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RESEARCH ARTICLE

WILEY

Salmon farming alters the structure and functioning of Norwegian maerl bed communities

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Abstract

1. Effluents resulting from fish farming activities can alter the structure and functioning of benthic ecosystems. In Norway, recent technological advances within the salmon industry have facilitated the expansion of aquaculture into shallower locations, leading to additional pressures upon coastal habitats.
2. Maerl/rhodolith beds are important bioengineers in coastal waters—supporting highly diverse associated macrofaunal communities—and are likely to be particularly at risk.
3. This study aims to investigate the environmental changes induced by fish farms in their vicinity and their impact on the structure and functioning of maerl bed macrofaunal communities.
4. High dissolved nutrients and organic enrichment levels were observed close to the cages, associated with lower live maerl cover.
5. Overall, the most substantial impact of salmon farms on macrofaunal communities was observed within 100 m from the cages. Nevertheless, changes in the structure and functioning of assemblages were evidenced up to 300 m.
6. In the vicinity of the cages, communities were characterized by the dominance of endobenthic subsurface deposit feeders and opportunistic species, notably the polychaetes *Chaetozone* sp., *Capitella* sp. and *Scoloplos armiger*. Conversely, sites situated farther away from the cages exhibited higher abundances of epibenthic taxa, including crawlers, grazers and species sensitive to organic enrichment.
7. Sites unaffected by the presence of fish farms were described by high abundances of the ophiuroid *Ophiura robusta*, the polychaete *Proclea graffi* and ostracods, reflecting more favourable environmental conditions.
8. Such changes in macrofaunal communities highlight the vulnerability of maerl beds to the impacts of aquaculture, thus emphasizing the importance of rigorous site selection when establishing new fish farming facilities.

KEYWORDS

functional diversity, functional traits, macrofaunal communities, maerl/rhodolith beds, salmon farming, taxonomic diversity

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1 | INTRODUCTION

The Atlantic salmon (*Salmo salar* [Linnaeus, 1758]) farming industry in Norway has witnessed substantial growth over the past two decades, increasing from 361,879 t in 1998 to about 1.6 million tonnes in 2021 (Directorate of Fisheries, 2023). Currently, Norwegian salmon farming accounts for about 50% of the world's production, representing one of the country's largest exports by economic value (Taranger et al., 2015). In 2021, a total of 1,243 marine farms were licenced in Norway for the production of both Atlantic salmon and rainbow trout (Directorate of Fisheries, 2023). In order to satisfy the increased global demand for food, salmon aquaculture is expected to continue expanding in the future, which will require the allocation of new aquaculture permits and localities (Norwegian Ministry of Trade Industry and Fisheries and Ministry of Petroleum and Energy, 2017). Such development raises concerns regarding the potential environmental impacts on coastal ecosystems, and management guidelines are necessary to determine the scope of production in coastal areas in the future.

Intensive finfish aquaculture exerts significant impacts on the structure and functioning of benthic coastal ecosystems due to the release of large amounts of effluents, such as organic matter, dissolved nutrients, heavy metals and chemotherapeutic substances (Burridge et al., 2010; Carroll et al., 2003; Dimech et al., 2002; Hall-Spencer et al., 2006; Keeley et al., 2014; Kutti et al., 2007; Taranger et al., 2015; Wilson et al., 2009). The extent of these impacts depends on a wide range of conditions of the fish farm (i.e., farm type, biomass production and age of the farm) as well as ambient environmental conditions (e.g., water depth, current velocities, topography and substrate) (Holmer et al., 2005; Parsons et al., 2020; Taranger et al., 2015). Negative effects from fish farming activities are frequently linked to the deposition of fish faeces and uneaten food pellets, resulting in localized increases in organic matter content within the sediments (Brooks et al., 2004; Burridge et al., 2010; Buschmann et al., 2006; Carroll et al., 2003; Karakassis et al., 2000; Kutti et al., 2007; Strain & Hargrave, 2005; Wilson et al., 2009). Many studies have investigated the impact of aquaculture on soft sediment benthic ecosystems, highlighting changes in macrofaunal communities along gradients of organic enrichment (Carroll et al., 2003; Macleod & Forbes, 2004; Pearson & Black, 2001; Sanz-Lázaro & Marín, 2011). These changes generally follow the model described by Pearson and Rosenberg (1978), characterized by reduced species diversity close to fish farms and increased abundance of opportunistic species (Sanz-Lázaro & Marín, 2011). Over the last decades, the major technological developments of the Norwegian salmon industry have enabled aquaculture to move into shallower and wave-exposed sites, leading to potential additional pressures on coastal benthic habitats, such as kelp forests (Haugland, 2019), seagrass meadows (Díaz-Almela et al., 2008; Dimech et al., 2002; Holmer et al., 2008) and maerl beds (Aguado-Giménez & Ruiz-Fernández, 2012; Hall-Spencer et al., 2006; Sanz-Lázaro et al., 2011).

Maerl beds, also referred to as rhodolith beds, are biogenic calcareous habitats formed by the accumulation of living and dead

free-living coralline algae, covering extensive benthic areas. These habitats have a worldwide distribution and typically thrive in shallow waters where conditions of light, temperature and sedimentation are favourable for photosynthetic, respiratory and calcification processes (Riosmena-Rodriguez et al., 2016). Coralline algae are recognized as bioengineers, forming complex three-dimensional habitats that foster highly diverse macroalgal communities and serve as nursery grounds and shelter for a wide range of invertebrates and fishes, including commercially important species (Barbera et al., 2003; Hall-Spencer, 1998; Helias & Burel, 2023; Neill et al., 2015; Nelson, 2009; Peña et al., 2014; Sciberras et al., 2009; Stelzer et al., 2021; Teichert, 2015). Additionally, maerl beds are one of the most important producers of calcium carbonate in temperate marine environments, thus exerting a significant role in the global carbon cycle within shallow coastal waters (Tuya et al., 2023; van der Heijden & Kamenos, 2015). Despite their ecological and economic importance, maerl beds are threatened by a rising number of environmental changes resulting from anthropogenic activities, including climate change (Martin & Gattuso, 2009; McCoy & Kamenos, 2015; Simon-Nutbrown et al., 2020), bottom trawling (Bernard et al., 2019; Hall-Spencer & Moore, 2000; Kamenos et al., 2003), eutrophication (Hall-Spencer et al., 2010), invasive species (Barbera et al., 2003; Grall & Hall-Spencer, 2003; Peña et al., 2014) and aquaculture (Aguado-Giménez & Ruiz-Fernández, 2012; Hall-Spencer et al., 2006; Sanz-Lázaro et al., 2011).

In Europe, the vulnerability of maerl beds has been recognized through the adoption of different conservation and management strategies such as directives and conventions. Since 2014, they have been included on the OSPAR List, underscoring their ecological significance and the need for their protection. However, in Norway, no protective management measures exist due to a significant lack of knowledge regarding the current distribution of maerl beds and the associated biodiversity (Gundersen et al., 2018). Moreover, it is likely that the most extensive maerl beds are located in the northern part of Norway (Gundersen et al., 2018), where most of the aquaculture industry's growth is planned (Aanesen et al., 2023). In their study, Hall-Spencer et al. (2006) highlighted the structural changes experienced by Scottish maerl beds and their associated faunal communities in response to effluents from salmon farms. While their findings are important for the management of Scottish maerl beds, specific studies on Norwegian maerl beds are necessary, given the environmental (e.g., hydrodynamic regime and temperature) and biological differences (e.g., engineer species forming maerl beds, diversity and composition of associated fauna) among these locations. Moreover, Norwegian salmon farms typically operate at higher production levels than Scottish farms (Asche et al., 2013), potentially leading to different environmental footprints. A thorough investigation is thus critical to understand the impact of Norwegian salmonid aquaculture on maerl beds and determine thresholds for better management of these habitats in aquaculture localities (Taranger et al., 2015).

In this context, the present study was conducted in 2019 in the Lofoten Islands, Northern Norway, and involved the investigation of

three salmon farms and two reference sites. The first objective was to understand how salmon farms modify the physical and chemical environment in their vicinity. In addition, the study aimed to assess changes in the structural integrity of maerl beds and modifications in the composition of associated faunal communities, along gradients of impact from the salmon farms. Finally, the study sought to highlight the functional changes occurring within the faunal communities through the analysis of the species' biological traits.

2 | MATERIAL AND METHODS

2.1 | Study sites

Three Norwegian fish farms (referred here as Farms A–C) were surveyed in the Lofoten Islands from 27 June 2019 to 9 July 2019. Farms were selected due to the presence of maerl beds in their vicinity. The three farms had a maximum total biomass capacity of 1,560 t of salmon. The farms presented differences in their production cycle, with a biomass peak reached in May 2019 (1,500 t) for Farm A, in July 2019 (1,306 t) for Farm B and in November 2019 for Farm C (1,145 t) (Figure S1). In addition, two reference maerl beds were selected at locations 1,580 to 2,170 m away from any fish farm or known anthropogenic source of organic enrichment. All studied maerl beds were formed by the accumulation of the coralline alga *Lithothamnion soriferum* Kjellman and *Lithothamnion glaciale* Kjellman (Peña et al., 2021), recently redefined as *Boreolithothamnion soriferum* (Kjellman) P.W. Gabrielson, Maneveldt, Hughey & V. Peña and *Boreolithothamnion glaciale* (Kjellman) P.W. Gabrielson, Maneveldt, Hughey & V. Peña, respectively (Gabrielson et al., 2023). Representative specimens from both maerl species are preserved in Trondheim Herbarium (TRH).

