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Seagrass-Associated Biodiversity Influences Organic Carbon in a Temperate Meadow

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Abstract: There is increasing interest in the role that seagrasses play in storing carbon in the context of climate mitigation, but many knowledge gaps in the factors controlling this storage exist. Here, we provide a small case study that examines the role of infaunal biodiversity in influencing seagrass and the carbon stored in its sediments. A total of 25 species of invertebrate were recorded in an intertidal *Zostera marina* meadow, where these species were dominated by polychaete worms with no bivalves present. We find organic carbon storage (within the top 20 cm) measured by AFDW to be highly variable within a small area of seagrass meadow ranging from 2961 gC.m^{-2} to 11,620 gC.m^{-2} with an average (±sd) of 6460^{2} ± 3274 gC.m^{-2}. Our analysis indicates that infaunal communities are significantly and negatively correlated with this sediment organic carbon. However, this effect is not as influential as hypothesised, and the relatively small sample size of the present study limits its ability to provide strong causality. Other factors, such as algal abundance, curiously had a potentially stronger influence on the carbon in the upper sediments. The increasing richness of infauna is likely reducing the build-up of organic carbon, reducing its ecosystem service role. We believe this to likely be the result of bioturbation by specific species such as *Arenicola marina* and *Ampharete acutifrons.* A change in sediment organic carbon suggests that these species could be key drivers of bioturbator-initiated redox-driven organic matter turnovers, influencing the microbial processes and remobilizing sediment compounds. Bioturbators should be considered as a limitation to C_{org} storage when managing seagrass C_{org} stocks; however, bioturbation is a natural process that can be moderated when an ecosystem is less influenced by anthropogenic change. The present study only provides small-scale correlative evidence with a range of surprising results; confirming these results within temperate seagrasses requires examining this process at large spatial scales or with targeted experiments.

Keywords: blue carbon; polychaetes; eelgrass; drivers

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1. Introduction

There is increasing evidence at regional and global scales that we are fishing down the marine food chain [1,2], creating a whole range of unintended consequences [3], which are restructuring marine ecosystems [4]. This restructuring is increasingly being observed at the base of many ecosystems where the abundance and structure of invertebrate communities are changing with respect to varying levels of predation [5–8]. These changes in invertebrate communities also happen with respect to increasing eutrophication and organic pollution [9]. Given the roles that invertebrate communities play in marine sediments in terms of carbon biochemistry [10], these changes are of increasing global importance.

Coastal vegetated ecosystems such as seagrass meadows, mangrove forests, salt marshes, and hypersaline tidal flats are blue carbon environments, largely contributing to global carbon sequestration [11–13]. Blue Carbon science has rapidly proliferated as a consequence of the realisation of the need to manage these resources in the context of the climate [14]; however, this management suffers from the presence of many knowledge gaps about the primary drivers of carbon storage and release [11,15].

Given what we know of how marine ecosystems are becoming increasingly restructured by over-exploitation, pollution, and increasingly climate-induced warming [16], understanding how different components of the food web influence carbon storage and release is of increasing importance. The implications of biotic factors on carbon stocks, such as bioturbation and microbial processes, have been proposed as a research priority but remain poorly understood [17]. In many marine ecosystems there is increasing realisation that numerous faunal communities re-work and re-mobilise sediment, often inducing numerous local benefits for the interaction of the ecological community. Crabs are well recorded to rework mangrove and salt marsh sediments [18,19] whilst in many environments bioturbating animals such as sea cucumbers play similar roles [20].

Bioturbation is defined as the reworking of soils and sediments by animals or plants, and it is an umbrella term that describes the process by which fauna rework the particles of sediment through ingestion, burrowing, and excretion. Bio-irrigation, a separate process that affects water movement through actively ventilating burrows with oxygenated overlying water, is often grouped with the term bioturbation [21]. Bioturbators are important ecosystem engineers that can rehabilitate polluted sediments and play crucial roles in shaping soil ecosystems as they are the foundation of biogeochemical processes in marine habitats [22]. In seagrass meadows, bioturbators have commonly been found to restructure communities and vice versa [23,24]. This therefore indicates that such roles will propagate into the seagrass sediments.

The microbial priming effect (MPE) is the remineralisation of carbon stimulated by disturbance [25]. Labile organic matter (LOM) inputs driven by bioturbator movement lead to disproportionate remineralisation of stable organic carbon (C_{org}) through MPE [26]. Bioturbators have close relationships with sediments and microbes. This is because bioturbators such as infauna rework and bring O_2 into anoxic sediment, which catalyses sediment metabolization and increases substrate permeability. This changes the depth distribution of organic material, enhances the quality and inventory of food for deposit feeders, and increases nutrient fluxes, leading to increased primary production by benthic fauna and elevated microbial activity, which promotes infaunal biodiversity [27]. Indirectly, they consume and alter microbial communities, which greatly influences nutrient cycling and sequestration [28]. Deeper O_2 penetration through oxygenation can reduce the organic content of sediment by up to 50% in situ [29].

Seagrass roots trap sediment, stabilising soil and creating three-dimensional habitats in support of diverse faunal (micro and macro) assemblages, enhancing foraging opportunities for infauna communities, including bioturbators [30]. As a result, seagrass meadows greatly increase infauna densities and assemblages, with significantly lower numbers of taxa recorded in fragmented meadows [31] and bare sediments [32].

