



# Spatial response of hard- and mixed-bottom benthic epifauna to organic enrichment from salmon aquaculture in northern Norway

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**ABSTRACT:** Norwegian Atlantic salmon aquaculture is continuing to expand in northern regions dominated by hard- and mixed-bottom substrates. Such habitats contain rich benthic epifaunal communities, including sponges and other sessile invertebrates susceptible to the impacts of particulate material released from finfish farms. Here, conventional soft-sediment sampling techniques are unable to discern the impacts of farm waste, and new monitoring methods and indicator taxa must be identified. This study improves understanding of the impacts of particulate waste released from salmon farms on the density and structure of benthic epifaunal communities on mixed- and hard-bottom substrates. The diversity, density, and composition of epifaunal communities and visually conspicuous benthic infauna were recorded in towed camera transects along the enrichment gradient (~50–800 m) of 3 salmon farms in northern Norway. Elevated fluxes of particulate material in the vicinity of all farms significantly affected epifaunal community composition, as did the coverage of some key substrate types. The defecated mounds of lugworms and the seastar *Asterias rubens* were notably more abundant near the farms where fluxes were elevated. The sponges *Polymastia* spp. and *Phakellia* spp. and the soft coral *Duva florida* showed significant declines in density with increasing sedimentation and were principal taxa in communities at natural sedimentation levels. Results identify taxa with both positive and negative spatial associations to particulate waste released from finfish farms and the potential for the development of an epifauna indicator-based index for monitoring the environmental impacts of aquaculture in hard- and mixed-bottom dominated substrates.

**KEY WORDS:** Benthic megafauna · Coastal aquaculture · Hard substrates · Sponge aggregations · Soft corals · Environmental assessment

## 1. INTRODUCTION

The deep-silled fjords and open coastal environments of inshore Norway provide well-flushed waters with stable salinities and temperatures as far north as the Subarctic regions of Troms and Finnmark. These conditions make coastal Norway particularly conducive to finfish farming. The Norwegian Atlantic salmon *Salmo salar* farming industry has experienced an average annual growth of 20% over the past 20 yr, with a total annual production of 1.35 mil-

lion t in 2018 (Statistics Norway 2019). The Norwegian aquaculture industry as a whole is predicted to experience continued growth and has the potential to reach a total annual production of 5 million t by 2050 (Olafsen et al. 2012). Much of the growth in Atlantic salmon farming is currently occurring in the fjords of northern Norway and in more exposed offshore areas, where space is not yet a constraint (Strat 2016, Aanesen & Mikkelsen 2020). In addition, rising seawater temperatures associated with global climate change will favor salmonid farming in the mid and

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northern regions of Norway (Lorentzen & Hannesson 2005, Hermansen & Heen 2012).

Organic enrichment from waste (uneaten food and faeces) released from open cage salmonid farms is known to impact benthic communities in the farms' local and broader scale environment (Kutti et al. 2007, Wilding et al. 2012, Bannister et al. 2014, Keeley et al. 2019). The rapid expansion of salmonid aquaculture in coastal Norway has led to increased concerns regarding the environmental impact both at current and future production levels. Current environmental monitoring procedures for finfish farming follow national and international directives; for example, the Norwegian standard NS9410 (Standards Norway 2016) and the Aquaculture Stewardship Council Salmon Standard (Aquaculture Stewardship Council 2019) that are centered around the analysis of chemical and biological parameters from soft-sediment and infauna samples. Monitoring is based on a well-established knowledge of the response of soft-sediment benthic infaunal communities to farm waste material, which is typified by a decrease in species diversity and a corresponding pronounced increase in the abundance of opportunistic species (Pearson & Rosenberg 1978, Henderson & Ross 1995). The seafloor of coastal northern Norway, however, commonly features hard and mixed substrates dominated by benthic epifaunal communities (Dunlop et al. 2020) and is thus unsuitable for conventional benthic monitoring techniques, such as benthic grabs or cores (Sutherland et al. 2018, 2019). Accordingly, there is a significant lack of knowledge regarding the impact of salmonid farming on hard- and mixed-bottom epifaunal communities in coastal Norway and how potential impacts can be monitored.

Benthic epifaunal communities on hard substrates in continental and coastal waters in northern Norway are known to be characterized by 'ostur' sponge communities and cold-water coral reef ecosystems (Kutti et al. 2013, Schöttner et al. 2013, Tjensvoll et al. 2013, Buhl-Mortensen et al. 2017, 2019, Dunlop et al. 2020). Soft corals of the family Nephtheidae, such as *Duva florida* and *Drifa* sp., have also been documented as a component of coastal and offshore benthic epifaunal communities on both sides of the North Atlantic (Buhl-Mortensen et al. 2012, 2019, Long et al. 2020). Often known to form 'cauliflower coral gardens', these soft coral communities are recognized to be vulnerable to physical disturbance and as a result represent a vulnerable marine ecosystem (Davies et al. 2017, Buhl-Mortensen et al. 2019, Devine et al. 2019). Aggregations of soft corals have been identified on mixed- and hard-substrate

habitats in mid and northern Norwegian fjords. Other key benthic epifauna within Subarctic coastal waters are encrusting bryozoans, cnidarians, asteroids, and solitary ascidians (Gulliksen & Bahr 2001, Liefmann et al. 2018, Dunlop et al. 2020).

Sessile benthic epifaunal species feed on suspended, recently settled, and detrital particulate material, whereas mobile benthic epifauna are predominantly predatory. The use of the substrate surface and the consumption of particulate material makes many epifauna taxa susceptible to anthropogenic sedimentation events (Trannum et al. 2019, Howell et al. 2016). In particular, sessile filter feeding sponges have an intricate and microscopic filtering system that draws in significant volumes of water ( $600 \text{ l kg}^{-1} \text{ wet weight d}^{-1}$ ) which can become clogged when exposed to enhanced levels of anthropogenic and natural suspended sediments (Kutti et al. 2013). This can lead to impacts on sponge physiological function, survivability, and reproduction (Maldonado et al. 2008, Bannister et al. 2012). Sessile soft coral communities have also been shown to be negatively impacted by increased sedimentation and suspended sediments, with elevated depositions of mine tailings suppressing feeding behaviour (Liefmann 2016). Conversely, some deposit feeding taxa are adapted to survive in high sedimentation environments where they glean energy and nutrients from enhanced organic materials (Bowden et al. 2016). The lugworm, for example, which is rarely captured in traditional infauna samples but can be visually identified by characteristic feeding pits and mounds of faeces on the seabed, is thought to be tolerant of coastal salmon farm wastes and can occur at high abundances close to farms (Keeley et al. 2020). Overall, however, there is a paucity of information regarding the responses of larger, more sparsely distributed benthic epifauna or conspicuous infaunal species to environmental disturbance from fish farms, including tolerance to sedimentation and organic waste, impacts on reproduction, larval settlement, and physiological function (Fields et al. 2019, Trannum et al. 2019). Without this knowledge, it is currently not possible to determine the risk of salmon farms to hard- and mixed-bottom benthic epifaunal communities and how these taxa could be used as possible biological indicators in environmental monitoring in the same manner as soft-sediment communities. Therefore, there is a need to gain a better understanding of potential changes in benthic epifauna exposed to particulate waste from finfish aquaculture to allow for the development of suitable monitoring methods in Norwegian coastal waters.

This hard-bottom monitoring challenge is not only relevant to Norwegian coastal waters, but also to other global finfish farming regions. Along Canada's coastlines, 90% of finfish facilities are situated over patchy mixed bedrock and cobbled seafloors (Hamoutene 2014, Hamoutene et al. 2015). As a result, monitoring programs that document changes in benthic conditions around finfish facilities at hard-bottom sites in British Columbia and Newfoundland, Canada, rely on visual approaches where grab sampling is challenging (Hamoutene et al. 2015, 2018). Here, visual indicators of organic enrichment (IOE), including the coverage of flocculent material, bacterial mats, and opportunistic polychaete complexes, are used to determine ecological state within the near-field (within 50 m of the cage) farm area (Salvo et al. 2015, Hamoutene et al. 2016, 2018). However, insights into the effects of sedimentation flux from finfish aquaculture facilities on hard-bottom epifaunal communities in the far-field (>50 m from the cage) are generally lacking. This is mostly due to the large volume of data required to detect statistically relevant differences in the traditionally patchy and sparse benthic epifauna communities.

In this study, we present an investigation of potential impacts of particulate material released from Atlantic salmon farming on the density and structure (also referred to as the composition) of benthic epifaunal communities on mixed- and hard-bottom dominated substrates in fjord systems in northern Norway. The spatial patterns of benthic epifaunal community composition in relation to their proximity to farms in the far-field area and the associated organic enrichment gradient were examined using substrate and biological mapping techniques that employed remote sensing and a low-cost towed camera system. The study was based on the hypothesis that increased bio-deposition from fish farming will alter the distribution and composition of benthic epifaunal communities on hard- and mixed-bottom habitats. Results bring forward new data valuable for the identification of potential biological IOE from fish farms in habitats dominated by hard and mixed substrates.

## 2. MATERIALS AND METHODS

### 2.1. Site selection, description, and farm production

Substrate and biological mapping were performed close to 3 Atlantic salmon farms in the county of Finnmark, northern Norway (Fig. 1a). Farms were situated in Øksfjorden (70.1–70.2° N, 22.3–22.5° E)

and Vargsundet (70.2–70.4° N, 23.2–23.7° E), a sound between the Norwegian mainland and the island of Seiland (Fig. 1b). Study farm 'A' was positioned on the western shore of the glacial fjord Øksfjorden (Fig. 1c). Farm 'B' was located at the northern side of Bekkarfjorden on the western coast of Vargsundet, whilst farm 'C' was situated along the eastern shore of Vargsundet south of Store Lerresfjorden (Fig. 1d). All 3 farms were in regions where the seabed predominantly consists of hard and mixed substrates, interspersed with gravelly sand or a mixture of gravel, cobbles, and boulders. Site details are provided in Table 1. Prior to the selection of these 3 study farms, multiple sites were surveyed in western Finnmark, i.e. an area stretching from Altafjorden in the south to Hammerfest in the north (Fig. 1b). Farms A, B, and C were selected because they reflected a range of hard- and mixed-habitat types common to northern Norwegian coastal regions utilized by aquaculture, benthic epifaunal communities that included potentially sensitive taxa (sponges and soft corals) were present, and farm layout (mooring line configurations) was suitable for the sampling procedures.

