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Temporal and spatial drivers of the structure of macroinvertebrate assemblages associated with *Laminaria hyperborea* detritus in the northeast Atlantic

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ABSTRACT

Kelp forests occur on more than a quarter of the world's coastlines, serving as foundation species supporting high levels of biodiversity. They are also a major source of organic matter in coastal ecosystems, with the majority of primary production released and exported as detritus. Kelp detritus also provides food and shelter for macroinvertebrates, which comprise important components of inshore food-webs. Hitherto, research on kelp detritus-associated macroinvertebrate assemblages remains relatively limited. We quantified spatiotemporal variability in the structure of detritus-associated macroinvertebrate assemblages within *Laminaria hyperborea* forests and evaluated the influence of putative drivers of the observed variability in assemblages across eight study sites within four regions of the United Kingdom in May and September 2015. We documented 5167 individuals from 106 taxa with Malacostraca, Gastropoda, Isopoda and Bivalvia the most abundant groups sampled. Assemblage structure varied across months, sites, and regions, with highest richness in September compared to May. Many taxa were unique to individual regions, with few documented in all regions. Finally, key drivers of assemblage structure included detritus tissue nitrogen content, depth, sea surface temperature, light intensity, as well as *L. hyperborea* canopy density and canopy biomass. Despite their dynamic composition and transient existence, accumulations of *L. hyperborea* detritus represent valuable repositories of biodiversity and represent an additional kelp forest component which influences secondary productivity, and potentially kelp forest food-web dynamics.

1. Introduction

Understanding patterns of biodiversity and explaining the mechanisms driving them is a fundamental aim of ecology (Wilson, 1993). In coastal marine environments, a number of highly complex and dynamic biotic and abiotic factors, operating across multiple temporal and spatial scales, are responsible for structuring communities and driving biodiversity patterns (Fraschetti et al., 2005). This biodiversity is extremely important, both ecologically and socioeconomically, ensuring provision of numerous ecosystem services (Costanza et al., 1997, 2014; Eger et al., 2023; Gray, 1997). To effectively manage and conserve coastal ecosystems and the services they underpin, and to improve prediction and detection of future changes, a better understanding of biodiversity patterns and the processes that shape them is required (Levin, 2000).

Kelp species are distributed along over a quarter of the world's coastlines, where they can form extensive, highly productive habitats (Jayathilake and Costello, 2021; Krumhansl et al., 2016; Pessarrodona et al., 2022; Wernberg and Filbee-Dexter, 2019). By offering complex, biogenic structures and altering environmental conditions, kelp species provide nursery, shelter and foraging areas for numerous invertebrates, fish, birds and mammals (Teagle et al., 2017). As a result, in addition to underpinning exceptionally high rates of primary productivity (Mann, 1973; Pessarrodona et al., 2022), kelp forests support rich and abundant faunal communities, elevated levels of secondary production, and maintain local biodiversity (Fredriksen, 2003; Norderhaug and Christie, 2011).

Kelp forests release large quantities of organic matter, the majority of which is exported from the habitat as detritus (Duggins et al., 1989; Smale et al., 2021; van der Mheen et al., 2024). Around 80% of total kelp habitat production is released as detritus (Krumhansl and Scheibling, 2012). While a significant fraction of this detritus will likely be exported to adjacent habitats or deeper waters, in some systems up to 50% of detrital matter may be retained in the shallows within kelp forests (Ramirez-Llodra et al., 2021). This retained detritus is either consumed by kelp forest associated fauna or microbes, thereby fuelling local inshore food-webs and highlighting its ecological importance

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(Krumhansl and Scheibling, 2012). Indeed, several studies have demonstrated that kelp detritus is an important resource for faunal assemblages both within kelp forests and in adjacent or distant habitats, providing food and shelter for a range of organisms, however a comprehensive understanding of these relationships is still lacking, especially within kelp forests themselves (Duggins et al., 1989, 2016; Duggins and Eckman, 1997; Vetter and Dayton, 1998). Furthermore, the sensitivity of kelp species to ocean warming and other anthropogenic stressors is altering their ecophysiological performance and productivity (Pessarrodona et al., 2018; Smale, 2020), which may have important consequences for secondary production and the structure and functioning of detritus-associated communities (Dayton, 1985; Steneck et al., 2002).

While much less research has been done of the importance of kelp detritus in supporting diversity, there is much research on other systems demonstrating the important role of detrital material in providing habitat and food for associated macrofauna across a wide range of marine, terrestrial and freshwater environments (Moore et al., 2004). Detrital inputs have been shown to support greater species diversity, larger predator populations and to make food chains longer than would be supported by living autotrophs alone (Hairston and Hairston, 1993). In addition to altering trophic dynamics, detritus also alters the physical structure of habitats (Schindler 1990; Williamson et al., 1999), providing habitats for some species, while inhibiting others (Peterson and Pickett, 1995). It is highly likely that kelp detritus plays a similarly structuring role both within the kelp forest itself, but also in near and far habitats where kelp detritus may be transported to (Krumhansl and Scheibling, 2012).

Kelp detritus-associated macroinvertebrates are an ecologically important component of kelp forest biodiversity and represent a critical trophic linkage as food for predators (Norderhaug et al., 2003). Nevertheless, research on the structure and diversity of these assemblages and the drivers of ecological patterns is limited in many regions. A lack of baseline information hinders the management and protection of wider kelp forest biodiversity in the face of rapid environmental change. Here, we quantified spatiotemporal variability in the structure and diversity of macroinvertebrate assemblages associated with kelp detritus within *Laminaria hyperborea* forests and examined the influence of putative biotic and abiotic drivers of the observed variability. To achieve this, we surveyed kelp detritus-associated assemblages across two time periods and eight sites situated along a 9° latitudinal gradient in the United Kingdom.

