



Potential novel habitat created by holdfasts from cultivated *Laminaria digitata*: assessing the macroinvertebrate assemblages

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ABSTRACT: Interest in the cultivation of native kelp species is increasing within Europe. Observations of seaweed farms suggest that they may act as a habitat for associated species, potentially altering the richness of the local area. Previous studies have generally focused on species associated with wild kelps, showing the holdfast to be relatively species-rich. Little research has, however, been conducted on the species associated with cultivated kelps. The habitat created by cultivated kelp holdfasts may act as a novel habitat and not simply an expansion of existing kelp habitat, due to differences in holdfast age, holdfast morphology and holdfast position in the water column. *Laminaria digitata* from the west of Ireland were examined to test if these differences result in the fauna of cultivated (suspended) holdfasts being distinct from wild (benthic) stands. To place the results in a broader context, patterns were compared to holdfast–richness relationships observed in comparable studies from the NE Atlantic. Total abundance of holdfast epifauna was similar across benthic and suspended holdfasts from the west of Ireland, although species richness was higher in suspended samples. Richness and abundance in suspended kelp holdfasts were consistent with the range of values recorded in other wild kelp studies. There were significant differences in assemblage composition between holdfast types (ANOSIM; $R = 0.383$, $p < 0.05$). The distributions of faunal feeding types did not, however, vary between suspended and benthic kelps. Suspended holdfasts in the west of Ireland represented a novel habitat with higher species richness and a different species assemblage when compared to adjacent benthic kelps.

KEY WORDS: *Laminaria* · Macroalgae · Aquaculture · Holdfasts · Macroinvertebrate · Multivariate analysis · Habitat volume

INTRODUCTION

Kelps (large seaweeds of the order Laminariales) are an existing and potentially expanding resource for the provision of food, fertilizers, food additives (e.g. alginates), pharmaceutical products (Guiry & Blunden 1991, Smit 2004), bioactive compounds (Holdt & Kraan 2011), biopolymers (Bella et al. 2015) and

biofuel production (Fasahati et al. 2015). Scientific interest in cultivating the Laminariales has been increasing with a doubling of the number of studies found using an ISI search of 'Laminaria and aquaculture' in 2005–2014 compared to the previous decade. Kelp farming is currently dominated by Japanese kelp *Laminaria japonica* and Wakame *Undaria pinnatifida*, together accounting for an annual produc-

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tion of over 7 million tonnes wet weight in 2012 (FAO 2014). Although there is currently little seaweed biomass cultivated in Europe, feasibility studies (e.g. Bruton et al. 2009) and experimental farms are being established to advance the cultivation of kelps native to the region (including several research projects, e.g. AtSea 2015 [www.atsea-project.eu], EnAlgae 2015 [www.enalgae.eu], MAB3 2015 [www.mab3.dk]).

As habitat-forming species and primary producers, kelps are often considered to be important parts of the ecosystem and providers of ecosystem services. The values of the kelp-associated ecosystem services (products, climate regulation, education, tourism, aesthetic) are currently not well quantified (Costanza et al. 2014). In contrast, there is an extensive literature on the species found living associated with kelps (e.g. Sloane et al. 1957, Schultze et al. 1990, Christie et al. 2003). The holdfast is generally found to host more species than other parts of the kelp (Jones 1972, Moore 1972, Thiel & Vásquez 2000, Arroyo et al. 2004). The relatively high biodiversity of the holdfast is thought to reflect the benefits of a more complex physical structure (the spaces within the holdfast as compared to relatively smooth stipes and fronds), a more sheltered and sediment-rich local environment and the longer time available for colonization when compared to annually renewing parts of the kelp, like fronds (Christie et al. 2003, 2007). Species composition of associated fauna have been found to be affected by differences in habitat architecture and size of other macrophytes (Knowles & Bell 1998, Christie et al. 2009).

Any increase in kelp farming will create new habitat for the associated species, potentially altering the richness and function of the areas where farms are sited. The majority of work conducted into the impact of seaweed cultivation on surrounding environments has been conducted either in tropical waters e.g. Zanzibar, East Africa (Eklöf et al. 2005) or with other seaweed species e.g. *Gracilaria* in Chile (Buschmann et al. 1996). The impacts of kelp cultivation in temperate seas are not greatly represented in the literature. However, the UK Crown Estate commissioned a report to understand the effects of large-scale seaweed farming off the west coast of Scotland (Aldridge et al. 2012). Using ecosystem-based modelling techniques Aldridge et al. (2012) concluded that the effect of seaweed farming on nutrient concentrations is expected to be 'marginally significant'; this conclusion reflects a focus on the effects of nutrient removal on plankton productivity, and the effects of habitat creation were not investigated. Studies on the impacts of aquaculture have often focused on a relatively narrow range of

pressures, although see Huntington et al. (2006). Evaluating the impact of seaweed aquaculture may be difficult as operations can be in areas away from the natural habitat and ecological reference points are not well defined. Although several of the pressures identified by Huntington et al. (2006) potentially associated with seaweed aquaculture have yet to be characterised, the creation of novel seaweed habitat represents a further process that requires consideration.

