Aquatic Conservation: Marine and Freshwater Ecosystems

WILEY

ARTICLE

Fish Community Structure and Habitat Complexity in Restored and Natural Eelgrass Meadows

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Received: 1 October 2024 | **Revised:** 21 January 2025 | **Accepted:** 7 February 2025

Funding: This work was funded by the European Union's Horizon 2020 Framework Programme under grant agreement no. 869300 'FutureMARES', the research contract 'Restoration of *Posidonia oceanica* meadow. REE Marine Forest' signed between Red Eléctrica de España and CSIC and the project PROFISH (PGC2018-096256-B-I00) funded by FEDER/Ministerio de Ciencia e Innovación–Agencia Estatal de Investigación. This work was carried out within the framework of the activities of the Spanish Government through the 'Maria de Maeztu Centre of Excellence' accreditation to the IMEDEA (CSIC-UIB) (CEX2021-001198). J.C.F. was supported by a PhD grant (FPU programme) from the Spanish Ministerio de Ciencia, Innovación y Universidades; and by an Erasmus+ Traineeship grant.

Keywords: ecosystem functions | ecosystem services | fish recovery | seagrass restoration

ABSTRACT

Seagrass meadows serve as nursery and permanent habitat for numerous fish species—an ecosystem function influenced by structural complexity. Rapid seagrass loss over recent decades has promoted restoration efforts aimed at recovering meadows and their ecological functions. This study assesses the restoration of habitat structural complexity and associated fish communities in two replanted eelgrass (*Zostera marina*) meadows on the west coast of Sweden, planted with a 2-year difference and comparing them to the inner and edge areas of natural meadows and unvegetated sandy areas. Eelgrass habitat structural complexity was assessed from seagrass samples collected to estimate shoot densities, shoot biomass, and canopy height of the meadows. Fish communities were assessed using two methods: diver-operated stereo-video transects, and traditional underwater visual census, testing the efficiency of both techniques. The two assessed methods produced similar results that sampled canopy-associated species well but were less accurate for cryptic bottom-dwelling species inside eelgrass meadows. Results indicated that structural complexity was statistically lower in the 2-year replanted area (Askerön) compared to the reference meadow, but in the 4-year replanted area (Gåsö), no significant differences were observed between the restored and reference meadows. Moreover, no differences were observed between the reference and restored meadows for canopy-associated fish species in Gåsö, indicating that the recovery of the habitat function was already underway. However, results from Askerön were inconclusive. Thus, despite rapid eelgrass growth, the recovery of ecosystem function and of the capacity to provide ecosystem services following seagrass replanting is not always immediate and may be dependent on factors such as time after restoration, environmental factors (e.g., water quality) or landscape configuration (e.g., meadow fragmentation, vicinity to natural meadows). A comprehensive understanding of how fish communities respond to seagrass restoration is necessary to effectively scale the restoration efforts.

1 | Introduction

Seagrass meadows are highly productive and diverse ecosystems (Duarte 2002; Gullström et al. 2008) that provide a wide range of ecosystem services, including carbon sequestration, water purification and coastal protection (Cullen-Unsworth and Unsworth 2013; Mtwana Nordlund et al. 2016). These ecosystems also serve as nurseries and/or permanent habitats for a variety of fishes, including commercially exploited species (Jackson et al. 2001). Compared to adjacent unvegetated areas, seagrass beds typically support more abundant and diverse fish assemblages, with distinct species compositions (e.g., Gray et al. 1998; Guidetti and Bussotti 2002; Pihl et al. 2006; Park and Kwak 2018). The structural complexity of seagrass at the local scale directly influences the provision of nursery and permanent habitats, correlating with higher fish abundances and diversity (Gullström et al. 2008; Ambo-Rappe 2016). Structural habitat complexity is defined as a multidimensional entity encompassing a set of qualitative and quantitative habitat traits that may interact (Carvalho and Barros 2017); and it is typically quantified by structural traits such as shoot density, shoot biomass, canopy height or leaf surface area (e.g., Hovel et al. 2002; Jinks et al. 2019).

The rapid loss of seagrass habitats in recent decades due to human activities has significantly affected the functioning of coastal ecosystems and their capacity to provide ecosystem services (Waycott et al. 2009; Unsworth and Cullen-Unsworth 2014). These disturbances are reducing fish abundance and altering the predominant species within the assemblages (Hughes et al. 2002; O'Leary et al. 2021). In response, global seagrass restoration efforts aim to mitigate this loss and restore associated ecosystem functions and services (Paling et al. 2009). Notably, eelgrass (*Zostera marina*) is the most commonly restored seagrass species (Van Katwijk et al. 2016) and is characterized by its rapid growth in comparison to other seagrass species like *Posidonia oceanica* (Borum et al. 2004).

Eelgrass meadows along the Swedish west coast have decreased by 58% in area over two decades (Baden et al. 2003; Moksnes et al. 2018). Nutrient pollution and overfishing have led to increased growth of fast-growing epiphytic algae and macroalgae mats, which cover eelgrass meadows and reduce their distribution (Moksnes et al. 2008), resulting in a substantial reduction in fish production (Pihl et al. 2006; Cole and Moksnes 2016). Small-scale restoration efforts in the area using eelgrass seeds and shoots have been undertaken (Eriander et al. 2016; Infantes, Crouzy, and Moksne 2016; Moksnes et al. 2016), showing a low success using seeds due to the low seed production in Swedish meadows and the presence of seed predators (Infantes, Eriander, and Moksnes 2016; Infantes and Moksnes 2018). In contrast, eelgrass shoot transplantation using the single shoot technique has shown to be successful (Eriander et al. 2016). Although a previous study examined epifaunal and infaunal recovery in one Swedish restored area (see Gagnon et al. 2023), no prior work has assessed the recovery of fish assemblages in these eelgrass habitats.

Monitoring fish assemblages in seagrass habitats using non-invasive techniques is challenging due to limited visibility beneath the dense canopy, which often favours trawling methods (French et al. 2021). However, trawls are inappropriate in sensitive areas such as MPAs or replanted seagrass meadows (Kiggins et al. 2018). Non-invasive techniques may detect fish more easily at meadow edges than within the interior, as visibility is greater at the seagrass-sand interface. Moreover, a real 'edge effect' is often observed at ecosystem boundaries, where preys like small crustaceans are more abundant, highlighting the ecological importance of habitat edges in supporting diverse fish assemblages (Tanner 2005; Smith et al. 2008).

Although Underwater Visual Census (UVC) is the most widespread non-destructive technique for monitoring fish assemblages (Cheal et al. 2021), the use of emerging video techniques such as Diver-Operated Stereo-Video (Stereo-DOV) has increased in the last decades due to their precision when counting and measuring fish (Harvey et al. 2002). Both methods have been compared in other habitats such as rocky bottoms (e.g., Grane-Feliu et al. 2019) or coral reefs (e.g., Holmes et al. 2013), but no comparison exists in seagrass meadows, because Stereo-DOV is not commonly used in this habitat.

