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Detecting sediment recovery below an offshore longline mussel farm: A macrobenthic Biological Trait Analysis (BTA)

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ABSTRACT

Expansion of bivalve aquaculture offshore reports lower environmental impacts compared to inshore farms. Taking a Before-After Control-Impact approach, this study presents the first functional diversity analysis and long-term Biological Trait Analysis (BTA) of infauna functional traits following the development of the United Kingdom's first large-scale, offshore longline mussel farm. Located in an area historically impacted by mobile fishing gear, farm sites had the greatest number of taxa and abundance compared to control sites. Functional diversity varied significantly across treatments (farm, near control, far control); while Functional Diversity, Richness, Divergence and Dispersion increased over time within the farm, Functional Evenness and Redundancy decreased. Bioturbation, body size, diet, feeding mode, life span, motility, sediment position, sensitivity and substrate type were chosen for Community-level Weighted Mean analysis, depicting the most frequently affected biological traits by shellfish farming. Farm sites developed a wider range of traits enhancing ecosystem function and habitat recovery after years of seabed damage. Outcomes support the use of functional diversity and BTA analysis to perform ecosystem assessment, supporting decision-makers implement policy and management.

1. Introduction

Offshore bivalve production has the potential to be a largescale, sustainable source of protein, that could play a major role in providing global food security with minimal environmental impact (FAO, 2016; Hilborn et al., 2018; Matarazzo Suplicy, 2018). Non-fed aquaculture such as bivalve farming can provide and/or, enhance a wide range of ecosystem services (ES) such as nutrient removal and nutrient cycling, reduce water turbidity and eutrophication, benthic sediment stabilisation and shoreline erosion protection, habitat provision and fish nursery, biodiversity increase and food source (Barrett et al., 2022; Benjamin et al., 2022) as well as acting as sustainable sea-bed and water quality mitigation measures (Nielsen et al., 2016; Ritzenhofen et al., 2022). The development of inshore mussel farms at large scale has been found to have repercussions on the surrounding environment through the accumulation of biodeposits beneath the farm. These can alter sediment characteristics, shifting benthic communities towards assemblages dominated by opportunistic deposit-feeders (Wilding and Nickell, 2013). These effects not only change the local biodiversity but also the ecosystem services that we are so dependent on (Alleway et al., 2019).

As with all human activities, aquaculture has the potential to impact

biodiversity, but also cause functional shifts as species with particular traits may be replaced by species with different functional traits (Loreau et al., 2001), leading to overarching ecosystem effects (Matarazzo Suplicy, 2018). But how we assess those depends not only on what we perceive to be a farm's 'positive' or 'negative' influence on the system but also, the level at which we evaluate them (Alleway et al., 2019; Mascorda-Cabre et al., 2021). For instance, some of the most productive ecosystems are characterised by low species diversity (Loreau et al., 2001). For this reason, we must keep in mind that there is a distinction between biodiversity focused areas and areas important for the ecosystem services they provide (Alleway et al., 2019; Rees et al., 2020).

As the industry moves offshore to avoid coastal saturation and space usage conflicts, mussel farms developed in high hydrodynamic areas can reduce spatial constraints and, have the potentially to reduce ecological effects while increasing productivity. Through the exclusion of mobile fishing activities from farmed grounds, these farms provide the prospect for benthic habitats to recover from years of mobile fishing, boost ecosystem services and, benefit biodiversity (Alleway et al., 2019; Lacoste et al., 2018; Mascorda-Cabre et al., 2021). Although there is an increasing amount of literature supporting the potential of offshore mussel farming as one of the most sustainable sources of protein, license

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procedures remain long, difficult and often, unfeasible. This is partly due to lack of clear policy and management, mainly governed by a need to minimise environmental and stakeholder impacts. Hence, the need for clearer impact assessments and guidance on what needs to be monitored to evaluate those (European Commission, 2019; Galparsoro et al., 2020; Mascorda-Cabre et al., 2021; Matarazzo Suplicy, 2018).

As part of the Blue Economy, aquaculture has a great role to play for its contribution to sustainable development (Sustainable Development Goals 2 and 14). If effectively managed, shellfish offshore aquaculture may have the ability to become part of a wider aquaculture conservation strategy as a nature-based solution, delivering socio-economic as well as ecological benefits in line with Other Effective Conservation Measures (OECMs) outcomes (Le Gouvello et al., 2022, 2017; Mascorda-Cabre et al., 2021). With the potential to support marine conservation targets (Aichi Target 11 and 6), an ecosystem approach to aquaculture (EAA) is paramount (Galparsoro et al., 2020; Le Gouvello et al., 2017; Matarazzo Suplicy, 2018; United Nations, 2015). However, our understanding of offshore aquaculture-environment interactions is limited, especially the long-term effects to ecosystems and the services they provide (Alleway et al., 2019; Mascorda-Cabre et al., 2021). Consequently, it is difficult for policy makers to support the expansion of this industry as part of a wider ecosystem approach to marine management (Galparsoro et al., 2020; Le Gouvello et al., 2017; Weitzman, 2019).

Benthic invertebrates are used as bio-indicators of anthropogenic stress for their ability to respond to organic enrichment (Borja et al., 2000; Fabi et al., 2009). Following Pearson and Rosenberg's (1978) paradigm, an improvement (or deterioration) in habitat quality is shown by a three-step progression: abundance increases; species diversity increases; and dominant species change from pollution-tolerant to pollution-sensitive species. There are various established ways to assess environmental impacts by aquaculture following the above however, these are all based on taxa abundances, richness, diversity and, certain degree of species characteristics. For instance, the Infauna Trophic Index (ITI) is based on organisms' feeding strategy but not all include their response to organic matter (OM) loading (Smith et al., 2001). AZTI's Marine Biotic Index (AMBI) uses taxa abundances, sensitivity or tolerance to a stress gradient, providing a comprehensive (qualitative and quantitative) measurement of impact to soft-bottom macrofauna (Borja et al., 2000) but, it doesn't account for ecosystem functions.

Ecosystem health assessment and the evaluation of anthropogenic impacts are often solely based on species richness and abundances (Cappelatti et al., 2020; Törnroos et al., 2015), combined with indexes such as AMBI which produce high sensitive results (Borja et al., 2000). However, solely based on assessing the ecological status of an area, these alone cannot show the full picture in terms of ecosystem services loss or gain (Cappelatti et al., 2020; Lam-Gordillo et al., 2021; Törnroos et al., 2015). Benthic macrofauna provide essential ecosystem functions to marine habitats in particular, it is the functional traits and characteristics of taxa that maintain 'ecosystem functioning' (Cappelatti et al., 2020; Lam-Gordillo et al., 2021). As certain biological traits are sensitive to habitat disturbances (Kenny et al., 2018), assessing and understanding changes or shifts in infauna traits, in combination with the role that rare or common taxa have, is crucial to understand long-lasting impacts to benthic habitats and the ecosystem services they provide.

Given the need for a robust scientific methodology to assess aquaculture-environment interactions at the ecosystem function level to inform consenting and, efficient marine spatial planning (MSP), 'biological trait analysis' (BTA) could be used to measure and assess aquaculture impacts (Beauchard et al., 2017; Cappelatti et al., 2020; Lam-Gordillo et al., 2021; Törnroos et al., 2015). Greater taxonomic biodiversity alone is not a sign of increased taxonomic traits and higher functional diversity with overall healthier ecosystem functions (Lam-Gordillo et al., 2021) thus, this study focused on BTA functional diversity analysis.

