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# Environmental impact of kelp (*Saccharina latissima*) aquaculture

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ABSTRACT

The aim of the study was to assess the effect of seaweed cultivation on the coastal environment. We analysed a multitude of environmental parameters using an asymmetrical before after control impact (BACI) design, comparing the seaweed farm (impact) with multiple unaffected locations (controls). The seaweed farm had a significant positive effect on benthic infauna ($p < 0.05$) and was found to attract 17 mobile faunal and 7 other seaweed species, indicating that the farmed crop may provide habitat to mobile faunal species. A light attenuation of approximately 40% at 5 m depth was noted at the peak of the seaweed biomass just before harvest. No changes were observed in benthic oxygen flux, dissolved nutrient concentrations, and benthic mobile fauna between farm and control sites. These results show that seaweed aquaculture has limited environmental effects, especially compared to other forms of aquaculture such as fish and bivalve farming.

## 1. Introduction

Seaweed cultivation is gaining increased interest world-wide for both food and non-food applications (Holdt and Kraan, 2011). Currently, the global seaweed aquaculture sector produces over 30 million tonnes, but is primarily dominated by two Asian countries, namely China (47.9%) and Indonesia (38.7%) (FAO, 2018). In order to meet future demands, seaweed aquaculture has to expand further beyond Asia into other regions with high production potential, such as the temperate regions of the North Atlantic. However, this development may be hampered by environmental concerns related to well-established impacts of aquaculture, more specifically fed fish and shellfish farming (FAO, 2018; Naylor et al., 2000; Wu, 1995). This includes effects on the benthic environment due to bio-deposition of (pseudo) faeces (Crawford et al., 2003; Edwards, 2015), genetic effects on wild fish populations of escapees (Jensen et al., 2010), transfer effects of associated pathogens and parasites (Arechavala-Lopez et al., 2013), and local alterations in biodiversity at the culture sites (Diana, 2009).

Seaweed farming is often considered as the least environmentally damaging form of aquaculture (Folke et al., 1998; Roberts and Upham, 2012), with a number of ecosystem services offered by the seaweed (Hasselström et al., 2018). In temperate regions, natural communities of the kelp serve key ecosystem functions in sublittoral marine ecosystems, being important perennial primary producers. Known to be habitat-creators they provide shelter, feeding and nursery areas for a highly diverse number of associated fauna (Christie et al., 2009). Kelp species have previously been identified as suitable candidate for the development of seaweed cultivation in new temperate waters (Kerrison et al., 2015). They are typically farmed on anchored long-lines suspended by buoys approximately 1–2 m below the surface. The culture period is from autumn until late spring, and there is no need for fresh-water or fertilizer, as the seaweed assimilates nutrients from the environment for their growth. Kelp farms are generally located in near-shore waters with sufficient water flow where they increase biological complexity to the otherwise structureless seawater column providing a three-dimensional habitat; such increases in local rugosity could benefit mobile fauna (e.g. invertebrates and fish), and anchors and other structures provide benthic substrate. In addition, seaweed aquaculture can mitigate eutrophication through the uptake of nutrients upon harvest (Seghetta et al., 2016).

Thus far, environmental risks associated with seaweed farming have mainly been assessed qualitatively (Campbell et al., 2019; Roberts and Upham, 2012; Titlyanov and Titlyanova, 2010; Wood et al., 2017), except for eucheumoid algae (i.e. *Kappaphycus* and *Eucheuma*) that are bottom-cultured in tropical and sub-tropical regions (Bergman et al., 2001; Eklöf et al., 2005; Eklöf et al., 2006; Ólafsson et al., 1995). In addition, large bottom cultivations of *Gracilaria* have shown to cause modification to the environment (Buschmann et al., 2001), such as sediment modification, infauna abundance, recruitment and abundance of sessile invertebrates and herbivores (Buschmann et al., 2001). Various potential drivers for environmental change caused by seaweed

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farming have been suggested by Campbell et al. (2019), such as the absorption of light, nutrients, carbon, and kinetic energy by a seaweed farm, which could potentially lead to alterations in the local environment. Numerous consequences of seaweed cultivation have been suggested. These include "crop-to-wild" gene flow by the release of reproductive material (Loureiro et al., 2015; Valero et al., 2017), habitat provisioning for diseases, parasites and the introduction of non-native species (Badis et al., 2019; Loureiro et al., 2015; Ribera and Boudouresque, 1995), effects on planktonic, epifauna, and megafauna species (Aldridge et al., 2012; Campbell et al., 2019), and benthic impacts through the release of dissolved and particulate matter by the seaweed biomass (Zhang et al., 2009; Zhou, 2012). However, there is a limited body of work providing primary data on environmental effects of kelp aquaculture. The few studies assessing the environmental effects associated with kelp farming indicate no or minimal impacts, but also highlight that scale and location of the seaweed farm might have a significant effect (Buschmann et al., 2014; Walls et al., 2017; Walls et al., 2016; Zhang et al., 2009).

Here we present an assessment of potential environmental impacts of a kelp (*Saccharina latissima*) farm on the Swedish west-coast. The assessment was based on an array of environmental parameters (i.e. benthic infauna and benthic mobile macrofauna, benthic oxygen flux, associated mobile and sessile organisms, dissolved nutrient composition and concentrations, and shading) during a two-year cultivation period using an asymmetrical before after impact control (BACI) design.

## 2. Materials and methods

### 2.1. Site description

The cultivation site is located in the Koster archipelago on the Swedish west coast within the Skagerrak region of the North Sea (Fig. 1). The Kosterhavet national park was formed in 2009 and is one of the most species rich marine areas in Sweden (Morf, 2010). Natural kelp populations at the rocky shores of the Swedish west coast are present from a depth of about 1 m. Governed by changes in atmospheric pressure and wind the coastline experiences a relatively small tidal range ( < 0.3 m), but differences between high and low water levels up to 2 m still occur (Johannesson, 1989). The 10-year (2008–2018) mean salinity of the surface water down to 10 m close to the farm site during the outgrow period (i.e. October until May) is 27.6 ± 3.3 psu and a temperature of 7.0 ± 4.2 °C (mean ± sd, n = 253) (SMHI, 2019). The cultivation period of kelp starts in September/October and the biomass is harvested in April/May. The local strains of *S. latissima* that were used in this study were collected from within the Kosterhavet National park (58°83.63′ N, − 10°99.42′ W). Seeded lines were produced through conventional cultivation techniques; spore release was induced and the spore solution (2000 spores/mL autoclaved seawater) was evenly distributed in tanks with collectors (Forbord et al., 2018). The motile spores were allowed to attach to the cultivation lines (1.2 mm diameter nylon), and further development of seedlings was done under laboratory conditions. The seeded cultivation lines were coiled around fabric long lines and attached to buoys with an anchor at each end. The substrate was placed at a depth of 1.5 m, with 4 m between each horizontal long line. The depth underneath the farm is approximately 10 m and the bottom substrate consists primarily of mud/sand, with no other macrophyte species present underneath the farm.

### 2.2. Sampling design

The experiment was designed using an asymmetrical approach (Underwood, 1991, 1994; Walls et al., 2017), with the seaweed farm as the impacted site (58°85.93′ N, − 11°06.82′ E), and four control locations (C1: 58°85.61′ N, − 11°01.79′ E; C2: 58°85.80′ N, − 11°00.89′ E; C3: 58°87.03′ N, − 11°01.80′ E; C4: 58°87.02′ N, − 10°99.60′ E) that were randomly selected from localities with a similar benthic sediment profile and depth as the impacted site. The distance to the farm was between 1.8 and 2.7 km, which was considered far enough for the

