



# Low-impact rearing of a commercially valuable shellfish: sea-based container culture of European lobster *Homarus gammarus* in the United Kingdom

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**ABSTRACT:** There is increasing interest in the aquaculture of high-value shellfish species such as European lobster *Homarus gammarus*. Recent years have seen the development of extractive rearing equipment requiring no additional feed input, including novel sea-based container culture (SBCC) systems designed specifically for lobster mariculture. Here, we report the results of a study which assessed the impact of SBCC systems on the local ecology surrounding a pilot-scale lobster farm (Lobster Grower) integrated into an existing mussel farm in St Austell Bay, Cornwall, UK, across 2 monitoring surveys. We assessed the impact of SBCC systems on the macrobenthic, epifaunal, and mobile species ecology across the study area through benthic grab sampling, drop-down camera, and baited-remote underwater video (BRUV) monitoring. We detected no changes to local sediment composition around SBCC systems, nor changes in macrobenthic diversity or community structure. Increased detritus and biodeposition originating from SBCC systems may be attracting increased epifaunal scavengers, while the presence of the containers and associated infrastructure may act as fish-aggregating devices and provide additional foraging opportunities for mobile fish. These extractive systems may provide low-impact and low-carbon opportunities for coastal mariculture in the face of increased global demand for shellfish.

**KEY WORDS:** Lobster · Shellfish · Sea-based container culture · Benthic ecology · Aquaculture impacts

## 1. INTRODUCTION

The Food and Agriculture Organisation (FAO) of the United Nations predict that the world's population will reach almost 10 billion people by 2050 (FAO 2020). Consequent rises in global food demand, al-

ready threatened by climate change, water scarcity, drought, and flooding, necessitate that food production must increase by up to 70% to feed this growing population (FAO 2020). Increased food production is often associated with environmental degradation and must be diversified to provide resilience to future im-

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pacts of climate change (De Silva et al. 2009). Since the 1980s, overall landings from wild capture fisheries have plateaued at around 90 million t yr<sup>-1</sup>, despite an increase in fishing effort (FAO 2020). With over one-third of marine capture fisheries currently defined as overfished or fished at their maximum sustainable level (FAO 2020), aquaculture production has increased dramatically in recent years (Mathiesen 2012). Aquaculture is now the main source of fish and shellfish for human consumption, and overall production is predicted to exceed wild capture fisheries, with shellfish (molluscs and crustaceans) comprising the majority of aquaculture species (FAO 2020).

Lobster is a valuable shellfish species globally, although chronic overexploitation of wild stocks and a dearth of commercial aquaculture has led to insufficient supply of European lobster *Homarus gammarus* to meet current demand (Drengstig & Bergheim 2013, Ellis et al. 2015). Around 80% of the approximately 5000 t of wild lobster caught globally each year is landed in the UK and Ireland and exported to Europe, where much of the demand for lobster is supplemented by imports of the American lobster *H. americanus* (Davies et al. 2014), with inherent issues around the potential ecological impacts of live non-native imports.

Efforts to enhance wild lobster stocks have been in place since the 1800s (Nicosia & Lavalli 1999), traditionally involving release of hatchery-reared juveniles (Bannister & Addison 1998, Browne 1999, Scovacicchi et al. 1999, Beal & Chapman 2001). This process reduces predation risk in the wild during planktonic larval phases (Lawton & Lavalli 1995), although lower-cost communal rearing is limited by nutrition, slow growth rates, and cannibalism (Fiore & Tlusty 2005, Powell et al. 2017). The species, therefore, requires high-cost and labour-intensive individual rearing, which, together with requirements for high-quality food and technological innovation, has limited the efficiency of rearing the species prior to release, and thus the potential for economically viable commercial aquaculture (Drengstig & Bergheim 2013).

In recent years, numerous studies have shown that sea-based container culture (SBCC) has the potential to offer an economically viable means of individually rearing juvenile lobsters (Knudsen & Tveite 1999, Perez Benavente et al. 2010, Browne et al. 2011, Beal & Protopopescu 2012, Beal 2012). Colonisation of SBCC systems by other marine species, along with plankton in the water column, provides a continuous food supply and negates the need for food inputs (Perez Benavente et al. 2010, Daniels et al. 2015), allowing high rates of juvenile growth and survival

and relatively low production costs. Further developmental benefits also apply to the stock through constant exposure to natural environmental conditions, which has the potential to further improve survival after release into the wild (Ellis et al. 2015). Therefore, there are 2 valuable potential utilities offered by SBCC systems: grow-out rearing of individual lobsters to market and on-growing of juveniles to a larger size to increase survival upon release to the wild (i.e. stock enhancement purposes).

The feasibility of SBCC as a technique for low carbon lobster cultivation was first investigated in Norway, the USA, and Ireland in the late 1990s and early 2000s (Knudsen & Tveite 1999, Beal 2012). In 2011, the National Lobster Hatchery (NLH) conducted the UK's first SBCC field trial at 6 sites around the coast of Cornwall, utilising container systems designed for rearing oysters (Daniels et al. 2015). This trial demonstrated the promising potential of SBCC as a mode of lobster mariculture, while also identifying limitations of the oyster system for this application. As a result, the NLH led a multi-disciplinary consortium in the Lobster Grower (LG) projects, which pioneered the development of the world's first SBCC system designed specifically for lobster culture (LG1). This was followed by the first semi-industrial-scale SBCC farm for rearing of *H. gammarus* (LG2), established at the site of an existing mussel farm operated by Westcountry Mussels of Fowey, in St. Austell Bay, Cornwall, UK.

The LG2 project ran from 2016–2018 and aimed to assess the potential for industrial development of lobster farming using SBCC systems through the collection of technical, environmental, economic, and social data. To assess the ecological sustainability of the systems, the present study focuses on understanding the impacts of SBCC on the wider marine environment in order to contribute to the growing evidence base for the development of this form of mariculture. According to the Aquaculture Production Intensity Scale (APIS) defined by Oddsson (2020), lobster SBCC culture is assigned a score of 1, defined as an extensive system involving only stocking, harvesting, and the prevention of escapes, but no treatment functions during rearing (Oddsson 2020). With no feed input and low stocking densities (<4 juveniles m<sup>-2</sup>), SBCC may minimise interactions with the wider ecosystem often associated with aquaculture systems through nutrient loading and organic enrichment driving local diversity loss (Grant et al. 2005, Kalantzi & Karakassis 2006). Yet the introduction of novel floating structures in pelagic and open water environments through the development of these systems

brings its own environmental interactions, including shading (Skinner et al. 2014), hydrodynamic alterations (Liu & Huguenard 2020), and the provision of new structures for species settlement and colonisation. Such structures may increase local diversity (Connell & Glasby 1999, Holloway & Connell 2002, Dafforn et al. 2015) and provide shelter and new foraging opportunities for mobile species (Rountree 1989, Nelson 2003, Sanchez-Jerez et al. 2011). However, these structures can also facilitate the establishment and transport of non-native species by acting as ‘stepping-stones’ for the dispersion of larval propagules (Bulleri & Airolidi 2005, Glasby et al. 2007, Dafforn et al. 2009).

To inform potential commercial expansion and management practices of lobster SBCC, the present study assessed the effects of the LG2 pilot-scale lobster farm on local benthic ecology and mobile benthopelagic species assemblages. We aimed to answer the following questions: (1) How does the presence of the SBCC systems affect the physical benthic environment compared to control areas outside of the site and areas within the existing mussel farm? (2) How does the presence of the SBCC systems affect macrofaunal, epifaunal, and mobile species assemblages compared to control areas, and to areas within the mussel farm? (3) How does the presence of the SBCC systems and the mussel farm affect hydrodynamics within the water column compared to control areas?

