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Is mussel farming helping to restore degraded seafloor habitats in Golden and Tasman Bays?

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Prepared for Envirolink and Marine Farming Association

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Executive summary

There is growing recognition that, in certain contexts, aquaculture can contribute positively to the environment. To contribute to this discussion, we compiled and analysed 13 years of monitoring data with the aim of detecting whether mussel farms have improved benthic habitat quality and ecosystem function in a region with a long history of environmental degradation.

Monitoring data on physical sediment characteristics (i.e. grain size) and benthic infauna and epifauna were collated for mussel farms within two large aquaculture management areas in Golden Bay / Mohua and Tasman Bay / Te Tai-o-Aorere. These data encompassed benthic conditions prior to the start of farming, immediately after the initial development (< 3 years) and at later stages (> 9 years). They also included consistent monitoring of benthic stations located within and outside the mussel farms. A range of univariate and multivariate analyses were conducted to investigate changes in physical habitat and benthic community structures.

One of the most conspicuous changes observed within one of the mussel farms (AMA 2) was the accumulation of live mussels, shells and shell debris on previously bare sediment, which was captured by surveys of the seafloor environment. Sediments within both farms also became coarser with time, likely driven by the accumulation of whole and fragmented shell material. Given that Golden and Tasman Bays have lost much of their shellfish reefs and suffer from excessive inputs of fine sediments, these observed changes may represent a positive step towards the recovery of structurally complex seafloor habitat.

Epifaunal data from AMA 2 showed this farm supported higher abundances of sea stars and sea cucumbers compared to reference stations. This is likely due to an increased abundance of mussels and other prey items on the seafloor, as well as higher levels of suspended and deposited organic matter, within mussel farms.

We also found shifts in benthic infaunal community structure for farm and reference sites, as communities became dominated by a small number of species known to be tolerant to organic enrichment. When assessing functional traits of benthic communities, we found evidence that shifts in benthic community structure may be leading to enhanced sediment stability and bioturbation as the farm ages.

Our study uncovered multiple lines of evidence that suggest benthic ecosystems have shifted over time within the wider region of Golden and Tasman Bays, both inside and outside of mussel farms. These more widespread changes could be due to ongoing environmental stress from sedimentation and bottom fishing, among other stressors.

This study focuses on mussel farms in Golden and Tasman Bays, as inconsistent monitoring methods, missing baseline data and inadequate controls rendered data from other regions unsuitable for analysis. Thus, we provide several monitoring and research recommendations, which include improving the standardisation of methods, making data and reports more publicly available, and supporting investigations into other ecosystem services provided by mussel aquaculture.

By drawing on 13 years of monitoring data, this study provides a unique insight into the long-term changes in benthic community structure

and functioning in Golden and Tasman Bays related to mussel farming. Overall, our study provides a method for generating additional value from previously gathered consent monitoring data that could be applied around the country. Furthermore, it furnishes a template that can be used to support an assessment of the restorative effects of mussel farming on the seafloor environment that also accommodates for signs of organic enrichment.

1. Introduction

Widespread degradation of coastal ecosystems has led to the extensive loss of critical habitats, including shellfish reefs (Duarte et al. 2009). Globally, recognition of the importance of shellfish reefs and a lack of natural recovery has prompted a rapid expansion of restoration initiatives (e.g. for oysters, see Schulte et al. 2009; for mussels, see Wilcox et al. 2018). However, shellfish reef restoration initiatives continue to face limitations due to the scalability of approaches, in terms of both cost and effort, and positive change may take decades, or longer, if environmental stressors are not addressed (Mann and Powell 2007; Bayraktarov et al. 2016). As a result, there is an urgent need to consider alternative pathways that may already support habitat restoration at ecologically meaningful scales.

Shellfish aquaculture is gaining international attention for the range of restorative benefits or ecosystem services marine farms provide to the environment at larger spatial scales (e.g. as reviewed in Stenton-Dozey and Broekhuizen 2019; Alleway et al. 2023; TNC 2024). In this context, the delivery of both economic and environmental benefits from farming is known as 'restorative aquaculture' (Alleway et al. 2023; TNC 2024). This emerging concept has primarily focused on the culture of species like macroalgae and shellfish, which generally contribute towards net neutral-to-positive effects on the environment (Slater and James 2023). For example, research into the ecosystem services provided by shellfish aquaculture has explored: (1) whether shellfish farms act as a net carbon source or sink (e.g. Burkholder and Shumway 2011; Petersen et al. 2016; Bricker et al. 2018; Ferreira and Bricker 2019; Petersen et al. 2019); (2) if high densities of filter-feeding bivalves can improve water quality by reducing dissolved nutrients and suspended organic particles (e.g. Iribarren et al. 2010; Martini et al. 2022; Feng et al. 2023); and (3) how farm structures and associated biomass provide feeding opportunities and habitat for fish and invertebrates (e.g. Morrisey et al. 2006; Chan et al. 2022; Theuerkauf et al. 2022; Underwood 2023; Underwood and Jeffs 2023; Underwood et al. 2023, 2024). In addition, shellfish farming could benefit benthic communities by creating novel seafloor habitats and increasing food availability. There is also potential for a *de facto* area-based conservation measure where the seafloor is allowed to recover in the absence of physical disturbance from stressors like mobile fishing gear (e.g. bottom trawling and dredging as seen in the United Kingdom; Mascorda-Cabre et al. 2024).

Mussels, shells and other organic material are frequently dislodged from mussel farms, where they accumulate on the underlying seafloor (Keeley et al. 2009; Stenton-Dozey and Broekhuizen 2019; Bridger et al. 2022). By increasing feeding opportunities and adding structural complexity to the seafloor, these accumulations can promote the development of benthic habitats and communities that are distinct from the surrounding area (Dumbauld et al. 2009; Alleway et al. 2019; Theuerkauf et al. 2022). Considering that shellfish reefs have declined globally (Lotze et al. 2006; Beck et al. 2011; Gillies et al. 2018; zu Ermgassen et al. 2020), the question remains whether these shell accumulations can mimic the properties, functions and communities associated with historic or wild shellfish reefs. If so, this would present an ideal scenario where farming is indirectly contributing to habitat restoration.

Despite the potential to deliver environmental benefits, historically, most research has focused on trying to identify the negative impacts of shellfish aquaculture. This is because the deposition of shellfish faeces and pseudofaeces (aka biodeposits) can lead to the organic enrichment of sediments beneath production lines (Crawford et al. 2003; Dumbauld et al. 2009). Organic enrichment is usually identified by reductions in sediment particle size and elevated bacterial activity. In extreme cases, studies have observed sites with localised oxygen depletion and increased sulphide concentrations in comparison to reference areas, particularly for semi-enclosed waterways with high shellfish stocking densities (Nizzoli et al. 2006; Richard et al. 2007; Hargrave et al. 2008; Vinther and Holmer 2008; Howarth et al. 2022). Under such scenarios that have been documented internationally (e.g. for Japanese oysters, see Ito and Imai 1955; Kusuki 1981), these changes displaced larger, more mobile fauna (e.g. echinoderms, bivalves, crustaceans, fish) and promoted the proliferation of smaller-bodied, faster growing, enrichment-tolerant organisms such as polychaetes and other marine worms (e.g. Tomassetti and Porrello 2005; Callier et al. 2008; Lacoste et al. 2019). The combined effects can manifest as a localised reduction in overall species diversity but an increase in infaunal abundance (Pearson and Rosenberg 1978; Keeley et al. 2009). Balancing these negative effects against potential benefits is essential for assessing the restorative effects of mussel aquaculture and guiding sustainable management.

Green-lipped mussel (*Perna canaliculus*) farming is the largest aquaculture sector in Aotearoa New Zealand, with most farms located in well-flushed, soft sediment areas (Keeley 2013b; AQNZ 2024). To operate, farm owners are required to conduct routine monitoring (e.g. on infaunal communities, sediment and water quality) to address potential negative effects on the surrounding environment. Reviews of monitoring data from academic and grey literature suggest that mussel aquaculture in Aotearoa New Zealand tends to result in ‘a mild, positive enrichment effect rather than a major disruption to the functional integrity of sediments’ (Keeley 2013b; and reviewed in Stenton-Dozey and Broekhuizen 2019). However, little to no work has been conducted to assess monitoring data on seafloor farm effects within a restorative context. Given the widespread loss and ongoing degradation of shellfish reefs and benthic habitats across the country (e.g. Cranfield et al. 1999; Handley 2006; Marsden and Adkins 2010; McLeod et al. 2014; Handley et al. 2017; Booth 2020), it is important to understand whether mussel aquaculture is indirectly supporting the recovery of seafloor habitats and communities. This question is particularly pertinent in Mohua / Golden Bay (hereafter Golden Bay), Te Tai-o-Aorere / Tasman Bay (hereafter Tasman Bay), Marlborough Sounds and the Coromandel Peninsula, as these are the largest mussel production regions (AQNZ 2024). Notably, these areas have also lost most of their natural shellfish reefs following centuries of environmental degradation (Handley 2006; Paul 2012; Handley et al. 2017; also see Section 2).

This study collated and analysed over a decade of benthic monitoring data from mussel farms within two large aquaculture management areas in Golden and Tasman Bays to investigate whether restorative effects could be detected beneath mussel farms via: (1) the development of novel seafloor habitat; (2) positive influences on benthic biodiversity; and (3) the enhancement of functional diversity. Our findings were then used to inform discussion on whether existing monitoring practices can be improved and address relevant research gaps to assess whether and how mussel farming may be helping to restore degraded seafloor habitats.

2. Golden and Tasman Bays

This study focuses on mussel farms within Golden and Tasman Bays. Although we initially aimed to include data from other production regions (e.g. Coromandel and Marlborough), environmental monitoring approaches were found to be too inconsistent across time and space. Furthermore, baseline data were often lacking, and control treatments were inadequately monitored. Consequently, datasets from these other regions were deemed unsuitable for inclusion in this study.

2.1 Environmental history

The seafloor of Golden and Tasman Bays was once replete with a mosaic of seafloor habitats, which included oyster and mussel reefs, scallop beds and algal meadows (Handley 2006). However, the clearing of native vegetation for forestry, agriculture and urban development has contributed to a fourteenfold increase in coastal sedimentation rates compared to pre-human settlement estimates (Handley et al. 2020a, 2020b). Furthermore, dredge fisheries for mussels (*Perna canaliculus*) and oysters (*Ostrea chilensis*) have been established since the 1800s, while dredging for scallops (*Pecten novaezelandiae*) and bottom trawling for demersal fish gained substantial momentum in the 1940s and 1950s (Handley 2006). Presently, much of the seafloor within the region is disturbed by fishing gears between 10 and 50 times a year (Michael et al. 2015; Prichard and Howarth 2025). The combination of excessive sedimentation and high fishing pressure has been linked to significant declines in shellfish populations, and water and benthic habitat quality (Handley 2006, 2022). Consequently, the seafloor is now predominantly characterised by silt and mud (Handley 2006; Handley et al. 2020a, 2020b).

2.2 Aquaculture

Over 3,207 ha of marine space is consented for mussel aquaculture in Golden and Tasman Bays, with another 3,978 ha consented for mussel and scallop spat collection (Mason and Bray 2020). Most operations in this region are situated within three aquaculture management areas (AMA; Figure 1). Each AMA is divided into sub-zones (a–q) consented for different activities (e.g. spat collection, outgrowing).

This study focuses on sub-zones p and q (AMA 2 in Golden Bay, covering 328.5 ha), and sub-zones i and k (AMA 3 in Tasman Bay, covering 749 ha), which represent the largest and longest-running mussel farms within the region. All four of these mussel sub-zones are currently undergoing staged development:

- **Stage 1** was initiated in 2011 and involved stocking a 50 ha area within each sub-zone (referred to as Stage 1 areas) at full density (i.e. 50 m spacing between lines). From an environmental perspective, Stage 1 essentially represented a high-impact scenario, going from an absence of farming to full-scale. This study focuses solely on Stage 1 areas (see Section 3).
- **Stage 2** was initiated between 2014 and 2016 and involved stocking the remainder of the sub-zones at two-thirds density.

- **Stage 3** is yet to commence but will involve stocking the remainder of the sub-zones at full density.

All monitoring to date has indicated that mussel farming is having minimal negative environmental impact on benthic communities and habitats within AMA 2 and 3 (Clark et al. 2012a, 2012b; Newcombe et al. 2017a, 2017b; Major and McMullin 2021a, 2021b). Consequently, the farms were progressed to Stage 2 and the operators are currently applying for permission to continue to Stage 3.