2. Materials and methods

2.1. Study area

Field samples were collected in May and September 2015 at two sites nested within four regions along the exposed west coast of the United Kingdom (UK) (Fig. 1), with regions separated by between ~180–500 km. The sites spanned 9° of latitude (~50° to ~59° N) which encompassed a gradient in mean sea temperature of ~2.5 °C (Smale et al., 2016, 2020b; Smale and Moore, 2017). All study sites were “open coast”, being moderately-to-fully exposed to wave action (Table 1) and were characterised by extensive subtidal rocky reef habitat dominated by the kelp *Laminaria hyperborea*. All sites were deemed representative of the coastal geomorphology of the wider region and were not impacted by local anthropogenic stressors (Smale et al., 2016; Smale and Moore, 2017).

2.2. Field collection

At each site on each sampling period, three replicate 1 × 1 m quadrats were haphazardly placed beneath dense *L. hyperborea* canopy

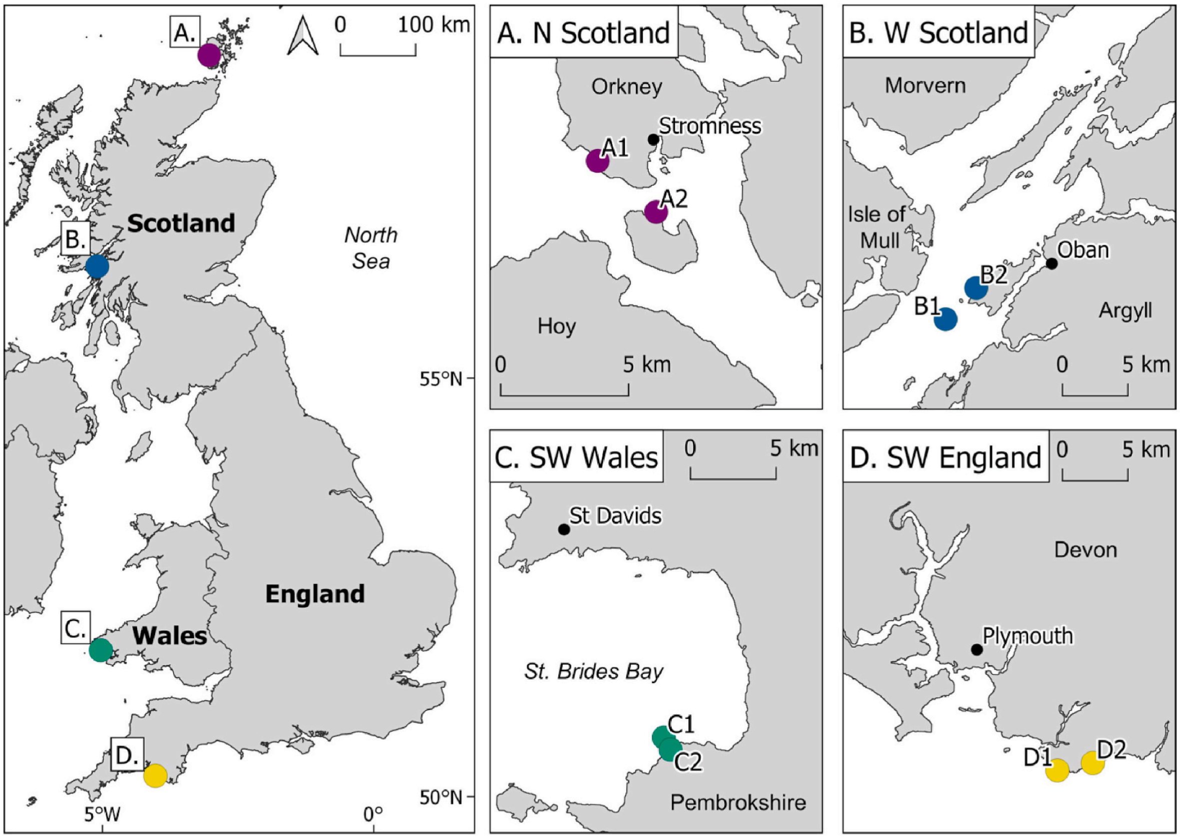

Fig. 1. Study area showing the position of the four study regions in the UK (left) and inset maps indicating positions of sites within these regions for A) northern Scotland, B) western Scotland, C) southwest Wales, and D) southwest England.

Table 1

Summary of biotic and abiotic variables measured at eight study sites located within four regions in the UK. "Detritus tissue nitrogen content" indicates mean percentage nitrogen content in detrital tissue samples. "Kelp density" is the mean density of canopy-forming *L. hyperborea* individuals found in eight replicate 1 m^2 quadrats. "Kelp biomass" refers to the mean fresh weight of 12–16 canopy-forming plants extracted from each site. "Urchin density" is the average number of sea urchins (exclusively *Echinus esculentus*) recorded in eight replicate 1 m^2 quadrats at each site. "Depth" indicates average depth below chart datum. "Mean SST" represents annual mean sea surface temperature (2005–2014) values calculated from satellite-derived data." Log chl a" is the average annual concentration of chlorophyll for each site (log 10 mg m^{-3} from MODIS Aqua satellite data, 2002 to 2012). "Log wave fetch" is a broad-scale metric of wave exposure obtained using a wave fetch model based on distances to nearest land in all directions around each 200 m coastal cell for the UK coastline (see Burrows et al., 2008). "Mean daily light" represents average daytime light levels (between 0800 and 2000 h) during 14-day deployment at each site.

