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Navigating biodiversity patterns in fragmented seagrass mosaics

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Human-driven fragmentation of natural habitats increasingly threatens biodiversity, particularly in coastal ecosystems like seagrass meadows. Fragmentation breaks continuous habitats into smaller, isolated patches, amplifying edge effects and disrupting community structures and ecosystem functions. This study examines the effects of habitat fragmentation on large (> 1 mm) and small (0.2–1 mm) epifauna, as well as infauna, within eelgrass (*Zostera marina*) meadows along the Skagerrak coast in western Sweden. We assessed faunal responses across three fragmentation levels (low, medium, and high) and patch zones (Edge, Near-Edge and Center), providing a novel multi-assemblage analysis of these dynamics. Field surveys and statistical modeling revealed distinct community responses: large epifauna, especially amphipods, dominated low and moderately fragmented meadows, whereas highly fragmented areas showed more even species distributions. In contrast, small epifauna exhibited consistent abundance across zones and fragmentation levels. Infaunal communities varied most, with high fragmentation linked to increased evenness and shifts in species composition. These findings underscore the importance of conserving less fragmented meadows and highlight the need for targeted restoration efforts to enhance biodiversity and ecological resilience in degraded areas. By addressing both patch- and seascape-level fragmentation effects, this study offers critical insights into the ecological impacts of habitat fragmentation, supporting the development of targeted conservation strategies for coastal ecosystems.

Keywords Seascape, Associated communities, Conservation, Meadows, Invertebrates

Human activities and environmental changes are transforming seascapes at unprecedented rates, breaking once-continuous ecosystems into smaller, isolated patches. This habitat fragmentation threatens global biodiversity by driving habitat loss, population isolation, and increased edge effects[1–3]. Its impacts include disrupted migration patterns, the loss of keystone species, and reduced ecosystem services[2,4,5]. Alongside habitat loss, fragmentation is one of the most critical threats to biodiversity[6,7], affecting both foundational habitats and the communities they support, from terrestrial insects to marine benthic invertebrates[8,9].

Marine ecosystems are especially vulnerable to habitat fragmentation, with significant declines in key coastal habitats such as kelp forests, wetlands, seagrass meadows, mangroves, and coral reefs[10–14]. Fragmentation in these areas is largely driven by human activities and environmental disturbances, which divide habitats into isolated patches and accelerate biodiversity loss[15]. The contrasting conditions between habitat edges and interiors - known as edge effects - intensify the impacts on community structure, habitat complexity, and species interactions, with variations across ecosystems[16–19]. While edge effects may not directly cause fragmentation, they compound its effects on biodiversity, species composition, and ecosystem functions[1,20].

Seagrass meadows, essential coastal habitats and nurseries for many marine species, serve as a valuable model for studying edge effects and fragmentation[18,21]. As transitional zones between seagrass beds and adjacent habitats like sandy substrates, these ecotones exhibit pronounced edge effects, which drive shifts in both epifaunal and infaunal communities[15,21,22]. These effects are often more pronounced at habitat edges, where exposure to predators and environmental stress is greater, leading to behavioral and physiological changes in both groups[23,24]. Additionally, nutrient and sediment dynamics shift within these ecotones, further influencing species distribution and ecosystem function[25,26]. Epifaunal species, such as annelids, crustaceans, and mollusks, are particularly sensitive to structural changes, with resulting shifts in species richness, abundance, and community dynamics[23,27]. Infaunal organisms, including polychaetes and burrowing crustaceans, are impacted by changes in sediment composition, which affects their distribution and survival rates[28,29]. Both groups play key

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roles in benthic food webs, connecting primary producers with higher trophic levels and serving as bioindicators of environmental stress[30,31].

Although the impacts of fragmentation and edge effects in seagrass meadows are well-documented, less is known about their specific effects on epifaunal and infaunal communities[18,32,33]. Previous research has often studied these communities separately, without fully examining the role of fragmentation in shaping their structure and dynamics[32,34]. This study addresses this gap by analyzing how edge effects vary in seagrass meadows with different fragmentation levels, with a particular focus on epifaunal and infaunal communities.

We hypothesize that increased fragmentation amplifies edge effects, resulting in distinct shifts in community structure. Specifically, we expect highly fragmented meadows to exhibit lower species richness and altered dynamics, especially among epifaunal species, which may face increased predation pressure and environmental stress at habitat edges. Infaunal communities, particularly smaller and less mobile species, are anticipated to respond sensitively to changes in sediment composition and structure within fragmented meadows. By investigating these dynamics, we aim to deepen our understanding of fragmentation's ecological impacts and support more effective conservation strategies for seagrass ecosystems.

Methods

Study area and experimental design

The distribution of *Zostera marina* (eelgrass) was assessed in three regions, Gåsö (Gullmars fjord area), Askeron (Hake fjord area) and Teneskär (Kosterhavet archipelago), selected based on the availability of historical data from the 1980s[35] and representing high, medium and low fragmentation levels, respectively (Fig. 1). Fragmentation levels were initially determined by comparing historical and contemporary aerial imagery, supplemented by in

