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Fish Assemblages in Seagrass (*Zostera marina* L.) Meadows and Mussel Reefs (*Mytilus edulis*): Implications for Coastal Fisheries, Restoration and Marine Spatial Planning

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Abstract: Seagrass meadows and mussel reefs provide favorable habitats for many fish species, but few studies have compared the associated fish assemblages directly and examined the influence of environmental variables. Knowledge of fish assemblages associated with disparate habitats is needed for the conservation of coastal fisheries and marine spatial planning. Catch per unit effort data derived from fyke nets showed similar species richness and diversity in seagrass meadows and mussel reefs, suggesting that both habitats support elevated marine biodiversity of mobile fauna. However, it was shown that fish assemblage structure differed between those habitats, and also fish abundance in seagrass meadows was significantly higher than in mussel reefs by comparing the data with a multivariate extension of Generalized Linear Models (GLM). Furthermore, employing underwater video recordings to compare fish abundances in high and low water current speed mussel reefs with a Generalized Linear Mixed Model with negative binomial distribution, data revealed similar fish abundances (in terms of the MaxN metric) despite the variation in current speed, probably because the mussel formations provide sufficient shelter, even from high water currents. The commercially important species Atlantic cod (*G. morhua*), however, was significantly more abundant in the low water current mussel reef. Therefore, restoration efforts targeting *G. morhua* could benefit from restoring low current mussel reefs. Our study provides input for the conservation of coastal recreational and commercial fisheries, habitat restoration and marine spatial planning where certain habitats may be prioritized.

Keywords: Atlantic cod (*Gadus morhua*); Baltic Sea; biogenic reef; eelgrass; fish abundance; fish assemblage; fisheries management; flow velocity; restoration

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1. Introduction

During recent decades, intensified human activities in coastal areas have degraded many marine habitats and caused subsequent declines in numerous organisms. Impacted organisms include seagrass and bivalves, which are considered significant habitat modifiers in coastal areas [1–6]. Importantly, seagrass meadows and bivalve reefs often support several important ecosystem services (ES), partly because the habitats act as nurseries for many marine species by providing nesting grounds, refuge from predators and habitats for foraging [7–13].

Bivalve reefs are often the target of restoration and management plans in coastal areas because of the associated ES; however, most restoration projects have targeted oyster species (e.g., European flat oyster; *Ostrea edulis* [14], Pacific oyster; *Crassostrea gigas* [9,15] and eastern oyster; *Crassostrea virginica* [8,16]). Fewer studies have targeted blue mussel (*Mytilus edulis*) [17], although *M. edulis* reefs often form biodiversity hotspots, including

habitats for many infaunal and epifaunal species [18,19]. For example, *M. edulis* reefs may augment seagrass growth [20] and fish production in the Baltic Sea [15,17,18].

In the Baltic Sea, seagrass meadows mainly consist of *Zostera marina* and provide several ES [3,4,21,22], and the meadows contribute to significant ecosystem functions, including carbon sequestration, nutrient cycling and alterations of water flows [3,7,21,23,24]. Moreover, *Z. marina* provides habitats for many organisms, including foraging habitats for several fish species [3,7,25] that may be exploited commercially and recreationally [10,26–28].

The important roles of *Z. marina* meadows and *M. edulis* reefs for coastal fishes have been documented by many studies suggesting that fish production is positively affected by the two habitats [2,3,7,9,10,17,29,30]. Importantly, both habitats may provide spatial refuges for predation and alleviate food limitations [2,31–33]. Few studies, however, have compared the fish assemblages associated with *Z. marina* meadows and *M. edulis* reefs to understand the relative significance of these habitats for a broad range of fish species.

Fish abundance and assemblage composition is often affected by the degree of structural complexity of the habitat [33–38]. For example, a previous study [37] showed that complex habitats, including seagrass and oyster habitats, are more diverse in terms of fish and invertebrate communities compared to mudflats. In addition to habitat complexity, environmental variables may affect fish assemblages. Recent studies have suggested that water currents may affect fish abundances and assemblage composition in freshwater [39,40] and marine ecosystems [41,42] and should be considered for integrated management plans [41]. Despite these findings in aquatic systems, the influence of contrasting water currents on fish assemblages associated with bivalve reefs remains largely unknown. This may be particularly relevant for reef restoration projects targeting bivalves to enhance fisheries production.

The ES provided by seagrass meadows and bivalve reefs may play a critical role for spatial management and coastal restoration plans [9,28]. Current challenges for management plans include gaining an integrated understanding of the processes that are taking place in marine habitats, and their threats, to design efficient plans [9,16,43]. Indeed, a thorough understanding of the relationships between seagrass meadows, bivalve reefs and fish assemblages can provide guidance for marine management and help to mitigate habitat degradation [16,30,44], as well as evaluate and protect the ES and ecosystem goods (EG) that the habitats provide [45,46].

