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**Seagrass-associated epifauna biodiversity
across the UK seascape**

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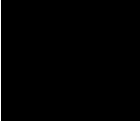
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Abstract

Seagrass meadows are critical habitats supporting diverse epifaunal communities. Many studies have explored epifauna biodiversity assemblage's changes across latitude gradients, yet the drivers of species assemblages across small-scale environments remain poorly understood. This study investigated how environmental drivers, such as nutrient inputs and seagrass structure, influence epifaunal species assemblages across four environments within the UK seascape: island, estuary, coastal, and lagoon. Multivariate analyses revealed significant differences in species assemblages among environments where coastal and estuaries environments showed most similarity but still significantly different ($R = 0.045$, $p = 0.7\%$). Island sites supported significantly higher species abundance ($p = 3.66 \times 10^{-5}$) and greater seagrass metrics, whereas coastal environments exhibited the lowest species richness ($p = 0.0081$) and lagoons showed lower seagrass metrics. Using spearman rank correlation coefficient, nitrogen emerged as the most influential driver ($\rho = 0.33$), where previous studies show indirect support for epifauna through epiphyte growth and seagrass metabolic processes, whereas carbon was strongly associated with seagrass growth and habitat formation ($\rho = 0.286$), enhancing protection for epifauna. Epiphyte coverage showed no significant effect on species composition or richness ($\rho = 0.210$), suggesting nitrogen's broader ecological role outweighs direct food-source contributions. These findings emphasize the importance of nutrient management and maintaining habitat structure to sustain biodiversity and enhance ecosystem resilience. This study provides critical insights for conservation and restoration strategies targeting seagrass meadows and their associated communities and environmental settings. Insights could include pre-planned site monitoring by taking nutrient readings to find ideal conditions for restoring and conserving seagrass meadows, thereby giving more opportunity for seagrass growth and biodiversity promotion.

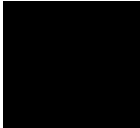
Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted for any degrees.

Signed: 

Date: 18/01/2025

This thesis is the result of my own investigation, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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The University's ethical procedures have been followed and, where appropriate, ethical approval has been granted.

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Introduction

Seagrass meadows are highly productive ecosystems that support diverse communities of organisms, shaped by the broad range of environments they inhabit. These habitats span climatic zones from warm Indo-Pacific tropical waters to cooler Atlantic temperate regions (Short et al., 2007). Despite these environmental differences, seagrass meadows often share similar food web structures, with epifaunal organisms playing crucial roles as intermediaries in trophic transfers (Coll et al., 2011; Park et al., 2013). Epifauna, which inhabits surfaces such as seagrass blades, sediments, and hard substrates, are fundamental to the biodiversity and ecological function of these ecosystems. They contribute to nutrient cycling and serve as prey for higher trophic levels, underscoring their importance to seagrass meadow dynamics (Cui et al., 2021).

Ecosystem resilience may be influenced by top-down trophic interactions, wherein predators regulate herbivore populations, potentially reducing grazing pressure on primary producers (Paine, 1966; Field et al., 2006; Fortuna et al., 2024). In some marine environments, such as rocky intertidal zones, evidence of top-down control has been demonstrated (Menge, 1992). For seagrass ecosystems, predation on mesograzers can indirectly support seagrass health by controlling algal overgrowth, highlighting the potential role of predators in maintaining ecological balance under stress (Vierucci, 2009). In a study conducted in Northern Baltic Sea eelgrass meadows, Gagnon et al. (2021) results showed the critical role of trophic pathways involving top predators that regulate mesograzers, such as crustaceans and gastropods. These mesograzers mitigate the effects of algal blooms resulting from nutrient input, with their functional redundancy, where one group compensates for the loss of another, providing additional resilience (Vierucci, 2009). This redundancy ensures that eelgrass meadows remain robust against environmental stressors, such as nutrient-driven algal blooms and trophic modifications.

Broad scale analyses across the Northern Hemisphere have found that latitudinal gradients significantly influence seagrass epifauna species composition and global biodiversity patterns (Whalen et al., 2020; Duffy et al., 2022). Generally, species richness and abundance decline with increasing latitude, reflecting complex interactions between environmental conditions and habitat complexity (Reynolds et al., 2018; Gross et al., 2022; Gross et al., 2024). For example, Reynolds et al. (2018) conducted a large-scale study on predation intensity across latitudinal gradients in eelgrass meadows. They found that predation rates decreased with latitude, with temperature gradients emerging as a significant predictor. Higher shoot densities in seagrass meadows were also associated with reduced predation, likely due to the shelter they provide, however unlike other variables in this study, this was not linked with changing latitude. These findings suggest that cooler, higher-latitude regions support distinct epifaunal community structures, shaped by reduced predation pressure and greater habitat complexity. This trend is not unique to seagrass communities but also observed in kelp forests with urchin abundance

(Estes & Duggins, 1995), soft-sediment systems such as mudflats (Ambrose, 1991), and increased latitude of freshwater lakes with a decrease fish predation and richer zooplankton community (Jeppesen et al., 2003).

Similarly, Gross et al. (2022) explored crustacean communities, a key component of epifauna, across latitudinal gradients in the Pacific and Atlantic Oceans. The findings revealed stronger predation pressures at lower latitudes, while Pacific communities exhibited greater trait diversity compared to the more clustered traits in the Atlantic. Higher epiphyte loads were linked to increased trait clustering, potentially altering epifaunal interactions. These studies suggest the influence of species interactions and environmental factors on epifaunal community composition across biogeographic gradients.

While these studies highlight the impact of latitudinal gradients on biodiversity, they often overlook the role of smaller-scale environmental variations. Seagrass meadows occur in diverse environments such as estuaries, coasts, islands, and lagoons, each with distinct environmental conditions that may influence species composition (Olsen et al., 2004). In the UK, Eelgrass (*Zostera marina*), the most abundant seagrass species in much of the Northern Hemisphere thrives in a range of environments, from muddy inshore waters of the Severn to the clear, deeper waters oceanic influenced islands (Davison et al., 1998). Across this range, hydrodynamics, intertidal emersion, light availability, nutrients, and salinity all fluctuate highly, influencing sediment types and general biochemistry of the sites (Gerbersdorf & Wieprecht, 2014; Tolhurst et al., 2020). Whilst we have some knowledge of how these pressures might influence the plants (e.g primary production rate (Collier et al., 2017), root stability (Carr et al., 2012), and growth (Cognat et al., 2018)), there exists limited understanding of how this variability influences the biodiversity and food-web within these systems.

Estuaries offer a dynamic ecosystem characterized by high and consistent nutrient input from terrestrial run-off, which promotes epiphyte growth and supports epifauna that depend on this food source (Whitfield et al., 2022). However, the benefits of nutrient availability are offset by stressors such as high turbidity, fluctuating salinity, and variable temperatures, leading to complex and adaptive species compositions (Wołowicz et al., 2007; Henriques et al., 2017). Conversely, island environments tend to have clearer waters and stable salinity, providing optimal conditions for seagrass growth. Yet, lower nutrient availability can limit epifaunal biodiversity, highlighting nutrient constraints in these regions (Gil et al., 2006; Anderson et al., 2013). Coastal environments present moderate nutrient levels compared to islands, with wave action reducing sediment accumulation and enhancing water clarity. These conditions promote seagrass growth, creating suitable habitats for epifauna. However, high wave energy can uproot seagrass, displacing epifauna and disrupting biodiversity (Reise, 2002). Lagoons, by contrast, are sheltered environments with minimal wave energy, providing habitat stability for epifauna. This

sheltering effect can lead to nutrient buildup, causing eutrophic conditions and oxygen depletion, which stress seagrass and epifauna communities (Han & Liu, 2014).

Understanding the influence of small-scale environmental changes on epifauna species composition is crucial for understanding the complexity and variability of biodiversity within seagrass meadows. These local environmental factors can significantly alter habitat quality, resource availability, and species interactions, which are often masked in broad-scale assessments (Ackerly, 2003). For example, the stressors in estuarine environments, such as fluctuating salinity and high turbidity, may drive the selection of more stress-tolerant epifauna species, creating distinct communities compared to the stable yet nutrient-limited island environments (Henriques et al., 2017). Similarly, the moderate conditions of coastal waters may favour generalist species, while lagoon habitats, despite their stability, could experience periodic biodiversity declines due to eutrophication and oxygen depletion.

Shifts in environmental conditions, particularly nutrient loading, can significantly alter epifaunal diversity in seagrass meadows. Increased terrestrial run-off in estuaries often leads to eutrophication, reducing water clarity and oxygen levels, which damages seagrass habitat and diminishes structural complexity essential for epifaunal assemblages (Macreadie et al., 2017). Excess nutrients also promote algal overgrowth, further displacing seagrass and associated fauna even if algal provides a food source for some epifauna (Åsmul, 2024). Conversely, natural nutrient inputs, such as deep-sea upwellings around islands, can enhance productivity and temporarily boost food availability for filter feeders (Alongi, 2020). However, prolonged or intense enrichment may still lead to ecological imbalance and reduced species evenness (Worm and Duffy, 2003). Both anthropogenic and natural nutrient fluxes can drive significant changes in epifaunal diversity.

This study aims to understand how smaller scale environmental changes affect epifauna seagrass biodiversity. By conducting a unique analysis of eelgrass communities across a range of environments integrating multivariate analyses with key environmental factors, this research will assess how differences in seascape characteristics affect epifaunal richness and community structure across diverse UK seagrass habitats.

Research questions:

- (i) How do epifauna assemblages vary across four distinct environments within UK seagrass habitats?
- (ii) Do small-scale environment gradients drive dissimilarities in epifauna species assemblages?
- (iii) If any, what are the main environmental predictors for seagrass-associated epifauna species composition?

By assessing small-scale environmental changes, we can better predict how shifts in environmental conditions might alter epifaunal diversity and the overall resilience of seagrass ecosystems. This fine-scale understanding is especially important for effective conservation strategies, as it highlights the need for specific management approaches to protect these habitats and their associated biodiversity.

Methods

Study site

The UK seascape falls under the temperate North Atlantic bioregion – the least diverse bioregion in terms of seagrass species. Collectively, the North Atlantic bioregion contains five species of seagrass, with the UK containing two out of the five species; *Zostera Marina* and *Zostera noltii* (Short et al., 2007). The UK seascape varies in environments, where four distinct environments were selected for this study; Lagoon, Estuary, Coastal, and Outer Island environments, to assess epifauna assemblages in the UK seascape.

A total of 16 sites were selected for this study; four sites per environment. Sample sites were selected from known established seagrass meadows across the UK seascape, with supporting documentation and interactive maps such as seagrass spotter. Some justifications had to be made for characterising some sample sites. Loch Craignish is a pseudo-estuary environment where it could be classified as a coastal site, however, in this study, we classified it as an estuary due to the site location and how far inland it was compared to other coastal sites as seen in figure 1. Inland Sea A and B were classified as lagoon sites, while not technically lagoons, the inland sea portrayed the same characteristics as lagoon environments. We used the Inland Sea as lagoon sites due to the fleet lagoon being the only true lagoon inhabited by seagrass in the UK, therefore, increasing sample size variability. Two sites; Thorness and Seaview, are both located on the Isle of Wight but classified as coastal sites. While the Isle of Wight is an island, it does not represent the same characteristics as other outer islands around the UK but more resembles characteristics of coastal environments.