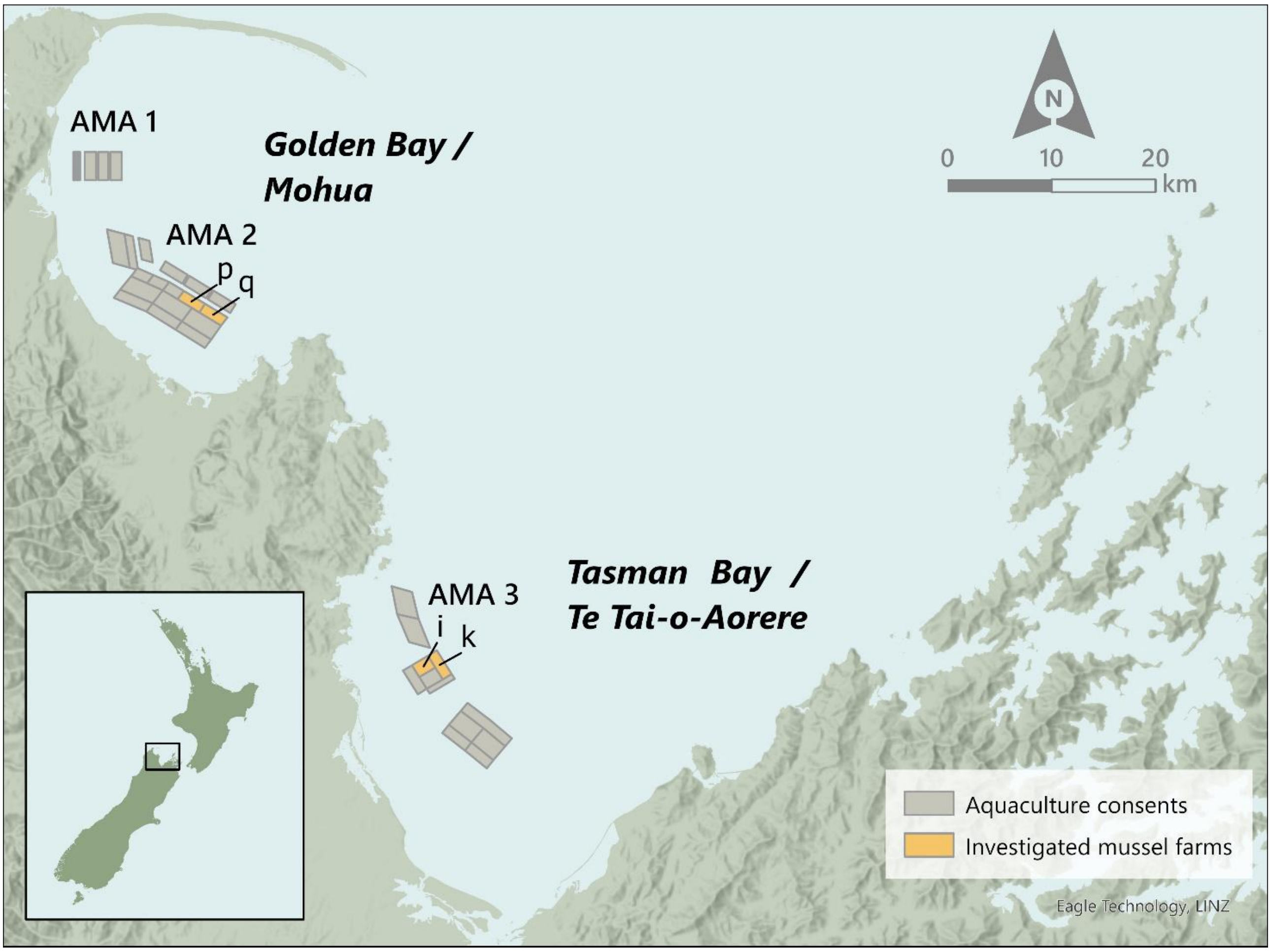

Figure 1. Map of Golden Bay / Mohua and Tasman Bay / Te Tai-o-Aorere showing aquaculture management areas (AMA) and associated consented areas. Each sub-zone is delineated, and the four mussel farms investigated in this study (sub-zones i, k, p and q) are highlighted. The inset shows the location of this region in Aotearoa New Zealand. Data provided by Tasman District Council.

2.3 Consent monitoring

To date, all benthic monitoring of AMA 2 and 3 has been undertaken by Cawthron Institute and has involved periodic sampling of sediments and infauna, alongside visual observations of shell drop-off and abundant epifauna, to help assess potential farm effects on the seafloor (methods described below). These data were considered as they can provide valuable insight of environmental effects such as the amount of enrichment and the frequency of disturbance. Baseline benthic monitoring of AMA 2 and 3 was first conducted in 2008–09 (Clark et al. 2012a, 2012b), and following this initial work, there have been surveys approximately every 2 years (see Section 3). Monitoring of Stage 1 areas continued even after the commencement of Stage 2 development. The most recent surveys of Stage 1 areas were conducted in 2021 (Major and McMullin 2021a, 2021b).

Benthic monitoring within AMA 2 and 3 was designed to enable comparisons between several distinct 'treatments' intended to reflect varying degrees of farm-related effects. 'Beneath-line' and 'between-line' sampling stations were respectively positioned directly beneath and between production lines, representing the areas of maximal farming effects on the immediate benthic environment. 'Near-control' stations, located 100 m and 250 m from sub-zone boundaries, were intended to capture the edges, or 'footprint,' of the farm's influence. Finally, 'reference' stations were situated 1 km from farm boundaries to represent broader environmental conditions beyond the influence of the mussel farms.

Sediment properties and benthic infauna

To collect information on infaunal communities and the physico-chemical properties of sediments, grab samples were collected at each station using a van Veen grab (0.1 m^2), or, when necessary, by scuba divers using hand corers (0.001 m^3). For infauna, a sediment sub-sample (130 mm diameter × 100 mm depth) was extracted from the grab and washed through a 0.5 mm sieve. Retained benthic infauna were preserved for subsequent taxonomic identification and enumeration.[1] The number of replicate samples taken at each station varied between one and four and was not consistent among stations and monitoring years due to differing monitoring requirements (see Table 2).

For physico-chemical analysis, additional sub-samples (63 mm diameter × 200–500 mm depth[2]) were extracted, refrigerated and later analysed for sediment grain size and other parameters.[3] As this study was focused on the development of physical habitat, only grain size was considered for the subsequent analysis. Grain size was measured using wet sieving and reported as the percentage of particles within either three or seven size categories (Table 1). Note that shell fragments contained within sediment samples were included in these estimates across all surveys. The number of samples analysed within this study is summarised in Table 2.

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[1] Note that different taxonomists have identified and counted benthic infauna over the 13 year time span; however, all identifications were standardised to a consistent taxonomic resolution.

[2] 200 mm for baseline surveys; 300–500 mm for all subsequent surveys.

[3] Depth of redox potential discontinuity, hydrogen sulphide, total organic content, total nitrogen, total phosphorus, total free sulphides.

Table 1. Grain sizes and descriptions used for the 3- and 7-size profile analyses.

Grain size	3-size profile	7-size profile
≥ 2 mm	Gravel	Gravel
< 2 mm ≥ 1 mm	Sand	Very coarse sand
< 1 mm ≥ 500 µm		Coarse sand
< 500 µm ≥ 250 µm		Medium sand
< 250 µm ≥ 125 µm		Fine sand
< 125 µm ≥ 63 µm		Very fine sand
< 63 µm	Silt and clay (mud)	Silt and clay (mud)

Benthic epifauna

Benthic epifauna were assessed through visual observations of the seafloor, but methods have varied over time as this monitoring was primarily used to provide additional context for changes to infaunal and sediment structure. Between 2008 and 2014, divers collected approximately 20 randomly positioned photo-quadrats (0.1 m^2) within a 20 m radius of each sampling station. Epifauna were then identified and counted from the photographs. From 2016, a towed video camera system (0.375 m^2) was used to accommodate for low visibility conditions, from which still images were extracted for analysis. In 2021, this system was replaced by a drop camera (0.125 m^2), which pointed directly downwards. In some years, the percentage cover of mussel shell, other shells and live mussels were estimated separately, while in other years they were combined. Between 2009 and 2012, the number of individual live mussels was counted. Similarly, the abundance of gastropods and hermit crabs was sometimes estimated separately or together. Due to differences in monitoring requirements over time, epifaunal classification and assessment in this study was restricted to general groupings.

3. Methods

3.1 Study design

A before–after control–impact (BACI) analysis is widely regarded as an effective approach for detecting ecological responses to human activities (Green 1979; Stewart-Oaten and Bence 2001). This design involves collecting data before (i.e. baseline surveys) and after the commencement of an activity at sites located within areas anticipated to be affected (e.g. within farming areas) and at comparable unaffected sites (e.g. reference sites).

3.2 Data sourcing and preparation

All monitoring reports related to AMA 2 and 3 were reviewed to establish a history of benthic monitoring (Clark et al. 2012a, 2012b; Newcombe and Berthelsen 2016; Newcombe et al. 2017a, 2017b; Major and McMullin 2021a, 2021b). Any associated benthic sampling data were then located and extracted from Cawthron's secure servers. To improve data consistency, simplify experimental design and focus on the largest expected differences, we excluded data from Stage 2 areas and near-control treatments. Due to issues in data accessibility and consistency, epifaunal and shell cover data were not included for AMA 2 in 2014, and no epifaunal data were investigated in AMA 3.

To further improve data consistency and enable statistical analysis, data from between- and beneath-production line treatments were combined into a single 'farm' treatment. Likewise, year of sampling was aggregated into three time periods: 'baseline' (2008 and 2009), early farming (2010, 2011 and 2012) and late farming (2013, 2014, 2016 and 2021).

There was substantial variation in sampling effort between years, farms, sub-zones, treatments and sampling methods (Table 2). For example, the number of samples collected in 2021 was comparatively lower than previous years. This is because a reduction in sampling effort was granted by the regional council after 6 years of Stage 1 monitoring, which had demonstrated minimal environmental effects from full-scale commercial mussel farming (Major and McMullin 2021a, 2021b). In contrast, AMA 3 was subjected to higher sampling effort than AMA 2 in 2012, as it was surveyed both at the beginning (main benthic survey) and the end of the year (supplementary survey to gather seafloor images; Newcombe and Berthelsen 2016).

Sediment size

To ensure consistency, any sediment grain-size data that underwent the 7-size profile analysis were converted to a 3-size profile by combining all sand fractions (≥ 63 µm ≤ 2 mm) into a single 'sand' category (Table 1).

Table 2. Number of samples (n) analysed in this study for each sampling method, farm location, sub-zone, treatment and year (grouped into baseline, and early and late farming periods). The number in brackets indicates the number of sampling stations, which was used as a random effect in analytical models. Note that the number of infaunal samples and epifaunal images per station varied over time and among stations. There was only one sample taken at each station for sediment grain size.

				Baseline		Early farming			Late farming			
Data	**Farm location**	**Sub-zone**	**Treatment**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2016**	**2021**
Sediment grain size (n = 154)	AMA 2	p	Farm	0	2	0	2	6	0	4	8	3
		q	Farm	0	2	0	2	6	0	4	12	3
			Reference	0	1	0	1	4	0	1	4	4
	AMA 3	i	Farm	6	0	6	0	6	0	0	12	3
		k	Farm	6	0	6	0	6	0	0	11	3
			Reference	4	0	4	0	4	0	0	4	4
Benthic epifauna (n = 1,365)	AMA 2	p	Farm	0	113 (6)	0	120 (6)	114 (6)	0	0	144 (8)	66 (3)
		q	Farm	0	120 (6)	0	120 (6)	120 (6)	0	0	144 (11)	51 (3)
			Reference	0	69 (4)	0	75 (4)	60 (4)	0	0	13 (4)	98 (4)
Benthic infauna (n = 481)	AMA 2	p	Farm	0	20 (6)	0	20 (6)	20 (6)	6 (6)	6 (6)	6 (6)	3 (3)
		q	Farm	0	20 (6)	0	20 (6)	20 (6)	6 (6)	6 (6)	6 (6)	3 (3)
			Reference	0	16 (4)	0	16 (4)	16 (4)	12 (4)	4 (4)	4 (4)	4 (4)
	AMA 3	i	Farm	28 (8)	0	20 (6)	0	41 (16)	0	0	10 (10)	3 (3)
		k	Farm	0	20 (6)	20 (6)	0	26 (12)	0	0	6 (6)	3 (3)
			Reference	16 (4)	0	16 (4)	0	29 (8)	0	0	4 (4)	5 (4)

Benthic epifauna and shell cover

Epifaunal abundance was standardised between years to number of individuals per m^2. To manage inconsistent identification (e.g. differences in the number of epifaunal species or groups recorded between surveys) and groupings of taxa between mussel farms and years, all taxa within the class Asteroidea were aggregated into 'sea stars', the class Holothuroidea into 'sea cucumbers', and the class Echinoidea into 'sea urchins'. Lastly, the percentage cover of live mussels and all shell types (e.g. bivalves and gastropods) were combined (the total never exceeded 100%). Early surveys indicated a wider variety of organisms occurring beneath mussel lines (e.g. ascidians, sponges, crab species). However, since these organisms were not recorded in subsequent surveys, they were removed from the analysis.

