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Quantification of finfish assemblages associated with mussel and seaweed farms in southwest UK provides evidence of potential benefits to fisheries

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ABSTRACT: Low trophic aquaculture, including shellfish and seaweed farming, offers a potentially sustainable food source and may provide additional environmental benefits, including the creation of new feeding, breeding and nursery areas for fish of commercial and ecological importance. However, quantitative assessments of fish assemblages associated with aquaculture sites are lacking. We used pelagic baited remote underwater videos (BRUVs) and hook and line catches to survey summer fish assemblages at 2 integrated blue mussel *Mytilus edulis* and kelp (predominantly *Saccharina latissima*) farms in southwest UK. We recorded at least 11 finfish species across the surveys, including several of commercial importance, with farmed mussels and/or kelps supporting significantly higher levels of abundance and richness than reference areas outside farm infrastructure. Farmed kelp provided temporary habitat due to seasonal harvesting schedules, whereas farmed mussels provided greater habitat stability due to overlapping interannual growth cycles. Stomach content analysis of fish caught at the farms revealed that some low trophic level species had high proportions of amphipods in their stomachs, which also dominated epibiont assemblages at the farms. Higher trophic level fish stomachs contained several lower trophic level fish species, suggesting that farms provide new foraging grounds and support secondary and tertiary production. Although not identified to species level, juvenile fish were abundant at both farms, suggesting potential provisioning of nursery or breeding grounds; however, this needs further verification. Overall, this study provides evidence that shellfish and seaweed aquaculture can support and enhance populations of commercially and ecologically important fish species through habitat provisioning.

KEY WORDS: Restorative aquaculture · Shellfish farming · Kelp farming · BRUV · Biodiversity · Habitat · IMTA

1. INTRODUCTION

Aquaculture, the farming of finfish, shellfish and algae in freshwater and saltwater environments, is one of the fastest growing food production systems globally (FAO 2022). Low-trophic or extractive aquaculture, such as shellfish or seaweed farming, is increasingly recognised for its potential environmental benefits, such as improved water quality regulation and nutrient cycling (van der Schatte Olivier et al. 2020, United Nations Environment Programme 2023). Recent work has focused on the habitats provided by shellfish and seaweed farms and their role in supporting coastal restoration efforts, particularly for fish species of commercial or ecological importance (Theuerkauf et al. 2021). The potential increase in

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secondary production of fish observed at oyster, mussel and seaweed aquaculture sites globally is estimated at 350–1000 kg ha^{-1} yr^{-1} relative to reference habitats, with additional value to commercial and recreational fishers of ~970–2850 USD ha^{-1} yr^{-1} (Barrett et al. 2022). Quantitative assessments of fish assemblages associated with shellfish and seaweed farms, however, are largely lacking, and in particular very few studies have been conducted at seaweed farms in temperate regions (Callier et al. 2018, Kelly et al. 2020, Fariñas-Franco et al. 2021, Theuerkauf et al. 2021, Corrigan et al. 2022, Forbes et al. 2022).

Shellfish and/or seaweed farms may provide novel structured habitat for fish species through both the provision of high densities of farmed organisms (i.e. bivalve shells and seaweed biomass) and their associated epibiont communities, as well as farm infrastructure (Callier et al. 2018, Barrett et al. 2019). This farmed biomass and infrastructure could provide valuable habitat in terms of spawning substrate, breeding grounds, shelter and/or food in the form of farmed biomass or associated epibionts, similar to wild populations of shellfish or seaweeds (Bergman et al. 2001, Callier et al. 2018, Theuerkauf et al. 2021). Hence there is growing interest surrounding the potential for farms to act as 'restorative' or 'regenerative' forms of aquaculture in areas where fish populations have been depleted due to degradation of natural habitats (Alleway et al. 2023). Shellfish and seaweed farming infrastructure may also restrict fishing activities in the immediate vicinity, which could benefit populations of fish and other organisms by excluding extractive activities such as bottom trawling, thereby acting as de facto 'no take zones' with potential spill-over benefits for fisheries in surrounding areas (Olsgard et al. 2008, Johnson et al. 2015, Wang et al. 2015, Gentry et al. 2020, Bridger et al. 2022). Farms may, however, induce changes in natural fish assemblages by altering food availability and quality (Oakes & Pondella 2009), or by replacing, modifying or damaging pre-existing habitats in the area, such as kelp forests, seagrass meadows or other important coastal habitats (McKindsey et al. 2011, Wood et al. 2017, Campbell et al. 2019, Kelly et al. 2020, Theuerkauf et al. 2021, United Nations Environment Programme 2023). It is also uncertain how farming operations and schedules may affect fish populations inhabiting farms. For example, in temperate seaweed farms, annual harvests remove cultivated biomass during summer months, which could disrupt important fish life stages such as spawning events and nursery habitat provisioning for juvenile fish (Corrigan et al. 2022, Forbes et al. 2022).

Recent reviews on the potential ecological benefits of seaweed farming have highlighted how farms will likely provide habitat distinct from natural seaweed beds, and so far the few reported effects on fish populations are highly variable between sites (Theuerkauf et al. 2021, Corrigan et al. 2022, Forbes et al. 2022, United Nations Environment Programme 2023). For instance, increased abundances of fish have been reported in some shallow-bottom tropical seaweed farms compared to reference areas (e.g. Eklöf et al. 2006, Radulovich et al. 2015), whereas in other similar farms, either negative or no effects on fish populations have been reported (as reviewed in Kelly et al. 2020). Little comparative evidence from suspended seaweed longline farms in temperate regions exists (Corrigan et al. 2022); however, a recent study in Maine, USA, found no difference in fish populations between kelp farms and reference sites, attributed to the seasonality of kelp farming in relation to fish migration patterns in the area (Schutt et al. 2023). Similarly, no effect on benthic fish assemblages was reported at a kelp farm in Sweden (Visch et al. 2020). Habitat provisioning for fish species at shellfish farms in temperate regions has been studied more widely, and although there is variation between sites, in general shellfish farms support comparable fish abundances and diversities to wild shellfish reefs (Callier et al. 2018, Ferriss et al. 2021, Martínez-Baena et al. 2022, Underwood & Jeffs 2023). In areas devoid of structural features, such as natural reefs, shellfish farms may act as aggregating devices and form relatively stable artificial reef-like habitats for fish species, as they tend to have longer and more overlapping growth periods than temperate seaweed farms, which persist for only several months of the year (Corrigan et al. 2022). However, more evidence from both seaweed and shellfish farming is needed, including from integrated seaweed and shellfish co-cultivation sites (Wang et al. 2015, Sheehan et al. 2020, Underwood & Jeffs 2023, United Nations Environment Programme 2023).

Most research on the ecological impacts of temperate shellfish and seaweed farms has focused on associated sessile and sedentary benthic organisms (Callier et al. 2018, Corrigan et al. 2022) rather than fish assemblages, which are highly mobile and difficult to quantify due to their pronounced spatiotemporal variability (Bicknell et al. 2019). Surveying coastal fishes in and around aquaculture sites provides additional challenges, such as reduced visibility and accessibility within farm infrastructure (Tonk et al. 2019, Sheehan et al. 2020, Bridger et al. 2022). Baited remote underwater video (BRUV) or camera

surveys are increasingly utilised for surveying fish assemblages in both natural and artificial habitats, as technological advances have made them relatively low cost and highly replicable (Langlois et al. 2010, 2018, Santana-Garcon et al. 2014, Tonk et al. 2019, Sheehan et al. 2020, Corrigan et al. 2022, Jackson-Bué et al. 2023). Furthermore, camera surveys have been designed specifically for suspended aquaculture monitoring: for instance, low cost video systems have recently proved effective in monitoring pelagic fauna in a large offshore UK mussel farm (Sheehan et al. 2020) and seaweed farms in the Netherlands (Tonk et al. 2019), and Maine, USA (Schutt et al. 2023). Camera surveys can capture multiple species simultaneously and are effective at monitoring the abundance and diversity of fish assemblages, as well as recording fish behaviour such as feeding. However, due to the relatively limited spatial and temporal coverage of static camera systems, they inevitably capture only a subset of the entire fish assemblage and should therefore be complemented with other approaches where possible, such as fishing surveys that also enable dietary analysis of caught individuals (Mallet & Pelletier 2014, Bicknell et al. 2016, 2019, Tonk et al. 2019, Corrigan et al. 2022).

