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**Ecological priming of artificial aquaculture structures: Kelp farms as an example**

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## ABSTRACT

*The continued development of the aquaculture industry is contributing to the proliferation of artificial structures in the marine environment. Observations of seaweed farms (infrastructure and biomass) suggest they act as a habitat for associated species. Seaweed farms differ from other forms of artificial infrastructure as the material deployed already has marine organisms (i.e. culture species) growing on it. This 'priming' of ropes with juvenile sporophytes may affect future development of communities by facilitating colonizing species or suppressing competitors. We call this process 'ecological priming': the provision of a biological platform that influences the successional development of specific communities. The communities that developed on ropes primed with *Alaria esculenta* individuals were compared to unprimed ropes to assess the ecological priming effect, at a commercial kelp farm in southwest Ireland. Species richness increased over two cultivation seasons and species composition was consistent between years, with distinct communities developing on primed and unprimed treatments. Timing of species occurrence on primed ropes was predictable with no predictable pattern occurring on unprimed ropes. Multivariate tests indicated distinct communities between treatments, with suppression of other algal species and potential facilitation of some species that have a particular association with *A. esculenta* on primed ropes. Communities from primed holdfasts contained a lower diversity of algal species compared to unprimed communities. Cultivated kelp holdfasts represent a habitat for distinct assemblages that reflect ecological priming of the substratum.*

## KEYWORDS

Artificial structures; Aquaculture; *Alaria esculenta*; Macroalgae; Holdfasts; Epibionts; Predictability; Facilitation; Kelp farm;

## INTRODUCTION

Over the last few decades there has been rapid proliferation of artificial structures in the marine environment (Firth *et al.*, 2016a) to enable the exploitation of the ocean's energy and food resources. Novel structures include oil and gas platforms, marine renewable energy installations and aquaculture facilities (Chapman & Underwood, 2011; Firth & Hawkins, 2011). The term 'ocean sprawl' has been used to describe this expansion of coastal and marine infrastructure (Duarte *et al.*, 2012; Firth *et al.*, 2016a, 2016b) and this is gaining recognition as one of the biggest threats to marine ecosystems (Airoldi & Beck, 2007; Firth *et al.*, 2013; Dafforn *et al.*, 2015; Bishop *et al.*, 2017; Heery *et al.*, 2017).

Specifically, the aquaculture industry has grown dramatically over the last 50 years to an all-time high of 101 million tonnes live weight in 2014 (FAO, 2016). Within the aquaculture sector, the cultivation of aquatic plants (dominated by marine macroalgae), is also expanding rapidly: by almost 8 % per year over the past decade (FAO, 2016). Over 33 % of the 27.3 million tonnes of global annual aquatic plant production came from just two kelp species (*Laminaria japonica* Areschoug, (1851) and *Undaria pinnatifida* (Harvey) Suringar (1873)) (FAO, 2016). Kelp species are cultivated to produce biomass to supply the many traditional (e.g. food) and expanding uses (e.g. biofuels) of kelp (Guiry, 1989; Walls *et al.*, 2016). Observations of the artificial infrastructure associated with seaweed farms and the kelp biomass itself suggest that farms provide important ecosystem functions and services such as habitat provision (Park *et al.*, 1990; Peteiro & Freire, 2013; Førde *et al.*, 2016; Walls *et al.*, 2016, 2017), protection from predators, and farms may act as nursery grounds for juvenile fish species, similar to that of wild kelp forests (Smale *et al.*, 2013; Walls *et al.*, 2016). However, cultivated kelps are grown suspended from ropes in the water column whereas wild kelps grow attached to the benthos, and this alteration of environments could modify the provision of these services (Walls *et al.*, 2016). Seaweed farms differ from other forms of artificial infrastructure in that the material placed in the sea already has marine organisms growing on it. This 'priming' of ropes with juvenile sporophytes may affect subsequent development of the fouling community by facilitating colonizing species or suppressing competitors. The intended consequence of seeding ropes with sporophytes is that a thick growth of harvestable kelp biomass develops. We term this process 'ecological priming' and define it as the practice of providing a biological platform that influences the successional development of specific communities. In this study, artificial structures (ropes), seeded with organisms, juvenile kelp (*Alaria esculenta* (Linnaeus) Greville (1830)) sporophytes, will be

referred to as ‘primed’ structures and conversely artificial structures with no seeding will be referred to as ‘unprimed’ structures.

To date the majority of research on the role of kelp as a habitat has focused on the holdfast structure (Jones, 1971; Moore, 1973; Schultze *et al.*, 1990; Smith, 1996; Thiel & Vásquez, 2000; Christie *et al.*, 2003; Blight & Thompson, 2008; Walls *et al.*, 2016; Teagle *et al.*, 2017). This focus on holdfasts is due in part to the relative ease in collecting these discrete sampling units (Walls *et al.*, 2016) and because the holdfast is generally found to host the highest diversity of all kelp structures (such as, kelp stipes and fronds) (Jones, 1972; Thiel & Vásquez, 2000; Norderhaug *et al.*, 2002; Christie *et al.*, 2003; Arroyo *et al.*, 2004). Within an individual holdfast, species richness typically reaches 30 – 70 macrofaunal species (Jones, 1972; Thiel & Vásquez, 2000; Teagle *et al.*, 2017), but in some cases, may reach up to 90 species (Christie *et al.*, 2003). This relatively high biodiversity is thought to reflect the complex physical structure provided by the holdfast, as the branched root-like shape of the holdfast provides a number of holes and crevices as living space (Christie *et al.*, 2003). This interstitial space may represent favourable habitat for colonising fauna, potentially providing protection from predators and during periods of adverse environmental conditions (Norderhaug *et al.*, 2002). The holdfast functions as a sediment trap accumulating detritus, which acts as a food source for many of the organisms inhabiting the structure (Moore, 1972). The holdfast also provides a stable environment which is persistent over seasons and years (Schaal *et al.*, 2009); with the lifespan of the holdfast being the same as that of the kelp individual (Kain, 1963; Christie *et al.*, 2003). This stability contrasts with the seasonally fluctuating habitat experienced by stipe-associated epiphytes (Norderhaug, 2004) and to the temporally renewing frond habitat (Christie *et al.*, 2003, 2007). It must be noted that, depending on cultivation practices, entire kelp individuals including the holdfast can be harvested from the farm thus the lifespan of cultivated holdfasts is only as long as the cultivation period.

A number of biotic and abiotic factors may influence the assemblages found on both seeded kelp droppers (ropes suspended vertically from seaweed farms which form substrate for cultivated kelps) and on submerged infrastructure like ropes. Where kelps form holdfasts, biotic factors include holdfast age, morphology and habitat volume. Wild holdfasts are perennial; Sheppard *et al.*, (1980) found that species richness increased for three different age classes of *Laminaria hyperborea* (Gunnerus) Foslie (1884) holdfasts. Age is linked to habitat volume, as holdfasts continually grow through the addition of more haptera and more space is enclosed within.

Here, habitat volume is defined as the space available for colonisation by organisms within the holdfast (see Walls *et al.*, (2016)). The volume and structure of these interstitial spaces have been shown to impact the diversity and abundance of associated assemblages (Jones, 1971; Thiel & Vásquez, 2000; Blight & Thompson, 2008; Tuya *et al.*, 2011; Walls *et al.*, 2016). The distinct holdfast morphologies of wild and cultivated *L. digitata* (Hudson) Lamourx (1813) were suggested as the cause of variations in species richness and community composition by Walls *et al.*, (2016). Wild kelps tend to grow a characteristic flat or slightly conical holdfast when attached to rock (Figure 1a in Walls *et al.*, 2016)), whilst cultivated kelps are seeded onto ropes, resulting in a different morphology, formed by intertwined haptera around the rope substratum (Figure 2A and Figure 1b in Walls *et al.*, 2016)). Alterations in abiotic conditions experienced by the holdfast can also cause variations in the assemblages inhabiting the holdfast (Smith, 2000; Walls *et al.*, 2016). Smith (1996) found differences in community structure between holdfasts sampled at different depths (2 m and 6 m), however depth also influences sediment load, structural complexity and water turbulence (Smith, 2000). Changing from a benthic to a suspended substratum can alter both the hydrodynamic environment and sedimentation rates experienced by fauna (Walls *et al.*, 2016). Shifts in other abiotic conditions that influence holdfast assemblages (and by extension, rope-attached assemblages) include hydrodynamic environment (Moore, 1972), sedimentation rates (Schaal *et al.*, 2012), light availability, and temperature (Scarratt, 1961).