This study performed, for the first time, a functional diversity analysis and the first long-term complete taxa biological trait-based analysis

of infauna changes in response to the operation of an offshore long-line mussel farm. This study used data from a long-term annual monitoring of soft sediment benthic communities. The aims of this field study were (i) to evaluate changes in taxonomic functional traits and functional diversity of benthic communities over time and across a seabed habitat gradient (farm, near controls and far controls) following a BTA approach, (ii) to provide a link between 'ecosystem functioning' and mussel farming-environmental interactions, and (iii) to evaluate the feasibility of using functional diversity or BTA as a metric to assess effects of offshore aquaculture to the environment and ecosystem services it provides offering a novel marine ecological indicator able to be used for rigorous marine management and policy-making.

2. Materials and methods

2.1. Study area

The study was conducted in the largest offshore longline mussel farm in the UK, operated by Offshore Shellfish Ltd., situated in Lyme Bay, the Southwest of England. Lyme Bay is a large, open embayment with a moderate slope from the intertidal zone to up to 50 m depth in the central outer reaches (Fig. 1). The Bay contains a mosaic of substrates including sand, mud, gravel, rock and mixed ground (Rees et al., 2016). The area protects UK Biodiversity Action Plan (BAP) species and habitats important in terms of ecology, conservation and socioeconomics (Sheehan et al., 2016) as they interact to support the delivery of several ecosystem processes (i.e. primary and secondary production) and ecosystem services (i.e. fish for food) (Rees et al., 2016; Sheehan et al., 2016; Singer and Jones, 2018).

Lyme Bay is home to important fishing grounds where different fishing methods are used contributing 12 % of the SW England Gross Value Added (GVA) in 2016. Traditionally, fishermen towing bottom-fishing gear (otter trawls, beam trawls, scallop dredging) avoid the rocky areas and fish on the mixed sediment areas (mud, sands, gravels, cobbles) (Rees et al., 2016; Sheehan et al., 2016; Singer and Jones, 2018). The farm is situated in a soft sediment area and prior to its development, the area was intensively fished using bottom mobile gear such as dredges and trawls (Bridger et al., 2022; Sheehan et al., 2013).

The farm leased 15 km² of seabed from the Crown Estate to deploy suspended longline ropes to cultivate the native blue mussel *Mytilus edulis*. The farm is located between 3 and 10 km from land and, at depths of 20 and 25 m relative to chart datum (Bridger et al., 2022). The farm is located in a highly hydrodynamic area where strong currents, waves and winds occur. Currents are predominantly driven by tides as well as more dynamic wind and density effects. Tidal streams are bidirectional travelling east and westward parallel to the coast in concordance with the main English Channel tidal stream (Cefas, 2015). A previous study found peak tidal current velocities in the vicinity of the mussel farm to be 0.51 ms⁻¹ on a west going tide and 0.36 ms⁻¹ on an east going tide, estimating a tidal excursion of about 7 km and 3.5 km during spring and neap tides respectively. Due to the effects of friction, near bed flows and flows in shallower near shore areas are likely to be slower. Following the main bidirectional pattern, any plumes would travel west parallel to the coast becoming progressively diluted with time and distance.

The farm was designed to withstand such conditions thus, headlines are highly separated from one another, suspended 3 m below the sea surface and placed in the same east-west direction to the flow, minimising the farm's drag. Mussel spat naturally collects on ropes in early spring. After six months, spat is reseeded onto new ropes and spread throughout the farm to grow. Mussels are harvested after 18–24 months. The farm currently produces 2000 t of mussels per year. While the farm is spread across two contiguous sites, this study focused on the most developed farm area (Site 2, Fig. 1).

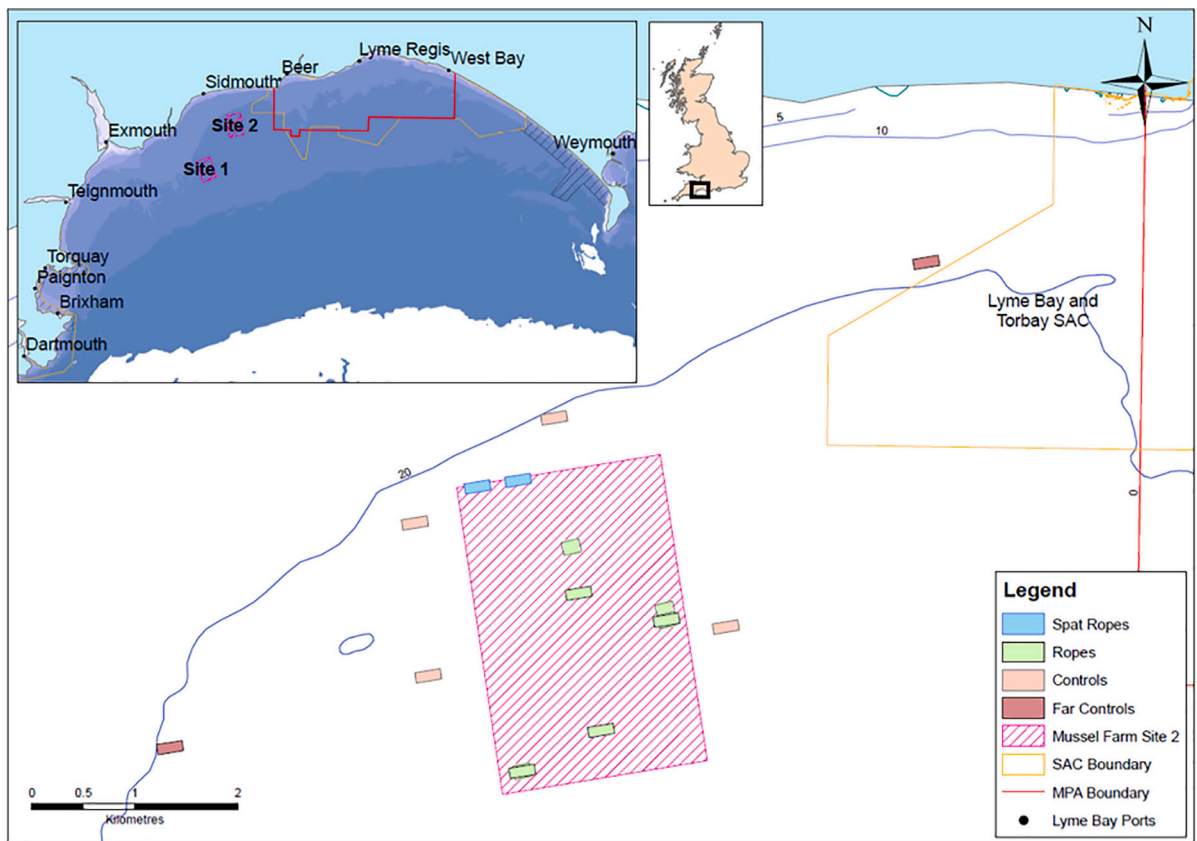


Fig. 1. Map of the study area showing the sites where grab sediment samples were taken throughout the long-term study (2013 to 2020).