We quantified the structure of fish assemblages associated with farmed shellfish and seaweeds, and in comparable pelagic negative control sites, or reference areas, over a summer season in southwest UK to determine whether aquaculture sites provide valuable habitat for coastal fish species. We repeatedly surveyed 2 integrated mussel and kelp farms at 2 locations, using pelagic BRUVS and hook and line fishing to examine fish abundance and species richness. We also analysed the stomach contents of captured fish to assess whether they were using the farms as feeding grounds based on similarities to epibionts present on the farmed kelps and mussels. We compared fish assemblages before kelp harvest (May), during harvest (June) and after harvest (August) at one farm site, to determine whether kelp farm habitat was temporary as a result of the farming cycle. We expected that farms would support greater levels of finfish abundance and richness than reference areas, as they provide structurally complex habitat and elevated food supply through both cultivated biomass and associated epibionts. An increased understanding of fish assemblages associated with mussel and seaweed farming will help determine whether low-trophic aquaculture sites can provide new or 'restorative' habitats for fish species of commercial or ecological importance.

2. MATERIALS AND METHODS

2.1. Study sites

Surveys were conducted at and around 2 integrated blue mussel *Mytilus edulis* and kelp (predominantly sugar kelp *Saccharina latissima*) farms in south Cornwall, UK (Fig. 1). Porthallow Bay farm (50° 04′ N, 5° 04′ W) is a small (~16 ha) site approximately 500 m from shore, while St Austell Bay farm (50° 18′ N, 4° 43′ W) is larger (~70 ha) and approximately 1–1.5 km from shore, with a second blue mussel farm (~30 ha) neighbouring it to the west. Both farm areas are exposed to wind and wave action from the east and southeast, but are sheltered from the predominant southwesterly winds and North Atlantic swells. Both farms are suspended over seabed depths of 8 to 15 m (below chart datum), with the seabed below consisting of mixed rocky substrate, soft sediments and maerl *Phymatolithon calcareum* gravel. Reference areas were randomly selected and located 200 to 600 m away from farm sites, in areas which did not contain any structural pelagic habitat, but experienced similar environmental conditions and seabed depths to the respective farm (as per Sheehan et al. 2020). Neighbouring benthic habitats around both Porthallow Bay and St Austell Bay include natural kelp beds, seagrass meadows and *P. calcareum* beds, and both sites are located within the Falmouth Bay to St Austell Bay Special Protected Area (Crosby et al. 2023). Porthallow and St Austell Bay farms use longline systems with ~200 m header lines anchored to the seabed and suspended 1–3 m below the surface, supporting either seaweed or mussel growth (Fig. 1). At both farms, mussel lines were seeded following the natural spawning and settlement cycle of *M. edulis*, whereby as seawater temperatures rise (typically from March to May), mussels spawn and their larvae settle naturally onto the dropper ropes as spat, and continue to grow for ~18 mo before harvest, by which time new spat will have settled for the next harvesting season. Seaweed lines in Porthallow Bay were seeded in late October 2021 with predominantly *S. latissima* gametophytes, and several *Alaria esculenta* lines were also deployed. The seeded lines were then spaced at 2–3 m distances along the header lines. Seaweed lines in St Austell Bay were set in January–February 2022, whereby carrier lines were wrapped in twine with juvenile *S. latissima* sporophytes attached. Several *A. esculenta* lines were deployed using the same method, which were then spaced 2–3 m apart along the header lines. At both farms, the cultivated seaweed and mussel lines were frequently colonised with *Saccorhiza polyschides*, a naturally settling pseudo-kelp, which sup-

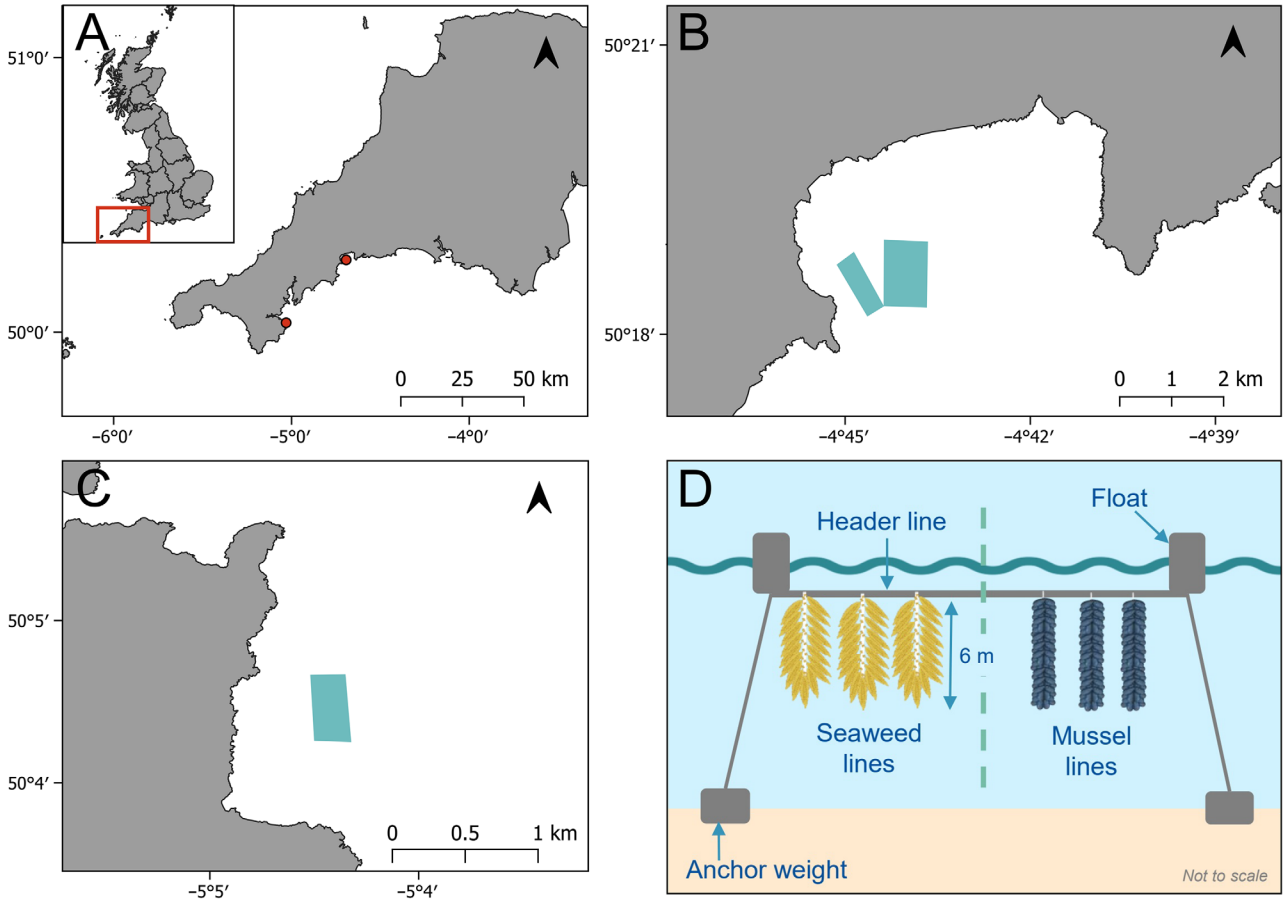


Fig. 1. Maps of study area indicating (A) location of farm sites in Cornwall, southwest UK (red dots); (B) St Austell Bay farm (shaded blue rectangle on right, with a second smaller mussel farm to the west); (C) Porthallow Bay farm (shaded blue rectangle); (D) simplified diagram of the farm system with suspended seaweed and mussel lines (created with BioRender.com). Note seaweed and mussel lines were set on separate header lines, not together as shown in diagram

ported similar epibiont assemblages to the seeded *S. latissima* lines, along with smaller red and green algal species (Corrigan et al. 2023a,b).

2.2. BRUV design, deployment and processing

At Porthallow Bay, surveys were conducted twice in May 2022, prior to kelp harvest, to compare assemblages across the 3 treatment areas (seaweed lines, mussel lines and reference areas). In St Austell Bay, surveys were conducted 3 times throughout the summer of 2022 in each of the 3 treatment areas, to compare assemblages prior to kelp harvest (May), during kelp harvest (June) and after kelp harvest (August). The mussel line areas surveyed were not harvested at either site during the survey period.

During each survey, BRUV units were deployed randomly throughout each treatment area 4 times, to give 4 independent replicates per treatment area per survey. After each deployment in a treatment area, BRUV units were moved to a new random location a minimum of 100 m away within the same treatment area, to ensure independence between the 4 replicates in each treatment (Ellis & Demartini 1995, Tonk et al. 2019). We also ensured that BRUVs in the seaweed and mussel treatments were >100 m apart to maintain independence between treatment areas. Reference areas were randomly selected 200 to 600 m away from farm sites to ensure they were not influenced by the farms (Ellis & Demartini 1995, Tonk et al. 2019). Deployments in all treatment areas occurred throughout daylight hours and across tidal cycles. Exact deployment locations of BRUV units in each survey treatment area were not consistent between survey dates; rather, for each survey, 4 new random locations were chosen within each treatment area.