The objective of this study was to investigate habitat use of marine fishes to improve ecosystem-based approaches for the management of marine resources and fisheries [47,48]. To this end, we compared fish assemblages in *Z. marina* meadows and *M. edulis* reefs in the Western Baltic Sea (i.e., Øresund between Denmark and Sweden). In addition, we contrasted fish assemblages representing two different *M. edulis* reefs with high and low water currents. Specifically, we tested the hypotheses that (1) *Z. marina* meadows support higher fish diversity and abundance than *M. edulis* reefs, and (2) fish abundance differs between *M. edulis* reefs exposed to high and low water currents.

2. Materials and Methods

2.1. Study Area

This study was carried out in the Sound (Øresund; ICES subdivision 23) between Denmark and Sweden (Figure 1). The Øresund represents transient waters between the Baltic Sea and Kattegat. Seagrass meadows (*Z. marina*) occur on sandy sediments at depths ranging between 1–6 m. In total, 162 km² are covered by seagrass meadows in Øresund [49], whereas blue mussel reefs (*M. edulis*) cover 46 km² [50].

Fish abundance and diversity were measured on three field sites near the island of Saltholm in Øresund. Southeast of the island (55°35′12.21″ N; 12°48′04.42″ E), field sites 1 and 2 had high water currents (range: 0.007–1.81 m s^{−1}) (Figure 2a,b). Field site 1 (0.22 km²) provided dense *Z. marina* meadows, whereas field site 2 (0.28 km²) provided extensive *M. edulis* reefs.

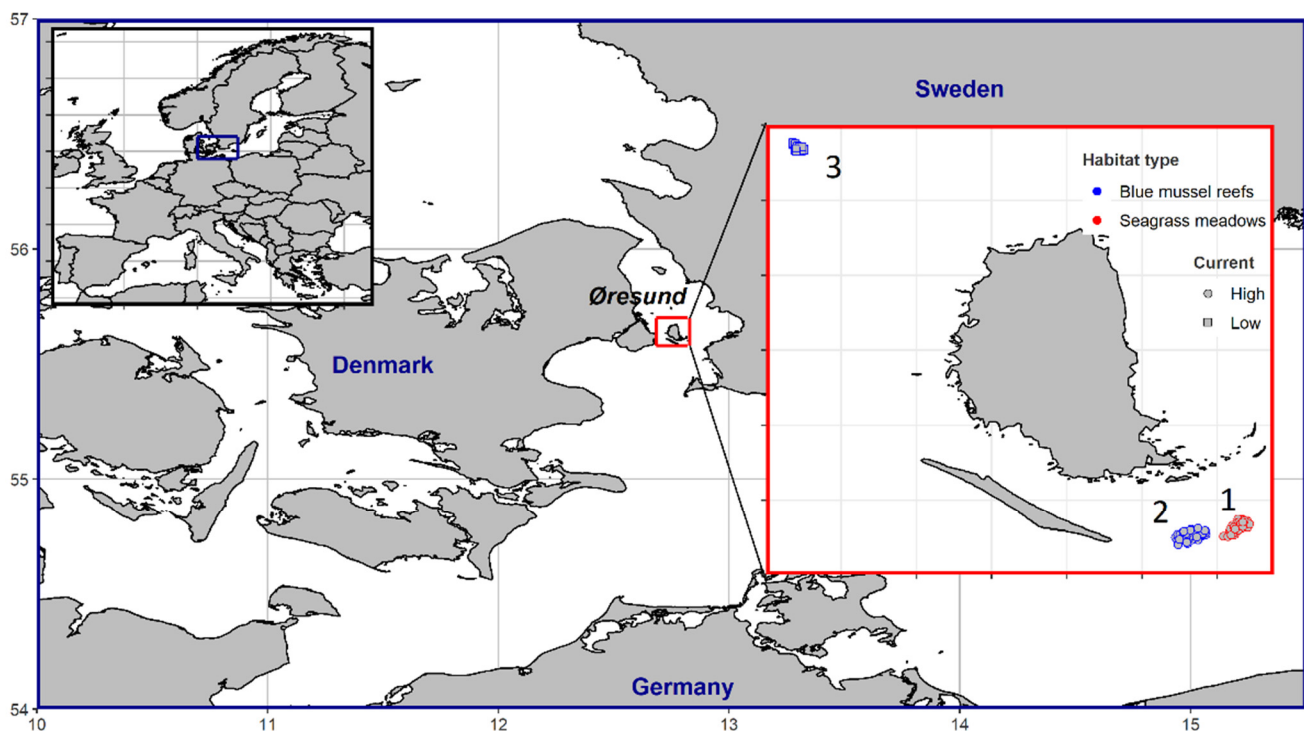


Figure 1. Map of the sampling area and sites. The red color dots indicate the seagrass meadows (field site 1), while the blue color dots indicate the mussel reefs. For the mussel reefs, circles refer to high water currents (field site 2) and squares refer to low water currents (field site 3).

