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

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

2

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12

13 ABSTRACT

14

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

31

32 KEYWORDS

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

35 INTRODUCTION

36 Over the last few decades there has been rapid proliferation of artificial structures in the marine environment
37 (Firth *et al.*, 2016a) to enable the exploitation of the ocean's energy and food resources. Novel structures include
38 oil and gas platforms, marine renewable energy installations and aquaculture facilities (Chapman & Underwood,
39 2011; Firth & Hawkins, 2011). The term 'ocean sprawl' has been used to describe this expansion of coastal and
40 marine infrastructure (Duarte *et al.*, 2012; Firth *et al.*, 2016a, 2016b) and this is gaining recognition as one of
41 the biggest threats to marine ecosystems (Airoldi & Beck, 2007; Firth *et al.*, 2013; Dafforn *et al.*, 2015; Bishop
42 *et al.*, 2017; Heery *et al.*, 2017).

43

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

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

66

67 To date the majority of research on the role of kelp as a habitat has focused on the holdfast structure (Jones,
68 1971; Moore, 1973; Schultze *et al.*, 1990; Smith, 1996; Thiel & Vásquez, 2000; Christie *et al.*, 2003; Blight &
69 Thompson, 2008; Walls *et al.*, 2016; Teagle *et al.*, 2017). This focus on holdfasts is due in part to the relative
70 ease in collecting these discrete sampling units (Walls *et al.*, 2016) and because the holdfast is generally found
71 to host the highest diversity of all kelp structures (such as, kelp stipes and fronds) (Jones, 1972; Thiel &
72 Vásquez, 2000; Norderhaug *et al.*, 2002; Christie *et al.*, 2003; Arroyo *et al.*, 2004). Within an individual
73 holdfast, species richness typically reaches 30 – 70 macrofaunal species (Jones, 1972; Thiel & Vásquez, 2000;
74 Teagle *et al.*, 2017), but in some cases, may reach up to 90 species (Christie *et al.*, 2003). This relatively high
75 biodiversity is thought to reflect the complex physical structure provided by the holdfast, as the branched root-
76 like shape of the holdfast provides a number of holes and crevices as living space (Christie *et al.*, 2003). This
77 interstitial space may represent favourable habitat for colonising fauna, potentially providing protection from
78 predators and during periods of adverse environmental conditions (Norderhaug *et al.*, 2002). The holdfast
79 functions as a sediment trap accumulating detritus, which acts as a food source for many of the organisms
80 inhabiting the structure (Moore, 1972). The holdfast also provides a stable environment which is persistent over
81 seasons and years (Schaal *et al.*, 2009); with the lifespan of the holdfast being the same as that of the kelp
82 individual (Kain, 1963; Christie *et al.*, 2003). This stability contrasts with the seasonally fluctuating habitat
83 experienced by stipe-associated epiphytes (Norderhaug, 2004) and to the temporally renewing frond habitat
84 (Christie *et al.*, 2003, 2007). It must be noted that, depending on cultivation practices, entire kelp individuals
85 including the holdfast can be harvested from the farm thus the lifespan of cultivated holdfasts is only as long as
86 the cultivation period.

87

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

94 Here, habitat volume is defined as the space available for colonisation by organisms within the holdfast (see
95 Walls *et al.*, (2016)). The volume and structure of these interstitial spaces have been shown to impact the
96 diversity and abundance of associated assemblages (Jones, 1971; Thiel & Vásquez, 2000; Blight & Thompson,
97 2008; Tuya *et al.*, 2011; Walls *et al.*, 2016). The distinct holdfast morphologies of wild and cultivated *L.*
98 *digitata* (Hudson) Lamourx (1813) were suggested as the cause of variations in species richness and community
99 composition by Walls *et al.*, (2016). Wild kelps tend to grow a characteristic flat or slightly conical holdfast
100 when attached to rock (Figure 1a in Walls *et al.*, 2016)), whilst cultivated kelps are seeded onto ropes, resulting
101 in a different morphology, formed by intertwined haptera around the rope substratum (Figure 2A and Figure 1b
102 in Walls *et al.*, 2016)). Alterations in abiotic conditions experienced by the holdfast can also cause variations in
103 the assemblages inhabiting the holdfast (Smith, 2000; Walls *et al.*, 2016). Smith (1996) found differences in
104 community structure between holdfasts sampled at different depths (2 m and 6 m), however depth also
105 influences sediment load, structural complexity and water turbulence (Smith, 2000). Changing from a benthic to
106 a suspended substratum can alter both the hydrodynamic environment and sedimentation rates experienced by
107 fauna (Walls *et al.*, 2016). Shifts in other abiotic conditions that influence holdfast assemblages (and by
108 extension, rope-attached assemblages) include hydrodynamic environment (Moore, 1972), sedimentation rates
109 (Schaal *et al.*, 2012), light availability, and temperature (Scarratt, 1961).