The maximum allowed biomass (MAB), i.e. the license-regulated maximum amount of live salmon stock on-site at any time of production under 'The Aquaculture Act' (Norwegian Ministry of Fisheries and Coastal Affairs 2005), was 3600 t at Farm A, 5460 t at Farm B, and 3480 t at Farm C. At both farms in Vargsundet (B and C), fish were set out during May 2017 and harvested in March 2019. Fish production started earlier at Farm A during Fall 2016 and fish were removed in July 2018. Farm production details are summarized in Table 2.

### 2.2. Survey design

The area leading ~50 m from each farm cage to ~800 m downstream of the farm was surveyed for spatial patterns in substrate and benthic epifaunal community composition in relation to the enrichment gradients from farm wastes. Using pre-existing knowledge from bathymetric and substrate mapping in the wider survey area (see Section 2.3), towed video techniques were conducted along pre-defined transects known to have a similar substrate range and depth profile throughout (Section 2.4). The same techniques were used to survey substrate and epifaunal community distribution in nearby reference locations (1–5 km from the farms). Reference sites and far-field farm transects had similar substrate compositions and depth profiles as confirmed by

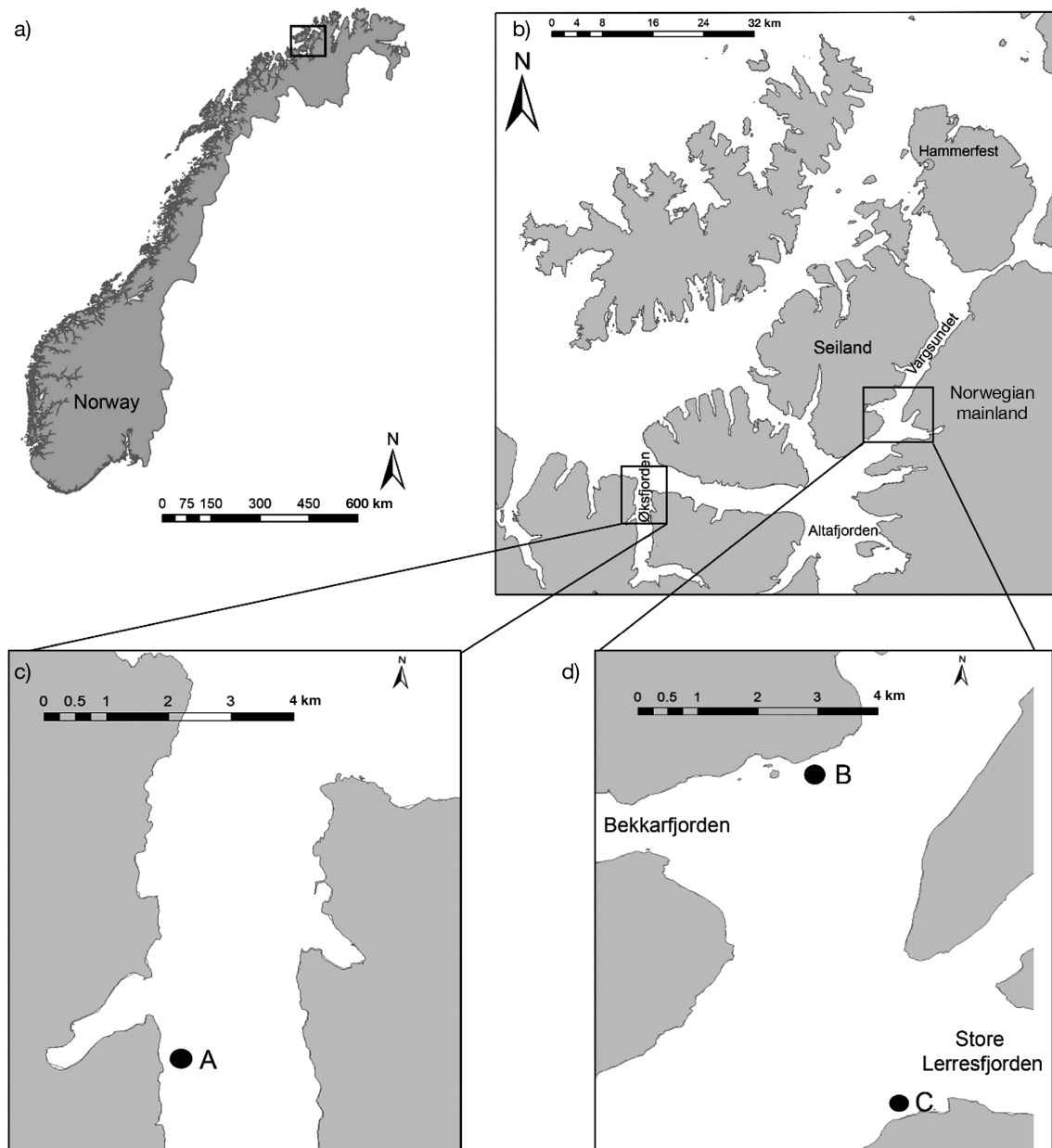


Fig. 1. (a) Location of sampling area in Norway, (b) Øksfjorden and Vargsundet and (c) Farm A and (d) Farms B and C

Table 1. Locations and environmental characteristics of the 3 salmon aquaculture study farms in northern Norway

Farm	Fjord	Farm position	Farm depth range (m)	Primary slope category	Mean ( $\pm$ SE) bottom current speed ( $m\ s^{-1}$ )	Primary substrate characteristics
A	Øksfjorden	70.2122° N, 22.2768° E	65–134	Steep (41–70°), near-vertical (70–90°)	0.032 $\pm$ 0.001	Boulder, bedrock and gravelly sand
B	Vargsundet	70.3416° N, 23.3902° E	35–122	Moderate (16–40°), steep (41–70°), near-vertical (70–90°)	0.086 $\pm$ 0.002	Gravelly sand, gravel and cobbles, bedrock and boulders
C	Vargsundet	70.2862° N, 23.3968° E	58–72	Flat (0–15°)	0.029 $\pm$ 0.001	Gravelly sand and gravel and cobbles

Table 2. Farm production characteristics of the 3 salmon aquaculture study farms described using maximum allowed fish biomass and total feed mass at full production and at the time of video and sediment trap surveys

Farm	Year est.	Max. allowed fish biomass (t)	Total feed mass during		
			Full production (t)	Video surveys (t)	Sediment trap surveys
A	2011	3600	6153	2942	5931
B	2005	5460	6257	621	5676
C	2001	3480	5475	3725	1456

bathymetric and substrate mapping (see Dunlop et al. 2020). The presence of farm moorings prohibited the use of the towed camera system in the vicinity of the cages, hence the proximity of each transect line to the cages varied between sites. Measurements of total particulate material (TPM) deposition and current velocity were collected along the same transects using sediment traps and data extracted from a hydrodynamic model (detailed in Section 2.3). Benthic infauna was sampled from near the cage edge out to 800 m along the transects where substrate conditions of the seabed allowed this (Section 2.6).

### 2.3. Environmental data collection (bathymetry and substrate composition, flow environment, and depositional flux)

Substrate composition and bathymetry were mapped in April 2018 in the wider survey area of Vargsundet and Øksfjorden using a Kongsberg™ EM2040 Dual RX multibeam echosounder (200 kHz) and a Kongsberg™ Topas PS 40 sub-bottom profiler (primary frequencies 36–39 and 41–44 kHz). The seafloor substrate structure was resolved by backscatter data, which was ground-truthed with drop-down video footage and sediment grain size samples collected by a Van Veen grab (0.1 m<sup>2</sup>). Bathymetric and substrate data were processed in ArcMap v.10.6 (ESRI) to create seabed maps at a resolution of 5 m.

The NorKyst 160 hydrodynamic model was used to model the hydrodynamic setting of the survey areas during the survey period in October 2017. NorKyst 160 is based on the Regional Ocean Modelling System (ROMS; <http://myroms.org>) (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008) and forced along the open boundaries of the larger-scale coastal model, NorKyst800 (Albretsen et al. 2011). The model has a grid resolution of 160 × 160 m and generates hourly data on the E–W and N–S component of the horizontal current flows throughout the water column. For

this study, modelled near-bottom velocities (1–2 m above the seabed) were extracted from 3 points along the towed camera transects.

Sediment traps were deployed to measure the depositional flux rate of suspended particulate matter along the enrichment gradient of each farm site. Suitable deployment locations were selected based on high-resolution bathymetry data, which allowed steep sloped terrain to be avoided.

Trap moorings consisted of a frame with a pair of sediment traps (diameter 10 cm; 90 cm apart) that collected suspended particulate matter at ca. 2.5 m above the seafloor. Cylinders were filled with clean 500 ml onsite seawater adjusted to a salinity of 45‰ with NaCl and buffered with 4% formalin prior to deployment to preserve samples. Upon retrieval, suspended material settled in the cylinders for a maximum of 2 h before excess water was decanted to leave ~2 l for subsequent analysis.

Trap moorings were deployed beside a cage at Farm A and 50, 100, 200, 400, and 600 m downstream of the farm for 12 d between 6 and 18 June 2018. At Farm B, a total of 5 trap moorings were deployed: 3 (100, 350, and 600 m downstream) for 10 d between 5 and 15 November and 2 at the cages for 11 d between 15 and 26 November 2018. The fish were unexpectedly harvested early at Farm C, which led to the postponement of the sediment trap deployments at that site until July 2020 when production was resumed. Seven sets of sediment trap moorings were deployed in the vicinity of Farm C: 2 at either side of the farm cages, 50, 150, 250, 450, and 650 m downstream of the farm between 4 and 15 July 2020. At each site, trap moorings were deployed ~1500 m from the farm cage to measure reference sedimentation flux. The mean TPM dry weight from each sediment trap mooring (TPM Trap; g m<sup>-2</sup> d<sup>-1</sup>) was quantified by filtering a known volume of the homogenized trap sample on pre-weighed filters that were subsequently oven-dried. TPM Trap was determined as the weight loss after drying. Further details on the laboratory analysis procedure are described in Keeley et al. (2019).

TPM values were corrected to reflect TPM at maximum production at each site using the equation: TPM max. production = [(full production feed / trap production feed) × TPM Trap]

A power function was fitted to the relationship between TPM at full production and distance to each farm. These relationships were used to estimate the

TPM input at 5–10 m intervals from each farm to correspond to the resolution of benthic towed camera transects (Section 2.4) and benthic infaunal grab samples (Section 2.6).

