

REVIEW ARTICLE

The restoration potential of offshore mussel farming on degraded seabed habitat

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Abstract

The United Kingdom's first large-scale, offshore, long-line mussel farm deployed its first ropes in 2013 in Lyme Bay, southwest United Kingdom, located in an area of seabed that was heavily degraded due to historic bottom-towed fishing. It was hypothesised that due to the artificial structures that accumulate mussels and exclude destructive fishing practices, the seabed could be restored. To assess the restoration potential of the farm and its ecosystem interactions over time, a multi-method, annual monitoring approach was undertaken. Here, we tested the effects of the farm trial stations on the seabed habitat, epifauna and demersal species over 5 years. Responses of % mussel cover, sessile and sedentary, and mobile taxa were measured using three video methods. Within 2 years of infrastructure deployment, mussel clumps and shells were detected below the headlines, increasing the structural complexity of the seabed. After 4 years, there was a significantly greater abundance of mobile taxa compared to the Controls that remained open to trawling. Commercial European lobster and edible crab were almost exclusively recorded within the farm. We discuss whether these findings can be considered a restoration of the seabed and how these data can be used to inform the future management of offshore mariculture globally.

KEYWORDS

aquaculture, artificial infrastructure, benthic macrofauna, blue growth, ecology, epibenthos, mariculture, *Mytilus edulis*, policy

1 | INTRODUCTION

To feed the world's growing population, and meet global fish consumption demands, aquaculture continues to expand rapidly. In 2018, aquaculture production made up 46% of global total production of seafood (FAO, 2020), making up the shortfall left by capture fisheries unable to keep up with an ever-increasing demand for fish and seafood (Jackson et al., 2001; Pauly et al., 2002). As capture

fishery production remains static (FAO, 2020), more ocean space needs to be utilised to feed the world. Therefore, aquaculture will play a key role in food production as demand for protein increases (Clavelle et al., 2019). As 37% of aquaculture production comes from the marine and coastal environment comprising mostly finfish and bivalve molluscs (FAO, 2020), concerns have been raised about the impact of this industry on the surrounding environment (McKindsey et al., 2011).

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Recently, bivalve mollusc aquaculture has been identified as providing one of the lowest impact animal source foods. Bivalve mollusc aquaculture requires very little energy input, has the lowest greenhouse gas production per portion of protein, absorbs nutrients and requires almost no fresh water and no antibiotics (Hilborn et al., 2018). Furthermore, bivalve aquaculture provides an important ecosystem service in the form of carbon sequestration (van der Schatte Olivier et al., 2018) as they use carbon in the water to form calcium carbonate, hence removing carbon from the ocean (Hickey, 2009). Within the United Kingdom, the native blue mussel *Mytilus edulis* contributes the most to cultivated bivalve landings (Laing & Spencer, 2006). Traditionally, mussel aquaculture has been located in sheltered coastal inlets where dispersal capacity is relatively low (Lacson et al., 2019). Mussel biodeposits (faeces and pseudofaeces) therefore accumulate on the seabed (Kumar & Cripps, 2012), impacting the chemical and physical characteristics of the seabed (Kaspar et al., 1985; Nizzoli et al., 2006).

Studies assessing the impacts of inshore mussel farms on the benthic community report reductions in infauna abundance and diversity (Grant et al., 2012) and reduced oxygen conditions, along with an increase in organic matter and finer sediment (Carlsson et al., 2012; Chamberlain et al., 2001; Hartstein & Rowden, 2004). While this is not always the case (Drouin et al., 2015; Inglis & Gust, 2003), there has been a call by the EU directive on Marine Spatial Planning to move aquaculture offshore in an attempt to mitigate environmental impact, resolve issues of space limitation in inshore areas and meet global protein demands (European Commission, 2012).

As offshore mussel farming is still relatively new, limited research has been done to quantify its environmental impact. To date, it seems that offshore mussel farming may be less impactful than inshore as evidence has shown little or no effect on sediment characteristics or the associated macroinfauna (Danovaro et al., 2004; Fabi et al., 2009; Lacoste et al., 2018). Due to the potential upscaling of this industry, it is now imperative to understand the long-term, ecosystem effects of offshore mussel farming (Gentry et al., 2017). Southwest United Kingdom has been identified as a key location for offshore aquaculture expansion (Department for International Trade, 2022; Dorset Aquaculture, 2022; South West Aquaculture Network, 2022), due to its level of exposure and good water quality (Masselink et al., 2016; Sheehan et al., 2021). As pioneers in this industry, Offshore Shellfish Ltd. began to develop the United Kingdom's first, large-scale, offshore long-line mussel farm. The area of seabed licensed is 15 km² of degraded sediment habitat due to intensive dredging and trawling (Sheehan et al., 2013). Historical fishing maps suggest that this area was once colonised by mussel and/or oyster reefs (Olsen, 1883). We hypothesised that by introducing mussel farm infrastructure that attract mussels and exclude destructive fishing activities, the mussel farm could have positive ecosystem benefits and a restorative effect on the benthos. Since before the first rope was deployed, an annual, multi-method, ecosystem monitoring survey began, including infauna, pelagic species, plankton, birds and mammals (Sheehan et al., 2019). Here, we focus on the effect of the mussel farm on the seabed

habitat, epifauna and demersal species, at two trial stations over 5 years.

2 | MATERIALS AND METHODS

2.1 | Site description

Lyme Bay, in the southwest of the United Kingdom, is home to the United Kingdom's first large-scale offshore long-line mussel farm. Offshore Shellfish Ltd. is cultivating the native blue mussel *M. edulis*. Once completed, the farm will be the largest of its type in European waters, situated over three sites covering a total area 15.4 km², between 4 and 10 km offshore. The farm consists of a series of 150 m headlines moored to the seabed with a pair of screw anchors, with continuous rope droppers hung from the headlines, positioned ~2–12 m below the sea surface. Buoys are placed at regular intervals along the headlines to keep the structures afloat (Figure 1a).

To assess the potential ecological effects of a large-scale mussel farm in the offshore environment, trial stations were designated within two of the mussel farm consented sites, each measuring 100 m × 650 m. The first is in the southeast corner of Site 1 (Trial Station 1), and the second is in the northwest corner of Site 2 (Trial Station 2) (Figure 1b). Within each Trial Station (TS), there are two Plots where headlines have been deployed and two Control Plots, one located 500 m to the southwest and the other 500 m to the northeast of the Rope Plots (Figure 1b). The number of headlines within Plots has varied over the sampling years. At TS2, the headlines were exclusively used to suspend spat ropes. However, at TS1, use changed from spat ropes to re-seeded ropes early on due to spat settling more successfully at TS2. TS1 was then used to grow mussels to harvestable size. The TSs were annually monitored from 2013, before the mussel ropes were deployed, to 2017, 4 years post-deployment.

