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Variability in epifaunal assemblages between *Sargassum muticum* and *Zostera marina*; a functional group approach

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Abstract

Marine macrophytes are globally important to coastal ecosystems, providing refugia, nutrients and important ecological processes. The structure and composition of macrophytes have a bottom-up effect on the epifauna they support. Due to their wide-reaching effects, invasive algae are considered one of the greatest threats facing marine ecosystems. *Sargassum muticum* is a Japanese algae increasing its non-native range in coastal habitats globally. A highly dispersive algae, able to colonise soft substratum, it is considered a threat to seagrass beds across the North East Atlantic. In Salcombe Estuary, Devon, beds of *Zostera marina* have seen increasing levels of invasion by *S. muticum*. Here, the epifaunal communities of *Z. marina* and *S. muticum* within the estuary were sampled and analysed. *Z. marina* hosted 1041 individuals from 36 taxa, with 11 unique species, whilst *S. muticum* hosted 2106 individuals from 37 taxa with 12 unique species. The community assemblages of *S. muticum* were characterised by higher abundance but lower diversity and species richness. Trophic functionality is compared using the functional group approach designed by Fauchald and Jumars (1979), with *S. muticum* hosting higher levels of surface detritivores and jawed carnivores, whilst *Z. marina* hosted higher numbers of suspension feeders and herbivores. Across both plants, a positive relationship was found between species diversity and functional diversity. The results suggest that a change in macrophyte assemblage could radically alter associated assemblages and thus functionality. Due to Covid-19 restrictions, data sampling was limited to one weekend in late October, so further studies would be required to test temporal and spatial variability between habitats.

Keywords: Ecosystem functionality, invasive species, macrophytes, *Sargassum muticum*, *Zostera marina*.

Introduction

Marine macrophytes such as seaweeds and seagrasses play vital roles in coastal ecosystem functioning, acting as habitat engineers and directly influencing the biotic assemblages which occur (Klein & Verlaque 2009, Egan et al. 2013). The presence of macrophytes provides refugia from environmental fluxes and pressures faced by subtidal and intertidal organisms (Hurd 2015, Xiao et al. 2021) and can greatly enhance the diversity of the otherwise homogenous environments in which they occur, such as sand and mud flats (Tweedley 2006). The increase in spatial complexity as well as the provision of nutrients and protection from predation (Henninger et al. 2009, Thiriet et al. 2014) can alter the co-occurring biotic assemblages, particularly the epifaunal assemblages, living directly on and around the macrophyte. In turn, the epifaunal assemblages determine the overall functionality of an ecosystem, performing fundamental ecological processes and creating vital links to higher trophic levels through the provision of a feeding landscape for predators (Warfe & Barmuta 2004, Tano et al. 2016). Patterns of diversity in both terrestrial and marine environments differ among host plants and algae. Though few species exhibit host specificity (Viejo 1999, Parker et al. 2001), many aspects of the structure and composition of the host plant will impact the organisms which can thrive. Size and complexity play an important role in shaping not only the amount but the variety of refugia offered to species (Thomaz & Cunha 2010), more complex habitats offer heterogenous interstitial spaces to support a range of sizes as well as life stages such as eggs and larvae (Thiriet et al. 2014, von Nordheim et al. 2018). Indirect associations between algae and epifauna have been known to alter with increasing or decreasing epiphyte load (Martin-Smith 1993, Viejo 1999) and the form of nutrients provided by the system determines the food availability for herbivores and detritivores (Duarte & Cebrián 1996). Additionally, variations in morphological and ecological aspects, such as biomass, height, percentage cover and longevity of the plant are known to be important, with differences in composition found between annual and perennial species (Wernberg et al. 2001). The composition of the habitat engineer species plays an important role in bottom-up ecosystem functioning.

Invasive macrophytes can alter the fundamental structure of ecosystems, causing a cascade of effects on the biotic assemblages (Schaffelke et al. 2006, Pyšek et al. 2020). As invasive species spread around the globe, the open and connected nature of marine ecosystems makes them particularly vulnerable to invasions, and within coastal environments the likelihood of invasions is greatly increased due to the proximity and quantity of anthropogenic pathways such as shipping and aquaculture (Carlton & Geller 1993). With high dispersive potential and colonisation ability, marine macrophytes are thought to pose one of the greatest threats to marine ecosystems (Schaffelke et al. 2006, Küpper & Kamenos 2018). The recruitment and colonisation of an invasive macrophyte can dramatically change the structure of the native macrophyte assemblage (Parker et al. 2001, Crooks 2002), although the full nature of these effects is still poorly understood and difficult to predict (Williams & Smith 2007). The impact of the invader on the recipient habitat is largely dependent on the structure of habitats. Epifaunal assemblages associated with invasive alga have found to be impoverished in comparison to native; however, this was linked to the lower complexity of the invader (Navarro-Barranco et al. 2018). Structural differences between invasive and native macrophytes can have both positive and negative effects on the epifaunal community structure, resulting in increased

abundance of fauna (Navarro-Barranco et al. 2019), reduced diversity (Klein & Verlaque 2009, Suárez-Jiménez et al. 2017) and in the case of some specific taxa such as molluscs, a reduction in population stability (Veiga et al. 2018). Although consistent predictions cannot be made about all invasion events, invasive habitat engineers will inevitably have an impact on associated biotic assemblages.

The effects of invasive habitat engineers on ecosystem functioning are less well known and in need of further study. The change in structure of the habitat may change light availability, nutrient provision, water flow regime and various other ecosystem level processes (Crooks 2002) as well as the associated food web dynamics (Warfe & Barmuta 2006, Farina et al. 2014). Although little is known about the impacts on functionality of the ecosystem, previous studies have shown that invasive macroalgae can result in biotic homogenization and a reduction in overall functionality in vital marine ecosystems (Navarro-Barranco et al. 2018). Biotic homogenization occurs when ecologically distinct communities become similar or indistinct, through the loss or gain of species, often because of anthropogenic activity, with invasion events known to be a primary driver of biotic homogenization (McKinney 2004). Invasion events often result in increased abundance of generalist species, outcompeting the rarer, more specialist species (Muthukrishnan & Larkin 2020). According to the insurance hypothesis, higher biodiversity increases resilience to disturbance, allowing disturbed ecosystems to retain functionality, as some species will be less impacted than others (Yachi & Loreau 1999). This view is contradicted by the idea that most communities are characterized by a few dominant species which perform the bulk of the ecosystem functioning (Cardinale et al. 2000) and the finding that the diversity of functional groups is more important than the diversity of species in controlling ecosystem processes (Tilman et al. 1997). Moreover, the relationship between productivity of an ecosystem and species diversity is thought to interact with environmental context, with the variation in productivity caused by species diversity changing with spatial heterogeneity, and variation caused by species composition changing with disturbance regime (Cardinale et al. 2000).

