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Temporal changes in visual organic enrichment indicators at an aquaculture site over mixed- and hard-bottom substrates

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ABSTRACT: Norway employs an environmental management system to assess benthic organic loading from aquaculture activities. Monitoring surveys, mostly performed through grab sampling, scrutinise responses to enrichment within soft-sediment macrofaunal communities. However, new methods and indicators of organic enrichment (IOE) need to be identified for mixed- and hard-bottom substrates. We used image characterisation to examine temporal changes in the abundance and coverage of benthic IOE on mixed- and hard-bottom substrates (organic pellets, sulphur-oxidising bacterial mats, opportunistic polychaete complexes [OPC], polychaete tube aggregations [PTA]) in relation to changes in organic deposition pressure through 1 yr of production at a rainbow trout farm on the western coast of Norway. Rates of organic deposition on the seafloor around the farm increased towards the end of the survey period as fish biomass increased. PTA were significantly associated with low levels of organic deposition and their abundance declined in 2 of the 3 study cages as the production cycle progressed. OPC coverage significantly increased with organic deposition and was greatest, 4 mo before the end of the production cycle. Organic pellet coverage closely followed the patterns of organic deposition on the seafloor, whereas bacterial mat coverage showed no relationship with deposition. Our findings provide new knowledge on the annual impact of organic enrichment on IOE beneath fish farms over mixed- and hard-bottom substrates, highlighting image characterisation methods as a means to improve benthic monitoring. This knowledge can contribute to the development of an environmental proxy to assess the enrichment stage around aquaculture farms placed over mixed- and hard-bottom areas.

KEY WORDS: Finfish aquaculture · Benthic communities · Organic sedimentation · Image characterisation · Environmental monitoring

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1. INTRODUCTION

With the potential to meet the increasing global demand for protein, marine aquaculture offers an alternative to capture fisheries (Merino et al. 2012, Gentry et al. 2017). However, several environmental impacts are associated with the finfish industry, such as the discharge of organic fish farm waste, the use of pesticides and chemicals, escaped fish cross-spawning with wild stocks, and animal welfare concerns (McGinnity et al. 2003, Forseth et al. 2017, FAO 2020, Parsons et al. 2020). This study specifically focuses on the release of organic waste, occurring in the form of uneaten feed pellets and faeces, from fish

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cages (Goldburg & Naylor 2005, Holmer et al. 2005, Kutti et al. 2007a). If areas do not benefit from strong enough currents, waste may not be dispersed and particles can sink directly to the seafloor (Sutherland et al. 2006), creating a layer of organic flocculent material. An accumulation of waste material (faeces, feed pellets, fish debris, sedimented organic matter) can represent a major change of substrate and habitat type for benthic communities, on both hard- and soft-bottom areas (Bannister et al. 2014, Salvo et al. 2015, Hamoutene et al. 2016). Organic enrichment from fish waste increases respiration rates and may lead to oxygen depletion on the seafloor, which favours the replacement of existent communities with benthic opportunistic organisms (Valdemarsen et al. 2012, 2015). These benthic communities are characterised by a few species with a high tolerance threshold to organic enrichment (e.g. complexes of opportunistic polychaetes [OPC] or sulphur-oxidising bacteria), leading to a decrease in overall species diversity (Pearson 1978, Henderson & Ross 1995, Wildish & Pohle 2005, Kutti et al. 2007b, Verhoeven et al. 2016).

In Norway, a system of mandatory monitoring investigations (Norwegian Standard NS9410:2016) is used for the assessment of benthic organic loading and benthic community responses based on an environmental management scheme called Modelling-Ongrowing fish farms-Monitoring (MOM) (Ervik et al. 1997, Hansen et al. 2001). The monitoring investigations are conducted under and in the vicinity of fish farms with a frequency that depends on the impact recorded and are based on chemical parameters such as pH and redox potential, benthic macrofauna, and qualitative sediment variables (Taranger et al. 2015, Standards Norway 2016). Benthic monitoring is mostly performed through grab-sampling surveys, suitable for soft sediment environments. Thresholds of benthic response were set to determine the level of impact from farm enrichment, categorised into 4 levels (1: low impact, 2: medium impact, 3: high impact-organic loading, 4: organic overloading) (Standards Norway 2016). However, challenges related to monitoring harder-bottom substrates with conventional sampling techniques (e.g. benthic grabs) have so far limited the monitoring of aquaculture sites placed over mixed- and hard-bottom substrates.

Hard-bottom substrates are common on the Norwegian coastline and are associated with high species richness and diversity (Howell et al. 2016, Keeley et al. 2021). Across Norway, approximately 25% of benthic grab sample sites directly beside fish farms under the Norwegian Standard NS9410 in 2022 and 2023 were on mixed- or hard-bottom substrates, where a grab could not be taken (Husa et al. 2024). Survey systems relying on remotely operated vehicles (ROVs) have been successfully used in deep-sea environments to monitor the spatial distribution of hard-bottom benthic communities (Lacharité & Metaxas 2017). However, the deployment of ROVs in near-shore areas and in the proximity of aquaculture sites can often be associated with high operational and maintenance costs and a need to manoeuvre large vessels near cages (Dunlop et al. 2020). Cost-effective visual monitoring techniques, such as drop camera surveys, allow for the identification and quantification of benthic communities under aquaculture sites placed over hard-bottom substrates (DFO 2013, Hamoutene et al. 2014, 2016, 2018). Image characterisation through drop-cameras can provide an agile and low-cost method to follow changes in the coverage of visual benthic indicators of organic enrichment (IOE), which provide quantitative information on the benthic ecologic state over mixed-bottom substrates (Salvo et al. 2017, 2018a).

In Canada, monitoring of hard substrates underneath fish cages through visual investigations has detected white sulphur-oxidising bacterial mats, OPC, and flocculent matter, which are considered the main visual IOE in Canadian waters (DFO 2013, Hamoutene et al. 2014). White mats of sulphur-oxidising bacteria can be found in association with high levels of sulphide and have been observed underneath or next to farms, over mixed- and hard-bottom substrates (Hamoutene 2014). In Norway, OPC containing individuals from the genera *Vigtorinella* sp. and *Ophryotrocha* sp. have been reported to fully cover the hard substrate beneath fish cages and to feed on the organic waste (Hansen et al. 2011, Eikje 2013). According to previous studies, the percentage coverage of bacterial mats and OPC increases closer to cages, indicating a spatial association with enhanced organic deposition from the farm (Hamoutene et al. 2016). These species are adapted to high sedimentation and have previously been found in high abundances beneath or close to Norwegian salmon farms over mixed- and hard-bottom substrates (Hansen et al. 2011, Keeley et al. 2019). Multiple studies have highlighted the necessity to acquire better knowledge of hard-bottom benthic communities, especially regarding their distribution under fish farms, sensitivity to organic loading from sedimentation, and overall ecological value (Hamoutene et al. 2014, 2015, Keeley et al. 2015, Armstrong et al. 2020, Dunlop et al. 2021). Further information on the impact of aquaculture on mixed- and hard-bottom habitats, and on the associated benthic communities, is needed to update the current MOM system, to encompass all Norwegian coastal habitats, and create a new hard substrates-specific monitoring tool (Dunlop et al. 2021, Keeley et al. 2021).

In this study, drop camera surveys were conducted underneath a finfish farm throughout a year of production to quantify the surface coverage and abundance of visual benthic indicators on mixed- and hard-bottom substrates. The surveys aimed to determine whether changes in the abundance and surface area coverage of visual benthic indicators of organic enrichment were associated with increased modelled daily rates (g total particulate matter [TPM] m^{-2} d^{-1}) of organic deposition and with different patterns of summed organic deposition (g m^{-2}) on the seafloor (i.e. summed dispersion over the production cycle and 10 d periods). New knowledge on these relationships in conjunction with the identified visual indicators offers an approach to improve the monitoring of organic enrichment state for finfish farms over habitats dominated by mixed- and hard-bottom substrates.

It was hypothesised that increased deposition of organic waste and summed deposition patterns on the seafloor would affect the presence, coverage, and abundance of benthic IOE throughout a 1 yr production cycle.

2. MATERIALS AND METHODS

2.1. Site description

Drop camera surveys were conducted around a fish farm producing rainbow trout *Oncorhynchus mykiss* near the northern coast of the island of Austevoll, western Norway (Fig. 1A,B). This farm site was established on 18 June 1996 and is licenced to produce a maximum allowed biomass (MAB) of 3120 t. Fish biomass is spread over 3 out of the 4 cages situated close to the shoreline, a common siting configuration for finfish farming on the west coast of Norway. The study farm is one of 21 farms producing finfish around the island of Austevoll. These farms are located at a water depth between 40 and 100 m and have an average MAB of 2580 t. In September 2021, the site was assigned an impact score of 2 (medium impact) based on soft-sediment grab and water samples, indicating mild organic enrichment from farm organic waste. The farm is situated over an area of mixed-bottom substrate at a water depth of between 80 and 90 m. Here the main substrate types under all cages were a mixture of sand, pebble/gravel, and boulders (CATAMI Technical Working Group 2014; Table 1). Current velocity measurements, carried out for approximately 1 mo in the upper 15 m of the water column, revealed average current velocities of 8 and 6 cm s^{-1} at 5 and 15 m water depth, respectively, and a northward prevailing current. Daily biomass and feed data for each of the 3 cages were provided by the farmer (see Fig. S3 in the Supplement at www.int-res.com/articles/suppl/q016p267_supp.pdf).