2.2 | Seabed sampling

Three remoted underwater video methods were employed to assess % mussel cover, species richness (number of taxa), total abundance (number of individuals) and assemblage composition of sessile and sedentary epifauna (those that are stationary or crawl slowly over the seabed), mobile epifauna and the abundance of five pre-selected key taxa/groupings: European lobster *Homarus gammarus* (Figure 2c: commercial species), edible crab *Cancer pagurus* (Figure 2d: commercial species) schooling fish (Figure 2e: Atlantic horse mackerel *Trachurus trachurus* and whiting *Merlangius merlangus*; commercial species), common whelk *Buccinum undatum* (commercial species) and common starfish *Asterias rubens* (Figure 2f: predator). We test the hypothesis that over time, the mussel farm trial station Rope Plots would change the epibenthic habitat (mussel shell cover and mussel clump size) and increase abundances of the associated taxa relative to Control Plots. These data will provide important evidence gaps for future licensing of

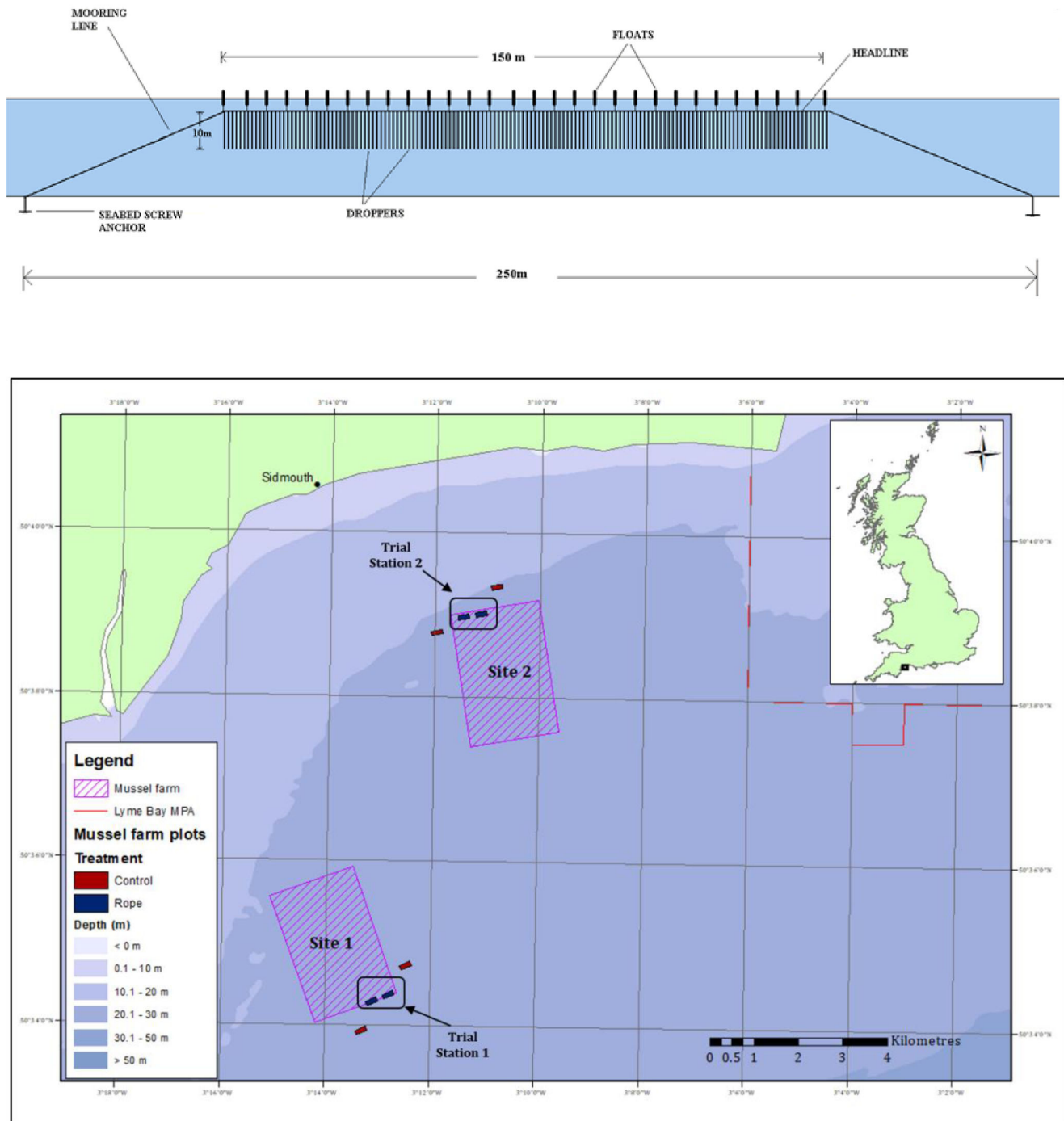


FIGURE 1 (a) Sectional view of a headline and (b) locations of Rope Plots at Trial Stations 1 and 2, and corresponding Control Plots at the Lyme Bay mussel farm

future aquaculture both in the United Kingdom and across the world. Sampling dates for each video survey method are provided in Table 1.

Sessile and sedentary taxa (including mussel cover): To optimise sampling efficiency, avoid entanglement with the mussel ropes and enable sampling directly under the ropes, two survey methods were used to record benthic video transects. The first method was a towed underwater video system (TUVS; Figure 3a) that was used ~1 m away from the mussel ropes, while a remotely operated vehicle (ROV: VideoRay

Pro 4; Figure 3b) was deployed to record transects under the ropes. Both systems were mounted with high-definition cameras, LED lights and scaling lasers (two parallel green 532 nm lasers were used to allow field of view calibration during video analysis) (Sheehan et al., 2010, 2016, 2021). Transects were measured using HYPACK GPS software.

Mobile taxa: Baited remote underwater video (BRUV) was used to quantify the benthic and demersal mobile taxa. Three BRUV units (Figure 3c) were deployed ~30 m apart in each Plot for 40 min. This