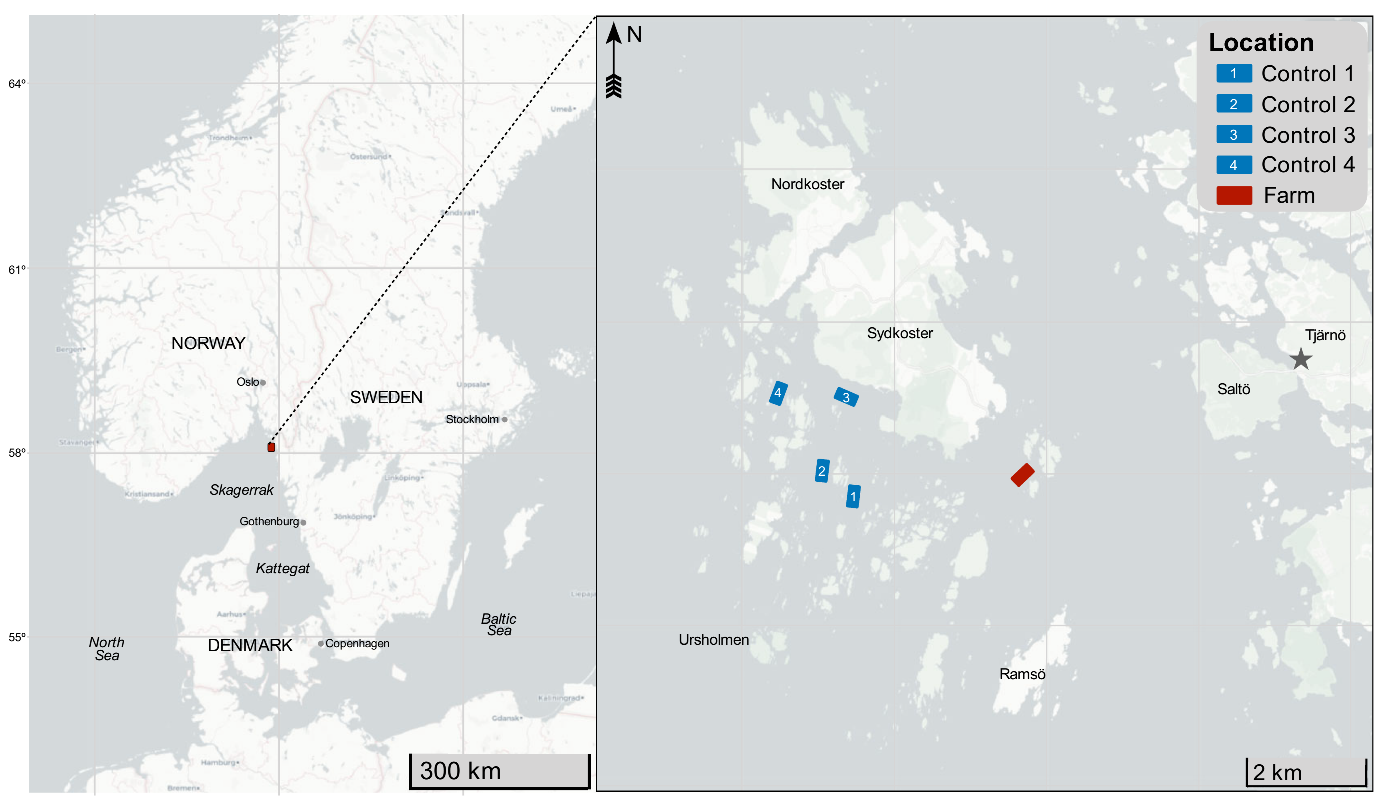


**Fig. 1.** The location of the seaweed farm and the four control sites within the archipelago of the Kosterhavet national Park, Sweden. The grey star marks the location of Tjärnö Marine Laboratory.

control locations to be unaffected by the seaweed farm but close enough to experience similar environmental conditions (Fig. 1). All sites were sampled during four sampling campaigns in February and May in 2016 and 2017, respectively, unless stated otherwise. All measurements and samples were taken randomly within a 2 ha (100 × 200 m) grid at the farm site or control locations. For logistical reasons the benthic oxygen flux measurements using benthic landers were done at the farm and three control locations (C1–3).

### 2.3. Benthic oxygen flux

Benthic oxygen flux (mmol $m^{-2}$ $day^{-1}$) was measured in situ using two benthic chamber landers: the small Göteborg benthic lander and the inner frame of the big Göteborg benthic lander (e.g. Almroth et al., 2009; Ståhl et al., 2004; Tengberg et al., 2003). The small lander has two and the big lander four open-bottomed incubation chambers. Each chamber incubated 400 $cm^2$ of sediment with up to 14 L of overlying bottom water. Each chamber on both landers was equipped with 10 injection/sampling syringes, a stirring device, and sensors for measuring dissolved oxygen, salinity and turbidity at 1-minute interval. Time series of chamber oxygen data were used to calculate oxygen flux values, and the in situ incubated water height essential for the flux calculation was obtained from chamber salinity measurements before and after injection of known volume of fresh water. Both landers were lowered to the sea floor with a rope vertically and very slowly to avoid any disturbance of sediment surface. Chamber ventilation lids were kept open during the lowering and initial ventilation phase (2–3 h of ventilation in total) to make sure that any surface water trapped by chambers was ventilated out and that ambient bottom water conditions were established within the chambers. The landers were deployed during morning to afternoon and from late afternoon to early next morning (for about 7–8 h and 17–18 h including the ventilation phase, respectively). The actual initial period, after the ventilation phase, used to calculate the oxygen flux was approximately 0.1–6 h hours. A more detailed description of the benthic landers and benthic oxygen flux calculations can be found in the supplementary material.

### 2.4. Benthic infauna

To examine changes in species composition of benthic infauna three sediment samples were randomly taken at the seaweed farm and the four control locations (C1–4) during each sampling time using a van Veen grab (0.1 $m^2$). All sediment samples were transferred into plastic containers, transported to the laboratory, and sieved through a 1 mm mesh. Any retained material was stored separately in plastic flasks and fixed in 70% ethanol pending laboratory analyses. To compare species diversity between sediment samples we calculated the rarefaction and the effective number of species. The rarefaction was calculated for a subset of the samples that contained 10 or more individuals, using the *rarefy* function of the *vegan* package in R (Oksanen, 2013). The effective number of species was calculated by converting the Shannon-Wiener entropy index exponentially (Jost, 2006), which was analysed using the *diversity* function of the *vegan* package. The benthic quality index (BQI) was also calculated for each sediment sample, as proposed for the Skagerrak region of the North Sea by Leonardsson et al., 2015. More details on the theory and calculation of the BQI can be found in (Rosenberg et al., 2004) and (Leonardsson et al., 2015; Leonardsson et al., 2009). The BQI borders for the classification status according to the EU Water Framework Directive (WFD) were set as follows: *Bad*: $\leq 3.4$; *Poor*: $3.4 \leq 6.9$; *Moderate*: $6.9 \leq 10.3$; *Good*: $10.3 \leq 13.9$; and *High*: $\geq 13.9$ (HavsARKiv, 2013).

### 2.5. Benthic mobile macrofauna

Effect of the seaweed farm on benthic mobile macrofauna was assessed using baited cages (Carapax cod cages; bait: five frozen herring per baiting, 300 ± 28 g (mean ± sd, n = 26)). At each sampling location four cages were randomly deployed on the sea floor (approx. 10 m depth). After 3–6 days the cages were inspected, the caught organisms were identified and counted, and the cages were re-baited for a second sampling. The accumulated catch per cages was used for comparing the species composition between the seaweed farm and the control locations (C1–4).

### 2.6. Associated organisms

Organisms associated with the farmed seaweeds was assessed in 2017 right before the harvest of the seaweed biomass by carefully wrapping seaweeds attached to 50 cm of long-line into a net-bag (200 µm mesh size). Five samples were taken randomly within the farm and included the blade, stipe, and holdfast of the attached seaweeds. The sampled seaweeds were rinsed with freshwater and any remaining attached organisms were carefully removed. The sampled associated organisms were fixed in 99% ethanol, stored at room temperature and species number and size was analysed after 48 h. Associated epiphytes were stored in natural seawater at 10 °C, identified to the lowest possible taxon, and absence or presence was denoted within 24 h after sampling.

### 2.7. Dissolved inorganic nutrients

Samples for dissolved inorganic nutrients (i.e. $NO_3^-$ + $NO_2^-$, $NH_4^+$, $PO_4^{3-}$, and $SiO_2$) were randomly collected at 2 and 5 m depth (n = 5) within all locations in February and May of 2016 and 2017. Samples were taken by carefully deploying a syringe (10 mL) attached to one rope, a second rope with a weight was released whereby the weight pulled out the syringe at the appropriate sampling depth (i.e. 2 or 5 m). Sampled seawater was syringe filtered (0.2 µm pore size acetate cellulose membrane) into 10 mL polyethylene vials immediately after collection and transported on ice to the laboratory before cold storage (−20 °C) and subsequent analysis using a SEAL Analytical QuAAtro AutoAnalyser (Seal Analytical, UK).