Region	Site	Detritus tissue nitrogen content (%)		Kelp density (inds m^2)	Kelp biomass (kg FW m^2)	Urchin density (inds/ m^2)	Depth (m below chart datum)	Mean SST (°C)	Log chl a (mg m^3)	Log wave fetch (km)	Mean daily light (lumens m^2)
		May	Sep								
N Scotland	A1	1.59	0.78	9.2	15.6	0	3	9.7	0.21	3.8	3290
N Scotland	A2	1.6	1.52	8.6	15.8	0.37	4	9.8	0.26	3.5	2592
W Scotland	B1	1.94	1.75	9.3	18.6	0.13	5	10.8	0.59	3.3	2543
W Scotland	B2	2.56	2.47	7.9	10.1	0.06	4	10.7	0.65	3.1	1696
SW Wales	C1	1.83	1.27	9.7	5.4	0.19	4	11.8	0.43	3.7	1519
SW Wales	C2	2.11	1.32	8.6	3.3	0.25	3	11.8	0.43	3.5	976
SW England	D1	1.88	1.64	9.1	7.9	0.06	3	12.4	0.28	4.1	1500
SW England	D2	2.15	1.27	8.2	4.4	0.13	3	12.5	0.38	3.5	1865

at depths of 3–5 m below chart datum (BCD) in areas of high detrital biomass. All detrital material within the quadrat was placed in a cloth bag underwater with the bag immediately sealed. All sites were dominated by *L. hyperborea*, although some other kelp species and abundant red algal assemblages on both the reef and kelp surfaces have been previously recorded (King et al., 2021; Smale et al., 2020a; Smale and Moore, 2017). Inspection of both detrital accumulations in the field and detritus samples in the laboratory (see below) suggested that the vast majority of material (i.e. >95%) originated from *L. hyperborea*.

On return to the laboratory all material was washed over a 1 mm sieve to collect macroinvertebrates. All macroinvertebrates retained on the sieve were preserved in 70% industrial methylated spirits (IMS) and subsequently identified to the lowest taxonomic level possible (most commonly species level) and enumerated. Excess water was removed from the kelp detritus using a salad spinner for approximately 1 min before samples were weighed to the nearest gram using an electronic scale (Ohaus Valor 2000) to determine wet weight biomass.

2.3. Biotic and abiotic predictor variables

A range of biotic and abiotic factors were quantified to examine the influence of putative drivers of macroinvertebrate assemblage structure (Table 1). At each study site, the density of *L. hyperborea* was quantified by haphazardly placing eight replicate 1 m^2 quadrats (placed >3 m apart) in dense canopy. The density was recorded by counting the total number of adult, canopy-forming plants within each quadrat. To determine L. *hyperborea* biomass 12–16 canopy-forming plants were removed from the substrate, brought to the surface, and weighed (wet weight). The density of sea urchins (exclusively *Echinus esculentus*) and the depth of each quadrat (BCD) were also recorded. Further information on the methods and habitat characteristics can be found in Smale et al. (2016), Smale and Moore (2017) and Smale et al. (2020). The total nitrogen content of kelp detritus was determined by freeze-drying the samples, grinding them to a fine powder and processing 200 g of each sample in an Elementar vario MAX cube combustion analyser (Table 1) (Muñoz-Huerta et al., 2013).

Remotely sensed data were obtained for each site to provide broad-scale metrics of sea surface temperature (SST), chlorophyll *a* (chl *a*) and wave exposure. Annual mean temperature (2005–2014) based on 9 km resolution data from the Pathfinder AVHRR satellite were downloaded from the NASA Giovanni Data Portal (http://giovanni.gsfc.nasa.gov/giovanni/) for each site. Estimates of chl *a* concentrations were generated from optical properties of seawater derived from satellite images (MODIS Aqua satellite at an estimated 9 km resolution) with data averaged for the period 2002 to 2012 (see Burrows 2012 for a similar approach). Wave exposure values were obtained using a wave fetch model (Burrows et al., 2008), based on distances to nearest land in all directions around each 200 m coastal cell for the UK coastline. Finally, light level sensors ('HOBO' Light weatherproof Pendant Data Logger 16 k) were deployed at each site for 14 days (during which time fouling by biofilms and epiphytes does not affect light measurements), in both May and September. To prevent any influence of shading on the light measurements, all kelp individuals within a ~2 m radius of the sensors were removed. The sensor data were used to generate average daytime light levels (between 0800 and 2000 h). All biotic and abiotic variables measured are summarised in Table 1.

2.4. Statistical analyses

All analyses were conducted using PRIMER v7 software (Clarke and Gorley, 2015) with the PERMANOVA add on (Anderson et al., 2008). Patterns of macroinvertebrate assemblage structure were visualised using non-metric multidimensional scaling (nMDS). Variability in the assemblage structure was examined using a 3-factor PERMANOVA, with the model comprising region (fixed, 4-levels), site (random, 2-levels nested within region) and month (fixed, 2-levels). Data were fourth-root transformed prior to analysis to down-weight the importance of numerically dominant taxa. Permutations (9999 under a reduced model) were based on a Bray–Curtis similarity matrix. In addition to the multivariate analyses, macroinvertebrate abundance and taxon richness were also examined. Macroinvertebrate abundance and taxon richness were examined using the same permutation-based model as the multivariate data but with matrices based on Euclidian distances between untransformed data (Clarke and Gorley, 2015). To account for potential effects of the detrital biomass on assemblage structure, this variable was included as a covariate in all analyses. Pairwise tests were performed wherever significant differences between terms were detected ($P < 0.05$). Prior to analysis, homogenous dispersion around the centroid was checked for all factors using the PERMDISP routine. Where significant differences in dispersion existed, a more conservative ($p < 0.01$) critical threshold of significance was used in order to reduce the risk of Type I errors.