Benthic infauna

Any taxonomic information within the benthic infaunal datasets was verified, and, where necessary, updated using the World Register of Marine Species (WoRMS 2025). This was done to standardise the taxonomic resolution of infaunal samples between surveys. Infauna were assessed based on occurrence and abundance across all surveys. To gain further insight into the ecological roles of each taxon (e.g. whether they contribute to functions like sediment stabilisation or nutrient cycling), taxa were matched to a series of biological traits using a database from Lam-Gordillo et al. (2023), describing their physical, behavioural and life-history characteristics.

This database categorises 'traits' (e.g. body size) into 'modalities' that represent a range of possible values for each trait (e.g. < 5 mm, 5–20 mm, > 20 mm), and assigns scores ranging from 0 to 1 to indicate each taxon's affinity to each modality, with values closer to 0 representing low affinity, and values closer to 1 representing high affinity. For example, an organism equally capable of both filter feeding and deposit feeding would be assigned a score of 0.5 for each. Thus, this 'fuzzy coding' approach allows taxa to be associated with multiple modalities that reflect its various ecological roles (reviewed in Bolam et al. 2016; Howarth et al. 2018).

Taxa listed within the traits database were also verified with WoRMS before matching with benthic infauna. Initially, 90.3% of all taxa were directly matched to the trait database. A remaining 7% were then matched to a trait using a higher taxonomic level. Following this, 2.7% of all taxa remained unmatched and were assigned the average scores of all taxa within the higher taxonomic rank. For example, an unmatched taxon within the class Gastropoda was assigned the average scores of all taxa within that class. This reduced the number of unmatched taxa to < 0.1%.

The original traits database contained 18 traits distributed across 77 modalities. However, for this study, the database was simplified to nine traits with a total of 28 modalities to facilitate data analysis and interpretation, reduce overlap, and focus on traits most relevant to the study's objectives (Table 3). For example, traits such as body shape (e.g. irregular, round), movement method (e.g. burrower, crawler) and reproductive technique (e.g. asexual, sexual) were excluded. Additionally, the trait 'bioturbation' was simplified from four modalities – biodiffusor, bioirrigator, surface modifier and none – to just two – bioturbator and none. To assist data visualisation, each modality was assigned a code reflecting its modality and trait name. For each sample, we then calculated the community weighted means (CWM) of each trait modality by multiplying the fuzzy-coded traits by the abundance of each taxon, summing the results across all taxa present in the sample, and dividing by the total abundance of fauna in the sample. These CWM represented the average trait modalities of all individuals within each sample, ranging from 0 to 1.

Table 3. Description of biological traits used in this study; adapted from Lam-Gordillo et al. (2023).

Trait	Code	Modality	Relevance
Bioturbation	bio_Tur	Bioturbator	Contributes to nutrient cycling and oxygen availability (Mermillod-Blondin 2011)
	bio_None	None	
Body size	bs_S	Small (< 5 mm)	Reflects an organism's energy requirements, trophic position, vulnerability to physical disturbance, and generation time (Brose et al. 2005; Sprules and Barth 2015)
	bs_M	Medium (5–20 mm)	
	bs_L	Large (> 20 mm)	
Feeding mode	f_Depos	Deposit feeder	Can reflect changes in nutrient availability, organic loading and food web dynamics (Rosenberg 1995; Bridger et al. 2022)
	f_Graze	Grazer	
	f_Omni	Omnivore	
	f_Pred	Predator	
	f_Scav	Scavenger	
	f_Susp	Suspension feeder	
Body fragility	fr_Fragile	Fragile / not durable	Determines susceptibility to physical disturbance (Beauchard et al. 2017)
	fr_Strong	Strong / durable	
Habitat provision	hab_Cavity	Creates pits / burrows	Physically complex structures on the seafloor increase biodiversity by providing habitat and shelter (Kazanidis et al. 2021)
	hab_Complex	Provides structural complexity	
	hab_None	None	
Living habit	lh_Att	Attached to seafloor	Indicates potential to evade physical disturbance, move towards areas of greater feeding opportunities, and potential to increase habitat complexity (Kaiser et al. 2000)
	lh_Burr	Burrow dwelling	
	lh_Free	Free-living	
	lh_Para	Parasitic	
	lh_Tube	Tube dwelling	
Mobility	m_Ltd	Limited / no mobility	Reflects the potential to evade disturbance and take advantage of greater feeding opportunities (Goodsell and Connell 2005)
	m_Mob	Mobile	
Sediment stabiliser	sed_Stable	Sediment stabiliser	Indicates whether taxa enhance sediment stability and reduce resuspension (Meadows et al. 1990)
	sed_None	None	
Longevity	yr_1	< 1 year	Reflects energy requirements and disturbance severity and frequency (Rosenberg 1995)
	yr_1_3	1–3 years	
	yr_3_10	> 3 years	

3.3 Data analysis

All data analysis was conducted using the software R (R Core Team 2024). Methods implemented in R are accompanied by the relevant package and function using the format ‘package::function’ followed by a reference.

Sediment grain size

Proportions of sediment grain-size fractions were modelled using Dirichlet regression using DirichletReg::DirichReg (Maier 2021). This method was selected as it can model compositional data (e.g. fractions or percentages) when the dependent variables are relative and sum up to a constant (e.g. 1 or 100%). For this, ‘farm location’ (2 levels: AMA 2 or AMA 3), ‘period’ (3 levels: baseline, early or late farming) and ‘treatment’ (2 levels: reference or farm) were included as categorical fixed effects. To account for varying temporal trends at different locations, interactions were added between farm location and period, as well as between period and treatment, to test for varying treatment effects over time. As the DirichletReg package currently does not support random effects, farm location was modelled as a fixed effect. As a result, the model was unable to make generalised predictions for both farm locations combined; therefore, results were plotted separately for each farm.

Benthic epifauna and shell cover

The epifaunal data presented several challenges for data analysis: (1) sample size was highly unbalanced between treatment–period combinations; (2) these combinations often comprised only zeros; and (3) the data were either counts (epifauna) or proportions (shell cover) data, which violated assumptions of normal distribution. These difficulties were overcome by plotting raw data in box plots and performing a non-parametric test – a Kruskal–Wallis test based on rank sums (Kruskal and Wallis 1952) to assess differences between treatment–period combinations. Where significant differences were detected, pairwise Kruskal–Wallis tests were used to examine differences between treatments within each period. P-values were adjusted for multiple testing using Bonferroni correction (Armstrong 2014).

Benthic infauna: taxa and traits composition

For analysing the composition of samples regarding taxonomic groups and traits, the abundance of benthic infauna was converted to relative abundance (within samples), and traits were considered as CWM. This was done to ensure that the following analysis reflected community composition in a way that was unaffected by overall trends in abundance. Note that samples were treated independently (i.e. no averaging), with nested random effects included to account for the nestedness of the data. A permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) using adonis2::vegan (Oksanen 2025) was performed to test for differences in taxa and trait composition of samples between farm locations, treatment and period, and the interaction between treatment and period. PERMANOVA and permutational multivariate analysis of dispersion (PERMDISP; Anderson 2006) using betadisper::vegan were then used to make pairwise comparisons between all unique combinations of treatment and period (six groups) with p-values adjusted for multiple comparisons. All permutation-based tests in this study were conducted using 10,000 iterations, with permutations blocked by farm (permute::how), and Bray–Curtis dissimilarities.

To visualise variations in taxa and trait composition between samples, both unconstrained and constrained ordination analyses were performed using non-metric multi-dimensional scaling (nMDS;

vegan::metaMDS) and distance-based redundancy analysis (dbRDA; vegan::dbrda), respectively. Unconstrained ordination visualises the overall variability in the data without accounting for or testing the effects of explanatory variables. In contrast, constrained ordination depicts the maximal variation in the data attributable to specified variables (Bakker 2024). For the constrained ordination, treatment, period and their interaction were included as constraining variables, while farm location was treated as a conditional factor to generalise the effects across different farm sites. Correlations between taxa and trait modalities were examined using the first two constrained dimensions of the dbRDA.

An indicator species analysis (ISA; Dufrêne and Legendre 1997; Cáceres and Legendre 2009) using indicspecies::isa was applied to test for associations between trait modalities and combinations of treatment and periods (Dufrêne and Legendre 1997; Cáceres and Legendre 2009). Only trait modalities that occurred at both farm locations were included in this analysis, and associations with a significance level of $p < 0.05$ were considered significant. Any significant associations in traits highlighted by the ISA were then visualised by plotting trait abundance (CWM) between treatments and periods.

Benthic infauna: diversity metrics

To support and explain multivariate comparisons of community structure over time, several benthic infaunal diversity metrics were calculated for each sample:

- **Infaunal abundance:** number of individuals.
- **Species richness (observed):** number of observed taxa.
- **Species richness (theoretical):** standardised species richness which accounts for estimated sample completeness (i.e. coverage) using the methods detailed in Chao and Jost (2012) and the iNEXT package (Hsieh et al. 2024). This metric excludes potential effects of different sample sizes and varying detection probability of (rare) species. The theoretical richness helps estimate the total number of species that would be expected in a complete sample so that different locations can be compared regardless of potential undersampling bias.
- **Functional diversity:** a measure of the diversity of traits within a population. Functional diversity was calculated as an abundance-weighted metric ($q = 2$) of modalities using mFD::alpha.fd.hill (Magneville et al. 2024).

Generalised linear mixed models (GLMM; glmmTMB:glmmTMB) were fitted for each metric above assuming negative binomial, Poisson, gamma and Gaussian distributions, respectively. Each model featured fixed effects for farm location, period and treatment. Like before, interactions were assessed between farm location and period, and between period and treatment. To account for potential temporal and spatial fluctuations in the data, random intercepts were fitted for each sampling event (i.e. survey; nested within farm location) and sampling station (nested within farm-sub-zone, which were nested within farm location). Sampling stations were unique per sampling event (206 levels), as samples were not taken from the exact same location each year. Model assumptions and residual patterns were inspected (Appendix 1) using the DHARMa package (Hartig et al. 2024). Pairwise comparisons between treatment group means at each period were conducted, with p-values adjusted for multiple comparisons using emmeans::emmeans and emmeans::pairs. As farm location only featured two levels, it was added as a fixed rather than a random effect in the GLMMs, and predictions were plotted individually since results were not generalised between farm locations.

4. Results

4.1 Sediment

Baseline monitoring showed no difference in sediment composition between farm and reference stations, with both dominated by muddy sediments comprising only small amounts of sand and gravel (< 5% combined, Figure 2). However, once farming commenced, sediments in farm stations became increasingly coarse, with the combined proportion of sand and gravel reaching 10% (for AMA 3) and 20% (for AMA 2) during the late farming period. In contrast, sediment grain size remained relatively stable over time at reference stations. A full summary table of the fitted Dirichlet regression, which accounted for 26.4% of the variance, is provided in Appendix 2. As post hoc tests are not available for model fit with the DirichletReg package, the significance of treatment–period combinations was not assessed.

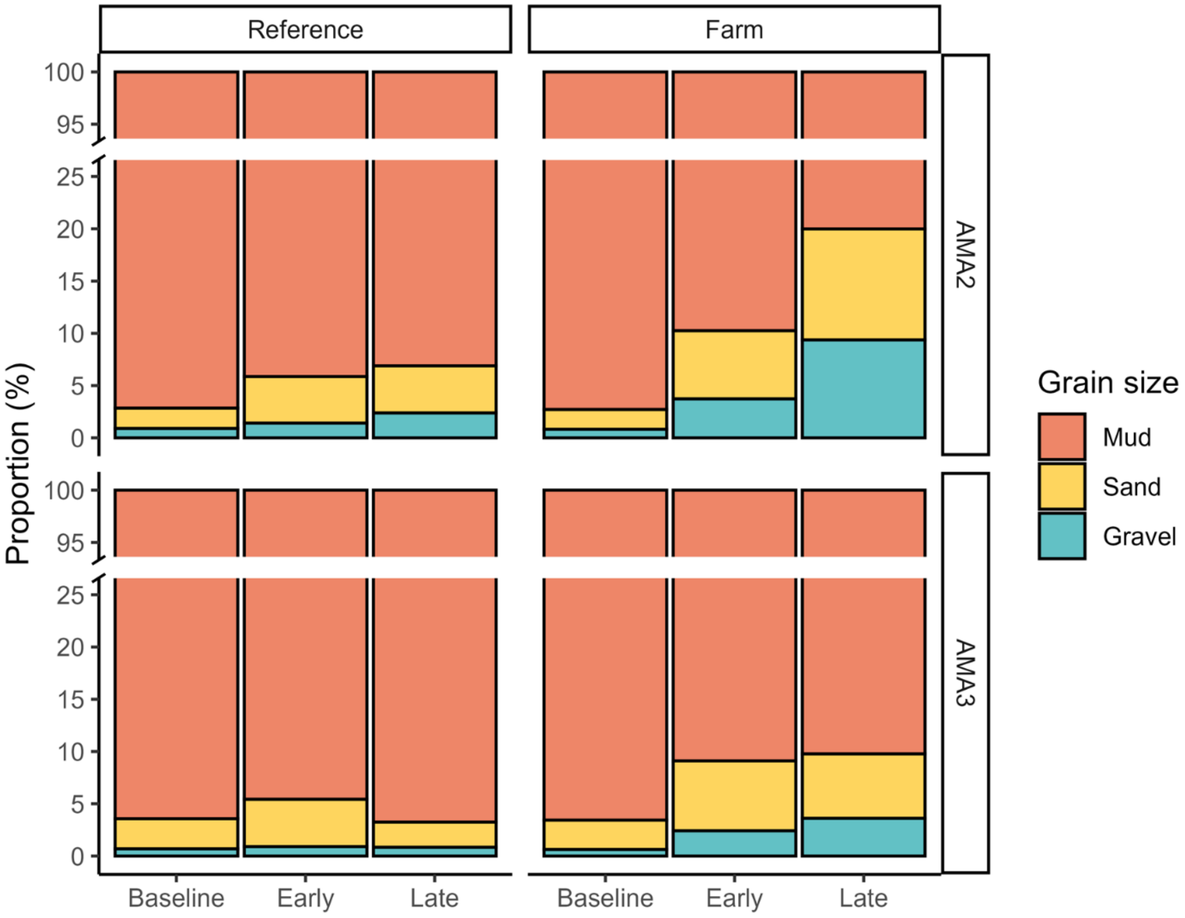


Figure 2. Predicted mean proportions of sediment grain-size fractions at farm and reference stations across different periods at the two mussel farm locations. The y-axis is broken to help visualise changes in the smaller sediment proportions.