### 2.8. Shading

Light loggers (Onset HOBO® Pendant UA-002-64) were used to measure light attenuation due to the seaweed farm. Loggers were randomly deployed at a depth of 5 m at three locations within the seaweed farm and the control sites (C1–4). Light was measured in lux at a 30-minute interval during the last 8 weeks of the cultivation before the harvest of the biomass in May. The mean from 11:00 h until 13:00 h (i.e. 5 data points per day) was used as daily average for statistical analysis. To estimate the biological relevant light irradiance, illuminance was converted to photosynthetically active radiation (PAR) as follows: 50 lx was approximated to 1 µmol photons $m^{-2}$ $s^{-1}$ (Fortes and Luning, 1980).

### 2.9. Statistical analysis

Univariate linear regression analyses were performed using the R software Version 1.1.423 (R Core Team, 2018), and prior to all univariate analysis data was graphically analysed and transformed if necessary. Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) and principle component analysis (PCO) were performed in PRIMER-e (Ivybridge, UK). Model simplifications where applied according to the principle of parsimony by pooling non-significant factors ($p \geq 0.25$) when using PERMANOVA and univariate linear regression models were compared using the AIC-values of which the model design with the lowest value by a margin of −2 was used in the analysis. PERMANOVA tests were carried out using 9999 unrestricted permutations. If the PERMANOVA test was found to be significant ($p \leq 0.05$), the analysis was accompanied by a test for homogeneity of multivariate dispersions (PERMDISP) to determine possible reasons for the rejection of the null hypotheses as PERMANOVA can be sensitive to sample dispersion (Anderson et al., 2006).

The BACI sampling design used to test for environmental effects of the seaweed farm differed somewhat between the different measured variables. The effect on benthic oxygen flux, benthic mobile macrofauna, benthic infauna, and the diversity measures (rarefaction, effective number of species, and BQI) was compared between years ('Before' is 2016 and 'After' is 2017) because the putative impact on these variables was expected to be fixed between years. Effects on the dissolved inorganic nutrients, however, were compared between sampling periods within years ('Before' is February and 'After' is May for both 2016 and 2017) as dissolved inorganic nutrients were not expected to be affected by the seaweed farm between years.

Changes in species richness and abundance of benthic infauna as well as benthic mobile macrofauna were tested using PERMANOVA and PCO using Bray-Curtis dissimilarities. The dissolved nutrients data were analysed using PERMANOVA and PCO using Euclidian distance dissimilarities. Benthic oxygen flux and benthic infauna diversity (rarefaction, effective number of species, and BQI) were tested using the mixed linear regression model *lmer* function from the lme4 package in R. The following model design was applied in the statistical test of benthic oxygen flux: 'Farm vs. Control' and 'Period' as fixed factors; 'Locality nested under Farm vs. Control', 'Sampling Time nested under Period' and 'Site nested under the interaction between Locality and Sampling Time' as random-factors. The model for benthic infauna and benthic mobile macrofauna was identical except that 'Site' was not included in the model. The statistical test of dissolved nutrients was performed using the following model design: 'Farm vs. Control', 'Period', and 'Depth' as fixed factors; 'Locality nested under Farm vs. Control' as random-factor. Changes in light penetration (i.e. shading), using pooled data from the four control locations, was tested by analysis of variances (one-way ANOVA) using linear regression model *lm* function, with 'location' (farm or controls) and 'date' as fixed factors. The estimated environmental impact, or how much the change differed between the control and farm sites, for the univariate test was assessed using the least square means (lsmeans) for calculating the BACI-contrast according to: $\text{Control}_{\text{AFTER}} - \text{Control}_{\text{BEFORE}} - \text{Farm}_{\text{AFTER}} + \text{Farm}_{\text{BEFORE}}$ (Schwarz, 2015).

## 3. Results

### 3.1. Benthic oxygen flux

No evidence was found that the seaweed farm had a significant effect on oxygen uptake of the sediment compared to the control sites between periods (i.e. the BACI-effect) (Table 1). The estimated change in oxygen uptake (i.e. the BACI-contrast) was $-8.95$ mmol m$^{-2}$ day$^{-1}$ (SE = 6), with lsmeans ± SE (in mmol m$^{-2}$ day$^{-1}$) of: $\text{Control}_{\text{BEFORE}} = -32.5 \pm 12.6$, $\text{Control}_{\text{AFTER}} = -41.5 \pm 12.6$, $\text{Farm}_{\text{BEFORE}} = -17.9 \pm 16.3$, and $\text{Farm}_{\text{AFTER}} = -18.0 \pm 16.4$. The differential change was mainly a result of site-to-site variation between control localities, as the mean oxygen uptake at the farm location remained largely unchanged after the placement of the seaweed farm (Fig. 2). In addition, there was significant variability in oxygen uptake of the sediment among 'Sampling times', 'Localities', and 'Sites' within localities, with highest variance contribution from 'Sampling time' (Table 1). Across all sites, oxygen uptake was higher in April ($-43.13 \pm 2.46$ mmol m$^{-2}$ day$^{-1}$ (mean ± SE, n = 52)) compared to February ($-21.94 \pm 2.06$ mmol m$^{-2}$ day$^{-1}$ (mean ± SE, n = 50)) (see Fig. 2).

### 3.2. Benthic infauna

A total of 65 benthic infaunal taxa and 1507 individuals were recorded at the four control locations or the farm site during the four sampling campaigns in February and May of 2016 and 2017 (see Table S1 for full species list and abundances). There was no significant BACI-effect on the benthic infauna species composition (Table 2). However, the PCO analysis showed a larger separation after impact between the farm site and the control locations (Fig. 3A and B). Vector plots using Pearson correlations showed that several species had increased at the seaweed farm after the impact. The species showing the greatest increase were: *Philine quadripartita* (gastropod), *Scoloplos armiger* (polychaeta), *Ampelisca tenuicornis* (amphipod), *Echinocardium cordatum* (sea urchin), *Galathowenia oculata* (polychaeta), *Phoronis muelleri* (horseshoe worm (Phoronidae)), *Amphiura filiformis* (brittle star), and *Harmothoe impar* (polychaete) (Fig. 3C and D). In addition, the PERMANOVA showed a significant interactive effect between 'Period' and 'Locality', although the PERMDISP analysis (Table 2) showed that the PERMANOVA result was inconclusive and could be a result of dispersion differences or a combination of dispersion and location differences.

The linear mixed model for the univariate analysis showed that the seaweed farm had a significant BACI-effect on the BQI, the rarefaction (E), effective number of species (D), species abundance (N) and richness (S) (Table 3 and S2). The estimated change in BQI (i.e. BACI-contrast) was $-4.4 \pm 1.2$ (mean ± SE), with lsmeans ± SE of: $\text{Control}_{\text{BEFORE}} = 4.7 \pm 0.9$, $\text{Control}_{\text{AFTER}} = 3.6 \pm 0.9$, $\text{Farm}_{\text{BEFORE}} = 8.2 \pm 1.8$, and $\text{Farm}_{\text{AFTER}} = 11.6 \pm 1.8$, demonstrating the significant effect of placement of the seaweed farm on the BQI. The increase in BQI at the farm site compared to a small decrease after impact at the control locations, largely explains this differential change. Accordingly, the ecological status of the impacted location was positively affected by the seaweed farm, and changed from "poor/moderate", to "good" after impact. This pattern was not found for the control locations (Table 4). In addition, the BACI-contrast analysis for the rarefaction, effective number of species, species abundance (N), and species richness (S) showed a similar pattern as the BACI-contrast for the BQI, with higher estimates for the farm site after impact and relatively low variance (Table S2).

**Table 1**
Benthic oxygen flux. Summary of mixed model analysis of variance of the mean benthic oxygen flux (mmol m$^{-2}$ day$^{-1}$) comparing three control sites and the farm location, testing the BACI-effect (i.e. FvC × Period) between 2016 ('Before') and 2017 ('After'). *ndf* and *ddf* indicate the calculated df in the nominator and denominator respectively, $\sigma^2$ is the variance, *sd* is the standard deviation, *LRT* is the likelihood ratio test, the marginal R$^2$ ($R_m^2$) is the variance explained by the fixed effects, and the conditional R$^2$ ($R_c^2$) is the variance explained by both fixed and random effects.

| Source of variance | | | |
|---|---|---|---|
| Fixed effects | ndf, ddf | F-value | p-Value |
| Farm vs. Control = FvC | 1, 2 | 1.75 | 0.319 |
| Period | 1, 2 | 0.10 | 0.786 |
| FvC × Period | 1, 30 | 1.72 | 0.200 |

| Source of variance | | | |
|---|---|---|---|
| Random effects | $\sigma^2$ ± sd | LRT | p-Value |
| Locality(FvC) | 146.83 ± 12.12 | 15.27 | < 0.001 |
| Sampling time(Period) | 205.92 ± 14.35 | 20.76 | < 0.001 |
| Site(Locality(FvC) × Sampling time (Period)) | 74.19 ± 8.61 | 57.01 | < 0.001 |
| Pooled[a] | 32.83 ± 5.73 | | |

Number of obs: 102; groups: Locality(FvC) = 4, Sampling time(Period) = 4, Site(Locality(FvC) × Sampling time(Period)) = 37.
$R_m^2/R_c^2$: 0.152/0.939.
[a] Pooled: Residuals + FvC × Sampling time(Period) + Locality (FvC) × Sampling time(Period) + Period × Locality(FvC).

