Norwegian
University of
Life Sciences

Master’s thesis 2025 45 ECTS
MINA

Mesofauna Assemblages Associated with the Introduced Seaweed *Sargassum muticum* and the Native Seagrass *Zostera marina*: A Comparative Study Across Four Eelgrass Meadows

Hanna Kristine Emhjellen Paulsen

Preface

This thesis marks the end of my master's degree in Natural Resource Management at NMBU.

I would like to thank my supervisors Eli Rinde, Kristina Øie Kvile, Camilla With Fagerli and Susanne Claudia Schneider for guidance and feedback throughout the process, and Marijana, Gunnhild and Hartvig from NIVA for assistance in identification of fauna.

I am also grateful to Hartvig and Eli for volunteering their time to look for suitable study locations, Truls Øygård for helping me in fieldwork at Drotningviga in Grimstad, and my field assistants Chloé, Alva, Rakel and Valerio for their patience and for keeping a lookout for me during fieldwork.

Hanna Kristine Emhjellen Paulsen

Ås, 14.05.2025

Abstract

Invasive habitat-forming macrophytes can alter native ecosystems directly, through competition with native macrophytes, or indirectly, by providing different habitat characteristics or supporting distinct faunal communities compared to that of the native macrophytes. *Sargassum muticum* (*Sargassum*), was previously thought unable to inhabit soft-sediment habitats, but is now found within *Zostera marina* (*Zostera*) meadows in Norway, potentially posing an additional threat to these habitats in decline. This study investigates how mesofauna assemblages differ between *Sargassum* and *Zostera* across four eelgrass meadows along a geographic gradient in the Oslofjord and Skagerrak. In July and August 2024, I sampled the macrophytes and measured habitat characteristics (fresh weight, C:N ratio). In the laboratory, I identified mesofauna (>250 μm) found on the macrophytes to set taxonomic levels.

Location was the strongest driver of faunal abundance and diversity, where location 1 had lowest diversity, linked to high dominance of juvenile bivalves and lower fresh weight of habitat-species. *Sargassum* supported higher faunal abundances overall, as well as for species groups gastropods, amphipods, and bivalves. Although habitat-species had similar taxa richness, *Sargassum* had greater richness of amphipods and gastropods, and also hosted more habitat-specific taxa, of which many are typically associated with seaweeds. However, *Sargassum* communities had lower evenness and Shannon-Wiener diversity compared to *Zostera*, reflecting dominance of a few taxa. Fresh weight was similar for the two habitat-species overall, while C:N ratio was higher for *Sargassum* but varied more across locations. The faunal responses to habitat-characteristics differed between macrophytes: for *Zostera*, abundance and diversity were best explained by fresh weight and location; for *Sargassum*, C:N ratio was the most consistent predictor, suggesting a more important role as a food source for fauna. NMDS and PERMANOVA revealed that location was the most important structuring factor for community composition, although the two habitat-species also hosted distinct faunal communities. There was also a significant interaction effect of habitat-species and location, highlighting the role of habitat-specific traits and site-specific variables in shaping mesofauna communities.

Faunal abundance in *Zostera* in this study, was lower than in meadows without *Sargassum*, suggesting that the invasion of *Sargassum* within these habitats may alter overall faunal abundance and/or distribution. If *Sargassum* continues to expand within *Zostera* meadows, its distinct faunal community, in combination with shifts in faunal abundance, could have broader ecological consequences, potentially altering trophic interactions and overall food web structure in these habitats.

Introduction

Habitat-forming macrophytes, like kelp, seaweed and seagrasses, are crucial for coastal biodiversity and ecological functioning (Edwards et al., 2020; Hemminga & Duarte, 2000; Unsworth et al., 2022). As ecosystem engineers, these macrophyte systems influence the coastal ecosystems by modifying local conditions, sedimentation rates and nutrient- and organic matter levels (Jones et al., 1994). In addition to shaping environmental conditions, these macrophytes act as miniature ecosystems in themselves, as habitats providing shelter and food for fauna, and serving as a substrate for various epibiont species (Christie et al., 2009; Wikström & Kautsky, 2004). Seagrasses are the main macrophyte species in shallow soft-sediment habitats, and in the temperate northern hemisphere, eelgrass (*Zostera marina,* hereafter *Zostera*) is the dominating species (Hemminga & Duarte, 2000; Short et al., 2007).

Zostera is a perennial marine vascular plant, with long narrow leaves – reaching up to 1cm in width and 1m in length (Sjøtun, 2025). In autumn and winter, above-ground biomass is reduced as the leaves are broken down, and in spring the leaves regrow from the rhizome embedded in the sediment (Pedersen & Borum, 1993; Sjøtun, 2025). In Norway, and along the coast of Skagerrak, *Zostera* is a common macrophyte, forming scattered populations along the coastline (Johannessen & Sollie, 1994). These meadows are highly productive habitats, both in primary and secondary production, with one study estimating the macrofaunal production rate to be 5 to 15 times greater than other estuarine habitats (Baden & Boström, 2001; Duarte et al., 2002; Heck et al., 1995). The *Zostera* plant provides a structural complex as habitat for fauna, both in the below-ground rhizome network and the above-ground biomass, supporting a unique and diverse assemblage of both sessile and mobile fauna (Boström et al., 2014; Fredriksen et al., 2005; Hall & Bell, 1988; Orth et al., 1984). These meadows are particularly important as nursery and feeding grounds for fish, including economically important taxa such as cod (*Gadus morhua),* as well as invertebrate mesofauna such as bivalves, gastropod and amphipods (Jackson et al., 2001; Pihl Baden, 1990; Pihl et al., 2006). These small invertebrates represent a diverse group and serve as a key food source for higher trophic levels, playing an essential role in the food web structure of Zostera meadows (Nelson, 1979; Solé et al., 2023; Virnstein, 1977).

Seagrass meadows are in decline globally, both in areal extent and depth distribution, with an estimated loss of 19.1% areal cover since the 1880s (Dunic et al., 2021). The rate of decline varies across and within regions, and in the Inner Oslo fjord, the lower growth limit has decreased for 67% of meadows in the region, which corresponds to an estimated loss of 57 000 m^2 (Dunic et al., 2021; Rinde et al., 2021). Threats to eelgrass ecosystems are largely driven by local anthropogenic influences, such as nutrient and sediment loading, overfishing and coastal habitat destruction (Boström et al., 2014; Vieira et al., 2020). But also more global influences linked to climate change such as increase in surface water temperature and increased intensity and frequency of storms (Orth et al., 2006). In the Skagerrak area, the main causes of the decline of eelgrass meadows are thought to be nutrient pollution and overfishing, leading to high epiphytic loads of algal species (Infantes et al., 2022). Shading from overgrowth of these epiphytic species or mats of filamentous- or macroalgae, can reduce or inhibit the growth and survival of seagrass species (Gustafsson & Boström, 2014; Hauxwell et al., 2001; Moksnes et al., 2018).

There is increased awareness of introduced habitat-forming species as stressors in native seagrass meadows (Belattmania et al., 2018; DeAmicis & Foggo, 2015; Navarro-Barranco et al., 2019; Tanner, 2011; Vieira et al., 2020). The effect of the introduced species on the overall seagrass ecosystem depends on many factors, such as its potential to modify native habitats, the biology of the species, and the state of the native habitat (Mateo-Ramírez et al., 2022). Highly eutrophicated areas, for example, favour algal growth and the presence of an introduced macroalgae may have greater impacts in such environments (Thomsen et al., 2012). The presence of introduced seaweed has generally been found to negatively affect the primary production of native seagrasses, dependent on the density of the seaweed, as well as presence of other stressors, like nutrient and sediment loading (DeAmicis & Foggo, 2015; Salvaterra et al., 2013; Thomsen et al., 2012; Vieira et al., 2020).

Change in habitat-related characteristics and macrophyte assemblage can also impact the associated fauna within these habitats, where the effect of an introduced macrophyte on native fauna can be related to competition between the native and introduced macrophyte, as well as the presence of specialist fauna or fauna-macrophyte interactions (Veiga et al., 2014; Viejo, 1999). The dissimilarity to the native macrophyte, in terms of taxonomy, morphology and biochemical composition, may also impact the associated faunal assemblages of the native habitats, for example by altered water flow regimes, predator/prey dynamics or trophic interactions (Buschbaum et al., 2006; Christie et al., 2009; DeAmicis & Foggo, 2015; Williams & Smith, 2007). Different studies have found both positive and negative effects of presence of seaweeds on faunal diversity in seagrass meadows, depending on the density of the introduced seaweed, presence of other stressors, as well as the identity of the fauna (DeAmicis & Foggo, 2015; Drouin et al., 2011; Thomsen et al., 2012; Vieira et al., 2020).

Sargassum muticum (hereafter *Sargassum*) has been described as the most successful macroalgal invader worldwide (Engelen et al., 2015). It is native to the Western Pacific but is today present across the North-Atlantic from Norway to Morocco (Belattmania et al., 2018; Engelen et al., 2015). *Sargassum* has a single stem and a heavily branched thallus, with side branches carrying pairs of small gas-filled vesicles. The thalli can grow up to 1 m long in intertidal environments, and up to 2–3 m in subtidal environments. *Sargassum* is pseudo-perennial, with a perennial holdfast which regenerates its side branches each year (Husa et al., 2023). In northern Europe, initial growth starts in spring and in autumn the branches fall off and float away carrying fertile propagules. This trait is thought to be one the reasons for its success as an introduced species, where the thalli can form large floating mats capable of spreading over long distances. In Europe, its introduction is also thought to be facilitated by "hitch-hiking" on oysters transported for cultivation purposes (Engelen et al., 2015). The first attached *Sargassum* in Norway was recorded in the late 1980's (Rueness, 1989). Today, *Sargassum* is distributed along the Norwegian coast - from the Swedish border in the South-East to Kristiansund in the North-West (Husa et al., 2023). *Sargassum* was first suggested as a potential threat to *Zostera* meadows in 1973, when found in habitats usually occupied by *Zostera* (Druehl, 1973). Studies prior to this claim suggested that *Sargassum* could not inhabit soft-substrate habitats, but required bedrock, boulders or stones larger than 10cm for attachment and therefore did not pose a threat to *Zostera* habitats (den Hartog, 1970). However, in recent years, *Sargassum* has been recorded within eelgrass meadows across northern Europe, and across the Oslo fjord and Skagerrak specifically (DeAmicis & Foggo, 2015; Rinde et al., 2022; Tweedley et al., 2008). Despite previous claims, it is able to inhabit soft-sediment habitats by attaching to substrates like small stones, shell fragments or even siphons of clams (Firth et al., 2024; White & Orr, 2011). Tweedley et al. (2008) suggests that eelgrass meadows may even facilitate establishment of *Sargassum* plants in these habitats, by trapping free-drifting *Sargassum*, and because higher sedimentation rates within the meadow enhance embedding of the *Sargassum* in the soft sediment.

As an introduced species, *Sargassum* presents a potential risk to eelgrass meadows in decline. Many studies have found a regression of local macrophyte species with the introduction of *Sargassum* in a new system, which a subsequent change in community structure of macrophytes (denHartog, 1997; Stæhr et al., 2000; Viejo, 1997). Apart from effects on *Zostera* cover, a central question in understanding the potential ecological effects of a *Sargassum* intrusion to *Zostera* meadows, is if *Sargassum* supports the same or similar diversity and faunal assemblages as *Zostera*. To my knowledge, only one study has compared the fauna assemblages associated with *Sargassum* and *Zostera* within an eelgrass meadow, but no studies have been conducted on the matter in Norway (DeAmicis & Foggo, 2015). In this study, my aim is to investigate if there are any differences in diversity and abundance of mesofauna assemblages associated to *Zostera* and *Sargassum* across four locations, as a baseline to understand the potential ecological impacts of the introduction of *Sargassum* in *Zostera* meadows. I also aim to investigate to what degree any potential differences can be explained by habitat-size and the nutritional quality of the macrophyte, and if there are any differences in these characteristics between *Zostera* and *Sargassum*. My research questions are as follows:

(1) Do habitat characteristics (i.e. fresh weight and C:N ratio) differ between *Zostera* and *Sargassum* and among locations, and how do species-specific traits such as length of thallus and leaves, as well as shoot density and leaf width of *Zostera* relate to these patterns?
(2) Does mesofauna abundance and diversity (taxa richness, Shannon-Wiener diversity and Pielou's evenness) vary between *Zostera* and *Sargassum* and among locations?
(3) Can variation in mesofauna abundance and diversity within the habitat-species be explained by the habitat characteristics (i.e. fresh weight and C:N ratio) or location?
(4) Does composition of the mesofauna community differ between *Zostera* and *Sargassum* and locations?
(5) How do habitat-species, location, and habitat-characteristics (i.e. fresh weight and C:N ratio) influence the abundance and richness of specific species groups?

Materials and Methods

Study sites

The study sites are located on a geographical gradient across the Oslo fjord and Skagerrak - from Drøbak in the North-East (NE) to Arendal in the South-West (SW) (Fig. 1). Location 1 Solbergstrand, Frogn (59.6152°N, 10.6508°E) is located in the middle Oslo fjord, and location 2 Mostranda, Færder (59.0814°N, 10.3916° E) in the outer Oslo fjord. Location 3 Stølsviga, Arendal (58.4253°N, 8.7617°E) and location 4 Drotningviga, Grimstad (58.3455°N, 8.6496°E) are located in Skagerrak.

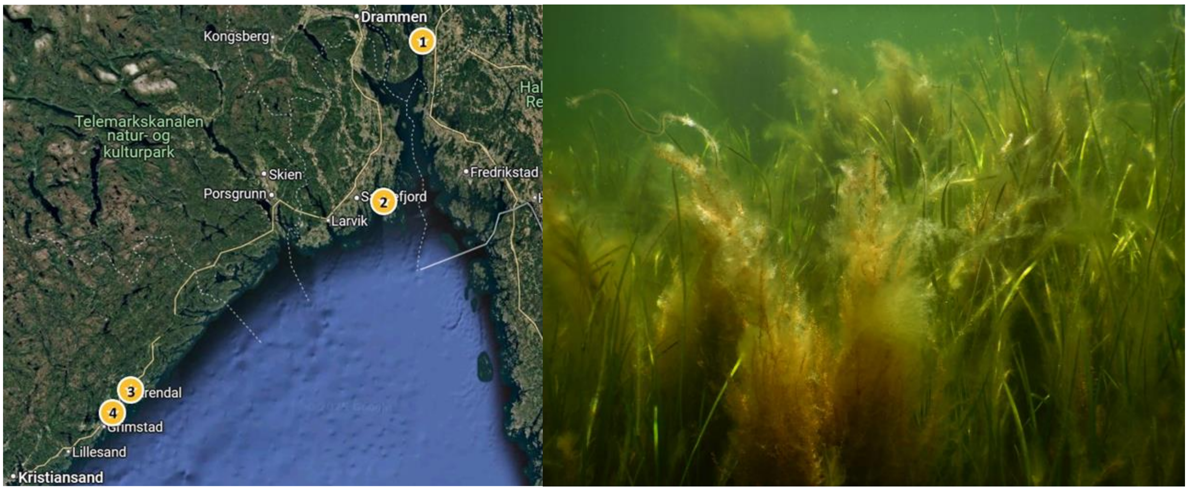

Figure 1 Map (left) with placement of the four study locations. Location 1 (Solbergstranda, Frogn), location 2 (Tjøme, Færder), location 3 (Stølsviga, Arendal) and location 4 (Drotningviga, Grimstad) (Google Maps, 2025). Photo (right) from location 2 showing side-by-side growth of Sargassum and Zostera (Rinde, n.d.).

