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Consistency and variation in the kelp microbiota: patterns of bacterial community structure across spatial scales

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Abstract

Kelp species are distributed along ~25% of the world's coastlines and the forests they form represent some of the world's most productive and diverse ecosystems. Like other marine habitat-formers, the associated microbial community is fundamental for host and, in turn, wider ecosystem functioning. Given there are thousands of bacteria-host associations, determining which relationships are important remains a major challenge. We characterised the associated bacteria of two habitat-forming kelp species, *Laminaria hyperborea* and *Saccharina latissima,* from eight sites across a range of spatial scales (10s of metres to 100s of km) in the northeast Atlantic. We found no difference in diversity or community structure between the two kelps but there was evidence of regional structuring (across 100s km) and considerable variation between individuals (10s of metres). Within sites, individuals shared few Amplicon Sequence Variants (ASVs) and supported a very small proportion of diversity found across the wider study area. However, consistent characteristics between individuals were observed with individual host communities containing a small conserved "core" (8-11 ASVs comprising 25 and 32% of sample abundances for *L. hyperborea* and *S. latissima,* respectively). At a coarser taxonomic resolution, communities were dominated by four classes (*Planctomycetes, Gammaproteobacteria, Alphaproteobacteria* and *Bacteroidia*) that made up ~84 % of sample abundances. Remaining taxa (47 classes) made up very little contribution to overall abundance but the majority of taxonomic diversity. Overall, our study demonstrates the consistent features of kelp bacterial communities across large spatial scales and environmental gradients and provides an ecologically meaningful baseline to track environmental change.

Introduction

Bacteria can be free living or form close associations with multicellular organisms. These associated bacterial assemblages form part of the wider “microbiome” (along with fungi, viruses and micro-eukaryotes), which strongly mediates the development and functioning of the host organism [1–3]. The host-bacteria relationship also influences acclimation and resilience to environmental stress and disruption can lead to dysbiosis, host disease and mass mortalities [4–7]. It is therefore becoming increasingly apparent that macro-organisms and their associated microbiota should be considered together as a single ecological unit known as the “holobiont” [8].

Host-bacteria relationships are dynamic and complex as microbial community structure is very responsive to stochastic and deterministic processes. These processes shift over environmental, geographic and evolutionary scales and, as such, deciphering ecologically meaningful associations from wider ecological noise is challenging. Attempts to achieve this have focused around describing “common-core” communities and such studies have been fundamental in identifying ecologically meaningful associations [9]. However, for most marine habitat forming species the necessary large-scale studies characterising the host-bacteria relationship over various environmental gradients are lacking.

Coastal marine ecosystems provide a wealth of ecological goods and services for human society [10]. The structure and functioning of these ecosystems is strongly mediated by habitat-forming foundation species (e.g., corals, mussels, seaweeds), which alter environmental conditions and elevate local biodiversity [11, 12]. In turn, the functioning of host foundation species is influenced by their associated microbiota and, as such, bacterial communities likely play a vital role in the healthy functioning of the wider ecosystem [13]. Given their importance, the role of foundation species in achieving conservation and restoration goals is increasingly recognised [14–17] and in turn it is increasingly clear this will also be dependent on a healthy host-bacteria relationship [18].

89 Kelps (large brown seaweeds belonging to the order Laminariales) are foundation species
90 distributed along around one-third of the world's coastlines [19, 20]. The forests they form are
91 fundamental wider ecosystem functioning and can represent some of the world's most
92 productive and diverse habitats [21, 22]. Like all seaweeds, the surfaces of kelp thalli
93 (hereafter 'plants') support dense bacterial communities, which are important in many aspects
94 of the host's biology, including metabolic function, nutrition and defence [23]. Moreover,
95 heterotrophic marine bacteria consume seaweed-derived compounds, providing a direct link
96 from primary to secondary production [24, 25] and may underpin a major pathway in coastal
97 nutrient cycling [26]. Therefore, describing the kelp-bacteria relationship is a critical step
98 towards understanding the wider coastal ecosystem. Recent studies have shown that bacterial
99 communities shift with host anatomy [27], across environmental gradients [28, 29], and
100 evidence from Australia demonstrated continental-scale structuring, high community turnover
101 and a small conserved core [30, 31]. However, our understanding in seaweeds still lags
102 considerably behind that of other benthic habitat formers (e.g., sponges and corals) and large-
103 scale multi-species studies are distinctly lacking for other kelp species and systems.

104 Along most of the Northeast (NE) Atlantic coastline, the kelps *Laminaria hyperborea*
105 (Gunnerus) Foslie 1885 and *Saccharina latissima* (Linnaeus) are the dominant foundation
106 species in shallow subtidal rocky habitats. Although these species have distinct environmental
107 requirements and occupy different niches, they co-exist in many coastal habitats [32] and
108 underpin productive and diverse ecosystems [33, 34]. Bacterial communities associated with
109 both species have been described previously but research has either been conducted in a
110 single location [35–37] or across a small-scale local environmental gradient [28]. Here, we
111 take a spatially structured approach to examine the bacteria-host relationship in both species
112 across a latitudinal gradient of ~ 9° in the United Kingdom, at scales from ~ 3 m to ~ 1000 km.
113 In doing so, we aim to determine i) at what scales host-bacteria relationships are structured
114 and ii) identify signatures of stability over spatial scales and between different hosts.

115

Methods

Sampling approach

Sampling followed a nested hierarchical approach based on four established study regions with two sampling sites nested within each region (Figure 1). Adjacent regions were 180 – 500 km apart, spanning a gradient of 9° in latitude (~1000 km) [38]. Sites within each sampling region were 2 – 10 km apart. The physical and biological attributes of these kelp forests sites has been previously described [39, 40]. In summer (August/September) 2015, 7 – 8 mature canopy-forming individuals of *Laminaria hyperborea* and *Saccharina latissima* were selected at random at a depth of 2 – 4 m (below chart datum) from each site. Individual plants were positioned at least 3 m and up to 10 m apart from one another, within the same continuous patch of kelp habitat. Sampled individuals were brought to the surface where an area of 24 cm^2 of tissue was excised from the basal section of the blade, above the meristematic area (i.e., ~ 10 cm above blade/stipe junction). Whilst seawater controls were not taken, studies have consistently shown seaweed surface communities to be distinct from those of the wider seawater environment [27, 29, 37, 41, 42]. The tissue was rinsed with sterilised seawater for 30 s to remove contamination of seawater DNA, and then scraped with a sterile razor blade. The sampled biofilm was placed in a 1.5 ml Eppendorf and stored at - 80 °C. DNA was extracted using Qiagen DNeasy Powersoil kits following the manufacturer's instructions. Library preparation and sequencing (MiSeq, Illumuna, San Diego, CA, United States) of the V4 region of the 16S rDNA gene using primers (515f - GTGCCAGCMGCCGCGGTAA + 806r - GGACTACHVHHHTWTCTAAT) was conducted by StarSEQ (StarSEQ GmbH, Mainz, DE) following an optimised protocol of [43]. At least one negative PCR control was run on each plate and demonstrated runs were free from contamination.