2.2. Data collection and laboratory procedures

The mussel farm site was monitored since 2013 (pre-development) following a BACI (Before-After Control-Impact) (Smith, 2002) and BAG (Before-After-Gradient) design (Methratta, 2021). Grab sampling was conducted each year (August) across three treatments: farm (which includes sites with spat headlines (Spat Ropes) and sites with mussel headlines (Ropes), near controls (located 250 m to 500 m from the nearest headline located either side of the farm) and, far controls (located 3 km either side from the farm) (Fig. 1 and S-Table I). Samples collected in 2017 (Time since deployment 4) were omitted from the analysis as the condition of the samples was compromised due to

laboratory equipment malfunction (S-Table I).

A 3-litre capacity Shipek sediment grab (0.04 m²) was used to sample infauna with 4 or 3 grab sample replicates taken per site (4 rep: 2013–2017 & 3 rep: 2018–2020) (S-Table I). From 2018, replication level was reduced from 4 to 3 grabs per site following the introduction of a more robust BAG design with an increase in sample effort by expanding the number of sample sites within the farm and near controls (Fig. 1 and S-Table I). Sediment samples were put into plastic bags and fixed with 10 % borax-buffered formalin to preserve the infauna until processing. Sediment samples were sieved through 2 mm, 1 mm and 0.5 mm Endecott sieves under a fume hood and placed in white trays (Fig. 2). Specimens were then systematically picked, identified under a

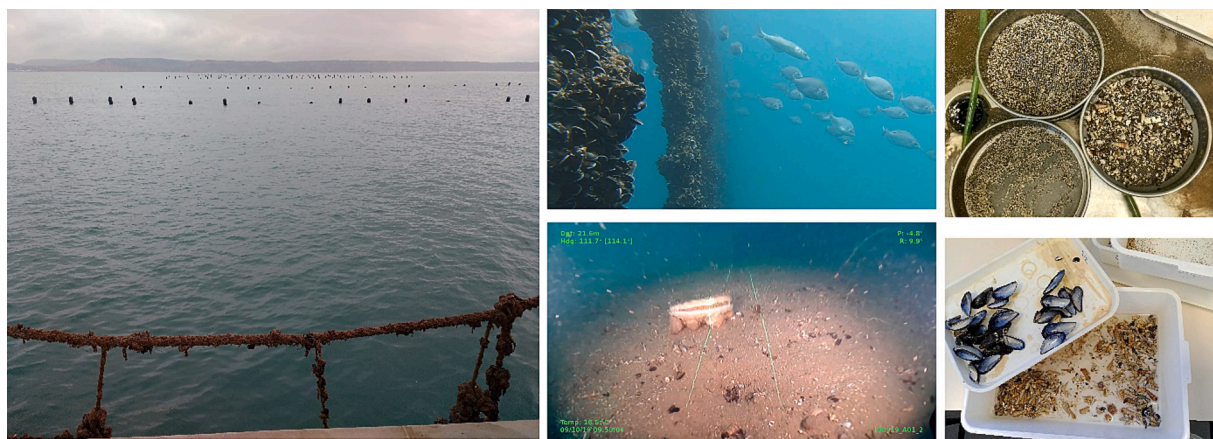


Fig. 2. Images taken of the offshore longline mussel farm (Offshore Shellfish Ltd). View of the farm from a boat (left), still frames taken from video surveys of the ropes (top middle) and seabed (bottom middle) and sediment samples in Endecott sieves (top right) and in trays ready to be picked (bottom right) (Mascorda-Cabre et al., 2021).

Leica EZ4 microscope using taxonomic keys (Hayward and Ryland, 1995) and placed into labelled glass vials filled with 70 % ethanol.

2.3. Taxonomic data

Organisms were identified to family level as this taxonomic resolution has been shown to provide information for assessing ecological impacts, functional trait analysis and community changes (Bolam et al., 2014; Dimitriou et al., 2015, 2012; Lampadariou et al., 2005). In line with NMBAQC's Processing Requirements Protocol for marine invertebrate samples (Worsfold et al., 2010), empty shells, empty worm tubes and cast skins from crustaceans were not counted.

2.4. Functional traits selection

In total, 14 functional traits with a cumulative 65 trait modes were selected (Table 1) as indicators of various aspects of marine function. Functional traits were carefully selected to describe behavioural, morphological and physiological attributes (Bremner et al., 2006) of benthic macrofauna. Traits were chosen as they directly or indirectly relate to: impacts of aquaculture developments; depict sensitivity and recoverability; are representative of several ecosystem functions (including nutrient cycling and sediment transport) and; are effective in assessing disturbance while avoiding redundancy (Board, 2022; Froese and Pauly, 2022; Lam-Gordillo et al., 2020; Shojaei et al., 2021; Tyler-Walters et al., 2022). The specific trait "Sensitivity (AMBI Ecological group)" was included following AMBI index ecological groups (Borja et al., 2000) where taxa were assigned one of the five ecological groups (I–V) following AZTI's most up to date list (AZTI, 2022). Trait information was obtained from multiple different sources: MarLIN BIOTIC, WORMS, SeaLifeBase, the South Australia Macrofaunal Trait (SAMT) database (Alomares and Pauly, 2022; Beauchard et al., 2017; Lam-Gordillo et al., 2020; MarLIN, 2006) and literature searches of peer-reviewed articles. When family trait data was limited or missing, trait data for close taxonomic relatives was used (Genus/Family). Every taxon of the same family was assumed to have the same traits. A fuzzy coding procedure assigning scores from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait, was used to quantify traits where individuals followed multiple modalities of a single trait (Lam-Gordillo et al., 2021). All modes within each individual trait summed to 1 so that a trait with more modalities would not be weighted higher than another (Laliberte and Legendre, 2010). Biological traits analysis (BTA) resulted in three infauna data matrices: (1) "taxa abundances by site" (survey sample data collected); (2) "taxa by traits" (trait information collected); and (3) "traits by site" (combinations of the previous two) (Bremner, 2008; Bremner et al., 2006).

2.5. Statistical analysis

Both Trait x Taxon and Site x Taxon matrices were input into the R packages 'FD' and 'funrar' to calculate multiple different functional diversity (FD) indices using Euclidean distance (Grenié et al., 2020; Laliberté et al., 2014; Laliberte and Legendre, 2010). To compare FD across the treatment gradient and over time, a range of functional metrics were calculated: Functional Diversity (FD) as a measure of how taxa characteristics affect its role within the community (Laliberte and Legendre, 2010; Ricotta et al., 2016); Functional Richness (FRic) as the amount of functional space occupied by a given taxon or trait within a community (Mason et al., 2005); Functional Evenness (FEve) as a measure of how uniform abundance is distributed across the traits (Mason et al., 2005); Functional Divergence (FDiv) as the degree to which FEve maximises trait variation across the community (Mason et al., 2005); Functional Redundancy (FR) as an important property of ecosystem stability, describing the overlap of taxon distribution across traits and how common these are (Mason et al., 2005; Van Der Linden et al., 2012) and; Functional Dispersion (FDis) as the spread of taxa

Table 1

Traits and traits-modes selected in alphabetical order (description of each trait can be found in S-Table II).