## 2. MATERIALS AND METHODS

### 2.1. Study site and SBCC system

The study focused on the LG2 pilot SBCC site located in St. Austell Bay, a 6 km wide embayment located in Cornwall in southwest England, UK (Fig. 1). Seabed habitats within the study area comprise poorly sorted mixed sediments, ranging from gravelly and sandy muds to sandy and muddy gravel ([https://](https://www.emodnet-seabedhabitats.eu/)

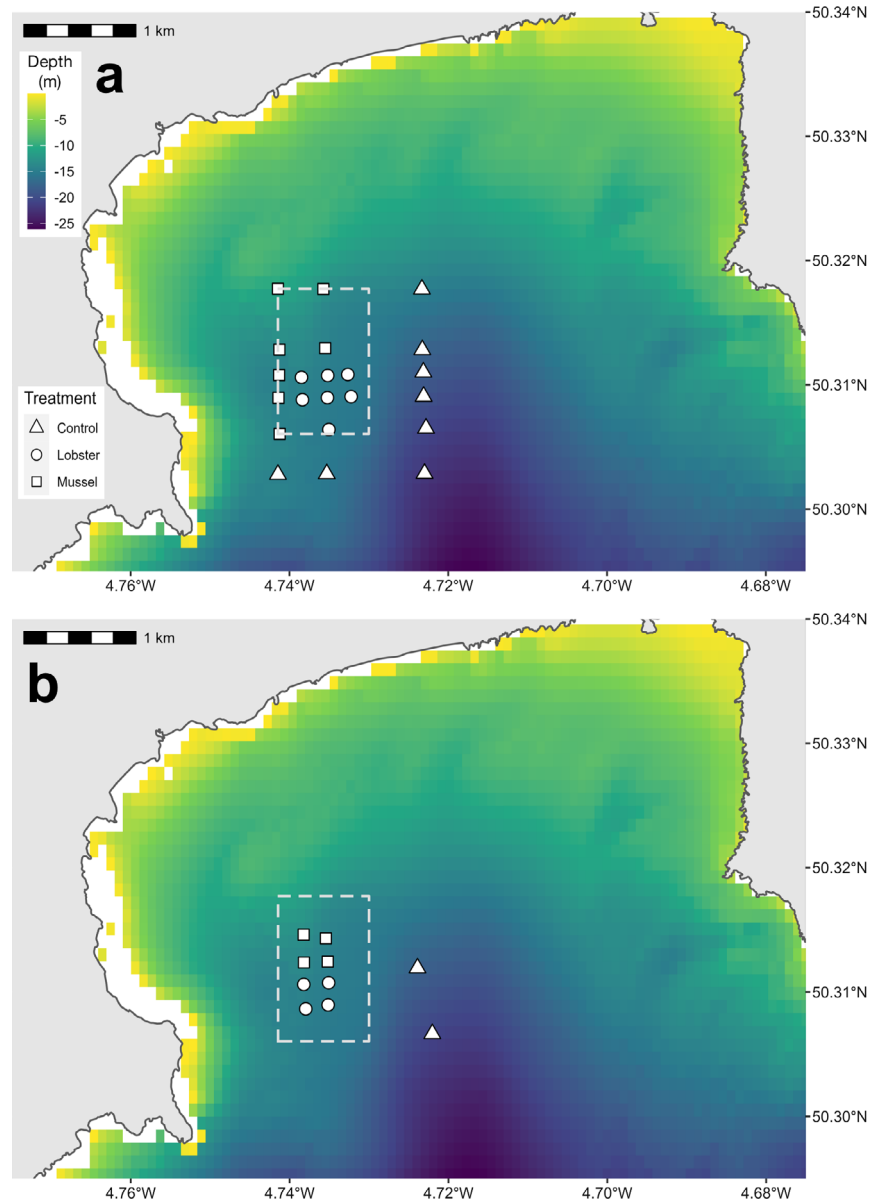


Fig. 1. Distribution of the stations across the mussel farm (dashed box) and the wider study area sampled by (a) grab and drop-down camera and (b) baited-remote underwater video

[www.emodnet-seabedhabitats.eu/](https://www.emodnet-seabedhabitats.eu/)) (Fig. 1). The bay has a tidal range of 4.7 m and is a low-energy site with depth-averaged mean water flows of  $0.05 \text{ m s}^{-1}$  and a maximum flow of  $0.14 \text{ m s}^{-1}$  (Tilsley 2020). This site was chosen after a 3 yr field investigation demonstrated consistently high production success of *Homarus gammarus* in oyster baskets compared to 5 alternative sites in the region (Daniels et al. 2015). Following these trials, the full pilot-scale system was installed as an extension to an existing mussel farm in the bay in June 2016.

Lobster rearing infrastructure comprising six 200 m long lines floated 2–4 m below the surface of the water, secured by 2 concrete end weights. Lobster containers were suspended on weighted dropper lines to depths of 4–8 m at 2 m intervals along these header lines (Fig. 2). Lobsters were housed in 2 types of containers: tiered oyster spat rearing baskets, stacked vertically ( $n = 225$ ), each of which holding up to 32 lobsters, and custom-designed lobster containers ( $n = 475$ ), each of which holding up to 40 lobsters. Containers were separated into individual compartments within which individual lobsters were held. Across both container types, approximately 26 000 juvenile lobsters were deployed over the course of the 3 yr study (2016: 13 163; 2017: 9040; 2018: 4600). Survival and growth of SBCC lobsters were recorded, but these findings are beyond the scope of this study and are intended to be reported separately. Juvenile SBCC lobsters were monitored over the project and showed good survival, development, and growth, with little maintenance and no regular dietary supplementation. SBCC lobsters showed greater growth and survival compared to their control counterparts reared in land-based recirculating aquaculture systems at the NLH (C. Daniels pers. comm.).

## 2.2. Sampling methods

A total of 22 stations were sampled across the farm area during the study period (Fig. 1a): once in late 2016–early 2017 during installation of the SBCC systems, and again in late 2018. This allowed a comparison of the ecology of the study area in order to inves-

tigate any impacts of the SBCC systems separately from those potentially arising from the existing mussel farm.

The 22 sampling stations were assigned to one of 3 treatments. Eight stations were located far from both the mussel farm and the SBCC systems (herein referred to as 'control' stations), 7 stations were located within the suspended SBCC systems (herein, 'lobster' stations), and 7 stations located within the mussel lines (herein, 'mussel' stations) (see Fig. 3). Stations were randomly located within each of these treatment zones, with a minimum distance of 200 m between stations.

### 2.2.1. Sediment and macrofaunal communities

Samples were collected using a 0.1 m<sup>2</sup> Day grab from all 22 stations from 31 May to 2 June 2017, and again on 31 August 2018, from aboard the survey vessel 'Tiger Lily'. Sample stations ranged from 16 to 28 m depth. A 10 g sediment subsample was taken from the sample for particle size analysis before the sample was filtered over a 0.5 mm sieve and all retained material was fixed in 10% buffered formalin. In the laboratory, macrofaunal samples were sorted, identified to the lowest taxonomic level possible, and all individuals counted. Sediment samples were passed over a 2 mm sieve to filter out gravel fractions before a Malvern Mastersizer 3000 (Malvern Panalytical 2017) laser particle size analyser was used to quantify the volume of finer (<2 mm) fractions. Cumulative sediment volume curves were produced and the % volume of gravel, sand, and mud was calculated.

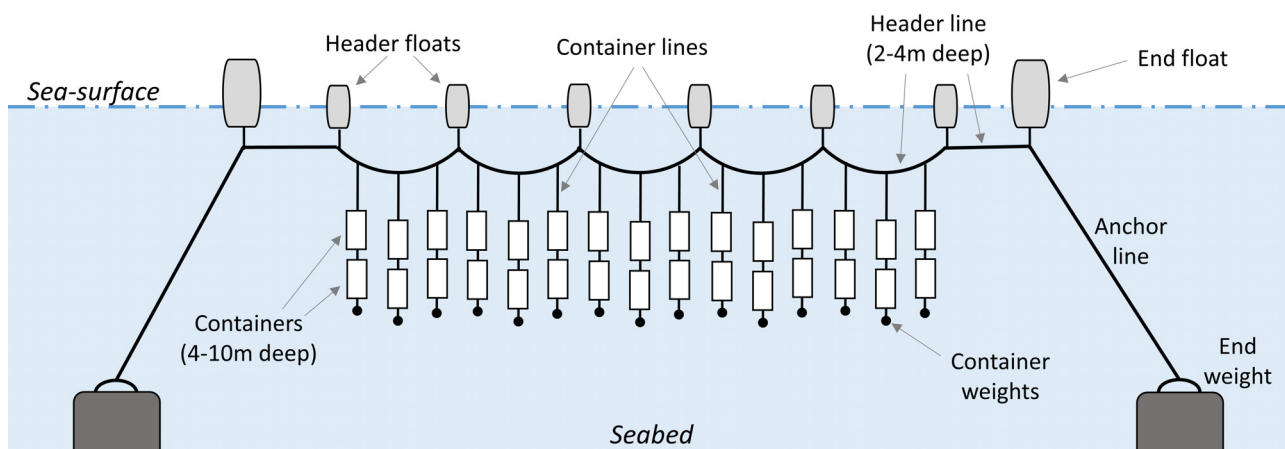


Fig. 2. Long line system used throughout the Lobster Grower LG2 project to suspend sea-based container culture systems; 2 to 3 container stacks were deployed per container dropper line. Diagram is not to scale