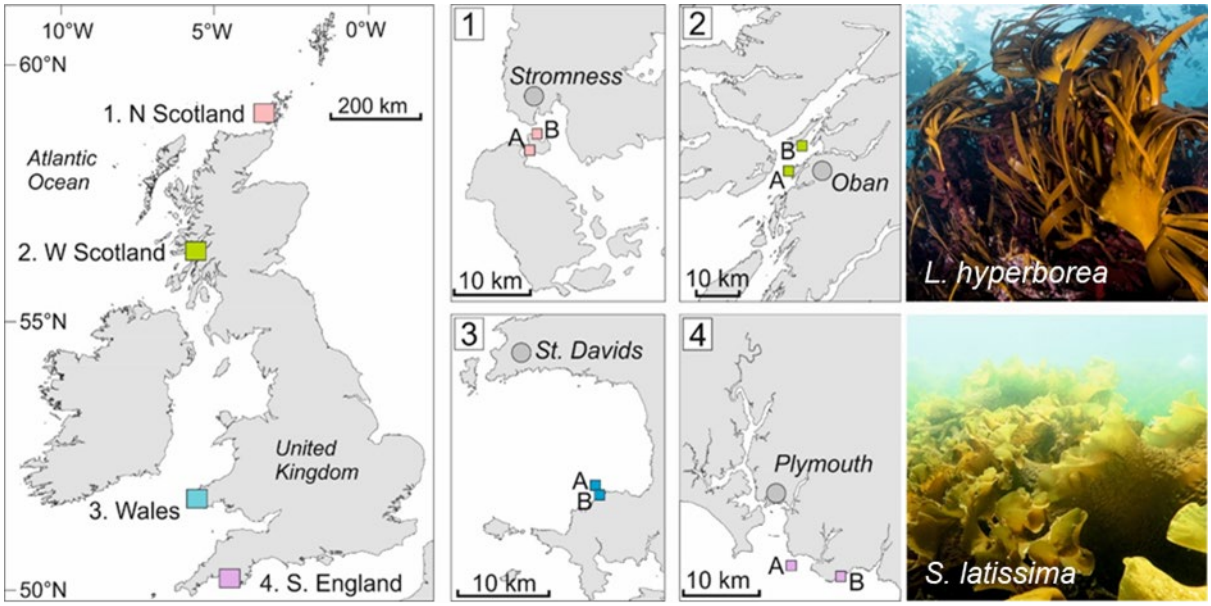

Figure 1. Map of study area showing position of four main study regions in the UK (left) and inset maps 1-4 indicating positions of paired sites (A + B) within each region (centre). Representative individuals of the host kelps *Laminaria hyperborea* (top right) and *Saccharina latissima* (bottom right) are also shown.

Sequence processing

All processing and analysis was conducted in the r statistical environment. Paired-end reads were processed according to the BIOCONDUCTER workflow [44]. Sequences were trimmed and truncated using the "filterAndTrim" function in DADA2 with the following parameters: truncLen, f= 240, r = 160; truncQ = 2; trimLeft, f = 20, r = 19, to remove primers and low quality reads. Amplicon Sequence Variants (ASVs) were resolved using DADA2 [44]. Chimeric sequences were removed using the "removeBimeraDenovo" function in DADA2. Sequence taxonomy was assigned using the RDP naïve Bayesian classifier against the SILVA release 132 database [45] using the "assignTaxonomy" function in DADA2. Sequence read counts, taxonomic assignments and metadata were assembled as an object in the r package "PHYLOSEQ" and was used in downstream analysis [46]. Samples containing < 10,000 reads, taxa contributing < 0.01% of the reads in the dataset and ASVs identified as mitochondria or chloroplast were then removed from the PHYLOSEQ object. Sequence counts were then expressed as relative abundance (in proportion to the total sample count). Rarefaction curves of the processed reads were saturated, indicating good coverage of bacterial diversity (Figure

S1). Sequences are accessible through the EMBL database (accession no. PRJEB50679). ASV table and metadata are available at (https://doi.org/10.6084/m9.figshare.19453889.v1).

Statistical analysis

To account for differences in sequence depth between samples in alpha diversity estimates, the dataset was rarefied to the minimum sample depth, using the "rarefy_even_depth" function in "PHYLOSEQ". Alpha diversity for each sample was estimated through the Chao1 index [47] implemented through the "estimate_richness" function in PHYLOSEQ. The Chao1 index estimates ASV richness, and the standard error surrounding this estimate, based on the observed number of ASVs, the observed number of ASVs occurring only once, and the observed number of ASVs occurring only twice [47]. Alpha diversity was compared using a three-way Analysis of Variance (ANOVA). Model factors consisted of Species (fixed factor; two levels: *L. hyperborea*, *S. latissima*), Region (fixed factor; four levels: N Scotland, W Scotland, Wales, S England) and Site (random factor; two levels: A, B). Differences in community structure were determined using PERMANOVA [48] based on Bray-Curtis dissimilarity and implemented through the "adonis" function in the package "VEGAN" [49]. Model design was the same as that for alpha diversity. The percent variation explained by each model factor was quantified as the coefficient of determination (R^2), which is one minus the ratio of the within-group sum of squares to the total sum of squares. Differences in multivariate dispersion between assemblages were examined using the "betadisper" function in "VEGAN". A similarity of percentage (SIMPER) procedure was conducted in "VEGAN" to determine which taxa contributed the most to observed dissimilarities.

To examine and define the "core bacterial community" we analysed each host kelp species separately. We based the core at the ASV level and used a compositional dataset. There is no consistent definition of a "core" in the literature with authors setting prevalence thresholds from 50 – 100 %. Here, we used two tiers with prevalence thresholds of 95 % and 80 % (of the total dataset with all regions included) in order to determine those taxa that a strictly

associated with each species, whilst also being comparable with recent studies in kelp [31]. In both tiers, a relative sample abundance threshold of 0.1 % was used.

Results

In total, we sampled bacterial communities from 115 kelps, which resulted in 4493603 paired end reads with an average coverage of 39052 reads per sample. We identified 2824 ASVs spanning 29 phyla, 52 classes, 121 orders and 236 families (Table S1, Figures 2 + S2 - S4). The classes that made up the vast majority of bacterial abundance (~ 93%) were Alphaproteobacteria (25.6%), Gammaproteobacteria (24.0%), Planctomycetes (21.0%), Bacteroidia (13.1%), Cyanobacteriia (5.0%) and Verrucomicrobiae (4.4%) (Figure 2) (Table S1). The relative contribution of these classes was remarkably consistent between species, regions and sites (Figure 2). Even at a finer taxonomic resolution, the relative abundances of bacterial taxa remained notably consistent across hosts and spatial scales (Figure S2 - S4). At the family level, Pirellulaceae (19.4%), Hyphomonadaceae (15.7%), Saprospiraceae (6.9%), Rhodobacteraceae (5.7%) and Flavobacteriaceae (5.5%) were the most abundant (Figure S3, Table S1). Whilst the underlying taxonomy of ~ 30% of ASVs did not resolve down to the genus level, 52% of sample abundance was made up of just twelve genera (Figure S4, Table S1).

Alpha Diversity

Shared ASVs

Of the 2824 ASVs identified in this study (all regions combined), 1201 ASVs (42.5%) were shared between both *L. hyperborea* and *S. latissima* (Figure S5). When *L. hyperborea* and *S. latissima* were combined, 505 ASVs (17.8 %) were found across all study regions. When the two species were examined separately, *L. hyperborea* shared 356 ASVs (17.2 %) and *S. latissima* 366 ASVs (15.2 %) across all regions (Figure S5). Shared ASVs between individual plants at the site level was far lower. When both kelp species were considered together estimates ranged from 0.4 % (S England A) to 2.1 % (Wales A). When the two kelp species were considered separately, estimates for *L. hyperborea* ranged from 1.0 % (W Scotland A)

to 3.9 % (Wales B), while estimates for *S. latissima* ranged from 1.1 % (S England A) to 4.9 % (Wales A) (Table S2).