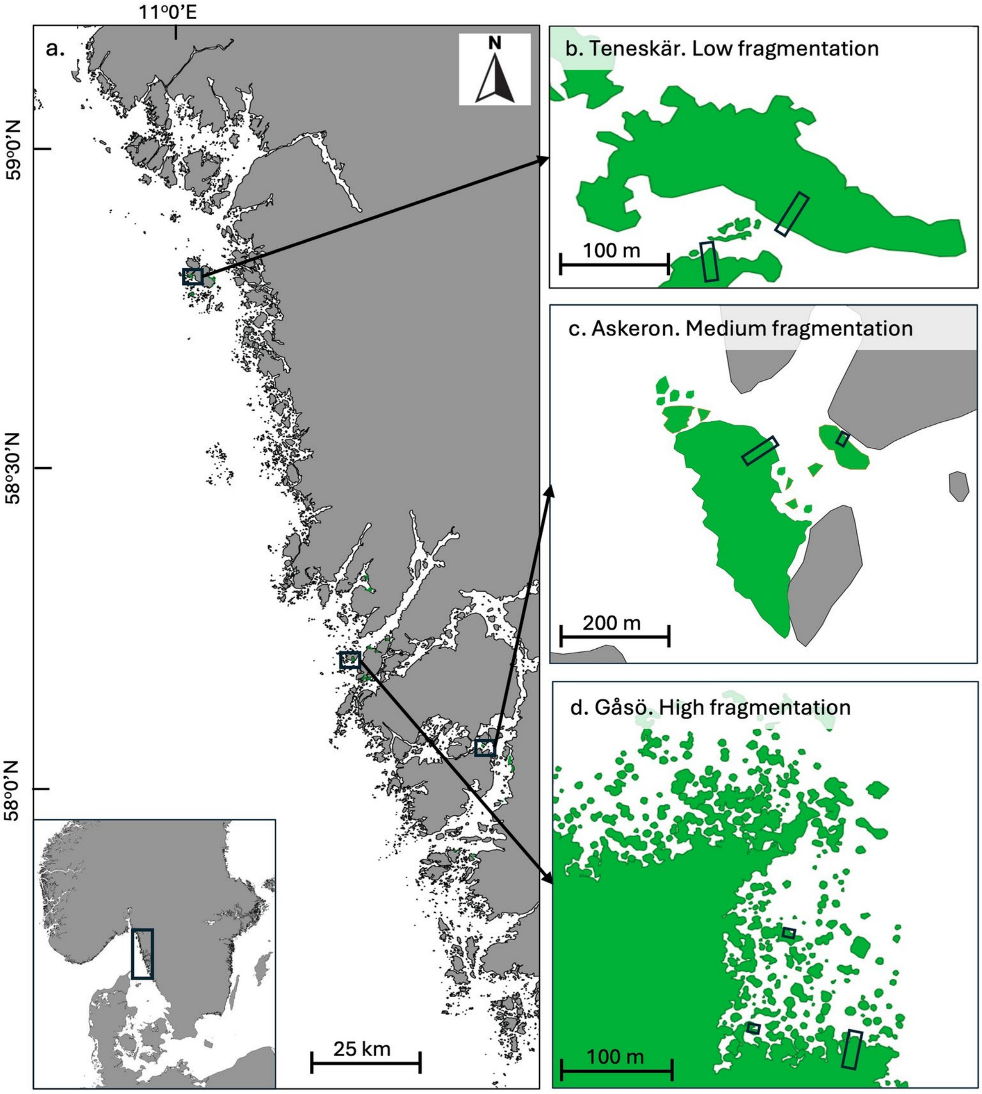

Fig. 1. Map of the sampling sites in the west coast of Sweden (**a**). Eelgrass meadows in Teneskär in the Kosterhavet National Park (**b**), Askeron Bay in the Hake fjord (**c**) and Gååsö island in the Gullmars fjord (**d**). Rectangles indicate the sampling transects at each location (QGIS, v3.2, https://qgis.org/).

situ observations, to establish the extent of habitat changes over time. To enhance precision, additional seascape metrics—total area, patch number, mean patch size, and patch isolation—were applied to characterize current fragmentation levels[36,37]. This combined approach captures the structure of the current habitat more effectively than the historical loss alone, with Gåsö classified as high fragmentation (70% loss, high patch number, small mean patch size), Askeron as medium (50% loss, moderate patch configuration), and Teneskär as low (under 25% loss, large patch sizes, low isolation). Field surveys validated these updated classifications, ensuring an accurate reflection of conditions impacting epifaunal and infaunal communities (see Table 1 for details).

At all sites, sampling was conducted at standardized distances within each eelgrass patch, measured from the edge toward the patch interior: (1) "Edge" (the first 1 m inside the meadow), (2) "Near-Edge" (1–2 m from the edge), and (3) "Center" (more than 5 m from the edge) (Fig. 1). To ensure robust sampling across each seascape, two of the largest patches (> 50 m in diameter) were chosen, minimizing the influence of patch size on fragmentation effects. A total of 15 epifauna and 15 infauna samples were collected within each patch, evenly distributed across the Edge, Near-Edge, and Center zones. This approach, aligned with established studies in seagrass meadows[38], provides comparability across zones and helps capture edge effects on community structure in fragmented seascapes. Fieldwork in July 2021 included snorkeling at approximately 1.5 m depth. Epifaunal communities were sampled by placing a 35 × 35 cm mesh bag (0.2 mm mesh) over eelgrass shoots, closing the bag, and cutting the shoots at the sediment surface, ensuring uniform sampling within a 0.043 m^3 volume. Infaunal samples were collected using a 10.5 cm diameter core to a depth of 10 cm, with density standardized to individuals per square meter by extrapolating from the core's surface area (86.6 cm^2). All samples were preserved in seawater and transported to the lab, facilitating cross-site and cross-zone comparisons.

In the laboratory, epifauna was carefully removed from eelgrass shoots, which were then counted and dried at 60 °C for 48 h to measure biomass. Epifauna samples were sieved into small and large size fractions using 0.2 mm and 1.0 mm mesh, respectively, and preserved in ethanol with Rose Bengal staining to facilitate counting and identification. This size-based separation aimed to reflect the distinct ecological roles of organisms within the eelgrass ecosystem. Smaller epifauna (typically juvenile stages, meiofauna, or small-bodied species) are often associated with microhabitats within the eelgrass canopy or sediment, feeding primarily on microalgae and detritus, while larger epifauna (such as grazers, predators, and larger-bodied species) engage in broader trophic interactions and may influence community dynamics through grazing, predation, and competition[35].

All organisms were counted and identified to the lowest taxonomic level possible. For infauna and the large epifauna fraction (> 0.5 mm), all organisms were counted in each sample. For the small fraction of epifauna (< 0.5 mm), the counts were estimated from three subsamples (0.5 g wet weight each), and total abundance was calculated based on the total weight of the sample. The combined small and large fractions provided overall epifaunal abundance, and densities were standardized to individuals per square meter (ind. m^{-2}) for comparability across sites and zones.

Assemblage structure

Principal Coordinate Analysis (PCoA) was initially applied to visualize assemblage structure variation in large (> 0.5 mm) and small (< 0.5 mm) epifauna, as well as infauna, among sampling zones within the seagrass patch, with each fragmentation level analyzed independently. This analysis used the R packages 'vegan'[39] and 'labdsv'[40]. Based on Bray-Curtis dissimilarity matrices of species abundances log10(x + 1) transformed to balance the contributions of dominant and rare species, the first two PCoA axes explained approximately 50% of total variability in species composition and abundance. Ellipsoids representing 95% confidence intervals encompassed sampling zones (Edge (E), Near-Edge (NE), and Center (C)). To identify species most responsible for community changes, correlations with PCoA axes were calculated by fitting a linear trend surface using the 'envit' function in 'vegan'[39], with these correlations shown as vectors in the ordination space.

We then assessed assemblage structure variation among sampling zones as a function of fragmentation level (two-way interaction: 'sampling zone × fragmentation') using a model-based approach for multivariate abundance data[41]. This approach addresses mean-variance relationship issues often seen in distance-based methods (e.g., PERMANOVA and ANOSIM)[42]. Generalized linear models (GLMs) with a negative binomial distribution were fitted to the species abundance matrix via the 'mvabund' R package[43], with p-values obtained from 999 PIT-trap resampling iterations. PIT-trap resampling, which transforms data using the cumulative distribution function (CDF) of the fitted model and then resamples the resulting probabilistic integral transform (PIT) values, provides robust p-value estimation by generating a reliable distribution of test statistics under the null hypothesis. This method is particularly effective for handling overdispersed data and assessing model fit. Model assumptions were visually inspected by plotting residuals against fitted values.