110
111 In this study, we focus on the assemblage that develops on suspended ropes primed with the cultivated kelp
112 *Alaria esculenta*. Kelp-associated holdfast epibionts were surveyed at different times during the two cultivation
113 periods to track changes in community composition and development. We compared these primed rope
114 communities with communities that developed on unprimed ropes. The comparison of primed and unprimed
115 treatments allows for an estimation of the effect of ‘ecological priming’. We tested the hypothesis that a priming
116 effect alters the development of assemblages differently across primed and unprimed treatments. An assessment
117 of an ecological priming effect associated with cultivated kelps is novel and, if present, may have important
118 implications for habitat restoration and enhancement of artificial structures. If the development of primed
119 communities is predictable, this would increase the capacity for planning and management in the seaweed
120 cultivation industry. Also, if cultivated holdfasts are found to have distinct assemblages when compared to
121 unprimed treatments, this suggests they supplement the habitat service provided by artificial structures, such as
122 mooring and anchor ropes, with the farm providing an alternative habitat for associated communities. This study
123 builds on previous work conducted in Walls *et al.*, 2017 on the ecological processes occurring on cultivated kelp

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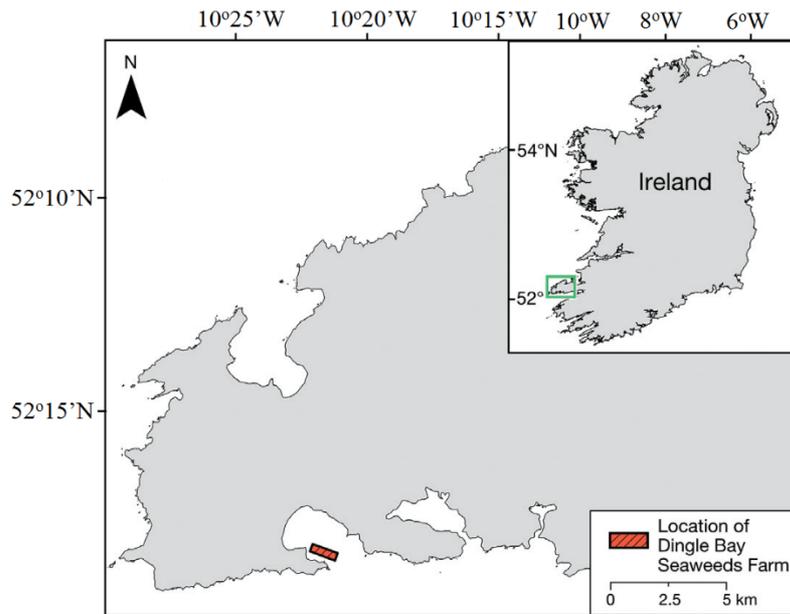
124 farms. However, the data presented here is related to the communities associated with the holdfast material
125 while, Walls *et al.*, 2017 studied the frond fouling communities and their impact on commercial aspects of
126 seaweed farming.

127 MATERIALS AND METHODS

128 **Study site**

129 This study was conducted in southwest Ireland in Ventry Harbour, County Kerry (52° 06' 49.45"N, 10°
130 21'20.17"W; Figure 1) at the largest operating commercial seaweed farm in Ireland (18 ha site). Ventry Harbour
131 is a moderately sheltered and shallow embayment orientated towards the southeast, approximately 2.5 x 1.5 km
132 (3.75 km²) with a wide mouth opening into Dingle Bay. The seagrass *Zostera marina* Linnaeus (1753) is
133 extensively distributed throughout the sandy seabed, leading to a rocky boulder reef towards the mouth of the
134 bay. Wild kelp populations are found at the mouth of Ventry Harbour and on the northeastern shore of the bay,
135 approximately 250 m- 1 km from the farm site). The licensed seaweed farm is orientated northwest to southeast,
136 and located to the westerly side of Ventry Harbour (Figure 1). The depth underneath the farm is approximately 6
137 m at the northwestern end before gently sloping to 20 m at the eastern edge of the farm at mean low water
138 spring tide (MLWS). The tidal range in Ventry Harbour is between 0.6 and 4.0 m. Monthly irradiance values,
139 obtained from nearby Valentia weather observatory (51° 56' 23" N, -10° 14' 40" W), ranged from 5,447 –
140 63,823 J cm⁻² for 2014; equivalent to approximately 3,356 to 40,364 mmol photons m⁻² day⁻¹ using the
141 approximation suggested by Tett (1990). Sea surface temperature data were obtained from the M3 offshore
142 weather buoy located approximately 56 km southwest of Mizen head (51° 13' 0" N, 10° 33' 0" W), and ranged
143 from 10.1 – 17.6 °C for 2014. Although offshore sea temperatures are less extreme than inshore waters, Ventry
144 Harbour is a well-flushed bay so values are broadly representative. The longline set-up and design of the
145 seaweed farm is described in detail in Walls *et al.*, 2017. The farm cultivates the kelps *Alaria esculenta* and
146 *Saccharina latissima* (Linnaeus) Lane, Mayes, Druehl & Saunders (2006) for human consumption, animal feed
147 and use in cosmetic products.

148



149

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

151

152 **Experimental set-up**

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

169

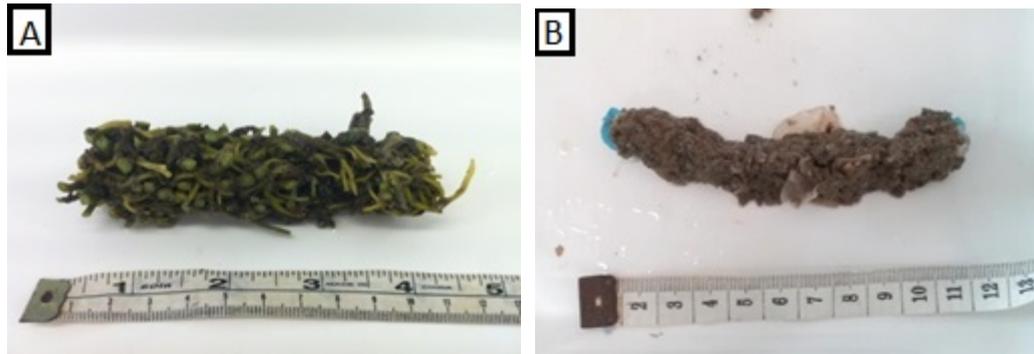
170 **Sampling protocol for primed and unprimed droppers**