### 2.2.2. Epifauna

Epifaunal communities at the 22 monitoring stations were surveyed by a drop-down camera (DDC) system, once from 30 November to 1 December 2016 and again on 30 October 2018. The camera system was deployed from the stern of the RV 'DevOcean' and consisted of an aluminium frame with a vertically positioned Panasonic HDC-HD60 camcorder (10 megapixel, 90× zoom) within a Seapro underwater housing. The camera was set with 2 lasers at either side of the housing, positioned 100 mm apart for scale. At each station, the camera system was deployed on the seabed for 4 min and a still image of the seabed was obtained once sediment had settled and the image was clear. Sediment type was identified from seabed imagery based on Folk (1954) and the European Union Nature Information System (EUNIS) Broad Scale Habitats (BSH) system.

### 2.3. Mobile species

At 10 sampling stations located across the study area (Fig. 1b), baited-remote underwater video (BRUV) deployments were also undertaken from the RV 'DevOcean' during the same survey as DDC deployments. These deployments aimed to assess whether there was any detectable change in mobile species assemblages as a result of the SBCC systems. Two control stations, 4 lobster stations, and 4 mussel monitoring stations were sampled. BRUV deployments used the same camera system described above, fitted with an LED lighting system and an aluminium pole to hold bait (~100 g of fresh Atlantic mackerel *Scomber scombrus* in a net bag) at 1 m from the camera. The system was stabilised by 40 kg of lead weights attached to the frame. All BRUV deployments were for a duration of 1 h during daylight. Videos were analysed in the specialist SeaGIS software Event Measure ([www.seagis.com.au](http://www.seagis.com.au)) and data separated into mobile fish fauna and motile epifauna. Motile epifauna were recorded as presence–absence data whilst the maximum abundance of mobile fish fauna (MaxN) was recorded.

### 2.4. Data analysis

Statistical analyses were conducted in RStudio version 1.1.456 (RStudio Team 2020). Differences in univariate responses (e.g. individual species abundances, diversity indices) between treatments and

survey years were identified by a 2-factorial general linear model with treatment and sampling year included as fixed factors. An interaction term between the 2 was included to identify any impact of the SBCC systems (i.e. if the change over time in any response differed between treatments). When variance was heterogeneous, ANOVA with White's adjustment was used to test for significance. Diagnostic plots of model residuals were used to assess normality and model fit. A significance level of  $\alpha = 0.05$  was used for all analyses.

Exploratory non-metric multidimensional scaling (nMDS) ordinations were produced for each of the multivariate biological data sets (macrofauna, epifauna, mobile species, fish species) to identify any notable grouping of samples taken from each of the 3 treatments and across the study period. For macrofaunal and fish data, this analysis was performed on a Bray-Curtis dissimilarity matrix, while for epifaunal community data and the entire mobile species assemblage, a Jaccard dissimilarity matrix based on presence–absence data was used due to the combination of presence–absence and abundance data.

To characterise similarities or differences in the macrofaunal, epifaunal, and mobile species assemblages between treatments and sampling years within the study area, we performed a similarity percentage (SIMPER) routine. Where this was performed on presence–absence data, the percentage occurrence of species at stations within each treatment was presented rather than mean abundance. Principal components analysis (PCA) identified patterns in epifaunal and mobile species communities in relation to the 3 treatments across the study area and between surveys. PCA ordination defines axes that best discriminate between a multivariate cloud of data points. Overlaid species vectors indicated species groups that best characterised group differences in the ordination. Where necessary, separate PCA ordinations were produced with and without overlaid species vectors for clarity.

Group differences in the multivariate datasets were formally assessed through permutational analysis of variance (PERMANOVA) (Anderson 2001, Anderson et al. 2008, Anderson & Walsh 2013) undertaken within the 'vegan' package in RStudio (Oksanen et al. 2019), which included treatment and sampling time as fixed model factors and an interaction between the 2 factors. PERMANOVA was performed on the similarity matrices described above for each biological dataset and on a Bray-Curtis dissimilarity matrix derived from the multivariate sediment data set. The PERMANOVA routine is robust to un-



balanced designs (Anderson & Walsh 2013) and is therefore appropriate for the unequal distribution of sampling stations across the 3 treatment areas. Where a significant interaction was found in the output of the PERMANOVA routine, pairwise comparisons were performed to investigate the changes over time at stations within each treatment across the study period.

To assess overall ecological condition at stations within each treatment, we calculated AZTI Marine Biotic Indices (AMBI) at each station (Borja et al. 2000). The AMBI index was developed specifically to assess ecological quality of European coastal benthic habitats and allows the assessment of any degradation of the ecological quality of the seabed habitats associated with the presence of the SBCC systems. AMBI values were calculated in the AMBI software version 5.0 (Borja et al. 2012).

### 3. RESULTS

#### 3.1. Sediment

Sediment composition was highly variable across the study area and typical of mixed sublittoral sediments, ranging from slightly gravelly sandy muds to muddy and sandy gravels (Fig. 3, see Table S1 in Supplement 1, all supplements available at [www.int-res.com/articles/suppl/q015p215\\_supp/](http://www.int-res.com/articles/suppl/q015p215_supp/)). PERMANOVA results indicated significant treatment differences in sediment composition (Table 1), although no significant effect of year or interaction between year and treatment was evident, indicating that

Table 1. Results of 2-factorial PERMANOVA performed on data obtained from stations in each treatment across the study area across monitoring surveys. Significant results ( $p < 0.05$ ) are indicated in **bold**. BRUV: baited-remote underwater vehicle

Source	df	SS	MS	F	p
<b>Particle size data</b>					
Year	1	437.69	437.69	0.971	0.375
Treatment	2	4484.6	2242.3	4.974	<b>0.002</b>
Year × treatment	2	331.35	165.67	0.368	0.965
Residuals	38	17130	450.79		
Total	43	22362			
<b>Macrofaunal assemblage</b>					
Year	1	0.70	0.70	2.349	<b>0.025</b>
Treatment	2	2.59	1.29	4.356	<b>0.001</b>
Year × treatment	2	0.65	0.32	1.088	0.312
Residuals	38	11.28	0.30		
Total	43	15.21			
<b>Epifaunal data</b>					
Year	1	1.94	1.94	5.326	<b>0.001</b>
Treatment	2	1.39	0.69	1.908	<b>0.012</b>
Year × treatment	2	1.27	0.64	1.748	<b>0.009</b>
Residuals	33	12.01	0.36		
Total	38	16.61			
<b>BRUV data (all species)</b>					
Year	1	0.40	0.40	1.285	0.169
Treatment	2	1.19	0.60	1.898	<b>0.003</b>
Year × treatment	2	0.99	0.49	1.576	<b>0.014</b>
Residuals	14	4.39	0.31		
Total	19	6.97			
<b>BRUV data (fish only)</b>					
Year	1	0.36	0.36	1.262	0.243
Treatment	2	0.97	0.49	1.697	0.061
Year × treatment	2	0.99	0.50	1.724	0.054
Residuals	14	4.02	0.29		
Total	19	6.35			