In this study, we investigated the short-term recovery of eelgrass structural complexity in two independent restoration trials along the Skagerrak (Swedish northwest coast) 2 and 4 years after eelgrass planting, respectively. We also assessed fish abundance, diversity and community structure recovery by comparing the communities from both replanted areas, nearby reference meadows and unvegetated sand areas. The main objective was to understand the recovery of associated ecosystem functions (i.e., habitat for fish) following eelgrass restoration in two meadows presenting different environmental contexts (i.e., level of eutrophication and turbidity, time since plantation and distance to the reference meadow), with an expectation that fish would start utilizing the replanted meadows as their structure recovers. Additionally, the study evaluates the efficiency of stereo-video transects for its use in eelgrass meadows compared to traditional visual census.

2 | Methods

2.1 | Study Area

The study was conducted in two separated bays, Askerön and Gåsö, on the west coast of Sweden (Skagerrak; see Figure 1a), where eelgrass shoot transplantations were implemented using the single shoot method described in Moksnes et al. (2016) in areas with previous historical presence of *Z. marina* (Baden et al. 2003; Moksnes et al. 2018).

Askerön is located deep in the Bohuslän archipelago (Figure 1b), in an area that is more affected by eutrophication and with lower water quality compared to the area around Gåsö (Moksnes et al. 2015) and where large losses of eelgrass have occurred in nearby areas (Baden et al. 2003). As a result of the loss of eelgrass and its stabilizing effect on the sediment, resuspension and high turbidity presently prevent eelgrass recovery in many areas (Moksnes et al. 2018). To reduce turbidity, the restoration area was sand capped with a thin layer of sand and gravel prior to the transplantation of eelgrass. A total of 80,000 eelgrass individual main shoots with 0–2 smaller side shoots collected from the closest natural meadow were planted by scuba divers in May–June 2021 at a depth of 1.2–1.8 m, covering a 1-ha plot (100 × 100 m) in a checkered pattern with a density of 16 shoots/m^2. The restored area is located ~200 m from the closest larger natural eelgrass meadow (Figure 1b).

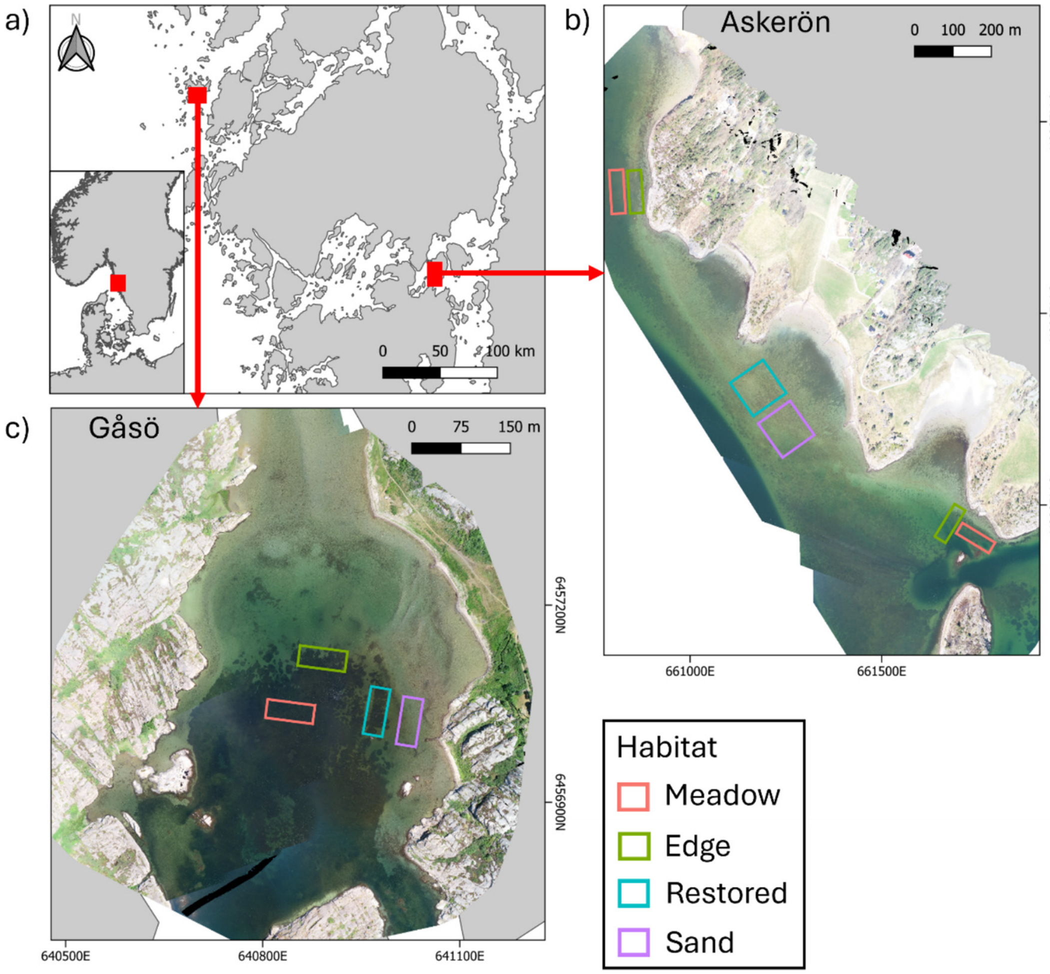

FIGURE 1 | Study areas. (a) West coast of Sweden (Skagerrak) where the study sites are located. (b) Bay of Askerön area (2-year plantation). (c) Bay in the island of Gåsö (4-year plantation). Coloured rectangles in the aerial drone photo mosaics represent the studied habitats.

Gåsö is a bay located on Gåsö island, in the archipelago outside the Gullmarn fjord (Figure 1c). This area has greater exchange of seawater from the Skagerrak Sea and better water quality compared to the area around Askerön (Moksnes et al. 2015), and the net loss of eelgrass area has been lower here than in other sites of the Swedish coast (Baden et al. 2003). In 2019, four plots of 400 m^2 each were planted on unvegetated soft sediment at depths of 1.2–2.5 m, which have since survived and expanded creating an almost continuous meadow of approximately 1600 m^2. All plots had an initial planting density of 16 shoots/m^2 at four planting pattern treatments, as explained in Gagnon et al. (2023), including one spatially continuous planting density and three checkered patterns with varying plot sizes (1, 4 and 16 m^2). In contrast to the restoration site at Askerön, these restoration plots are located next to a large natural meadow (Figure 1c). The after-four-years continuous restored meadow, which includes the four types of planted plot patterns (continuous, 1, 4 and 16 m^2 checkered), was sampled in this study.

On both sites, the size of the planted areas has not increased considerably, but the canopy structure has notably increased in density over time, and it was considered in the study (see Section 3.1).

An adjacent unvegetated sand area with a lack of seagrass-associated structural complexity, hereafter referred to as 'sand', near each replanted site was used to assess the effect of eelgrass replanting on fish assemblages. Two structurally complex reference habitats positioned in natural meadows were also selected nearby each replanted site: one parallel to the meadow edge and another within the meadow's interior (> 4 m from the edge), hereafter referred to as 'edge' and 'meadow', respectively (see Figure 1b,c). These two types of reference habitats (sand vs. edge/meadow) were selected to investigate sampling biases linked to distinct structural complexities of seagrass habitats. The total sampling areas were 10,000 m^2 for each habitat in Askerön and 1600 m^2 in Gåsö.