In seagrass meadows, burying activities by deposit feeders are thought to increase the growth rate of seagrass through improving sediment oxygenation and organic matter (OM) remineralisation enhancement. Alternatively, head-down ‘conveyor belt’ feeders, such as *Arenicola marina*, can disturb the root–rhizome matrix and bury seeds below their critical depth, which stops seedling development [33]. Prolonged top-down trophic cascades through unsustainable harvest of predators have indirectly affected benthic seagrass communities, resulting in a global increase in bioturbator densities that enhance transport of O_2 into deeper sediments, ultimately effecting the plants photosynthetic C fixation, storage, and remineralisation [34]. Given these active management concerns, it is vital to understand the extent of the impacts bioturbators may be having on seagrass productivity and carbon storage.

Current research indicates there is a relationship between infaunal assemblages and seagrass carbon storage in the tropics [35]. However, little to no literature covering this theme is available in temperate seagrass ecosystems, resulting in a lack of discussion around this concept in Blue Carbon research and policy. A significant knowledge gap exists in the context of degraded food webs [36], such as that observed in the North Atlantic [2]. The previous literature on seagrass has not measured animal density and biodiversity in relation to both carbon storage and productivity but instead has focused on the effects of bioturbation on one or the other. Overall, there is a lack of infauna studies in seagrass meadows that relate to the properties of the ecosystem, such as carbon storage and productivity.

The present case study hypothesises that infauna density and biodiversity influence carbon storage in a temperate *Zostera marina* meadow. Surprisingly, this is the first study to investigate the relationship between infaunal animal density and biodiversity and seagrass, as well as carbon storage and productivity in northern temperate seagrass systems.

2. Methods

2.1. Study Area

The influence of bioturbation on seagrass productivity and carbon storage was investigated in Porthdinllaen (PD, Wales, UK) (Figure 1). Porthdinllaen contains over 28 ha of seagrass, with its full range spanning from the intertidal zone to the subtidal areas of the harbour [37]. Despite all effort to achieve favourable conservation status of habitat and species features, seagrass here continues to exist in unfavourable conditions, mainly due to damage caused by moorings and vehicles [38] and is one of the largest and most extensive meadows in Wales [39]. The seagrass has some excess nutrients from nearby golf courses [40], but overall has limited impacts from land due to its significant distance from any riverine input. The region suffers from a degraded food web as a result of centuries of overfishing [2], leading to a loss of predators.

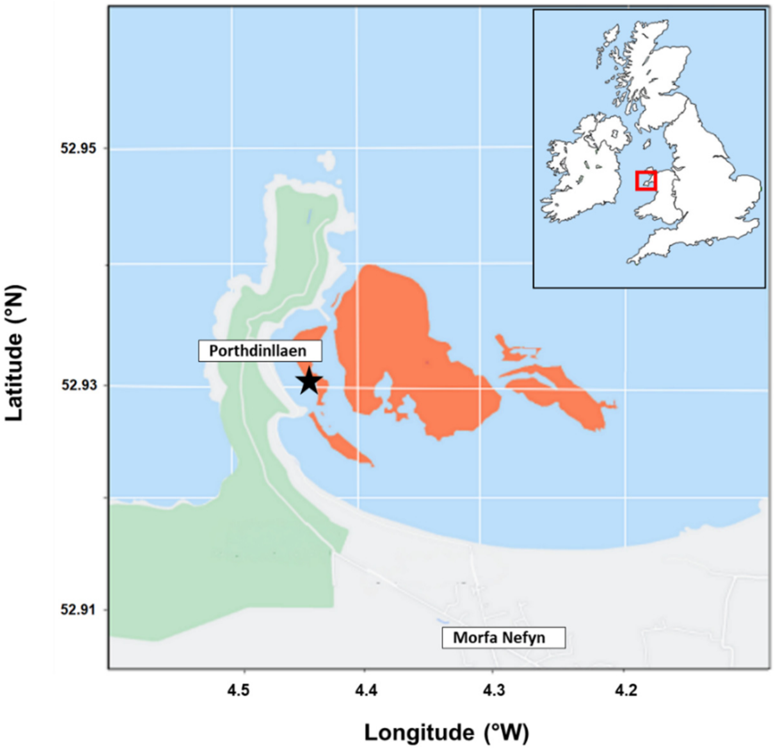

Figure 1. Seagrass study site, Porthdinllaen, North Wales, UK. Orange overlay shows mapped seagrass meadow (*Zostera marina*). Black Star is the location of the nine sampling sites spread over a 250 m long transect.

2.2. Seagrass and Sediment Assessment

A 0.25 m^2 quadrat was used to sample eelgrass (*Zostera marina*) throughout the intertidal meadow in Porthdinllaen. These quadrats were spread over a 250 m long section of intertidal seagrass. Nine sites were stratified a priori into those with high, medium, and low levels of expected bioturbation intensity determined by the density of lugworm (*Arenicola marina*) casts in each quadrat (observed on the seabed surface). Quadrats containing three or more worm casts were considered areas of high bioturbation; those containing one or two worm casts were considered areas of medium bioturbation; and those with no worm casts were considered areas of low bioturbation. Quadrats were placed intertidally on the seagrass at low tide at the shoreline as the tide went out and the seagrass was then assessed. Shoot density was determined alongside seagrass percentage cover of seagrass and macroalgae using percentage cover standards. In addition, percentage cover of epiphytes (using the Seagrass Watch method), sediment type, and coverage of leaves with wasting disease were also quantified. Measurements of the redox layer depth were assessed visually using a ruler. This visual method provides an integrated long-term average of redox conditions (aRPD) [41]. Reduction and oxidisation of ferric sulphides, the primary reaction responsible for sediment colour change, do not occur instantly, and therefore, although the visual method may have short-term inaccuracies, we believe it makes a better longer-term indication of the conditions influencing the carbon stored in the sediments [41,42].