BRUV units comprised 2 cameras (AKASO EK7000 Pro 4K Action Camera) placed back to back, which were each set to face a 35 cm bait arm holding a bait box with 100 g mixed bait (consisting of sardines or mackerel, mussels and prawns) to attract diverse fish species (Fig. 2). BRUV units were suspended at 3 m depths to correspond with seaweed and mussel growth while maintaining good visibility (Fig. 2), and bait was replenished for each deployment. BRUV units were set to record continuously for ~1 h, as restricted by battery life, and once deployed were avoided by the vessel for the hour to prevent disturbance. Visibility during each BRUV deployment was also measured using Secchi depth. Visibility in the water column remained sufficient to detect fish associated with the farm lines within a close proximity throughout surveys, ranging from 4 to 11 m (mean ± SE, 8 ± 0.34 m).

In total, 118 of the 120 videos from the 60 BRUV unit deployments were successful, with footage from 2 videos being completely obscured by kelp biomass on the first survey in St Austell Bay farm (3 May 2022). In these 2 instances, only footage from the unobscured cameras on the BRUV units were used. After this initial survey, the BRUV unit design used to survey in the seaweed treatments was changed from the attached header line unit (Fig. 2B) to the independent unit (Fig. 2A) to distance the cameras slightly further from the kelp biomass and prevent further videos from being obscured.

Footage from both cameras in each BRUV unit was analysed, as different fish species and abundances were observed between the 2 cameras; data were then averaged to yield 4 replicates per treatment per survey. Fifty minutes of footage were analysed from the start of each video, once cameras had stabilised at their sampling depth following deployment. A 50 min period was chosen as this was the minimum length of footage recorded by any one camera, and most fish species are typically observed within the first 40 to 60 min of BRUV deployment (Unsworth et al. 2014, Jackson-Bué et al. 2023). Fish species were identified to the lowest taxonomic level possible, with species richness defined as number of different taxa observed per video (taxa richness). The maximum number of individuals from each species visible in a single frame (MaxN) was recorded as a conservative measure of relative abundance that reduces the possibility of double counting an individual (Cappo et al. 2003, Langlois et al. 2010). Total MaxN was calculated for each video as the sum of all MaxN values for each species observed. $MaxN^{-min}$ was also recorded as the maximum number of individuals of each species observed in the field of view at the same time per 1 min of video, and then averaged across the 50 min of video, to give the relative abundance (mean min^{-1}) of every species and allow comparisons with similar studies (e.g. Bicknell et al. 2019, Sheehan et al. 2020). The total time fish of each species spent in view per video was also recorded in seconds (MaxT), along with the total time spent in view by all fish species per video (total MaxT).

Shoals of lesser sand eels *Ammodytes* spp., which can comprise several species, were included in taxa richness estimates as a single species as a conservative estimate. However, as shoals of *Ammodytes* spp. observed were large, frequently consisting of >200 individuals, their abundance was not included in

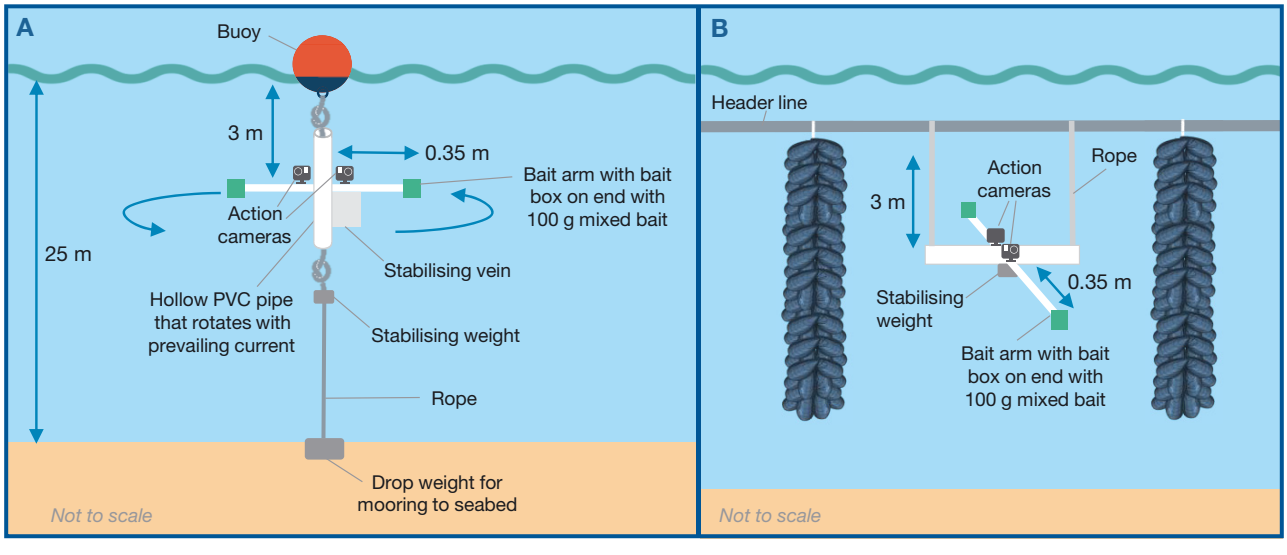


Fig. 2. BRUV unit setup for (A) reference and seaweed areas and (B) farm deployments between mussel cultivation lines

MaxN estimates as this would heavily skew other fish species abundance estimates. The number of shoals of *Ammodytes* spp. per video was recorded and compared across survey dates and treatments; however, no statistical differences were recorded, except for a higher number of *Ammodytes* spp. shoals in mussel lines than seaweed lines at St Austell Bay farm on 14 June 2022 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/q016p145_supp.pdf).

2.3. Fishing and stomach content analysis

To sample fish for stomach content analysis, hook and line fishing was conducted concurrently with BRUV surveys, using a range of lures and baits to attract different species. Fishing of the whole water column was conducted on an ad hoc basis around camera deployments, with approximately 30 min spent in each treatment area across the survey day (~1 tidal cycle). Up to 10 fish were caught per species per survey, and fish were terminated using schedule one procedure (destruction of the brain). Fish were measured (maximum standard length, fork length, maximum total length and body depth) and weighed. Fish stomachs were removed and their contents preserved in 70% ethanol for later identification. Each stomach sample was subsequently rinsed in fresh water and its contents identified to coarse taxonomic group, enumerated (if applicable, e.g. whole organisms seen) and then weighed (blotted wet weight). Stomach contents were qualitatively compared with the structure of epifaunal communities found on seaweed and mussels grown at Porthallow farm in 2020 (as per Corrigan et al. 2023b), to tentatively determine whether prey items were sourced from farm infrastructure. In June 2020, epibiont assemblages were quantified from kelp and mussel lines in Porthallow Bay; 50 cm of each line type was sampled from 2 to 2.5 m water depth, consistent with the growing depth of both species (Corrigan et al. 2023b). Three replicate sections from each line type were collected and epifaunal individuals were identified down to the finest practicable taxonomic resolution (e.g. family) and blotted wet weight biomasses for each taxonomic group were recorded (Corrigan et al. 2023b).

2.4. Statistical analysis

The statistical approaches described below involve univariate and multivariate permutational analyses using the PERMANOVA add on for PRIMER v7® software (Anderson et al. 2008, Clarke & Gorley 2015). Due to the different sampling schedules at Porthallow and St Austell Bay, data from each farm were analysed separately and qualitative comparisons were then made between sites. For comparisons of fish assemblages between treatments (mussel lines, seaweed lines and reference areas), and over the sampling season, univariate assemblage metrics (total MaxN, total $MaxN^{-min}$, taxa richness and total MaxT) were examined using 2-way permutational analyses of variance (PERMANOVA) with treatment and survey date as fixed factors. For each univariate comparison, PERMANOVAs with permutations (999 under an unrestricted model) were based on Euclidean distances between untransformed data with different dummy variables added to each metric (detailed in Table 1). Pairwise tests in PERMANOVA were then conducted wherever main effects or interactions were significant ($p < 0.05$).

Variability in multivariate fish assemblage structure (MaxN, $MaxN^{-min}$ and MaxT) between factors was also examined using a 2-way PERMANOVA and visualised using metric multidimensional scaling (mMDS) ordination. Multivariate assemblages were examined using the models described above, but with permutations based on Bray-Curtis resemblance matrices constructed from each metric, with either a square root or fourth root transformation applied to down-weight the influence of highly abundant fish species and different dummy variables added to each metric (detailed in Table 1). SIMPER analysis was then performed to determine which taxa contributed most to the observed dissimilarity between treatments and survey dates in multivariate analysis. For both the univariate and multivariate metrics, differences in within-treatment variability between levels of factors were also examined using the permutational dispersion (PERMDISP) routine. Where within-treatment dispersion differed between groups, a more conservative p-value ($p < 0.01$) was adopted for the main PERMANOVA test for that response variable (Anderson 2017). Values presented in the text and figures are means ± SE.