2.2 | Habitat Structural Complexity

The structural complexity was quantified by structural traits through three metrics: *Z. marina* shoot density (shoots/m^2), dry shoot biomass (g/m^2) and canopy height (cm). Samples were collected *in-situ* at the planted area and the interior part of the reference meadow, not at the edge, by snorkelling divers in June 2023, 2 and 4 years after the restoration units were planted in Askerön and Gåsö, respectively. Ten and five replicates of 452 cm^2 were sampled in Askerön and Gåsö, respectively, in natural and restored *Z. marina* meadows by placing a 24-cm-diameter bucket over the sediment and collecting by hand all the eelgrass shoots inside. Shoots were then placed in a plastic bag and transported to the laboratory. All shoots were counted, and the length of each leaf within a shoot was measured in 10 shoots per each habitat and site. Subsequently, canopy height was estimated as 80% of the average maximum leaf length per shoot (Duarte and Kirkman 2001). All collected shoots were dried at 60°C for 48 h and weighed to quantify dry shoot biomass.

2.3 | Fish Communities

Fish communities were surveyed on transects by snorkelling divers using a stereo-video system (Stereo-DOV). Simultaneously, the divers used the traditional method of UVC (Harmelin-Vivien et al. 1985) to record all fish observed on an underwater pad to compare between methods and assess the viability of the Stereo-DOV method in Swedish *Z. marina* meadows. Due to the low number of fish present in the area, including various transects where no fish was observed, the same snorkeler diver performed each transect simultaneously for both methods (Stereo-DOV and UVC) while operating the camera and counting fish at the same time. Additionally, the snorkelling divers carried a buoy with GPS (Garmin eTrex 22x) to track and record the transects. Each transect lasted 7 min, covering an average of 140 m^2 (70×2 m), and was separated to the next transect by at least 10 m.

The samplings took place during daylight hours within the two study areas in June 2023. The highest species richness, abundance and biomass occurs during June, and during this month, most species have already settled in coastal habitats, providing a comprehensive representation of all age groups within the community (Pihl et al. 2006). In Askerön, a total of 6 transects for each method were performed on each habitat (i.e., edge, meadow and sand) except for the replanted habitat, where 10 transects were performed. In Gåsö, 9 transects for each method were performed on both the meadow and edge habitats and 13 on each of the replanted and sand habitats. Between 3 and 4 transects for both methods were conducted for each habitat and sampling day, covering an area of 420 or 560 m^2.

Although both methods present some limitations in detecting fish in complex habitats compared to traditional methods like trawl nets, they were chosen for its capacity of monitoring fish communities non-invasively, which is essential in restored areas. Each observed fish with both methods was identified to the lowest taxonomic level (species level when possible). With Stereo-DOV, fish were measured for total length (TL) to enable subsequent biomass estimations. However, with UVC, fish were only counted, and their TL was not estimated with this method.

The low-cost Stereo-DOV system comprised two GoPro Hero 7 Black digital video cameras (GoPro, Colorado, USA) in underwater housings mounted on an aluminium frame with a 6° inward inclination angle and lenses separated by 34 cm. The distance and angle between the cameras were determined through pilot trials to ensure accurate fish detection and size estimation of juvenile and adult fish. Camera settings were optimized for image quality and battery consumption, using wide mode, 30 frames per second and 1440-pixel resolution. The system was calibrated in a pool, and the calibration videos were processed with CAL SeaGIS software (www.seagis.com.au), generating unique camera orientation files for subsequent length measurements using EventMeasure software (SeaGIS, Version 3.22). The stereo pairs of recorded videos were analysed with this software, where fish TL was measured by marking each fish from the tip of the snout to the tip of the tail in both videos (left and right; Figure S1). To ensure accuracy and precision to the millimetre level, fish lengths were only measured when individuals were at less than 7 m from the cameras and exhibited one of their body sides straight to the cameras. Fish individuals that did not meet these criteria were excluded from measurement and only identified and counted. For individuals that were not measured, the average TL of the measured individuals within the same species and site was assigned. The video processing was performed by a single observer trained to identify local species, with experts consulted when needed.

Before analysing the fish communities, we compared Stereo-DOV and UVC methods. Given the similarity in results obtained from both approaches (all identified taxa are listed in Table 1; see Section 3), we chose to use Stereo-DOV data for all subsequent analyses due to its capacity to also provide fish total length measurements. Ammodytidae sp. and *Aphia minuta* were excluded from all the analyses because of their shoaling behaviour and sporadic occurrence. Once these species were excluded, two analyses were conducted: one for the entire community and another including only the 'canopy-living' species commonly associated to dense, healthy natural eelgrass meadows that could be accurately sampled with the methods used. The latter analysis excluded cryptic species lying on the bottom, very difficult to detect inside eelgrass meadows by the visual census methods performed swimming above the canopy but easier to detect in unvegetated habitats, creating a biased sampling for these species (see Table 2 from Section 3). The excluded species included both fish that are common inside eelgrass meadows (i.e., *Gobius niger* and *Anguilla anguilla*; Pihl et al. 2006) and species that are mainly associated with sandy habitats or very sparse seagrass, such as the family Pleuronectidae and the sand gobies *Pomatoschistus* spp. (including *Pomatoschistus minutus*, *Pomatoschistus pictus* and *Pomatoschistus microps*) (Louisy 2002; Schultz and Kruschel 2010; Boissin et al. 2011).

For the whole community, the species composition on each habitat was assessed (multivariate descriptor) using the density of the different species within the assemblages. For the 'canopy-associated' community, both univariate and multivariate descriptors were used: taxonomic richness, total density, total biomass and species composition. All descriptors were standardized to m^2 except taxonomic richness. The biomass was calculated from the TL measured using the formula: $a \times (TL^b) \times density$; where 'a' and 'b' represent empirical parameters derived from length–weight relationships documented in FishBase (Froese and Pauly 2023).

2.4 | Data Analysis

The shoot density (shoots/m^2), dry shoot biomass (g/m^2) and canopy height (cm) of *Z. marina* were analysed separately on both sites using the Mann–Whitney U non-parametric test

TABLE 1 | Taxonomic classification, total abundances and percentage of similarity between methods for the fish found in the two study sites using Stereo-DOV and UVC. *Pomatoschistus* spp. includes *Pomatoschistus microps*, *Pomatoschistus minutus* and *Pomatoschistus pictus*.

	Askerön			**Gåsö**		
Taxa	**Stereo-DOV**	**UVC**	**Similarity (%)**	**Stereo-DOV**	**UVC**	**Similarity (%)**
Ammodytidae sp.	—	—	—	402	350	86.17
Anguilla anguilla	—	—	—	2	2	100
Aphia minuta	—	—	—	3635	3311	91.34
Ctenolabrus rupestris	3	3	100	2	2	100
Gasterosteus aculeatus	1	1	100	—	—	—
Gobius niger	25	23	91.67	40	36	89.47
Pleuronectidae sp.	—	—	—	5	5	100
Pomatoschistus flavescens	61	57	93.22	54	49	90.29
Pomatoschistus spp.	10	10	100	30	29	96.61
Symphodus melops	1	1	100	—	—	—
Syngnathus acus	1	1	100	2	2	100
Syngnathus rostellatus	1	1	100	—	—	—
Syngnathus typhle	2	2	100	2	2	100
Total	105	99	98.32	4174	3788	95.39

(Mann and Whitney 1947) with habitat as a factor with two levels: restored and meadow.