Sargassum muticum (Yendo) Fensholt is a finely branched macroalgae native to Japan, but now widely dispersed in coastal regions around the globe (Engelen et al. 2015). Its arrival to, and presence in, the East Atlantic Ocean has been documented since the early 1970's (Farnham et al. 1973) and by 1976 it had arrived in Plymouth, South West Devon (Boalch & Potts 1977). Contrary to predictions that it would not threaten seagrass beds due to its reliance upon hard substratum, it quickly began colonising disturbed patches of seagrass (Den Hartog 1997). The spread of *S. muticum* is thought to be facilitated through the drifting of detached fertile branches with air filled gas bladders (Engelen et al. 2015), and recruitment in to soft substratum aided by the thick rhizome mats created by the seagrass (Tweedley et al. 2008) and its ability to "stone walk;" or attach to a stone a drift to a new habitat (Critchley 1983). *S. muticum* exhibits fast growth throughout the summer months, and an annual period of senescence through winter, in which the vegetative thallus is shed and the holdfast remains (Wernberg et al., 2001), eliminating the need for it to expend energy maintaining the thallus through the winter, or to recolonise the next year.

Seagrass meadows are highly important coastal habitats, distributed globally across tropical and temperate oceans (Jayatilake & Costello 2018), and providing significant ecosystem services including primary productivity and carbon storage (Kennedy & Björk 2009, Nordlund et al. 2018). Occurring exclusively in soft substratum, seagrass meadows significantly increase habitat complexity and consequently the diversity and abundance of associated fauna of the homogenous environments in which they occur (Tweedley 2006), a phenomenon which interacts with changes in meadow characteristics such as complexity (Boström & Bonsdorff 2000) and biomass (Attrill et al. 2000, Smale et al. 2019). In areas otherwise dominated by sand or mud flats, seagrasses provide important nursery habitats for juvenile fish and invertebrates; however, this importance is reduced in the presence of other structurally complex habitats such as coral reefs and algae (McDevitt-Irwin et al. 2016). Due to their coastal range, seagrass beds are particularly susceptible to multiple pressures from marine and land based activities (Griffiths et al. 2020) including introduced species, dispersed through anthropogenic activity, many of which have negative effects on the associated ecology (Williams 2007). Around the UK, seagrass beds, dominated by *Zostera marina* (L), are believed to have declined by up to 92%, with around 44% of the decline occurring since the 1980's (Green et al. 2021). The increasing colonisation of degraded seagrass beds by *S. muticum* is considered a threat to *Zostera* species and their associated fauna.

Few studies have looked in depth at the differences in community assemblage of *S. muticum* and *Z. marina* (see: Tweedley 2006, DeAmicis 2012). This study aims to discern the differences in epifaunal assemblages supported by these two co-occurring habitat species through a) using field and laboratory-based methods to sample, identify and quantify epifauna, b) utilising univariate and multivariate community measures to highlight and investigate differences including species diversity, richness and abundance between assemblages and c) assigning trophic functionality groups to each species to detect possible changes to functionality which could occur as a result of a changing environment.

Methodology

Study site and sampling methodology

The study was conducted in the subtidal mixed beds of *Zostera marina* and *Sargassum muticum* in Salcombe-Kingsbridge estuary in Devon, South west England (**Figure 1**). Due to COVID-19 restrictions, data collection was limited to one site, Woodville Rocks (50°13'56"N, 03°46'18"W) across 3 low tides (0.5m below chart datum) from October 17th – 19th 2020.

Salcombe-Kingsbridge is a dendritic estuary, meaning it has very little freshwater input, and experiences almost fully marine conditions in which both *Z. marina* and *S. muticum* can thrive (DeAmicis 2012). Due to the large seagrass beds and the highly biodiverse flora and fauna found in and around the estuary, Salcombe has been classified as a Site of Special Scientific Interest (SSSI). With a number of small villages situated along the banks of the estuary, most of the estuary experiences some level of anthropogenic activity, from agriculture to boating activities, meaning anthropogenic pressures include increased nutrients from run off and seabed scarring from boat anchors. Due to Salcombe Estuary being classified as an SSSI and *Zostera marina* being protected under the Wildlife and Countryside Act 1981,

permission to sample the site was obtained from the South Devon Area of Natural Beauty estuaries officer.



Figure 1: Location of study site; Woodville Rocks, Salcombe-Kingsbridge Estuary (50°13'56"N, 03°46'18"W)

Sampling was conducted by wading in water depths of 0.5 - 1m at low spring tides and haphazardly placing 1m² quadrats within areas of *Z. marina* or *S. muticum*. An FBA net with a 900 µm mesh was used to sweep in random directions within the quadrat for 30 seconds per sample and 30 replicates were collected of each vegetation type. Samples were emptied into a tray, large and easily identified fauna such as large gastropods were noted and released. The remainder of the sample was transferred in to sampling pots, preserved in 70% ethanol and labelled.

Laboratory analysis

In the laboratory, samples were rinsed in freshwater over a 500µm sieve and hand sorted with forceps to remove all vegetation and separate fauna into small pots. Fauna was then identified to the lowest taxonomic level possible (species and family level) using microscopy and Hayward and Ryland dichotomous keys (Hayward & Ryland 1995).