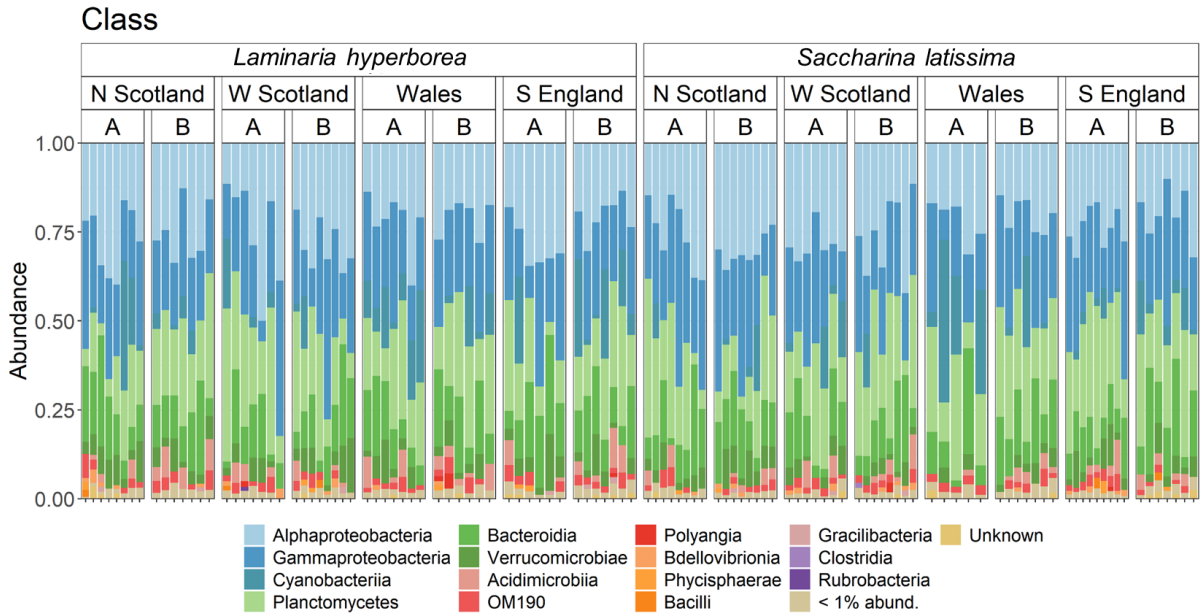

Figure 2. Relative abundance bacterial classes in the kelps *Laminaria hyperborea* (left) and *Saccharina latissima* (right) from four study regions (two sites A + B within each region) in the UK. Site locations can be seen in Figure 1. Classes that made a contribution of < 1% to overall study wide abundance were collapsed into a separate category. "Unknown" represents taxa where underlying taxonomy was not resolved.

Bacterial ASV richness (Chao1 index) was not significantly different between Species or Regions or their interaction (Table 1). Our study wide estimate of mean richness for both species combined was 179.8 ± 5.2 S.E, which ranged from 152.7 ± 11.20 S.E. (W Scotland A) to 214.3 ± 17.5 S.E. (S England B). For *L. hyperborea,* mean richness was 182.9 ± 8.3 S.E. and ranged from 147.3 ± 16.9 S.E. (W Scotland A) to 217 ± 26.1 S.E. (S England B) (Figure 3). For *S. latissima,* mean richness was 176.7 ± 7.4 and ranged from 158 ± 15.1 (W Scotland A) to 211 ± 25.3 (S England B) (Figure 3).

Table 1. Results of univariate (ANOVA) for alpha diversity and multivariate community structure (PERMANOVA) between Species, Regions and site variability within region.

	Alpha diversity (Chao1 index) (ANOVA)			Multivariate structure (PERMANOVA)			
	df	F	p	df	Pseudo-F	R^2	p
Species	1	0.66	0.42	1	0.81	0.01	0.64
Region	3	2.18	0.09	3	2.23	0.06	0.001
Species*Region	3	0.97	0.41	3	0.78	0.02	0.85
Species*Region(Site)	8	1.01	0.40	8	1.01	0.07	0.47
Residual	99					0.84	

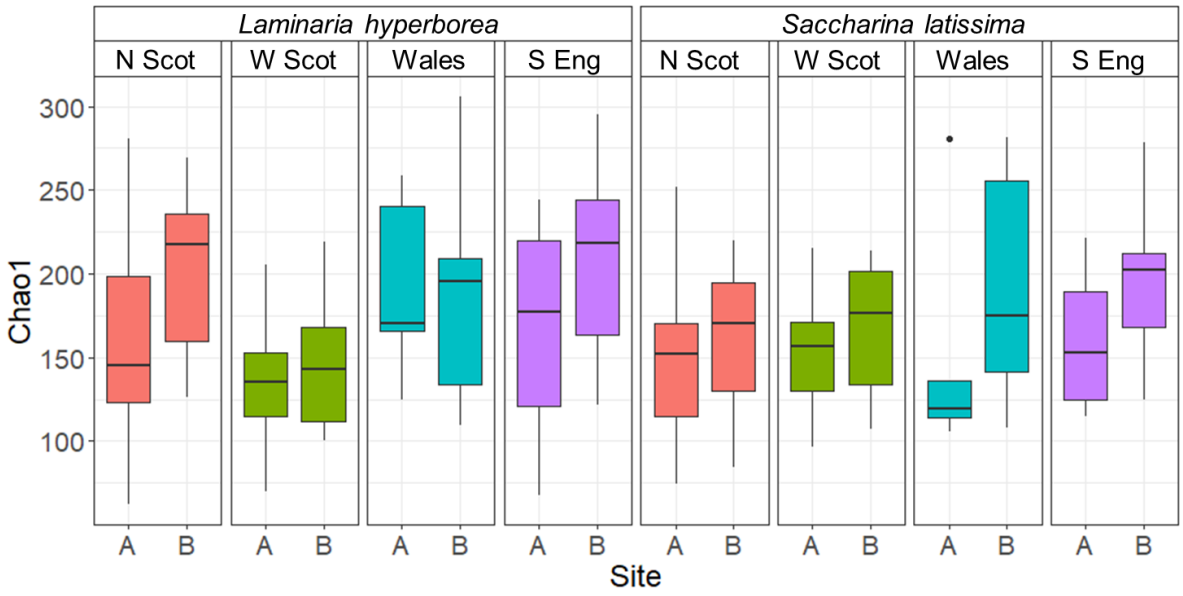

Figure 3. Box plots representing alpha diversity (Chao1 index) for bacterial communities associated with the kelps *Laminaria hyperborea* (left) and *Saccharina latissima* (right) from eight study sites in the UK. Site locations can be seen in Figure 1.

Core Community

Both species exhibited similar core bacterial communities. The first tier core (ASVs present in 95% of samples), consisted of the same five ASVs for both kelp species. These were ASV3: *Blastopirellula* sp., ASV8: *Hellea balneolensis*, ASV11: *Litorimonas cladophorae*, ASV14: *Litorimonas* sp. and ASV21 *Croceitalea* sp. (Figure 4). Together, these five ASVs made up 13.8 ± 0.9% and 13.7% ± 0.9% of the relative sample abundance for *L. hyperborea* and *S. latissima* respectively (Figure 4). The second tier core (ASVs present in 80% of samples) consisted of an additional six ASVs for *L. hyperborea* (11 total) and eight for *S. latissima* (13 total). This wider core made up 25.4 ± 0.9% and 32.7 ± 1.8% of the relative sample abundance for *L. hyperborea* and *S. latissima* respectively (Figure 4).