The % similarity between fish monitoring methods was calculated for each species and site as 100 − (|Abundance Stereo-DOV − Abundance UVC| × 100)/Average Abundance (Stereo-DOV, UVC). If the result was higher than 95% for low-abundance species (<10 average individuals between methods) or 90% for medium- to high-abundance species (>10 average individuals), the methods were considered to similarly detect the species.

Differences between habitats (four levels: restored, sand, edge and meadow) in terms of species composition (multivariate descriptor) at each site were graphically represented by multidimensional scaling (MDS) means plots for both the entire and the canopy-living communities. MDS means plots provide a summary of the mean centroid of each habitat and its deviation following 75 bootstrap runs. The bootstrap runs of each habitat were represented by point clouds of different shapes and colours. Additionally, beneath these clouds, coloured areas represented the 95% smoothed confidence envelopes of bootstrapped centroids for respective habitats. The arrangement of point clouds within the MDS means plots, along with the extent of their overlap, indicated the similarity of the habitats, corresponding to the similarity in the species composition of habitats. To validate visual observations and verify whether the observed differences in the MDS means plots were statistically significant, the associated ANOSIM tests (Bakker 2024) were performed using the Bray–Curtis similarity matrices. Then, the species contributing to the differences observed between habitats for the whole community were obtained with a SIMPER analysis (Clarke 1993). The density of the species accounting for the higher % difference between habitats was then plotted for visual comparison.

All fish community univariate descriptors (taxonomic richness, total density and total biomass) were analysed separately on both sites using Kruskal–Wallis (K-W) non-parametrical test (Kruskal and Wallis 1952) with habitat as a single factor with four levels: restored, sand, edge and meadow. For the descriptors in which the K-W results were significant, a Dunn's pairwise test with a Bonferroni adjustment (Dinno 2015) was performed to evaluate the differences between each pair of levels within the significant factor.

All statistical analyses and graphs were conducted and generated with PRIMER v6 and v7 software and the R packages ggplot2 (Wickham 2016), dplyr (Wickham et al. 2018), tidyr (Wickham et al. 2022) and dunn.test (Dinno 2024).

3 | Results

3.1 | Habitat Structural Complexity

The habitat structural complexity of the replanted and reference meadow's interior from Askerön, analysed 2 years after planting, exhibited significant differences for shoot density ($p = 0.006$), dry shoot biomass ($p = 0.002$) and canopy height ($p = 0.023$). The reference meadow presented higher values of complexity compared to the planted area (Figure 2). For instance, average shoot density and canopy height were around 1.6 higher in the reference that in the restored meadow, and shoot biomass was 2 times higher in the reference meadow. However, a notable increase in shoot density was observed since planting. Shoot

TABLE 2 | Total fish abundances by taxon across different habitats (E = edge; M = meadow; R = restored; S = sand) at the two study sites, obtained using Stereo-DOV. *Pomatoschistus* spp. includes *Pomatoschistus microps*, *Pomatoschistus minutus* and *Pomatoschistus pictus*. Species marked in orange were excluded from all the analysis. Abundance data represent the total count from multiple transects as follows: In Askerön six transects were conducted in each of the edge, meadow and sand habitats and ten transects in the restored habitat; and in Gåsö, nine transects were conducted in the meadow and edge habitats and thirteen in the restored and sand habitats.

	Askerön				**Gåsö**			
	M	**E**	**R**	**S**	**M**	**E**	**R**	**S**
Ammodytidae sp.	—	—	—	—	—	—	—	402
Anguilla anguilla	—	—	—	—	—	2	—	—
Aphia minuta	—	—	—	—	9	2255	1204	167
Ctenolabrus rupestris	3	—	—	—	1	1	—	—
Gasterosteus aculeatus	1	—	—	—	—	—	—	—
Gobius niger	—	16	4	5	—	3	4	33
Pleuronectidae sp.	—	—	—	—	—	2	—	3
Pomatoschistus flavescens	35	22	2	2	4	8	42	—
Pomatoschistus spp.	—	5	3	2	—	24	1	5
Symphodus melops	—	—	—	1	—	—	—	—
Syngnathus acus	1	—	—	—	—	1	1	—
Syngnathus rostellatus	—	—	1	—	—	—	—	—
Syngnathus typhle	—	—	1	1	1	—	1	—
Total	40	43	11	11	15	2296	1253	610
	105				4174			

density increased from 16 shoots/m^2 to an average of almost 300 shoots/m^2 in 2 years.

Although the same pattern was observed in Gåsö, analysed 4 years after planting (Figure 2), these differences in complexity between the natural and restored habitats were not significant for neither shoot density, shoot biomass or canopy height ($p = 0.090$, 0.548 and 0.753, respectively). Structural complexity reached reference levels in 4 years increasing from initial densities of 16 shoots/m^2 to an average of approximately 300 shoots/m^2, in contrast to the 2 years, it took to reach this level in Askerön.

Notable natural differences were also observed between the reference meadows on both sites. For instance, shoot biomass from Gåsö was approximately 2.5 times higher than that from Askerön (Figure 2b).

3.2 | Comparison of Fish Sampling Methods

A total of 4279 and 3887 fish were counted and identified with the Stereo-DOV and UVC methods, respectively, during the sampling period at the two sites (see Table 1). The precise counts provided by Stereo-DOV and the estimates provided by UVC for shoaling species (i.e., Ammodytidae sp. and *A. minuta*) were responsible for the differing total abundances obtained (lower with UVC). These two species accounted for 94.34% of the total (4037 individuals) for the Stereo-DOV and a 94.19% (3661 individuals) of the total for UVC, although they were all observed in Gåsö during 1 day of sampling. Ammodytidae sp. and *A. minuta* were therefore removed for all subsequent analysis (as explained in Section 2), which were performed with the remaining 242 individuals observed by Stereo-DOV. Most of the remaining species were ‘rare’, as they were only observed once or a few times in each habitat (see Table S1). Overall, Stereo-DOV detected 9.16% more individuals than UVC, particularly when small fish like *A. minuta* were present in large groups.

The results from Stereo-DOV and UVC detected the same species and similar abundances for most species (Table 1). A similarity over 95% was observed for all low-abundance species (< 10 average individuals between methods) and over 90% for all high-abundance species (> 10 individuals) in Askerön. In Gåsö, however, although a similarity over 95% was observed for all low-abundance species, not all high-abundance species were observed with a similarity over 90% between methods (e.g., Ammodytidae sp. and *G. niger*) (Table 1). Stereo-DOV detected significantly higher abundances of these species than UVC.