3. RESULTS

3.1. BRUV surveys

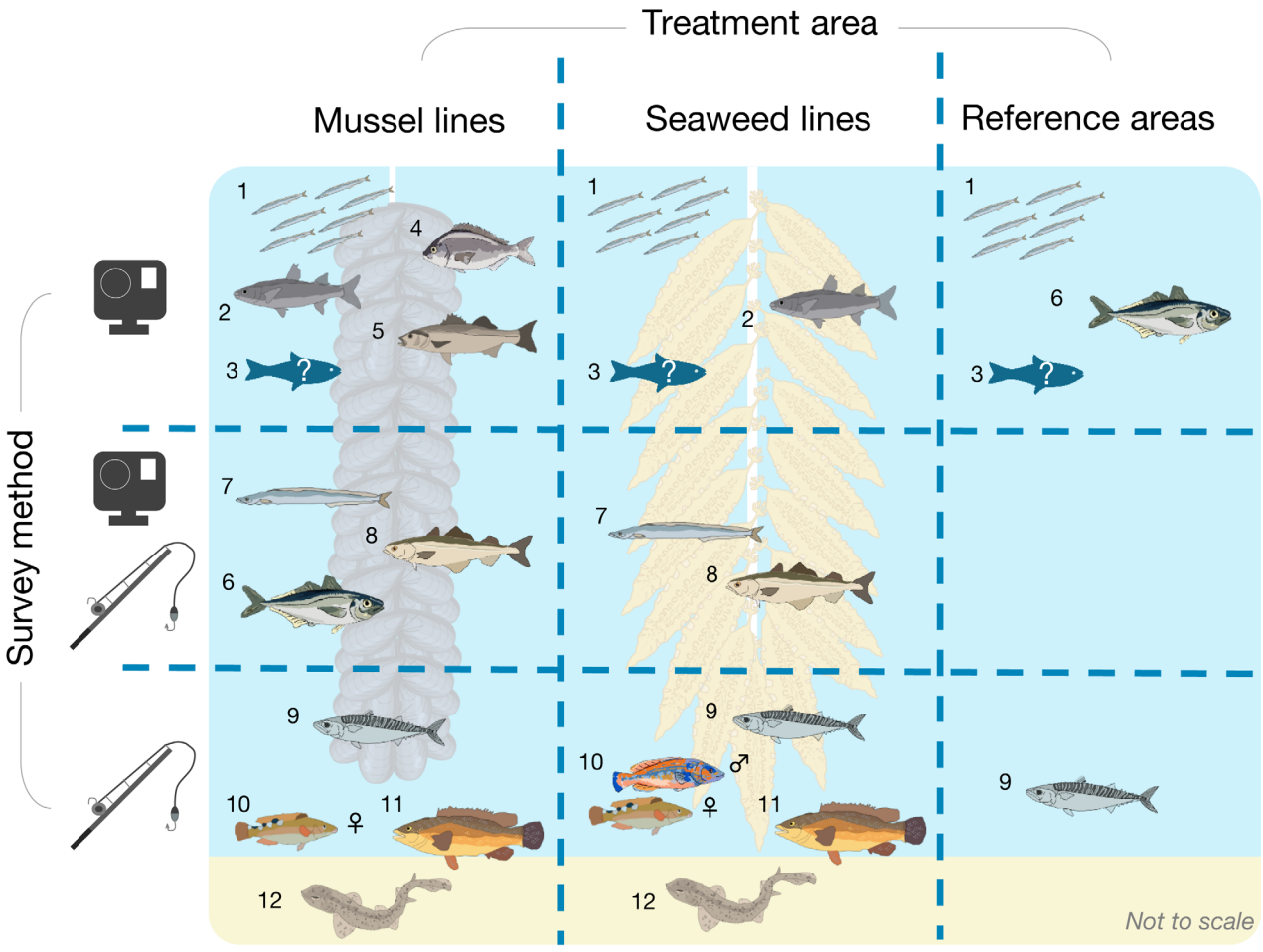
Across all 118 BRUV recordings, a total of 1067 individuals (excluding shoals of lesser sand eels *Ammodytes* spp.), representing at least 7 fish taxa were recorded (including *Ammodytes* spp. as one taxonomic group, and excluding unidentified juveniles) (Figs. 3

Table 1. Results of univariate (Uv) and multivariate (Mv) PERMANOVAs to test for differences in fish assemblages between treatment areas — mussel (M), seaweed (S) and reference (R) — and survey dates at Porthallow and St Austell Bay farms. Asterisks show significant differences; where significant differences between treatment and/or date were detected, the results of pairwise post hoc tests are shown. NA: not applicable

	Transformation	Factor	PERMANOVA df	PERMANOVA *F*	PERMANOVA p	PERMDISP *F*	PERMDISP p	Post-hoc significance differences between treatments and survey dates
Porthallow Bay								
(Uv) total MaxN	Dummy variable added = 1	Treatment	2	7.08	0.006*	5.64	0.04*	M & S > R
		Survey date	1	1.57	0.22	0.72	0.46	NA
		Treatment × survey date	2	1.26	0.29	NA	NA	NA
(Uv) Taxa richness	Dummy variable added = 1	Treatment	2	13.17	0.001*	3.24	0.07	M & S > R
		Survey date	1	1.27	0.27	0.12	0.71	NA
		Treatment × survey date	2	0.97	0.41	NA	NA	NA
(Mv) MaxN	Square root Dummy variable added = 1	Treatment	2	10.06	0.001*	34.57	0.001*	M & S - R
		Survey date	1	0.97	0.45	0.74	0.31	NA
		Treatment × survey date	2	1.06	0.41	NA	NA	NA
St Austell Bay								
(Uv) total MaxN	Dummy variable added = 1	Treatment	2	9.23	0.001*	7.27	0.001*	M > S & R
		Survey date	2	1.75	0.17	3.89	0.19	NA
		Treatment × survey date	4	2.19	0.053	NA	NA	NA
(Uv) Taxa richness	Dummy variable added = 1	Treatment	2	13.96	0.001*	7.15	0.004*	NA
		Survey date	2	7.49	0.007*	2.19	0.26	NA
		Treatment × survey date	4	10.13	0.001*	NA	NA	3 May: no difference 14 June: M > S & R 16 August: M > S
(Mv) MaxN	Square root Dummy variable added = 1	Treatment	2	18.22	0.001*	7.18	0.013*	NA
		Survey date	2	8.35	0.001*	0.15	0.92	NA
		Treatment × survey date	4	5.31	0.001*	NA	NA	3 May: all different 14 June: M — S & R 16 August: M — S & R

& 4). Horse mackerel *Trachurus trachurus* were the most abundant species recorded (~45%) in terms of MaxN; however, they were almost exclusively recorded in the mussel lines in St Austell Bay, particularly from June onwards (Fig. 4). Thick lipped grey mullet *Chelon labrosus* and greater sand eel or lance *Hyperoplus lanceolatus* were also abundant (~20 and ~15% of total fish abundance, respectively) in both farms, but were not recorded in reference areas, and became less abundant later in the season (Fig. 4). Juvenile fish, which could not be identified to species level as they were typically <5 cm in length (hereafter 'juveniles'), contributed ~12% of fish abundance and were present in all treatment areas; however, they were predominantly recorded inside the farms, particularly in May (Fig. 4).

Taxa richness per video ranged from 0 to 5 taxa, with the highest average richness of 3.0 ± 0.5 recorded in the mussel lines in Porthallow Bay on 31 May (Fig. 4). Total fish abundance (total MaxN) ranged from 0 to ~200 per video (0.0 to 7.4^{-min} in terms of $MaxN^{-min}$), with the highest average abundance at 55.0 ± 23.9 (5.7 ± 1.2^{-min} in terms of $MaxN^{-min}$) in the mussel lines in St Austell on 16 August (Figs. 4 & S1). This high abundance value was largely driven by *T. trachurus*, which were present in up to 68% (~34 min) of video footage captured from the mussel lines in August, giving the highest total MaxT value of the study (Table S1, Fig. S1). In general, throughout the season, total MaxN, $MaxN^{-min}$, MaxT and taxa richness were greater in the mussel and unharvested seaweed lines than the reference areas (Figs. 4 & S1, Tables 1 & S1). There was no significant interaction between survey date and treatment for total MaxN at either site (Table 1). However, in St Austell Bay, total $MaxN^{-min}$ was initially higher in both mussel and seaweed lines than reference areas, whereas after the seaweed had been partially or totally harvested in



1) Lesser sand eels (*Ammodytes* spp.). 2) Grey mullet (*Chelon labrosus*). 3) Unidentified juveniles. 4) Black sea bream (*Spondyliosoma cantharus*). 5) European seabass (*Dicentrarchus labrax*). 6) Atlantic horsemackerel (*Trachurus trachurus*). 7) Greater sand eel (*Hyperoplus lanceolatus*). 8) Atlantic pollack (*Pollachius pollachius*). 9) Atlantic mackerel (*Scomber scombrus*). 10) Cuckoo wrasse (*Labrus mixtus*). 11) Ballan wrasse (*Labrus bergylta*). 12) Nursehound (*Scyliorhinus stellaris*)

Fig. 3. Fish species observed using BRUV, fishing or both in mussel, seaweed and reference areas across all surveys (May to August). Fish illustrations are adapted from Jackson-Bué et al. (2023) with permission. Mussel illustrations are created with BioRender.com; seaweed illustrations by S. Corrigan

June and August, total MaxN^{-min} was higher in mussel areas than both seaweed and reference areas, with few, or no, fish seen in the harvested seaweed areas of the farm (Table S1). Taxa richness and total MaxT were also lower in the seaweed areas after harvest than the mussel lines and were instead more comparable to the reference areas (Figs. 4 & S1, Tables 1 & S1).