Observations of the fauna growing on existing seaweed farms suggest that both the longline infrastructure and the growing kelps may function as a habitat or refuge for a number of species (M. D. Edwards pers. obs.). There are, however, at least 3 reasons why the cultivated habitat may not act simply as an extension of existing kelp habitat for the associated species. (1) The holdfast morphologies of wild and cultivated kelp differ. Wild kelps tend to grow a characteristic flat or slightly conical holdfast when attached to rock (Fig. 1a). Cultivated kelps are seeded onto ropes for growth, resulting in a different morphology, formed by intertwined haptera (Fig. 1b). Such differences in the arrangement of space within holdfasts are thought to affect the associated community (Vasquez 1993, Tuya et al. 2011). (2) Depending on culture practices, kelp may be seeded fresh to rope for each growing season, so cultivated holdfasts are younger, on average, than those from wild stands. (3) Finally, cultivated kelp are suspended from ropes in the water column; this will alter both the hydrodynamic environment (discussed as an influence on epifauna by Moore 1972) and the accumulation of sediments thought to provide the bulk of carbon supply to the associated species (Schaal et al. 2012). Changing from a benthic to a suspended growth form may also alter the environmental conditions experienced by kelp epifauna: changes in depth (Coleman et al. 2007), salinity (Jones 1973), oxygen availability (Scarratt 1961), and temperature (Scarratt 1961). Ecological processes may also be altered between benthic and suspended growth forms. Potential changes include variations in the presence of structural epibiota e.g. sponges (Smith 1996, Anderson et al. 2005a), changes in predation pressures on the communities (Vasquez 1993, Dumont et al. 2011) and variation in recruitment associated with dispersal abilities of adults and larvae (Edgar 1987, Thiel & Vásquez 2000, Norderhaug et al. 2002). To emphasize the differences in habitat between the wild and cultivated holdfasts, we refer to wild holdfasts as benthic holdfasts and cultivated holdfasts as suspended holdfasts. But it is important to note that this is not the only difference between the 2 holdfast types.



Fig. 1. Morphology of (a) benthic and (b) suspended *Laminaria digitata* holdfast

This study set out to test whether the differences in habitat and growth form of suspended kelp result in a holdfast fauna that is different from benthic stands. Studies of holdfast fauna emphasize that the patterns of species richness and abundance depend on the volume of space in the holdfast (e.g. Anderson et al. 2005a). We therefore included habitat volume as a covariate in statistical analyses of community structure. The goals of this study were, firstly, to test the difference in species richness and abundance between benthic and suspended *L. digitata* holdfast communities. Secondly, to put samples from the west of Ireland in a broader context, the patterns were compared to holdfast–richness relationships generated in comparable studies from the NE Atlantic. Multivariate tests were conducted on benthic and suspended holdfasts to assess differences in species composition. Furthermore, to assess the functional roles of the 2 holdfast types, differences in feeding strategies of their associated fauna were compared.

MATERIALS AND METHODS

Study sites

Laminaria digitata (Hudson) J.V. Lamourx holdfasts were collected at Mweenish Island, Galway, on the west coast of Ireland; from an established suspended longline structure and from the closest accessible stand of natural *L. digitata* (Fig. 2). Both locations were moderately exposed with southwest winds, situated approximately 10 m offshore, with a tidal range of 2.5–5 m. The suspended site (53° 18' N, 9° 53' W), at Ard Bay, held a single longline structure (Fig. 3) over sandy substratum, in water depth of approx. 8 m at mean low water spring tide (MLWS). The 60 m longline structure consisted of a header rope suspended approx. 1 m below the sea surface by buoys and kept in position by anchor ropes and 500 kg weights at either end. Polypropylene dropper ropes (10 mm diameter, 3 m in length) with 1 kg weights were seeded with juvenile *L. digitata* sporophytes and suspended from the header rope 2 m apart. Dropper deployments were made in November 2010 and January 2011. The benthic site of natural stands of *L. digitata* (53° 17' N, 9° 51' W) was approximately 200 m long, on rocky substratum and in a water depth of 2 m at MLWS.

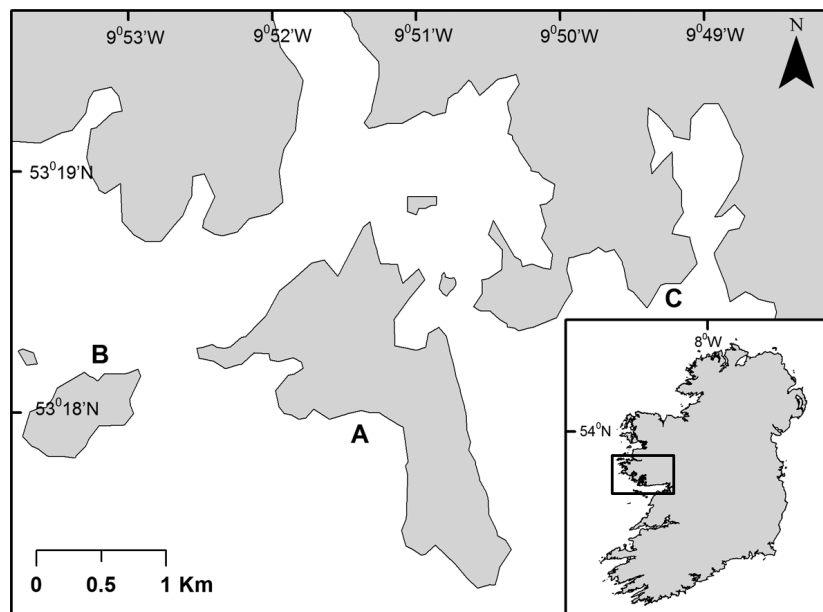


Fig. 2. Location of sampling sites at Mweenish Island, Galway, Ireland. A: benthic sampling site; B: suspended longline sampling site in Ard Bay; C: location of Ryan Institute's Carna Research Laboratory

