Large-scale salmon farming in Norway impacts the epiphytic community of _Laminaria hyperborea_

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ABSTRACT: Large-scale finfish farms are increasingly located in dispersive hard-bottom environments where _Laminaria hyperborea_ forests dominate; however, the interactions between farm effluents and kelp forests are poorly understood. Effects of 2 levels of salmonid fish-farming effluents (high and low) on _L. hyperborea_ epiphytic communities were studied by sampling canopy plants from 12 sites in 2 high-energy dispersive environments. Specifically, we assessed if farm effluents stimulated fast-growing epiphytic algae and faunal species on _L. hyperborea_ stipes — as this can impact the kelp forest community composition — and/or an increased lamina epiphytic growth, which could negatively impact the kelp itself. We found that bryozoan biomass on the stipes was significantly higher at high-effluent farm sites compared to low-effluent farm and reference sites, resulting in a significantly different epiphytic community. Macroalgal biomass also increased with increasing effluent levels, including opportunistic _Ectocarpus_ spp., resulting in a less heterogeneous macroalgae community at high-effluent farm sites. This habitat heterogeneity was further reduced by the high bryozoan biomass at the high-effluent sites. Such changes in the epiphyte community could have implications for the faunal community that relies on the epiphytes for food and refuge. On the kelp lamina, no clear response to farm effluents was found.

KEY WORDS: _Laminaria hyperborea_ · Kelp · Epiphytes · Epiphytic community · _Salmo salar_ · Atlantic salmon · Norway · Bryozoa

1. INTRODUCTION

Increased loading of nutrients from anthropogenic activities can be a driver of ecosystem change in coastal hard-bottom systems (e.g. Filbee-Dexter & Wernberg 2018) and has in some cases contributed to slow-growing perennial macrophytes such as kelp forests being replaced by fast-growing ephemeral algae mats (e.g. Kraufvelin et al. 2006, Worm & Lotze 2006, Filbee-Dexter & Wernberg 2018). Along the Norwegian coast, salmonid fish farming is currently the largest anthropogenic source of nutrients in coastal waters, contributing 55% of the total anthropogenic nitrogen emissions (Selvik & Sample 2018). However, the interactions between nutrient effluents from fish farming and kelp forests are poorly understood. Kelp forests face several stressors, such as sea urchin overgrazing, climate change, and harvesting (reviewed by Steneck et al. 2002, Araújo et al. 2016). With more than a third of kelp forests worldwide having been in decline over the last 50 yr (Krumhansl et al. 2016) and better management of kelp forests being called for (Teagle et al. 2017), it is imperative to discern the potential response of kelp forest ecosystems to localised increased nutrient loadings such as fish farming effluents.

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Kelps (Laminariales) are important seaweeds in temperate coastal seas, as they provide important ecosystem services, e.g. supporting a diverse community of associated epiphytic macroalgae (e.g. Christie et al. 2003) and fauna (e.g. seabirds: Fredriksen 2003; macrofauna: Christie et al. 2003, Fredriksen 2003; fish: Norderhaug et al. 2005), having exceptionally high primary production and carbon assimilation (Chapry-Roubaud & Sournia 1990, Steneck et al. 2002, Christie et al. 2009) with resulting kelp detritus providing a significant food source for local secondary production (Fredriksen 2003, Norderhaug et al. 2003), in addition to subsidizing other habitats in deeper waters (Krumhansl & Scheibling 2012, Pedersen et al. 2020). Changes in our kelp forests could therefore have cascading effects on ecosystem function and services, both locally and beyond the coastal zone.

The rapid growth of the Norwegian aquaculture industry, from ca. 490 000 t in 2000 (Gullestad et al. 2011) to ca. 1340 000 t in 2018 (Fiskeridirektoratet 2019), has made Norway one of the leading countries worldwide in marine aquaculture production (FAO 2018). A continuous restructuring of the industry has followed this expansion; from small farms in sheltered fjords (3000–5000 t maximum total biomass [MTB]) to larger farms (ca. 6000–14000 t MTB) in more exposed and shallow coastal locations—locations where Laminaria hyperborea (Gunnerus) Foslie kelp forests typically thrive down to a depth of ca. 30 m (Kain 1979, Lüning 1990, Bekkby et al. 2009). Indeed, the majority of the Norwegian aquaculture expansion over the last 10 yr can be attributed to a developing industry in the Frøya-Smøla archipelago (63° N) in the county of Trøndelag, an area where L. hyperborea forests is currently listed as ‘near threatened’ (Gundersen et al. 2018), making impact-studies on this habitat type particularly relevant. Few studies have examined the effect of salmonid fish farm effluents in exposed coastal locations or on kelp forests, with most previous work focussing on soft-bottom habitats (Holmer 2010) and fjords (Kutti et al. 2007a,b). Effluents being released from the fish farms that are located at more exposed sites are likely to be more dispersed (hence the allowance of larger farms compared to in sheltered fjords), potentially resulting in environmental responses being more diffuse and difficult to detect compared to in-fjord systems. Future expansion of the aquaculture industry, both in Norway and globally, will include further relocations to exposed, dispersive coastal environments due to the observed higher resiliency of soft-bottom habitats at such locations (Keeley et al. 2013, 2019, Valdemarsen et al. 2015), increasingly overlapping with kelp forest habitats, making it critical to quantify any potential effects aquaculture effluents may have on kelp forest conditions.

Fish farming releases large amounts of effluents in the form of dissolved nutrients and particulate organic matter (POM), which have the potential to affect kelp forests, both directly and indirectly. The amount of these effluents released along the Norwegian coast in 2018 was estimated by Husa (2019) to be 52 000 t of dissolved inorganic nitrogen (DIN) (mainly ammonia; e.g. Sanderson et al. 2008), 7000 t of dissolved inorganic phosphorus (DIP) (Husa 2019), and 540 000–670 000 t of POM (Hansen 2019). Effluent amount and dispersal from individual farms will depend on the farm characteristics (biomass and feed levels, related to the stage of the production cycle) and location (i.e. the depth, wave exposure, and current strength and direction at the site) (Jansen et al. 2016). DIN is most likely to become a limiting nutrient for seaweed growth in undisturbed temperate coastal waters (and DIP in freshwater systems) (e.g. Kain 1989, Howarth & Marino 2006), especially in the warm summer months following the spring bloom (Rey 2004), which is when effluent release from fish farms tends to be highest (Wang et al. 2012). Ephemer al macroalgae, many of which grow as epiphytes on kelp, can respond faster to increased nutrient availability than perennial slow-growing macroalgae (Pedersen & Børum 1996). Ephemeral macroalgae also grow during summer, with L. hyperborea stipe and lamina epiphyte biomass peaking in August (Christie et al. 2003), whereas the main growth season for Laminariales is during winter and early spring (Kain 1979). Hence, although fish-farm derived DIN may have a positive effect on kelp, fast-growing ephemeral macroalgae are thought to benefit more, and an increase in epiphytic algae growth on perennial macrophytes with nutrient enrichment is well documented (e.g. Rönnberg et al. 1992, Worm & Sommer 2000, Oh et al. 2015).