Seascape metrics	Teneskär	Askeron	Gåsö
Patch area	Large	Intermediate	Low
Patch number	< 5	5–15	> 15
Patch size	Large	Large-intermediate	Small
Patch isolation	High	Intermediate	Small
Fragmentation level	Low	Intermediate	High

Table 1. Seascape metrics used at the study locations to identify fragmentation levels, based on historical and current imagery as well as recent field observations.

Alpha diversity

We used a unified framework based on generalizations of Hill numbers to measure the taxonomic (species-level) alpha diversity of large (> 0.5 mm) and small (< 0.5 mm) epifauna, as well as infaunal assemblages. Hill numbers offer a family of diversity indices varying by a parameter ‘*q*’ that determines sensitivity to species relative abundances: ‘*q*’ = 0 (species composition only), ‘*q*’ = 1 (emphasis on common species), and ‘*q*’ = 2 (emphasis on dominant species)[44]. This parameter allowed us to assess whether diversity differences were driven by rare, common, or dominant species[45]. All indices were calculated in R using the ‘hillR’ package[46].

To test taxonomic alpha diversity differences among sampling zones in the seagrass patch as a function of fragmentation level (two-way interaction: ‘sampling zone in the patch x fragmentation’), we applied Generalized Linear Mixed Effects Models (GLMMs) via the ‘glmmTMB’ package[47]. Models used a “Gamma” error distribution with an “inverse” link function for large epifauna, a Gaussian distribution with an identity link for small epifauna and infauna at ‘*q*’ = 0, and a “Gamma” distribution for infauna at ‘*q*’ = 1 and ‘*q*’ = 2. Each model included “seagrass patch” (n = 2 per region) as a random effect to control for spatio-temporal non-independence. Violation of model assumptions were visually inspected through residuals *vs.* fitted values plots.

Results

A total of 44,398 individuals of large epifauna (> 0.5 mm) were recorded, representing 8 phyla (Annelida, Cnidaria, Arthropoda, Echinodermata, Chordata, Mollusca, Nemertea, and Platyhelmintha), 14 classes, 25 orders and 64 species (Suppl. Table S1). The small epifauna group (< 0.5 mm) included 31,650 individuals from 7 phyla (Annelida, Arthropoda, Echinodermata, Mollusca, Nemertea, Nematoda, and Platyhelmintha), 12 classes, 17 orders, and 37 species (Table S1a). We also recorded 285,243 infaunal individuals from 11 phyla (including Platyhelmintha, Polychaeta, Oligochaeta, Mollusca, Amphipoda, Crustacea, Chironomid, Echinodermata, Nemertea, Cnidaria, and Chordata), 4 classes, 21 orders, and 41 species (Supplementary Table S2).

Assemblage structure

Large Epifauna

The first two axes of the ordination explained approximately 50% of the overall variation in the species composition and abundance of large (> 0.5 mm) epifauna. Specifically, the variation explained was highest in high fragmentation meadows (46.95%), followed by low fragmentation meadows (45.97%) (Fig. 2a, c). In medium fragmentation meadows, the first two axes accounted for only 38.2% of the variation (Fig. 2b). The ‘mvabund’ analysis indicated that the assemblage structure of large epifauna varied significantly among sampling zones in the seagrass patch depending on fragmentation level (‘mvabund’, $\alpha < 0.05$), although there was considerable overlap among zones regardless of fragmentation level (Fig. 2a–c). The greatest differentiation among zones was observed in medium fragmentation meadows, while zones in low and high-fragmented meadows exhibited nearly complete overlap. Multivariate dispersion was highest in near-edge areas of medium and high fragmentation meadows and in center areas of low fragmentation meadows. A wide range of epifaunal species contributed to the observed variation, especially in low and medium fragmentation meadows. Notably, the amphipod *Gammarus locusta*, the polychaete *Capitella capitata*, and the Nemertean sp1 were major contributors to variation in center samples of low fragmentation meadows (Fig. 2a–c).

Small epifauna

For small (< 0.5 mm) epifauna, the two PCoA axes explained approximately 50% of the overall variation, with over 50% explained in low (56.49%) and high (53.88%) fragmentation meadows (Fig. 2d, f). In medium fragmentation meadows, only 48.42% of the variation was explained (Fig. 2e). The ‘mvabund’ analysis showed significant variation in assemblage structure among zones in the seagrass patch depending on fragmentation level (‘mvabund’, $\alpha < 0.05$), though a high degree of overlap was observed across all fragmentation levels. Multivariate dispersion was notably higher in edge samples, except in medium fragmentation meadows, where the abundances of the polychaete *Platynereis dumerilii* and Chironomid larvae influenced the variation. This overlap is partly due to a limited number of epifaunal species present across all meadows, including the oligochaete Naididae, nematode Chromadoridae sp1, Nemertean sp1, and Ostracoda sp1 (Fig. 2d–f).

Infauna

Infaunal assemblages showed that the two PCoA axes explained about 45-60% of the overall variation, with 45.6% in medium-fragmented and 62.6% in highv fragmentation meadows (Fig. 2g–i). According to the ‘mvabund’ analysis, variation in infaunal assemblage structure among zones in the seagrass patch was significant as a function of fragmentation level (‘mvabund’, $\alpha < 0.05$), though there was considerable overlap across all fragmentation levels. The highest differentiation was observed in low fragmentation meadows, while medium and high fragmentation meadows showed nearly complete overlap. Multivariate dispersion was notably higher in edge samples across all fragmentation levels. Only a few species contributed to the observed variation, most of which were shared among patch areas (Center, Near-Edge, and Edge). Notable exceptions included the polychaete *Platynereis dumerilii*, which dominated assemblages in high fragmentation meadows from the center area, and the polychaetes *Eteone longa, Alitta virens* and *Capitella capitata*, which partially explained the variability in edge areas of high fragmentation meadows. However, a general trend was difficult to discern due to the overlap among Edge, Near-Edge, and Center areas of the studied meadows (Fig. 2g–i).

Alpha diversity

Large epifauna

For large epifauna, there was no significant variation in alpha diversity among the three zones (Edge, Near-Edge and Center) at any fragmentation level when considering any value of the ‘*q*’ parameter (Fig. 3a–c, Table 2).