The locations have a similar substrate with sandy bottoms mixed with small stones and shell fragments. The locations are all sheltered, however there is some variation in wave exposure – with highest exposure at location 3 and 4 (~30000), intermediate at location 1 (~15000) and lowest at location 4 (~5000) (Table 1). At location 1, there is also wave impact due to ship-traffic close by. The average temperature in the growth season is similar across locations 1, 3 and 4, with temperatures around 13°C. At location 2, temperatures are slightly higher (14.6°C). There is a shift in salinity between the inner and outer locations, with lower salinities (~26 psu) for locations 1 and 2, and higher salinities (~29 psu) at locations 3 and 4. There is also a gradient of nitrogen content – with increasing total nitrogen (mmol N/m^3) from SW to NE (location 4 to 1).

Table 1 Coordinates, collection depth and environmental variables at the four study location.

The simplified index of wave exposure (swm) is extracted from Isæus' wave exposure model (spatial resolution of model: 25x25m) (Isæus, 2004). Average temperatures (°C), salinity (psu) and nitrogen content (mmol N/m^3) are extracted from NIVAs 3D hydrographic MARTINI-800 model (spatial resolution is 800 x 800m) (Staalstrøm et al., 2022). Temperature, salinity and nitrogen content are averaged for the upper 30m of the water column and for the main growth season of Zostera and Sargassum (May-September).

Location		**Solbergstrand**	**Mostranda**	**Stølsviga**	**Drotningviga**
	no.	1	2	3	4
Coordinates		59.6152°N, 10.6508°E	59.0814°N, 10.3916° E	58.4253°N, 8.7617°E	58.3455°N, 8.6496°E
Collection depth	[m]	1.5-2.0	1.0-1.5	1.5-2.0	3.0-5.0
Exposure	grade	Protected	Highly protected	Protected	Protected
		15468	4029	30095	35624
Temperature	[°C]	12.6	14.6	12.9	13.0
Salinity	[psu]	26.54	26.46	28.81	29.24
Nitrogen content	[mmol N/m^3]	14.12	12.20	11.51	11.14

Field sampling

Sampling was conducted on July 23rd and 24th at locations 2 and 1, respectively, and on August 15th and 16th at locations 4 and 3, respectively. For locations 1, 2 and 3, I collected samples by snorkelling at low tide. At location 4, collection was done by a volunteer diver because of greater growing depths of the two habitat-species. All samples were collected within a 15m distance to the shore. For each location, I measured the collection depth of one of the samples with a ruler and estimated the depth variation across the sampling location. The sampling depth was similar across locations 1 through 3 (1-2 m), but for location 4, samples were collected at depths between 3-5m depth.

For each location, I collected 3 samples per habitat-species. Replicate samples were collected >5 metres apart, to ensure independence of replicates. *Zostera* samples were collected at least 1 m from the edges of the meadow, to avoid edge effects. *Sargassum* were haphazardly collected from within the meadow. I collected the samples using a fine mesh bag, which was lowered over the macrophytes. I then cut off the macrophytes at the base with scissors, closed the bag while still submerged and removed it from the water. All *Sargassum* samples had one single thallus per bag. To account for shoot density, *Zostera* samples were collected with the opening of the mesh bag held open by a ring of known diameter. The diameter of rings corresponded to either 0.03, 0.07 or 0.08 m^2. All shoots within the area of the ring were cut at the base and collected as one sample.

In the laboratory, I emptied each sample bag into a bucket. The inside of the bag was carefully rinsed to flush all visible animals into the bucket. I then shook the macrophyte around in the bucket filled with water by hand, and the bucket content was sieved through a 250 µm sieve. This process was repeated three times to ensure all fauna was released from the macrophytes. The fauna was preserved with a 70% ethanol solution and stored for analysis. I shook the macrophyte samples for excess water and measured the fresh weight and length of each sample. For *Sargassum* samples, the whole length of the thallus was measured. For *Zostera* samples, shoot length and width per sample was estimated over an average of three shoots. I also counted shoots per sample and calculated the shoot density according to the diameter of the ring opening of the sampling bag. To measure C and N content, I cut off three leaf-samples of *Zostera* and three samples of main- or side branches of *Sargassum*. The samples were cut off from the top of the blades, or near the top of the thallus, and frozen for analysis of dry weight and percentage carbon and nitrogen content. The samples were analysed by LabTek at NMBU, where they were dried to constant weight and analysed for C:N content using the Dumas method of analysis.

To estimate cover of filamentous algae for *Sargassum* per location, I selected a random branch of the thallus and plucked off the filamentous algae with a tweezer. I towel dried both the *Sargassum* branch and filamentous algae, weighed both separately and then calculated an average percentage cover. For *Zostera*, filamentous algae cover was visually estimated by comparison to *Sargassum* per location, because of lower filamentous algae cover as well as difficulty in separating the algae from the leaves. Apart from filamentous algae, some samples were contaminated by presence of other species than *Zostera* and *Sargassum*: many *Zostera* samples had epiphytic macroalgae present and some *Sargassum* samples had *Zostera* present. For all samples with contamination, I measured the fresh weight of the contaminant species.

Fauna identification

Because of high abundance of individuals per sample, I sub-sampled 1/8 of the faunal samples, according to NIVAs internal procedure described below. Before sub-sampling, I visually inspected samples in a tray. If any rare taxa were observed in the tray, I identified these and counted them for the overall sample. Then, I divided the tray into eight equal squares, and after mixing well and spreading the sample evenly within the tray, I chose one square at random. For the sub-sample, I identified most fauna to lowest taxonomic level possible (see paragraph below). If a taxon was counted less than 5 times in the sub-sample, I counted two squares for the specific taxon. The average of the two sub-samples was multiplied to calculate the total abundance for the sample. For all other taxa, the sub-sample was multiplied by eight to get the total abundance of the sample.

Fauna was identified with guidance from staff at NIVA, and by using the following literature for the specified taxa: amphipods, isopods, mysid shrimps and true shrimps were identified using Enckell (1980), as well as figures of amphipods from Sars (1895); brachyura were identified using Christiansen (1972); and remaining taxa were identified by Hayward and Ryland (2017) (Christiansen, 1972; Enckell, 1980; Hayward & Ryland, 2017; Sars, 1895). All oligochaetes and barnacles were identified to the subclasses “Oligochaeta indet” and “Cirripedia indet”. Chironomid larvae, halacaridae, polychaetes and stenothoidae were identified to family level. All other taxa were identified to species level where possible, however, because many individuals were juvenile or small in size, the taxonomic resolution is generally low. Nematodes, copepods, ostracods, bryozoa and foraminifera were registered as present when found in samples, but not included in analyses as the research questions are focused on mesofauna. Names of taxa were updated to the current scientific name using WoRMS Taxon match (*WoRMS Taxon match*, n.d.).

Diversity calculations

For each sample, I calculated the individual abundance and richness of taxa. As well as Shannon-Wiener diversity and Pielou's evenness. The two latter calculations are both based on natural algorithms, and Shannon-Wiener diversity incorporates both taxa richness and Pielou’s evenness (hereafter evenness). For calculation of taxa richness, taxa were presented with absence/presence in a taxa list with adjustment to avoid duplicated presence-counts of taxa within same taxonomic group. This was done by removing presence of higher taxonomic levels where a taxon was determined to two levels in one sample. For example, in a sample where both *Eualus sp.* and *Eualus pusiolus* were present, I removed the presence count of *Eualus sp.*. For samples where lowest taxon in sample is present both as unidentified and unidentified juvenile, for example polychaeta indet. and polychaeta indet. juv., then the presence of one of the categories were removed in taxa counts. I identified taxa with habitat-species specificity based on the species list, defined as those with 80% or more of counts in one habitat-species and more than 3 counts overall.

Data analyses

Because of many samples with contamination (n=11), I considered including a «mixed» category of habitat-species for samples with contamination higher than 20% of total fresh weight. However, this was difficult to include in the analyses, because of few parallels per habitat-category. Also, there was seemingly no effect of contamination on diversity indices nor abundance of individuals when investigated using linear models. Hence, I decided not to include mixed-habitat as a category in the analyses.

I used a fully crossed study design where all categories of the first factor (habitat: *Zostera* or *Sargassum*) occur in all levels of the second factor (location: 1-4). All statistical analyses were performed in RStudio (version 4.3.3) (R Core Team, 2024; RStudio Team, 2024). All continuous variables were tested for normality, using Shapiro-Wilk's test as well as with visual inspection of Q-Q plots. Non-normal data were converted to normal distribution where possible, by square (^2), cube (^3) or log- transformation. To identify potential covariation, I tested correlation for continuous variables using Pearson's correlation (if normal) or Spearman's correlation (if non-normal). Differences in diversity (i.e. Shannon-Wiener diversity, evenness and taxa richness), individual abundance, fresh weight and C:N ratio across habitat-species and locations was tested using a two-way analysis of variance (ANOVA) with and without interaction (habitat-species and location). The significance threshold for all analyses was set at $p < 0.05$. I made all graphs and boxplots using the ggplot-package from R.

All models testing the effect of predictor variables on diversity indices and individual abundance were run separately on data subsets for *Sargassum* and *Zostera* samples. Because of small sample size and non-normal distribution of variables within the subsets, I used Spearman's rank correlation to test correlation with abundance and diversity indices with fresh weight and C:N ratio. To test which predictor variables (i.e. location, fresh weight and C:N ratio) best explained variation of diversity indices and abundance, I used the dredge function from the MuMin package in R on generalised linear models. Model selection was conducted with forward and backward stepwise selection based on Akaike Information Criterion corrected for small sample size (AICc). Because of slight collinearity of C:N ratio and location in the *Sargassum* subset, I rerun all models where C:N ratio was significant, substituting C:N ratio with location and compared AIC values. The model with the lowest AIC-value was kept.

To visualize and test patterns in community composition, I performed non-metric multidimensional scaling (NMDS) and permutational analysis of variance (PERMANOVA) using the vegan package in R. To evaluate the influence of rare taxa on the multivariate structure, I created filtered taxa lists by removing taxa with fewer than 3 and 5 individuals across all samples. Stress was assessed according to the thresholds defined by Clarke (1993): stress <0.05 gives an excellent representation; stress <0.1 corresponds to a good ordination, etc. The lowest stress value was achieved for NMDS5 (taxa with fewer counts than 5 removed; stress= 0.078) compared to NMDS0 (no taxa removed; stress = 0.162) and NMDS3 (taxa with fewer counts than 3 removed; stress = 0.150). PERMANOVA was therefore performed on the NMDS5 dataset based on Bray-Curtis dissimilarities with 999 permutations. Community composition was tested for habitat-species, location, as well as habitat-species and location interaction. Ellipses representing 95% confidence intervals for centroids of groups were plotted in NMDS ordination plots.

All models testing the effect of predictor variables (i.e. fresh weight and C:N ratio) on species group richness and abundance were run separately on data subsets for *Sargassum* and *Zostera* samples. Species groups are polychaeta, amphipods, crustaceans (other than amphipods), gastropods and bivalves. Because of non-normal distributions, richness and abundance of species groups was tested with generalised linear models (GLM). Amphipod abundance showed overdispersion, and therefore a negative binomial GLM was used. To compare variance of species groups across habitat-species and locations, I used the car and emmeans packages in R, so I could perform an ANOVA-test and Tukey's post-hoc analysis on the generalised linear models. All models were tested for habitat-species and location interaction, and the type of ANOVA-test was chosen accordingly. If there was no significant interaction, I used a type 2 ANOVA-test. If interaction was significant, I used a type 3 ANOVA-test. For post-hoc analyses I used estimated marginal means analysis adjusted for Tukey for pairwise comparison. For testing the effect of C:N ratio and fresh weight on abundance and richness, I used Spearman's rank correlation test.

Results

Habitat-size and nutritional quality

For *Sargassum* – thallus length was relatively consistent across locations, with an average length of 55 cm (Fig. 2a). The average width and length of *Zostera* leaves in the study sites was 0,4cm and 44 cm respectively, with a trend of increasing width and length of leaves from NE (location 1) to SW (location 4) (Fig. 2a and 2b). Average shoot density overall was 217 ± 45 shoots per m^2. Shoot density was similar for location 1, 3 and 4, but was markedly higher at location 2 (Fig. 2c). Although not precisely determined, I observed less fouling of filamentous algae for *Zostera* (~7%) than *Sargassum*. There was also a gradient of filamentous algae cover from NE to SW – with an average of ~10%, ~15%, ~18% and ~23% cover across location 1 to 4.

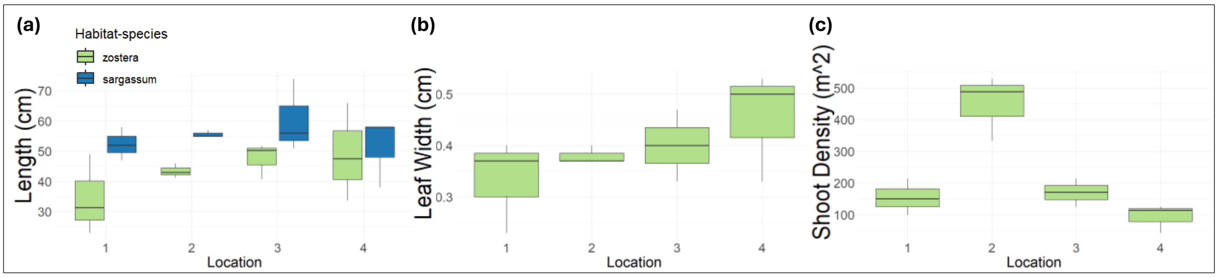

Figure 2 Morphometric measurements across site locations of (a) length of Sargassum (blue) and Zostera (green), (b) width of Zostera leaves and (c) shoot density of Zostera leaves.

Fresh weight seemed to increase slightly from NE to SW for both habitat-species, apart from fresh weight of *Zostera* at location 2 which is markedly higher and coinciding with the high shoot density at the site (Fig. 3a, see also Fig. 2c). There was no consistent size hierarchy between *Sargassum* and *Zostera* across locations. ANOVA results revealed no significant difference of fresh weight between habitat-species, locations, nor the interaction between habitat-species and location. For C:N ratio, *Sargassum* had higher values than *Zostera* for all locations except location 1 - where both habitat-species had the lowest C:N ratio, and the trend was inverted (Fig. 3b). The C:N ratios were significantly different among locations ($p = 0.003$) and there was a significant interaction between habitat-species and location ($p = 0.045$). Post-hoc analyses revealed that the difference between locations was driven by *Sargassum*, with significantly higher C:N ratios at locations 2, 3, and 4 compared to location 1 (2-1: p = 0.007; 3-1: p = 0.010; 4-1: p = 0.009).