Some degree of epiphytic fouling on kelp laminae is common in natural communities and tends to decrease with increasing wave exposure (Jorde 1966, Pedersen et al. 2012). However, increased lamina epiphytic load can reduce growth and survival of kelp (Levin et al. 2002) by affecting the kelp’s photosynthetic performance and nutrient uptake (Andersen et al. 2011) and can reduce the light available to the kelp by 90% (Andersen et al. 2019). Epiphytic fil-
 Epiphytic feeders (e.g. bryozoans and colonial tunicates) are common on kelp and may benefit from increased nutrients (both in the form of DIN and POM), and an increase in epiphytic bryozoan cover has been observed for Mediterranean seagrass communities with increasing nutrients (Balata et al. 2010). Encrustation by bryozoans can weaken the kelp lamina, leaving it more prone to breakage (Krumhansl et al. 2011). Enhanced epiphytic load on *L. hyperborea* stipes can result in an increased habitat complexity of the kelp forest, but nutrient enrichment tends to homogenize communities (Balata et al. 2010, Oh et al. 2015). As positive relationships between epiphytes and faunal abundance are present on large macrophytes (Christie et al. 2003, 2009, Norderhaug et al. 2014, Armitage & Sjøtun 2016), such changes in the epiphytic community could have knock-on effects on ecosystem functioning via changes to the faunal community.

The aim of this study was to assess the effect of 2 levels (high and low) of effluents (DIN and POM) from large-scale salmonid fish farms in dispersive environments on *L. hyperborea* forest functioning. Specifically, we assessed if the amount of epiphytes (macroalgae, colonial tunicates, and bryozoans) living on the kelp stipe and lamina increased as a response to fish farm effluents, and if the community structure of the stipe epiphytes changed.

### 2. MATERIALS AND METHODS

#### 2.1. Sampling sites

We chose 12 sites for this study: 6 sites near salmonid fish farms (FF) and 6 reference sites (Ref) located in the same area, but considered unaffected from effluents. Sites were chosen in 2 archipelagic areas on the west coast of Norway, about 40 km apart: Frøya (3 Ref, 3 FF) and Smøla (3 Ref, 3 FF) (Fig. 1). This part of the coast is characterized by ocean swells, waves and strong currents resulting in a highly dynamic area. The terrain in this area is mostly hard-bottom mixed with shell sand, with *Laminaria hyperborea* dominating the sublittoral rocks down to about 30 m (Steen 2017, 2018). Salinity ranges from 31 to 34‰ (IMR 2017). Both areas are subject to a high intensity of fish farming, producing more than 420,000 t of salmonid biomass in our sampling year of 2015 (Fiskerdirektoratet 2019). A typical farm cycle lasts 12–18 mo, with the farms in the present study having cycles around 18 mo (excluding the falling period). At the time of the study, farms in Frøya were early in the production cycle (Month 5–6), with low fish biomass and feed levels (FF-L). Farms in Smøla were at the end of their production cycle (ca. Month 17), with effluent loads at the time of sampling, respectively.
Mean monthly feed use at the FF-H farms was 3.5–11 times higher than at the FF-L farms in the 6 mo preceding sampling (Table 1). Sampling in both areas gave the opportunity to compare the effects of a high versus a low effluent load while at the same time assessing whether potential impacts were short term (i.e. if impacts were only observed at FF-H sites and not FF-L sites) or long term (i.e. if the same level of impacts was found at both FF-H and FF-L sites), as the effluent load level varies with farm cycle stage. Wave exposure levels differed between the FF locations, hence, to take the potential effect of wave exposure into account, the study location at Ref sites was chosen based on 2 criteria: similar wave exposure levels as the FF locations and >2 km from any fish farm or other major industries. Due to wave-exposure and ocean current patterns in the sampling area, the impact of effluents is not believed to follow a clear gradient as in calm fjords (Kutti et al. 2007a,b), but rather, impacts are evident in patches in the prevailing current direction (particle modelling conducted herein), with benthic effects observed up to 1000 m away (Keeley et al. 2019). Thus, within each study location, a skerry with L. hyperborea forest was chosen as the sampling site, itself based on 2 criteria: presence of L. hyperborea forest at 5 m depth (relative to the nautical chart zero, i.e. the lower astronomical tide [LAT]), as depth can have an impact on kelp communities (Kain 1977), and that the skerry was located within the main effluent plume of the farm. To ensure that L. hyperborea plants at FF locations were sampled from effluent-impacted kelp forest, the direction of the main effluent plume was determined from ocean current models, and the closest suitable skerry to the farm within the plume was selected as the sampling site. Maps of modelled particle movement and dissolved nutrients were consulted after the study to check that the farm sites were in the area of effect of the farm (see Section 2.5 for details, and see Figs. 3 & 4).

2.2. Sampling design

Sampling was conducted over 6 consecutive days, from 8 to 14 August 2015, the time of year when epiphyte abundance on L. hyperborea normally peaks (Christie et al. 2003). At each site, a 25 m transect was laid out along the sea floor, following contours so the depth remained at 5 m LAT. The living canopy plant closest to the metre mark every 2 m for 20 m was collected by SCUBA divers, giving a total of 10 thalli (holdfasts were collected along the last 5 m of the 25 m transect; B. T. Haugland unpubl.). The density of the L. hyperborea forest was determined by counting the number of living canopy thalli within 5 randomly selected 1 m² quadrants along the transect. Collected L. hyperborea plants were kept in fresh seawater until processed. The thallus of each collected plant was divided into lamina and stipe, where the lamina was cut off 1 cm below the stipe−lamina transition zone, and the stipe right above the holdfast−stipe transition zone. A summary of sampled kelp variables is given in Table S1 in the Supplement at www.int-res.com/articles/suppl/q013p081_supp.pdf.