171 All samples were collected by SCUBA divers. In April, May and June 2014 and 2015 five droppers were
172 randomly chosen and collected from the primed and unprimed treatments using open-ended mesh bags (150 x
173 55 cm, 0.5 mm mesh size). If a dropper was not uniformly covered in developing sporophytes (i.e. showed
174 evidence of rubbing or entanglement), another dropper replicate was selected. The mesh bag was carefully
175 slipped up over the dropper and tightly secured at top and bottom (just above the weight) using cable ties,
176 enclosing the entire 1 m dropper and kelp biomass. The focus for the current study was to compare the
177 assemblages associated most closely with the dropper rope. There are potential issues of habitat extent when
178 comparing the assemblages of entire kelp sporophytes with organisms attached to unprimed rope (where large
179 kelp blades did not develop in the experimental time period). We therefore compared the near-rope assemblages
180 of the holdfast with those on unprimed droppers.

181

182 All samples were transferred back to nearby facilities at Dingle Oceanworld Aquarium for initial processing
183 within 6 hours. The sampling technique of bagging fronds and holdfast before separating the material on land
184 potentially risks mixing species attached to the frond with those of the holdfast. However, fronds mainly host
185 attached organisms such as hydroids and bryozoans and fewer mobile species (Walls *et al.*, 2017) so this form
186 of contamination is likely to be minimal. The alternative, of cutting fronds in situ, risks dislodging loosely
187 attached species on one treatment (primed ropes), but not the other (unprimed ropes). The mesh bags were
188 untied before randomly pre-selected 10 cm sections (n=3) of each dropper were excised from the 1 m dropper
189 (Figure 2A+B). In the rare event that any randomly selected section of primed dropper was not entirely covered
190 in holdfast structures, an alternative section was chosen. The frond and stipe material of primed samples were
191 cut just above the holdfast and stored in sealed plastic bags containing 100 % ethanol for a separate study. The
192 10 cm primed and unprimed rope sections were stored in separate sealed plastic bags containing 100 % ethanol.
193 All samples were transported back to the laboratory for further processing.

194



195

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

197 **Sample processing**

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

206

207 **Statistical analysis**

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

218 unprimed treatments using the model of month (fixed factor) crossed with treatment (fixed factor) for years
219 2014 and 2015 separately. Dropper sections were pooled to make droppers rather than 10 cm sections the basic
220 unit of replication. The pooling was carried out as variation within droppers and between sections was not part
221 of the hypothesis of interest.

222 The differences between community composition from different months and years for the primed and unprimed
223 treatments were compared using multivariate tests. A Simpson's dissimilarity matrix was generated from the
224 presence/absence data for pooled dropper communities from years 2014 and 2015 separately for the 3 primed
225 and 3 unprimed treatments and different months (April, May and June). Simpson's dissimilarity values are 0
226 when assemblages from separate samples are identical and scaled to 100 when there are no species in common
227 between separate samples. Simpson's dissimilarity has the advantage that it only measures the compositional
228 turnover and is not affected by the relative difference in species richness between samples (Baselga, 2010). This
229 makes dissimilarities measured by Simpson's index easier to interpret than is the case for indices that mix
230 turnover and species richness components of dissimilarity (e.g. Sørensen's index). The PRIMER software used
231 for multivariate analysis does not calculate Simpson's dissimilarities, so these were calculated from species
232 presence/absence data in EXCEL using the PopTools add-on (Hood, 2014) and dissimilarity matrices were
233 subsequently imported into PRIMER. All samples were ordinated using a multidimensional scaling plot (MDS)
234 (Shepard, 1962; Kruskal, 1964a, 1964b) in PRIMER V6®, giving the position of each dropper community (n=3
235 sections pooled) in two-dimensional space based on its species composition for years 2014 and 2015 separately.
236

237 Permutational multivariate analysis of variance (PERMANOVA, Anderson *et al.*, 2008) was used to test for
238 differences in multivariate species assemblages among primed and unprimed communities using the model of
239 month (fixed factor) crossed with treatment (fixed factor) for years 2014 and 2015 separately, based on 9999
240 unrestricted permutations of raw data. PERMDISP routine revealed that the variation in multivariate dispersion
241 (around the centroid) was not significant ($p > 0.5$) for all factors (month and treatment).

242

243 Where significant differences between sampling dates and treatments were detected, a variation on SIMPER
244 analysis was conducted to highlight the species that contributed most to the observed differences. The SIMPER
245 programme in PRIMER could not be used as Simpson's dissimilarity is not compatible with the algorithm used
246 in the programme. Instead, we conducted a SIMPER-like analysis, hereafter referred to as a test of species
247 influence (Walls *et al.*, 2017), by comparing the observed dissimilarity within and between samples when all