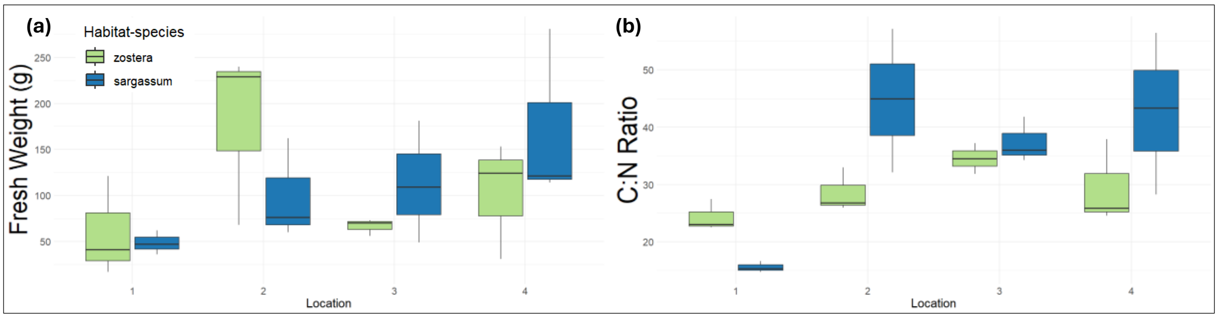

Figure 3 Boxplots of (a) fresh weight and (b) C:N ratio for Zostera (green) and Sargassum (blue) across site locations.

Mesofauna abundance and diversity

Per sample, the two habitat-species supported approximately the same taxa richness, with an average of 20 ± 3 taxa for *Sargassum,* compared to 18 ± 4 taxa for *Zostera*. In terms of individual abundance, *Sargassum* supported markedly higher average individual abundance (7400 ± 6200 individuals) than *Zostera* (2600 ± 2000 individuals) per sample.

There was an increasing trend of Shannon-Wiener diversity and evenness for *Sargassum* from NE (location 1) to SW (location 4) (Fig. 4a and 4b). ANOVA results revealed that Shannon-Wiener diversity differed significantly between locations (p < 0.001) and habitat-species (p = 0.031). Tukey's post-hoc analysis revealed that Shannon-Wiener diversity was lower for *Sargassum* (p = 0.031) and location 1 compared to locations 2, 3, and 4 (all p < 0.001). ANOVA results for evenness displayed the same pattern. Evenness differed significantly between locations (p < 0.001) and habitat-species (p = 0.007). Post-hoc comparisons showed that *Sargassum* had lower evenness than *Zostera* (p = 0.007), and location 1 had significantly lower evenness than all other locations (all p < 0.001).

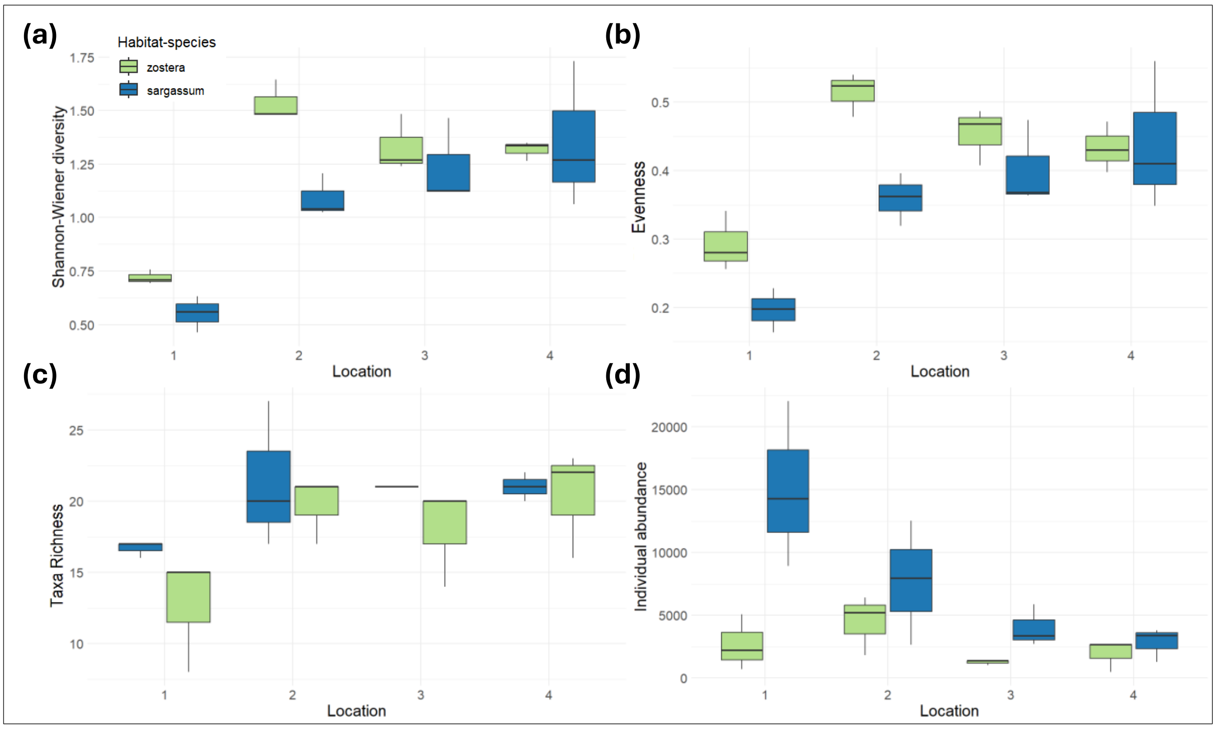

Figure 4 Diversity indices and individual abundance across Zostera (green) and Sargassum (blue) habitat-species at site locations. (a) Shannon-Wiener diversity, (b) evenness, (c) taxa richness and (d) individual abundance.

Parallel to the increasing trend of Shannon-Wiener diversity and evenness, there was a decreasing trend of individual abundance from NE (location 1) to SW (location 4) for *Sargassum* (Fig. 4d). ANOVA revealed significant differences in individual abundance between habitat-species ($p = 0.002$) and location ($p = 0.041$). Tukey's post-hoc test showed that *Sargassum* had significantly higher individual abundance than *Zostera* ($p = 0.002$). No significant pairwise differences were found between locations. Taxa richness was generally similar between habitat-species and was lowest at location 1 for both (Fig. 4c). Taxa richness varied significantly between locations ($p = 0.006$), and Tukey's post-hoc analysis indicated that location 1 had significantly lower taxa richness than the other sites (2-1: $p = 0.013$; 3-1: $p = 0.044$; 4-1: $p = 0.010$). All ANOVA models were tested for interaction between habitat-species and location; however, the interaction was not significant in any of the four models.

Effect of habitat-size, nutritional quality and location

Linear models of fresh weight and C:N ratio with diversity and abundance are shown in Fig. 5 to illustrate habitat-specific trends; however, statistical significance was assessed using Spearman's rank correlation, because of small sample size and non-normal distribution of variables. Across both habitat-species, all diversity indices showed positive trends with both fresh weight and C:N ratio (Fig. 5a and 5b). Fresh weight was significantly positively correlated with individual abundance (p < 0.001) and taxa richness (p = 0.001) for *Zostera* but showed no significant correlation with diversity indices or abundance for *Sargassum*. However, there was a bordering trend of increasing taxa richness with fresh weight for *Sargassum* (p = 0.066) (Fig. 5a). C:N ratio exhibited no significant correlation with abundance for either habitat-species. However, for *Sargassum*, C:N ratio was positively correlated with evenness (p = 0.032) and taxa richness (p = 0.045) and showed a borderline positive correlation with Shannon-Wiener diversity (p = 0.059) (Fig. 5b). No significant relationships were found between C:N ratio and individual abundance nor diversity indices for *Zostera*.

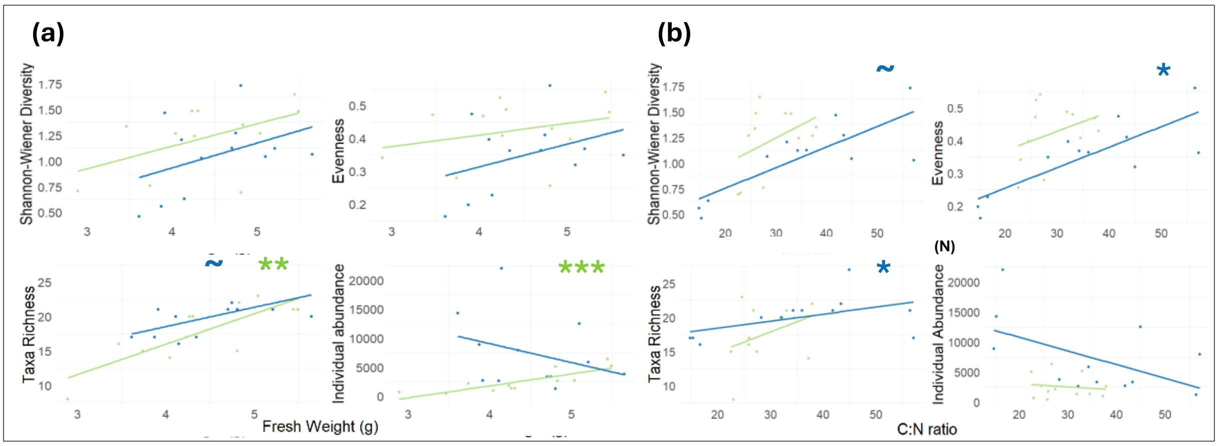

Figure 5 Scatter plots with points and linear regression models for Zostera (green) and Sargassum (blue) between (a) fresh weight (g) and (b) C:N ratio with: Shannon–Wiener diversity, evenness, taxa richness and individual abundance. Asterix (coloured for habitat-species) denote the significance of Spearman's rank correlation: p < 0.05 (*), p < 0.01 (**), p < 0.001 (***) and ~ indicates borderline significance.

According to AICc models accounting for all variables (location, C:N ratio and fresh weight), location best explained Shannon-Wiener diversity (p < 0.001) and evenness (p < 0.001) for *Zostera*, whereas fresh weight best explained taxa richness (p = 0.027) and abundance (p = 0.002). For *Sargassum*, C:N ratio best explained Shannon-Wiener diversity (p = 0.002), evenness (p = 0.003), as well as individual abundance (p = 0.019). Neither location, C:N ratio or fresh weight were kept in the *Sargassum* taxa richness model.

Community composition

The five most dominating taxa overall (across habitat-species and locations) were *Mytilus edulis*, juvenile (juv.) *Rissoa spp.*, and indetermined juvenile (indet. juv.) bivalves, gastropods and amphipods, with counts and relative abundances of respectively 43,776 (36.6%), 16,240 (13.6%), 12,864 (10.7%), 11,736 (9,8%) and 8,616 (7.2%) (Table 2). *M. edulis, Rissoa spp.* (juv.) and amphipods (indet. juv.) were among the top five most dominating taxa for both habitat-species. Including indetermined juvenile bivalves and gastropods for *Sargassum*, and barnacles (Cirripedia indet.) and *Ischyroceridae* (indet. juv.) for *Zostera*.

Table 2 Excerpt from species list for all locations, sorted by most abundant taxa. Full species list provided in Appendix I.

Species	**3-letter code**	**Habitat specificity**	**Found in locations**	**Total count**	**% of total individuals (n=119740)**	**% occurrence in samples (n=24)**
Mytilus edulis	MYT		1, 2, 3, 4	43,776	36.6	100.0
Rissoa spp. juv.	RIS		1, 2, 3, 4	16,240	13.6	100.0
Bivalvia indet. juv.	BIV	*Sargassum*	1, 2, 3, 4	12,864	10.7	58.3
Gastropoda indet. juv.	GAS	*Sargassum*	1, 2, 3, 4	11,736	9.8	100.0
Amphipoda indet. juv.	AMI		1, 2, 3, 4	8,616	7.2	87.5
Ischyroceridae indet.	ISC		1, 2, 3, 4	6,624	5.5	100.0
Aoridae indet.	AOR		1, 2, 3, 4	2,680	2.2	91.7
Cirripedia indet.	CIR	*Zostera*	1, 2, 3	2,592	2.2	54.2

Taxa specific to *Zostera* (9 in total) included *Jassa falcata* (8 individuals), Cirripedia indet. (2,592 individuals), *Myidae* indet. (1,685 individuals), *Sabellidae* indet. juv. (85 individuals), *Eualus* sp. (21 individuals), *Microdeutopus sp.* (16 individuals), *Eualus pusiolus* (5 individuals), Nudibranchia (indet. juv.) (4 individuals) and *Polybius navigator* (3 individuals). Taxa specific to *Sargassum* (15 in total) included indetermined juvenile bivalves (12,864 individuals) and gastropods (11,736 individuals), *Stenothoidae* indet. (2,305 individuals), *Nereididae* indet. (181 individuals), *Omalogyra atomus* (64 individuals), *Gammaridae* indet. (49 individuals), *Gammarus locusta* (38 individuals), *Apherusa bispinosa* (32 individuals), *Iphimedia obesa* (32 individuals), *Polychaeta* indet. (19 individuals), *Ericthonius rubricornis* (16 individuals), *Lacuna pallidula* (7 individuals), *Onoba* sp. (6 individuals), fish (*Pisces* indet. juv.) (7 individuals) and *Idotea granulosa* (5 individuals).

Juvenile *Rissoa spp.*, and indetermined juvenile gastropods and amphipods were in the top five most dominating taxa for all locations. The remaining most abundant taxa for each location is bivalves (indet. juv) and *Halacaridae* (indet.) for location 1, *Ischyroceridae* (indet. juv.) and *M. edulis* for location 2, *Corophiidae* (juv. indet) and *Stenothoidae* (indet.) for location 3, and *Bittium reticulatum and Halacaridae* (indet.) for location 4.

Non-metric multidimensional scaling (NMDS-stress = 0.078) show stronger clustering for locations than habitat-species, but with overlap between location 3 and 4 (Fig. 6b). The fauna communities associated with the two habitat-species are not entirely separated but also show distinct clustering (Fig. 6a). PERMANOVA reveal that both habitat-species (p = 0.001) and location (p = 0.001) significantly explain community composition. PERMANOVA tested for interaction habitat-species and location (p = 0.005) was also significant.