#### 2.4. Towed video transects

Densities of benthic epifauna were quantitatively assessed along transects using a towed underwater video system (UVS), deployed from RV 'Fangst'. The UVS used a HD GoPro™ Hero 4, a live feed Splashcam Delta Vision industrial underwater video camera (1/3" 960 H High Sensitivity CCS, > 750 TVL) and 2 Keldan 4X video lights (9000 lm) mounted on a stainless-steel frame with an aerodynamic fin. The UVS was manually flown over the seafloor at  $\sim 0.3 \text{ m s}^{-1}$  using the live feed camera cable. A pair of crossed Sea Beam™ lasers, visible at the bottom of the live feed camera field of view, were used as a guide for manual cable adjustments to fly the UVS  $\sim 1 \text{ m}$  above the seafloor. This resulted in a mean ( $\pm$ SD) image width of  $1.3 (\pm 0.2) \text{ m}$ .

UVS camera transects began  $\sim 50 \text{ m}$  from the fish cage and ran parallel to the coastline along the 70 and 100 m depth contours to  $\sim 800 \text{ m}$  downstream of each farm. Depths of 70 and 100 m were selected as they represent typical depth ranges for northern Norwegian finfish farm locations. At Farms A and B, 2 replicate transects were recorded along each depth contour (70 and 100 m), while the shallower waters at Farm C only allowed for a pair of replicate transects along the 70 m depth contour. Details of the UVS transects are provided in Table 3. A GPS recorded the vessel position on average every 4 s, which was used to calculate the distance of the camera to the farm and the accumulated distance travelled along the seabed (using basic trigonometry). Layback of the camera rig to the vessel was minimized as much as possible by continually assessing the wire angle, adapting survey direction to the prevailing current, and only lifting the rig onboard once vertical under the vessel. GPS, time, and depth information were later overlaid onto the HD GoPro™ video footage for annotation.

#### 2.5. Video transect annotation

For the analysis of the UVS footage, transects were subdivided into 5–10 m swath sections to capture the patchy distribution of habitats and epifaunal communities. The seafloor area covered by each swath was

calculated by multiplying swath length (or distance travelled) and average swath width, scaled by the paired laser lines. A substantial change in the field of view or a new substrate type initiated the start of a new swath and led to some variation in swath length. Substrate types were classified as (1) solid bedrock, (2) patchy bedrock/broken reef, (3) boulders, (4) broken rocks, (5) gravel and cobbles, (6) shellsand, (7) sand, and (8) gravelly sand; slope categories were classified as (1) flat, (2) moderate, (3) steep, (4) near-vertical, or (5) overhang. Primary, secondary, and tertiary substrate types and their percentage contribution were recorded for each swath along with the corresponding slope category. Tables with further substrate and slope category details are provided in Dunlop et al. (2020).

Videos were viewed in VLC player, and all conspicuous benthic epifaunal taxa were identified to the lowest possible taxonomic level. The number of individuals or individual colonies from each taxon were enumerated in the video footage. DNA sequencing was used to confirm the identity of key benthic epifaunal taxa. Counts were also made of the visually conspicuous faecal mounds of the deposit-feeding lugworm. The lugworm lives within sediments but, similar to benthic epifauna, its overall distribution is challenging to capture with conventional grab sampling, and needs to be enumerated by visual surface surveys that cover a greater spatial area. Although the lugworm is part of the benthic infauna, for practical reasons this visually conspicuous species will hereafter be referred to under the general term 'benthic epifauna'. Counts of individual taxa within each swath were converted into densities by dividing by the estimated covered seafloor area ( $\text{m}^2$ ), scaled using paired lasers.

#### 2.6. Benthic infauna sampling and taxonomy

A weighted Van Veen grab ( $0.1 \text{ m}^2$ ) was used to sample sediments downstream of each farm from the cage edge to  $\sim 1500 \text{ m}$  at Farm A (total 20 grabs), Farm B (total 12 grabs), and Farm C (total 10 grabs). High-resolution substrate maps, based on the collected backscatter multibeam data (Section 2.3), were used to target areas of suitable soft sediment interspersed between mixed and hard substrates for grab sampling. Obtaining grab samples was challenging, and grabs were only accepted when they provided at least 10 cm deep undisturbed sediment. Each sample was sieved through a 1 mm mesh, and the remaining benthic infauna was preserved in buffered 4 % forma-

Table 3. Details of towed camera transect surveys conducted at each of the 3 salmon aquaculture study farms. Transect positions are provided in decimal degree format (WGS84)

Date (dd/mm/yyyy)	Farm	Mean ( $\pm$ SE) survey depth (m)	Transect start position (Lat, Lon)	Transect end position (Lat, Lon)	Transect length (distance from cage) (m)
08/10/2017	A	79.3 ( $\pm$ 7.2)	70.21409, 22.27818	70.22097, 22.28176	779 (36–815)
08/10/2017	A	80.1 ( $\pm$ 9.5)	70.21411, 22.27815	70.22098, 22.28232	781 (39–820)
08/10/2017	A	112.2 ( $\pm$ 9.6)	70.21408, 22.28039	70.22093, 22.28327	774 (48–822)
08/10/2017	A	110.0 ( $\pm$ 8.1)	70.21417, 22.28013	70.22118, 22.28305	789 (56–845)
13/10/2017	B	77.4 ( $\pm$ 7.5)	70.34227, 23.40069	70.34645, 23.41864	778 (56–834)
13/10/2017	B	70.5 ( $\pm$ 10.9)	70.34236, 23.40053	70.34614, 23.41865	795 (129–924)
13/10/2017	B	104.7 ( $\pm$ 7.6)	70.34132, 23.40136	70.34552, 23.41908	775 (132–907)
13/10/2017	B	101.9 ( $\pm$ 6.0)	70.34132, 23.40044	70.34487, 23.41878	771 (97–868)
13/10/2017	B	67.2 ( $\pm$ 9.1)	70.34213, 23.39864	70.34416, 23.39995	924 (16–88)
12/10/2017	C	63.5 ( $\pm$ 2.4)	70.28610, 23.40676	70.29016, 23.42376	799 (47–826)
12/10/2017	C	65.5 ( $\pm$ 4.1)	70.28663, 23.40510	70.29005, 23.42243	734 (49–783)

lin and later transferred to ethanol for identification in the laboratory at Akvaplan-niva AS. The composition of benthic infaunal communities was quantified to the lowest taxonomic level following the Norwegian standard NS16665 (Standards Norway 2013).

## 2.7. Data analysis

Sequential bar plots of the substrate composition recorded along UVS transects were created. Plots depicting the relative densities (ind. m<sup>-2</sup>) of numerically dominant benthic epifaunal taxa with distance from the farm were aligned to visualize substrate associations. Multivariate analysis was performed using Bray-Curtis dissimilarity coefficients on fourth-root transformed benthic epifauna density data and Euclidean dissimilarity coefficients on normalized environmental data (TPM flux, slope, and depth). Substrate percentage cover was treated with a square-root transformation prior to analysis. TPM flux is directly linked to distance to farm with a negative power function; therefore, TPM flux was used in subsequent analysis. Variation in the benthic epifaunal communities between the farm survey sites was examined using a non-metric multidimensional scaling plot (nMDS) and PERMANOVA analysis in PRIMER-E v.7 (Clarke & Gorley 2015).

A multivariate regression analysis using the distance-based linear model (DISTLM) was applied to determine the role of TPM flux, substrate (% cover of the 8 substrate categories), current velocity, depth, and seafloor slope on the variation in benthic epifaunal community structure at a scale across all farms and also at each farm site. The BEST selection and Akaike's information criterion (AIC) were used to

select the environmental variables with the greatest explanatory power.

Variation in benthic epifaunal community composition between different levels of TPM flux (g m<sup>-2</sup> d<sup>-1</sup>) output from the 3 farms was examined with a 2-dimensional principal coordinates (PCO) plot and PERMANOVA test. The key benthic epifaunal species contributing to the dissimilarity between benthic epifaunal communities were overlaid as a vector plot upon the PCO ordination. In addition, a PCO analysis was used to examine structural differences (based on a Bray-Curtis similarity matrix from fourth-root transformed raw data) of the benthic infaunal community with varying TPM deposition along the enrichment gradient of the 3 farm sites. TPM at maximum production was plotted against distance to farm at each study site alongside the established benthic infaunal indexes AZTI marine biotic index (AMBI) (Borja et al. 2000) and the Norwegian sensitivity index (NSI) (Rygg & Norling 2013), and the mean epifaunal Shannon-Wiener Index ( $H'$ ) was calculated for each 50 m transect section.

Generalized additive models (GAMs) were used to model the relationship between the densities per swath of the identified key benthic epifaunal taxa (lugworm, common seastar *Asterias rubens*, cushion star *Ceraster granularis*, soft coral *Duva florida*, sponge *Polymastia* spp., sea anemone *Hormathia digitata*, and fan-sponge *Phakellia* spp.), species diversity per swath in the benthic epifaunal community as expressed by  $H'$ , and TPM flux. GAMs are generalized models based on an exponential relationship between the response and predictor variables and therefore are suitable to examine non-linear relationships (Zuur & Ieno 2016). The data contained a high proportion of zeros, and therefore GAMs with

a negative binomial distribution were applied to the data sets and plots of the relationship between the density of key epifaunal taxa and TPM flux.

### 3. RESULTS

#### 3.1. Environmental and biological site characteristics

The bottom substrate in the vicinity of Farm A, at depths of 70 and 100 m, consisted of bedrock and boulders interspersed with patches of mixed gravelly sand and gravel and cobbles (Fig. S1 & S2 in the Supplement at [www.int-res.com/articles/suppl/q013p455\\_supp.pdf](http://www.int-res.com/articles/suppl/q013p455_supp.pdf)). The topography was predominantly steep and often near-vertical, and the mean ( $\pm$ SE) modelled bottom current velocity was  $0.032 \pm 0.001$  m s<sup>-1</sup>. TPM flux at maximum production was  $24.0$  g m<sup>-2</sup> d<sup>-1</sup> 10 m from the cage edge and declined to  $1.5$  g m<sup>-2</sup> d<sup>-1</sup> 600 m from Farm A, which is close to background TPM flux levels at ~1000 m from the cages (Fig. 2a). A separation of benthic epifaunal communities existed between the 3 farm sites identified by a significant PERMANOVA test result ( $p = 0.001$ ) (pseudo- $F_{2,1011} = 116.4$ ,  $p = 0.001$ ) (Table S1a). The numerically dominant taxa *Phakellia* spp., *Geodia* spp., and *Ceramaster granularis* were seen to particularly influence the structure of epifaunal communities at Farm A in the nMDS plot (Fig. 3a).