In this study, we focus on the assemblage that develops on suspended ropes primed with the cultivated kelp *Alaria esculenta*. Kelp-associated holdfast epibionts were surveyed at different times during the two cultivation periods to track changes in community composition and development. We compared these primed rope communities with communities that developed on unprimed ropes. The comparison of primed and unprimed treatments allows for an estimation of the effect of ‘ecological priming’. We tested the hypothesis that a priming effect alters the development of assemblages differently across primed and unprimed treatments. An assessment of an ecological priming effect associated with cultivated kelps is novel and, if present, may have important implications for habitat restoration and enhancement of artificial structures. If the development of primed communities is predictable, this would increase the capacity for planning and management in the seaweed cultivation industry. Also, if cultivated holdfasts are found to have distinct assemblages when compared to unprimed treatments, this suggests they supplement the habitat service provided by artificial structures, such as mooring and anchor ropes, with the farm providing an alternative habitat for associated communities. This study builds on previous work conducted in Walls *et al.*, 2017 on the ecological processes occurring on cultivated kelp

124 farms. However, the data presented here is related to the communities associated with the holdfast material  
125 while, Walls *et al.*, 2017 studied the frond fouling communities and their impact on commercial aspects of  
126 seaweed farming.

## MATERIALS AND METHODS

### Study site

This study was conducted in southwest Ireland in Ventry Harbour, County Kerry (52° 06' 49.45"N, 10° 21' 20.17"W; Figure 1) at the largest operating commercial seaweed farm in Ireland (18 ha site). Ventry Harbour is a moderately sheltered and shallow embayment orientated towards the southeast, approximately 2.5 x 1.5 km (3.75 km<sup>2</sup>) with a wide mouth opening into Dingle Bay. The seagrass *Zostera marina* Linnaeus (1753) is extensively distributed throughout the sandy seabed, leading to a rocky boulder reef towards the mouth of the bay. Wild kelp populations are found at the mouth of Ventry Harbour and on the northeastern shore of the bay, approximately 250 m- 1 km from the farm site). The licensed seaweed farm is orientated northwest to southeast, and located to the westerly side of Ventry Harbour (Figure 1). The depth underneath the farm is approximately 6 m at the northwestern end before gently sloping to 20 m at the eastern edge of the farm at mean low water spring tide (MLWS). The tidal range in Ventry Harbour is between 0.6 and 4.0 m. Monthly irradiance values, obtained from nearby Valentia weather observatory (51° 56' 23" N, -10° 14' 40" W), ranged from 5,447 – 63,823 J cm<sup>-2</sup> for 2014; equivalent to approximately 3,356 to 40,364 mmol photons m<sup>-2</sup> day<sup>-1</sup> using the approximation suggested by Tett (1990). Sea surface temperature data were obtained from the M3 offshore weather buoy located approximately 56 km southwest of Mizen head (51° 13' 0" N, 10° 33' 0" W), and ranged from 10.1 – 17.6 °C for 2014. Although offshore sea temperatures are less extreme than inshore waters, Ventry Harbour is a well-flushed bay so values are broadly representative. The longline set-up and design of the seaweed farm is described in detail in Walls *et al.*, 2017. The farm cultivates the kelps *Alaria esculenta* and *Saccharina latissima* (Linnaeus) Lane, Mayes, Druehl & Saunders (2006) for human consumption, animal feed and use in cosmetic products.



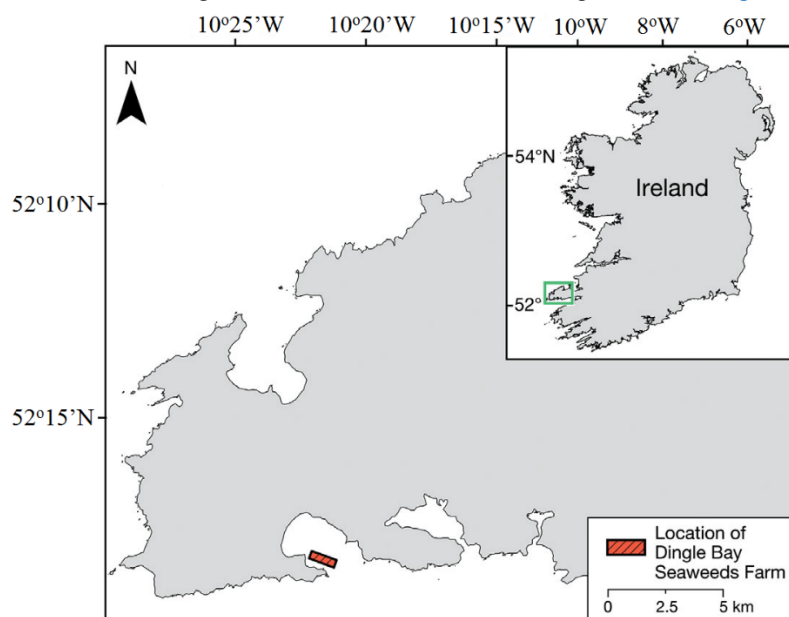


Fig. 1. Location of Dingle Bay Seaweeds farm and sampling site at Ventry Harbour, Co. Kerry, Ireland.

## Experimental set-up

Experimental treatments were based on 1 m polypropylene dropper ropes (10 mm diameter) with two initial set-ups. Treatment 1 “primed droppers” consisted of ropes sprayed directly with juvenile *A. esculenta* sporophytes that had been developed from gametophyte cultures held in the seaweed hatchery at the NUIG Carna Research Station (County Galway), following standard industry protocols. The primed ropes were left to develop under controlled growth conditions (Edwards & Watson, 2011) for between 5 to 12 weeks. Sporophytes were ca. 10 mm at time of deployment. Treatment 2 dropper ropes consisted of clean polypropylene rope and will be referred to as “unprimed droppers” hereafter. Unprimed droppers were submerged in tanks of seawater under the same laboratory conditions as the primed droppers for the same length of time prior to deployment. At deployment, all dropper replicates had a 1 kg concrete weight attached to the end of the rope and were deployed vertically on the longline header rope and spaced 1.5 m apart to mitigate against rubbing and tangling (Walls *et al.*, 2016). Dropper ropes were suspended at a depth of between 1.5 to 2.5 m below the surface of the water, which is a depth range experienced at commercial seaweed farms. Each dropper was randomly assigned to a location on the longline header rope prior to deployment. Primed (n=35) and unprimed (n=35) droppers were deployed on the 18<sup>th</sup> February 2014 for the 2013/2014 growing season (Year 1); deployment was delayed in Year 1 due to winter storms in early 2014. The experiment was repeated for the 2014/2015 growing season (Year 2), when the primed (n=35) and unprimed (n=35) treatments were deployed on the 15<sup>th</sup> December 2014.

## **Sampling protocol for primed and unprimed droppers**

All samples were collected by SCUBA divers. In April, May and June 2014 and 2015 five droppers were randomly chosen and collected from the primed and unprimed treatments using open-ended mesh bags (150 x 55 cm, 0.5 mm mesh size). If a dropper was not uniformly covered in developing sporophytes (i.e. showed evidence of rubbing or entanglement), another dropper replicate was selected. The mesh bag was carefully slipped up over the dropper and tightly secured at top and bottom (just above the weight) using cable ties, enclosing the entire 1 m dropper and kelp biomass. The focus for the current study was to compare the assemblages associated most closely with the dropper rope. There are potential issues of habitat extent when comparing the assemblages of entire kelp sporophytes with organisms attached to unprimed rope (where large kelp blades did not develop in the experimental time period). We therefore compared the near-rope assemblages of the holdfast with those on unprimed droppers.