Functional Groupings

For the purposes of this study, functional groups have been defined as groups of species which perform similar ecological functions within an environment. The method used to group these is known as trophic analysis and was originally devised by Fauchald and Jumars (1979) for assessing the ecological function of Polychaetes,

then further developed by Pearson and Rosenberg (1987) to include other benthic fauna. This method assigns each species a three-letter functional group based on three aspects of their biology: trophic type, level of mobility and feeding type (**Table 1**). Groups were assigned using Hayward and Ryland (1995) and further information from primary and secondary literature. Some species are known to have more than one feeding method; in this instance feeding type was assigned based on the primary feeding method. For example, a growing body of evidence suggests *Gammarus zaddachi* exhibits predatory and cannibalistic behaviours, but is known to be primarily a detritivore, therefore S (surface detritivore) was assigned. This grouping method was chosen as it has demonstrated ability to identify some interesting differences between groups and has proven successful in other similar studies (see: Bonsdorff & Blomqvist 1993, Bonsdorff & Pearson 1999) although criticism has been raised that limiting fauna to such a small number of categories can minimise the importance of other functions and interactions to structuring ecosystems (Bremner et al. 2003). Further studies into the change of functionality may find interesting results when using a more in-depth analysis such as Biological Trait Analysis; but a higher level of species expertise will most likely be required for accurate analysis (Bremner et al. 2003). Each species was assigned a functional group. In most cases, particularly in the dominant groups, multiple species were assigned the same functional group, and data from these were accumulated to form one group. A total of 12 functional groups were identified and are presented in **Table 1** along with the number of contributing species and examples of species assigned. A full list of species and functional groups can be found in Appendix 1 (available as a supplementary file).

Statistical analysis

Both univariate and multivariate techniques were applied to the data using the VEGAN package in R Studio (R Core team 2020). Multivariate analysis was carried out to investigate the differences in assemblages of *Z. marina* and *S. muticum*. A square root transformation was applied to reduce the influence of highly abundant species and homogeneity of variance was verified using a betadisperser permutest. A Bray-Curtis similarity index was generated using the transformed data and visualised using non-metric multidimensional scaling ordinations (nMDS). Differences between habitats were compared using a PERMANOVA (function `adonis`, 999 permutations) and further investigated using a SIMPER analysis to identify which taxa contributed the most to the differences.

Functional group data were first transformed using a 4th root transformation to satisfy the assumption of homogeneity of variance (Permutest $p > 0.05$). The same analysis as above was run on these data; a Bray-Curtis similarity index followed by nMDS scaling, a PERMANOVA and a SIMPER analysis. For further analysis, the functional groups were then categorized into trophic groups using the first letter of the Functional group description (for the purposes of this analysis, Burrowing Detritivores and Surface Detritivores were grouped together as Detritivores) into "Herbivores," "Carnivores," "Detritivores," and "Suspension feeders." As the data for carnivores and suspension feeders did not initially meet the assumptions of normal distribution, they were transformed using square root and log transformations (respectively). Welch's T-tests were run on all groups to compare levels of abundance between vegetation.

Welch's T-tests were run on raw, untransformed data to identify differences between assemblages on *Sargassum* and *Zostera* for metrics such as Species richness, Shannon-Weiner diversity index and Pielou's Evenness Index on both the overall assemblage data and the functional group data. The most abundant taxonomic groups (crustaceans and molluscs) were identified and Welch's T-tests were run to check differences in diversity between these. A linear regression model was applied to identify any significant relationship between species diversity and functional diversity

Table 1: Adapted from Boström et al. 2006. Lists Functional Groups identified, number of contributing species and examples of taxons assigned.

Group	Description	No. species	Example
BDJ	Burrowing Semi mobile Detritivore	1	<i>Corophidae spp.</i>
CMJ	Mobile Jawed Carnivore	11	<i>Crangon crangon</i>
CMX	Mobile Carnivore	5	<i>Nucella lapilus</i>
FDC	Semi mobile Carnivorous Suspension feeder	3	<i>Antedon bifida</i>
FDJ	Semi mobile Jawed Suspension feeder	1	<i>Phtisica marina</i>
FDT	Semi mobile Tentaculate Suspension feeder	1	<i>Anemonia viridis</i>
FDX	Semi mobile Suspension feeder	2	<i>Caprella linearis</i>
FMX	Mobile Suspension feeder	3	<i>Ophiocomina nigra</i>
HMJ	Mobile Jawed Herbivore	1	<i>Macropodia rostrata</i>
HMX	Mobile Herbivore	9	<i>Bittium reticulatum</i>
SMJ	Mobile Jawed Surface detritivore	7	<i>Hippolyte varians</i>
SMX	Mobile Surface Detritivore	4	<i>Rissoa guerini</i>

Three letter code refers to Feeding Type (*H* = Herbivore, *F* = Suspension Feeder, *S* = Surface Detritivore, *B* = Burrowing Detritivore, *C* = Carnivore), Motility (*M* = Mobile, *D* = Semi Mobile, *S* = Sessile), Feeding habit (*J* = Jawed, *C* = Ciliary Mechanism, *T* = Tentaculate, *X* = Other method not covered). No. species column shows how many species in total contributed to each functional group.

Results

A total of 3147 individuals belonging to 48 taxa were collected and identified. 1041 individuals from 36 taxa were identified in *Zostera marina* whilst 2106 individuals were identified from 37 taxa in *Sargassum muticum*. Crustaceans were the most abundant and the most species rich group, contributing 77% and 69% of the total abundance and 61% and 54% of the species of *Z. marina* and *S. muticum*, respectively. Molluscs were the second most abundant and species rich, contributing 13% and 30% of total abundance and 22% and 30% of species of *Z. marina* and *S. muticum*, respectively. The most numerically abundant species overall (totals listed as *Z. marina* and *S. muticum*, respectively) were *Hippolyte varians* (143, 474) followed by *Rissoa parva* (24, 546) and *Ischyrocerus anguipes* (205, 203). The diversity of crustaceans was lower on *S. muticum* than on *Z.marina* (Welch's two sample t-test $t = -2.1559$, $df = 27.989$, $p < 0.05$) but there was no significant difference found in mollusc diversity between treatments (Welch's two sample t-test $t = -1.1702$, $df = 23.821$, $p > 0.05$) (**Figure 2a**). *Z. marina* was found to host 11 unique

species, i.e., species not found on *S. muticum*, whilst *S. muticum* hosted 12. Results are presented in **Table 2**.