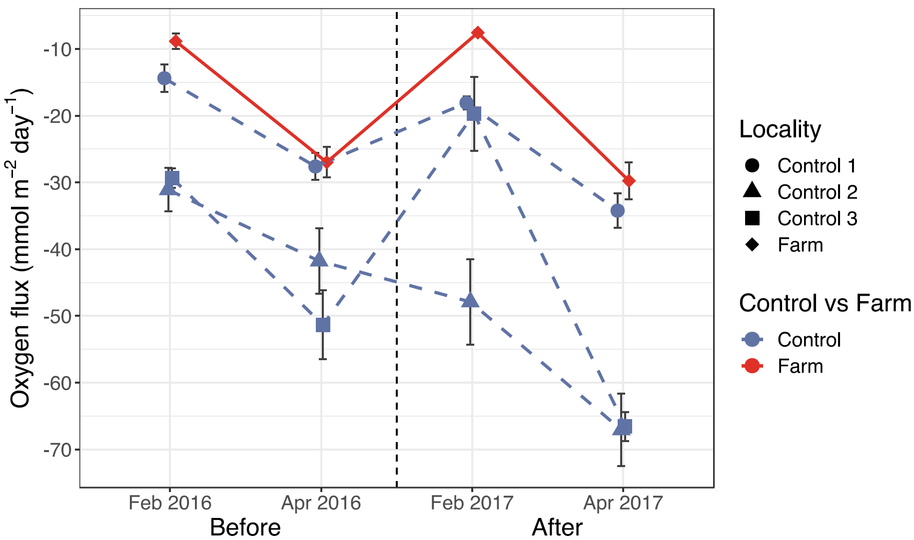


**Fig. 2.** Oxygen uptake by the sediment at three control sites (dashed lines) and the seaweed farm (solid line) of two years (2016/2017) at two time points (February and April). Error bars show SE (n = 6).

**Table 2**
Benthic infauna. Summary of results from PERMANOVA and PERMDISP testing the BACI-effect (i.e. FvC × Period) on the benthic infauna based on Bray-Curtis dissimilarity matrices. df: degrees of freedom; SS: sum of squares; MS: mean squares; Pseudo-F: ratio of within-group variation to between-group variation; P(perm): permutational probability value. Numbers in bold are considered significant ($p < 0.05$).

| | | PERMANOVA | | | | | PERMDISP | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | df1 | df2 | F | P(perm) |
| Fixed effects | | | | | | | | | | |
| Farm vs. control = FvC | 1 | 35,231 | 35,231 | 4.153 | 0.065 | 4348 | | | | |
| Period | 1 | 6153 | 6153 | 1.326 | 0.314 | 9780 | | | | |
| FvC × Period | 1 | 5291 | 5291 | 1.196 | 0.092 | 9899 | | | | |
| Random effects | | | | | | | | | | |
| Locality(FvC) | 3 | 21,435 | 7145 | 5.073 | **< 0.001** | 9920 | 4 | 54 | 1.124 | 0.518 |
| Sampling time(Period) | 2 | 3285 | 1643 | 1.166 | 0.293 | 9922 | | | | |
| FvC × Sampling time(Period) | 2 | 3089 | 1544 | 1.097 | 0.353 | 9917 | | | | |
| Period × Locality(FvC) | 3 | 12,008 | 4003 | 2.842 | **< 0.001** | 9910 | 9 | 49 | 3.928 | **0.017** |
| Pooled[a] | 45 | 63,376 | 1408 | | | | | | | |
| Total | 58 | 153,220 | | | | | | | | |

[a] Pooled: Residuals + Locality(FvC) × Sampling time(Period).

### 3.3. Benthic mobile macrofauna

At the four control locations and the farm site, a total of 9 mobile benthic species were sampled during the four sampling campaigns in February and May of 2016 and 2017 (see supplementary Table S3 for full species list and abundances). The 6 most abundant species were included in the statistical analysis. The PERMANOVA analysis showed no evidence of an altered species composition and abundance at the farm compared to the control localities (Table 5). This is corroborated by the PCO analysis that did not indicate a separation between the farm and the control localities both before and after impact (Fig. 4). In addition, the PERMANOVA analysis showed a significant interactive effect between 'Farm vs. Control' and 'Sampling time'. However, the PERMDISP analysis (Table 5) suggested that the effect could be due to dispersion differences, which was corroborated by the PCO showing clear dispersion differences between the sampling times (Fig. 4).

### 3.4. Associated organisms

In total 24 species, consisting of 17 faunal and 7 other seaweed species, were observed associated with the cultured seaweed biomass (see supplementary Table S4 for full species list and abundances). The most abundant species in the samples were *Harmothoe imbricate* (polychaete) and *Lacuna vincta* (gastropod), with an abundance of 184 ± 16 (mean ± SE) and 93 ± 18 (mean ± SE) per 50 cm cultivation line, respectively. In addition, we found 3 lumpfish (*Cyclopterus lumpus*) within the sampled 2.5 m of farmed seaweed line. Based on these data, it was approximated that there were 3000 lumpfish per ha$^{-1}$ in the seaweed farm at the time of harvest (the farm set-up with 26 × 100 m horizontal long-line per hectare). The presence of many lumpfish in the seaweed farm was confirmed by observations during the actual harvest (personal observations by the authors).

### 3.5. Dissolved inorganic nutrients

Ammonium ($NH_4^+$) concentrations were for the majority of the samples below the detection limit (< 0.20 µmol/l), and therefore not included in the analysis. The PERMANOVA analysis of the dissolved nutrient data (i.e. $NO_3^-$ + $NO_2^-$, $PO_4^{3-}$, and $SiO_2$) showed significant interactive effects between 'Period' and 'Farm vs. control' for both years (i.e. 2016 and 2017; see Tables 6 and 7). However, PERMDISP and PCO showed that the significant result for this factor was primarily an effect of dispersion differences due to larger variability in samples from February compared to May, and not due to location differences (Tables 6 and 7, Fig. 5). This implied that there was no effect of the seaweed farm on dissolved nutrients. In addition, for both years we found a