In contrast, field site 3 (0.17 km²) northwest of the island (55°41′32.63″ N; 12°41′31.68″ E) had low water currents (range: 0.003–0.88 m s^{−1}) (Figure 2a,b) combined with widely developed *M. edulis* reefs. Comparing additional environmental parameters derived from a numerical operational model, which estimates hourly the hydrographic conditions in the surface water column of Øresund basin (Western Baltic Sea), both sites (site 2 and 3) were characterized by similar water temperature (°C) (Figure 2c,d) and salinity (ppt) (Figure 2e,f). All data were collected during autumn and winter of 2014.

2.2. Fish Assemblages in *Z. marina* Meadows and *M. edulis* Reefs

A total of 60 double fyke nets were deployed in *Z. marina* meadows (field site 1) and *M. edulis* reefs (field site 2) (high water currents). The lead lengths of fyke nets were 8 m, heights were 0.6 m and mesh sizes were 18 mm. Diameters of the seven sequential hoops were 60, 55, 50, 45, 40, 35 and 35 cm, similar to earlier studies [51]. All fyke nets were deployed identically and with the same orientation to current direction in random positions at field sites 1 and 2 in the afternoon and fished for about 24 h. Deployment and retrieval of the fyke nets followed standard procedures [51,52]. After retrieval, fishes were identified to species or family levels. Catch per unit effort (CPUE) data were derived as the total catch (in numbers) of each taxon for each deployment (i.e., per 24 h). CPUE data were considered proxies of the relative fish abundance following previous studies [53–55].

2.3. Fish Assemblages in *M. edulis* Reefs with High and Low Water Currents

A total of 50 underwater cameras were deployed from 11 September 2014 to 8 December 2014 in contrasting mussel reefs with high currents (HC) and low currents (LC) (i.e., field sites 2 and 3), similar to previous studies using remote underwater video systems to describe fish assemblages in different habitats [56]. Each camera (Hero 3+ Black Edition; GoPro Inc., San Mateo, CA, USA) was mounted with a scheduler (TL-004A Intervalometer; CamDo Solutions Inc, Vancouver, BC, Canada). The scheduler ensured that each camera

recorded one 30 s video sequence every hour. Videos were recorded in HDTV resolution (1080 p) with a 30 Hz frame rate and were stored on 32 GB micro-SD cards.