2.2 | Sampling

2.2.1 | Faunal sampling and identification

Sampling of maerl bed communities was conducted using a box corer (0.1 m²) at depths ranging from 10 to 27 m. For each farm, macrofaunal samples were taken along three transects (two to five cores per transect; Figure 1). The length and direction of the transects were selected in order to follow the distribution area of maerl beds. At reference sites, macrofauna was sampled along one transect. Only samples containing coralline algae (live or dead) were kept for analysis (41 cores in total). GPS coordinates were used to determine accurate location for each sample and determine its distance from the fish farm (calculated as the shortest distance between the sampling site and the edge of the farm, according to the *Norwegian Aquaculture Register*; Directorate of Fisheries, 2023). Pictures of each core were taken in order to estimate the proportion of live maerl (see Section 2.3.2). Then, samples were washed through a 1 mm sieve and immediately preserved in 4% formalin. In the laboratory in Bergen, Norway, macrofauna was sorted, counted and identified to the lowest taxonomic level.

All samples are abbreviated below according to the farm (A, B or C), the transect number (1, 2 or 3) and the distance to the farm (e.g., A1_{75m} for Farm A, transect 1, 75 m from the farm). Reference Sites 1 and 2 are abbreviated as R1 and R2, respectively, followed by the sample number (R1S1 for Reference Site 1, Sample 1).

2.2.2 | Environmental characterization

For each macrofaunal sample, seawater was collected beforehand at the exact same location using a water collector. Water samples were taken 1 m above the seabed. Nitrite (NO₂[−], μmol l^{−1}), nitrate (NO₃[−], μmol l^{−1}), phosphate (PO₄^{3−}, μmol l^{−1}) and silicate (SiO₄^{4−}, μmol l^{−1}) were measured from 20 ml water samples, fixated with 1 drop of chloroform. Samples were analysed using a *Skalar autoanalyzer* with an accuracy of 1 μmol l^{−1} for NO₂, 0.02 μmol l^{−1} for NO₃[−], 1 μmol l^{−1} for PO₄^{3−} and 0.01 μmol l^{−1} for SiO₄^{4−} (Bendschneider & Robinson, 1952; Grasshoff, 1965). Twenty-millilitre water samples were collected and stored frozen (−20°C) for fluorometric determination of ammonium (NH₄⁺, μmol l^{−1}) by direct segmented flow analysis (Alpkem Flow Solution IV autoanalyser: Kérouel & Aminot, 1997). Depth (m), temperature (°C) and salinity were obtained using a conductivity-temperature-depth (CTD) instrument at each sampling site.

Surface sediment samples were taken from each transect at the site closest to the farms using a Van-Veen grab. About 50 g of sediment was sampled and stored in plastic bags at −20°C pending analysis. Concentrations of copper (Cu; mg kg^{−1}), chromium (Cr; mg kg^{−1}), nickel (Ni; mg kg^{−1}), zinc (Zn; mg kg^{−1}), arsenic (As; mg kg^{−1}), lead (Pb; mg kg^{−1}), cadmium (Cd; mg kg^{−1}) and mercury (Hg; mg kg^{−1}) were measured according to standardized methods at an accredited laboratory (Eurofins, Linköping, Sweden).

2.3 | Data treatment

2.3.1 | Current models

Ocean currents within the study region were modelled using the Regional Ocean Modelling System (ROMS, Shchepetkin & McWilliams, 2005). The model setup is based on NorKyst800 (Albretsen et al., 2011), which covers the Norwegian coastal waters with a horizontal resolution of 800 m and a vertical resolution of 35 terrain-following layers. In a 200 km × 300 km subregion around the farms, ocean currents were computed on a one-way nested subgrid with a horizontal resolution of 160 m, with boundary values taken from the coarser model, as a part of the NorFjords160 system at the Institute of Marine Research (<https://www.hi.no>). The model includes atmospheric forcing from AROME MetCoOp (Müller et al., 2017) and river runoff from the Norwegian Water Resources and Energy Directorate (NVE, <https://nve.no>). The model period used for this paper is August 2018 to July 2019. For each sampling location, mean ocean currents at 10 m depth were extracted from the model.

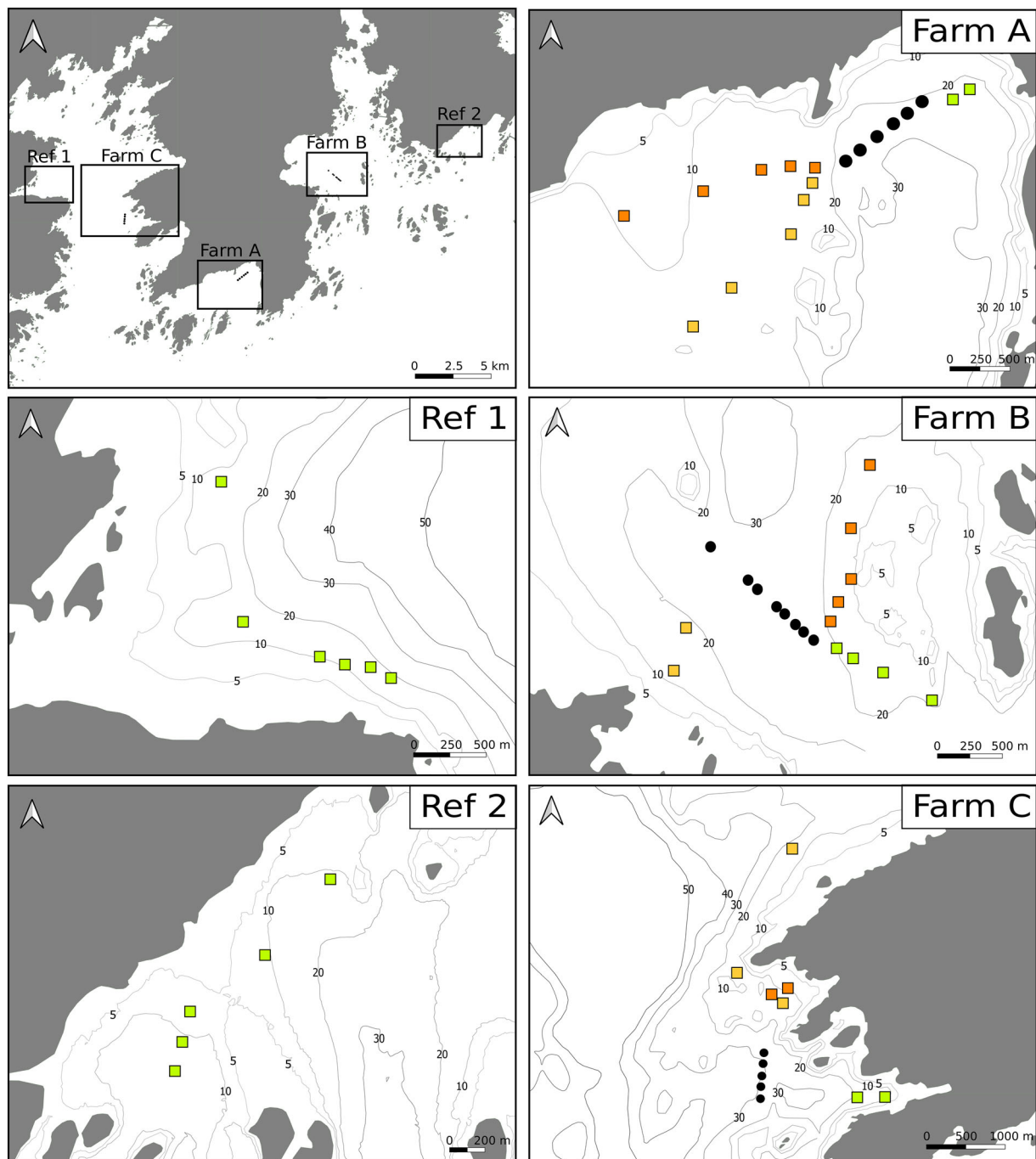


FIGURE 1 Location of the three salmon farms (Farms A, B and C) and two reference sites (Refs 1 and 2). For each farm, the location of net cages is presented as black circles. Coloured squares show the location of samples (box cores and water samples) taken from each transect (light green = transect 1; light orange = transect 2; dark orange = transect 3). Isobaths are presented for each location (depth in m).

2.3.2 | Live maerl cover

Core imagerys were analysed using the ImageJ software (Schneider et al., 2012), and the surface covered by the live maerl was calculated for each sampling site through manual contour tracing. The proportion of live maerl cover was obtained by dividing the surface covered by live maerl by the total surface of the core. Proportion data were then transformed to percentages and displayed according to their distance from the

farm, divided in five groups (≤ 100 m [$n = 4$], 101–200 m [$n = 7$], 201–400 m [$n = 11$], 401–1,000 m [$n = 8$] and $>1,000$ m [$n = 11$]).

2.3.3 | Collection of biological traits

For each identified taxa, biological traits were collected from different published sources (e.g., species identification guides, scientific papers

and online databases). A total of seven traits, divided into 29 modalities, were considered (Table 1): feeding method, maximum size, life span, living habit, substrate position, development mode and AMBI groups (AZTI's Marine Biotic Index, calculated using AMBI 4.1 software; <http://ambi.azti.es>; Borja et al., 2000). AMBI was developed as a proxy of species sensitivity/tolerance to organic enrichment. Taxa-specific groups were displayed according to species sensitivity to organic enrichment and ranging from 'I' (sensitive species) to 'V' (first-order opportunistic species) (Grall & Glémarec, 1997). The species affinity to each modality was scored with 0, 1, 2 and 3 using a fuzzy coding approach (Chevenet et al., 1994), with 0 indicating the absence of affinity to a modality and 3 a complete affinity (D'Alessandro et al., 2020; Dong et al., 2021; van der Linden et al., 2016).