2.3. Biodiversity Assessment

Nine biodiversity and nine carbon cores were taken, one of each within each quadrat, and hammered down to collect a core with a sediment depth of 20 cm. These were collected using PVC pipes with a diameter of 10 cm. Cores were retrieved and subsampled in the field into 10 cm intervals (0–10 cm and 10–20 cm), placed in a freezer box for transportation, and stored in a freezer until analysis. These 10 cm intervals were used for biodiversity samples, and samples were sieved through 0.5 mm using seawater to separate the invertebrates from the fine sedimentary material according to international standard methods (ISO, 2022). Invertebrates were stored using 70% ethanol and 10% glycerol until further laboratory analysis. Invertebrates were identified to species levels using a 40 X–2500 X LED Trinocular Lab Compound Microscope (OMAX, Gyeonggi-do, Republic of Korea) and [43]. Species accumulation curves indicate that the number of samples was sufficient to characterise the assemblage (see Appendix A).

2.4. Carbon Core Analysis

Nine carbon cores were taken, one within each quadrat, and hammered down to collect a core with a sediment depth of 20 cm. These were collected using PVC pipes with a diameter of 10 cm. Cores were retrieved and subsampled in the field into 10 cm intervals (0–10 cm and 10–20 cm), placed in a freezer box for transportation, and stored in a freezer until analysis. Cores were analysed following the established methods outlined in the Blue Carbon Manual [44]. Samples were left to thaw for 24 h before being weighed and oven-dried at 60 °C for 72 h or until a constant weight was achieved. After drying, the sediment was weighed again to determine the dry bulk density.

Aliquots of 5 cm^3 of each subsample were placed into pre-weighed crucibles and placed in the muffled furnace at 650 °C for 6 h to determine the loss of ignition (% LOI). Organic matter was determined according to [45], due to its comparability to the environment.

The literature commonly extrapolates organic carbon (C_{org}) stocks in *Z. marina* meadows to a 100 cm depth from a 25 cm depth [12,46]. Although we recognise the uncertainty in performing so, we have calculated values to 25 cm from our values of 20 cm in order to make comparisons with other literature values [47].

2.5. Statistical Analysis

In order to examine differences in the community composition of the infaunal communities and link this to environmental parameters, nonmetric multidimensional scaling ordination (nMDS) was used with Bray–Curtis similarity using the software PRIMER v7 with PERMANOVA+ [48]. The Bray–Curtis similarity index was applied to square-root transformed data, which created a ranked similarity matrix [49]. This scale was used to determine if key species could be drivers of seagrass productivity or carbon storage.

Additional Partial Least Squares regression analysis [50] was conducted to determine those parameters of the seagrass community (plants and infauna) that most strongly correlate to the amount of organic carbon within different depth segments of the seabed (top 10 cm, 10 to 20 cm, and the whole of the top 20 cm). This analysis is particularly suited to incidences when the matrix of predictors has more variables than observations and when there is multi-co-linearity among variables [50,51].

3. Results

3.1. Invertebrate Communities

A total of 25 species of invertebrates were recorded from biodiversity cores across nine study quadrats in PD. In total, 74 individuals were recorded, with an average of 8.2 animals per sample. A total of 24 annelids were sampled (22 Polychaetes and 2 Nemertea), one crustacean was sampled (Arthropoda), and 0.014 organisms per L of sediment. *Ampharete acutifrons* (present in 89% of samples) was the most abundantly recorded species across the study area (22 individuals in total sampled) and of samples (Appendix A), followed by *Notomastus latericeus* and *Neoamphitrite edwardsi.* Five species dominated the assemblages, making up 63% of all the animals observed (see Table 1). These dominant species were all categorised in terms of their reworking traits as being ‘upward and downward conveyors’, two of them were living in fixed tubes, and the other three defined as having ‘limited movement’ (Table 1) [52].

Table 1. Bioturbation potential allocations (adapted from [52]) for the five most abundant macrofaunal species (that accounted for 63% of the abundance) recorded in the seagrass at Porthdinllaen, North Wales, UK. M_i and R_i are the reworking and mobility traits, and Ft_i is the corresponding sediment reworking functional types. Two of the species had no allocation, and therefore, data from closely related species was used in lieu (see * and **).

Species	Reworking Traits (R_i)	Motility Traits (M_i)	Sediment Reworking Types (Ft_i)
Neoamphitrite edwardsi *	Upward and downward conveyors	Fixed Tubes	DC
Ampharete acutifrons	Upward and downward conveyors	Limited Movement	UC/DC
Notomastus latericeus	Upward and downward conveyors	Limited Movement	UC
Terebellides stroemii	Upward and downward conveyors	Fixed Tubes	DC
Malacoceros vulgaris **	Upward and downward conveyors	Limited Movement	UC/DC

* *Neoamphitrite affinis*, ** *Malacoceros fuliginosus*.