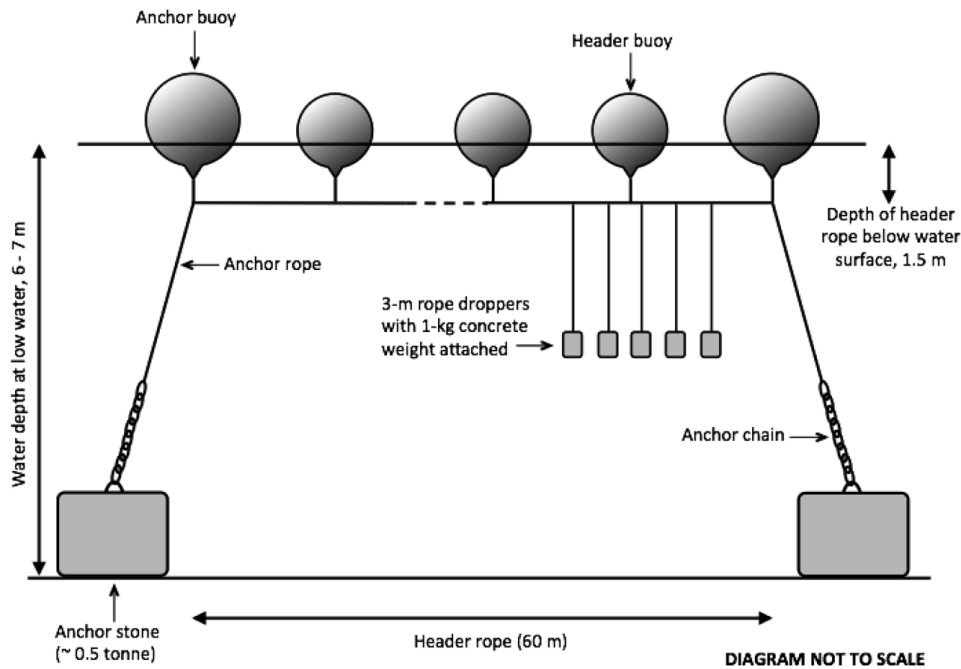


Fig. 3. Schematic of suspended longline structure in Ard Bay

Sampling protocol for the benthic and suspended *L. digitata* populations

Samples were taken using SCUBA on 20th October 2011 for the benthic samples and on the 4th November 2011 for the suspended samples. Five random *L. digitata* individuals in 5 replicate areas ($n = 25$) within the benthic site were collected using a mesh bag (1 mm mesh size). The entire plant was enclosed in the bag, the holdfast of the individual was pried away from the substratum using a dive knife and enclosed in the bag which was secured using string. At the suspended site, 5 dropper ropes from both deployment dates (November and January, $n = 10$) were collected using open-ended mesh bags (1 mm mesh size). The bag was slipped over the middle 1 m section of each dropper enclosing entire kelp plants and secured using string, taking care not to disturb the fauna. Unfortunately, it was not possible to remove the stipe and frond material from the suspended holdfasts during sampling as this would involve cutting fronds from suspended holdfasts while diving, potentially losing dislodged animals. All stipe and frond material was therefore collected in the field for both benthic and suspended holdfasts so that both treatments were comparable. Both the benthic and suspended samples were transferred back to the nearby laboratory (Fig. 2) and processed within 8 h. The benthic samples were removed from the mesh bags and the holdfast was cut at the base of the stipe

using a scalpel and measurements were taken to calculate habitat volume (described below). The suspended samples were removed from the mesh bags and a 10 cm rope section of continuous holdfast material was excised (Fig. 1b) from the 1 m dropper section. The fronds and stipes were removed leaving only the 10 cm section of holdfast biomass; individual holdfasts could not be removed as the morphology of suspended holdfasts mean the haptera grow intertwined with each other. The rope substratum was removed and measurements were taken to calculate habitat volume (described below). After all measurements were taken both benthic and suspended holdfasts were stored in sealable plastic bags containing 70% ethanol until further processing.

Habitat volume measurements

To compare holdfast communities a standard unit of habitat volume was used, i.e. the volume of space within the holdfast haptera available for colonisation by epibionts. There are 2 main methods used to measure the habitat volume; these methods were compared to investigate whether results from different studies are comparable. The first approach is an algebraic method described by Jones (1971) and the second uses displacement to calculate habitat volume, described by Sheppard et al. (1980) and used more recently by Blight & Thompson (2008). A metho-

dological miscalculation was discovered in both methods (Jones 1971, Blight & Thompson 2008) when calculating tissue volume; the tissue weight should have been *divided* by specific gravity and not multiplied as stated in the original texts. We compared the algebraic and displacement methods (adjusting for the miscalculation) using additional data obtained from Blight & Thompson (2008). Analysis of these data suggests that holdfast volume can be compared across studies that use the algebraic or displacement methods (regression of volume [displacement] against volume [algebraic] is significant, $R^2 = 0.4556$). For our samples, the habitable volume of benthic and suspended holdfasts was calculated using the corrected Jones (1971) algebraic method. From the 10 cm suspended section, the holdfast volume was calculated by treating the holdfast structure as rectangular cuboid in shape.

Sample processing

Holdfast samples were removed from bags and washed over large trays with freshwater. For both benthic and suspended samples, holdfast haptera were carefully removed with frequent pauses for collections of exposed fauna (Jones 1971). Haptera were rinsed with freshwater and the remaining contents in the trays and bags were washed over a 0.5 mm sieve and stored in 70% ethanol for later identification. All collected fauna were sorted from the residue and identified down to species level where possible using (Hayward 1988, Hayward & Ryland 2002), with taxonomy cross-checked (using WoRMS Editorial Board 2016), enumerated and stored in 70% ethanol.

Statistical analyses

Species richness and total abundance were compared across holdfast type (benthic or suspended) using holdfast volume as a covariate in ANCOVA. The optimal regression model, with homogenous slopes or heterogeneity of slopes (a holdfast type \times holdfast volume interaction), was found to minimise the value of the Akaike information criterion (AIC). To determine if the suspended samples from Ard Bay sown at different dates (November and January) could be pooled, the data were initially analysed separately from benthic samples. The relationship of seeded date and species abundance and richness was tested using ANCOVA with habitat volume as the covariate.

Following the determination of whether sowing date should be kept as a separate independent variable, data from this study (benthic and suspended *L. digitata*) were compared to natural stands of *L. digitata* and *L. ochroleuca* sampled off the southwest coast of England near Plymouth (Blight & Thompson 2008). Algal counts were removed from the Plymouth data set as we did not enumerate algae. Other potential sources of northeast Atlantic holdfast richness and abundance data could not be compared directly as the studies did not present the data in a comparable form or the definition of holdfast volume was different. If suspended holdfasts represent similar habitat to epifauna as benthic holdfasts, then there were expected to be few differences in slope of richness against holdfast volume and no differences in intercept value. Unfortunately, the Blight & Thompson (2008) study scored species presence-absence, so direct comparisons of abundance cannot be made. However, comparison of benthic and suspended holdfast abundance was possible.