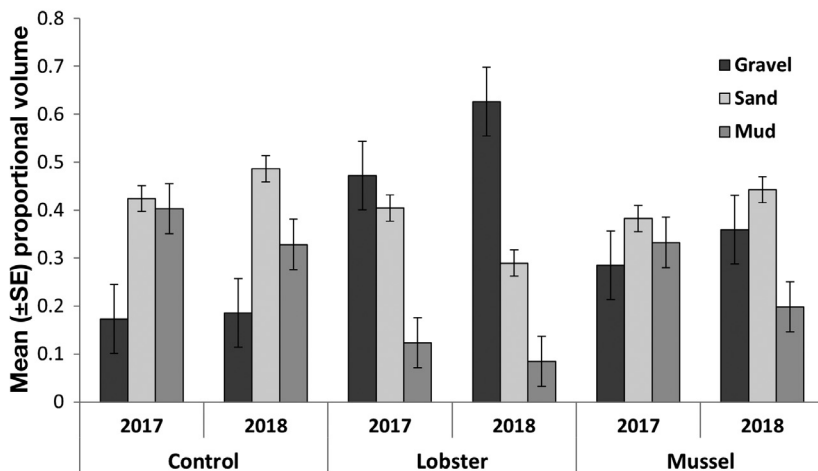


Fig. 3. Proportional contribution of each main sediment group at stations within each treatment across the study area in 2017 and 2018

despite significant spatial differences between treatments, no change in the overall sediment composition occurred between surveys throughout the study area (Table 1). Stations within the lobster systems were characterised by a lower volume of muddy fractions compared to control stations and those within the wider mussel farm, and they generally had a higher proportion of gravel, although there was high variability (Fig. 3). Despite the non-significance of survey year in the PERMANOVA results, both the proportional volume of each sediment type and cumulative sediment volume curves (Fig. 4) indicate a general loss of finer sediments between surveys,

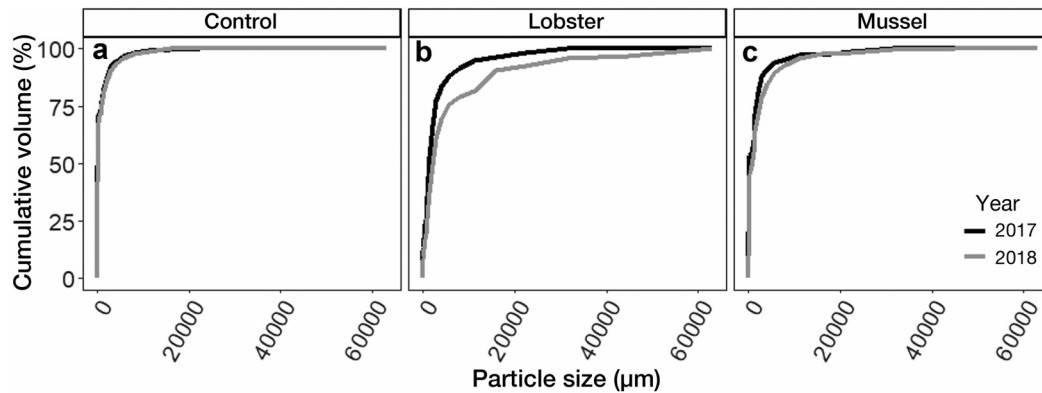


Fig. 4. Cumulative volume curves against particle size for benthic grab samples taken at stations within each treatment across the study area in 2017 and 2018

which was most pronounced at stations within the lobster systems (see Fig. 5).

### 3.2. Biological assemblage

#### 3.2.1. Macrofaunal communities

A total of 332 individual macrofaunal species were recorded across the study area during the 2 surveys. Species assemblages were broadly similar across the site and between monitoring years, and typical of shallow sublittoral sediment communities, dominated by polychaetes (e.g. *Mediomastus fragilis*, *Lumbrineris cingulata*) and small bivalves such as *Kurtiella bidentata*, *Abra alba*, and *Nucula nitidosa*. The biotope throughout the study area, therefore, appears to be best characterised by the EUNIS Habitat A5.142: 'Mediomastus fragilis, Lumbrineris spp. and venerid bivalves in circalittoral coarse sand'. Whilst venerid bivalves, a characterising species of this biotope, were relatively scarce in samples, such species are often under-represented in grab samples.

**Community descriptors.** A significant main effect of sampling time indicated significant increases in all diversity indices except Pielou's evenness index between the 2 survey years (Table 2). Stations within the mussel farm were generally less diverse than those at control locations or within the lobster systems, with significant spatial differences evident in Pielou's, Simpson's, and Shannon's diversity indices (Table 2).

The observed increases in diversity were largely consistent across the survey area, with a significant model interaction term only evident for total abundance (Table 2). Whilst overall abundance was similar between surveys at control locations, significant

increases occurred at stations within the lobster and mussel systems, with the largest increase occurring at stations within the lobster systems (Table 2).

**Species assemblage.** An nMDS ordination of the macrofaunal data showed some clustering of control stations separate from lobster and mussel stations (Fig. S1a in Supplement 1). PERMANOVA results indicate significant main effects of both treatment (control vs. lobster:  $F_{2,38} = 6.76$ ,  $p = 0.003$ ; control vs. mussel:  $F_{2,38} = 2.61$ ,  $p = 0.030$ ; lobster vs. mussel:  $F_{2,38} = 3.36$ ,  $p = 0.009$ ) and sampling time (Table 1). The lack of a significant interaction term indicates that the change in the macrofaunal assemblages across the survey area between surveys was consistent across stations within all 3 treatments (Table 1). Temporal pairwise comparisons (Table 3) indicate that while the macrofaunal assemblage remained similar between surveys within each treatment, the magnitude of these changes (as indicated by  $F$ -value test statistics; Table 3) demonstrate that the largest change occurred at lobster stations and the lowest at mussel stations. Results of the SIMPER routine (Supplement 2) show that this change within the lobster farm appears to be largely due to increases in the abundance of a number of the dominant species (e.g. the polychaetes *M. fragilis*, *L. cingulata*, *Psamathe fusca*, Polynoidae, and the bivalve mollusc *Timoclea ovata*). Variability in the direction and magnitude of change is evident at control stations, whilst the abundance of the dominant species at stations within the shellfish farm remained relatively constant in comparison (Supplement 2).

**Ecological status.** Mean AMBI scores show that benthic habitats across the study area were of 'good' ecological status (Fig. 5), consistent across treatments and surveys. Results show significant differences between treatments, however (Table 2),

Table 2. Mean ( $\pm$ SE) diversity indices calculated from grab samples (per 0.1 m<sup>2</sup>), drop-down camera deployments, and BRUV deployments undertaken within each treatment across the study area between surveys. Significant changes across surveys and ANOVA results are indicated in **bold**. Total N: total macrofaunal abundance; MaxN: maximum number of individuals observed. Sample sizes: macrofauna: control = 8; lobster = 7; mussel = 7; epifauna: control = 8; lobster = 7; mussel = 7; BRUV: control = 2; lobster = 4, mussel = 4