The multivariate analysis revealed that in Porthallow Bay, both mussel and seaweed treatments hosted distinct fish assemblages (in terms of MaxN, MaxN^{-min} and MaxT) compared to the reference areas on both survey dates (Figs. 5 & S2, Tables 1 & S1). In St Austell Bay, fish assemblages in all treatment areas were distinct from one another at the start of the survey season; however, as more seaweed was harvested over the season, seaweed areas became more similar to reference areas, and only fish assemblages associated with mussel lines remained distinct in June and August (Figs. 5 & S2, Tables 1 & S1). SIMPER analysis showed that in Porthallow Bay, differences in MaxN and MaxN^{-min} between farmed and reference areas were due to higher abundances of *H. lanceolatus*, *C. labrosus* and unidentified juveniles (Tables S3 & S5). These species also differed in abundances between the mussel and seaweed lines, with

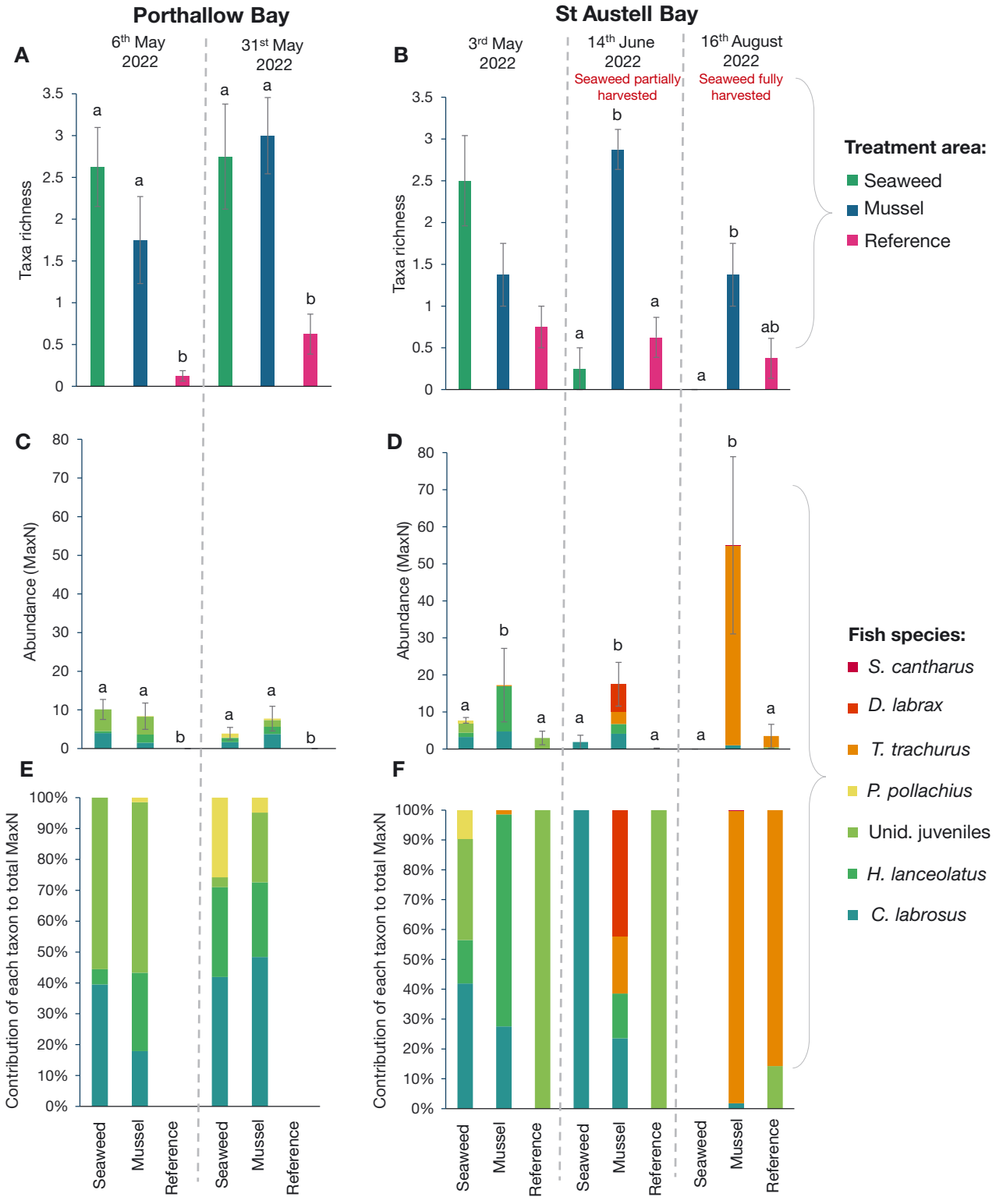


Fig. 4. Differences in fish assemblages between seaweed, mussel and reference areas across survey dates at Porthallow Bay farm and St Austell Bay farm in terms of (A,B) taxa richness (including *Ammodytes* spp); (C,D) abundance based on MaxN (the maximum number of individuals of each species visible in a single frame) of all species (excluding *Ammodytes* spp); (E,F) percentage contribution of each taxon to total abundance (excluding *Ammodytes* spp). Bars indicate mean values per area (unless otherwise stated) and error bars represent SE (n=4 per survey). Significant differences between treatments on a given survey date are denoted with letters. See Fig. 3 for full species names