4.2 Benthic epifauna

Before farming commenced, no shell material (including live mussels) was present on the seafloor at either farm or reference stations for AMA 2 (Figure 3). Once farming began, shell cover increased substantially at farm stations, reaching 75–100 % in many cases. Similarly, sea cucumbers and sea stars were absent during baseline monitoring but subsequently increased at farm stations, reaching densities up to 30–40 individuals per m^2 in some instances. In contrast, sea urchins were significantly more abundant at reference stations during baseline monitoring, with densities reaching up to 145 individuals per m^2. However, their abundance declined markedly across both treatments over time, decreasing to fewer than 10 individuals per m^2 during late farming. Full results are provided in Appendix 3.

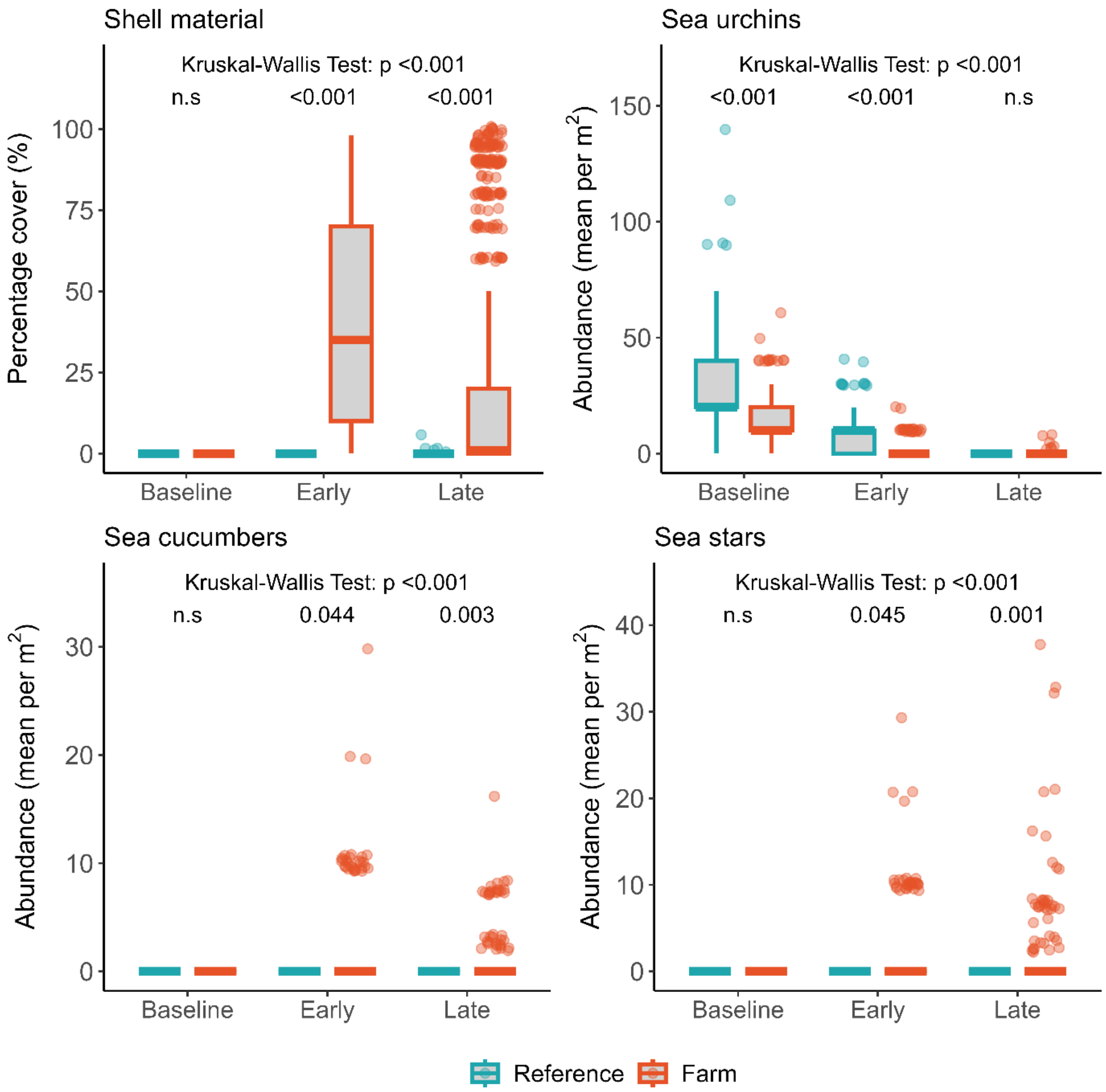


Figure 3. Boxplots of percentage cover of shell material and abundance of epifauna at AMA 2. Bars indicate median values. Dots represent outliers (i.e. exceeding the 0.75 quantile + 1.5 * interquartile range). P-values at the top of each plot represent Kruskal–Wallis tests for period–treatment combinations. P-values below this represent Kruskal–Wallis tests between treatments within each period. Note that y-axis scales differ across graphs.

4.3 Benthic infauna

Taxa-based community structure

The PERMANOVA revealed significant differences in infaunal community structure between farm locations, and for the interaction of treatment and period (Table 4). Pairwise comparisons showed significant differences between farm and reference stations in every period, including baseline (Table 5). These trends were generally supported by the ordinations (Figure 4A, 4B), which indicated these communities changed over time, and treatments increasingly diverged, with communities within the mussel farm experiencing the most change.

The ordinations and PERMDISP results (Tables 4 and 5) indicated that dispersion (within-group variability) was consistent across treatments but increased over time. This indicates treatment differences were driven by shifts in community structure (i.e. changes in centroid location), rather than by variability (i.e. dispersion).

The dbRDA (Figure 4C) suggested that similarities between farm and reference baseline communities were driven by high abundances of small crustaceans, including cumaceans, ostracods and amphipods. However, as farming activity progressed, farm stations became more associated with high abundances of polychaetes, such as *Prionospio* spp., *Heteromastus filiformis, Theora lubrica* and *Armandia maculata*. In contrast, reference stations became increasingly associated with polychaetes from the family Cirratulidae and *Cossura consimilis*.

Table 4. PERMANOVA and PERMDISP results of infaunal taxonomic community structure between treatments (reference and farm), locations (AMA 2 or AMA 3), and periods (baseline, early and late farming). Df = degrees of freedom, SS = sum of squares, R^2 = coefficient of determination. Significant results ($p < 0.05$) are denoted by *.

Test	Term	df	SS	R^2	F	p
PERMANOVA	Farm location	1	2.778	0.022	12.681	< 0.001*
	Treatment	1	4.132	0.033	18.866	< 0.001*
	Period	2	10.383	0.084	23.701	< 0.001*
	Treatment * Period	2	2.354	0.019	5.374	< 0.001*
	Residual	474	103.826	0.841		
PERMDISP	Group (Treatment * Period)	5	0.595		15.814	< 0.001*
	Residual	475	3.575			

Table 5. Pairwise comparisons of infaunal community structure between treatments (reference and farm) in different farming periods. df = degrees of freedom, SS = sum of squares, R^2 = coefficient of determination. Significant results ($p < 0.05$) are denoted by *.

Test	Term	df	SS	R^2	F	p
PERMANOVA	Baseline	1	0.423	0.021	2.486	0.002*
	Early	1	3.595	0.054	15.091	< 0.001*
	Late	1	2.599	0.098	10.373	< 0.001*
PERMDISP	Baseline	1			0.786	0.431
	Early	1			0.643	0.528
	Late	1			-1.448	0.160

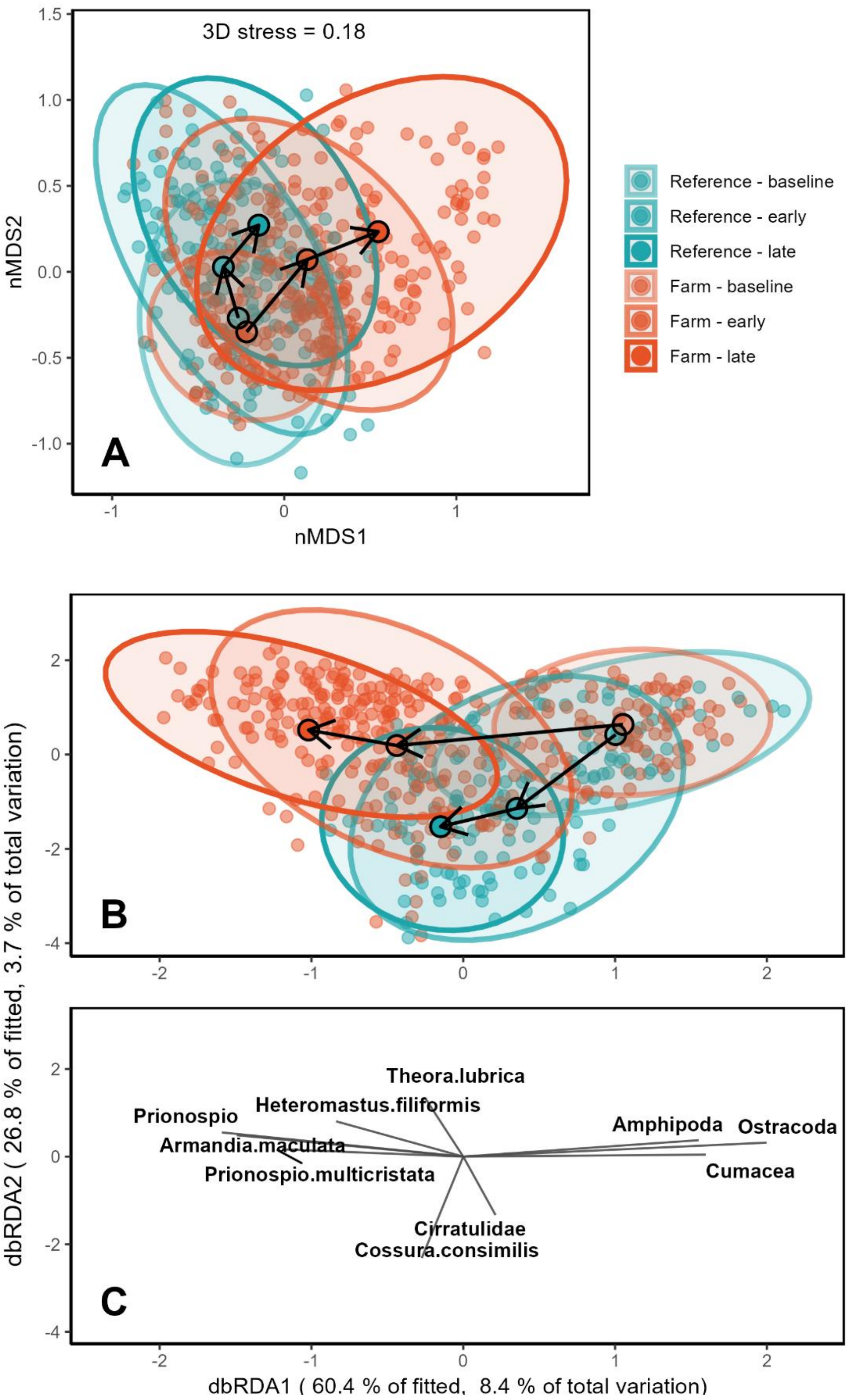


Figure 4. Unconstrained (A) and constrained (B) ordinations of benthic infaunal community structure. Ellipsoids indicate the 95% confidence intervals for each group. Large dots indicate group centroids, with arrows illustrating their directional shifts over time. Bottom plot (C) is the same ordination as (B) but overlaid with the 10 taxa most strongly correlated with the dbRDA axes.