Fish were set out in 3 of the 4 farm cages between the 23 August (Cage 4) and the 11 September (Cages 2 and 3) 2020. Prior to the beginning of the production cycle, cages had no fish for approximately 6 mo, as the previous production cycle took place between September 2018 and February 2020. Since 2014, the farm has undergone 5 full production cycles. At the end of May 2021, approximately half the fish in the cages were moved into 3 newly established additional cages that were placed directly adjacent (i.e. less than 30 m distance) to the 4 original ones. All fish were finally harvested in October and November 2021.

2.2. Sampling design

The surface area coverage and abundance of benthic visual indicators on the substrate directly beneath the farm cages were investigated on an approximately monthly basis with drop camera surveys. Surveys were conducted around 3 of the 4 original farm cages: Cage 2, Cage 3, and Cage 4, and 1 additional site situated approximately 100 m west of the farm (Fig. 1C, Table 1). Images of the substrate directly beside and under the farm cages were collected with a drop camera at 11 time points throughout a year of production, starting in September 2020 and ending in September 2021. Image collection was carried out every 4 to 5 wk, except for February and June 2021, when images were collected twice a month, and a gap in April to May and July 2021. Images were collected downstream of the main current direction (northward).

2.3. Deposition of organic waste

2.3.1. Modelled organic deposition. We set up a deposition model to model the dispersal and estimate the deposition of organic waste from the study farm cages. Faeces and excess feed were modelled as discrete particles that move with ambient currents and have individual sinking velocities. The approach is

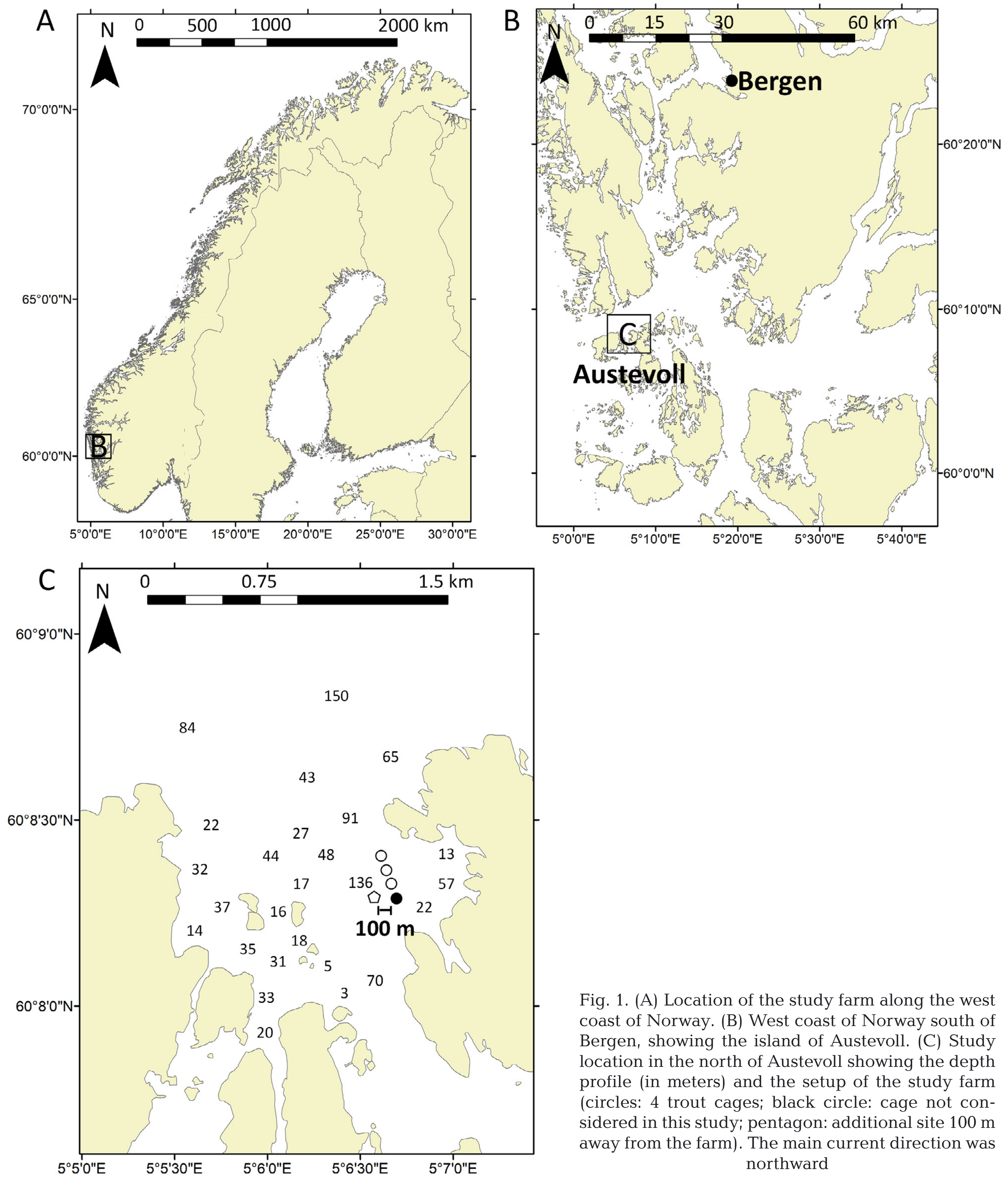

Fig. 1. (A) Location of the study farm along the west coast of Norway. (B) West coast of Norway south of Bergen, showing the island of Austevoll. (C) Study location in the north of Austevoll showing the depth profile (in meters) and the setup of the study farm (circles: 4 trout cages; black circle: cage not considered in this study; pentagon: additional site 100 m away from the farm). The main current direction was northward

similar to that used by Carvajalino-Fernández et al. (2020), but without resuspension mechanics. Cage-specific daily feed data were supplied by the farm and used to compute faecal output as well as feed spill throughout the production cycle (September 2020 to September 2021). All 3 farm cages were included in the model and positioned on the map using aerial photographs. We used a feed-to-waste conversion factor of 24% (Cubillo et al. 2016, their Fig. 4) and sinking velocities according to Bannister et al. (2016).

Table 1. Summary of survey sites, substrate features, sampling depth, and maximum fish biomass in each cage at the beginning of the fish production cycle. Dates are given as dd/mm/yy; na: not applicable

Site (date)	Substrate characteristics	Depth (m)	Max. fish biomass (t)
100 m from farm	Sand, pebble/gravel, boulders	80–90	na
Cage 2 (15/10/2021)	Sand, pebble/gravel, boulders	90	338
Cage 3 (21/09/2021)	Sand, pebble/gravel	84	360
Cage 4 (30/09/2021)	Sand, pebble/gravel	84	524

The release depth was set to 20 m below sea surface. Particle transport was modelled using the particle-tracking software Ladim (Ådlandsvik & Sundby 1994). Hydrodynamic currents were modelled using the regional oceanic modelling system (ROMS; Shchepetkin & McWilliams 2005), with a horizontal resolution of 160 m. Except for the finer resolution and a smaller model domain, the setup is identical to the NorKyst800 setup described by Albretsen et al. (2011). Hydrodynamic models on the 160 m scale were run routinely by the Norwegian Institute of Marine Research for the entire Norwegian coast. Final results were converted to a daily depositional rate on a 15 m resolution map (g TPM m^{-2} d^{-1}). In the model, changes in cage-specific daily feed data account for the changes in fish biomass at the end of May 2021.

2.3.2. Measured organic waste deposition (sediment traps). Sediment traps were deployed by hand next to the 3 fish cages and at the site 100 m from the farm cages to measure the depositional flux of suspended organic particles to the seafloor and validate modelled depositional values. In September 2020, traps were only deployed directly beside Cage 3 and at the site 100 m from the farm, while in February and April 2021 measurements were taken next to all 3 cages and at the additional site away from the farm.

Sediment traps were deployed for approximately 2 wk each and were situated 6 m above the seafloor. Each sediment trap frame consisted of 3 cylinders (diameter 9 cm) that collected suspended particles 6 m above the seafloor. Each cylinder was filled with 0.5 l of seawater enriched with 5 g of NaCl and buffered with a 4% formalin solution (Keeley et al. 2019). The high salinity seawater solution maintained the formalin solution at the bottom of the cylinder, preserving organic matter against decomposition. Each sediment rig was anchored to the bottom with 100 kg of weight. Upon retrieval with a hydraulic winch, suspended material in the cylinders was allowed to settle and excess water was removed. Finally, cylinders were sealed and brought to the lab for content analysis. TPM dry weight daily flux (g m^{-2} d^{-1}) was determined from 3 sub-samples of a known volume of suspended organic material from the sediment trap cylinders filtered on pre-weighed filters (47 mm Whatman GF/F, porosity 1.2 µm). Filters were oven-dried and reweighed to determine TPM dry weight.