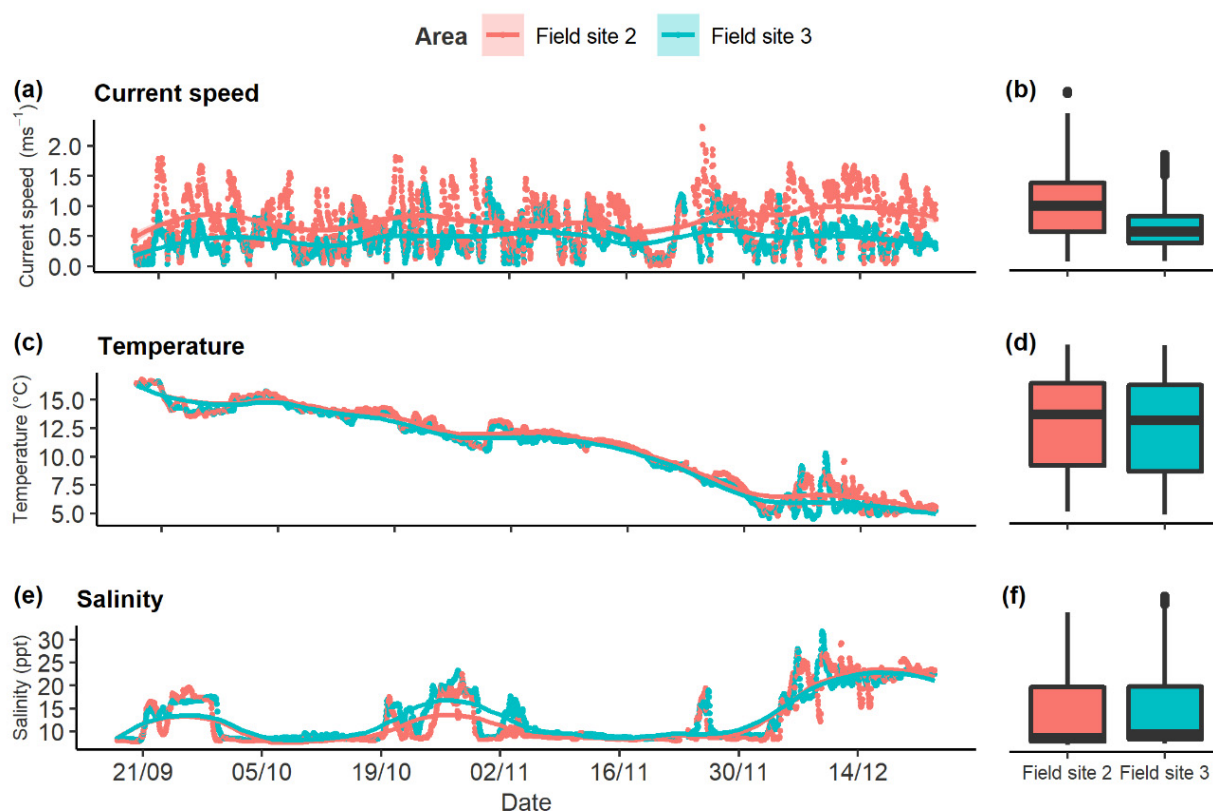


Figure 2. Environmental variables across the study period (September to December 2014) in the mussel reef areas with high currents (HC) (red color) (field site 2) and with low currents (LC) (green color) (field site 3): (a) water current speeds (m s^{-1}); (c), water temperature ($^{\circ}\text{C}$); (e) water salinity (ppt); (b,d,f) boxplots representing the mean values of the environmental parameters (a,c,e, respectively) for each site with 95% confidence intervals. The environmental data are derived from a numerical operational model, which estimates the hydrographic conditions in the Øresund basin (Western Baltic Sea). The database Baltic Sea Analyses Forecast was used, accessible via COPERNICUS (<https://marine.copernicus.eu/>, accessed on 16 November 2021).

Each camera was mounted for horizontal recording on a vertical pole attached to a concrete tile ($40 \times 40 \times 5$ cm). A 10 m line connected the tile to an anchor and surface float. The camera tile was deployed from a boat and lowered to the seafloor with a rope temporarily attached to the tile. After positioning the tile on the seafloor, the rope was retrieved and the anchor line and surface float were deployed.

Similar to previous studies [57,58], video analyses included identifications of fish species or families (when identification to the species level was unreliable) and measurements of the maximum number of each taxon that appeared within the video sequence at one time, known as the MaxN metric. MaxN is a conservative metric of relative abundance and it is used in order to avoid multiple counts of the same individuals appearing in the videos [59,60]. Only daylight recordings were analyzed because no artificial light source was deployed. This approach assumed that recordings between dawn and dusk are sufficient to describe fish assemblages [61,62].

2.4. Statistical Analysis

2.4.1. Statistical Analysis of Fyke Nets Data

Hypothesis 1 stated that fish diversity (i.e., species) and abundance would be higher in seagrass meadows compared to mussel reefs because of higher structural complexities in seagrass meadows [63]. To compare species diversity between *Z. marina* meadows (field

site 1) and *M. edulis* reefs (field site 2), species richness, Shannon and Pielou's evenness indices were estimated (R package: vegan, functions: specnumber, diversity [64]). Next, the diversity metrics for each habitat (*Z. marina* meadow and *M. edulis* reef) were compared using non-parametric Mann–Whitney tests [65,66] because data were incompatible with a normal distribution, even after transformations.

To contrast fish abundances and composition between *Z. marina* meadows and *M. edulis* reefs, a multivariate extension of Generalized Linear Models (GLM), suitable to model abundances of community data (R package: mvabund, function: manyglm [67]) was applied. Due to many zero abundances, leading to overdispersion, a negative binomial regression version of the model was fitted with two levels (mussel reef and seagrass meadow) of habitat as predictor. Multivariate extensions of GLM are considered to increase the statistical power, in comparison to conventional distance-based multivariate analyses, by taking into account the endogenous mean–variance relationship of count type data [68]. To test for significant effects of habitat on fish abundance, univariate analyses of deviance with 999 resampling iterations for each species separately were applied (R package: mvabund, function: anova.manylm [67]). In addition, for the inspection and visualization of the influence of habitat on fish assemblages, a distance-based redundancy analysis (db-RDA) (R package: vegan, function: capscale [64]), using habitat as predictor and Bray–Curtis dissimilarity coefficient, was applied. Finally, a Permutational multivariate analysis of variance (PERMANOVA) [69] (R package: vegan, function: adonis [64]) with Bray–Curtis dissimilarity matrix, was run to test the importance of habitat in explaining the assemblage composition.

2.4.2. Statistical Analysis of Video Cameras' Data

Hypothesis 2 stated that fish abundance would differ between *M. edulis* reefs exposed to high (HC) and low (LC) water currents. To address the hypothesis, underwater recordings were analyzed to detect differences between the two habitats. Therefore, differences in the maximum numbers of fish (MaxN) between the two habitats (HC *M. edulis* reef and LC *M. edulis* reef) were tested for each species or family separately using a Generalized Linear Mixed Model with negative binomial distribution to avoid pseudoreplication and to account for overdispersion (GLMM, R package: lm4, function: glmer.nb [70]), similar to previous studies [71,72]. The model selection followed [73] and integrated the Akaike Information Criterion (AIC). In addition to the fixed variables of habitat and environmental parameters (salinity, temperature and current), random variables of camera id, hour and month were also included in the model to account for random effects. The species *Aphia minuta* and sand lances (Ammodytidae) were registered rarely and, thus, were excluded from the analysis. Due to uncertainty in the video identification of gobies (Gobiidae), other than *Gobiusculus flavescens* and *Gobius niger*, flatfish (Pleuronectidae) and wrasses (Labridae), other than *Ctenolabrus rupestris*, they were identified to the family level, while the rest of the fishes were identified to species level.

