The structure and diversity of macroinvertebrate assemblages associated with the understudied pseudo-kelp *Saccorhiza polyschides* in the Western English Channel (UK)

Nora Salland [a,b,*], Antony Jensen [b], Dan A. Smale [a]

[a] *The Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, PL1 2PB, Plymouth, UK*
[b] *School of Ocean and Earth Science, University of Southampton, European Way, SO14 3ZH, Southampton, UK*

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ABSTRACT

We examined spatiotemporal variability in the structure of faunal assemblages associated with the warm-temperate pseudo-kelp *Saccorhiza polyschides* towards its range centre (Western English Channel, southwest UK), to better understand its role as a habitat-former in the northeast Atlantic. A total of 180 sporophytes and their associated fauna were sampled across three months, three sites, and two depths. Assemblage abundance and biomass varied markedly between three morpho-functional sporophyte components (i.e., holdfast, stipe, blade). We recorded rich and abundant macroinvertebrate assemblages, comprising nine phyla, 28 coarse taxonomic groups, and 57 species of molluscs, which consistently dominated assemblages. We observed pronounced seasonality in faunal assemblage structure, marked variability between sites and depths, and strong positive relationships between biogenic habitat availability and faunal abundance/biomass. *S. polyschides* sporophytes are short-lived and offer temporary, less-stable habitat compared with dominant perennial *Laminaria* species, so shifts in the relative abundances of habitat-formers will likely alter local biodiversity patterns.

1. Introduction

Large brown macroalgae, including species of kelps and fucoids, serve as foundation organisms along temperate and subpolar coastlines, where they form extensive marine forests and provide complex biogenic habitat for a variety of associated species, including understory seaweeds, epiphytes and benthic invertebrates, and support nursery and feeding grounds for highly mobile species, such as fishes, mammals and seabirds (Steneck et al., 2002; Smale et al., 2013). In addition to direct habitat provisioning, large macroalgae alter local environmental conditions and influence resource availability and, as such, marine forests are widely recognised as hotspots of biodiversity and productivity (Steneck et al., 2002; Pessarrodona et al., 2022; UN, 2023). These forests also underpin wider ecosystem services, such as habitat provisioning for commercially important fisheries species and nutrient cycling, which have significant socioeconomic benefits to human societies (Bennett et al., 2015; Blamey and Bolton, 2018; Eger et al., 2023; UN, 2023).

Kelps, fucoids and other large brown macroalgae typically form complex biogenic structures that offer favourable habitats for associated organisms. Kelp sporophytes, for example, can be divided into three morphological and structural compartments: the blade, stipe, and holdfast (Fig. 1). All three tissue components serve a different function for the macroalga (e.g., energy uptake/photosynthesis, stability, attachment), and also offer distinct microhabitats for a diversity of flora and fauna (Christie et al., 2003; Teagle et al., 2017). Field studies on macroalgae-fauna interactions have shown that many species of invertebrates and fishes rely (at least partially) on habitat provisioning by marine forest-formers (Steneck et al., 2002; Teagle et al., 2017; Shaffer et al., 2023). That said, these studies have tended to focus on a few model host species within well-studied regions, such as *Ecklonia radiata* in New Zealand and Australia (Smith et al., 1996; Smith, 2000; Anderson et al., 2005), *Laminaria hyperborea* in the northeast Atlantic (Moore, 1973a, 1973b; Christie et al., 2003, 2009, 2022; Norderhaug et al., 2005; Teagle et al., 2018) and *Macrocystis pyrifera* along the Pacific coast of North and South America (Coyer, 1984; Ojeda and Santelices, 1984; Ríos et al., 2007; Winkler et al., 2017). The ecological role of many other habitat-forming macroalgal species, however, remains poorly described.

A better understanding of the ecological functioning of marine forest-formers is needed to predict the wider consequences of shifts in species distributions and abundances under rapid environmental change

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(Wernberg et al., 2024). Macroalgae are strongly influenced by changes in environmental conditions, and anthropogenic stressors such as ocean warming (Wernberg et al., 2011, 2013; Coleman et al., 2022), the spread of epiphytic and invasive species (Lambert et al., 1992; Piazzi et al., 2001), decreased coastal water quality, and fishing-induced trophic cascades have caused widespread shifts in the distribution of macroalgal species and the structure of marine forests (Johnson et al., 2011; Vergés et al., 2014). Changes in the identity and/or abundance of these foundation species can have implications for local biodiversity, as different macroalgae may support different communities (Smale et al., 2015; Teagle and Smale, 2018; Thomsen and South, 2019). As such, quantifying habitat value and provisioning for associated assemblages is needed to benchmark current biodiversity patterns and generate robust predictions of future changes. Further, faunal assemblages in themselves are sensitive indicators of environmental change, stress and pollution (Smith, 2000 and references therein). Collecting robust baseline data on the structure, composition and diversity of these assemblages can therefore effectively illustrate, identify and contribute to the prediction of future changes in these environments and ecosystems.

Saccorhiza polyschides (LIGHTFOOT) BATTERS 1902, or 'Furbelows', is a pseudo-kelp (belonging to the order Tilopteridales) that is widely distributed across the northeast Atlantic coastline. The current distribution of *S. polyschides* extends from its poleward range edge in Norway to its equatorward limit in Morocco, and it is commonly recorded in both low intertidal and shallow subtidal habitats within a range of low to moderately exposed wave exposure. In recent years, population declines and local extinctions have been recorded towards its equatorward trailing range edge, most likely driven by recent ocean warming, increased marine heatwave activity and changes in coastal upwelling (Fernández, 2011; Díez et al., 2012; Casado-Amezúa et al., 2019). However, further north towards the range centre (i.e., Western English Channel), anecdotal evidence suggests that *S. polyschides* has increased in abundance (Smale et al., 2013), and is now a dominant habitat-forming species in some regions (Salland et al., 2023). This species has a pseudo-annual life cycle (sporophytes typically persist for less than a year in most populations, but up to 12–18 months in some regions), exhibits a unique and distinct morphology (including a large bulbous holdfast and flattened stipe; see Fig. 1) and, as such, contrasts with other dominant (Laminarian) kelps in the region. It may support

distinct communities and harbour different levels of biodiversity, yet few studies have examined its role as a habitat former.

Previous studies on faunal assemblages associated with *S. polyschides* have been conducted in coastal habitats in both the UK (Norton, 1971; McKenzie and Moore, 1981; Gordon, 1983; Salland and Smale, 2021) and on the Iberian Peninsula (Tuya et al., 2011; Fernández et al., 2022). These studies have shown that *S. polyschides* may support lower levels of faunal abundance and diversity compared with longer-lived perennial species, such as *Laminaria hyperborea*, which is characterised by rich and abundant stipe epiphytes and a complex claw-like holdfast (McKenzie and Moore, 1981; Tuya et al., 2011). Even so, remnant *S. polyschides* holdfasts may offer important microhabitat and refugia for over-wintering faunal species (Salland and Smale, 2021). Some previous studies were, however, relatively limited in scope, in terms of spatio-temporal resolution within the short lifespan of this seaweed (McKenzie and Moore, 1981), encompassing environmental gradients or exploring a range of diversity measures (Norton, 1971). Without robust information on spatiotemporal variability in the structure and diversity of faunal assemblages associated with *S. polyschides*, it is not possible to predict how current and future changes in *S. polyschides* populations might affect habitat provisioning and local biodiversity patterns in the Western English Channel, where *S. polyschides* is now a dominant space occupier on low intertidal rocky reefs during its peak-growth season (Salland et al., 2023), and is thought to have proliferated in response to recent environmental changes (Smale et al., 2013).