2.4. Benthic surveys

2.4.1. Image collection. Drop-camera surveys were conducted to estimate the changes in the abundance and seafloor coverage of visual IOE throughout a year of farm production. A GoPro Hero 7 (f2.8, shutter speed 1/161 s, ISO-666, focal length 3 mm) was used to record HD images of the seafloor at ca. 80 m depth. The camera was attached to a steel frame of area 0.1 m^2 and dropped to the seafloor on a 110 m long rope. One Keldan 4X video light (9000 lm) was placed next to the camera and angled towards the centre of the photo frame to illuminate the seafloor. Additionally, the steel frame was marked with a 1 cm scale bar which was placed in contact with the substrate to estimate surface area per cm^2 (Fig. S1). At each cage, images were taken approximately every 2 m around an 18 m long section of the circular cage, to create 10 image stations per cage (Fig. S2). At the side of the cage, where the camera was dropped, the image stations were marked to keep the camera placement consistent throughout the study period. At each of the 10 image stations, 5 different frames were shot with 5 s between each frame.

2.4.2. Image annotation. The Bio-Image Indexing and Graphical Labelling Environment (BIIGLE 2.0) software was used to annotate images to estimate surface coverage and abundance of IOE (Langenkämper et al. 2017). From each time period, the best-resolution image (out of the 5 shots recorded) was chosen and annotated at each image station. The 4 additional recorded images were used to detect movements and help in the identification of visual indicators. Thus, 10 images were analysed and annotated per cage at each time point. A label tree system was created to collate the labels used to annotate the images (e.g. pellets, OPC, bacterial mats). The annotation catalogue allowed all annotations within a label to be visualised together. Visual indicators were annotated according to either surface area coverage or total count, as illustrated in Fig. 2. To measure surface area coverage, the BIIGLE magic wand annotation tool was used to detect regions where pixels share similar colours and automatically draw a polygon around the object. Total counts were determined using the BIIGLE point annotation tools. The laser point detection tool, calibrated with the 1 cm scale bar, was used to determine the pixel-to-cm ratio of the surface area. Organic pellets (uneaten feed and faeces), sulphur-oxidising bacterial

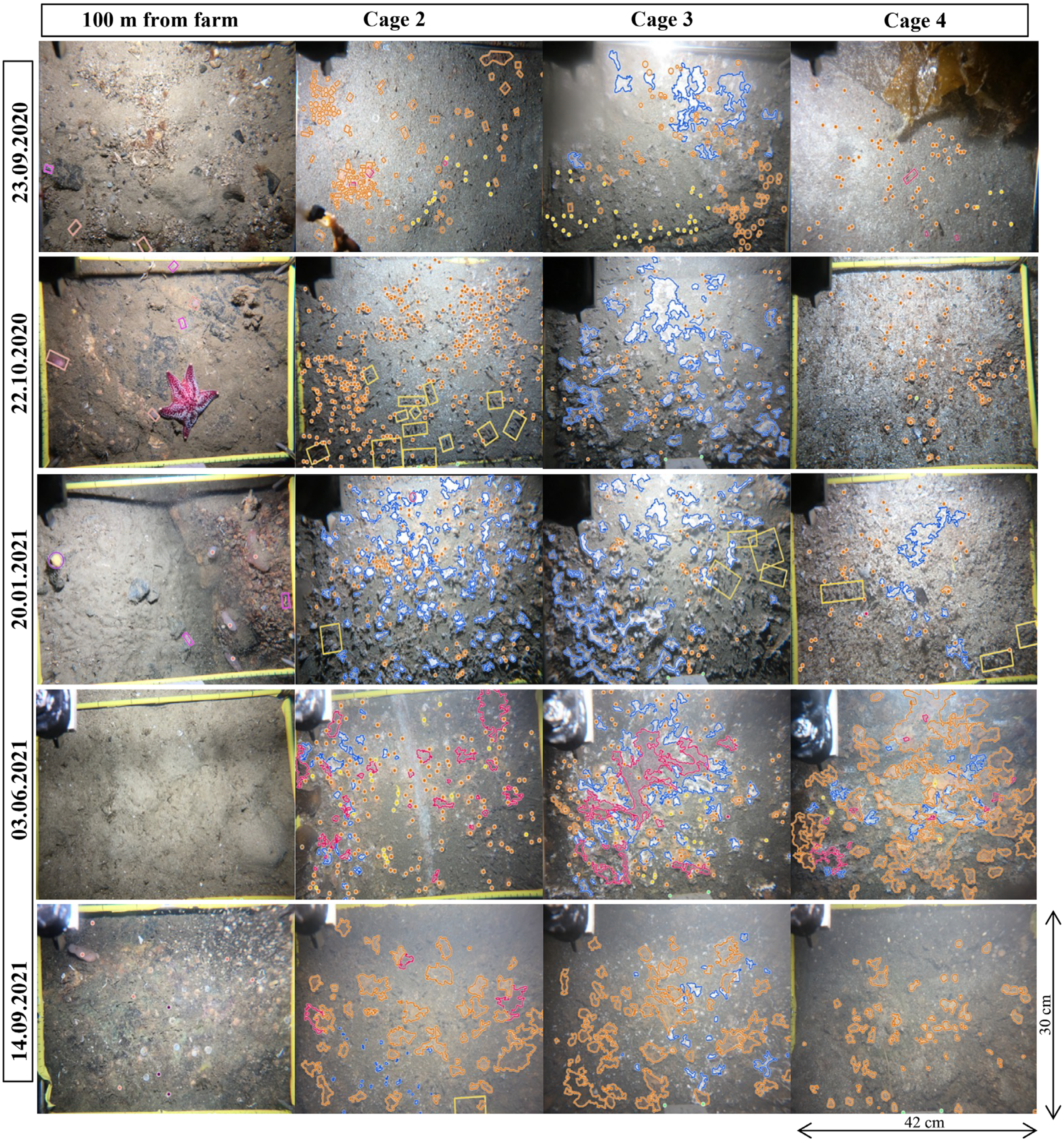

Fig. 2. Examples of images of the sea floor underneath farm cages. Each column represents a different location (100 m from the farm, Cages 2, 3 and 4) and each row a different date (dd/mm/yy). IOE are highlighted by colours, as annotated using the BIIGLE software: surface covered by (blue) bacterial mats, (orange) organic pellets, and (pink) opportunistic polychaete complexes (OPC), and (yellow squares) counts of polychaete aggregations

mats (presumably from a *Beggiatoa*-like species), and OPC were measured for surface area coverage. In cases of overlapping indicators, the most visible one (i.e. the one on top) was annotated. Polychaete tube aggregations (PTA) were counted for abundance.

2.4.3. Taxonomic analysis of OPC and PTA. In March 2021, 2 samples of the OPC from 2 of the study fish cages were collected for taxonomic identification. Samples collection was performed through the positioning of 4 perforated metal trays, each with 4 boxes (18 × 26 × 8 cm each) equipped with a fitted lid, on the seafloor under the cages. The metal trays, which were directly attached to the study cages through ropes, were left on the seafloor for 2 wk. Upon retrieval, the trays were manually lifted from the seafloor and boxes containing samples were sealed by their lids, preventing the loss of sampling material (Svensson et al. 2023). After collection, samples were sieved through a 900 µm mesh, sorted in the laboratory, and preserved in a 96% alcohol solution. Taxonomic analysis was performed on samples collected from under Cages 2 and 3. The aim was to determine the polychaete species composition within the complexes and assess the presence of other non-polychaete taxa in the complex. Due to a lack of samples, taxonomic identification of PTA could not be performed and this IOE was not identified at the species level.

2.5. Statistical analysis

To delineate changes in the abundance and surface area coverage (%) of IOE under the 3 farm cages and at the site 100 m from the farm, the coverage and abundance of each indicator at the 10 image stations was plotted through time. For each cage, we used the average coverage and abundance values from the 10 image stations (N = 1 per cage and time point) for plots and statistical analyses. Changes in mean coverage and abundance were examined in relation to 3 organic waste depositional patterns modelled per cage: (1) daily organic deposition (g TPM m^{-2} d^{-1}), (2) organic deposition summed since the start of the production year (g TPM m^{-2}), and (3) organic deposition summed over the 10 d prior to each survey date (g TPM m^{-2}).

The 2 summed deposition estimates were based on the sum of (modelled) daily deposition rates (g TPM m^{-2} d^{-1}). The 'summed deposition over the production cycle' pattern provided an estimation of the total waste deposition pressure to the seafloor since the start of fish production in September 2020. This measure did not account for flushing dynamics and the removal of organic material by benthic infauna organisms. The 'deposition summed over 10 d' represents the total of the daily deposition (g TPM m^{-2}) modelled over the 10 d leading up to each sampling time point. This measure was included in the analysis as recent experiments have shown that benthic infauna removes salmon faecal material from enriched sediments within 200 h (Keeley et al. in press), meaning 10 d represents an estimate of how long organic material remains present on the seafloor.

Eleven time points were considered for each location (i.e. 3 cages, 100 m distant site). Count values of PTA were plotted for abundance, while surface area coverage (%) data was plotted for organic pellets, bacterial mats, and OPC. As no IOE were detected at the site 100 m from the farm, only data from the farm cages were used in the statistical analyses.