Trait	Trait modes	Acronym
Bioturbation	Biodiffusor	B_Diff
	Bioirrigator	B_Irrig
	Surface modifier	B_Surf
Body size	None	B_None
	Small	BS_S
	Medium	BS_M
Diet	Large	BS_L
	Algae	D_Al
	Bacteria	D_Bact
	Detritus	D_Det
	Macrofauna	D_Macro
	Phytoplankton	D_Phyto
	Particulate OM (POM)	D_POM
Feeding mode	Suspended OM (SOP)	D_SOP
	Zooplankton	D_Zoo
	Deposit feeder	Feed_Dep
	Filter/Suspension	Feed_FilSusp
	Grazer/Scraper	Feed_GrazSc
	Omnivore	Feed_Omni
	Predator	Feed_Pred
Larvae	Parasite	Feed_Para
	Scavenger/Opportunist	Feed_ScavOpp
	Sub-Surface deposit feeder	Feed_SSDep
	Benthic	L_Bent
	Brooder direct developer	L_Brood
	None	L_None
	Pelagic Lecihotrophic	L_PelLec
Life span	Pelagic Planktotrophic	L_PelPlan
	Short (< 2 year)	LS_S
	Medium (2–5 years)	LS_M
Mobility	Long (> 5 years)	LS_L
	Mobile	M_Mob
Morphology	Sessile/Attached	M_Sess
	Fragile soft	Morp_Soft
	Hard	Morp_H
	Hard Exoskeleton	Morp_HE
	Hard Shell	Morp_HS
Motility	Fragile intermediate	Morp_Inter
	Burrower	Mot_Burr
	Crawler	Mot_Craw
	None	Mot_None
	Swimmer	Mot_Swim
Reproductive Frequency	Annual	RepFreq_An
	Continuous	RepFreq_Cont
	Seasonal	RepFreq_Sea
Reproductive mode	Asexual	RepMod_Asex
	Sexual Benthic Shed Eggs	RepMod_SBent
	Sexual Direct Development	RepMod_SDD
	Sexual Encapsulation	RepMod_SE
	Sexual Ovigerous Broad Eggs	RepMod_SO
	Sexual Pelagic Shed Eggs	RepMod_SPel
	Attached	Sed_Att
Sediment position	Benthic/Pelagic	Sed_BP
	Deep (> 3 cm)	Sed_Deep
	Surface/Shallow (< 3 cm)	Sed_Shall
	Sensitive	AMBI_I
Sensitivity (AMBI Ecological group)	Indifferent	AMBI_II
	Tolerant	AMBI_III
	Second-order Opportunistic	AMBI_IV
	First-order Opportunistic	AMBI_V
	Substrate type	Bedrock
Gravel		Subs_Gra
Mud		Subs_M
Sand		Subs_S
Sandy mud		Subs_SM

across community traits (Laliberte and Legendre, 2010).

FR can be calculated by using the ratio between FD and H', when the ratio increases, FR decreases and vice versa (Van Der Linden et al., 2012). However, this approach assumes that functional traits may be objectively defined, hence a more coherent approach was used based on

functional (dis)similarities amongst families taking into account abundances (Ricotta et al., 2016). FR was calculated as one minus the mean functional distinctiveness of the community (Davies et al., 2022; Ricotta et al., 2016), thus low functional redundancy (values close to zero) indicate habitats vulnerable to functional loss (Davies et al., 2022; Lam-Gordillo et al., 2021).

Community-level weighted means (CWMs) of trait values represent the relative proportions and functional composition of all traits following the “biomass ratio hypothesis” (Laliberte and Legendre, 2010). Proved to be a fundamental driver of ecosystem process, used to relate traits to environmental pressures, and also referred to as functional identity, CWMs were calculated to compare trait expression across treatments and time where equal weight was given to all traits (Beauchard et al., 2017; Laliberte and Legendre, 2010; Mokany et al., 2008). CWM was calculated from the ‘FD’ package in R (Laliberté et al., 2014). Specific traits, known to be affected by coastal and inshore shellfish farming, were then selected for statistical analysis: bioturbation, diet, feeding mode, life span, motility, sediment position, sensitivity and, substrate type.

To assess the hypothesis that there were changes in functional diversity over time and gradient between the mussel farm sites and control sites, Linear Mixed Models were used (using a Poisson and Gamma distribution as required). Models were fitted using R package ‘lme4’ (Bates et al., 2020). Response metrics were assessed as a function of Time since deployment (continuous: 0–7) and Treatment (categorical: Rope, Near Control and Far Control) with Station (categorical) as a random factor. The interaction term (Time x Treatment) was included in each model. Sample vs fitted residuals, quartile-quartile and autocorrelation of temporally sequential samples were assessed visually, to fit assumptions of the models used. Models were used to test differences in Functional Diversity metrics and CWMs. Data were $\text{Log}_{10}(x + 1)$ transformed to reduce the influence of dominant taxa without losing the abundance effect.

3. Results

3.1. Taxa and functional diversity

A total of 76 different taxa were identified in this study of those, 24 taxa had an abundance of >500 individuals per m^2 (S-Table III). Polychaetes were the dominant class (24 families). Polychaetes (81 % mainly led by Ampharetidae, Magelonidae, Cirratulidae), amphipods (4.2 %), gastropods (2.7 %) and decapods (1.4 %) were the principal groups at both farm and control sites. At 5.6 %, bivalves were exclusively found within the farm with Mytilidae accounting for 70 % of the total bivalve abundance. Turritellidae and Philinidae were 64 % and 31 % of the total gastropod abundance while Paguridae accounted for 49 % of the total decapod abundance. The highest number of taxa identified in a single sediment grab, 26 taxa, was found in the farm in 2020, while the lowest number of taxa, one, was found in a near control in 2014. The overall number of taxa significantly increased over time within the farm ($p < 0.0001$) and near controls while it decreased in the far controls (Fig. 3, S-Fig. IA and S-Table IV). Amongst the highest contributing taxa across sites and sampling periods, the only taxa considered to be opportunistic (belonging to AMBI groups IV or V) were those found in the Cirratulidae (IV) and Capitellidae (V) families. In line with the overall increase in organisms’ abundance across all taxa, Cirratulidae and Capitellidae polychaetes were found at considerably higher abundances within the farm and near controls compared to far controls, especially high during the last sampling year (Year 7).

Functional Diversity had higher values within the farm than in controls, overall showing <50 % levels in the far control. FD significantly increased over time across all treatments ($p < 0.0001$) with the farm displaying the highest level of FD after seven years of farming (Fig. 3B, S-Fig. IB and S-Table IV). Functional Richness increased significantly over time across the farm and near controls ($p < 0.0001$)

while it significantly decreased over time in the far control ($p < 0.0001$) with the farm showing the highest level of FRic after seven years of farming (Fig. 3C, S-Fig. IC and S-Table IV). Functional Evenness significantly decreased over time ($p < 0.0001$) across the near controls, it increased over time in the far control ($p < 0.0001$) while remaining stable within the farm (Fig. 3D, S-Fig. ID and S-Table IV). Functional Divergence significantly increased over time in the farm ($p < 0.0001$), while it remained stable in near controls and significantly decreased in far controls over time ($p < 0.0001$) (Fig. 3E, S-Fig. IE and S-Table IV). Functional Redundancy significantly changed over time ($p < 0.0001$) decreasing across the farm and near controls while remained stable in far controls (Fig. 3F, S-Fig. IF and S-Table IV). Functional Dispersion was higher within the farm compared to the far controls ($p < 0.0001$) where it significantly increased over time ($p < 0.0001$) (Fig. 3G, S-Fig. IG and S-Table IV).