Measure	Control			Lobster			Mussel			Year	Treatment	Year $\times$ treatment
	2017	2018	2018	2017	2018	2018	2017	2018	2018			
<b>Macrofaunal assemblage</b>												
Species richness	<b>29.10 <math>\pm</math> 1.98</b>	<b>43.9 <math>\pm</math> 4.40</b>	<b>29.10 <math>\pm</math> 3.47</b>	<b>62.60 <math>\pm</math> 4.88</b>	<b>30.70 <math>\pm</math> 3.21</b>	<b>49.70 <math>\pm</math> 5.62</b>	<b>F<sub>1,38</sub> = 43.60, p = &lt;0.001</b>	<b>F<sub>2,38</sub> = 2.53, p = 0.093</b>	<b>F<sub>2,38</sub> = 2.62, p = 0.086</b>			
Total N	46.80 $\pm$ 4.63	69.10 $\pm$ 7.11	<b>44.50 <math>\pm</math> 6.53</b>	<b>107.00 <math>\pm</math> 12.70</b>	<b>57.40 <math>\pm</math> 4.16</b>	<b>86.20 <math>\pm</math> 9.97</b>	<b>F<sub>1,38</sub> = 32.18, p = &lt;0.001</b>	<b>F<sub>2,38</sub> = 2.25, p = 0.120</b>	<b>F<sub>2,38</sub> = 3.76, p = 0.032</b>			
Pielou's	0.96 $\pm$ 0.01	0.97 $\pm$ 0.00	0.96 $\pm$ 0.01	0.96 $\pm$ 0.01	0.93 $\pm$ 0.01	0.95 $\pm$ 0.00	<b>F<sub>1,38</sub> = 2.42, p = 0.128</b>	<b>F<sub>2,38</sub> = 8.36, p = 0.001</b>	<b>F<sub>2,38</sub> = 2.72, p = 0.117</b>			
Simpson's	<b>0.97 <math>\pm</math> 0.01</b>	<b>0.98 <math>\pm</math> 0.00</b>	<b>0.98 <math>\pm</math> 0.00</b>	<b>0.99 <math>\pm</math> 0.00</b>	<b>0.98 <math>\pm</math> 0.01</b>	<b>0.98 <math>\pm</math> 0.00</b>	<b>F<sub>1,38</sub> = 18.08, p = &lt;0.001</b>	<b>F<sub>2,38</sub> = 7.53, p = 0.002</b>	<b>F<sub>2,38</sub> = 1.41, p = 0.257</b>			
Shannon	<b>3.20 <math>\pm</math> 0.08</b>	<b>3.62 <math>\pm</math> 0.10</b>	<b>3.20 <math>\pm</math> 0.12</b>	<b>3.96 <math>\pm</math> 0.06</b>	<b>3.17 <math>\pm</math> 0.11</b>	<b>3.65 <math>\pm</math> 0.11</b>	<b>F<sub>1,38</sub> = 44.30, p = &lt;0.001</b>	<b>F<sub>2,38</sub> = 2.03, p = 0.145</b>	<b>F<sub>2,38</sub> = 1.18, p = 0.319</b>			
AMBI	1.91 $\pm$ 0.05	1.43 $\pm$ 0.14	1.68 $\pm$ 0.13	1.48 $\pm$ 0.15	1.96 $\pm$ 0.20	2.02 $\pm$ 0.10	<b>F<sub>1,38</sub> = 3.78, p = 0.06</b>	<b>F<sub>2,38</sub> = 4.74, p = 0.01</b>	<b>F<sub>2,38</sub> = 1.98, p = 0.15</b>			
<b>Epifaunal assemblage</b>												
Species richness	3.14 $\pm$ 0.88	3.40 $\pm$ 0.81	4.43 $\pm$ 0.20	4.86 $\pm$ 0.40	2.43 $\pm$ 0.61	3.17 $\pm$ 0.54	<b>F<sub>1,33</sub> = 1.25, p = 0.272</b>	<b>F<sub>2,33</sub> = 5.19, p = 0.011</b>	<b>F<sub>2,33</sub> = 0.08, p = 0.926</b>			
<b>BRUV (all mobile species)</b>												
Species richness	5.00 $\pm$ 1.00	5.00 $\pm$ 1.00	<b>3.00 <math>\pm</math> 0.71</b>	<b>5.50 <math>\pm</math> 0.87</b>	6.75 $\pm$ 0.63	4.00 $\pm$ 0.41	<b>F<sub>1,14</sub> = 0.03, p = 0.871</b>	<b>F<sub>2,14</sub> = 1.41, p = 0.278</b>	<b>F<sub>2,14</sub> = 7.50, p = 0.006</b>			
<b>BRUV (fish only)</b>												
Species richness	1.50 $\pm$ 0.50	2.50 $\pm$ 0.50	2.25 $\pm$ 0.48	2.75 $\pm$ 0.85	2.50 $\pm$ 0.29	1.25 $\pm$ 0.25	<b>F<sub>1,14</sub> = 0.05, p = 0.827</b>	<b>F<sub>2,14</sub> = 0.823, p = 0.459</b>	<b>F<sub>2,14</sub> = 2.25, p = 0.142</b>			
MaxN	2.50 $\pm$ 1.50	18.00 $\pm$ 10.00	8.25 $\pm$ 3.77	5.75 $\pm$ 2.75	<b>17.00 <math>\pm</math> 8.03</b>	<b>1.75 <math>\pm</math> 0.48</b>	<b>F<sub>1,14</sub> = 0.90, p = 0.359</b>	<b>F<sub>2,14</sub> = 0.204, p = 0.818</b>	<b>F<sub>2,14</sub> = 3.59, p = 0.06</b>			

with lower AMBI values at lobster sites than mussel sites ( $t_{38} = -2.91$ ,  $p = 0.016$ ), while all other pairwise comparisons were similar. Individual sampling stations did drop below the boundaries of 'good' status, although these were across all treatments and no station remained below the threshold across both surveys (Fig. S2 in Supplement 1).

### 3.2.2. Epifaunal communities

DDC sampling of the study area recorded 17 epifaunal species across the 2 monitoring surveys (Supplement 3), dominated by live and dead maerl *Phymatolithon calcareum* and red algae (Rhodophyta), along with other taxa typical of shallow sublittoral habitats such as the hermit crab *Pagurus prideaux* and turf-forming hydroids and bryozoans. Epifaunal communities across the study area, therefore, appear best described by EUNIS Habitat A5.51: '*Phymatolithon calcareum* maerl beds in infralittoral clean gravel or coarse sand'.

**Community descriptors.** Analysis of abundance-based indices was not undertaken on seabed imagery data due to the subjective nature of quantifying epibiotic taxa from seabed imagery and issues merging count and percentage coverage data for mobile and colonial taxa. However, results showed significant differences in species richness between the treatments across the study area (Table 2), with pairwise comparisons indicating more diverse epifaunal communities within lobster sites than mussel sites (Table 2). SIMPER results indicate the absence of a number of taxa at mussel stations that were present at lobster stations (Supplement 2) such as spiny starfish (*Marthasterias glacialis*, Asteroidea), the hermit crab *P. prideaux*, dragonet *Callionymus lyra*, coralline algae, and other encrusting fauna. Diversity at control stations was similar to that in both the lobster and mussel systems. No significant difference between surveys or a significant interaction term were detected (Table 2).

**Species assemblage.** An nMDS ordination of presence-absence epifaunal data



Table 3. Pairwise comparisons of macrofaunal, epifaunal, and BRUV mobile species assemblages between survey years recorded at stations in each treatment across the study area, following the PERMANOVA routine. Significant results are indicated in **bold**

Treatment (2017 vs. 2018)	<i>F</i>	<i>R</i> <sup>2</sup>	<i>p</i>
<b>Macrofauna</b>			
Control (n = 8)	1.84	0.12	0.555
Lobster (n = 7)	2.24	0.16	0.060
Mussel (n = 7)	0.70	0.05	1.00
<b>Epifauna</b>			
Control (n = 8)	4.13	0.29	0.240
Lobster (n = 7)	6.32	0.34	<b>0.045</b>
Mussel (n = 7)	1.14	0.09	1.00
<b>BRUV data (all species)</b>			
Control (n = 2)	3.03	0.60	1.00
Lobster (n = 4)	1.55	0.21	1.00
Mussel (n = 4)	0.59	0.09	1.00

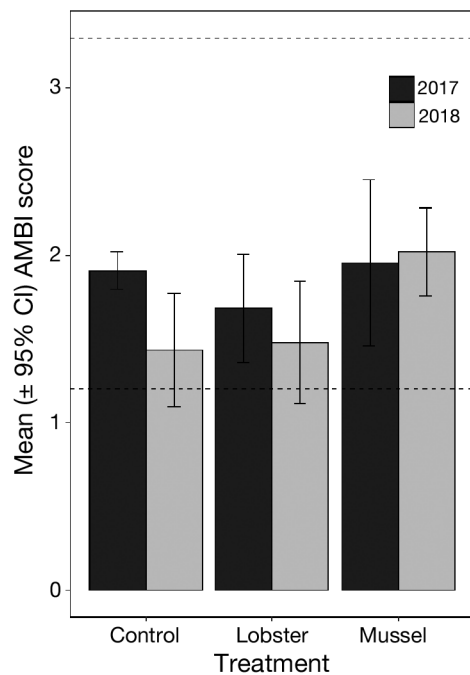


Fig. 5. AZTI Marine Biotic Index (AMBI) values recorded at stations within each treatment across the LG2 survey area in 2017 and 2018. Dashed lines: upper (3.3) and lower (1.2) boundaries of the 'good ecological status' category of the Water Framework Directive (Borja et al. 2000)