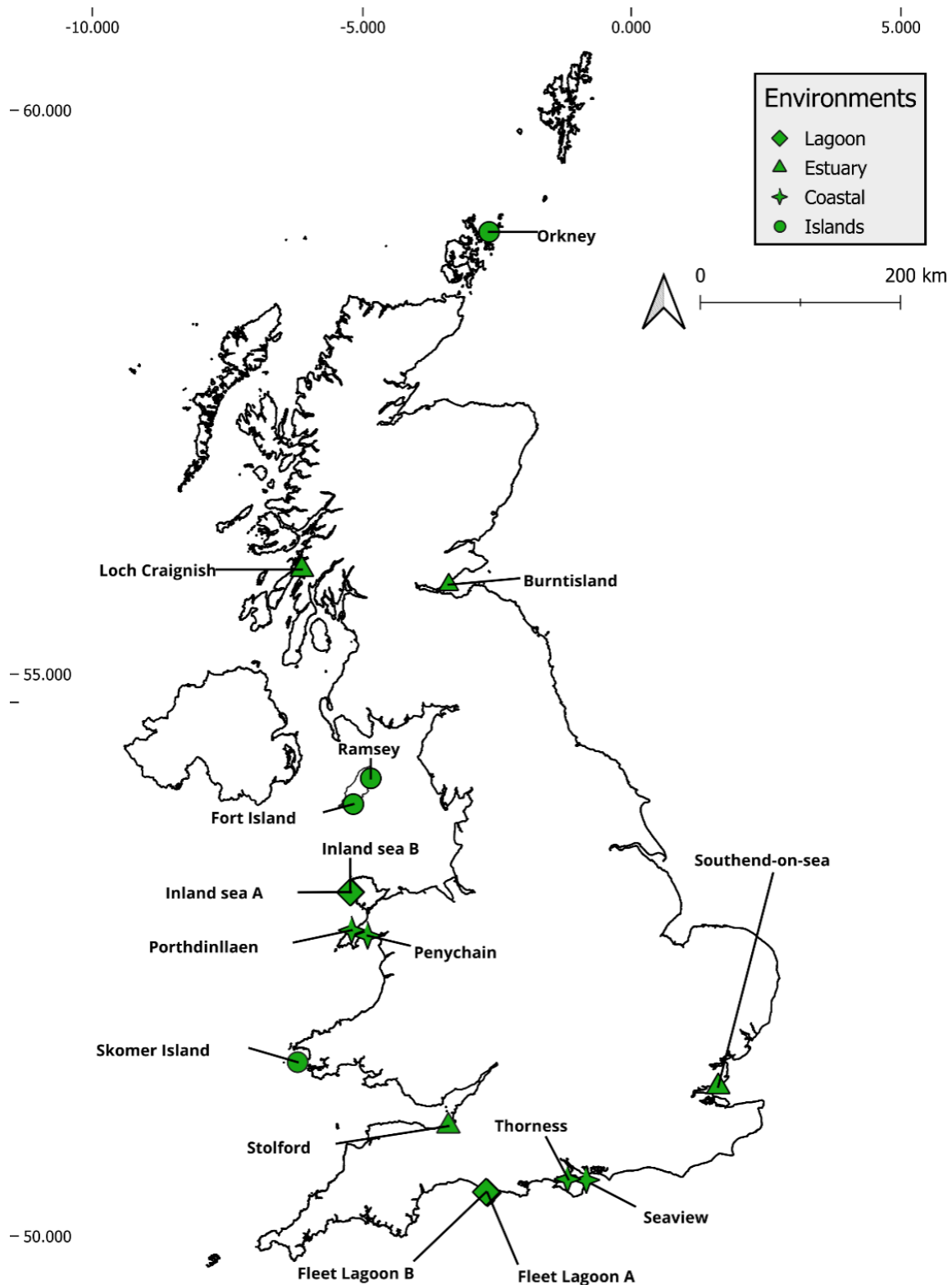


Figure 1: Map of all the sample sites across the UK seascape, categorized by environmental type. Seagrass and associated biodiversity data were collected from 16 distinct sites, classified into four environments: Lagoon (diamond), Estuary (triangle), Coastal (star), and Island (circle).

Study design

The study design for this research is based on the premise of the *Zostera* Experimental Network (ZEN) handbook section II. Field surveys & collections: A.3. Field Survey – Epibiota, Epifauna and *Zostera* Collections and B.3. Laboratory Processing of Plot Samples – Epifaunal Processing. We built upon this methodology by investigating additional factors such as nutrient content and seagrass parameters to see how the functional diversity of epifauna varies across different environments. As suggested by the ZEN handbook, 20 samples are taken per site. However, using previous data provided by ZEN, we could run a power-to-analysis statistical test with an 80% confidence level with a significance level of 0.05. Findings show that we could reduce the 20 samples to 10 samples per site, without significant change.

Data collection

Sampling begins at the first point of contact with a seagrass meadow perpendicular to the shoreline. Each sample is spaced a metre apart along a transect line. In each sample; five shoots are cut just above the meristem within a 0.25m² quadrat, having a 200µm mesh size sample bag flush over the seagrass blades. Bags are sealed (to avoid any epifauna escape) and labelled for onshore processing. GPS coordinates and photos are taken for mapping and percentage cover respectively. Samples are first processed as soon as possible, taking seagrass measurements before drying and altering measurements, and to ensure no damage to epifauna tissue by preserving it in 70% ethanol for later processing in the laboratory (See Woan Shian et al., 2016).

Habitat and Environmental data

Sheath length measurements were measured from where it was cut just above the meristem, to allow regrowth, to the highest intact leaf sheath where leaf bundles surround it (Gaeckle et al., 2006). If the meristem was not visible during seagrass collection due to the meristem being under the sediment, sheath length measurements were measured where the shoot was cut at level with the sediment to avoid uprooting the seagrass. The number of leaves was recorded per shoot while taking the longest leaf width and length, from the top of the sheath to the tip of the blade. The number of leaves, leaf length and width are used to approximate the surface area of each shoot and show the growth metrics, conditions, and stressors of different environments.

To assess the nutrient levels, we can examine seagrass internal Carbon (C) and Nitrogen (N) ratios by drying seagrass samples at 50°C for 24 hours. The dried seagrass is ground into a fine powder and then sent to OEA labs for Carbon and Nitrogen analysis. We can measure the percentage cover of epiphytes that grow on seagrass to get an overall visual health assessment of the environment. A high abundance of epiphytes signifies nutrient-rich waters, potentially leading to reduced oxygen levels and blocked sunlight, negatively impacting seagrass health (Brodersen et

al., 2015; Ralph et al., 2007). Using a 0.25m² quadrat, we can determine the seagrass density per sample, per site. We can use the density to determine the stability and health of the seagrass.

Identification

Identification of species collected was done through dichotomous keys using the Hayward and Ryland (2017) Handbook of the Marine Fauna of North-West Europe. Species-level identification was achieved by first keying out higher taxonomic categories that being either Class, Order, or Family. Once a species was identified, a cross-check with global distribution, habitat preference, and images was often researched to ensure we had made a correct conclusion. Once we were satisfied with our taxonomical identification, we used the World Register of Marine Species (WoRMs) to ensure the taxonomical names were up to date.

Data analysis

A two-way ANOVA was conducted to analyze species abundance and richness across different environments, followed by the post hoc test TukeyHSD to identify significant pairwise differences. Seagrass metrics were compared among environments using one-way ANOVA. Similarly, environmental conditions such as C:N ratios and epiphyte coverage were analyzed across environments using ANOVA. Various multivariate analyses were used to examine changes in species assemblages across environments with incorporating environmental (nutrient) and ecological factors (seagrass metrics). Non-metric multidimensional scaling (nMDS) was used to visualize patterns of species similarity across sites, with a 50% similarity threshold and a stress value of 0.17 indicating a reliable ordination. Analysis of Similarities (ANOSIM) was performed to quantify the influence of environmental grouping on species assemblages. Principal Component Analysis (PCA) was used to explore relationships between seagrass metrics and environmental variables across environments. Finally, a RELATE analysis, supported by Spearman's rank correlation, was conducted to assess the correlation between environmental/seagrass variables and epifauna community composition. All average values were presented along with their standard deviation. All the analyses were done using PRIMER 7 and R, where statistical significance was determined at $p < 0.05$ (PRIMER-e, 2025; RStudio Team, 2023).

Results

Across all sampled sites, 50 distinct species were identified with a collective abundance of 397 individuals. Island sites showed the highest abundance with a total of 185 individuals and a moderately high species richness of 21 species where *Dynamene bidentate* and *Apherusa cirrus* contributed to 65% (120 individuals) of species observed. Coastal sites had the lowest species abundance totaling 40 individuals with a richness of 16 species. Estuary sites show moderate species abundance and the highest richness with 93 individuals and 24 species. Lagoon sites showed the lowest species richness with 13 species with 79 individuals. *Dexamine spinosa*, *Pullilina sarsii*, and *Idotea chelpes* were the most widespread species (5 unique sites each), in contrast, 28 unique species were found at one site.

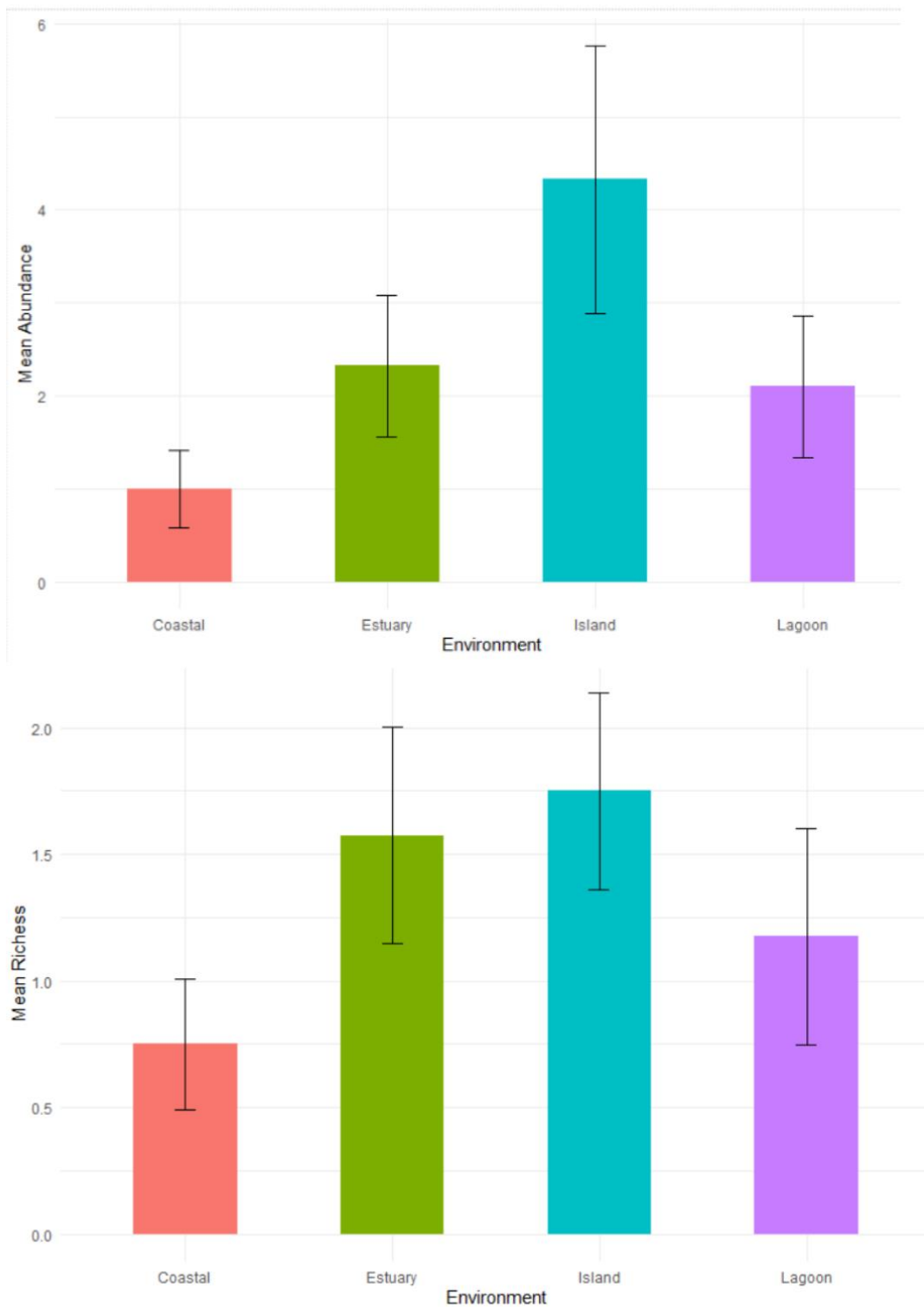


Figure 2: The mean species abundance (top) and mean species richness (bottom) across all sites, per quadrat, are categorized within their respective environment. Error bars represent 95% confidence intervals.

A two-way ANOVA examining species abundance across environments revealed a significant effect of site ($p = 1.13 \times 10^{-5}$). Post hoc Tukey HSD tests indicated that island sites differed significantly from the other environments. The most significant difference was between Island and Coastal sites ($p = 4.3 \times 10^{-6}$), followed by Island–Lagoon ($p = 0.004$) and Island–Estuary ($p = 0.012$), as shown in Figure 2 (top). No other environment pairings showed significant differences in species abundance. Similarly, ANOVA results for species richness indicated a significant difference among environments ($p = 1.18 \times 10^{-3}$). Post hoc comparisons revealed that Coastal–Island ($p = 1.4 \times 10^{-3}$) and Coastal–Estuary ($p = 0.012$) pairs were significantly different, as illustrated in Figure 2 (bottom).

Malacostraca and Gastropoda showed the highest species richness with 21 species each, with Malacostraca being the most abundant with 133 individuals. Gastropoda had 5 different orders (Archaeogastropoda, Aplysiida, Caenogastropoda, Littorinimorpha, and Trochida) while Malacostraca only had 3 different orders (Amphipoda, Decapoda, and Isopoda) shown in table 1. Gastropoda was widespread across all environmental types, with estuary being the most predominant containing 13 different Gastropoda species. While Malacostraca was widespread, only *Microprotopus maculatus* was observed in coastal environments. *Pusillina sarsii* was the only species found across each environmental type as shown in Table 1.

Table 1: List of species that were found across all sample sites. Each species is categorized under Class, then Order, and then species name and is shown which environments they were found with the labels *I* (Island), *C* (Coastal), *E* (Estuary), and *L* (Lagoon). Species that were unidentified due to genetics analysis needed (nematode ssp.) or damaged samples have been excluded from this list.