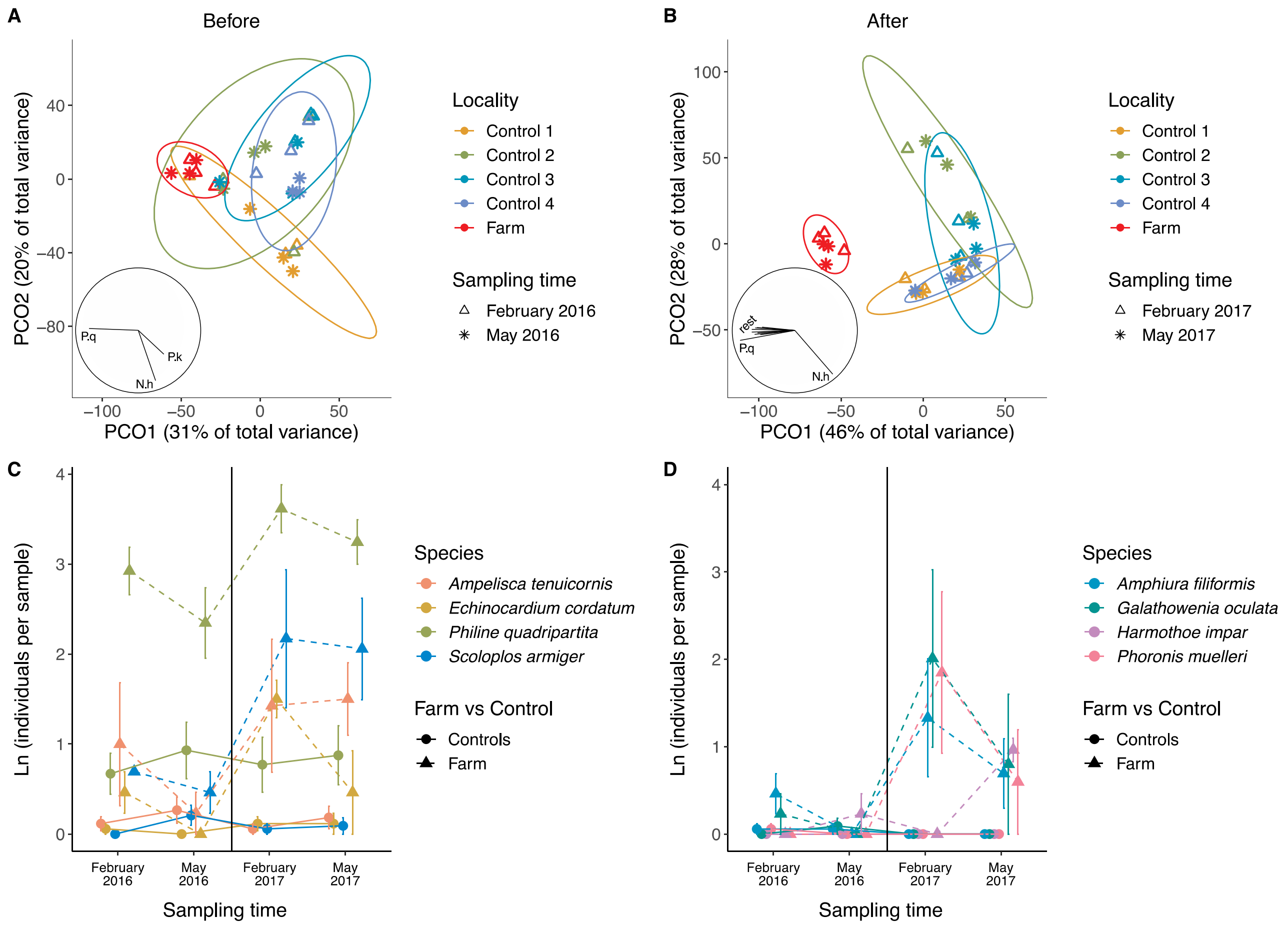


**Fig. 3.** Graphical representation of benthic infauna species composition and abundance. (A) and (B): Principle component ordination (PCO) diagram of benthic infauna species composition before (A) and after (B) the placement of the seaweed farm. Each dot represents a sediment sample from the seaweed farm or the control areas (C1–4) at each sampling time, the ellipses represent the 95% confidence intervals per locality of both sampling times combined, and vectors represent species with a correlation ≥0.5 to the PCO axes. (C) and (D): abundance change of individual species with the highest correlation with the PCO axes for the species composition after the placement of the farm. Error bars show SE. Abbreviations: N.h., *Nephtys hombergii*; P.k., *Pectinaria koreni*; P.q., *Philine quadripartita*; "rest" (n = 12): *Amphiura filiformis*, *Ampelisca tenuicornis*; *Corbula gibba*, *Diastylis lucifera*, *Echinocardium cordatum*, *Eteone* sp., *Galathowenia oculate*, *Harmothoe impar*, *Kurtiella bidentate*, *Nephtys caeca*, *Phoronis muelleri*, *Scoloplos armiger*.

significant effect of 'Period', reflecting seasonal differences for all localities with higher concentration of nutrients in February compared to May as indicated by vector plots (Fig. 5). PERMANOVA also showed a significant interactive effect between 'Period' and 'Depth' in 2017 (Table 7). However, the PERMDISP analysis showed that the PERMANOVA result could be a result of dispersion differences or a combination of dispersion and location differences. Accordingly, the PCO showed clear dispersion differences between periods for both 2016 and 2017, but also weak separation between depths in May (stronger depth separation in 2016 compared to 2017) indicating different nutrient profiles between 2 and 5 m in May.

### 3.6. Shading

The light irradiance (lux) at 5 m depth fluctuated extensively between days (Fig. 6). Light irradiance increased over the full sampling period, and was found to be significantly reduced underneath the seaweed farm (Table 8). The seaweed farm reduced the average light irradiance (lux) with approximately 40% during the last week before the biomass harvest. The irradiance at the control locations during that period was 5610 ± 162 lx (mean ± SE, n = 374) and 3192 ± 225 lx (mean ± SE, n = 102) at the seaweed farm. This corresponds to approximately 112 ± 3.2 μmol $m^{-2} s^{-1}$ (mean ± SE) at the control locations and 64 ± 4.5 μmol $m^{-2} s^{-1}$ (mean ± SE) at the seaweed farm.

## 4. Discussion

This paper shows that a seaweed farm of 2 ha. has limited negative environmental effects, but can rather have a positive effect on some environmental parameters. More specifically, the assessment of an extensive number of environmental variables indicate no significant effect of the seaweed farm on the sediment oxygen uptake, mobile benthic macrofauna, nor in the concentration of dissolved inorganic nutrients ($NO_{2+3}$, $PO_4$, and $SiO_2$). We did, however, observe an increase in benthic infaunal species diversity and abundance, resulting in improved Benthic Quality Index (BQI) at the farm site. Furthermore, the seaweed farm attracted a range of different species, thus increasing the local biodiversity. As expected, a reduction in light irradiance under the farm was observed due to shading at the peak of the farmed seaweed biomass.

In the present study we found an increase in benthic infaunal species abundance, richness, rarefaction, effective number of species, and an improvement of the benthic quality index (BQI) at the farm site. These results imply that the seaweed farm included in this study had a positive effect on the endobenthos rather than a negative effect. This contrasts with other aquaculture practices such as fish or shellfish aquaculture (Edwards, 2015; Smaal et al., 2018), where changes in benthic infauna have often been related to organic enrichment (Pearson and Rosenberg, 1978), caused by organic matter loading of the

**Table 3**
Benthic Quality Index (BQI) infauna. Summary of mixed model analysis of variance of the mean BQI from three control sites and the farm location testing the BACI-effect (i.e. FvC × Period) between 2016 ('Before') and 2017 ('After'). With *ndf* and *ddf* indicating the calculated df in the nominator and denominator respectively, $\sigma^2$ is the variance, *sd* is the standard deviation, *LRT* is the likelihood ratio test, the marginal $R^2$ ($R_m^2$) is the variance explained by the fixed effects, and the conditional $R^2$ ($R_c^2$) is the variance explained by both fixed and random effects.

| Source of variance | | | |
|---|---|---|---|
| Fixed effects | ndf, ddf | F-value | p-Value |
| Farm vs. Control = FvC | 1, 3 | 9.15 | 0.057 |
| Period | 1, 5 | 3.76 | 0.114 |
| FvC × Period | 1, 50 | 13.57 | < 0.001 |

| Source of variance | | | |
|---|---|---|---|
| Random effects | $\sigma^2$ ± sd | LRT | p-Value |
| Locality(FvC) | 2.55 ± 1.60 | 14.42 | < 0.001 |
| Pooled[a] | 3.48 ± 1.87 | | |

Number of obs: 59; groups: Locality(FvC) = 5.
$R_m^2/R_c^2$: 0.505/0.715.
[a] Pooled: Residuals + FvC × Sampling time(Period) + Locality(FvC) × Sampling time(Period) + Period × Locality(FvC) + Sampling time(Period).

sediment as a result of bio-deposition of faeces and pseudofaeces (Crawford et al., 2003), and (for fish farms) excess feed deposition (Edwards, 2015). Specific effects on benthic meiofauna and infauna community (i.e. abundance and diversity) responses have shown to vary greatly due to organic enrichment produced by shellfish aquaculture, from reported lower diversity (Callier et al., 2007; Chamberlain et al., 2001; Hartstein and Rowden, 2004; Matisson and Lindén, 1983), to neutral (Crawford et al., 2003; Danovaro et al., 2004) or positive (Callier et al., 2008). So far, few studies have investigated benthic effects of kelp cultivation, but they report minimal negative impacts on benthic infaunal communities (Buschmann et al., 2014; Walls et al., 2017; Zhang et al., 2009; Zhou, 2012). Changes in species richness and diversity at these kelp farm sites were found to be rather seasonal and affected by stochastic weather events such as storms, and not related to the seafarms per se (Walls et al., 2017; Zhang et al., 2009). However, long-term impact of seaweed farming on natural meiofauna and macrofauna has been reported for other types of seaweed aquaculture (Eklöf et al., 2005; Ólafsson et al., 1995). These studies examined the "off-bottom" cultivation of *Eucheuma denticulatum* and *Kappaphycus alvarezii* in shallow tropical lagoons. Here, clonal seaweed thalli are tied to lines and placed between wooden sticks, stuck into the sea bottom, and the biomass is harvested every 2–3 months. Thus, these types of cultivation methods and environments differ substantially from kelp cultivation in the coastal temperate regions, and inferences when comparing the two are hard to make.