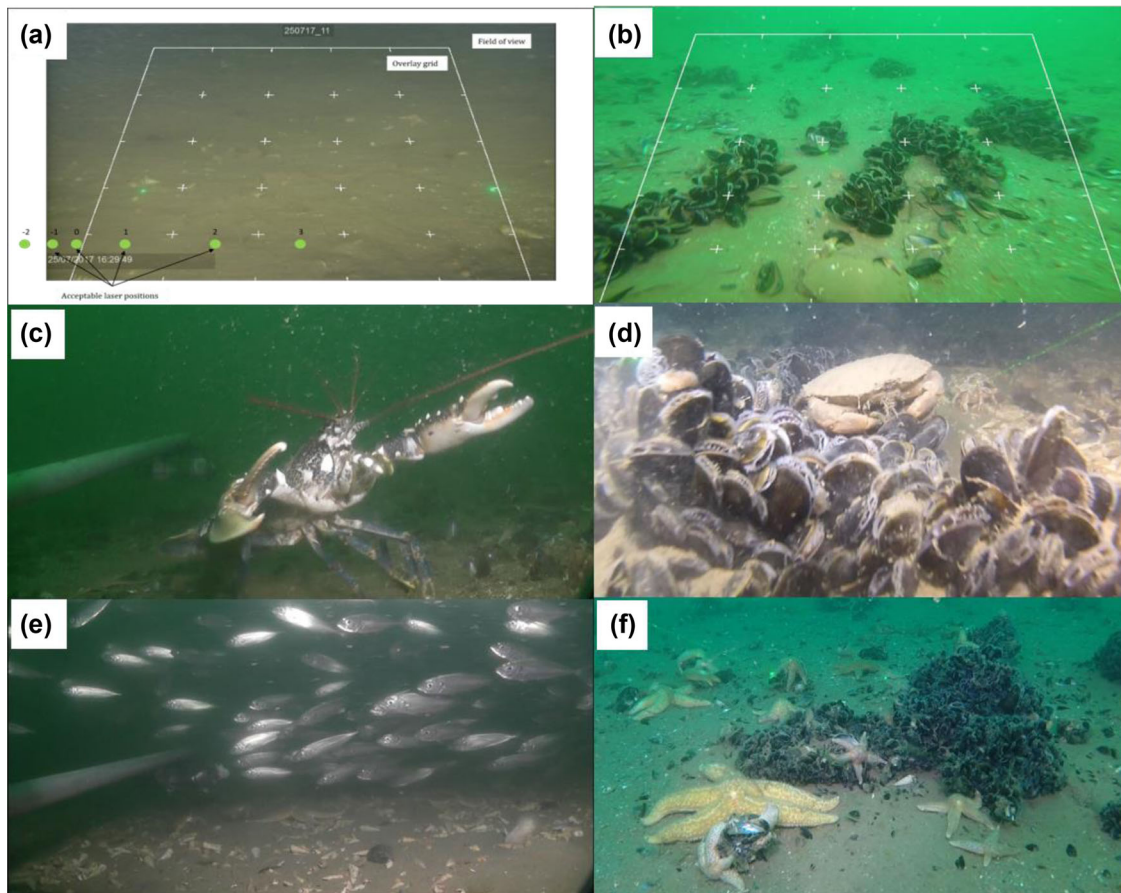


FIGURE 2 Frame grabs showing (a) overlay grid and acceptable laser positions, (b) mussel shells and clumps contributing to % cover of mussels, (c) European lobster *Homarus gammarus*, (d) edible crab *Cancer pagurus*, (e) schooling fish (whiting *Merlangius merlangus* and Atlantic horse mackerel *Trachurus trachurus* and (f) common starfish *Asterias rubens*

TABLE 1 Sampling dates for each video method

Year	TUVS	ROV	BRUV
2013	9/12/20 August	No sampling	13/14/19/21 August
2014	3–4 September	4–5 September	5–7 September
2015	11–13 August	7 September	23/30 July, 11–12 August
2016	17–21 July	25 August	21–24 June
2017	25–31 July	30–31 August	27–30 June

Abbreviations: BRUV, baited remote underwater video; ROV, remotely operated vehicle; TUVS, towed underwater video system.

allowed for 30 min of filming, with a 5-min 'settling' period after the unit had reached the seabed. Thirty minutes of video captures on average 75% or more of the species richness and abundance that would have been seen in 60 min of footage (Bicknell et al., 2019), and so was chosen in interest of time and cost-effectiveness, and to limit the spread of the bait plume. Each BRUV unit was equipped with a pole holding a wire mesh bait box 1 m in front of the camera. Note that 100 g of bait (*Scomber scombrus*) was replenished for each deployment. See Rees et al. (2021) and Davies, Holmes, Rees, et al. (2021) for detailed information on BRUV structure and configuration.

2.3 | Video data extraction and analysis

Sessile and sedentary taxa (including mussel cover): Video footage from the TUVS and the ROV was analysed according to a standard procedure carried out in previous work by Sheehan et al. (2010, 2021) and Davies, Holmes, Bicknell, et al. (2021). First, mobile and infrequent fauna were enumerated by viewing each video transect and counting individuals that passed through the 'gate' formed by the two laser dots. Second, smaller and more frequent organisms were counted from still images obtained from randomly selected frame grabs. Frame grabs were extracted from the video footage at 5-s intervals and overlaid with a digital quadrat using bespoke software (Cybertronix CXOverlay) (Figure 2a). Frames were quality controlled and only included if they met certain criteria of laser placement (within the boundary of the digital quadrat) and focus (taxa and substrate within focus and identifiable). The useable frames were then randomly subsampled in order to obtain 30 frames from the transects. These were then averaged for each transect. To quantify the % cover of mussel debris (dead shells and live clumps) on the seabed, a grid overlay with 25 squares was superimposed over each frame and the number of squares containing mussel shell recorded (Sheehan, Bridger & Attrill, 2015; Sheehan, Bridger, Cousens, et al., 2015). The score was then converted into %