Animal abundance (p = 0.025, $F_{1,17}$ = 6.11) and richness (p = 0.033, $F_{1,17}$ = 5.45) were significantly higher in the first 10 cm of sediment and decreased with depth (Figure 2); however, the whole assemblage structure was not changed with depth ($F_{1,17}$ = 1.9383, p = 0.067). Across the nine sediment cores, there was an average of 8.2 ± 3.9 animals per core; this was 5.4 ± 2.6 animals in the top 10 cm and 2.8 ± 2.0 animals in a depth of 10–20 cm. Species richness (number of taxa recorded) was on average 4.2 ± 1.6 animals per core in the upper 10 cm and 2.4 ± 1.7 animals per core in the deeper depths from 10 to 20 cm.

3.2. Sediment Carbon

The average carbon storage (based on a 20 cm core depth) was 6460 gC.m^{-2} ± 3274 and ranged from 2961 to 11,620 gC.m^{-2} (Figure 3). When extrapolated to a 25 cm depth for alignment with existing *Z. marina* data across the Northern Hemisphere [47], the mean value becomes 8075 ± 4092 gC.m^{-2}. This indicates that carbon stocks in Porthdinllaen are on average higher than the Northern Hemisphere average of 2721 gC.m^{-2} [47]. The carbon levels did not significantly differ between depths (p = 0.76, $F_{1,17}$ = 0.10); however, the data from the first 10 cm is far more variable than that at deeper depths (Figure 3).

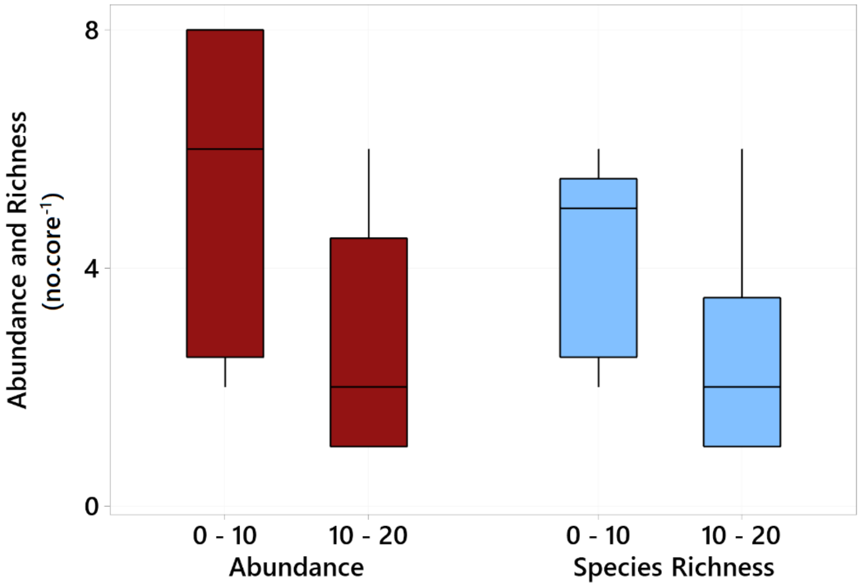

Figure 2. Box plots of infaunal abundance (red) and species richness (blue) at two depths (cm) in sediment cores (10 cm diameter) within the Porthdinllaen seagrass meadow (*Zostera marina*) in North Wales, UK.

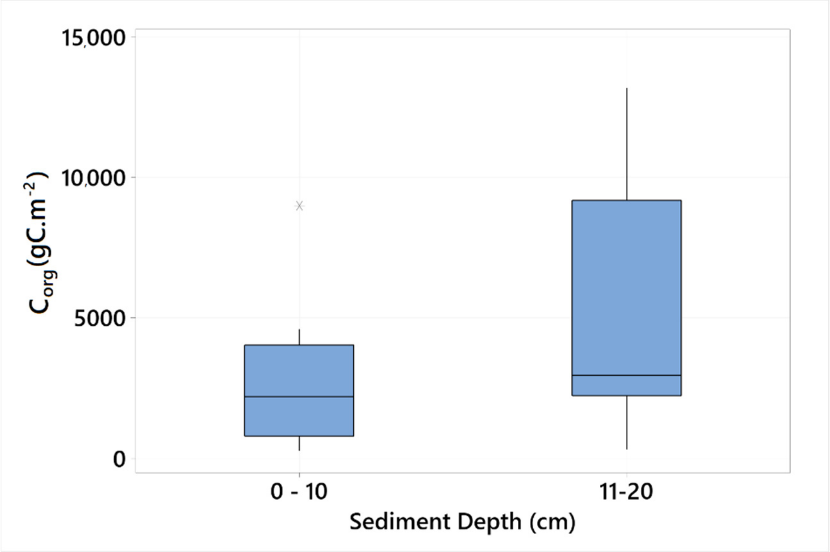

Figure 3. Box plot of total organic carbon (gC.m^{-2}) at two depth intervals recorded in sediment cores within the Porthdinllaen seagrass meadow (*Zostera marina*).

3.3. Seagrass Characteristics

Seagrass % cover was on average (±SD) 32 ± 19% and ranged from 9 to 73%. Shoot density was on average 75 ± 34 shoots per 0.25 m^2, ranging from 26 to 128 shoots. The redox layer was also quite variable between cores, ranging from a depth of 16 cm to 28 cm with an average depth of 21.16 ± 4.13 cm. Epiphytes coverage was also highly variable, ranging from 1 to 17% cover with an average cover of 6.8 ± 5.7.