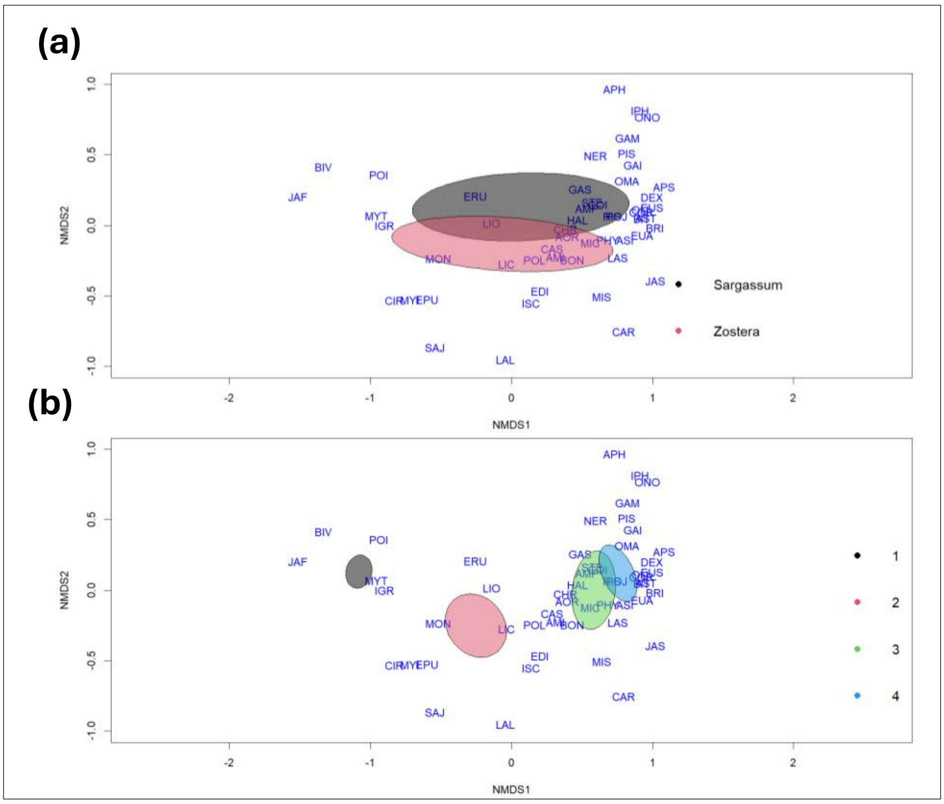

Figure 6 Non-metric multidimensional scaling (NMDS) of (a) habitat-species and (b) locations 1-4. In (a) Sargassum ellipse is black, and Zostera ellipse red. In (b) loc 1 is ellipse is represented by black colour, 2 (red), 3 (green) and 4 (blue). 3-letter codes (in blue) represent taxa, corresponding names found in species list (Appendix I).

Relative abundance of species groups showed similar patterns for the habitat-species within locations and differed more between locations than between habitat-species (Fig. 7). Relative abundance of gastropods increased from NE (location 1) to SW (location 4). Relative abundance of bivalves decreased from NE to SW, with strong dominance of bivalves in location 1. Difference between habitat-species was largest at location 2 – where the dominating species group for *Sargassum* was amphipods, while bivalves and barnacles (Cirripedia indet.) were most abundant for *Zostera* (Fig. 7a). This was also the location with largest difference in fresh weight between the two habitat-species; however, taxa richness was almost the same (Fig. 7b, see also Fig. 4).

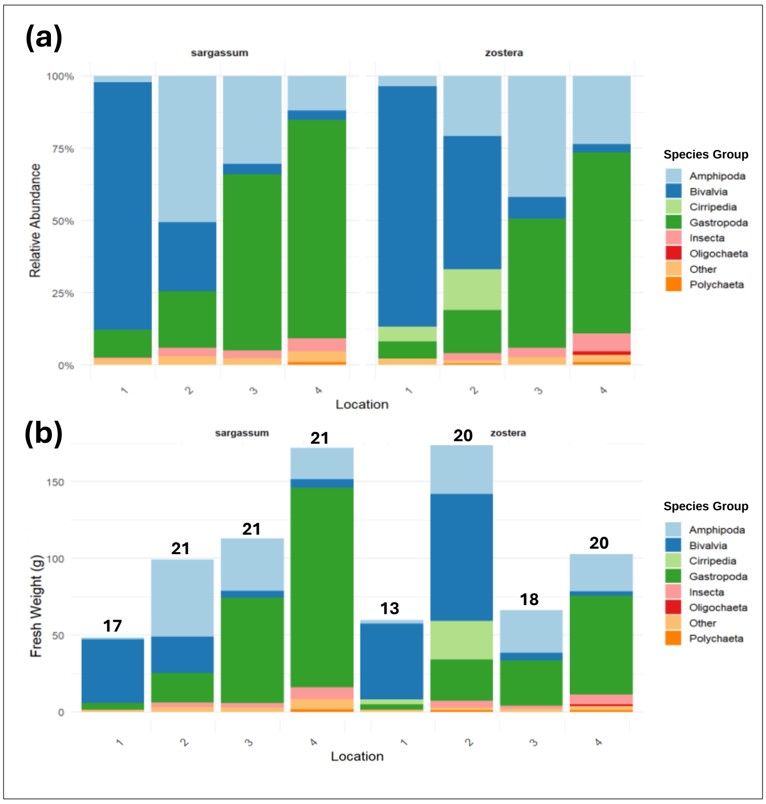

Figure 7 Bar plots showing relative abundance of main taxonomic groups (amphipoda, bivalvia, cirripedia, gastropoda, insecta, oligochaeta, other, polychaeta) for Sargassum and Zostera across site locations standardised to (a) 100% and (b) fresh weight of habitat-species. Numbers above bars represent the average taxa richness. "Other" category is all groups with less than 0.5% contribution of abundance at the specific habitat-species and location combination.

Species groups abundance and richness

Gastropod abundance increased from NE to SW, with higher abundance for *Sargassum* overall ($p = 0.002$) (Fig. 8d). Amphipod richness displayed a similar pattern, also with higher taxa richness for *Sargassum* overall ($p = 0.012$) (Fig. 9b). Amphipod ($p = 0.045$) and bivalve ($p < 0.001$) abundance was higher overall for *Sargassum* - with significantly higher abundances of amphipods for *Sargassum* at location 2 compared to location 1 and 4 (1-2: $p = 0.082$; 2-4: $p = 0.079$) and of bivalves for *Sargassum* at location 1 compared to all other locations (1-2: $p = 0.005$; 1-3: $p = 0.002$; 1-4: $p = 0.002$) (Fig. 8c and 8e).

There was a peak of crustacean (other than amphipod) abundance at location 2 for *Zostera* where the dominating taxon was barnacles (Cirripedia indet.) (Fig. 8b). Abundance of crustaceans (other than amphipods) was significant for location ($p = 0.018$), however there was no significant interaction with habitat-species and location, nor any significant pairwise comparisons between locations. Abundance of polychaeta was significantly higher at location 2 and 4 than 1 and 3 (2–1: p = 0.014; 4–1: p = 0.020; 3–2: p = 0.031; 4–3: p = 0.045) but with no clear pattern between habitat-species (Fig. 8a). Gastropod richness was higher overall for *Sargassum* (p = 0.010), with highest taxa richness found in location 3 and lowest in location 1 (3-1: p = 0.046) (Fig. 9a). Bivalve richness was generally low, but with significant difference between locations (p = 0.005), where bivalve richness at location 2 was higher compared to 3 and 4 (2-3: p = 0.026; 2-4: p = 0.026) (Fig. 9c). I found no significant variation between habitat-species, location or their interaction for polychaeta richness or crustacean (other than amphipod) richness.

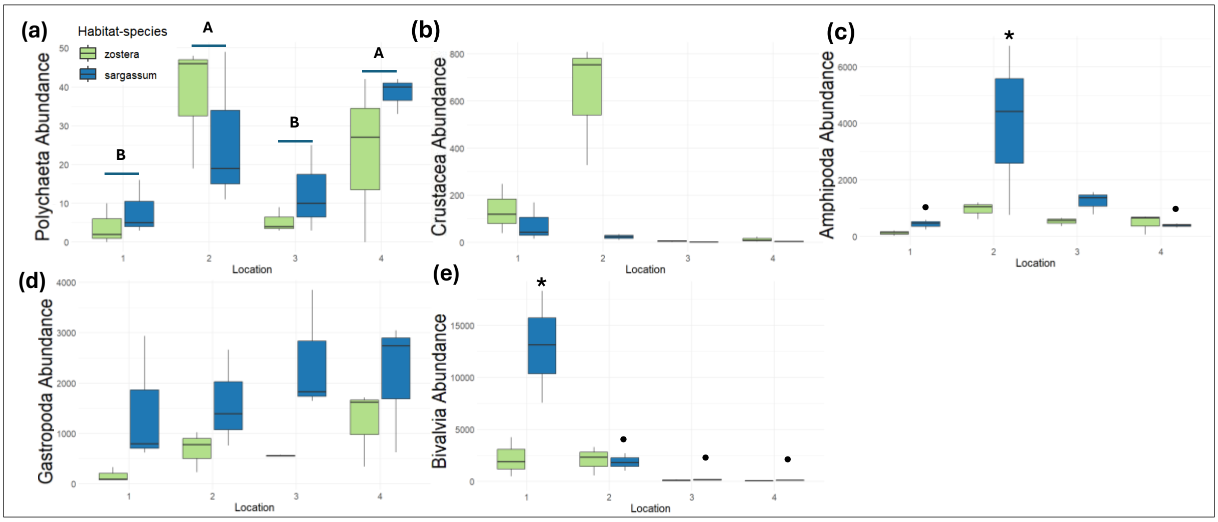

Figure 8 Species group abundances for Zostera (green) and Sargassum (blue) across site locations. Significance across locations is marked with A/B. Significance across locations within habitat-species is marked with asterix (*) and a point symbol (•). Only species groups which abundance varied significantly between either habitat-species or locations are included.

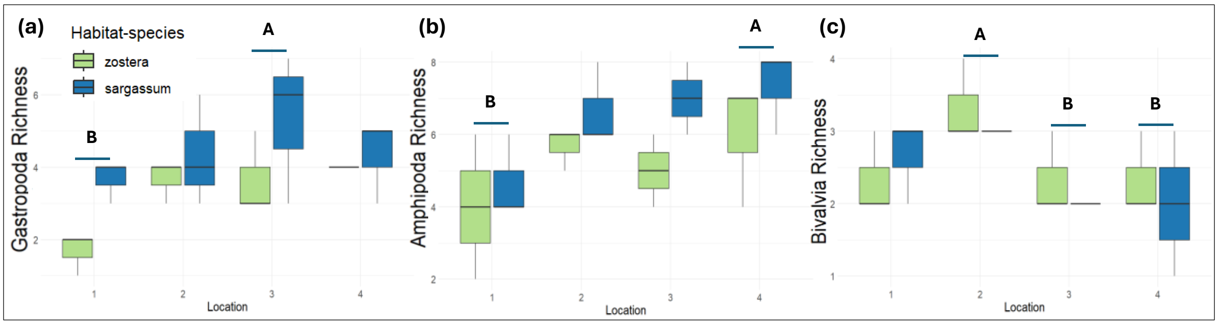

Figure 9 Species group richness for Zostera (green) and Sargassum (blue) across site locations. Significance across locations is marked with A/B. Only species groups which taxa richness varied significantly between either habitat-species or locations are included.

C:N ratio was not significantly correlated with abundance or richness for any of the species groups. Positive relationships were found between species groups abundance and richness and fresh weight for both habitat-species. Polychaeta abundance was positively correlated with fresh weight for *Sargassum* ($p = 0.007$) and *Zostera* ($p < 0.001$). However, polychaeta richness was positively correlated with fresh weight only for *Zostera* ($p = 0.021$). Amphipod abundance showed a positive correlation with *Zostera* fresh weight ($p < 0.001$), while amphipod richness was also positively correlated for *Zostera* ($p = 0.022$), and marginally so for *Sargassum* ($p = 0.063$). Gastropod abundance was positively correlated with fresh weight for both *Sargassum* ($p = 0.028$) and *Zostera* ($p = 0.005$).

Discussion

The aim of this study was to investigate the difference in faunal diversity and abundances as well as community composition between *Sargassum* to that of the native *Zostera* within eelgrass meadows, as a baseline to understand the ecological consequences of the introduction of *Sargassum* within these habitats. This is particularly important to investigate in a time where eelgrass meadows are in decline globally, as well as in the studied areas, where the introduction of *Sargassum* may pose an additional threat to *Zostera* ecosystems and the fauna associated with them (Dunic et al., 2021; Rinde et al., 2021). Here, I discuss the ecological implications of my findings considering habitat characteristics, site-specific conditions, and patterns of habitat-specific taxa.

Habitat-size and nutritional quality

There was no significant difference in fresh weight between the two habitat-species. Thallus length was similar for *Sargassum* across locations, but there was a trend of increasing fresh weight from NE (location 1) to SW (location 4), parallel to a trend of longer and wider leaves of *Zostera*. Additionally, *Zostera* showed a peak of fresh weight at location 2, which seemed to relate to the high shoot density at the site. C:N ratio was generally higher for *Sargassum*, with a significantly lower C:N ratio at location 1, where it was even lower than that of *Zostera*.

Although the fresh weight was similar between the two habitat-species, a direct comparison of fresh weight per areal unit is challenging due to their different growth forms. In this study, fresh weight of *Sargassum* was not standardised to area, as was done for *Zostera* using shoot density. This is due to difficulty in defining a sampling area given that the thallus has a large circumference, whereas the holdfast takes up a small area, and that sampling using a fixed diameter would likely have included *Zostera* shoots, confounding comparisons. Therefore, when comparing fresh weight, it is important to consider that *Sargassum* likely offers greater biomass per areal unit, related to its holdfast's small footprint within the meadow.

Time of sampling may have influenced the geographical trend of fresh weight, as locations 3 and 4 were collected a month later than locations 1 and 2. However, the effect of sampling time was not tested for in this study. Apart from sampling time, the observed patterns of fresh weight and C:N ratio may reflect species-specific growth and assimilation strategies in response to environmental conditions such as temperature, nutrient availability, tidal regime, exposure, substrate and light availability (Arenas et al., 2002; Boyé et al., 2022; Marba et al., 2004; Pedersen et al., 2005). Aboveground biomass of *Zostera* is linked to shoot density, as well as the length and width of shoots (Boyé et al., 2022). There was a trend of slight increase in fresh weight, as well as leaf length and width from NE (location 1) to SW (location 4). However, shoot density varied most – where the peak of fresh weight for *Zostera* at location 2 seems to relate to the high shoot density at the site, which was 450 shoots/m^2, compared to 170 shoots/m^2 at the next highest site (location 3). Shoot density may be driven by local environmental conditions such as higher water temperatures, which is known to enhance growth, and low exposure, which is associated with higher above to belowground allocation (Baden & Pihl, 1984; Marba et al., 2004). For *Sargassum,* biomass is correlated with both thallus length, canopy volume and branching density (Hacker & Steneck, 1990; Wernberg et al., 2001). Length was relatively consistent across locations and my findings of thalli length were shorter compared to other studies, which might relate to smaller hard-surface substrates for holdfasts within soft-sediment habitats (Sjøtun et al., 2021; Tweedley et al., 2008; Wernberg et al., 2001). While length of thalli was similar across locations, fresh weight varied (though not significantly), suggesting a difference of length to volume and/or density relationship between locations. This aligns with the findings of Sjøtun et al. (2021), who reported large variation in branching densities across sampling stations. Higher branching densities have been associated with higher exposure, which may have contributed to observed differences in fresh weight compared to length of thalli across locations (Baer & Stengel, 2010).