Trait-based community structure

Similar to taxonomic structure, the PERMANOVA indicated trait community structure was significantly different between farm locations, with a significant interaction between treatment and period (Table 6). Pairwise comparisons indicated that differences between farm and reference stations only emerged after farming had commenced (Table 7). Likewise, ordination plots (Figure 5A, 5B) indicated little difference between treatments during baseline monitoring. However, these communities then began to shift and diverge as farming activity progressed, with farm stations experiencing the greatest levels of change. The ordinations and PERMDISP suggested these differences were driven by shifts in the trait structure (group centroids) and by increased dispersion over time. Greatest within-group variability occurred underneath mussel farms during late farming.

Together, the results of the dBRDA (Figure 5C) and ISA (Table 8) indicated little difference in the abundance of trait modalities between farm and reference stations during baseline monitoring. However, as farming activity commenced and progressed, farm stations supported increased abundances of sediment-stabilising organisms (Figure 6A), bioturbators (Figure 6B) and tube-dwelling organisms (Figure 6C). In contrast, burrow-dwelling organisms increased slightly at reference stations but decreased at farm stations (Figure 6D). Conversely, free-living organisms and grazers declined over time at both treatments (Appendix 4).

Table 6. PERMANOVA and PERMDISP results of infaunal trait community structure**.** df = degrees of freedom, SS = sum of squares. Significant results ($p < 0.05$) are denoted by *.

Test	Term	df	SS	R^2	F	*p*
PERMANOVA	Farm location	1	0.216	0.024	12.728	< 0.001*
	Treatment	1	0.153	0.017	9.002	< 0.001*
	Period	2	0.613	0.067	18.021	< 0.001*
	Treatment * Period	2	0.119	0.013	3.500	0.002*
	Residual	474	8.056	0.880		
PERMDISP	Group (Treatment * Period)	5	0.153		11.366	< 0.001*
	Residual	475	1.2818			

Table 7. Pairwise comparisons of infaunal trait community structure between treatments (reference and farm) in different farming periods. df = degrees of freedom, SS = sum of squares, R^2 = coefficient of determination. Significant results ($p < 0.05$) are denoted by *.

Test	Term	df	SS	R^2	F	*p*
PERMANOVA	Baseline	1	0.017	0.014	1.638	0.122
	Early	1	0.105	0.021	5.522	< 0.001*
	Late	1	0.167	0.076	7.836	< 0.001*
PERMDISP	Baseline	1			1.155	0.253
	Early	1			1.034	0.301
	Late	1			2.997	0.003*

Table 8. All trait modalities identified by the indicator species analysis to exhibit a significant ($p < 0.05$) association with the various treatments and periods at both farms. Stat = test statistic, a measure of association ranging between 0 and 1, was averaged between the two farms.

<table>
<tr><th></th><th>Baseline</th><th>Early farming</th><th>Late farming</th></tr>
<tr><th>Reference</th><td rowspan="2">f_Graze (stat = 0.75)
lh_Free (stat = 0.68)
sed_None (stat = 0.59)</td><td colspan="2">lh_Burr (stat = 0.62)</td></tr>
<tr><th>Farm</th><td colspan="2">lh_Tube (stat = 0.74)
sed_Stable (stat = 0.74)
bio_Tur (stat = 0.61)</td></tr>
</table>

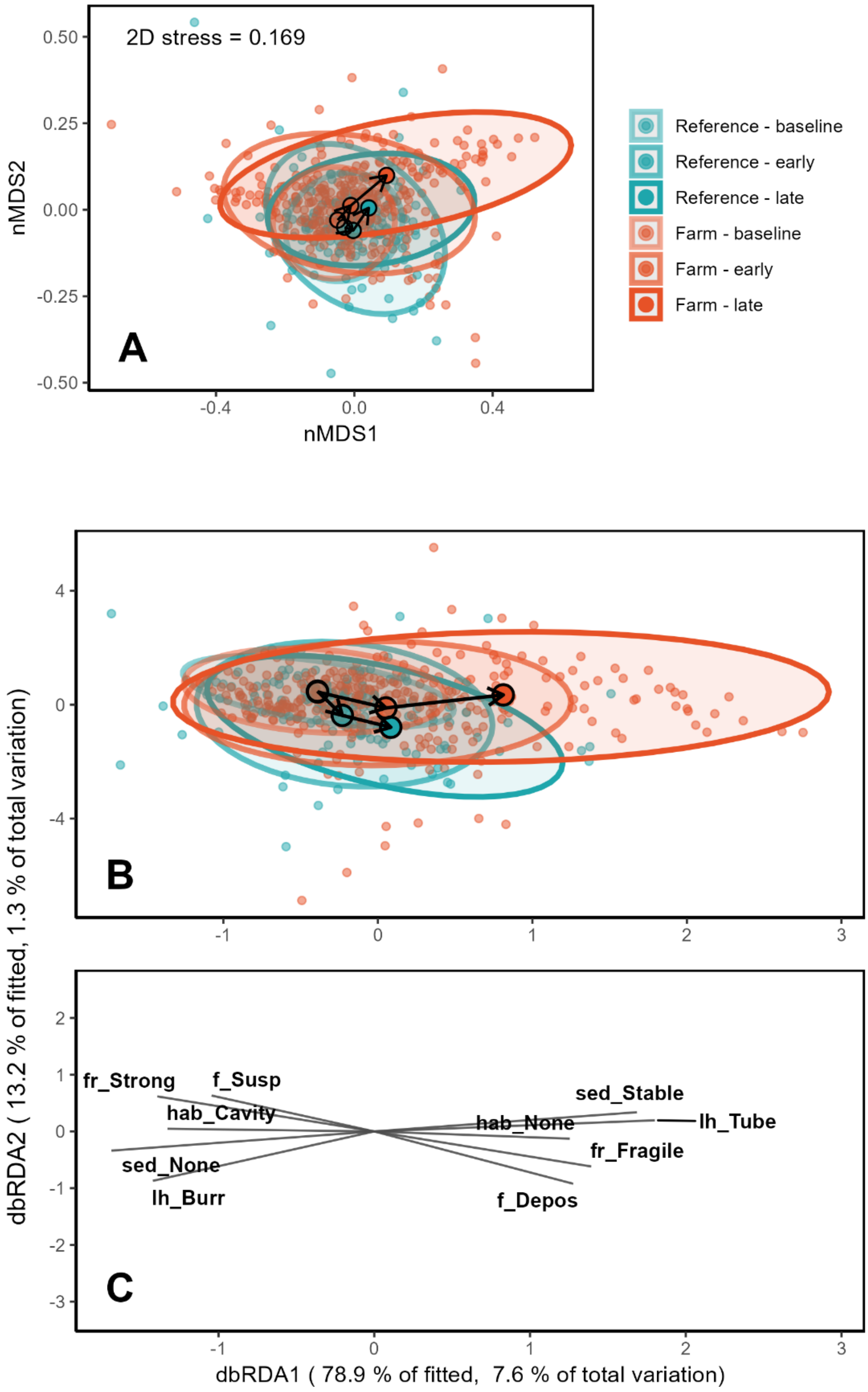


Figure 5. Unconstrained (A) and constrained (B) ordinations of benthic infaunal traits composition. Ellipsoids indicate the 95% confidence intervals for each group. Large dots indicate group centroids, with arrows illustrating their directional shifts over time. Bottom plot (C) is the same ordination as (B) but overlaid with the 10 taxa most strongly correlated with the dbRDA axes.

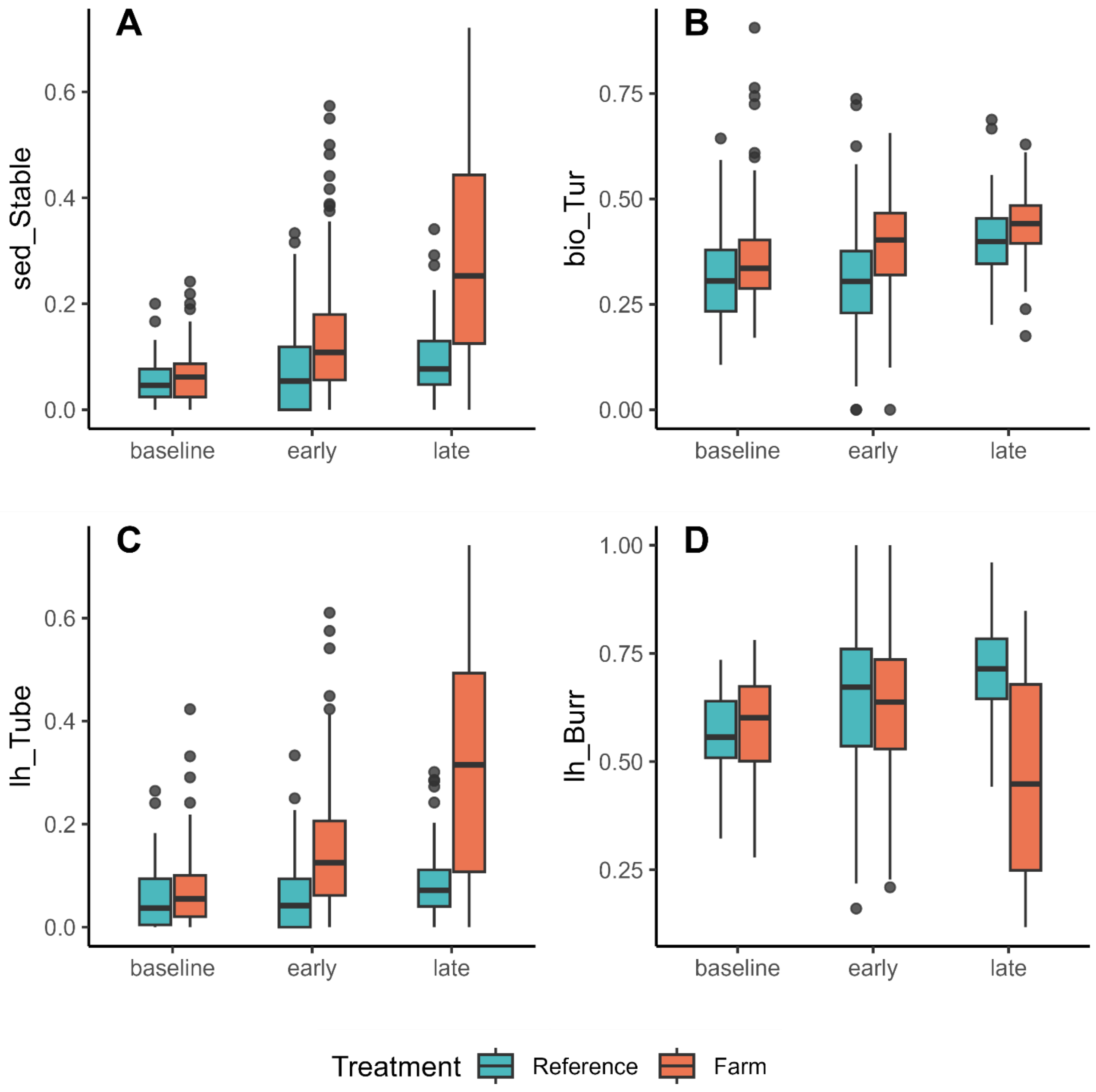


Figure 6. Abundance (community weighted means) of the four trait modalities identified by indicator species analysis to be significantly associated with different treatments and periods. Sed_Stable = sediment stabilisers, bio_Tur = bioturbators, lh_Tube = tube-dwellers, and lh-Burr = burrow-dwellers.

Diversity metrics

All diversity metrics were comparable between farm and reference stations during baseline monitoring (Figure 4, Appendix 5). After farming commenced, infaunal abundance doubled at farm stations, while numbers remained comparatively stable at reference sites. In contrast, species richness remained relatively stable over time but was consistently higher at farm stations. The observation that theoretical species richness did not differ between treatments suggests that this trend was due to higher infaunal abundance, leading to greater detection probability of rarer taxa. Functional diversity was marginally higher at farming stations during early farming but did not differ between treatments in any other period. No significant differences were found between farm locations (AMA 2 vs AMA 3) for any metric across periods and treatments.