Alongside differences in species richness and abundance, the differences between the assemblage structures of fauna from benthic and suspended holdfasts from Ireland were compared with a multivariate test. A Simpson's dissimilarity matrix was generated from the presence-absence data for the 2 treatments (1 benthic [5 levels] and 1 suspended [2 levels; November and January]) using the PopTools (Hood 2014) add-on in Excel. Simpson's dissimilarity has the advantage that it only measures the turnover of species and is not affected by changes in species richness between samples (Baselga 2010). This makes dissimilarities measured by Simpson's index easier to interpret than in the case for indices that mix the turnover and species richness components of dissimilarity (e.g. Sørensen's index). MDS (Shepard 1962, Kruskal 1964a,b) ordination was carried out using PRIMER V6®, giving the position of each holdfast in 2-dimensional space based on its species composition. Nested ANOSIM was used to test for differences between the faunal assemblages of the holdfast types and between spatially (benthic) or temporally (suspended) separated samples within holdfast type. Post-hoc results were pooled for a summary representation of differences between groups. Expected number of species for rarefaction analysis was also conducted using PRIMER V6®.

To test for an effect of holdfast type on the functional roles of associated species, fauna were grouped into categories based on their feeding strategies: suspension feeder, deposit feeder, carnivore, herbivore, or omnivore. Where species spanned these catego-

ries, their predominant mode of feeding was recorded (Sheppard et al. 1980). Chi-squared analysis was used to test the hypothesis that feeding types were randomly associated with holdfast type (benthic or suspended). This chi-squared test involved a contingency table, although 4 of the expected values were <5. In a clarification of the rule of thumb that chi-squared is unreliable with expected values <5, Zar (1996) suggests that a better threshold is for the average expected frequency to be at least 6 when testing at 0.05 level of significance. For the chi-squared test presented in the current study, the average expected frequency was 9.4. The test was therefore considered reliable.

RESULTS

A total of 2434 individuals in 61 taxa over 42 families were identified: 1801 individuals from the benthic and 633 individuals from the suspended holdfasts. Nematodes, polychaetes and molluscs were the 3 most frequently found groups in the benthic holdfasts, and accounted for 48, 26 and 13% of abundance (number of individuals), respectively, whereas amphipods, polychaetes and decapods were the 3 most frequently found groups in the suspended holdfasts and accounted for 30, 27 and 16% of abundance, respectively. Thirty-one percent of all taxa were unique to benthic holdfasts including the sponges *Halichondria panicea*, *Hymeniacion perleve*, the polychaete *Prionospio multibranchiata* and the gastropod molluscs *Lacuna parva* and *Onoba semicostata*. Thirteen percent of all taxa were unique to suspended holdfasts including the decapod crustacean *Hippolyte varians*, the ascidian *Ascidia mentula*, and the polychaetes *Dasybranchus* spp. and *Nereimyra punctata*. A total of 58% of all taxa were common to both holdfast types. Where species are rare, presence in a particular type of holdfast may not be distinguishable from random placement. As species occur more frequently, random placement of individuals becomes an unlikely hypothesis for cases where all individuals are found in a single holdfast type. Random placement is an unlikely hypothesis for the exclusivity of *Hippolyte varians*, *Dasybranchus* spp. and *Nereimyra punctata* in suspended holdfasts (binomial test, $p < 0.05$). Similarly, the observations of *Prionospio multibranchiata* and *Hymeniacion perleve* in benthic holdfasts were too frequent for random placement to be a suitable hypothesis (binomial test, $p < 0.05$). A full list of species recorded, their abundance and the taxonomic level to which they

were identified is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/q008p157_supp.pdf.

Species abundance in suspended holdfasts was not affected by habitat volume or holdfast deployment date (habitat volume: $F_{1,7} = 1.69$, $p > 0.05$; holdfast deployment date: $F_{1,7} = 0.14$, $p > 0.05$; interaction was not fitted in the optimum model). Abundance data from suspended holdfasts from 2 different sowing dates were therefore pooled. In the ANCOVA comparing abundance–volume relationships between holdfast types, the number of associated individuals was related to habitat volume, but not the source of the holdfast (Table 1, Fig. 4). The pooled regression slope relating abundances to habitat volume had $R^2 = 0.4861$ and slope 1.19 (± 15.796 SE).

Species richness in suspended holdfasts was affected by both habitat volume and holdfast deployment date (habitat volume: $F_{1,7} = 6.54$, $p < 0.05$; holdfast deployment date: $F_{1,7} = 5.64$, $p < 0.05$; interaction was not fitted in the optimum model). Species richness values from *Laminaria digitata* sown in November and January were therefore kept separate for further analysis. The combined data for species richness showed evidence for an interaction between habitat volume and type (Table 2, Fig. 5). Species richness always increased with habitat volume, but the rate of increase and mean richness differed among benthic and suspended *L. digitata* and *L. ochroleuca*. Benthic *L. digitata* holdfasts from Plymouth were the most species-rich, followed by *L. ochroleuca*. For the material collected in the west of Ireland, suspended holdfasts were generally more species-rich than benthic holdfasts of an equivalent volume. Holdfasts sown in January were more species-rich than holdfasts sown 2 mo earlier in November considering their smaller volume.