In terms of nutrient assimilation, the two habitat-species are morphologically and taxonomically very different. *Zostera* has the possibility of nutrient uptake both from the sediment and water phase, whereas *Sargassum* only from the water phase (Short & McRoy, 1984). The observed shift in C:N ratio at location 1, may relate to the higher total nitrogen values at the site. In low-nitrogen environments, seagrasses have a competitive advantage in nitrogen assimilation to seaweeds, as they respond more quickly to surges of nitrogen (Alexandre et al., 2017). In contrast, nitrogen uptake by *Sargassum* is favoured with high nutrient loads over time, and macroalgae generally assimilate more nitrogen compared to seagrass in such conditions (Dillon & Chanton, 2008; Incera et al., 2009).

Mesofauna abundance and diversity

Mesofauna abundance and diversity varied between both habitat-species and locations. Diversity was lowest at location 1, in terms of taxa richness, evenness and Shannon-Wiener diversity, which was related to the high dominance of juvenile bivalves at the site. Taxa richness was similar between the habitat-species, but evenness and Shannon-Wiener diversity was higher overall for *Zostera*. Individual abundance, however, was markedly higher overall for *Sargassum*.

Different studies have found both lower and higher diversity of associated fauna with *Sargassum* compared to native macrophytes, where higher diversity is usually linked to dominant taxa groups (Belattmania et al., 2018; Salvaterra et al., 2013; Thomsen et al., 2012). My findings of taxa richness for *Sargassum* were at the lower end of the range reported in previous studies from Norway but slightly exceeded values observed in Danish waters (Sjøtun et al., 2021; Wernberg et al., 2004). Abundance of individuals, however, was substantially higher than both reports, which is likely due to the smaller mesh size used in this study (0,25 mm compared to 0,5 and 1mm). For *Zostera*, individual abundance was at the lower range of previous studies, while taxa richness was markedly lower (Baden & Boström, 2001; Fredriksen et al., 2005). This gap may be explained by the high proportion of juvenile taxa, and an overall lower taxonomic resolution which may underestimate taxa richness. However, these numbers should still be comparable between the two habitat-species in this study. The lower individual abundance for *Zostera* in this study (compared to meadows with no *Sargassum* presence and same mesh size for fauna), may indicate that the co-occurrence of the two habitat-species influences the distribution and perhaps total abundance of individuals associated with a *Zostera* meadow. This aligns with the findings of DeAmicis and Foggo (2015) that found that the associated epibiota assemblages differed with the presence of *Sargassum* in species composition, but mostly in biomass distribution.

Although *Sargassum* supported slightly higher average taxa richness (20 ± 3, compared to 18 ± 4 for *Zostera*), overall taxa richness was best explained by location, with lowest richness at location 1. The low diversity (richness, evenness and Shannon-Wiener diversity) observed at location 1, likely reflects lower habitat fresh weight and reduced evenness due to dominance of juvenile bivalves (likely juvenile *M.* edulis) at the site. Their high abundance may be linked to site-specific factors such as the locations position, wave exposure, and wave impact due to nearby ship traffic. Due to the poor-swimming ability of the larvae, larval settlement is influenced by currents and passive depositional forces (Butman, 1989). The combination of high local retention of blue mussel larvae in the area, as well as the exposure and wave impact at the site, may explain the high bivalve abundances found here (Gullström et al., 2012; Gustafsson et al., 2024; Kitching, 1937; Muntz et al., 1965).

The low evenness observed for *Sargassum,* despite its similar taxa richness to Zostera, likely underlies its lower Shannon-Wiener diversity. The pattern of low evenness and high abundances may be explained by *Sargassum's* habitat architecture. Higher faunal abundances and lower evenness has been associated with branched macroalgae and bushy substrates, compared to simpler habitat-structures and macrophytes (Christie et al., 2007; Hacker & Steneck, 1990; Parker et al., 2001; Taylor & Cole, 1994). The dense branching as well as a higher observed cover of filamentous algae of *Sargassum*, can provide additional refugia and niche space for small invertebrates, increase variety of food organisms, more suitable feeding surfaces, as well as reducing wave impact (Dean & Connell, 1987; Gartner et al., 2013; Kraufvelin & Salovius, 2004; Taylor & Cole, 1994). Bivalve abundances, has also been associated with more complex habitat structures (Christie et al., 2007). This may explain the particularly high abundances of juvenile bivalves on *Sargassum* at location 1, where the difference in complexity of the two habitat-species may have been exaggerated by the low shoot density and length of *Zostera*.

Effect of habitat-size, nutritional quality and location

Variation in mesofauna abundance and diversity within each habitat-species was partially explained by habitat characteristics and location, but the strength and relevance of each predictor varied between *Zostera* and *Sargassum*. For *Zostera,* fresh weight was the most important predictor for taxa richness and individual abundance, where there was a positive correlation with both indices with fresh weight. Shannon-Wiener diversity and evenness was best described by location, which seemed to relate to the large variation in evenness across locations. For *Sargassum*, C:N ratio was the most consistent predictor, where lower C:N ratios, indicating higher nutritional quality, correlated with higher individual abundances, and the higher C:N ratios, indicating lower nutritional quality, with lower evenness and Shannon-Wiener diversity. In terms of taxa richness, no predictors were kept in the best fit model.

Abundance and diversity of fauna is generally found to increase with habitat size, which aligns with the correlation of fresh weight with *Zostera* found in this study (Christie et al., 2009; Rodil et al., 2021). However, no such correlation was found for *Sargassum*. The lack of correlation may be due to an asymptotic relationship or "saturation" effect, where biomass beyond a certain threshold does not support further increase in individuals (Sjøtun et al., 2021). Additionally, *Sargassum* fresh weight had little variation compared to *Zostera*, which may have limited the ability to observe any potential relationship between biomass and individual abundance. The lack of variation in *Sargassum* fresh weight might relate to the shorter length of thalli within soft-sediment habitats where the observed fresh weight might reflect an upper limit within these habitats.

The smaller range in C:N ratio might also be related to the lack of correlation between C:N ratio and diversity and individual abundance for *Zostera,* although C:N ratio was lower overall for *Zostera* compared to *Sargassum*. However, this relationship might also be related to the fact that the majority of small grazing invertebrates graze on epiphytes and detritus rather than the seagrass themselves because the cellulose-rich leaves make them difficult to digest (Duarte, 1990; France, 2015; Thayer et al., 1984). Although, grazers have been found to generally prefer native seaweeds over *Sargassum,* C:N ratio was the most consistent predictor, indicating a more important role of *Sargassum* as a food source for fauna within seagrass meadows. This aligns with previous studies which have found that 98% of the fauna associated with *Sargassum* are usually herbivorous (Viejo, 1999). However, the strength and significance of the relationships differed among diversity indices and statistical tests. Because C:N ratio was slightly collinear with location, the strength of correlation of C:N ratio with abundance and diversity might be exaggerated. The collinearity is due to the especially low C:N ratio values and very high abundance (mainly of juvenile bivalves) for *Sargassum* at location 1. Lower C:N ratio was consistently associated with evenness across tests which suggests that nutritional quality predominantly affects the dominance structure of the associated community. Since gastropods, bivalves and many amphipods, which are the most abundant species groups for *Sargassum* across locations, are mostly grazers, detritus-feeding or filter-feeding, the lower nutritional quality of *Sargassum* and its detritus may reduce the dominance of these groups, and consequently increase evenness (Steneck & Watling, 1982; Valentine & Heck, 1993).

Although both fresh weight (bordering on significance) and C:N ratio (significant) were both weakly positively correlated with taxa richness for *Sargassum*, neither were kept as predictors in the best fit model. These patterns suggest that other habitat-specific variables not measured or tested for in this study, may explain the variation in taxa richness associated with *Sargassum* better. Such as the previously discussed habitat-complexity (i.e. branching density or epiphytic and filamentous algae cover), which fresh weight might not accurately portray. Other variables which may explain the associated taxa richness are rate of production or nutritional quality of the macroalgal detritus, or the content of secondary metabolites which may deter grazers or settlement of larvae (Hay & Fenical, 1992; Leduc & Probert, 2009; Norderhaug et al., 2003; Williams, 1964).

Community composition

Community composition varied between both habitat-species and locations, which is consistent with findings of other studies (Buschbaum et al., 2006; Engelen et al., 2013; Sjøtun et al., 2021). Location seemed to be the most important factor in structuring the associated faunal assemblage, with a more distinct pattern of community composition between locations compared to between habitat-species within locations. It should be noted that the degree of dissimilarity between *Sargassum* and *Zostera* associated communities may have been even larger, due to the presence of *Zostera* within some *Sargassum* samples. There was also a significant interaction between habitat-species and location in PERMANOVA-analysis, which suggests that site-specific variables may exaggerate or lessen the difference between associated faunal assemblages. For example, environmental variables related to different growth or assimilation strategies in the two habitat-species, as discussed in the first section. However, these variables were not tested for in the present study.

Bivalves, gastropods and amphipods comprised most of the individuals for both habitat-species across locations, which are typically the taxa associated with *Zostera* meadows (Virnstein et al., 1984). The presence or absence of a species in a habitat, is dependent on both site-specific variables such as the primary production, exposure or sediment quality, as well as species-specific variables, such as the physiological tolerances of the taxa and distribution and settling patterns of juvenile larvae (Boström et al., 2006; Guidetti & Bussotti, 2000; Gullström et al., 2012; Heck & Wetstone, 1977; Isaksson & Pihl, 1992; Roughgarden et al., 1985; Virnstein et al., 1984). Community composition across location seemed to reflect the geographical distribution and the environmental variables across the sites. There was a closer NMDS-clustering proximity for location 1 and 2, as well as between location 2 to location 3 and 4. Location 3 and 4 has had similar community composition, with a dominance of gastropods at both locations. As well as close geographical proximity, these locations had more similar exposure, salinity, nitrogen-values and temperature. Location 1 and 2 had more different community compositions, with a dominance of bivalves at location 1, and bivalves as well as amphipods at location 2. These locations are geographically more distant and differ more in environmental variables. The difference between the locations may also be related to the large difference in *Zostera* fresh weight between sites, which has been suggested as the most important factor explaining differences in community composition between *Zostera* meadows (Attrill et al., 2000).

Though some overlap was observed, *Sargassum* and *Zostera* supported distinct faunal communities, which is consistent with the findings of other studies comparing *Sargassum* faunal communities with that of native seagrasses (Belattmania et al., 2018; DeAmicis & Foggo, 2015; Nohrén & Odelgård, 2010). The majority of taxa were not associated with one or the other habitat, suggesting that most taxa are generalist species. The small number of specialised fauna in marine compared to terrestrial systems has been linked to the dominance of generalist herbivores (Hay et al., 1990). Specialist fauna may also be generalist in terms of being associated to epiphyte growing on the macrophytes, rather than the macrophytes themselves (Armitage & Sjøtun, 2016; Viejo, 1999). Although most taxa were generalist, I found affinities of some taxa to *Zostera* and *Sargassum,* with more taxa being associated with the latter (15 compared to 9 taxa).

Some taxa may be incorrectly associated with habitat-species, because of the calculation method, the overall higher individual abundances of *Sargassum*, or limitations in sampling and identification effort. The habitat-affinities should therefore be interpreted with caution. For example, juvenile bivalves which are associated with *Sargassum* were found in very high abundances on *Sargassum* at location 1 but made up an equal proportion of relative abundances for *Zostera* at the location, and even higher relative abundances for *Zostera* at location 2. Another example is, *Jassa falcata*, which I found association to for *Zostera* but is usually associated with *Fucus serratus* when directly comparing these two habitat-species (Fredriksen et al., 2005; Nilsen, 2007). Taxa living on or within sediment, such as the bivalve *Myidae indet.*, could wrongfully be associated with *Zostera* due to upwelling of sand during sampling efforts (Tyler-Walters, 2003). Moreover, as fauna samples were sub-sampled, some associations may be due to overestimation of individual numbers.

Most species associated with *Sargassum* were gastropods and amphipods, whereas crustaceans were most typical for *Zostera* (*Cirripedia indet., Polybius navigator, Eualus sp., Microdeutopus sp. and Jassa falcata*). *Microdeutopus Gryllotalpa* has been associated with *Zostera* (Fredriksen et al., 2005; Hayward & Ryland, 2017). Several of the species associated with *Sargassum* in my studies, are typically associated with seaweeds or *Fucus serratus* specifically, such as *Lacuna pallidula, Idotea granulosa* and the amphipod taxa *Stenothoidae* and *Gammarus locusta* (Fredriksen et al., 2005; Hayward & Ryland, 2017; Southgate, 1982). Nohrén et al. (2010) also found that *F. serratus* and *Sargassum* had the most similar community composition, in terms of biomass and abundance, when compared to *Zostera* and filamentous algae. Other species with affinities to *Sargassum* in this study are typically associated with the holdfast of seaweeds, such as *Apherusa bispinosa* (Hayward & Ryland, 2017; Norderhaug et al., 2002). These findings suggest that within a *Zostera* meadow, *Sargassum* may serve a similar ecological role for fauna as *F. serratus* and other seaweeds, potentially offering a more suitable habitat for fauna typically associated with seaweeds.

The association of species with one over the other habitat-species may be related to predator-prey dynamics. Rather than choosing habitat according to macrophyte identity, invertebrate fauna has been found to choose habitats of increased complexity (due to branching or higher filamentous algae cover) which enhances survival by offering refuge from predation. (Dean & Connell, 1987; Moksnes et al., 1998; Russo, 1987). In this study, fish (*Pisces indet.*) were associated with *Sargassum*, which had the highest abundance of gastropods and amphipods, an important part of the diet for many marine predators (Vázquez-Luis et al., 2013). At the same time, high densities of vegetation can also reduce the predation success of fish (Isaksson & Pihl, 1992). The combination of higher prey availability, as well as enhanced shelter from predation, may explain the high faunal abundances, as well as the higher number of associated species on *Sargassum*.

Barnacles (*Cirripedia indet.*) were associated with *Zostera*, with a particularly high abundance at location 2. This location also exhibited the most pronounced differences in community composition between the two habitat-species, in terms of relative abundances of species groups. The higher dissimilarity between the two habitat-species at this location, might relate to the large difference in fresh weight at the site, which in turn was related to the high shoot density of *Zostera*. In addition to barnacles, *Zostera* also had high relative abundances of bivalves at this location. Filter feeders, such as these two taxa, have been found in higher abundances with higher shoot density of *Zostera* (Gullström et al., 2012). Unlike macroalgal canopies, which have been suggested to negatively affect barnacle recruitment due to reduced water flow, a more open structure such as that of *Zostera* has been found to benefits sessile filter-feeding taxa, perhaps by allowing higher water flow and transport of food particles (Beermann et al., 2013; Sjøtun et al., 2021).