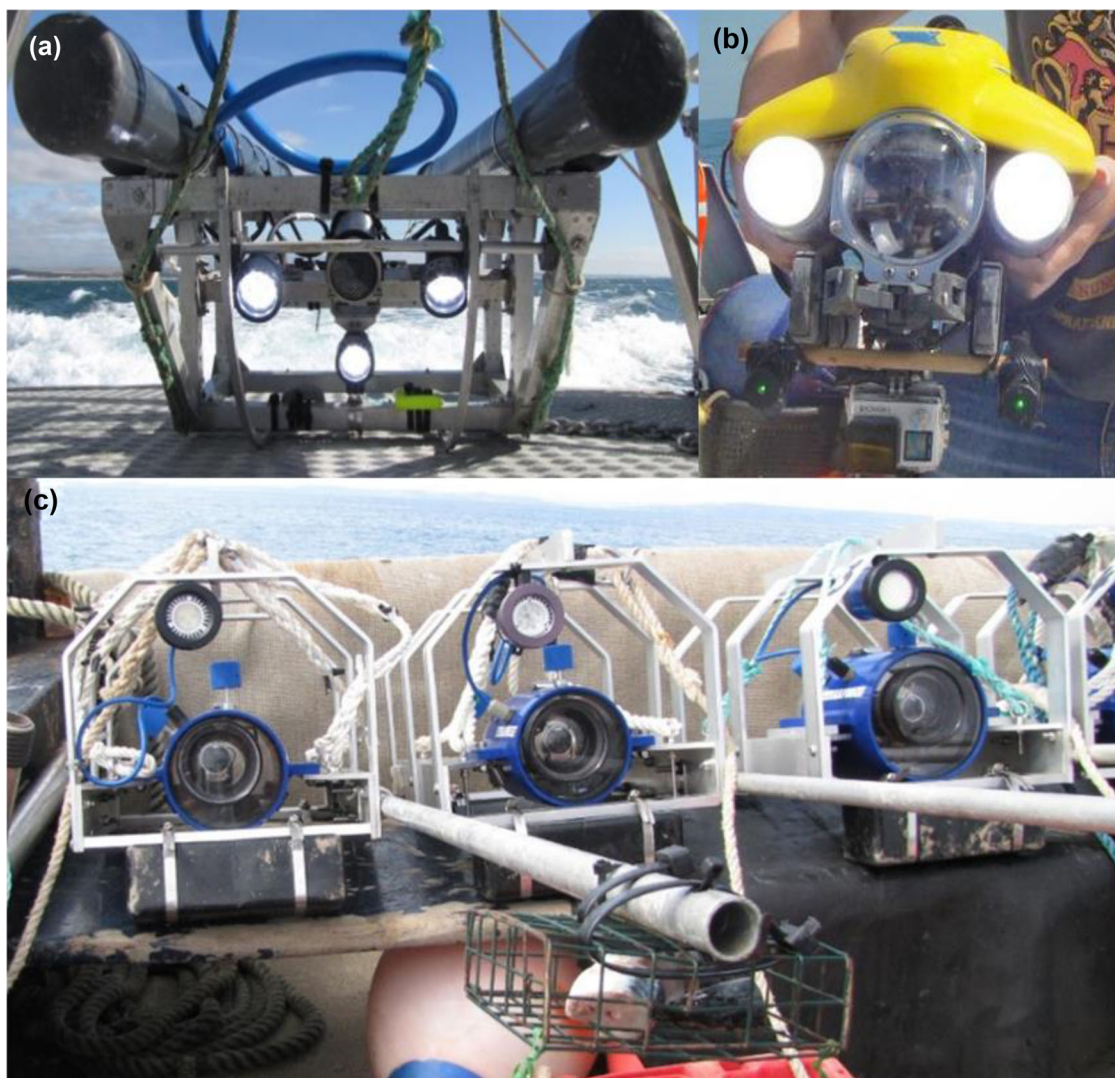


FIGURE 3 Images of video equipment used for data collection (a) towed underwater video system (TUVS) showing high-definition (HD) video camera, LED lights and lasers, (b) remotely operated vehicle (ROV) with mounted GoPro camera, LED lights and lasers and (c) baited remote underwater video (BRUV) units with camera module, LED light and pole with bait box

cover (4% per square; Figure 2b). The length of the clump at the longest point was measured using ImageJ (version 1.52p).

Mobile taxa: Quantitative data were extracted from BRUV samples by viewing the video footage at normal speed for 30 min. For each 1-min segment of the video, the maximum number of individuals on screen (maxN) was recorded for each taxon. Relative abundance of each taxon was recorded as the greatest maxN value within the 30 min analysed (maxN min^{-1}) (Willis et al., 2000). This gives a conservative estimate of abundance of mobile taxa and decreases the chance of an individual being repeatedly recorded (Bicknell et al., 2019; Cappo et al., 2003).

Organisms were identified to the lowest taxonomic level possible. Morphologically similar species that were difficult to identify were grouped, for example, spider crab genera *Inachus* and *Macropodia* were recorded as *Inachus* spp. and *Macropodia* spp., and all species within the family Gobiidae were recorded as 'Grouped gobies'.

2.4 | Data analysis

Univariate response metrics (number of taxa, total abundance, abundance of indicator species) were analysed using generalised linear mixed effects models. Models were fit using the R packages 'glmmADMB' and 'lme4' (Bates et al., 2020; Fournier et al., 2012; Skaug et al., 2016). Response metrics were assessed as a function of Time since deployment (continuous: 0–4) and Treatment (categorical: Rope and Control) with Trial Station (categorical: TS1 and TS2) as a random factor. Number of taxa and total abundance of Sessile and Sedentary taxa were derived from TUVS and ROV (modelled using a Poisson and Gamma distribution, respectively); Number of taxa and total abundance of Mobile taxa were derived from BRUV (both modelled using a Poisson distribution). Abundance of *A. rubens* was derived from TUVS and ROV (using a Gamma distribution), and abundance of schooling fish was derived from BRUV (using a Poisson distribution). The

interaction term (Time since deployment \times Treatment) was included in each model. Sample versus fitted residuals, quartile-quartile and autocorrelation of temporally sequential samples were assessed visually, to fit assumptions of the models used.

Multivariate assemblage composition data were analysed using Permutational multivariate analysis of variance (PERMANOVA+, using PRIMER v7 software package) (Anderson, 2001). Differences in assemblage composition for sessile and sedentary taxa, and mobile taxa were compared between the following factors: Time since deployment (fixed: 0–4), Trial Station (random: TS1, TS2) and Treatment (fixed, nested in TS: Rope, Control) with two replicate Plots per Treatment within each Trial Station. Resemblance matrices were based on Bray Curtis similarity of square root transformed data to down weight dominant and highly clustered taxa (Clarke et al., 2006). Significant interactions between Time since deployment and Treatment in univariate and multivariate metrics were further explored using pairwise tests. Similarity percentages (SIMPER) were conducted to identify the species driving the differences in assemblage composition (Clarke & Warwick, 2001). Multivariate patterns were visualised using non-metric multi-dimensional scaling (nMDS) ordination plots using the centroids of each Time since deployment \times Trial Station \times Treatment combination (Terlizzi et al., 2005).

3 | RESULTS

3.1 | Mussel cover

Mussel shells and clumps were first observed under the mussel headlines 6 months and 18 months, respectively, after headlines were first deployed (Figure 4a). They continued to be detected in subsequent years in the Rope treatment, but never in the Control plots located 500 m away.

Abundance of mussel shells was greatest in Year 2 at both TSs (TS1 = $36.42 \pm 13.64 \text{ m}^{-2}$, TS2 = $74.66 \pm 20.51 \text{ m}^{-2}$) and decreased in Years 3 and 4, particularly at TS2 (Figure 4b). Abundance of mussel clumps was similar across Years 2–4 at TS1. At TS2, abundance was highest in Year 2 ($1.54 \pm 0.92 \text{ m}^{-2}$). There was a decrease in abundance from Years 2 to 3, and then a slight increase again in Year 4 ($0.87 \pm 0.54 \text{ m}^{-2}$) (Figure 4c).

Mussel clump length was greatest at TS1 in Year 4 at a mean length of $15.88 \pm 4.56 \text{ cm}$ (Figure 4d). At TS2, mussel clump length was greatest in Year 2 ($11.08 \pm 4.95 \text{ cm}$), dropped in Year 3 ($2.08 \pm 2.08 \text{ cm}$) and then rose again in Year 4 ($7.47 \pm 3.76 \text{ cm}$) (Figure 4d).

3.2 | Sessile and sedentary taxa

A total of 58 sessile and sedentary taxa were identified: 20.7% or which were chordates, 17.2% were crustaceans and 15.5% were cnidarians. A full list of taxa with mean, maximum and minimum abundances can be found in Table S1. There were several taxa that were present through the survey, for example, *Pecten maximus*, *Alcyonium digitatum* and *Cal-*

lionymus lyra (Table S2). Other taxa were present in the Rope treatment after the deployment of the mussel headlines. For example, *Metridium dianthus*, *Maja squinado* and *C. pagurus* were present from Year 2, and *Syngnathus acus* was present from Year 3 (Table S2). However, there were instances of taxa becoming absent after headline deployment including Sagartiidae, *Molgula manhattensis* and *Cellepora pumicosa*. Further to this, *Cereus pedunculatus* and *Suberites* spp. were absent in the Rope treatment after the headline deployment but were then present again from Year 3 (Table S2).

The number of sessile and sedentary taxa showed no statistically significant change across treatments over time since deployment ($p > 0.05$; Table S3). Figure 5a shows that the number of taxa decreased marginally in the Rope treatment over time. The total abundance of sessile and sedentary taxa also showed no statistically significant change across treatments over time since deployment ($p > 0.05$; Table S3). Total abundance was similar in the Rope and Control treatments throughout the survey (Figure 5b).