Furthermore, similarity percentage analyses (SIMPER) were performed to determine which taxa contributed most to any observed dissimilarity between regions (Clarke and Gorley, 2006). The routine was based on breaking down the Bray-Curtis dissimilarity between samples into contributions for each taxon ($\bar{\delta}i$), with a cut-off at 50% for cumulative contribution (Clarke and Warwick, 2001).

Relationships between environmental variables and macroinvertebrate assemblage structure and macroinvertebrate diversity metrics were examined using the DISTLM (distance-based linear model) routine in PERMANOVA. Predictor variables included all quantified abiotic and biotic predictor variables (Table 1), as well as the detrital biomass. Prior to analyses Pearson's correlation coefficient was used to check for collinearity between the predictor variables. None of the variables demonstrated a high degree of correlation ($r \geq 0.85$), and therefore all were retained in the analyses (Anderson et al., 2008). The DISTLM routine was then used (with normalised predictor variables) to obtain the most parsimonious model using a stepwise selection procedure and AICc selection criterion (Anderson et al., 2008). According to the most parsimonious DISTLM model, distance-based redundancy analysis (dbRDA), a constrained ordination technique, was used to provide a 2D visualisation of the relationship between macroinvertebrate assemblage structure and significant predictor variables, with vectors representing the strength (i.e., vector length) and direction of influence (Laliberté and Legendre, 2010).

3. Results

A total of 5167 macroinvertebrates representing 102 taxa were recorded across the study. Malacostraca, with 2164 individuals belonging to 58 taxa and gastropoda, with 2162 individuals from 26 taxa were the most dominant and diverse groups. Isopoda (694 individuals and 6 taxa) and bivalvia (102 individuals and 3 taxa) were also abundant groups (Supplementary Table 1). The abundance of individuals recorded in September (3115) was over a third greater than in May (2052), while the number of taxa was more than double, with 91 recorded in September and 42 in May (Supplementary Table 2). The relative contribution of major taxonomic groups to total faunal abundance remained similar across sampling months (Fig. 2).

Across the different regions, southwest Wales (C) had the highest number of taxa and second highest abundance (62 and 1,710, respectively), northern Scotland (A) had second highest number of taxa and the highest abundance of individuals (57 and 2566), in western Scotland (B) 45 taxa and 518 individuals were recorded, while southwest England (D) had both the lowest number of taxa (36) and individuals (373) (Fig. 2 and Supplementary Table 3). The contributions of major taxonomic groups also differed across regions, with relatively higher abundances of isopods in southwest Wales and gastropods in north Scotland and southwest England (Fig. 2 and Supplementary Table 3). Overall, taxa exhibited regional-scale specificity, with nearly half (46.6%) found exclusively within one of the four regions, indicating that certain taxa were unique to each region and a small fraction (12.6%) of taxa were found in all four study regions.

Non-metric MDS plots indicated clear partitioning in the macroinvertebrate assemblage structure between months and some clustering by region albeit with considerable variation observed between sites and replicate samples (Fig. 3).

Detrital biomass did not influence macroinvertebrate assemblage structure, abundance or taxon richness (Table 2). At the assemblage level there was a significant site (nested within region) by month interaction (Table 2), with pairwise comparisons identifying a single site in northern Scotland, western Scotland and southwest England supporting different assemblages between May and September (Fig. 3). There were also significant effects of region and month, with all regions supporting different assemblages between the two months, as well between regions, except for western Scotland and southwest England and southwest Wales and southwest England, as identified by the pairwise comparisons. According to the pairwise comparisons, macroinvertebrate abundance was significantly different and higher in northern Scotland compared to western Scotland and in northern Scotland compared to southwest England (Fig. 4a). While not significant, abundance tended towards being higher in southwest Wales compared to western Scotland and southwest England (Fig. 4a). Faunal richness was affected by an interaction between region and month (Table 2). Pairwise comparisons indicated richness was higher in northern Scotland compared to western Scotland and western Scotland had higher richness compared to southwest Wales (Fig. 2b). Higher macroinvertebrate richness was observed in all regions in September compared to May (Table 2 and Fig. 4b).

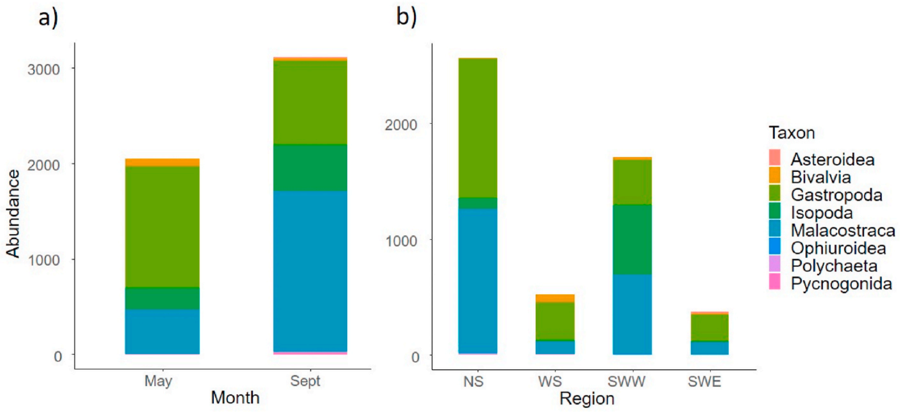

Fig. 2. Total abundance of macroinvertebrates shown by contributions of major taxonomic groups for each a) month and b) region (NS: northern Scotland; WS: western Scotland; SWW: southwest Wales; SWE: southwest England).