Substrate at Farm B consisted of mixed hard bottom with gravelly sand and gravel and cobbles interspersed with bedrock and boulders (Figs. S3 & S4). The topography along the 70 and 100 m depth contours was highly varied, changing from flat to near-vertical in some sections. Farm B was located close to a headland reaching into the sound of Vargsundet and showed the fastest mean ( $\pm$ SE) modelled current velocity at  $0.086 \pm 0.002$  m s<sup>-1</sup>. TPM deposition directly downstream of the cages was  $44.2$  g m<sup>-2</sup> d<sup>-1</sup> and declined to  $6.2$  g m<sup>-2</sup> d<sup>-1</sup> 600 m from the farm. Background TPM flux was  $5$  g m<sup>-2</sup> 1400 m from the farm (Fig. 2b). The asteroids *C. granularis*, *Henricia* spp., and *Asterias rubens* were dominant around Farm B alongside sponges from the genus *Polymastia*, *Myxilla*, and *Geodia*. The soft coral *Duva florida*, was however, the single most prominent benthic epifaunal species (Fig. 3b).

The seabed around Farm C at the 70 and 100 m contours primarily consisted of gravel and cobbles and sand substrates on a flat to moderately sloped seabed (Fig. S5). Farm C was in the relative shelter of Store Lerresfjorden where the slowest mean ( $\pm$ SE) modelled

bottom current velocity ( $0.029 \pm 0.001$  m s<sup>-1</sup>) of all study sites occurred. TPM flux at maximum production at Farm C and up to 600 m away were  $51.1$  and  $6.5$  g m<sup>-2</sup> d<sup>-1</sup> respectively. TPM flux was  $5$  g m<sup>-2</sup> 1500 m from Farm C (Fig. 2c). The asteroid *A. rubens*, the sea anemone *Hormathia digitata*, and a species of lug-worm were major drivers of the community structure (Fig. 3c). A full list of the benthic epifaunal taxa observed at all farm sites is provided in Table 4.

#### 3.2. Comparison of environmental drivers of community composition

Farm-specific DISTLM analyses demonstrated that at all farms the TPM flux and current velocity, alongside hard-substrate seabed characteristics, had significant effects on benthic epifaunal community composition (Table S2a). Along the 70 and 100 m transects at Farm A, TPM flux had the greatest impact on total variation in community composition, as did the coverage of boulders, depth, and slope on the 70 m transects (Table S2b,c). Along the 70 m transect at Farm B, TPM flux and the coverage of bedrock and boulders were the dominant explanatory variables for benthic epifaunal community composition (Table S2d). TPM flux, depth, slope, and the coverage of boulders explained the greatest proportion of the variation in community composition at the 100 m transect at Farm B (Table S2e). The total variation in community composition around Farm C was best explained by the variables TPM flux, the coverage of sand, and gravel and cobbles (Table S2f).

Changes in benthic infaunal community composition along the enrichment gradient of Farm A were not clearly distinguishable between sampling stations with increasing TPM input (Fig. 3a). The benthic infauna indexes (AMBI and NSI) at Farm A indicated an irregular pattern with regards to distance and organic enrichment (Fig. 2a). The NSI was generally reduced and the AMBI slightly elevated (indicative of an unbalanced or slightly impacted state) within 500 m of the cages, but some of the closest samples to the farm were atypically unenriched. The diversity of benthic epifaunal communities ( $H'$ ) at Farm A declined with increasing TPM input (GAM;  $\chi^2 = 0.1$ ,  $p < 0.0001$ ) (Fig. 2a). Along the enrichment gradient at Farm A, the PCO ordination plot indicated that some division in the clustering of benthic epifaunal communities existed between communities at a TPM input level of less than and greater than  $4$  g m<sup>-2</sup> d<sup>-1</sup> occurring at approximately 200 m from the farm cage, which was supported by a significant PERM-



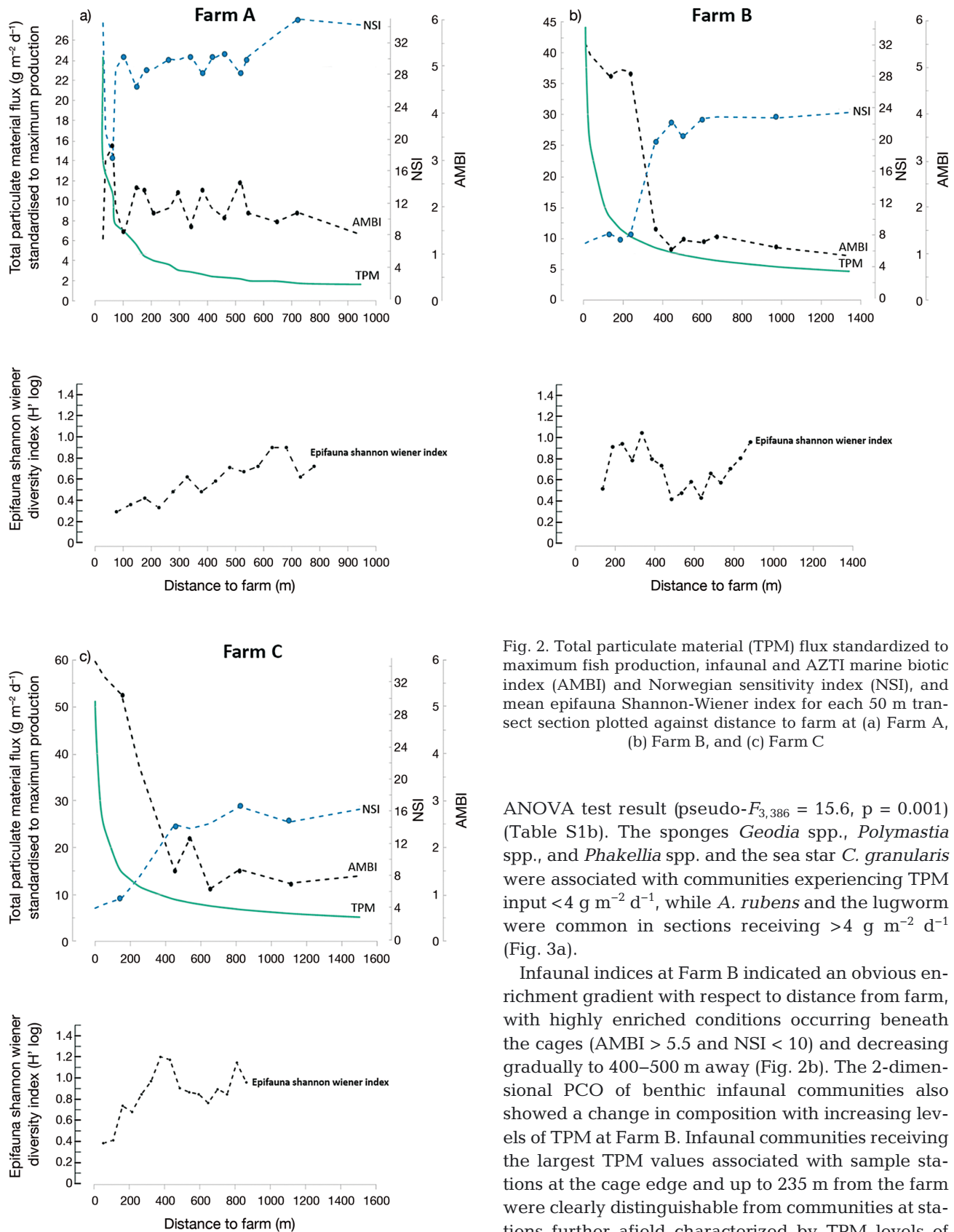


Fig. 2. Total particulate material (TPM) flux standardized to maximum fish production, infaunal and AZTI marine biotic index (AMBI) and Norwegian sensitivity index (NSI), and mean epifauna Shannon-Wiener index for each 50 m transect section plotted against distance to farm at (a) Farm A, (b) Farm B, and (c) Farm C

ANOVA test result (pseudo- $F_{3,386} = 15.6$ ,  $p = 0.001$ ) (Table S1b). The sponges *Geodia* spp., *Polymastia* spp., and *Phakellia* spp. and the sea star *C. granularis* were associated with communities experiencing TPM input  $<4 \text{ g m}^{-2} \text{ d}^{-1}$ , while *A. rubens* and the lugworm were common in sections receiving  $>4 \text{ g m}^{-2} \text{ d}^{-1}$  (Fig. 3a).