Class: Bivalve

- ⌚ **Order: Cardiida**
 - *Abra tenuis* (Montagu, 1803) (C)
 - *Cerastoderma edule* (Linnaeus, 1758) (E)

Class: Enteropneusta

- ⌚ **Order: Enteropneusta *incertae sedis***
- ⌚ *Saccoglossus ruber* (Tattersall, 1905) (I)

Class: Gastropoda

- ⌚ **Order: Archaeogastropoda**
 - ⌚ *Patella pellucida* (Linnaeus, 1758) (E, I)
- ⌚ **Order: Aplysiida**
 - ⌚ *Aplysia punctata* (Cuvier, 1803) (I)
- ⌚ **Order: Caenogastropoda**
 - ⌚ *Bittium reticulatum* (da Costa, 1778) (C, E)
 - ⌚ **Order: Littorinimorpha**
 - ⌚ *Alvania punctata* (Montagu, 1803) (C)
 - ⌚ *Cingula trifasciata* (J. Adams, 1800) (C)
 - ⌚ *Ecrobia ventrosa* (Montagu, 1803) (L)
 - ⌚ *Hydrobia acuta neglecta* (Muus, 1963) (E)
 - ⌚ *Lacuna crassior* (Montagu, 1803) (C)
 - ⌚ *Lacuna vincta* (Montagu, 1803) (E)
 - ⌚ *Littorina littorea* (Linnaeus, 1758) (E, I)
 - ⌚ *Littorina obtusata* (Linnaeus, 1758) (C)
 - ⌚ *Littorina saxatilis* (Olivi, 1792) (C, E, L)
 - ⌚ *Melarhapha neritoides* (Linnaeus, 1758) (C)
 - ⌚ *Obtusella intersecta* (S. V. Wood, 1857) (E)
 - ⌚ *Peringia ulvae* (Pennant, 1777) (E)
 - ⌚ *Potamopyrgus antipodarum* (J. E. Gray, 1843) (E)
 - ⌚ *Pusillina sarsii* (Lovén, 1846) (C, E, I, L)
 - ⌚ *Rissoa membranacea* (J. Adams, 1800) (C, E, L)
 - ⌚ *Rissoella opalina* (Jeffreys, 1848) (I)
 - ⌚ **Order: Trochida**
 - ⌚ *Steromphala pennanti* (R. A. Philippi, 1851) (I)
 - ⌚ *Steromphala umbilicalis* (da Costa, 1778) (C, E, I)

Class: Hexacorallia

- ⌚ **Order: Actiniaria**
 - ⌚ *Anemonia viridis* (Forsskål, 1775) (C, E)

Class: Malacostraca

- ⌚ **Order: Amphipoda**
 - ⌚ *Apherusa cirrus* (Spence Bate, 1863) (I)
 - ⌚ *Corophium arenarium* (Crawford, 1937) (L)
 - ⌚ *Corophium multisetosum* (Stock, 1952) (L)
 - ⌚ *Dexamine spinosa* (Montagu, 1813) (E, I, L)
 - ⌚ *Erichthonius difformis* (H. Milne Edwards, 1830) (I, L)
 - ⌚ *Gammarus locusta* (Linnaeus, 1758) (I)
 - ⌚ *Gammarus zaddachi* (Sexton, 1912) (E)
 - ⌚ *Leptocheirus pilosus* (Zaddach, 1844) (L)
 - ⌚ *Microprotopus maculatus* (Norman, 1867) (C, I)
 - ⌚ *Nototropis swammerdamei* (H. Milne Edwards, 1830) (E, I)
 - ⌚ *Nototropis vedlomensis* (Spence Bate & Westwood, 1862) (E)
- ⌚ **Order: Decapoda**
 - ⌚ *Eualus gaimardii* (H. Milne Edwards, 1837) (E)
 - ⌚ *Rhithropanopeus harrisii* (Gould, 1841) (E)
- ⌚ **Order: Isopoda**
 - ⌚ *Cleantis prismatica* (Risso, 1827) (E, I, L)
 - ⌚ *Dynamene bidentata* (Adams, 1800) (I)
 - ⌚ *Idotea balthica* (Pallas, 1772) (I)
 - ⌚ *Idotea chelipes* (Pallas, 1766) (E, L)
 - ⌚ *Idotea linearis* (Linnaeus, 1767) (I)
 - ⌚ *Idotea neglecta* (G. O. Sars, 1897) (E)
 - ⌚ *Idotea pelagica* (Leach, 1816) (E)
 - ⌚ *Lekanesphaera rugicauda* (Leach, 1814) (L)

Class: Polychaeta

- ⌚ **Order: Eunicida**
 - ⌚ *Hyalinoecia tubicola* (O.F. Müller, 1776) (I, L)
- ⌚ **Order: Terebellida**
 - ⌚ *Nicolea zostericola* (Örsted, 1844) (I)
- ⌚ **Order: Phyllodocida**
 - ⌚ *Parexogone hebes* (Webster & Benedict, 1884) (I)

As well as species differences across sites, seagrass parameters and environmental conditions varied. The longest leaf measured ranged from 40mm to 750mm, with the leaf sheath length ranging from 5mm to 220mm. Leaf width (mm), number of leaves and percentage cover averaged 3.28 ± 1.08 mm, 3.60 ± 1.01 , and 52.92 ± 28.69 % respectively as seen in Table 2.

Table 2: Seagrass parameters are shown with the respective range and average, with the lowest and highest ranges sites included.

Parameter	Range	Lowest range site	Highest range site	Average
Sheath Length (mm)	5mm – 220mm	Ramsey	Fort Island	46.58 ± 36.19 mm
Longest Leaf (mm)	40mm – 750mm	Inland Sea B	Fort Island	228.81 ± 118.61 mm
Leaf Width (mm)	1mm – 7mm	Fleet Lagoon A, Fleet Lagoon B	Skomer Island, Loch Craignish	3.28 ± 1.08 mm
Percentage Cover (%)	4% - 95%	Skomer Island	Loch Craignish	52.92 ± 22.50 %
Number of Leaves	1 - 7	Orkney, Skomer Island	Loch Craignish	3.60 ± 1.01

Across sites, Island environments showed the highest averages for sheath length (55.48 ± 40.60 mm), longest leaf length (306.21 ± 157.73 mm) and leaf width (4.02 ± 0.96 mm) but had the lowest average for seagrass percentage cover (26.93 ± 27.30 %). Lagoon environments showed the lowest average for longest leaf length (171.5 ± 87.16 mm), leaf width (2.39 ± 0.71 mm), and number of leaves (3.39 ± 0.96). Coastal environments showed the highest average number of leaves (3.81 ± 0.94) while Estuaries showed the highest average seagrass percentage cover (64.27 ± 22.0 %).

ANOVA results indicated significant differences among environments for seagrass morphological traits, including leaf width, longest leaf length, and sheath length (all $p < 2.2 \times 10^{-16}$). The number of leaves per shoot also showed a significant difference between environments ($p = 4.15 \times 10^{-7}$). In contrast, percentage cover did not differ significantly between environments ($p = 0.61$). Post hoc comparisons using Tukey HSD tests were conducted to identify which environment pairs contributed to these differences, with results summarized in Table 3.

Table 3: Tukey HSD values for each combination of environments for different seagrass parameters. Where * there is significance. No significance was found between any sites in seagrass percentage cover

Environment combination	Longest leaf p-value	Leaf Width p-value	No. of Leaves p-value	Sheath Length p-value
Estuary-Coastal	0.48	0.01*	0.01*	0.99
Island-Coastal	0.01*	0.01*	0.01*	0.01*
Lagoon-Coastal	0.01*	0.01*	0.01*	0.01*
Island-Estuary	0.01*	0.01*	0.01*	0.01*
Lagoon-Estuary	0.01*	0.01*	0.07	0.01*
Lagoon-Island	0.01*	0.01*	0.01*	0.99

Significant differences were observed in seagrass parameters across environmental combinations. Leaf width consistently differed across all pairwise comparisons whereas seagrass cover showed no significant differences across any environment pairs. The number of leaves and longest leaf also displayed significant variation in most comparisons, except for Lagoon vs. Estuary ($p = 0.066$) for the number of leaves and Estuary vs. Coastal ($p = 0.482$) for the longest leaf. Sheath length showed significance in most environment combinations besides Estuary vs. Coastal ($p = 0.999$) and Lagoon-Island ($p = 0.999$).

Nitrogen contents ranged from 1.019% (Orkney) – 3.064% (Southend-on-Sea) with an average of $1.84 \pm 0.57\%$ across all sites. On average Estuary environments had the highest nitrogen content of $2.44 \pm 0.57\%$ while Lagoon environments showed the lowest nitrogen content of $1.58 \pm 0.12\%$. Both Coastal and Island sites showed an average content of nitrogen of $1.67 \pm 0.53\%$ and $1.67 \pm 0.47\%$ respectively. Carbon contents ranged from 26.69% (Inland Sea 2A) – 40.91% (Fort Island C) with an average of $32.09 \pm 3.16\%$ across all sites. Island environments showed the highest average carbon content of $33.56 \pm 3.69\%$ while lagoon environments showed the lowest average carbon content of $30.04 \pm 2.55\%$. Coastal and Estuary environments showed the average carbon content to be $32.59 \pm 3.26\%$ and $32.28 \pm 2.31\%$ respectively.

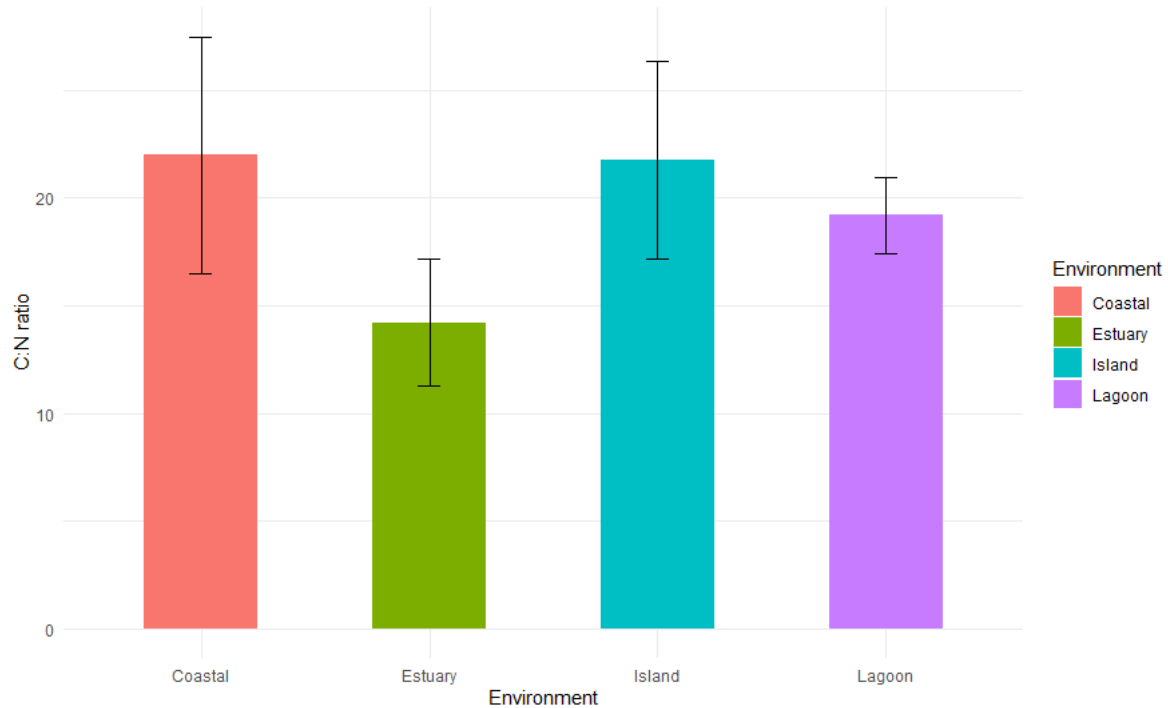


Figure 3: Carbon:Nitrogen (C:N) ratio for each environment where error bars are represented by 95% confidence interval.

Performing an ANOVA test between C:N showed a significant difference between environments ($p = 0.01$). Further analysis using TukeyHSD showed a significant difference between Estuary – Coastal ($p = 0.02$) and Estuary – Island ($p = 0.02$) as seen in Figure 3. These results suggest that Estuary environments are more nutrient-rich than island and coastal environments.

Epiphyte percentage cover ranged from 0% to 75% with an average of $8.78 \pm 13.89\%$. Out of 795 seagrass samples, 384 samples contained 0% epiphyte coverage; those that did showed an average of $16.98 \pm 15.29\%$. Estuary and Lagoon environments tended towards a higher average of epiphyte percentage coverage with $13.80 \pm 18.30\%$ and $13.03 \pm 14.60\%$ respectively while Coastal and Island environments showed lower averages with $3.08 \pm 5.10\%$ and $5.13 \pm 10.40\%$. Macroalgae percentage cover ranged from 0% to 77% with an average of $11.42 \pm 12.72\%$. Island environments had the highest average macroalgae cover at $19.90 \pm 13.70\%$ followed by Coastal environments at $14.60 \pm 12.80\%$. Lagoon environments showed the lowest average macroalgae cover at $2.60 \pm 4.98\%$ while Estuary environments had $8.50 \pm 10.50\%$ average macroalgae cover.

Species Composition

A non-metric Multi-Dimensional Scaling (nMDS) analysis was conducted to assess the similarity in species composition across all sample sites, categorized by environmental types (Estuary,

Island, Lagoon, and Coastal). 2D and 3D configurations were explored over 50 iterations. The 2D solution showed a stress value of 0.17 in 6 out of 50 iterations.