3.3 | Complete Fish Community

The community composition in the different habitats was calculated using the Stereo-DOV density data (Table 2), excluding Ammodytidae sp. and *A. minuta* for their shoaling behaviour. Although some habitats seemed to differ in both sites (e.g., edge vs. sand; Figure 3), overall ANOSIM statistical differences

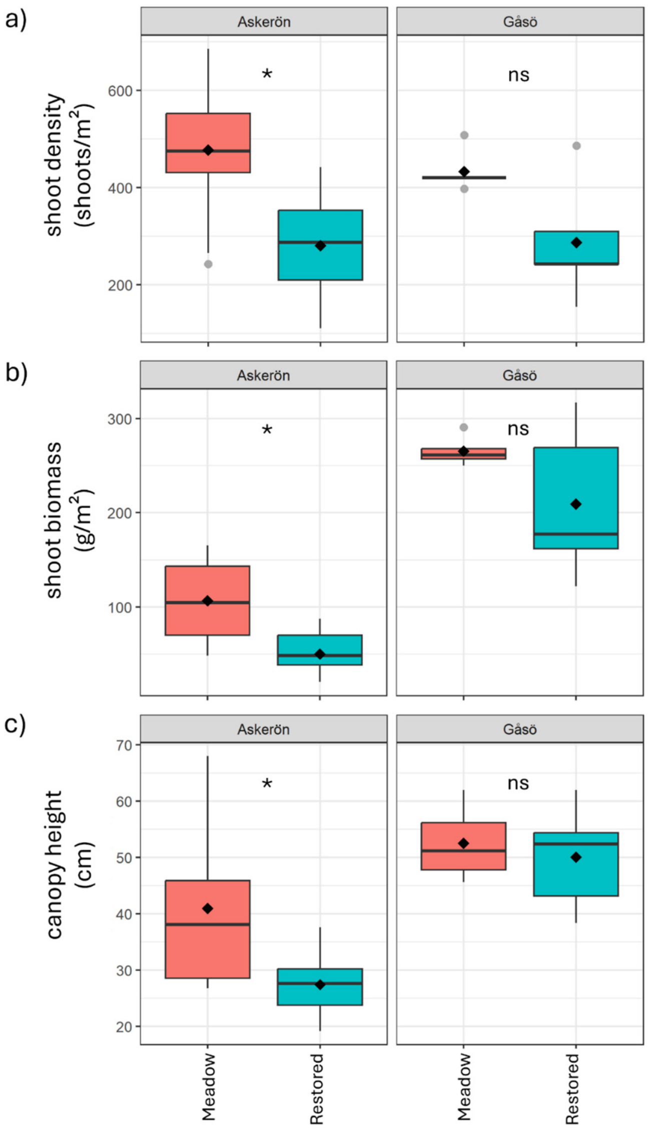

FIGURE 2 | Boxplots of (a) shoot density (shoots/m^2), (b) shoot biomass (g/m^2) and (c) canopy height (cm) in both study sites for the inner part of the reference meadow and the restored meadow. Boxes: Difference between the third and the first quartile or the interquartile range (IQR) of the data. Horizontal lines: median values. Black rhombus: mean. Error bars: Minimum and maximum values within 1.5 times the IQR. Grey dots: Individual data points beyond this range (outliers). Asterisks: Significant differences ($p < 0.05$); ns = non-significant differences.

between habitats were found in Gåsö ($p = 0.001$) but not in Askerön ($p = 0.209$). Certain pairs of habitats were statistically different in Gåsö (i.e., restored vs. edge, $p = 0.037$, and sand vs. edge/meadow/restored, $p = 0.001$, 0.015 and 0.029) (Figure 3b). However, meadow vs. edge/restored presented no significant differences ($p = 0.111$ and 0.786, respectively).

Among all the species observed (Table 2), the SIMPER analysis revealed that in Gåsö, *Pomatoschistus flavescens*, *Pomatoschistus* spp. and *G. niger* were the species accounting for most dissimilarities between habitats (Table S1). These were also the only species that were observed in greater numbers and across most habitats in both sites (Table 2). The higher difference in the assemblage composition in Gåsö was between the sand and edge/meadow areas ($p = 0.001$ and 0.015). *P. flavescens* was absent in the sand area, present in the edge and dominating the meadow; *G. niger* was not detected in the meadow, but it was observed in the edge and dominating in the sand; and *Pomatoschistus* spp. was absent in the meadow, present in the sand and dominating the edge (Table S1 and Figure 4b). In Askerön, where significant differences were not observed between habitats, these three dominating species were present at similar densities except for the absence of *G. niger* and *Pomatoschistus* spp. in the meadow (Figure 4a).

Canopy-Associated Fish Community

Taxonomic richness, total fish density, total fish biomass and community composition were also evaluated excluding cryptic bottom dwelling species that were not well sampled by the visual method, including both species common in eelgrass (*G. niger* and *A. anguilla*) and sand-associated species (Pleuronectidae sp. and *Pomatoschistus* spp.). Once excluded, the three univariate community descriptors did not differ significantly across habitats in Askerön ($p = 0.148$, 0.173 and 0.134, for richness, density and biomass, respectively). In Gåsö, they were all significantly different ($p = 0.002$, 0.002 and 0.008). These differences were significant between the sand vs. the edge/meadow habitats (Figure 5 and Table S2), as none of the remaining fish analysed were observed in the sand on this site (see Table 2).

The multivariate analysis of the community showed no significant differences between habitats for any of the sites ($p = 0.463$ for Askerön and 0.379 for Gåsö), considering that in Gåsö only the eelgrass meadows were analysed as no canopy-living species were detected in the sand. The MDS means plot showed a strong overlap between all habitats in both sites, except between the edge and the sand and restored habitats in Askerön (Figure 6).

4 | Discussion

The goal of seagrass restoration is not only to recover the meadow structure but also to regenerate ecosystem integrity by enhancing the associated ecosystem functions and services, such as the return of fauna (Paling et al. 2009; McSkimming et al. 2016). Regarding the habitat function for fish provided by *Z. marina*, our results suggest that the recovery of eelgrass structural complexity and the favourable environmental conditions (e.g., good water quality) in Gåsö may be promoting the recovery of this ecosystem function for the canopy-associated fish species from the community. The lack of complete structural recovery in Askerön, together with worse environmental conditions, resulted in inconclusive results in terms of recovery of the fish habitat function for these species.

Both sites exhibited a fast initial increase of eelgrass aboveground structural complexity compared to restoration actions carried out with slow growing species like *P. oceanica* in the Mediterranean, where structural complexity after similar periods of time was still far from reaching reference values (authors, pers. obs.). The high survivorship and increased shoot density of the planted eelgrass fragments indicate the replanting success of