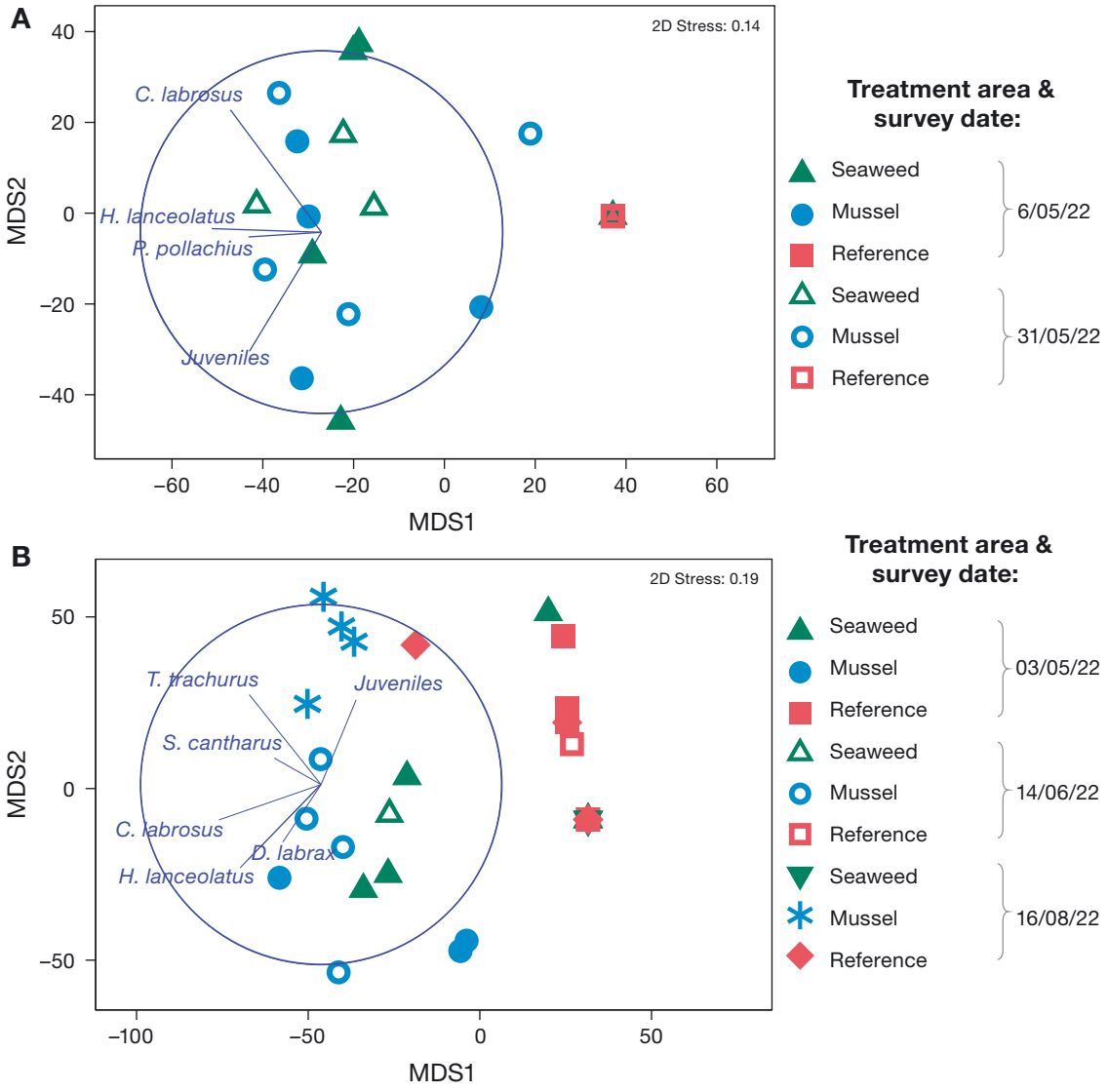


Fig. 5. Metric multidimensional scaling (MDS) plots depicting multivariate analyses of fish assemblages between seaweed lines, mussel lines and reference areas across survey dates at (A) Porthallow Bay farm and (B) St Austell Bay farm. Assemblages represent MaxN (the maximum number of individuals from each species visible in a single frame) of all fish species present, excluding *Ammodytes* spp., with data square root transformed with a dummy variable of 1 added. Both plots are ordinated based on Bray-Curtis similarity matrices of species. n = 4 for each treatment in each survey. Vectors overlaying the plots are based on Pearson's correlation coefficients r > 0.2 for MaxN and depict species that drive separation among treatments in fish assemblages. Dates are given as d/mo/yr

higher abundances of *C. labrosus* observed in the seaweed treatment (in terms of MaxN but not $MaxN^{-min}$, which was the same for both treatments) and higher abundances of *H. lanceolatus* and juveniles observed in the mussel lines (for both Max N and $MaxN^{-min}$) (Tables S3 & S5). In St Austell Bay, higher abundances of *T. trachurus* and *H. lanceolatus* distinguished fish assemblages in the mussel treatment from those in the seaweed and reference areas, while seaweed lines hosted higher abundances of *C. labrosus* but lower numbers of juveniles than reference areas throughout the season (for both Max N and $MaxN^{-min}$), although only a maximum of 3 ± 1.84 juveniles were reported in control areas (Tables S4 & S6). SIMPER analysis also revealed that across both farms, juvenile abundances were highest in early May, and in St Austell Bay, *C. labrosus* abundance declined over the survey season, while *T. trachurus* abundances increased (for both Max N and $MaxN^{-min}$) (Figs. 4 & S1, Tables S3–S6). SIMPER analysis revealed that *Ammodytes* spp., *H. lanceolatus* and *C. labrosus* spent more time (MaxT) in the seaweed and mussel areas than the ref-

erence areas at both sites, and *T. trachurus* spent more time in the mussel lines in St Austell Bay than the seaweed and reference areas (Table S7 & S8). Juveniles also spent longer durations of time in the seaweed and mussel areas than reference areas in Porthallow; however, in St Austell Bay, they spent longer in reference areas, predominantly due to a few individuals that were attracted to the bait box during 2 deployments (Tables S7 & S8). With those exceptions, however, fish did not generally seem to be attracted to or interact with the bait box.

3.2. Fishing and stomach content analysis

Across fishing surveys, 94 fish were caught, representing 7 different species (Fig. 6, Table S2). These were primarily *H. lanceolatus*, with 10 caught per survey; however, during the last survey in St Austell Bay in August, none were caught. A total of 7 fish species were caught around mussel lines, 6 around seaweed lines and only 1 in reference areas, despite comparable fishing effort across all 3 areas (Fig. 3). Comparing across sampling methods, fishing captured 4 additional species not recorded on BRUVs, namely Atlantic mackerel *Scomber scombrus* and 3 demersal species: Ballan wrasse *Labrus bergylta*, Cuckoo wrasse *Labrus mixtus*, and nursehound or bull huss *Scyliorhinus stellaris*. Five species recorded in BRUV videos were not caught using fishing methods (Fig. 3).

In total, 89 fish (94.7%) had stomach contents that could be analysed, with the remaining 5 being empty (Figs. 6 & S3, Table S2). Of the 4 pelagic species studied (*H. lanceolatus, T. trachurus, P. pollachius* and *S. scombrus*), ~40–90% of stomach content biomass averaged across the surveys constituted amphipods, primarily *Jassa falcata*, with the remaining majority comprising fish species (Figs. 6 & S3). *J. falcata* amphipods were also the primary colonising epibiont in terms of abundance and biomass on both seaweed and mussel lines at the Porthallow farm in 2020 (Corrigan et al. 2023a,b) (Fig. 6), which was consistent with epibionts observed on both farms in 2022 (S. Corrigan pers. obs.). On several occasions in the BRUV footage, *H. lanceolatus, T. trachurus, P. pollachius* and *Ammodytes* spp. could be seen feeding on amphipods present in the farm. Of the 8 wrasse individuals sampled across the surveys, there was a high proportion (~34–95%) of mussel biomass in the stomach contents, particularly for *L. bergylta*, whereas *L. mixtus* stomach contents were dominated by crab biomass (Figs. 6 & S3). The 2 analysed samples of *S. stellaris,* a predatory species, confirmed a mixed diet consisting primarily of crabs, fish and worms, with 1 stomach containing a whole *S. scombrus* tail (Figs. 6 & S3). Differences between fish species in terms of prey composition were not assessed statistically (e.g. using prey accumulation curves), due to lack of replication for some species and within-species variation in stomach contents in relation to fish size and survey date (Table S2). Nevertheless, qualitative comparisons of stomach contents indicated notable differences in prey composition between even closely related species (e.g. *L. mixtus* versus *L. bergylta*) and between juveniles and sub-adults (e.g. for *P. pollachius*) (Fig. S3).

4. DISCUSSION

This study presents the first comparison of fish assemblages between farmed mussels, kelp and non-farm reference areas in the UK, which, like other European countries, has a growing cultivation industry for both shellfish and seaweed species (Capuzzo & McKie 2016, Hughes & Black 2016). We found that farmed mussels and/or kelp lines hosted higher taxa richness and abundances of fish species than reference areas away from farmed sites. However, as seaweed biomass was harvested through the summer, valuable fish habitats were seemingly lost, whereas cultivated mussel lines offered more temporally stable habitat due to overlapping interannual growth cycles. Stomach content analysis revealed that several of the pelagic fish species inhabiting the farm had high proportions of amphipods in their diet (~40–90%), consistent with the species recorded at the farms. Amphipods, primarily *Jassa falcata,* were the dominant epibiont found on both mussel and seaweed lines, occurring in huge numbers and contributing substantial biomass to secondary production at the farm sites (Corrigan et al. 2023a,b). Indeed, in several of the videos, pelagic fish were seen feeding on amphipods in the farm. Demersal wrasse species caught beneath farm infrastructure had high proportions of mussels in their stomachs, suggesting that they were also feeding directly from the farm or on mussels that had been detached from lines and accumulated on the seabed. However, further research (using stable isotopes or biomarkers, for example) is needed to confirm prey sources and trophic linkages. High abundances of juvenile fish were also recorded around both seaweed and mussel lines, suggesting farms could act as potential spawning and nursery grounds; however, these juveniles could not be identified to species from videos due to their small size (<5 cm) and further investigation is needed to confirm this.