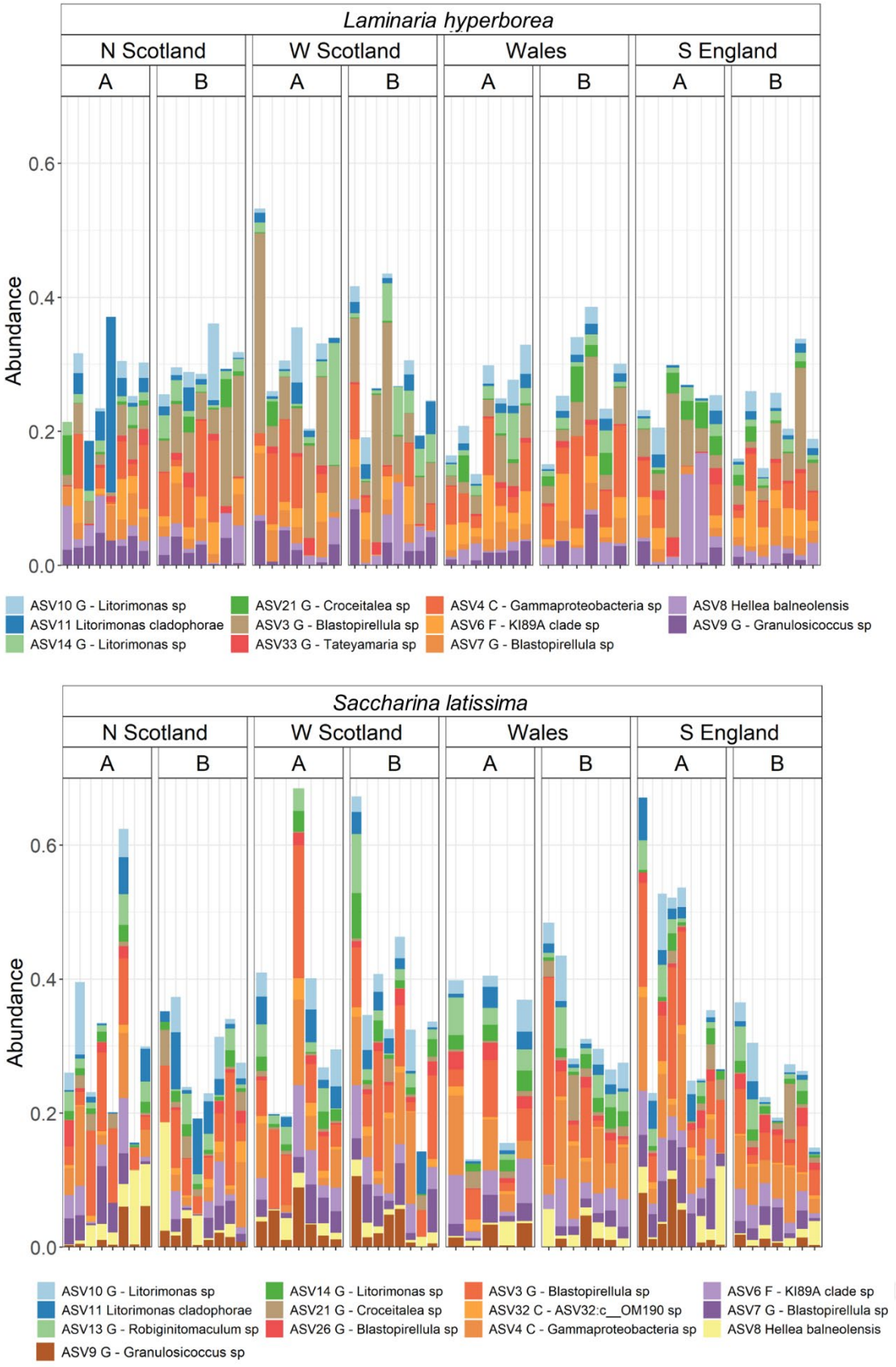

Figure 4. Relative abundance of the core bacteria community (defined at taxa present in > 80% of samples at a relative abundance > 0.1%) associated with the blade of the kelps *Laminaria hyperborea* and *Saccharina latissima*. Abundance is expressed as proportion of entire sample. Letter represents lowest resolved taxonomic rank C = Class, F = Family, G = Genus.

Community Structure

PERMDISP showed no significant differences in within-factor multivariate dispersion for either Species ($F_{(1, 119)}$ = 0.4, p = 0.5) or Region ($F_{(3, 117)}$ = 0.4, p = 0.8). PERMANOVA showed community structure varied significantly between regions but there was no significant effect of Species or within Region variability between sites. This pattern was consistent when analysis was performed at the higher taxonomic ranks of class and family (Table S3). Pairwise comparisons and nMDS visualisation showed Wales to be significantly different to N Scotland and W Scotland (Table 1, Figure 5). SIMPER analysis revealed the ASVs driving this difference were similar between W Scotland and N Scotland with only one different ASV in those contributing to 70% of observed dissimilarity (33 ASVs). Most notably, ASV5 – *Chroococcidiopsis sp.* (Phylum; Cyanobacteria) and ASV4 - Gammaproteobacteria (Phylum; Proteobacteria) were found in higher abundances in Wales, while ASV3 - *Blastopirellula* sp (Phylum; Planctomycetes) was found in greater abundances in N and W Scotland (Table 2). Regional structuring was evident but the magnitude of variance explained (R^2) by each model component showed that residual scales were the major contributor to overall variability. Here, 85% of variation remained unexplained (Table 1).

Table 2. SIMPER analysis on significant pairwise comparisons identified by PERMANOVA analysis. Presented taxa represent the top five that contributed most to the observed Bray-Curtis dissimilarities between comparisons. Letter represents lowest resolved taxonomic rank C = Class, F = Family, G = Genus.

Taxa	Average abundance		Average dissimilarity between comparisons	Dissimilarity / SD	Contribution (%) to dissimilarity	Cumulative contribution to dissimilarity (%)
	N Scotland	**Wales**				
ASV 5 (G) *Chroococcidiopsis*	0.021	0.069	0.037	0.77	5.1	5.1
ASV 4 (C) *Gammaproteobacteria*	0.037	0.059	0.024	1.40	3.3	8.4
ASV 3 (G) *Blastopirellula*	0.069	0.049	0.0223	0.96	2.8	11.2
ASV 20 (F) *Saprospiraceae*	0.007	0.031	0.016	0.78	2.6	13.8
ASV 24 (G) *Granulosicoccus*	0.008	0.032	0.015	0.71	2.1	15.9
	W Scotland	**Wales**				
ASV 5 (G) *Chroococcidiopsis*	0.031	0.069	0.036	0.78	5.0	5.0
ASV 3 (G) *Blastopirellula*	0.094	0.049	0.033	1.01	4.7	9.7
ASV 4 (*C*) *Gammaproteobacteria*	0.047	0.059	0.024	1.44	3.5	13.2
ASV 20 (F) *Saprospiraceae*	0.010	0.031	0.016	0.81	2.3	15.5

ASV 24 (G)	*Granulosicoccus*	0.005	0.032	0.015	0.68	2.2	17.7

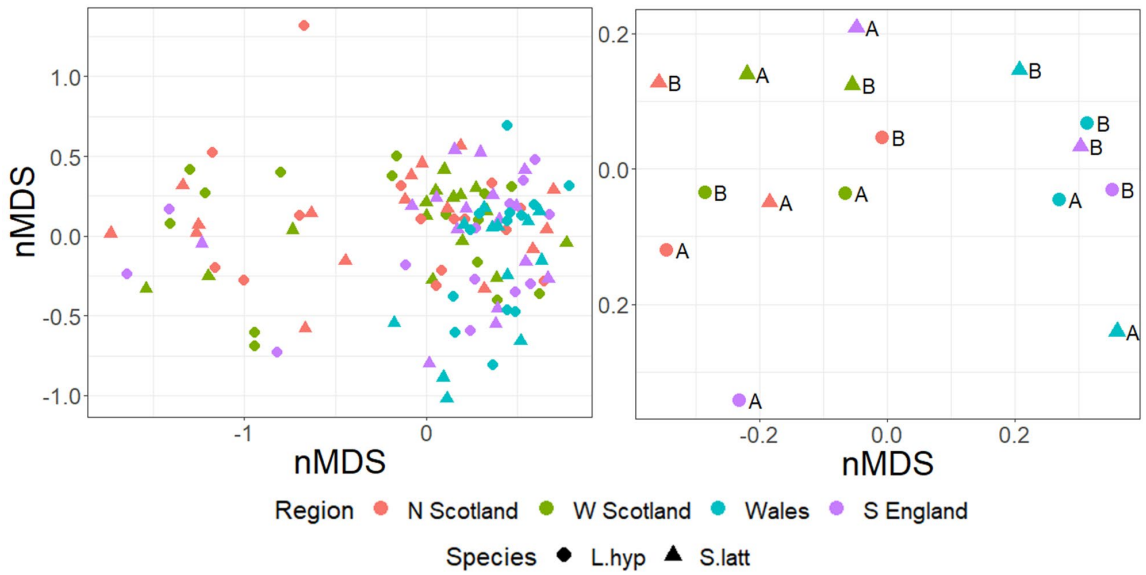

Figure 5. nMDS plots depicting the structure of bacterial assemblages associated with the kelps *Laminaria hyperborea* and *Saccharina latissima* from eight study sites in the UK. Symbols represent individual kelp communities (left) and site averages (right). Data are based on Bray-Curtis similarity. Site locations can be seen in Figure 1.