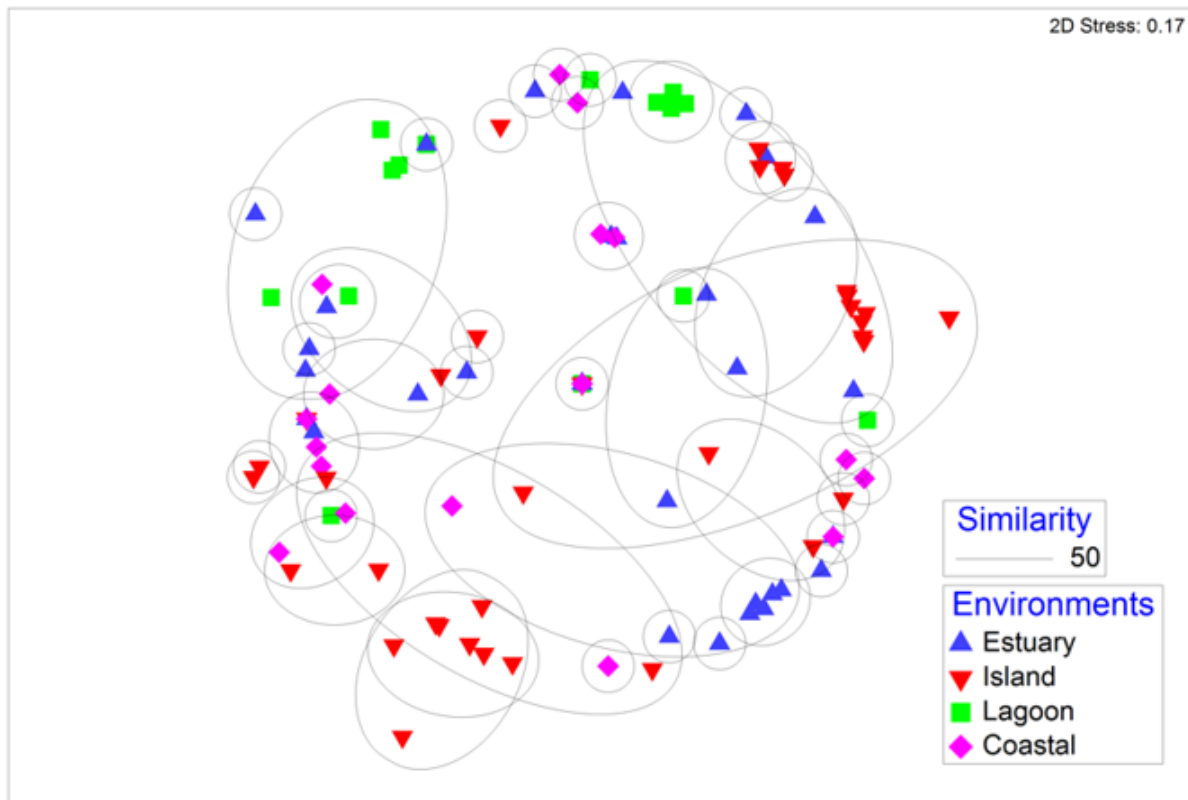


Figure 4: A 2D nMDS ordination of sampling sites, grouped into their respective environments, based on community composition. The ordination is derived from Bray-Curtis similarities at a stress level of 0.17. The similarity was set at 50% with clustering analysis having a cophenetic correlation coefficient of 0.980, showing a good representation of the original resemblance data.

The nMDS ordination shows the variation in species composition across sampling sites in different environments. Clustering at 50% similarity highlights groupings among the sites. Many sites and environments show cross-over in similarity. Some individual clustering does occur in island sites, estuary sites and lagoon sites as seen in Figure 4, however, coastal sites tend to mix more often across all environments suggesting no distinct species composition.

A One-Way Analysis of Similarity (ANOSIM) was conducted to further analyse the differences in species composition among four environmental groups. The global test revealed a sample statistic (R) of 0.123, with a significance level of 0.1% ($p = 0.001$), indicating significant differences in assemblage structure among the environments but is only explained by 12.3% variability in species composition.

Table 4: Pairwise comparisons of species composition among environmental groups.

Comparison	R-value	Significance level (%)	Number \geq Observed
Estuary vs. Island	0.14	0.10	0
Estuary vs. Lagoon	0.11	0.10	0
Estuary vs. Coastal	0.04	0.70	6
Island vs. Lagoon	0.20	0.10	0
Island vs. Coastal	0.12	0.10	0
Lagoon vs. Coastal	0.13	0.10	0

The pairwise comparisons between environmental groups revealed significant differences in community composition for most group pairs (table 4). However, Estuary vs. Coastal showed a higher significance level ($R = 0.04$, $p = 0.7\%$), suggesting a more similar species composition. While different assemblages are significant across environments, further analysis is needed to explain the remaining variability in species composition.

Environmental factors

The principal component analysis (PCA) of environmental variables across the study sites extracted four principal components (PCs) that cumulatively accounted for 100% of the total variation in the data. PC1 and PC2 together explained 77.40% of the variation, while the addition of PC3 increased the cumulative variance and explained 100% of the variation. The eigenvector loadings on each principal component revealed insights into the contributions of the measured environmental variables (Surface, Epiphytes and C:N ratio) to each component as seen in Table 5.

Table 5: The eigenvector values shown with the coefficient in the linear combinations of variables making up PC's

Variable	PC1	PC2	PC3
Surface	0.395	-0.912	-0.114
Epiphytes	-0.662	-0.197	-0.723
C:N ratio	0.637	0.361	-0.681

PC1 shows the eigenvector values for C:N ratio (0.637) has a strong positive contributing factor whereas epiphytes (-0.662) showed a strong negative contributing factor seen in Table 5. Estuary showed an average PC1 score of -1.292 indicating high nutrients and epiphytes, followed by lagoon environments with a PC1 score of -0.310. Whereas the coastal environment average score was 1.171 showing low nutrient input and epiphytes, island sites had a score of 0.679.

PC2, with an eigenvector value of -0.912 for surface area, indicates a strong negative contribution of this variable (Table 5). Coastal environments, with an average PC2 score of 0.679, suggest lower surface area and nutrient availability. Island sites, with a score of -0.317, indicate higher surface area and relatively greater nutrient availability compared to coastal sites. Lagoon environments, with a score of 0.546, are similar to coastal environments, while estuary environments, with a score of -0.160, align more closely with island environments.

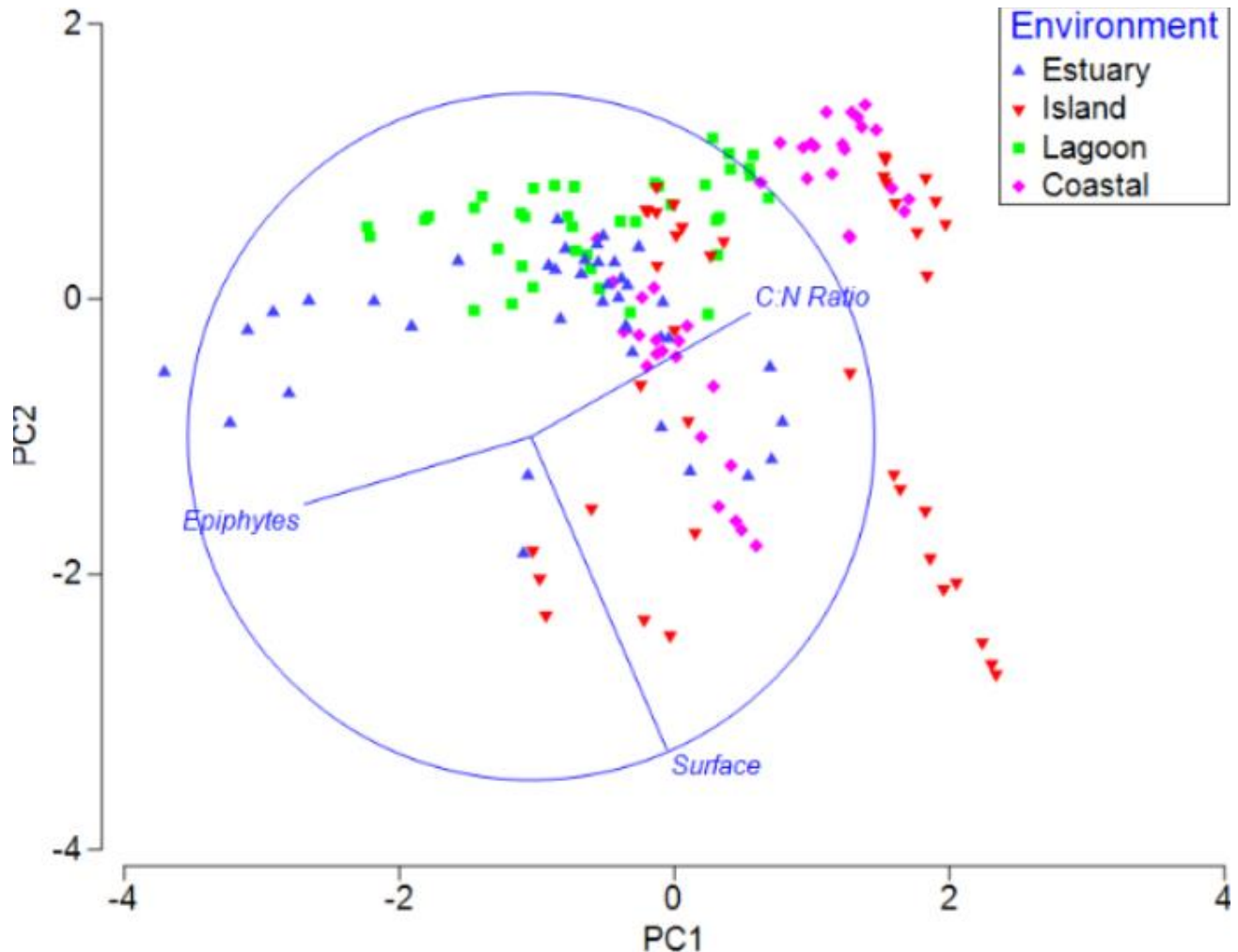


Figure 5: PC1 and PC2 scores are used, due to 77.4% of the variation accounted for, to plot how changes influence each site in their respective environments in terms of environmental factors. The variable lines indicate that there is an increase in value.

As C:N ratio values increase, nutrient availability decreases. In Figure 5, values that tend towards a higher C:N value, the lower epiphyte coverage there is. Estuary environments have higher epiphyte coverage due to more nutrient availability (Nitrogen). As surface area increases, many sites tend to have a higher C:N ratio shown in Figure 5, this is due to higher values of Carbon for increased photosynthetic mechanisms.

Species assemblages' relation with environmental factors

Environmental and ecological factors (C:N ratio, Leaf surface area, and epiphytes) moderately correlate (RELATE analysis) with species composition ($\rho = 0.25$). C:N ratio (and indicator of light availability) was the most influential environmental factor explaining biological community patterns, with a Spearman rank correlation co-efficient (ρ) of 0.33. Surface area and epiphyte coverage had correlation co-efficient (ρ) of 0.29 and 0.21 respectively, indicating that while these factors contribute to community structure, the C:N ratio is the dominant predictor.

Discussion

The findings of this study show significant differences between seagrass epifaunal species assemblages across varied environmental settings within the UK seascape. Species abundance was significantly higher in island sites compared to other environments, likely due to the stable, isolated conditions that reduce anthropogenic, predation, and environmental pressures supporting higher abundances (Francesco Ficetola & De Bernardi, 2004; Hein & Gillooly, 2011; Mori et al., 2012; Jones et al., 2020). These results differ from other studies on seagrass epifauna, which show no significant associations between environmental variables and abundance patterns across small spatial scales (Murphy et al., 2021). However, due to these reduced pressures, disproportionate shifts in epifauna abundance can occur, decreasing resource availability and increasing competition, especially in predator-prey interactions (Bailey et al., 2010; Ritchie & Johnson, 2009). With limited top-down trophic interactions, this may result in reduced ecosystem resilience and unstable food web dynamics (Morozov et al., 2012) where Jephson et al. (2008) showed that epifaunal grazers in seagrass meadows are top-down controlled where larger predators and eutrophic conditions play an important role.

Species richness, however, was significantly lower in coastal environments compared to estuary and island sites. Coastal environments experience higher exposure to anthropogenic stressors such as increased boat traffic, anchoring and tourism than islands (Collins et al., 2010; Murphy et al., 2019). These areas lack the sheltered conditions and nutrient input characteristic of estuaries, where species have adapted to survive under specific environmental conditions (McGarigal & Cushman, 2002). Lagoon environments showed no significant difference in species abundance or richness compared to other sites. This suggests that, like coastal environments, they are not biodiversity hotspots relative to estuaries and islands. This study underscores that biodiversity hotspots within small-scale environments are influenced by a combination of environmental factors, which are similar to other marine ecosystems such as coral reefs (with temperature fluctuations) or mangroves (with salinity and rainfall changes) (Mellin et al., 2010; Osland et al., 2017).