All samples were transferred back to nearby facilities at Dingle Oceanworld Aquarium for initial processing within 6 hours. The sampling technique of bagging fronds and holdfast before separating the material on land potentially risks mixing species attached to the frond with those of the holdfast. However, fronds mainly host attached organisms such as hydroids and bryozoans and fewer mobile species (Walls *et al.*, 2017) so this form of contamination is likely to be minimal. The alternative, of cutting fronds in situ, risks dislodging loosely attached species on one treatment (primed ropes), but not the other (unprimed ropes). The mesh bags were untied before randomly pre-selected 10 cm sections (n=3) of each dropper were excised from the 1 m dropper (Figure 2A+B). In the rare event that any randomly selected section of primed dropper was not entirely covered in holdfast structures, an alternative section was chosen. The frond and stipe material of primed samples were cut just above the holdfast and stored in sealed plastic bags containing 100 % ethanol for a separate study. The 10 cm primed and unprimed rope sections were stored in separate sealed plastic bags containing 100 % ethanol. All samples were transported back to the laboratory for further processing.

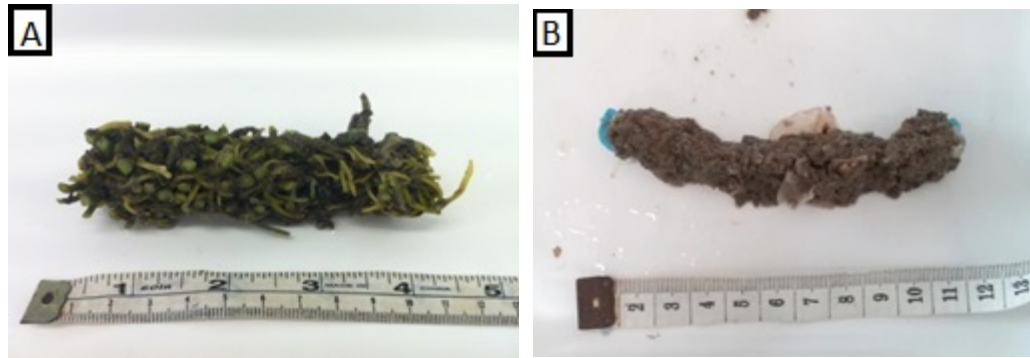


Fig. 2. Morphology of 10 cm section (A) primed *Alaria esculenta* holdfast, (B) unprimed section

### Sample processing

The 10 cm replicate primed *A. esculenta* and unprimed sections were removed from the plastic bag and all material (i.e. kelp holdfasts, epiphytes and fauna) was cleaned from the substratum. Due to the morphology of cultivated kelp holdfasts, individual holdfasts could not be removed as the haptera grow intertwined with each other (Figure 2A, also see Walls *et al.*, (2016) for comparison of morphology of wild and cultivated kelp holdfasts). All collected epibionts from primed and unprimed samples were washed over a 0.5 mm sieve and stored in 100 % ethanol for later identification. All collected flora and fauna were identified to species level where possible (using Hayward, 1988; Hayward & Ryland, 2002; Bunker *et al.*, 2012). Taxonomy was cross-checked using web resources (WoRMS Editorial Board 2016) and samples were stored in 100 % ethanol.

### Statistical analysis

The impact of priming ropes with kelp sporophytes was examined using univariate tests of diversity, multivariate tests of assemblage composition and regressions of mean occurrence days for different treatment and year combinations. To compare functional diversity between primed and unprimed treatments, species were grouped into categories based on morphology (algae): thin filamentous algae, foliose algae and leathery macrophyte (Steneck & Dethier, 1994; Eriksson *et al.*, 2002); and feeding strategies (fauna): suspension feeder, detritivore, carnivore, omnivore or herbivore. Where species spanned these categories, their predominant model of feeding was recorded (Sheppard *et al.*, 1980). Occurrences of functional groups were pooled by treatment/month combinations and tested using a two-way sampling date x treatment model with functional group number as a response variable. Univariate analysis of variance (ANOVA) was used to examine temporal differences in species richness of dropper communities ( $n = 3$  10 cm sections pooled) between primed and

unprimed treatments using the model of month (fixed factor) crossed with treatment (fixed factor) for years

2014 and 2015 separately. Dropper sections were pooled to make droppers rather than 10 cm sections the basic

unit of replication. The pooling was carried out as variation within droppers and between sections was not part

of the hypothesis of interest.

The differences between community composition from different months and years for the primed and unprimed

treatments were compared using multivariate tests. A Simpson's dissimilarity matrix was generated from the

presence/absence data for pooled dropper communities from years 2014 and 2015 separately for the 3 primed

and 3 unprimed treatments and different months (April, May and June). Simpson's dissimilarity values are 0

when assemblages from separate samples are identical and scaled to 100 when there are no species in common

between separate samples. Simpson's dissimilarity has the advantage that it only measures the compositional

turnover and is not affected by the relative difference in species richness between samples (Baselga, 2010). This

makes dissimilarities measured by Simpson's index easier to interpret than is the case for indices that mix

turnover and species richness components of dissimilarity (e.g. Sørensen's index). The PRIMER software used

for multivariate analysis does not calculate Simpson's dissimilarities, so these were calculated from species

presence/absence data in EXCEL using the PopTools add-on (Hood, 2014) and dissimilarity matrices were

subsequently imported into PRIMER. All samples were ordinated using a multidimensional scaling plot (MDS)

(Shepard, 1962; Kruskal, 1964a, 1964b) in PRIMER V6®, giving the position of each dropper community (n=3

sections pooled) in two-dimensional space based on its species composition for years 2014 and 2015 separately.

Permutational multivariate analysis of variance (PERMANOVA, Anderson *et al.*, 2008) was used to test for

differences in multivariate species assemblages among primed and unprimed communities using the model of

month (fixed factor) crossed with treatment (fixed factor) for years 2014 and 2015 separately, based on 9999

unrestricted permutations of raw data. PERMDISP routine revealed that the variation in multivariate dispersion

(around the centroid) was not significant ( $p > 0.5$ ) for all factors (month and treatment).

Where significant differences between sampling dates and treatments were detected, a variation on SIMPER

analysis was conducted to highlight the species that contributed most to the observed differences. The SIMPER

programme in PRIMER could not be used as Simpson's dissimilarity is not compatible with the algorithm used

in the programme. Instead, we conducted a SIMPER-like analysis, hereafter referred to as a test of species

influence (Walls *et al.*, 2017), by comparing the observed dissimilarity within and between samples when all

species were included to the dissimilarities generated by excluding each species individually. The average between-group and within-group dissimilarities were compared to see whether omitting a species made the groups appear more or less similar. In summary, if a species makes groups more similar when excluded from the matrix, it suggests that the species makes a contribution to the observed differences between groups. Ratios of between to within group dissimilarities were normalized to facilitate comparisons. Any species greater than one standard deviation of the mean normalized score was identified as having an above average contribution to the overall dissimilarity between the groups.

To test the predictability of the presence of species on primed and unprimed droppers from Year 1 (2014) to Year 2 (2015), we used day of year to calculate the central tendency of species occurrence. Day of year is the number assigned to a whole solar day that starts at 1 on the 1<sup>st</sup> of January and finishes at 365 on 31<sup>st</sup> of December (non-leap year), e.g., sampling took place on 7<sup>th</sup> April 2015 which is day of year 97. Central tendency is the average day when a species was observed, weighted by the frequency of occurrence. For example, if a species has high occurrence in the first sampling date, lower occurrence in the middle sampling date and does not occur in the final sampling date then the mean occurrence day will be somewhere between the first and second sampling date. The central tendency method as described by Colebrook (1979) can identify changes in the timing of seasonal cycles (Edwards & Richardson, 2004; Moore *et al.*, 2011). To test if species arrival times were similar between the different treatment droppers within the same year the mean species arrival times were compared between treatments within years 2014 and 2015 separately. Regression analysis was conducted using Minitab v16 to test if arrival times of commonly occurring species were significantly related. A slope close to 1 is expected if the timing of species presences is the same from year to year. If the relationship between occurrence days is significant, but the slope is not close to 1, this implies that the order of species occurrence is similar between sets of samples, but the rate of species arrival varies between years.