TABLE 1 List of the functional traits, their modalities and abbreviations, used in the present study.

Trait	Modality	Abbreviation
Feeding method (FM)	Subsurface deposit feeder (SSDF)	FM_SSDF
	Surface deposit feeder (SDF)	FM_SDF
	Filter feeder (FF)	FM_FF
	Grazer (G)	FM_G
	Scavenger (S)	FM_S
	Predator (P)	FM_P
Maximum size (MS)	Very small (<1 cm)	MS_<1
	Small (1 to 2 cm)	MS_1-2
	Medium (2 to 5 cm)	MS_2-5
	Large (5 to 10 cm)	MS_5-10
	Very large (>10 cm)	MS_>10
Life span (LS)	Very short (<1 year)	LS_<1
	Short (1 to 3 years)	LS_1-3
	Medium (3 to 5 years)	LS_3-5
	Long (>5 years)	LS_>5
Living habit (LH)	Sessile (Se)	LH_Se
	Burrower (B)	LH_B
	Crawler (C)	LH_C
	Swimmer (Sw)	LH_Sw
Substrate position (SP)	Endobenthic (En)	SP_En
	Epibenthic (Ep)	SP_Ep
Development mode (DM)	Direct (D)	DM_D
	Indirect—lecitotrophic (L)	DM_L
	Indirect—planktotrophic (P)	DM_P
AMBI group (AMBI)	Sensitive species I	AMBI_I
	Indifferent species II	AMBI_II
	Tolerant species III	AMBI_III
	Second-order opportunistic species IV	AMBI_IV
	First-order opportunistic species IV	AMBI_V

2.3.4 | Statistical analyses

The environmental variations among the different sampling sites were visualized using a principal component analysis (PCA). Due to its strong correlation with temperature, salinity was removed from the analysis. Prior to the PCA analysis, Pearson's correlation was performed on the environmental data to check for the correlation between the environmental variables. NO_2^- and salinity were not considered for the analysis due to their strong correlation with NO_3^- and temperature, respectively.

A beta-regression model was used to examine the amount of variation in live maerl cover explained by the distance from fish farms. Beta-regression is useful because live maerl cover data are continuous and restricted to the unit interval (0, 1) (Cribari-Neto & Zeileis, 2010). The model predictors significance for the beta regression was assessed using a likelihood ratio test (Ferrari & Cribari-Neto, 2004). The proportion data were transformed beforehand according to Equation (1) to avoid issues due to the presence of zeroes and ones (Smithson & Verkuilen, 2006):

$$p^* = \frac{p(n-1) + 0.5}{n} \quad (1)$$

with p the proportion of live maerl and n the total number of observations in the dataset.

A post hoc multiple comparison test (Tukey's honestly significant difference test) was then performed to determine specific differences between distance categories.

Local diversity (i.e., α diversity) indices were calculated on macrofaunal abundance data for each sampling site: taxonomic richness (S), Shannon diversity (N, calculated as the exponential of Shannon entropy H') Inverse Simpson Index ($1/\lambda$) and Pielou's evenness (J') (Jost, 2006). Using biological traits matrix and abundance, several functional diversity indices were calculated: the functional richness (FRic), functional evenness (FEve) and the functional divergence (FDiv) (Villéger et al., 2008). In the multidimensional trait space, FRic corresponds to the volume occupied by the community; high value indicates a major space occupied by the community, and thus a high functional diversity; FEve measures the regularity of species abundances within the volume, accounting for both the evenness of abundance distribution among species and for the regularity of the functional distances among species; and FDiv represents the changes in the proportion of total abundance that is supported by species with the most extreme functional traits (Villéger et al., 2008). For each index, the mean diversity values (mean \pm standard error; SE) were calculated for the five groups of distance from fish farms: ≤ 100 m ($n = 4$), 101–200 m ($n = 7$), 201–400 m ($n = 11$), 401–1,000 m ($n = 8$) and $>1,000$ m ($n = 11$). Generalized linear models (GLM) and ANOVA analyses were used with a gamma error distribution to analyse the effect of distance groups on macrofaunal abundance, and taxonomic and functional diversity indices. When significant, post hoc multiple comparison tests (Tukey post hoc test) were performed to determine differences between distance categories.

Hellinger-transformed data were used in all multivariate analyses. PCAs were used to visualize among-sample variation in macrofauna and functional traits by farm and reference site. Ward's hierarchical clustering was computed with each PCA to illustrate clusters of samples. For each PCA, the sampling sites were displayed according to their distance from the farm, divided in five groups (≤ 100 m [$n = 4$], 101–200 m [$n = 7$], 201–400 m [$n = 11$], 401–1,000 m [$n = 8$] and $>1,000$ m [$n = 11$]). The relative contribution of sampling sites to β -diversity was calculated using the Local Contribution to Beta Diversity (LCBD) (Legendre & De Cáceres, 2013). LCBD scores were calculated for both macrofaunal assemblage and biological trait data. LCBD represents the degree of ecological uniqueness of the sampling sites in terms of taxonomic and traits-based functional composition. Hence, large LCBD values indicate samples with significantly different species and/or biological trait composition (Legendre & de Cáceres, 2013). In order to define main functional groups, the 'species by trait' matrix was ordinated based on Euclidian distances between taxa by the fuzzy correspondence analysis (FCA). Ward's hierarchical cluster analysis was performed—based on the Euclidian distance of the taxon coordinates along the first two FCA axes—to define functional groups of macrobenthos that share similar patterns of trait structure (Dong et al., 2021; Marchini et al., 2008; Paganelli et al., 2012).

All statistical analyses were conducted in R (R Core Team, 2021). Diversity indices and PCA were conducted using the *vegan* package (Oksanen et al., 2022). Beta-regression was performed using the *betareg* package (Cribari-Neto & Zeileis, 2010). LCBD indices were calculated using the *adespatial* package (Dray et al., 2023). Functional analysis was performed using the *FD* package (Laliberté et al., 2014). GLM were performed using the *stats* package (R Core Team, 2021).

3 | RESULTS

3.1 | Environmental characteristics and live maerl cover

Physical and chemical variables and heavy metal concentrations are presented for each sampling site in Tables S2 and S3, respectively. Data from current models revealed different hydrodynamical conditions between sites and farm localities, with average current velocities ranging from 0.16 cm s^{-1} (Farm C, C1_{333m}) to 3.99 cm s^{-1} (Farm A, A2_{516m}) (Figure S4). The PCA generated on environmental variables explains 63.5% of the data variability along the first two axes (axis 1: 45.9%; axis 2: 17.6%) (Figure 2). Axis 1 is positively correlated with nutrients (SiO_4^{4-} , NO_3^- and PO_4^{3-}) and depth but negatively correlated with temperature, distance from farms and live maerl cover. Axis 2 is positively correlated with modelled average current velocity and NH_4^+ and negatively correlated with PO_4^{3-} . Reference sites were described by higher live maerl cover and low concentrations of nutrients. However, the sample R1S6 (Reference 1) presented high PO_4^{3-} and SiO_4^{4-} concentrations (1.37 and $1.80 \mu\text{mol l}^{-1}$, respectively) compared to other sites. The PCA reveals a strong variability in nutrient concentrations between sites, depending on the farm and the distance. Overall, nutrient concentrations measured close to Farm A were higher than other locations, with the highest values recorded within 200 m distance. Farm B showed the highest nutrient concentrations within 100 m distance, although these values were much lower than the concentrations recorded close to Farm A (up to sevenfold lower for NO_3^-). The sites at Farm C presented low concentrations of nutrients compared to other farms—regardless the distance to the farm—with values close to those measured at reference sites.

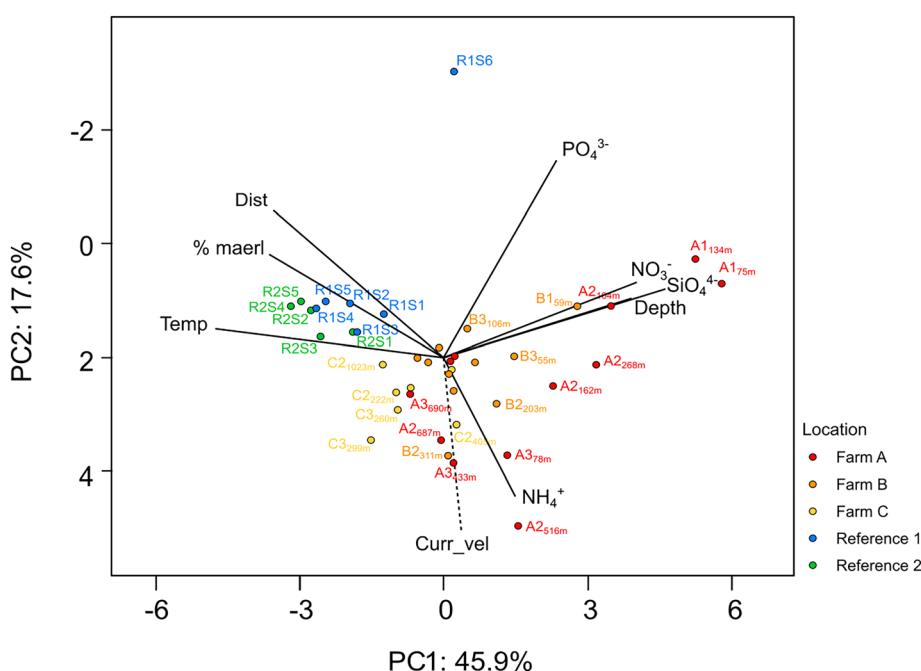


FIGURE 2 Principal component analysis (PCA) of environmental variables (Dist = distance from farms; Temp = temperature; % maerl = live maerl cover). The length of a vector is proportional to the importance of the descriptor to the sites. Each point represents a sampling site at: Farm A (red), Farm B (orange), Farm C (yellow), Reference 1 (blue) and Reference 2 (green). The dotted line vector represents the current velocity obtained from models (Curr_vel). Labels for sites contributing least to variability have been removed from the PCA for clarity.