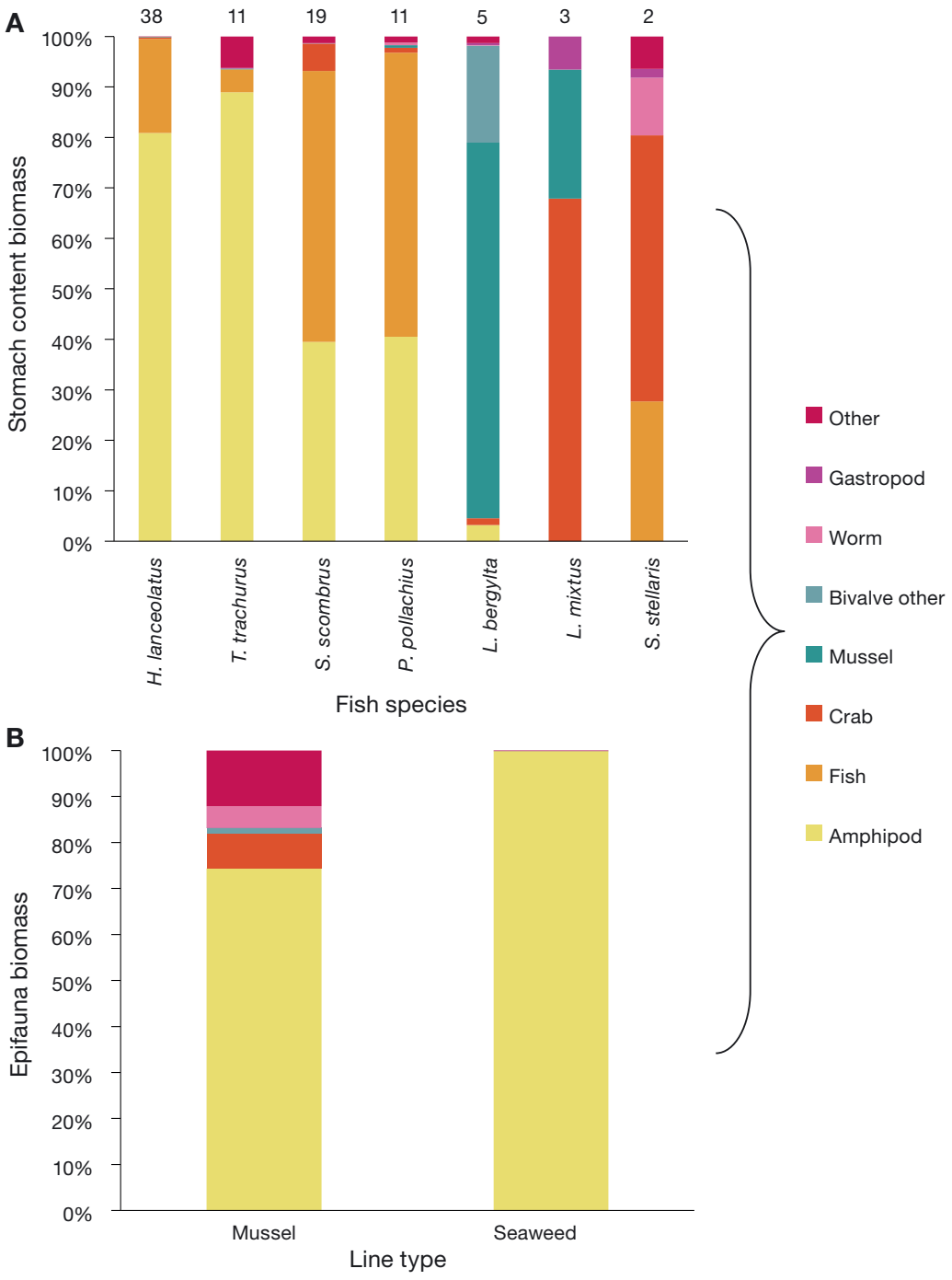


Fig. 6. (A) Stomach contents of fish species caught over all surveys throughout the study, presented as percentage contributions of total stomach content biomass (wet weight). Number of fish sampled per species is shown at the top of each bar. See Fig. 3 for full species names. (B) Percentage contributions of total epifauna biomass (wet weight) from mussel and seaweed lines sampled at Porthallow Bay farm in 2020 (adapted from Corrigan et al. 2023b)

Overall, this study demonstrates that shellfish and seaweed aquaculture may provide new, valuable habitat for fish species in coastal environments, particularly in areas that lack structural habitats that attract or maintain fish populations.

The fish species found to be present in this study were consistent with those expected around the southwest UK for the time of year (Naylor 2021), and with those previously recorded at seaweed and mussel farm sites in Europe more widely (e.g. Sheehan et

al. 2020, Fariñas-Franco et al. 2021, Bridger et al. 2022, Clarke et al. 2023). The most abundant taxa found across our surveys was *Trachurus trachurus*, a commercial bentho-pelagic species which has also been reported as the dominant fish species in other European mussel and seaweed farms (Tonk et al. 2019, Sheehan et al. 2020, Fariñas-Franco et al. 2021, Bridger et al. 2022). In this study, *T. trachurus* were mainly observed around the mussel lines, particularly later in the season once the seaweed had been harvested, suggesting a seasonal visiting pattern that has been observed in other fish species in temperate seaweed farms in Maine, USA (Schutt et al. 2023). On several occasions *T. trachurus* were observed to be feeding on amphipods associated with the mussel lines, and the stomach contents analysed from the fish caught at the farms confirmed this as their main prey source, with the most predominant amphipod, *J. falcata*, consistent with that most commonly recorded at the farms (Corrigan et al. 2023a,b). *Hyperoplus lanceolatus* were also abundant during the surveys; however, they became less common towards the end of the survey season, with none seen or caught in the last survey in August. *H. lanceolatus* are commercially and ecologically important due to their high fat content, which makes them desirable for marine predators including mammals, seabirds and predatory fish, and targets for fisheries that use *H. lanceolatus* for fish meal, oil production, human consumption and fishing bait (Frimodt & Dore 1995, Winter et al. 2023). *H. lanceolatus* stomach contents sampled in this study were similarly dominated by *J. falcata* amphipods and small fish, often juvenile *H. lanceolatus* or *Ammodytes* spp., also frequently reported across the surveys. *Chelon labrosus* was also commonly observed in the farm BRUV footage, particularly in May and June; however, none were caught using hook and line methods, and therefore their stomach contents could not be analysed. This demonstrates how different survey techniques are biased towards recording certain species and why a combination of methods should be used to more holistically survey fish assemblages at farm sites in the future (Corrigan et al. 2022).

Using a wider range of survey techniques, such as fish traps or eDNA methodologies (e.g. Schutt et al. 2023, Underwood & Jeffs 2023), could also help to identify the many juvenile fish that were detected in the videos, which likely comprised several different species. Several fish species identified in this study spawn during the kelp farming period (typically November through June), including *Pollachius pollachius*, which spawns from January to May in the northeast Atlantic (Svetovidov 1986, Naylor 2021) (Table S9). Juvenile *P. pollachius* could be identified by their characteristic 3 dorsal fins, and several mature *P. pollachius* juveniles were caught around the mussel lines in St Austell Bay in August (Table S2), which might suggest that the farm could be providing a nursery or spawning ground for this species. Previously, there has been uncertainty as to whether shellfish and seaweed farms enhance juvenile fish recruitment or simply aggregate existing adult fish populations from other local areas (Gentry et al. 2020). A recent study in New Zealand successfully used standard monitoring units for the recruitment of fishes (SMURFs) as temporary settlement substrates to determine that juvenile recruitment and diversity was equivalent to natural habitats in both mussel monoculture and mussel and seaweed co-cultivation sites (Underwood & Jeffs 2023). In the same study, for at least the most abundant species of fish present, the aquaculture sites had sufficient epibiont food resources to support growth from settlement to juvenile size classes. This, in turn, offers a promising new insight into how farms may create valuable habitat for fish across different life stages, particularly in relation to soft-bottom habitats that have limited structural complexity (Underwood & Jeffs 2023).

In China, the abundance of juvenile fish at mussel farms was also not found to differ from natural rocky reefs, although assemblages at mussel farms were structurally more similar to those found in soft-bottom habitats than those associated with artificial and natural reefs (Wang et al. 2015). This contradicts the findings from New Zealand that showed no difference in juvenile assemblages between a mussel farm and surrounding natural habitats, including soft-bottom areas and shellfish reefs (Underwood & Jeffs 2023), suggesting that aquaculture–environment interactions may vary between sites. In future, collecting more data on size classes and ages of fish present at aquaculture sites will help determine the importance of farm habitat for fish at different life stages. Additionally long-term surveys with appropriate reference areas are needed to inform more ecosystem-based approaches to farm management. For instance, harvesting of cultivated biomass could be planned to avoid interrupting key life stages of fish species, such as juvenile recruitment windows, which would help maximise the habitat value of cultivation sites, rather than leading to increased mortality through the untimely removal of food and shelter, and increased predation (Barrett et al. 2022, Corrigan et al. 2022, Forbes et al. 2022, Schutt et al. 2023). However, given that the farms in Porthallow Bay and

St Austell Bay are situated in close proximity to other structured habitats, including seagrass meadows and kelp beds (Crosby et al. 2023), the fish associated with these farms would have the opportunity to migrate to these surrounding natural habitats after biomass has been harvested (Fariñas-Franco et al. 2021), although this was not tested in our study. Evidence as to whether seaweed and/or mussel farms aggregate fish from neighbouring habitats or vice versa could be confirmed through medium to long-term telemetry studies, following the tagging of individual fish caught in the farm and surrounding areas (Bjordal & Johnstone 1993, Otterå & Skilbrei 2014, Arechavala-Lopez et al. 2015, McPeek et al. 2015).