2.3. Stipe measurements and epiphytes

Epiphytic macroalgae and fauna were collected by scraping them off the stipe; samples were frozen until processed in the laboratory at the Institute of Marine Research in Bergen, Norway. Large bundles of Desmarestia aculeata were occasionally tangled around the top of the stipe, or a second L. hyperborea (typically several years old) was growing out from the sampled thallus. These were identified and weighed in situ but excluded from further data analysis. To determine the area available for epiphytic growth, the surface area (SA) of the stipes was calculated by recording

| Site | Group | MTB (t) | Mean feed (kg mo⁻¹) | Distance to farm (m) |
|------|-------|---------|---------------------|---------------------|
| Frøya | S-1 FF-L | 10 920 | 122 000 | 380 |
|       | S-2 Ref-L | 3 850 | 2 890 |
|       | S-3 Ref-L | 21 600 | 60 |
|       | S-4 FF-L | 8 580 | 131 000 | 200 |
|       | S-5 FF-L | 7 800 | 79 000 | 2 890 |
|       | S-6 Ref-L | 2 890 |
| Smøla | S-7 Ref-H | 7 100 | 150 |
|       | S-8 FF-H | 8 580 | 857 000 | 520 |
|       | S-9 FF-H | 6 240 | 466 000 | 3 530 |
|       | S-10 FF-H | 5 460 | 577 000 | 6 020 |
|       | S-11 Ref-H | 3 530 |

Table 1. Overview of sampling sites for Laminaria hyperborea kelp plants collected from salmonid fish farming (FF) sites (low effluent load: FF-L, high effluent load: FF-H) and reference sites (Ref-L, Ref-H) in the Frøya (Ref-L, FF-L) and Smøla (Ref-H, FF-H) archipelagos, Norway, August 2015. Information is also given on the maximum total fish biomass (MTB) permitted at the farm, the mean amount of feed-use at farms for the 6 mo prior to sampling (January–July 2015), and the distance to the nearest farm.
the length and the diameter at the top and bottom of the stipe. As stipes can be oval in cross-section, the diameter was measured twice perpendicular to each other, and the average was used. Grazing by urchins was common in the study area (75–100% of the stipe epiphytes were grazed in most samples), distinguished by short stubble left on the stipe, in most cases the bottom section (see Fig. 2 for comparison). Stipe epiphyte biomass was therefore standardized to 10 cm² ungrazed SA to allow comparisons across sites independent of stipe length, and as grazing would reduce epiphyte biomass irrespective of the effect of farm effluents on epiphyte growth. Grazed SA was calculated using the same method as for stipe SA (using the diameters of the upper and lower grazing boundary and length of the grazed stipe) where whole sections of the stipe had been grazed, which was mostly the case. When grazing was patchy or inconsistent along the stipe, a percentage in relation to total stipe SA was estimated to the nearest 10%. Stipe age was determined by counting growth rings (Kain 1963).

To study changes in biomass and community structure, epiphytic macroalgae >0.5 cm in length were defrosted in the laboratory and identified to the lowest possible taxonomic level (genus, species) by the use of relevant literature (Dixon & Irvine 1977, Rueness 1977, Prud’homme van Reine 1982, Irvine 1983, Fletcher 1987, Maggs & Hommersand 1993, Irvine & Chamberlain 1994, Brodie et al. 2007). The biomass of each species was determined (fresh weight, FW) after spinning the sample in a salad spinner for 5 rounds to remove excess water. Freezing and defrosting have little impact on distinguishing features of macroalgae. The biomass may be slightly reduced due to cells breaking and consequently leaking, but this was not observed. Macroalgae <0.5 cm were grouped and blotted to determine FW and included in the univariate analysis of total biomass. Bryozoans (encrusting [thin sheets] and erect [plant-/bush-like]), and macroalgae which had bryozoans covering >40% of their surface, were grouped as ‘Bryozoa’. These were not identified further, as different bryozoan species were frequently overgrowing each other. One level of epiphytic growth was identified and quantified (except in the case of bryozoans); small epiphytic algae that were loosely attached to the epiphytic community were occasionally observed but were excluded due to uncertainty regarding whether they were actually part of the attached community or simply drifting seaweed that had become entangled.

2.4. Lamina measurements and epiphytes

The biomass (FW) and maximum length of the lamina were recorded after removal of epiphytes. Presence of dominant epiphytes was quantified using different methods depending on the group: SA for encrusting colony-forming fauna (bryozoans and tunicates); number of colonies for erect bryozoans; and biomass (FW) for macroalgae. SA and the number of erect colonies were determined by laying the lamina out on a flat surface and taking photographs. Five randomly selected photographs from each site were later processed using the program ImageJ (Schneider et al. 2012) by tracing the edge of the lamina and subsequently the edge of the attached fauna. Macroalgae were gently scraped off the lamina and frozen until processing in the laboratory at the Institute of Marine Research in Bergen. Lamina macroalgae were sorted in the following categories to assess changes in biomass of dominant macroalgae groups: Rhodophyta leaf-forming, Rhodophyta branched (Polysiphonia/Ceramium-like), Ectocarpales thread
(thin *Ectocarpus*-like filaments), and Ulvales. Biomass in FW was determined in the same way as the stipe epiphytes.

### 2.5. Modelling of abiotic variables and farm effluents

Site information on abiotic data, particle settlement, and DIN was made available from different models (see Table S1 for summary of abiotic data used).

Mean current speeds for analysis were taken from the NorKyst800 model (Albretsen et al. 2011, Asplin et al. 2020) interpolated onto a 500 × 500 m grid. In addition, a higher-resolution model (160 × 160 m) nested into the NorKyst800 model was run for the Frøya/Smøla area. Both models are based on the Regional Ocean Modelling System (ROMS, www.myroms.org; Shchepetkin & McWilliams 2005). Realistic forcing of the ocean model from atmosphere, tides, and rivers are included as described by Asplin et al. (2014). The NorKyst800 model has been validated (e.g. Asplin et al. 2020).

The higher-resolution circulation fields from the ROMS model were also used to force the Lagrangian transport model LADiM (Ådlandsvik 2019), to predict the transport of particle waste from the FF in the study area and verify whether the sampling sites were located within the effluent plume of the nearby farm. LADiM calculates active transport of individual particles using the modelled currents as inputs, as well as particle-specific dynamics including settling and lifespan via an individual-based model. Constant settling velocity of 7.5 cm s⁻¹ and a particle lifespan of approximately 12 d were used as model parameters based on previous research (Bannister et al. 2016, Carvajalino-Fernández et al. 2020). Particle distribution at the sampling sites was calculated and presented as particle accumulation maps in order to identify the plume trajectories for the periods of interest.

Using sampling to adequately capture the effect of FF effluents on dissolved nutrient concentrations can be extremely challenging, due to the high spatial-temporal variation and utilization/transformation (Jansen et al. 2016). Hence the NORWECOM model (Skogen et al. 1995, Skogen & Søiland 1998) was used to predict the dispersion and ambient concentrations of DIN at the sampling sites. The NORWECOM model is a full 3-dimensional nutrient−phytoplankton−zooplankton−detritus model, and the processes included are primary and secondary production, grazing, respiration, algae death, remineralization of inorganic nutrients from dead organic matter, self-shading, turbidity, sedimentation, resus-
colony-forming tunicates) according to lamina SA. No statistical analysis was conducted for bush-forming bryozoans and colony-forming tunicates due to low abundances and large within-group variation. The stipe epiphytes (algal and bryozoan biomass) were standardized according to stipe ungrazed SA. Note that 5 stipes were recorded as 100% grazed at the same time as some epiphytic biomass was sampled (due to rounding up to nearest 10%, see Section 2.3). For these, 5% of their total stipe SA was used for standardization, as this was considered a relevant margin of error.