3.2. Community-level weighted means (CWMs) of biological traits

The most expressed functional trait modalities based on community-level weighted mean (CWM) analyses of trait values (weight of >0.55) found before any development of the farm (both within the farm sites and near control sites) were: mobility, reproductive frequency, bioturbation, motility, morphology and diet (Fig. 4A). After one year of development, the most expressed functional traits were: Farm - mobility, reproductive frequency, bioturbation, motility, morphology and body size; Near controls - mobility, AMBI, reproductive frequency, motility, bioturbation, morphology, body size and diet; and Far controls - mobility, reproductive frequency, bioturbation, motility, morphology, body size and larvae (Fig. 4B). Seven years after development, the most expressed functional trait modes in the studied benthic communities were: Farm - mobility, reproductive frequency, bioturbation, motility, life span and larvae; Near controls - mobility, reproductive frequency, AMBI, bioturbation, motility, life span, morphology and body size; and Far controls - mobility, AMBI, reproductive frequency, bioturbation, life span, morphology, motility, diet and body size trait mode (Fig. 4C). Overall, the most commonly expressed traits found in all sites over the period under study were mobility, reproductive frequency, bioturbation and motility. Within the farm and near controls, trait modes were better distributed, especially within the farm where more variation was observed across trait mode weights over time (Fig. 4).

3.2.1. Bioturbation

When looking at the traits chosen for further analysis, bioturbation (Fig. 5A and S-Table V), the bioirrigation capacity of the infaunal community fluctuated over time across all sites ($p < 0.0001$), always remaining around 70 % of the CWM. A closer look into the CWM for this particular trait showed that within the farm sites, bioturbation is dominated by bioirrigation, but surface modification organisms have started to gain more weight while are barely present in the far control sites (Fig. 4).

3.2.2. Body size

The body size of the infaunal community was affected by time ($p < 0.0001$), slightly increasing on the far controls and to lesser extent on the near controls while slightly decreasing within the farm (Fig. 5B and S-Table V). Larger organisms within the farm and near controls increased from about 50 % to 60 % over time while in far controls remained stable at 60 %. Medium and small organisms did not change.

3.2.3. Diet

The type of diet significantly decreased over time and between treatments ($p < 0.0001$) with its overall CWM decreasing within the farm and near controls from 60 % to 40 % weight over the seven year period (Fig. 5C and S-Table V). Detritus was the preferred trait mode across all treatments however, over time, diet had become more varied with macrofauna and phytoplankton acquiring more weight, which is

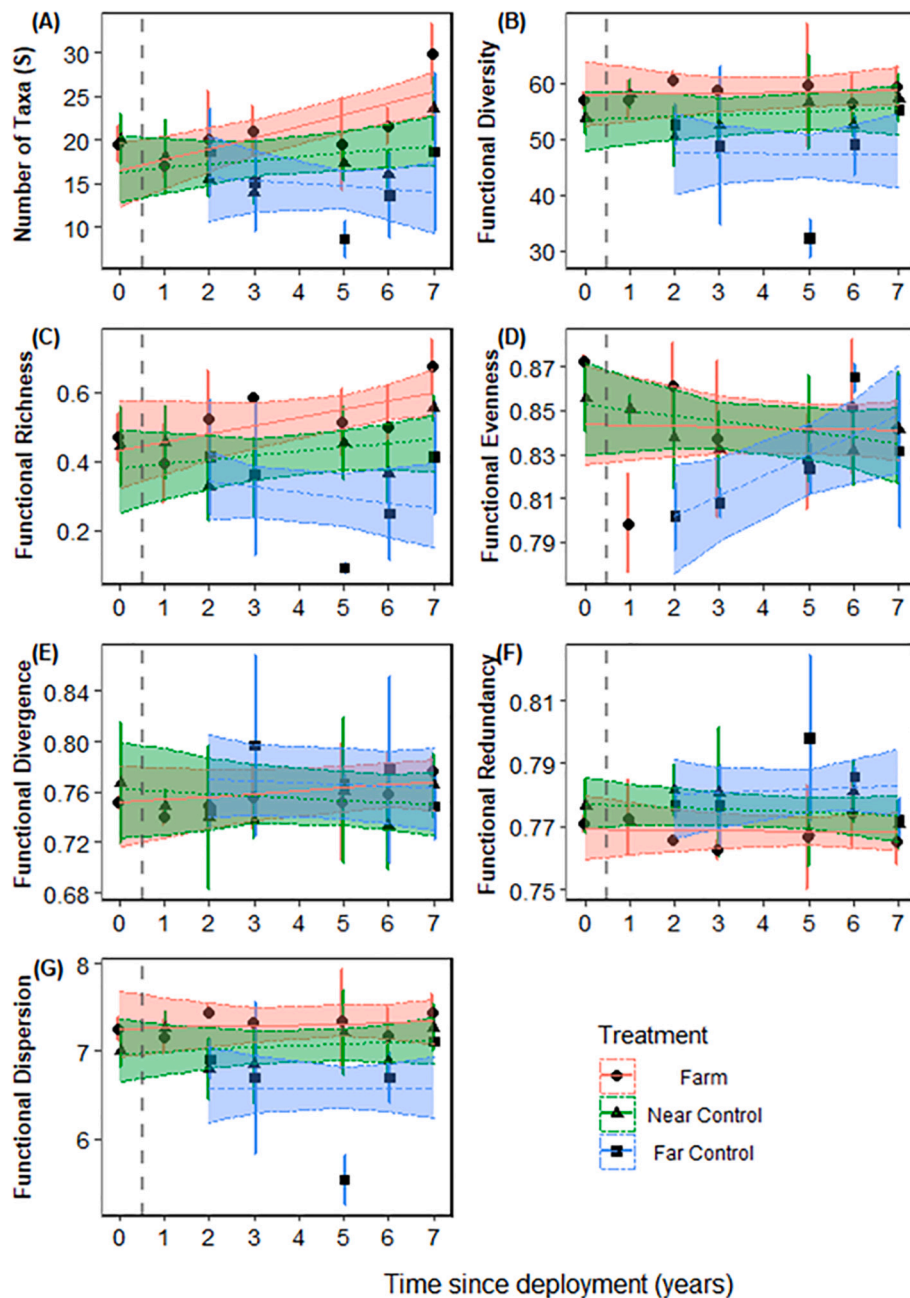


Fig. 3. Linear Mixed model outputs (linear regression) showing temporal changes in (A) Number of taxa and Functional Diversity (FD) Metrics; (B) Functional Richness, (C) Functional Evenness, (D) Functional Divergence, (E) Functional Redundancy and (F) Functional Dispersion. Dash line marks deployment of the first mussel ropes. Note: Far controls were introduced in T2.

especially true within the farm (Fig. 4).

3.2.4. Feeding mode

The CWMs of feeding mode traits gained more weight over time in the far controls (up to 60 %) ($p < 0.0001$) and near controls while remaining stable within the farm (Fig. 5D and S-Table V). Deposit feeder and to lesser extent, predator were the most important trait modes throughout. Over time, the weight of feeding mode within the farm and near control sites had a more distributed weight range amongst the different traits and expanded the variety of trait modes to include filter/suspension feeder organisms, not found in the far controls (Fig. 4).

3.2.5. Life span

During the seven years of monitoring, the CWMs of life span

increased throughout all treatments being statistically significant in the controls ($p < 0.0001$) (Fig. 5E and S-Table V). A life span of 2–5 years (medium) was the dominant trait mode increasing from 50 % to 60 % of the CWMs. Longer living organisms (> 5 years) were also present in all sites with weight fluctuating around 30 % (Fig. 4).