A univariate analysis was carried out in R (R Core Team 2021) to model the relationships between the 3 modelled depositional estimates (daily, total summed, and summed over 10 d) and the mean abundance or surface area coverage of IOE. Generalised additive models (GAMs) were used to model the relationships between the 3 depositional estimates (predictor variables) and surface coverage of organic pellets, bacterial mats, and OPC (dependent variables). GAMs use a flexible function that allows the modelling of nonlinear relationships. Relationships between the explanatory variable waste deposition and the response variable (IOE) were smoothed to remove the need to make assumptions about the relationship form (Wood 2006, Zuur & Ieno 2016). Models also included the effect of cage (i.e. inter-cage variability) on the distribution of the IOE. The fit of the GAMs for the data was assessed using Akaike's information criterion (AIC).

3. RESULTS

3.1. Sedimentation rates

Around all 3 cages, measured daily organic deposition rates increased considerably from February 2021 (average TPM = 27.4 g m^{-2} d^{-1}) to April 2021 (average TPM = 87.75 g m^{-2} d^{-1}) (Table 2). While daily deposition rates increased throughout the survey period around the farm, values remained low at the site 100 m away from the cages (~2 ± 0.2 g m^{-2} d^{-1}). Compared to this site, measured daily deposition rates (g m^{-2} d^{-1}) were 10 times higher in September 2020 around Cage 3, and 40 times higher in April 2021 around the 3 cages (average) (Table 2). Modelled deposition confirmed that only a small fraction of the organic waste reached the location 100 m away from the farm.

Table 2. Comparison of mean (±SE) sedimentation rates (g total particulate matter m^{-2} d^{-1}) around the farm and at 100 m distance based on (1) measurements from sediment traps (measured) and (2) modelled rates based on feed data and hydrodynamics (modelled). Dates are given as dd/mm/yy

Date	Site	Measured	Modelled
24/09/2020	Cage 3	22.90 (±5.8)	14.36
	100 m from farm	2.52 (±0.2)	0.21
16/02/2021	Cage 2	26.86 (±0.5)	23.95
	Cage 3	19.98 (±3.6)	27.90
	Cage 4	35.45 (±10.8)	9.33
	100 m from farm	1.14 (±0.1)	0.57
16/04/2021	Cage 2	102.81 (±34.0)	61.74
	Cage 3	78.61 (±2.9)	70.06
	Cage 4	66.84 (±13.0)	36.34
	100 m from farm	2.55 (±0.2)	0

The general pattern of modelled daily deposition rates agreed with the changes in measured deposition rates across the production cycle; however, modelled rates were generally lower than the measurements from the sediment traps. The deviation was higher in April 2021, when the average deposition rate under the 3 cages was above 50 g m^{-2} d^{-1} (Table 2).

Modelled daily deposition rates (g m^{-2} d^{-1}) highlighted 2 different stages of production: (1) an early stage, from September 2020 to March 2021, during which deposition rates ranged between 0 and 70 g m^{-2} d^{-1}, and (2) a late stage, starting in April 2021 and stretching until the end of the production cycle in September 2021, when deposition rates were between 50 and 110 g m^{-2} d^{-1} (Table 2, Fig. 3).

The modelled organic deposition summed over the entire production cycle (g TPM m^{-2}) increased linearly with time (Fig. 4A). Between September and November 2020, when fish biomass was approximately 100 t, the summed deposition to the seafloor was around 2000 g m^{-2}. During the December 2020 to March 2021 period, when fish biomass increased from 100 to 300 t, the summed deposition reached approximately 5000 g m^{-2}. Finally, after April 2021, at the peak of fish production, deposition was around 20 000 g m^{-2} (Fig. 4A, Table S1, Fig. S3).

The modelled organic deposition summed over 10 d (g TPM m^{-2}) showed an overall non-linear increase over time, with a drop in deposition levels around February to March 2021, followed by a second rapid increase and peak in June 2021 and then a further drop around August 2021 (Fig. 4B).

3.2. Changes in benthic enrichment indicators through the farm production cycle

3.2.1. Presence of organic pellets. Some organic pellets covering the seafloor were visible in images during the entire production period (Figs. 2 & 5A). However, changes in the extent of organic pellet coverage (%) showed a significant positive relationship with organic deposition summed over 10 d ($p < 0.05$) (Table 3). For example, a reduction in summed organic deposition in February and March coincided with a reduction in the surface area covered by organic pellets, while a rise in 10 d summed depositions in late June occurred at the same time as an increase in coverage by organic pellets, mainly in Cages 3 and 4 (Fig. 5A). The GAMs and generalised linear models (GLMs) showed a significant interaction between ‘cage’ and the ‘modelled deposition over 10 d’ ($p = 0.001$) due to high variability between cage deposition and organic pellets coverage (Fig. 5A). The between-cage variation increased towards the end of the production cycle, which also coincided with the removal of some fish in May 2021. For example, in late June 2021, up to 50% of the total

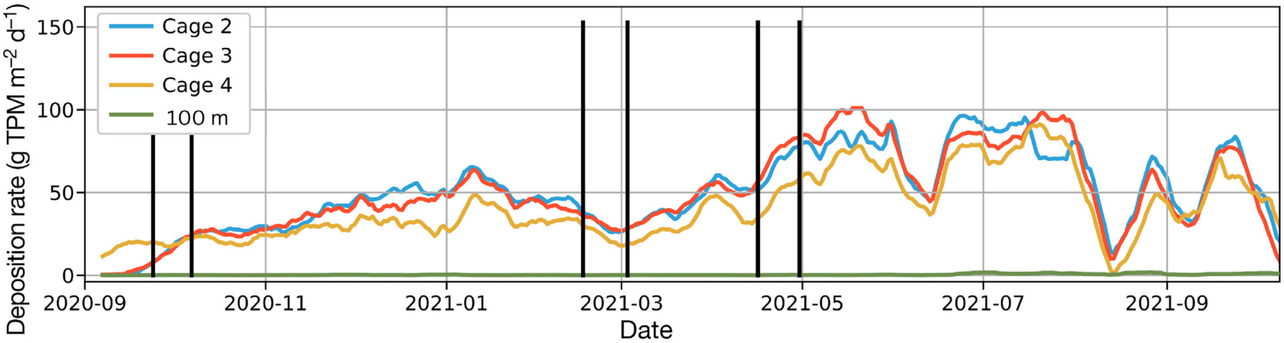

Fig. 3. Modelled total particulate (organic) matter deposition rates (g TPM m^{-2} d^{-1}) under the 3 cages and at 100 m distance modelled over time from September 2020 to September 2021 (14 d moving average). Black bars: deployment and retrieval of sediment traps

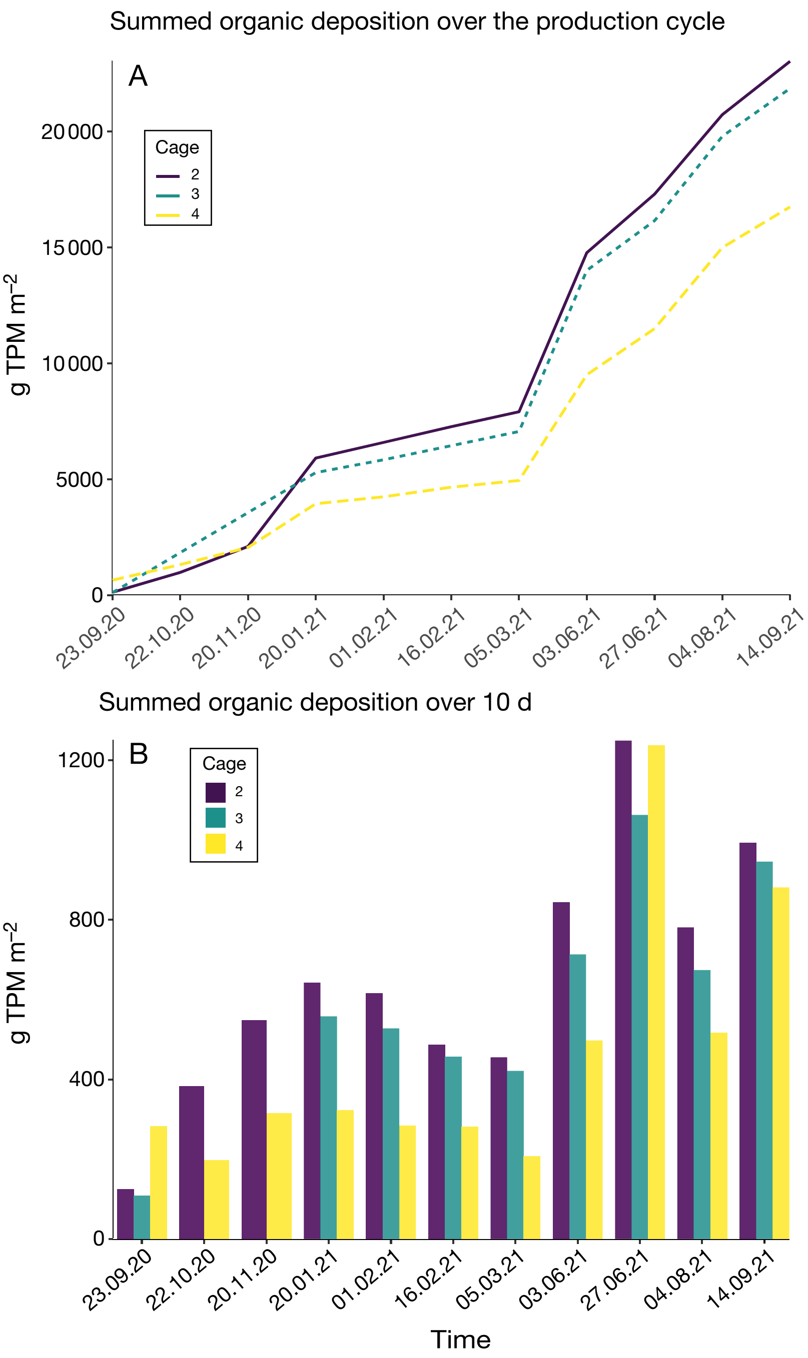

Fig. 4. (A) Modelled summed total particulate (organic) matter deposition (g TPM m^{-2}) over the entire production cycle under the 3 cages from September 2020 to September 2021. (B) Modelled organic deposition (g TPM m^{-2}) summed over the 10 d before the sampling date under the 3 cages, over a year of production

surface area under Cage 4 was covered by pellets, compared to only ca. 8% under Cage 2 (SD = 20.4; Fig. S4). At 100 m from the farm, pellets were rarely detected, and the highest surface area coverage of pellets at any time was 0.04%.