Figure 3 presents the mean percentage of live maerl (\pm standard error; SE) in the cores, according to the distance from fish farms. Our results evidenced a significant relationship between the proportion of live maerl and the distance from fish farm (β -regression, $p < 0.001$). The lowest live maerl cover was observed next to the cages (≤ 100 m; $1.1 \pm 0.5\%$), while the highest cover was found at sites $>1,000$ m from the farms, reaching $82.9 \pm 6.9\%$ (mean \pm SE). Most of the maerl present around the farms (≤ 100 m) was dead and surrounded by a thick layer of organic sediments (Figure 3).

3.2 | Macrofaunal composition of maerl bed communities

During this survey, a total of 41 macrofaunal samples were collected. In total, 284 macroinvertebrate taxa were identified from sampling sites across the three fish farms and the two reference sites: Farm A (183 taxa; $n = 12$), Farm B (193 taxa; $n = 11$), Farm C (152 taxa; $n = 7$), Reference 1 (151 taxa; $n = 6$) and Reference 2 (103 taxa; $n = 5$), with a total of 17,653 individuals (Table S5). Distance from farms did not significantly affect the abundance of macrofauna (GLM, $p = 0.471$). However, the relative abundance of the four main taxa (Polychaeta, Mollusca, Crustacea and Echinodermata) varied with distance (Figure 4).

For instance, the polychaetes represented 83% of the macrofauna in samples ≤ 100 m from the cages (Mollusca: 8%, Crustacea: 6% and Echinodermata: 2%). The relative abundance of polychaetes then decreased with the distance from the farms, reaching 28% in the reference sites. The relative abundance of the other three taxa increased with distance from cages, up to 25%, 20% and 25% in reference sites for molluscs, crustaceans and echinoderms, respectively.

Table 2 presents mean values (\pm SE) of taxonomic diversity indices for the different categories of distance from fish farms (detailed results for each sampling site are presented in Table S6). Taxonomic richness and Pielou's evenness (J') were not significantly affected by the distance from farms (GLM; $p = 0.940$ and $p = 0.054$, respectively), although a marginal trend is observed for the latter. Conversely, Shannon diversity (N) and inverse Simpson concentration ($1/\lambda$) indices varied significantly with the distance from farms (GLM; $p = 0.027$ and $p = 0.023$, respectively). Both N and $1/\lambda$ exhibited the lowest values at a distance ≤ 100 m (12.4 ± 1.8 and 5.4 ± 1.2 , respectively) and the highest values at 400–1,000 m (24.4 ± 3.0 and 13.0 ± 1.9 , respectively). No significant difference in N and $1/\lambda$ was detected between distance categories using Tukey's post hoc test ($p > 0.05$), although a marginal trend was observed between ≤ 100 m and 400–1,000 m for both indices (Tukey HSD test, $p = 0.06$ and 0.09 for N and $1/\lambda$, respectively).

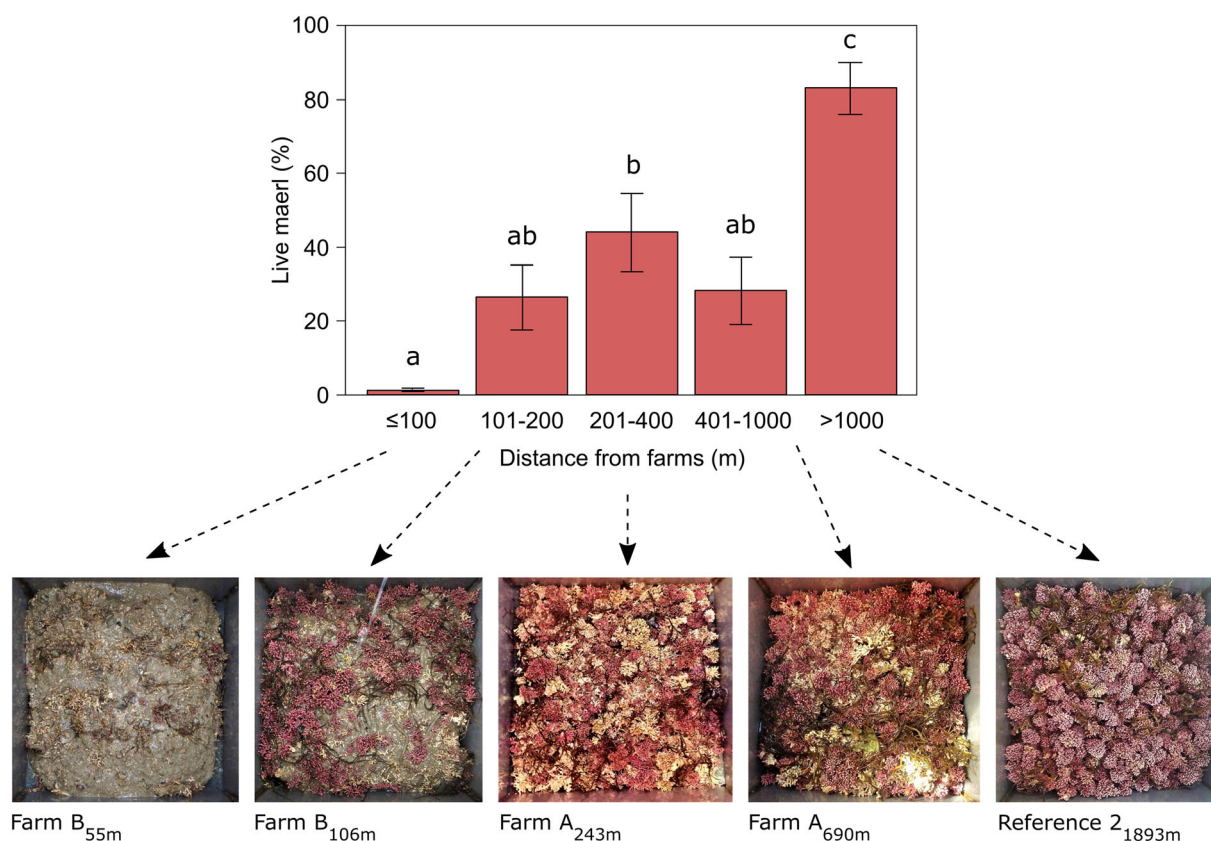


FIGURE 3 Mean percentage (\pm SE) of live maerl measured in each box core sample collected at different distances from salmon cages and at two reference sites ($>1,000$ m from cages). Percentages were obtained through picture analysis (≤ 100 m: $n = 4$; 101–200 m: $n = 7$; 200–400 m: $n = 11$; 401–1,000 m: $n = 8$; $>1,000$ m: $n = 11$). Different letters above bars indicate significant differences between distance categories ($p = 0.05$, Tukey post hoc test).

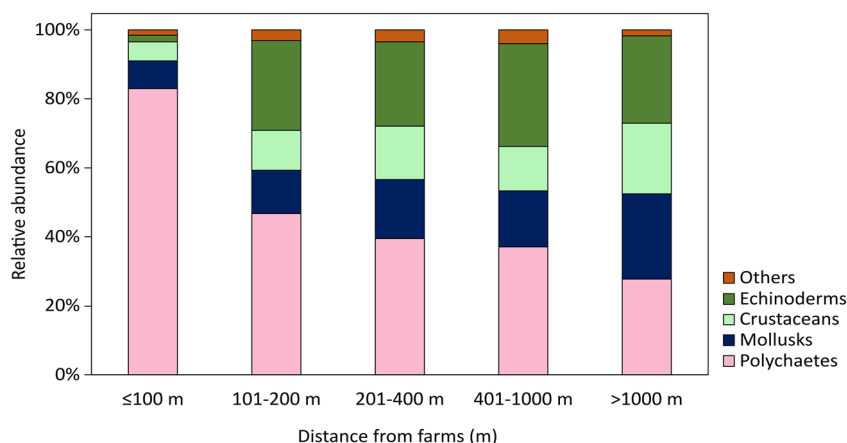


FIGURE 4 Relative abundance of echinoderms, crustaceans, molluscs, polychaetes and other taxa found in 0.1 m² box core samples collected at different distances from salmon cages and at two reference sites (>1,000 m from cages). (≤100 m: $n = 4$; 101–200 m: $n = 7$; 200–400 m: $n = 11$; 401–1,000 m: $n = 8$; >1,000 m: $n = 11$).

TABLE 2 Mean values (\pm SE) of taxonomic diversity indices calculated for the different categories of distance from fish farms.