3.2.6. Motility

Over time, the CWMs of the type of motility (movement strategy) used by the infauna community lost weight outside the farm ($p < 0.0001$) while slightly increased its dominance within (Fig. 5F and S-Table V). This was produced by an increase in the weight of burrower organisms within the farm (from 20 % to 30 %). Free surface crawler was the predominant trait mode with a CWM fluctuating between 60 % and 70 %. These two traits were present over time in both farm and

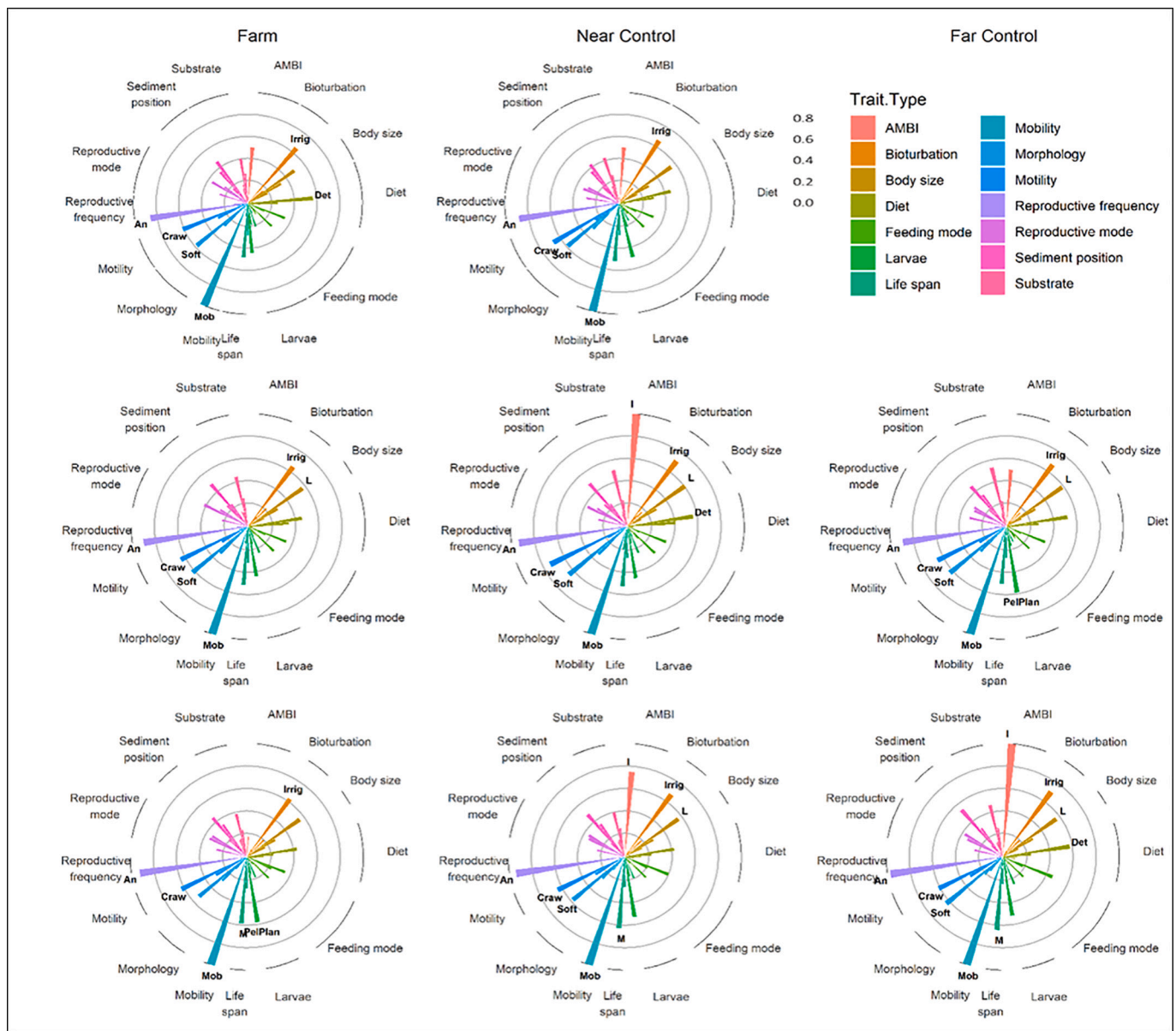


Fig. 4. Community-weighted means (CWM) of trait modalities expressions over time in different treatments. Scales represent the percentage contribution to CWM. Trait modalities labels (acronyms) are defined in Table 1. Each row represents the different times since deployment of the farm: (A) Year 0; (B) Year 2; and (C) Year 7.

control sites (Fig. 4).

3.2.7. Sediment position

CWMs of sediment position traits were affected by time in all treatments ($p < 0.0001$) where CWMs increased in the near controls ($p < 0.0001$) and controls but remained stable within the farm (Fig. 5G and S-Table V). This was driven by an overall increase in the relevance of the dominant trait mode deep (> 3 cm) in the far controls (fluctuating from 40 % up to 70 %) while near controls and specially the farm, showed a uniform distribution between deep and subsurface/shallow (< 3 cm) organisms (around 40 % each) and an increase of benthic/pelagic organisms over the seven-year monitoring period (up to 20 %).

3.2.8. Sensitivity - AMBI

The CWMs dominance of the sensitivity (AMBI Ecological Group) trait remained very stable over time within the farm and near controls while it increased in the far controls ($p < 0.0001$) (Fig. 5H and S-Table V). The main trait mode found is AMBI_I which over time fluctuated from 50 % to up to 100 % in the far and near controls while it

fluctuated between 20 % and 50 % within the farm (Fig. 4).

3.2.9. Substrate type

The CWMs of the substrate type used by the infauna community decreased over time ($p < 0.0001$) showing a difference between the farm and controls ($p < 0.0001$) (Fig. 5I and S-Table V). Sand and sandy mud were the dominant trait modes which over time fluctuated around the 40 % and 20 % weight respectively. Overall, both the farm and controls followed very similar sediment type trends (Fig. 4).

4. Discussion

Poorly sorted muddy sediments such as those predominant in Lyme Bay are known to be highly sensitive to trawling. However, Lyme Bay infauna have been classed to be of low long-term sensitivity to mobile fishing gear, suggesting that the area has a good recovery potential (Bolam et al., 2014). Our results suggest a transformation of within-farm ecosystem functions due to a halt in mobile fishing activities after seven years of mussel aquaculture development in the area. On the contrary,