Species richness did not differ significantly between treatments (Welch's two sample t-test $t = -0.7922$, $df = 25.432$, $p > 0.05$) (**Figure 2b**) but significant differences were found in Shannons Diversity Index (Welch's t-test $t = -4.6952$, $df = 27.355$, $p < 0.001$) (**Figure 2c**) and Pielou's Evenness Index (Welch's t-test $t = -3.8884$, $df = 24.902$, $p < 0.001$) (**Figure 2d**) with *Z. marina* ranking higher in both. This is likely to be at least in part due to the high abundance of some species found in *S. muticum*.

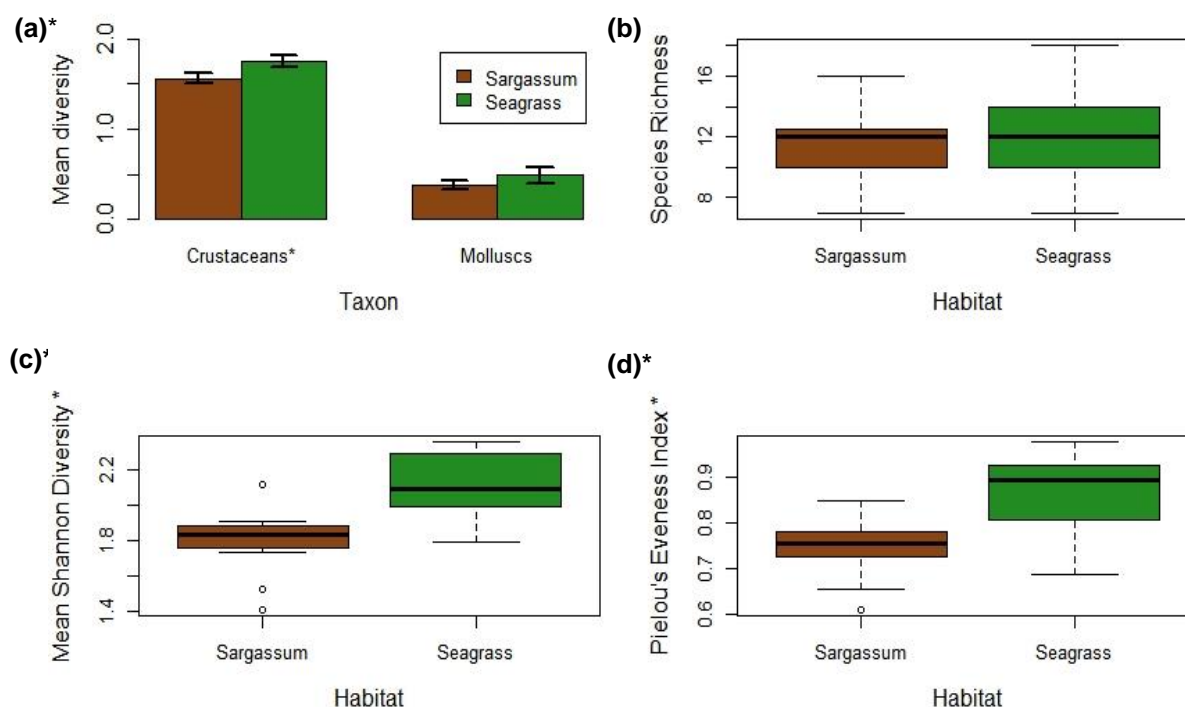


Figure 2: (a) Bar plots showing the results of T-Tests comparing mean diversity of crustaceans and molluscs (b) Box and whisker plots showing mean species richness (c) mean species diversity and (d) mean Pielou's Evenness Index between *S. muticum* and *Z. marina*. *indicates significant difference found.

Table 2: Results of data collected on community assemblages on *Z. marina* and *S. muticum* plants

	Total Abundance	Total Species	Unique sp.	% species Mollusc	% species Crustacean	% Crust abund	% Moll abund
<i>S. muticum</i>	2106	37	12	30%	54%	69%	30%
<i>Z. marina</i>	1031	36	11	22%	61%	77%	13%

Multivariate analysis was used to assess differences in communities between the vegetation. MDS ordination revealed distinct communities in each habitat (**Figure**

3a) and to confirm significance, a PERMANOVA was applied (PERMANOVA $r^2=0.279$; $F=10.881$; $d.f.= 1,28$; $p < 0.001$). Further investigation through a SIMPER analysis revealed the top contributors to the difference as *Rissoa parva*, *Hippolyte varians*, *Orchestia gammarellus*, *Processa canaliculata*, *Gammarellus zaddachi*, *Ophiocomina nigra* and *Jujubinus striatus* (**Figure 3b**).