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

255
256 To test the predictability of the presence of species on primed and unprimed droppers from Year 1 (2014) to
257 Year 2 (2015), we used day of year to calculate the central tendency of species occurrence. Day of year is the
258 number assigned to a whole solar day that starts at 1 on the 1st of January and finishes at 365 on 31st of
259 December (non-leap year), e.g., sampling took place on 7th April 2015 which is day of year 97. Central tendency
260 is the average day when a species was observed, weighted by the frequency of occurrence. For example, if a
261 species has high occurrence in the first sampling date, lower occurrence in the middle sampling date and does
262 not occur in the final sampling date then the mean occurrence day will be somewhere between the first and
263 second sampling date. The central tendency method as described by Colebrook (1979) can identify changes in
264 the timing of seasonal cycles (Edwards & Richardson, 2004; Moore *et al.*, 2011). To test if species arrival times
265 were similar between the different treatment droppers within the same year the mean species arrival times were
266 compared between treatments within years 2014 and 2015 separately. Regression analysis was conducted using
267 Minitab v16 to test if arrival times of commonly occurring species were significantly related. A slope close to 1
268 is expected if the timing of species presences is the same from year to year. If the relationship between
269 occurrence days is significant, but the slope is not close to 1, this implies that the order of species occurrence is
270 similar between sets of samples, but the rate of species arrival varies between years.

271 RESULTS

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

285
286 Thin filamentous algae were the most dominant algal functional group for both treatments, with algal diversity
287 higher (4/6 dates) in unprimed treatments when compared to primed treatments in the same month. The
288 suspension feeders were the most common faunal groups for both treatments, followed by omnivores and
289 detritivores (Table 1). A full list of species recorded and their abundance is provided in Supplementary Material
290 (Table S1). Functional group richness increased with time since deployment ($F_{2,6} = 5.7, p < 0.05$), but there were
291 no effects of treatment.

292
293
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302 Table 1. Number of species in each functional group for primed (P) and unprimed (UP) dropper treatments
 303 sampled in April, May and June 2014 and 2015.

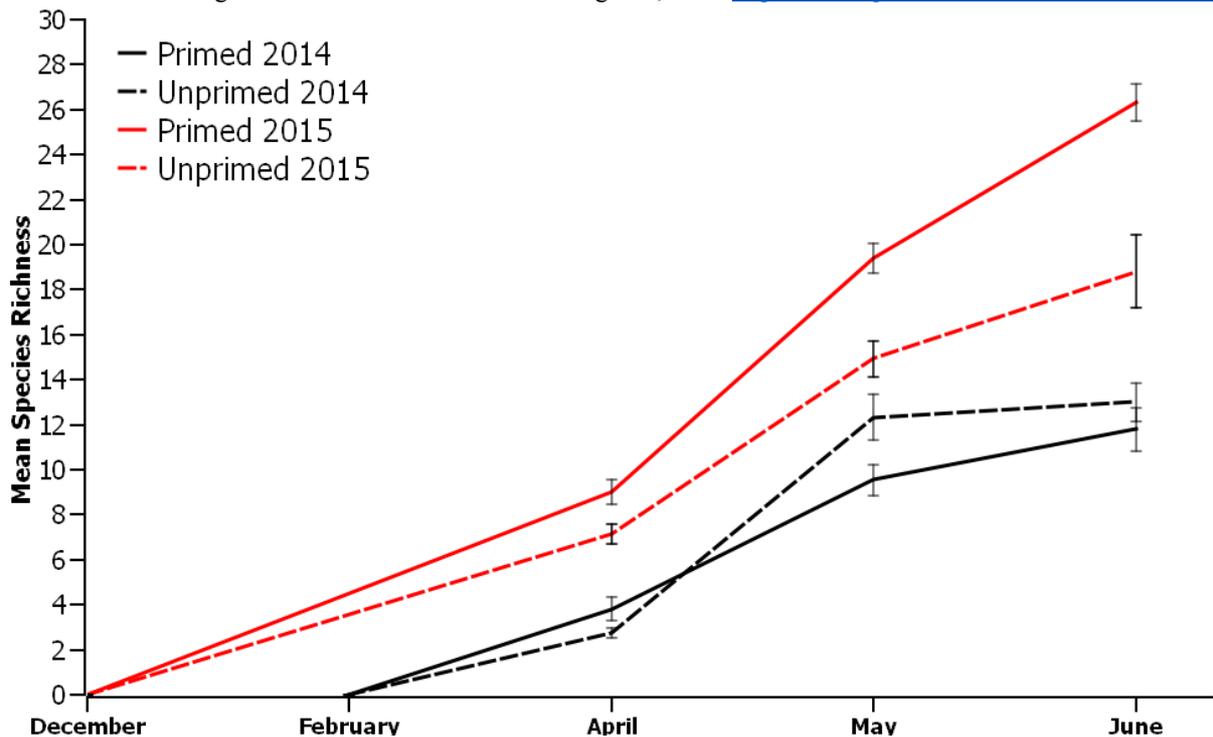
Functional Groups	April 2014 P	April 2014 UP	May 2014 P	May 2014 UP	June 2014 P	June 2014 UP	April 2015 P	April 2015 UP	May 2015 P	May 2015 UP	June 2015 P	June 2015 UP
Thin Filamentous Algae	1	2	2	3	3	4	4	4	3	4	4	5
Foliose Algae	0	0	0	0	0	0	0	0	0	1	0	2
Leathery Macrophyte	1	0	1	1	1	2	1	1	1	3	1	3
Suspension 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

304

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

307 Species richness at the seaweed farm site in Ventry increased from time of deployment until the end of the
 308 study, for both primed and unprimed treatments. Apart from the accumulation of species with time, the patterns
 309 of species richness were not consistent across factors (Treatment 2014 $F_{1,24} = 0.126$, $P = 0.725$, Treatment 2014
 310 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
 311 differences in species richness were recorded for month for both years (Months 2014 $F_{2,24} = 34.608$, $P = <$
 312 0.001 ; Months 2015 $F_{2,24} = 91.555$, $P = < 0.001$), and treatment is significant for 2015 from the ANOVA (Figure
 313 3, Treatment 2015 $F_{1,24} = 16.796$, $P = < 0.001$). Species richness within 2015 was higher in the primed treatment
 314 than in the unprimed treatment for each sampling month. For 2014 primed species richness was higher than
 315 unprimed species richness for April samples, however, richness was lower for primed samples from May and
 316 June than unprimed samples (Figure 3).