3.4. Correlations

The creation of a Pearson's correlation matrix between fourteen variables assessed in the cores (see Figure 4) revealed a range of significant correlations. This shows a range of strong correlations between the infaunal invertebrate communities and aspects of the seagrass and the carbon storage.

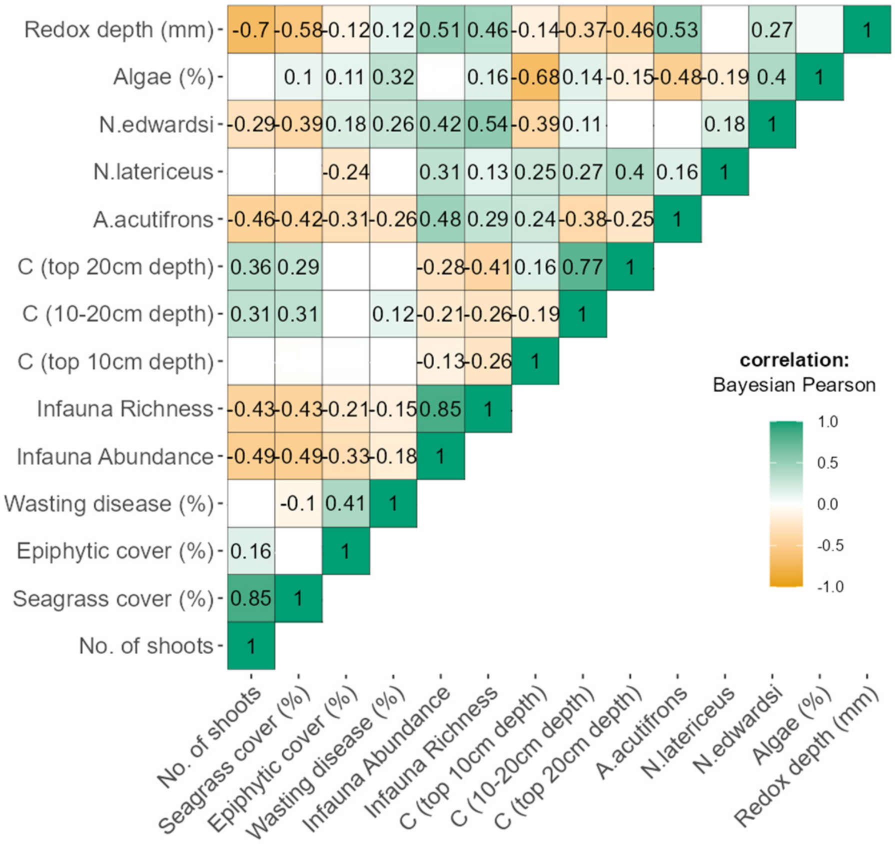

Figure 4. Pairwise Bayesian Pearson correlation coefficients between variables quantified in the seagrass meadow in Porthdinllaen, Wales, UK.

A significant negative correlation ($p < 0.05$) was observed between the redox depth and seagrass cover (-0.58) as well as shoot density ($r = -0.7$). This redox parameter was also found to have positive correlations with infaunal abundance (0.51) and richness ($r = 0.46$). Additionally, a similar negative correlation was observed between the number of surface worm casts and the density of seagrass shoots. The cover of algae on the seabed was also negatively correlated with the amount of organic carbon in the top 10 cm of the sediment. The small sample size relative to the number of potential drivers led to the need to examine the data using a targeted partial least squares statistical approach [50].

When applying a partial least squares (PLS) regression analysis of sediment carbon content in different depth ranges relative to environmental and ecological parameters measured within the seagrass, we found that 72% of the variability in the carbon content in the top 10 cm was best explained by the negative effect of algae cover and *Neoamphitrite edwardsi* (a downward conveyor) and the positive effect of the ringworm species *Notomastus latericeus* (Figure 5, Table 2). Furthermore, 52% of the carbon content of the deeper 10 cm (10–20 cm) was explained by a combination of the positive effect of seagrass shoot density and the density of the ringworm species *Notomastus latericeus,* together with a negative effect of *Ampharete acutifrons*. Meanwhile, 74% of the variability of the carbon content of the entire core sample (top 20 cm) was explained by the negative effect of algae cover, *A. acutifrons* and *N. edwardsi* (a downward conveyor), and the positive effect of the ringworm species *Notomastus latericeus* (Table 2).