All statistical analysis and plotting were conducted in R statistical and programming environment (version 3.6.3) [74].

3. Results

3.1. Using Fyke Nets to Estimate Fish Assemblage in Seagrass Meadows and Mussel Reefs

A total of 380 individual fish, covering 14 different species, were caught by the 60 fyke nets deployed in this study. Eelpout (*Zoarces viviparus*) was the most abundant species in both surveyed habitats (i.e., seagrass meadow and mussel reef). The eelpout was followed by the two-spotted goby (*Gobiusculus flavescens*) and the European eel (*Anguilla anguilla*) in the seagrass meadow and the two-spotted (*Gobiusculus flavescens*) and black goby (*Gobius niger*) in the mussel reef habitat. According to the Mann–Whitney test, the habitats provided similar species richness ($W = 422, p = 1$), the Shannon index ($W = 380, p = 0.5$) and Pielou's evenness index ($W = 285, p = 0.5$) suggested comparative fish species diversities in the two habitats.

The five species broadnosed pipefish (*Syngnathus typhle*), Atlantic cod (*Gadus morhua*), corkwing wrasse (*Symphodus melops*), goldsinny wrasse (*Ctenolabrus rupestris*) and ninespine stickleback (*Pungitius pungitius*) were only observed in the mussel habitat, while shorthorn sculpin (*Myoxocephalus scorpius*) was only found in the seagrass meadows. The total CPUE (i.e., abundance) for all species together was, however, significantly higher in the seagrass meadow ($p < 0.001$).

The univariate tests comparing the species abundances between the two habitats showed that the CPUE for *A. anguilla* ($p < 0.001$) and *Z. viviparus* ($p = 0.02$) was significantly higher in the seagrass compared to mussel reef, while the abundance of *G. niger* was significantly higher ($p = 0.01$) in the mussel reefs compared to seagrass. All the other species exhibited similar CPUE numbers in both habitats (Table 1).

Table 1. Comparison of fish species abundances estimated using catch per unit effort (CPUE) data from seagrass meadows and mussel reefs in the Øresund between Denmark and Sweden. The p values were derived from the univariate analyses of deviance with 999 resampling iterations, comparing the number of each species separately in each habitat. The bold cells indicate the statistically significant differences and the asterisks show the level of significance, where *** $p < 0.001$ and * $p < 0.05$.

Family	Fish Species Latin Name	Common Name	CPUE Mussel	CPUE Seagrass	p	Dev
Anguillidae	<i>Anguilla anguilla</i>	European eel	0.3	2.429	<0.001 ***	12.15
Labridae	<i>Ctenolabrus rupestris</i>	Goldsinny wrasse	0.067	0	0.18	2.64
Gadidae	<i>Gadus morhua</i>	Atlantic cod	0.067	0	0.14	2.64
Gobiidae	<i>Gobius niger</i>	Black goby	1.2	0.429	0.01 *	6.45
Gobiidae	<i>Gobiusculus flavescens</i>	Two-spotted goby	1.333	1.714	0.61	0.28
Cottidae	<i>Myoxocephalus scorpius</i>	Shorthorn sculpin	0	0.071	0.13	2.91
Pleuronectidae	<i>Platichthys flesus</i>	European flounder	0.067	0.036	0.68	0.27
Pleuronectidae	<i>Pleuronectes platessa</i>	European plaice	0.033	0.036	0.86	0
Gasterosteidae	<i>Pungitius pungitius</i>	Ninespine stickleback	0.033	0	0.47	1.32
Gasterosteidae	<i>Spinachia spinachia</i>	Sea stickleback	0.133	0.607	0.11	2.96
Labridae	<i>Symphodus melops</i>	Corkwing wrasse	0.033	0.286	0.06	4.1
Syngnathidae	<i>Syngnathus typhle</i>	Broadnosed pipefish	0.033	0	0.44	1.32
Cottidae	<i>Taurulus bubalis</i>	Longspined bullhead	0.067	0.036	0.65	0.27
Zoarcidae	<i>Zoarcas viviparus</i>	Eelpout	1.6	2.607	0.02 *	5.79

Based on the distance-based redundancy analysis, the axis of the constrained component (CAP) explained a minor proportion (6.15%) of the variance and the axis of the unconstrained component (MDS1) explained 25% of the residual variation (Figure 3). Even though the proportion of variance explained by habitat in db-RDA was relatively low, the PERMANOVA analysis showed a significant effect of habitat (PERMANOVA, $p = 0.003$) in distinguishing the assemblages in the two habitats (seagrass meadows and mussel reefs). These findings supported the belief that fish assemblages between seagrass meadows and mussel reefs differ.