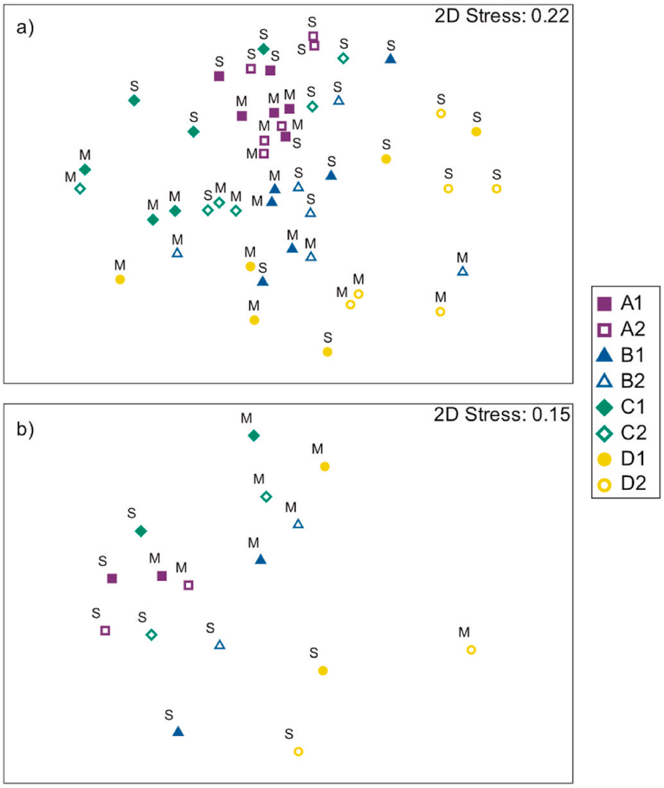

Fig. 3. Non-metric MDS plots depicting variation in macroinvertebrate assemblage structure across regions, sites (nested within regions) and months (a) and with centroids as averages for each region/site/month combinations (b). Symbols/colours represent different regions, fills indicate site and text indicates sampling month (M = May, S = September). Data were fourth-root transformed, and similarities were based on Bray–Curtis similarity matrices.

Between-region dissimilarity identified by SIMPER ranged from 69% to 82%. Overall, the dissimilarities were driven by taxa including the gastropods *Margarites helicinus*, *Tricolia pullus* and *Steromphala cineraria*, amphipods *Jassa* sp. and *Gammarus* sp. and isopoda *Idotea neglecta* (Table 3).

The DISTLM routine was used to determine relationships between predictor variables and variability in macroinvertebrate assemblage structure, abundance, and richness. Marginal tests showed that kelp detritus tissue nitrogen content, depth, SST, light intensity, canopy density and canopy biomass were overall the most important individual predictor variables explaining macroinvertebrate assemblage structure. For abundance, SST, chl *a*, canopy density and canopy biomass were the most important individual predictor variables, while for taxon richness it was kelp detritus tissue nitrogen content, SST and light intensity (Table 4). The stepwise selection procedure indicated that the most parsimonious model for the macroinvertebrate assemblage structure included kelp detritus tissue nitrogen content, depth, SST, light intensity, canopy density and canopy biomass, which explained 39% of the total observed variability (Table 4 and Fig. 5). The most parsimonious model for macroinvertebrate abundance included, SST, chl *a*, canopy density and canopy biomass and explained 41% of the total observed variability (Table 4). Finally, the most parsimonious model for macroinvertebrate richness included kelp detritus tissue nitrogen content, SST and light intensity, explaining 38% of the variability. The outcome of the most parsimonious model for macroinvertebrate assemblage structure was visualised in dbRDA. The most variation was explained across the x-axis with regions separated across this axis (Fig. 5). Along this axis mean SST temperature was the greatest influence, especially on sites in SW England. The y-axis explained less of the observed variation with regional differences also evident. In this case Mean canopy biomass and mean light intensity had a sting influence on sites in NW Scotland and N Scotland, while mean canopy density was a strong influence on sites In SW Wales and to a less extent detritus tissue nitrogen content had an influence at one site in SW England (Fig. 5).

4. Discussion

Macroinvertebrate assemblages associated with kelp detritus within *Laminaria hyperborea* forests in the UK were both rich (106 distinct taxa) and abundant (total of 5167 individuals), and represent an important and largely overlooked component of kelp forest biodiversity. Our study-wide estimate of macroinvertebrate richness is notably higher than previously reported values for detritus-associated assemblages. For example, a study by Duggins et al. (2016) identified 24 and 15 macrofauna taxa associated with kelp detritus derived from *Nereocystis luetkeana* and *Agarum fimbriatum*, respectively. Due to the lack of similar research on detritus within *L. hyperborea* forests, we are unable to make direct comparisons, nevertheless our study-wide richness value is comparable to those reported along the same study gradient for macroinvertebrate assemblages associated with holdfasts (187 taxa; Teagle et al., 2018), stipes (134 taxa; King et al., 2021), understorey algal mimics (173 taxa; Bué et al., 2020) and understory algae (179 taxa; Earp et al. in review). The richness observed in our study is comparable to macroinvertebrate assemblages of seagrass meadows in the Mediterranean (Como et al., 2008) and Western Australia (Edgar, 1990), which are commonly regarded as habitats of high biodiversity value (Unsworth and Cullen-Unsworth, 2014). Consequently, macroinvertebrate assemblages associated with kelp detritus appear to be diverse and similar to those associated with other habitats within *L. hyperborea* forests, as well as being comparable with some other marine habitats characterised by high faunal diversity.