All statistical analyses were done using R (R Core Team 2017) with plots created using the package ‘ggplot2’ (Wickham 2016). The effect of farming on the abundance of epiphytes was analysed by constructing linear mixed-effects models (R package ‘nlme’; Pinheiro et al. 2017). These allow for the inclusion of a random effect, ‘site’ (12 levels), which accounts for the potential inter-dependence of thalli sampled from the same site. The effect of farming was examined using the variable ‘group’ (categorical, 4 levels: Ref-L, Ref-H, FF-L, FF-H). A number of control variables were chosen for inclusion, based on biological theory that they could influence the response variables: kelp age (continuous), kelp density (continuous), wave exposure (continuous, modelled), current speed (continuous, modelled), and light (continuous, modelled). Variables were tested for collinearity by calculating the variance inflation factor (VIF) and examining pairwise correlations. All VIF values were low (≤3.2; Table S2). The dataset did not allow for testing interactions between control variables and is also limited for making conclusions about the impact of these factors on epiphyte communities. One site had much higher wave exposure than the rest (Site 7, Ref-H; >2.5× higher than any other site), which could unduly influence the analyses. The analyses were therefore run once with, and once without, this site.

Before any testing, plots of residuals for the models were examined to check for homogeneity of variance and normality. To meet these assumptions, some response variables were square-root transformed, and variance structure functions were included to allow the residual variation to vary along certain variables (selected based on plots of residuals and AIC and likelihood ratio testing, following Zuur et al. 2009; see Table 2). Significance testing was done using likelihood ratio tests (comparisons of the model with and without the variable of interest, Zuur et al. 2009). To test for differences between levels of ‘group’, Dunnett contrasts were done, which compared a treatment (FF-H or FF-L) to controls (Ref-H and Ref-L averaged), using an approximation of the Dunnett p-value adjustment for multiple comparisons (R package ‘lsmeans’; Lenth 2016). After analysis, the epiphytic algae were grouped by morphology (corticated, foliose, uniseriate, other; Karez et al. 2004), and by higher taxon (Rhodophyta, Phaeophyceae, Chlorophyta) to visually explore any shifts correlating with FF effluents.

Non-metric multi-dimensional scaling (NMDS) was chosen to graphically present the stipe epiphytic community. NMDS ordination plots (2-dimensional) were applied to a Bray-Curtis distance matrix calculated from species biomass data (R package ‘vegan’; Oksanen et al. 2018). The data were first square-root transformed to prevent very abundant species having an overwhelming effect, and stipes with a total biomass of zero were omitted (Clarke & Warwick 2001). Vectors of scaled control variables (kelp age, kelp density, wave exposure, current speed, and light) were generated utilizing data positioning obtained in the NMDS (‘envfit’ function). Relative lengths of vectors correspond to their strength (i.e. magnitude of change and variability) in the positioning of samples relative to each other in NMDS plots and can thus be used to aid in NMDS interpretations. The significance of vectors and the a priori set ‘group’ were tested via 999 permutations. Vector fitting was conducted both with and without the high wave exposure site (Site 7). Ellipses representing 95% confidence intervals around the centroid for each level within group (Ref-L, FF-L, Ref-H, FF-H) were plotted to aid graphical representation (‘ordiellipse’ function), where a shift in centroid location indicates a different species composition.

To test if the stipe community composition differed between levels within group, a pairwise PERMANOVA was run (R package ‘pairwiseAdonis’; Martínez Arbizu 2017). A 5-way PERMANOVA (R package ‘vegan’; Oksanen et al. 2018) was used to test the significance of the chosen control variables on the epiphytic community, and to assess the amount of variation explained by these compared to the a priori set factor. P-values (α = 0.05, based on 999 permutations) were adjusted for multiple comparisons in the pairwise PERMANOVA. SIMPER (R package ‘vegan’; Oksanen et al. 2018) was run to investigate contribution of each species to potential differences between ‘group’ community compositions. PERMDISP, (‘betadisp’ function) was conducted to assess the multivariate dispersion of the stipe epiphytic community within the 4 different groups (i.e. beta-diversity), where a lower average distance to centroid indicates a more homogeneous community. Significance was determined with an ANOVA. Based on statistical results obtained so far,
the analysis was conducted twice to assess if the observed patterns were caused by the macroalgae community, and/or caused by bryozoan biomass.

3. RESULTS

3.1. DIN and abiotic variables

The model of DIN and particle movements predicted that all farm sampling sites were within the main effluent plume of the respective farms. DIN levels in March (prior to the spring bloom) were predicted to range between 7.00 and 7.45 μmol l$^{-1}$ at all sites. A lower elevation in DIN levels was predicted at FF-L sites (up to 1.4 times higher than at Ref sites) compared to FF-H sites (up to 1.8 times higher than at Ref sites) (Fig. 3). DIN levels in the study area were dynamic for the period (March to August) prior to sampling, with weekly fluctuations varying in magnitude from 0.03 μmol l$^{-1}$ (7.19–7.22 μmol l$^{-1}$) to 4.42 μmol l$^{-1}$ (2.07–6.50 μmol l$^{-1}$). However, a consistently higher DIN concentration was predicted at farm sites (FF-L, FF-H) compared to Ref sites (Ref-L, Ref-H) (FF-L: 0.01–0.30 μmol l$^{-1}$ higher; FF-H: 0.07–0.40 μmol l$^{-1}$ higher; Fig. 3). Modelled particle trajectories predicted that farm sampling sites were located in areas with medium exposure to the particle plume (within 40–60% of the maximum registered depositions) from the respective fish farms (Fig. 4).

Modelled wave exposure levels ranged from 7206 to 700125 m$^2$ s$^{-1}$ across sites, which is classified from ‘very sheltered’ to ‘exposed’ according to the classification system of Davies et al. (2004). Modelled mean current speed ranged from 0 to 0.07 m s$^{-1}$ across sites. The Ref-H sites all had relatively high wave exposure (Fig. S1). The modelled light exposure index ranged from −0.14 to 0.07 (with 1 being optimal).