Species similarity analyses revealed similarity within environments due to low R values, where coastal and estuarine environments showed the most similar species composition. Estuarine and coastal share the most overlap in species similarities, which could be explained by their biogeographical closeness, migration access, or similarities in habitat structure and environmental drivers (Connor et al., 2019; Harrison & Whitfield, 2024). However, with a low variability percentage (12.3%), these low R values are only showing a small portion of how similar species composition is due environments alone. Other environmental (nutrient input and epiphytes) and ecological (habitat structure) factors play a significant role in influencing species composition. Looking at species level specimens, we found only one species, *Pusillina*

sarsii, was found across all four environments types out of the 50 observed species, demonstrating the high dissimilarity in species composition between these environments. This highlights the importance of niche differentiation, where species thrive under specific environmental and ecological conditions, contributing to small-scale differences in assemblages and community composition.

Environmental drivers can indirectly shape seagrass habitat complexity by limiting or promoting seagrass growth through differences in light availability and nutrient input (Ralph et al., 2007). Our results show that environmental factors in small-scale environments across the UK seascape differ significantly. Nutrient input, often inversely related to light availability, influences seagrass photosynthetic activities and growth (Dennison et al., 1993). High carbon content in seagrass tissue indicates high light availability, as increased photosynthetic activity creates a positive feedback loop with larger leaf surface areas (Enríquez & Pantoja-Reyes, 2005). Conversely, high nitrogen content correlates with lower light levels, which decreases photosynthesis. High nitrogen levels can encourage epiphyte and algae blooms, reducing light penetration and negatively affecting seagrass growth (Cambridge & McComb, 1984; Dennison et al., 1993; Short & Wyllie-Echeverria, 1996; Ralph et al., 2006). Our results show that environments with larger seagrass metrics had higher carbon content, lower nitrogen, and fewer epiphytes, suggesting higher light availability and, consequently, higher photosynthetic activity and seagrass growth.

Island environments significantly showed larger average seagrass metrics, coupled with the highest carbon content and lower nitrogen content compared to estuary and coastal environments. Island sites are less affected by terrestrial runoff and primarily receive nitrogen from hydrodynamic mixing (Fabricius, 2005; Dahl et al., 2020). With lower nitrogen, seagrass in island environments grows larger due to a higher carbon capacity (Liu et al., 2020). Estuary environments, while showing higher nitrogen content, did not exhibit the lowest carbon content or seagrass metrics. Estuaries experience varied nutrient loads from terrestrial runoff and intertidal dynamics (Lee et al., 2006). Lagoon environments had the lowest average carbon and nitrogen content and the lowest seagrass metrics, emphasizing that carbon is a stronger driver of seagrass growth than nitrogen. Studies such as Liu et al. (2020) have shown that high nitrogen levels can reduce carbon storage capacity and, in turn, seagrass growth, giving more canopy cover for epifauna protection, reducing predator-prey interactions and increases epifauna abundance (Chen et al., 2021). Our results reflect that island sites, with the highest seagrass metrics, also supported the highest species abundance.

Nitrogen, however, shapes ecosystems by promoting epiphyte and algae growth, providing stable food sources for mesograzers and other epifauna (Thornber et al., 2016). Our results show that estuary environments had the highest average nitrogen percentage and epiphyte

coverage. While increased epiphyte coverage can negatively affect seagrass growth, it provides food stability, allowing complex food-web dynamics to form and enhance ecosystem resilience (Ralph et al., 2006; Horn et al., 2020). Estuaries did not support the highest species abundance but did support significantly higher species richness compared to coastal environments, demonstrating their role in supporting biodiversity. Habitat complexity and environmental drivers can explain why certain species are present in specific environments and how small-scale changes influence species assemblages and niche roles.

A higher leaf surface area provides more opportunities for site selection and offers increased shelter and protection for epifauna (Sirota & Hovel, 2006). Our results indicate that leaf surface area moderately contributes to epifauna community structure. Although not the most influential factor, larger seagrass leaf areas were significantly associated with increased species abundance and richness. Similar studies have reported that greater seagrass density and cover enhance epifauna abundance (Schneider & Mann, 1991; Murphy et al., 2021), likely due to reduced predator-prey interactions and the protective structure provided by seagrass (Horinouchi, 2007; Farina et al., 2009). York et al. (2018) similarly highlighted the role of heterogeneous seagrass habitats in shaping food webs through bottom-up processes, where invertebrate prey influence consumer productivity and predator spatial patterns. Our results revealed a significant increase in species abundance and richness, but this trend was not specific to any environment, indicating that larger leaf area positively impacts small-scale environments across the UK seascape. Increased leaf area is typically associated with higher light availability and elevated photosynthetic rates (Hirose et al., 1997), producing more internal carbon to support seagrass growth (Tanaka et al., 2008). This suggests that higher carbon percentages may contribute to increased abundance in seagrass-associated epifauna. However, our findings indicate that nutrient loads, particularly nitrogen, are a more significant factor in shaping epifauna assemblages than carbon percentages.

With studies showing that increased carbon promotes seagrass growth and leaf area, which in turn increase protection for epifauna and promotes species abundance (Schneider & Mann, 1991; Sirota & Hovel, 2006; Murphy et al., 2021). Our results showed that higher nitrogen ratio played a more significant role in shaping epifauna composition. Internal nitrogen helps maintain seagrass metabolic rates and contributes to productivity but can also stimulate epiphyte and algae production, which serve as food sources for epifauna (Touchette & Burkholder, 2007; Williams & Ruckelshaus, 1993; Jaschinski & Sommer, 2010). Although increased nitrogen can help maintain productivity and metabolism for seagrass, the high production of epiphytes can inhibit the growth of seagrass by blocking sunlight (Nelson, 2017). Without epifauna grazers to reduce the cover of epiphytes, meadows would not be able to sustain high nitrogen areas, demonstrating the ecological importance of epifauna (Prado et al., 2007; McSkimming et al., 2015). Increased nitrogen levels around estuary and island sites were

reflected in significantly lower C:N ratios, significantly increased abundance and correlating with higher epiphyte coverage in estuaries and macroalgae in islands. Interestingly, unusually high nitrogen levels around islands sites like Ramsey, Fort Island, and Skomer were likely influenced by seabird activity (Puffin breeding site around Skomer) and industrial runoff (Isle of Man), contributing to nutrient enrichment (Wainright et al., 1998; Otero et al., 2018; Kazama, 2019). Conversely, Lagoon environments epifauna abundance significantly increased with higher C:N ratios, demonstrated that seagrass cover was a stronger driver of epifauna abundance than food reliability in these settings. These results indicate that nitrogen and carbon are indirectly important for food-web stability, habitat complexity, and epifauna assemblages. Increased carbon indirectly provides protection through increased seagrass surface area for epifauna, while increased nitrogen indirectly provides a food source for epifauna, allowing stable trophic transfer.

When there is an increase in nitrogen, epiphytes and macroalgae growth tend to follow, initially creating an ideal food source for epifauna (Jaschinski & Sommer, 2010). However, if epiphytes are not controlled, this can impair seagrass growth by blocking sunlight. Our results show that epiphytes were the least significant factor contributing to species composition and showed no significant effect on species abundance and richness across any of the environments. As epiphyte growth is related to nitrogen inputs, this suggests that the observed significance in species composition from increased nitrogen influences epifauna abundance not only through food production but also by affecting other ecological factors. Alexandre et al. (2012) explored the effects of elevated carbon dioxide (CO₂) on seagrass growth, and their results showed that CO₂ increased growth only when nitrogen levels were also elevated. These findings along with our results underscore the importance of nitrogen for seagrass growth and provide insights into why nitrogen is critical, having multiple contributing factors toward epifauna abundance and species composition.

Our results indicate that nutrients play a more significant role in shaping epifauna assemblages than carbon and surface area while epiphytes showed no significance. However, Gartner et al. (2013) explored how habitat complexity shapes faunal communities, and their study found that small-scale variation in habitat complexity was a bigger factor in canopy morphology than larger-scale variation. The results also show that the structure of seagrass meadows was equally important for epifauna abundance as food sources. We can conclude that species assemblages in small-scale environments across the UK seascape significantly change, with environmental drivers being the largest contributors to dissimilarity. Nitrogen had the largest effect on species assemblages, acting as both an indirect food source for epifauna via epiphytes and as a promoter of seagrass growth. Carbon was linked to increased surface area, both significant factors contributing to increased epifauna abundance and richness, due to enhanced canopy cover that provides protection. Finally, epiphytes showed no significant effect on

epifauna assemblages, suggesting that nitrogen has broader ecological implications in small-scale environments. Further implications of these findings suggest that nutrient management, especially nitrogen, could be a key factor in the conservation and management of seagrass meadows. These results also highlight the importance of habitat structure in influencing biodiversity, which may guide future restoration efforts, especially in areas impacted by nutrient loading. Further research into understanding the connectivity between nutrients, habitat complexity, and food sources could inform strategies for maintaining or enhancing epifauna diversity and ecosystem stability across the UK seascape along with seagrass restoration plans.

Conclusion

This study demonstrates significant differences in species assemblages across different environments within the UK seascape, highlighting the critical role of environmental drivers in shaping biodiversity. Island environments supported the highest species abundance and largest seagrass metrics, likely due to their stable, isolated conditions with reduced anthropogenic and environmental pressures. In contrast, coastal environments exhibited the lowest species richness, likely influenced by increased exposure to stressors and limited habitat complexity. Estuarine sites, with high nitrogen levels and epiphyte coverage, supported greater species richness, emphasizing the importance of nutrient inputs in maintaining and increasing biodiversity. Lagoon environments, however, showed no distinct patterns in species abundance or richness, suggesting that their ecological role is less pronounced compared to other environments.

Our results show that nitrogen emerged as the most influential factor shaping species composition, with previous studies demonstrating that nitrogen indirectly supports epifaunal communities through enhanced epiphyte growth and stimulation of seagrass metabolic processes. Conversely, carbon was strongly associated with larger seagrass surface areas, which enhanced habitat complexity and provided structural protection for epifauna. The limited significance of epiphyte coverage across environments suggests that nitrogen's broader ecological influence outweighs its direct effects on epiphyte-driven food sources.

These findings show the importance of managing nutrient dynamics, particularly nitrogen inputs, to sustain seagrass meadows and their associated biodiversity. Conservation efforts should prioritize reducing anthropogenic nutrient runoff while maintaining habitat complexity to enhance ecosystem resilience. Future research should focus on seasonal and regional nutrient fluctuations, connectivity between environments, and the long-term impacts of nitrogen and carbon dynamics on food-web stability. By understanding these relationships, management strategies can better protect seagrass ecosystems and the biodiversity they support in the UK seascape and beyond.

Appendix

#Data set up

```
Simpledata <- Species.richness.and.abundance.R[,-1]
```

#Anova and tukey test for abundance

```
X1 <- aov(Abundance ~ Environment+site, data = Simpledata)
```

```
summary(X1)
```

```
X2 <- TukeyHSD(X1)
```

```
print(X2)
```

```
install.packages("dplyr")
```

```
library(dplyr)
```