Infaunal indices at Farm B indicated an obvious enrichment gradient with respect to distance from farm, with highly enriched conditions occurring beneath the cages (AMBI  $> 5.5$  and NSI  $< 10$ ) and decreasing gradually to 400–500 m away (Fig. 2b). The 2-dimensional PCO of benthic infaunal communities also showed a change in composition with increasing levels of TPM at Farm B. Infaunal communities receiving the largest TPM values associated with sample stations at the cage edge and up to 235 m from the farm were clearly distinguishable from communities at stations further afield characterized by TPM levels of

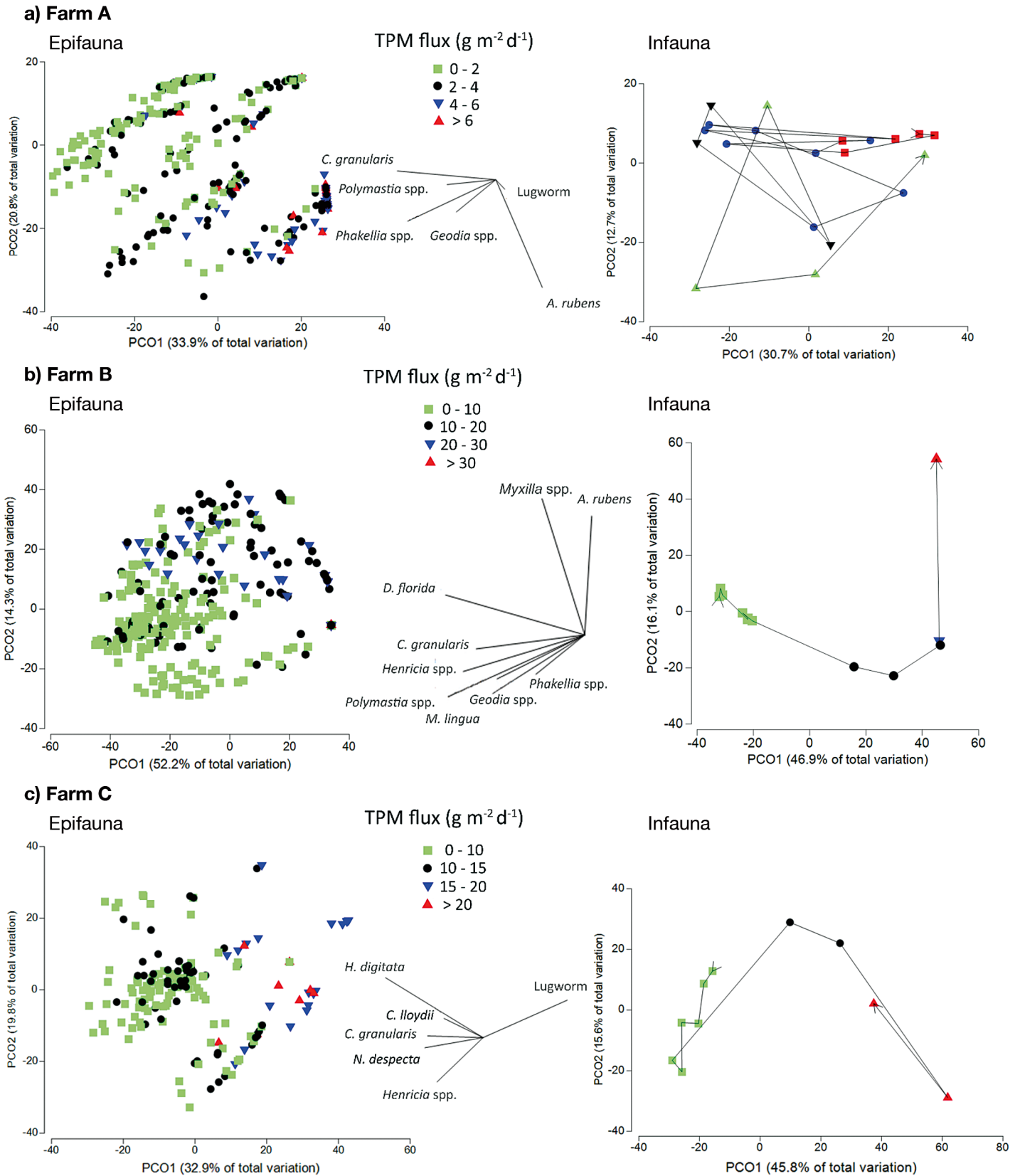


Fig. 3. Non-metric multidimensional scaling (nMDS) plot of benthic epifaunal and infaunal community composition at (a) Farm A, (b) Farm B, and (c) Farm C. Each point represents the benthic epifaunal community abundance at each 10 m transect section and benthic infaunal community abundance in individual grabs. MDS points are coloured to represent the total particulate material input (TPM flux; standardized to maximum fish production) received at transect sections and grab locations. Overlay represents the key benthic epifaunal taxa involved in structuring the epifaunal community composition at each farm

Table 4. Epifaunal taxa observed in towed camera transects at each farm site and corresponding mean taxa densities recorded within each swath (ind. m<sup>-2</sup>)

Taxa	Farm A	Farm B	Farm C
<b>Porifera</b>			
<i>Mycale lingua</i>	0.005	0.03	0.006
<i>Axinella infundibuliformis</i>	0.01	0.01	0.0006
<i>Polymastia</i> spp.	0.02	0.24	0.004
<i>Craniella</i> spp. / <i>Tethya</i> spp.	0.006	0.03	0.001
<i>Myxilla</i> spp.	0	0.10	0.0004
<i>Phakellia</i> spp.	0.11	0.01	0
<i>Isodictya palmata</i>	0.0004	0.01	0
<i>Geodia</i> spp.	0.06	0.06	0
<b>Cnidaria</b>			
<i>Hormathia digitata</i>	0.01	0.01	0.16
<i>Cerianthus lloydii</i>	0.001	0.0002	0.014
<i>Bolocera tuediae</i>	0	0.0002	0.0009
<i>Duva florida</i>	0.0003	1.12	0
<i>Urticina</i> spp.	0.006	0	0
<i>Primnoa resedaeformis</i>	0	0.01	0
<b>Echinodermata</b>			
<i>Ceramaster granularis</i>	0.10	0.05	0.032
<i>Asterias rubens</i>	0.06	0.03	0.21
<i>Henricia</i> spp.	0.01	0.06	0.027
<i>Hippasteria phrygiana</i>	0.02	0.03	0.011
<i>Gorgonocephalus lamarckii</i>	0.0004	0.0005	0.002
<i>Stichopus tremulus</i>	0	0	0.0008
<i>Cucumaria frondosa</i>	0	0.006	0
<i>Solaster endeca</i>	0.001	0.005	0.02
<i>Ophuira</i> spp.	0.001	0.004	0.0006
<i>Stichastrella rosea</i>	0.0009	0.004	0.0008
<b>Gastropoda</b>			
<i>Neptunea despecta</i>	0.0005	0.015	0.024
<i>Buccinum undatum</i>	0	0.0002	0.006
<b>Annelida</b>			
Lugworm	0.0006	0.01	0.15
<b>Arthropoda</b>			
<i>Munida</i> spp.	0.0002	0.02	0.002
<b>Bryozoa</b>			
<i>Omalosecosa ramulosa</i>	0	0.004	0
<i>Securiflustra</i> spp.	0	0.02	0
<i>Porella compressa</i>	0.0006	0	0
<b>Chordata</b>			
<i>Ascidia</i> spp.	0.007	0.008	0.002

<10 g m<sup>-2</sup> d<sup>-1</sup> (Fig. 3b). No significant relationship between the diversity of benthic epifaunal communities ( $H'$ ) recorded on Farm B transects and TPM input was observed (Fig. 2b). A separation existed in the PCO plot between the composition of benthic epifaunal communities along transect sections around Farm B receiving TPM less than and greater than 10 g m<sup>-2</sup> d<sup>-1</sup> within 200–250 m from the cage (Fig. 3b). The PERMANOVA test reported a significant test result for the effect of TPM input on benthic epifaunal community composition (pseudo- $F_{3,444} = 7.3$ ,  $p = 0.001$ ). Pairwise tests, however, only showed signifi-

cant separation between communities receiving less than and greater than 10 g TPM m<sup>-2</sup> d<sup>-1</sup> (Table S1c). Community composition on transect sections receiving lower TPM input was primarily driven by the presence of the sponges *Geodia* spp. and *Polymastia* spp., the soft coral *Duva florida*, and the sea stars *Henricia* spp. and *C. granularis*. In areas receiving >10 g m<sup>-2</sup> d<sup>-1</sup>, benthic epifaunal communities were dominated by *A. rubens* and the sponge *Myxilla* spp. (Fig. 3b).

The patterns observed for the infaunal indices at Farm B recurred at Farm C (Fig. 2c) and can be supported by the respective PCO ordination where the composition of infauna communities near the farm (<250 m, >10 g TPM m<sup>-2</sup> d<sup>-1</sup>) is clearly separated from those further afield and exposed to lower TPM (Fig. 3c). The diversity of the benthic epifaunal community ( $H'$ ) at Farm C was significantly affected by TPM input (GAM;  $\chi^2 = 0.2$ ,  $p < 0.005$ ) and generally increased with distance to farm and reduced TPM (Fig. 2c). The PCO ordination plot of benthic epifaunal community composition demonstrated separation at a level of 15 g TPM m<sup>-2</sup> d<sup>-1</sup>, which occurred at approximately 200 m from the cage (Fig. 3c); this was supported by a significant PERMANOVA test result (pseudo- $F_{3,179} = 16.9$ ,  $p = 0.001$ ) (Table S1d). Along transect sections receiving <15 g TPM m<sup>-2</sup> d<sup>-1</sup>, community composition was characterized by a number of benthic epifaunal taxa (*Hormathia digitata*, *Henricia* spp., *Cerianthus lloydii*, *Ceramaster*

*granularis*, *Neptunea despecta*), whilst the visually conspicuous lugworm dominated on transect areas receiving >15 g TPM m<sup>-2</sup> d<sup>-1</sup> (Fig. 3c).

### 3.3. Responses of dominant conspicuous benthic infauna in relation to sedimentation

The fan sponge *Phakellia* spp. was not present in the vicinity of Farm A (i.e. within ≤200 m from the cage edge where TPM flux was >4 g m<sup>-2</sup> d<sup>-1</sup>) but dominated bedrock outcrops beyond the 200 m range

(Figs. S1 & S2). At this site, its density was negatively related to TPM input at 100 m depth (GAM;  $\chi^2 = 4.9$ ,  $p < 0.05$ ) (Fig. 4a). Sponges of the genus *Geodia* were distributed throughout the transects at both Farms A and B. Their distribution was more affected by the presence of gravel and cobbles than TPM deposition (GAM;  $\chi^2 = 17.2$ ,  $p < 0.001$ ).

The visually conspicuous lugworm only occurred in patches at densities of 0.2–2 ind.  $m^{-2}$  in transect sections adjacent (~50–160 m) to Farm B at 70 m water depth (Fig. S3). Here, TPM input was in the higher range (10–22  $g\ m^{-2}\ d^{-1}$ ), and lugworm densities were significantly related to TPM input (GAM;  $\chi^2 = 8.9$ ,  $p = 0.05$ ) (Fig. 4b). Lugworms also gathered (0.3–2.5 ind.  $m^{-2}$ ) close to Farm C ( $\leq 150$  m from the cage edge), where the TPM flux was between 15 and 25  $g\ m^{-2}\ d^{-1}$ . TPM input explained a significant proportion of the variation in lugworm density (GAM;  $\chi^2 = 17.3$ ,  $p < 0.01$ ). Lugworm density at Farm C was also significantly related to the coverage of sand (GAM;  $\chi^2 = 4.3$ ,  $p < 0.05$ ) (Figs. 4c & S5). It should be noted that in the case of Farm C, more sand habitat was observed closest to the farm, making it impossible to separate the effects of TPM input or the presence of sand on lugworm density. Lugworms were not present on transects around Farm A or at 100 m depth at Farm B.