(Fig. S1b) indicated clear grouping of stations within the lobster systems during the second monitoring survey alongside some of those from within the mussel systems, while control samples show higher dispersion between stations. PERMANOVA results show treatment differences in the epifaunal assemblage (Table 1), and pairwise comparisons indicate

similarity between control and mussel stations ( $F_{2,33} = 1.46$ ,  $p = 0.825$ ) but differences between both control and mussel stations and those within the lobster systems (control vs. lobster:  $F_{2,33} = 3.55$ ,  $p = 0.039$ , mussel vs. lobster:  $F_{2,33} = 4.41$ ,  $p = 0.012$ ). A significant main effect of sampling time was also evident, as was a significant interaction term (Table 1). Pairwise comparisons show that a significant change in the epifaunal assemblage between surveys occurred only within the lobster farm (Table 3), with SIMPER results indicating that this was largely driven by an increase in the occurrence of caridean shrimp and encrusting hydroids and bryozoans, dragonet, *P. prideaux* and starfish (Fig. S3 in Supplement 1, Supplement 3), and a decrease in the occurrence of other taxa (e.g. serpulid polychaetes, gobies, maerl). These differences are seen in a PCA ordination of the epifaunal data set (Fig. 6), which shows clear grouping of lobster stations separate from samples from the other 2 treatments, as well as separation of samples from the lobster systems between monitoring surveys. Overlaid species vectors provide an indication of the dominant species that characterise samples from within each treatment, with control stations and those from within the mussel farm largely characterised by polychaetes and decapod crustaceans during both surveys. Lobster stations were dominated by maerl and serpulid polychaetes during the first survey, while in the second year were dominated by epibenthic opportunistic predators and scavengers such as *M. glacialis*, other starfish (Asteroidea), *P. prideaux* and a hydrozoan and bryozoan turf. These changes characterise the significant differences identified through PERMANOVA (Fig. 6, Table 1).

### 3.2.3. Mobile species assemblages

*Community descriptors.* In total, 21 mobile taxa were recorded during BRUV deployments throughout the study period (Supplement 4). Model results showed no treatment or sampling differences in mobile species richness (Table 2), although a significant interaction term was present, with an increase in richness within the lobster farm between surveys, which remained similar at control and mussel stations (Table 2). SIMPER results suggest that this increase within the lobster farm was driven by the presence of various species in 2018 that were absent in 2017 (Supplement 4), including crustaceans (*Maja* sp., *Pagurus* sp., *Palaemon serratus*), fish (Mullidae, Ammodytidae, *Sprattus sprattus*, *Ctenolabrus rupestris*), starfish Asteroidea, and scallops Pectinidae.

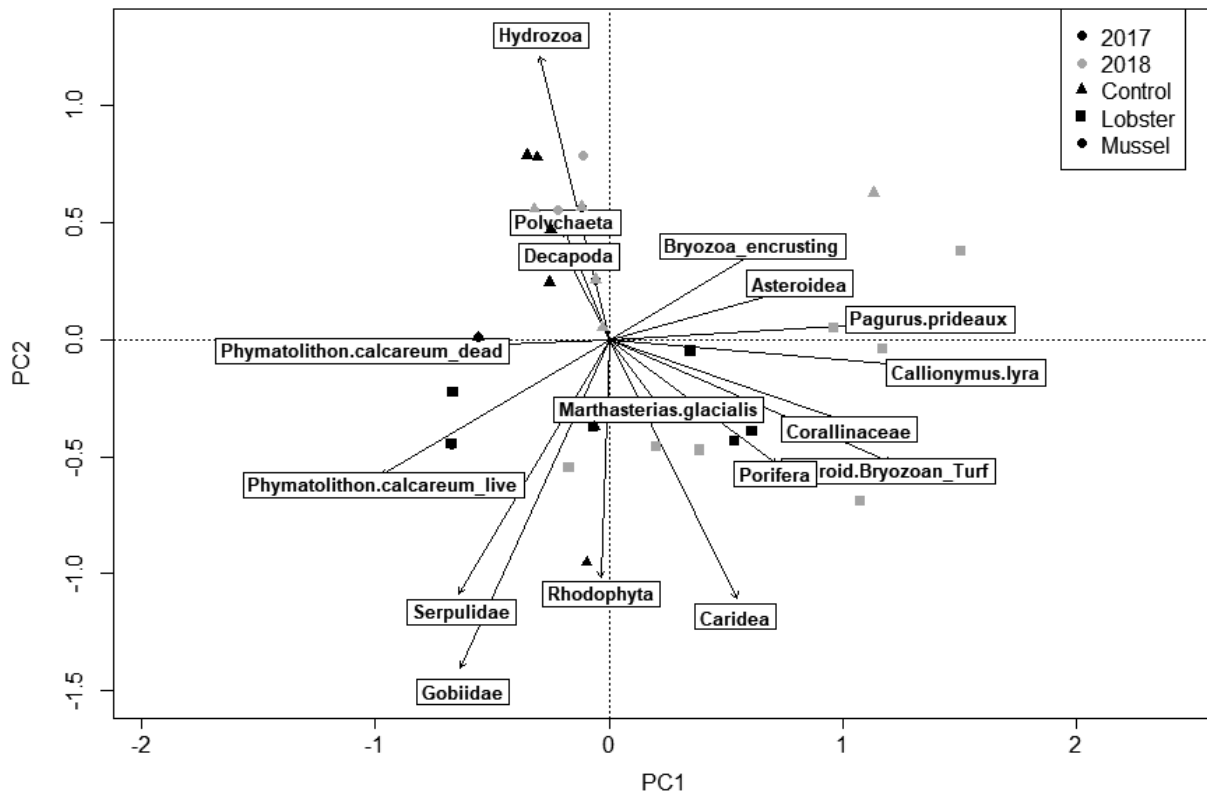


Fig. 6. Principal components analysis ordination of presence–absence epifaunal data obtained at stations in each treatment across the study area and across monitoring surveys, with overlaid species vectors

Analysis of the fish assemblage only shows clear trends in species richness or total, with no significant treatment or sampling differences in species richness or MaxN, likely due to high variability in the data (Table 2).

**Species assemblage.** No clear grouping of sampling stations was evident in nMDS ordinations derived from either presence–absence data of all mobile species (Fig. S1c in Supplement 1) or untransformed fish abundance data (Fig. S1d). The PERMANOVA model results, however, show a significant treatment effect and a significant interaction term (Table 1) on the entire mobile species assemblage. Pairwise comparisons show similarity between the mobile species assemblage at mussel and control stations ( $F_{2,14} = 0.69$ ,  $p = 1.000$ ) but significant differences between stations within the lobster and mussel farms ( $F_{2,14} = 2.89$ ,  $p = 0.006$ ) and lobster and control stations ( $F_{2,14} = 2.31$ ,  $p = 0.033$ ). Despite significance of the model interaction term, pairwise comparisons show no significant change in the overall mobile species assemblage between surveys within any treatment (Table 3), again likely due to high variability. The model test statistics, however, show that the largest difference between years oc-

curred at control stations, with the smallest change occurring at stations within the shellfish farm. SIMPER results (Fig. S4, Supplement 4) suggest that the larger change at control stations is likely due to the complete absence of some species in the second monitoring survey that were widely recorded in the first survey (e.g. *Portunidae* sp., *Goneplax rhomboides*), or vice versa (e.g. *Sprattus sprattus*, *Asteriidae*), whilst the magnitude of change within other treatments was relatively smaller (Fig. S4, Supplement 4).

The results of PERMANOVA performed on the fish assemblage showed similarity across treatments within the study area in both monitoring surveys (Table 1). A total of 9 fish taxa were recorded during BRUV deployments across the 2 surveys, although the abundance of each was highly variable between surveys and treatments (Fig. 7). Of the 4 taxa most consistently recorded during the 2 surveys, no significant trend was evident in abundance between survey years, or between treatments across the study area (Table 3), consistent with the model results for the overall fish assemblage. However, the fish assemblage within the lobster farm was characterised by more frequent occurrence of sandeel *Ammodytes*