3.2. Stipe epiphyte biomass

Macroalgae and bryozoans were the dominating stipe epiphytes, with a total of 67 macroalgal taxa identified, where the majority were red algae (Table S3). Sponges and non-colonial tunicates commonly grow on Laminaria hyperborea stipes (Christie et al. 2003), but the former were not observed and the latter were only sporadically observed, and therefore not included further. Average total epiphytic biomass on stipes ranged from 0.01 to 34.4 g FW between sites. Standardized to 10 cm$^2$ ungrazed stipe, average macroalgal and bryozoan epiphytes were 1.25 and 0.48 g FW, respectively. Bryozoans were predominantly Membranipora membranacea, Electra pilosa, and species in the genera Scruparia and Crisia. Kelp density varied, ranging from 1 to 14 canopy plants m$^{-2}$ at the sampled sites. Mean kelp density was slightly higher at reference sites (mean ± SD, Ref-L: 9 ± 8, Ref-H: 7 ± 7 plants m$^{-2}$) compared to farms (FF-L: 3 ± 3, FF-H: 5 ± 2 plants m$^{-2}$; Table S1).

For epiphytic algae on the stipe, the biomass was higher at farm sites than at reference sites and increased with wave exposure level and kelp age (Fig. 5). Group (levels: Ref-L, FF-L [low effluent load], Ref-H, FF-H [high effluent load]) was a significant explanatory factor in the model ($p = 0.014$, Table 2). However, post hoc contrasts did not find significant differences between reference sites and farm sites (FF-H vs. Ref-L/H: $p = 0.14$, FF-L vs. Ref-L/H: $p = 0.38$).

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Fig. 3. Predicted effect of salmonid fish farm effluents (low levels: FF-L; high levels: FF-H) on background (reference, Ref) dissolved inorganic nitrogen concentration (DIN) in the upper 5 m of the water column at 3 farm sites and 3 reference sites in the Frøya (FF-L, Ref-L) and Smøla (FF-H, Ref-H) archipelagos, Norway (see Fig. 1). The difference in predicted DIN concentrations is between 2 model simulations (NORWECOM) run for 4.5 mo prior to sampling: one simulation conducted with, and one simulation without, the presence of the study farms. The grey bar marks the sampling time. For farm sites, the distance to the closest farm is included in brackets.
Fig. 4. Predicted effluent plume and movement of particles released from fish farms (low effluent levels: FF-L; high effluent levels: FF-H) at 3 farm sites (FF-L) located in the Frøya archipelago and at 3 farm sites (FF-H) located in the Smøla archipelago, Norway. Red diamonds are sampling sites for the collection of *Laminaria hyperborea*, black squares are fish farms. For Site 1, modelled ocean currents are also presented (inset), as the resolution of the particle model did not capture small skerries north of the sampling site in this specific area, resulting in an unrealistic prediction of particle movement.
Of the control variables, kelp age and wave exposure had positive significant relationships with epiphyte biomass (Table 2, Fig. S1), although the relationship with wave exposure became insignificant when the site with much higher wave exposure (Site 7) was excluded. When the macroalgal epiphytes were divided into morphological and taxonomic groups (Fig. 6),

Table 2. Results of likelihood ratio tests of the effect of location (group: farm or reference, high or low effluent), kelp age, kelp density, and environmental conditions on Laminaria hyperborea stipe and lamina epiphytes. LR: likelihood ratio for each predictor with degrees of freedom as subscript. Italics show the results when the site with high wave-exposure (Site 7 in Ref-H) was excluded; bold indicates significant results (p < 0.05); a dash indicates that a variable was not included. $R^2$ is calculated as a comparison of the residual variance of the full model against the residual variance of an intercept-only null model (Xu 2003). Model structure is included in the footnotes.

| Response variable | n | Group | Kelp age | Kelp density | Predictors | R² |
|-------------------|---|-------|----------|-------------|------------|----|
|                   |   | LR p  | LR p     | LR p        | Current speed | LR p | Wave exposure | LR p | Light exposure | LR p |
| Algal epiphytes   | 110| 10.63 | 0.014    | 16.41       | <0.001      | 9.02 | 0.430         | 5.01 | 0.026         | 0.61 |
| (g per 10 cm² stipe)² | 100| 9.91  | 0.020    | 12.21       | <0.001      | 9.02 | 0.430         | 5.01 | 0.026         | 0.61 |
| Bryozoan epiphytes| 110| 28.03 | <0.001   | 1.41        | 0.232       | 0.042 | 0.012         | 4.21 | 0.041         | 5.21 |
| (g per 10 cm² stipe)² | 100| 23.33 | <0.001   | 1.11        | 0.300       | 0.042 | 0.012         | 4.21 | 0.041         | 5.21 |
| Algal epiphytes   | 115| 11.13 | 0.011    | –           | –           | 4.11  | 0.042         | 2.51 | 0.112         | 7.41 |
| (g per 100 g lamina)³ | 105| 14.41 | 0.002    | –           | –           | 10.61 | 0.001         | 0.71 | 0.414         | 4.15 |
| Encrusting bryozoan cover | 60| 32.73 | 0.001    | –           | –           | 5.21  | 0.022         | 0.41 | 0.529         | 8.01 |
| (cm² per 100 cm² lamina)³ | 55| 27.63 | <0.001   | –           | –           | 4.51  | 0.034         | 0.61 | 0.448         | 1.01 |

²Square-root transformed. Variance structures: varIdent(Group), varExp(Kelp age); ³square-root transformed. Variance structures: varIdent(Group), varExp(Kelp age); ⁴variance structure: varExp(Current Speed); ⁵variance structures: varIdent(Group), varExp(Current speed)
they all showed the same trend of increasing biomass with increasing effluents (except for phaeophyceans, which were constantly at very low abundances).

For epiphytic bryozoans on the stipe, the biomass increased with farm effluent load (Fig. 5), and with wave exposure level and light exposure. Group was significant \( (p < 0.001, \text{Table 2}) \), and the post hoc contrasts showed that FF-H sites had a significantly higher biomass than reference sites (FF-H vs. Ref-L/H: \( p = 0.034 \), FF-L vs. Ref-L/H: \( p = 0.50 \)). Light exposure and wave exposure level were significantly positively related to biomass (Fig. S2), although the relationship with the latter became insignificant when the site with much higher wave exposure level was excluded (Table 2). In general, the biomass of epiphytes could be very variable between sites and between individual stipes at the same site (Fig. S3). Most stipes were heavily grazed. The lowest levels of grazing were recorded at 2 of 3 FF-H sites (Fig. S4).

### 3.3. Stipe epiphyte composition

The NMDS indicated that both the community composition and the community similarity between stipes (i.e. multivariate dispersion) were affected by farm effluents (Fig. 7). This was confirmed by the statistical analysis. The community composition on stipes in the high effluent load (FF-H) group was significantly different compared to stipes exposed to low effluent load (FF-L vs. FF-H: \( p = 0.008 \)) and the reference (Ref-H vs. FF-H: \( p = 0.006, \text{Table 3} \)). SIMPER analysis revealed that this difference was primarily driven by the higher bryozoan biomass at FF-H sites. Bryozoan biomass contributed 61 and 47% to the dissimilarity between FF-H vs. Ref-H and FF-H vs. FF-L, respectively (Table 4). Among the few other species that contributed to the difference between groups, *Ectocarpus* spp. showed an increase in biomass with increasing effluent load, whereas there was no consistent pattern for the other contributing...
species (Palmaria palmata, Membranoptera alata, Phycodrys rubens, Polysiphonia stricta) (Table 4).