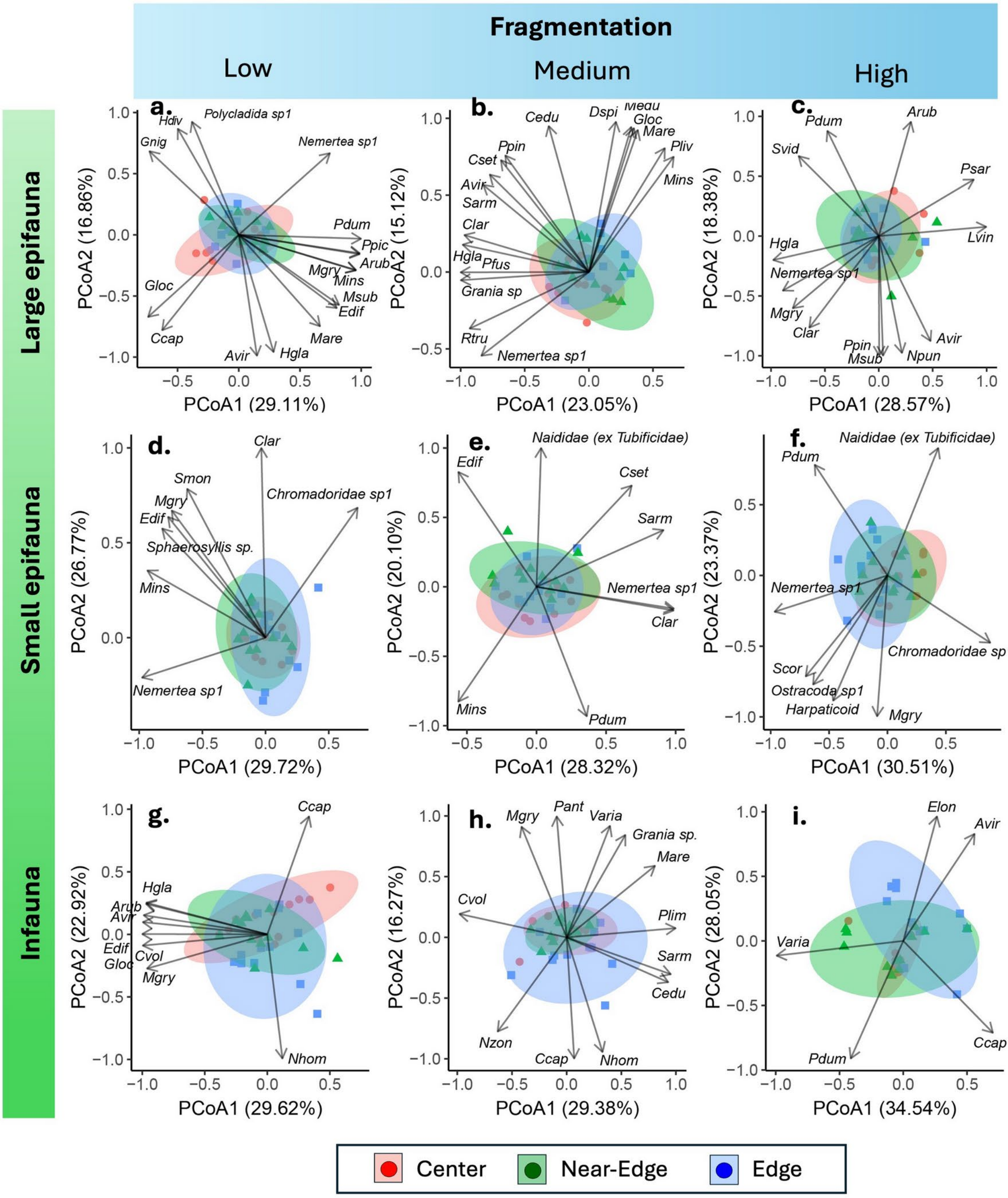

Fig. 2. Principal coordinate analyses (PCoA) represents variation in large epifauna (> 0.5 mm), small epifauna (< 0.5 mm) and infauna among zones in the seagrass patch (red = Center, green = Near-Edge, blue = Edge) for each fragmentation level: (**a**, **g**, **d**) low, (**b**, **e**, **h**) medium, and (**c**, **f**, **i**) high. Overlaid vectors indicate species significantly ($p \leqslant 0.05$) correlated with PCoA axes, whilst ellipses delineate the 95% confidence interval around the mean bivariate coordinate (i.e., centroid). Abbreviations for species names are provided in Table S2.

Significant differences in alpha diversity were observed solely among different levels of fragmentation (low, medium, and high). The patterns varied depending on the weight given to species abundances, as indicated by the *'q'* parameter. When focusing on rare species (i.e., *'q'* = 0), taxonomic diversity was highest in medium fragmentation meadows, with lower and comparable values in low and high fragmentation meadows. In contrast, for common (i.e., *'q'* = 1) and dominant species (i.e., *q'* = 2), there was a general trend of increasing taxonomic diversity from low to high fragmentation levels.

Small epifauna

For small epifauna, the patterns of alpha diversity differed according to the *'q'* parameter. In low and medium fragmentation levels, the results were similar, but varied based on the weight of species relative abundances.