The BQI used for the Swedish assessment within the EU-Water Framework Directive (WFD) classifies the ecological status of a water body corresponding the EU-WFD recommendations (Leonardsson et al., 2009). In the present study, most control locations were in 'Bad' or 'Poor' status, and the response over time (i.e. before vs. after impact) was either neutral or slightly negative, whilst the status at the farm site improved from 'Poor'/'Moderate' to 'Good' ecological status. In addition, we found large variation, ranging from 3 to 21, in sensitivity values of taxa that had a significant contribution to the difference between the farm site and control locations. Sensitivity values used in the BQI are indicative for a species' tolerance to disturbance and their capacity to coexist with other species (Rosenberg et al., 2004). A high sensitivity value means that the species occurs in a high diversity community and has a high competitive ability; it is seldom found in species-poor and disturbed environments. A low sensitivity value on the other hand means that the species has been found predominantly in species-poor environments (Leonardsson et al., 2015). We found that the species with the largest differential change in abundance at the farm site consisted of a diverse group of taxa with a relatively high sensitivity values. This implies that the response to the placement of a seaweed farm varies between taxa, and confirms that more sensitive species with a high sensitivity value are most likely to be affected (Leonardsson et al., 2015). Noteworthy is that BQI-values can be highly variable between 10 and 20 m depth, which was the dominating benthic biotope in the present study (Leonardsson et al., 2016). The use of a robust sampling design such as the asymmetrical "before after impact control" (BACI) design with multiple controls, as used here, is therefore essential to handle the inherent variability within sampling sites at these depths (Underwood, 1991, 1994).

Kelp farms have previously been suggested to locally increase the biodiversity (Campbell et al., 2019; Walls et al., 2016; Wood et al., 2017). Our results confirm that a multitude of organisms use the cultured seaweed biomass either as habitat or as shelter. However, baited cage fishing on the sea floor indicated that the benthic mobile macrofauna was not affected by the seaweed farm. Previous studies show that bivalve aquaculture attracts benthic mobile fauna due to increased food supply and the creation of new artificial habitat on the sea floor (D'Amours et al., 2008; Morrisey et al., 2006). Seaweed aquaculture can be expected to be similar in benthic habitat creation (e.g. anchors), but is likely to differ from mussel cultivation in terms of food supply for benthic macrofauna. Furthermore, effects on species biodiversity of associated organisms through the provisioning of habitat by the farmed kelp biomass in the pelagic zone are not yet fully understood. For example, many taxa found to be associated with the kelp biomass in the present study are reproductive in the spring or summer, which is after or at the time of harvest of the seaweed biomass and it is therefore expected that these species will not be able to spawn before the provided habitat is removed. Mobile fauna might find new habitats in the surrounding area, but for sessile organisms the habitat removal is irreversible. This does not necessarily affect these species negatively, but depends on whether or not the farm attracts dispersing planktonic larvae that otherwise would have settled in high-quality habitats, or if the farm creates a temporal habitat for a small portion of larvae that otherwise would not have settled elsewhere. Adjusting the timing of the harvest might resolve some issues related to reproduction, however, harvesting timing is primarily governed by biofouling that reduces the quality of the crop (Bruhn et al., 2016; Førde et al., 2015; Matsson et al., 2019). Accordingly, the timing of the harvest of a commercially operating seaweed farm will most likely only be adjusted (i.e. reduced or prolonged) such that it does not impeach commercial interests. Analogous to agriculture, an improvement of the local biodiversity could be achieved through crop harvesting regimes or farming method, such as organic agriculture or intercropping (Bengtsson et al., 2005; McLaughlin and Mineau, 1995). It is obvious that better knowledge is needed on the long-term effects of habitat provisioning by seaweed farms. Until that, assertions that the placement of a seaweed farm will positively affect and contribute to the biodiversity on the local scale need to be done carefully.

It has been suggested that a seaweed farm may shade underlying habitats containing autotrophic communities (Campbell et al., 2019). We found a 40% reduction in light irradiance at 5 m below the seaweed farm during the peak of the biomass. The seaweed farm investigated here was located such that there were no macrophytes at the sea floor. Analysis of benthic primary producers was not included in the present study, but the non-significant BACI-effect of oxygen uptake suggests that light attenuation of the seaweed farm had no major influence on benthic primary production. Benthic communities that are sensitive to change, such as seagrass meadows or maerl beds, are more likely to be affected by shading (Eriander et al., 2017; Wilson et al., 2004), although an assessment of the impact of an 18 ha. kelp farm showed no

**Table 4**
Summary of mean diversity of benthic infauna community at the control locations (C1–4) and the seaweed farm, sampled over 4 sampling times in the Kosterhavet national park. S: the total number of taxa per sample; N: total number of individuals per sample; E: rarefaction (N ≥ 10); D: Effective number of species; BQI: benthic quality index. Standard error of means is included in parenthesis and colour represents the EU-WFD classification status for the BQI corresponding to: red = bad (≤3.4); orange = poor (3.4 ≤ 6.9); yellow = moderate (6.9 ≤ 10.3); and green = good (10.3 ≤ 13.9).

| Location | Sampling time | S | N | E | D | BQI |
|---|---|---|---|---|---|---|
| Control 1 | Feb 2016 | 3.3 (1.2) | 20.3 (8.8) | 3.46 (0.36) | 2.31 (0.74) | 3.71 (0.92) |
| | April 2016 | 5.0 (0.6) | 33.7 (10.5) | 3.84 (0.02) | 3.84 (0.22) | 4.82 (0.79) |
| | Feb 2017 | 4.0 (0.6) | 29.3 (3.2) | 3.08 (0.17) | 2.33 (0.29) | 4.79 (0.57) |
| | April 2017 | 4.3 (0.3) | 32.7 (5.8) | 3.15 (0.06) | 2.42 (0.13) | 4.69 (0.30) |
| Control 2 | Feb 2016 | 2.3 (0.3) | 16.0 (6.1) | 3.09 (0.18) | 2.09 (0.24) | 2.96 (0.37) |
| | April 2016 | 2.7 (0.3) | 15.7 (4.7) | 3.28 (0.18) | 2.39 (0.20) | 3.57 (0.14) |
| | Feb 2017 | 1.3 (0.7) | 4.0 (3.1) | 2.50 ( - ) | 1.69 (0.31) | 1.75 (0.87) |
| | April 2017 | 1.7 (0.3) | 5.7 (2.3) | 2.42 (0.23) | 1.34 (0.19) | 2.14 (0.32) |
| Control 3 | Feb 2016 | 1.7 (0.3) | 4.3 (0.9) | - | 1.44 (0.23) | 2.72 (0.70) |
| | April 2016 | 3.3 (0.3) | 17.0 (5.0) | 3.08 (0.00) | 2.23 (0.01) | 4.52 (0.14) |
| | Feb 2017 | 2.0 (0.0) | 10.0 (3.5) | 2.72 (0.04) | 1.67 (0.04) | 2.91 (0.16) |
| | April 2017 | 1.3 (0.3) | 13.7 (2.0) | 2.00 ( - ) | 1.24 (0.24) | 1.95 (0.44) |
| Control 4 | Feb 2016 | 6.3 (1.2) | 14.3 (4.9) | 4.47 (0.51) | 4.79 (1.00) | 8.80 (1.36) |
| | April 2016 | 5.3 (0.7) | 21.0 (3.5) | 3.71 (0.14) | 3.58 (0.49) | 6.69 (0.74) |
| | Feb 2017 | 4.7 (1.8) | 23.7 (3.5) | 2.84 (0.33) | 2.17 (0.61) | 4.73 (1.35) |
| | April 2017 | 4.7 (1.3) | 30.7 (7.8) | 3.21 (0.55) | 2.89 (0.99) | 5.61 (1.50) |
| Farm | Feb 2016 | 7.7 (1.5) | 32.0 (6.0) | 3.55 (0.50) | 3.85 (1.50) | 9.94 (2.13) |
| | April 2016 | 4.3 (1.2) | 15.0 (5.3) | 3.34 (0.26) | 2.37 (0.41) | 6.47 (1.19) |
| | Feb 2017 | 14.7 (3.8) | 101.0 (36.9) | 4.14 (0.41) | 6.55 (1.85) | 12.41 (1.92) |
| | April 2017 | 10.3 (1.9) | 57.0 (15.0) | 3.86 (0.42) | 4.91 (1.57) | 10.79 (1.53) |
| Mean: | | 4.6 (0.5) | 24.9 (3.4) | 3.32 (0.10) | 2.81 (0.23) | 5.30 (0.43) |