We observed marked differences in the structure, richness, and

Table 2

Results of PERMANOVA tests for differences in multivariate macrofaunal assemblage structure and univariate abundance and taxon richness, between regions (fixed), sites (nested in region, random) and month (fixed). Detrital biomass was included as a covariate in all analyses. Permutations (9,999) were conducted under a reduced model and were based on a Bray-Curtis similarity matrix of forth-root transformed data for the multivariate assemblage and Euclidean distance and untransformed data for univariate analyses. Significant values ($P < 0.05$) are indicated in bold and underlined values indicate main factors where PERMDISP revealed significant differences in within-group dispersion.

	Assemblage				Abundance				Richness			
Source	df	MS	F	P	df	MS	F	P	df	MS	F	P
Detrital biomass	1	3033.1	1.32	0.22	1	26076.0	4.24	0.05	1	1.0	0.05	0.82
Region	3	11374.0	2.86	**0.01**	3	84747.0	29.71	**0.01**	3	240.4	11.48	**0.02**
Month	1	11531.0	3.93	**0.04**	1	28066.0	1.21	0.33	1	674.0	29.35	**0.01**
Site (Region)	4	3783.4	2.61	**0.001**	4	2712.0	0.33	0.86	4	19.9	1.03	0.41
Region x Month	3	2882.0	1.06	0.44	3	6489.0	0.31	0.84	3	24.1	1.17	0.43
Site (Region) x Month	4	2624.3	1.81	**0.001**	4	21335.0	2.63	0.05	4	20.3	1.05	0.39
Residual	31	1447.2			31	8122.0			31	19.3		
Total	47				47				47			

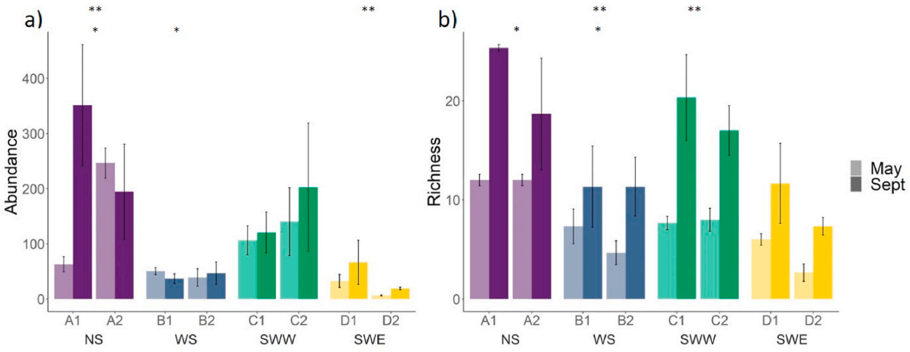

Fig. 4. Mean (±SE) a) total macrofaunal abundance, and b) richness, by region, site and month (NS: northern Scotland; WS: western Scotland; SWW: southwest Wales; SWE: southwest England). Asterisks indicate regions with statistically significant differences.

Table 3
Results of the SIMPER analysis, with a cut-off at 50% cumulative contribution, showing the contributions in dissimilarity of taxa and their total abundances between regions with statistically different macrofaunal assemblages. The taxa are ordered by decreasing contribution. ***δi***: average dissimilarity, ***δi***%: percentage contribution of each taxon to the average dissimilarity, ***δi***/SD: standard deviation. Total abundance of the contributing taxa in each region (northern Scotland (A), western Scotland (B), southwest Wales (C) and southwest England (D)) is provided in corresponding columns.

	δi A & B = 68.19					δi A & C = 69.96			
Taxon	A	B	δi%	δi/SD	Taxon	A	C	δi%	δi/SD
Margarites helicinus	406	28	7.18	1.41	*Margarites helicinus*	406	2	6.36	1.5
Jassa sp	702	16	7.04	1.64	*Gammarus* sp	23	392	6.11	1.19
Rissoa sp	359	19	6.69	1.35	*Jassa* sp	702	105	5.29	1.46
Ischyrocerus anguipes	97	6	5.37	1.64	*Idotea neglecta*	30	597	5.08	1.12
Jassa falcata	29	2	4.17	1.4	*Rissoa* sp	359	191	4.97	1.25
Ampithoe rubricata	87	1	4.14	1.24	*Ischyrocerus anguipes*	97	4	4.64	1.77
Lacuna vincta	148	37	4.02	1.28	*Lacuna vincta*	148	29	4.31	1.62
Tricolia pullus	0	49	3.41	0.84	*Ampithoe rubricata*	87	4	3.42	1.25
Idotea neglecta	30	1	2.97	1.09	*Jassa falcata*	29	5	3.12	1.27
Stenothoe monoculoides	172	0	2.96	0.8	*Modiolula phaseolina*	3	24	2.88	1.12
Lacuna parva	148	1	2.88	1.05	*Tricolia pullus*	0	31	2.78	0.94