*Polymastia* spp. was present on 70 and 100 m transects at Farm A, predominantly at a distance of  $\geq 250$  m from the farm. However, only a few isolated individuals were observed and densities were not significantly related to TPM flux (Figs. S1 & 2). At Farm B (70 and 100 m depth), *Polymastia* spp. densities declined with increasing TPM input (GAM; 70 m:  $\chi^2 = 12.1$ ,  $p < 0.01$ ; 100 m:  $\chi^2 = 58.2$ ,  $p < 0.0001$ ) (Fig. 4b). For example, at 70 m depth, *Polymastia* spp. densities were depressed (mean: 0.06 ind.  $m^{-2}$ ) up to 200 m from the farm, whilst at a distance  $> 200$  m, densities between 0.2 and 6 ind.  $m^{-2}$  were recorded. *Polymastia* spp. density was also significantly related to the presence of bedrock and boulders at 70 m (GAM;  $\chi^2 = 10.4$ ,  $p < 0.05$ ) and various substrate types at 100 m depth.

The highest density aggregations of the soft coral *D. florida* recorded in this study were present on transects at Farm B (up to 15 ind.  $m^{-2}$ ). Here, the density of *D. florida* was negatively related to TPM input on both the 70 and 100 m transects (GAM; 70 m:  $\chi^2 = 62.9$ ,  $p < 0.0001$ ; 100 m:  $\chi^2 = 48.8$ ,  $p < 0.0001$ ) respectively (Fig. 4b) and were also affected by the distribution of gravel and cobbles and gravelly sand substrates (GAM;  $\chi^2 = 12.1$ ,  $p < 0.05$ ;  $\chi^2 = 14.5$ ,  $p < 0.005$ ). On both transects, relative densities of *D. florida* were generally suppressed ( $< 1$  ind.  $m^{-2}$ ) from the farm edge to 200 m downstream where TPM flux

was  $> 10\ g\ m^{-2}\ d^{-1}$ . However, some isolated accumulations of *D. florida* were observed in close proximity to the cage edge ( $< 100$  m) (Figs. S3 & S4). *D. florida* was rarely observed at the other 2 study sites.

*A. rubens* was present at all sites and at highest densities (up to 1.4 ind.  $m^{-2}$ ) within 50–200 m of Farm B at 70 m depth. Along this transect, the relationship between the density of seastars and TPM flux was close to significant (GAM;  $\chi^2 = 8.9$ ,  $p = 0.08$ ). *A. rubens* was rarely observed on 100 m transects at Farm B. At Farm A, *A. rubens* was present along the 100 m transect but its density did not show a significant relationship with TPM. On the 70 m transect of Farm A, however, the density of *A. rubens* was relatively elevated (up to 1.0 ind.  $m^{-2}$ ) within 200 m of the farm and significantly related to TPM input (GAM;  $\chi^2 = 8.2$ ,  $p < 0.05$ ) (Figs. 4a, S1 & S2). Other seastar taxa (*C. granularis* and *Henricia* spp.) were prominent throughout transects at Farms A and B. Along the 100 m transect at Farm B, the density of both taxa showed a negative relationship with TPM flux and a significant relationship with coarse substrates. A visual assessment of Figs. S1 & S2 shows that at Farm A, *C. granularis* coexists with the distribution of the sponge taxa *Polymastia* spp. and *Phakellia* spp.

#### 4. DISCUSSION

This study improves understanding of the effect of sedimentation fluxes from finfish farms on the distribution of benthic epifaunal groups and taxa across mixed- and hard-bottom habitats along an enrichment gradient in the far-field farm area ( $> 50$  m from the farm cages). It demonstrates that elevated TPM flux arising from salmon farming activity affects benthic epifaunal community composition, along with other dominant natural physical factors such as substrate type. Species-specific responses were observed in several common hard-bottom epifaunal taxa, whereby they were found to be either enhanced, depressed, or unaffected by the processes of sedimentation. The burrowing lugworm and the predatory seastar *Asterias rubens* showed evidence of elevated densities with increasing proximity to the study farms. In contrast, densities of the filter feeding sponges *Phakellia* spp. and *Polymastia* spp. were relatively low in close proximity (i.e. 50–200 m) to the farms. The soft coral *Duva florida* was only observed in high densities around one farm, which was situated on mixed bedrock and cobbles substrate with moderate to strong currents (mean current velocity 0.086  $m\ s^{-1}$ ). When present, *D. florida* distribution

had a negative relationship with depositional flux whereby densities were generally depressed near the farm (between 50 and 200 m). This information on both species- and community-level responses is valuable for decision making on the ecological status of hard- and mixed-bottom habitats.

#### 4.1. Comparative influence of abiotic drivers of epibenthic assemblages

The 3 study farm locations were all situated on hard- and mixed-bottom substrates; however, variation in depth, seafloor structure (slope, aspect, and rugosity), dominant substrate type, current velocity, and TPM flux created site-specific habitat characteristics and thus unique epibenthic communities. On a broad spatial scale (10s of km, site comparative) the environmental variables current velocity, depth, sea-

bed slope, and TPM flux rate were the most important drivers of epibenthic community distribution and composition. The identified environmental variables with the highest contribution to the best-fitting multivariate model are a selection of well-established benthic abiotic drivers: geomorphology (slope), depth, and exposure (current flow) (Harris & Baker 2020).

On a site-specific scale (10s of m), TPM flux followed by the presence of hard substrata (bedrock, boulders, and gravel and cobbles) were the overall dominating drivers of the structure of epibenthic communities along the surveyed transects. Stable hard substrate surfaces are essential for the settlement and sustained growth of associated sessile epibenthic species (Harms & Anger 1983, Howell et al. 2016). Current velocity, depth, slope, and sedimentation (natural or anthropogenic) have previously been shown as major structuring forces of sponge assemblages (Bell & Barnes 2000a,b,c) and have

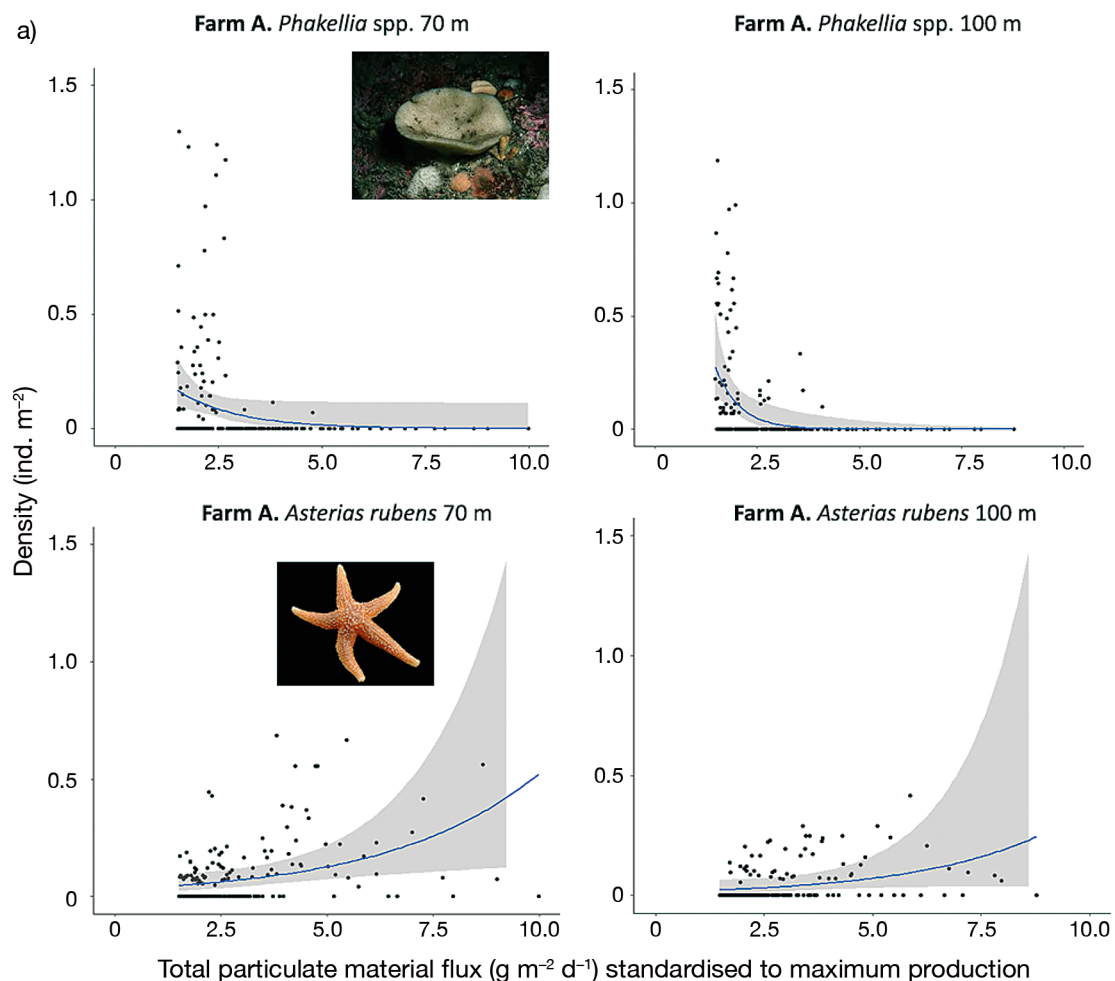


Fig. 4. Distribution of the density of benthic epifaunal key taxa at (a) Farm A, (b) Farm B, and (c) Farm C with total particulate material flux standardized to maximum fish production