Species groups abundance and richness

Species group richness and abundance were influenced by both habitat-species and location, but location was the most consistent driver of variation. Some species groups, such as gastropod abundance and amphipod richness, displayed a gradual increase across locations from NE (location 1) to SW (location 4). Other species groups displayed peaks at locations, within habitat-species, such as amphipods for *Sargassum* at location 3, and the previously discussed bivalves at location 1 for *Sargassum* and crustaceans (dominated by barnacles) for *Zostera* at location 2.

Sargassum supported higher abundance and richness for most species groups, however *Zostera* had highest abundance of crustaceans. In terms of habitat-characteristics, fresh weight was the only significant predictor, with positive correlation with some species groups for both habitat-species, but more groups correlating with fresh weight for *Zostera*.

The trend of increasing abundance and richness of some species groups across locations appears to mirror the increase in fresh weight across locations. Gastropod abundance and amphipod richness did indeed correlate positively with increasing fresh weight for both habitat-species. The trend may also be linked to the observed increase in filamentous algae cover across locations, providing more food for grazers such as gastropods, as well as increased niche space (Heck & Valentine, 2006).

Some species groups, such as polychaeta richness and amphipod abundance, only positively correlated with *Zostera* fresh weight. This aligns with the finding that fresh weight was a stronger predictor of overall abundance and diversity for *Zostera* than *Sargassum*. The stronger association with *Zostera* fresh weight and fauna might relate to it being a more stable habitat across seasons, as northern *Zostera* populations in stable environments are found to maintain a large overwintering biomass (Clausen et al., 2014; Pedersen & Borum, 1993; Törnblom & Søndergaard, 1999). In contrast, the thallus of *Sargassum* is shed every autumn, which might not give sufficient time for less mobile taxa such as polychaeta, or taxa without a larval stage, to respond to the increased fresh weight of *Sargassum* within one season (Nohrén & Odelgård, 2010). For example the polychaete genus *Sabellidae*, which are associated with *Zostera* in this study, of which some species have no larval stage (Hill et al., 2018). Although adult gastropods also have low mobility, the larval stage facilitates colonisation, which might explain the higher abundances and taxa richness associated with *Sargassum* despite its short-lived thalli (Hadfield, 1986). Other groups, such as crustaceans and amphipods, have been found to colonise new habitat more quickly, either by active swimming or passive transport with currents, and may therefore still be found in high abundances on *Sargassum* (Russell et al., 2005). Over longer timescales, however, more locally-bound species (i.e. species with no larval stage or migration into deeper waters in winter) are dependent on a stable habitat to maintain their local populations (Christie, 2025).

Interestingly, although overall diversity indices and abundance was associated with C:N ratio, no species groups were correlated with C:N ratio for either *Zostera* or *Sargassum*. This suggests that grouping species by taxonomy, may not thoroughly explain the response of fauna with increased nutritional quality. *Sargassum* has a fast biomass turnover and a large proportion of its production is found to be channelled directly into detritus pools (Pedersen et al., 2005). Lower C:N ratios may be associated with higher abundances not only of grazers, but also detritivores or filter-feeding species (Baden & Boström, 2001; Duggins et al., 1989; Walton et al., 2022). Therefore, the relationship between the C:N ratio of *Sargassum* and fauna abundance and diversity might be more apparent if fauna are grouped by functional feeding groups rather than taxonomic classifications as in this study.

Conclusion

This study highlights how both habitat-specific traits, like nutritional value and habitat-size, as well as site specific environmental conditions shape the faunal abundance, diversity and composition associated with *Sargassum* and *Zostera* within eelgrass meadows. *Sargassum* supports a different community composition to *Zostera,* with higher faunal abundances and species group richness, but lower evenness and Shannon-Wiener diversity, indicating a higher dominance of certain taxa.

The presence of *Sargassum* provides habitat heterogeneity and an additional food source within a *Zostera* meadow, offering a potentially more suitable habitat for grazers and detritus-dependent species, as well as seaweed-associated fauna. However, as the individual abundances associated with *Zostera* in this study were lower compared to studies without presence of *Sargassum*, this could suggest a potential change in distribution or overall reduction of individuals within the *Zostera* meadow. If *Sargassum* continues to expand within these habitats, this observed shift in faunal abundance, combined with its distinct faunal assemblage, could lead to shift in community composition and dominant feeding groups, potentially impacting the trophic interactions and overall food web structure associated with *Zostera* meadows.

Moreover, the short-lived *Sargassum* thalli within an eelgrass meadow, provides only a short-term habitat for fauna, potentially to the disadvantage of more locally bound species. Its presence may also indirectly impact *Zostera* and its associated fauna, by shading and reduced primary production, or inhibiting re-growth of *Zostera* where it has established its holdfast. Further studies are needed to determine the long-term effect of its presence on overall *Zostera* distribution and growth within a meadow, as well as the long-term effect on faunal community, abundance and diversity within *Zostera* meadows, particularly regarding its short-lived nature as habitat.

References

Alexandre, A., Baeta, A., Engelen, A. H. & Santos, R. (2017). Interactions between seagrasses and seaweeds during surge nitrogen acquisition determine interspecific competition. *Scientific Reports*, 7 (1). doi: 10.1038/s41598-017-13962-4.

Arenas, F., Viejo, R. M. & Fernández, C. (2002). Density-dependent regulation in an invasive seaweed: responses at plant and modular levels. *Journal of Ecology*, 90 (5): 820-829. doi: 10.1046/j.1365-2745.2002.00720.x.

Armitage, C. S. & Sjøtun, K. (2016). Epiphytic macroalgae mediate the impact of a non-native alga on associated fauna. *Hydrobiologia*, 776 (1): 35-49. doi: 10.1007/s10750-016-2707-9.

Attrill, M., Strong, J. & Rowden, A. (2000). Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography*

23: 114-121. doi: 10.1111/j.1600-0587.2000.tb00266.x.

Baden, S. P. & Pihl, L. (1984). Abundance, biomass and production of mobile epibenthic fauna inZostera marina(L.) meadows, western Sweden. *Ophelia*, 23 (1): 65-90. doi: 10.1080/00785236.1984.10426605.

Baden, S. P. & Boström, C. (2001). The Leaf Canopy of Seagrass Beds: Faunal Community Structure and Function in a Salinity Gradient Along the Swedish Coast. In, pp. 213-236: Springer Berlin Heidelberg.

Baer, J. & Stengel, D. B. (2010). Variability in growth, development and reproduction of the non-native seaweed Sargassum muticum (Phaeophyceae) on the Irish west coast. *Estuarine, Coastal and Shelf Science*, 90 (4): 185-194. doi: 10.1016/j.ecss.2010.08.011.

Beermann, A. J., Ellrich, J. A., Molis, M. & Scrosati, R. A. (2013). Effects of seaweed canopies and adult barnacles on barnacle recruitment: The interplay of positive and negative influences. *Journal of Experimental Marine Biology and Ecology*, 448: 162-170. doi: 10.1016/j.jembe.2013.07.001.

Belattmania, Z., Chaouti, A., Reani, A., Engelen, A. H., Machado, M., Serrão, E. A. & Sabour, B. (2018). The introduction of<i>Sargassum muticum</i>modifies epifaunal patterns in a Moroccan seagrass meadow. *Marine Ecology*, 39 (3): e12507. doi: 10.1111/maec.12507.

Boström, C., O'Brien, K., Roos, C. & Ekebom, J. (2006). Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. *Journal of Experimental Marine Biology and Ecology*, 335 (1): 52-73. doi: 10.1016/j.jembe.2006.02.015.

Boström, C., Baden, S., Bockelmann, A. C., Dromph, K., Fredriksen, S., Gustafsson, C., Krause-Jensen, D., Möller, T., Nielsen, S. L., Olesen, B., et al. (2014). Distribution, structure and function of Nordic eelgrass (Zostera marina) ecosystems: implications for coastal management and conservation. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 24 (3): 410-434. doi: 10.1002/aqc.2424.

Boyé, A., Gauthier, O., Becheler, R., Le Garrec, V., Hily, C., Maguer, M. & Grall, J. (2022). Drivers and limits of phenotypic responses in vulnerable seagrass populations:<i>Zostera marina</i>in the intertidal. *Journal of Ecology*, 110 (1): 144-161. doi: 10.1111/1365-2745.13791.

Buschbaum, C., Chapman, A. S. & Saier, B. (2006). How an introduced seaweed can affect epibiota diversity in different coastal systems. *Marine Biology*, 148 (4): 743-754. doi: 10.1007/s00227-005-0128-9.

Butman, C. A. (1989). SEDIMENT-TRAP EXPERIMENTS ON THE IMPORTANCE OF HYDRODYNAMICAL PROCESSES IN DISTRIBUTING SETTLING INVERTEBRATE LARVAE IN NEAR-BOTTOM WATERS. *Journal of Experimental Marine Biology and Ecology*, 134 (1): 37-88.

Christiansen, M. E. (1972). *Crustacea decapoda*. Zoologiske bestemmelsestabeller. Oslo: Universitetsforlaget.

Christie, H., Jørgensen, N. M. & Norderhaug, K. M. (2007). Bushy or smooth, high or low; importance of habitat architecture and vertical position for distribution of fauna on kelp. *Journal of Sea Research*, 58 (3): 198-208. doi: 10.1016/j.seares.2007.03.006.

Christie, H., Norderhaug, K. & Fredriksen, S. (2009). Macrophytes as habitat for fauna. *Marine Ecology Progress Series*, 396: 221-233. doi: 10.3354/meps08351.

Christie, H. (2025). *Email to Hartvig Christie, 13 February*.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18 (1): 117-143. doi: 10.1111/j.1442-9993.1993.tb00438.x.

Clausen, K., Krause-Jensen, D., Olesen, B. & Marbà, N. (2014). Seasonality of eelgrass biomass across gradients in temperature and latitude. *Marine Ecology Progress Series*, 506: 71-85. doi: 10.3354/meps10800.

DeAmicis, S. & Foggo, A. (2015). Long-Term Field Study Reveals Subtle Effects of the Invasive Alga <i>Sargassum muticum</i> upon the Epibiota of <i>Zostera marina</i>. *Plos One*, 10 (9). doi: 10.1371/journal.pone.0137861.

Dean, R. L. & Connell, J. H. (1987). Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology*, 109 (3): 249-273. doi: 10.1016/0022-0981(87)90057-8.

den Hartog, C. (1970). *The sea-grasses of the world*. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, vol. 51: North-Holland Publishing Company.

denHartog, C. (1997). Is Sargassum muticum a threat to eelgrass beds? *Aquatic Botany*, 58 (1): 37-41. doi: 10.1016/s0304-3770(97)00007-7.

Dillon, K. S. & Chanton, J. P. (2008). Nitrogen Stable Isotopes of Macrophytes Assess Stormwater Nitrogen Inputs to an Urbanized Estuary. *Estuaries and Coasts*, 31 (2): 360-370. doi: 10.1007/s12237-007-9028-1.

Drouin, A., McKindsey, C. & Johnson, L. (2011). Higher abundance and diversity in faunal assemblages with the invasion of Codium fragile ssp. fragile in eelgrass meadows. *Marine Ecology Progress Series*, 424: 105-117. doi: 10.3354/meps08961.

Druehl, L. D. (1973). Marine Transplantations. *Science*, 179 (4068): 12-12. doi: 10.1126/science.179.4068.12.

Duarte, C. M. (1990). Seagrass nutrient content. *Marine Ecology Progress Series*, 67: 201-207. doi: http://dx.doi.org/10.3354/meps067201.

Duarte, C. M., MartíNez, R. & Barrón, C. (2002). Biomass, production and rhizome growth near the northern limit of seagrass (Zostera marina) distribution. *Aquatic Botany*, 72 (2): 183-189. doi: 10.1016/s0304-3770(01)00225-x.

Duggins, D. O., Simenstad, C. A. & Estes, J. A. (1989). Magnification of Secondary Production by Kelp Detritus in Coastal Marine Ecosystems. *Science*, 245 (4914): 170-173. doi: 10.1126/science.245.4914.170.

Dunic, J. C., Brown, C. J., Connolly, R. M., Turschwell, M. P. & Côté, I. M. (2021). Long-term declines and recovery of meadow area across the world’s seagrass bioregions. *Global Change Biology*, 27 (17): 4096-4109. doi: 10.1111/gcb.15684.

Edwards, M., Konar, B., Kim, J.-H., Gabara, S., Sullaway, G., McHugh, T., Spector, M. & Small, S. (2020). Marine deforestation leads to widespread loss of ecosystem function. *PLOS ONE*, 15 (3): e0226173. doi: 10.1371/journal.pone.0226173.

Enckell, P. H. (1980). *Kräftdjur*. Fältfauna. Lund: Signum.

Engelen, A. H., Primo, A. L., Cruz, T. & Santos, R. (2013). Faunal differences between the invasive brown macroalga Sargassum muticum and competing native macroalgae. *Biological Invasions*, 15 (1): 171-183. doi: 10.1007/s10530-012-0276-z.

Engelen, A. H., Serebryakova, A., Ang, P., Britton-Simmons, K., Mineur, F., Pedersen, M. F., Arenas, F., Fernández, C., Steen, H., Svenson, R., et al. (2015). CIRCUMGLOBAL INVASION BY THE BROWN SEAWEED <i>SARGASSUM MUTICUM</i>. In Hughes, R. N., Hughes, D. J., Smith, I. P. & Dale, A. C. (eds) Oceanography and Marine Biology, vol. 53 *Oceanography and Marine Biology: An Annual Review, Vol 53*, pp. 81-126.

Firth, L. B., Foggo, A., Watts, T., Knights, A. M. & Deamicis, S. (2024). Invasive macroalgae in native seagrass beds: vectors of spread and impacts. *Annals of Botany*, 133 (1): 41-50. doi: 10.1093/aob/mcad143.

France, R. L. (2015). Feeding on the edge: δ¹³C analysis of a macrofauna food web from disappearing seagrass beds in a polluted urban harbour – implications for biomonitoring and restoration efforts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25 (1): 81-90. doi: 10.1002/aqc.2353.

Fredriksen, S., Christie, H. & Andre Sæthre, B. (2005). Species richness in macroalgae and macrofauna assemblages on<i>Fucus serratus</i>L. (Phaeophyceae) and<i>Zostera marina</i>L. (Angiospermae) in Skagerrak, Norway. *Marine Biology Research*, 1 (1): 2-19. doi: 10.1080/17451000510018953.

Gartner, A., Tuya, F., Lavery, P. S. & McMahon, K. (2013). Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *Journal of Experimental Marine Biology and Ecology*, 439: 143-151. doi: 10.1016/j.jembe.2012.11.009.

Google Maps. (2025). Google Maps.

Guidetti, P. & Bussotti, S. (2000). Fish fauna of a mixed meadow composed by the seagrasses Cymodocea nodosa and Zostera noltii in the Western Mediterranean. *Oceanologica Acta*, 23 (7): 759-770. doi: 10.1016/s0399-1784(00)01117-8.

Gullström, M., Baden, S. & Lindegarth, M. (2012). Spatial patterns and environmental correlates in leaf-associated epifaunal assemblages of temperate seagrass (Zostera marina) meadows. *Marine Biology*, 159 (2): 413-425. doi: 10.1007/s00227-011-1819-z.