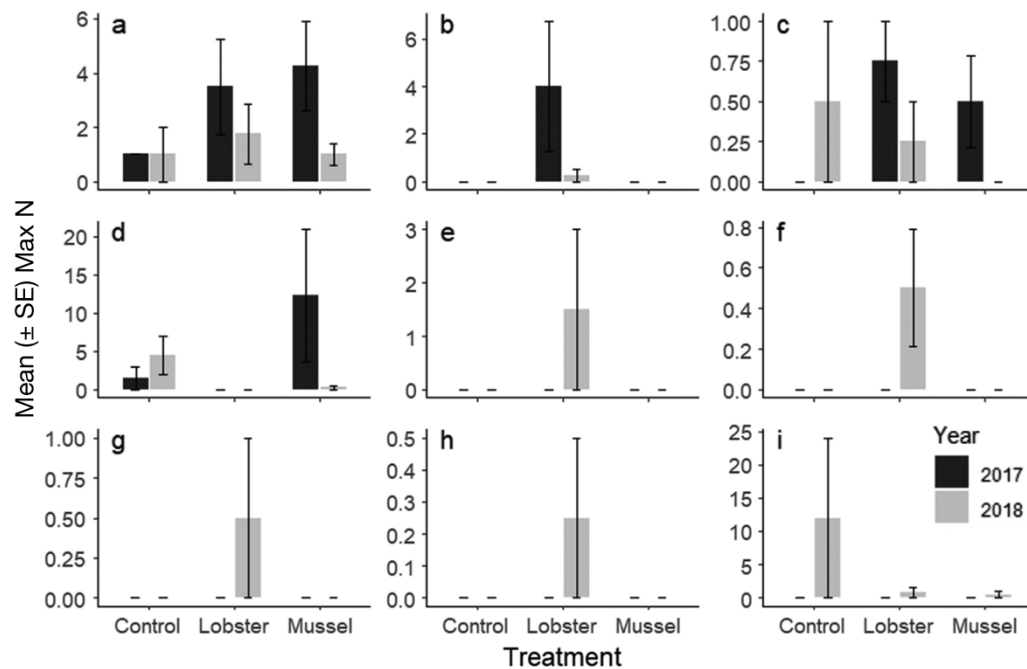


Fig. 7. Maximum abundance (MaxN) of (a) Gobiidae (b) Labridae (c) Scyliorhinidae (d) whiting *Merlangius merlangus* (e) sandeel *Ammodytidae* spp. (f) Gadidae (g) Mullidae (h) goldsinny wrasse *Ctenolabrus rupestris* and (i) sprat *Sprattus sprattus* observed during 1 h BRUV deployments across each treatment during surveys in 2017 and 2018

spp. gadoids, wrasse (Labridae spp. goldsinny *C. rupestris*), and mullet in 2018, which were absent from control stations and within the mussel farm (Fig. 7). Control stations and those within the mussel farm were characterised by increased occurrence of whiting *Merlangius merlangus* (Fig. 7).

#### 4. DISCUSSION

Whilst previous work has documented the effectiveness of SBCC systems on the growth and survival of the target species (Jeffs & James 2001, Beal 2012, Beal & Protopopescu 2012, Daniels et al. 2015), this study is the first to investigate potential impacts of the technique on wider ecosystems. As interest in low-cost and low-carbon food production increases, a better understanding of both the effectiveness and the environmental interactions of these systems is necessary to inform regulatory decisions around their implementation. Our results indicate that SBCC can provide a sustainable, low-impact method of rearing lobsters, which can contribute to the sustainable development of shellfish mariculture, benefiting industry stakeholders, policymakers and regulators, and seafood consumers.

Our sampling design allows the detection of any impacts of lobster SBCC systems on the local ecol-

ogy in relation to the existing mussel farm and control locations in the bay. Given that the mussel farm was already established, our study does not represent a true BACI design, with no sampling prior to any possible sources of disturbance, although sampling across monitoring years and between treatments should allow a reliable assessment of any changes over time as a result of the introduction of the SBCC systems and is a well-established method of detecting environmental impacts (Underwood 1993). DDC and BRUV surveys were undertaken shortly after establishment of the SBCC systems, providing an accurate representation of baseline conditions against which comparisons can be made. Although sampling limitations meant that initial grab sampling was not undertaken until May–June 2017, 11 mo after the first lobster containers were installed, our survey should still have been robust enough to identify any impacts of the systems on local benthic ecology at the monitoring stations over the course of the subsequent 15 mo, particularly given the cumulative nature of container density and resultant biofouling.

The introduction of mid-water structures can change the physical environment and alter hydro-sedimentary processes by reducing current speeds (Gibbs et al. 1991, Plew et al. 2005, Liu & Huguenard 2020) and increasing local sedimentation rates



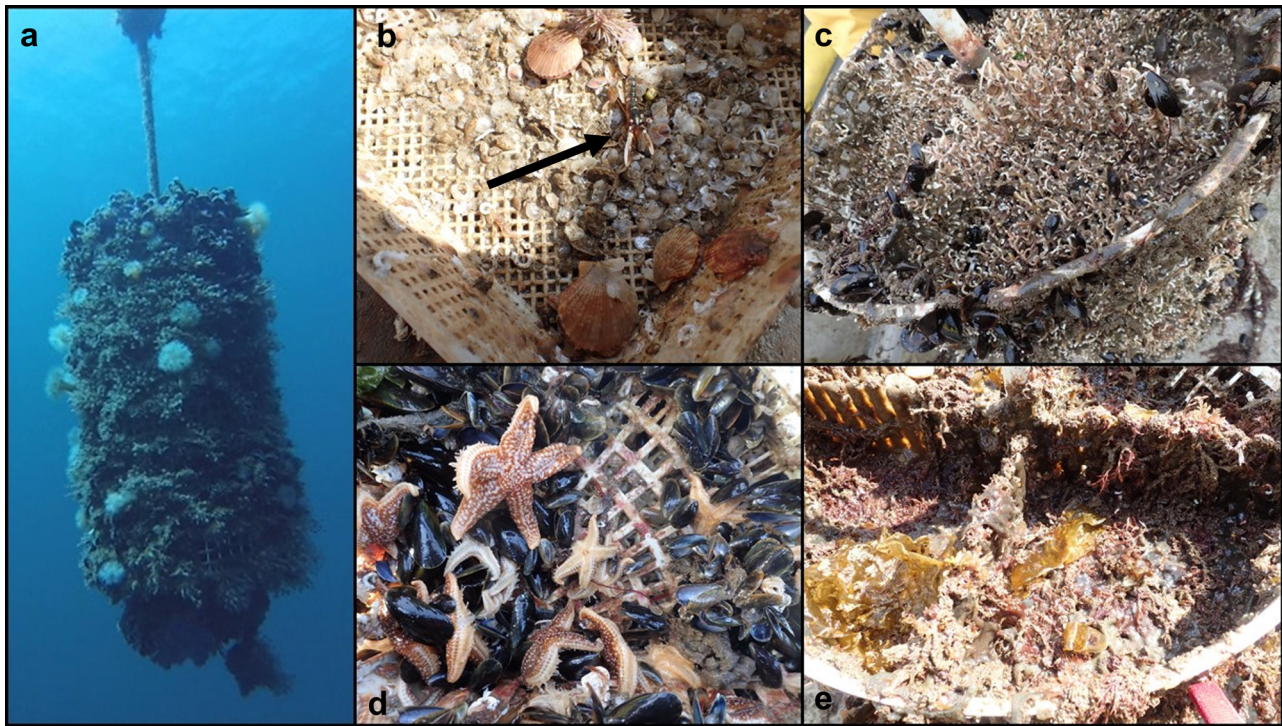


Fig. 8. (a) An *in situ* sea-based container culture system in the water column, with examples of the various colonising taxa, including (b) bivalve molluscs (mussels, scallop [king, queen and variegated], saddle oyster), nudibranch gastropods, cnidarians (anemones and hydroids), (c) encrusting polychaete tube worms, (d) echinoderms (Asteroidea, Ophiuroidea, Chirinoidea, Echinoidea), decapod crustaceans (brown crab, velvet swimming crab) and (e) brown (Pheophyta), red (Rhodophyta) and green (Chlorophyta) algae, tunicates (ascidians). The cultured species, a juvenile European lobster, can also be seen in the container in (b), as indicated by the black arrow

(Hatcher et al. 1994). Biological changes associated with the presence of aquaculture systems are typically characterised by the settlement and colonisation of pelagic floating structures by epifauna (Daniels et al. 2015), reduced levels of dissolved oxygen and nitrogen flushing in the water column (Price et al. 2015), and organic enrichment in surrounding sediments (Hargrave 2010). In the present study system, the suspended containers attracted settlement of various marine fauna, including Annelida, Arthropoda, Chlorophyta, Chordata, Echinodermata, Mollusca, Porifera, and Rhodophyta (Fig. 8), comparable to the existing mussel lines. Whilst water sampling would have allowed for a detailed assessment of nitrogen loading and dissolved oxygen, it was beyond the scope of project resources. Nonetheless, none of our monitoring results provide any indication of subsequent biological impacts that may occur due to reduced dissolved oxygen and increased nitrogen loading.