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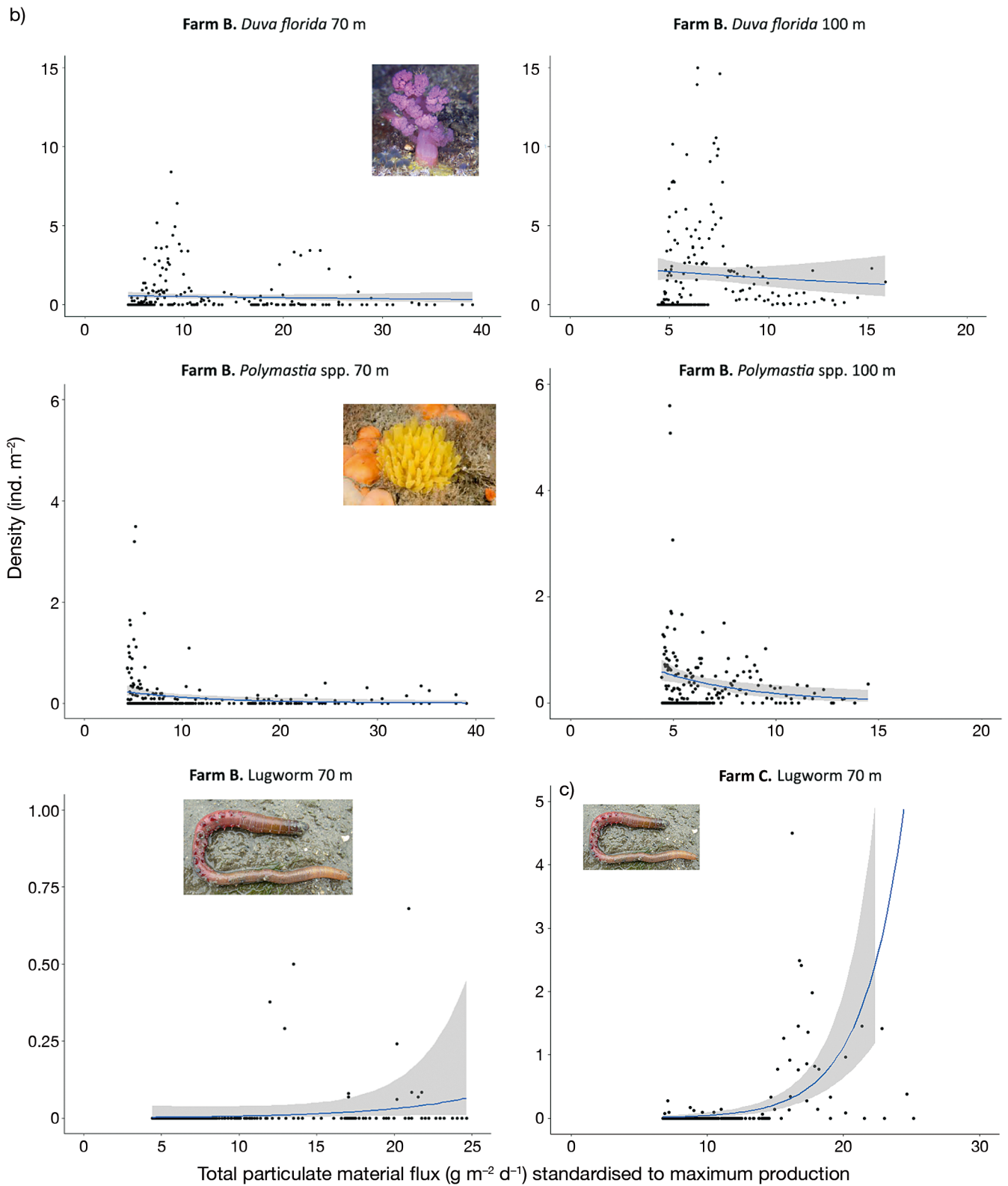


Fig. 4 (continued)

been observed to play a primary role in the structure and distribution of sponges dominating Norwegian coastal and fjord areas (Klitgaard & Tendal 2004, Kutti et al. 2015, Dunlop et al. 2020). The reliance of fan- or cup-shaped sponges (*Phakellia ventilabrum* and *Axinella infundibuliformis*) on hard substrate in northern European waters has been recorded in several studies (Connor et al. 2004, Buhl-Mortensen et al. 2012, Kutti et al. 2015, Dunlop et al. 2020). Sponges of the genus *Polymastia* have similarly been associated with gravel, cobbles, and boulders on morainic ridges on the eastern Tromsøflaket (Buhl-Mortensen et al. 2012). Soft corals of the family Nephtheidae have been recorded on varied substrata ranging from bedrock, boulder, cobbles and pebbles to coarse sands (Murillo et al. 2011). Elevated TPM fluxes, however, will lead to a loss of exposed hard-substrate surfaces, thus altering suitable habitat availability for larval settlement and indirectly affecting species presence (Maughan 2001). Overall, TPM flux emerged as the strongest driver of benthic epifaunal community composition and the spatial abundance of key epifaunal taxa. Reflecting the enrichment status of the sampled benthic infaunal communities along the transects (Section 4.4), elevated TPM flux led to a decrease in epibenthic biodiversity ( $H'$ ) along the majority of the transects. Distance to farm (and thus TPM flux) has also been shown to be the most important explanatory variable determining the presence of visual IOE and epibenthic taxa within a range of ca. 200 m of finfish farms over hard-bottom substrates in Newfoundland. In these studies, substrate type, current velocity, and depth had a significant effect on the structure of epibenthic communities, but effects were secondary to distance to farm (Hamoutene et al. 2016, Salvo et al. 2017).

Our results support the importance of the selected environmental variables but also imply shortcomings, as a proportion of variation in community composition remained unexplained by the multivariate models. This is likely the result of high spatial variability that is implicit in benthic epifaunal communities but may also be because other potentially important structuring factors such as nutrient levels, larval life span, competition for space, grazing, and predation were not measured. For example, the broadscale distribution of geodic sponge habitats is largely driven by the concentration of dissolved silicate, temperature, and depth in addition to the particulate organic carbon available (Howell et al. 2016). Additionally, while hydrodynamic data were available at a resolution sufficient for broad-scale comparisons, it was not possible to resolve the fine-scale changes in

boundary layer flow that are inevitably associated with the complex topography observed at these sites (e.g. accelerated currents over and vortices behind large rocks that may be important at an individual organism level) (Danny 2016).

#### 4.2. Effects of elevated sedimentation on sensitive epibenthic taxa

Epibenthic sessile filter feeders are thought to be especially vulnerable to anthropogenic sedimentation, either from particulate material suspended in the water column or deposited on the seabed (Howell et al. 2016). Sessile filter feeders have no mode of escape from an impacted area nor the option of an alternative feed source or mechanism. Direct impacts include habitat loss by sedimentation and gradual burial potentially leading to mortality (Larsson & Purser 2011, Topçu et al. 2019, Last et al. 2020). Elevated suspended particulate levels can clog respiration and feeding apparatuses or cause smothering, leading to physiological alterations such as reduced feeding capacity, metabolic rates, and tissue oxygenation, which in turn affects growth, survival, and reproductive output (Roberts et al. 2006, Maldonado et al. 2008, Bannister et al. 2012, Tjensvoll et al. 2013, Edge et al. 2016). In addition, increased use of clearing and cleaning mechanisms as well as avoidance behaviour is expected, raising the organism's energetic demands and thus reducing general condition and reproductive output (Bell et al. 2015, Liefmann et al. 2018). Indirectly, sedimentation can alter substrate surfaces and deter settlement of larvae and reduce recruitment. Furthermore, sedimentation can indirectly cause tissue abrasion or harmful anoxic and sulphide-producing conditions on tissue surfaces and, in the case of contaminated sediments, lead to toxic effects (Bak & Elgershuizen 1976, Sun et al. 2010, Bell et al. 2015).

Epibenthic communities at 2 of the study farm sites were dominated by several sponge taxa and the soft coral *D. florida*, which showed taxa-specific varied tolerances to the TPM gradient. Most profound changes occurred within 50–200 m of the farms, which corresponded to the area with the highest depositional flux rates and visually conspicuous deposits on the seabed. This approximate boundary also corresponded to the compositional changes that were observed in the infauna samples, which were generally consistent with the well-established organic enrichment gradient. Waste particulates released from finfish farms differ in size and weight (Bannister et al. 2016) and have

correspondingly varied settling velocities, with the largest and heaviest particles being swiftly deposited close to the farm whilst smaller fractions stay longer in suspension and are transported further afield. In close proximity to all 3 farms (<50–150 m), the natural substrata and any associated epibenthic communities were observed to be covered by a layer of fine sediments, interspersed with feed pellets and faeces. The increased load of deposited sediments thus clearly altered habitat availability and posed the risk of gradual burial and smothering for some epifauna.

At Farms A and B, the sponges *Phakellia* spp. and *Polymastia* spp. were common in areas >200 m downstream of the farm where TPM fluxes were <5 or 10 g m<sup>-2</sup> d<sup>-1</sup> respectively. Low densities of these sponges close to the farm indicate that these taxa are susceptible to adverse effects from higher depositional fluxes. Fan- and cup-shaped Axinellidae (*Phakellia*/*Axinella*) were found to be particularly susceptible to the physical damage and sedimentation from bottom trawling in the Barents Sea (Buhl-Mortensen et al. 2016). Laboratory experiments involving the exposure of *Phakellia ventilabrum* to sedimentation showed no significant changes in sponge oxygen consumption, but the expression of stress proteins was enhanced (Schuster 2013). The highest level of sedimentation (0.1 g l<sup>-1</sup>) used in these experiments was similar to levels recorded approximately 50 m from Farm A and 100 m from Farm B, where *Phakellia* sponges were uncommon. During these experiments, the cup-shaped *P. ventilabrum* accumulated significant quantities of particles over 14 d, and therefore over longer exposure periods (e.g. one production cycle of the study farms typically takes 18 mo), this would lead to even greater accumulation of organically enriched biodeposits. *Polymastia* spp. sponges have previously been found to be relatively resilient to natural sedimentation and to survive under layers of sediment, using papillae protruding above the sediment surface to continue feeding (Bell & Barnes 2000a). Here, it can only be speculated that either the anthropogenic sedimentation rate within 50–200 m of the farm was high enough to cause rapid and complete burial or that a change to unfavorable sediment conditions from several years of organic enrichment could preclude larvae settlement and *Polymastia* spp. survival. There were some indications in our results that the relative density of the seastars *Ceramaster granularis* and *Henricia* spp. declined with increasing TPM flux. These seastars are known sponge predators (Sheild & Witman 1993, Gale et al. 2013), and thus their recorded distribution could simply be a response to changes in sponge distribution close to the farms.