Distance from farms (m)	n	Taxonomic richness (S)	Shannon Diversity (N)	Inverse Simpson Concentration ($1/\lambda$)	Pielou's evenness (J')
≤100	4	53.5 (\pm 6.1)	12.4 (\pm 1.8)	5.4 (\pm 1.2)	0.43 (\pm 0.02)
101–200	7	55.9 (\pm 6.6)	22.7 (\pm 3.8)	12.3 (\pm 2.3)	0.50 (\pm 0.05)
201–400	11	59.2 (\pm 3.8)	23.2 (\pm 2.5)	12.8 (\pm 1.8)	0.52 (\pm 0.01)
401–1,000	8	57.2 (\pm 6.5)	24.4 (\pm 3.0)	13.0 (\pm 1.9)	0.54 (\pm 0.01)
>1,000	11	58.2 (\pm 5.1)	20.0 (\pm 1.8)	10.2 (\pm 1.2)	0.50 (\pm 0.01)

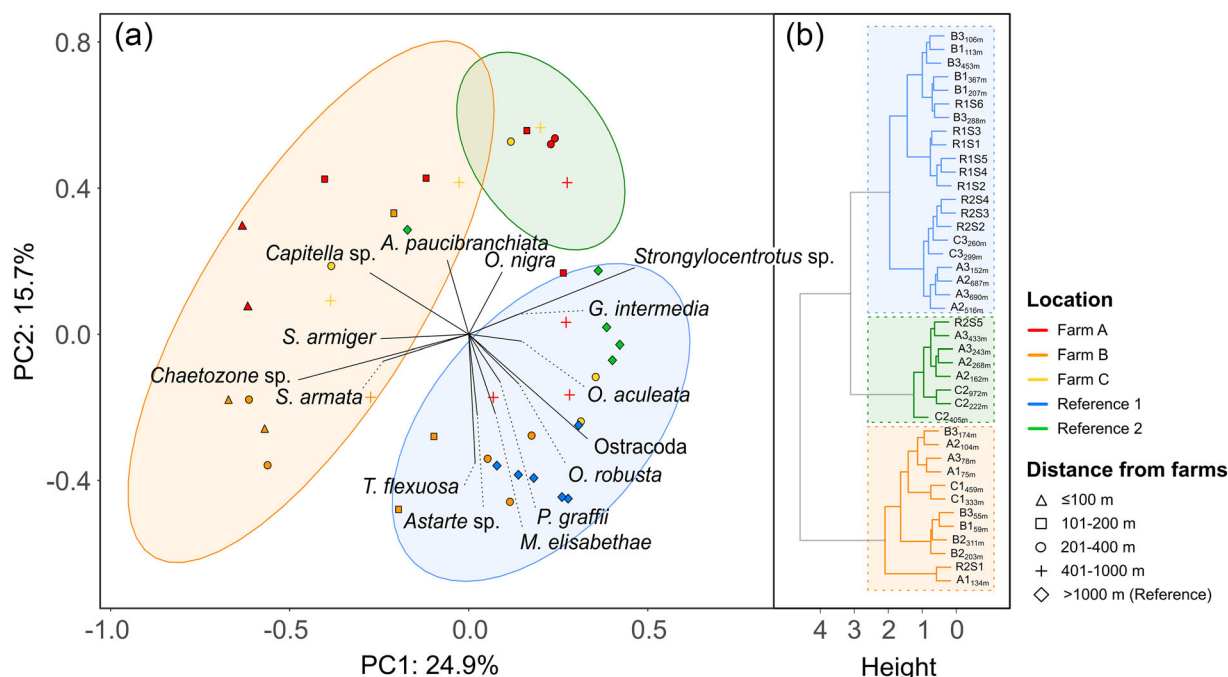


FIGURE 5 (a) Principal component analysis (PCA) of macrofaunal assemblages from the three farms (red: Farm A; orange: Farm B; yellow: Farm C) and two reference sites (blue: Reference 1; green: Reference 2). Only 5% of species contributing the most to variability are represented. The shape of each point shows the distance between the sampling site and fish farms: ≤100 m (triangles), 101–200 m (squares), 201–400 m (circles), 401–1,000 m (crosses) and >1,000 m (diamonds). Ninety-five per cent confidence ellipses represent the different groups obtained from Ward's hierarchical clustering. (b) Ward's hierarchical clustering performed with Hellinger-transformed data.

The PCA of the Hellinger-transformed abundances for the macrofauna explains 40.6% of the data variability along the first two axes (axis 1: 24.9%; axis 2: 15.7%) (Figure 5). Three main groups could

be differentiated using Ward's hierarchical clustering. The first group was composed of 12 samples, including all samples ≤100 m from the farms. This group had an average distance from the cages of 298 m.

Only two samples >400 m were part of this group: C1_{459m} and R2S1. This group was dominated by high abundances of the Polychaeta *Chaetozone* sp. (Malmgren, 1867), *Capitella* sp. (Blainville, 1828), *Scoloplos armiger* (Müller, 1776) and *Spio armata* (Thulin, 1957). The second group contained 21 samples and had an average distance from the farms of 964 m. Only three samples taken within 200 m were part of this group: A3_{152m}, B1_{113m} and B3_{106m}. This group was described

by high abundances of the echinoderms *Strongylocentrotus* sp. (Brandt, 1835), *Ophiura robusta* (Ayres, 1852) and *Ophiopholis aculeata* (Linnaeus, 1767), the crustaceans Ostracoda and *Galathea intermedia* (Lilljeborg, 1851), the bivalves *Thyasira flexuosa* (Montagu, 1803) and *Astarte* sp. (J. Sowerby, 1816) and the polychaete *Proclea graffi* (Langerhans, 1884). The polychaete *Melinna elisabethae* (McIntosh, 1885) presented high abundances at Reference 1 but was

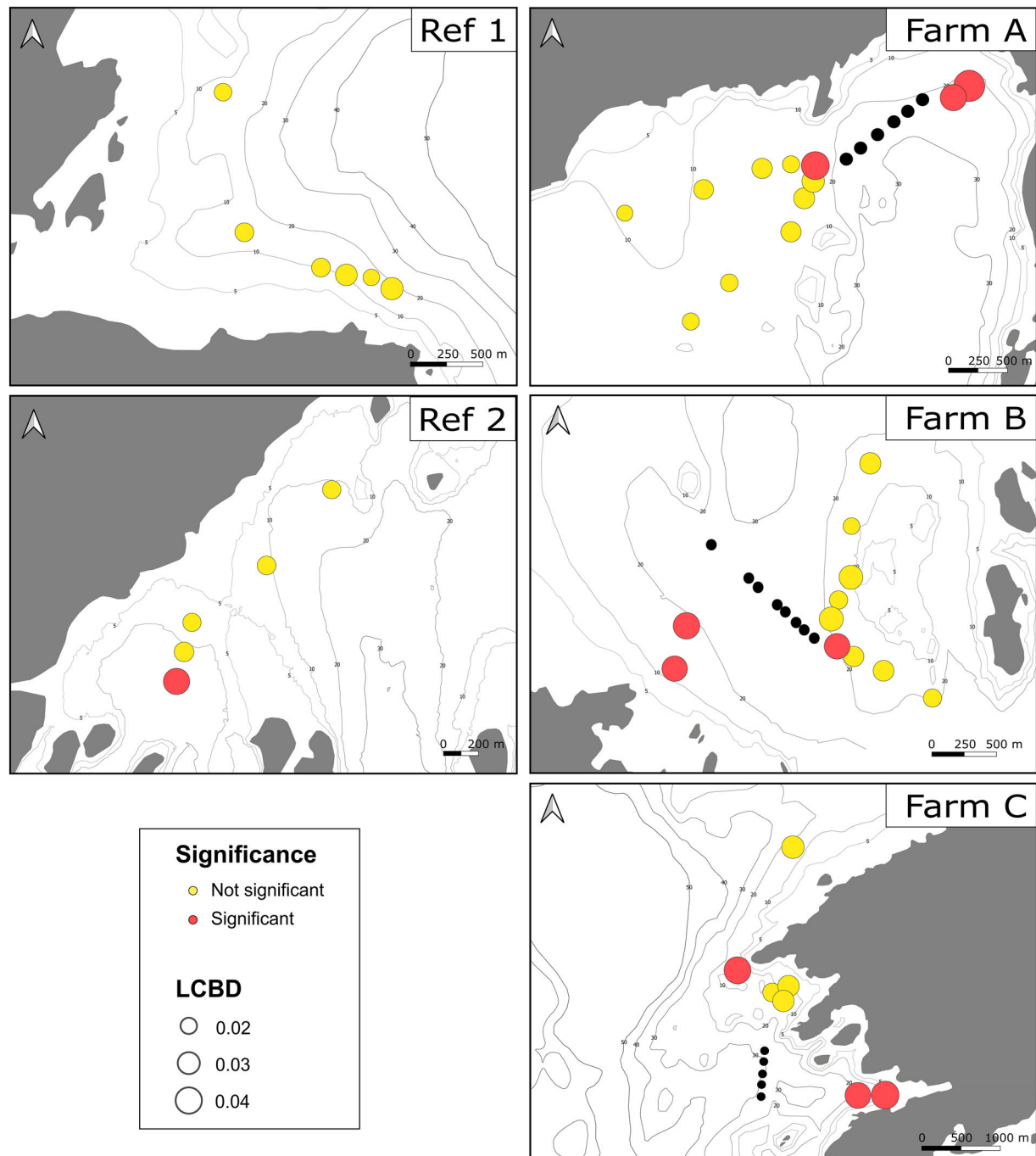


FIGURE 6 Local contribution to beta-diversity (LCBD) of the macrofaunal assemblage data. For each farm, the location of net cages is presented as black circles. The radius of the coloured circles is proportional to the LCBD scores. Red circles indicate significant LCBD ($p < 0.05$) and represent samples that are significantly different in terms of macrofaunal community composition compared to all sampling sites. Yellow circles show non-significant samples. Detailed LCBD scores are given in Table S7.

completely absent from Reference 2. The third group was composed of eight samples, located on average 600 m from the farms and included the site R255. It was described by high abundances of *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789) and comprised species from the second group, such as *Strongylocentrotus* sp. and *G. intermedia*.