**Table 5**
Benthic mobile macrofauna. Summary of results from PERMANOVA and PERMDISP testing the BACI-effect (i.e. FvC × Period) on benthic mobile species based on Bray-Curtis dissimilarity matrices. df: degrees of freedom; SS: sum of squares; MS: mean squares; Pseudo-F: ratio of within-group variation to between-group variation; P(perm): permutational probability value. Numbers in bold are considered significant (p < 0.05).

| Source | df | PERMANOVA | | | | | PERMDISP | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SS | MS | Pseudo-F | P(perm) | Unique perms | df1 | df2 | F | P(perm) |
| Fixed effects | | | | | | | | | | |
| Farm vs. Control = FvC | 1 | 9944 | 9944 | 1.210 | 0.325 | 9939 | | | | |
| Period | 1 | 4327 | 4327 | 0.275 | 0.343 | 6 | | | | |
| FvC × Period | 1 | 1499 | 1499 | 0.187 | 0.947 | 4307 | | | | |
| Random effects | | | | | | | | | | |
| Locality(FvC) | 3 | 6397 | 2133 | 0.917 | 0.500 | 9934 | | | | |
| Sampling time(Period) | 2 | 31,431 | 15,715 | 6.411 | **< 0.001** | 9936 | 3 | 73 | 4.828 | **0.019** |
| FvC × Sampling time(Period) | 2 | 15,999 | 8000 | 3.269 | **0.007** | 9941 | 7 | 69 | 9.341 | **< 0.001** |
| Pooled[a] | 9 | 21,190 | 2354 | 3.936 | **< 0.001** | 9854 | | | | |
| Residuals | 57 | 34,099 | 598 | | | | | | | |
| Total | 76 | 156,620 | | | | | | | | |

[a] Pooled: Period × Locality(FvC) + Locality(FvC) × Sampling time(Period).

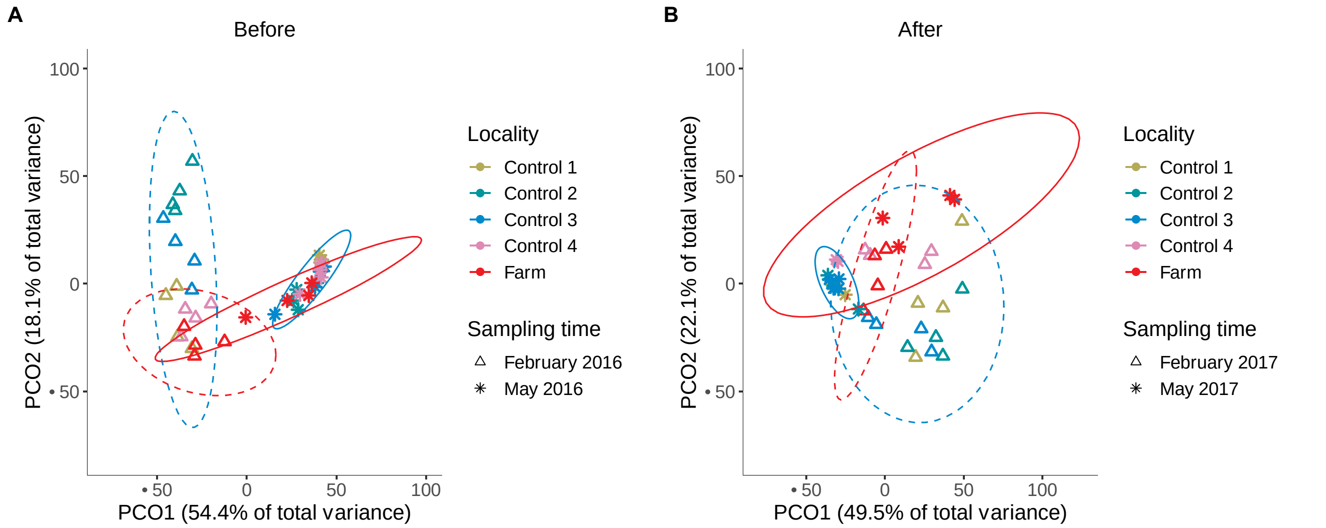


**Fig. 4.** Principle component ordination (PCO) diagram of benthic mobile species composition before (A) and after (B) the placement of the seaweed farm. Each dot (40 in total) represents a landing of benthic fishing cages (n = 4) underneath the seaweed farm or in the control areas (C1–4) at each sampling time. The ellipses represent the 95% CI averaged per sampling time of the control localities and the farm site, with the dashed lines are February and the solid lines are May.

effect on the seagrass (*Zostera marina*) biomass underneath the farm (Walls et al., 2017). Since the peak of the biomass is during a relatively short period in the last phase of the growing season, it is likely that the shading by a seaweed farm has limited functional and ecological effect on photosynthetic benthic communities. Nevertheless, avoiding well vegetated areas and habitats that are protected under the EU-WFD is still recommended (Campbell et al., 2019), especially since rapid expansion of the seaweed industry and increased farm sizes can result in unforeseen ecological impacts (Cottier-Cook et al., 2016).

Dissolved inorganic nutrients were found to be unaffected by the installation of the seaweed farm. Seasonal differences in dissolved inorganic nutrients found in the present study can ecologically be explained by the annual occurrence of the phytoplankton spring bloom, which naturally depletes the coastal ecosystem from its dissolved nutrients, and seasonal differences in nutrient rich river runoff water from land. The uptake of dissolved inorganic nutrients by seaweed aquaculture has been studied extensively (Seghetta et al., 2016; Xiao et al., 2017). For example, large scale seaweed aquaculture practices did not exceed the carrying capacity in one of the most intensely farmed location in China (Zhang et al., 2009), a 21-ha kelp farm in Chile did not negatively affected dissolved nitrogen levels (Buschmann et al., 2014), and no difference was detected by the cultivation of *Kappaphycus* in India (Abhilash et al., 2019). Seaweed cultivation can reduce inorganic nutrients thereby competing with phytoplankton (Yang et al., 2015a), as demonstrated by the inhibitory effect on harmful algal blooms (HABs) of large-scale commercial cultivation of *Gracilaria* in China (Yang et al., 2015b). In addition, studies that model the effects of seaweed farms on the dissolved nutrients within Europe suggest no negative effects on the local environment (Broch et al., 2019; van der Molen et al., 2018). On the contrary, the production of seaweed in eutrophicated coastal waters has been suggested to positively affect the environment by extracting nutrients upon harvest (Seghetta et al., 2016).

Oxygen uptake by the sediment was found to be unaffected by the seaweed farm, indicating that detached seaweeds or release of organic matter from the blades did not significantly affect the organic content of the sediment under the farm. Instead, the observed fluctuations in oxygen uptake rates were attributed to differences in locality and

**Table 6**
Dissolved inorganic nutrients for 2016. Summary of results from PERMANOVA and PERMDISP for the year 2016 testing the BACI-effect (i.e. FvC × Period) on the dissolved inorganic nutrients (nitrate + nitrite ($NO_3^- + NO_2^-$), phosphate ($PO_4^{3-}$), and silicate ($SiO_2$)) based on Euclidean similarity matrices. df: degrees of freedom; SS: sum of squares; MS: mean squares; Pseudo-F: ratio of within-group variation to between-group variation; P(perm): permutational probability value. Numbers in bold are considered significant (p < 0.05).

| Source | df | PERMANOVA | | | | | PERMDISP | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SS | MS | Pseudo-F | P(perm) | Unique perms | df1 | df2 | F | P(perm) |
| Fixed effects | | | | | | | | | | |
| Farm vs. Control = FvC | 1 | 1.892 | 1.892 | 19.003 | < **0.001** | 20 | 1 | 96 | 3.0661 | 0.157 |
| Period | 1 | 185.280 | 185.280 | 1294.800 | < **0.001** | 9916 | 1 | 96 | 75.415 | < **0.001** |
| Depth | 1 | 1.207 | 1.207 | 3.836 | 0.099 | 9790 | | | | |
| FvC × Period | 1 | 0.623 | 0.623 | 4.353 | **0.038** | 9914 | 1 | 3 | 27.851 | < **0.001** |
| FvC × Depth | 1 | 0.459 | 0.459 | 1.466 | 0.297 | 9803 | | | | |
| Period × Depth | 1 | 1.291 | 1.291 | 4.327 | 0.121 | 9914 | | | | |
| FvC × Period × Depth | 1 | 0.605 | 0.605 | 2.034 | 0.243 | 9939 | | | | |
| Random effects | | | | | | | | | | |
| Locality(FvC) | 3 | 0.293 | 0.098 | 0.682 | 0.567 | 9956 | | | | |
| Depth × Locality(FvC) | 3 | 0.925 | 0.308 | 2.155 | 0.103 | 9964 | | | | |
| Period × Depth × Locality(FvC) | 3 | 0.877 | 0.292 | 2.043 | 0.112 | 9950 | | | | |
| Pooled[a] | 81 | 11.591 | 0.143 | | | | | | | |
| Total | 97 | 291.000 | | | | | | | | |

[a] Pooled: Residuals + Period × Locality(FvC).