## RESULTS

In total, we recorded 81 species inhabiting the primed and unprimed 10 cm dropper sections. 54 species were recorded on 2014 primed sections and 63 species were recorded on the 2015 primed sections. 28 % of all taxa were unique to primed samples including the lumpsucker *Cyclopterus lumpus* Linnaeus (1758), the ascidian *Ciona intestinalis* Linnaeus (1767), and the polychaete *Nereimyra punctata* Müller (1788). Only 6 % of taxa (5 species) were unique to the unprimed ropes, 4 of these were algal species including the kelps *Saccorhiza polyschides* (Lightfoot) Batters (1902) and *Saccharina latissima*, the brown algae *Desmarestia viridis* (O.F. Müller) J.V. Lamourx (1813) and the green algae *Ulva* sp. Linnaeus (1753). The only faunal species unique to unprimed samples was the gastropod *Patella pellucida* Linnaeus (1758) which is usually associated with the kelp fronds on which it exclusively feeds (Hayward, 1988). As only one individual was recorded, the occurrence of this species is not particularly informative. Variation in sample depth along the 1 m dropper ropes or location of the droppers within the farm did not cause any differences in the species richness or community composition of primed and unprimed 10 cm sections. A full list of species sampled on both primed and unprimed samples can be found in Table S1 in supplementary material.

Thin filamentous algae were the most dominant algal functional group for both treatments, with algal diversity higher (4/6 dates) in unprimed treatments when compared to primed treatments in the same month. The suspension feeders were the most common faunal groups for both treatments, followed by omnivores and detritivores (Table 1). A full list of species recorded and their abundance is provided in Supplementary Material (Table S1). Functional group richness increased with time since deployment ( $F_{2,6} = 5.7$ ,  $p < 0.05$ ), but there were no effects of treatment.

Table 1. Number of species in each functional group for primed (P) and unprimed (UP) dropper treatments sampled in April, May and June 2014 and 2015.

Functional Groups	April 2014 P	April 2014 UP	May 2014 P	May 2014 UP	June 2014 P	June 2014 UP	April 2015 P	April 2015 UP	May 2015 P	May 2015 UP	June 2015 P	June 2015 UP
Thin Filamentous Algae	1	2	2	3	3	4	4	4	3	4	4	5
Foliose Algae	0	0	0	0	0	0	0	0	0	1	0	2
Leathery Macrophyte	1	0	1	1	1	2	1	1	1	3	1	3
Suspension Feeder	5	3	9	9	15	12	8	7	16	13	22	17
Detritivore	2	2	6	3	7	4	3	4	8	5	6	7
Carnivore	1	1	5	6	6	1	4	1	6	3	7	4
Omnivore	7	4	8	8	10	8	6	5	8	7	10	10
Herbivore	0	0	1	1	1	2	0	0	1	1	1	1
Other	0	0	0	0	0	0	0	0	0	1	1	1

# Community composition and development of epibionts on primed *Alaria esculenta* 10 cm holdfast sections and unprimed sections.

Species richness at the seaweed farm site in Ventry increased from time of deployment until the end of the study, for both primed and unprimed treatments. Apart from the accumulation of species with time, the patterns of species richness were not consistent across factors (Treatment 2014  $F_{1,24} = 0.126$ ,  $P = 0.725$ , Treatment 2014 x Months 2014  $F_{2,24} = 1.433$ ,  $P = 0.258$ ; Treatment 2015 x Months  $F_{2,24} = 0.088$ , 2015  $P = 0.914$ ). Significant differences in species richness were recorded for month for both years (Months 2014  $F_{2,24} = 34.608$ ,  $P = < 0.001$ ; Months 2015  $F_{2,24} = 91.555$ ,  $P = < 0.001$ ), and treatment is significant for 2015 from the ANOVA (Figure 3, Treatment 2015  $F_{1,24} = 16.796$ ,  $P = < 0.001$ ). Species richness within 2015 was higher in the primed treatment than in the unprimed treatment for each sampling month. For 2014 primed species richness was higher than unprimed species richness for April samples, however, richness was lower for primed samples from May and June than unprimed samples (Figure 3).

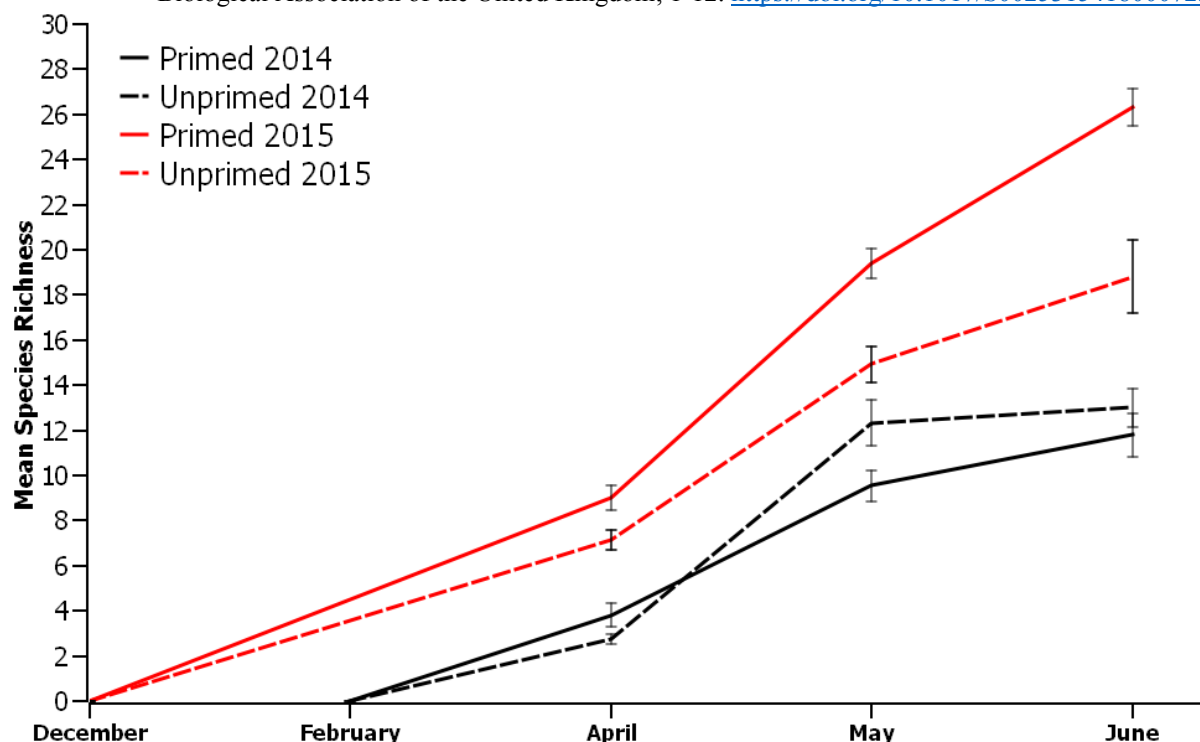


Fig.3. Species richness (mean  $\pm$  SE) on primed *Alaria esculenta* holdfast sections and unprimed sections sampled in April, May and June 2014 and 2015. Species richness represents the number of taxa identified on 10 cm section ( $n = 3$ ) from each dropper ( $n = 5$ ).

Due to the high stress values of the MDS plots for year 2014 (0.22 Figure 4A) and for year 2015 (0.23 Figure 4B) patterns of differences among assemblages from separate months and treatments were difficult to examine. A stress value of  $> 0.20$  indicates the data are only partially represented by the two-dimensional plot and little reliance should be placed on the finer detail of the plot (Clarke & Warwick, 1994). However, the broad-scale pattern shows a separation of early April communities to later May and June communities which show little separation, with month also being significant from the PERMANOVA analysis for both years 2014 and 2015 (Table 2A+B,  $p < 0.05$ ). There is also a separation of community assemblages between primed and unprimed treatments. This pattern is evident from the PERMANOVA analysis with species assemblage composition differing between treatment (primed and unprimed) from the analysis again for both years 2014 and 2015 (Table 2A+B,  $p < 0.01$ ). Interestingly, the month crossed with treatment interaction was significant for year 2015 only (Table 2B,  $p < 0.05$ ). The pairwise tests reveal that this significant interaction is not due to whether treatments are different in one particular month, but the interaction implies that month within a treatment are sometimes different and sometimes not.