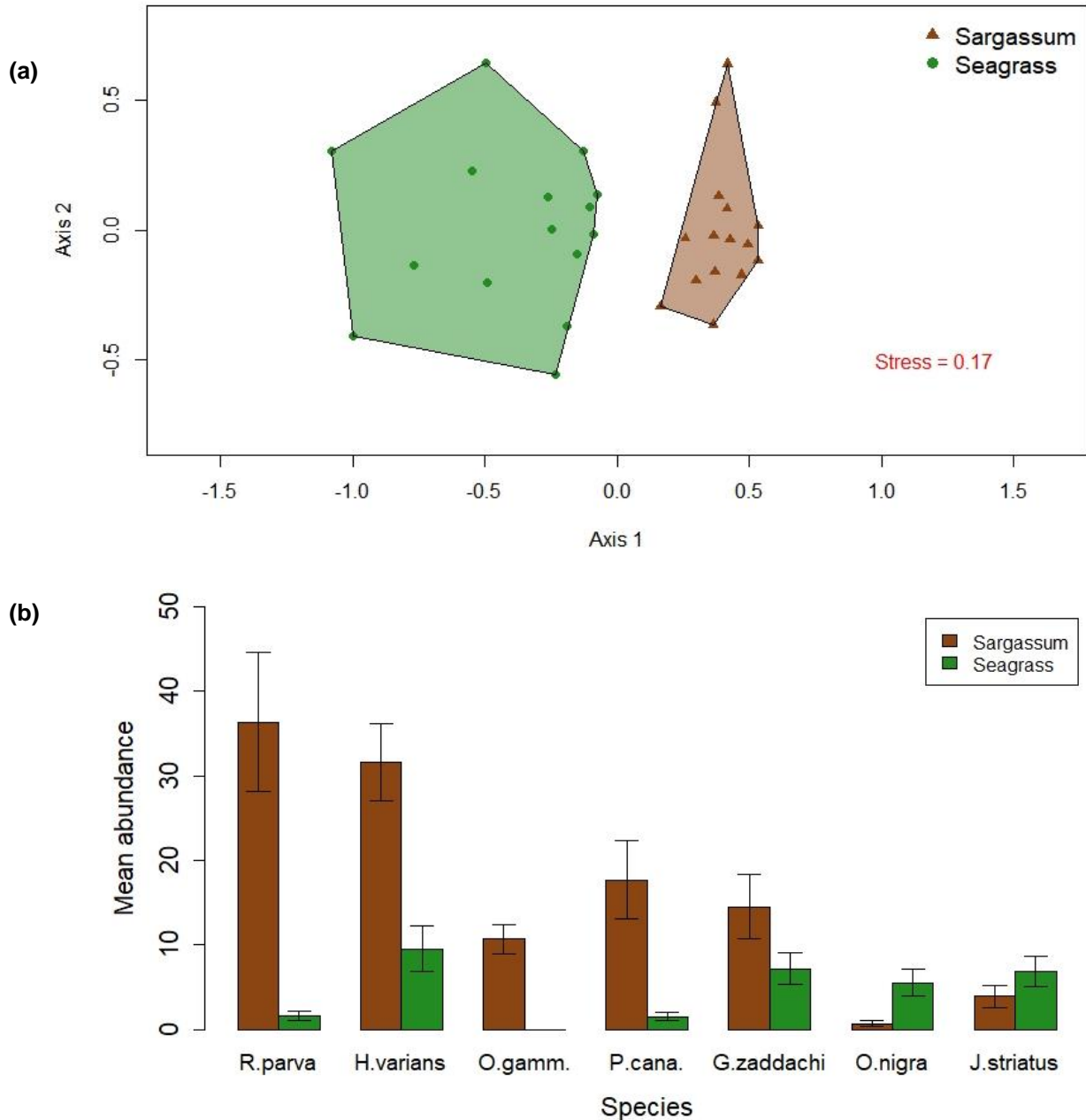


Figure 3 (a) nMDS ordination showing differences between *Z. marina* and *S. muticum* in community group assemblages and **(b)** mean abundance of the species contributing highest to the differences, identified by SIMPER analysis.

Functional group data satisfied the assumptions of the permutest and significant groupings were found in the nMDS ordination (**Figure 4a**), confirmed by the

PERMANOVA (PERMANOVA $r^2=0.296$; $F=11.786$; $d.f.= 1,28$; $p < 0.001$). SIMPER analysis revealed the top contributors to the differences to be SMX, FDJ, FMX, FDX, SMJ, CMJ, HMX (**Figure 4b**). *S. muticum* hosted higher levels of mobile surface detritivores and mobile jawed carnivores but ranked lower in mobile and semi mobile filter feeding species, as well as herbivores, all of which were present in higher numbers on *Z. marina*.

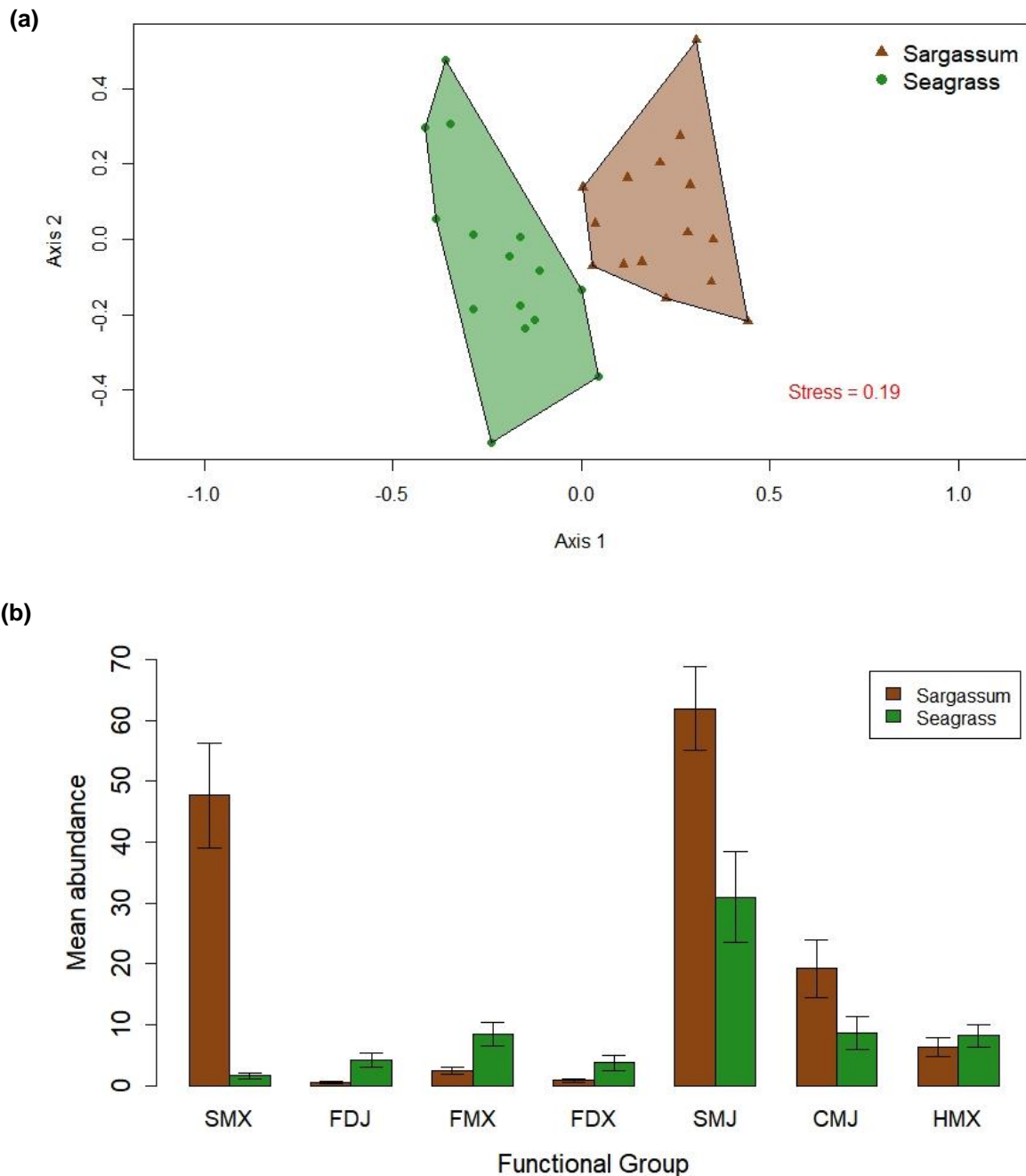


Figure 4 (a) nMDS ordination showing differences between *Z. marina* and *S. muticum* in functional group assemblages and (b) mean abundance of the species contributing highest to the differences, identified by SIMPER analysis. For Functional Group codes, see **Table 1**