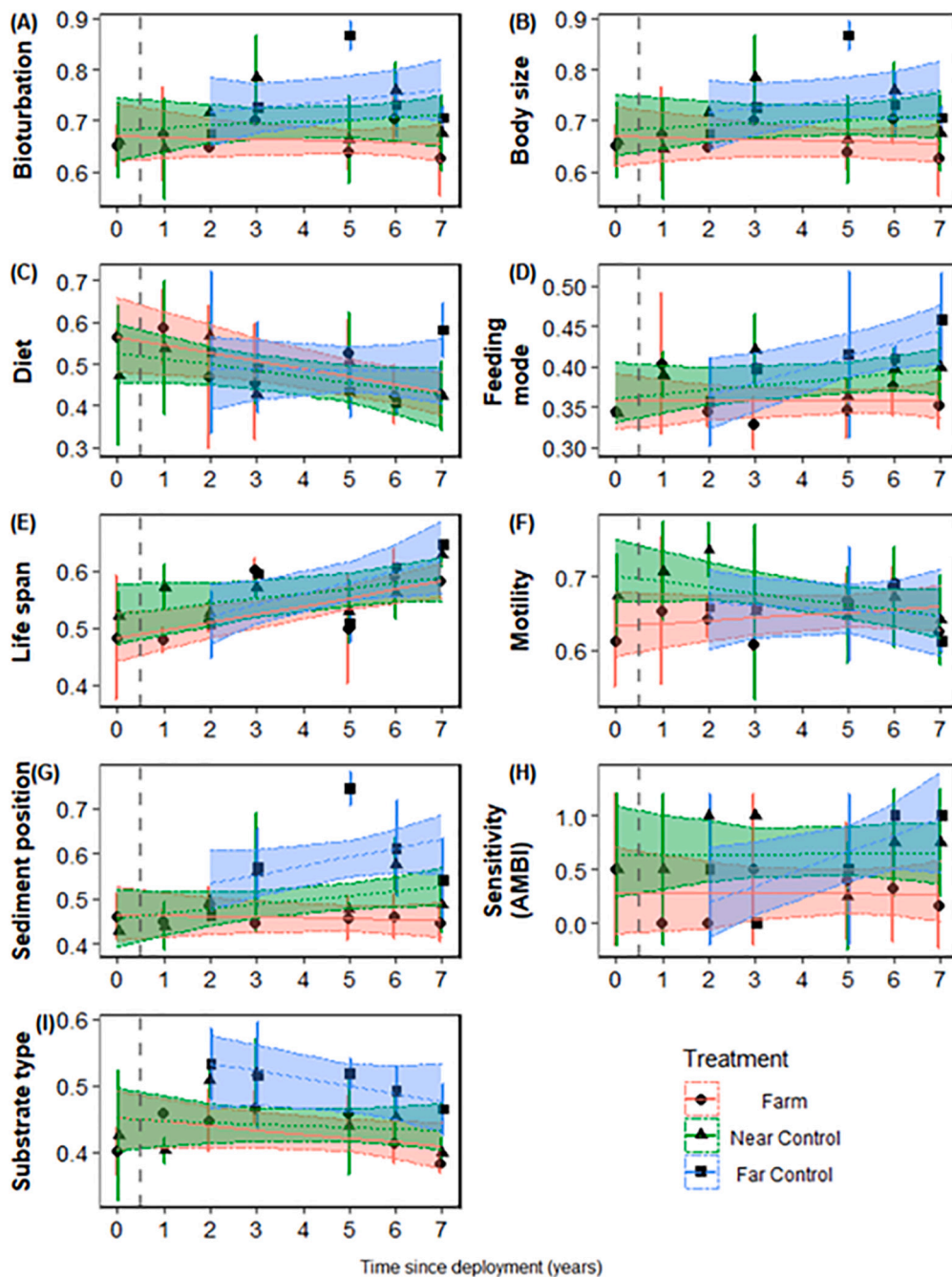


Fig. 5. Linear Mixed model outputs (linear regression) for the cumulative weighted means (CWM) of a priori selected set of trait modalities: (A) Bioturbation, (B) Body size, (C) Diet, (D) Feeding mode, (E) Life span, (F) Motility, (G) Sediment position, (H) Sensitivity (AMBI Group) and (I) Substrate type derived from infauna sediment grabs as functions of Time and Treatment with Site as a random factor. Dash line marks deployment of the first mussel ropes. Note: Far controls were introduced in T2.

ecosystem functions in the far controls remained similar over time, typical of an impacted and/or degraded ecosystem where mobile fishing activities regularly take place. This spatial and temporal analysis revealed patterns and differences in infauna diversity and functional traits across years and habitat gradient. We believe this study has produced a more comprehensive and systematic analysis than prior comparable studies which have either been limited by time of priori selection of functional traits (Kenny et al., 2018; Lacson et al., 2019).

4.1. Detecting aquaculture impact

4.1.1. Effects of the farm on biological traits

Traits such as body size, diet, feeding mode, life span, motility or sediment position are important for vertical trophic transfer and horizontal carbon cycling processes (Bremner, 2008; Törnroos et al., 2015),

for their relevance to the long-term community structure (Lacson et al., 2019; Pearson and Rosenberg, 1978) and to assess sensitivity to human pressures such as trawling (Bolam et al., 2014). Such traits can be shaped by organic matter loading, especially following the development of a farm, by selecting small and short-lived opportunistic organisms that have limited penetration into the sediment and are dominated by surface deposit feeders (Lacson et al., 2019; Ysebaert et al., 2009). While in trawled impacted areas, smaller, faster-growing and short-lived taxa with soft shells replace large, slow-growing (long-lived) fauna with hard shells (Bolam et al., 2014).

As infauna communities are connected to the characteristics of their environment and the degree of disturbance, taxa are expected to shift following a change in human pressure (Beauchard et al., 2017; Bolam et al., 2016; Kenny et al., 2018; Lacson et al., 2019). The offshore farm showed to develop a more complex combination of trait modes not

typical of smothered habitats by organic matter debris (Lacson et al., 2019; Ysebaert et al., 2009) or impacted by mobile fishing gear (Bolam et al., 2014). Farm sites and to a lesser extent, near control sites, showed an overall increase: of burrower organisms and surface crawlers with implications in the way carbon is moved across the system; in body size; greater diet variety; a shift from deposit-feeder dominance towards the inclusion of predators and filter/suspension-feeders; an increasing lifespan and; an increase in bioturbators with sediment transport consequences, facilitating oxygenation and microbial recycling of nutrients, detoxification of pollutants and, organic matter remineralisation (Lam-Gordillo et al., 2021; Törnroos et al., 2015). Overall suggesting within-farm ecosystem changes in nutrient and sediment cycling.

After 4 years of farming an offshore mussel farm in Portugal, Lacson et al. found no changes in biological traits compared to controls with no other impacts. The farm produced twice as many mussels per year (3990 tons) and covered an area double in size (15 km²) under similar hydrodynamic conditions. However, our results showed a shift in the infaunal community and the heterogeneity of the habitat beneath and surrounding the farm, from one impacted by mobile fishing gear, towards a more complex and productive ecosystem (Bridger et al., 2022; Lacson et al., 2019; Mascorda-Cabre et al., 2021).

4.1.2. Effects of the farm on functional diversity

As hypothesised, number of taxa, abundance, and functional diversity increased over time within the farm boundaries and the near controls showing a spillover effect. An increasing FRich and FDis within the farm further supports a shift in ecosystem stability, resilience and resistance of the habitat to impacts and invasions while boosting the system's productivity (Laliberte and Legendre, 2010; Mason et al., 2005; Ricotta et al., 2016; Törnroos et al., 2015). This is further supported by within-farm decreasing levels of FEve and increasing FR, illustrating that the farm has more predominant traits than far controls (less uniform across traits), showing better productivity and resilience to functional loss or the introduction of opportunistic organisms, enhancing temporal stability (Lam-Gordillo et al., 2021; Ricotta et al., 2016; Törnroos et al., 2015; Van Der Linden et al., 2012).