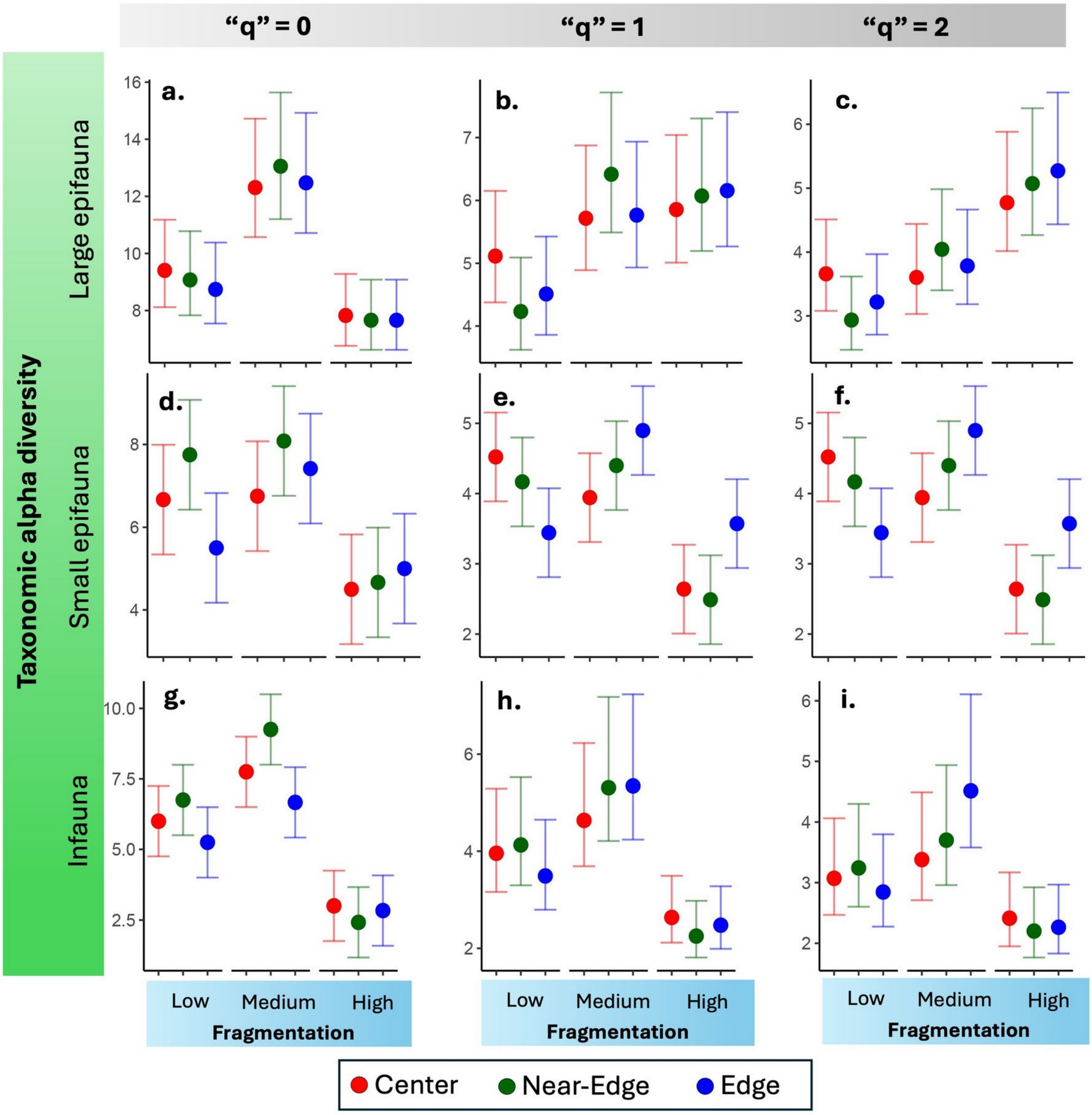

Fig. 3. Predicted differences in the taxonomic alpha diversity of large epifauna (> 0.5 mm), small epifauna (< 0.5 mm) and infauna among zones in the seagrass patch as a function of fragmentation level, for each 'q' parameter: (**a**, **d**, **g**) '*q*' = 0 (i.e., species composition only, analogous to species richness), (**b**, **e**, **h**) '*q*' = 1 (i.e. weighted in proportion to species abundances, analogous to Shannon entropy), and (**c**, **f**, **i**) '*q*' = 2 (i.e. more weight on very abundant species, analogous to inverse Simpson index). Dots are model-averaged predictions from GLMMs, and whiskers are standard errors around the predicted mean, (Mean ± SE).

When focusing on rare species ('*q*' = 0), higher taxonomic diversity was observed at near-edge areas compared to the center and edge communities, which had similar values. However, when emphasizing common ('*q*' = 1) and dominant species ('*q*' = 2), a distinct pattern emerged: taxonomic diversity declined from the center to the edge in low-fragmented patches, while it increased from the center to the edge in medium-fragmented patches (Fig. 3d–f, Table 2). At high fragmentation levels, local-edge effects were detected only when accounting for species abundances ('*q*' = 1 and '*q*' = 2). Here, higher taxonomic diversity was found at the edge compared to both the center and near-edge, suggesting that edge effects become more apparent when common and dominant species are considered.

Infauna

For infaunal assemblages, a significant local-edge effect on alpha diversity was observed, but only when species abundances were not considered ('*q*' = 0) (Fig. 3g–i, Table 2). Although similar trends were noted when accounting for species abundances (i.e., '*q*' = 1 and '*q*' = 2), the results were less clear due to higher uncertainty in the estimates. When focusing on rare species ('*q*' = 0), taxonomic diversity was comparable among zones in low and high fragmentation levels, but significant differences were found in medium-fragmented meadows.

			Large		Small		Infauna	
TD	Model	df	Chisq	p	Chisq	p	Chisq	p
‘q’ = 0	Fragmentation	2	56.01	<0.001*	11.18	<0.003*	105.02	<0.001*
	Zone	2	0.24	0.88	7.33	< 0.03*	5.82	0.05
	Fragmentation*Zone	4	0.56	0.96	10.23	< 0.03*	6.28	0.17
‘q’ = 1	Fragmentation	2	15.75	< 0.001*	26.081	< 0.001*	41.68	< 0.001*
	Zone	2	0.1	0.95	2.06	0.35	0.15	0.92
	Fragmentation*Zone	4	3.79	0.43	21.26	< 0.001*	2.44	0.65
‘q’ = 2	Fragmentation	2	30.29	< 0.001*	29.95	< 0.001*	23.34	< 0.001*
	Zone	2	0.05	0.97	5.51	0.06	0.87	0.64
	Fragmentation*Zone	4	3.88	0.42	23.8	< 0.001*	3.36	0.5

Table 2. GLMM results testing for differences in the taxonomic alpha diversity (TD) of large epifauna (> 0.5 mm), small epifauna (< 0.5 mm) and infauna among zones in the seagrass patch as a function of fragmentation level (two-way interaction, ‘zone × fragmentation’), for each ‘q’ parameter: ‘q’ = 0 (i.e., species composition only, analogous to species richness), ‘q’ = 1 (i.e. weighted in proportion to species abundances, analogous to Shannon entropy), and ‘q’ = 2 (i.e. more weight on very abundant species, analogous to inverse Simpson index). Significant values ($p \leq 0.05$) are indicated with an asterisk and highlighted in bold.

Specifically, higher diversity was observed near the edge, followed by the center, with the lowest diversity at the edge.

Species abundance curves

A highly skewed distribution of species abundance was observed within this associated community, emphasizing differences in evenness across fragmentation levels. This pattern reflects how fragmentation influences community structure, with varying levels of dominance and diversity depending on habitat configuration. In meadows with low to medium fragmentation levels, the amphipod species *Microdeutopus gryllotalpa* exhibited overwhelming dominance among the large epifauna, particularly pronounced in samples taken near the edges of medium fragmented meadows. Conversely, high fragmented meadows displayed a distinct trend, with several species exhibiting more evenly distributed abundances. Among these, chironomid larvae and the polychaete *Platynereis dumerilii* were the most abundant. In high fragmented meadows, a range of 7–9 species were well represented, whereas in low and medium fragmented meadows, only 1–3 species were abundant, with the remaining taxa being sparsely represented (Fig. 4).

The faunal composition of small epifauna displayed an inverse trend compared to that observed in the context of larger epifaunal organisms. Within low and moderately fragmented meadows, dominance was evident among two amphipod species, namely *Microdeutopus gryllotalpa* and *Monocorophium insidiosum*, alongside a lesser presence of Chironomid larvae and the amphipod *Ericthonius difformis*. In contrast, highly fragmented meadows were characterized by the prevalence of a single species, namely Chironomid larvae, with a significant disparity in abundance compared to other species such as, the nematode Chromadoridae sp1, the amphipod *M. gryllotalpa*, or the nemertean Nemertea sp1, among others (Fig. 5).