Gustafsson, C. & Boström, C. (2014). Algal mats reduce eelgrass (Zostera marina L.) growth in mixed and monospecific meadows. *Journal of Experimental Marine Biology and Ecology*, 461: 85-92. doi: 10.1016/j.jembe.2014.07.020.

Gustafsson, M., Strand, Å., Laugen, A. T., Albretsen, J., André, C., Broström, G., Jorde, P. E., Knutsen, H., Ortega-Martinez, O., Sodeland, M., et al. (2024). Unlocking the secret life of blue mussels: Exploring connectivity in the Skagerrak through biophysical modeling and population genomics. *Evolutionary Applications*, 17 (5). doi: 10.1111/eva.13704.

Hacker, S. D. & Steneck, R. S. (1990). Habitat Architecture and the Abundance and Body-Size-Dependent Habitat Selection of a Phytal Amphipod. *Ecology*, 71 (6): 2269-2285. doi: 10.2307/1938638.

Hadfield, M. G. (1986). SETTLEMENT AND RECRUITMENT OF MARINE-INVERTEBRATES - A PERSPECTIVE AND SOME PROPOSALS. *Bulletin of Marine Science*, 39 (2): 418-425.

Hall, M. O. & Bell, S. S. (1988). RESPONSE OF SMALL MOTILE EPIFAUNA TO COMPLEXITY OF EPIPHYTIC ALGAE ON SEAGRASS BLADES. *Journal of Marine Research*, 46 (3): 613-630.

Hauxwell, J., Cebrian, J., Furlong, C. & Valiela, I. (2001). Macroalgal Canopies Contribute to Eelgrass (Zostera marina) Decline in Temperate Estuarine Ecosystems. *Ecology*, 82 (4): 1007. doi: 10.2307/2679899.

Hay, M. E., Duffy, J. E. & Fenical, W. (1990). Host-Plant Specialization Decreases Predation on a Marine Amphipod: An Herbivore in Plant's Clothing. *Ecology*, 71 (2): 733-743. doi: 10.2307/1940326.

Hay, M. E. & Fenical, W. (1992). Chemical mediation of seaweed-herbivore interactions. In, pp. 319-338: Oxford University PressOxford.

Hayward, P. J. & Ryland, J. S. (eds). (2017). *Handbook of the marine fauna of the North-West Europe*. Second ed. Oxford: Oxford University Press.

Heck, K. L. & Wetstone, G. S. (1977). HABITAT COMPLEXITY AND INVERTEBRATE SPECIES RICHNESS AND ABUNDANCE IN TROPICAL SEAGRASS MEADOWS. *Journal of Biogeography*, 4 (2): 135-142. doi: 10.2307/3038158.

Heck, K. L., Able, K. W., Roman, C. T. & Fahay, M. P. (1995). Composition, Abundance, Biomass, and Production of Macrofauna in a New England Estuary: Comparisons among Eelgrass Meadows and Other Nursery Habitats. *Estuaries*, 18 (2): 379. doi: 10.2307/1352320.

Heck, K. L. & Valentine, J. F. (2006). Plant–herbivore interactions in seagrass meadows. *Journal of Experimental Marine Biology and Ecology*, 330 (1): 420-436. doi: 10.1016/j.jembe.2005.12.044.

Hemminga, M. A. & Duarte, C. M. (2000). *Seagrass ecology*. Limnology and Oceanography: Cambridge University Press.

Hill, S. D., Saglam, N. & Shain, D. H. (2018). Reproduction in the Annelida. In, pp. 526-532: Elsevier.

Husa, V., M., E., Haugland, B. & Steen, H. (2023). *Phaeophyceae: Vurdering av japansk drivtang Sargassum muticum for Fastlands-Norge med havområder*. Fremmedartslista 2023: Artsdatabanken. Available at: http://www.artsdatabanken.no/lister/fremmedartslista/2023/2799 (accessed: 09.04.2025).

Incera, M., Olabarria, C., Troncoso, J. & López, J. (2009). Response of the invader Sargassum muticum to variability in nutrient supply. *Marine Ecology Progress Series*, 377: 91-101. doi: 10.3354/meps07866.

Infantes, E., Rinde, E. & Kvile, K. Ø. (2022). *Restaurering av ålegrasenger - En praktisk veileder utviklet for Oslo kommune*, 7693-2022: NIVA.

Isaksson, I. & Pihl, L. (1992). Structural changes in benthic macrovegetation and associated epibenthic faunal communities. *Netherlands Journal of Sea Research*, 30: 131-140. doi: 10.1016/0077-7579(92)90052-g.

Jackson, E. L., Rowden, A., Attrill, M., Bossey, S. J. & Jones, M. B. (2001). The importance of seagrass beds as a habitat for fishery species. In Gibson, R. N., Barnes, M. & Atkinson, R. J. A. (eds) vol. 39 *Oceanography and Marine Biology*, pp. 269-304. London: CRC Press. doi: https://doi.org/10.1201/b12588.

Johannessen, T. & Sollie, A. (1994). *Overvåking av gruntvannsfauna på Skagerrakkysten - historiske forandinger i fiskefauna 1919-1993, og ettervirkninger av den giftige algeoppblomstringen i mai 1988* In HFI (ed.). Fisken og Havet.

Jones, C. G., Lawton, J. H. & Shachak, M. (1994). Organisms as Ecosystem Engineers. *Oikos*, 69 (3): 373. doi: 10.2307/3545850.

Kitching, J. A. (1937). Studies in Sublittoral Ecology: II. Recolonization at the Upper Margin of the Sublittoral Region; with a Note on the Denudation of Laminaria Forest by Storms. *The Journal of Ecology*, 25 (2): 482. doi: 10.2307/2256206.

Kraufvelin, P. & Salovius, S. (2004). Animal diversity in Baltic rocky shore macroalgae: can Cladophora glomerata compensate for lost Fucus vesiculosus? *Estuarine, Coastal and Shelf Science*, 61 (2): 369-378. doi: 10.1016/j.ecss.2004.06.006.

Leduc, D. & Probert, P. K. (2009). The effect of bacterivorous nematodes on detritus incorporation by macrofaunal detritivores: A study using stable isotope and fatty acid analyses. *Journal of Experimental Marine Biology and Ecology*, 371 (2): 130-139. doi: 10.1016/j.jembe.2009.01.011.

Marba, N., Duarte, C. M., Alexandre, A. & Cabaço, S. (2004). How do seagrasses grow and spread? In Borum, J., Duarte, C. M., Krause-Jensen, D. & Greve, T. M. (eds) *European seagrasses: an introduction to monitoring and management*, pp. 11-18: M&MS Project.

Mateo-Ramírez, Á., Máñez-Crespo, J., Royo, L., Tuya, F., Castejón-Silvo, I., Hernan, G., Pereda-Briones, L., Terrados, J. & Tomas, F. (2022). A Tropical Macroalga (Halimeda incrassata) Enhances Diversity and Abundance of Epifaunal Assemblages in Mediterranean Seagrass Meadows. *Frontiers in Marine Science*, 9. doi: 10.3389/fmars.2022.886009.

Moksnes, P., Pihl, L. & Van Montfrans, J. (1998). Predation on postlarvae and juveniles of the shore crab Carcinus maenas:importance of shelter, size and cannibalism. *Marine Ecology Progress Series*, 166: 211-225. doi: 10.3354/meps166211.

Moksnes, P. O., Eriander, L., Infantes, E. & Holmer, M. (2018). Local Regime Shifts Prevent Natural Recovery and Restoration of Lost Eelgrass Beds Along the Swedish West Coast. *Estuaries and Coasts*, 41 (6): 1712-1731. doi: 10.1007/s12237-018-0382-y.

Muntz, L., Ebling, F. J. & Kitching, J. A. (1965). The Ecology of Lough Ine. *The Journal of Animal Ecology*, 34 (2): 315. doi: 10.2307/2653.

Navarro-Barranco, C., Muñoz-Gómez, B., Saiz, D., Ros, M., Guerra-García, J. M., Altamirano, M., Ostalé-Valriberas, E. & Moreira, J. (2019). Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga Rugulopteryx okamurae in the Strait of Gibraltar. *Biological Invasions*, 21 (11): 3319-3334. doi: 10.1007/s10530-019-02049-y.

Nelson, W. G. (1979). Experimental studies of selective predation on ampibpods: Consequences for amphipod distribution and abundance. *Journal of Experimental Marine Biology and Ecology*, 38 (3): 225-245. doi: 10.1016/0022-0981(79)90069-8.

Nilsen, H. L. (2007). *Habitattilhørighet og romlig variasjon hos mobil fauna (invertebrater) knyttet til ålegress, Zostera marina L., og sagtang, Fucus serratus L., på Skagerrakkysten*. Marinbiologi og limnologi: University of Oslo.

Nohrén, E. & Odelgård, E. (2010). Response of epibenthic faunal assemblages to varying vegetation structures and habitat patch size. *Aquatic Biology*, 9 (2): 139-148. doi: 10.3354/ab00247.

Norderhaug, K., Fredriksen, S. & Nygaard, K. (2003). Trophic importance of Laminaria hyperborea to kelp forest consumers and the importance of bacterial degradation to food quality. *Marine Ecology Progress Series*, 255: 135-144. doi: 10.3354/meps255135.

Norderhaug, K. M., Christie, H. & Rinde, E. (2002). Colonisation of kelp imitations by epiphyte and holdfast fauna; a study of mobility patterns. *Marine Biology*, 141 (5): 965-973. doi: 10.1007/s00227-002-0893-7.

Orth, R. J., Heck, K. L. & Van Montfrans, J. (1984). Faunal Communities in Seagrass Beds: A Review of the Influence of Plant Structure and Prey Characteristics on Predator: Prey Relationships. *Estuaries*, 7 (4): 339. doi: 10.2307/1351618.

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., et al. (2006). A Global Crisis for Seagrass Ecosystems. 56 (12). doi: https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2.

Parker, J., Duffy, J. & Orth, R. (2001). Plant species diversity and composition: experimental effects on marine epifaunal assemblages. *Marine Ecology Progress Series*, 224: 55-67. doi: 10.3354/meps224055.

Pedersen, M. F. & Borum, J. (1993). AN ANNUAL NITROGEN BUDGET FOR A SEAGRASS ZOSTERA-MARINA POPULATION. *Marine Ecology Progress Series*, 101 (1-2): 169-177.

Pedersen, M. F., Stæhr, P. A., Wernberg, T. & Thomsen, M. S. (2005). Biomass dynamics of exotic Sargassum muticum and native Halidrys siliquosa in Limfjorden, Denmark—Implications of species replacements on turnover rates. *Aquatic Botany*, 83 (1): 31-47. doi: 10.1016/j.aquabot.2005.05.004.

Pihl Baden, S. (1990). The cryptofauna of Zostera marina (L.): Abundance, biomass and population dynamics. *Netherlands Journal of Sea Research*, 27 (1): 81-92. doi: 10.1016/0077-7579(90)90036-g.

Pihl, L., Baden, S., Kautsky, N., Rönnbäck, P., Söderqvist, T., Max.Troell & Wennhage, H. (2006). Shift in fish assemblage structure due to loss of seagrass Zostera marina habitats in Sweden. *Estuarine, Coastal and Shelf Science*, 67 (1-2): 123-132. doi: 10.1016/j.ecss.2005.10.016.

R Core Team. (2024). *R: A Language and Environment for Statistical Computing* (Version 4.3.3). Software. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

Rinde, E., Bekkby, T., Kvile, K., Andersen, G. S., Brkljacic, M., d'Auriac, M. A., Christie, H., Fagerli, C. W., Fredriksen, S., Moy, S., et al. (2021). *Kartlegging av et utvalg marine naturtyper i Oslofjorden*. Miljødirektoratet: NIVA.

Rinde, E., Moy, S. R., Tveiten, L. A., Kvile, K. Ø., Walday, M. G., Christie, H., Stenrud, M. B., Kile, M. R., Bekkby, T., Gitmark, J. K., et al. (2022). *Feltbasert kunnskap, metodikk og kriterier for økologisk kvalitet til et utvalg av marine naturtyper*. NIVA-rapport.

Rinde, E. (n.d.).

Rodil, I. F., Lohrer, A. M., Attard, K. M., Hewitt, J. E., Thrush, S. F. & Norkko, A. (2021). Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications. *Biodiversity and Conservation*, 30 (11): 3023-3043. doi: 10.1007/s10531-021-02234-3.

Roughgarden, J., Iwasa, Y. & Baxter, C. (1985). Demographic Theory for an Open Marine Population with Space-Limited Recruitment. *Ecology*, 66 (1): 54-67. doi: 10.2307/1941306.

RStudio Team. (2024). *RStudio: Integrated development environment for R* (Version 2024.09.1). Software: Posit Software, PBC. Available at: www.posit.co.

Rueness, J. (1989). Sargassum muticum and other introduced Japanese macroalgae: Biological pollution of European coasts. *Marine Pollution Bulletin*, 20 (4): 173-176. doi: 10.1016/0025-326x(89)90488-8.

Russell, B., Gillanders, B. & Connell, S. (2005). Proximity and size of neighbouring habitat affects invertebrate diversity. *Marine Ecology Progress Series*, 296: 31-38. doi: 10.3354/meps296031.

Russo, A. R. (1987). ROLE OF HABITAT COMPLEXITY IN MEDIATING PREDATION BY THE GRAY DAMSELFISH ABUDEFDUF-SORDIDUS ON EPIPHYTAL AMPHIPODS. *Marine Ecology Progress Series*, 36 (2): 101-105.

Salvaterra, T., Green, D. S., Crowe, T. P. & O'Gorman, E. J. (2013). Impacts of the invasive alga Sargassum muticum on ecosystem functioning and food web structure. *Biological Invasions*, 15 (11): 2563-2576. doi: 10.1007/s10530-013-0473-4.

Sars, G. O. (1895). Amphipoda (Plates). In vol. 1 *An account of the Crustacea of Norway*. Christiania: ALB Cammermeyers Forlag.

Short, F., Carruthers, T., Dennison, W. & Waycott, M. (2007). Global seagrass distribution and diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology*, 350 (1-2): 3-20. doi: 10.1016/j.jembe.2007.06.012.

Short, F. T. & McRoy, C. P. (1984). Nitrogen Uptake by Leaves and Roots of the Seagrass <i>Zostera marina </i>L. *botm*, 27 (12): 547-556. doi: 10.1515/botm.1984.27.12.547.

Sjøtun, I. K. (2025). *ålegras*. In Leksikon, S. N. (ed.). Available at: https://snl.no/%C3%A5legras (accessed: 14.04.2025).

Sjøtun, K., Armitage, C. S., Eilertsen, M. & Todt, C. (2021). Fauna associated with non-native<i>Sargassum muticum</i>(Fucales, Phaeophyceae) vary with thallus morphology and site type (sounds and bays). *Marine Biology Research*, 17 (5-6): 454-466. doi: 10.1080/17451000.2021.1994999.