To address this knowledge gap, we quantified the structure and diversity of faunal assemblages associated with three distinct, morphological microhabitats formed by *S. polyschides* sporophytes at multiple sites situated along a wave-exposure gradient in Plymouth Sound (Western English Channel, southwest UK). We conducted surveys across multiple months, in both intertidal and subtidal habitats, to yield robust information on habitat provisioning and patterns of faunal assemblage structure and diversity within populations of an understudied, yet increasingly dominant, habitat-forming foundation species. The specific research questions of this study are as follows:

- How much biogenic habitat does *S. polyschides* provide for associated assemblages? How much living space is provided by different morpho-functional tissue compartments of the seaweed?
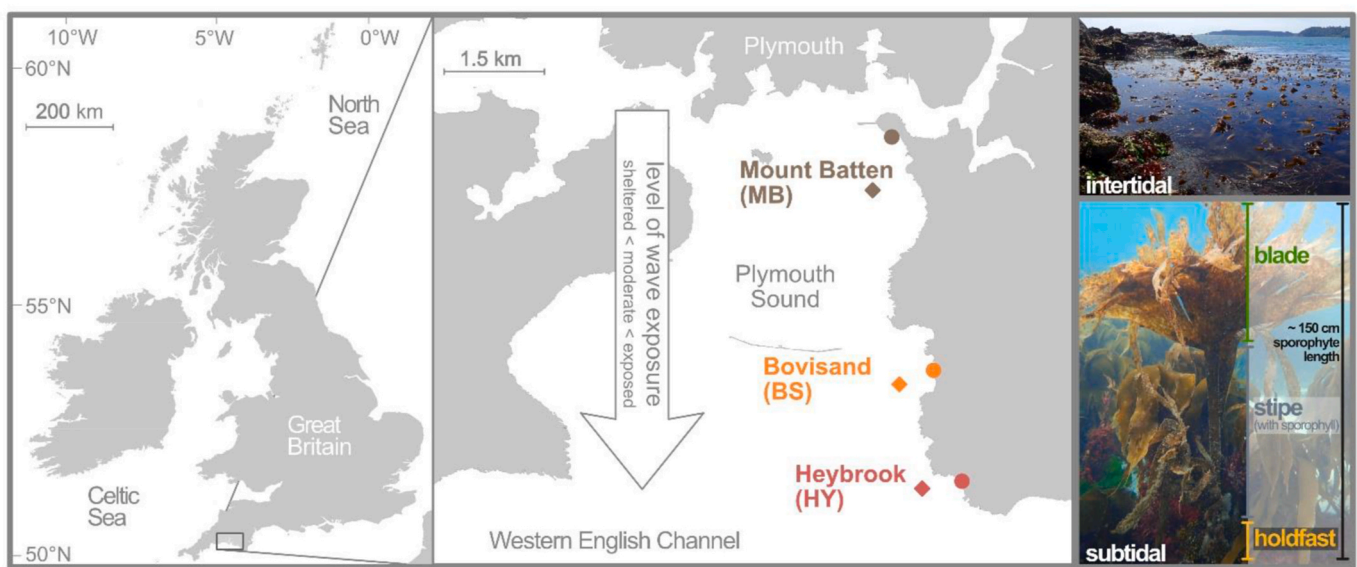

Fig. 1. Map of study area in southwest UK (left), with detailed map of Plymouth Sound (middle). Shown are intertidal (●) and subtidal (◆) sites from North to South and from 'sheltered' through 'moderately exposed' to 'fully exposed'), respectively: Mount Batten (MB), Bovisand (BS), Heybrook (HY). Images (top right) show a typical intertidal stand of *S. polyschides* and a subtidal sporophyte (bottom right) with three morphological components (blade, stipe, holdfast). See Salland et al. (2023) for detailed site location descriptions and biometric information regarding all three morphological components.

- How many invertebrates and how much biomass of faunal assemblages are associated with *S. polyschides* sporophytes?
- Which are the dominating phyla, coarse taxonomic groups and species and how much faunal richness does *S. polyschides* support?
- Does abundance, biomass, richness, and dominating species (i.e., molluscs) differ between sites, months and depths?
- What is the abundance of key invertebrate species across the lifespan of intertidal *S. polyschides* sporophytes in the Western English Channel?

2. Material and methods

2.1. Study region and survey design

Surveys were conducted at three sites within Plymouth Sound, southwest UK (50°N), which were situated along a gradient of wave exposure (sheltered Mount Batten 'MB' < moderately-exposed Bovisand 'BS' < fully exposed Heybrook Bay 'HY') (Fig. 1) (see Salland et al., 2023). Sites were characterised by extensive rocky reef platforms, extending from the high shore to depths of ~5 m (below chart datum), which support dense macroalgal stands. Sites were deemed to be representative of the wider region and largely unimpacted by localised anthropogenic stressors (for further description of the sites and location characteristics see Salland and Smale, 2021; Salland et al., 2023). The principal survey in the current study involved the collection of 10 representative *S. polyschides* sporophytes in 3 months during the summer peak growth season (sampling in June, August, and October 2020). Samples were collected from both intertidal (+0.5 to +0.8 m relative to chart datum, sampled during periods of low tide emersion) and subtidal habitats (2–4 m below chart datum, sampled by SCUBA divers) at each site. Individual sporophytes were randomly selected from mixed macroalgal stands and were situated > 2 m apart from one another. Specimens were cut into three morpho-functional components (i.e., blade, stipe, and holdfast; see Fig. 1), which were directly transferred and separately sealed in a bag to prevent loss of mobile fauna (conducted underwater at the subtidal sites), and then transported to the laboratory for processing.

A secondary survey component focussed specifically on common molluscan grazers and involved the collection of (only) intertidal sporophytes, across an extended period of 15 months from February 2020 until April 2021 (apart from January 2021 due to unfeasible weather conditions). Again, 10 sporophytes were randomly selected, carefully removed from the substratum, transferred to a labelled bag and transported to the laboratory for processing. However, for this secondary survey, only large molluscan grazers were identified and enumerated (see below), and fauna was assigned to the entire sporophyte rather than the separate morphological components.

2.2. Sample processing

On return to the laboratory, morphological measurements were obtained for each of the 540 sporophyte components (3 sites × 3 months × 2 depths × 3 tissue components × 10 replicates). The blade of each sporophyte was laid flat on a white surface with a scale measure and photographed from above (~90° angle). Images were later analysed with ImageJ V1.53f51 with the 'Fiji' plugin (Schindelin et al., 2012; Rueden et al., 2017), to estimate surface area. If the blade tissue was absent (e.g., during months of sporophyte decay) the blade surface area was recorded as zero. Area estimates were doubled to give the combined area of both blade surfaces. The surface area of the stipe was calculated by multiplying the stipe length by the average width (measured along three points along the stipe); values were then doubled to give the combined surface area of both sides of the flattened stipe. The internal holdfast volume (i.e., internal living space of the bulbous, hollow holdfast) was quantified by first measuring the volume through water displacement of the holdfast wrapped in cling film, and then again with unwrapped fragments of the holdfast, and calculating the difference between the two (see Sheppard et al., 1980; Teagle et al., 2018).

For the primary survey (3 months, intertidal and subtidal), all fauna associated with each sporophyte component retained on a 500 μm sieve (Anderson et al., 2005) were preserved in 70% ethanol and later identified, enumerated, and weighed (blotted tissue dry) for biomass. Our taxonomic analysis of the 540 samples adopted a two-pronged approach; first, the entire faunal assemblage was identified to a coarse taxonomic resolution (grouped mostly to class or order level), and secondly, all specimens of molluscs were identified to the species level. This approach allowed the analyse of patterns across the entire assemblages whilst also examining species-level patterns for a subset of the assemblage. Taxonomic analysis did not include sessile, colony-forming mat-like taxa (e.g., bryozoans, hydrozoans).

For the secondary survey, species-level abundances of large molluscan grazers (e.g., *Patella pellucida, Steromphala cineraria*) were recorded for each whole sporophyte (i.e., not separated into microhabitat components) collected across the three intertidal sites and 15 months.

2.3. Statistical analysis

Variability in assemblage structures between sites, months and depths was examined with permutational analysis of variance (PERMANOVA), conducted with PRIMER 7.0.21 and the PERMANOVA add-on (Anderson et al., 2008; Clarke et al., 2014). For the primary survey data, the full model included 'site' (3 levels), 'month' (3 levels) and 'depth' (2 levels) as fixed factors, and 9999 permutations, with the entire sporophyte assemblage (i.e., all tissue components combined) as replicate samples. The 'whole assemblage' dataset based on the abundance of coarse taxonomic groups and the 'mollusc only' dataset based on species-level abundances were analysed separately. For the secondary survey data, the model included 'site' (3 levels) and 'month' (14 levels) as fixed factors, and 9999 permutations, with the assemblage of key molluscan grazers (*Patella pellucida*, *Steromphala* spp., other large gastropods grouping *Tricolia pullus*, *Calliostoma zizyphinum*, *Littorina* spp., *Trivia* spp.) on the entire sporophytes. For both surveys, data were square-root transformed prior to the construction of Bray-Curtis similarity matrices, and a dummy variable (with a value of '1') was included if necessary. Where significant effects or interactions were detected (at $p < 0.05$), pairwise *post-hoc* tests were conducted to determine which groups differed. Similarity percentage (SIMPER) analysis of the primary survey was used to determine which taxa and species contributed most to any observed dissimilarities. Multivariate assemblage structure was visualised with non-metric Multi-Dimensional Scaling (nMDS), conducted with R version 4.3.2 (R Core Team, 2023), RStudio/Posit version 2023.12.0.369 (Posit Team, 2023).

For univariate responses (i.e., living space, total abundance, total biomass and richness), similarity matrices were constructed based on Euclidean distances between untransformed data, before using a univariate permutational analysis approach with the same model described above (with dummy value of '1' if necessary). Furthermore, a one-way PERMANOVA was conducted on the entire dataset to examine variability in total abundance and biomass between the three tissue components (one fixed factor, 3 levels, using 9999 permutations). When unique permutations were below 100, permutations were conducted under a reduced model with Monte-Carlo correction. Finally, relationships between living space and total abundance and biomass were tested for each tissue component with simple linear regression.