There was a significant difference in assemblage composition of sessile and sedentary taxa between the Rope and Control treatments ($p = 0.0002$; Table S3). The assemblage composition was also different between TS1 and TS2.

At TS1, assemblage composition between the two treatments was consistently significantly different from Years 0 to 4 (all $p < 0.05$; Table S3). SIMPER analysis showed the average dissimilarity between treatments increased with time since deployment, from 26.8% in Year 0 to 36.7% in Year 4 (Table S4). This is visualised in the nMDS where the distance between the two treatments on the plot is greatest in Year 4 (Figure 5c). Of the top species contributing to this dissimilarity between treatments in Year 4, common starfish *A. rubens* and hermit crabs *Pagurus* spp. had a greater average abundance in the Rope treatment (*A. rubens*: Rope = 1.79, Control = 0.59, *Pagurus* spp.: Rope = 3.30, Control = 2.25; Table S4), whereas common tower shell *Turritellinella tricarinata* and cylinder anemones *Cerianthus* spp. had a greater average abundance in the Control treatment (*T. tricarinata*: Rope = 2.73, Control = 3.77, *Cerianthus* spp.: Rope = 1.83, Control = 2.46; Table S4).

At TS2, assemblage composition was significantly different between treatments in Years 1, 3 and 4 after headline deployment (all $p < 0.05$; Table S3). The average dissimilarity between treatments increased with time since deployment (Year 0 = 20.4%, Year 4 = 47.4%; Table S4), which is visualised in the nMDS plot (Figure 5c). Hydroids substantially contributed to the dissimilarity, with a greater average abundance in the Control treatment in all years, except Year 2. After Year 0, *Pagurus* spp. had a consistently greater average abundance in the Rope treatment (Table S4).

3.3 | Mobile taxa

A total of 11 mobile taxa were identified: 10 chordates and one crustacean. A full list of taxa can be found in Table S1. *Scyliorhinus canicula*, *Merlangius merlangius* and *T. trachurus* were present throughout the survey (Table S2). Both *Trisopterus minutus* and *Trisopterus luscus* were present after the deployment of the mussel headlines, after Years 2

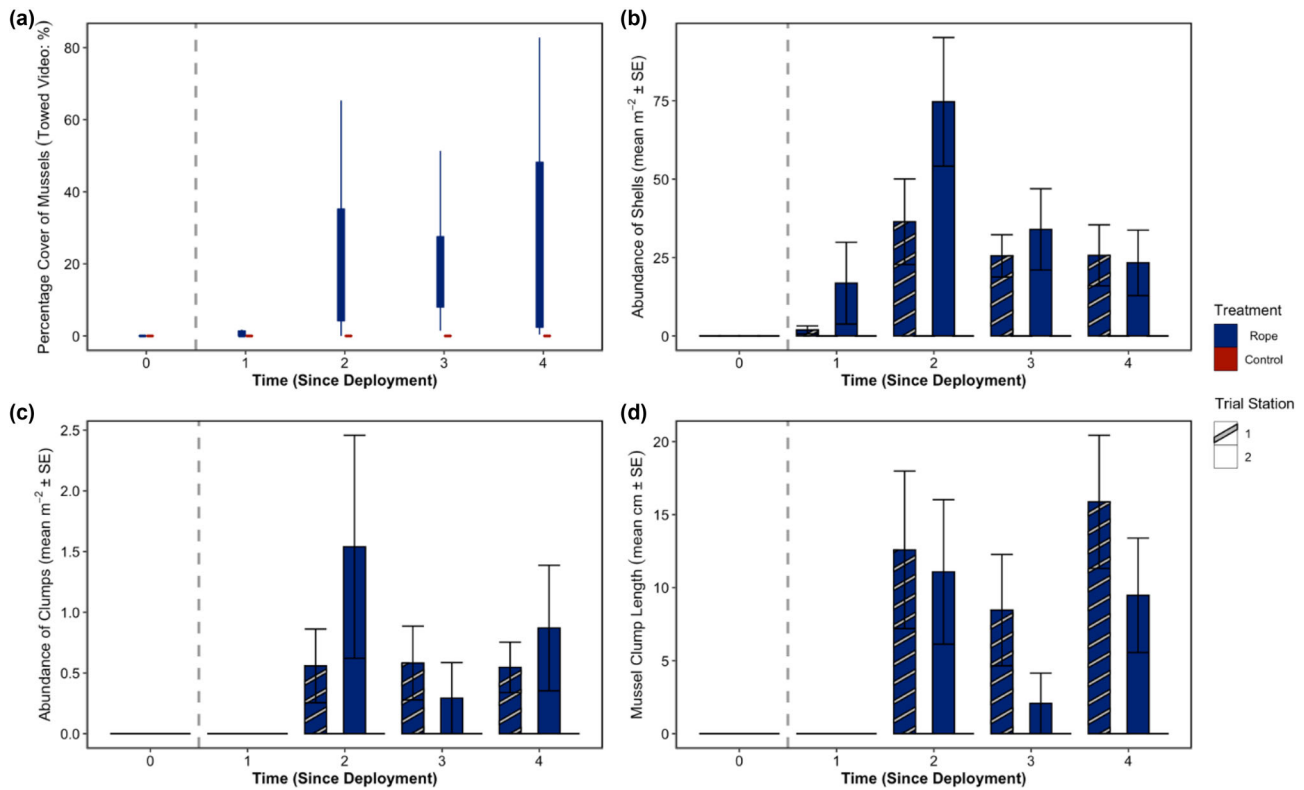


FIGURE 4 Temporal change in (a) percentage cover of mussels, (b) abundance of shells, (c) abundance of clumps, and (d) mussel clump length derived from towed underwater video system (TUVS) and remotely operated vehicle (ROV) from Rope (blue) and Control (red) treatments

and 3. However, *Zeus faber* was only present in Year 0, before headline deployment (Table S2).

The number of mobile taxa was not statistically significantly different between treatments over time since deployment ($p > 0.05$; Table S5). Figure 6a shows an increase in the number of taxa over time, with a greater number of taxa in the Rope than the Control treatment from Year 1, after the headlines were deployed. There was a statistically significant difference in total abundance of mobile taxa between treatments over time since deployment ($p = 0.0001$; Table S5). From the start of the survey, there was a greater total abundance in the Rope treatment. The difference between the two treatments increased over time as total abundance increased in the Rope treatment and decreased in the Control (Figure 6b). The greatest difference between treatments was in Year 4 (Rope = 92.17 ± 17.39 MaxN min^{-1} , Control = 47.81 ± 10.80 MaxN min^{-1}). Pairwise tests show that in this year, there was a significantly greater total abundance of mobile taxa in the Rope compared to the Control treatment at TS1 ($p = 0.001$; Table S5).