#Abundance

```
summary_data_Abundance <- Simpledata %>%
```

```
  group_by(Environment) %>%
```

```
  summarise(
```

```
    mean_abundance = mean(Abundance),
```

```
    SD_abundance = sd(Abundance),
```

```
    n = n(),
```

```
    CI = qt(0.975, df = n - 1)* (SD_abundance / sqrt(n))
```

```
  )
```

```
print(summary_data_Abundance)
```

```
#Richness
summary_data_Rich <- Simpledata %>%
  group_by(Environment) %>%
  summarise(
    mean_Richness = mean(Richness),
    SD_Richness = sd(Richness),
    n = n(),
    CI = qt(0.975, df = n - 1)* (SD_Richness / sqrt(n))
  )
```

```
print(summary_data_Rich)
```

```
#Graphs
```

```
install.packages("ggplot2")
```

```
library(ggplot2)
```

```
#Abundance
```

```
ggplot(summary_data_Abundance, aes(x = Environment, y = mean_abundance, fill = Environment)) +
```

```
  geom_bar(stat = "identity", width = 0.5) + # Adjust bar width here
```

```
  geom_errorbar(aes(ymin = mean_abundance - CI, ymax = mean_abundance + CI), width = 0.1)
+ # Error bars
```

```
  theme_minimal() +
```

```
  labs(x = "Environment", y = "Mean Abundance")
```

```
#Richness
```

```
ggplot(summary_data_Rich, aes(x = Environment, y = mean_Richness, fill = Environment)) +  
  geom_bar(stat = "identity", width = 0.5) + # Adjust bar width here  
  geom_errorbar(aes(ymin = mean_Richness - CI, ymax = mean_Richness + CI), width = 0.1) + #  
Error bars  
  
  theme_minimal() +  
  labs(x = "Environment", y = "Mean Richness")
```

```
#Anova and tukeyHSD for Richness
```

```
X3 <- aov(Richness ~ Environment, data = Simpledata)  
summary(X3)  
X4 <- TukeyHSD(X3)  
print(X4)
```

```
#Standard deviation for environmental data
```

```
#SD for Number of Leaves
```

```
Leaves_SD <- sd(Environmental.data$Number.of.leaves)  
print(Leaves_SD)
```

```
SD_Leaves_Env <- Environmental.data %>%
```

```
  group_by(Environment) %>%
```

```
  summarize(sd_value = sd(Number.of.leaves, na.rm = TRUE))
```

```
print(SD_Leaves_Env)
```

```
#SD for Longest leaf
```

```
Long_SD <- sd(Environmental.data$Longest.Leaf.Length..mm.)  
print(Long_SD)
```

```
SD_Longest_Env <- Environmental.data %>%  
  group_by(Environment) %>%  
  summarize(sd_value = sd(Longest.Leaf.Length..mm., na.rm = TRUE))
```

```
print(SD_Longest_Env)
```

```
#SD for Leaf Width
```

```
Width_SD <- sd(Environmental.data$Leaf.Width..mm.)  
print(Width_SD)
```

```
SD_Width_Env <- Environmental.data %>%  
  group_by(Environment) %>%  
  summarize(sd_value = sd(Leaf.Width..mm., na.rm = TRUE))
```

```
print(SD_Width_Env)
```

```
#SD for Sheath lenght
```

```
Environmental.data$Sheath.Length..mm. <-  
as.numeric(Environmental.data$Sheath.Length..mm.)
```

```
Sheath_SD <- sd(Environmental.data$Sheath.Length..mm.)  
print(Sheath_SD)
```

```
SD_Sheath_Env <- Environmental.data %>%  
  group_by(Environment) %>%  
  summarize(sd_value = sd(Sheath.Length..mm., na.rm = TRUE))
```

```
print(SD_Sheath_Env)
```

```
#SD for epiphyte cover
```

```
Epip_SD <- sd(Environmental.data$Epiphyte.cover....)  
print(Epip_SD)
```

```
Epip_Mean <- mean(Environmental.data$Epiphyte.cover....)  
print(Epip_Mean)
```

```
SD_Epip_Env <- Environmental.data %>%  
  group_by(Environment) %>%  
  summarize(sd_value = sd(Epiphyte.cover...., na.rm = TRUE))
```

```
print(SD_Epip_Env)
```

```
Epip_Mean_Env <- Environmental.data %>%  
  group_by(Environment) %>%  
  summarise(  
    Nitrogen_Mean = mean(Epiphyte.cover...., na.rm = TRUE))
```

```
print(Epip_Mean_Env)
```

```
Epip_filtered <-  
Environmental.data$Epiphyte.cover....[Environmental.data$Epiphyte.cover.... != 0]  
Epip_Mean_Filtered <- mean(Epip_filtered)  
print(Epip_Mean_Filtered)  
Epip_SD_Filter <- sd(Epip_filtered)  
print(Epip_SD_Filter)
```

```
#SD for seagrass cover
```

```
SeagrassCover$Seagrass.Percentage.Cover <-  
as.numeric(SeagrassCover$Seagrass.Percentage.Cover)
```

```
Cover_SD <- sd(SeagrassCover$Seagrass.Percentage.Cover)  
print(Cover_SD)
```

```
SD_Cover_Env <- SeagrassCover %>%  
  group_by(Environment) %>%  
  summarize(sd_value = sd(Seagrass.Percentage.Cover, na.rm = TRUE))  
  
print(SD_Cover_Env)
```

```
#Macro cover
```

```
SeagrassCover$Macroalgae.Percentage.Cover <-  
as.numeric(SeagrassCover$Macroalgae.Percentage.Cover)
```

```
Macro_Mean <- mean(SeagrassCover$Macroalgae.Percentage.Cover)  
print(Macro_Mean)
```

```
Macro_SD <- sd(SeagrassCover$Macroalgae.Percentage.Cover)
print(Macro_SD)
```

```
Macro_Mean_SD_Env <- SeagrassCover %>%
  group_by(Environment) %>%
  summarise(
    Macro_Mean = mean(Macroalgae.Percentage.Cover, na.rm = TRUE),
    Macro_SD = sd(Macroalgae.Percentage.Cover, na.rm = TRUE),
  )
print(Macro_Mean_SD_Env)
```

```
#Nutrient
```

```
Nutrient_summary_data <- Nutrients %>%
  group_by(Environment) %>%
  summarise(
    Nitrogen_Mean = mean(Nitrogen, na.rm = TRUE),
    Nitrogen_SD = sd(Nitrogen, na.rm = TRUE),
    Carbon_Mean = mean(Carbon, na.rm = TRUE),
    Carbon_SD = sd(Carbon, na.rm = TRUE)
  )
```

```
print(Nutrient_summary_data)
```

```
#C:N ratio
```

```
Nutrients$C_N_ratio <- Nutrients$Carbon / Nutrients$Nitrogen
```

```

summary_data_Nutrients <- Nutrients %>%
  group_by(Environment) %>%
  summarise(
    mean_Nutrient = mean(C_N_ratio),
    SD_Nutrient = sd(C_N_ratio),
    n = n(),
    CI = qt(0.975, df = n - 1)* (SD_Nutrient / sqrt(n))
  )

install.packages("ggplot2")
library(ggplot2)

ggplot(summary_data_Nutrients, aes(x = Environment, y = mean_Nutrient, fill = Environment))
+
  geom_bar(stat = "identity", width = 0.5) + # Adjust bar width here
  geom_errorbar(aes(ymin = mean_Nutrient - CI, ymax = mean_Nutrient + CI), width = 0.1) + #
Error bars
  theme_minimal() +
  labs(x = "Environment", y = "C:N ratio")

Nutrients_anova <- aov(C_N_ratio ~ Environment, data = Nutrients)
summary(Nutrients_anova)

Post_Nutrients <- TukeyHSD(Nutrients_anova)
print(Post_Nutrients)

```

```
#Manover attempt

attach(Environmental.data)

test1 <- manova(cbind(Leaf.Width..mm., Longest.Leaf.Length..mm., Sheath.Length..mm.,
Number.of.leaves)
               ~ Environment)

summary(test1)
summary.aov(test1)

TukeyHSD(aov(Longest.Leaf.Length..mm. ~ Environment))
TukeyHSD(aov(Leaf.Width..mm. ~ Environment))
TukeyHSD(aov(Sheath.Length..mm. ~ Environment))
TukeyHSD(aov(Number.of.leaves ~ Environment))

detach(Environmental.data)

summary(aov(Seagrass.Percentage.Cover ~ Environment, data = SeagrassCover))
TukeyHSD(aov(Seagrass.Percentage.Cover ~ Environment, data = SeagrassCover))

#Graphs of Nitrogen and Carbon

library(dplyr)
install.packages("tidyr")
library(tidyr)
```

```
library(ggplot2)
```

```
Nutrient_plot_data <- Nutrient_summary_data %>%
```

```
  pivot_longer(
```

```
    cols = c(Nitrogen_Mean, Nitrogen_SD, Carbon_Mean, Carbon_SD),
```

```
    names_to = c("Variable", "Stat"),
```

```
    names_sep = "_",
```

```
    values_to = "Value"
```

```
  ) %>%
```

```
  pivot_wider(names_from = "Stat", values_from = "Value")
```

```
ggplot(Nutrient_plot_data, aes(x = Environment, y = Mean, fill = Variable)) +
```

```
  geom_bar(stat = "identity", position = position_dodge(width = 0.8), width = 0.6) +
```

```
  geom_errorbar(
```

```
    aes(ymin = Mean - SD, ymax = Mean + SD),
```

```
    position = position_dodge(width = 0.8),
```

```
    width = 0.2
```

```
  ) + # Error bars
```

```
  labs(
```

```
    x = "Environment", y = "Percentage (%)"
```

```
  ) +
```

```
  theme_minimal() +
```

```
  scale_fill_brewer(palette = "Set2")
```

```
#Stats for Nitrogen and Carbon
```

```
Anova_N <- aov(Nitrogen ~ Environment, data = Nutrients)
```

```
summary(Anova_N)
```

```
TukeyHSD(Anova_N)
```

```
Anova_C <- aov(Carbon ~ Environment, data = Nutrients)
```

```
summary(Anova_C)
```

```
TukeyHSD(Anova_C)
```

References

- Ackerly, David D., 2003. Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. *International Journal of Plant Sciences* 164: S165–S184.
- Alexandre, A., J. Silva, P. Buapet, M. Björk, & R. Santos, 2012. Effects of CO₂ enrichment on photosynthesis, growth, and nitrogen metabolism of the seagrass *Zostera noltii*. *Ecology and Evolution* 2: 2625–2635.
- Alongi, D. M., 2020. Coastal Ecosystem Processes. CRC Press eBooks. Informa.
- Ambrose, W. G., 1991. Are Infaunal Predators Important in Structuring Marine SoftBottom Communities? *American Zoologist Oxford University Press* 31: 849–860, <https://www.jstor.org/stable/3883672>.
- Anderson, T. J., M. A. McArthur, C. Syms, S. Nichol, & B. Brooke, 2013. Infaunal biodiversity and ecological function on a remote oceanic island: The role of biogeography and bio-physical surrogates. *Estuarine, coastal and shelf science (Print) Elsevier BV* 117: 227–237.
- Åsmul, M., 2024. Investigating shifts in epifaunal communities in *Zostera marina* meadows and *Fucus serratus* beds in the Norwegian Skagerrak. Bora.uib.no The University of Bergen, <https://bora.uib.no/bora-xmlui/handle/11250/3164201>.
- Atkinson, C. L., C. C. Vaughn, K. J. Forshay, & J. T. Cooper, 2013. Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. *Ecology* 94: 1359–1369.
- Bailey, D., M. H. Schmidt-Entling, P. Eberhart, J. D. Herrmann, G. Hofer, U. Kormann, & F. Herzog, 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology* 47: 1003–1013.
- Bradley, M. P., & M. H. Stolt, 2006. Landscape-level seagrass–sediment relations in a coastal lagoon. *Aquatic Botany* 84: 121–128.
- Brito, A. C., A. Newton, P. Tett, & T. F. Fernandes, 2012. How will shallow coastal lagoons respond to climate change? A modelling investigation. *Estuarine, Coastal and Shelf Science* 112: 98–104.
- Brodersen, K. E., M. Lichtenberg, L.-C. Paz, & M. Kühl, 2015. Epiphyte-cover on seagrass (*Zostera marina* L.) leaves impedes plant performance and radial O₂ loss from the below-ground tissue. *Frontiers in Marine Science* 2:

Cambridge, M. L., & A. J. McComb, 1984. The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* 20: 229–243.

Canuel, E. A., & A. K. Hardison, 2016. Sources, Ages, and Alteration of Organic Matter in Estuaries. *Annual Review of Marine Science* 8: 409–434.

Carr, J. A., P. D’Odorico, K. J. McGlathery, & P. L. Wiberg, 2012. Stability and resilience of seagrass meadows to seasonal and interannual dynamics and environmental stress. *Journal of Geophysical Research: Biogeosciences* 117:

Chen, Y.-Y., G. Edgar, & R. J. Fox, 2021. The Nature and Ecological Significance of Epifaunal Communities within Marine Ecosystems. CRC Press eBooks 585–719.

Clare, D. S., S. G. Bolam, P. S. O. McIlwaine, C. Garcia, J. M. Murray, & J. D. Eggleton, 2022. Biological traits of marine benthic invertebrates in Northwest Europe. *Scientific Data* 9:

Cognat, M., F. Ganthy, I. Auby, F. Barraquand, L. Rigouin, & A. Sottolichio, 2018. Environmental factors controlling biomass development of seagrass meadows of *Zostera noltei* after a drastic decline (Arcachon Bay, France). *Journal of Sea Research* 140: 87–104.

Coll, M., A. Schmidt, T. Romanuk, & H. K. Lotze, 2011. Food-Web Structure of Seagrass Communities across Different Spatial Scales and Human Impacts. *PLoS ONE* 6: e22591, <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0022591>.

Collier, C. J., Y. X. Ow, L. Langlois, S. Uthicke, C. L. Johansson, K. R. O’Brien, V. Hrebien, & M. P. Adams, 2017. Optimum Temperatures for Net Primary Productivity of Three Tropical Seagrass Species. *Frontiers in Plant Science* 8:, <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5572403/>.

Collins, K., A. Suonpää, & J. Mallinson, 2010. The impacts of anchoring and mooring in seagrass, Studland Bay, Dorset, UK. *Underwater Technology* 29: 117–123.

Connor, L., D. Ryan, R. Feeney, W. K. Roche, S. Shephard, & F. L. Kelly, 2019. Biogeography and fish community structure in Irish estuaries. *Regional Studies in Marine Science* 32: 100836.

Contti Neto, N., A. Pomeroy, R. Lowe, & M. Ghisalberti, 2022. Seagrass Meadows Reduce Wind-Wave Driven Sediment Resuspension in a Sheltered Environment. *Frontiers in Marine Science* 8:

Cui, L., Z. Jiang, X. Huang, Q. Chen, Y. Wu, S. Liu, J. Li, & P. I. Macreadie, 2021a. Eutrophication reduces seagrass contribution to coastal food webs. *Ecosphere* 12:

Cui, L., Z. Jiang, X. Huang, S. Liu, Y. Wu, & M. Fan, 2021b. Decade changes of the food web structure in tropical seagrass meadow: Implication of eutrophication effects. *Marine Pollution Bulletin* 173: 113122.