In this study, we focused mainly on pelagic fish assemblages, as these directly interact with farmed biomass suspended in the water column. However, in order to more comprehensively understand farm effects on fish assemblages, demersal and benthic fish also need to be quantified (e.g. via use of BRUVS deployed on the seabed), as the abundance and richness of fish assemblages typically varies throughout the water column and with seabed depth and habitat (Schutt et al. 2023, Underwood & Jeffs 2023). Benthic surveys will also allow for comparisons of fish assemblages between farms and naturally occurring shellfish reefs and seaweed beds. In the present study, no demersal species were caught in reference areas, compared to several wrasse (*Labrus mixtus* and *L. bergylta*) and 2 *Scyliorhinus stellaris* caught inside the farms, which may suggest that demersal fish abundances were lower outside the farm; however, this needs to be quantitatively assessed in further surveys. A benthic BRUV survey conducted previously at St Austell Bay farm found 9 fish taxa in the farm area, including lesser sand eels, gadoids, wrasse species, and grey mullet *Chelon labrosus* (Clarke et al. 2023), which were consistent with our pelagic fish findings. This previous study, however, found no difference in species richness or MaxN between benthic farm or reference areas, which was attributed to high variability in the data and only 2 reference areas surveyed (Clarke et al. 2023).

In 4 seaweed farms in Maine, USA, there were also no observable differences in benthic fish and invertebrate assemblages between farms and reference areas, which were dominated by crab and lobster species (Schutt et al. 2023). These authors did however report differences in species assemblages between benthic and pelagic areas within farms. This suggests that farms offer different habitat spatially between the benthos and the water column, with benthic habitats below farms potentially offering greater stability and similarity to reference sites than pelagic areas. Shellfish and seaweed farms can alter the benthic environment through shading, organic enrichment and biodeposition, increases in structural complexity, changes to hydrodynamic flow and increased sedimentation (Mascorda Cabre et al. 2021, Corrigan et al. 2022). For mussel farms in particular, if they are placed over degraded or soft-bottom habitats, mussel fall-off or shell debris from the lines and farm infrastructure on the seabed can increase structural complexity, making the seabed more closely resemble natural reefs (Callier et al. 2018, Mascorda Cabre et al. 2021, Bridger et al. 2022). Indeed, in the UK, restoration success was seen in an area of seabed previously degraded due to bottom trawling fisheries after only 4 yr of an offshore long-line mussel farm being implemented, with increased abundances of macroinvertebrate and fish species compared to reference areas (Bridger et al. 2022). In areas where shellfish and seaweed farms have been placed over pre-existing structurally complex habitats such as seagrass meadows, however, there is concern that farms will have a negative effect on demersal fish assemblages, particularly in tropical off-bottom seaweed farms (United Nations Environment Programme 2023). Nevertheless, in temperate suspended seaweed farms, negligible impacts on seagrass beds have been reported (Walls et al. 2017, Fariñas-Franco et al. 2021), so effects are site and culturing method dependent. Given the degradation of many coastal habitats and the cost of their restoration, it is important to understand how aquaculture could have low cost restorative or regenerative benefits for fish species (Theuerkauf et al. 2019, Alleway et al. 2023).

It is necessary to understand how shellfish and seaweed farms affect pelagic fish species, as they form an ecologically important prey source for larger marine predators, such as seabirds, mammals and sharks, which may also be attracted to farms if they support high abundances of pelagic fish (Callier et al. 2018). At both farms in this study, fish from varying trophic levels with different feeding patterns were recorded (Table S9), indicating that shellfish and seaweed farms may interact with or attract a variety of fish species and functional groups, rather than just the herbivorous species that have been the focus of previous studies conducted at tropical seaweed farms (Eklöf et al. 2006, Hehre & Meeuwig 2015, 2016, Mirera et al. 2020). In a mussel farm in Croatia, it was reported that some predatory fish were present because they prey upon other smaller fish present at the farm (Šegvić-Bubić et al. 2011). In our study, 2 *S. stellaris* were caught below the seaweed and mussel lines in St Austell Bay. These are high-trophic level demersal predatory sharks of con-

servation and commercial importance, and are listed as Near Threatened in Europe and Vulnerable in the Mediterranean on the IUCN Red List (Finucci et al. 2021). The stomach contents of both *S. stellaris* were typical of their normal predatory feeding patterns (Table S9), containing high proportions of crabs, fish and worms, with one sample containing a whole *Scomber scombrus* tail. *S. scombrus* are also an important commercial species and were themselves frequently caught around the farms. Their stomach contents consisted primarily of amphipods and smaller fish (including lesser sand eels also seen at the farms). This small insight into one aspect of the many potential trophic interactions at the farm highlights why further studies are needed to confirm wider trophic dynamics surrounding aquaculture systems and how they might have knock-on implications for broader ecosystem functioning. Previous research has assessed how other high trophic level species may be affected by farms, particularly in terms of food provisioning (Callier et al. 2018, Corrigan et al. 2022). For example, seals and other pinnipeds may be attracted to mussel farms as they occasionally consume mussels as well as crabs and fish which are associated with them (Roycroft et al. 2004). Studies from Chile and Spain have reported dolphins feeding on fish in mussel farms (Ribeiro et al. 2007, Díaz López & Methion 2017, Methion & López 2019), and in Maine, USA, predatory harbour seals and porpoises were also recorded on pelagic and benthic cameras around seaweed farms, suggesting that they are not excluded from farm areas (Schutt et al. 2023). In New Zealand, Australia and in another study in Chile, however, dolphins have been reported to avoid shellfish farms due to the presence of farm infrastructure (Markowitz et al. 2004, Watson-Capps & Mann 2005, Heinrich 2006, Pearson et al. 2012). It is therefore important to understand how aquaculture may change natural fish assemblages and distributions to ensure farms are not displacing larger predators that depend on them (Callier et al. 2018).

Shellfish and seaweed farms may also displace fishing activity from an area, acting as de facto 'no take zones' (Wang et al. 2015), as the structure of longline mussel and seaweed farms ensures that fishermen cannot fish safely within the farm (Bridger et al. 2022). For instance, in China, the age structure of fish populations associated with caged fish farms was more diverse than those sampled in reference areas, likely due to limited fishing in the area (Wang et al. 2015). Instead of fishing directly in the farm, fisheries may benefit from 'spill-over' effects, where an increase in fish abundance at farm sites spreads into surrounding fishing grounds (Bridger et al. 2022). We found that Porthallow and St Austell Bay farms supported several commercially important fish species, such as *P. pollachius* and *S. scombrus*, which are commonly targeted in both recreational and commercial fisheries. Surrounding reference areas were less populated with commercial species, and additional spatial sampling is required in future to better resolve and quantify spill-over. Previous studies in Indonesia, Malaysia and the Philippines found a positive correlation between landings of herbivorous reef fishes and seaweed production at a national scale (Hehre & Meeuwig 2016), highlighting how large-scale low-trophic farming could support fisheries. It is unlikely that the small-scale shellfish and seaweed farms currently in operation in Europe affect fisheries landings; however, as the footprint of cultivation in Europe increases in the future (Capuzzo & McKie 2016, Hughes & Black 2016), they may come to do so and studies are needed to investigate how fish from farms may contribute to local and regional fish stocks.

5. CONCLUSION

Our results demonstrate that shellfish and seaweed farms located in southwest UK provide valuable habitats that support a high abundance and richness of coastal fish species, many of which are of commercial and/or ecological importance. It is likely that these farming structures provide shelter, feeding, breeding and/or nursery grounds; however, further investigation is needed to confirm which of these are provisioned for different fish species and how this compares to natural kelp and shellfish beds. For nearshore pelagic environments, which are often degraded and lack any structural complexity in the water column, low-trophic farms may enhance fish numbers and help to regenerate fish populations, especially where they have been depleted. The habitat provisioning for seaweed cultivation lines, however, is markedly affected by harvesting, with dramatic declines in fish abundance and richness subsequent to crop removal highlighting that farms are not a replacement for natural kelp habitats. In contrast, mussels that were grown in continuous overlapping cycles at the study farms provided temporally stable habitat for fish species for the duration of this study. Looking ahead, greater recognition by legislative and governmental bodies on the potential environmental benefits of low-trophic aquaculture sites is needed, together with the provision of financial subsidies to support their development as sustainable food production systems. Greater understanding of the environmental benefits

and ecosystem services these low-trophic aquaculture systems provide will help facilitate expansion of the industry and farmers should be encouraged to maintain habitat provisioning and increase environmental stewardship at their sites.

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