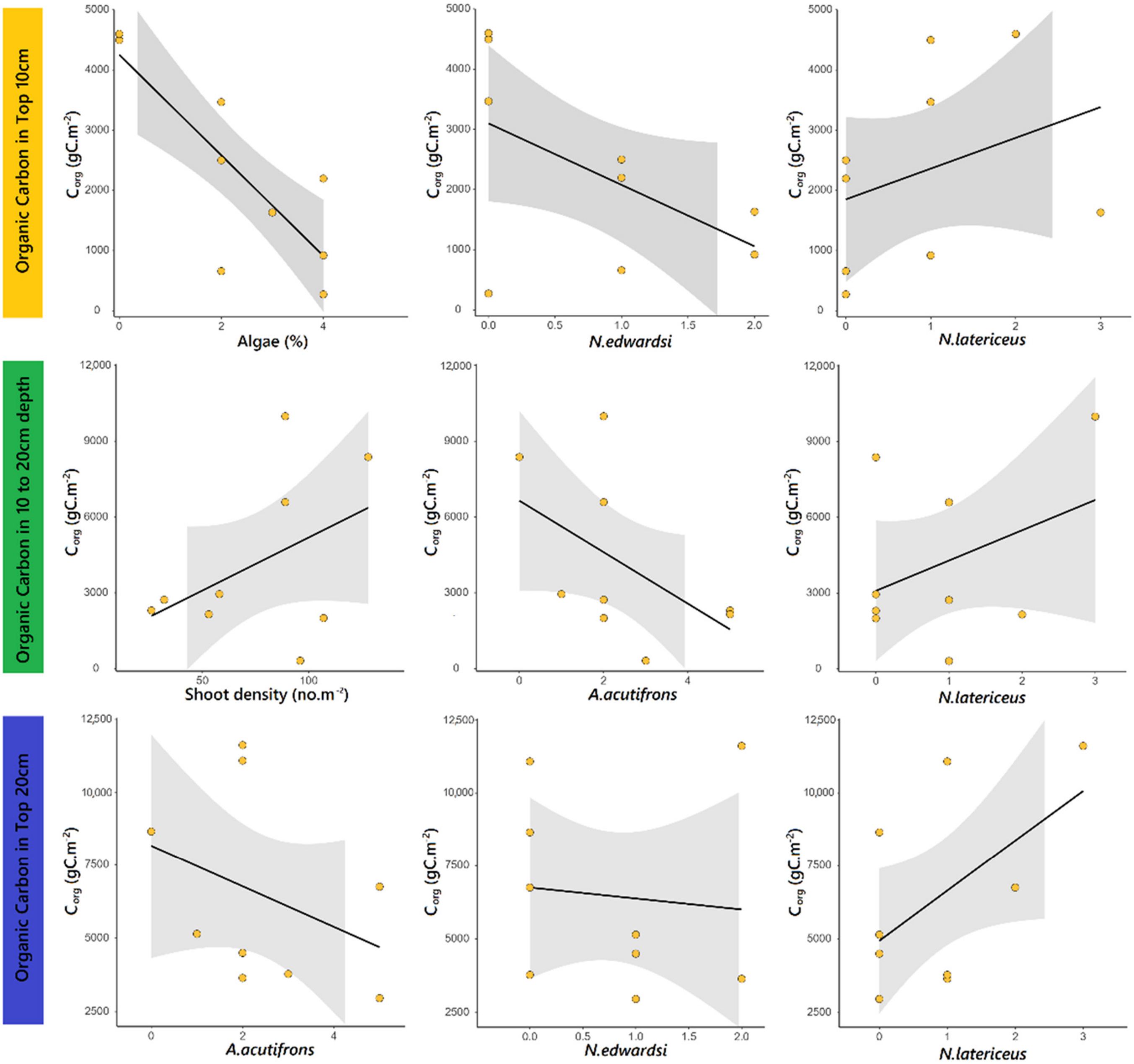

Figure 5. Correlations and 95% CI between variables observed to contribute to three partial least squares regression models (see Table 2), explaining carbon stores in different depth fractions of seagrass sediment in Porthdinllaen, North Wales, UK.

Infaunal assemblage composition varied between the samples (Figure 6). However, samples did not show significantly high levels of similarities. Bray–Curtis similarity scaling showed some 30% similarity clusters between cores containing low and medium total organic carbon levels; however, there was no consistency in this pattern. ANOSIM indicated that neither bioturbation (no. of worm casts) nor carbon content explained the variability in the assemblage ($p > 0.7$).

Table 2. Partial least squares (PLS) regression analysis (final models following stepwise analysis) of sediment carbon content in different depth ranges relative to environmental and ecological parameters measured within the seagrass. Table shows the overall 'global' ANOVA statistics for each of the regression models, the individual principal components, and their cumulative R2 values. The table also shows the values computed by the PLS model of the variance explained with the *x*-axis (x-var.). Individual regression coefficients of the specific carbon predictors are also shown.

	R2	**R2**	**F**	**P**		**Coeff**				
Carbon	Comp 1	Comp 2			X variance	Algae (%)	Shoot density	*Ampharete acutifrons*	*Notomastus latericeus*	*Neoamphitrite edwardsi*
Corg in Top 10 cm	0.71	0.72	17.38	0.004	0.50	−0.55			0.22	−0.36
Corg in 10 to 20 cm	0.47	0.53	6.25	0.041	0.47		0.35	−0.4	0.3	
Corg in Top 20	0.69	0.74	14.16	0.007		−0.29		−0.49	0.77	−0.13