3.2. Using Stationary Underwater Cameras to Estimate Fish Assemblage in Two Different Mussel Reef Habitats

For each underwater camera, recordings lasted for 6–7 days (i.e., 300–350 camera days were recorded in total). A total number of 28,535 fish were registered during the video analyses covering the high current (HC) and low current (LC) mussel reefs. The total maximum number of fish was similar (GLMM, $p = 0.14$) in both habitats. However, the univariate analysis of the maximum number of fish representing each family or species in the two habitats indicated that four species differed significantly. More specifically, *G. morhua* and *C. rupestris* exhibited significantly higher abundances in LC mussel reefs, while abundances of *G. niger* and *S. spinachia* were higher in HC mussel reefs (Table 2). In addition, flatfish (Pleuronectidae) abundance was higher in LC compared to HC mussel reef, but the statistical test was marginally insignificant ($p = 0.0745$). Except for habitat, water temperature and salinity demonstrated significant effects on some species. Specifically, temperature had a negative effect on *G. morhua* abundance (GLMM, $p < 0.001$), whereas

salinity showed a positive effect (GLMM, $p = 0.004$). Thus, *G. morhua* abundance appeared to decrease in warmer water and increase at elevated salinities. Concerning the *G. flavescens*, both water temperature and salinity affected abundance positively (GLMM, $p = 0.003$ for temperature and $p < 0.001$ for salinity). Finally, the abundance of *C. rupestris* was positively affected only by salinity (GLMM, $p < 0.001$), while the rest of the species and families remained unaffected by environmental variables.

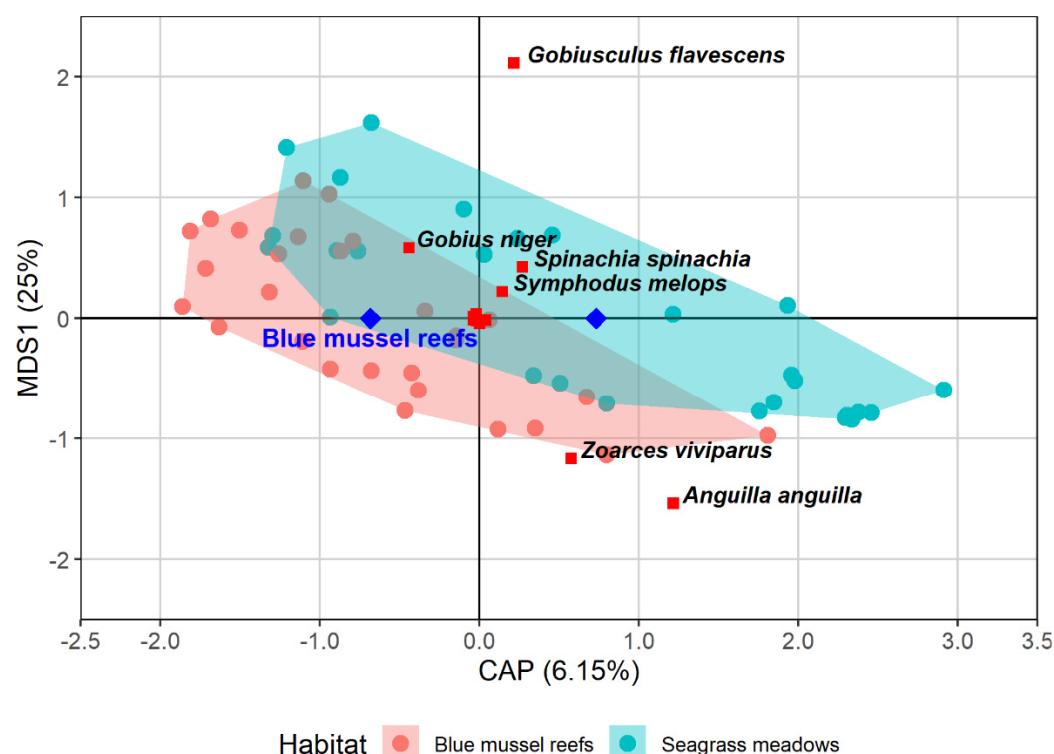


Figure 3. Distance-based redundancy analysis (db-RDA) of the abundances of fish families and species with habitat (i.e., seagrass meadow and mussel reef) as predictor. The green convex hull and point (circles) refer to the seagrass meadows (high current; field site 1), while the red convex hull and point (circles) refer to the mussel reefs (high current; field site 2) in the Western Baltic Sea (Øresund). Red square represents the species (species names are shown when the distance from the center of the axes is >0.1).