**Table 7**
Dissolved inorganic nutrients for 2017. Summary of results from PERMANOVA and PERMDISP for the year 2017 testing the BACI-effect (i.e. FvC × Period) on the dissolved inorganic nutrients (nitrate + nitrite ($NO_3^-$ + $NO_2^-$), phosphate ($PO_4^{3-}$), and silicate ($SiO_2$)) based on Euclidean similarity matrices. df: degrees of freedom; SS: sum of squares; MS: mean squares; Pseudo-F: ratio of within-group variation to between-group variation; P(perm): permutational probability value. Numbers in bold are considered significant (p < 0.05).

| Source | df | PERMANOVA | | | | | PERMDISP | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SS | MS | Pseudo-F | P(perm) | Unique perms | df1 | df2 | F | P(perm) |
| Fixed effects | | | | | | | | | | |
| Farm vs. Control = FvC | 1 | 0.356 | 0.356 | 2.249 | 0.398 | 5 | | | | |
| Period | 1 | 168.720 | 168.720 | 1734.900 | **< 0.001** | 9922 | 1 | 98 | 44.165 | **< 0.001** |
| Depth | 1 | 1.241 | 1.241 | 12.759 | **< 0.001** | 9934 | 1 | 98 | 1.827 | 0.125 |
| FvC × Period | 1 | 1.016 | 1.016 | 10.445 | **0.001** | 9921 | 3 | 96 | 12.276 | **< 0.001** |
| FvC × Depth | 1 | 0.075 | 0.075 | 0.776 | 0.384 | 9921 | | | | |
| Period × Depth | 1 | 0.512 | 0.512 | 5.262 | **0.021** | 9909 | 3 | 96 | 16.949 | **< 0.001** |
| Random effects | | | | | | | | | | |
| Locality(FvC) | 3 | 0.474 | 0.158 | 1.626 | 0.187 | 9947 | | | | |
| Pooled[a] | 90 | 8.753 | 0.097 | | | | | | | |
| Total | 99 | 297.000 | | | | | | | | |

[a] Pooled: Residuals + Period × Locality(FvC) + Depth × Locality(FvC) + FvC × Period × Depth + Period × Depth × Locality(FvC).

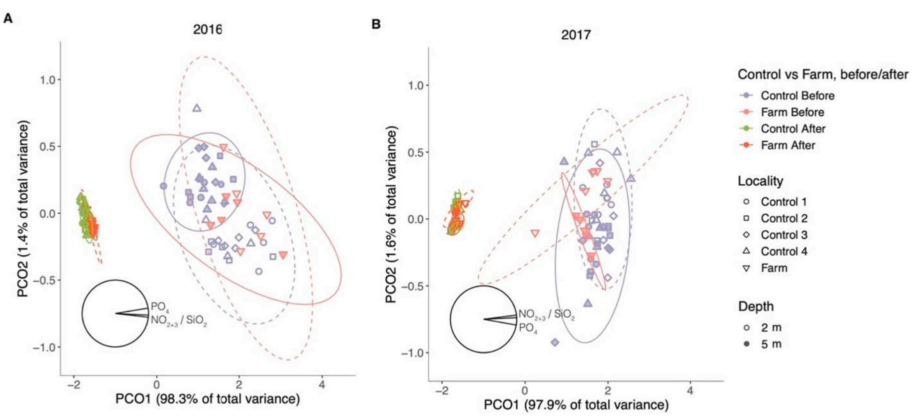


**Fig. 5.** Principle component ordination (PCO) diagram of the composition of dissolved inorganic nutrients. Each dot (200 in total) represents a sample from two depths at the control locations (C1–4) and the seaweed farm, sampled in 2016 (A) and 2017 (B). The BACI-effect was tested separately for each year as follows: before is February, and after is May. The ellipses represent the 95% CI averaged before and after impact for both the pooled control locations and the farm. Filled shapes with solid ellipse lines where sampled at a depth of 5 m, and open shapes with dashed ellipse lines where sampled 2 m deep. The vectors represent correlation of each dissolved nutrient to the PCO axes. Abbreviations: $NO_{2+3}$, nitrate and nitrite ($NO_3^-$ + $NO_2^-$); $PO_4$, phosphate ($PO_4^{3-}$); and $SiO_2$, silicate ($SiO_2$).

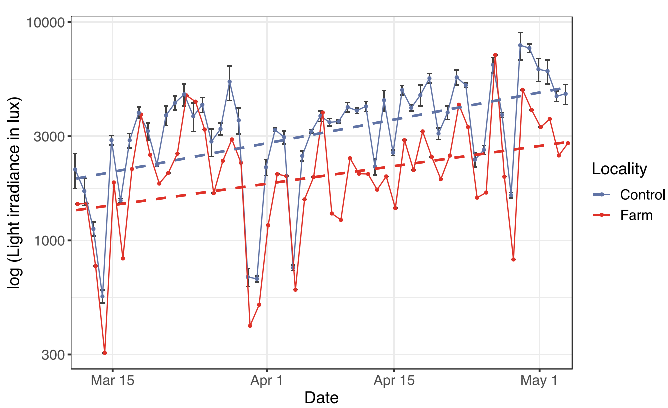


**Fig. 6.** Variance in light irradiance (lux) at 5 m depth between the farm and control areas during the last 8 weeks of the cultivation period. Dashed lines represent linear regression, data points are daily means of three loggers, and error bars show standard error (SE) for mean light irradiance between control areas (n = 4).

**Table 8**
Shading. Summary of linear regression of mean light irradiance (lux) at 5 m. depth comparing the pooled control locations (n = 4) and the seaweed farm. Numbers in bold are considered significant (p < 0.05).

| Source of variance | Estimates | CI (95%) | p-Value |
|---|---|---|---|
| Intercept | 1972.64 | 1698.70–2246.57 | **< 0.001** |
| Date | 56.49 | 47.98–65.00 | **< 0.001** |
| $Location_{(Farm)}$ | −386.41 | −978.18–205.35 | 0.200 |
| Date × $Location_{(Farm)}$ | −30.53 | −48.92 to −12.15 | **0.001** |

Number of obs: 770.
$R^2$/adjusted $R^2$: 0.246/0.243.
F-statistics: 83.1 on 3, and 766 df, p-value: < 0.001.

season. The increased benthic oxygen uptake rates in April compared to February were most likely due to temperature differences, and variation among localities was likely the result of spatial heterogeneity such as minor differences in sediment type or composition between the analysed sites. In a previous study, Ren et al. (2014) estimated that 5% of the suspended particulate matter in a coastal embayment in China, heavily used for kelp cultivation, came from kelp. Furthermore, measured contribution by the kelp to the sediments was even lower. In addition, Buschmann et al. (2014) found no significant trend of increased organic matter under the seaweed farm and noted few seaweed blades on the bottom under the kelp farm. These studies together with our results strongly suggest that seaweed cultivation at the scale currently done in Europe does not lead to any substantial organic enrichment of the sediment.

## 5. Conclusion

Our study demonstrates that the environmental impact of seaweed cultivation is minimal. The seaweed farm (in relation to control sites) caused minimal effects on dissolved inorganic nutrient concentrations and benthic oxygen flux compared to natural fluctuations. More research is needed to better understand and evaluate the interactive effects between seaweed farming and the environment at different temporal and spatial scales, such as genetic effects on wild populations and facilitation of pathogen and/or pests. Together with our findings, this may offer a basis for the development of management policy for future seaweed aquaculture. This is of main importance as farm operations are expected to increase.

## CRediT authorship contribution statement

**Wouter Visch:**Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft.**Mikhail Kononets:**Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing - review & editing.**Per O.J. Hall:**Conceptualization, Investigation, - Methodology, Writing - review & editing.**Göran M. Nylund:** Conceptualization, Methodology, Project administration, Resources, Supervision, Validation, Writing - review & editing.**Henrik Pavia:**Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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