Trophic group analysis found no significant differences between herbivores (Welch's two sample t-test $t = -0.65145$, $df = 27.676$, $p > 0.05$) or carnivores (Welch's two sample t-test $t = 1.8452$, $df = 24.769$, $p > 0.05$) but found a significantly higher number of suspension feeders in *Z.marina* (Welch's two sample t-test $t = -3.3613$, $df = 26.474$, $p < 0.005$) and a higher number of detritivores in *S. muticum* (Welch's two sample t-test $t = 4.956$, $df = 22.616$, $p < 0.001$) (**Figure 5a**).

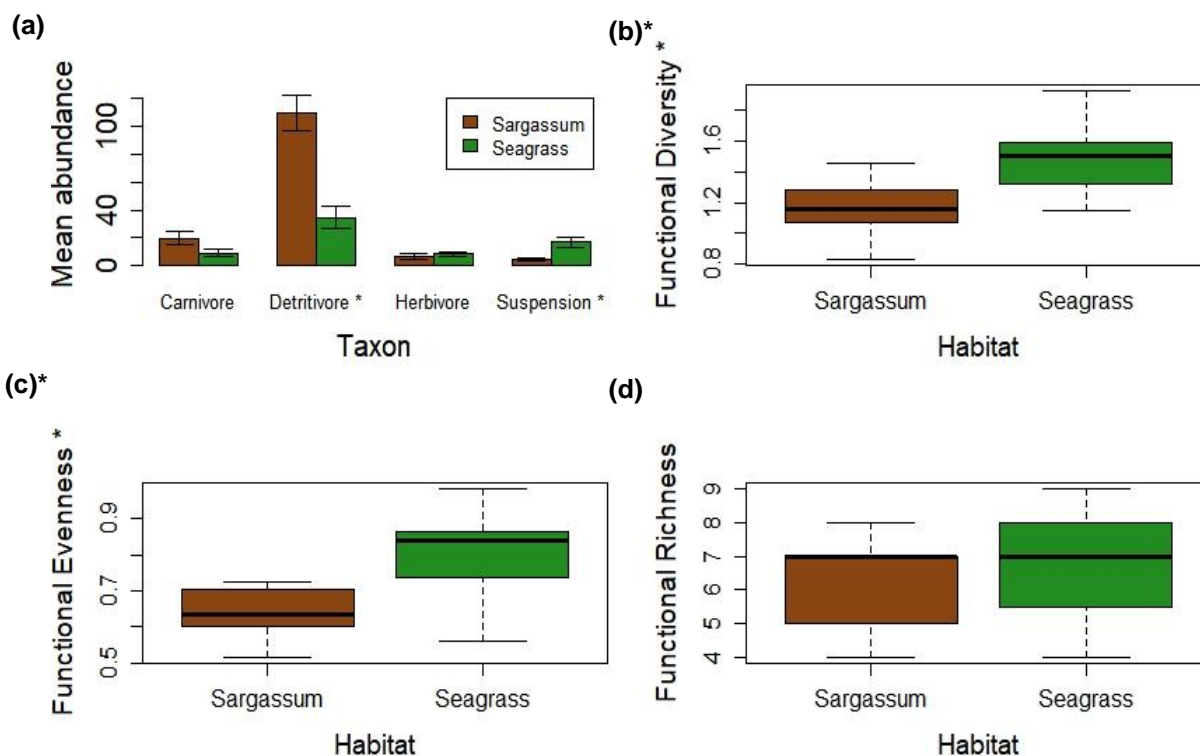


Figure 5: (a) Bar plots showing the results of T-Tests comparing mean abundance of four main trophic groups (b) Box and whisker plots showing mean Functional Diversity (c) mean Functional Evenness and (d) mean Functional Richness between *S. muticum* and *Z.marina*. * indicates significant difference found.

Within the Functional groups, both Shannons diversity and Pielou's evenness indexes were found to be significantly higher in *Z. marina* (Welch's two sample t-tests; $t = -4.1014$, $df = 24.954$, $p < 0.001$ (**Figure 5b**); $t = -4.2225$, $df = 21.611$, $p < 0.001$, (**Figure 5c**) respectively) but no difference was found in functional group richness (Welch's two sample t-test $t = -0.95814$, $df = 25.927$, $p > 0.05$) (**Figure 5d**). A significant positive relationship was found between species diversity and functional diversity ($R^2 = 0.645$, $p < 0.001$) (**Figure 6**).