317



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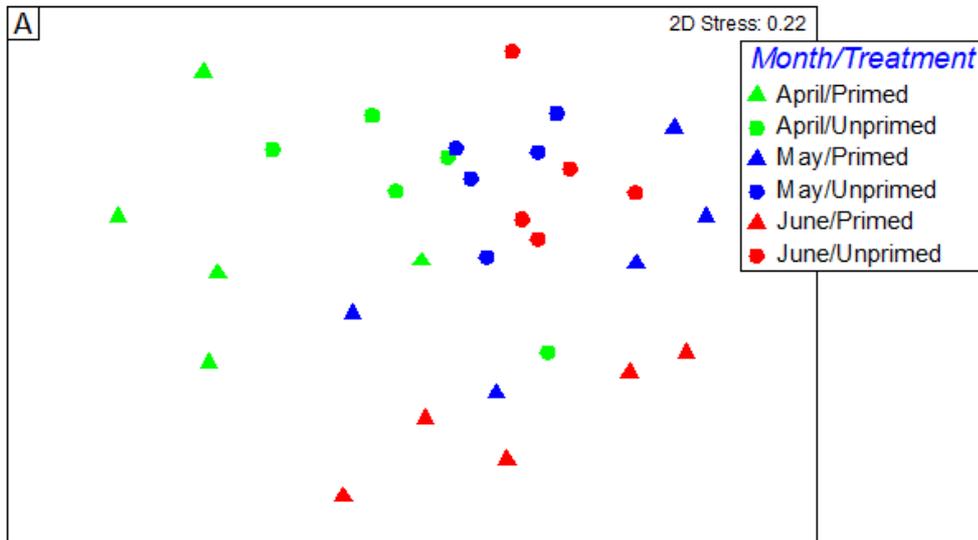
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320 Fig.3. Species richness (mean \pm SE) on primed *Alaria esculenta* holdfast sections and unprimed sections
321 sampled in April, May and June 2014 and 2015. Species richness represents the number of taxa identified on 10
322 cm section ($n = 3$)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

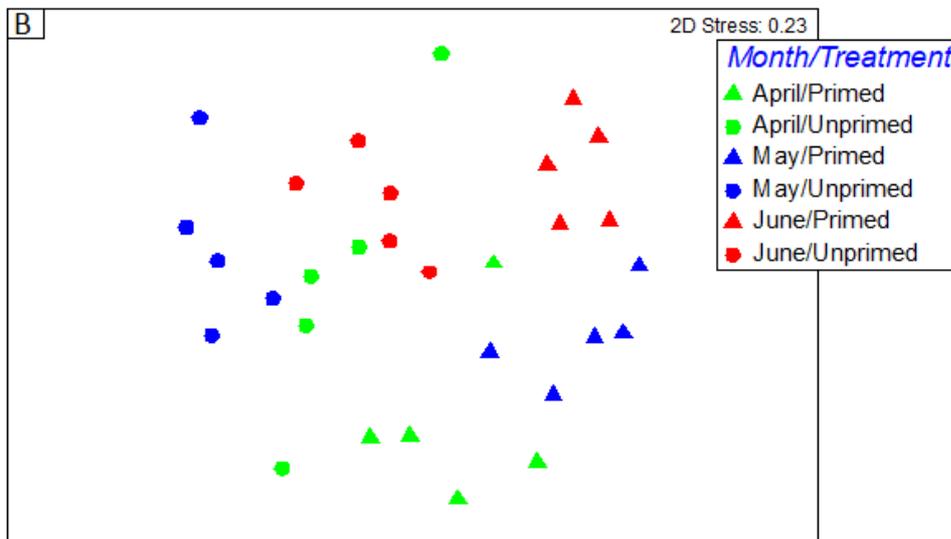
323

324 Due to the high stress values of the MDS plots for year 2014 (0.22 Figure 4A) and for year 2015 (0.23 Figure
325 4B) patterns of differences among assemblages from separate months and treatments were difficult to examine.
326 A stress value of > 0.20 indicates the data are only partially represented by the two-dimensional plot and little
327 reliance should be placed on the finer detail of the plot (Clarke & Warwick, 1994). However, the broad-scale
328 pattern shows a separation of early April communities to later May and June communities which show little
329 separation, with month also being significant from the PERMANOVA analysis for both years 2014 and 2015
330 (Table 2A+B, $p < 0.05$). There is also a separation of community assemblages between primed and unprimed
331 treatments. This pattern is evident from the PERMANOVA analysis with species assemblage composition
332 differing between treatment (primed and unprimed) from the analysis again for both years 2014 and 2015 (Table
333 2A+B, $p < 0.01$). Interestingly, the month crossed with treatment interaction was significant for year 2015 only
334 (Table 2B, $p < 0.05$). The pairwise tests reveal that this significant interaction is not due to whether treatments
335 are different in one particular month, but the interaction implies that month within a treatment are sometimes
336 different and sometimes not.