The highest amount of the variation in the epiphytic community was explained by the group factor (PERMANOVA: 13%, Table 3). All control variables except wave exposure level were significant by PERMANOVA, although each explained only 4% or less of the community variation (Table 3). In the constrained 2-dimensional space, the control variables explained more of the variation in the community than the group factor (Fig. 7, Table S4).

The multivariate dispersion of the macroalgae community was significantly different between group levels (ANOVA: $F = 6.64, p < 0.001$), with FF-H sites having the lowest dispersion (Table S5). The dispersion was also significantly different between groups when including the bryozoans (ANOVA: $F = \ldots$)

Table 3. Output of PERMANOVA for the epiphytic community on Laminaria hyperborea stipes collected from fish farm sites (low effluent load: FF-L, high effluent load: FF-H) and reference sites (Ref-L, Ref-H) in the Frøya (Ref-L, FF-L) and Smøla (Ref-H, FF-H) archipelagos. The significance of chosen control variables in explaining the variation in the data, and pairwise comparisons of levels within the a priori set factor ‘group’, are shown ($p$-values based on permutations and adjusted for multiple testing in the former). Bold indicates significance (based on permutations, $\alpha = 0.05$).

| Control variable     | df | SS   | Mean SS | F      | $R^2$ | p    |
|----------------------|----|------|---------|--------|-------|------|
| Group                | 3  | 3.462| 1.154   | 4.813  | 0.13  | 0.001|
| Kelp age             | 1  | 0.881| 0.881   | 3.676  | 0.03  | 0.001|
| Kelp density         | 1  | 1.172| 1.172   | 4.888  | 0.04  | 0.001|
| Current speed        | 1  | 0.616| 0.616   | 2.570  | 0.02  | 0.002|
| Wave exposure        | 1  | 0.325| 0.325   | 1.357  | 0.01  | 0.150|
| Light exposure       | 1  | 0.697| 0.697   | 2.905  | 0.03  | 0.002|
| Residuals            | 84 | 20.137| 0.240   | 0.74   |       |      |
| Total                | 92 | 27.290| 1.00     | 1.00   |       |      |

Pairwise test: group  | $F$ | $R^2$ | p    |
|----------------------|-----|-------|------|
| FF-L vs. Ref-L       | 0.803| 0.02  | 0.754|
| FF-H vs. Ref-H       | 12.047| 0.19  | 0.006|
| FF-L vs. FF-H        | 5.283| 0.10  | 0.008|
| Ref-L vs. Ref-H      | 1.584| 0.04  | 0.642|

Table 4. Results from SIMPER analysis of Laminaria hyperborea stipe epiphytes sampled from fish farm sites. Cumulative contribution of species up to 90% of the dissimilarities between tested group-pairs is presented, with the average biomass (standardized to 10 cm² ungrazed stipe) for each contributing species. Bold indicates the highest biomass for each species within each group-pair. Percent in brackets refers to overall dissimilarity for the respective group-pairs (see Table S3 for species authorities).

| Farm effect        | Cumulative contribution | Average biomass (g) |
|--------------------|-------------------------|---------------------|
| FF-L vs. Ref-L     | (91%)                   | FF-L                |
| Phycodrys rubens   | 0.26                    | 0.643               |
| Palmaria palmata   | 0.47                    | 0.031               |
| Bryozoa            | 0.62                    | 0.272               |
| Polysiphonia stricta| 0.72                   | 0.051               |
| Membranoptera alata| 0.79                   | 0.130               |
| Ulva lactuca       | 0.83                    | 0.069               |
| Delesseria sanguinea| 0.87                  | 0.180               |
| Ectocarpus spp.    | 0.91                    | 0.033               |
| FF-H vs. Ref-H     | (82%)                   | FF-H                |
| Bryozoa            | 0.61                    | 1.256               |
| Palmaria palmata   | 0.69                    | 0.468               |
| Phycodrys rubens   | 0.76                    | 0.046               |
| Membranoptera alata| 0.82                   | 0.092               |
| Ectocarpus spp.    | 0.87                    | 0.278               |
| Polysiphonia stricta| 0.91                   | 0.021               |
| FF-L vs. FF-H      | (83%)                   | FF-H                |
| Bryozoa            | 0.47                    | 1.256               |
| Phycodrys rubens   | 0.64                    | 0.046               |
| Palmaria palmata   | 0.71                    | 0.468               |
| Membranoptera alata| 0.78                   | 0.092               |
| Ectocarpus spp.    | 0.83                    | 0.278               |
| Delesseria sanguinea| 0.87                  | 0.000               |
| Polysiphonia stricta| 0.90                   | 0.021               |
21.123.91, \( p = 0.010, \) Fig. 7), with the high bryozoan biomass at FF-H sites (Fig. 5) further decreasing the dispersion at these sites by 30% (Table S5).

### 3.4. Lamina epiphytes

For epiphytic algal biomass on the lamina, group was a significant factor in the model (\( p = 0.011, \) Table 2), although post hoc comparisons of farm vs. reference were insignificant (FF-H vs. Ref-L/H: \( p = 0.304, \) FF-L vs. Ref-L/H: \( p = 0.322 \)). The model predicted that farm sites would have lower levels of epiphytic algae than the reference sites if all other variables were equal. This was not apparent from a plot of epiphytes by group, which showed a trend of higher macroalgal biomass at farm sites (FF-L and FF-H; Fig. 8). The model results were most likely caused by the varying kelp density, wave exposure, and light between the sites, all of which were significantly negatively associated with epiphyte biomass (Fig. S5). Again, the importance of wave exposure level was mainly driven by the 1 high-exposure site. The epiphytic biomass was mostly made up of brown algae categorized as Ectocarpales thread (on average 77% of the lamina macroalgal epiphytes by weight).