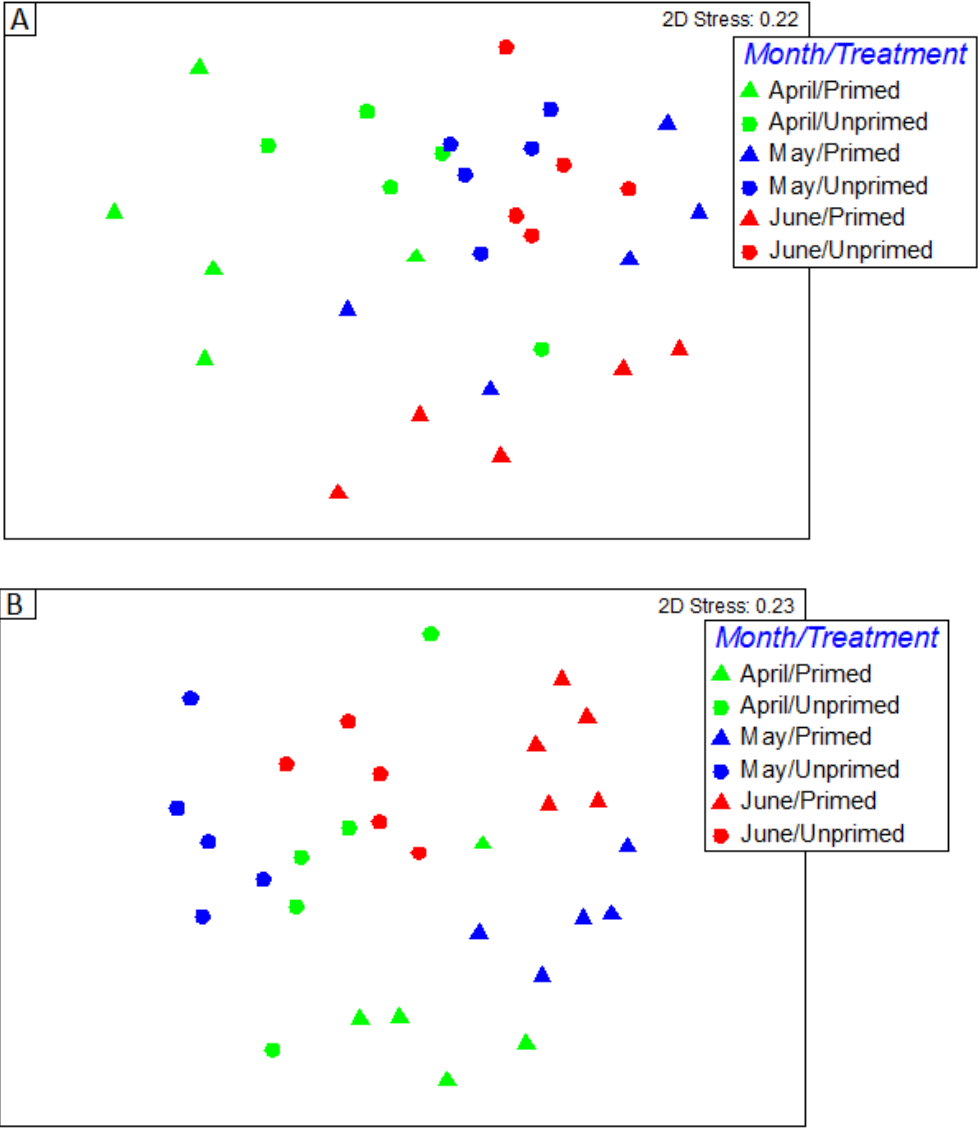


Fig. 4. Two-dimensional multidimensional scaling plot of 30 primed and unprimed dropper samples ( $n = 3$  pooled): 15 from primed treatment and 15 from unprimed treatment, based on presence/absence Simpson's dissimilarity matrix of species collected from each primed and unprimed section. (A) Samples from year 2014 (stress = 0.22). (B) Samples from year 2015 (stress = 0.23).

Table 2: Permutational multivariate analyses of variance based on Simpsons dissimilarity matrix based on presence/ absence data for dropper community (n = 3 10 cm rope sections pooled) sampled over months (April, May and June) on different treatments (primed and unprimed) for (A) year 2104 and (B) year 2015. All tests were conducted using unrestricted permutation of raw data with 9999 permutations.

Table 2A: PERMANOVA Year 2014					
Source	df	SS	MS	F	P (perm)
Month	2	0.7802	0.3901	7.3524	0.0001**
Treatment	1	0.32709	0.32709	6.1649	0.0011**
Month x Treatment	2	0.14437	7.2187 x10 <sup>-2</sup>	1.3606	0.2803
Residuals	24	1.2734	5.3057 x10 <sup>-2</sup>		
Total	29	2.525			

Table 2B: PERMANOVA Year 2015					
Source	df	SS	MS	F	P (perm)
Month	2	0.10493	5.2466 x10 <sup>-2</sup>	2.1916	0.0496*
Treatment	1	0.39384	0.39384	16.452	0.0001**
Month x Treatment	2	0.11995	5.9977 x10 <sup>-2</sup>	2.5054	0.0298*
Residuals	24	0.57454	2.3939 x10 <sup>-2</sup>		
Total	29	0.1933			

df: degrees of freedom; SS: sum of squares; MS: mean squares; F-ratio of within-group variation to between-group variation, P (perm) permutational probability value, \* p < 0.05, \*\* p < 0.001

A test of species influence was conducted to determine which taxa were the major contributors to the observed dissimilarity in assemblage structure between primed and unprimed treatments within the same sampling months (Table 3). Most of the species responsible for dissimilarity between treatments were algae and sessile faunal species. The species with higher occurrence on the primed samples were from a variety of different phyla and dissimilarities were not characterised by any specific group. These included the amphipod *Jassa* fem. Montague (1808) present in April 2014 samples, and the polychaete *Harmothoe* sp. Kinberg (1856) present in May 2014 samples, the bryozoan *Electra pilosa* Lamourx (1816) which contributed to differences between treatments in both June 2014 and May 2015, the amphipod *Gammarellus homari* Herbst (1793) present in April 2015 and the bivalve molluscs *Anomia eippium* Linnaeus (1758) and *Hiattella arctica* Linnaeus (1767) which were responsible for some of the differences observed in June 2015. The unprimed treatment was generally characterised by a higher occurrence of algal species during each sampling month. The filamentous brown algae sp. and the red alga *Ceramium* sp. Wiggers (1780) were major contributors to the observed differences between

treatments and were present in April 2014 (filamentous brown algae sp. only), May 2014 and 2015 and June 2015. Laminariales juveniles *Migula* (1909) were present in higher occurrence in all sampling months except May 2014 when they did not contribute to observed dissimilarities. The red algae *Polysiphonia* sp. Greville (1823) and *Lomentaria clavellosa* Lyngbye (1819) were present in June 2015. The only non-algal species which contributed to the dissimilarity between treatments with higher occurrence in the unprimed treatment was *Harpacticoida* indent. Sars (1903) present in June 2014. From the dissimilarity scores May 2014 and April 2015 treatments are less dissimilar than June 2015, however primed and unprimed treatments sampled in June 2014 and May 2015 are the most dissimilar (> 2.00 dissimilarity score, Table 3).

Table 3: Test of species influence to determine the species contributing to observed differences in the structure of assemblages between primed and unprimed treatments. Dissimilarity scores are the ratio of average between-group dissimilarities to within-group dissimilarities for each pairwise comparison. Normalized score is the reduction in dissimilarity score when excluding the species of interest, normalized to mean = 0, SD = 1 using the mean and standard deviation of all individual species' scores. A higher loss in dissimilarity indicates that a species is important in distinguishing the dates compared.