337



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339

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

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350 Table 2: Permutational multivariate analyses of variance based on Simpsons dissimilarity matrix based on
 351 presence/ absence data for dropper community (n = 3 10 cm rope sections pooled) sampled over months (April,
 352 May and June) on different treatments (primed and unprimed) for (A) year 2104 and (B) year 2015. All tests
 353 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 ⁻²	1.3606	0.2803
Residuals	24	1.2734	5.3057 x10 ⁻²		
Total	29	2.525			

354

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

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

357

358 A test of species influence was conducted to determine which taxa were the major contributors to the observed
 359 dissimilarity in assemblage structure between primed and unprimed treatments within the same sampling
 360 months (Table 3). Most of the species responsible for dissimilarity between treatments were algae and sessile
 361 faunal species. The species with higher occurrence on the primed samples were from a variety of different phyla
 362 and dissimilarities were not characterised by any specific group. These included the amphipod *Jassa* fem.
 363 Montague (1808) present in April 2014 samples, and the polychaete *Harmothoe* sp. Kinberg (1856) present in
 364 May 2014 samples, the bryozoan *Electra pilosa* Lamourx (1816) which contributed to differences between
 365 treatments in both June 2014 and May 2015, the amphipod *Gammarellus homari* Herbst (1793) present in April
 366 2015 and the bivalve molluscs *Anomia eippium* Linnaeus (1758) and *Hiatella arctica* Linnaeus (1767) which
 367 were responsible for some of the differences observed in June 2015. The unprimed treatment was generally
 368 characterised by a higher occurrence of algal species during each sampling month. The filamentous brown algae
 369 sp. and the red alga *Ceramium* sp. Wiggers (1780) were major contributors to the observed differences between

370 treatments and were present in April 2014 (filamentous brown algae sp. only), May 2014 and 2015 and June
 371 2015. Laminariales juveniles *Migula* (1909) were present in higher occurrence in all sampling months except
 372 May 2014 when they did not contribute to observed dissimilarities. The red algae *Polysiphonia* sp. Greville
 373 (1823) and *Lomentaria clavellosa* Lyngbye (1819) were present in June 2015. The only non-algal species which
 374 contributed to the dissimilarity between treatments with higher occurrence in the unprimed treatment was
 375 *Harpacticoida* indent. Sars (1903) present in June 2014. From the dissimilarity scores May 2014 and April 2015
 376 treatments are less dissimilar than June 2015, however primed and unprimed treatments sampled in June 2014
 377 and May 2015 are the most dissimilar (> 2.00 dissimilarity score, Table 3).

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390 Table 3: Test of species influence to determine the species contributing to observed differences in the structure
 391 of assemblages between primed and unprimed treatments. Dissimilarity scores are the ratio of average between-
 392 group dissimilarities to within-group dissimilarities for each pairwise comparison. Normalized score is the
 393 reduction in dissimilarity score when excluding the species of interest, normalized to mean = 0, SD = 1 using
 394 the mean and standard deviation of all individual species' scores. A higher loss in dissimilarity indicates that a
 395 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 ⁻¹)	
				Primed	Unprimed
April 2014 Primed & Unprimed	1.17	Filamentous brown algae sp.	2.36	7	< 10
		Jassa fem.	1.05	15	> 12

May 2014 Primed & Unprimed	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
June 2014 Primed & Unprimed	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
April 2015 Primed & Unprimed	1.62	<i>Laminariales</i> juv.	4.70	0	<	12
		<i>Gammarellus homari</i>	1.37	10	>	0
May 2015 Primed & Unprimed	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
June 2015 Primed & Unprimed	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

396

397 **Predictability of holdfast assemblages on primed and unprimed treatments**

398

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

400 The temporal pattern of shared holdfast species was consistent between years for the primed treatment;

401 however, this pattern was not the same in the unprimed treatment. The regression of mean species occurrence in

402 2014 and 2015 was significant in primed treatments ($p < 0.001$; Figure 5A). In contrast, patterns of mean

403 species arrival on unprimed treatments were not consistent between 2014 and 2015 ($p > 0.05$; Figure 5B).