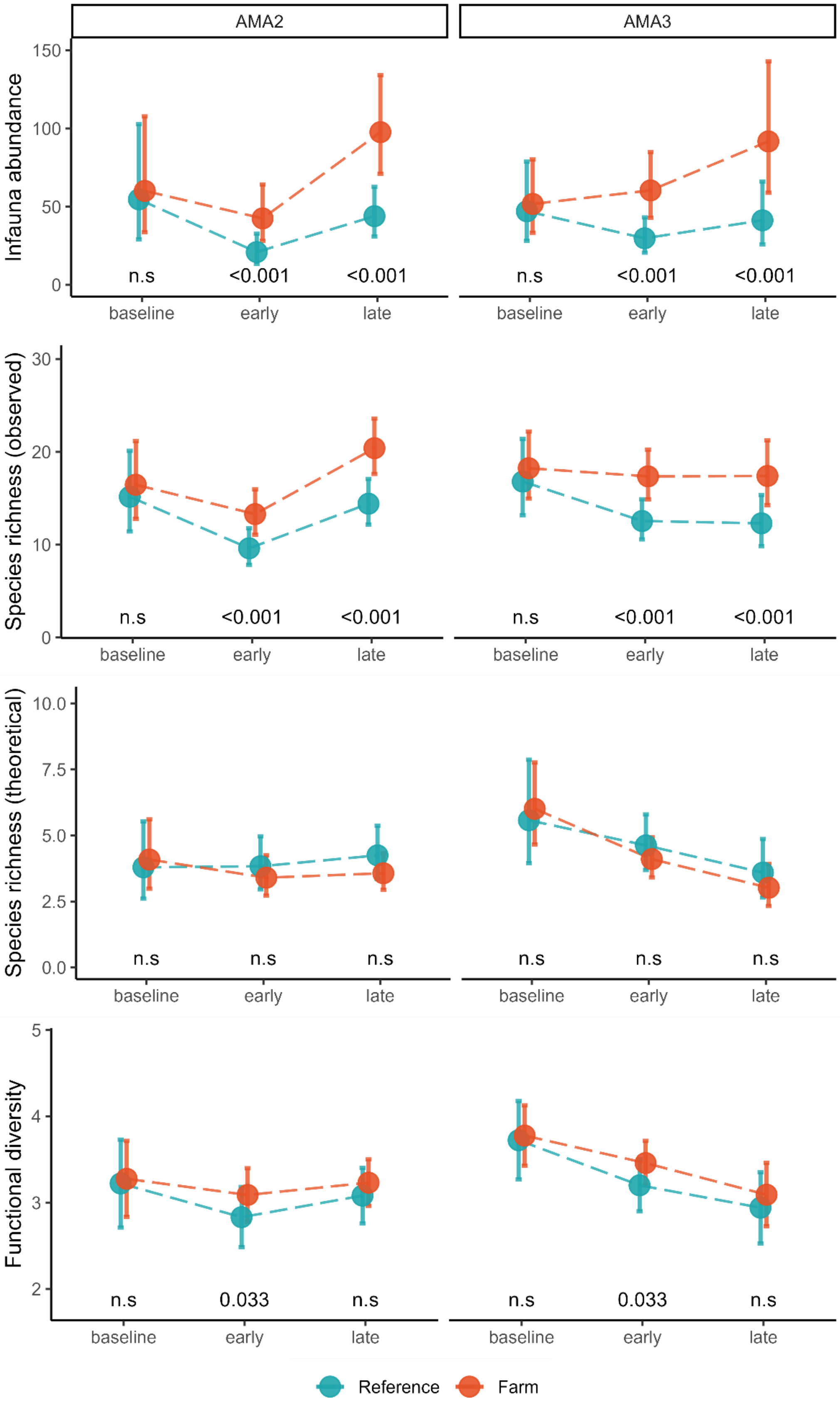


Figure 7. Mean species diversity metrics and 95% confidence intervals predicted by the generalised linear mixed models. P-values or 'n.s' indicate significant and non-significant pairwise comparisons, respectively.

5. Discussion

With the rapid, ongoing degradation of coastal ecosystems, there is growing interest in the potential for shellfish aquaculture to assist local recovery through the delivery of environmental benefits (Alleway et al. 2019; Stenton-Dozey and Broekhuizen 2019; Gentry et al. 2020; Alleway et al. 2023; TNC 2024). To contribute to this discussion, we analysed 13 years of benthic monitoring data from mussel farms within two large aquaculture management areas located in Golden and Tasman Bays – a region with a long history of environmental degradation. The primary aim of this study was to investigate whether consent monitoring of farming activity had captured nature-positive changes to seafloor habitats and communities.

5.1 Creation of novel seafloor habitat

In alignment with other studies (reviewed in Keeley et al. 2009; Stenton-Dozey and Broekhuizen 2019), consent monitoring data revealed that mussel farming promoted the accumulation of live mussels, shells and shell debris on previously bare sediment. Historic shellfish reefs also naturally accumulated live shellfish and shell material, modifying the soft sediment seafloor environment (e.g. as suggested by Commito and Dankers 2001) and supporting additional reef building through the establishment of a biogenic legacy (e.g. Commito et al. 2018; Albertson et al. 2024). Given that Golden and Tasman Bays have lost most of their natural shellfish reefs (Handley 2006), the changes identified in our data analyses could represent a positive step towards the recovery of structurally complex benthic habitats via biogenic subsidies. Given the extent of consented marine space (over 3,200 ha) in the region and an annual harvest of 2,400–6,300 tonnes (Newcombe et al. 2015), this novel habitat could already occupy substantial areas of the seafloor. As the farms progress towards full stocking density, it is possible that the magnitude of biogenic material reaching the seafloor over time could contribute to a form of large-scale seafloor recovery. However, additional work is needed to verify this process and consider potential restorative trade-offs with effects like the localised depletion of planktonic resources (e.g. as suggested in Keeley et al. 2009).

The mussel aquaculture industry already supplies mussels and shells to habitat restoration programmes across Aotearoa New Zealand (e.g. Wilcox et al. 2018; Alder et al. 2021; Benjamin et al. 2022, 2024). However, our study suggests mussel farms may also be indirectly contributing to habitat restoration goals by promoting the development of structurally complex shell-based habitat on the seafloor. Further research is required to determine whether these shell accumulations and their associated benthic communities function similarly to naturally occurring shellfish reefs. Ideally, our results would be compared with historical data of naturally occurring mussel reefs in the region, but to our knowledge, such data or reefs do not exist. Nonetheless, emerging evidence suggests that, while shell and live mussel accumulations form patchy reef-like habitat beneath farms, they are unlikely to fully resemble historic reefs for the following reasons. First, the survival of dislodged mussels tends to be very low due to predation from sea stars and other predators (e.g. Sean et al. 2022; Benjamin 2023), and because food availability for mussels is likely lower on the seafloor than the overlying water column (e.g. as suggested by Alder et al. 2022). Second, the persistence of this habitat and community is likely dependent on ongoing farming activity providing continuous inputs of shell material and organic deposition (e.g. Davidson et al. 2024). If farming was to stop in Golden and Tasman Bays, the large volumes of sediment discharged from the two local rivers, combined with sediment resuspension from bottom trawling, would likely bury accumulated shell material and associated communities, potentially resetting the seafloor to pre-farming conditions (Handley 2006; Handley et al. 2020b; Davidson et al. 2024). Finally, living mussel reefs improve water quality, enhance nutrient cycling, actively bind substrates, and form highly complex three-dimensional structures that support high levels of biodiversity (Wilcox et al. 2018; Sea et al. 2021; Alder and Hillman 2024). Given the limitations of the data used in this study, future work should evaluate whether dislodged mussels are likely to survive and form living structures that function similarly to ongoing restored reefs.

Changes in benthic habitat were also detected by sediment grain-size analysis, which indicated that sediments within the mussel farms became coarser over time. However, as grain-size analysis cannot distinguish between sediment particles and shell fragments (Hill Labs, pers. comm.), this trend was likely driven by the accumulation of shell material within the sediment matrix, rather than a true increase in large sediment particles. Furthermore, the range in depths sediment samples were collected over the different surveys (e.g. 2–5 cm) could also have impacted the perceived coarsening of the substrate. This is because small differences in collection depths could have led to differences in the proportions of grain sizes collected. However, it is worth noting that this increase in grain size appears to have occurred despite the expectation that areas beneath production lines would experience continual deposition of biodeposits and other fine organic particles, which should make sediments finer, not coarser (Howarth et al. 2022). It is also possible that the presence of farm structures and the accumulation of shell material are altering local hydrodynamics, potentially increasing both scouring, leading to sediment coarsening, and sediment deposition, leading to sediment fining (McKindsey et al. 2011; Davidson et al. 2024). Future monitoring or targeted research should consider sediment analyses that account for the presence of shell to better clarify whether coarsening of the benthic substrate is taking place.

5.2 Influence on benthic biodiversity

Consent monitoring data provided evidence that benthic infaunal communities within mussel farms underwent greater structural shifts than those at reference stations. Over time, communities shifted away from high abundances of mobile crustaceans (e.g. amphipods, cumaceans, and ostracods), which are generally sensitive to organic enrichment and disturbance (Ruiz et al. 2005; Hyne 2011; Stępień et al. 2021), towards communities characterised by Prionospid polychaete worms *A. maculata, H. filliformis* and *T. lubrica*, which are considered opportunistic species and tolerant of mild to moderate organic enrichment (Dean 2008; Keeley 2013a). Consequently, infaunal abundance increased while species richness remained relatively stable at farms when compared to reference areas, which is a pattern commonly reported in other studies of organically enriched environments (Pearson and Rosenberg 1978; Keeley et al. 2009). However, a similar community shift also occurred at reference sites, becoming increasingly dominated by burrowing polychaetes such as Cirratulidae and *Cossura consimilis*, (Keeley et al. 2012) suggesting that changes to the wider environment could have also promoted the development of enrichment-tolerant communities. These lines of evidence mean it is difficult to fully disentangle effects from the wider environment on benthic communities (e.g. sedimentation) and farming specifically.

The deposition of mussels and organic material from production lines can enhance feeding opportunities for a diverse range of benthic organisms (reviewed in Stenton-Dozey and Broekhuizen 2019; Howarth et al. 2022). This likely explains the variable but significant increase in sea stars within the AMA 2 mussel farms, as these are commonly reported to aggregate near farms in response to increased availability of mussels and other prey items on the seafloor (Benjamin et al. 2022; Benjamin 2023; Davidson et al. 2024; Mascorda-Cabre et al. 2024). This is one of the reasons why mussels tend not to survive under production lines, which can potentially limit the habitat restoration benefits provided by mussel farms (Slater et al. 2011; Zamora et al. 2022).

The abundance of suspension- and deposit-feeding sea cucumbers also increased within the mussel farm, likely in response to elevated levels of organic matter in the water column and on the seafloor (Slater et al. 2011; Zamora et al. 2022). Elevated organic matter may also help explain the increase in *A. maculata*, which is also a deposit feeder, and the increase in tube-dwelling polychaetes, which tend to employ either or both suspension and deposit feeding (Fauchald and Jumars 1979). All of these organisms can help recycle organic matter in sediments and the water column and contribute to forms of bioturbation.

Conversely, sea urchins (predominantly the heart urchin *Echinocardium australe*) declined markedly at both farm and reference stations over time. Heart urchins are important soft sediment fauna that can have an outsized influence on bioturbation in high densities. Their conspicuous loss at both farm and reference stations also suggests that longer-term, broader environmental changes have occurred across the Golden and Tasman Bay region.

5.3 Enhancement of functional diversity

When examined through the lens of biological traits, ecological shifts to infaunal communities only became conspicuous at the later stages of farming. This result supports the need for monitoring data to be considered over longer time frames, as certain ecological phenomena may take longer than current monitoring cycles before they become apparent. In addition, as the farm aged, infaunal samples gathered from within the farm demonstrated increased variation, which could be indicative of increased habitat heterogeneity over time. Similarities in functional diversity between farm and reference sites suggest that, apart from the early stages of farming, farm sites retain a similar balance of functional attributes to natural areas in the longer term. For instance, increased abundances of *A. maculata* and other burrowing organisms within the mussel farms and at reference sites contribute to bioturbation, enhancing nutrient and oxygen cycling within sediments (Mermillod-Blondin 2011). Alternatively, greater abundances of *Prionospio* spp. beneath farms may be improving sediment stability, as these worms construct tubes by secreting mucus to bind sediments and suspended particles. These biogenic structures can therefore reduce sediment resuspension by dampening water movements and consolidating the surrounding substrate (e.g. as discussed by Volkenborn et al. 2009). Sediment resuspension may also be lower within the mussel farms due to sediment coarsening, the potential for shell accumulations to dissipate water energy, and the indirect effect of farming operations restricting the use of mobile fishing gear (Benjamin et al. 2024; Mascorda-Cabre et al. 2024). The finding that mussel farming may be improving sediment stability and benthic habitat quality is particularly significant in Golden and Tasman Bays, as sedimentation and resuspension have been linked to declines and a lack of recovery in scallop, oyster and other shellfish populations (Gillespie et al. 2000; Handley 2006; Michael et al. 2015; Handley et al. 2020a, 2020b). Thus, these new conditions could potentially provide a more suitable environment for the recovery of naturally occurring shellfish populations.