Assemblage composition was statistically significantly different between treatments over time since deployment ($p = 0.005$; Table S5). At TS1, assemblage composition of the mobile species became significantly different in Year 4, 3 years after headline deployment ($p = 0.003$; Table S5). This result is visually represented in the nMDS plot, which shows the distance between the two treatments in Year 4 is greater than in any other year (Figure 6c). The dissimilarity between the Rope and Control treatments at TS1 was 46.0% in Year 4, compared to 31.8%

before headline deployment (Table S6). Over 50% of this dissimilarity was due to *T. trachurus*, which was twice as abundant in the Rope treatment (Table S6). This is illustrated in the nMDS plot: the treatments within years with a greater abundance of *T. trachurus* are separated from those with a lesser abundance (Figure 6c). At TS2, there were no significant differences in assemblage composition in any year (all $p > 0.05$; Table S5).

3.4 | Key taxa/groupings

Abundance of *A. rubens* showed no change between treatments over time ($p > 0.05$; Table S7); however, there was a significant difference between treatments ($p = 0.04$; Table S7). This is reflected in Figure 7a which shows an increase in *A. rubens* in the Rope treatment, but not in the Control. Conversely, the relative abundance of schooling fish (cumulative abundance of whiting *M. merlangus* and Atlantic horse mackerel *T. trachurus*) changed significantly between treatments over time ($p < 0.0001$; Table S7), with abundances staying consistent in the Rope and decreasing over time since deployment in the Control (Figure 7b). Pairwise tests show a significantly greater abundance of schooling fish in the Rope compared to the Control treatment in Year 4 at TS1 ($p = 0.01$; Table S7).

There were few incidents of *H. gammarus*, *C. pagurus* and *B. undatum* across all treatments and years. There were four recordings of *H. gammarus* across all years, all within the Rope treatment. *Cancer*

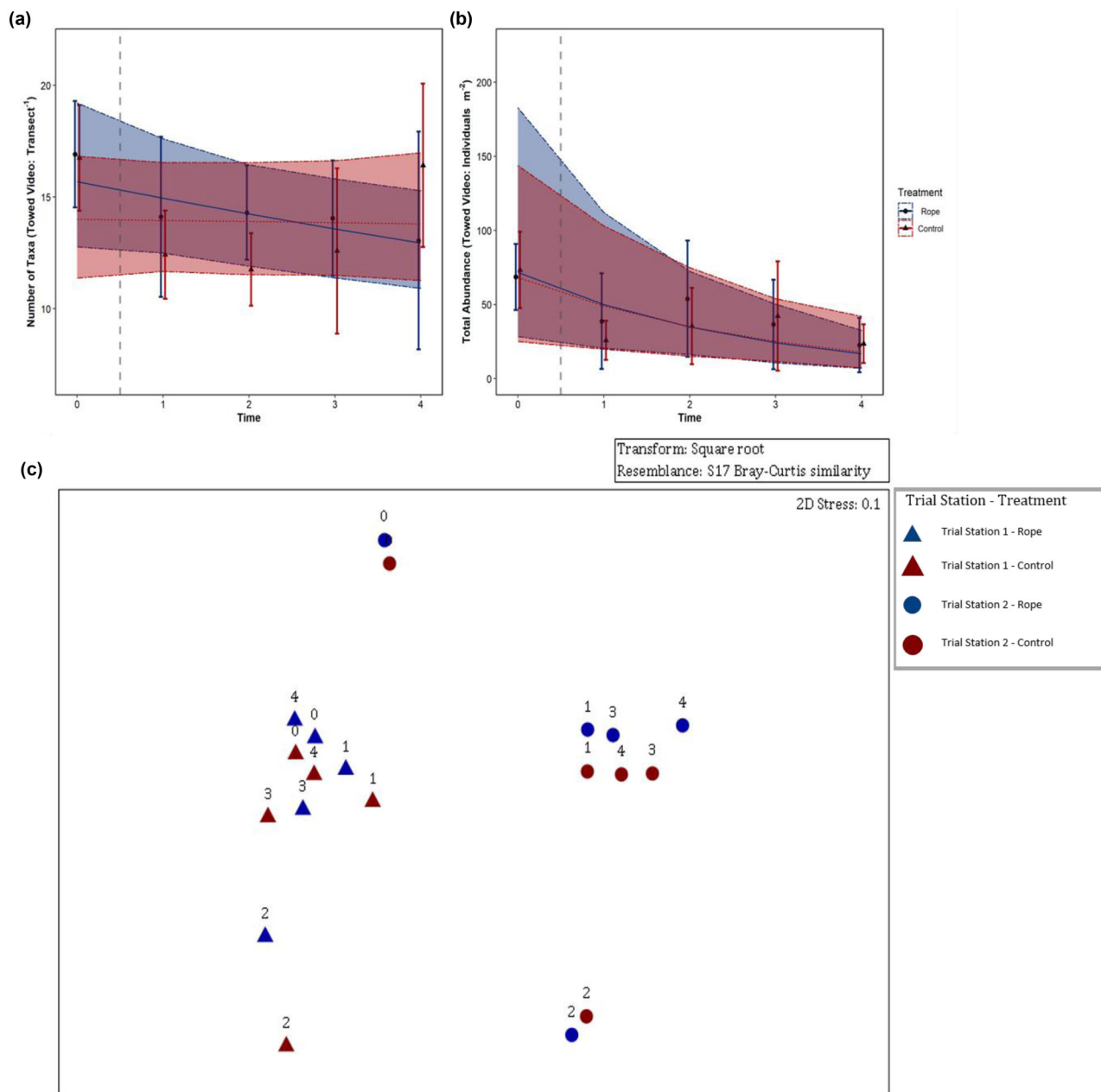


FIGURE 5 Temporal change in (a) number of taxa, (b) total abundance and (c) non-metric multidimensional scaling (nMDS) ordination plot illustrating differences in assemblage composition of sessile and sedentary taxa derived from towed underwater video system (TUVS) and remotely operated vehicle (ROV) from Rope (blue) and Control (red) Treatments. Lines show model estimates with shading and dotted lines indicating 95% confidence intervals. Symbols with error bars show raw mean values and 95% confidence intervals. Vertical dashed line denotes when first headlines were installed.

pagurus was recorded 12 times, all but one within the Rope treatment. *Buccinum undatum* was recorded 34 times, with 16 in the Rope and 18 in the Control.