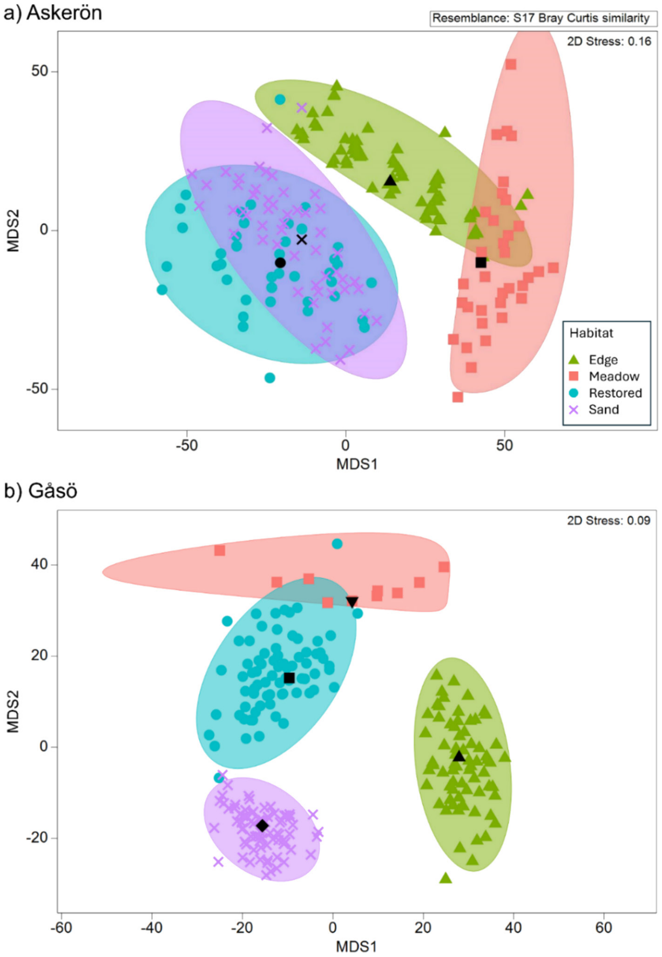

FIGURE 3 | MDS means plot illustrating the differences in species composition densities across habitats in (a) Askerön and (b) Gåsö. Mean centroid (black points), bootstrapped centroids (coloured points) and 95% confident envelopes (coloured areas) are represented for each habitat. Transects with no fish detected were excluded from this graphical analysis, not from the statistical analysis, to enhance the visualization of the primary patterns across the majority of transects. In Gåsö, a dummy variable of value 1 was added when creating the resemblance matrix.

both independent restoration trials. Although a single 1-ha plot was planted in Askerön in 2021, and four plots of 0.16-ha were planted in Gåsö in 2019, the average shoot densities increased from 16 shoots/m^2 at the time of plantation to 300 shoots/m^2 in both sites 2 and 4 years after plantation, respectively. Whereas Gåsö's plantation site had already reached structural complexity values of the reference meadow and a continuous landscape configuration 4 years after planting, Askerön's plantation has not yet achieved the reference state after 2 years.

Besides time since plantation, Gåsö restored area is located next to the reference natural meadow in contrast to Askerön, where they were approximately 200 m away. Moreover, although it was not formally measured, habitat fragmentation differed between the two sites. Although the checkered pattern was almost gone at Gåsö due to lateral growth, Askerön still presented very fragmented and patchy eelgrass, with very low density in some areas. Moreover, shoots from Gåsö tended to be larger and exhibited higher biomass compared to those from Askerön. Differences between the reference meadows on both sites may also reflect the more disturbed environment around Askerön. Given these differences between sites, we hypothesize that inter-site variability in eelgrass structural recovery could be caused by the time elapsed since plantation, by the inherent plasticity of eelgrass, modulated by environmental factors such as light availability, salinity, depth, wave exposure, turbidity and temperature (Bertelli et al. 2021), or by a combination between these factors.

These differences in landscape configuration and environmental conditions between sites may also affect the fish communities (Yeager et al. 2016). The different recovery stages of eelgrass structural complexity between sites may influence the provision of refuge and better access to prey and, therefore, the recovery of the habitat function for fish. For instance, the epifaunal community seems to rapidly recover after replantation. A preceding study by Gagnon et al. (2023) documented rapid epifaunal colonization in Gåsö's restored area, achieving similar density, biodiversity and functional diversity values to the reference meadow 15 months post-transplantation. However, epifaunal recovery has not yet been studied in Askerön. Results from Gåsö indicated that a relatively low threshold of eelgrass biomass was sufficient to sustain a diverse and large invertebrate community (Gagnon et al. 2023). Similar findings were observed by Gräfnings et al. (2024) in the Dutch Wadden Sea, where benthic communities recovered after 2 years regardless of eelgrass meadow structure. McSkimming et al. (2016) also observed that in an *Amphibolis antarctica* plantation, epifaunal richness and

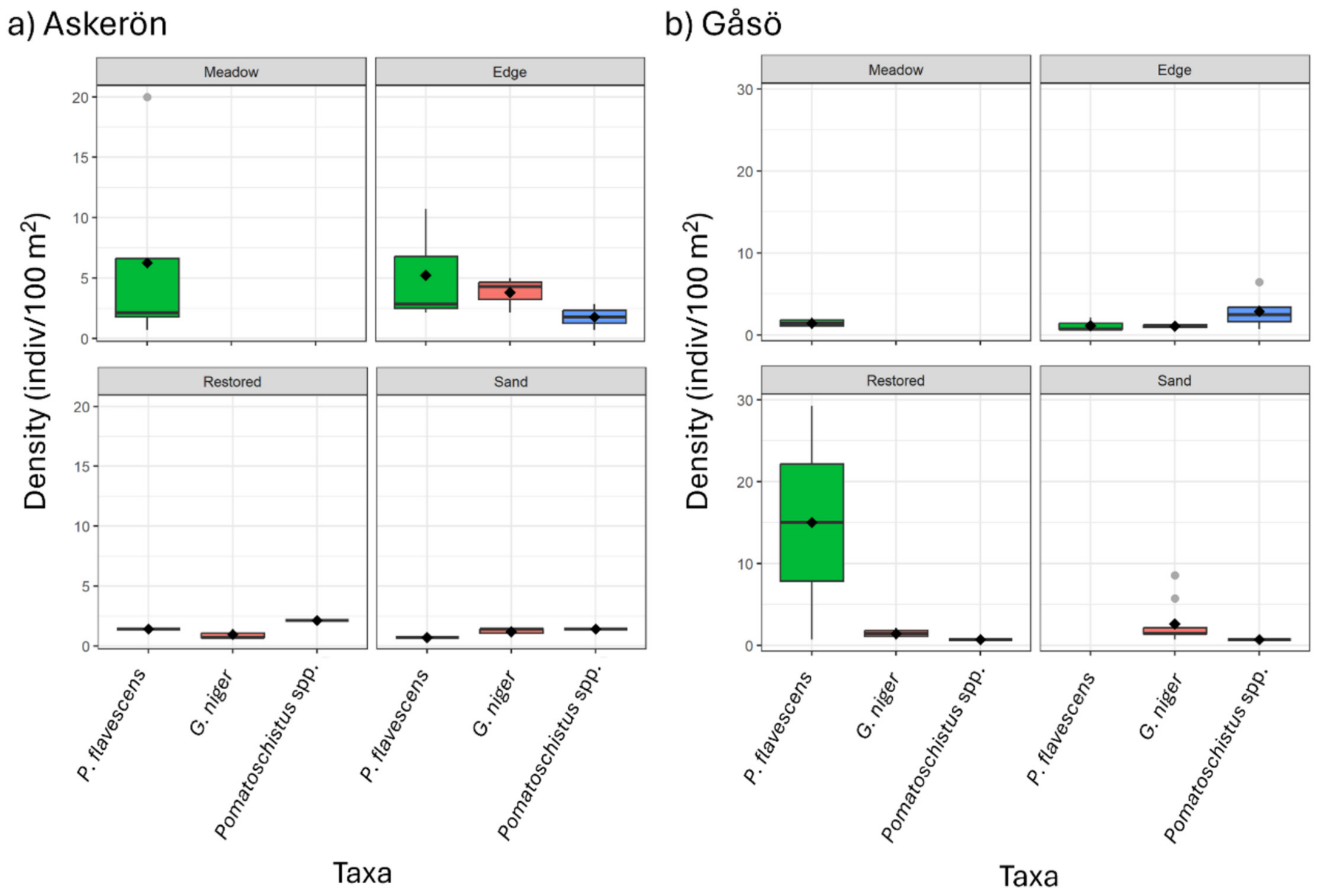

FIGURE 4 | Fish density of the three fish taxa that were responsible for the higher % dissimilarities between habitats in (a) Askerön and (b) Gåsö.

abundance recovered within 1 year, whereas seagrass structural complexity took 3 years to recover after plantation. However, the recovery of the epifaunal community composition did not reach reference levels until seagrass structure was fully restored.