3. Results

3.1. Biogenic habitat structure (living space)

For *S. polyschides* sporophytes collected from intertidal habitats, the amount of living space provided by the blade, stipe and holdfast

components increased markedly between June and August, followed by a decline to October for blade and stipe surface area but an increase in internal holdfast volume (Fig. 2a, c, e). This observation was less evident for sporophytes collected from subtidal habitats, as trends in blade surface area and holdfast volume differed between sites (Fig. 2b, d, f). Across the survey, the maximum mean blade surface area was recorded for intertidal sporophytes at HY in August (6584 ± 1088 cm^2), the maximum stipe surface area was recorded for subtidal sporophytes at BS in August (761 ± 75 cm^2), and the maximum internal holdfast volume recorded for subtidal sporophytes at MB in October (435 ± 54 cm^3).

For blade surface area, PERMANOVA detected significant variability across the 3-way 'site × month × depth' interaction term, as well as for 'month' and 'depth' and their interaction term, and for 'site × month' (Table 1). Post-hoc tests within the interaction terms (Table S1) indicated that patterns between sites and months were dissimilar between depths. For stipe surface area, PERMANOVA detected a significant interaction for 'month × depth' and a significant main effect of 'month' (Table 1), with post-hoc tests showing that differences between depths were statistically greater in October (Table S1). For internal holdfast volume, a significant 'site × month' interaction was recorded (Table 1), which was related to increasing dissimilarity between sites through time (Table S1). In general, the main effect of 'month', or its interaction with 'site' or 'depth', was the greatest source of variability in biogenic structure, indicating shifts in *S. polyschides* sporophyte morphology through time.

3.2. Variability in faunal assemblage structure (primary survey)

A total of 40,046 macroinvertebrate individuals were recorded across all 180 sporophyte samples (with a maximum of 1150 organisms per sporophyte). Mean total abundance values were generally low in June but increased markedly in August, with 3- to 30-fold increases recorded at all sites and depths (Fig. 3a and b). Between August and October, total abundance values decreased in the intertidal at HY and in the subtidal at BS and HY (Fig. 3a and b). Abundances at MB (intertidally and subtidally) continued to increase slightly during the same time period, whereas abundances in the intertidal at BS more than doubled, to attain a study-wide maximum abundance value of 835 ± 2 individuals per sporophyte by October (Fig. 3a and b). In general, invertebrate abundance was highest within holdfasts, although blade surfaces also supported notable abundances, particularly in August. Linear regressions indicated significant positive relationships between the living space provided by each morphological tissue components and total faunal abundance (Fig. 4a–c). One-way PERMANOVA detected a significant difference in total abundance between the tissue components (df = 2, F = 44.49, $p \leq 0.0001$), with post-hoc results indicating that abundances were higher on holdfasts than on blades, which in turn were higher than on stipes.

Mean total biomass increased from June to August across all sites and depths (Fig. 3c and d). At most sites, total biomass increased steadily from June to October, except for the intertidal samples at HY where a
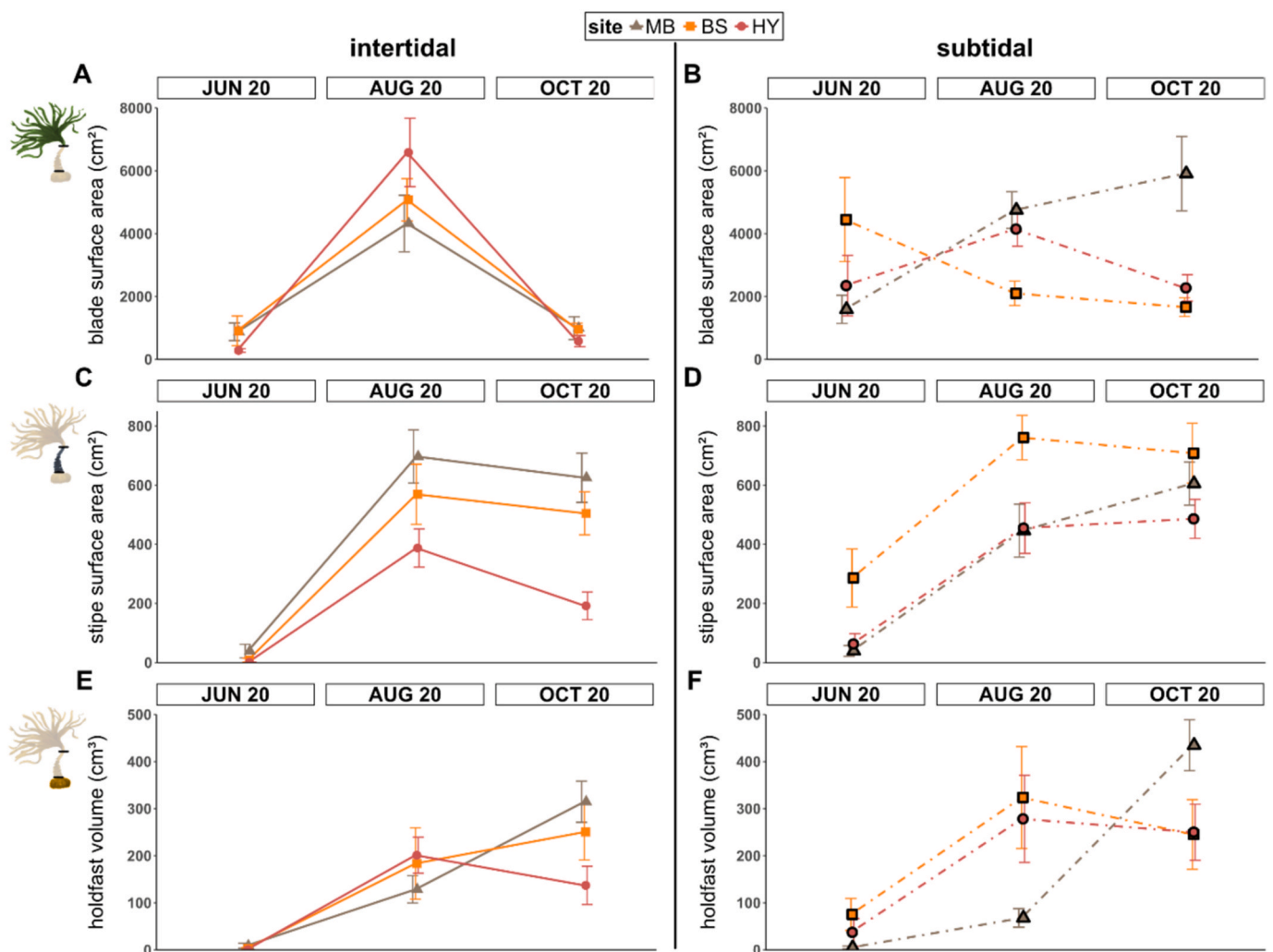

Fig. 2. Living space provided by three tissue compartments of *S. polyschides* sporophytes samples at each month and site in both intertidal **(A, C, E)** and subtidal **(B, D, F)** habitats. Values shown are means (±SE) for blade surface area **(A, B)**, stipe surface area **(C, D)**, and internal holdfast volume **(E, F)**.

Table 1

Results of a univariate PERMANOVA to test for differences in living space provided by distinct morphological tissue components of *S. polyschides* sporophytes samples across sites, months and depths. Results shown for tissue components of blades **(A)**, stipes **(B)**, and holdfasts **(C)**. PERMANOVAs (9999 permutations) are based on Euclidean distances between untransformed data, with 'site' (3 levels), 'depth' (2 levels) and 'month' (3 levels) as fixed factors. Significant values are indicated in bold ($p \leq 0.05$). Post-hoc pairwise test followed PERMANOVAs (Table S1).