Months	Dissimilarity score all species included	Species responsible for dissimilarity	Normalized score	Species occurrence (max. 15 mo <sup>-1</sup> )		
				Primed		Unprimed
April 2014 Primed & Unprimed	1.17	Filamentous brown algae sp.	2.36	7	<	10
		Jassa fem.	1.05	15	>	12

<b>May 2014 Primed &amp; Unprimed</b>	1.56	Filamentous brown algae sp.	4.25	1	<	14
		<i>Ceramium</i> sp.	1.72	2	<	12
		<i>Harmothoe</i> sp.	1.34	6	>	2
<b>June 2014 Primed &amp; Unprimed</b>	2.00	<i>Electra pilosa</i>	4.13	12	>	0
		<i>Laminariales</i> juv.	3.28	0	<	15
		<i>Harpacticoida</i> indent.	1.94	3	<	15
<b>April 2015 Primed &amp; Unprimed</b>	1.62	<i>Laminariales</i> juv.	4.70	0	<	12
		<i>Gammarellus homari</i>	1.37	10	>	0
<b>May 2015 Primed &amp; Unprimed</b>	2.06	Filamentous brown algae sp.	4.42	0	<	14
		<i>Laminariales</i> juv.	4.37	0	<	14
		<i>Electra pilosa</i>	1.19	15	>	1
		<i>Ceramium</i> sp.	1.15	7	<	14
<b>June 2015 Primed &amp; Unprimed</b>	1.84	<i>Ceramium</i> sp.	4.09	4	<	15
		Filamentous brown algae sp.	3.07	1	<	11
		<i>Polysiphonia</i> sp.	2.64	5	<	14
		<i>Laminariales</i> juv.	1.89	5	<	12
		<i>Anomia eippium</i>	1.59	15	>	1
		<i>Hiatella arctica</i>	1.10	15	>	2
		<i>Lomentaria clavellosa</i>	1.06	1	<	8

## Predictability of holdfast assemblages on primed and unprimed treatments

Shared species between and within treatments included algal species and both sessile and mobile faunal species.

The temporal pattern of shared holdfast species was consistent between years for the primed treatment; however, this pattern was not the same in the unprimed treatment. The regression of mean species occurrence in 2014 and 2015 was significant in primed treatments ( $p < 0.001$ ; Figure 5A). In contrast, patterns of mean species arrival on unprimed treatments were not consistent between 2014 and 2015 ( $p > 0.05$ ; Figure 5B).

Recruitment by shared species to both treatments was similar within a year. The timing of species occurrence was consistent across treatments within the same year for both 2014 and 2015. The regression slope relating mean day of year of shared species occurrence samples was significant within both years ( $p < 0.05$ ; Figure S1A & S1B Supplementary Material).

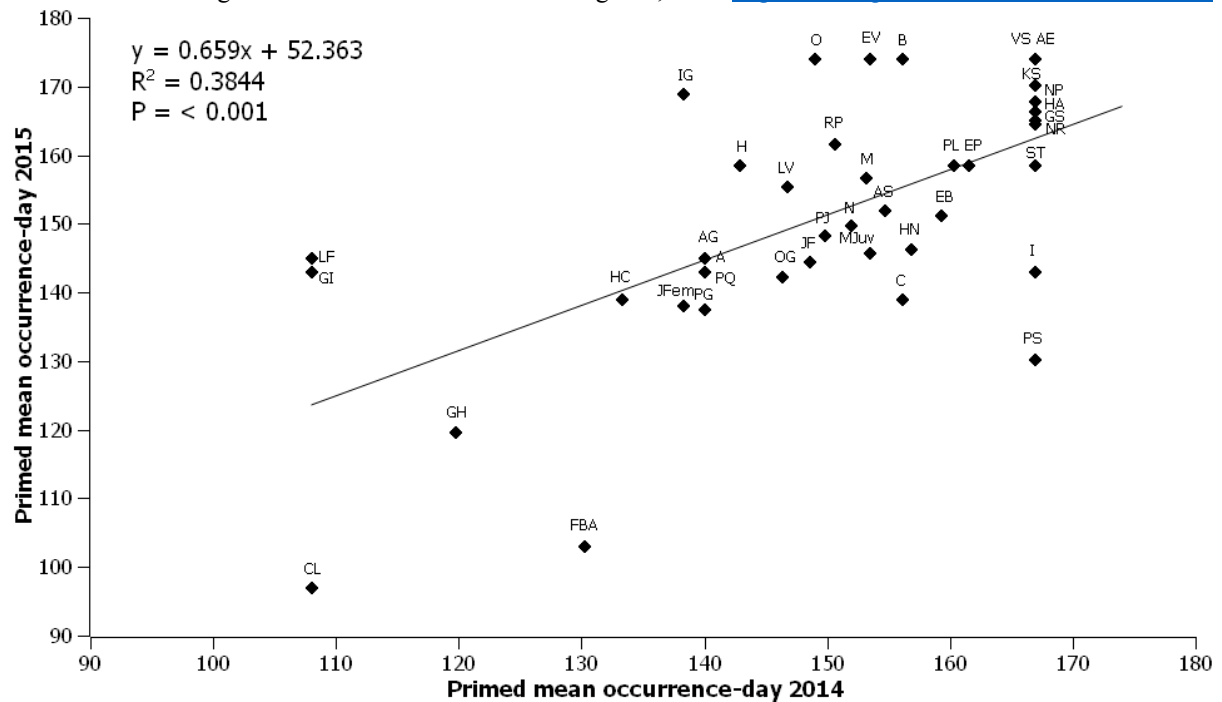


Fig. 5A. The relationship between mean day of year occurrences for all shared species in 2014 and 2015 on primed holdfast samples.

Legend: CL: *Cyclopterus lumpus*; LF: *Laomedea flexuosa*; GI: *Gammarus insensibilis*; GH: *Gammarus homari*; FBA: filamentous brown algae sp; HC: Harpacticoid Copepods; JFem: *Jassa* sp. female; IG: *Idotea granulosa*; PG: Pycnogonida indent.; A: *Aora* sp.; AG: *Aora gracilis*; PQ: *Polycera quadrilineata*; H: *Harmothoe* sp.; OG: *Obelia geniculata*; LV: *Lacuna vineta*; JF: *Jassa falcata*; O: Ostracoda indent.; PJ: *Parajassa pelagica*; RP: *Rissoa parva*; N: Nematoda indent.; M: *Myrianida* sp.; EV: *Eulalia viridis*; MJuv: *Mytilus* sp. juvenile; AS: *Asterias* sp.; B: *Balanus* sp.; C: *Ceramiales* sp.; HN: *Hardametopa nasuta*; EB: *Eusyllis blomstrandii*; PL: *Pisidia longicornis*; EP: *Electra pilosa*; ST: *Spirobranchus triqueter*; NR: *Nereiphylla rubiginosa*; NP: *Nereimyra punctata*; GS: *Gitana sarsi*; KS: *Kellia suborbicularis*; HA: *Hiatella arctica*; I: *Idotea* sp.; PS: *Polysiphonia* sp.; AE: *Anomia eippium*; VS: *Vesicularia spinosa*