3.2.2. White bacterial mats. The presence of bacterial mats was detected underneath all 3 farm cages, while no bacterial mats were observed 100 m from the cages (Fig. 2). Unlike organic pellets, changes in the mean percentage surface area covered by bacterial mats could not be explained by any of the modelled deposition estimates (Table 3). Following an initial increase, the percentage of surface covered by bacterial mats peaked in February 2021 to an average of 20% under all farm cages and decreased after March 2021. However, organic deposition continued to increase after March and peaked in June 2021, when bacterial mats only covered around an average of 3% of the seafloor (Fig. 5B). While inter-cage variation in surface area coverage by bacterial mats was observed, the general pattern of increased coverage midway throughout the production cycle was detected at all 3 cages (Fig. 5B, Fig. S5).

3.2.3. PTA. PTA abundance had a significant negative linear relationship with organic deposition on the seafloor summed over the entire production cycle under Cages 2 and 3 ($p < 0.05$) (Table 3). The total number of aggregations of polychaete tubes went from approximately 200 per photo-station in September and November 2020, when summed dispersion was approximately 2000 g m^{-2}, to less than 10 individuals in September 2021, when the levels of summed deposition around the farm since the beginning of the production cycle were approximately 17 000 g TPM m^{-2} (Fig. 5D, Table S1). Under Cage 4, PTA abundances were low throughout the entire production cycle and showed no association with any of the modelled deposition estimates on the seafloor (Fig. S6). No aggregations were detected 100 m away from the farm (Fig. S6).

3.2.4. OPC. Percentage coverage by OPC throughout the production cycle was lower than that of other IOE (organic pellets and bacterial mats) and peaked at around 4% in early June 2021. Changes in the OPC percentage surface area coverage showed a significant positive relationship with the organic deposition on the seafloor summed

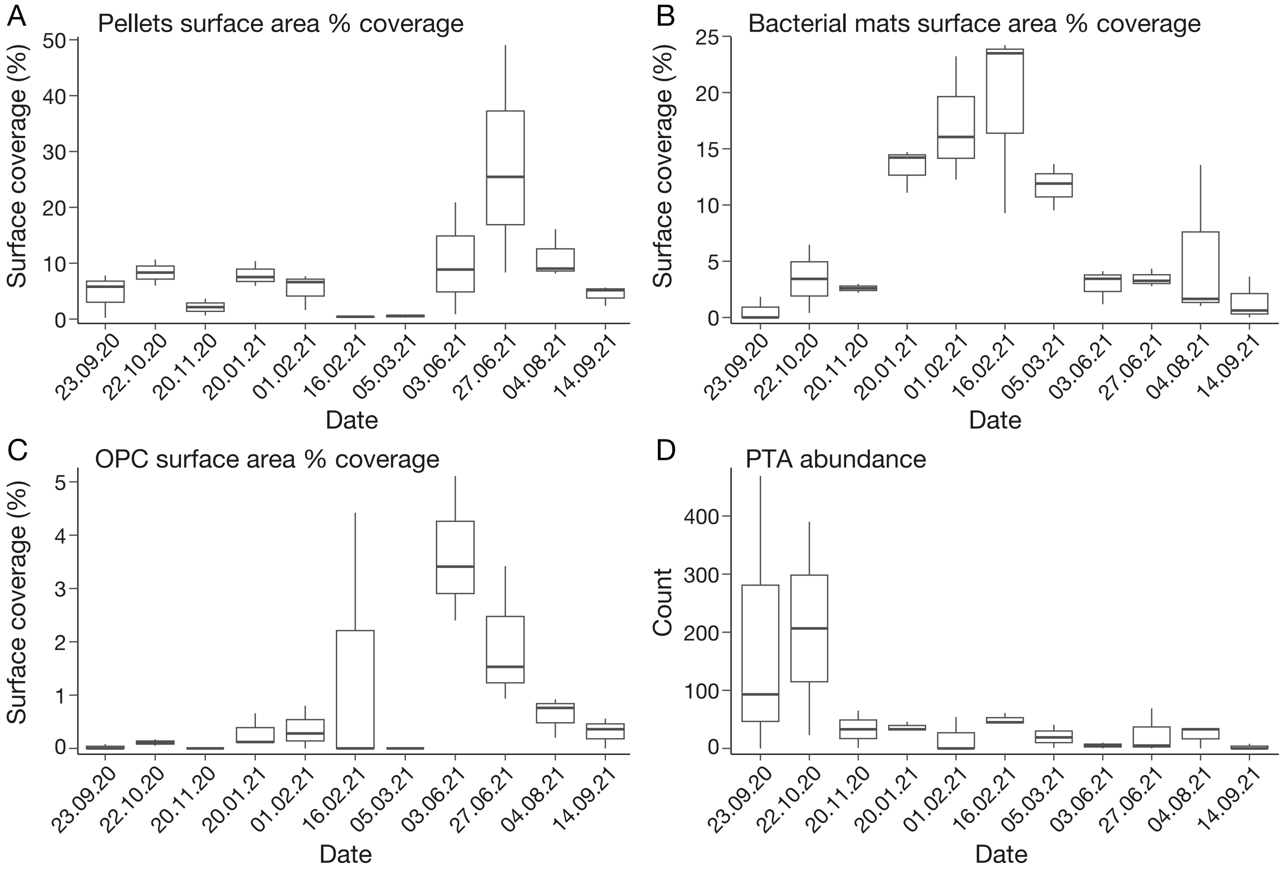

Fig. 5. Changes in surface area coverage (%) of (A) organic pellets, (B) bacterial mats, and (C) opportunistic polychaete complexes (OPC), and (D) abundance of polychaete tube aggregations (PTA) over the survey period. Bar: median; box: interquartile range; whiskers: max./min. values

over the whole production cycle ($p = 0.04$) and over 10 d periods ($p = 0.01$). However, the 'organic deposition summed over 10 d' pattern was the best-fit model to explain changes in the percentage coverage of OPC (Table 3). The linear increase in the summed deposition over 10 d corresponded to an increase in the surface area covered by polychaete complexes until the IOE peaked in early June 2021, when the organic deposition summed over 10 d was around 700 g TPM m^{-2} (Fig. 5C). When organic deposition peaked (TPM > 1100 g m^{-2} over 10 d), OPC coverage started to decrease (to ~2%) and kept declining until the end of the production cycle (Fig. 5C). Variability in the mean percentage coverage of OPC between cages was detected throughout the entire production cycle and increased in early June 2021 (SD = 1.4; Fig. S7). Eventually, a peak in OPC surface area coverage was followed by a gradual drop during the final stage of fish production (Fig. 5C). No OPC were observed at 100 m from the farm site.

Table 3. Results of (1) the generalised additive model on the surface coverage (%) of pellets, bacterial mats, and opportunistic polychaete complexes (OPC), and (2) the generalised linear model on the abundance of polychaete tube aggregations (PTA), for the effect of modelled daily total particulate (organic) matter deposition rate (g TPM m^{-2} d^{-1}), summed organic deposition (g TPM m^{-2}) over 10 d, and summed organic deposition (g TPM m^{-2}) over the production cycle. **Bold**: significant at $p < 0.05$

Modelled deposition	Organic pellets			Bacterial mats			OPC			PTA		
	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p
Daily rate	1	0.79	0.381	1	1.04	0.316	1	0.14	0.711	1	0.28	0.599
Summed over 10 d	1	15.3	**0.0005**	1	1.34	0.255	1	6.56	**0.016**	1	3.56	0.069
Summed over production cycle	1	1.58	0.218	1	1.34	0.255	1	4.47	**0.043**	1	4.98	**0.034**

3.3. Taxonomic identification of OPC

Taxonomic analysis of the samples revealed the presence of 2 different taxa, namely Polychaeta and Nematoda, within the 2 OPC formations. The polychaete component was represented by 8 species, including 4 *Ophryotrocha* sp. species (*O. eutrofila*, *O. maculata*, unknown), *Palpiphitime lobifera*, *Capitella capitata*, *Malacoceros vulgaris*, and *Eusyllis blomstrandi*. A comparison of benthic images with taxonomic data revealed that a considerable fraction of the opportunistic complexes found in the intermediate stage of production consisted of nematodes.