Discussion

Kelp are foundation species that play a disproportionately important role in the healthy functioning of the wider reef ecosystem [21, 50]. However, the dynamic and variable nature of its associated microbial community make it difficult to interpret. Here, we characterised this relationship in two sympatric kelp species over a range of spatial scales in the UK. We found communities were highly variable and differences between plants separated by 10s of metres was often greater than between hosts, sites or regions. However, despite this high inter-individual variation, consistencies and signals of stability were evident between the host species and across large geographic scales.

Variation across scales

The bacterial communities associated with seaweeds have been shown to be structured over a range of spatial scales, including microns [51], centimetres [27], tens [29], thousands [31] and tens of thousands of kilometres [52]. In the most geographically extensive study to date,

Bonthold *et al.,* (2020) explicitly examined the relative importance of different spatial scales across the distribution of the red alga, *Gracilaria vermiculophylla* (previously *Agarophyton vermiculophyllum*), on associated microbiomes. They found hierarchal structuring across all scales tested (10 - 10000 km) but processes operating at the site level (10's of kilometres) to be the most important source of variation. Some structuring was observed at a regional scale (100's km) but we did not observe any difference in community structure at the site level (10's of km). Instead, we saw greatest variability between individual plants. This is in contrast to other brown seaweeds, including kelp, that have found site level structuring [28, 29] and may be due to a relatively similar environmental conditions across sites, or greater connectivity overriding ecological drift.

The high levels of inter-individual variability is in contrast to bacterioplankton assemblages, which show strong and robust geographical patterns in community structure [53–55]. Whilst we do not have seawater comparisons, this suggests that host traits may play a stronger role in community assembly than patterns in the wider environment. The high variability between individuals also suggest a dominance of stochastic factors at the individual plant level. Burke et al., (2011) [56] proposed the "competitive lottery model", originally developed for the macroecology of reef fish [57], as a way of explaining the high variability between individual algal hosts. Here, different subsets of bacteria, from the wider environmental species pool, may have similar affinities for host traits and may provide similar suitable functions. However, the final taxonomic community structure will be dependent on the randomness of the initial colonisation. In our study, this may be exacerbated by the position of sampling on the host itself. We sampled the meristem, which is the area of new growth in both hosts and may represent an early stage in the bacterial succession trajectory. Indeed, previous studies have found species richness to increase and community structure to shift on older parts of the kelp blade [27, 29] and high variability between individuals where the meristem has been sampled [31]. This means variability could decrease on older tissue as there is more time for deterministic processes imposed by the host, site or region to take effect. However, given

growth of both kelp hosts is minimal in summer and autumn [32, 58] when our samples were collected, our bacterial communities do not represent “newly settled” communities.

Whilst the vast majority of variation was unexplained, some regional structuring was also evident. Specifically, differences were driven by bacterial communities in Wales being significantly different to those in North and West Scotland. The prevailing climate of our Wales sites is 2.5 °C (mean annual sea surface temperature) warmer than the northern cooler sites of N and W Scotland and temperature has been found to impact various aspects of kelp physiology and population structure across the same study site investigated here [38, 39]. However, given S England, which represents our warmest region, was not clearly differentiated from the cooler regions it is unlikely temperature alone is responsible for this structuring. A number of other regional scale factors have been associated with shifts in host-bacteria community structure including variation in salinity [29], wave exposure [28], turbidity [59], nutrient concentrations [31] and host genetic factors [60] and these could be responsible for driving regional differences observed here.

Signatures of Stability

Despite high between-host variation, consistencies were observed across all the spatial scales of our study. At a coarser taxonomic resolution, out of the 52 classes we observed, the vast majority of sample abundance was constrained to *Alphaproteobacteria*, *Gammaproteobacteria*, *Planctomycetes*, and *Bacteroidia*. Whilst we do not have appropriate environmental controls (seawater and other biofilms) to make direct comparisons, the consistently high abundance of *Planctomycetes* is interesting. This group have been found enriched in many seaweeds around the world, including *S. latissima* and *L. hyperborea* [36, 56, 61–64]. *Planctomycetes* have high numbers of sulfatase genes that can degrade agars associated with macroalgae providing them with resources [65]. The precise role of *Planctomycetes* for the host remains speculative but their consistent association across all scales tested here and more widely for seaweeds generally suggests they may play an

346 important role for the host. Ultimately, such an understanding will be gained as our knowledge
347 of Planctomycetal physiology increases and full genomes of taxa in this group become
348 available.

349 **Core community**

350 The “core community” concept aims to identify stable, functionally important taxa rather than
351 transient or opportunistic components of the community [66]. In this study, both kelp hosts
352 possessed a small core community that was similar in size and composition. The ASVs that
353 were present in > 80% of samples made up 25.4% (*L. hyperborea* – 11 ASVs) and 32.7% (*S.*
354 *latissima* – 13 ASVs) of the overall sample relative abundance, despite representing < 5 % of
355 the ASVs present in a typical plant. The stability of this core community contrasts with recent
356 attempts to characterise a common core in three species of green algae in the *Ulva* genus,
357 where taxonomic composition was too variable. However, such communities have been
358 effectively described in a range of other seaweeds [52, 67] and the size and composition is
359 comparable to estimates across large spatial scales in the kelp, *E. radiata,* in Australia [31].
360 Indeed, the core community associated with *E. radiata* is similar in size (15-55 taxa making
361 up 33-35% of relative sample abundance) and shares many taxa that form the core
362 communities of our two host species, including the genera *Blastopirerllula* (Planctomycetes)*,*
363 *Granulosicoccus* (Gammaproteobacteria) and *Hellea* (Alphaproteobacteria) [30, 31].

364 Many of our core taxa have been reported in association with seaweeds in systems and
365 species across the world [29, 36, 64, 67–70]. Such interspecific consistencies suggests that a
366 “core bacterial community” may encompass seaweeds more generally and particular taxa may
367 be associated with diverse host phylogenies even across large geographic scales. Whilst our
368 core community is based on taxonomy, the ecology and genome profiles of many ASVs
369 suggest they may be functionally important. Specifically, *Litorimonas* (3 core ASVs) may aid
370 in photosynthesis through oxygen detoxification and CO_2 evolution [71], while
371 *Granulosicoccus* are chemo-heterotrophic bacteria capable of reducing nitrate [68, 72].
372 However, further large-scale studies incorporating other hosts and a greater understanding of

their functional profiles are required before the ubiquity and utility of this core can be determined.

Outside of the four dominant classes and core-ASVs associated with each host, the remaining bacterial community was generally made up of classes with low diversity, abundance and only appeared in a small number of samples. This highly variable constituent of the bacteria community is likely reflective of both deterministic and stochastic processes operating within the reef environment and the interaction between plants, other organisms and the surrounding seawater. Shallow subtidal reef habitats are highly dynamic and influenced by a number of factors that vary across multiple scales, including wave exposure, light and nutrient availability, sedimentation rates and salinity fluctuations [73–75]. These factors may interact in a multitude of ways to influence bacteria communities found at any given time or host. Future studies using high-resolution *in situ* measurements of physical and biological variables will provide insights into the drivers of bacterial community structure.

