 7 m (mean=41.42 %, SD±31.57 and mean=72.33 %, SD±24.38, respectively). The reason for this difference may be the same as for Frøya, where the kelp closer to the surface has a higher growth rate than the kelp at greater depths, thus lowering the cover ratio. However, the depth difference (2–7 m) was not as high as at the Frøya location (3–15 m). Neither was the difference in median total size of the lamina between the depths.

Abundance of cyphonaut larvae in the water column The cyphonaut larvae of *E. pilosa* are mainly produced in late summer and remain present in the plankton throughout the year (Ryland 1965). According to Ryland and Stebbing (1971), the larval stage of *M. membranacea* may remain in the water column for several weeks or months before settling, which usually occurs during the early spring to early summer. Some colonies are able to survive the cold winter season and may be the source of the spring larvae (Lutaud 1961; Menon 1972). The semi-quantitative zooplankton sampling done in this study showed the presence of bryozoan larvae on all the sampling dates. This finding supports the literature on cyphonaut larvae being present in coastal waters throughout the year in the North Atlantic Ocean (Ryland 1965). The relative abundance of bryozoan larvae in the water samples was, however, low until the end of June. The settlement of colonies on the seaweed coincided with the highest abundance of cyphonaut larvae in the water column. This may be due to an increase in plankton generally, a rise in temperature, or to spawning from the already settled colonies in the seaweed farm area.

Biofouling and seaweed cultivation/concluding remarks Biofouling is a major challenge in global commercial macroalgae cultivation (Fletcher 1995; Handå et al. 2013; Peteiro and Freire 2013). Fouling organisms degrade the seaweed and decrease the value of the biomass. This study has documented the development of bryozoan growth and coverage on cultivated *S. latissima* in Norway, and the results show that cultivation during July and August is not feasible for the industry as the deterioration of the product is high during these months due to the heavy fouling of bryozoan colonies. The bryozoan coverage does not just make the product more indelicate, but causes a substantial loss of biomass due to breakage of the fronds.

From a commercial point of view, the best solution at this point will be to harvest the crops of kelp in June before the bryozoan colonies settle and spread extensionally. Other solutions like submerging the crops to greater depths during the late season will not have a large impact as the bryozoans settle and grow also at depths of 15 m as documented in this study.

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