The relative contribution of sampling sites to LCBF of the macrofaunal assemblage data ranged from 0.013 to 0.050. In total, 10 sites presented a significant degree of uniqueness in terms of species composition (LCBF; $p < 0.05$) (Figure 6; Table S7): three sites at each fish farm (A–C) and one site at Reference 2. At Farm A, the highest LCBF scores are observed for the sites A1_{75m} (0.036; $p = 0.011$), A1_{134m} (0.050; $p = 0.001$) and A3_{78m} (0.041; $p = 0.002$). The highest LCBF values were obtained at sites B1_{59m} (0.034; $p = 0.018$), B2_{203m} (0.036; $p = 0.007$) and B2_{311m} (0.034; $p = 0.028$) for Farm B, and C1_{333m} (0.034; $p = 0.028$), C1_{459m} (0.040; $p = 0.003$) and C2_{405m} (0.037; $p = 0.008$) for Farm C. Reference sites presented LCBF scores ranging from 0.014 to 0.026, except for the sample R251 that evidenced a significant value of 0.036, therefore characterized by a high degree of uniqueness.

3.3 | Functional traits analysis

The mean values (\pm SE) of functional diversity indices are presented in Table 3 (detailed results for each sampling site are presented in Table S6). We did not observe significant effects of distance from farms on functional richness (FRic; GLM, $p = 0.377$) and divergence (FDiv; GLM, $p = 0.241$). However, functional evenness (FEve) varied significantly according to distance from cages (GLM, $p = 0.035$), showing the highest value at a distance ≤ 100 m (0.67 ± 0.02) and low and similar values for all other distances. A significant difference was observed between ≤ 100 m and 400–1,000 m (Tukey HSD test, $p = 0.03$), while a marginal trend was detected between ≤ 100 m and 100–200 m (Tukey HSD test, $p = 0.08$) and ≤ 100 m and $> 1,000$ m (Tukey HSD test, $p = 0.06$).

The PCA indicates a clear impact of the farms on functional traits within macrofaunal communities (Figure 7). Based on the PCA and Ward's hierarchical clustering, three distinct groups have been identified. The first group included all samples collected within 100 m from the farms and had an average distance from the cages of 339 m. This group was described by the functional traits: subsurface deposit

feeders (FM_SSDF), endobenthic (SP_En), burrower (LH_B), short life span (LS_1–3), lecithotrophic (DM_L) and opportunistic species (AMBI groups IV and V). The second group was mainly characterized by samples distant from fish farms (849 m on average). This group was dominated by grazers (FM_G), crawlers (LH_C), medium life span (LS_3–5), epibenthic (SP_Ep) and sensitive species (AMBI group I). Four samples from Farm A and one from Farm C, located between 152 and 268 m from the farms, were also part of this second group. The third group was mainly composed of surface deposit feeder (FM_SDF), medium size (MS_2–5) and tolerant species (AMBI group III) and was also described by samples distant from cages (786 m on average).

The relative contribution of sampling sites to LCBF of the biological trait data varied from 0.003 to 0.116. In total, eight sites presented a significant degree of uniqueness in terms of traits-based functional composition (Figure 8; Table S7): three sites at Farm A, four sites at Farm B and one site at Reference 2. The highest LCBF scores were obtained at sites A1_{75m} (0.051; $p = 0.002$), A1_{134m} (0.116; $p = 0.001$) and A3_{78m} (0.060; $p = 0.001$) for Farm A, and B1_{59m} (0.044; $p = 0.009$), B2_{203m} (0.037; $p = 0.023$), B2_{311m} (0.059; $p = 0.001$) and B3_{55m} (0.038; $p = 0.016$) for Farm B. At reference sites, the sample R251 presented a significant degree of uniqueness, with a score of 0.064 ($p < 0.001$).

The FCA calculated on the 'species by trait' matrix shows that the first two axes accounted for 22.7% of the total variability with 13.7% explained by axis 1 and 9.0% by axis 2 (Figure 9). Based on this ordination, three main functional groups were defined. The first group was mainly described by subsurface deposit feeder (FM-SSDF) and opportunistic species (AMBI index IV and V). The second group mainly comprised filter feeder (FM_FF) and sessile species (LH_Se). The third group was mainly characterized by crawlers (LH_C) and epibenthic species (SP_Ep), as well as a greater diversity of feeding modes compared to other groups, including scavengers (FM_S), predators (FM_P) and grazers (FM_G). Group 1 represents 73% of the relative abundance of functional groups close to the cages (25% for Group 3) (Figure 9). The mean relative abundance of functional Group 1 then quickly decreased, reaching about 40% at 300 m from the farms. Conversely, the mean relative abundance of functional Group 3 increased up to 55% at 300 m from the cages. The mean relative abundance of functional Group 2 was lower than the two other groups. A detailed analysis for this group showed the lowest values close to the farms (2%) and the highest values about 400 m distance (5%).

TABLE 3 Mean values (\pm SE) of functional diversity indices calculated for the different categories of distance from fish farms.

Distance from farms (m)	n	Functional richness (FRic)	Functional evenness (FEve)	Functional divergence (FDiv)
≤ 100	4	0.25 (± 0.03)	0.67 (± 0.02) ^a	0.88 (± 0.03)
101–200	7	0.32 (± 0.04)	0.59 (± 0.02) ^{ab}	0.87 (± 0.02)
201–400	11	0.33 (± 0.02)	0.60 (± 0.02) ^{ab}	0.84 (± 0.02)
401–1,000	8	0.31 (± 0.04)	0.59 (± 0.02) ^b	0.85 (± 0.04)
$> 1,000$	11	0.29 (± 0.02)	0.59 (± 0.01) ^{ab}	0.84 (± 0.01)

Note: Different letters indicate significant differences in functional diversity indices between distance categories ($p < 0.05$, Tukey post hoc test).

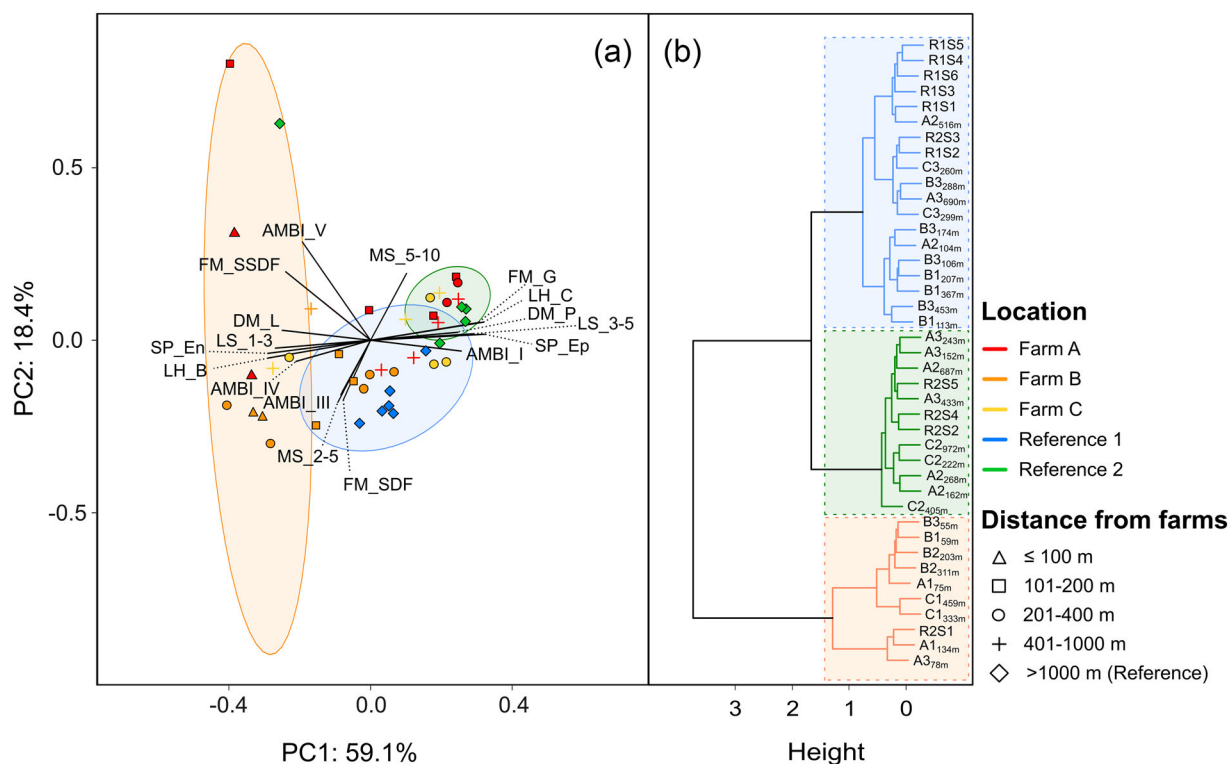


FIGURE 7 (a) Principal component analysis (PCA) of Hellinger-transformed trait-modalities density data of macrofaunal assemblages from the three farms (red: Farm A; orange: Farm B; yellow: Farm C) and two reference sites (blue: Reference 1; green: Reference 2). The shape of each point represents the distance between the sampling site and fish farms: ≤ 100 m (triangles), 101–200 m (squares), 201–400 m (circles), 401–1,000 m (crosses) and $>1,000$ m (diamonds). Ninety-five per cent confidence ellipses represent the different groups obtained from Ward's hierarchical clustering. A full description of functional trait-modalities abbreviations is given in Table 1. (b) Ward's hierarchical clustering performed with Hellinger-transformed trait-modality data.