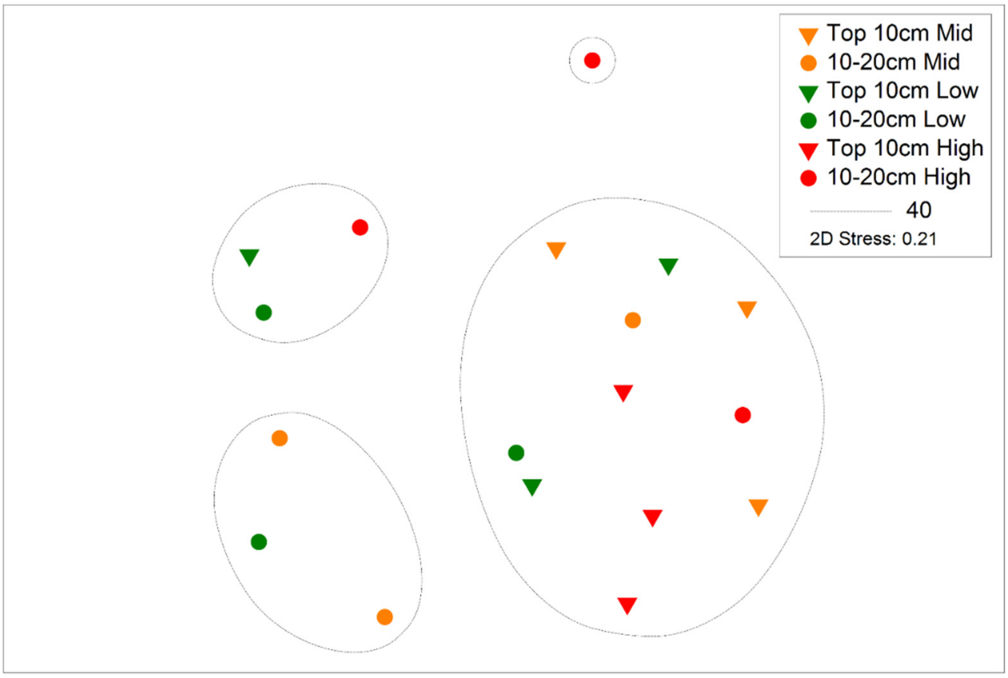

Figure 6. Non-metric multi-dimensional scale (nMDS) representation (showing 40% similarity groups) of infaunal species assemblages at two sediment depths within seagrass sites of varying levels of expected bioturbation (as defined by surface worm casts) in Porthdinllaen, North Wales, UK.

4. Discussion

There is limited discussion in the literature on the interaction of sedimentary organic carbon in seagrass meadows in the context of its associated biota. By their very nature, vegetated habitats support biodiverse and productive faunal communities that influence carbon cycling through processes of herbivory, bioturbation, and decomposition [53]. Many of these species exist in the sediment and in close proximity to the root systems of seagrass due to the radial oxygen loss (ROL) [54] that creates an oxic layer in otherwise potentially anoxic sediment. The present study is a novel example of assessing seagrass infaunal communities relative to seagrass sedimentary organic carbon storage accumulation and finds that specific abundant infaunal species, the cover of algae, and the seagrass density combine to be explanatory variables of the amount of carbon within the shallower sediment depths.

Shoot density and the abundance of the *Notomastus latericeus* were positive explanatory variables of the carbon, whereas algal cover, *Ampharete acutifrons*, and *Neoamphitrite edwardsi* were potentially negatively influencing carbon storage and accumulation. In addition, faunal assemblages present in sediments with relatively high C_{org} were significantly different from those present in sediments with low C_{org}. This raises two hypotheses: either seagrass infauna prefer sediment with specific organic content or the abundant assemblages of infauna are effective at remobilising the sediment, which alters the total organic C content in the sediment. We hypothesise the latter explanation is more likely.

As particular dominant infauna increased in abundance, the amount of C_{org} stored in the area decreased correspondingly, most likely due to the actions of bioturbating infauna of varied function [35]; however, this was not observed as a strong linear correlation but as a component of a partial least squares model that was also influenced by increasing macroalgal abundance and decreasing seagrass shoot density. We did not measure the particle size distribution of sediment in this study, and given the potential for this to influence carbon accumulation [55] and also act as an indicator of variable hydrodynamics [56] we cannot rule out this influence. However, we suspect it to be minimal due to the relatively small spatial area (200 × 10 m) and consistent sediment type from all sample areas that were classified as muddy sand, an observation from long-term data that has not changed over a decadal period [57].

Although infaunal richness was a significant driver of carbon, this did not explain the full variability, and other factors, such as algal and seagrass cover, were significant and possibly greater drivers of carbon storage. The negative correlation of algal cover with sediment carbon is an unexpected result and cannot be fully explained; however, we know that algal cover can have a negative impact on seagrass systems, leading to reduced density and patchiness [58], potentially further proliferating its cover as habitat gaps expand. This presence may also negatively influence the faunal communities, creating further complex interactions. In addition, the negative influence of macroalgae might relate to reduced productivity within the seagrass and therefore the reduced exudation of labile organic carbon or the reduced accumulation of plant detritus [59]. These explanations, however, remain speculative.

Infaunal richness and abundance were much lower at deeper depths in the sediment, where carbon levels were not significantly different and a lot less variable. We hypothesise that this reduced variability is the result of less prevalent and different infauna influencing sediment composition.

Ampharete acutifrons was the most abundant species sampled (on average three times higher density than other species) during this study and is described as a soft-bodied deposit feeding polychaete [60]. Higher *A. acutifrons* densities were most abundant in sample areas with low C_{org} content. *A. acutifrons* exert strong effects on the sediment by mechanically and chemically altering dissolved and particulate organic matter (POM), which might also enhance seagrass growth through the deep burial of O_2 [61]. *A. acutifrons* can reduce the concentration of H_2S in sediment porewater, facilitating seagrass growth in organic carbon-rich sediments, allowing the plant to thrive in areas of poor water quality [62], which have been recorded at the sampling site, Porthdinllaen [40].

Some specific species of infauna that were unexpectedly lower in density (e.g., *Arenicola marina*) are thought to have a stronger effect on biogeochemical processes [10], significantly influencing seagrass carbon stocks through burrowing activities by stimulating the remineralisation of carbon through mediated disturbance. This causes labile organic matter input and reduces the carbon capture capacity [63]. Previous lab studies have also shown how such burrowing played an important role in the cycling of iron and sulphur across the sediment–water interface [64].