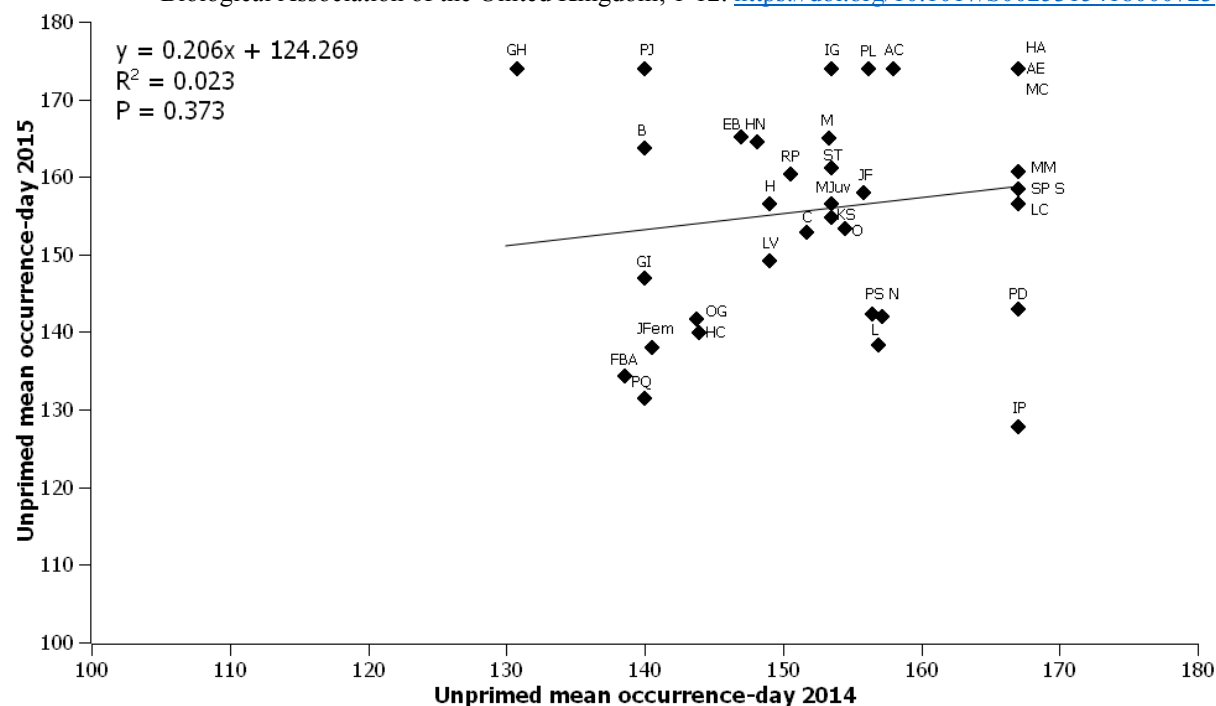


Fig. 5B. The relationship between mean day of year occurrences for all shared species in 2014 and 2015 on unprimed samples.

Legend: GH: *Gammarellus homari*; FBA: filamentous brown algae sp; GI: *Gammarus insensibilis*; B: *Balanus* sp.; PQ: *Polycera quadrilineata*; .; PJ: *Parajassa pelagica*; JFem: *Jassa* sp. female; OG: *Obelia geniculata*; HC: Harpacticoid Copepods; EB: *Eusyllis blomstrandii*; HN: *Hardametopa nasuta*; LV: *Lacuna vincta*; H: *Harmothoe* sp.; RP: *Rissoa parva*; C: *Ceramiales* sp; M: *Myrianida* sp.; ST: *Spirobranchus triqueter*; IG: *Idotea granulosa*; MJuv: *Mytilus* sp. juvenile; KS: *Kellia suborbicularis*; O: Ostracoda indent; JF: *Jassa falcata*; PL: *Pisidia longicornis*; PS: *Polysiphonia* sp; L: *Laminariales* juvenile.; N: Nematoda indent.; AC: *Acari* sp.; SP: *Saccorhiza polyschides*; LC: *Lomentaria clavellousa*; MM: *Membranipora membranacea*; PD: *Platynereis dumerilii*; S: *Sipuncula* indent.; IP: *Idotea pelagica*; MC: *Musculus costulatus*; AE: *Anomia eippium*; HA: *Hiatella arctica*

## DISCUSSION

### **Community composition and development of epibionts on primed *Alaria esculenta* 10 cm holdfast sections and unprimed sections.**

Diverse assemblages developed on both primed *Alaria esculenta* sections and unprimed sections. The assemblage developed from unfouled material at deployment to 63 individual taxa sampled on the primed treatment and 54 taxa sampled on the unprimed treatment in 2015 which had higher species richness than 2014. This general build-up of species over sampling months followed a seasonal pattern of development from time of deployment in February (2014) and December (2015) until harvest in June for both growing seasons. The species identified on our primed samples have all been previously recorded on wild or cultivated kelp holdfasts (Jones, 1971; Christie *et al.*, 2003; Blight & Thompson, 2008; Tuya *et al.*, 2011; Schaal *et al.*, 2012; Walls *et al.*, 2016). Although we did not record species abundance directly, the dominant faunal groups based on species occurrence in our primed samples were amphipod crustaceans, polychaetes and molluscs. This agrees with previous studies of wild kelp holdfasts from European waters including Blight & Thompson (2008), Christie *et al.*, (2003) and Walls *et al.*, (2016), the latter of which is the only previous study of cultivated holdfast assemblages to our knowledge.

Functional diversity was dominated by suspension feeders, omnivores and detritivores for both our primed and unprimed samples. However, algal diversity was higher on unprimed samples with 4 of the 5-unique species on unprimed samples being algae, e.g. the kelps *Saccorhiza polyschides* and *Saccharina latissima*, the green algae *Ulva* sp., and *Desmarestia viridis* a filamentous brown alga. Consistently higher species richness in primed samples during early sampling suggests that habitat availability is very important for the colonization of species during early successional stages (April). This importance lessens as communities develop, leading to less consistency in the treatments with higher species richness. The rapid colonisation of this novel habitat suggests that the species have either planktonic larval settlement or if they have direct development, species are highly mobile (Walls *et al.*, 2016). Fouling epibionts such as bryozoans, hydroids, molluscs and crustaceans begin to settle in spring and early summer, which coincides with deployment and the cultivation period for kelps (Walls *et al.*, 2017). The sources of these colonizing species remain unknown. The nearest wild kelp populations are between 250 m (mouth of Ventry Harbour opening up to Dingle Bay) and 1 km (northeast direction from farm in Ventry Harbour) away from the farm site. Cultivation practices are not harmonized within the sector or even

between years at the same site, however at Ventry Harbour over the duration of this study, the header and dropper ropes were taken in from sea and cleaned after each harvest season, also anchor chains are cleaned *in situ* by divers at irregular intervals. Thus, over-wintering of fauna on the farm and re-colonization of the growing kelp and infrastructure in spring is unlikely to occur.

Analysis of the community composition of primed and unprimed treatments revealed several important patterns, which remained constant between years. Communities were distinct between treatments and also between months, with primed samples showing more separation during community development than unprimed samples. The dissimilarity results imply that species are not simply accumulated over time; there are compositional differences between early and later samples. Change in community composition was through addition of new species and replacement of early colonisers. This pattern was more evident in primed samples: with the species filamentous brown algae sp., showing higher occurrence in April samples with much reduced occurrence in later May and June samples.

Algal species were revealed to be the main cause of variation between community composition of treatments from the test of species influence. Filamentous brown algae sp., *Ceramiales* sp., *Laminariales* juveniles, *Polysiphonia* sp. and *Lomentaria clavellosa* were more closely associated with the unprimed treatment. The presence of *A. esculenta* from the beginning of colonisation may pre-empt other algal species from settling and dominating the primed droppers. Benedetti-Cecchi (2000) studied the effect of disturbance on turf and canopy-forming algae in Italy. He found that canopy-forming algae dominated cleared patches of substratum during their main recruitment period; even though turf-forming algae were initially present they were replaced by canopy-forming algae. However, turf-forming algae would characterise early stages of colonisation and mature assemblages in patches that were cleared outside of the main recruitment period of the canopy-forming algae. In our study, unprimed samples were dominated by filamentous and ephemeral algae species, which seemed unable to colonise primed samples potentially because of the presence of *A. esculenta*. Furthermore, the bryozoan *Electra pilosa* was only present on primed samples late in the sampling period with very low occurrence in the unprimed treatment. *E. pilosa* settles in early spring (Ryland & Hayward, 1977) and is found to be out competed by *Membranipora membranacea* Linnaeus (1767) on kelp fronds (Førde *et al.*, 2016; Walls *et al.*, 2017), however because *M. membranacea* is highly selective in habitat (Ryland, 1962) it does not thrive in other habitats thus *E. pilosa* is the dominant bryozoan on these samples. Additionally, in the absence of *M.*



*membranacea*, *E. pilosa* is also selective and was unable to settle on the unprimed samples. The polychaete *Harmothoe* sp., the amphipod *Gammarellus homari*, and the bivalves *Anomia ephippium* and *Hiattella arctica*, were all more closely associated with the primed treatment and have all been previously recorded on kelp holdfasts (Christie *et al.*, 2003; Blight & Thompson, 2008; Walls *et al.*, 2016) and are suggested to utilise the crevices provided by the structurally complex holdfast morphology.