Suspended *L. digitata* holdfasts held the same number of individuals as benthic holdfasts, but had more species in samples of equivalent volume. These patterns are reflected in rarefaction plots (Fig. S1 in

Table 1. ANCOVA data from *Laminaria digitata* number of individuals vs. holdfast types (benthic and suspended) with habitat volume as a covariate. *Significant difference at $p < 0.001$

Source	df	SS	MS	F	p
Habitat volume	1	48503	48503	28.93	<0.001*
Holdfast type	1	1467	1467	0.86	0.361
Error	32	54669	1708		
Total	34	104693			

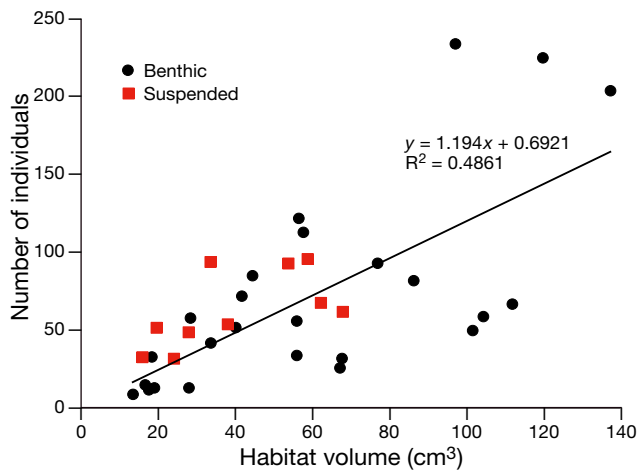


Fig. 4. The relationship between holdfast habitat volume and number of individuals per holdfast for benthic and suspended *Laminaria digitata*

the Supplement), with suspended holdfasts having more species per individual counted.

Some separation and clustering of epifaunal assemblages of *L. digitata* holdfasts can be seen for the 2 treatments (1 benthic [5 levels B1–B5] and 2 suspended (2 levels, November and January) in the MDS plot (Fig. 6). A stress value of 0.21 in the MDS indicates that the data are only partially represented by a 2-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 the benthic holdfast samples and the suspended November and January holdfast samples.

The nested ANOSIM indicated significant differences in assemblage composition among holdfast types: between sowing dates and between samples collected in separate areas of the natural kelp bed

Table 2. ANCOVA data from number of species vs. holdfast types with habitat volume as a covariate. There are 5 holdfast types: the *Laminaria digitata* and *L. ochroleuca* from the Blight & Thompson (2008) study benthic material collected in Ireland and 2 sowing dates of suspended *L. digitata* holdfasts from aquaculture longlines (present study). The 2 sowing dates were not pooled for species richness as a preliminary ANCOVA suggested inhomogeneity of slopes.

*Significant difference at $p < 0.05$

Source	df	SS	MS	F	p
Habitat volume (V)	1	11.3	160.02	10.64	0.002*
Holdfast type (T)	4	1425.82	8.60	0.57	0.684
V × T	4	245.47	61.37	4.08	0.006*
Error	55	827.35	15.04		
Total	64	2509.94			

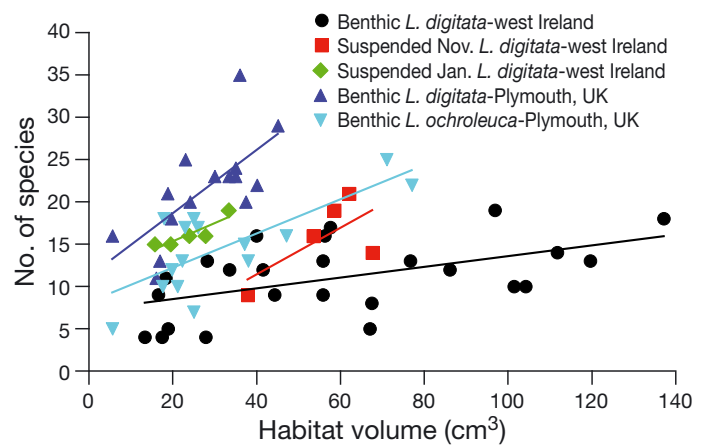


Fig. 5. The relationship between holdfast habitat volume and number of species per holdfast for Blight & Thompson (2008, Plymouth, UK) benthic *Laminaria digitata* ($r^2 = 48\%$, slope = 0.376, SE = 0.545) and benthic *L. ochroleuca* ($r^2 = 56\%$, slope = 0.202, SE = 0.262), and, from the current study (west Ireland), benthic *L. digitata* ($r^2 = 27\%$, slope = 0.063, SE = 0.164), suspended November *L. digitata* ($r^2 = 81\%$, slope = 0.276, SE = 5.019) and suspended January *L. digitata* ($r^2 = 45\%$, slope = 0.214, SE = 6.951)

sampled ($R = 0.383$, $p < 0.01$). There was also significant difference in structure between holdfast types ($R = 1$, $p < 0.05$). The R value of 1 indicates that all samples from suspended holdfasts were more similar to another suspended sample than they were to any benthic sample (and vice versa). The R values from post-hoc tests were pooled to summarise the pattern of pairwise differences between the 'within' groups of 5 samples (7 groups in total, 5 benthic and 2 suspended). There was a high dissimilarity between the

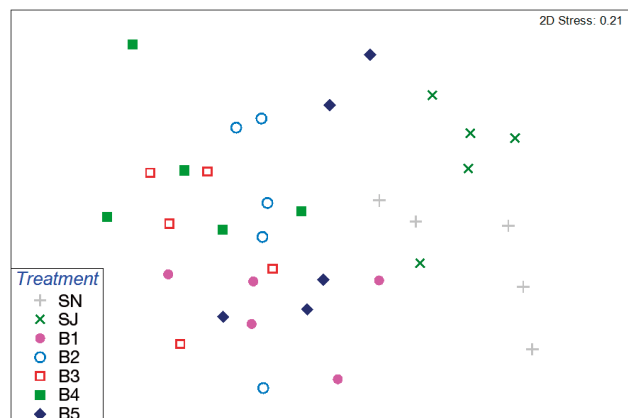


Fig. 6. Two-dimensional MDS plot of 35 holdfasts: 25 benthic samples (B1–B5, spatially separate locations in kelp bed) and 5 suspended samples (different droppers from longline) sown in November (SN) and 5 sown in January (SJ), based on presence-absence Simpson's dissimilarity matrix of faunal species collected from each holdfast

suspended samples from the November and January sowing ($R = 0.82$, no SE as only one comparison can be made), whereas the Benthic-Benthic pairs from separate areas of the same bed were relatively similar (mean $R = 0.29$, $SE = 0.030$). Benthic-Suspended pairs were generally quite different, as would be expected from the overall result (mean $R = 0.80$, $SE = 0.255$).