Table 2. Comparison of mean fish abundances (in terms of MaxN) with associated confidence intervals (CI), recorded by underwater cameras in mussel reefs with high and low water currents in Øresund. The p values were derived from tests using a GLMM model with negative binomial distribution comparing the maximum number of fish between mussel reefs with high and low current speeds. The asterisks show the level of significance, where *** $p < 0.001$ and * $p < 0.05$.

Family	Fish Species	Common Name	Mean Abundance in High Current Mussel Reef	CI for High Current	Mean Abundance in Low Current Mussel Reef	CI for Low Current	p
Gadidae	<i>Gadus morhua</i>	Atlantic cod	0.000	0	0.621	0.446–0.864	<0.001 ***
Gasterosteidae	<i>Gasterosteus aculeatus</i>	Three-spined stickleback	0.000	0–0.038	0.000	0–0.004	0.485
Gobiidae	<i>Gobius niger</i>	Black goby	0.379	0.154–0.931	0.023	0.006–0.087	<0.001 ***
Gobiidae	<i>Gobiusculus flavescens</i>	Two-spotted goby	10.135	3.112–33.002	21.221	6.107–73.736	0.3876
Gobiidae		Other gobies	0.084	0.012–0.609	0.283	0.022–3.607	0.2511
Labridae	<i>Ctenolabrus rupestris</i>	Goldsinny wrasse	0.017	0.003–0.086	0.515	0.157–1.694	<0.001 ***
Labridae		Other wrasses	0.000	0–0.006	0.000	0–0.005	0.7568
Pleuronectidae		Flatfish	0.010	0.001–0.166	0.041	0.002–0.945	0.0745
Gasterosteidae	<i>Spinachia spinachia</i>	Sea stickleback	0.058	0.022–0.149	0.006	0.001–0.048	0.043 *

4. Discussion

This study investigated the fish assemblages associated with seagrass meadows and mussel reefs. The study highlights that fish abundance in seagrass meadows is significantly higher compared to mussel reefs. Although the habitats examined supported similar species diversity and richness, the fish assemblages differed slightly in structure. In addition, mussel reef habitats with different water current speeds exhibited similar fish abundances, regardless of the water current regime, revealing minor differences in assemblage composition. However, commercially important species, such as *G. morhua* and Pleuronectidae, were more abundant in low current mussel reefs. The findings suggest that mussel reef restoration projects should target low current areas if the goal is to support *G. morhua* and flatfish. Our comparative analysis provides fundamental knowledge for marine habitats and the associated fish assemblages, and plays an important role in the implementation of policies to protect and enhance marine resources, such as coastal fisheries [28,46]. Furthermore, the information combined with species distribution models could be used to define the “essential habitats” for fish life cycles, which should be taken into account in marine spatial planning [75].

Species selectivity of our two sampling methods (fyke nets and underwater cameras) in the same HC mussel bed habitat seemed to differ. More specifically, the two methods presented consistent differences in fish abundance and species composition probably due to different sampling designs, gear selectivity and the sampled area covered by the methods [76,77]. Some species were more effectively targeted by fyke nets (*A. anguilla* and *Z. viviparus*), others by the underwater cameras (Labridae and *G. morhua*), while sampling for other fishes appeared to be unaffected by the gear type (Gobiidae and Pleuronectidae), although the overall fish species spectrum was consistent with previous studies in coastal habitats in the Baltic Sea [17,78–80].

The results of this study suggest that species composition may differ between mussel reef and seagrass habitats, highlighting the different ecological value of each habitat. For example, *C. rupestris*, *G. morhua*, *P. pungitius* and *S. typhle* were only observed at the mussel reefs. The two habitats were, however, characterized by similar species richness (total number of species), e.g., Shannon and Pielou’s evenness indices. These findings are contrary to a previous study [37] that sampled fish with fyke nets in seagrass, oyster and mudflats habitats, and suggested that species composition is more related to location within the estuary than to different habitats. Moreover, in the same study, the authors documented similar fish species richness but marginally higher Shannon diversity in oyster habitats compared to seagrass meadows.

In contrast to the diversity metrics, the overall fish abundance as indexed by CPUE was higher in seagrass meadows, which is in accordance with previous studies [63,81], endorsing that seagrasses support higher fish densities and provide more complex habitats compared to oyster reefs. Additionally, Tomas and Waldbusse [77], comparing seagrass, long-line and on-bottom oyster aquaculture habitats, found higher fish densities in seagrass and long-line oyster habitats compared to on-bottom oyster aquaculture habitats. In contrast, a comparison of fish assemblages in mudflats, oyster reefs and seagrass meadows in North Humboldt Bay, California, showed significantly higher fish CPUE in oyster reefs [44]. To summarize, the majority of previous studies support higher fish abundance in seagrass meadows compared to oyster reefs, a habitat which is similar to mussel reefs as both organisms (oyster and mussel) are bivalves, form biogenic reefs and may offer similar ES.