4. DISCUSSION

4.1. Summary of results

Changes in the surface area coverage and abundance of visual benthic indicators throughout a year of finfish production revealed a clear impact of the release and accumulation of total particulate matter. Whereas bacterial mat coverage showed no relationship with waste deposition, the surface coverage of organic pellets closely followed the pattern of modelled organic deposition summed over 10 d periods. PTA were associated with low levels of summed deposition on the seafloor and decreased throughout the production cycle, while the lower prevalence of OPC was positively influenced by the higher levels of organic deposition during the later stages of the production cycle.

4.2. Visual indicators of enrichment present throughout the production cycle

4.2.1. Organic pellets. The presence of organic pellets beside the cages could be explained by the production of fish, as no pellets were detected at the site 100 m away from the farm. The close association between the coverage of organic pellets and the 'organic deposition summed over 10 d' pattern could be explained by the combination of sediment deposition cycles, rates of organic matter consumption by infauna organisms, and flushing dynamics on the seafloor over several days. Results are also in agreement with an experiment that showed that infauna removes Atlantic salmon faecal pellets from enriched seafloor sediments over a 200 h period (Keeley et al. in press). Similarly, hydrodynamic and flushing dynamics along the water column and at the seafloor, removing and distributing organic matter released from the farm, could be related to the discrepancy in peaks and troughs of pellet coverage detected between cages (Alongi 1996, Sarà et al. 2006). Previous studies (e.g. Hamoutene et al. 2016, Dunlop et al. 2021) have already described the importance of these abiotic factors in changes in benthic community distribution and abundances.

4.2.2. Mat-forming sulphur-oxidising bacteria. The presence of mat-forming sulphur-oxidising bacteria under the farm supports the previously observed relationship between benthic organic enrichment and a shift in communities towards sulphur-oxidising bacteria under aquaculture sites (Preisler et al. 2007, Hamoutene et al. 2014). This bacterial composition is characterised by a combination of naturally occurring sediment bacteria and bacteria associated with flocculent matter (Verhoeven et al. 2016). In our study, fluctuations in the total surface coverage of this IOE were detected throughout the production cycle and between the 3 cages but showed no correlation with temporal sedimentation patterns. Bacterial mats have also been observed around farm sites in Newfoundland, Canada, and no clear pattern in temporal distribution with enrichment status was observed (Salvo et al. 2017).

The difference between cages could be related to hydrodynamics, as water current patterns and flushing dynamics can change within a few metres span, and throughout the production cycle. Sulphur-oxidising bacteria live in environments where sulphide and oxygen meet and need low levels of oxygen in the water while they oxidise hydrogen sulphide produced in the sediment (Fenchel et al. 2012). Sulphide concentration within the sediment has also been used as an explanation for bacterial mat distribution on sandy substrates by Hamoutene et al. (2014). On hard substrates, sulphur-oxidising bacteria can exploit the oxygen–sulphide interface created by the layer of organic matter. A patchy distribution of organic matter on the sandy sediment or hard bottoms (e.g. due to an uneven seabed) can thus result in a patchy distribution of bacterial mats. Moreover, a decreased coverage of bacterial mats was observed in association with an increased coverage of organic pellets (i.e. June 2021), and vice versa (i.e. February and March 2021). This reverse relationship, alongside the observed drop in bacterial mat surface coverage during the late stage of production, could be explained by high sulphide levels and a lack of oxygen caused by the increasing levels of organic material reaching the seafloor (TPM $\geqslant$ 100 g m^{-2} d^{-1}) but also the potential smothering of bacterial mats by increased pellets and OPC coverage. This process will break down the oxic–anoxic interface at the sediment–water juncture necessary for the proliferation of these bacteria.

4.3. Early indicators of enrichment — disappearance of PTA

Tube-forming polychaetes are common and naturally abundant on many types of soft sediments and can adopt deposit-feeding mechanisms (Haanes & Gulliksen 2011). The presence of tube-forming polychaetes under fish cages indicates their disposition to colonise organically enriched areas during the early stages of farm production when organic loading is low. The bottom deposition and accumulation of fine sediments and organic pellets provide these suspension-feeding organisms with higher amounts of organic matter and can smother them. At the same time, these organisms play a crucial role in ecosystem functioning and biodiversity preservation as the formation of reef-like structures is associated with several ecological benefits such as sediment stabilisation, provision of habitat and food for other organisms, and biofiltration properties (Fornós et al. 1997, Dubois et al. 2002, Murray et al. 2002, Bruschetti et al. 2008, 2009). It has been demonstrated that these aggregations can remain constant in a specific location for a prolonged period, but physical disturbances can alter their abundance and spatial distribution (Callaway et al. 2010). Previous studies on large-scale aquaculture activities have shown how enhanced particulate matter fluxes and altered hydrodynamics regimes can lead to the loss of PTA in the areas surrounding farms (Davenport et al. 2000). In our study, the low resistance to environmental disturbances explains the decreased abundance of these aggregations in combination with higher modelled organic depositional rates to the seafloor (TPM $\geqslant 40$ g m^{-2} d^{-1}). The disappearance of this IOE in conjunction with increased levels of organic enrichment suggests the presence of a tolerance threshold to organic loading and the inability of this IOE to withstand medium to high levels of organic enrichment.

4.4. Late indicators of enrichment — OPC arrival

Opportunistic polychaetes are complex-forming organisms often encountered under aquaculture sites, particularly hard-bottom ones, and are considered an important indicator of organic enrichment (Hansen et al. 2011, Eijke 2013, Hamoutene et al. 2015, Jansen et al. 2019). The presence of OPC has been previously described by Hamoutene et al. (2016) in close association with *Beggiatoa*-like bacterial mats and organic pellets under aquaculture sites placed over mixed- and hard-bottom substrates. The reliance on organic material for their nutrients and energy requirements can explain the presence beneath cages of opportunistic taxa, such as polychaetes and nematodes, especially when organic enrichment is high. Overall, these opportunistic polychaete-dominated complexes hold a high bio-mitigation potential and can be beneficial under farm sites to mitigate organic pollution on the seafloor (Kinoshita et al. 2008, Brown et al. 2011, Nederlof et al. 2020). However, video or image-based estimations of OPC abundances can be hindered by the presence of bacterial mats and organic pellets, covering the substrate and concealing the presence of OPC (Hamoutene et al. 2015). Similarly, the thickness of these complexes cannot be estimated by means of image analysis.

Our results revealed that OPC coverage was low (<1%) between September 2020 and January 2021, when daily organic deposition rates were low (TPM < 50 g m^{-2} d^{-1}). Around February 2021, increasing modelled organic deposition summed over the whole production cycle and 10 d was positively correlated with the observed OPC coverage, indicating the need for higher amounts of organic material for these organisms to start colonising the seafloor. OPC are also small in size and need a substantial mass of individuals to become complexes that can be identified visually; therefore, indicating a high level of enrichment. As organic enrichment increases, the recruitment of these opportunistic species could be enhanced by the accumulation of sulphides in the sediments, acting as a cue for larval settlement (Cuomo 1985). The peak of OPC coverage in early June did not correspond to the peak of summed deposition to the seafloor in late June, suggesting a tolerance threshold for this IOE and the existence of an organic enrichment optimum window that favours the presence of OPC. This tolerance maximum could be explained by the formation of anoxic conditions due to increasing levels of organic enrichment, the offset of organic matter degradation processes, and the presence of oxygen (Salvo et al. 2017, 2018b). Alongside waste deposition, the presence and coverage of these complexes could be influenced by other factors, such as seawater temperature, not included in this study.

In our study, visual inspections allowed the identification of 2 different complex-forming organisms. The distinction between these 2 opportunistic organisms was confirmed by taxonomic analyses, revealing the presence of both polychaetes and nematodes in the OPC. Based on our limited ability to identify fauna from images, we established that the OPC were dominated by nematodes until June 2021, while opportunistic polychaetes such as *Ophryotrocha* spp. became more prevalent in August and September 2021. A change in taxonomic dominance within these complexes during the late stage of production could explain temporal changes in seafloor coverage.

4.5. Use of IOE for monitoring systems

Video and image monitoring represents a viable solution for collecting information about benthic communities inhabiting mixed- and hard-bottom substrate types, where grab sampling is hindered (Hamoutene et al. 2015). Benthic responses to organic enrichment, visually characterised by changes in distribution and abundance/surface coverage, could be used to evaluate and make informed decisions regarding the activity of fish farms located over mixed- and hard-bottom habitats (Hansen et al. 2011). The use of image annotation software for the characterisation of benthic indicators can make the evaluation faster, more accessible, and more precise, as data on presence, distribution, abundance, and surface area coverage is readily provided to the user. Image annotation holds the potential for inclusion in a substrate-specific monitoring system for mixed- and hard-bottom substrates in ongoing monitoring schemes (e.g. the MOM system in Norway).

Although bacterial mats are widely used as an indicator of excess organic enrichment (Armstrong et al. 2020), our results suggest that this IOE fails to indicate a specific level of organic enrichment on mixed- and hard-bottom substrates. The organic pellet coverage, however, could be used as a proxy of summed organic deposition on the seafloor, particularly over short periods (e.g. 10 d periods). On mixed substrates, the presence of IOE such as tube-forming polychaetes can be related to low levels of sediment accumulation, while their consequent disappearance could be indicative of increasing organic matter on the seafloor. Finally, the presence and coverage of OPC can reveal high levels of summed organic deposition during stages of peak production on mixed- and hard-bottom substrates.