The assessment of the functional traits within ecological communities is uncommon within the realm of consent monitoring but is gaining traction within ecological restoration (e.g. Carlucci et al 2020; Gimenez et al 2024). This study provides some evidence that assigning these traits to existing data sets can provide additional context for directly assessing how farm activity can promote restorative effects in seafloor communities. Furthermore, it presents an opportunity to compare infaunal communities across areas that may support different species assemblages but similar functional attributes, such as those in different production regions. Future work should include a functional assessment of benthic communities from the different production regions across Aotearoa New Zealand to investigate if the patterns observed in Golden and Tasman Bays are reflected elsewhere. If so, this could help signal, more broadly, the restorative effects mussel farming is providing to areas of degraded soft sediment seafloor.

5.4 Limitations and recommendations

Consent monitoring of mussel aquaculture has been conducted to a relatively high standard in Golden and Tasman Bays (Newcombe and Cornelisen 2014). Most notably, baseline conditions were assessed, and multiple treatments (i.e. reference, near-control and farm) were surveyed approximately every 2 years for the first 6 years of farming activity. Nonetheless, we provide several recommendations and identify priority areas for future research to better capture the restorative benefits of shellfish farms in Golden and Tasman Bays, and more broadly across Aotearoa New Zealand:

- Where monitoring is deemed necessary, standardise consent monitoring practices across Aotearoa New Zealand to facilitate other studies that address more than compliance assessments.
- Make data publicly accessible through a centralised, online repository to support future research and transparency.
- Where epifaunal monitoring is deemed necessary, improve epifaunal survey methods to better resolve taxa identification and quantify abundance and percent cover estimates of benthic habitats. For example, epifaunal assemblages in this study had to be aggregated into broad categories such as ‘sea star’ and ‘shell material’ due to the level of taxonomic resolution captured during certain monitoring events.
- Consider discontinuing the monitoring of near-control treatments for existing farm sites, as these have exhibited minimal environmental impact (Major and McMullin 2021a, 2021b). The time and resources saved could instead be directed towards improving monitoring or research on benthic epifauna, or to better investigate other benefits potentially provided by mussel aquaculture.
- Undertake additional research to improve understanding of the broader suite of ecosystem services that are potentially provided by shellfish aquaculture but not captured by current consent

monitoring, such as the provision of benthic fish habitat, water filtration or carbon sequestration (Alleway et al. 2023; TNC 2024). Furthermore, marine farmers and other stakeholders have shown a growing interest in better assessing and formally recognising these benefits through mechanisms like carbon or voluntary biodiversity credits.

- Support targeted research to assess whether:
  - shell accumulations and associated communities can mimic wild shellfish reefs
  - returning post-harvest mussel shells to farm consent areas can provide additional environmental benefits
  - dislodged mussels can persist over time or are simply replenished by subsequent drop-off.

6. Conclusion

By drawing on 13 years of environmental monitoring data, this study provides a valuable insight into the long-term effects of mussel farming on seafloor habitats and community structure. Overall, we found mussel farming had promoted the development of a structurally complex habitat and may be enhancing sediment stability and bioturbation for aquaculture areas in Golden and Tasman Bays. Our analyses also revealed that mussel farming and reference sites experienced a shift in seafloor communities towards greater dominance of small-bodied, opportunistic, enrichment-tolerant species, signalling a potential interaction between farm effects and the wider environment. Our findings support a growing body of research that is quickly refining indicators that can be used to measure the restorative effects of aquaculture.

7. Appendices

Appendix 1. Diagnostic plots of the fitted generalised linear mixed model residuals

The diagnostic plots include: (Figure A1.1) infaunal abundance model, (Figure A1.2) observed species richness, (Figure A1.3) theoretical species richness and (Figure A1.4) functional diversity. The quantile–quantile plot (QQ) plot (left) shows that the simulated residuals follow the expected distribution, with no significant deviation detected by the Kolmogorov–Smirnov (KS), dispersion or outlier tests. The residuals vs predicted plot (right) confirms no significant patterns or deviations, indicating an adequate model fit and no evidence of overdispersion, zero inflation or non-linearity.

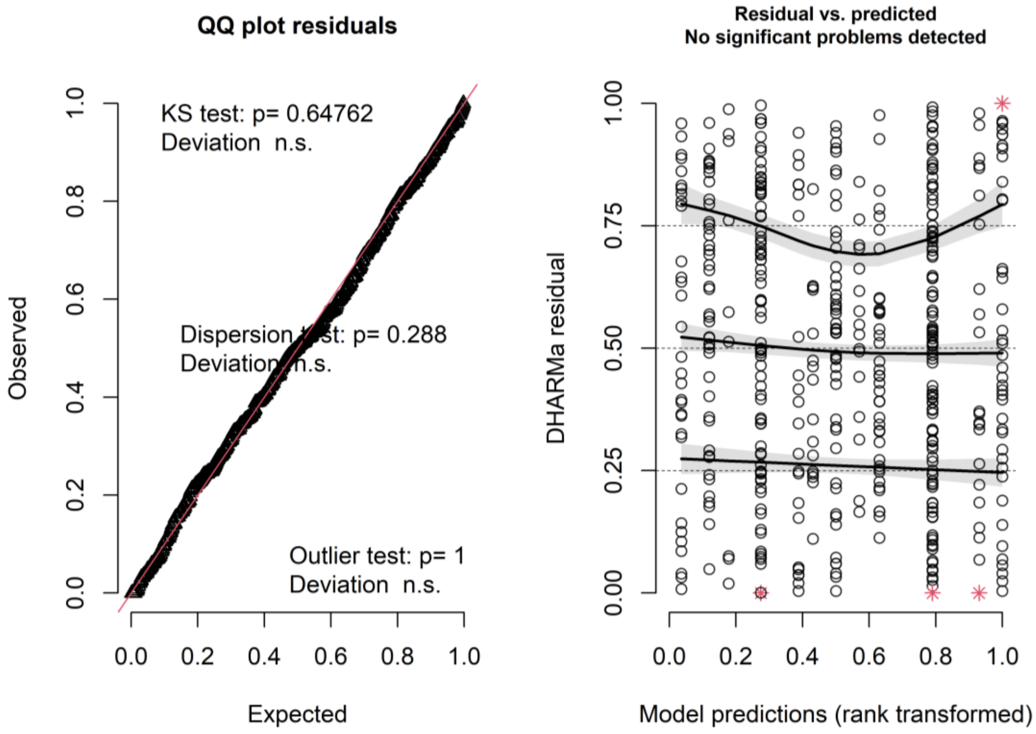


Figure A1.1. Infaunal abundance model.

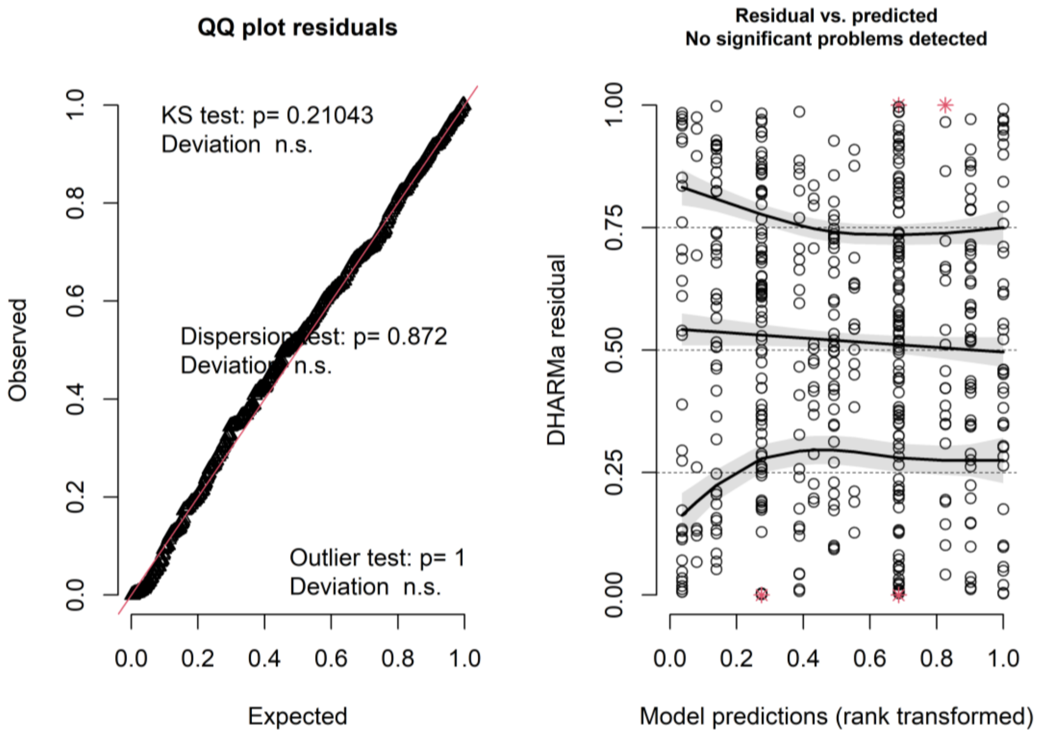


Figure A1.2. Observed species richness.

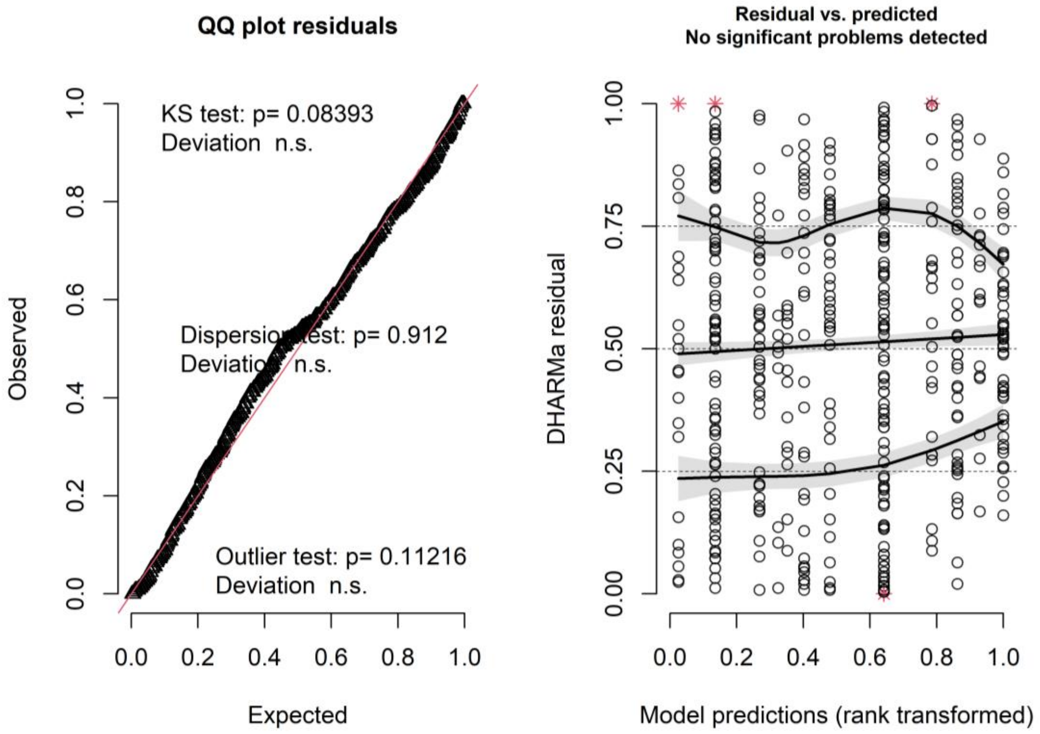


Figure A1.3. Theoretical species richness.

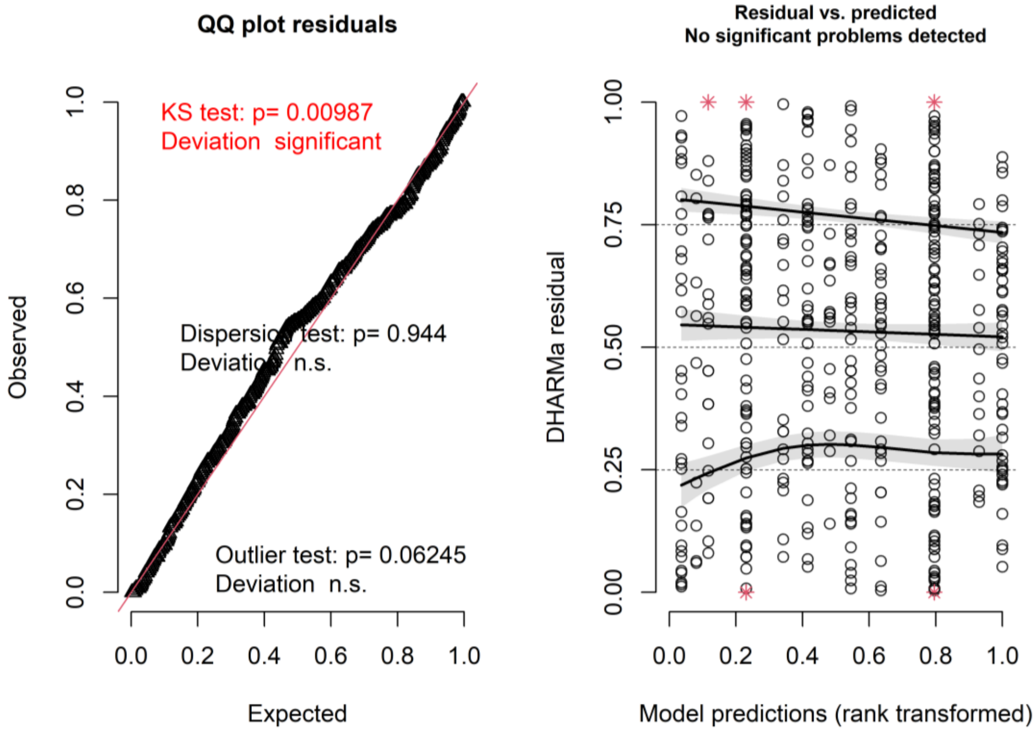


Figure A1.4. Functional diversity.