The complete fish communities observed in both studied sites and across all habitats were dominated by the same three intermediate predator species: the two-spotted goby *Pomatoschistus flavescens*, the black goby *G. niger* and the sand gobies *Pomatoschistus* spp. These species typically feed on epifauna (i.e., crustaceans, annelids and molluscs), and sometimes smaller fish or fish larvae (Utne-Palm 2000; Leitão et al. 2006; Matern et al. 2021). The overall dominance of these species may be explained by a top-down cascading effect caused by overfishing of Atlantic cod (*Gadus morhua*), an economically important species, along the Swedish coast. Stocks of this top predator species have declined by up to 90% in recent decades (Moksnes et al. 2008; Baden et al. 2012; Boström et al. 2014). Eelgrass meadows have historically been used by Atlantic cod 0-group juveniles as nursery habitats (Lilley and Unsworth 2014), as they improve their chances of avoiding predation (Gotceitas et al. 1997), thereby contributing to their stocks as they reach maturation (Lilley and Unsworth 2014). However, we did not observe any juvenile *G. morhua* individuals during our samplings.

P. flavescens, *G. niger* and *Pomatoschistus* spp. were responsible for the different community compositions observed between certain pairs of habitats in Gåsö. However, these differences should be interpreted with caution, because a sampling bias was detected due to the difficulty for detecting some species inside eelgrass meadows (e.g., *G. niger*), and differences between the edge and the restored habitats disappeared when evaluating only the canopy-associated fish community, which includes labrids and pipefish among other species. In Askerön, although the communities did not differ significantly between habitats, the natural meadow was separated from the sand and restored habitats in the MDS plots when analysing the complete community, but they overlapped when analysing only the canopy-associated species.

The visual methods used in this study, UVC and Stereo-DOV, were conducted swimming above the canopy and failed to detect cryptic species that hide on the bottom between the stems of eelgrass (e.g., *G. niger*, *A. anguilla* or Cottidae sp.). These species were more easily observed on unvegetated bottoms than within the meadows, resulting in a methodological limitation that biased the results. Consequently, these species were excluded from subsequent analysis, highlighting that visual census methods may not be suitable for comparing vegetated and unvegetated habitats for these species. Previous studies on the Swedish west coast using a beach-seine (e.g., Pihl et al. 2006) reported black gobies as significantly more abundant inside eelgrass meadows compared to unvegetated habitats, with up to 2.5 times greater abundance. Thus, it is important to recognize this species-specific limitation when using visual methods in dense vegetated habitats.

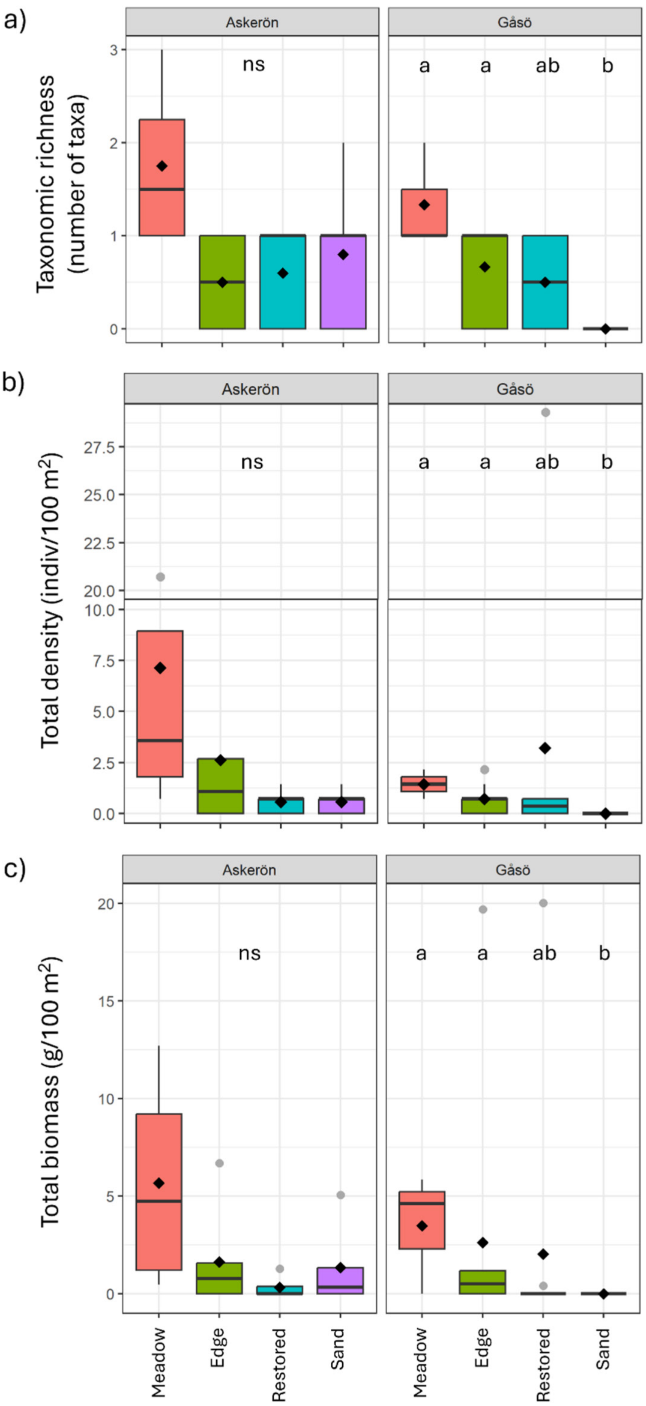

FIGURE 5 | Boxplots of (a) taxonomic richness, (b) total density and (c) total biomass between habitats of the canopy-associated fish community in both study sites. a,b: Significant differences across habitats ($p < 0.05$); ns = non-significant differences.

Stereo-DOV, used for the first time in Swedish *Z. marina* meadows, demonstrated its ability to detect the same species and comparable or higher abundance levels than traditional UVC surveys conducted by divers, including juvenile fish and some cryptic species like pipefish. Interestingly, Stereo-DOV detected significantly higher total abundances of species such as sand eels (Ammodytidae sp.)—small, shoaling fish potentially underestimated by divers but more precisely counted in the video analyses. The black goby was also underestimated by UVC in Gåsö. Despite these capabilities, overall taxonomic richness, density and biomass values obtained using both Stereo-DOV and UVC were very low compared to results from Pihl et al. (2006) using the beach-seine method. Both diver-based methods showed limitations in estimating fish diversity and abundance for certain species compared to the traditional beach seine. Stereo-DOV, like UVC, was unable to detect bottom-dwelling species such as the black goby or cottids within eelgrass methods, underestimating their abundance relative to unvegetated areas.