For some visual indicators, visual biomonitoring techniques struggle to differentiate enriched from highly enriched conditions and may also struggle to discriminate between low and moderate levels of summed organic deposition. Therefore, in addition to visual monitoring techniques, the isolation and analysis of microbial environmental DNA (eDNA) sequences may be deployed in the characterisation of hard-bottoms indicators of organic enrichment (Keeley et al. 2021, Knight et al. 2021). Site-specific factors such as hydrodynamics, temperature, depth profile, and the morphological features of endemic benthic organisms (e.g. sensitivity to organic enrichment) should be considered alongside organic matter sedimentation (Lin & Bailey-Brock 2008, Macleod et al. 2006, 2007). The combination of these factors can make the correlation between waste deposition and the presence and/or abundance of indicators difficult to interpret (Armstrong et al. 2020). Finally, the development of an inclusive hard-bottom habitat monitoring system may be challenged by the patchy nature of rocky substrates, which can be naturally barren of faunal coverage, and by the strong regional variability in the distribution of hard-bottom substrate organisms (Keeley et al. 2021). Extending research over a longer period and applying the method to farm sites with different geographical profiles and layouts would help determine the validity of our results on a broader scale and contribute to the development of an overarching monitoring tool for mixed- and hard-bottom substrates. Furthermore, these visual methods would ideally be based on substantial baseline information collected at the start of the farm establishment through systematic benthic mapping around farms (Kutti & Husa 2021).

4.6. Limitations

A limitation of this study was the lack of sufficient resolution data on hydrodynamics, current velocities, water temperatures, and benthic processes (i.e. faunal respiration, resuspension events). Previous studies (e.g. Hamoutene et al. 2016, Dunlop et al. 2021) have described the importance of these abiotic factors in changes in the distribution and abundance of hard-bottom epibenthic organisms. Spatial measurements of current velocity at the seabed are necessary to detect the difference in potential erosion of sediment and the distribution of organic waste. Such a limitation highlights the importance of future research to create a sampling design embracing all the environmental conditions at the site. Another limitation was the unexpected fish-relocation events, which occurred several times during the survey period. Trout were occasionally moved from their original cage to a fourth cage for short periods (e.g. during sea lice treatments). Furthermore, half of the fish present in the 3 farm cages were moved in May 2021 to 3 new cages, placed adjacent to the original ones. Modelling, however, took these changes in fish stocking into account by using daily feed input as a proxy of fish biomass. Finally, image analysis methods can be limited by the occasional spatial overlaps between indicators. This circumstance may lead to underestimations of the surface area coverage or abundance of indicators that are covered by others, resulting in their incomplete detection.

5. CONCLUSIONS

This study quantified the impact of organic waste released from fish farming on visual benthic indicators inhabiting the mixed- and hard-bottom substrates beneath finfish cages. Contrasting responses, in time and spatial extent, were detected between different benthic indicators of organic enrichment. Image collection coupled with image characterisation software can provide an alternative approach to data collection for monitoring purposes, especially where grab sampling is hindered by hard substrates. Characterising the response of different visual indicators on mixed- and hard-bottom substrates permitted us to observe the relationship between the indicators and organic deposition patterns on the seafloor. These findings can contribute to the development of a quantitative monitoring scheme for mixed- and hard-bottom benthic communities that would facilitate defensible monitoring and better management of aquaculture farms placed over mixed- and hard-bottom substrate areas.

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LITERATURE CITED

Ådlandsvik B, Sundby S (1994) Modelling the transport of cod larvae from the Lofoten area. ICES Mar Sci Symp 198:379–392

Albretsen J, Sperrevik AK, Staalstrøm A, Sandvik AD, Vikebø F, Asplin L (2011) NorKyst-800 report no. 1: User manual and technical descriptions. Fisken Havet 2-2011

Alongi DM (1996) The dynamics of benthic nutrient pools and fluxes in tropical mangrove forests. J Mar Res 54: 123–148

Armstrong EG, Mersereau J, Salvo F, Hamoutene D, Dufour SC (2020) Temporal change in the spatial distribution of visual organic enrichment indicators at aquaculture sites in Newfoundland, Canada. Aquacult Int 28:569–586

Bannister RJ, Valdemarsen T, Hansen PK, Holmer M, Ervik A (2014) Changes in benthic sediment conditions under an Atlantic salmon farm at a deep, well-flushed coastal site. Aquacult Environ Interact 5:29–47

Bannister RJ, Johnsen IA, Hansen PK, Kutti T, Asplin L (2016) Near- and far-field dispersal modelling of organic waste from Atlantic salmon aquaculture in fjord systems. ICES J Mar Sci 73:2408–2419

Brown N, Eddy S, Plaud S (2011) Utilization of waste from a marine recirculating fish culture system as a feed source for the polychaete worm, *Nereis virens*. Aquaculture 322–323:177–183

Bruschetti M, Luppi T, Fanjul E, Rosenthal A, Iribarne O (2008) Grazing effect of the invasive reef-forming polychaete *Ficopomatus enigmaticus* (Fauvel) on phytoplankton biomass in a SW Atlantic coastal lagoon. J Exp Mar Biol Ecol 354:212–219

Bruschetti M, Bazterrica C, Luppi T, Iribarne O (2009) An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon. J Exp Mar Biol Ecol 375: 76–83

Callaway R, Desroy N, Dubois SF, Fournier J and others (2010) Ephemeral bio-engineers or reef-building polychaetes: how stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? Integr Comp Biol 50: 237–250

Carvajalino-Fernández MA, Sævik PN, Johnsen IA, Albretsen J, Keeley NB (2020) Simulating particle organic matter dispersal beneath Atlantic salmon fish farms using different resuspension approaches. Mar Pollut Bull 161:111685

CATAMI Technical Working Group (2014) CATAMI classification scheme for scoring marine biota and sub-strata in underwater imagery. Version 1.4. National Environmental Research Program, Marine Biodiversity Hub, Canberra

Cubillo AM, Ferreira JG, Robinson SMC, Pearce CM, Corner RA, Johansen J (2016) Role of deposit feeders in integrated multi-trophic aquaculture — a model analysis. Aquaculture 453:54–66

Cuomo MC (1985) Sulphide as a larval settlement cue for *Capitella* sp. I. Biogeochemistry 1:169–181

Davenport J, Smith RJJW, Packer M (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Mar Ecol Prog Ser 198:131–137

DFO (Fisheries and Oceans Canada) (2013) Potential effects surrounding the importation of European-origin cultured Atlantic salmon to Atlantic salmon populations and habitats in Newfoundland. DFO Can Sci Advis Sec Sci Advis Rep 2013/050

Dubois S, Retière C, Olivier F (2002) Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs: effects of human disturbances. J Mar Biol Assoc UK 82:817–826

Dunlop K, Harendza A, Plassen L, Keeley N (2020) Epifaunal habitat a ssociations on mixed and hard bottom substrates in coastal waters of northern Norway. Front Mar Sci 7: 568802

Dunlop K, Harendza A, Bannister R, Keeley N (2021) Spatial response of hard- and mixed-bottom benthic epifauna to organic enrichment from salmon aquaculture in northern Norway. Aquacult Environ Interact 13:455–475

Eikje EM (2013) Benthic impacts of fish-farm waste on hard bottom habitats, the ecology of opportunistic epifauna polychaetes. MSc thesis, University of Bergen

Ervik A, Hansen PK, Aure J, Stigebrandt A, Johannsen P, Jahnsen T (1997) Regulating the local environmental impact of intensive marine fish farming. I. The concept of the MOM system (Modelling-Ongrowing fish farms-Monitoring). Aquaculture 158:85–94

FAO (Food and Agriculture Organization of the United Nations) (2020) The state of world fisheries and aquaculture 2020. Sustainability in action. FAO, Rome

Fenchel T, Blackburn H, Blackburn TH, King GM (2012) Bacterial biochemistry: the ecophysiology of mineral cycling. Academic Press, London

Fornós JJ, Forteza V, Martínez-Taberner A (1997) Modern polychaete reefs in western Mediterranean lagoons: *Ficopomatus enigmaticus* (Fauvel) in the Albufera of Menorca, Balearic Islands. Palaeogeogr Palaeoclimatol Palaeoecol 128:175–186

Forseth T, Barlaup BT, Finstad B, Fiske P and others (2017) The major threats to Atlantic salmon in Norway. ICES J Mar Sci 74:1496–1513

Gentry RR, Froehlich HE, Grimm D, Kareiva P and others (2017) Mapping the global potential for marine aquaculture. Nat Ecol Evol 1:1317–1324

Goldburg R, Naylor R (2005) Future seascapes, fishing, and fish farming. Front Ecol Environ 3:21–28

Haanes H, Gulliksen B (2011) A high local species richness and biodiversity within high-latitude calcareous aggregates of tube-building polychaetes. Biodiv Conserv 20: 793–806

Hamoutene D (2014) Sediment sulphides and redox potential associated with spatial coverage of *Beggiatoa* spp. at finfish aquaculture sites in Newfoundland, Canada. ICES J Mar Sci 71:1153–1157

Hamoutene D, Sheppard L, Mersereau J, Oldford V and others (2014) Applicability of the use of visual indicators [presence of *Beggiatoa* and/or opportunistic polychaete complexes (OPC)] to identify benthic changes due to aquaculture on various substrates. DFO Can Sci Advis Sec Res Doc 2014/063