	δi B & C = 73.60					δi A & D = 81.88			
Taxon	B	C	δi%	δi/SD	Taxon	A	D	δi%	δi/SD
Gammarus sp	1	392	9.33	1.29	*Jassa* sp	702	1	8.45	2.64
Idotea neglecta	1	597	7.92	1.05	*Margarites helicinus*	406	0	7.77	1.63
Rissoa sp	19	191	5.49	0.98	*Rissoa* sp	359	79	6.53	1.35
Modiolula phaseolina	1	24	4.39	1.17	*Ischyrocerus anguipes*	97	0	5.78	2.02
Jassa sp	16	105	4.35	1.25	*Lacuna vincta*	148	0	5.68	2.32
Tricolia pullus	49	31	4.34	1.05	*Steromphala cineraria*	149	15	4.68	1.42
Lacuna vincta	37	29	4.02	1.18	*Jassa falcata*	29	0	4.05	1.45
Atylus guttatus	0	20	3.26	0.9	*Ampithoe rubricata*	87	0	3.83	1.24
Patella pellucidia	39	32	3.24	1.06	*Idotea neglecta*	30	2	2.76	1.09
Steromphala cineraria	148	91	3.08	0.98	*Stenothoe monoculoides*	172	0	2.68	0.79

abundance of detritus-associated macroinvertebrate assemblages between survey months. Macroinvertebrates were more abundant, by over a third, and were composed of twice as many taxa in September compared to May, while assemblage composition was dissimilar between months. Similar findings, where higher abundance and richness values were observed in September compared to May was also found for faunal assemblages associated with understorey algae in the same *L. hyperborea* forests (Earp et al. in review). Pronounced seasonality in ecological structure and functioning is a characteristic feature of temperate marine ecosystems more broadly, being primarily driven by intra-annual variation in key factors such as light, nutrients, temperature, and food supply, as well as strong seasonality in life histories (Pessarrodona et al., 2018). With regards to kelp forests specifically, previous studies have highlighted strong seasonality in community structure related to temporal patterns in food availability (Teagle et al., 2018), recruitment of key species (Teagle et al., 2017), and seasonal growth patterns of secondary habitat formers (Bué et al., 2020). Our study suggests that detritus-associated macroinvertebrate assemblages also exhibit marked seasonality in structure, likely due to temporal patterns of faunal recruitment, growth, and development, shifts in food quality and responses to environmental variability. Further surveys conducted at a finer temporal resolution and across larger scales are needed to fully explore seasonal patterns.

We did not observe any differences in detrital biomass at different months and detrital biomass did not play a role in structuring the macroinvertebrate assemblage. In L. *hyperborea*, detritus is produced via the three discrete processes of ”May cast”, chronic erosion and the dislodgement of whole (or partial) plants (Lüning, 1969; Pessarrodona et al., 2018). “May cast” produces a major detrital pulse resulting in shedding of the previous season’s lamina growth, which remains attached to the newly growing lamina until it is lost entirely between March and May. This process accounts for ~30% of the total amount of kelp organic matter released as detritus each year (Pessarrodona et al., 2018), and the volume of fresh detritus found within these habitats is generally greater in May compared with September as a result (Smale et al., 2021). However, due to the highly energetic nature of these shallow reefs, the flux of organic matter is highly dynamic. Whilst we did not observe between-month differences in detrital biomass, it should be

Table 4
DISTLM marginal test results for macroinvertebrate assemblage structure, abundance and taxon richness based on a set of 10 predictor variables (Table 1 plus detrital biomass). Values indicate proportion of variance (R^2) explained by each individual predictor from marginal testing. The terms in bold indicate the most parsimonious models based on stepwise selection and AICc criterion. The terms in italics indicate significant ($P < 0.05$) individual predictors from marginal testing.

	R^2 marginal tests		
Variable	Assemblage	Abundance	Richness
Detrital biomass	0.02	0.04	0.0004
Detrital tissue N [%]	***0.06***	*0.1*	***0.18***
Mean depth	**0.04**	0.002	0.0006
Mean SST	***0.13***	***0.17***	***0.16***
Log wave fetch	*0.05*	0.03	0.01
Log chl *a*	*0.06*	***0.14***	*0.09*
Mean light intensity	***0.10***	*0.09*	**0.05**
Mean canopy density	***0.06***	***0.08***	0.03
Mean canopy biomass	***0.09***	**0.03**	0.05
Mean urchin density	*0.02*	0.04	*0.10*
R^2 of best solution	0.39	0.41	0.38

noted that our surveys targeted areas of high accumulation and did not yield a habitat-wide estimate of detritus load. Intuitively, the quantity and quality of available detritus will influence the structure of microbial and macrofaunal assemblages, as has been shown in both marine (Olabarria et al., 2010) and freshwater systems (König et al., 2014).

Macroinvertebrate assemblages were highly variable over multiple spatial scales, although we observed clear partitioning between regions. A regional-scale specificity was observed, with almost half of the macroinvertebrate taxa found only in a single region and just over 10% of the taxa found in all regions, resulting in high between-region dissimilarities. Macroinvertebrate assemblages associated with algal mimics placed within *L. hyperborea* forests exhibited a similar pattern, whereby several taxa, a number of which were also recorded in our study, resided only in specific regions or were found in much greater abundances in those regions (Bué et al., 2020). Although considerable regional-scale variability was observed, there were no detectable latitudinal patterns. Differences between regions did not correspond to sequential shifts in latitude, with higher and lower abundances and numbers of taxa observed both in the northern and southern study regions. The lack of interaction between *L. hyperborea* macroinvertebrate assemblages and latitude we observed is contrary to the findings of several other studies along the same gradient. For example, Teagle et al. (2018) discovered a latitudinal shift in structure of macroinvertebrate assemblages associated with *L. hyperborea* holdfasts, while Bué et al. (2020) reported a north-south increase in the richness and diversity of understorey macroinvertebrate assemblages.