The differences in faunal assemblage across holdfast type did not seem to reflect any pattern of variation in categorization of feeding strategy (Table 3). The distribution of feeding types was not significantly different from a random allocation to holdfast types (chi-squared test, $\chi^2 = 3.161$, $df = 4$, $p > 0.1$).

DISCUSSION

Benthic and suspended holdfast fauna in comparison with other studies

Kelps collected in Ireland show a pattern where suspended holdfasts hold similar numbers of individuals for an equivalent habitat volume as benthic holdfasts, but the species richness was higher in suspended holdfasts. Although the distribution of feeding types did not change across holdfast types, there were differences in the structure of the associated assemblage (identified using multivariate tests). The relatively high richness in suspended holdfasts from Ireland was within the range of values observed from samples taken off Plymouth by Blight & Thompson (2008).

The results from Ireland can be compared to other studies to assess if the relatively low species richness recorded for benthic holdfasts was due to the low

Table 3. Number of epibiontic species in each feeding category for benthic and suspended *Laminaria digitata* holdfasts

No. of species	Benthic	Suspended
Suspension feeders	16	12
Deposit feeders	19	12
Carnivores	13	14
Omnivores	1	3
Herbivores	3	1

numbers of individuals sampled or other factors. Unfortunately, the Blight & Thompson (2008) study did not record individuals so the comparisons for abundance need to be drawn from elsewhere. Comparisons with previous studies are slightly complicated by the different methodologies employed for the measurement of volume: whether estimated as holdfast volume or habitat volume. To compare studies, we calculated the mean abundance per 10 ml of holdfast volume and the mean abundance per 10 ml of habitat volume (Table 4). This provides data that can be compared across studies using different denominators. Comparisons are also complicated by mesh size when sampling and the taxonomic resolution to which organisms were identified. For mesh size the studies we selected for comparison varied from 250 μm to 1 mm or were unreported, and the taxonomic resolution of these studies ranged from identification to species level or only specialist groups were identified, i.e. peracarid crustaceans studied by Thiel & Vásquez (2000). However, these differences show no patterns in the results calculated but should be further studied. Mean abundance per 10 ml holdfast volume for our benthic and suspended *Laminaria digitata* samples fell within the range of

Table 4. Comparison of mean abundance per 10 ml of holdfast volume or habitat volume across a number of studies from varying locations and varying kelp species (*L.*: *Laminaria*, *S.*: *Saccorhiza*, *E.*: *Ecklonia*, *M.*: *Macrocystis*). Range values given when differential samples from species, location and other factors were provided

Location	Species	Abundance per 10 ml holdfast volume	Abundance per 10 ml habitat volume	Study
West of Ireland	<i>L. digitata</i>	82.5	11.89	Present study, benthic
West of Ireland	<i>L. digitata</i>	51.26	17.54	Present study, suspended
Norway	<i>L. hyperborea</i>	17.75–63.1 ^a		Christie et al. (2003)
Northern Portugal	<i>S. polyschides</i>	79.93		Tuya et al. (2011)
Northern Portugal	<i>L. ochroleuca</i>	114.03		
New Zealand	<i>E. radiata</i>	47.67		Anderson et al. (2005a)
Australia	<i>E. radiata</i>	9.9–62.9		Smith et al. (1996)
United Kingdom	<i>L. hyperborea</i>		1.78–9.59	Jones (1971)
Chile	<i>L. trabeculata</i>	41.68		Thiel & Vásquez (2000)
Chile	<i>L. nigrescens</i>	44.97		
Chile	<i>M. integrifolia</i>	12.21		

^aExcluding Stn 1 outlier = 352.73

previous studies in Europe of kelps *L. hyperborea* (Christie et al. 2003), *Saccorhiza polyschides* and *L. ochroleuca* (Tuya et al. 2011), and from southern hemisphere studies, including *Ecklonia radiata* (Smith et al. 1996, Anderson et al. 2005a), and *Lessonia trabeculata*, *L. nigrescens* and *Macrocystis integrifolia* (Thiel & Vásquez 2000). Mean abundance per 10 ml habitat volume for our benthic and suspended holdfasts was compared with *L. hyperborea* (years 2–7) from the UK (Jones 1971) correcting for miscalculation (Table 4). We conducted the same comparison between studies but for mean species per 10 ml holdfast volume and per 10 ml of habitat volume (Table 5). Our *L. digitata* holdfast values again fell within the range of other studies, with Blight & Thompson (2008) holdfasts being more species-rich per 10 ml of holdfast volume, and our habitat volume values were similar when compared with other available studies (Jones 1971).

Overall, in the context of data from other studies, we can say that the relatively low species richness of our benthic holdfasts (as seen in Fig. 5) is not likely to be a sampling artefact from material with a particularly low abundance of individuals, as our values for mean species and abundance per 10 ml of holdfast and habitat volume are within the bounds of values from previous authors.