A. marina was recorded as the principle bioturbator during this study and was present in three samples, which contained the lowest amount of C_{org}. These animals were the biggest species encountered, and therefore, physically, their effect would have been disproportionally bigger. *A. marina* is an upward conveyor with an impressive capacity for particle reworking and the transport of deep sediment particles to the surface [65].

Overall, it seems the interactions of multiple components of the infaunal assemblage are potentially exerting some level of influence over the seagrass carbon stocks rather than just one specific species of infauna, but this influence is not as pronounced as we hypothesised. In a broader sense, the interaction between the infauna and the seagrass is also a two-way process, as seagrass roots improve oxygenation and labile organic carbon, potentially promoting infauna abundance and diversity [66,67]. In addition, the presence of the organisms likely increases oxygen movement within the sediment, increasing the oxidation of toxic sulphide [68]. Bioturbator burrows such as those of *A. marina* are rich in organic carbon and can support up to 11 times more microbes than sediment without burrows [69]. Bioturbator-stimulated microbial priming accounts for approximately 15% of released C_{org} in controlled environments [70], which likely explains why C_{org} was lowest in samples that contained this species.

The environment created by the seagrass might attract animals (e.g., through enhanced oxygenated sediments with a deeper redox layer). Undisturbed seagrass habitats with greater complexity in relation to shoot density, plant biomass, and canopy height greatly increase infauna communities and assemblages [31,71]. In the present study, as seagrass density varied, we found little impact of this upon the abundance and diversity of the infauna but some interaction with the carbon. This may reflect the fact that only basic parameters of the seagrass were assessed (e.g., cover and density) rather than a detailed assessment of the root and rhizome biomass.

Bioturbators play crucial roles in sediment nutrient recycling and removing pollutants and contaminants from sediment through burial and oxygenation, which promotes seagrass growth through bioirrigation, a process that differs from bioturbation [72]. However, bioturbators also disturb the root–rhizome matrix, which damages the anchoring system of the plant and reduces overall productivity [62]. Our results do find some influence of the infaunal community on the carbon, but limited effect on the seagrass. In addition, bivalves were not recorded within the sediment at the site; given the known role many of these species play in assisting with the detoxification of sulphide-rich sediments [73], this was a surprise. The detoxification influence of *A. acutifrons* may be playing this role (assuming the sediments are sulphide rich) instead rather than just the effect of the seagrass alone [74]. Although we focus on the potential negative influence of infauna on carbon storage within sediments, there exists some evidence that bioturbation might facilitate carbon storage due to the movement of organic matter deeper into the sediments [75]. Whilst we do not show such a process within our data, there exists potential for some species to do so.

Trophic cascades caused by over-exploitation of top predators have been recorded to affect C sediment stocks in tropical seagrass ecosystems [34]. Marine ecosystems in the North Atlantic are heavily overexploited and largely anthropogenically modified, leading to the presence of numerous potential trophic cascades [76] including seagrass ecosystems [77]. Within seagrass ecosystems, a loss of predators is thought to have released secondary consumers from control, leading to a loss of grazers and reduced resilience to eutrophication [77]. Previous studies have recorded cascades from changes in predatory fish density to densities of polychaete worms [78,79]. This suggests that trophic cascades with increased polychaete abundances could negatively influence seagrass carbon storage, as it has happened with other keystone predators, influencing grazing in tropical seagrass systems to affect sediment C_{org} stocks [34]. Findings of the present study show that bioturbators have the potential to turn seagrass meadows from carbon sinks to carbon sources [28] and should be considered as a negative factor when estimating seagrass C_{org} stocks.

In conclusion, we recorded infaunal communities within a temperate seagrass meadow to potentially influence the ability of the plant community to trap and store organic carbon. However, this effect is not as pronounced as expected. The increasing density of infauna is likely to have some effect in reducing the storage of organic carbon, which might affect its ecosystem service role, but other factors (algae and seagrass cover) are also influencing this over small scales. When in high densities, infauna can bury seedlings, uproot patches of seagrass, and reduce light availability by increasing turbidity. High bioturbation makes seagrass more susceptible to erosion via reducing sediment cohesion [62]. This study highlights the importance of including bioturbator processes when managing temperate seagrass C_{org} stocks and the need to examine this process in more detail.

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Appendix A

Table A1. Species List of All Invertebrates Recorded from Biodiversity Cores Across Nine Study Areas in Porthdinllaen, Wales, UK.

Annelida	Crustacea
(Polychaeta)	(Arthropoda)
Ampharete acutifrons	*Urothoe marina*
Arenicola marina	
Cirriformia tentaculata	
Eteone picta	
Euclymene lombricoides	
Eumida sanguinea	
Eurnereis longissma Johnston	
Lumbrineris latreilli	
Malacoceros vulgaris	
Marphysa bellii	
Mediomastus fragilis Rasmussen	
Melinna palmata	
Myriochele heeri	
Neoamphitrite edwardsi	
Nephtys caeca	
Nicolea zostericola	
Notomastus latericeus	
Parexgone hebes	
Scoloplos armiger	
Terebellides stroemii	
Thelepus setosus	
Polychaete sp.	
(Nemertea)	
Emplectonema echinoderma	
Tetrastemma coronatum	

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