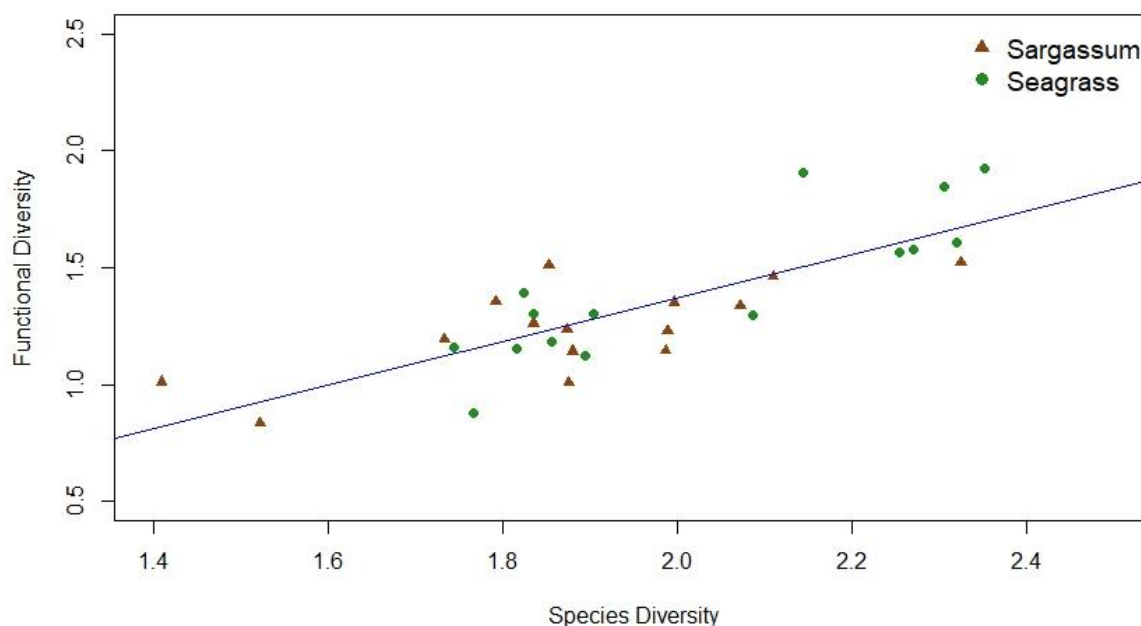


Figure 6: A linear regression model showing a significant positive relationship between Species Diversity and Functional Diversity within *Z. marina* and *S. muticum* assemblages.

Discussion

Sargassum muticum supports a functionally different epifaunal community to *Zostera marina*, characterized by higher abundance and lower diversity. *Z. marina* hosted less than half the numerical total of individual organisms hosted by *S. muticum*, but ranked higher in species diversity and evenness, including diversity of the most abundant group, crustaceans. An even number of species were supported by both macrophytes. Distinct functional communities were found to exist between species, with *S. muticum* hosting a far higher number of mobile surface detritivores and carnivores whereas *Z. marina* hosted higher numbers of herbivores and suspension feeders.

Although some studies have exposed detrimental impacts of invasive species on epifaunal communities (Gordon 1998, Molnar et al. 2008, Navarro-Barranco et al. 2018), others have found that morphology is the most important factor in shaping assemblages, and a morphologically complex species, whether native or invasive, will harbour a more diverse community than one of lower complexity (Parker et al. 2001, Suárez-Jiménez et al. 2017). A study on *S. muticum* stands in Australia showed a positive correlation of epifaunal abundance with increased habitat complexity created by an abundance of epiphytes which peaked in the winter months (Martin-Smith 1993), consequentially resulting in a peak abundance of crustaceans, as seen in this study. Anecdotally, a high number of epiphytes were seen in the *S. muticum* samples (Hickman pers. obs.), although no data were collected on this. This could explain the abundance of *Hippolyte varians* which, although able to exploit a broad range of habitats, have shown preference for algae with a “bushy” structure, and an abundance of epiphytes (Berggren 1993). The increased abundance of individuals on morphologically complex *S. muticum* is consistent with

previous studies finding that *S. muticum* is likely to host a small number of species in great abundance (Norton & Benson 1983, Harries et al. 2007) and can host up to 250% more individuals than *Z. marina* (Tweedley 2006). Within seagrass beds themselves, biomass, and amount of plant available are thought to be important in shaping assemblages (Attrill et al. 2000, Smale et al. 2019). In this environment, *Z. marina* experiences die back in autumn and winter, therefore would naturally not have been at its peak levels of growth during sampling, potentially impacting the fauna present. However; it should be noted that *S. muticum* has proven detrimental impacts on the defensive phenol production (DeAmicis & Foggo 2015) and the photosynthetic ability (Tweedley 2006) of *Z. marina*, potentially increasing its vulnerability to grazing and lowering its growth rate, and has significantly reduced the cover of native macrophytes in other settings (Staehr et al. 2000, Sánchez et al. 2005), so a reduction of *Z. marina* biomass as a direct result of *S. muticum* spread cannot be ruled out. The shape, biomass and complexity of a habitat engineer is important in shaping species assemblages and should be measured seasonally and at different stages of life history to fully assess the strength of this relationship.

Other temporal variations seem to play a significant role in shaping epifaunal communities. Although this study revealed no differences in species richness, this contradicts findings of a long-term study on the same area, in which species richness positively correlated with presence of *S. muticum* (Tweedley 2006). Due to Covid-19 restrictions, this study was conducted over a short period of time (2 days) during stormy conditions in late October, when both macrophytes would have experienced some die back and disturbance.

S. muticum has a period of fast growth in the summer, reaching heights of 120cm, followed by senescence and detachment of primary laterals from around September (Wernberg et al. 2001) and this is associated with strong seasonal variations in epifauna (Wernberg et al. 2004), including a loss of diversity (Norton & Benson 1983). Due to this, it can be assumed that with a longer study period and repeated sampling to monitor temporal changes, the results would have been different. It is also likely that in a habitat in which *Z. marina* is perennial and *S. muticum* is an annual (DeAmicis & Foggo 2015), *Z. marina* may be vital for the survival of some species and a dominance of *S. muticum* could result in a long term loss of diversity as the slower growing, longer lived or less disturbance resilient species may not survive the annual dieback of the habitat (Strong et al. 2006). The reduced diversity of communities could indicate that *S. muticum* assemblages are exhibiting biotic homogenization, as suggested by previous studies which found high levels of similarity in *S. muticum* replicates (Staehr et al. 2000, Harries et al. 2007). If the findings of reduced diversity and biotic homogenization are consistent, the reduction in biodiversity could impact the ecosystems resilience and ability to survive disturbance events (Yachi & Loreau 1999) or cause a loss of unique species (Muthukrishnan & Larkin 2020), a theory which is supported by the positive relationship found in this study between species diversity and functional group diversity. However, the finding that *S. muticum* hosted more unique species than *Z. marina* indicates that although some species may be unable to inhabit the invader, others may well fill the niche they leave. Long term studies on patterns of diversity and functionality would provide a clearer picture of ecosystem level impacts of the invasion.