4 | DISCUSSION

4.1 | Impact of fish farms on environmental characteristics

Sea-cage salmon farming discharges substantial quantities of effluents into the environment, comprising organic waste and inorganic nutrients generated from remains of uneaten food, fish faeces and excretion (Redmond et al., 2010; Taranger et al., 2015; Wang et al., 2012). Notably, Wang et al. (2012) conducted research on Norwegian salmon farms and estimated that 70% of carbon, 62% of nitrogen and 70% of phosphorus from the total feed input were lost into the environment. Overall, the nutrient enhancement has received extensive attention in close proximity to fish farms, with a release pattern closely linked to feed use and production cycle (Davies, 2000; Demirak et al., 2006; Islam, 2005; Mente et al., 2006; Navarro et al., 2008; Sanderson et al., 2008). Here, we demonstrate higher concentrations of dissolved nutrients due to fish farming. The extent of nutrient emission varies among the different farms, possibly in connection with temporal differences in fish production. Farm A, which showed the highest nutrient concentrations, had a fish biomass peak in May 2019 (1,500 t) and still showed a high biomass in July 2019 (1,380 t) when the study was carried out. In

contrast, the lower nutrient enrichment close to Farm B is likely to reflect the onset of the production peak in July 2019 (1,310 t). Overall, the low nutrient concentrations measured at Farm C can be related to the absence of samples within 200 m from the farm due to the absence of maerl beds. Moreover, the fish biomass at Farm C remained at approximately half the levels of Farms A and B during the survey (664 t), with its peak being reached only in November 2019 (1,145 t).

The large amounts of carbon, nitrogen and phosphorus contained in the particulate fraction of waste have the potential to generate anoxic conditions in close proximity to aquaculture facilities, thereby exerting profound impacts on benthic communities (Brooks et al., 2002; Diaz & Rosenberg, 1995; Keeley et al., 2012). Models used to predict the dispersion of organic waste from salmon cages generally predict a gradient of particle sedimentation that decreases with increasing distance from the cages (Carvajalino-Fernández et al., 2020; Pérez et al., 2002). The spatial extent of particle dispersal varies is contingent upon various factors, including current velocities, fish farm production levels and seasonal variations in production (Carvajalino-Fernández et al., 2020). Prior investigations have reported a relatively limited spatial dispersion of organic wastes, with substantial deposition primarily occurring within the initial 100 m from the farm, with a levelling off observed after 200–250 m

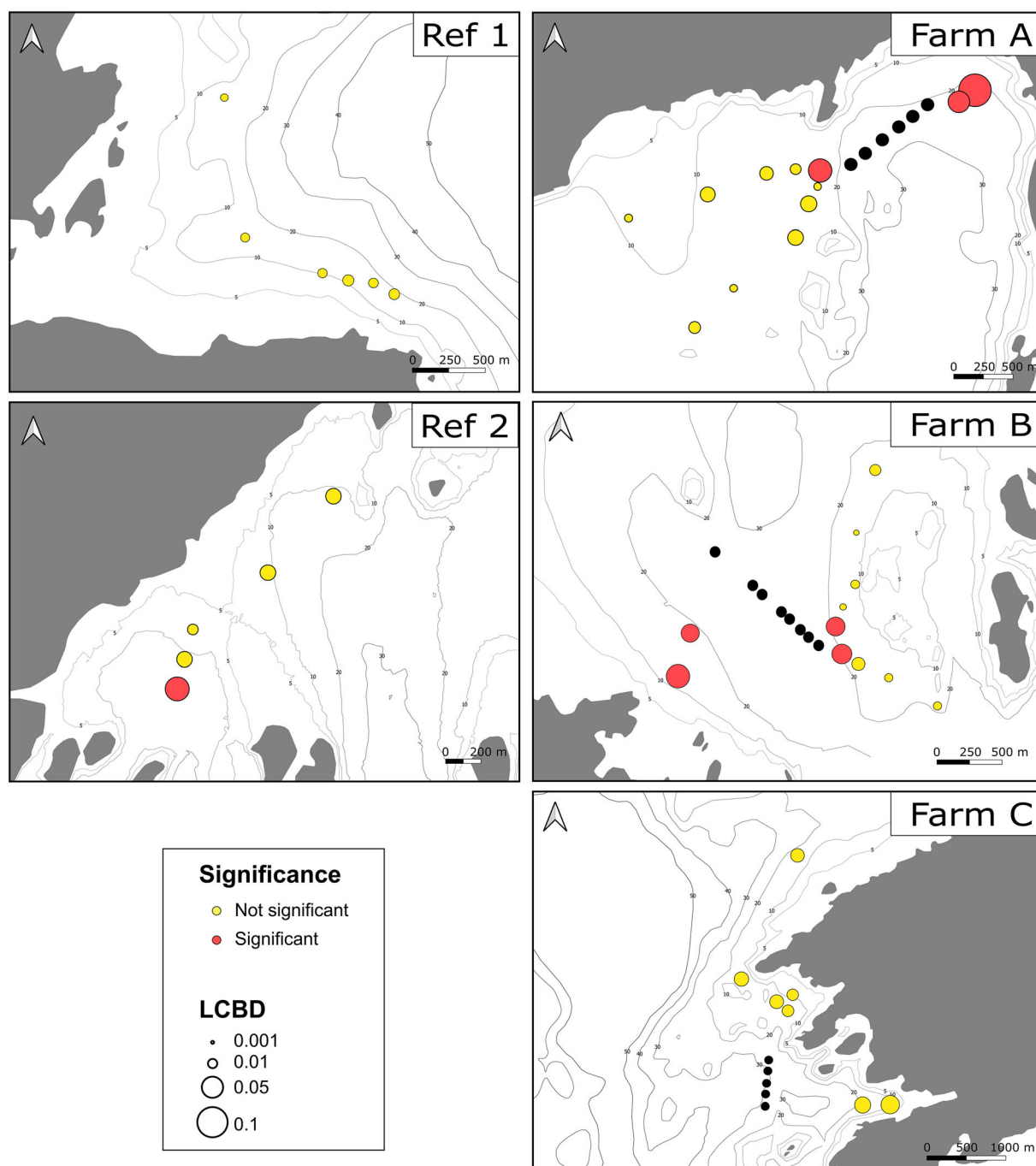


FIGURE 8 Local contribution to beta-diversity (LCBD) of the biological trait data. For each farm, the location of net cages is presented as black circles. The radius of the coloured circles is proportional to the LCBD scores. Red circles indicate significant LCBD ($p < 0.05$) and represent samples that are significantly different in terms of traits-based functional composition compared to all sampling sites. Yellow circles show non-significant samples. Detailed LCBD scores are given in Table S7.

(Carvajalino-Fernández et al., 2020; Johannessen et al., 1994; Kutti et al., 2007). In Gokasho Bay (Japan), Yokoyama et al. (2006) documented the dispersion of organic waste from fish farms producing the yellowtail fish *Seriola quinqueradiata* (Temminck & Schlegel, 1845), extending up to 300 m. The dispersion occurred under conditions characterized by a similar biomass production (1,248 t), current velocities (2.8 to 7.1 cm s^{-1}) and depths (16–19 m)

as those observed in our study. Apart from organic enrichment, fish farms can potentially release toxic contaminants, including sea lice therapeutants and heavy metals, which may exert deleterious effects on species both in the water column and in the sediments beneath the cages (Brooks & Mahnken, 2003; Burrige et al., 2010; Dean et al., 2007). In accordance with the quality guideline for heavy metals in marine sediment outlined by Pazi (2011), our findings suggest that

Hall-Spencer, 1998; Sciberras et al., 2009). Our findings suggest that the total abundance and taxonomic richness were not significantly affected by the distance from the farms. Due to sampling constraints, such as the presence of mooring lines, the samples were collected at a minimum distance of 59 m from the fish farms. This implies that any substantial changes in abundance and taxonomic richness, if they exist, are likely to occur directly beneath the fish farms and in their immediate vicinity (within 50 m) but could not be described in this study. Nevertheless, variations in several taxonomic diversity indices were observed. Notably, a marginal trend was observed for N and $1/\lambda$, which tend to be lower within 100 m from the cages. The N and $1/\lambda$ indices consider not only species richness but also species evenness, therefore suggesting higher dominance of one or a few species near to the cages. This is consistent with the results of Hall-Spencer et al. (2006), who documented a similar pattern in mael beds situated near salmon farms in Scotland, where N values ranged from 10.1 to 47.9 within 0 to 100 m from the cages. In the Western Mediterranean, a reduction in diversity was observed within 200 m from gilthead sea bream (*Sparus aurata*) and European sea bass (*Dicentrarchus labrax* [Linnaeus, 1758]) farms, with N values varying from 17.1 (at 0 m from cages) to 71.6 (at 200 m from cages) (Sanz-Lázaro et al., 2011).