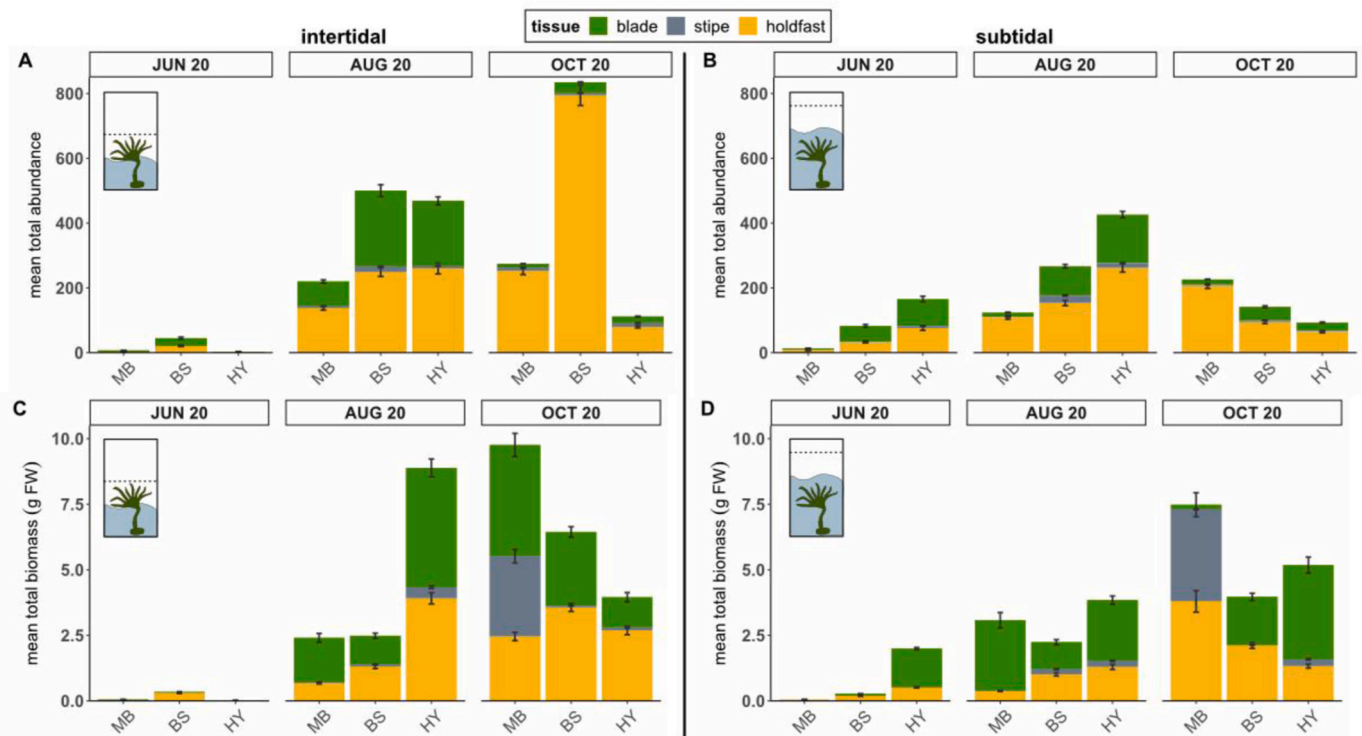|	living space on *S. polyschides* sporophytes								
	A) blade surface area			B) stipe surface area			C) holdfast volume (internal)		
	df	F	p	df	F	p	df	F	p
site	2	1.0199	*0.3684*	2	0.78902	*0.4561*	2	0.49339	*0.6176*
month	2	29.469	***0.0001***	2	158.42	***0.0001***	2	35.861	***0.0001***
depth	1	8.9825	***0.003***	1	1.9451	*0.1588*	1	4.8326	***0.027***
site x month	4	5.762	***0.0001***	4	2.3986	*0.051*	4	5.6498	***0.0002***
site x depth	2	2.7301	*0.0712*	2	0.25844	*0.7674*	2	0.53217	*0.5931*
month x depth	2	16.819	***0.0001***	2	4.4347	***0.0116***	2	0.22705	*0.7985*
site x month x depth	4	4.1488	***0.0027***	4	2.7608	***0.027***	4	1.2669	*0.2866*
Res	162			162			162		

Fig. 3. Mean total abundance (count $\pm$ SE) and total biomass (g $\pm$ SE) of faunal assemblages associated with *S. polyschides* sporophytes collected at each site and month in both intertidal **(A, C)** and subtidal **(B, D)** habitats. Mean values are shown for each sporophyte component separately, entire stacked bar indicates total abundance/biomass per sporophyte.

marked decline in total biomass occurred between August and October (Fig. 3c and d). The maximum mean biomass value was recorded for intertidal sporophytes at MB in October (9.8 ± 0.3 g). The total biomass of associated invertebrates was relatively high in holdfasts and on blades, and comparatively low on stipes, except for MB samples in October in both intertidal and subtidal habitats (Fig. 3c and d). Linear regressions revealed significant positive relationships between the living space offered by each morphological tissue components and total faunal biomass (Fig. 4d–f). One-way PERMANOVA detected a significant difference in total biomass between tissue components (df = 2, F = 21.16, $p \leq 0.0001$), with post-hoc tests indicating that biomass values were similar between blades and holdfasts, which were both higher than on stipes.

Univariate PERMANOVA showed that total abundance varied significantly between main effects and their interaction terms (Table 2). Post-hoc comparisons within levels of the interaction terms showed that

magnitudes of differences were not consistent (Table S2). Univariate PERMANOVA for total biomass detected a significant main effect of 'month' as well as a significant interaction for 'site × month' and 'site × month × depth' (Table 2). Post-hoc comparisons within levels of the interaction terms showed that differences were pronounced in August and October, but not in June (Table S2).

Faunal assemblages comprised a total of nine phyla (Fig. 5) and 28 coarse taxonomic groups (Table S3; Figure S4). Dominant phyla were arthropods, molluscs and annelids (Fig. 5). In terms of faunal abundances, in intertidal habitats, the relative contribution of annelids (mostly polychaetes) increased through the sampling period whereas in subtidal habitats arthropods (mostly amphipods) and molluscs (mostly gastropods) remained dominant throughout (Fig. 5a and b; Figure S4). With regards to total faunal biomass, assemblages in both the intertidal and subtidal were dominated by molluscs (mostly gastropods) throughout the survey at all sites (Fig. 5c and d; Figure S4).
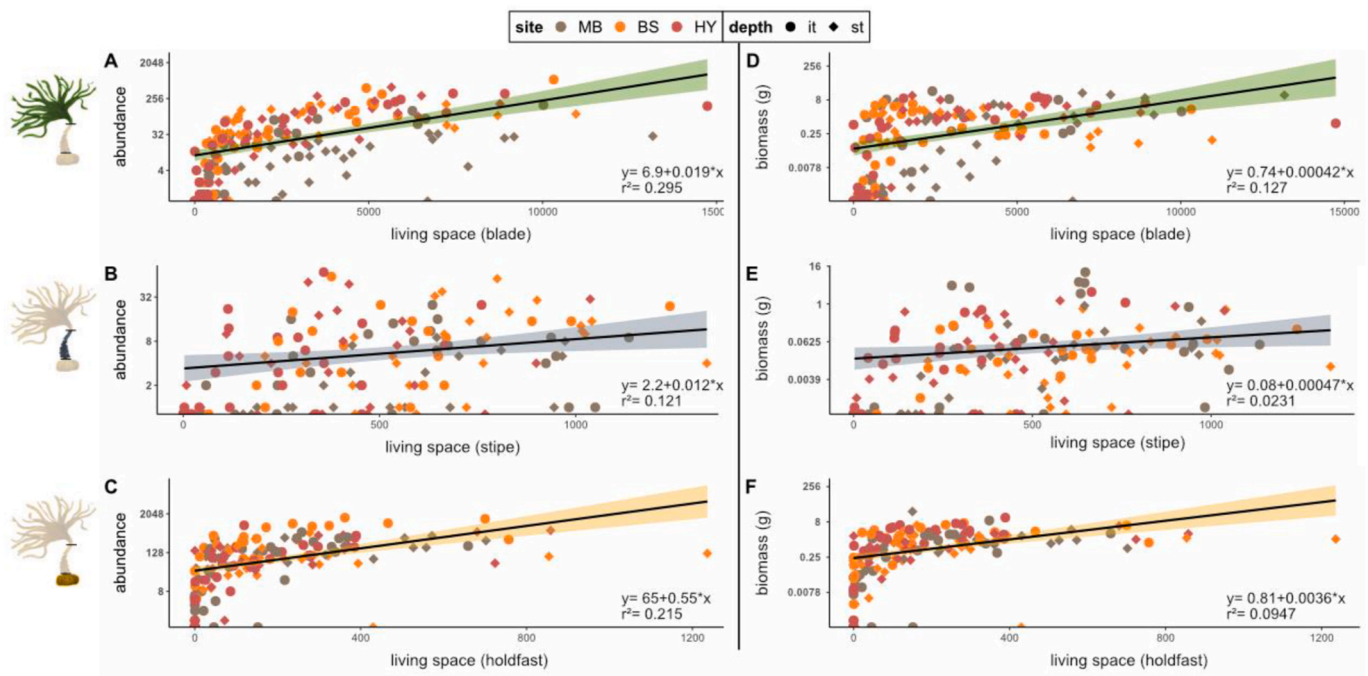
Fig. 4. Relation of total invertebrate abundance **(A, B, C)** and total biomass **(D, E, F)** against living space, separated by morphological and functional tissue components: blades **(A, D)**, stipes **(B, E)** and holdfasts **(C, F)** (x-axes scale consistent within each tissue component type). Significant, linear regressions (p < 0.05) with 95% confidence interval.