A change in macrophyte assemblage can change the rate of organic decomposition and nutrient availability. *S. muticum* is known to exhibit high levels of productivity, with faster decomposition than perennial species with thicker tissues (Pederson et al. 2005). This nutrient availability could explain the far higher abundance of detritivores found in *S. muticum* stands. Food sources for species found living on *S. muticum* are likely to be different to those on *Z. marina* and therefore attract different species. *S. muticum* is known to accumulate high levels of silt and detritus in the autumn months (Norton & Benson 1983). Five out of six of the species identified as the highest contributors to the community differences via SIMPER analysis were mobile surface detritivores and present in high abundance on *S. muticum*. *Rissoa parva*, the top contributor; is a species of minute gastropod which is known to be abundant in finely branched algae where detritus and silt collect (Hayward & Ryland 1995) and relies heavily on detritus in its diet (Wigham 1976), and *Hippolyte varians*, the second highest contributor; is known to stir and sweep the sediment for organic matter (Coombs & Allen 1978). Conversely, previous studies have suggested that up to 98% of epifauna associated with *S. muticum* tend to be herbivorous (Viejo 1999), therefore environmental conditions and time of year could have resulted in higher levels of siltation, facilitating less herbivorous grazing than the summer months. Higher plants, including *Z. marina*, lock much of their nutrient production underground in roots and rhizomes, meaning that whilst their carbon storage is around 4 times more effective than macroalgae, the nutrients available for epifauna is reduced (Duarte & Cebrián 1996). The slightly higher number of herbivores on seagrass beds could be supported by vast diatom assemblages which contribute up to 83% of primary production in seagrass beds (Cox et al. 2020). Alternatively, herbivory could of course be on the seagrass itself, due to the afore mentioned lowered defensive compounds produced in the presence of *S. muticum* (DeAmicis & Foggo 2015). The increased siltation on *S. muticum* could suggest the canopy is slowing or interrupting the flow regime and stratifying the water column, as seen in previous studies (see: Strong et al. 2006). This could limit the movement of sediment offshore and result in an increase in suspended particles which has the potential to reduce the abundance of filter feeding species (Ostroumov 2005). The low numbers of suspension feeders found on *S. muticum* could alter the water quality and further inhibit the growth of *Z. marina*. Shading by *S. muticum* is already known to be a problem to native macrophytes (Britton-Simmons 2004), but, additionally, filters feeders are known to clear the water in turbid environments such as estuaries, enhancing the light availability for photosynthesis by *Z. marina* (Wall et al. 2008). If filter feeders are unable to inhabit *S. muticum* to the same extent as *Z. marina*, this could have implications for the future of *Z. marina* beds within the system. Although macrophytes often produce nutrient levels in excess of that required by the systems they support (Duarte & Cebrián 1996), the availability of these nutrients will vary dramatically and alter the species which are able to exploit it.

The open landscape of seagrass beds are important landscapes for predation by fish (Tano et al. 2016) which may contribute to the lower abundance of individuals than on the comparatively closed, protected seaweed stands. Previous experiments removing fish from *S. muticum* stands by caging revealed no differences in the levels of epifauna, indicating potentially low effects of predation of epifauna from *S. muticum* (Martin-Smith 1993). The change of epifauna and high structural complexity of *S. muticum* as a habitat could restrict important feeding opportunities and inhibit predator success (Warfe & Barmuta 2004), breaking trophic links in coastal food

webs. In tropical areas, however, this has not been found to be the case and seaweed has proven to be potentially even more important as a feeding ground than adjacent seagrass beds (Tano et al. 2016) and in temperate marine systems, the presence of *S. muticum* is thought to have increased food web connectivity (Salvaterra et al. 2013). Though this study shows some changes in ecosystem functionality, other studies have highlighted the importance of size and location of patch sampled on the functionality, citing for example a higher abundance of HMX species in outer beds of seagrass and a general lack of representation from CMJ species (Boström et al. 2006). The lack of CMJ species within seagrass beds could potentially be a normal and expected pattern of nearshore seagrass beds and may not be related to the presence of *S. muticum*. A study of 13 seagrass beds over 80km in the Baltic sea found that physical and environmental characteristics such as fetch, and shore angle were among the most important in shaping functionality (Boström et al. 2006). Therefore, whilst this study reveals some interesting considerations, a longer-term study would have to be conducted over a broader spatial scale in order to develop a clearer understanding on the functional impacts of *S. muticum* invasion.

Conclusions

Sargassum muticum supports different epifaunal assemblage to *Zostera marina*, assemblages which are higher in abundance but lower in diversity and evenness. The assemblages on *S. muticum* are comprised largely of surface detritivores, with slightly more mobile carnivores, less herbivores and a significant loss of filter feeders. An increase in mobile surface detritivores and decrease of herbivores in *S. muticum* is suggested to be a result of the increased availability of detritus due the timing of the study, the slowing of water flow by the *S. muticum* canopy and the complexity of the habitat providing smaller niches and accumulating silt, whereas the reduction in filter feeding could be a result of increased sedimentation. Temporal variations such as annual senescence of *S. muticum* stands could have disproportionate impacts on sensitive species, resulting in a loss of diversity. However, an equal level of species richness and a similar number of unique species on both habitats suggest that whilst some species may be lost to *S. muticum*, others may be gained. The loss of diversity seems to be mostly due to the high abundance of species such as *Rissoa parva* and *Hippolyte varians* in *S. muticum* stands, yet the positive relationship between species diversity and functional group diversity identified indicates that this could impact functionality at an ecosystem level.

At a given time of the year, *S. muticum* epifaunal assemblages are measurably different to those of *Z. marina*. An increased spread of *S. muticum* throughout seagrass habitats could have a lasting impact on epifaunal assemblages supported, nutrient levels in the system, trophic links to the higher levels of the food web and fundamental ecological processes performed by seagrass. However, whilst this is clear, what is not clear is the exact nature of the effects which could result from the spread. The changes caused by *S. muticum* interact with both spatial and temporal environmental conditions. The results are difficult to predict and seem to be nonlinear in nature. Whilst this study provides an insight in to the changes which can be seen at an epifaunal level, it does not clearly show how this might change at different times of the year, across different geographically connected sites, or what the wider impacts on the marine food webs supported by seagrass could be.

Invasive macrophytes undeniably alter the assemblages present in an ecosystem, but the broader implications of those changes are unpredictable and require in more depth, long term studies.

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