Interestingly, our findings indicate a lack of correlation between taxonomic and functional diversity patterns. This contrasts with the general theory that greater taxonomic diversity results in increased functional diversity, due to the presence of greater number of biological traits within a community (Tilman et al., 2014). The spatial patterns in functional traits indices (FRic, FEve and FDiv) have been explored in several studies conducted along gradients of anthropogenic stressors (D'Alessandro et al., 2020; Dong et al., 2021). These investigations generally indicate a decrease in functional diversity at high levels of disturbance, leading to lower FRic, FEve and FDiv values (D'Alessandro et al., 2020). Here, the FRic and FDiv indices did not exhibit significant changes in relation to the distance from the fish farms, and only FEve increased in close proximity to the cages. Low FEve values are commonly associated with highly disturbed community and a heterogeneously occupied functional space (D'Alessandro et al., 2020; Mason et al., 2005; Villéger et al., 2008). Surprisingly, our results do not support this statement, as they indicate higher FEve values near the farms. FEve is a heterogeneous index of functional evenness, combining two different components into a single value: the evenness of abundance distribution among species and the regularity of the functional distances among species (Villéger et al., 2008). Therefore, FEve may not consistently represent a reliable indicator of functional evenness, as its value can increase when the evenness of abundance distribution decreases, even though the regularity of functional distances among species remains unchanged (Legras and Gaertner, 2018). Such an increase in FEve may hide the impact of disturbance on communities due to the proliferation of one or a few dominant species within the community, potentially leading to inaccurate view of the functional evenness (Legras and Gaertner, 2018).

4.2.2 | Beta diversity

Our study indicates that most of the sampling sites exhibiting a high degree of ecological uniqueness were located near the farms, highlighting significant changes in both the taxonomic and functional composition of macrofaunal communities, associated with the activity of fish farms. Polychaetes represent the dominant taxonomic group in close proximity to the cages (83% of macrofauna within 100 m). Notably, impacted sites are characterized by high abundances of the polychaetes *Chaetozone* sp., *S. armiger*, *Capitella* sp. and *S. armata*, which are widely recognized as indicator species of polluted environments (Henriksson, 1969; Keeley et al., 2020; Kutti et al., 2008; Macleod et al., 2008; Pearson & Rosenberg, 1978; Rygg, 1985; Wada et al., 2008) and are rare at Reference Sites 1 and 2. From a functional perspective, impacted sites exhibit increased abundances of endobenthic burrowers, deposit feeders, opportunistic and short-lived (lifespan 1 to 3 years) species. This observation is consistent with the findings of previous studies, which also reported a selection of short-lived opportunistic species near fish farms, capable of surface deposit feeding behavior (Keeley et al., 2020; Macleod et al., 2008; Papageorgiou et al., 2009; Sanz-Lázaro et al., 2011; Sanz-Lázaro & Marin, 2006). Overall, we observed an impact of fish farms on the functional structure of communities up to a distance of 300 m, with assemblages being significantly dominated by opportunistic subsurface deposit feeders within 200 m from the farms.

Sites located farther from the cages tend to be characterized by higher abundances of echinoderms, crustaceans and molluscs. The effluents from the farms appear to have deleterious effects on the ophiuroid *O. robusta* and the polychaete *P. graffi*, which are relatively scarce near the cages but become more abundant as distance from the farms increases. Furthermore, the establishment of ostracods in sites further from the farms can be considered as an indicator of more favourable environmental conditions, which is consistent with the results from previous studies that demonstrated a decrease in ostracods in the vicinity of farm cages (Hall-Spencer et al., 2006; Mazzola et al., 1999). Unimpacted sites tend to be dominated by epibenthic crawlers and exhibit higher abundances of grazers, medium-lived species (3 to 5 years) and species that are sensitive to organic enrichment. These findings are consistent with the observations of previous studies, which have also reported higher abundances of grazers (Handley et al., 2020; Sanz-Lázaro et al., 2011), larger-sized (Brooks et al., 2004; Handley et al., 2020) and sensitive species (Brooks et al., 2004; Keeley et al., 2012) at greater distances from fish farms. The sea urchin *Strongylocentrotus* sp. emerges as the main grazer at reference sites and shows marked reductions in populations within 100 m from the cages. Interestingly, *Strongylocentrotus* sp. is also abundant at moderately impacted sites, in combination with high abundances of the brittle star *O. nigra*. This supports the findings of previous studies, suggesting that both species are capable of feeding on organic matter derived from aquaculture when concentrations are low (Graydon et al., 2012; Orr et al., 2014; Woodcock et al., 2018). Regarding *O. nigra*, a threshold was observed at approximately 150 m from the farms, inside of which abundances decrease to near-zero.

4.2.3 | Spatial extent of the impact of salmon farms

Interestingly, the sites C1_{333m} and C1_{459m} exhibit both taxonomic and functional characteristics that suggest a significant impact from the fish farm, despite their intermediate distance from the cages. While distance plays a significant role in explaining macrofaunal community changes, it is important to consider that water depth and hydrodynamic regime are also crucial abiotic factors that must be considered for a more comprehensive understanding of the environmental impacts of fish farming (Dauvin et al., 2020; Frid & Mercer, 1989; Hall-Spencer et al., 2006; Merceron et al., 2002). It is commonly acknowledged that strong currents (exceeding 10 cm s⁻¹) play crucial role in preventing the accumulation of organic waste beneath fish farm, as they promote the dispersion and resuspension of particles (Bannister et al., 2016; Black et al., 1996; Canal-Vergés et al., 2010; Cromey et al., 2002; Keeley, Cromey, et al., 2013). Here, the sampling sites are characterized by generally low current speeds (up to 4 cm s⁻¹), with a minimum of 0.16 cm s⁻¹ on average estimated for the site C1_{333m}. Consequently, sites located in sheltered bays, such as C1_{333m} and C1_{459m}, are particularly at risk due to the reduced current velocities, which hinder the effective dispersion of organic matter and potential contaminants, including heavy metals.

Understanding the spatial extent of fish farm impacts is critical for the implementation of adequate monitoring programmes and conservation strategies, aimed at mitigating interference with sensitive ecosystems such as maerl beds (Keeley et al., 2019). In our study, we have demonstrated a main impact of salmon farms on maerl bed communities within 100 m from the cages, with changes in the structure and functioning of assemblages extending up to 300 m. For high-production farms (~9,000 t) operating in relatively shallow waters (depths of 30–50 m), Keeley et al. (2019) provided clear evidence of ecological changes in macrofaunal communities extending up to 600 m from a farm. These production levels are approximately six times greater than those of the farms investigated in the present study (~1,500 t), which may account for the differences in ecological footprint observed herein. Indeed, the higher the production of the farm, the greater the amount of effluent released into the surrounding environment, leading to an increased ecological footprint. This highlights the necessity of considering production capacity when locating new fish farms to prevent damage to maerl beds. The impact of fish farms may also vary temporally depending on their production cycle, given that farms typically generate a larger footprint during production peaks (Haugland, 2019; Keeley et al., 2019). Finally, this study was conducted in early summer and did not consider potential seasonal differences in the impact of farms on macrofaunal communities. Further work is therefore needed to better understand the temporal differences in the impact of fish farms on maerl beds, considering both the production cycle and the seasonal variations in environmental conditions.

4.3 | Implications for conservation

In Norway, salmon are usually farmed on a 2-year cycle, followed by a fallowing period usually of 6 to 8 weeks (Black et al., 2008). After the

cessation of fish farm activities, some benthic communities may recover rapidly within a few months (Lu & Wu, 1998; Ritz et al., 1989; Zhulay et al., 2015). However, most are likely to require years for a full recovery (Karakassis et al., 1999; Kraufvelin et al., 2001; Macleod et al., 2004; Pereira et al., 2004; Sanz-Lázaro & Marin, 2006). Regarding maerl beds, the recovery of macrofaunal communities is expected to be extremely slow, especially due to the slow growth of the coralline algae (ca. 1 mm year⁻¹) that form this unique habitat (Hall-Spencer et al., 2006). Consequently, the cumulative impacts of multiple production cycles are likely to lead to irreversible damage to coralline algae and the associated communities, ultimately resulting in a complete loss of the structure and function of this habitat in the vicinity of fish farms.

Measures that address key pressures from human activities or conserve maerl beds have been recommended by OSPAR, and conservation actions have been implemented in several countries in Europe (OSPAR, 2019). In Norway, the assessment of maerl beds is based on expert judgement and the Norwegian Red List Assessment (Gundersen et al., 2018), which relied on limited data. Although their conservation is suggested in the white paper 'Norway's integrated plan for the conservation of areas of special importance for marine biodiversity' (Norwegian Ministry of Climate and Environment, 2021), maerl beds have not been included in any national plan for coastal protection measures. In the light of our findings, the implementation of conservation strategies is necessary to mitigate the adverse effects of salmon aquaculture on Norwegian maerl beds. Based on the characteristics of the farms investigated in this study (size, production capacity and cycle), it is important to consider a minimum distance of 300 m from any maerl bed when selecting new fish farm locations. However, it is essential to acknowledge that the production capacity of the studied farms (1,560 t of salmon) is relatively low compared to the average Norwegian salmon farms (3,120–4,800 t of fish). As a precautionary measure, we recommend increasing the distance to 500 m in case of maximum total biomass capacities exceeding 3,000 t, pending more detailed investigations. Moreover, it is critical to consider the direction and intensity of currents to maximize the dispersion of organic particles and maintain the ecological integrity of maerl bed communities. Currently, the significant knowledge gap regarding the distribution of maerl beds in Norway complicates the accurate prediction of potential overlaps between aquaculture localities and this biogenic habitat. Hence, coastal monitoring initiatives are necessary to ensure that the environmental impacts of fish farming, along with other anthropogenic activities, on this biogenic habitat are maintained at an acceptable level.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information of this article.

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