Composition of fauna

The 3 most dominant groups, in terms of abundance, in benthic holdfasts were nematodes, polychaetes and molluscs and, for suspended holdfasts, the dominant epifaunal groups were amphipods, polychaetes and decapods. These results agree with previous studies of the Laminariales from European

waters including Blight & Thompson (2008) from the UK and Christie et al. (2003) from Norway, Tuya et al. (2011) from Portugal; also from the Southern Hemisphere, Smith et al. (1996) found that amphipod crustaceans and polychaete worms accounted for 78% of the total number of organisms counted in *E. radiata* holdfasts sampled in Australia, and Włodarska-Kowalczyk et al. (2009) found dominant taxa in the dominant kelp species in the Arctic were polychaetes, molluscs and amphipods. Although nematodes were present in these studies, they were not a dominant group as found in our benthic samples. The presence of nematodes can suggest a source of organic pollution (Platt et al. 1984); however, this is unlikely as Ard Bay is situated in a sparsely populated area in west Galway. There may be nematode population increases in response to transient resource availability in the present study as increased detrital food source after kelp die back in autumn (Krumhansl & Scheibling 2012). Moore (1971) studied the nematode fauna of kelp holdfasts in the UK and found, among other species, omnivorous species that exploited the sediment-feeding niche provided by holdfasts. Nematodes were found in less abundance in suspended holdfasts, which could be due to the different hydrodynamic environment around these suspended holdfasts, inhibiting the accumulation of detrital material within. Juvenile decapods were a dominant group in our suspended holdfasts and, although present in other studies (Christie et al. 2003, Tuya et al. 2005), they were generally not found to be dominant in previous work (but see Ojeda & Santelices 1984). Decapods are omnivorous and may prefer increased water flow on the suspended holdfasts, which are suspended in the water column compared to benthic holdfast on the seabed.

Table 5. Comparison of mean species per 10 ml of holdfast volume or habitat volume across a number of studies from varying locations and varying kelp species (*L.*: *Laminaria*, *E.*: *Ecklonia*, *M.*: *Macrocystis*). Range values given when differential samples from species, location and other factors were provided

Location	Species	Species per 10 ml holdfast volume	Species per 10 ml habitat volume	Study
West of Ireland	<i>L. digitata</i>	16.21	2.41	Present study, benthic
West of Ireland	<i>L. digitata</i>	14.04	4.96	Present study, suspended
SW England	<i>L. hyperborea</i>	32.85		Blight & Thompson (2008)
SW England	<i>L. ochroleuca</i>	20.04		
Norway	<i>L. hyperborea</i>	0.61–1.58 ^a		Christie et al. (2003)
New Zealand	<i>E. radiata</i>	7.17		Anderson et al. (2005a)
United Kingdom	<i>L. hyperborea</i>		0.42–5.99	Jones (1971)
Chile	<i>L. trabeculata</i>	8.55		Thiel & Vásquez (2000)
Chile	<i>L. nigrescens</i>	10.73		
Chile	<i>M. integrifolia</i>	5.25		

^aExcluding Stn 1 outlier = 37.27

Although the most dominant groups vary slightly between studies, their contribution as a proportion of overall epifaunal abundance varies considerably; probably due to species, location and time of sampling. Smith (2000) found that, regardless of kelp species, the same functional groups tend to dominate. Polychaete worms and peracarid crustaceans are the most abundant, with molluscs, decapod crustaceans, echinoderms and ascidians providing the majority of the additional taxa (Smith 2000). The fauna found in our suspended samples was not functionally dissimilar to that in natural kelp beds.

Do species richness and abundance increase as habitat volume increase?

Our results show that the epifaunal abundances and species richness increase when habitat volume within the holdfast increases, agreeing with other studies (Ojeda & Santelices 1984, Smith et al. 1996, Thiel & Vásquez 2000, Blight & Thompson 2008, Tuya et al. 2011). However, our data did not reach a plateau as found in Anderson et al. (2005a) who suggested that encrusting species increase in size over time as holdfasts age and may decrease the overall space within the holdfast. No difference in age or size between organisms inhabiting the farmed and benthic holdfasts was observed. Although standardization of the age of *L. digitata* was not possible, as *L. digitata* cannot be aged accurately, no exceptionally large holdfasts were observed or sampled in our benthic kelp populations. We estimate the benthic holdfasts to be between 3 and 5 yr old in comparison to suspended holdfasts that were 11–13 mo old. Thus, age of the holdfasts did not seem to affect the size of the individuals inhabiting them, e.g. smaller individuals were not found on the younger suspended kelps. For future studies with kelp species that can be accurately aged, e.g. *L. hyperborea*, standardization should be employed when comparing holdfasts.

Holdfast as sampling unit

Kelp holdfasts represent a discrete sampling unit which is easily collected and which have been used by many studies for the purpose of monitoring pollution (Jones 1971, Moore 1971, Sheppard et al. 1980, Smith 1993), stress (Smith 2000) and evaluating patterns of biodiversity at different taxonomic resolutions in marine ecosystems (Anderson et al. 2005a,b). Fauna in kelp holdfasts often have higher species richness and abundance compared to other adjacent

habitats and kelp forests offer uniform habitats across large spatial scales; these are just a few of the advantages of using kelp holdfasts as a sampling unit (Smith 2000).

However, as is clear from attempts to synthesize the literature, problems occur in the definition of volume when comparing different studies, i.e. holdfast volume vs. habitat volume. Standardization is needed across all future studies with habitable volume (space available for colonisation by fauna within holdfast) being our preferred method. Holdfast volume and habitat volume are correlated (data from correlation for benthic holdfasts, $R^2 = 0.81$; for suspended holdfasts: $R^2 = 0.87$). However, habitable volume is more logically consistent as its use avoids possible issues in deciding where the stipe should be cut, which is an important measurement in holdfast volume. Habitable volume is also a more reasonable measure to use, as the indirect nature of holdfast volume as an estimate of habitat can cause problems when correlation does not hold, e.g. comparison across different holdfast morphologies. Further, care must be taken not to continue to use Jones' (1971) miscalculation for tissue volume. In addition to defining holdfast/habitat volume, other issues arise when using holdfasts as a sampling unit, including variations in the age of the holdfasts sampled (which should be standardised where possible) and the process of separating the stipe and frond material from the holdfast. Most studies remove the stipe and holdfast before collection of the holdfast (but see Thiel & Vásquez 2000, Włodarska-Kowalczyk et al. 2009). Separation of stipe and holdfast at the time of sampling seems the least likely to introduce artefacts; however, for this study, we were unable to do so due to the major disturbance it would have caused to the suspended holdfasts, and benthic samples were therefore treated the same for comparison. Tuya et al. (2011) suggests that loss of animals during sampling is likely low since animals tend to attach to the holdfast in response to the detected disturbance. Observations of frond fauna suggest fronds are mainly dominated by sessile organisms such as hydroids and bryozoans and less mobile species, e.g. *Patella pellucida* and other gastropod species. Also, the stipes of *L. digitata* are smooth, unlike the rough *L. hyperborea* stipes; thus, epiphytes and their associated fauna are rare. For these reasons we suggest that collecting stipe and frond material along with the holdfasts may not have caused significant intra-sample confusion of attached fauna. Finally, both species identities and abundances should be recorded for deeper understanding and more robust comparisons between studies so

that richness per individual counted can be compared and rarefaction curves calculated.