404

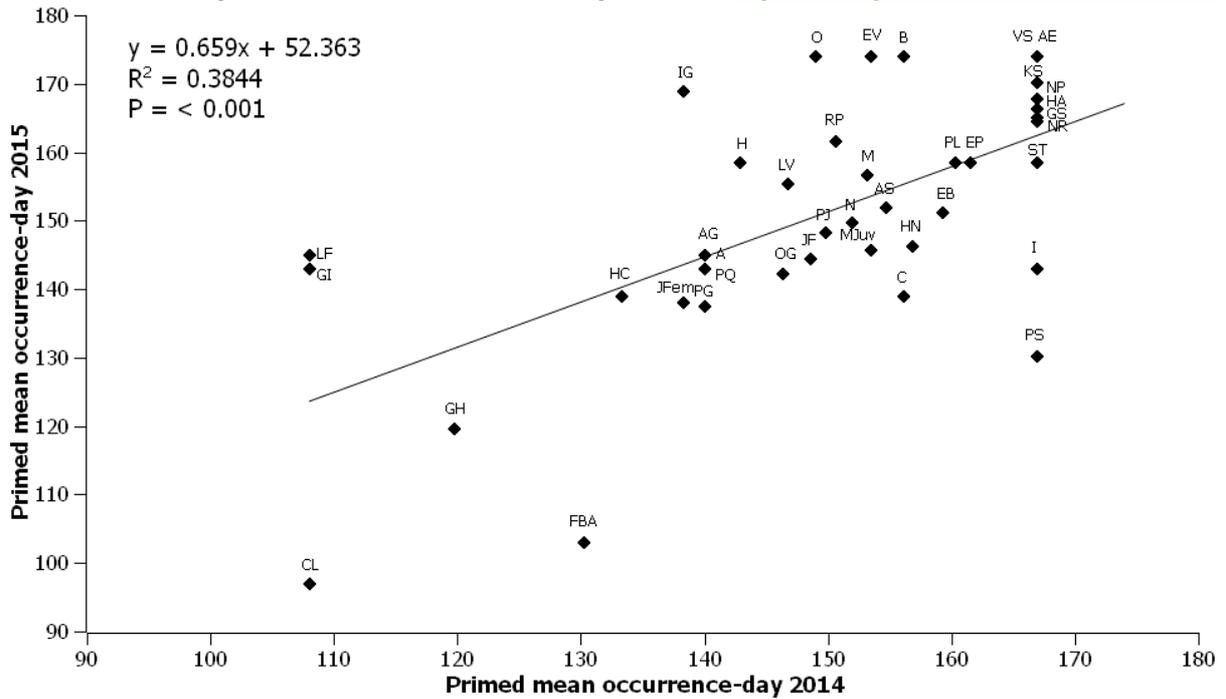
405 Recruitment by shared species to both treatments was similar within a year. The timing of species occurrence

406 was consistent across treatments within the same year for both 2014 and 2015. The regression slope relating

407 mean day of year of shared species occurrence samples was significant within both years ($p < 0.05$; Figure S1A

408 & S1B Supplementary Material).

409



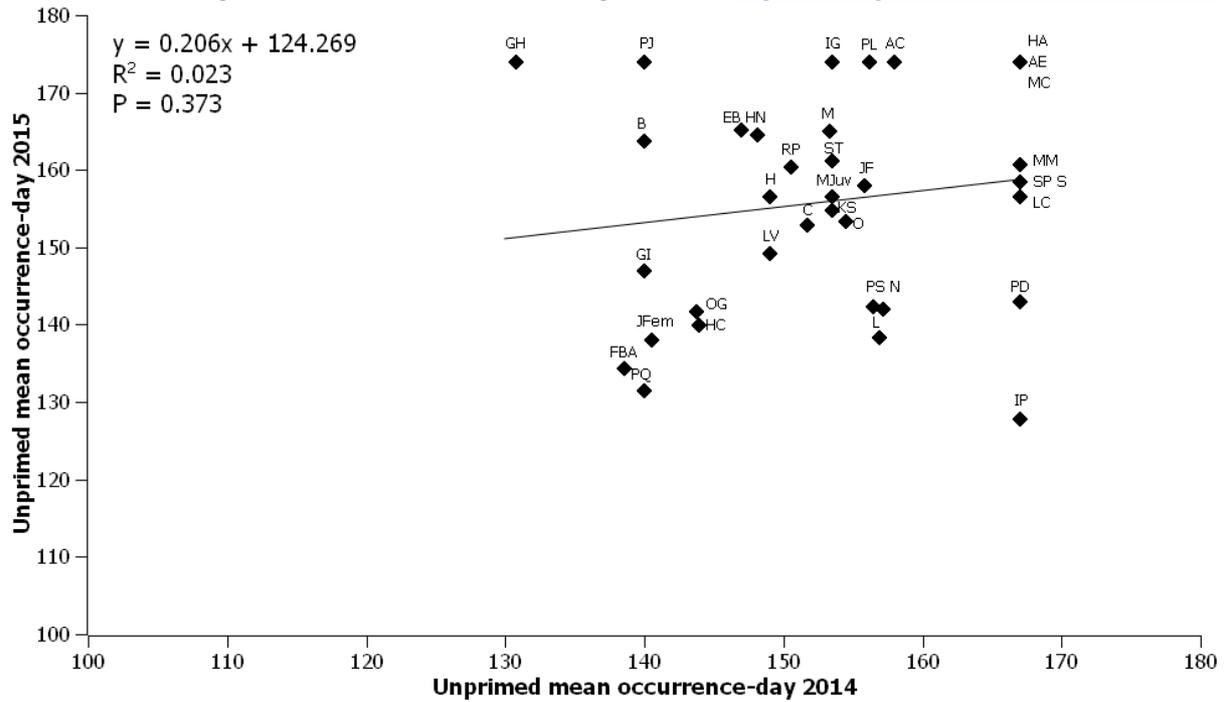
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411

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

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

423



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

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

436 DISCUSSION

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

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

451
452 Functional diversity was dominated by suspension feeders, omnivores and detritivores for both our primed and
453 unprimed samples. However, algal diversity was higher on unprimed samples with 4 of the 5-unique species on
454 unprimed samples being algae, e.g. the kelps *Saccorhiza polyschides* and *Saccharina latissima*, the green algae
455 *Ulva* sp., and *Desmarestia viridis* a filamentous brown alga. Consistently higher species richness in primed
456 samples during early sampling suggests that habitat availability is very important for the colonization of species
457 during early successional stages (April). This importance lessens as communities develop, leading to less
458 consistency in the treatments with higher species richness. The rapid colonisation of this novel habitat suggests
459 that the species have either planktonic larval settlement or if they have direct development, species are highly
460 mobile (Walls *et al.*, 2016). Fouling epibionts such as bryozoans, hydroids, molluscs and crustaceans begin to
461 settle in spring and early summer, which coincides with deployment and the cultivation period for kelps (Walls
462 *et al.*, 2017). The sources of these colonizing species remain unknown. The nearest wild kelp populations are
463 between 250 m (mouth of Ventry Harbour opening up to Dingle Bay) and 1 km (northeast direction from farm
464 in Ventry Harbour) away from the farm site. Cultivation practices are not harmonized within the sector or even