Hamoutene D, Salvo F, Bungay T, Mabrouk G, Couturier C, Ratsimandresy A, Dufour SC (2015) Assessment of finfish aquaculture effect on Newfoundland epibenthic communities through video monitoring. N Am J Aquaculture 77: 117–127

Hamoutene D, Salvo F, Donnet S, Dufour SC (2016) The usage of visual indicators in regulatory monitoring at hard-bottom finfish aquaculture sites in Newfoundland (Canada). Mar Pollut Bull 108:232–241

Hamoutene D, Salvo F, Cross S, Dufour SC, Donnet S (2018) Linking the presence of visual indicators of aquaculture deposition to changes in epibenthic richness at finfish sites installed over hard bottom substrates. Environ Monit Assess 190:750

Hansen PK, Ervik A, Schaanning M, Johannessen P, Aure J, Jahnsen T, Stigebrandt A (2001) Regulating the local environmental impact of intensive, marine fish farming: II. The monitoring programme of the MOM system (Modelling–Ongrowing fish farms–Monitoring). Aquaculture 194:75–92

Hansen PK, Bannister R, Husa V (2011) Waste from fish farms. Impact on shallow and deep hardbottom sites. Institute of Marine Research, Bergen (in Norwegian)

Henderson AR, Ross DJ (1995) Use of macrobenthic infaunal communities in the monitoring and control of the impact of marine cage fish farming. Aquacult Res 26:659–678

Holmer M, Wildish D, Hargrave B (2005) Environmental effects of marine finfish aquaculture. In: Hargrave B (ed) Handbook of environmental chemistry. Springer-Verlag, Berlin, p 181–206.

Howell KL, Piechaud N, Downie AL, Kenny A (2016) The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management. Deep Sea Res I 115:309–320

Husa V, Fossøy F, Davey M, Agnalt AL and others (2024) Monitoring marine alien species in Norway — a pilot study for implementing a national program. Rapport fra havforskningen 2024-1

Jansen HM, Hansen PK, Brennan N, Dahlgren TG and others (2019) Enhancing opportunistic polychaete communities under fish farms: an alternative concept for integrated aquaculture. Aquacult Environ Interact 11: 331–336

Keeley NB, Forrest BM, Macleod CK (2015) Benthic recovery and re-impact responses from salmon farm enrichment: implications for farm management. Aquaculture 435:412–423

Keeley N, Valdemarsen T, Woodcock S, Holmer M, Husa V, Bannister R (2019) Resilience of dynamic coastal benthic ecosystems in response to large-scale finfish farming. Aquacult Environ Interact 11:161–179

Keeley N, Laroche O, Birch M, Pochon X (2021) A substrate-independent benthic sampler (SIBS) for hard and mixed-bottom marine habitats: a proof-of-concept study. Front Mar Sci 8:627687

Keeley N, Dunlop K, Laroche O, Watts E, Sævik P, Albretsen J (in press) Disaggregation rates of salmon feces and microbial inoculation of sediments: new insight for particle dispersal modelers. Aquacult Environ Interact doi: 10.3354/aei00489

Kinoshita K, Tamaki S, Yoshioka M, Srithonguthai S, Kunihiro T, Ohwada K, Tsutsumi H (2008) Bioremediation of organically enriched sediment deposited below fish farms with artificially mass-cultured colonies of a deposit-feeding polychaete *Capitella* sp. I. Fish Sci 74: 77–87

Knight R, Verhoeven JTP, Salvo F, Hamoutene D, Dufour SC (2021) Validation of visual bacterial mat assessment at aquaculture sites through abiotic and biotic indicators. Ecol Indic 122:107283

Kutti T, Husa V, (2021) Proposal for a method for mapping vulnerable species and habitat types in deep water for applications for aquaculture in the sea. Rapport fra havforskningen 2021-39 (in Norwegian)

Kutti T, Ervik A, Hansen PK (2007a) Effects of organic effluents from a salmon farm on a fjord system. I. Vertical export and dispersal processes. Aquaculture 262:367–381

Kutti T, Hansen PK, Ervik A, Høisæter T, Johannessen P (2007b) Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. Aquaculture 262:355–366

Lacharité M, Metaxas A (2017) Hard substrate in the deep ocean: how sediment features influence epibenthic megafauna on the eastern Canadian margin. Deep Sea Res I 126: 50–61

Langenkämper D, Zurowietz M, Schoening T, Nattkemper TW (2017) BIIGLE 2.0-browsing and annotating large marine image collections. Front Mar Sci 4:83

Lin DT, Bailey-Brock JH (2008) Partial recovery of infaunal communities during a fallow period at an open-ocean aquaculture. Mar Ecol Prog Ser 371:65–72

Macleod CK, Moltschaniwskyj NA, Crawford CM (2006) Evaluation of short-term fallowing as a strategy for the management of recurring organic enrichment under salmon cages. Mar Pollut Bull 52:1458–1466

Macleod CK, Moltschaniwskyj NA, Crawford CM, Forbes SE (2007) Biological recovery from organic enrichment: some systems cope better than others. Mar Ecol Prog Ser 342:41–53

McGinnity P, Prodöhl P, Ferguson A, Hynes R and others (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc Biol Sci 270: 2443–2450

Merino G, Barange M, Blanchard JL, Harle J and others (2012) Can marine fisheries and aquaculture meet fish demand from a growing human population in a changing climate? Glob Environ Change 22:795–806

Murray JM, Meadows A, Meadows PS (2002) Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. Geomorphology 47:15–30

Nederlof MAJ, Fang J, Dahlgren TG, Rastrick SPS and others (2020) Application of polychaetes in (de)coupled integrated aquaculture: an approach for fish waste bioremediation. Aquacult Environ Interact 12:385–399

Parsons AE, Escobar-Lux RH, Sævik PN, Samuelsen OB, Agnalt AL (2020) The impact of anti-sea lice pesticides, azamethiphos and deltamethrin, on European lobster (*Homarus gammarus*) larvae in the Norwegian marine environment. Environ Pollut 264:114725

Pearson TH (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

Preisler A, De Beer D, Lichtschlag A, Lavik G, Boetius A, Jørgensen BB (2007) Biological and chemical sulfide oxidation in a *Beggiatoa* inhabited marine sediment. ISME J 1: 341–353

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Salvo F, Hamoutene D, Dufour SC (2015) Trophic analyses of opportunistic polychaetes (*Ophryotrocha cyclops*) at salmonid aquaculture sites. J Mar Biol Assoc UK 95: 713–722

Salvo F, Dufour SC, Hamoutene D (2017) Temperature thresholds of opportunistic annelids used as benthic indicators of aquaculture impact in Newfoundland (Canada). Ecol Indic 79:103–105

Salvo F, Oldford V, Bungay T, Boone C, Hamoutene D (2018a) Guide for video monitoring of hard bottom benthic communities of the south coast of Newfoundland for aquaculture impact assessments. Can Data Rep Fish Aquat SciFs 97-13/1284E-PDF.

Salvo F, Marshall K, Hamoutene D (2018b) Mesocosm trials to determine survival of *Ophryotrocha cyclops* (Salvo, 2014) to different oxygen conditions. Ecol Indic 89:572–575

Sarà G, Scilipoti D, Milazzo M, Modica A (2006) Use of stable isotopes to investigate dispersal of waste from fish farms as a function of hydrodynamics. Mar Ecol Prog Ser 313: 261–270

Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model 9:347–404

Standards Norway (2016) Environmental monitoring of benthic impact from marine aquaculture. Norwegian Standard NS9410:2016. Standards Norway, Lyskard (in Norwegian)

Sutherland TF, Amos CL, Ridley C, Droppo IG, Petersen SA (2006) The settling behavior and benthic transport of fish feed pellets under steady flows. Estuaries Coasts 29: 810–819

Svensson SGB, Strohmeier T, Rastrick H, Garcia AA, Lock EJ, Sveier H, Jansen HM (2023) Life history traits for *Ophryotrocha craigsmithi* (Wiklund, Glover & Dahlgren, 2009), a candidate species in integrated multitrophic aquaculture. Front Mar Sci 10:1116765

Taranger GL, Karlsen Ø, Bannister RJ, Glover KA and others (2015) Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES J Mar Sci 72: 997–1021

Valdemarsen T, Bannister RJ, Hansen PK, Holmer M, Ervik A (2012) Biogeochemical malfunctioning in sediments beneath a Norwegian deep-water fish farm. Environ Pollut 170:15–25

Valdemarsen T, Hansen PK, Ervik A, Bannister RJ (2015) Impact of deep-water fish farms on benthic macrofauna communities under different hydrodynamic conditions. Mar Pollut Bull 101:776–783

Verhoeven JTP, Salvo F, Hamoutene D, Dufour SC (2016) Bacterial community composition of flocculent matter under a salmonid aquaculture site in Newfoundland, Canada. Aquacult Environ Interact 8:637–646

Wildish DJ, Pohle GW (2005) Benthic macrofaunal changes resulting from finfish mariculture. In: Hargrave B (ed) Environmental effects of marine finfish aquaculture. Springer, Berlin, p 275–304

Wood SN (2006) Generalized additive models: an introduction with R. CRC Press, Boca Raton, FL

Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. Methods Ecol Evol 7:636–645

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