Appendix 2. Dirichlet regression examining the effects of location, period and treatment on sediment grain-size proportions

Predictors	Sediment grain size			
	Odds ratios	*CI*	*p*	*Response*
(Intercept)	10.55	2.81 – 39.62	< 0.001	rel_gravel
location [AMA 3]	0.17	0.06 – 0.50	0.001	rel_gravel
period [early]	0.14	0.03 – 0.66	0.013	rel_gravel
period [late]	0.16	0.04 – 0.65	0.010	rel_gravel
treatment [Farm]	1.22	0.43 – 3.43	0.710	rel_gravel
location [AMA 3] × period [early]	9.69	2.87 – 32.73	< 0.001	rel_gravel
location [AMA 3] × period [late]	2.90	0.92 – 9.20	0.070	rel_gravel
period [early] × treatment [Farm]	0.30	0.09 – 1.06	0.062	rel_gravel
period [late] × treatment [Farm]	0.69	0.21 – 2.25	0.543	rel_gravel
(Intercept)	22.73	5.62 – 91.92	< 0.001	rel_sand
location [AMA 3]	0.33	0.11 – 0.99	0.047	rel_sand
period [early]	0.21	0.04 – 1.02	0.053	rel_sand
period [late]	0.14	0.03 – 0.61	0.009	rel_sand
treatment [Farm]	1.29	0.44 – 3.78	0.637	rel_sand
location [AMA 3] × period [early]	7.95	2.30 – 27.49	0.001	rel_sand
location [AMA 3] × period [late]	2.26	0.70 – 7.35	0.175	rel_sand
period [early] × treatment [Farm]	0.16	0.04 – 0.58	0.005l	rel_sand
period [late] × treatment [Farm]	0.39	0.12 – 1.33	0.132	rel_sand
(Intercept)	1,135.09	293.82 – 4,385.13	< 0.001	rel_mud
location [AMA 3]	0.22	0.08 – 0.65	0.006	rel_mud
period [early]	0.09	0.02 – 0.44	0.003	rel_mud
period [late]	0.06	0.01 – 0.24	< 0.001	rel_mud
treatment [Farm]	1.33	0.46 – 3.83	0.594	rel_mud
location [AMA 3] × period [early]	11.72	3.31 – 41.49	< 0.001	rel_mud
location [AMA 3] × period [late]	6.56	2.01 – 21.38	0.002	rel_mud
period [early] × treatment [Farm]	0.10	0.03 – 0.37	0.001	rel_mud
period [late] × treatment [Farm]	0.14	0.04 – 0.47	0.001	rel_mud
Observations	154			
R^2 Nagelkerke	0.264			

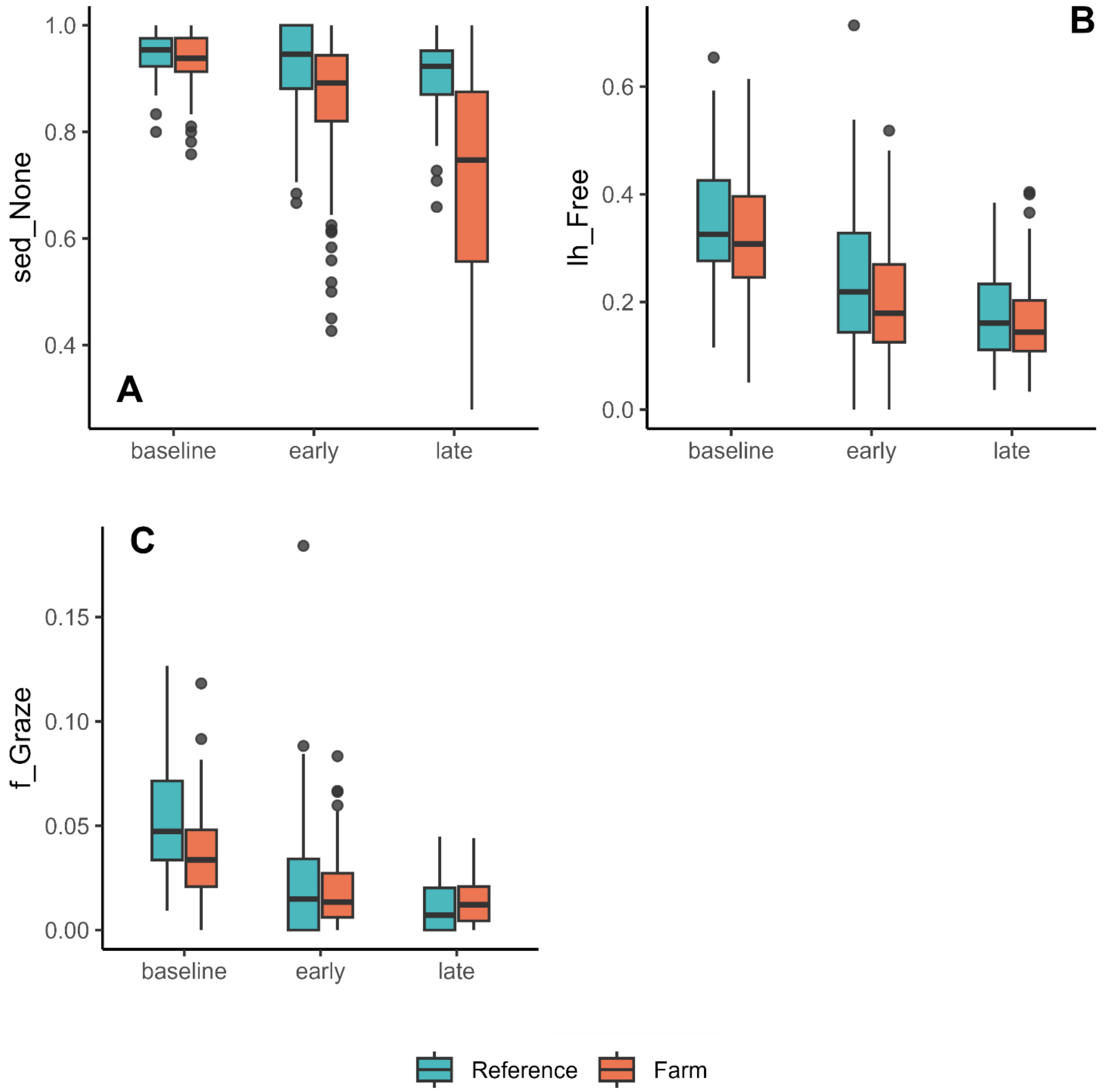
Appendix 3. Bonferroni-adjusted pairwise comparisons for epifaunal groups and shell cover across baseline, early and late farming periods

Asterisks indicate statistically significant results.

Group	Test		Chi-squared	Z statistic	P value	P value (adjusted*)
Shell cover	Kruskal–Wallis		1,058.900		< 0.001*	
	Pairwise KW	Baseline		0	1	1
		Early		19.063	< 0.001*	< 0.001*
		Late		15.435	< 0.001*	< 0.001*
Sea urchins	Kruskal–Wallis		813.660		< 0.001*	
	Pairwise KW	Baseline		-4.566	< 0.001*	< 0.001*
		Early		-11.308	< 0.001*	< 0.001*
		Late		0.266	0.790	1
Sea stars	Kruskal–Wallis		53.772		< 0.001*	
	Pairwise KW	Baseline		0	1	1
		Early		2.967	0.003*	0.045*
		Late		3.956	< 0.001*	< 0.001*
Sea cucumbers	Kruskal–Wallis		48.930		< 0.001*	
	Pairwise KW	Baseline		0	1	1
		Early		2.978	0.003*	0.043*
		Late		3.738	< 0.001*	< 0.001*

Appendix 4. Abundance (community weighted mean) of the three trait modalities identified by indicator species analysis as significantly associated with both farm and reference stations during baseline monitoring

Boxplots show changes over time (baseline, early, late) for (A) taxa with no sediment stabiliser modality (sed_None), (B) free-living habitat (ln_Free) and (C) grazing feeding mode (f_Graze).



Appendix 5. Generalised linear mixed models examining the effects of location, period and treatment of infaunal abundance, species richness (observed and theoretical) and functional diversity

Reference levels used for comparisons are indicated in brackets. CI = confidence intervals, σ^2 = residual variance, τ_{00} = variance of random intercepts, ICC = intraclass correlation coefficient, *N* = number of groups, observations = total number of samples, marginal R^2 = the variance explained by fixed effects alone, and conditional R^2 = variance explained by both fixed and random effects.

Predictors	Infaunal abundance			Species richness (observed)			Species richness (theoretical)			Functional diversity		
	Log-Mean	*CI*	*p*	*Log-Mean*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	4.0007	3.3695 – 4.6318	**< 0.001**	2.7186	2.4357 – 3.0015	**< 0.001**	1.3331	0.9566 – 1.7095	**< 0.001**	3.2216	2.7128 – 3.7304	**< 0.001**
Location [AMA3]	-0.1499	-0.8723 – 0.5725	0.684	0.1028	-0.2096 – 0.4153	0.519	0.3851	-0.0086 – 0.7789	0.055	0.5011	-0.0470 – 1.0491	0.073
Period [early]	-0.9598	-1.7269 – -0.1926	**0.014**	-0.4557	-0.7971 – -0.1143	**0.009**	0.0104	-0.4470 – 0.4678	0.964	-0.3904	-1.0076 – 0.2267	0.215
Period [late]	-0.2189	-0.9412 – 0.5034	0.552	-0.0503	-0.3759 – 0.2752	0.762	0.1129	-0.3310 – 0.5569	0.618	-0.1410	-0.7439 – 0.4619	0.647
Treatment [Farm]	0.0948	-0.2523 – 0.4418	0.592	0.0820	-0.1093 – 0.2734	0.401	0.0750	-0.2253 – 0.3754	0.624	0.0537	-0.3208 – 0.4282	0.779
Farm [AMA3]: period [early]	0.5016	-0.3901 – 1.3934	0.270	0.1640	-0.2151 – 0.5432	0.396	-0.1973	-0.6802 – 0.2856	0.423	-0.1316	-0.8056 – 0.5424	0.702
Farm [AMA3]: period [late]	0.0874	-0.8064 – 0.9811	0.848	-0.2616	-0.6448 – 0.1217	0.181	-0.5522	-1.0527 – -0.0517	**0.031**	-0.6406	-1.3404 – 0.0591	0.073
period [early]: treatment [Farm]	0.6130	0.2061 – 1.0199	**0.003**	0.2423	0.0216 – 0.4630	**0.031**	-0.1945	-0.5505 – 0.1615	0.284	0.2037	-0.2392 – 0.6465	0.367
Period [late]: treatment [Farm]	0.7046	0.2747 – 1.1345	**0.001**	0.2650	0.0311 – 0.4989	**0.026**	-0.2489	-0.6269 – 0.1291	0.197	0.0967	-0.3849 – 0.5783	0.694
Random effects												
σ^2	0.17			0.06			0.15			0.36		
τ_{00}	0.07 farm:sampling_event			0.01 farm:sampling_event			0.02 farm:sampling_event			0.03 farm:sampling_event		
	0.00 farm:subzone			0.00 farm:subzone			0.00 farm:subzone			0.00 farm:subzone		
	0.12 farm:subzone:station			0.03 farm:subzone:station			0.09 farm:subzone:station			0.11 farm:subzone:station		
ICC	0.52			0.42								
N	2 farm			2 farm			2 farm			2 farm		
	14 sampling_event			14 sampling_event			14 sampling_event			14 sampling_event		
	12 subzone			12 subzone			12 subzone			12 subzone		
	206 station			206 station			206 station			206 station		
Observations	481			481			477			481		
Marginal R^2 / conditional R^2	0.290 / 0.660			0.259 / 0.568			0.174 / -			0.153 / -		

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