We found no significant changes to sedimentary habitats within and around the systems, something usually attributed to changes in water flow. The size of the SBCC systems and associated biofouling is comparable to existing mussel lines and may be ex-

pected to lead to similar flow reductions. Indeed, acoustic Doppler current profiler deployments undertaken throughout the mussel farm in 2016–2018 as part of a separate study (Tilsley 2020) suggest that the mussel farm and SBCC systems contribute to a reduction in flow speeds across the site, with a 30% reduction in mean flow speeds in the centre of the farm area compared to a reference location to the southwest corner of the farm (Tilsley 2020). Yet we observed a loss, although non-significant, of finer sediments within the lobster farm, something generally associated with higher water flows rather than flow reductions usually associated with the introduction of mid-water structures. Lobster stations consistently showed a higher proportion of gravelly sediments compared to our other 2 treatments, which were predominantly in sandy substrates (Fig. 3), and these physical differences may be the driver of the treatment differences observed in our diversity indices, particularly a higher diversity of epifaunal species (Table 2). Whilst it would provide greater insight into any changes to organic carbon or nitrogen loading, detailed chemical analysis of sediments was beyond the scope of this study.

Macrofaunal diversity showed significant changes in species richness, total abundance, and Simpson's and Shannon's indices between monitoring surveys, although this was consistent across all treatments (i.e. seen at control stations as well as mussel and lobster stations). The model interaction term was only significant for total abundance, which increased within the SBCC systems and mussel farm but not at control stations (Table 2), indicating a potential effect of the systems on overall macrofaunal abundance. SIMPER analyses indicate that this change was characterised by increases in the abundance of various species at these stations, a number of which are highly sensitive to environmental disturbance (*Timoclea ovata*, *Leptochiton cancellatus*, *Polyopthalmus pictus*, *Ampelisca tenuicornis*), as well as species indifferent or tolerant to environmental disturbance and organic pollution (*Mediomastus fragilis*, *Psammthe fusca*, *Lumbrineris cingulata*, *Pholoe inornata*) (WoRMS Editorial Board 2023). Whilst the SBCC and mussel systems are extractive, 'no-feed' systems (Oddsson 2020), biodeposition of faeces and pseudo-faeces (Grant et al. 2005), and/or fall-off of colonising organisms (Kaspar et al. 1985, Inglis & Gust 2003) may increase organic input and food availability and drive such an increase in abundance, biomass, and productivity (Robichaud et al. 2022), which did not occur at control stations. If it were the case, however, this was not sufficient to elicit a significant change in the overall community structure, as indicated by the lack of a significant interaction in the PERMANOVA model (Table 1), with the species driving these changes mostly present across both surveys.

Furthermore, mean AMBI values showed no change throughout the study period and remained in 'good ecological status' across both surveys, with the exception of 2 control stations and a single station within the SBCC systems (Fig. S2 in Supplement 1). Thus, we found little evidence that either the mussel farm, consistent with previous work (Fabi et al. 2009), or the SBCC systems negatively affected local benthic communities throughout the study period. Given that the species driving the increased abundance within the mussel farm and SBCC systems relative to control locations were present across surveys, it is more likely that these changes reflect variability in recruitment patterns, which are strongly affected by environmental fluctuations (Pearson & Rosenberg 1978). Whilst such processes may be affected by aquaculture systems through alterations to benthic-pelagic coupling, biogeochemical processes, increased sedimentation loads, and organic input through deposition of metabolic prod-

ucts as pseudofeces (Newell 2004, Alonso-Pérez et al. 2010), our results show little evidence that this occurred within the present study.

The epifaunal changes we detected around the SBCC systems were not recorded at control or mussel stations (Table 1) and were characterised by an increase in the presence of mobile epifauna, generally scavenging species (e.g. *Pagurus prideaux*, *Marthasterias glacialis*, Asteroidea, Caridea). This may be indicative of increased detritus from the SBCC systems and associated fouling organisms that can attract scavenging and benthivorous species into an area (Inglis & Gust 2003, Clynick et al. 2008, D'Amours et al. 2008, Drouin et al. 2015). Indeed, dive surveys in May 2018, led by Cornwall Wildlife Trust, recorded diverse epibenthic communities in and around both the mussel farm and the SBCC systems, with recorded fauna including European spiny lobster *Palinurus elephas*, spider crab *Maja brachydactyla*, and abundant *M. glacialis*, consistent with our epifaunal monitoring, particularly in areas where mature mussels had fallen from their culture ropes. Dive surveys identified a high density of fouling organisms, hydroids *Ectopleura larynx*, sponges, anemones *Metridium dianthus*, and sea squirts *Diplosoma spongioformae* on the SBCC cages, which were home to other species such as the tube dwelling amphipods *Jassa* sp., and a large diversity of nudibranchs (M. Slater pers. comm.). Whilst individual SBCC containers are of a greater surface area than mussel lines, the total surface area and thus biomass of fouling organisms on mussel lines was higher due to the high number and density of mussel lines. As a pilot study, however, the SBCC systems were periodically hauled for stock checks and monitoring, dislodging biofouling organisms and thus causing the observed increase in epifaunal scavengers and mobile fish species. Although not formally analysed, researchers monitoring SBCC systems noted that initial settlement was dominated by different taxa depending on the seasonality of deployment, with whole cohorts of deployments tending to be encrusted by the same locally abundant species, especially kelp *Laminaria digitatum*, tube-building annelid worms *Pomatoceros triqueter*, or Japanese skeleton shrimps *Caprella mutica*. This last species is aggressively invasive, and although aquaculture infrastructure may be a conduit to localised proliferation, *C. mutica* was previously established at the mussel farm and is already widely introduced throughout the UK, with shipping considered the major mechanism of long-range dispersal (Cook et al. 2007). Thus, the presence of the SBCC systems in addition to the mussel lines appears to provide additional mid-water



habitat, elevating local diversity and promoting an influx of scavenging species in the immediate vicinity of the systems. Any increase in scavengers may not be of the magnitude observed by our monitoring for commercial scale operations, during which containers will not be hauled for monitoring and only for annual harvesting and container changes.

Our BRUV monitoring of mobile species suffers from low replication, with only 2 control sites sampled, and our results should hence be interpreted with caution. Despite this, and whilst acknowledging high natural variability in mobile species assemblages, our results offer an insight into the potential interaction with the mussel farm, SBCC systems, and mobile species within the area. A number of fish taxa were observed at higher abundances around the SBCC systems or solely at these stations (Fig. 7), such as sandeel *Ammodytes* spp., gadoids, goldsinny wrasse *Ctenolabrus rupestris*, and other Labridae, and a significant increase in species richness was observed within these systems between surveys that was not observed elsewhere.

Aggregations of mobile species may occur around the SBCC systems, as novel structures provide shelter and additional foraging opportunities through fouling organisms and increased detritus and prey, acting as 'fish-aggregating devices' (Klima & Wickham 1971, Rountree 1989, Nelson 2003, Sanchez-Jerez et al. 2011). Such structures can increase local biodiversity around the systems relative to the surrounding environment, and, indeed, our BRUV results identified an increase in diversity at lobster stations relative to that at mussel or control stations, characterised by higher numbers of gadoids and wrasse. The effect of floating aquaculture structures in providing mid-water reef habitat for motile species has been documented in previous studies (Morrissey et al. 2006, Mohammed et al. 2010, Clark et al. 2012), and this increase in diversity at lobster stations may be due to the introduction of the SBCC containers, providing additional opportunities for feeding and shelter that have increased local mobile species diversity. This may indicate a future positive effect of the systems on local mobile species diversity, with both demersal and pelagic fish potentially gaining additional abundance of prey species and shelter, similar to other manmade marine structures (Callaway et al. 2017).

The results of this work contribute to the evidence base upon which regulatory and management decisions can be made in implementing novel SBCC systems elsewhere in the future, contributing to the sustainable culture of European lobster as a high-value

species, particularly as UK fisheries adapt to the exit from the European Union's Common Fisheries Policy and Single Market. Whilst further monitoring data will allow for a longer-term assessment, we show minimal impacts of SBCC culture systems on the local ecology within St Austell Bay, UK, and suggest that such systems may provide low-impact and low-carbon opportunities for coastal shellfish mariculture in the face of increased pressure on wild stocks and global food demand.

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