Some of the other species observed, such as flatfish (family Pleuronectidae) and the sand gobies, are primarily associated with sand substrates or sparse seagrass (Louisy 2002; Schultz and Kruschel 2010; Boissin et al. 2011). When removing both cryptic bottom-dwelling species and sand-associated species, differences between habitats were not detected between the edge and restored meadows in Gåsö. This result indicates that previous differences were caused by the methodological bias or by sand-associated species and that the canopy-associated community may have already recovered in the restored eelgrass from Gåsö. In Askerön, the removal of these species also homogenized the natural and restored meadows' communities.

When analysing only this fraction of the fish community, taxonomic richness, density and biomass in Gåsö were significantly higher in the natural meadows compared to the sand, where no fish were detected. The restored meadow did not present significant differences either with the natural meadow or with the sand, which may indicate an ongoing recovery process. The lack of significant differences between habitats in Askerön, including the sand, does not necessarily support a lack of recovery. If there was no recovery, natural meadows would be expected to present significantly higher diversity and abundance than restored meadows. This inconclusive result may be partly influenced by the visual census methods being less efficient inside eelgrass meadows even for some canopy-associated species (e.g., pipefish), which may also explain why the abundance and diversity was lower in this study compared to other studies from the west coast of Sweden (Pihl et al. 2006). For instance, only eight pipefish individuals were observed among all habitats and sites of which four were observed in restored meadows. This result indicates that both restored meadows function as habitat for this group of species, which are most strongly affected when eelgrass beds are lost (Masonjones et al. 2010).

Despite the suitability of Stereo-DOV for use in protected and restored environments we recommend the implementation of this method with caution in future eelgrass studies and always in combination with an alternative method where possible (i.e., the beach-seine method). It would be useful to also formally compare the performance of Stereo-DOV vs. beach-seine in future studies to quantify the inherent bias of Stereo-DOV in detecting bottom-dwelling species in vegetated habitats.

Apart from the above-mentioned methodological limitation of Stereo-DOV, it is also essential to address the temporal limitations of the data presented. To gain a more comprehensive understanding of fish community dynamics, future studies should incorporate data collection that accounts for diel (day and night) differences, as well as variations across monthly, seasonal and annual timeframes. Such approaches would enable a

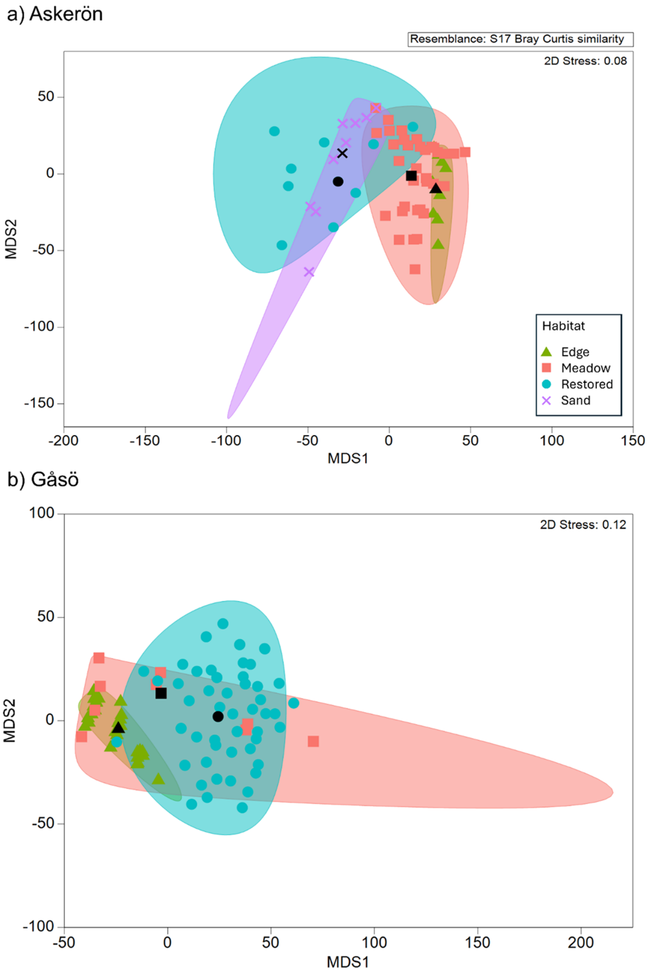

FIGURE 6 | MDS means plot illustrating the differences in species composition densities across habitats in (a) Askerön and (b) Gåsö for the canopy-associated communities. Transects with no fish detected were excluded from this graphical analysis to enhance the visualization of the primary patterns across the majority of transects.

more detailed assessment of habitat and site-specific variations, as well as provide insights into the fish recovery process in restored eelgrass meadows. The partially inconclusive results regarding the detectable recovery effect in Askerön may also be attributed to the sampling approach used in this study. Sampling was conducted only after restoration had taken place, and the habitats were near one another. It is possible that habitat restoration benefited the fish fauna across the broader area, creating a landscape-level effect rather than increasing abundances solely within the restored meadow. This is particularly likely for mobile species with weak habitat affiliations. Detecting such effects would have required sampling the general area prior to replanting. We recommend that future replanting studies aiming to assess restoration effects should incorporate pre-restoration sampling at both local and landscape scales.

In conclusion, our results indicate a relatively fast increase and recovery of structural complexity in both restored eelgrass meadows. Elapsed time since plantation and other environmental variables (i.e., habitat fragmentation or water quality, among others) may be playing a role in the different eelgrass recovery stages observed between sites. These environmental factors may also influence the differential recovery in terms of habitat provisioning for fish when considering only the canopy-living fraction of the fish community. The natural eelgrass meadows exhibited higher fish richness, density or biomass in Gåsö compared to the unvegetated habitat, but no differences were observed compared to the restored habitat. In Askerön, these parameters did not show any significant differences between habitats, although slightly higher values were detected for the inner meadow. Furthermore, community composition across all eelgrass habitats were similar at both sites, suggesting that the restored meadow functioned similarly to natural meadows on a structural level. Given these results, restoration practitioners should manage expectations regarding the recovery of ecosystem functions. The natural presence or replanting of *Z. marina*, a fast-growing seagrass species, may not necessarily imply an increase in all associated ecosystem functions compared to unvegetated habitats. Nevertheless, it is important to note that this study did not include pre-restoration sampling and that it compared differences between contrasting habitat types located in close proximity to the restored sites. As a result, we could not draw firm conclusions about fish recovery on a broader temporal and spatial scale. Future replanting studies evaluating restoration effects on habitat provision for fish should therefore incorporate pre-restoration sampling at both local and seascape scales.

Ethics Statement

The research required no permit approvals.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in DIGITAL.CSIC at https://doi.org/10.20350/digitalCSIC/17059, reference number 10261/379990.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.