Similarities between hosts

We observed no difference in community structure between associated bacterial communities of *L. hyperborea* and *S. latissima,* with these two hosts sharing 40% of observed ASVs. This is similar to the 37% of bacterial taxa shared between eight sympatric kelp hosts in British Columbia [42]. Moreover, many of the most diverse families observed in our study (e.g., Flavobacteriaceae, Saprospiraceae, Rhodobacteraceae) (Figure S3) have been identified as seaweed generalists [76]. Therefore, it may not be surprising that our hosts share a large proportion of bacteria taxa between them. The lack of structure may also be a product of similarities in the chemical and physical properties of the both kelp hosts [77], reflective of their recent evolutionary divergence [78]. Indeed, differences in bacterial community structure exist between other sympatric species from the three different algal lineages (red, green and brown algae) that have far greater evolutionary distance [63]. However, it is important to note that we sampled the meristematic region, which represents an early stage in the colonisation and

development of bacterial communities [28] and, as such, interspecific differences may manifest at later stages of bacterial succession.

In summary, kelp harbour thousands of bacterial associations but individual communities are largely constrained to four taxonomic classes and have a small conserved core at the ASV level. This was consistent across large spatial scales and between different host species and may be a common characteristic of kelp bacterial communities more generally. Given host-associated microbial communities are increasingly recognised for their role in mediating host resilience to environmental perturbations, and kelps are threatened by a range of stressors, these data provides critical insight into the stability of the healthy host-microbiome complex. Future studies documenting how the breakdown of this relationship may impact host condition may lead to robust microbial indicators of stress across large spatial scales.

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Author Contribution

PJM and DAS designed the experiment. NGK and JT conducted all laboratory work and analysis. NGK lead the manuscript preparation and all authors contributed equally to subsequent edits. All authors read and approved the final manuscript

Data Accessibility

Sequences are accessible through the EMBL database (accession no. PRJEB50679). ASV table and metadata are available at (https://doi.org/10.6084/m9.figshare.19453889.v1)

Statements and Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical Declaration No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted on unregulated kelp species.

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Supplementary Information

Table S1. Relative abundance and number of ASVs (nASV) per class, order and genus of 121 kelp samples (*L. hyperborea* and *S. latissima* combined) from eight sites in the United Kingdom. Taxa shown represent those contributing over > 1% to overall sample abundance.

Class	Relative abundance	nASV
Alphaproteobacteria	25.6	519
Gammaproteobacteria	24.0	482
Planctomycetes	21.0	105
Bacteroidia	13.1	612
Cyanobacteriia	5	36
Verrucomicrobiae	4.4	126
Acidimicrobiia	2.1	26
OM190	2.0	63
Order		
Pirellulales	19.4	75
Caulobacterales	16.4	51
Chitinophagales	6.9	161
Flavobacteriales	5.7	283
Rhodobacterales	5.7	85
Granulosicoccales	5.4	21
Verrucomicrobiales	4.4	104
Pseudomonadales	4.2	155
Cyanobacteriales	4.1	16
Microtrichales	2.1	25
Thiotrichales	2.1	19
Arenicellales	1.8	33
Planctomycetales	1.6	29
Unknown	12.9	
< 1 %	7.4	
Family		
Pirellulaceae	19.4	75
Hyphomonadaceae	15.7	40
Saprospiraceae	6.9	157
Rhodobacteraceae	5.7	85
Flavobacteriaceae	5.5	199
Granulosicoccaceae	5.4	21
Xenococcaceae	4.1	8
Rubritaleaceae	3.4	73
K189A clade	3.1	16
Microtrichaceae	2.1	24
Thiotrichaceae	2.1	19
Arenicellaceae	1.8	33
Rubinisphaeraceae	1.6	24
Unknown	13	

< 1%	10.8	
Genus		
Blastopirellula	17.9	46
Litorimonas	7.6	12
Granulosicoccus	5.4	21
Chroococcidiopsis	3.4	3
Hellea	3.0	2
Sva0996 marine group	2.1	14
Roseibacillus	2.1	28
Cocleimonas	2.0	12
Robiginitomaculum	2.0	4
Arenicella	1.7	21
Octadecabacter	1.4	5
Croceitalea	1.3	3
Unknown	27.9	
<1%	22.4	

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645 **Table S2.** Shared ASVs between all host plants (*S. latissima* and *L. hyperborea*) at study region and sites in the
646 United Kingdom.
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L. hyperborea* + *S. latissima				
Region	Site	Shared ASVs	Total Site ASVs	%
N Scotland	A	4	987	0.40
N Scotland	B	5	963	0.51
W Scotland	A	5	846	0.59
W Scotland	B	5	1014	0.49
Wales	A	19	897	2.11
Wales	B	16	951	1.68
S England	A	4	964	0.41
S England	B	22	1046	2.10
L. hyperborea				
N Scotland	A	9	671	1.34
N Scotland	B	11	709	1.55
W Scotland	A	6	581	1.03
W Scotland	B	8	701	1.14
Wales	A	26	716	3.63
Wales	B	26	670	3.88
S England	A	10	615	1.62
S England	B	26	749	3.47
S. latissima				
N Scotland	A	8	700	1.14
N Scotland	B	10	644	1.55
W Scotland	A	17	558	3.04

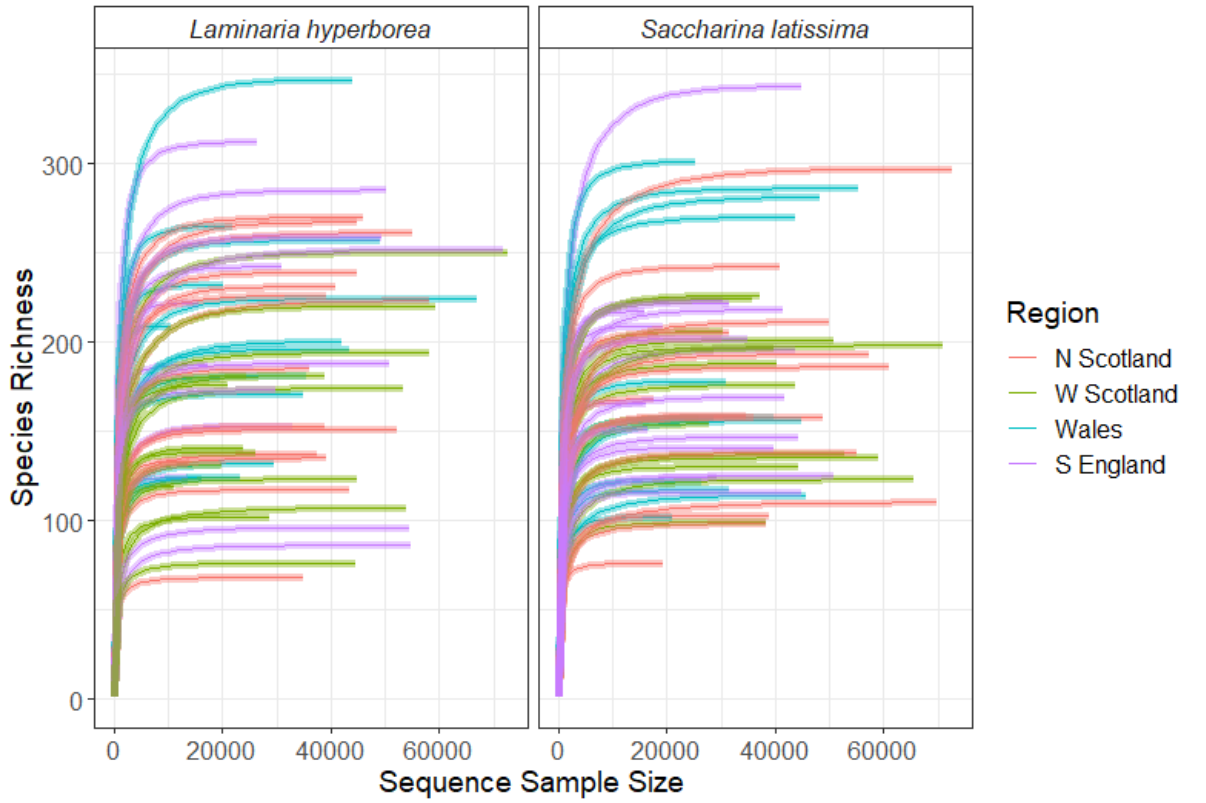
W Scotland	B	8	694	1.15
Wales	A	24	485	4.94
Wales	B	25	662	3.77
S England	A	8	721	1.10
S England	B	27	735	3.67