A number of biotic and abiotic predictor variables explained some of the observed variability in macroinvertebrate assemblage structure. The most important variables influencing ecological structure included detritus tissue nitrogen content, SST, canopy density and canopy biomass. It was somewhat expected that tissue nitrogen content would be an important driver, as increased nitrogen content generally renders kelp tissue more readily available to consumers (Duggins and Eckman, 1997), although high nitrogen levels in *L. hyperborea* may reduce its palatability (Norderhaug et al., 2006). We observed markedly higher nitrogen content in May compared to September, which could have influenced macroinvertebrate assemblage structure, richness and abundance. Similar to our study, sea temperature has previously been identified as important in driving macroinvertebrate assemblages of *L. hyperborea* along the same gradient as used in this research (e.g. Teagle et al., 2018; Bué et al., 2020, Earp et al. in review). Finally, since the majority of *L. hyperborea* detritus is produced by shedding of the lamina (Pessarrodona et al., 2018), kelp canopy density and biomass could have had a direct influence on the habitat provision for the detritus-associated macroinvertebrate assemblages.

Despite high rates of detritus production by kelp forests (Krumhansl et al., 2016; Pessarrodona et al., 2022), accumulations of which offer distinct habitat and food for a wide range of fauna, few studies have investigated the structure and diversity of their associated macroinvertebrate assemblages. To our knowledge, this is the first study to examine spatiotemporal variability in the structure of detritus-associated macrofaunal assemblages within *L. hyperborea* forests, particularly across a large latitudinal gradient. Here we

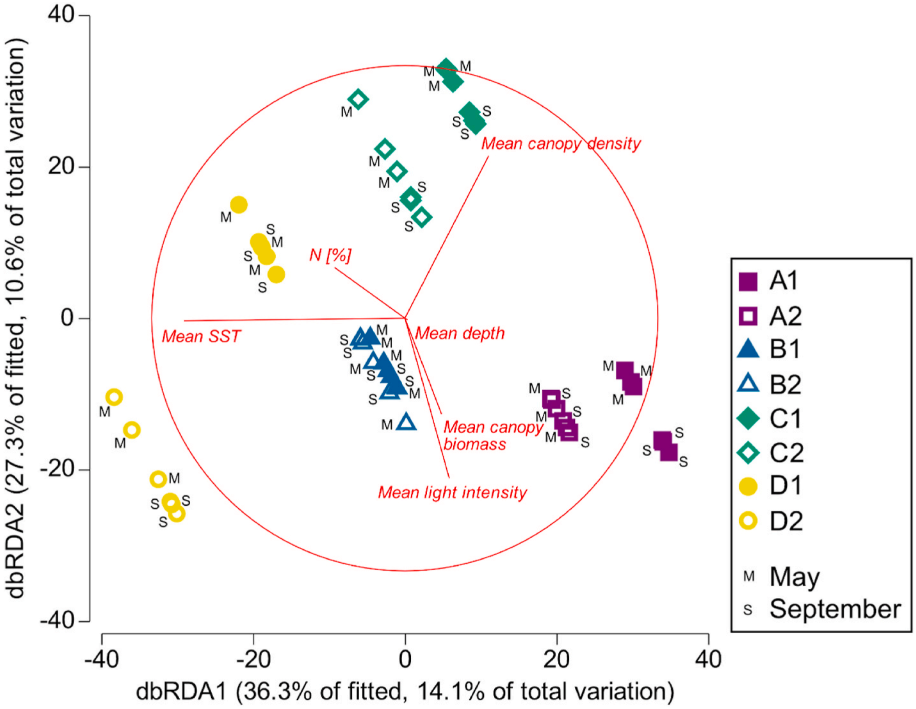

Fig. 5. Relationship between macroinvertebrate assemblage structure and predictor variables represented by distance-based redundancy analysis (dbRDA).

demonstrate that *L. hyperborea* detritus habitats attract and harbour highly diverse macroinvertebrate assemblages, acting as important repositories of biodiversity and a food source for higher trophic levels within coastal marine ecosystems. Many studies have emphasised the role of kelp holdfast communities in driving secondary productivity (e.g. Ojeda and Santelices, 1984; Teagle et al., 2018), but this study and others (e.g. Bué et al., 2020; Smale et al., 2020; King et al., 2021, Earp et al. in review) have highlighted the often overlooked contribution of other components of kelp forest biodiversity in driving secondary productivity and likely foodweb dynamics. We encourage future studies to focus further on disentangling the links between kelp detritus associated communities and secondary productivity and food web dynamics. To do so, quantifying the biomass and functionality of macroinvertebrate detritovores, and trophic linkages between them and other components of the kelp forest ecosystem, will be a useful addition to the community metrics recorded in this study.

CRediT authorship contribution statement

Adam Gouraguine: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Dan A. Smale:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Arwyn Edwards:** Writing – review & editing, Validation, Resources, Methodology, Formal analysis. **Nathan G. King:** Writing – review & editing, Investigation, Data curation. **Mathilde Jackson-Bué:** Writing – review & editing, Investigation, Data curation. **Sean Kelly:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Hannah S. Earp:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Pippa J. Moore:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106518.

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