Dahl, M., M. E. Asplund, M. Björk, D. Deyanova, E. Infantes, M. Isaeus, A. Nyström Sandman, & M. Gullström, 2020. The influence of hydrodynamic exposure on carbon storage and nutrient retention in eelgrass (*Zostera marina* L.) meadows on the Swedish Skagerrak coast. *Scientific Reports* 10:

Davison, D., D. Hughes, & D. Davison Associates, 1998. *Zostera* biotopes Prepared by Scottish Association for Marine Science (SAMS) for the UK Marine SACs Project, Task Manager. , http://ukmpa.marinebiodiversity.org/uk_sacs/pdfs/zostera.pdf.

Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, & R. A. Batiuk, 1993. Assessing Water Quality with Submersed Aquatic Vegetation. *BioScience* 43: 86–94, https://www.jstor.org/stable/1311969?seq=1#metadata_info_tab_contents.

Enríquez, S., & N. I. Pantoja-Reyes, 2005. Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. *Oecologia* 145: 234–242.

Estes, J. A., & D. O. Duggins, 1995. Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm. *Ecological Monographs* 65: 75–100.

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50: 125–146.

Farina, S., F. Tomas, P. Prado, J. Romero, & T. Alcoverro, 2009. Seagrass meadow structure alters interactions between the sea urchin *Paracentrotus lividus* and its predators. *Marine Ecology Progress Series* 377: 131–137.

Field, J. C., R. C. Francis, & K. Aydin, 2006. Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography* 68: 238–270.

Fonseca, M. S., J. C. Zieman, G. W. Thayer, & J. S. Fisher, 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* 17: 367–380.

Fortuna, C. M., T. Fortibuoni, J. Bueno-Pardo, M. Coll, A. Franco, J. Giménez, Y. Stranga, M. A. Peck, C. Claver, S. Brasseur, E. Fernández-Corredor, S. Fraschetti, Odei Garcia-Garin, Anieke van Leeuwen, Maite Louzao, Arkaitz Pedrajas, Saša Raicevich, F. Ramírez, Janneke Ransijn, & D. Russell, 2024. Top predator status and trends: ecological implications, monitoring and

mitigation strategies to promote ecosystem-based management. *Frontiers in Marine Science* Frontiers Media 11:

Francesco Ficetola, G., & F. De Bernardi, 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation* 119: 219–230.

Gagnon, K., C. Gustafsson, T. Salo, F. Rossi, S. Gunell, J. P. Richardson, P. L. Reynolds, J. E. Duffy, & C. Boström, 2021. Role of food web interactions in promoting resilience to nutrient enrichment in a brackish water eelgrass (*Zostera marina*) ecosystem. *Limnology and Oceanography* 66: 2810–2826.

Gartner, A., F. Tuya, P. S. Lavery, & K. McMahon, 2013. Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *Journal of Experimental Marine Biology and Ecology* 439: 143–151.

Gerbersdorf, S. U., & S. Wieprecht, 2014. Biostabilization of cohesive sediments: revisiting the role of abiotic conditions, physiology and diversity of microbes, polymeric secretion, and biofilm architecture. *Geobiology* 13: 68–97.

Gil, M., A. R. Armitage, & J. W. Fourqurean, 2006. Nutrient impacts on epifaunal density and species composition in a subtropical seagrass bed. *Hydrobiologia* 569: 437–447.

Gross, C., J. Emmett Duffy, K. Hovel, P. Reynolds, Christoffer Boström, K. Boyer, M. Cusson, Johan Eklöf, A. Engelen, B. Eriksson, F. Joel Fodrie, J. Griffin, Clara M. Hereu, M. Hori, A. Randall Hughes, M. Ivanov, P. Jorgensen, Melissa R. Kardish, C. Kruschel, & K. Lee, 2024. A Latitudinal Cline in the Taxonomic Structure of Eelgrass Epifaunal Communities is Associated With Plant Genetic Diversity. *Global Ecology and Biogeography* Wiley.

Gross, C., J. Emmett Duffy, K. A. Hovel, M. R. Kardish, P. L. Reynolds, Christoffer Boström, K. E. Boyer, M. Cusson, Johan Eklöf, A. H. Engelen, Britas Klemens Eriksson, F. J. Fodrie, J. N. Griffin, C. M. Hereu, M. Hori, A. J. Hughes, M. V. Ivanov, P. Jorgensen, C. Kruschel, & K. Lee, 2022. The biogeography of community assembly: latitude and predation drive variation in community trait distribution in a guild of epifaunal crustaceans. *Proceedings of The Royal Society B: Biological Sciences* Royal Society 289:

Han, Q., & D. Liu, 2014. Macroalgae blooms and their effects on seagrass ecosystems. *Journal of Ocean University of China* 13: 791–798.

Harrison, T. D., & A. K. Whitfield, 2024. A global functional analysis of fish-estuary associations and selected environmental factors. *Reviews in Fish Biology and Fisheries* 34: 805–825.

- Hayward, P., & J. Ryland, 2017. Handbook of the Marine Fauna of North-West Europe. academic.oup.com. Oxford University Press, <https://academic.oup.com/book/26914>.
- Hein, A. M., & J. F. Gillooly, 2011. Predators, prey, and transient states in the assembly of spatially structured communities. *Ecology* 92: 549–555.
- Henriques, S., P. Cardoso, Inês Lopes Cardoso, M. I. Laborde, H. N. Cabral, & R. P. Vasconcelos, 2017. Processes underpinning fish species composition patterns in estuarine ecosystems worldwide. *44*: 627–639.
- Hirose, T., D. D. Ackerly, M. B. Traw, D. Ramseier, & F. A. Bazzaz, 1997. CO₂ELEVATION, CANOPY PHOTOSYNTHESIS, AND OPTIMAL LEAF AREA INDEX. *Ecology* 78: 2339–2350.
- Horinouchi, M., 2007. Review of the effects of within-patch scale structural complexity on seagrass fishes. *Journal of Experimental Marine Biology and Ecology* 350: 111–129.
- Horn, S., M. Coll, H. Asmus, & T. Dolch, 2020. Food web models reveal potential ecosystem effects of seagrass recovery in the northern Wadden Sea. *Restoration Ecology* .
- J. Emmett Duffy, J. J. Stachowicz, P. L. Reynolds, K. A. Hovel, M. Jahnke, E. E. Sotka, Christoffer Boström, K. E. Boyer, M. Cusson, Johan Eklöf, A. H. Engelen, Britas Klemens Eriksson, F. J. Fodrie, J. N. Griffin, C. M. Hereu, M. Hori, A. Randall Hughes, M. V. Ivanov, P. Jorgensen, & C. Kruschel, 2022. A Pleistocene legacy structures variation in modern seagrass ecosystems. *Proceedings of the National Academy of Sciences of the United States of America National Academy of Sciences* 119:
- J.L. Gaeckle, F. T. Short, S.E. Ibarra-Obando, & A.E. Meling-López, 2006. Sheath length as a monitoring tool for calculating leaf growth in eelgrass (*Zostera marina* L.). *Aquatic botany Elsevier BV* 84: 226–232.
- Jaschinski, S., & U. Sommer, 2010. How do nutrient conditions and species identity influence the impact of mesograzers in eelgrass-epiphyte systems? *Marine Biology* 158: 193–203.
- Jephson, T., P. Nyström, P. Moksnes, & S. Baden, 2008. Trophic interactions in *Zostera marina* beds along the Swedish coast. *Marine Ecology Progress Series* 369: 63–76.
- Jeppesen, E., J. Jensen, C. Jensen, B. Faafeng, D. O. Hessen, M. Søndergaard, T. L. Lauridsen, Pål Brettum, & K. Christoffersen, 2003. The Impact of Nutrient State and Lake Depth on Top-down Control in the Pelagic Zone of Lakes: A Study of 466 Lakes from the Temperate Zone to the Arctic. *6*: 313–325.
- Jones, G. P., G. Barone, K. Sambrook, & M. C. Bonin, 2020. Isolation promotes abundance and species richness of fishes recruiting to coral reef patches. *Marine Biology* 167:

Kazama, K., 2019. Bottom-up effects on coastal marine ecosystems due to nitrogen input from seabird feces. *ORNITHOLOGICAL SCIENCE The Ornithological Society of Japan* 18: 117–126, https://www.jstage.jst.go.jp/article/osj/18/2/18_117/article/-char/ja/.

Kelaher, B., J. Van den Broek, P. York, M. Bishop, & D. Booth, 2013. Positive responses of a seagrass ecosystem to experimental nutrient enrichment. *Marine Ecology Progress Series* 487: 15–25.

Lattanzi, A., B. Bellisario, & R. Cimmaruta, 2024. A review of fish diversity in Mediterranean seagrass habitats, with a focus on functional traits. *Reviews in Fish Biology and Fisheries* Springer Science+Business Media.

Lawson, S. E., P. L. Wiberg, K. J. McGlathery, & D. C. Fugate, 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and Coasts* 30: 102–112.

LEE, S. Y., R. J. K. DUNN, R. A. YOUNG, R. M. CONNOLLY, P. E. R. DALE, R. DEHAYR, C. J. LEMCKERT, S. MCKINNON, B. POWELL, P. R. TEASDALE, & D. T. WELSH, 2006. Impact of urbanization on coastal wetland structure and function. *Austral Ecology* 31: 149–163.

Liu, S., Y. Deng, Z. Jiang, Y. Wu, X. Huang, & P. I. Macreadie, 2020. Nutrient loading diminishes the dissolved organic carbon drawdown capacity of seagrass ecosystems. *Science of The Total Environment* 740: 140185, <https://www.sciencedirect.com/science/article/pii/S0048969720337062>.

Macreadie, P. I., J. Jarvis, S. M. Trevathan-Tackett, & A. Bellgrove, 2017. Seagrasses and Macroalgae: Importance, Vulnerability and Impacts. *Climate Change Impacts on Fisheries and Aquaculture* 729–770, <http://doi.wiley.com/10.1002/9781119154051.ch22>.

McGarigal, K., & S. A. Cushman, 2002. Comparative Evaluation of Experimental Approaches to the Study of Habitat Fragmentation Effects. *Ecological Applications* Wiley-Blackwell 12: 335–335.

McSkimming, C., J. E. Tanner, B. D. Russell, & S. D. Connell, 2015. Compensation of nutrient pollution by herbivores in seagrass meadows. *Journal of Experimental Marine Biology and Ecology* 471: 112–118.

Mellin, C., C. J. A. Bradshaw, M. G. Meekan, & M. J. Caley, 2010. Environmental and spatial predictors of species richness and abundance in coral reef fishes. *Global Ecology and Biogeography* 19: 212–222.

Menge, B. A., 1992. Community Regulation: Under What Conditions Are Bottom-Up Factors Important on Rocky Shores? *Ecology* 73: 755–765.

Middelburg, J. J., & P. M. J. Herman, 2007. Organic matter processing in tidal estuaries. *Marine Chemistry* 106: 127–147.

Mori, A. S., T. Furukawa, & T. Sasaki, 2012. Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews* 88: 349–364,
<https://onlinelibrary.wiley.com/doi/abs/10.1111/brv.12004>.

Morozov, A., M. Sen, & M. Banerjee, 2012. Top-down control in a patchy environment: Revisiting the stabilizing role of food-dependent predator dispersal. *Theoretical Population Biology* 81: 9–19.

Mounir Ben Brahim, L. Mabrouk, A. Hamza, & Imed Jribi, 2019. Comparison of spatial scale variability of shoot density and epiphytic leaf assemblages of *Halophila stipulacea* and *Cymodocea nodosa* on the Eastern Coast of Tunisia. *Plant biosystems Taylor & Francis* 154: 413–426.

Murphy, C. E., R. J. Orth, & J. S. Lefcheck, 2021. Habitat Primarily Structures Seagrass Epifaunal Communities: a Regional-Scale Assessment in the Chesapeake Bay. *Estuaries and Coasts* 44: 442–452.

Murphy, G. E. P., M. C. Wong, & H. K. Lotze, 2019. A human impact metric for coastal ecosystems with application to seagrass beds in Atlantic Canada. *FACETS* 4: 210–237.

Nelson, W. G., 2017. Development of an epiphyte indicator of nutrient enrichment: Threshold values for seagrass epiphyte load. *Ecological Indicators* 74: 343–356.

Olivier, P. E. N., M. Lindegren, E. Bonsdorff, & M.C. Nordström, 2024. A network of biological traits: Profiling consumer-resource interactions. *Food webs Elsevier BV* 38: e00333–e00333.

OLSEN, J. L., W. T. STAM, J. A. COYER, T. B. H. REUSCH, M. BILLINGHAM, C. BOSTRÖM, E. CALVERT, H. CHRISTIE, S. GRANGER, R. L. LUMIÈRE, N. MILCHAKOVA, M.-P. OUDOT-LE SECQ, G. PROCACCINI, B. SANJABI, E. SERRÃO, J. VELDSINK, S. WIDDICOMBE, & S. WYLLIE-ECHEVERRIA, 2004. North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology* 13: 1923–1941.