Table 2
Results of univariate PERMANOVAs to test for differences in the total abundance, biomass and richness (of different taxonomic classifications). Total abundance (count of specimen) **(A)**, and total biomass **(B)** of invertebrate assemblages, richness of phyla **(C)**, richness of coarse taxonomic groups **(D)**, and richness of molluscan species **(E)**, all associated with *S. polyschides* sporophytes sampled across sites, months and depths. PERMANOVAs (9999 permutations) are based on Euclidian distances between untransformed data, with 'site' (3 levels), 'month' (3 levels) and 'depth' (2 levels) as fixed factors. Significant values are indicated in bold ($p \leq 0.05$). Post-hoc tests see Table S2.

	A) total abundance			B) total biomass			richness C) phyla			D) coarse taxonomic groups			E) mollusc species		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
site	2	11.206	**0.0002**	2	2.8324	0.0623	2	0.68726	0.5076	2	0.86973	0.4261	2	0.99197	0.3699
month	2	35.119	**0.0001**	2	40.003	**0.0001**	2	81.448	**0.0001**	2	100.12	**0.0001**	2	75.136	**0.0001**
depth	1	12.427	**0.0005**	1	0.91001	0.3466	1	0.18251	0.6773	1	0.01599	0.9015	1	1.3623	0.2473
site x month	4	10.172	**0.0001**	4	7.4383	**0.0002**	4	5.3413	**0.0007**	4	7.073	**0.0001**	4	7.2224	**0.0001**
site x depth	2	11.672	**0.0001**	2	0.18555	0.8322	2	2.1074	0.118	2	3.66	**0.0288**	2	4.4883	**0.013**
month x depth	2	10.347	**0.0001**	2	1.3081	0.2777	2	1.2519	0.2844	2	2.8882	0.0602	2	1.9395	0.1457
site x month x depth	4	4.7703	**0.0008**	4	2.6286	**0.0359**	4	1.4829	0.2107	4	0.90493	0.4688	4	2.4883	**0.04**
Res	162			162			162			162			162		

The richness of phyla increased markedly between June and August at all sites and both depths and remained relatively constant between August and October (Fig. 6a and b). The maximum mean richness of six phyla was recorded in the intertidal at HY in August. Richness trends of coarse taxonomic groups exhibited variation across sites, with an increase observed throughout the survey at BS, while richness at MB and HY peaked in August, but had declined by October (Fig. 6c and d). Univariate PERMANOVA showed that the richness of phyla, coarse taxonomic groups, and molluscs varied significantly between months (Table 2). We recorded a significant interaction term of 'site × month' for all richness metrics, a significant interaction term of 'site × depth' for richness of coarse taxonomic groups and molluscs species, and a significant interaction term of 'site × month × depth' for mollusc species (Table 2). Post-hoc results detected different magnitudes of differences between the interaction of 'site × month' and 'site × depth', respectively (Table S2). Post-hoc comparisons between 'site × month × depth' of mollusc species showed differences between sites in October, but not in the remaining two months (Table S2).

Faunal assemblage structure (based on abundances of coarse taxonomic groups) in multivariate analysis (nMDS) showed clusters of the centroids of main factors, despite high variability with the main factors (Fig. 7a, c, e). PERMANOVAs detected significant two-way interactions between all main factors (Table 3) and their interaction terms, and post-hoc tests (Table S5) showed that variability between 'site' was not consistent between 'depth' or 'month'. Interactions between 'month × depth' were highly variable (Table S5). Differences between site, month and depth were only evident in the intertidal between August and October, whereas in the subtidal the magnitude of differences showed no patterns (Table S5). SIMPER analysis (Table S6) showed that the gastropods were the taxonomic key group driving observed variability between factors, followed by amphipods and polychaetes.

For the subset of the assemblage that we identified to a fine taxonomic resolution (i.e., the molluscs), we recorded a total of 57 species (Table S7), belonging to taxonomic groups of gastropods, bivalves, polyplacophores and the development stage of veliger larvae (Figure S4; Table S7). Trends in species-level richness (Fig. 6e and f) were similar to
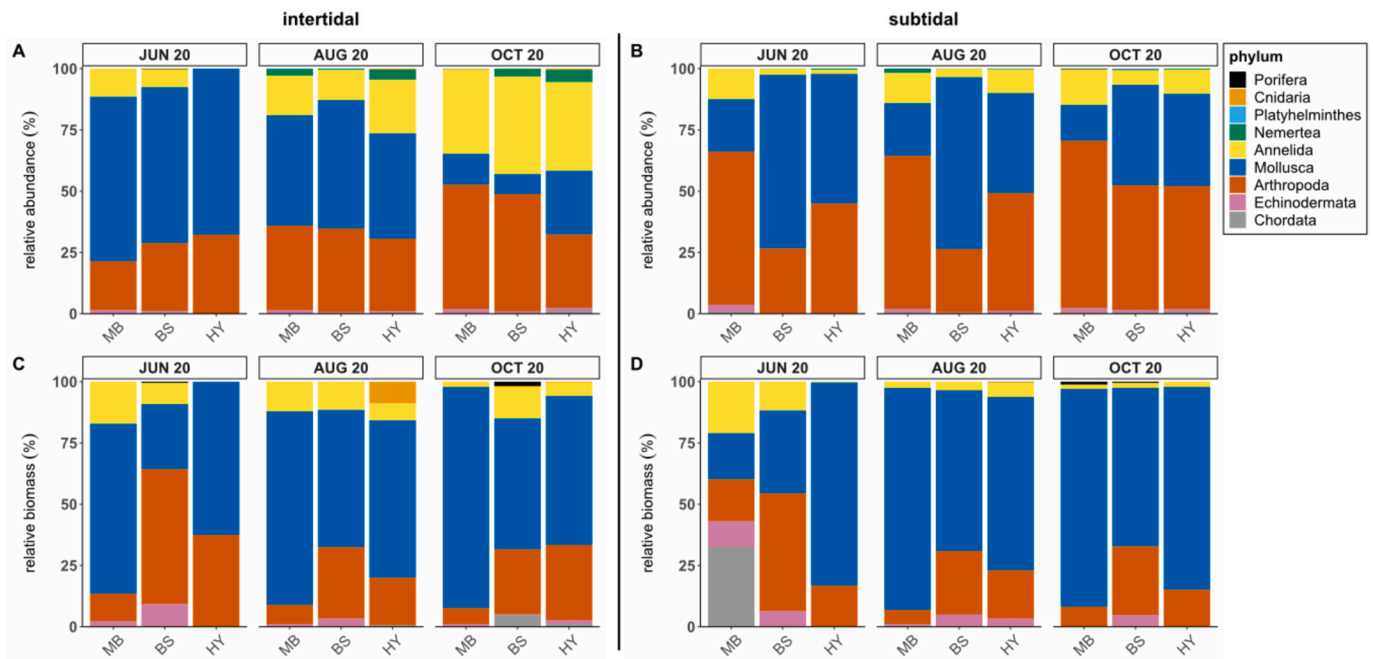
Fig. 5. Relative abundance (%) and relative biomass (%) of faunal assemblages (phyla) associated with *S. polyschides* sporophytes collected at each site and month in both intertidal **(A, C)** and subtidal **(B, D)** habitats.

those observed at coarser taxonomic levels, with a general increase in richness through the survey period, except for HY which showed a slight decline between August and October. Multivariate assemblage structure (based on the abundances of molluscs species), as depicted by nMDS plots, was highly variable with limited structuring across all factors (Fig. 7b, d, f), but evident structure when highlighting the centroids (especially for site and depth, see Fig. 7b). However, PERMANOVA detected significant two-way and three-way interaction terms between all factors (Table 3). SIMPER analysis (Table S8) showed that the gastropod *Patella pellucida* was the key species driving observed variability between factors (28–52% contribution), followed by the bivalve *Modiolula phaseolina* (6–18% contribution) and the gastropod *Steromphala cineraria* (7–18% contribution).

3.3. Abundances of key molluscan grazers (secondary survey)

Over the 15-months study period of the secondary survey, *S. polyschides* sporophytes sampled from intertidal habitats showed marked variability in morphology (i.e., living space) at all survey sites (Figure S9). The living space provided by blades, stipes and holdfasts (morphological tissue compartments) increased rapidly in late spring/early summer, with maximum blade and stipe surface area values attained by July/August, and maximum holdfast volume reached by August/September/October, depending on sites (Figure S9).

The abundance of gastropod grazers was also highly seasonal, with high densities of the blue-rayed limpet *Patella pellucida* (up to 301 ± 123 individuals per sporophyte) observed between July and September (Fig. 8a). The abundance of top shells (primarily *Steromphala cineraria* and to a minor extent *S. umbilicalis*) showed significant variation throughout the year (Fig. 8b). However, during summer, their abundance was 30 times lower than that of *P. pellucida*. The abundance of other large gastropod grazers (i.e., *Tricolia pullus*, *Calliostoma zizyphinum*, *Littorina* spp., *Trivia* spp.) was generally low (Fig. 8c) but peaked in October at BS (3 ± 1 individuals per sporophyte).