The relative species composition and fish abundance in both examined habitats (*Z. marina* meadows and *M. edulis* reefs) were in agreement with previous studies [4,78,79]. The higher abundance of *Z. viviparus* in seagrass habitats supports the findings of Thormar et al. [80], reporting that *Z. viviparus* account for the largest proportion of the fish species in another seagrass area in the western Baltic Sea. Moreover, seagrass meadows exhibited a significantly higher abundance of adult *A. anguilla* compared to the mussel reefs. In contrast, mussel reefs, as well as medium size gravel habitats, are often favored by juvenile

eels [82,83]. *A. anguilla* is a critically endangered species as stated in the HELCOM Red list [84], as well as in the Danish Red list [85], while *Z. viviparous* is a near threatened species [84]. *A. anguilla* is targeted by both commercial and recreational fisheries, although this is highly regulated due to the vulnerable status of the species. On the other hand, *Z. viviparous* is only occasionally taken for consumption in recreational fisheries. The high abundance of these species in the seagrass habitat and the status of their stocks, as mentioned above, underlines the significant role of seagrass in the ecosystem structure and demonstrates the value of the specific habitats when considering spatial management plans. On the other hand, the only species with significantly higher abundance in mussel reefs compared to seagrass was *G. niger*, which is a species of “least concern” [86].

The outcomes from the comparison of the two mussel habitats exposed to different current regimes indicated similar total abundance (MaxN) of species in the low and high current habitats, which is consistent with a previous study [41], indicating that the relative fish abundance and fish assemblages of benthic fish species are not strongly structured by current regimes. This finding supports that benthic structures, including biogenic reefs, may act as flow refuges for fish. Other studies have, however, shown increased fish assemblages in high current habitats [39]. In any case, although the outcomes of our research are in accordance with previous studies, conclusions here should be drawn with caution, since the distance between sampling stations was limited, potentially raising issues concerning pseudo-replication.

The distribution of dominant fish species in our study was similar to the distribution of species found in a previous study [17]. Differences in species composition between the mussel reefs with disparate water current regimes may be explained by the absence or presence of the dominant species [87,88]. Specifically, the higher abundance of *G. niger* in the in HC mussel habitat may be driven by the lower abundance of *G. morhua* compared to LC mussel reefs, as *G. morhua* is a major predator of *G. niger* and the presence of *G. morhua* alters the behavior of *G. niger* [89]. Additionally, assemblage structure differences could be explained by the ability of the species to minimize the energy costs in the water current and increase the foraging rates [90]. According to Hamner et al. [91], high current areas could be favored by planktivorous species as the concentration of zooplankton is high in those areas. Thus, the higher abundance of *S. spinachia* in HC mussel reefs compared to LC could be explained by its slender and elongated body shape, a characteristic which allows for efficient and elevated swimming speeds [92], as well as by its diet preference of small invertebrates including copepods [93].

On the other hand, higher densities of *G. morhua* and *C. rupestris* in LC mussel reefs could be attributed to the relatively large body sizes of the fishes with limited opportunity to find shelter against current speeds in the mussel reefs. The negative effect of increasing temperature on *G. morhua* abundance could be explained by its preference for cooler waters [94]. In addition, the Pleuronectidae family including European flounder (*Platichthys flesus*), which is a keystone species for the specific area [86], was marginally more abundant in LC mussel reefs than in HC mussel reefs. Therefore, the higher abundances of Pleuronectidae, as well as *G. morhua*, which is a vulnerable keystone species [84] with high commercial value [95], in the low current mussel reefs compared to the high current mussel reef enforce the importance of protecting low current mussel reefs when spatial management actions are implemented. Thus, it could be most favorable to protect and restore low current mussel reef habitats in management plans to support Pleuronectidae and *G. morhua* stocks and the economy of various coastal fisheries.

Further research comparing fish assemblages in seagrass and mussel habitats is warranted as it could contribute to a better understanding of habitat use by marine species. In addition, to adequately describe fish assemblages, the selection of the sampling method(s) should be made with caution, especially when management decisions are considered. For example, equipment improvements in cameras, including the use of infrared light (IR), which allows filming in darkness, would allow recordings of the abundance and behavior of nocturnal species. Including sampling of the full diel cycle is important for

the evaluation of habitat use, because fish metabolism and behavior may be affected by circadian rhythms [96], potentially resulting in an underestimation of the fish abundances and, subsequently, the importance of the habitat [78,87,94].

5. Conclusions

In this study, we showed that seagrass meadows and mussel reefs in Øresund have a similar fish species diversity and species richness. On the other hand, fish abundance was higher in seagrass meadows as compared to mussel reefs and fish assemblages differed, suggesting that specific habitats may have different ecological and economic value. Concerning the effect of current speeds in mussel reef habitats, fish appeared largely unaffected by the observed variation in current speeds, exhibiting few differences in assemblage structure, although some commercially important species revealed higher abundances in low current mussel reefs. The information should be taken into account by policy makers when management and restoration actions are planned to protect coastal habitats and fisheries [28,45,46,75].

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