Infauna communities showed a skewed distribution of species abundance, notably in low and medium fragmented meadows. The amphipod *Gammarus locusta* was the most abundant species in low fragmented areas whilst the opportunistic *Microdeutopus gryllotalpa* dominated the medium fragmented meadows. The remaining species were characterized by low abundances, highlighting the polychaete *Capitella capitata* and the amphipods *M. gryllotalpa* and *Corophium volutator* in low fragmented meadows. Medium fragmented meadows showed the oligochaete *Grania* sp. and the polychaete *Chaetozone setosa* as important contributors to the overall abundance, and to a lesser extent, the polychaete *Scoloplos armiger*. The highly fragmented patches were dominated by the polychaetes *Capitella capitata* and *Alitta virens* (Fig. 6).

Discussion

This study explores the effects of edge and habitat fragmentation on seagrass meadows, focusing on three key groups: large epifauna, small epifauna, and infauna. Through field surveys, we analysed how these taxonomic groups respond to varying fragmentation levels and edge conditions, uncovering distinct ecological roles and complex dynamics in seagrass ecosystems. Fragmented meadows showed reduced taxonomic diversity in large and small epifauna and infauna, with declines in infauna and large epifauna abundance and notable shifts in species composition across all three community types. Large epifauna showed significant local edge effects, especially in moderately fragmented meadows, supporting ecological theories on edge habitats as unique resources or microhabitats that shape species distributions[48]. Small epifauna, however, demonstrated consistent edge effects across all fragmentation levels, suggesting adaptability to changing conditions, possibly due to their small size and ecological flexibility. In contrast, infauna exhibited variable responses, lacking a clear trend in edge effects-indicating complex interactions with local environmental factors and highlighting the importance of habitat-specific assessments in understanding ecological responses.

The contrasting responses among large epifauna, small epifauna, and infauna emphasize the intricate community dynamics within fragmented seagrass habitats. Certain species, like *Microdeutopus gryllotalpa*,

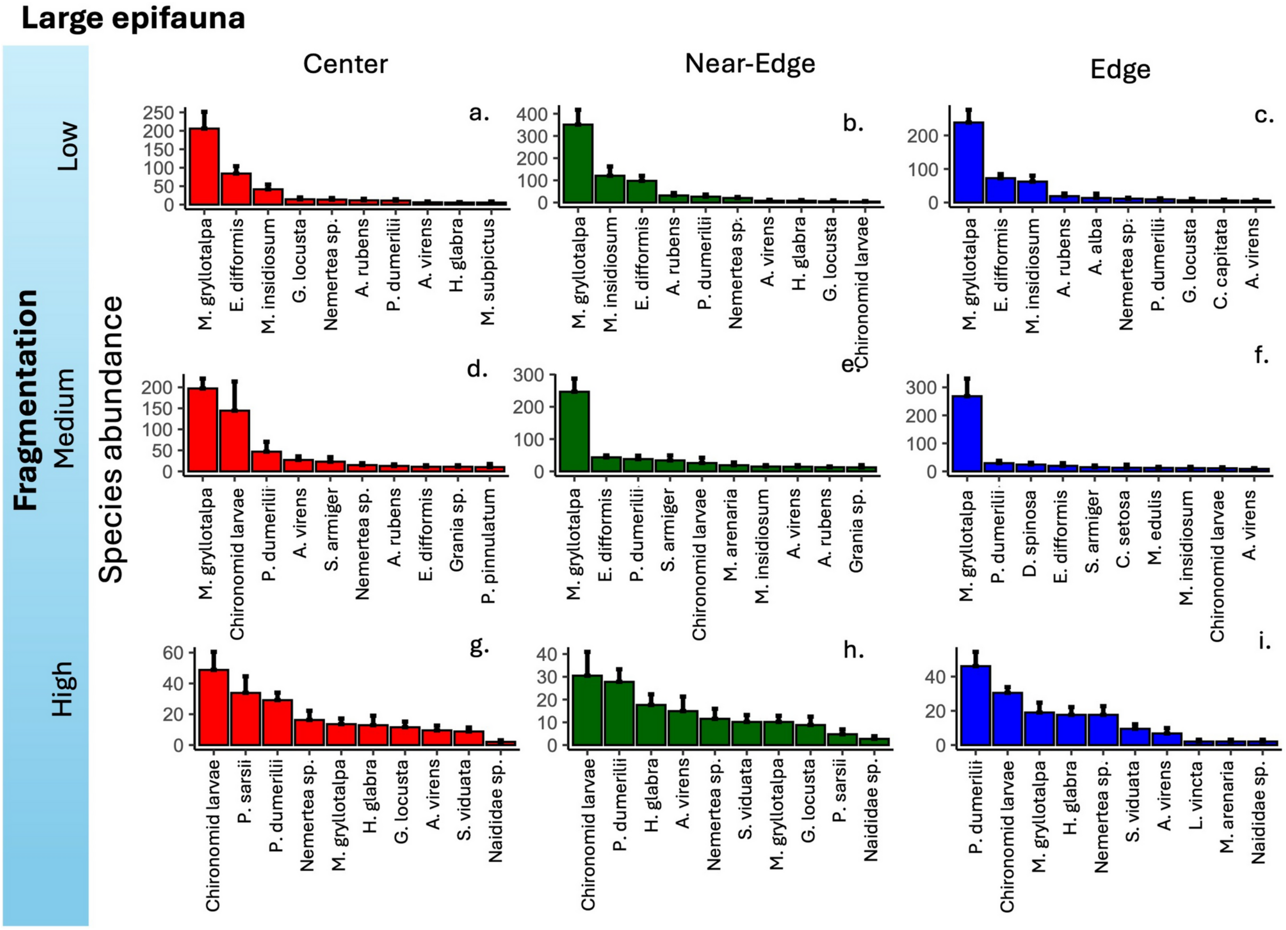

Fig. 4. Species abundance of the ten most common taxa of large epifauna in each zone of the patch for each fragmentation level (Mean ± SE).

thrived in low to moderately fragmented meadows, while others, such as chironomid larvae, dominated highly fragmented areas, reflecting a decline in species diversity. These findings align with ecological theories on species competition and resource availability, indicating that fragmentation disrupts established community structures and interactions[49]. However, the responses of these groups likely reflect additional environmental and ecological factors. Co-varying factors such as fish community composition[50], sediment organic content[51], human activity[52], and seagrass patch size[53] significantly influence these ecosystems. Physical and biological conditions, including wave exposure[54], water flow[52], light availability[53], nutrient levels[51], and salinity[50], also shape community responses. The complexity introduced by these factors[54] can obscure clear patterns in community responses. Additionally, anthropogenic pressures, such as coastal development and boating, impact connectivity and the resilience of seagrass meadows[50–53]. Thus, while fragmentation directly affects these communities, the interplay of environmental and human-induced factors complicates the observed patterns.

To our knowledge, while several field-based studies have investigated fragmentation effects in seagrass meadows (see[18]), none have simultaneously assessed both epifauna and infauna communities. Previous experimental research has documented changes in species composition, reduced biodiversity, and compromised ecological functions within fragmented seagrass habitats[55,56]. For instance,[49] found that while epifaunal amphipod densities decreased in fragmented habitats, the overall community structure remained stable, preserving their role in controlling epiphyte populations. In contrast, our study revealed marked differences in epifaunal assemblage between highly fragmented habitats and those with medium and low fragmentation levels, suggesting that fragmentation may impact epifaunal community structure more significantly than previously reported. This discrepancy might stem from differences in study design, habitat characteristics, or the specific community metrics assessed.