4 | DISCUSSION

The development of an offshore, longline mussel farm at two trial stations in Lyme Bay was found to modify the benthic habitat and species

below the ropes after just 2 years. Mussel shells and clumps were observed every year from 6 months and 18 months, respectively, after headlines were first deployed. Both the size of mussel clumps and the % cover of mussel shell accumulating under the farm also increased over time. Similar patterns were also observed for the associated epifauna and mobile species. The abundance of benthic mobile species such as *T. trachurus* increased over time in both trial stations, especially at TS1 Rope plots where adult mussels are grown to harvest. Here, they increased by over 300% over 4 years. *Homarus gammarus* and *C. pagurus*

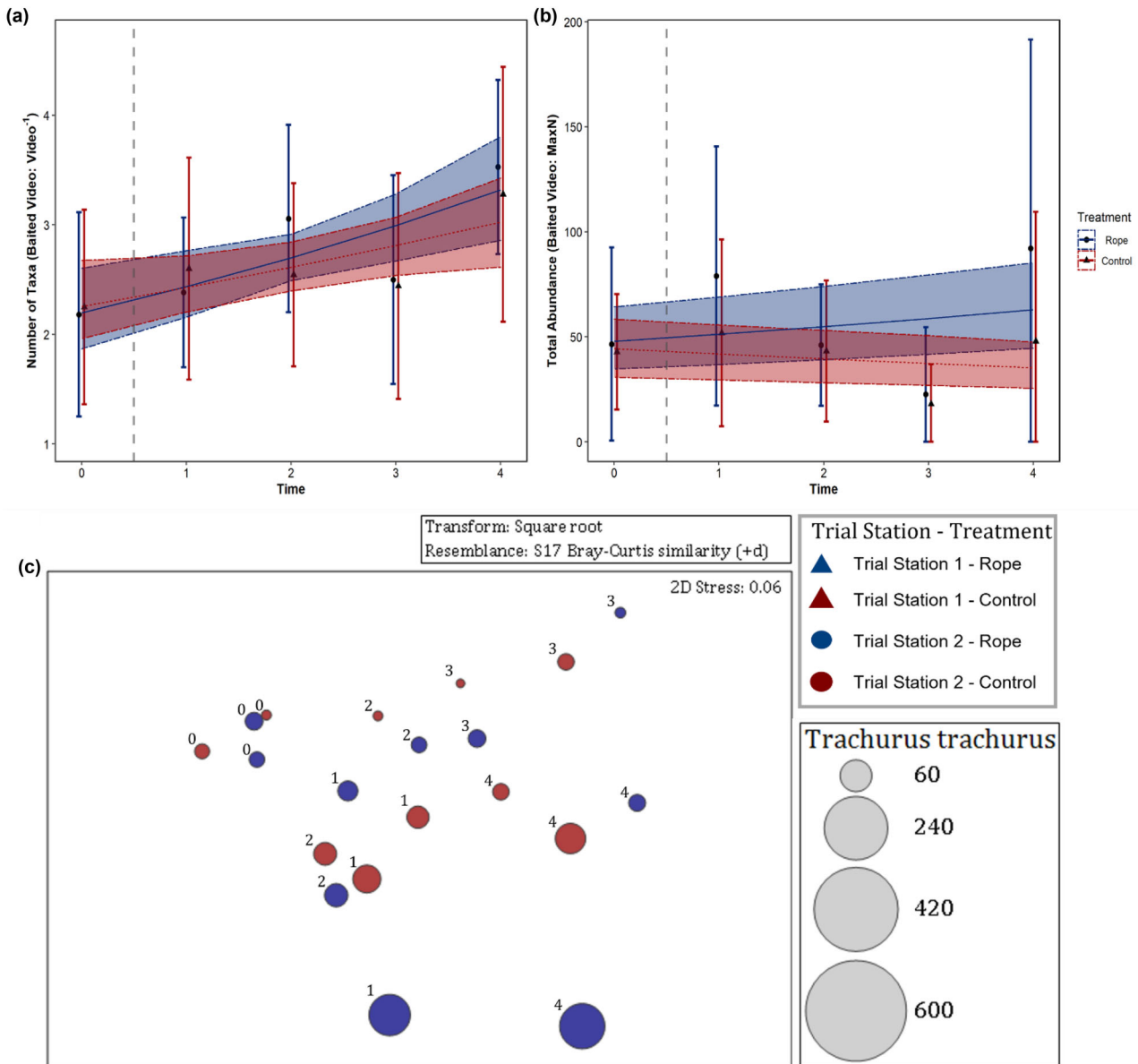


FIGURE 6 Temporal change in (a) number of taxa, (b) total abundance and (c) non-metric multidimensional scaling (nMDS) ordination plot illustrating differences in assemblage composition of mobile taxa derived from baited remote underwater video (BRUV) from Rope (blue) and Control (red) Treatments. Lines show model estimates with shading and dotted lines indicating 95% confidence intervals. Symbols with error bars show raw mean values and 95% confidence intervals. Vertical dashed line denotes when first headlines were installed.

were almost exclusively recorded beneath the mussel headlines. This is the first experimental, long-term ecological evidence that offshore mussel farming can deliver positive, restorative effects on degraded seabed habitats.

Prior to the installation of Lyme Bay mussel farm, the area was part of a busy fishing ground off the southwest United Kingdom, with vessels operating from Brixham, Lyme Regis, Axmouth, Beer and West Bay. Historically, the area was believed to house extensive biogenic shellfish reef, but there is no evidence of this in the literature. However, ancient seabed maps show a wide coverage of oyster and mussel reefs along the southwest UK coastline (Olsen, 1883). This lack of information can lead to 'shifting baselines', where fisheries scientists accept the stock size

and species composition that existed at the beginning of their experience as the baseline for which changes are evaluated (Pauly, 1995). This is apparent for Australian oyster reefs where it is often forgotten that they once characterised the Australian coastline, which are now areas of sand and mud (Alleway & Connell, 2015). This illustrates the acceptance that soft sediment is the natural habitat, when perhaps it is not. There is evidence that the reefs in Lyme Bay should be home to slow growing and long-lived sessile species, including pink sea fan *Eunicella verrucosa* and ross coral *Pentapora foliacea* (Sheehan et al., 2013). Due to intensive demersal trawling and scallop dredging, these habitats have been degraded and are dominated instead by fast-growing, short-lived species (Sheehan et al., 2013).

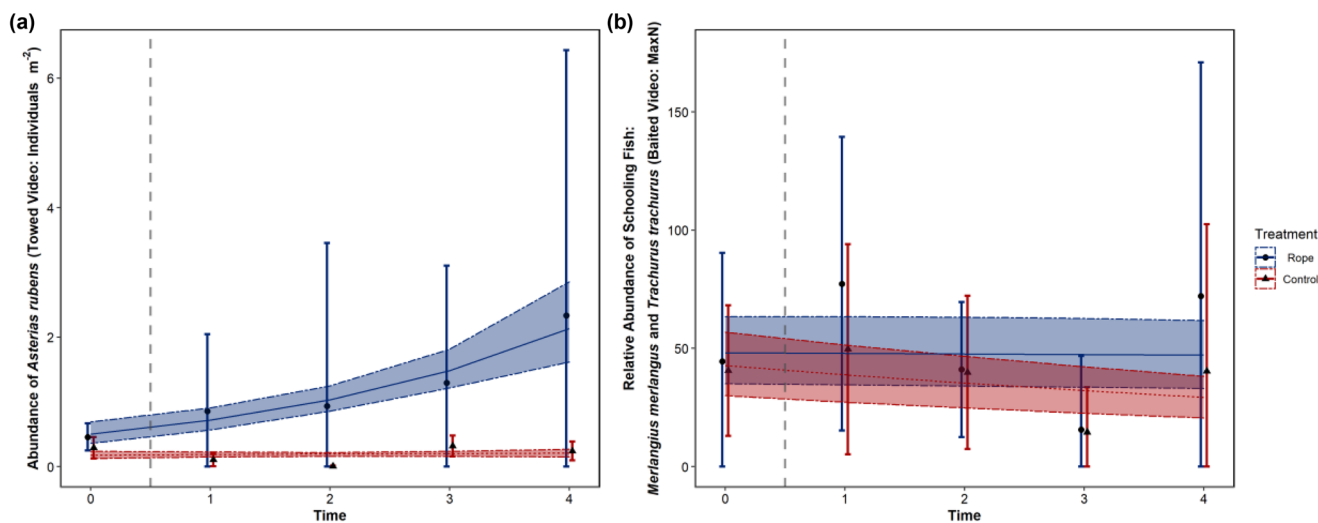


FIGURE 7 Temporal change in abundance of (a) *Asterias rubens* and (b) schooling fish derived from towed underwater video system (TUVS) + remotely operated vehicle (ROV), and baited remote underwater video (BRUV), respectively, from Rope (blue) and Control (red) treatments. Lines show model estimates with shading and dotted lines indicating 95% confidence intervals. Symbols with error bars show raw mean values and 95% confidence intervals. Vertical dashed line denotes when first headlines were installed.