Osland, M. J., L. C. Feher, K. T. Griffith, K. C. Cavanaugh, N. M. Enwright, R. H. Day, C. L. Stagg, K. W. Krauss, R. J. Howard, J. B. Grace, & K. Rogers, 2017. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs* 87: 341–359.

Otero, X. L., S. De La Peña-Lastra, A. Pérez-Alberti, T. O. Ferreira, & M. A. Huerta-Diaz, 2018. Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nature Communications* 9:

- Paine, R. T., 1966. Food Web Complexity and Species Diversity. *The American Naturalist* 100: 65–75, <https://www.jstor.org/stable/2459379>.
- Park, H. J., E. J. Choy, K.-S. Lee, & C.-K. Kang, 2013. Trophic transfer between coastal habitats in a seagrass-dominated macrotidal embayment system as determined by stable isotope and fatty acid signatures. *Marine and Freshwater Research* 64: 1169.
- Prado, P., T. Alcoverro, Begoña Martínez-Crego, A. Vergés, M. Pérez, & J. Romero, 2007. Macrograzers strongly influence patterns of epiphytic assemblages in seagrass meadows. *Journal of Experimental Marine Biology and Ecology Elsevier BV* 350: 130–143.
- PRIMER-e, 2024. *PRIMER 7: Statistical software for multivariate analysis*. Version 7.0.23. Auckland: PRIMER-e Ltd.
- R Studio Team, 2024. *RStudio: Integrated development environment for R*. Version 2024.12.0+467. Boston: RStudio, PBC
- Ralph, P. J., M. J. Durako, S. Enríquez, C. J. Collier, & M. A. Doblin, 2007. Impact of light limitation on seagrasses. *Journal of Experimental Marine Biology and Ecology* 350: 176–193, [https://www.sciencedirect.com/science/article/pii/S0022098107003152#:~:text=As%20the%20quantity%20\(and%20quality](https://www.sciencedirect.com/science/article/pii/S0022098107003152#:~:text=As%20the%20quantity%20(and%20quality).
- Ralph, P. J., D. Tomasko, K. Moore, S. Seddon, & C. M. O. Macinnis-Ng, 2006. Human Impacts on Seagrasses: Eutrophication, Sedimentation, and Contamination. *SEAGRASSES: BIOLOGY, ECOLOGY AND CONSERVATION* 567–593.
- Reise, K., 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48: 127–141.
- Reynolds, P. L., J. J. Stachowicz, K. Hovel, C. Boström, K. Boyer, M. Cusson, J. S. Eklöf, F. G. Engel, A. H. Engelen, B. K. Eriksson, F. J. Fodrie, J. N. Griffin, C. M. Hereu, M. Hori, T. C. Hanley, M. Ivanov, P. Jørgensen, C. Kruschel, K. Lee, & K. McGlathery, 2018. Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. *Ecology* 99: 29–35.
- Ritchie, E. G., & C. N. Johnson, 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12: 982–998.
- Schneider, F. I., & K. H. Mann, 1991. Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *Journal of Experimental Marine Biology and Ecology* 145: 119–139.

See Woan Shian, Arifin Soenggono, & Sawkar Vijay Pramod, 2016. Comparison of Tissue Preservation using Formalin and Ethanol as Preservative Formula. *Althea Medical Journal* 3: 359–363, <https://journal.fk.unpad.ac.id/index.php/amj/article/view/880>.

Short, F. T., & S. Wyllie-Echeverria, 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17–27.

Short, F., T. Carruthers, W. Dennison, & M. Waycott, 2007a. Global seagrass distribution and diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology* 350: 3–20, <https://www.sciencedirect.com/science/article/pii/S002209810700305X>.

Short, F., T. Carruthers, W. Dennison, & M. Waycott, 2007b. Global seagrass distribution and diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology* 350: 3–20, <https://www.sciencedirect.com/science/article/pii/S002209810700305X>.

Sirota, L., & K. Hovel, 2006. Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the epifaunal community of San Diego Bay, California, USA. *Marine Ecology Progress Series* 326: 115–131.

Speed, M. P., M. A. Brockhurst, & G. D. Ruxton, 2009. THE DUAL BENEFITS OF APOSEMATISM: PREDATOR AVOIDANCE AND ENHANCED RESOURCE COLLECTION. *Evolution* 64: 1622–1633.

Tanaka, Y., T. Miyajima, K. Yamada, M. Hori, N. Hasegawa, Y. Umezawa, & I. Koike, 2008. Specific growth rate as a determinant of the carbon isotope composition of the temperate seagrass *Zostera marina*. *Aquatic Botany* 89: 331–336.

Taugbøl, A., T. P. Quinn, K. Østbye, & L. Asbjørn Vøllestad, 2020. Allometric relationships in morphological traits associated with foraging, swimming ability, and predator defense reveal adaptations toward brackish and freshwater environments in the threespine stickleback. *Ecology and Evolution* 10: 13412–13426.

Thornber, C., E. Jones, & M. Thomsen, 2016. Epibiont-Marine Macrophyte Assemblages. , 43–75, https://www.researchgate.net/publication/307466738_Epibiont-Marine_Macrophyte_Assemblages.

Tolhurst, T. J., M. G. Chapman, & R. J. Murphy, 2020. The Effect of Shading and Nutrient Addition on the Microphytobenthos, Macrofauna, and Biogeochemical Properties of Intertidal Flat Sediments. *Frontiers in Marine Science* 7:

Touchette, B. W., & J. M. Burkholder, 2007. Carbon and nitrogen metabolism in the seagrass, *Zostera marina* L.: Environmental control of enzymes involved in carbon allocation and nitrogen assimilation. *Journal of Experimental Marine Biology and Ecology* 350: 216–233.

Vierucci, E., 2009. Multiple stressor effect on the recovery of marine benthic community. Unisalento.it Università del Salento, <http://salentoarch.unisalento.it:8080/xmlui/handle/11092/15>.

Wainright, S. C., J. C. Haney, C. Kerr, A. N. Golovkin, & M. V. Flint, 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. *Marine Biology* 131: 63–71.

Whalen, M. A., R. D. B. Whippo, J. J. Stachowicz, P. H. York, E. Aiello, T. Alcoverro, A. H. Altieri, L. Benedetti-Cecchi, C. Bertolini, M. Bresch, F. Bulleri, P. E. Carnell, S. Cimon, R. M. Connolly, M. Cusson, M. S. Diskin, E. D'Souza, A. A. V. Flores, F. J. Fodrie, & A. W. E. Galloway, 2020. Climate drives the geography of marine consumption by changing predator communities. *Proceedings of the National Academy of Sciences* 117: 28160–28166, <https://www.pnas.org/content/117/45/28160>.

Whitfield, A. K., K. W. Able, S. J. M. Blaber, M. Elliott, A. Franco, T. D. Harrison, & E. D. Houde, 2022. Feeding Ecology and Trophic Dynamics. *Fish and Fisheries in Estuaries* 255–331.

Williams, S. L., & M. H. Ruckelshaus, 1993. Effects of Nitrogen Availability and Herbivory on Eelgrass (*Zostera Marina*) and Epiphytes. *Ecology* 74: 904–918.

Wołowicz, M., A. Sokołowski, & R. Lasota, 2007a. Estuaries — a biological point of view. *Oceanological and Hydrobiological Studies* 36: 113–130.

Wołowicz, M., A. Sokołowski, & R. Lasota, 2007b. Estuaries — a biological point of view. *Oceanological and Hydrobiological Studies* 36: 113–130.

WOODWARD, G., B. EBENMAN, M. EMMERSON, J. MONTOYA, J. OLESEN, A. VALIDO, & P. WARREN, 2005. Body size in ecological networks. *Trends in Ecology & Evolution* 20: 402–409.

Worm, B., & J. Emmett. Duffy, 2003. Biodiversity, productivity and stability in real food webs. *Trends in Ecology & Evolution* 18: 628–632.

York, P. H., G. A. Hyndes, M. J. Bishop, & R. S. K. Barnes, 2018. Faunal Assemblages of Seagrass Ecosystems. *Seagrasses of Australia* 541–588.

Expenditure

Item	Supplier	Specs	Price
Travel (train)	Trainline	N/A	£477.12
Travel (boat)	IOM Steam Packet	N/A	£87.00
Accommodation	Campsites	N/A	£83.00
Mesh bags	Yuxi shop	x20	£62.60
Lab analysis	OEA Laboratories Limited	x46	£1188.86
Total			£1898.58

Statement of Contributions

Contributor Role	Persons involved
Conceptualization	MH, RU
Data Curation	MH, Project Seagrass team
Formal Analysis	MH
Funding Acquisition	MH
Investigation	N/A
Methodology	MH, RU
Project Administration	MH, RU
Resources	MH, RU
Software	MH
Supervision	RU
Validation	N/A
Visualization	MH
Writing – Original Draft	MH
Writing – Review & Editing	MH, RU

Ethics



Swansea University
Prifysgol Abertawe

Approval Date: 14/02/2025

Research Ethics Approval Number: 2 2025 8772 11960

Thank you for completing a research ethics application for ethical approval and submitting the required documentation via the online platform.

Project Title Seagrass associated biodiversity in the temperate seascape
Applicant name MR MANNING EDWARD HOPE
Submitted by MR MANNING EDWARD HOPE /
Full application form link <https://swansea.forms.ethicalreviewmanager.com/Project/Index/10744>

The Science and Engineering ethics committee has approved the ethics application, subject to the conditions outlined below:

Approval conditions

1. The approval is based on the information given within the application and the work will be conducted in line with this. It is the responsibility of the applicant to ensure all relevant external and internal regulations, policies, and legislations are met.
2. This project may be subject to periodic review by the committee. The approval may be suspended or revoked at any time if there has been a breach of conditions.
3. Any substantial amendments to the approved proposal will be submitted to the ethics committee prior to implementing any such changes.

Specific conditions in respect of this application:

The application has been classified as *Low Risk* to the University.

No additional conditions.

Statement of compliance

The Committee is constituted in accordance with the Governance Arrangements for Research Ethics Committees. It complies with [the guidelines of UKRI](#) and the concordat to support [Research Integrity](#).

Science and Engineering Research and Ethics Chair

Swansea University.

If you have any queries regarding this notification, then please contact your research ethics administrator for the faculty.

- For Science and Engineering contact FSE-Ethics@swansea.ac.uk
- For Medicine, Health and Life Science contact FMHLS-Ethics@swansea.ac.uk
- For Humanities and Social Sciences contact FHSS-Ethics@swansea.ac.uk

Dyddiad Cymeradwyo: 14/02/2025

Rhif Cymeradwyo Moeseg Ymchwil:

Diolch am gwblhau cais moeseg ymchwil am gymeradwyaeth foesegol ac am gyflwyno'r ddogfennaeth ofynnol drwy'r plaffform ar-lein.

Tcitiŷ y Proiect Seagrass associated biodiversity in the temperate seascape
Enw'r Ymgeisydd MR MANNING EDWARD HOPE
Cyflwynwyd gan MR MANNING EDWARD HOPE /
Dolen i'r ffurflen gais lawr <https://swansea.forms.ethicalreviewmanager.com/Project/Index/10744>

Mae'r pwyllgor moeseg Science and Engineering wedi cymeradwyo'r cais moeseg ymchwil, yn amodol ar yr amodau a amlinellir isod:

Amodau cymeradwyo

1. Mae'r gymeradwyaeth yn seiliedig ar yr wybodaeth a roddir yn y cais, a gwneir y gwaith yn unol â hyn. Yr ymgeisydd sy'n gyfrifol am sicrhau bod yr holl reoliadau, polisiâu a deddfau mewnol ac allanol perthnasol yn cael eu dilyn.
- Gall y prosiect hwn gael ei adolygu gan y pwyllgor o bryd i'w gilydd. Gellir atal neu ddirymu'r gymeradwyaeth ar unhyw adeg os bydd yr amodau'n cael eu torri.
 - Caiff unhyw addasiadau sylweddol i'r cais a gymeradwywyd eu cyflwyno i'r pwyllgor moeseg cyn i'r fath newidiadau gael eu rhoi ar waith.

Amodau penodol ynghylch y cais hwn:

Barnwyd bod y cais yn risg Low i'r Brifysgol.

Dim amodau ychwanegol.

Datganiad o gydymffurfiaeth

Penodir y pwyllgor yn unol â'r trefniadau llywodraethu ar gyfer pwyllgorau moeseg ymchwil. Mae'n cydymffurfio â [chanllawiau Ymchwil ac Arloesi yn y DU \(UKRI\)](#) a'r concordat i gefnogi [ymchwil ymchwil](#).

Cadeirydd Ymchwil a Moeseg, Science and Engineering

Prifysgol Abertawe.

Os oes gennych ymholiadau ynghylch yr hysbysiad hwn, yna mae croeso i chi gysylltu â gweinyddwr moeseg ymchwil eich cyfadrn.

- Ar gyfer Gwyddoniaeth a Pheirïanneg, e-bostiwech FSE-Ethics@abertawe.ac.uk
- Ar gyfer Meddygaeth, Iechyd a Gwyddor Bywyd, e-bostiwech FMHLS-Ethics@abertawe.ac.uk
- Ar gyfer y Dyniaethau a'r Gwyddorau Cymdeithasol, e-bostiwech FHSS-Ethics@abertawe.ac.uk