Table S3. Results of multivariate community structure (PERMANOVA) between Species, Regions and site variability within region. Analysis was performed on data agglomerated back to the taxonomic ranks of class and family/

		Class		Family	
	df	**F**	**p**	**F**	**p**
Species	1	0.725	0.577	0.732	0.614
Region	3	1.789	0.05	2.20	0.005
Species*Region	3	0.631	0.765	0.724	0.797
Species*Region(Site)	8	1.207	0.205	1.016	0.452
Residual	99				

Table S4. Pairwise comparisons of significant factors (Region) from multivariate PERMANOVA analysis. p values are with Bonferroni correction applied.

Comparison	**df**	**Pseudo-F**	**R^2**	**p**
W Scot vs N Scot	1	0.66	0.001	1.0
W Scot vs S Eng	1	1.85	0.03	0.228
W Scot vs Wales	1	4.04	0.07	**0.013**
N Scot vs S Eng	1	1.69	0.03	0.312
N Scot vs Wales	1	4.24	0.07	**0.006**
S Eng vs Wales	1	1.45	0.03	0.630



677
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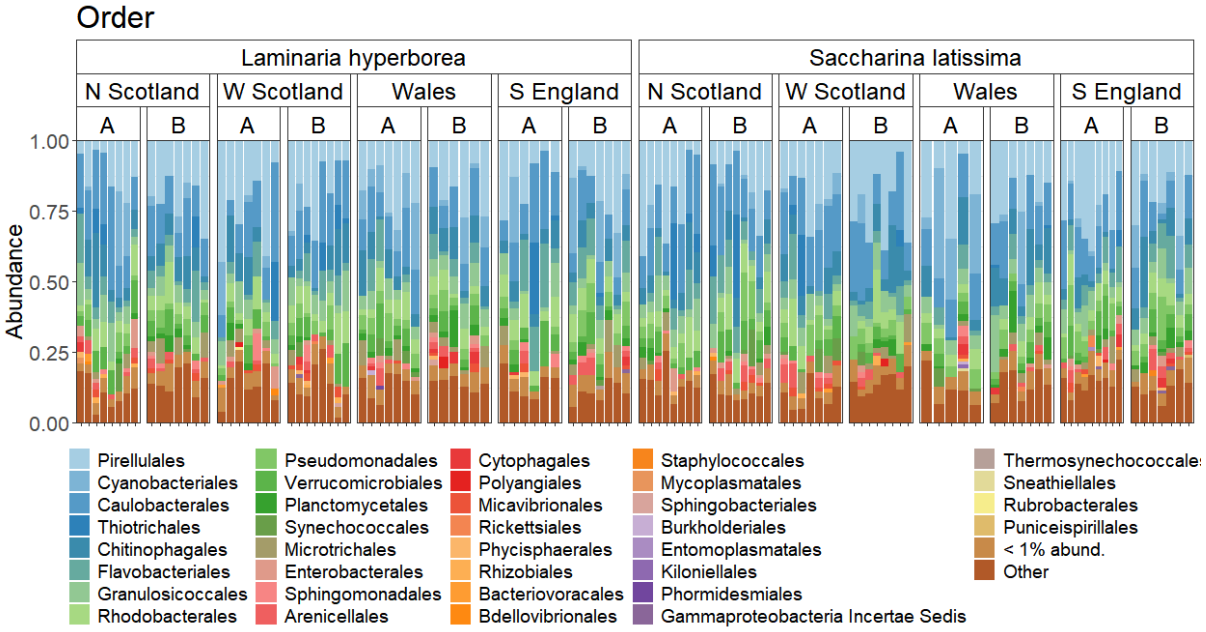
679 **Figure S1**. Rarefaction curves of Amplicon Sequence Variants and sequencing depth of 115 kelp samples from
680 eight sites in the United Kingdom



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683 **Figure S2.** Relative abundance of bacterial orders in the kelps *Laminaria hyperborea* (left) and *Saccharina*
684 *latissima* (right) from four study regions (two sites A + B within each region) in the UK. Site locations can be seen
685 in Figure 1. Orders that made a contribution of < 1% to overall study wide abundance were collapsed into a separate
686 category. “Other” represents taxa where underlying taxonomy was not resolved.
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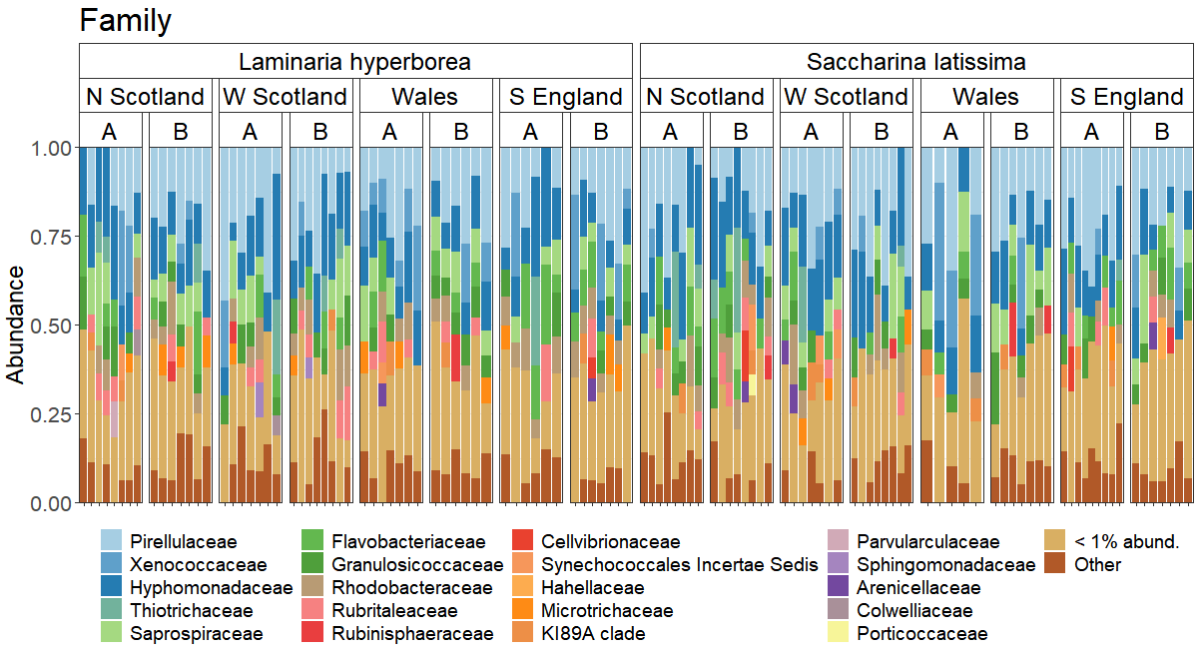

Figure S3. Relative abundance of bacterial Families in the kelps *Laminaria hyperborea* (left) and *Saccharina latissima* (right) from four study regions (two sites A + B within each region) in the UK. Site locations can be seen in Figure 1. Orders that made a contribution of < 1% to overall study wide abundance were collapsed into a separate category. “Other” represents taxa where underlying taxonomy was not resolved.