Notably,[55] showed that seagrass plots with 90% habitat loss had significantly lower epifaunal density and species richness compared to plots with 0%, 10%, or 50% habitat removal, indicating a critical threshold where both richness and abundance decline sharply. However, our findings did not reveal such a clear-cut threshold; while we observed significant differences between highly fragmented meadows (70% loss) and those with medium (50%) and low (25%) fragmentation, the trends were less pronounced. Specifically, we noted reduced taxonomic diversity of large epifauna, small epifauna, and infauna in highly fragmented meadows, along with declines in infauna and large epifauna abundances and shifts in species composition across all groups. This

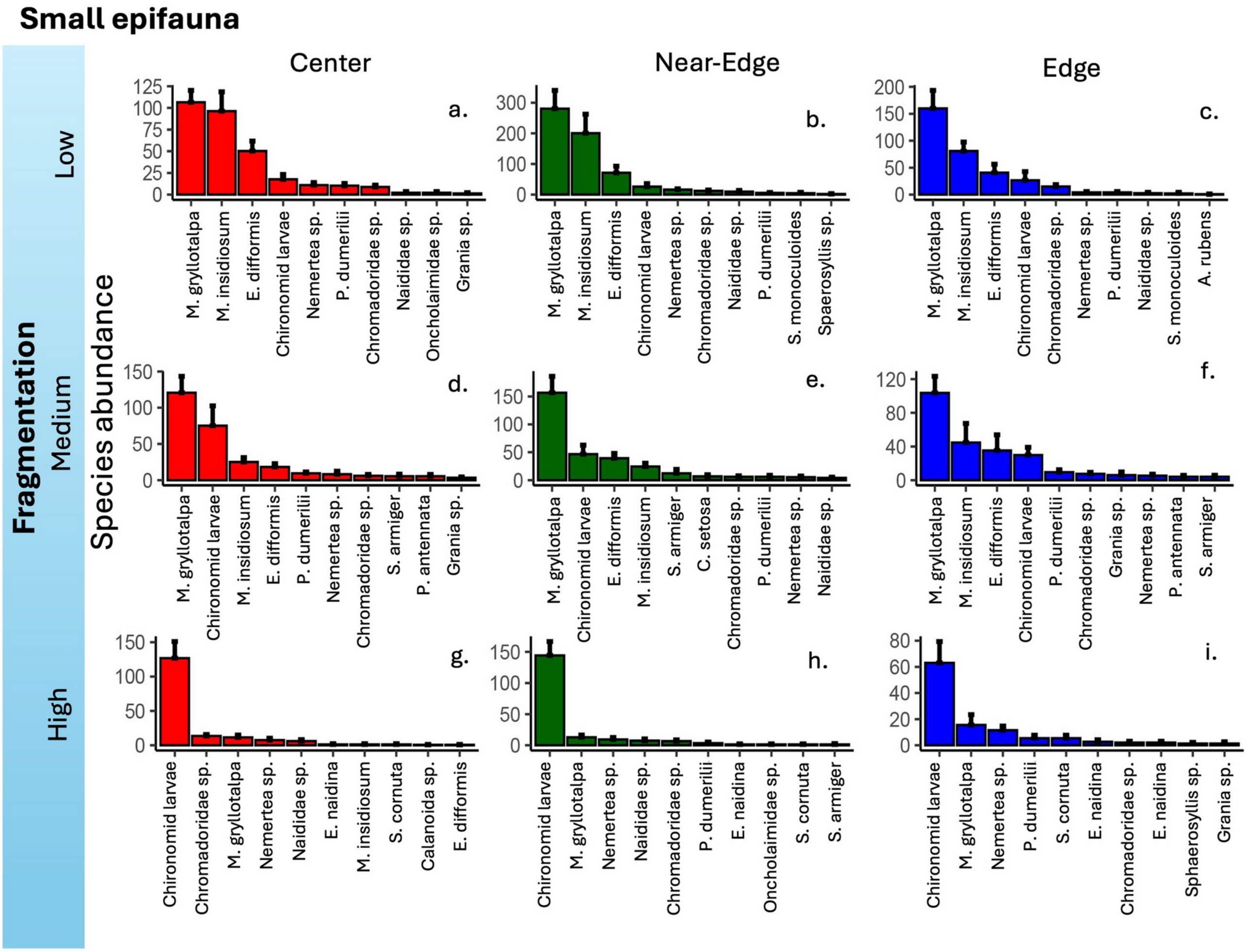

Fig. 5. Species abundance of the ten most common taxa of small epifauna in each zone of the patch for each fragmentation level (Mean ± SE).

suggests that while fragmentation influences these communities, the impact does not align with the sharp threshold-based decline highlighted by[55].

The distribution patterns of small epifauna, large epifauna, and infauna in fragmented seagrass meadows offer valuable insights into how habitat structure shapes community dynamics. Among large epifauna, the amphipod *Microdeutopus gryllotalpa* is most abundant in low to moderately disturbed meadows, particularly at the edges of moderately disturbed areas. In contrast, highly disturbed meadows exhibit a more even distribution, with chironomid larvae and *Platynereis dumerilii* becoming more prominent. Small epifauna show co-dominance of *Microdeutopus gryllotalpa* and *Monocorophium insidiosum* in less disturbed areas, while highly disturbed areas are dominated by chironomid larvae, indicating a reduction in species diversity. Infaunal communities respond differently; for instance, *Gammarus locusta* is prevalent in low disturbance areas, while *Microdeutopus gryllotalpa* dominates in moderately disturbed meadows. These patterns reveal that different taxa exhibit species-specific shifts in abundance in response to environmental change, reflecting broader ecological impacts.

Our findings diverge from previous studies[33,48] that reported increased abundance or biodiversity near seagrass meadows edges. Unlike these studies, we found large epifauna, such as *Microdeutopus gryllotalpa*, more abundant in less disturbed areas, with pronounced edge effects only in moderately disturbed meadows. Additionally, small epifauna exhibited decreased diversity and a shift in dominance towards chironomid larvae in highly disturbed areas, contrasting with earlier observations of greater biodiversity at meadow edges or interiors. These variations suggest that habitat structure influences community dynamics in complex ways, varying by taxa and disturbance level. This highlights the intricate relationship between environmental conditions and community composition, emphasizing the importance of considering spatial and taxonomic diversity in conservation strategies. Addressing these varied ecological responses is essential for effectively mitigating impacts on seagrass ecosystems and enhancing their resilience.