## **Predictability of primed and unprimed communities from one year to the next**

Between growing seasons, the mean occurrence-days of common species on primed samples were found to be predictable. This consistent pattern for primed samples was significant despite variation in deployment date and sampling date between years and factors such as water temperature, turbidity, irradiance and salinity presumably also varying from one year to the next (Walls *et al.*, 2017). This pattern was not replicated for shared species on unprimed samples between years (Figure 5B). However, the colonisation of shared species between treatments within the same year was shown to be predictable (Figure S1A & S1B in Supplementary Material). This informs us that treatment did not affect arrival and colonisation of shared epibionts within years and suggests that primed *A. esculenta* ropes are habitat to a specific assemblage whereas the unprimed habitat had more loosely associated assemblages. Interestingly, a predictable pattern was also observed between shared frond epibionts on cultivated *A. esculenta* (Walls *et al.*, 2017), but patterns of mobile fauna from the same site sampled at the same time were not predictable (un published data). Walls *et al.*, (2017) suggested that the predictability of organism arrival times observed on their frond samples could be attributed to flushing times within the bay affecting local larval pools; this could also be a probable explanation for our primed holdfast assemblages (Herben, 2005; Jessopp *et al.*, 2007). Ecological priming with juvenile *A. esculenta* sporophytes provides a biological platform that influences the development of predictable communities whereas the unprimed substratum leads to the development of unpredictable communities. This is an important consideration from a management perspective and the ability to understand the timing of occurrence of organisms and predict their arrival has significant benefits for the seaweed cultivation industry and management (Walls *et al.*, 2017). With this knowledge, seaweed farmers can exert some control over the quality of their crop by being able to decide on a date-by-site basis when the optimum time to harvest is to avoid detrimental fouling species attaching to their crop. This study was only conducted over a two-year period and analysis of communities over longer durations would be required before definitive conclusions can be made.

Ecological priming using kelp sporophytes provides the complex physical structure that is the holdfast, which has many interstitial spaces for epibionts to colonise. The holdfast also offers protection from predators and adverse environmental conditions (Norderhaug *et al.*, 2002), accumulates food sources (Moore, 1972) and increases the area of substratum and volume of habitable space available for colonisation (Ojeda & Santelices, 1984; Teagle *et al.*, 2017). Cultivated kelp holdfasts likely provide similar resources to colonising communities as wild kelps (Walls *et al.*, 2016). Hauser *et al.*, (2006) experimentally altered the complexity of artificial holdfast mimics and found significantly lower diversity on low complexity mimics in comparison to those with higher complexity. The organisms inhabiting low complexity habitats need to be highly mobile to escape predation as there is less physical structure for refuge and food may be more difficult to find as it is not concentrated within the structure (Hauser *et al.*, 2006). Hauser *et al.*, (2006) also suggests that higher complexity habitats offer a greater surface area for attachment of species, in addition to providing a larger surface area to catch organisms floating in that water column. The latter point is especially interesting in the context of our droppers which are suspended within the water column, and thus are more likely to attract larvae and pelagic organisms drifting in the water. As a consequence of ecological priming our primed samples are more predictable than unprimed samples potentially due to the foundational structure provided by kelp holdfasts.

### **Succession of epibiont assemblages of primed *Alaria esculenta* holdfasts**

There appear to be no published descriptions of succession on cultivated holdfasts so comparisons must be drawn from wild holdfast studies and successional studies from alternative systems. Kelp successional studies used holdfast volume rather than holdfast age to analyse succession, due to difficulties in determining the age of holdfasts partly because of the indistinct nature of growth rings and the lack of comparative data using age rather than volume in other studies (Smith *et al.*, 1996). Interestingly, several studies suggest that successional processes do not involve species replacement but rather an additive progression (Ojeda & Santelices, 1984; Smith *et al.*, 1996; Smith, 2000; Teagle *et al.*, 2017). Smith *et al.*, (1996) found that while early colonists on *Ecklonia radiata* (Agardh) Agardh (1848) holdfasts generally had a shift in dominance in larger holdfasts, all species that were recorded in smaller holdfasts were also present in larger samples. This was evident in *Macrocystis pyrifera* (Linnaeus) C. Agardh (1820) holdfasts that had a shift in dominance of polychaetes in smaller samples to a more diverse community in larger samples in which echinoids and decapod crustaceans were dominant (Ojeda & Santelices, 1984). Ojeda & Santelices (1984) suggested that this form of succession

may be more characteristic of habitats that grow, such as corals and sponges. This type of successional process is dissimilar to many other habitats where succession has been studied, including our cultivated kelp holdfasts, in which community change involved the replacement of early colonists with later species (Connell & Slatyer, 1977; Dean & Connell, 1987; Platt & Connell, 2003; Cifuentes *et al.*, 2010). In rocky shore and artificial habitats, the timing of disturbance or the creation of free-space can influence richness and abundance of initial colonizers which in turn affects succession, (Sousa, 1979; Dayton *et al.*, 1984; Benedetti-Cecchi & Cinelli, 1993; Underwood & Chapman, 2006; Cifuentes *et al.*, 2010; Valdivia *et al.*, 2014). This is partly due to seasonality in organisms' reproductive patterns and/or growth and seasonal variation in environmental conditions (Jenkins & Martins, 2010). This effect of timing was observed in the initial differences between early primed samples. However, as clearly evident from our primed samples and a number of other successional studies, varying successional trajectories subsequently converge towards a local climax community (Underwood & Chapman, 2006; Cifuentes *et al.*, 2010; Antoniadou, 2014; Evans *et al.*, 2016; Walls *et al.*, 2017). One such study, Cifuentes *et al.*, (2010), proposed that initial and intermediate successional stages can be highly variable, while late stages are highly deterministic if a dominant species is present that uses the available energy efficiently. This leads to a convergence of communities with different start points. As our study followed succession over the first 4-7 months of development of primed and unprimed communities we do not know if these communities will converge into one climax state dominated by a superior competitor(s), either within the individual treatments or between treatments. However, from previously conducted studies it is highly probable that they could converge to similar end-point communities.

## Outlook

This study identifies a unique habitat provided by the ecological priming of droppers with *A. esculenta* sporophytes, creating a complex physical structure with a distinct community when compared to unprimed ropes. This distinct community may be attracted to the habitat and refuge provided by the interstitial spaces between the holdfast haptera and its ability to accumulate food. The effect of primed ropes may reflect suppression of algal species that would otherwise colonize suspended ropes, and the facilitation of species that have a particular association with kelps. The restoration of kelp forests (Carney *et al.*, 2005; Yu *et al.*, 2012; Marzinelli *et al.*, 2016) and the transplantation of habitat forming species (Perkol-Finkel *et al.*, 2012; Ferrario *et al.*, 2016; Strain *et al.*, 2017) onto artificial structures have gained increased interest recently with attempts to mitigate the potential negative anthropogenic impacts of ocean sprawl (Airoldi & Beck, 2007; Firth *et al.*,

2016a, 2016b; Strain *et al.*, 2017). Rope has even been used as a method for enhancing productivity and biodiversity enhancement on pier pilings (Paalvast *et al.*, 2012), and its physical structure mimicked on pre-cast concrete habitat enhancement units (Perkol-Finkel & Sella, 2015). Deployment of seaweed lines may aid in habitat restoration by supplying spores and gametophytes to wild kelp beds that have been damaged by anthropogenic impacts, or by transplanting seeded kelp juveniles directly onto artificial structures (Marzinelli *et al.*, 2009). Ecologically priming the substratum with kelp seems likely to lead to the development of particular predictable associated communities. Colonisation onto kelps can occur from settlement of larvae or migration by mobile fauna (Walls *et al.*, 2016, 2017). The duration of the ‘seeding’ effect remains to be defined. Communities may become more similar over time (depending on successional processes and dominant species), or the influence of a kelp-dominated habitat may increase the longer the longlines are left in the water column. The cultivation practices for kelps are subject to change and development. Harvesting practices may be adjusted so that holdfasts, stipes and small fronds remain in place for more than one growing season, however the applicability of these techniques depends on culture species. Another area for future research is the impact of primed ropes on primary and secondary productivity associated with these communities. An assessment of productivity could increase the importance of primed communities through quantification of the ecosystem services they provide (Beaumont *et al.*, 2007). The importance of priming effects may depend on the case-by-case details of cultivation practice, and there is a need for further research to fully understand the novelty of habitats created by seaweed cultivation.

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