Do cultivated kelps provide a novel habitat?

The evidence from this study suggests that suspended holdfasts represents a novel habitat for fauna which is different to the habitat provided by benthic kelp species. The species found on suspended kelps are not unexpected for benthic kelp populations. The multivariate differences, however, demonstrate that suspended kelps can complement diversity in an area to produce higher richness than that just provided by benthic kelp. This was a preliminary study of suspended kelp faunal communities with comparisons to the existing literature. It seems likely that site-specific characteristics will affect the degree of difference between suspended and benthic epifauna. Similarly, holdfast age and seasonal effects are likely to affect comparisons. In this respect it is remarkable that suspended kelp were only in the sea for 11–13 mo, but had higher species richness than adjacent holdfasts from an established kelp bed. Even though holdfasts have been shown to be the tissues hosting the highest richness and abundance of fauna on kelp (Jones 1972, Moore 1972, Christie et al. 2003), the stipe and frond faunal communities can host different assemblages in terms of composition and structure (Christie et al. 2003) and, thus, also need to be analysed. If the communities associated with suspended kelps were found to be beneficial to the ecosystem, different harvesting techniques could be employed to maintain the holdfast, stipe and some frond material to allow the community to continue to grow.

Causes of differences in faunal assemblages

As this is a preliminary study, the specific mechanisms that cause the difference in assemblage structure between the 2 holdfast types cannot be determined, however, the 3 main factors identified; morphology, age and habitat may help explain the variation in species richness. As seen in Fig. 1, the morphologies of the holdfasts are distinctly different. Tuya et al. (2011) found holdfast morphology to be the best physical predictor to explain variation in epifaunal assemblage structure between 2 holdfasts with different morphologies. Vásquez (1993) noted that in drifting *Macrocystis pyrifera*, without substrate limiting its vertical growth, the holdfasts acquire a cylin-

dric morphology. This, he suggests, could be a reason for differences in faunal diversity and density between drifting and attached holdfasts. As discussed above, the age of our benthic and suspended holdfasts varied considerably. Interestingly, Sheppard et al. (1980) found species richness increased for 3 different age classes of *L. hyperborea* holdfasts. Thus age should be studied as a possible factor to explain the differences in faunal communities. Change in habitat from benthic to suspended has many associated changes which could all cause variations in faunal communities. Changes in abiotic conditions, such as hydrodynamic environment (Moore 1972), sedimentation rates (Schaal et al. 2012), depth (Coleman et al. 2007), salinity (Jones 1973), oxygen availability (Scarratt 1961) and temperature (Scarratt 1961) are all associated with changes in kelp fauna. These factors could be measured relatively easily in the field to determine their degree of influence on suspended communities. The influences of habitat on ecological processes are a little more difficult to estimate. Dispersal abilities of fauna inhabiting benthic holdfasts can affect their ability to inhabit suspended holdfasts. Highly mobile organisms and those with pelagic larval dispersal rates will have a greater opportunity to inhabit and establish on suspended kelps. Other animals with direct development of offspring or low mobility rates may not be able to establish on the suspended holdfasts or may need more time. Thiel & Vásquez (2000) showed that the distribution of peracarid aggregations may be a consequence of their reproductive biology as they are brooders and juveniles recruit to the immediate vicinity of their mother and may stay and reproduce in the natural holdfast. *Fabricia stellaris* was found in our benthic holdfasts but was not present in our suspended samples and so could be an example of a species which was limited by its dispersal abilities, and could not reach the suspended holdfasts, as its offspring brood in the mother's tube and move very short distances (Hayward & Ryland 2002). As shown by Dumont et al. (2011) predation pressures on suspended structures may be considerably less than those of benthic habitats. Some species may thrive in suspended habitats but may not establish in similar benthic communities due to predation by other organisms.

Implications

This study identifies a habitat value associated with suspended kelp holdfasts as, although they hold similar numbers of individuals for equivalent volume

as benthic holdfasts, the species richness of macroinvertebrates was greater in suspended populations. The habitat may provide a structure for fauna to inhabit or act as a food source. The presence of an epifaunal assemblage suggests possible ecosystem services provided by seaweed farms that should be quantified. Ecosystem services are the goods and services provided by an ecosystem that benefit humans (Millennium Ecosystem Assessment 2005). In addition to biodiversity, seaweed farms may provide nursery grounds and protection from predators for juvenile invertebrates and fish similar to that of benthic kelp forests (Smale et al. 2013). Kelp also assists in the uptake of excess nutrients that cause eutrophication, reflected in the use of kelps for Integrated Multi-trophic Aquaculture (IMTA) (Neori et al. 2004, Troell et al. 2009). The filter feeding organisms attached to kelp may influence particulate and plankton concentrations by biofiltration. It is also possible that the deployment of seaweed lines could assist in habitat restoration by supplying spores and gametophytes where benthic kelp beds have been destroyed by anthropogenic impacts. The extent of such 'seeding' influences will increase with the time that longlines are left in the water. Harvesting practices are not yet harmonized and holdfasts and small fronds may potentially remain in place for some time after the blades are removed. The potential additional benefits need to be assessed and quantified, allowing a valuation of seaweed aquaculture beyond the basic price for the crop.

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