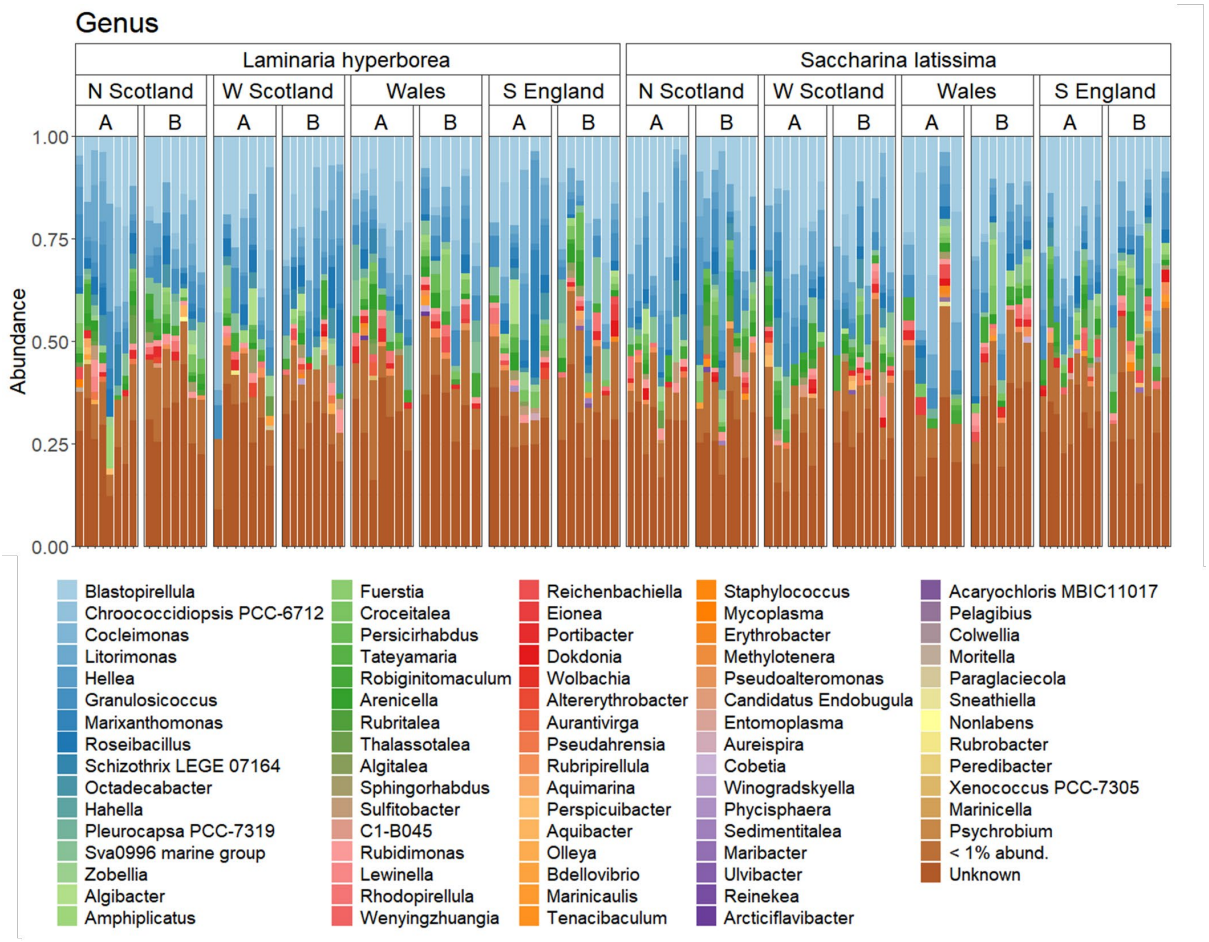

Figure S4. Relative abundance of bacterial orders in the kelps *Laminaria hyperborea* (left) and *Saccharina latissima* (right) from four study regions (two sites A + B within each region) in the UK. Site locations can be seen in Figure 1. Orders that made a contribution of < 1% to overall study wide abundance were collapsed into a separate category. “Unknown” represents taxa where underlying taxonomy was not resolved.

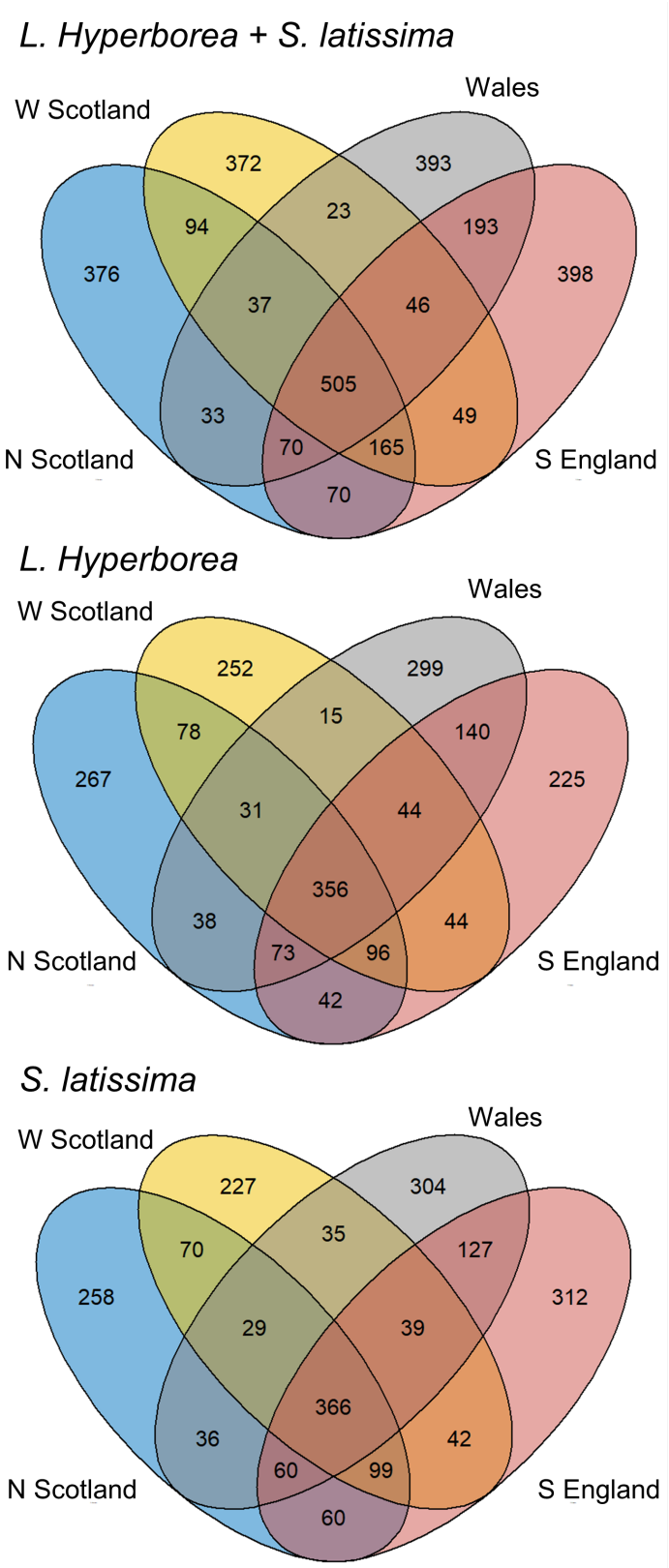

Figure S5. Venn diagrams showing shared amplicon sequence variants between regions for the kelps *Laminaria hyperborea* and *Saccharina latissima* in the United Kingdom. Locations of study regions are shown in Figure 1.