Although *D. florida* populations appeared to be generally suppressed within 200 m of Farm B, there was also evidence of some resilience or tolerance in the peripheral 'impact zone' (i.e. 250–400 m downstream of the farm), where depositional fluxes were still elevated (10 and 7.5 TPM g m<sup>-2</sup> d<sup>-1</sup>). This is possibly attributed to the soft coral's morphology, i.e. the erect shape elevates its polyp structure into faster current flow, thus providing a natural cleansing mechanism. In addition, *D. florida* has the capability of contracting into a small ball (ca. 0.5–2 cm<sup>2</sup>) when disturbed, which presumably also provides a cleansing mechanism and may allow the species to close down during periods of excessively high sedimentation such as peak fish feeding time.

Boreal sponges of the genus *Geodia* occurred along transects at Farm A and B with several observations close to the farm cages (~50 m) and no apparent trend with TPM flux. This could imply some tolerance to extended periods of sedimentation. Previous studies indicate a comparatively high tolerance to elevated sedimentation for this sponge group (Hoffmann et al. 2003, Kutti et al. 2013, Fang et al. 2018), with *G. barretti* exhibiting high recovery capabilities following sedimentation events (Kutti et al. 2013). Oxygen consumption and metabolic function, however, have been shown to be impaired when exposed to elevated suspended particulate compounds found in oil drilling wastes (Fang et al. 2018). In this study, *Geodia* spp. was recorded not just on exposed flat surfaces, but often nestled under overhangs in steep reef sections or within complex boulder gardens, both of which will provide some shelter from extensive sedimentation. Nonetheless, several *Geodia* sponges found in close proximity to the farm showed signs of disease in the form of altered tissue colour and structure, potentially indicating a lowering of metabolic function and fitness from prolonged exposure to elevated levels of sedimentation (Luter et al. 2017).

A general suppression of most sessile filter feeding epibiota (aside from *Geodia* spp.) within ca. 200 m of fish farms is consistent with findings from analogous studies conducted elsewhere in the world. In British Columbia, the susceptibility of upwards-facing, cup-shaped sponge taxa to the accumulation of particulate material was also observed by Sutherland et al. (2018). The study found that locally abundant glass sponges were only present in areas >80 m from the net pens, where modelled aquaculture depositional carbon flux was low. Similarly, the abundance of hard-bottom suspension and filter feeding taxa including soft corals, crinoids, serpulids, and poriferans recorded in drop-camera transects between the farm



cage and 220 m downstream of farms in Newfoundland were relatively low. In general, epibenthic abundance increased with distance from farm and suspension and filter feeders were lacking in near cage areas containing other indicators of acute enrichment (Salvo et al. 2017). The sessile epifaunal taxa in studies from Newfoundland and British Columbia are dominated by pulmonate anemones and glass lyssacine and dictyonine sponges and therefore represent relatively different epifaunal communities to northern Norway. However, sponges of the genus *Polymastia* and soft corals of the genus *Drifa* were observed in hard-bottom communities in Newfoundland (Salvo et al. 2017).

#### 4.3. Conspicuous fauna with a positive response to elevated sedimentation

Several taxa that were commonly observed in video transects had generally enhanced densities in regions of elevated TPM flux close to the study farms. Densities of a lugworm species were elevated over sandy gravel seafloor habitats at 70 m water depth at Farms B and C. Lugworms are commonly found in the shallow sandy intertidal zone and were therefore understandably not present along 100 m survey sites. Elevated densities of the lugworm *Arenicola marina* have previously been observed near salmon and mussel farms (Sánchez-Mata & Mora 2000, Keeley et al. 2020). The lugworm can benefit from increased deposition rates and subsequent change of habitat as natural substrates were smothered with finer sediments, which they favor. Lugworms also feed on organic debris, and waste from farms is an attractive food source. By breaking down organic waste, the lugworm reduces sediment organic content as well as oxidizing and lowering sulphate production (Papaspyrou et al. 2007, Wendelboe et al. 2013). In this manner, aggregations of *A. marina* have been suggested to help prohibit the enrichment and anoxia of sediments (Keeley et al. 2020). Results from this study also present some indication that the asteroid *A. rubens*, a species common to coastal regions of the North Atlantic and a primary predator in benthic communities, can be found at relatively higher densities in association with salmon farms. This supports the findings of previous studies, which have also shown elevated biomass of *Asterias* spp. around mussel and salmon farms where it is thought they are feeding on increased abundances of opportunistic infauna and epifauna (Hall-Spencer et al. 2006, D'Amours et al. 2008, Wilding et al. 2012). At Farm B,

the encrusting sponge *Myxilla* spp. showed elevated densities in proximity to the farm (<300 m) on the 70 m transect. Other encrusting sponges, for example *Eurypon* sp., are known to live permanently under layers of sediment (Bell & Barnes 2000b,c), and the distribution of *Myxilla* spp. could indicate both a resilience to sedimentation effects and the ability to gain some nutritional benefit from enhanced suspended particulate material.

#### 4.4. Benthic infaunal and epifaunal indexes

Benthic infauna communities along the transect generally reflected the expected enrichment gradient. The irregular pattern in infauna biotic indexes at Farm A was attributed to the dispersive nature of the site and the complex hard-bottom bathymetry. This was presumably influenced by near-bottom hydrodynamics and spatial heterogeneity with respect to particle settlement. At Farm A, the enrichment gradient that was not well reflected in the established infauna indices was apparent in changes in the epibenthic biodiversity index ( $H'$ ). At both Farms B and C, elevated TPM flux did lead to the expected changes in infauna indices; however, only at Farm C was there an equivalent decrease in the epibenthic biodiversity index. The absence of a clear enrichment gradient in the epifauna index at Farm B was attributed to substrate changes (i.e. the prevalence of rocks between 200 and 400 m from the farm), which strongly influenced the faunal assemblage and associated diversity. Collectively, these findings suggest that an epifaunal diversity index can elucidate community responses to changes in TPM flux along the enrichment gradient in locations dominated by hard substrate where grab sampling is challenging. The varied response of these traditional indexes, however, also highlights the need for a more holistic approach to the assessment of the environmental status of hard-bottom-dominated locations, as they show shortcomings in reliably resolving the complexity of the sites, especially where substrates are highly variable.

#### 4.5. Ecological indicators and implications for aquaculture environmental monitoring

This study has contributed significantly to our understanding of the effects of elevated sedimentation from finfish farms on the distribution of benthic epifaunal communities across mixed- and hard-bottom habitats. This information is essential for informed

decisions on the establishment and expansion of finfish aquaculture sites in coastal areas dominated by hard and mixed habitats to minimize adverse impacts on potentially ecologically important and vulnerable species and communities. Despite the importance of relevant knowledge on the risks to these species in aquaculture management planning, the ecological role and services provided by these communities and their overall distribution are currently poorly known. Deep-sea sponges are generally known to provide structurally complex habitats and refuge for fish and invertebrates and enhance benthic biodiversity (Klitgaard 1995, Knudby et al. 2013, Kutti et al. 2013) as well as providing important services in benthic–pelagic coupling (Maldonado et al. 2012). For management purposes, it is necessary to determine the ecological value and uniqueness of communities encountered to decide if the risk of loss or severe impairment within the impact area is acceptable and ecologically sustainable. The composition of sponges (*Geodia* spp., *Phakellia* spp., *Polymastia* spp., and *Mycale lingua*) and the densities observed around Farms A and B are comparable to those found in regions containing protected boreal ‘ostur’ sponge beds (Klitgaard & Tendal 2004, Kutti et al. 2013). There is a general lack of knowledge on the life history of many of these northern ostur sponges, including reproduction, how to discern between adults and juveniles, and life expectancy. It is, however, thought that many are long-lived and have intermittent reproduction cycles (Spetland et al. 2007). A full site recovery is thus likely to take substantially longer than the 10 yr expected for soft-bottom locations dominated by benthic infaunal communities and should be factored into aquaculture management decisions.

Furthermore, the type of information obtained regarding the relative densities of visually conspicuous epifauna along the enrichment gradient has considerable potential for making informed judgements about the ecological status of hard- and mixed-bottom habitats. For example, once a sufficient number of species are classified in terms of their enrichment tolerance it should be possible to develop a simple index that utilizes their relative dominance to rank the site according to disturbance or organic enrichment level—akin to those based on benthic infaunal ‘ecological groupings’ (Borja et al. 2000). This approach has its challenges, mainly due to the patchy nature of many of the species (i.e. not always naturally present) in conjunction with potentially high regional species-specificity, which in turn means the species tolerance library would need to be relatively large to make it broadly applicable. However, cur-

rent findings from northern Norwegian fjord systems include prominent taxonomic groups distributed throughout the northern Atlantic and other temperate waters. Sedimentation-associated sensitivity thresholds of these taxa can also inform the ecological status of similar biological habitats in association with aquaculture in other locations. The collection of corresponding infaunal and epifaunal information across the enrichment gradient used here is valuable in the development of epifaunal ecological indicators. If it is possible to collect grab samples between hard substrate, infauna community composition helps to determine benthic state and its relationship to epifaunal distributions and enrichment tolerance.

The development of an epibenthic enrichment index based on the current visual assessments is, however, limited to presence–absence. Sub-lethal effects and signs of ‘stress’ are difficult if not impossible to distinguish. This is compounded by the fact that there is limited knowledge regarding the physiology, life history, and reproduction of the sponge and soft coral species common in coastal northern Norway, and therefore a lack of guidance as to what to look for. These long-lived sessile organisms could undergo a slow and gradual impairment of function over time before disappearance. A suite of species-specific sub-lethal stress indicators, especially those possible through new genomics techniques (metabarcoding, metagenomics, and functional profiling) should therefore be considered to refine differentiation of intermediate impact stages and enhance the visual assessment methods. For example, the sponge *Weberella bursa* tends to have reduced ribosomal activity and increased expression of genes controlling cell apoptosis when exposed to farm waste (Laroche et al. 2021). However, approaches based on epibenthos alone will inevitably be challenged by the patchy and stochastic nature of the habitats, regional changes in composition, and the prevalence of specific species.

In conclusion, this study demonstrates that epifaunal distribution is decidedly impacted by farm-derived waste, but also by other abiotic factors (current velocity, substrate type, and seafloor slope). This means that visual assessments reflect an effect of several interconnected factors. Therefore, visual assessments should ultimately be coupled with stress-indicator genes and novel quantitative measures of enrichment or waste prevalence, e.g. microbial eDNA (Keeley et al. 2018, Stoeck et al. 2018, Cordier et al. 2021), which can also be evaluated from flocculent material that overlies most hard-bottom habitats (Keeley et al. 2021) to create a universal adaptable monitoring toolbox which can address site-specific needs.

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