While our research provides valuable insights, we acknowledge limitations that warrant consideration. First, the temporal variability inherent in seagrass ecosystems suggests that our single sampling approach in July 2021 may not fully capture the dynamic community composition and edge effects. Future studies incorporating multi-season and interannual sampling could better reveal how temporal changes influence species dynamics.

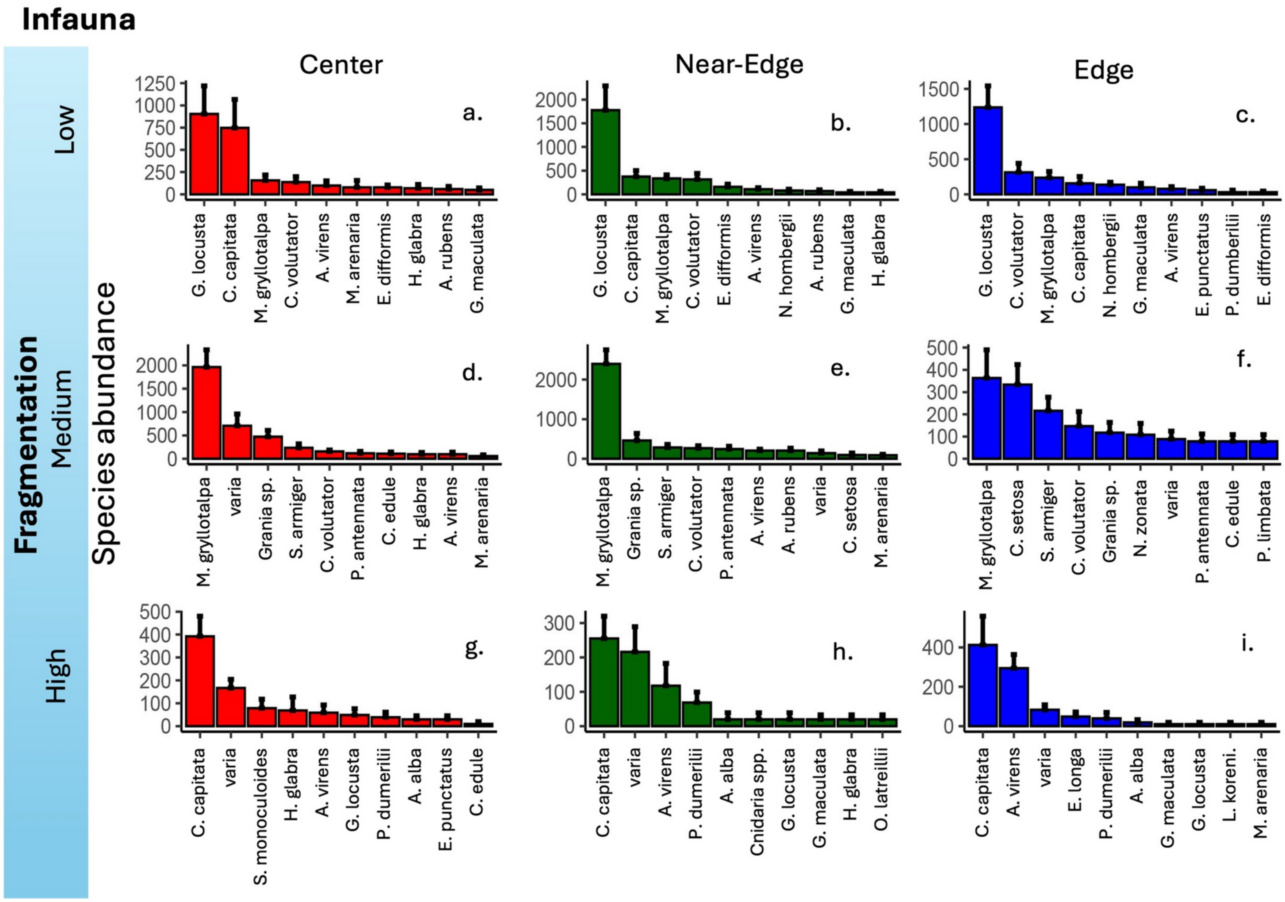

Fig. 6. Species abundance of the ten most common taxa of infauna in each zone of the patch for each fragmentation level (Mean ± SE).

Additionally, though our study sites represent a fragmentation gradient, the limited number of sites restricts the scalability of our findings. Future research should expand to a wider array of sites with vvaried disturbance levels, allowing for more comprehensive assessments across different environmental contexts[57].

Future studies would benefit from examining fragmentation effects at both patch and seascape scales[58]. Patch-level analyses, as emphasized by Riva and Fahrig[57], allow for a detailed exploration of how specific habitat features and edge effects shape community structure. Investigating these fine-scale dynamics can provide insights into how habitat attributes influence species responses to disturbances. At the seascape level, studies such as Chase et al.[59] underscore the importance of examining spatial configuration, connectivity, and habitat patch distribution, which collectively affect species dispersal, colonization, and extinction dynamics. Recognizing the role of small patches, as highlighted by Riva & Fahrig[60], is also essential. Despite their size, small patches often harbor disproportionately high biodiversity, acting as important refuges for rare species and enhancing overall seascape connectivity[61–63]. Integrating patch- and seascape-level perspectives in future research will enable a more nuanced understanding of the complex interactions between environmental structure and community dynamics. Such interdisciplinary approaches are essential for developing conservation strategies that mitigate disturbances and support biodiversity and ecosystem function within seagrass habitats.

In conclusion, our study demonstrates that habitat fragmentation in seagrass meadows distinctly affects different faunal groups. High fragmentation led to a significant reduction in the taxonomic diversity and abundance of large epifauna and infauna, alongside notable shifts in species composition across all groups. Large epifauna exhibited pronounced edge effects, particularly in moderately fragmented areas, while small epifauna showed consistent edge responses across fragmentation levels, suggesting resilience. In contrast, infaunal responses varied widely, likely due to local environmental conditions. These findings underscore that fragmentation uniquely shapes community dynamics, highlighting the need for conservation strategies tailored to specific habitat structures and the fragmentation impacts on diverse taxonomic groups.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

R.R.: Conceptualization, biological sampling, data acquisition, data curation, methodology, formal analysis, validation, critical analysis, project administration, funding, supervision, writing—original draft preparation, and writing—review and editing; N.E.B.: formal analysis, critical analysis; E.I.: resources, biological sampling, validation, critical analysis and writing—review and editing; J.V.: biological sampling, data acquisition, data curation, critical analysis, validation, funding, supervision, writing—review and editing. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Ethical and legal considerations

Permission for the collection of *Zostera marina* specimens along the Swedish west coast was obtained from the relevant authorities prior to sampling. All necessary permits and licenses were acquired in accordance with national and regional regulations governing seagrass research and conservation. Voucher specimens have been deposited at Kristineberg Research Center, University of Gothenburg. The identification of the specimens was conducted by Dr. Rodrigo Riera and Dr. Joana Vasconcelos, ensuring taxonomic accuracy.

Additional information

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