Multivariate PERMANOVA results detected a highly significant effect of the main factors 'site' (df = 2, F = 7.1866, *p = 0.0001*), 'month' (df = 13, F = 46.953, *p = 0.0001*) as well as the 'site × month' interaction term (df = 26, F = 3.4154, *p = 0.0001*). Post-hoc comparison within the

interaction term showed high variability of magnitudes and differences between the levels and did not exhibit seasonal patterns between the sites (Table S10).

4. Discussion

Our study contributes to a wider understanding of macroalgae-fauna interactions and specifically on the role of an understudied species, *S. polyschides*, a habitat-former on intertidal and subtidal reefs in the northeast Atlantic. The biogenic habitat provided by *S. polyschides* sporophytes exhibited pronounced seasonal variability, increasing markedly from spring into summer, which coincided with seasonal patterns in assemblage structure and faunal abundance, biomass and richness. Although sporophytes of this species offer habitat for only a limited period of time (12–18 months in the centre of their distribution), its rapid growth rate, large sporophyte size and spacious bulbous holdfast morphology likely enhance the habitat provisioning function of *S. polyschides* within the temperate reef ecosystem. It is also likely that populations of *S. polyschides* found towards the centre of its range, such as in the Western English Channel, are proliferating in response to recent ocean warming trends (Smale et al., 2013; Assis et al., 2018; Salland et al., 2023) and, as such, the relative importance of this species as a habitat-former and driver of local community structure is increasing.

We recorded over 40,000 macroinvertebrates, belonging to 57 mollusc species, 28 coarse taxonomic groups and nine phyla, associated with the 180 sporophytes, and revealed strong positive relationships between biogenic living space, faunal abundance and biomass. While the abundance and richness of faunal assemblages associated with *S. polyschides* may be lower compared to *Laminaria hyperborea* (Christie et al., 2003), the current dominant habitat-former in the Western English Channel, our study shows that *S. polyschides* provides important, well used, habitat, particularly during periods of peak sporophyte biomass in late summer and early autumn (Salland et al., 2023). Based on mean standing density of ~14 sporophytes m^{-2} across all sites and depths in August (see Salland et al., 2023) and an average faunal abundance of ~330 individuals per sporophyte across all sites and depths in August, we estimate a total faunal abundance of > 4600 individuals m^{-2} associated with *S. polyschides* populations in summer.
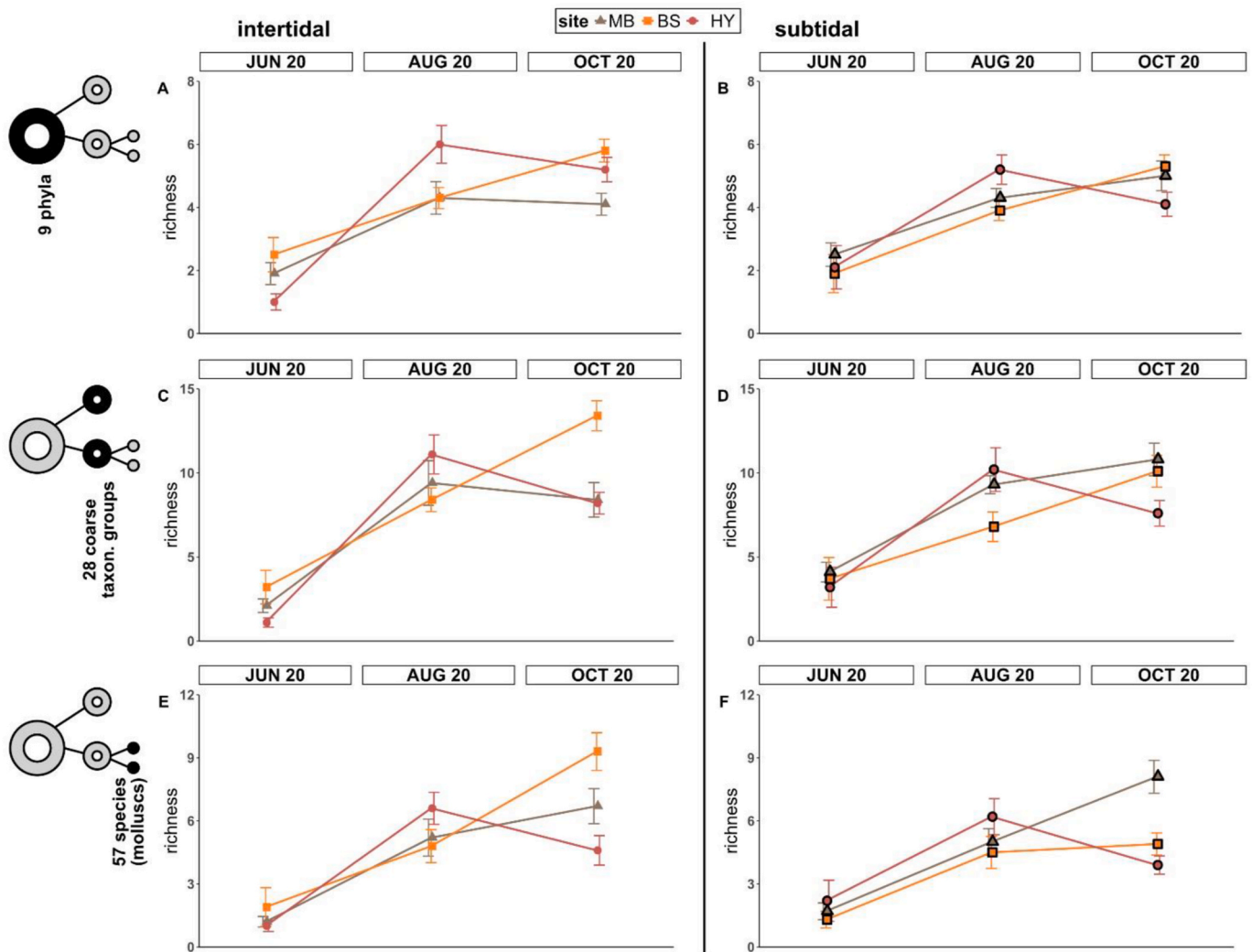
Fig. 6. Mean richness (±SE) of faunal assemblages associated with *S. polyschides* sporophytes collected at each site and month in both intertidal **(A, C, E)** and subtidal **(B, D, F)** habitats. Richness measures were calculated at three taxonomic resolutions: phyla **(A, B)**, coarse taxonomic groupings **(C, D)**, and richness of mollusc species **(E, F)**. Note the change of scale in y-axis.

Similarly, holdfasts alone supported a mean total abundance of ~200 individuals across all sites and depths in August, which can be scaled up to > 2700 invertebrate specimens m^{-2} exclusively associated with *S. polyschides* holdfasts. A previous study conducted in the region recorded faunal abundance values of ~1500 individuals m^{-2} associated with holdfasts of the cold-temperate kelp *L. hyperborea* (Teagle et al., 2018), suggesting that *S. polyschides* holdfasts support nearly twice the amount of invertebrates during the peak summer month of August.

We recorded high levels of variability in living space and faunal abundance, richness and biomass across survey months. The total abundance and biomass of associated organisms differed between the three tissue components. Norton (1971) found that some invertebrate taxa prefer living space associated with the blades, whereas other species may be associated with stipes or holdfasts, largely dependent on size, feeding strategy or life stage. A recent study on microbial assemblages associated with seaweed hosts also found that bacterial richness varied between tissue components (Lemay et al., 2021). Strong seasonality in faunal diversity and community structure is characteristic of mid-latitude temperate reef ecosystems, which experience pronounced intra-annual variation in key factors such as temperature, nutrients, light, disturbance and food availability (Ríos et al., 2007; Winkler et al., 2017, Akita et al., 2019). Many invertebrate taxa exhibit strong seasonality in population demography, leading to intra-annual variation in