Cover of encrusting bryozoans on the lamina (predominately Membranipora membranacea and Elec- trina pilosa) was significantly different between group levels (\( p < 0.001, \) Table 2). Again, the model predicted a lower cover at farm sites (Fig. S6), and kelp density was a significant factor (Table 2). FF-L had a significantly lower bryozoan cover compared to the other groups (post hoc: FF-H vs. Ref-L/H, \( p = 0.736; \) FF-L vs. Ref-L/H, \( p = 0.011 \)), but had a higher presence of colony-forming tunicates (Fig. 8). The density

![Epiphytes present on Laminaria hyperborea kelp canopy laminas collected from fish farm sites (low effluent levels: FF-L; high effluent levels: FF-H) and reference sites (Ref-L, Ref-H) in the Frøya (Ref-L, FF-L) and Smøla (Ref-H, FF-H) archipelagos, Norway. (A) Algal epiphytes; (B,C) encrusting and erect bryozoans; (D) colony-forming tunicates. Note different units and use of different square-root scales on the \( y \)-axes. Different letters denote significant difference (Dunnett’s post-hoc, \( \alpha = 0.05 \)). For plot explanation, see Fig. 5](image-url)
of erect bryozoan tufts (identified to *Crisia* spp.) was slightly higher at FF-L and Ref-H compared to FF-H and Ref-L (Fig. 8). The natural variation in epiphytic fauna was in general high and could be very variable both within and between sites.

4. DISCUSSION

Large-scale salmonid fish farms are increasingly situated in exposed locations where soft-bottom communities have shown high resilience to the large amounts of nutrients released (e.g. Keeley et al. 2013, 2019). However, the impact of these effluents on hard-bottom communities, such as kelp forests, has received little focus. We have demonstrated that some components of the epiphytic community living on *Laminaria hyperborea* canopy plants are impacted by fish farming effluents in such dispersive environments. Bryozoan biomass on the kelp stipes increased with proximity to high-effluent fish farms, resulting in an altered and more homogeneous stipe community composition. The epiphyte load on the kelp lamina was impacted by wave exposure and kelp density, but a clear connection with fish farming effluents was not found. In general, natural variables, such as wave exposure, kelp age, and kelp density, had a very strong influence on variation within epiphyte communities, making further explorations of the interaction between kelp epiphytic communities and aquaculture necessary to understand the extent of the impacts.

4.1. Stipe-associated epiphyte biomass and community structure

The response of the stipe epiphytes to the effluent level was consistent with the expectation that dissolved nutrients and particulate matter released from fish farms may supply extra nutrition to the surrounding community. Filter feeders may be able to utilize both the dissolved nutrients and the POM released from farms, as this can increase their food supply, directly in the case of POM (Lojen et al. 2005) or via an increased abundance of phytoplankton with nutrients (Worm & Lotze 2006). Bryozoans tend to feed on small phytoplankton (Winston 1977), and this could explain the strong association between bryozoan biomass and high effluents. Higher bryozoan cover with increasing dissolved nutrients has also been observed on seagrass *Posidonia oceanica* (Balata et al. 2010), but studies looking at uptake of farm-derived DIN or POM for these animals is limited. Bryozoans (species not specified) at a seabream farm in the Red Sea took up little nitrogen from POM compared to other filter feeders (Lojen et al. 2005), but food selection and uptake rates vary between species (Winston 1977, Riisgård & Maríquez 1997) and could therefore differ for the bryozoans in the present study.

Macroalgae can take up DIN released from farms (Carballeira et al. 2013) and incorporate ammonium (Deutsch & Voss 2006), and it was anticipated that this should benefit small, fast-growing epiphytic algae species particularly. Although not significant at the post hoc test level, the results suggest an increase in total macroalgae biomass with effluents, in addition to the increase in filamentous opportunistic *Ectocarpus* spp. and a more homogeneous macroalgae community at the high-effluent sites. This is indicative of a farm impact. The predicted farm effect on local DIN levels suggests that dissolved nutrients are diluted at a much faster rate in this dispersive area compared to reports for smaller farms at less exposed locations (Sanderson et al. 2008, Jansen et al. 2018). This could explain why the trend on total macroalgae biomass was not clearer, and why the patterns within morphological and taxonomic groups were not clearly affected. The chosen methodology could also have contributed to the larger response of bryozoans compared to macroalgae; bryozoan-covered macroalgae were counted as 'Bryozoa', and therefore any extra growth of macroalgal epiphytes that later became extensively covered by bryozoans would have contributed to bryozoan differences rather than macroalgal differences. Phytoplankton may also have played a role; by having a higher growth rate than macroalgae, phytoplankton might take up DIN before the macroalgae have time to respond (Hadley et al. 2015). Higher phytoplankton biomass could potentially also benefit the bryozoans, although in this dispersive environment it is not likely that this would only benefit local bryozoan growth.

A more homogeneous epiphytic community, as observed in this study at sites exposed to high effluent levels, is a known response of communities exposed to stress, and has been reported for macroalgae communities (Oh et al. 2015) and the epiphytic community on seagrass (Balata et al. 2010). An important question following these results is how this response could affect the associated fauna. *L. hyperborea* forests can support over 500,000 animals m$^{-2}$, with a single kelp thallus supporting 80–90 faunal species on average (Christie et al. 2009). Faunal diversity and abundance in kelp forests increase with habitat diversity (Eilertsen et al. 2011, Norderhaug et al. 2014), hence lower heterogeneity could nega-
tively affect the wide range of faunal species that depend on the kelp forest as a habitat. The change in community composition caused by the high bryozoan biomass could further alter the faunal composition of kelp forests, as mobile fauna are well known to be affected by the community structure of different macroalgae habitats (e.g. Wikström & Kautsky 2007). Some faunal species also have preferences for epiphytic algae with specific morphologies, influenced by characteristics such as interstitial space, surface, and colour (Hacker & Steneck 1990, Norderhaug 2004, Christie et al. 2007, 2009, Eilertsen et al. 2011), hence algae encrusted with bryozoans may be less favourable for such faunal species. The changes caused by farm effluents could thus have implications for the mobility patterns of the faunal community that directly depends on the stipe community. This in turn could affect the food availability for higher trophic levels, such as the economically important Atlantic cod Gadus morhua, saithe Pollachius virens, and seabirds that forage in the kelp forest (Fredriksen 2003, Norderhaug et al. 2005).

The impacts on community and bryozoan biomass were found at the sites where the fish farms were at the end of their production cycle (FF-H). This could indicate that this effect was short-term and that epiphyte presence and biomass can respond quickly to effluent levels within a year. Compared to that seen in benthic soft-bottom macrofaunal communities exposed to fish farm effluents, this would be a faster response (Macleod et al. 2004, Keeley et al. 2019). This could imply that L. hyperborea forest as habitat is more resilient to fish farming than other systems. The natural seasonal fluctuation in epiphytic biomass, which peaks in the summer and decreases in winter (Whittick 1983) could mediate recovery. It is likely also related to the dispersive nature of the study area, as more dispersive sites generally show higher resilience (Keeley et al. 2013, Valdemarsen et al. 2015). Recovery speed should be further explored, e.g. by including samples from farms at the end of their fallowing period, or examining areas where farms are being moved.