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

469

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

478

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

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

500

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

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

524

525 Ecological priming using kelp sporophytes provides the complex physical structure that is the holdfast, which
526 has many interstitial spaces for epibionts to colonise. The holdfast also offers protection from predators and
527 adverse environmental conditions (Norderhaug *et al.*, 2002), accumulates food sources (Moore, 1972) and
528 increases the area of substratum and volume of habitable space available for colonisation (Ojeda & Santelices,
529 1984; Teagle *et al.*, 2017). Cultivated kelp holdfasts likely provide similar resources to colonising communities
530 as wild kelps (Walls *et al.*, 2016). Hauser *et al.*, (2006) experimentally altered the complexity of artificial
531 holdfast mimics and found significantly lower diversity on low complexity mimics in comparison to those with
532 higher complexity. The organisms inhabiting low complexity habitats need to be highly mobile to escape
533 predation as there is less physical structure for refuge and food may be more difficult to find as it is not
534 concentrated within the structure (Hauser *et al.*, 2006). Hauser *et al.*, (2006) also suggests that higher
535 complexity habitats offer a greater surface area for attachment of species, in addition to providing a larger
536 surface area to catch organisms floating in that water column. The latter point is especially interesting in the
537 context of our droppers which are suspended within the water column, and thus are more likely to attract larvae
538 and pelagic organisms drifting in the water. As a consequence of ecological priming our primed samples are
539 more predictable than unprimed samples potentially due to the foundational structure provided by kelp
540 holdfasts.

541

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

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

555 may be more characteristic of habitats that grow, such as corals and sponges. This type of successional process
556 is dissimilar to many other habitats where succession has been studied, including our cultivated kelp holdfasts,
557 in which community change involved the replacement of early colonists with later species (Connell & Slatyer,
558 1977; Dean & Connell, 1987; Platt & Connell, 2003; Cifuentes *et al.*, 2010). In rocky shore and artificial
559 habitats, the timing of disturbance or the creation of free-space can influence richness and abundance of initial
560 colonizers which in turn affects succession, (Sousa, 1979; Dayton *et al.*, 1984; Benedetti-Cecchi & Cinelli,
561 1993; Underwood & Chapman, 2006; Cifuentes *et al.*, 2010; Valdivia *et al.*, 2014). This is partly due to
562 seasonality in organisms' reproductive patterns and/or growth and seasonal variation in environmental
563 conditions (Jenkins & Martins, 2010). This effect of timing was observed in the initial differences between early
564 primed samples. However, as clearly evident from our primed samples and a number of other successional
565 studies, varying successional trajectories subsequently converge towards a local climax community (Underwood
566 & Chapman, 2006; Cifuentes *et al.*, 2010; Antoniadou, 2014; Evans *et al.*, 2016; Walls *et al.*, 2017). One such
567 study, Cifuentes *et al.*, (2010), proposed that initial and intermediate successional stages can be highly variable,
568 while late stages are highly deterministic if a dominant species is present that uses the available energy
569 efficiently. This leads to a convergence of communities with different start points. As our study followed
570 succession over the first 4-7 months of development of primed and unprimed communities we do not know if
571 these communities will converge into one climax state dominated by a superior competitor(s), either within the
572 individual treatments or between treatments. However, from previously conducted studies it is highly probable
573 that they could converge to similar end-point communities.

574

575 **Outlook**

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

585 2016a, 2016b; Strain *et al.*, 2017). Rope has even been used as a method for enhancing productivity and
586 biodiversity enhancement on pier pilings (Paalvast *et al.*, 2012), and its physical structure mimicked on pre-cast
587 concrete habitat enhancement units (Perkol-Finkel & Sella, 2015). Deployment of seaweed lines may aid in
588 habitat restoration by supplying spores and gametophytes to wild kelp beds that have been damaged by
589 anthropogenic impacts, or by transplanting seeded kelp juveniles directly onto artificial structures (Marzinelli *et*
590 *al.*, 2009). Ecologically priming the substratum with kelp seems likely to lead to the development of particular
591 predictable associated communities. Colonisation onto kelps can occur from settlement of larvae or migration by
592 mobile fauna (Walls *et al.*, 2016, 2017). The duration of the ‘seeding’ effect remains to be defined.
593 Communities may become more similar over time (depending on successional processes and dominant species),
594 or the influence of a kelp-dominated habitat may increase the longer the longlines are left in the water column.
595 The cultivation practices for kelps are subject to change and development. Harvesting practices may be adjusted
596 so that holdfasts, stipes and small fronds remain in place for more than one growing season, however the
597 applicability of these techniques depends on culture species. Another area for future research is the impact of
598 primed ropes on primary and secondary productivity associated with these communities. An assessment of
599 productivity could increase the importance of primed communities through quantification of the ecosystem
600 services they provide (Beaumont *et al.*, 2007). The importance of priming effects may depend on the case-by-
601 case details of cultivation practice, and there is a need for further research to fully understand the novelty of
602 habitats created by seaweed cultivation.

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611

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