wider community structure (Wing et al., 2003; Broitman et al., 2008). Here, a combination of the seasonality in biogenic habitat availability related to the life cycle of *S. polyschides* sporophytes and seasonal patterns in invertebrate recruitment and growth resulted in high between-month variation in faunal assemblage structure. Similar patterns and links between the structural complexity of habitat-formers and the structure of associated assemblages have been recorded for other seaweeds (Gibbons and Quijón, 2023), such as brown macroalgae in the Mediterranean Sea and their associated meiofaunal communities (Losi et al., 2018). When comparing the findings of this study with assemblage-level data gathered from the same locations during winter (see Salland and Smale, 2021), we observed a notable exponential increase in the abundance, biomass, and richness of associated invertebrate assemblages from winter to late summer/autumn, again indicating the marked seasonality in these assemblages. General increases in faunal abundance and richness from spring through summer have been reported previously for both annual and perennial habitat-forming kelp species (Arnold et al., 2016, Akita et al., 2019), and are likely a common feature of temperate reef ecosystems. Variation between 'site' and 'depth' was less pronounced, although these factors had an interactive effect with 'month' for some assemblage metrics. Variability in the structure of assemblages associated with kelp is driven by abiotic and biotic factors such as wave exposure (Norderhaug et al., 2012),
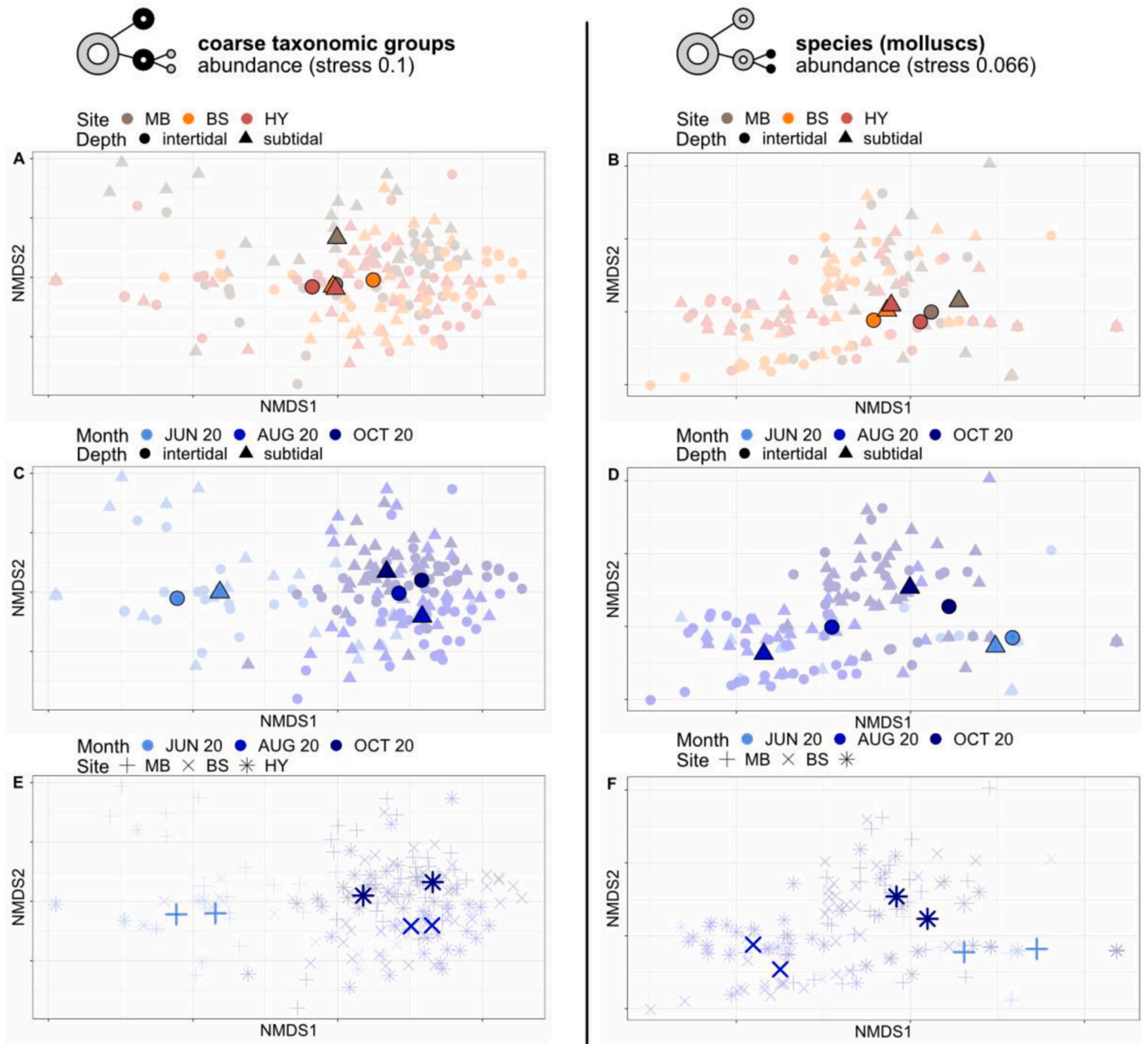
Fig. 7. Non-metric MDS plots depicting multivariate structure of invertebrate assemblages associated with *S. polyschides* sporophytes across three sites and two depths over three sampling occasions. Ordinations are based on square-root transformed abundances of coarse taxonomic groups **(A, C, E)** and species-level abundances of molluscs **(B, D, F)**. Plots show the interaction of terms 'site × depth' **(A, B)**, 'month × depth' **(C, D)** and 'month × site' **(E, F)** (centroids are highlighted).

storminess (Byrnes et al., 2011), light availability (Connell, 2003), sedimentation rates (Moore, 1972; Connell, 2003; Traiger, 2019), predation (Byrnes et al., 2006; Shelton et al., 2018), and, recruitment patterns (Almanza et al., 2012). These factors, particularly wave exposure and light levels, were likely important here and further work across broader gradients is warranted.

Prior research on communities associated with *S. polyschides* predominantly focused on the bulbous holdfast (Barber, 1889; McKenzie and Moore, 1981; Gordon, 1983), which is known for its considerable structural complexity. Notably, we observed the highest abundance, richness, and biomass of associated invertebrates either on or within these holdfasts. Despite this, the blades of *S. polyschides* play a significant role, particularly as a habitat for grazing gastropods during the summer months before sporophyte senescence. In contrast, stipes represent the least valuable microhabitat having supported the lowest abundance and

richness values. Overall, the abundance and biomass of invertebrates exhibited a positive correlation with the living space provided by all three tissue component structures. Similar correlations have been established in previous studies regarding faunal diversity and abundance concerning the holdfast volume and size of *L. hyperborea* and *E. radiata* (Sheppard et al., 1980; Ojeda and Santelices, 1984; Smith et al., 1996; Anderson et al., 2005). The facilitative positive relationships between the biogenic living space offered by *S. polyschides* and faunal assemblage structure indicate the importance of this macroalga as a habitat-forming foundation species.

Mollusca was the dominant phylum comprising invertebrate assemblages associated with *S. polyschides* sporophytes in the Western English Channel, with species of gastropods (e.g., *Patella pellucida* and *Steromphala cineraria*) and bivalves (e.g., *Modiolula phaseolina*) exhibiting high abundance (maximum abundance of *P. pellucida* > 800

Table 3

Results of multivariate PERMANOVA to test for differences in the structure of invertebrate assemblages associated with *S. polyschides* sporophytes sampled across sites, months and depths. Assemblage structure was based on both the abundances of coarse taxonomic groups (whole assemblage) **(A)** and species-level abundances of molluscs **(B)**. PERMANOVAs (9999 permutations) are based on square-root transformed data and Bray-Curtis resemblance matrices with 'site' (3 levels), 'month' (3 levels) and 'depth' (2 levels) as fixed factors. Significant values are indicated in bold ($p \leq 0.05$). Post-hoc pairwise test followed PERMANOVAs (Table S5) and SIMPER analysis (Table S6 for coarse taxonomic groups; Table S8 for molluscan species).

	A) coarse taxonomic groups (abundance)			B) mollusca species (abundance)		
	df	F	*p*	df	F	*p*
site	2	4.7385	**0.0001**	2	7.7411	**0.0001**
month	2	59.901	**0.0001**	2	57.949	**0.0001**
depth	1	6.8093	**0.0001**	1	4.0943	**0.0007**
site x month	4	4.6914	**0.0001**	4	3.0325	**0.0001**
site x depth	2	4.4707	**0.0001**	2	3.4382	**0.0002**
month x depth	2	5.8891	**0.0001**	2	3.5588	**0.0002**
site x month x depth	4	1.8752	**0.0089**	4	2.1215	**0.0013**
Res	162			162		