The combination results of these the functional diversity analysis (Villéger et al., 2008) shows that although the farm has increased the taxonomic richness of the area, there has been no significant detrimental impact on the overall functional trait capacity of the community. Instead, the development of the farm in an area of damaged seabed has increased the functional diversity of the area. This is especially crucial when assessing benthic infauna changes after a halt on trawling historically heavily damaged soft-sediment habitats where large community changes and trends might take years to appear (Szostek et al., 2015; Wan Hussin et al., 2012).

4.2. Management implications

Results from this study reiterate the importance of not only using alpha diversity indices to assess ecological changes and impacts but the value of performing BTA analysis using ecological traits and functions to measure and evaluate anthropogenic activities (Bremner, 2008; Lacson et al., 2019; Törnroos et al., 2015). Taxa may change from one ecosystem to another hence assessing changes over large-scale environmental gradients might infer anthropogenic impacts where there's natural or environmental variation. Instead, assessing ecological traits and functional diversity provides an insight into changes to ecosystem services as traits are enduring characteristics of ecological communities (Costello et al., 2015; Lacson et al., 2019) supporting the ecosystem approach (Bolam et al., 2014). This is especially true for complex offshore ecosystems with highly variable hydrodynamic conditions which can induce patchiness, crucial when assessing large-scale aquaculture developments.

There are no 'magic' indicator traits to irrefutably assess environmental impacts as decision-making tools (Beauchard et al., 2017; Bolam

et al., 2014). This study has carefully chosen a set of meaningful traits representative of sensitivity and recoverability. These have been tailored to the specific given pressures and environmental conditions (high hydrodynamic regime) and can be reproduced to assess potential changes and impacts following the development of an offshore shellfish aquaculture. It is important to note that evaluating ecosystem impacts from anthropogenic activities depends on what has been used to weigh the different factors which would determine what is a 'positive' or 'negative' impact and this delicate balance is regulated by fickle societal values (Alleway et al., 2019; Kenny et al., 2018; Mascorda-Cabre et al., 2021).

The present study therefore offers crucial evidence not only on the benefits of offshore mussel farming, but it presents what we think is the best approach to help policymakers, managers and aquaculture stakeholders evaluate and understand aquaculture-environmental impacts. This type of analysis can support MSP, help identify the most suitable aquaculture development areas and adopt an integrated ecosystem-based management. Unfortunately, there is no 'quick' way around it but to continue monitoring benthic communities underneath farms and include a wide range of control sites to detect a farm's footprint (Bridger et al., 2022; Lacson et al., 2019; Mascorda-Cabre et al., 2021).

4.3. Limitations and further work

Although the authors have performed a wider ecological and oceanographic study of the Lyme Bay offshore mussel farm which includes surveys of larger mobile macrobenthic and pelagic organisms, data is yet to be analysed. The functional analysis of this other component of the seabed and water column is likely to be diverse and help understand not only patterns seen within the infaunal community but the wider impact that the farm has on its surrounding environment.

Despite our effort to compile a well-informed list of traits to study sensitivity and recoverability, to date, functional trait analysis is still evolving as detailed trait data for many taxa are still lacking, especially when it comes to understanding which traits are essential in regulating principal ecosystem functions (e.g. nutrient or carbon cycle) (Beauchard et al., 2017; Bolam et al., 2016; Kenny et al., 2018; Lacson et al., 2019; Paganelli et al., 2012; Van Der Linden et al., 2012). The use of functional diversity indexes (BTA) to evaluate and assess anthropogenic impact and disturbance is still in its early days, especially when identifying causality between human pressures and biological traits and functions, isolating those from natural environmental variables and interpreting the implications to the ecosystem and the services it provides (Beauchard et al., 2017; Kenny et al., 2018; Lacson et al., 2019).

The authors understand that there is an important naturally occurring sediment cycle factor when analysing infaunal community changes however, due to the length and nature of this study, we believe that these results are representative of the potential effects that an offshore longline mussel farm of this type can have on its surrounding ecosystem. This study is a valuable illustration of offshore aquaculture-environment interaction and how to assess them but there is still a lack of research to compare results and strategies. It is important that studies like this one are replicated providing essential knowledge to our understanding of ecosystem responses to farming to support effective governance.

This study highlights the importance of locating a shellfish farm in an adequate offshore environment, under high hydrodynamic conditions, where currents and waves disperse organic matter loading (Lacson et al., 2019). Thus, caution is needed when using the results from this study as these are true for a farm of this characteristics under similar environmental conditions. We cannot predict environmental interactions of a larger farm or one with greater abundance and carrying capacity. Hence, it is important to keep monitoring aquaculture-environmental interactions, not only as farms increase in size but as benthic habitats are transformed.

5. Conclusions

This study provides the first long-term BACI and BAG study of functional diversity and BTA analysis of infaunal communities following the development of an offshore longline mussel farm, quantifying impacts to benthic ecosystems. Our results demonstrate that ecological interactions of offshore developments of this kind have the potential to not only increase taxonomic richness but also expand the amount and selection of traits and functions shaping the community. These results provide a further insight into the impacts of offshore mussel aquaculture suggesting that the highly hydrodynamic conditions weaken the environmental effects of shellfish farming and, have the potential to support habitat restoration. This, in conjunction with the ceasing of seabed damaging activities (i.e trawling) within the farm, is allowing the seabed to recover.

With a focus on specific traits known to be modified by shellfish farming and taking into account sensitivity and recoverability, the findings from this study showed that advanced functional diversity and trait approaches are necessary to complement classical diversity indexes and tests, providing a clearer picture of ecological impact. This highlights the importance of considering multifunctionality in assessments of ecosystem functioning, the use of a wide range of functional diversity indices and traits as well as how crucial it is to perform long-term studies to be able to show not only trends but well-established long-term effects.

The outcomes of this study can help support decision-makers implement marine policy, especially regarding the licensing, monitoring requirements and assessment to adopt an integrated ecosystem-based management in order to support the offshore aquaculture industry grow sustainably. For these reasons, we strongly recommend the use of BTA when evaluating aquaculture-environment interactions.

It can be concluded that aquaculture developments like the one under study can not only provide the opportunity for seabed to recover after years of damaging activities but also can have the capacity to restore benthic habitats, boost biodiversity, provide spillover effect, improve the health of the ecosystem and the ecosystem services provided acting as de facto OECMs.

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CRedit authorship contribution statement

Experimental study was designed by LL.M-C, E.V.S, P.H, M.J.A and D.B. The article was conceived by LL.M-C with supervision by E.V.S, P.H and M.J.A. Sampling was carried out by LL.M-C, D.B and E.V.S. Laboratory analysis and taxonomical identification was carried out by LL.M-C and D.B. Article analysis was completed by LL.M-C. Results were discussed by LL.M-C, E.V.S, P.H and M.J.A. The manuscript was written by LL.M-C with contributions from E.V.S, P.H and M.J.A. Reviewer comments were addressed by LL.M-C with contributions from P.H, E.V.S, and M.J.A.

Declaration of competing interest

Offshore Shellfish Ltd. was not involved in the study design, data collection and analysis, preparation of the manuscript or decision to publish. Independent researchers at the University of Plymouth have undertaken the work. None of the co-authors are, or have ever been, a collaborator or employee of Offshore Shellfish Ltd. Reviewer comments were addressed by LL.M-C with contributions from P.H, E.V.S, and M.J.A.

Data availability

Data will be made available on request.

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