Factors other than farm effluents also play a role in epiphyte abundance and composition. Wave exposure and kelp age are reported to positively affect stipe epiphyte density (Norderhaug et al. 2012, Bekkby et al. 2015, Steen et al. 2016) and composition (Pedersen et al. 2014), which was mostly supported by our results for both macroalgae and bryozoans (depending on the inclusion of the high-exposure site; Table 2). The total stipe epiphytic biomass reported here was low compared to other reports for L. hyperborea stipes (Norton et al. 1977, Whittick 1983, Steen et al. 2016), most likely caused by the observed high grazing activity in the study area. Large grazing fronts of the sea urchin Echinus esculentus (Linnaeus, 1758) were regularly observed and are known to feed on algae and associated epiphytes (Jorde & Klavestad 1963, Comely & Ansell 1988). Sea urchins can also exploit and assimilate farm waste (White et al. 2017, 2018), and may benefit from intensive farming. This is a potential ecological factor that was not within the scope of this study but needs to be further examined. The grazing may have affected our results in 2 ways. As L. hyperborea stipe communities show vertical zonation (Whittick 1983, Christie et al. 2007), the upper-stipe epiphyte community could have been disproportionately represented in this study (as the lower part of stipes were often grazed). However, this is unlikely to have affected the main results, as these zonation patterns have only been reported for rhodophytes, and not for bryozoans and Ectocarpus spp. Secondly, during short-term increases in nutrients, grazing can mediate the growth of epiphytes (Balata et al. 2010) and macroalgae communities (Karez et al. 2004, Russell & Connell 2007). Top-down control of epiphytes via grazing could therefore have limited any epiphyte biomass increase in response to farm effluents, making impacts harder to detect. Given this, the low level of replication at the site level in this study (n = 3), and the substantial influence of natural variables on epiphyte communities, our detection of a significant relationship between fish farm effluents and kelp epiphytes is highly noteworthy.

4.2. Lamina epiphytes

In contrast to the stipe, there were no significant increases in lamina-associated epiphyte abundance that could be related to nutrients from fish farming, suggesting that the kelp lamina could be more resilient to an increased epiphyte load than the kelp stipe in dispersive environments. For the range of wave exposure levels modelled at our sampling sites, lamina epiphyte load decreases with exposure (Pedersen et al. 2012), which could contribute to this potential higher resilience. The way nutrients are released from fish farms could also have contributed to the lack of a clear response. Along the southern coast of Australia, macroalgal epiphyte load on lamina of the kelp Ecklonia radiata increased significantly under high and constant nitrogen conditions (1.8 times higher than ambient waters) (Russell et al. 2005). The elevation in nutrient levels was compara-
ble to the maximum that was predicted at the high-effluent farm sites herein, but the contrasting results could be related to the nature of nutrient pulses from fish farms. Longer, constant nitrogen pulses have a higher impact on epiphytic communities than several shorter-duration pulses (Worm & Sommer 2000), and the nitrogen plume from fish farms would be much more variable compared to the artificial nutrient source used by Russell et al. (2005). However, the dominant lamina epiphytes were thread-forming Ectocarpales algae, thus including the stipe algae (*Ectocarpus* spp.) that were found to respond to farm effluents. The differing response of the epiphytic algae herein compared to that observed on *E. radiata* could also be related to oligotrophic conditions at the Australian study sites (Russell et al. 2005), different levels of wave exposure (not reported for Australian sites), or different anti-fouling mechanisms between the 2 kelp species (reviewed by Bartsch et al. 2008).

The lowest cover of encrusting lamina bryozoans was found at the sites with low-effluent fish farming. However, a higher cover of colony-forming tunicates was observed at these sites, which could indicate competition for space between epiphytic invertebrates. Competition for space between colony-forming invertebrates on host plants is common (Boaden et al. 1976, O’Connor et al. 1980). Other factors not examined in the present study could also have played a role in epiphyte abundance, for example, the growth rate of kelp (Andersen et al. 2011) or grazer density (Worm & Lotze 2006, Balata et al. 2010). In addition, both lamina bryozoans and epiphytes showed a negative relationship with kelp density. One potential explanation for this relationship is that higher kelp density could directly reduce epiphyte settlement via increased mechanical abrasion by sweeping laminas, as shown for settlement of sessile invertebrates in the understorey community (Jenkins et al. 1999, Connell 2003). Sampling time could also have had an effect; sampling was conducted in August, and a higher lamina epiphyte diversity is present in May compared to August for kelp species *Saccharina latissima* and *Laminaria digitata* (Carlsen et al. 2007), and this could also be true for *L. hyperborea*. Hence, sampling laminas earlier in the summer could have yielded different results.

The epiphytic kelp community documented in this study was highly variable both within and between sites at small scales, as has also been found in previous work (Karez et al. 2004, Oh et al. 2015). For impact studies, this means that a high number of sites are needed to detect impacts, especially when abiotic and biotic factors, which can also affect the community, vary between sites. Although we sampled from relatively many sites for this type of study and a number of factors could be controlled for (e.g. the abiotic modelled factors, kelp density, depth), the resolution of the abiotic modelled factors could miss small-scale variations that influence the kelp community.

### 4.3. Future perspectives

Changes in epiphytic communities on perennial algae can be seen as early warning signs of eutrophication (Balata et al. 2010) and can, over time, be followed by a degradation of the perennial species itself (e.g. Worm & Sommer 2000). Eutrophication has been a driver implicated in shifts from kelp forests to ephemeral algae communities along the coasts of Norway, Australia, Brazil, Russia, and in the Mediterranean (Filbee-Dexter & Wernberg 2018), although the mechanisms behind these shifts can be complex and hard to discern. The natural variation is high in these communities, which often requires a rigorous sampling regime to be able to identify real changes. At the level of sampling conducted herein, impacts from nutrients were found on the epiphytic stipe community, which could have implications for the fauna associated with this habitat and should be further explored. More knowledge on the interaction between kelp density and lamina epiphytes could also further our understanding of the mechanism(s) behind degradation of kelp forests seen worldwide. Although no increase in lamina epiphytes was detected with increasing fish farm effluents, elevated nutrients derived from fish farming may interact with other stressors in unpredictable ways. Climate change is one potential stressor, as higher temperatures have negative impacts on kelp (Araújo et al. 2016, Krumhansl et al. 2016) while promoting recruitment and growth rates of bryozoans such as *M. membranacea* (Saunders & Metaxas 2008, Scheibling & Gagnon 2009). The fish-farming industry is expected to expand quickly in the future, both in Norway (NFD 2014) and globally (FAO 2018), and dispersive coastal sites will most likely be favoured due to their higher resilience. More understanding of the interactions between kelp forest and nutrients from aquaculture is needed to be able to monitor, detect potential changes, and underpin good management of kelp forest ecosystems in the future.

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