Overall, mussel clump size has increased over time, creating large patches with a variety of epibiota. Mussels, when aggregated in beds, are ecosystem engineers, creating habitat, which increases habitat heterogeneity and diversity (Jones et al., 1994, 1997). This effect has the potential to increase species richness through the provision of substrata for colonisation (Borthagaray & Carranza, 2007) and provide refuges from predation, nursery areas (Díaz et al., 2015) and can become an important food provision for benthic communities (Freire & González-Gurriarán, 1995). The mussel cover also contributes to the sequestration of carbon by 'locking' carbon into the seabed; an important regulating ecosystem service in the drive to mitigate climate change (van der Schatte Olivier et al., 2018).

Asterias rubens were consistently more abundant beneath the mussel farm headlines compared to control plots, increasing in abundance year on year within the farm. This result compliments work by Inglis and Gust (2003), which found that starfish were up to 39 times more abundant at farmed sites at an inshore mussel farm in New Zealand, than surrounding unfarmed areas and was correlated with the abundance of living mussels on the seabed. Anchor blocks have the potential to act as artificial reef structure, which are used around the world for various purposes including improving fishery production and rehabilitating habitats (Lee et al., 2018).

Large schools of *T. trachurus* and *T. minutus* within the mussel farm caused this significant difference in assemblage composition, perhaps a result of the increase in food availability or because of the farm structures on the benthos (e.g., anchor blocks) acting as fish aggregation devices (Kingsford, 1993). At Site 1, the abundance of schooling fish (*M. merlangus* and *T. trachurus*) was significantly greater within the farm compared to control plots after 4 years of headline deployment. This could be a result of the difference in headline use between the two trial stations; TS1 was being used for the further growth of older

mussels, which could be providing a larger food source for these fish. Furthermore, two important commercial species to Lyme Bay were consistently more abundant in the farm compared to control areas: *C. pagurus* and *H. gammarus*. Drouin et al. (2015) found that lobsters were more abundant where mussel fall-off was more frequent and were found to be more abundant close to the mussel farm structures, like anchor blocks. Although the lobsters in this study were enumerated from the baited remote underwater video survey, they were often observed sheltering next to the anchor block during the remotely operated vehicle survey.

It is evident that the epibenthic habitat within the offshore mussel farm has changed as a direct effect of the aquaculture installation. Mussel cover on the seabed has increased year on year, and benthic assemblages are beginning to respond to the change in habitat. Future monitoring is needed to understand how these assemblages respond as the capacity of the mussel farm increases. The increasing abundance of schooling fish will also need continued monitoring. The fish within the farm are unable to be fished safely, due to the nature of the arrangement of headlines. As a result, the farm is unlikely to become an 'ecological trap', where aggregated fish are targeted by fishers. This can happen to fish aggregated around fish farms (Fernandez-Jover et al., 2008). If the abundance of schooling fish continues to increase, catch per unit effort in fishing ground around the mussel farm could increase in time, as these fish 'spillover' into fishing areas (Rowley, 1994). It is unclear, however, whether the mussel headlines are contributing to the production of epibenthic fauna or whether they are redistributing the species in the area and pulling them away from their other areas into, perhaps, a more attractive habitat with a reliable food source. To monitor this, The University of Plymouth, funded by the European Maritime and Fisheries Fund, is using acoustic telemetry to focus on how commercial species, including *C. pagurus* and *H. gammarus*, move around the

mussel farm and how long they remain resident to the farm compared to the surrounding area and the nearby Lyme Bay Marine Protected Area (ROPE, 2022).

The Lyme Bay offshore mussel farm has increased the hard structure on the seabed; both in terms of man-made structures (e.g., anchor blocks and rope) and mussel shell cover. In time, this may increase the provision of feeding areas along with the abundance and number of taxa utilising the area, restoring the degraded seabed habitat from historical bottom towed fishing. However, caution is needed when predicting how assemblages will interact with the farm when the carrying capacity of the farm increases. As the farm upscales, the effects of headline development are crucial to investigate how offshore mussel farms interact with the benthic habitat.

There is some evidence that the development of the Lyme Bay offshore mussel farm has contributed to the restoration of the seabed. Restoration is defined as the process of assisting the recovery of a degraded, destroyed or damaged ecosystem (Society for Ecological Restoration, 2004). This includes improving the structural diversity, species composition and ecosystem function (McDonald et al., 2016), which the introduction of mussel cover to the seabed beneath the headlines has contributed to, by providing a different habitat type to a heavily trawled, damaged area of seabed. Further research on the effects of offshore mussel farming could benefit from seasonal sampling. The present study sampled exclusively during the summer which may not have been sufficient in monitoring benthic and demersal species that are more common during the winter months.

This study has increased the evidence base available to policy makers that can be used to help guide the initiative to move aquaculture installations offshore, supporting the Blue Growth agenda. It can also inform Maritime UK Southwest (MUK SW) which brings together the ocean economy of Southwest England to grow the marine sector. As part of MUK SW, The Southwest Aquaculture network aims to sustainably enhance aquaculture production and feed into the developing Great South West strategy to support initiatives for sustainable development.

AUTHOR CONTRIBUTIONS

Danielle Bridger: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; writing—original draft. **Martin Attrill:** Conceptualization; funding acquisition; methodology; project administration; supervision; validation; writing—review & editing. **Bede Davies:** Formal analysis. **Luke Holmes:** Conceptualization; investigation; methodology; project administration. **Amy Cartwright:** Data curation. **Sian Rees:** Project administration; supervision; validation; writing—review & editing. **Lucia Mascorda Cabre:** Data curation. **Emma Sheehan:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; writing—review & editing.

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CONFLICTS OF INTEREST

The funder Offshore Shellfish Ltd. was not involved in the study design, data collection and analysis, decision to publish or preparation of the manuscript, all of which were undertaken by independent researchers at the University of Plymouth. None of the co-authors are, or ever have been, a collaborator or employee of Offshore Shellfish Ltd.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ETHICS STATEMENT

The authors declare that the present research is the authors' own original work, which has not been previously published elsewhere, and the paper is not currently being considered for publication elsewhere.

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SUPPORTING INFORMATION

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