individuals per sporophyte) and biomass (maximum biomass of *S. cineraria* > 21 g per sporophyte) values. These gastropods are typically grazers/herbivores, feeding either directly on the seaweed tissue and often inhabiting 'living homescars' (rather than homescars in rocks, as described in Firth, 2021) or consuming epiphytic biofilms (Schaal et al., 2010; Mayombo et al., 2020). Even so, only a small portion of the seaweed biomass is likely to be directly consumed, as the vast majority enters coastal carbon cycles as detritus, and is generally consumed by detritivores, such as amphipods, or bacteria (Krumhansl and Scheibling, 2012). An increase in availability or processing rates of organic matter can also contribute to the diet of filter-feeders (Leblanc et al., 2011), such as bivalves. Results from our secondary survey (15 months, intertidal) showed that the abundance of the gastropods *P. pellucida* and *S. cineraria* followed the seasonal growth cycle and habitat provision of the kelp (i.e., living space), declining when kelp sporophytes senesced. Similar demographic patterns for these species have also been observed on the Isle of Man (Norton, 1971). Interestingly, in June, August, and October 1964, Norton (1971) recorded 98% of *S. cineraria* individuals occurring on the blades of *S. polyschides*, with the remaining 2% associated with holdfasts. In contrast, we recorded only 62% of individuals occurring on blades, about 7% on stipes, and 31% associated with holdfasts in the same months in 2020 (at both depths in Plymouth Sound). Moreover, total abundances of *S. cineraria* in the Western English Channel were about six times higher than those previously
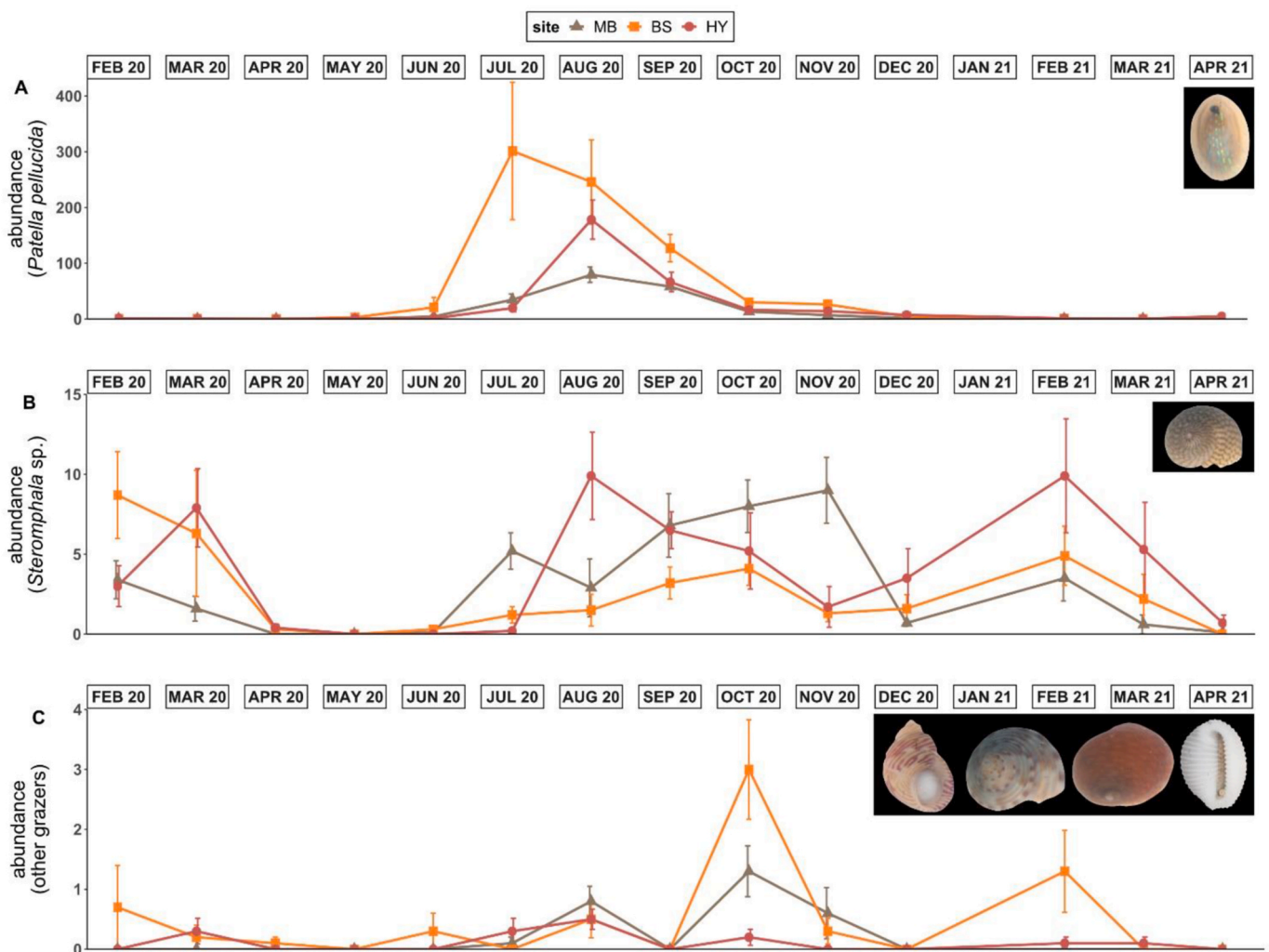

Fig. 8. Mean abundance values (count ± SE) of dominant molluscan grazers associated with intertidal *S. polyschides* sporophytes at three sites over 15 months. Abundances shown for the Blue-rayed limpet *Patella pellucida* **(A)**, Topshell *Steromphala* spp. **(B)**, and other dominant gastropods (i.e., *Tricolia pullus*, *Calliostoma zizyphinum*, *Littorina* spp., *Trivia* spp.) **(C)**. Note the change in abundance scale on the y-axis.

recorded by Norton (1971) in the late 1960s. Further, records of *P. pellucida* were over 100-fold greater in Plymouth Sound in 2020 than at the Isle of Man in the 1960s. As such, the population structure, behavioural patterns and microhabitat preferences of key gastropod grazers may vary considerably across *S. polyschides* populations within the UK.

The taxa richness of stipes and holdfasts we observed for *S. polyschides* was lower than that reported previously for the cold-water kelp *L. hyperborea* (McKenzie and Moore, 1981; Christie et al., 2003; Teagle and Smale, 2018), but similar to the warm-water kelp *L. ochroleuca* (Teagle and Smale, 2018). The local dominant, *L. hyperborea* (Smale and Moore, 2017), typically supports a rich and abundant stipe-associated epiphytic assemblage, which underpins a facilitative habitat cascade and supports high levels of biodiversity (Teagle and Smale, 2018; King et al., 2021). In contrast, the minimal attachment of epiphytic algae on *S. polyschides* stipes (authors' personal observation) offered far less complex secondary habitat and supported far lower faunal abundance, richness and biomass. Total invertebrate biomass values we recorded for *S. polyschides* holdfasts (maximum mean of 3.9 g per holdfast) by late summer were, however, broadly comparable to those reported for *L. hyperborea* holdfasts (estimated mean of 4.5 g per holdfast) in the same study region (Teagle and Smale, 2018).

In an earlier study, McKenzie and Moore (1981) compared the composition, richness, and abundance of faunal assemblages associated with *S. polyschides* and *L. hyperborea*. They found that the large, bulbous, hollow holdfasts formed by *S. polyschides* were inhabited by some mid-size to larger species (e.g., larger decapods and fishes), whereas the complex, claw-like haptera of *L. hyperborea* holdfasts supported smaller to mid-size species. In contrast, Tuya et al. (2011) did not record differences in functional groups of fauna associated with *S. polyschides* and *L. hyperborea* populations in northern Portugal. A recent study conducted in Spain by Fernández et al. (2022) showed that, in a region where both species are found towards their equatorward range edges, the holdfasts of *S. polyschides* offered less favourable habitat than those of *L. ochroleuca*, but both kelps supported similar richness, and total abundances of associated species. Overall, our results suggest that *S. polyschides* in the Wester English Channel may offer a similar function as perennial, habitat forming Laminariales in summer, when its sporophytes are large and complex and standing stock is high, but not during other seasons when sporophytes are either absent, small, or decaying. Our results showed that the total abundance of invertebrates associated with holdfasts may be up to twice as high in *S. polyschides* when compared to *L. hyperborea* (Teagle et al., 2018), although comparisons are only valid during summer, when sporophytes of both species are present and in good condition. As such, any climate-driven shift in dominance from cold-adapted kelp species (e.g., *L. hyperborea*, *L. digitata* and *S. latissima*) towards the more southerly warm-adapted *S. polyschides* would represent a shift towards a less stable habitat, with implications for local biodiversity and community structure. During winter, however, *S. polyschides* offers living space for a reduced abundance of invertebrates and provides unstable, short-lived habitat.

In conclusion, the habitat provision by *S. polyschides* has been undervalued in the NE Atlantic. Despite the short lifespan of its sporophytes, it offers three distinct microhabitats formed by morphofunctional tissue components, rapid growth rates and extensive biogenic habitat (Salland et al., 2023). The unusual, unique morphology of the bulbous holdfast varies a lot from the functional structure of other regional habitat-forming kelps (i.e., *Laminaria* spp.). We believe that its role as a foundation species for a diverse marine, benthic community is crucial and has been previously undervalued. Our survey results deliver beneficial baseline data and insight to understand habitat provision by *S. polyschides* in the Western English Channel, which is located in a biogeographic transition zone (Forbes, 1853; Dinter, 2001; Hiscock et al., 2004). Our observations offer a monitoring foundation for future comparisons with assemblages under climate change scenarios (Gibbons and Quijón, 2023), and faunal communities across the broader distribution area of *S. polyschides*.

CRediT authorship contribution statement

Nora Salland: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Antony Jensen:** Writing – review & editing, Supervision. **Dan A. Smale:** Writing – review & editing, Supervision, Conceptualization.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106519.

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