Solé, M., Kaifu, K., Mooney, T. A., Nedelec, S. L., Olivier, F., Radford, A. N., Vazzana, M., Wale, M. A., Semmens, J. M., Simpson, S. D., et al. (2023). Marine invertebrates and noise. *Frontiers in Marine Science*, 10. doi: 10.3389/fmars.2023.1129057.

Southgate, T. (1982). A COMPARATIVE STUDY OF LACUNA VINCTA AND LACUNA PALLIDULA (GASTROPODA: PROSOBRANCHIA) IN LITTORAL ALGAL TURFS. *Journal of Molluscan Studies*, 48 (3): 302-309. doi: 10.1093/oxfordjournals.mollus.a065652.

Steneck, R. S. & Watling, L. (1982). Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. *Marine Biology*, 68 (3): 299-319. doi: 10.1007/bf00409596.

Stæhr, P., Pedersen, M., Thomsen, M., Wernberg, T. & Krause-Jensen, D. (2000). Invasion of Sargassum muticum in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Marine Ecology Progress Series*, 207: 79-88. doi: 10.3354/meps207079.

Tanner, J. E. (2011). Utilisation of the Invasive Alga Caulerpa taxifolia as Habitat by Faunal Assemblages in the Port River–Barker Inlet Estuary, South Australia. *Estuaries and Coasts*, 34 (4): 831-838. doi: 10.1007/s12237-010-9370-6.

Taylor, R. B. & Cole, R. G. (1994). MOBILE EPIFAUNA ON SUBTIDAL BROWN SEAWEEDS IN NORTHEASTERN NEW-ZEALAND. *Marine Ecology Progress Series*, 115 (3): 271-282. doi: 10.3354/meps115271.

Thayer, G. W., Bjorndal, K. A., Ogden, J. C., Williams, S. L. & Zieman, J. C. (1984). Role of Larger Herbivores in Seagrass Communities. *Estuaries*, 7 (4): 351. doi: 10.2307/1351619.

Thomsen, M. S., De Bettignies, T., Wernberg, T., Holmer, M. & Debeuf, B. (2012). Harmful algae are not harmful to everyone. *Harmful Algae*, 16: 74-80. doi: 10.1016/j.hal.2012.01.005.

Tweedley, Jr., Jackson, E. & Attrill, M. (2008). Zostera marina seagrass beds enhance the attachment of the invasive alga Sargassum muticum in soft sediments. *Marine Ecology Progress Series*, 354: 305-309. doi: 10.3354/meps07242.

Tyler-Walters, H. (2003). *Mya arenaria*. In Tyler-Walters, H. (ed.). Marine Life Information Network: Biology and Sensitivity Key Information Reviews. Plymouth: Marine Biological Association of the United Kingdom. Available at: https://www.marlin.ac.uk/species/detail/1404 (accessed: 01.05.2025).

Törnblom, E. & Søndergaard, M. (1999). Seasonal dynamics of bacterial biomass and production on eelgrass Zostera marina leaves. *Marine Ecology Progress Series*, 179: 231-240. doi: 10.3354/meps179231.

Unsworth, R. K. F., Cullen-Unsworth, L. C., Jones, B. L. H. & Lilley, R. J. (2022). The planetary role of seagrass conservation. *Science*, 377 (6606): 609-613. doi: 10.1126/science.abq6923.

Valentine, J. F. & Heck, K. L. (1993). MUSSELS IN SEAGRASS MEADOWS - THEIR INFLUENCE ON MACROINVERTEBRATE ABUNDANCE AND SECONDARY PRODUCTION IN THE NORTHERN GULF-OF-MEXICO. *Marine Ecology Progress Series*, 96 (1): 63-74.

Vázquez-Luis, M., Sanchez-Jerez, P. & Bayle-Sempere, J. T. (2013). Does the invasion of<i>Caulerpa racemosa</i>var.<i>cylindracea</i>affect the feeding habits of amphipods (Crustacea: Amphipoda)? *Journal of the Marine Biological Association of the United Kingdom*, 93 (1): 87-94. doi: 10.1017/s0025315412000288.

Veiga, P., Rubal, M. & Sousa-Pinto, I. (2014). Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species.

Marine Environmental Research, 101: 115-123. doi: 10.1016/j.marenvres.2014.09.007.

Vieira, R., Martin, A., Engelen, A. H., Thomsen, M. S. & Arenas, F. (2020). Interactive effects of co-occurring anthropogenic stressors on the seagrass, Zostera noltei. *Ecological Indicators*, 109: 105780. doi: 10.1016/j.ecolind.2019.105780.

Viejo, R. M. (1997). The effects of colonization by Sargassum muticum on tidepool macroalgal assemblages. *Journal of the Marine Biological Association of the United Kingdom*, 77 (2): 325-340. doi: 10.1017/s0025315400071708.

Viejo, R. M. (1999). Mobile epifauna inhabiting the invasive Sargassum muticum and two local seaweeds in northern Spain. *Aquatic Botany*, 64 (2): 131-149. doi: 10.1016/s0304-3770(99)00011-x.

Virnstein, R. W. (1977). The Importance of Predation by Crabs and Fishes on Benthic Infauna in Chesapeake Bay. *Ecology*, 58 (6): 1199-1217. doi: 10.2307/1935076.

Virnstein, R. W., Nelson, W. G., Lewis, F. G. & Howard, R. K. (1984). Latitudinal Patterns in Seagrass Epifauna: Do Patterns Exist, and Can They be Explained? *Estuaries*, 7 (4): 310. doi: 10.2307/1351616.

Walton, M. E. M., Browne, R., Griffiths, J. N., Cartwright, D., Robins, P., Malham, S. K. & Le Vay, L. (2022). Kelp detritus: Unutilized productivity or an unacknowledged trophic resource? *Science of The Total Environment*, 820: 153191. doi: 10.1016/j.scitotenv.2022.153191.

Wernberg, T., Thomsen, M. S., Stæhr, P. A. & Pedersen, M. F. (2001). Comparative Phenology of Sargassum muticum and Halidrys siliquosa (Phaeophyceae: Fucales) in Limfjorden, Denmark. *Botanica Marina*, 44 (1). doi: 10.1515/bot.2001.005.

Wernberg, T., Thomsen, M. S., Staehr, P. A. & Pedersen, M. F. (2004). Epibiota communities of the introduced and indigenous macroalgal relatives Sargassum muticum and Halidrys siliquosa in Limfjorden (Denmark). *Helgoland Marine Research*, 58 (3): 154-161. doi: 10.1007/s10152-004-0180-8.

White, L. & Orr, L. (2011). Native clams facilitate invasive species in an eelgrass bed. *Marine Ecology Progress Series*, 424: 87-95. doi: 10.3354/meps08958.

Wikström, S. A. & Kautsky, L. (2004). Invasion of a Habitat-Forming Seaweed: Effects on Associated Biota. *Biological Invasions*, 6 (2): 141-150. doi: 10.1023/b:binv.0000022132.00398.14.

Williams, G. B. (1964). The Effect of Extracts of<i>Fucus Serratus</i>in Promoting the Settlement of Larvae of<i>Spirorbis Borealis</i>[Polychaeta]. *Journal of the Marine Biological Association of the United Kingdom*, 44 (2): 397-414. doi: 10.1017/s0025315400024917.

Williams, S. L. & Smith, J. E. (2007). A Global Review of the Distribution, Taxonomy, and Impacts of Introduced Seaweeds. *Annual Review of Ecology, Evolution, and Systematics*, 38 (1): 327-359. doi: 10.1146/annurev.ecolsys.38.091206.095543.

WoRMS Taxon match. (n.d.). World Register of Marine Species. Available at: https://www.marinespecies.org/aphia.php?p=match (accessed: 15.01.2025).

Appendix I

Appendix I Species list for all locations, sorted by most abundant taxa, including 3-letter code, habitat-specificity of taxa, which locations taxa are found in, total count, relative abundance (n = 119740) and percentage occurrence in samples (n = 24).

Species	3-letter code	Habitat specificity	Found in locations	Total count	% Relative abundance (n= 119740)	% Occurrence (n =24)
Mytilus edulis	MYT		1, 2, 3, 4	43,776	36.6	100.0
Rissoa spp. juv.	RIS		1, 2, 3, 4	16,240	13.6	100.0
Bivalvia indet. juv.	BIV	*Sargassum*	1, 2, 3, 4	12,864	10.7	58.3
Gastropoda indet. juv.	GAS	*Sargassum*	1, 2, 3, 4	11,736	9.8	100.0
Amphipoda indet. juv.	AMI		1, 2, 3, 4	8,616	7.2	87.5
Ischyroceridae indet.	ISC		1, 2, 3, 4	6,624	5.5	100.0
Aoridae indet.	AOR		1, 2, 3, 4	2,680	2.2	91.7
Cirripedia indet.	CIR	*Zostera*	1, 2, 3	2,592	2.2	54.2
Corophiidae indet. juv.	COI		1, 2, 3, 4	2,481	2.1	83.3
Stenothoidae indet	STE	*Sargassum*	1, 2, 3, 4	2,305	1.9	70.8
Myidae indet.	MYI	*Zostera*	1, 2, 3, 4	1,685	1.4	58.3
Lacuna sp.	LAS		1, 2, 3, 4	1,393	1.2	91.7
Halacaridae indet.	HAL		1, 2, 3, 4	1,273	1.1	87.5
Chironomidae indet.	CHR		1, 2, 3, 4	1,265	1.1	100.0
Bittium reticulatum	BIT		1, 2, 3, 4	1,019	0.9	66.7
Crassicorophium bonnellii	BON		1, 2, 3, 4	617	0.5	83.3
Cardiidae indet.	CAS		1, 2, 3, 4	430	0.4	83.3
Ericthonius punctatus	EPU		1, 2, 4	282	0.2	50.0
Littorina cf. Littorea	LIC		1, 2, 3, 4	259	0.2	66.7
Nereididae indet.	NER	*Sargassum*	1, 2, 3, 4	181	0.2	66.7
Polychaeta indet. juv.	POJ		1, 2, 3, 4	156	0.1	50.0
Monocorophium insidiosum	MON		1, 2, 3	150	0.1	25.0
Erichtonius difformis	EDI		1, 2, 3, 4	140	0.1	45.8
Oligochaeta indet.	OLI		1, 2, 3, 4	131	0.1	37.5
Microdeutopus gryllotalpa	MIC		2, 3, 4	114	0.1	37.5
Sabellidae indet. juv.	SAJ	*Zostera*	1, 2	85	0.1	25.0
Ampithoe rubricata	AMP		2, 3, 4	82	0.1	41.7
Omalogyra atomus	OMA	*Sargassum*	2, 3, 4	64	0.1	20.8
Gammaridae indet.	GAI	*Sargassum*	1, 2, 3, 4	49	0.0	16.7
Apherusa sp.	APS		4	41	0.0	12.5
Gammarus locusta	GAM	*Sargassum*	3, 4	38	0.0	20.8
Apherusa bispinosa	APH	*Sargassum*	4	32	0.0	8.3

Iphimedia obesa	IPH	*Sargassum*	4	32	0.0	8.3
Jassa sp.	JAS		2, 4	26	0.0	16.7
Littorina obtusata	LIO		1, 2, 3	25	0.0	12.5
Asteroidea indet. juv.	ASI		2, 3, 4	22	0.0	50.0
Eualus sp.	EUS	*Zostera*	4	21	0.0	8.3
Polychaeta indet.	POI	*Sargassum*	1, 2	19	0.0	16.7
Polynoidae indet	POL		1, 2, 3, 4	17	0.0	41.7
Corophium voluntator	COR		3, 4	16	0.0	8.3
Dexamine Sp.	DEX		3, 4	16	0.0	20.8
Ericthonius rubricornis	ERU	*Sargassum*	2	16	0.0	4.2
Microdeutopus sp.	MIS	*Zostera*	3	16	0.0	4.2
Asterias rubens	AST		3, 4	10	0.0	37.5
Brachyura indet. juv.	BRI		1, 3, 4	10	0.0	25.0
Jassa falcata	JAF	*Zostera*	1	8	0.0	4.2
Lacuna pallidula	LAL	*Sargassum*	2	7	0.0	8.3
Pisces indet. juv.	PIS	*Sargassum*	1, 2, 3, 4	7	0.0	20.8
Onoba sp.	ONO	*Sargassum*	4	6	0.0	8.3
Carcinus maenas	CAR		2, 3, 4	5	0.0	16.7
Eualus pusiolus	EUA	*Zostera*	4	5	0.0	4.2
Idotea granulosa	IGR	*Sargassum*	1, 2	5	0.0	8.3
Phyllodocidae indet.	PHY		3, 4	5	0.0	12.5
Nudibranchia indet. juv.	NUD	*Zostera*	4	4	0.0	4.2
Athanas nitescens	ATH		4	3	0.0	12.5
Polybius navigator	PON	*Zostera*	4	3	0.0	8.3
Praunus sp.	PRS		2, 4	3	0.0	8.3
Brachyura larvae indet.	BRL		3	2	0.0	8.3
Caridea indet. juv.	CAI		4	2	0.0	4.2
Idotea pelagica	IPE		3	2	0.0	4.2
Nassarius reticulatus	NAS		3	2	0.0	8.3
Paguridae indet.	PAG		3, 4	2	0.0	8.3
Phoxocephalidae indet.	PHO		4	2	0.0	4.2
Sabellidae indet.	SAB		1, 3	2	0.0	8.3
Apohyale prevosti	APO		1	1	0.0	4.2
Ascidiacea indet. juv.	ASC		2	1	0.0	4.2
Chiton indet.	CHI		4	1	0.0	4.2
Haliclystus sp.	CLY		3	1	0.0	4.2
Crangon crangon	CRA		2	1	0.0	4.2
Goobidae indet. juv.	GOB		4	1	0.0	4.2

Hemiaclis ventrosa	HEM	3	1	0.0	4.2
Hippolyte varians	HIP	4	1	0.0	4.2
Idotea balthica	IBA	3	1	0.0	4.2
Idotea sp.	IDS	3	1	0.0	4.2
Iphimedia sp.	IPS	3	1	0.0	4.2
Jaera sp.	JAE	2	1	0.0	4.2
Lacuna parva	LAR	4	1	0.0	4.2
Lacuna vincta	LAV	2	1	0.0	4.2
Littorina littorea	LIL	2	1	0.0	4.2
Musculus sp.	MUS	2	1	0.0	4.2
Orbiniidae indet.	ORB	4	1	0.0	4.2
Palaemon adspersus	PAL	3	1	0.0	4.2
Palaemon sp.	PAS	3	1	0.0	4.2
Philocheras trispinosus	PHI	2	1	0.0	4.2
Platyhelminthes indet.	PLA	1	1	0.0	4.2
Platyhelminthes indet. juv.	PLJ	3	1	0.0	4.2
Pomatoschistus pictus	POM	1	1	0.0	4.2
Praunus inermis	PRA	4	1	0.0	4.2
Pycnogonida indet.	PYC	2	1	0.0	4.2
Veneridae indet.	VEN	4	1	0.0	4.2

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway