MASTER THESIS

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BI309F MSc in Marine Ecology

A comparison of the associated fauna of habitats of seagrass (*Zostera marina* L.), macroalgae (*Fucus* spp.) and bare sediment in a subarctic fjord in northern Norway

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Sofie Gundersen

Abstract

This study compares abundance, species richness and community composition of associated fauna in habitats of seagrass (*Zostera marina* L.), macroalgae (*Fucus* spp.) and bare sediment, at three different sites in a subarctic fjord in northern Norway. Epifauna, infauna and mobile mesopredators were sampled at three seagrass meadows with patches of *Fucus* and bare sediment. The locations Røvika and Juvika shared environmental characteristics, such as coarse sediment and high salinity, while Valnesfjorden had softer sediments and relatively low salinity. Epifauna abundance and species richness were higher in *Fucus* habitats than in *Zostera* habitats at all sites. Infauna abundance and species richness were higher in vegetated meadows compared to bare sediment. However, infauna species and abundances varied greatly across habitats and sites, with the highest values found at Valnesfjorden. Community composition analyses showed strong groupings of *Zostera* and *Fucus* habitats across sites for epifauna, while the infauna communities showed more clustering among sites than among habitats. Mesopredator species richness was higher in vegetated habitats than on bare sediment. Overall mesopredator abundance was largely driven by one species (*Gasterosteus aculeatus*) at one location (Valnesfjorden). Excluding the effect of this species, mesopredator abundance was higher in vegetated habitats, with no difference between *Zostera* and *Fucus*. Differences in abundance and species richness of epifauna between *Fucus* and *Zostera* are likely driven by the different physical architecture of the vegetation, while belowground structures (*Zostera* root-rhizomes) had no general effect on infauna. Rather, aboveground vegetation per se increased their abundance and species richness. I conclude from the study that vegetated habitats support higher abundances and species richness´s than unvegetated habitats.

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1. Introduction

Seagrasses and macroalgae are important ecosystem engineers in the subtidal zone, physically modifying, maintaining and creating habitats by altering biotic and abiotic materials, supporting a wide range of associated fauna (Christie et al., 2009; Eklöf et al., 2015; Jones et al., 1997). Vegetation provides multifunctional structures to an otherwise structureless environment (Boström & Bonsdorff, 1997; Christie et al., 2009; Heck et al., 1989). The seagrass leaves and macroalgae canopy slow down the water current, enhance sediment accretion and increase the silt content of the sediments (Bos et al., 2007; Boström & Mattila, 1999; Orth et al., 1984). These structures are important to the productivity of the subtidal zone, enhancing the success of the associated fauna as they rely on the trophic interactions within these systems (Alfaro, 2006; Christie et al., 2009; Thormar et al., 2016). The vegetation provides shelter from predators and acts as a nursery habitat for mobile fauna (Duarte et al., 2002; Heck Jnr et al., 2003).

Seagrass beds houses a wide range of fauna, from deposit feeders and grazers, to scavengers and predators, utilizing the vegetation all through its lifecycle (Alfaro, 2006). The physical architecture and lifespan of the vegetation are of great importance to the system, as different vegetation structures have been found to house different species and community compositions (Edgar, 1990). The seagrass leaves are thin and elongated, and will be renewed several times trough the season, while the extensive root-rhizome system may persist for years (Christie et al., 2009; Pinnerup, 1980). The root-rhizomes stabilize the sediments, and provide shelter for infauna species through preventing predator's access to the prey species in the sediments (Boström et al., 2006; Orth et al., 2006; Orth et al., 1984). The three-dimensional canopy of macroalgae has a large surface area, and protects the associated fauna from dehydration through providing a moist shelter underneath the canopy as it gets exposed to air and irradiation at low tide (Christie et al., 2009; Eriksson & Johansson, 2003; Orth et al., 1984).

Vegetated sediments possess higher species diversities than adjacent unvegetated sediment, and an increase in habitat heterogeneity increases the abundances and species richness of the habitat (Bologna & Heck, 1999; Boström & Bonsdorff, 1997; Edgar & Robertson, 1992; González‐Ortiz et al., 2016; Lewis III & Stoner, 1983; Stoner, 1980). Thus, seagrass beds with patches of macroalgae will host higher numbers of species and abundances than a seagrass bed without. An investigation by Klumpp and Kwak (2005) revealed that polychaetes, amphipods, decapods, and in some cases molluscs, were the dominant macrofauna groups in seagrass beds, regardless of location and climate. Investigations from the southern part of Norway comparing the associated epifauna in habitats of seagrass (*Zostera marina* L.) and macroalgae (*Fucus serratus* L.), found that macroalgae are inhabited by larger individuals of gastropods, amphipods and isopod than those inhabiting seagrasses, while seagrasses showed a higher species diversity than macroalgae (Fredriksen & Christie, 2003; Fredriksen et al., 2005)

Organisms inhabiting the coastal zone are exposed to continuous change throughout the day, and must be able to tolerate fluctuating abiotic stress such as tidal changes, air exposure, water turbidity, nutrient input, salinity, temperature and light availability (Boström et al., 2014; Raffaelli & Hawkins, 1996). As a primary producer, the depth distribution and complexity of seagrass beds are affected by light availability (Duarte, 1991; Krause-Jensen et al., 2003). The light availability of the subarctic regions varies greatly through the season, from no sunlight midwinter, to 24hours of sunlight midsummer, making the growing season of seagrasses in subarctic systems short. Even small changes in light availability and temperature may have major effects on seagrass growth, thus affecting the whole ecosystem (Olesen et al., 2015), as an increase in shoot length increases the surface area and biomass of the seagrass.

Investigations comparing epifaunal (Fredriksen et al., 2005) and infaunal (Fredriksen et al., 2010) diversities in habitats of *Z. marina* and *F. serratus*, as well as the infaunal diversity of habitats of *Z. marina* compared to bare sediment habitats (Fredriksen & Christie, 2003), has been conducted at several locations in the southern, and at one location at the western part (64°N) of Norway. These studies were conducted at depths of 2-5 meters through SCUBA diving at several occasions from April to November, and found higher abundances and species richness´s for both epifauna and infauna in habitats of *Z. marina,* than in habitats of *F. serratus* and bare sediment. No similar studies have been published from the northern part of Norway, where the environmental conditions are somewhat harsher. The water temperatures are lower, and the light availability fluctuates between two extremes. This leads us to the overall objective of this study, to assess the associated fauna of assemblages of *Z. marina, Fucus* spp. and bare sediment habitats at different locations in a subarctic fjord. The specific research questions were:

i. Do infauna, epifauna and mobile mesopredators differ among habitats (*Z. marina* vs. *Fucus* spp. vs. bare sediment) in terms of abundance, species richness and community composition?
ii. Are these differences consistent across locations (within location vs. between location variability)?

2. Materials and methods

2.1. Study locations

This study was conducted at three locations in Skjerstadfjorden: Røvika, Valnesfjorden and Juvika, in the summer of 2016 (Fig. 1, Table 1). The requirement for the locations was the presence of seagrass beds with patches of *Fucus* spp. and bare sediment. The habitat requirement were a size >1m^2, and due to this the plots were semi-randomly chosen.

Figure 1. Overview of Skjerstadfjorden and the study locations (red dots) (Norgeskart, 2016)

Table 1.Characteristics of the study locations (Miljødirektoratet, 2011a, 2011b, 2011c, 2014)

	Røvika	**Valnesfjorden**	**Juvika**
Geographical location	67.2724°N 15.2347°E	67.2910°N 15.1647°E	67.1904°N 14.9472°E
Location in Skjerstadfjorden	Klungsetvika	Valnesfjorden	Misværfjorden
Coverage *Z. marina* bed	24 000 m^2	60 000 m^2	4 900 m^2
Description of the *Z. marina* bed	A small, medium dense bed with tall plants	A dense, medium big solid bed with tall plants	A small, patchy bed with average sized plants
Depth limit *Z. marina*	~6m	~4m	~4.5 m
Fucus specie	*F. serratus*	*F. vesiculosus*	*F. serratus*

2.2. Sampling

Epifauna, infauna and mobile mesopredators were sampled in each habitat at each location, together with measurements of environmental parameters and sediment composition. Both epifauna and infauna were sampled five times at each location, resulting in 10 (*Fucus* and *Zostera*) and 15 (*Fucus, Zostera* and bare sediment) samples per site respectively. The mesopredators was sampled through n trap deployments with three traps being deployed in each habitat at each location, resulting in n*9 samples per site.

The fieldwork was conducted from the mid June until the mid July 2016. Røvika was the first location to be sampled, followed by Valnesfjorden and lastly Juvika (Fig 2.). The sampling was performed while snorkelling at low tide (Table 2).

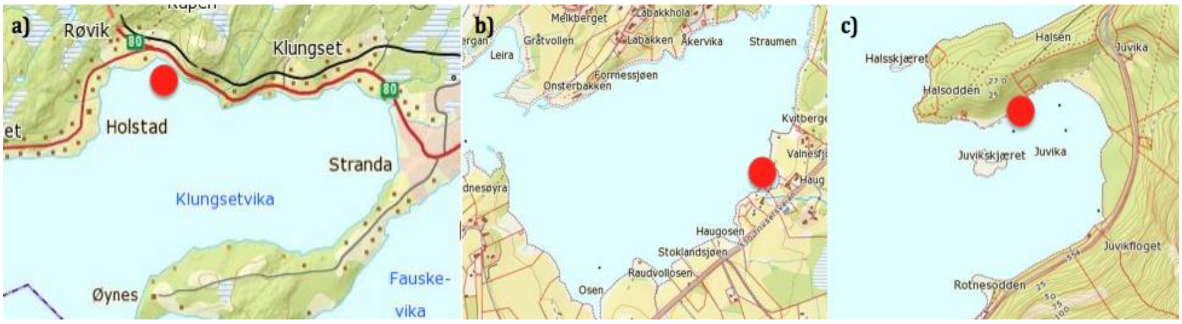

Figure 2. Location of study site (red circle) at a) Røvika, b) Valnesfjorden & c) Juvika (Kartverket, 2016)

2.2.1. Epifauna

The epifauna was collected by placing a cylinder (d=30 cm, h=30 cm), with a meshed bag (200 μm) attached, down in the selected plot and carefully cutting all the vegetation inside the cylinder loose from the sediments. The meshed bag was removed from the cylinder under water and closed for transport. At Mørkvedbukta research station, the samples were washed, sieved through a sieve with mesh size of 1 mm, fixed in 4% formaldehyde and stored for 3+ weeks. After which, the individuals were identified down to the lowest possible taxonomic level (Appendix A, Table i & Appendix B) and transferred to 70% ethanol for preservation. All the species in this thesis were determined according to World Register of Marine Species (WoRMS) (http://www.marinespecies.org/).

To determine the biomass of the sampled vegetation, the vegetation was spun 30 times in a salad spinner in order to remove the remaining water before weighing (Appendix A, Table iii). In order to record highly abundant sessile fauna on the macroalgae, a subsample from each of the *Fucus* samples was collected. Each subsample was weighted, and the individuals were identified and counted (Appendix A, Table ii). Unfortunately, the *Fucus* subsamples were discarded before the phylum Bryozoa could be further identified down to species level.

2.2.2. Infauna

Infauna samples were collected using a plastic corer (h=50 cm, d=10 cm). The plastic corer was pushed down in the sediment to a depth of 20-30cm and a lid was placed on the top of the corer to create vacuum, in order to extract the entire core without loosing any material. The samples were transferred from the corer to a plastic bag for transportation. At Mørkvedbukta research station, the samples were rinsed over a 1mm sieve, and fixed in 4% formaldehyde for 3+ weeks. After which, the formaldehyde was washed out of the samples in a 1 mm sieve, with a 0.5 mm meshed sieve placed underneath the upper sieve, in order to collect material smaller than 1 mm. The 0.5 mm fraction was saved, but not further processed. The 1 mm fraction was stained with "Rose Bengal" to make sorting of the fauna easier, and sorted. The fauna was identified down to the lowest possible taxonomic level and put on 70% ethanol for preservation (Appendix A, Table iv).

Additionally, the abundance of *Arenicola marina*, an ecosystem engineering annelid, in the seagrass beds was recorded through the use of quadrats. A quadrat (50*50 cm) was put down at each plot, and every faecal cast inside the quadrant was recorded. Each cast was considered to represent one individual.

2.2.3. Mobile mesopredators

Mobile mesopredators were recorded by randomly placing three minnow traps, with three pieces of dog food as bait, in each habitat for 24 hours. The caught fauna was identified down to species level before being released back into the fjord (Appendix A, Table v). Due to lack of time and equipment, the amount of trap deployments varied between the locations. At Røvika traps were deployed on 11 days, at Valnesfjorden on 10 days and at Juvika on four days.

Seagrass shoot density

Shoot density of *Z. marina* within the *Zostera* habitats was measured by using the same counting frames as for *A. marina*. However, the shoot densities were very high, and therefore only ¼ of the quadrat was counted in each plot at each location. At Juvika, two counts per replicate were made.

2.2.4. Environmental parameters

Salinity and temperature were measured by the use of a CTD recorder (SAIV SD204 CTD profiler), which was held approximately 30 cm above the seabed for 10 seconds. Three parallel measurements were conducted, covering the entire study area. The environmental data was collected at two different dates, in order to account for variations. The water depths at each plot was measured at low tide, and adjusted according to recordings by Kartverket (2016) at the same date and time.

Sediment samples were collected from each plot, except for four plots where the position of the original sample could not be recognised anymore. The upper 5 cm of the sediment were sampled with a 20 ml syringe. At each plot, two sediment samples were collected, merged in a plastic bag and frozen at -20ºC for preservation. Continued processing consisted of sieving each sample through a sieve cascade by wet sieving, separating the sediment into seven size fractions; 2000 µm, 1000 µm, 500 µm, 250 µm, 125 µm, 63 µm and <63 µm. Each fraction was dried at 85 ºC for three days before weighing. The sediment analysis was performed through the use of GRADISTAT, a particle-size analysis software (Blott & Pye, 2001).

2.3. Statistical analysis

Univariate measurements and analysis

Abundance, species richness as well as the environmental parameters (temperature, salinity) were tested for significant differences across habitats, locations and their interaction through Analysis of Variance (ANOVA) or Generalized Least Square model (GLS).

Prior to the analysis, a Shapiro-Wilk normality test, and a Fligner-Kileen test for homogeneity of variance were applied, in order to check whether the assumptions for a parametric test (normal distribution and homogeneity of variance) were fulfilled or not. For the data that met the assumptions for a parametric test, an ANOVA was applied. If the ANOVA gave significant p-values on one or more of the tested effects (habitat, location, habitat x location), a post-hoc test using the method Tukey for pair-wise comparison of the means was applied in order to test the single levels of each effect against each other. For data exhibiting large heterogeneity of variance, a Generalised Least Square model (GLS) using the nlme package (Pinheiro et al., 2015) was applied, with the location, habitat and their interactions as predictors and species abundance and richness as response variables, similar to the ANOVA. The univariate analyses were performed through the statistical program R (RStudio Team, 2015).

Multivariate analysis

The multivariate statistical analysis were performed in PRIMER v6 (Clarke & Gorley, 2006). In order to decrease the influence of the most abundant species, the count data was square root transformed prior to analysis, and the Bray Curtis similarity index was applied (Bray & Curtis, 1957). The community composition was tested for significant differences between habitats within locations as well as between habitats at different locations through analysis of similarities (ANOSIM). A similarity percentage analysis (SIMPER) was applied to the data in order to identify the species, which contributed the most to the dissimilarities between the habitats. A non-metric multidimensional-scaling (nMDS) ordination plot (100 restarts) was created to visualize the differences habitats and locations with all replicates.

3. Results

3.1. Environment

The salinity was considerably higher at both Røvika and Juvika (on average 21.4 and 29.2 psu respectively) than in Valnesfjorden (on average 8.3 psu), and varied strongly with the tidal cycles. The temperature at all sites varied between 11.5 °C (Juvika) and 16.2°C (Valnesfjorden). The water level ranged from on average 132 cm (Juvika) to 154 cm (Valnesfjorden) at low tide.

The sediment at Røvika and Juvika was relatively similar, and consisted mostly of sand (mean = 96.6%) with small contributions of gravel and mud in all three habitats. In contrast, the sediment at Valnesfjorden contained higher proportions of mud (mean = 15.9%), and less sand (mean = 83.5%). Comparing sediment composition of vegetated habitats only, *Zostera* habitats contained on average more sand (mean = 93.5%) and less mud (mean = 6.2%) than the *Fucus* habitats (mean = 89% and 8.7%), while *Fucus* habitats contained more gravel (mean = 1.8%). In addition to the quantified sediment composition, a clay layer of 10-15cm in the infauna cores was observed at Røvika only, which was not reflected by the sediment analysis based on samples taken from the upper 5 cm.

Z. marina mean shoot densities varied from 410 $\pm$ 90 shoots m^{-2} at Juvika, to 528 $\pm$ 110 shoots m^{-2} at Valnesfjorden.

Table 2. Mean and standard deviation of environmental parameters, water depth and sediment structure (n = 3), *Z. marina* shoot densities (n = 5, shoot m^{-2}) and *A. marina* abundance (n = 5, Ind. m^{-2}) at each location and habitat.

		Røvika			Valnesfjorden			Juvika		
Salinity (psu)		16.2			2.7			29.2		
		26.5			13.8			29.1		
Temperature (°C)		13.8			15.6			11.5		
		13.5			16.2			11.5		
		Zostera	***Fucus***	**Bare sediment**	***Zostera***	***Fucus***	**Bare sediment**	***Zostera***	***Fucus***	**Bare sediment**
Water depth	cm	137±7	152±22	139±2	156±5	166±9	139±25	127±3	119 ±3	149±4
Sediment (%)	Gravel	0	4.3±4	0.7±1.3	0.7±0.4	0.9±0.1	0.2±0.2	0.1±0.1	0.2±0.4	0
grain size	Sand	98.7±0.3	93.6 ±4.4	98.1±1.4	84.7±4.1	77.8±3.4	87.9±8.2	97.2±0.7	97.1 ±0.8	96.4±1.2
	Mud	1.3±0.3	2.1±0.6	1.2±0.2	14.6±3.9	21.3±3.4	11.9±8	2.7±0.7	2.7±0.7	3.6±1.2
A. marina	Ind. m^{-2}	36±7	0	36±12	4±4	0	6±5	22±5	0	22±5
Z. marina shoot density	Shoots m^{-2}	416±105			528±110			410 ±90		

3.2. Benthic fauna

3.2.1. Abundance and species richness

Epifauna

Habitat had a strong effect on epifauna abundance (ANOVA, F = 86.54, p < 0.0001, Table 3), while location did not (ANOVA, F = 0.21, p = 0.8145). However, the habitat effect on epifauna varied among sites (ANOVA, Habitat:Location, F = 9.71, p = 0.0008). The epifauna was significantly more abundant in the *Fucus* habitat than the *Zostera* habitats at Røvika and Juvika (post-hoc, p < 0.000, Appendix C, table vi) (Fig 3a), but not at Valnesfjorden (post-hoc, p = 0.1271). In the *Fucus* habitats across locations only the *Fucus* habitats at Røvika and Valnesfjorden were significantly different (post-hoc, p = 0.0065), while there were no significant differences between the *Zostera* habitats (post-hoc, p > 0.05).

Epifauna species richness was strongly affected by habitat (ANOVA, F = 66.41, p < 0.0001), but also by location (ANOVA, F = 6.55, p = 0.005). Species richness was significantly higher in the *Fucus* habitats than in the *Zostera* habitats at al three locations (post-hoc, p < 0.0001) (Fig 3b). Across habitats, Røvika had significantly higher mean species richness than Valnesfjorden (post-hoc, p = 0.0156) in both habitats.

Table 3. ANOVA results of total abundance and species richness of epifauna. Significant results are highlighted (p < 0.05).

Response variable	Factor	df	F-values	p-values
Abundance	Habitat	1	86.54	**<.0001**
	Location	2	0.21	0.8145
	Habitat:Location	2	9.71	**0.0008**
Species richness	Habitat	1	66.41	**<.0001**
	Location	2	6.55	**0.005**

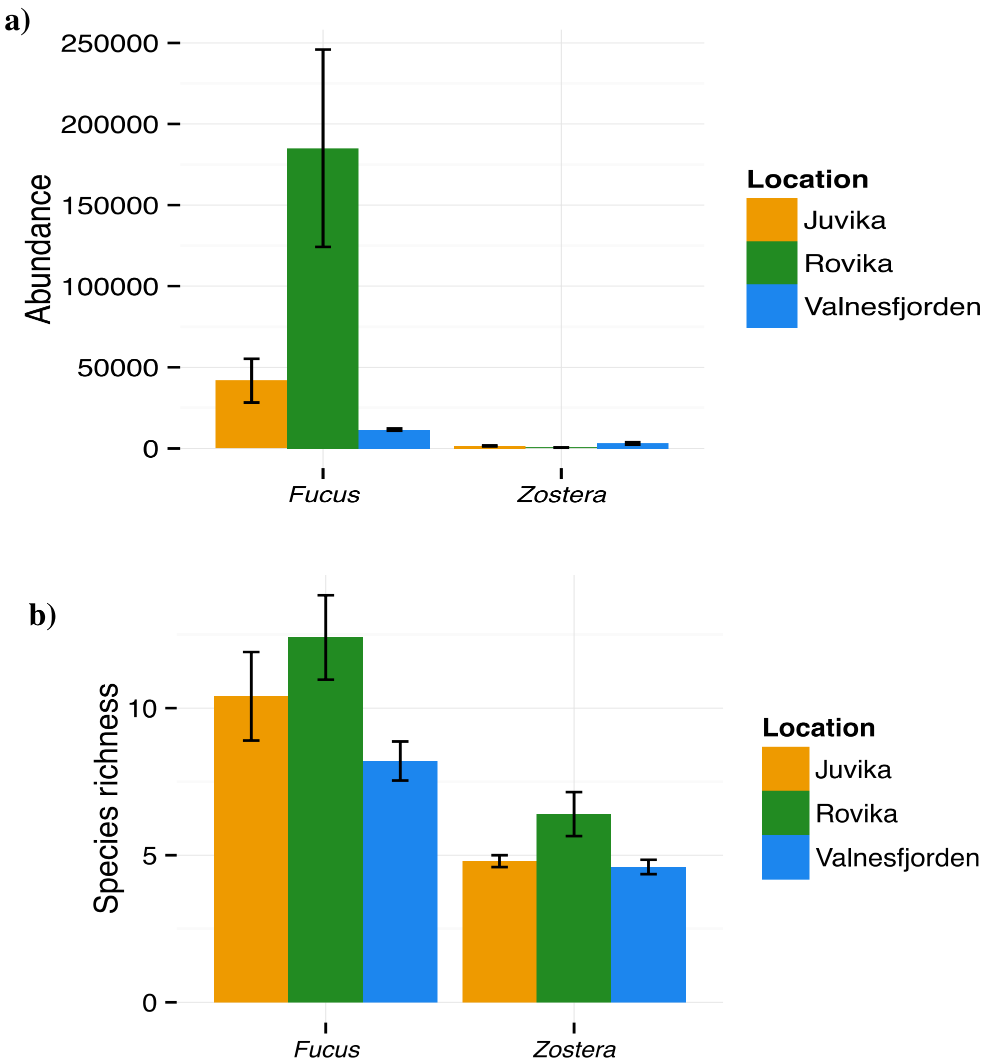

Figure 3. Epifauna a) mean abundance of ind. m^{-2} (±SE) and b) mean species richness

Infauna

Infauna abundance was strongly affected by habitat (ANOVA, $F = 6.52$, $p = 0.0038$, Table 4), and location (ANOVA, $F = 55.31$, $p < 0.0001$), as well as their interaction (ANOVA, $F = 4.75$, $p = 0.0035$). The infauna abundance was significantly higher in the bare sediment habitats compared to the *Fucus* habitats at Røvika (post-hoc, $p = 0.0263$) and Valnesfjorden (post-hoc, $p = 0.0019$, Appendix C, Table vi). However, infauna did not differ between the *Fucus* and *Zostera* habitats. Infauna abundance at Juvika did not differ across habitats.

Infauna species richness was significantly affected by habitat (ANOVA, $F = 11.83$, $p = 0.0001$), but also differed across location (ANOVA, $F = 24.45$, $p < 0.0001$). Furthermore, habitat effects on infauna species richness differed across locations (ANOVA, Habitat:Location, $F = 3.87$, $p = 0.0102$). Species richness was the highest in the *Zostera* habitat compared to both *Fucus* (post-hoc, $p = 0.0308$) and bare sediment (post-hoc, $p = 0.0010$) at Røvika (Fig 4b). There was no significant difference across habitats at Valnesfjorden and Juvika (post-hoc, $p > 0.05$).

Table 4. ANOVA results on total abundance and species richness of infauna. Significant results are highlighted ($p<0.05$).

Response variable	Factor	df	F-values	p-values
Abundance	Habitat	2	6.52	**0.0038**
	Location	2	55.31	**<.0001**
	Habitat:Location	4	4.75	**0.0035**
Species Richness	Habitat	2	11.83	**0.0001**
	Location	2	24.45	**<.0001**
	Habitat:Location	4	3.87	**0.0102**

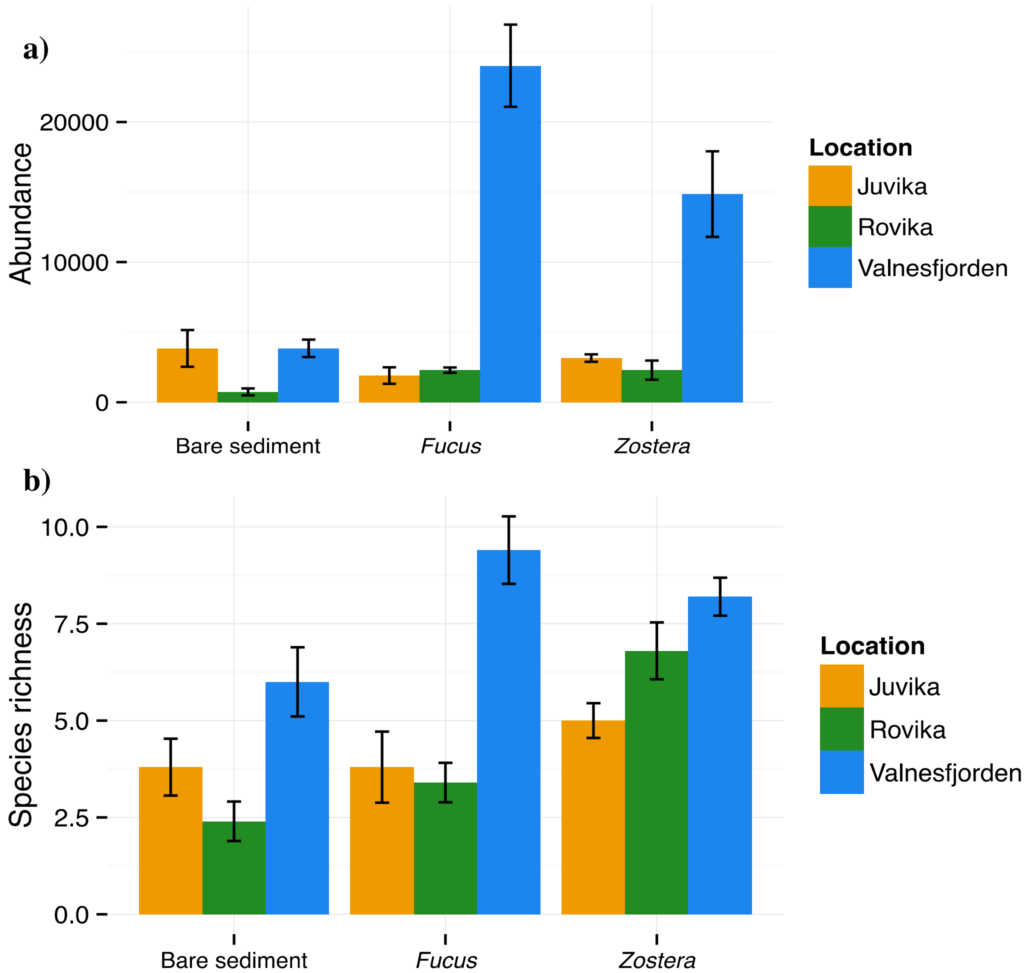

Figure 4. Infauna a) mean abundance of ind. m^{-2} (±SE) and b) mean species richness (±SE), for each habitat at each location

Densities of Arenicola marina

Mean densities of *A. marina* (Ind. m^{-2}) were much higher at Røvika (*Zostera:* 36 ± 7 and bare sediment: 36 ± 12 Ind. m^{-2}) and Juvika (*Zostera*/ bare sediment: 22 ± 5 Ind. m^{-2}) than at Valnesfjorden (*Zostera:* 4 ± 4 and bare sediment: 6 ± 5 Ind. m^{-2}) (Table 2). Thus, the *A. marina* densities in the *Zostera* habitats were similar to the densities in bare sediment habitats, while no faecal casts were observed in any of the *Fucus* habitats.

3.2.2. Phylum composition

Epifauna

In total, 34 taxa from seven phyla were identified in the epifauna samples: Annelida (6 taxa), Arthropoda (11 taxa), Bryozoa (1 taxon), Echinodermata (1 taxon), Mollusca (12 taxa), Nemertea (1 taxon) and Platyhelminthes (1 taxon) (Appendix A, Table i). In the *Fucus* habitats at Røvika and Juvika Annelida (Oligochaeta) occurred in very high numbers, while in the corresponding *Zostera* habitat, as well as in both habitats at Valnesfjorden, Mollusca and Arthropoda dominated (Fig 5.).

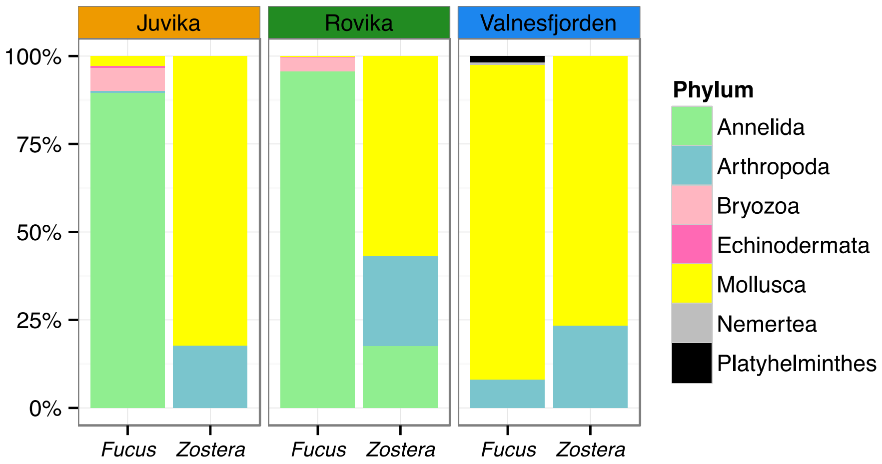

Figure 5. Relative abundance (%) of epifauna phyla

Infauna

In total, 27 taxa from four phyla were identified in the infauna samples; Annelida (15 taxa), Arthropoda (5 taxa), Mollusca (6 taxa) and Nemertea (1 taxon) (Appendix A, Table iv). In all habitats Annelida were the dominating phyla with significant contributions of Mollusca (Fig.6).

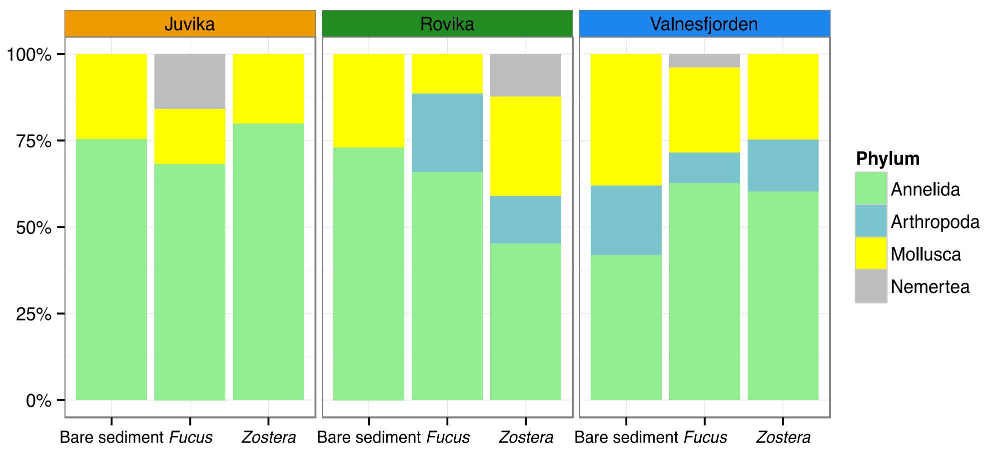

Figure 6. Relative abundance (%) of infauna phyla

3.2.3. Community composition

Epifauna

Epifauna communities were structured according to their habitat macrophyte: both *Zostera* as well as *Fucus* epifauna communities were similar across sites (Fig. 7), except for *Fucus* epifauna at Valnesfjorden that were more structured according to site. All communities were significantly different to each other (ANOSIM, $p<0.05$, Table 5). Dominating species in the communities from both habitats included *Littorina* spp., *Littorina obtusata, Gammarus oceanicus, Peringia ulvae, Mytilus edulis* and *Idotea balthica*. In addition, *Spirorbis spirorbis,* Bryozoa*, Pussilina inconspicua,* Chironomidae and *Trocochaeta multisetosa* were dominating in the *Fucus* habitats (Appendix A, Table i). The dissimilarities between the communities within locations, as well as across the *Fucus* communities was mainly caused by the dominance by *S. spirorbis* in the *Fucus* communities of Røvika and Juvika (Appendix D, Table vii & viii). The dissimilarities between the *Zostera* habitats were caused by the dominance of *P. ulvae* and *Littorina* spp. at Valnesfjorden and Juvika.

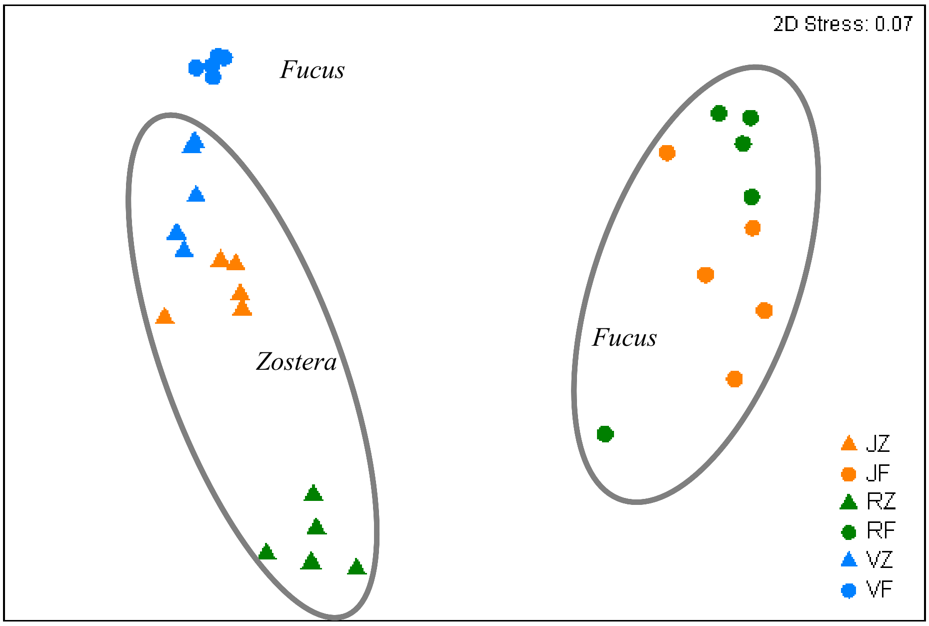

Figure 7. nMDS plots of epifauna abundance in *Zostera* (triangles) and *Fucus* (circles) habitats at all sites. The habitat groupings are indicated by grey circles (JZ = Juvika *Zostera*, JF= Juvika *Fucus*, RZ = Røvika *Zostera*, RF= Røvika *Fucus*, VZ = Valnesfjorden *Zostera*, VF= Valnesfjorden *Fucus*).

Table 5. SIMPER and ANOSIM results of epifauna a) differences between the habitats within each location and b) differences between habitats across locations. Significant results are highlighted (p<0.05).

	SIMPER	**ANOSIM**	
a) Between habitats within locations	**Average dissimilarity (%)**	**R-statistics**	**p-value**
Røvika *Fucus* - Røvika *Zostera*	83.21	0.948	**0.008**
Valnesfjorden *Fucus* - Valnesfjorden *Zostera*	42.16	0.844	**0.008**
Juvika *Fucus* - Juvika *Zostera*	84.69	1	**0.008**
b) Between habitats across locations			
Juvika *Fucu*s - Røvika *Fucus*	50.69	0.412	**0.032**
Juvika *Fucus* - Valnesfjorden *Fucus*	89.29	1	**0.008**
Røvika *Fucu*s - Valnesfjorden *Fucus*	89.64	1	**0.008**
Juvika *Zostera* - Røvika *Zostera*	62.65	1	**0.008**
Juvika *Zostera* - Valnesfjorden *Zostera*	36.61	0.632	**0.008**
Røvika *Zostera* - Valnesfjorden *Zostera*	75.50	1	**0.008**

Infauna

Infauna composition was not affected by habitat, but depended more on location (Fig. 8). There were significant differences between all habitats at Røvika, and between bare sediment and *Fucus*/ *Zostera* at Valnesfjorden (ANOSIM, $p < 0.05$, Table 6). At Juvika, none of the habitats were significantly different to each other. The community compositions were dominated by Oligochaeta, Tubificoides, *Scoloplos armiger, P. ulvae, Pygospio elegans,* Chironomidae, *G. oceanicus, Mya arenaria* and *Littorina* spp. (Appendix A, Table iv). Across the communities the dissimilarities were mainly caused by these taxa being highly more dominant at Valnesfjorden than at Røvika and Juvika, except for *S. armiger* who dominated more in the communities at Røvika and Juvika than at Valnesfjorden (Appendix D, Table ix & x).

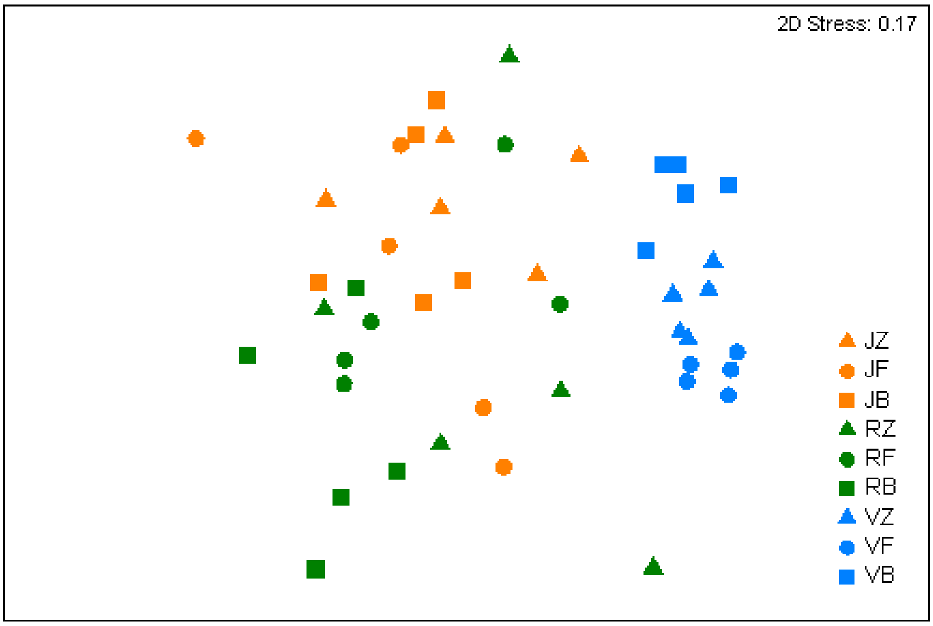

Figure 8. nMDS plots of epifauna abundance in *Zostera* (triangles), *Fucus* (circles) and bare sediment (squares) habitats at all sites (JZ = Juvika *Zostera,* JF= Juvika *Fucus*, JB = Juvika bare sediment, RZ = Røvika *Zostera,* RF= Røvika *Fucus*, RB = Røvika bare sediment, VZ = Valnesfjorden *Zostera,* VF= Valnesfjorden *Fucus*, VB = Valnesfjorden bare sediment).

Table 6. SIMPER and ANOSIM results of infauna a) differences between the habitats within each location and b) differences between habitats across locations. Significant results are highlighted (p<0.05).

	SIMPER	**ANOSIM**	
a) Between habitats within locations	**Average dissimilarity (%)**	**R-statistics**	**p-value**
Røvika bare sediment - Røvika *Fucus*	63.71	0.272	**0.040**
Røvika bare sediment - Røvika *Zostera*	77.58	0.564	**0.008**
Røvika *Fucus* - Røvika *Zostera*	73.55	0.372	**0.032**
Valnesfjorden bare sediment - Valnesfjorden *Fucus*	65.09	1	**0.008**
Valnesfjorden bare sediment - Valnesfjorden *Zostera*	47.27	0.772	**0.008**
Valnesfjorden *Fucus* - Valnesfjorden *Zostera*	36.54	0.28	0.071
Juvika bare sediment - Juvika *Fucus*	61.36	0.086	0.270
Juvika bare sediment - Juvika *Zostera*	54.69	0.112	0.230
Juvika *Fucus* - Juvika *Zostera*	61.26	0.074	0.254
b) Between habitats across locations			
Juvika bare sediment - Røvika bare sediment	70.86	0.544	**0.008**
Juvika bare sediment - Valnesfjorden bare sediment	76.91	0.92	**0.008**
Røvika bare sediment - Valnesfjorden bare sediment	92.69	1	**0.008**
Juvika *Fucus* - Røvika *Fucus*	62.31	-0.038	0.563
Juvika *Fucus* - Valnesfjorden *Fucus*	84.59	0.786	**0.008**
Røvika *Fucus* - Valnesfjorden *Fucus*	78.10	0.912	**0.008**
Juvika *Zostera* - Røvika *Zostera*	75.80	0.58	**0.008**
Juvika *Zostera* - Valnesfjorden *Zostera*	73.08	0.852	**0.008**
Røvika *Zostera* - Valnesfjorden *Zostera*	77.61	0.76	**0.008**

3.3. Mobile mesopredators

In total, nine taxa were identified in the mesopredator traps (Appendix A, Table iv). The highest mesopredator abundance, when pooled over locations, was found in the bare sediment habitats, and the lowest abundance in the *Zostera* habitats. The differences between the habitats can be explained by the high abundance of *Gasterosteus aculeatus* in the habitats at Valnesfjorden, which accounted for more than 2/3 of the total mesopredator abundance. At Røvika and Juvika, the mesopredator abundances were higher in the vegetated habitats than in the bare sediment habitat (Fig. 9a). The overall species richness was highest in the *Zostera* habitats and lowest in the bare sediment habitats (Fig. 9b).

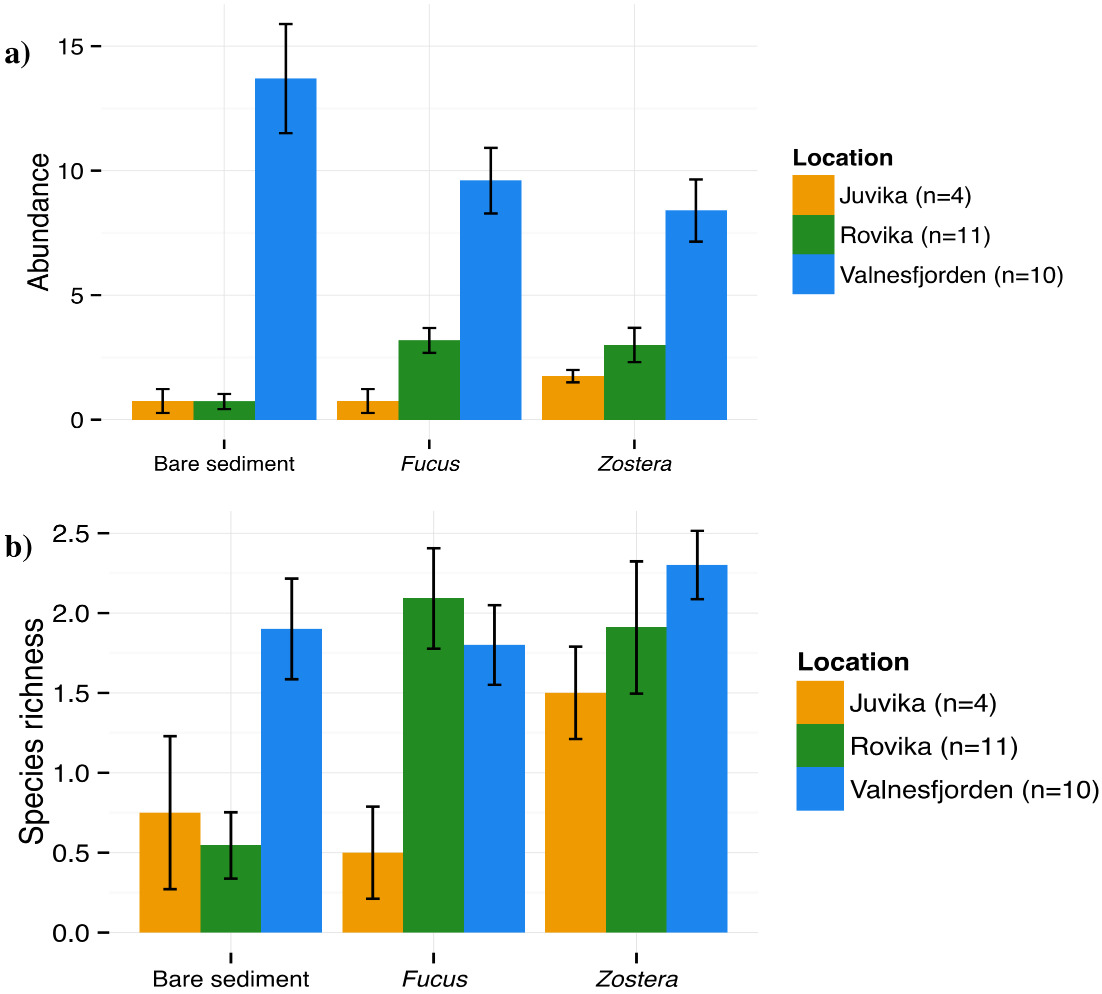

Figure 9. Mesopredator a) mean abundance (±SE) and b) mean species richness (±SE), for each habitat at each location with n trap deployments.

Two phyla, Arthropoda (2 taxa) and Chordata (7 taxa), were identified in the mesopredator traps (Fig.10). The species composition at Valnesfjorden was markedly different to that identified at the two other locations, mainly caused by the presence of *G. aculeatus* at this location, which were absent at Røvika and Juvika. The scorpion fish *Myoxocephalus scorpius* was present at Røvika and Juvika, and absent Valnesfjorden. Some species, such as *Gadus morhua* and *Pomatoschistuz minutus* were only found in vegetated habitats.

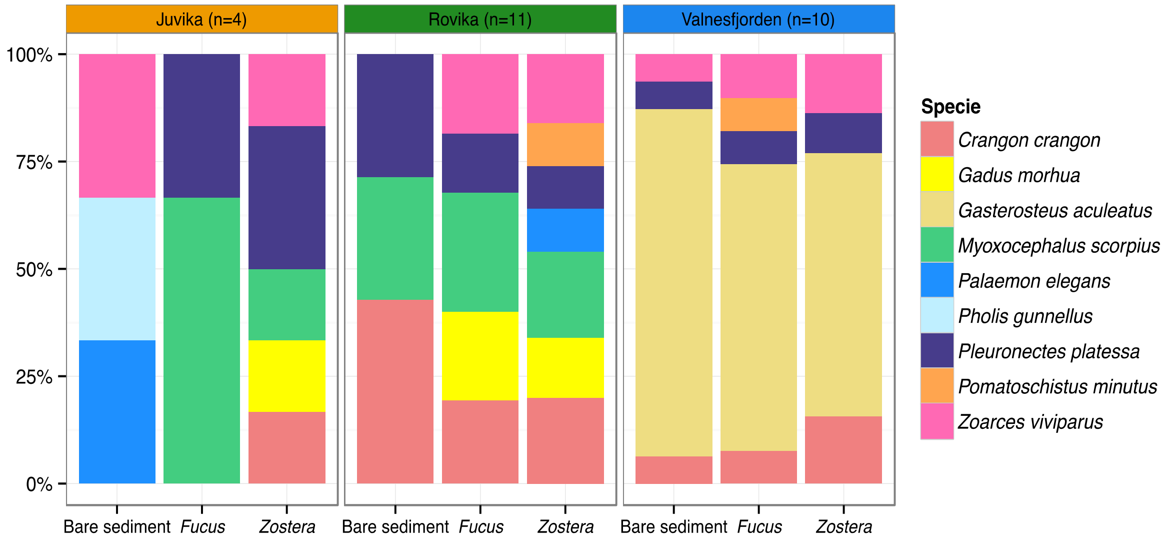

Figure 10. Relative abundance (%) of mesopredator species in the different habitats and sites with n trap deployments

4. Discussion

In this study the associated fauna of habitats of seagrass (*Z. marina*), macroalgae (*Fucus* spp.) and bare sediment was compared. In general, vegetated habitats possessed higher abundances and species richness than adjacent bare sediment. However, specific differences between vegetation type (*Zostera* vs *Fucus*) were site-dependent. Epifauna abundance and species richness were higher on *Fucus* than on *Zostera*, and the differences was mainly driven by the presence/ absence and abundance of *S. spirorbis,* Bryozoa, *Littorina* spp. and *P. ulvae*. Infauna abundance was higher in the *Fucus* habitat compared to the bare sediment habitat at Røvika and Valnesfjorden, but not at Juvika. Infauna species richness was higher in *Zostera* compared to both *Fucus* and bare sediment at Røvika, but not at Valnesfjorden and Juvika. The highest infauna species richness was found in the *Zostera* habitats at both Røvika and Juvika, while the highest species richness at Valnesfjorden was found in the *Fucus* habitat. The dissimilarity between infauna habitats was mainly caused by the dominance of the species Oligochaeta, Tubificoides, *S.armiger,* and *P. ulvae*. Mesopredators were abundant and occurred in higher species numbers in vegetated habitats than on bare sediment at Røvika and Juvika, while at Valnesfjorden the highest abundance was found in the bare sediment habitat.

4.1. Epifauna

Epifauna abundance and species richness were higher in the *Fucus* habitats compared to *Zostera* habitats. This is partly in contrast to studies from the south of Norway, which found the highest abundance in the *Fucus* habitats but highest species richness in the *Zostera* habitats (Christie et al., 2009; Fredriksen & Christie, 2003; Fredriksen et al., 2005). The difference between the former and the present study in regards to species richness may be explained by the overall fauna and flora investigated, as the former studies included epiphytes and this study did not. Higher epifauna abundance on *Fucus* than on *Zostera* may be explained through different architectures and life spans of *Z. marina* and *Fucus* spp. Both species are canopy-forming, providing three-dimensional structures to their environments (Fredriksen et al., 2005). However, while seagrass leaves are thin and simple, macroalgae form large structures with large surfaces areas, and are thus able to house larger individuals and abundances than seagrasses (Christie et al., 2003; Christie et al., 2009; Orth et al., 1984). The life span of *Z. marina* leaves is markedly shorter than that of the fucoid canopy. The seagrass leaves will be lost and renewed several times throughout the season, being a habitat of continuous change, while the fucoids are perennial, change little throughout the season and may live for more than three years (Christie et al., 2009). Macroalgae are therefor able to accumulate larger abundances of sessile fauna over time than seagrasses. The highest *Fucus* abundance in this study was found at Røvika, where two sessile organisms recorded on the *Fucus* spp. subsamples, *S. spirorbis* and Bryozoa, contributed to 99.2% of the habitat's abundance.

The sessile filter feeding polychaeta *S. spirorbis* were highly abundant at Røvika and Juvika, but absent at Valnesfjorden. The community composition analyses showed strong groupings of *Zostera* and *Fucus* habitats across sites, mainly contributed to by the dominance by *S. spirorbis* and Bryozoa in the *Fucus* habitats at Røvika and Juvika. The settlement and survivorship of *S. spirorbis* is linked to salinity, as the *S. spirorbis* larvae have a lower salinity tolerance of 5 psu, and the highest success of survival and settlement is in salinities of 25-30 psu (Ushakova, 2003). At Valnesfjorden the salinity was on average 8.3 psu, while Røvika and Juvika had on average a salinity of 25.3 psu, providing more suitable conditions for the larvae. The absence of *S. spirorbis* at Valnesfjorden may therefore be explained by the low salinity.

Two phyla, Mollusca and Arthropoda, were mainly driving the dissimilarities between habitats. Apart from *S. spirorbis,* the two gastropods *Littorina* spp. and *P.ulvae* contributed to the dissimilarities between the *Fucus* and *Zostera* habitats. The gastropod *Littorina* spp. was highly abundant at all three locations. At Røvika and Valnesfjorden, the highest abundances of *Littorina* spp. were found in the *Fucus* habitat, while at Juvika the highest abundance was found in the *Zostera* habitat. *Littorin*a are herbivorous grazers, mainly feeding on *Fucus* spp. (Watson & Norton, 1987), which may explain the difference in abundance between the two habitats. When excluding *S. spirorbis,* Valnesfjorden would have the highest epifauna abundance of both habitats, due to its high dominance of *Littorina* spp. and *P. ulvae*.

4.2. Infauna

Infauna abundance and species richness varied strongly between habitats. Overall, the abundance and species richness of the vegetated habitats were higher than the ones found in the bare sediment habitats, consistent with previous studies (Boström & Bonsdorff, 1997; Fredriksen et al., 2010; Mattila et al., 1999). Infauna abundance was higher in *Fucus*

compared to bare sediment at Valnesfjorden and Røvika, but not at Juvika. No significant difference in abundance in *Zostera* compared to *Fucus* or bare sediment were found.
The physical properties of the vegetation are of great importance when assessing these differences. Seagrasses anchors themselves to the sediment through its root-rhizomes system and is thus a structured system, while macroalgae don't have roots but attaches themselves to rocks and boulders by a disc and settles wherever they find suitable conditions (Kaiser & Attrill, 2011). Seagrasses, therefore, provide a belowground structured habitat through their roots, while the macroalgae do not (Orth et al., 1984). Both vegetation types will slow down the water current and trap detritus, increasing the abundance of detritus feeding organisms (Alfaro, 2006), while the bare sediment habitat will likely be preferred by mobile fauna moving between vegetated habitats.

The polychaeta *A. marina* is an ecosystem engineer in marine ecosystems through destabilizing the sediment as a bioturbator. In contrast, seagrasses are sediment-stabilisers through their root-rhizome system. Thus, both *A. marina* and *Z. marina* are ecosystem engineers in soft sediments, but with contrasting effects on the sediment, and may therefore facilitate different macrofauna communities (Eklöf et al., 2015). High abundances of *A. marina* may therefore increase the species richness of the *Zostera* habitat. Seagrass shoot density is positively correlated with infauna abundance and community structure, because a higher shoot density increases the trapping of detritus, reduces predation of the associated infauna and correlates with higher below-ground biomass (Fredriksen et al., 2010; Webster et al., 1998). As the macroalgae canopy performs similar functions as the seagrass leaves, the density of the vegetation may be an important factor when explaining the differences in abundances and species richness between the habitats. The *Fucus* canopy has a larger surface area than the seagrass leaves, and may therefor be able to trap more detritus in its adjacent sediment, which may partly explain why the higher abundance and species richness at Valnesfjorden were found in the *Fucus* habitat, and not the *Zostera* habitat.

The highest abundances of infauna were found at Valnesfjorden, with a dominance of Oligochaeta (here: including the Oligochaeta genus Tubificoides) and the gastropod *P. ulvae*, which were also the main contributing species to the dissimilarities between the habitats. Oligochaeta are generally able to tolerate low levels of oxygen, which may be caused by high levels of detritus in the sediment (Fredriksen et al., 2010). The high mud content and dead *Z. marina* leaves observed at the study site may indicate that Valnesfjorden is an accumulating site for fine particles and detritus. This may explain the locations higher abundances compared to Røvika and Juvika, as these species are detritus feeders and grazers (Ieno et al., 2006). Røvika had a thick layer of hypoxic clay in its habitats, and the lowest abundance of general infauna, as well as of Oligochaeta. The conditions at this location may therefor have been too harsh for the organisms to thrive. However, Røvika had a high species richness, which indicates that other factors may have contributed to the differences observed.

Fredriksen et al. (2010) compared infauna from habitats of *Zostera* and bare sediment from four sampling sites, three in the south of Norway and one in the western part of Norway. Their investigations showed higher abundance and species richness in the vegetated habitat than in the unvegetated habitat, with the exception of one station. Even though their study was performed later in the season (August and November) and at greater depths through SCUBA diving (3-5m), their results coincide with the result of this study, indicating that the physical architecture of the vegetated habitats may be of greater importance to the associated infauna than other factors such as latitude, season and depth.

4.3. Mobile mesopredators

Mesopredator abundance and species richness were higher in vegetated habitats than in the bare sediment habitat, except for Valnesfjorden, where the highest abundance was found in the bare sediment habitat. Vegetation functions as a nursery habitat for mobile fauna, through providing shelter from larger predators, and a source of food through its associated fauna (Duarte, 2002; Heck Jnr et al., 2003). Increased seagrass shoot density increases the complexity of the seagrass bed, and may increase the abundance and species richness of associated mesopredators, as it offers more protections than less dense seagrass beds. The preference of high/low complexity habitats varies from species to species (Tait & Hovel, 2012), and as the highest shoot density per square meter was found at Valnesfjorden, other factors may be of grater importance when explaining these differences found in this study.

Valnesfjorden was the only location where the highest mesopredator abundance was found in the bare sediment habitat, mainly caused by the dominance of *G. aculeatus* at this location. The higher abundance in this habitat may be explained by the traps adding a structure to a structure less habitat (Layman & Smith, 2001; Petrik & Levin, 2000), however this effect is likely of minor importance, as the abundances at Røvika and Juvika were lower in the bare sediment habitats than in the vegetated habitats. *G. aculeatus* exhibit schooling behaviour (Ward et al., 2002), and may therefore be less dependent on vegetation for protection, and may prefer the bare sediment habitats as prey is are more accessible in this habitat than in vegetated habitats. Their schooling behaviour may also have contributed to several individuals entering the trap at once, explaining the high abundances found in the traps.

Several taxa, such as *Carcinus maenas* (shore crab), juvenile flatfish and high abundances of juvenile *Pollachius virens* (saithe) were observed while working in the seagrass bed, but were not caught in the traps. This indicates that the mesopredator data is biased toward mesopredator species that were attracted by the baited traps, as some species may have a higher preference to the bait and traps than others. Thus, the mesopredator distribution found in this study only represents part of the mesopredator fauna at the different locations, and trapping of the additionally observed species could potentially have affected the variances between the habitats seen in this study. Also, the mesopredators were released back into the fjord after measurements were completed, and the same individuals may therefore have been recorded multiple times thus affecting the results.

5. Conclusion

In this study I showed that vegetation of seagrass and macroalgae had strong effects on abundance and species richness of the epifauna, infauna and mesopredators compared to adjacent bare sediment habitats. The habitats physical architecture was probably the main contributing factor to the differences observed. Epifauna abundance and species richness were higher in *Fucus* than in *Zostera* habitats at all locations. Infauna abundance and species richness were higher in *Fucus* than in bare sediment at Røvika and Valnesfjorden, but not at Juvika. No difference between *Zostera* and *Fucus* or bare sediment abundance was found. Species richness was higher in *Zostera* compared to both *Fucus* and bare sediment at Røvika, while no significant difference was found between the habitats at Valnesfjorden and Juvika. The surface area of the detritus-trapping canopy of both vegetation types, as well as the root system of seagrass, are likely of great importance for the infauna community. Mesopredator abundance and species richness were higher in vegetated habitats than in unvegetated habitats, except for at Valnesfjorden, supporting the important role of vegetation as a habitat for mesopredators.

To conclude, the overall results showed that vegetated habitats houses higher abundances and species richness than unvegetated habitats, although differences between vegetation types (*Fucus* vs *Zostera*) were site dependent.

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7. Appendix

Appendix A – Species lists and sample information

Epifauna

Table i. Species list epifauna. This list includes counts of the collected individuals from the epifauna samples, as well as the counts from the *Fucus* subsamples (Table ii). Note that the infaunal specie *S.armiger* is present in this species list, but excluded from the analysis, as it defined as an infauna specie.

	RØVIKA		**VALNESFJORDEN**		**JUVIKA**	
	Zostera	***Fucus***	***Zostera***	***Fucus***	***Zostera***	***Fucus***
PHYLUM ANNELIDA						
CLASS POLYCHAETA						
ORDER SPIONIDA						
Harmothoe spp.	0	4	0	0	0	14
Trocochaeta multisetosa	0	0	0	0	0	99
ORDER PHYLLODOCIDA						
Phyllodoce mucosa	0	0	0	0	0	1
ORDER ORBINIIDA						
Scoloplos armiger	0	1	0	0	8	1
ORDER SABELLIDA						
Spirobranchus triqueter	0	0	0	0	0	52
Spirorbis spirorbis	5	64012	0	0	0	14050
PHYLUM ARTHROPODA						
CLASS MALACOSTRACA						
ORDER DECAPODA						
Crangon crangon	3	3	0	0	0	0
Eualus cranchii	0	3	0	0	0	8
Hyas coarctatus	0	1	0	0	0	0
Hyas areneus	0	0	0	0	0	1
ORDER AMPHIPODA						
Gammarus oceanicus	1	6	63	166	0	2
ORDER ISOPODA						
Idotea balthica	31	39	0	0	34	28
Idotea cf. metallica	1	0	0	0	0	0
Jaera albifrons	0	7	0	26	1	2
ORDER MYSIDA						
Pranus inermis	0	20	0	0	0	2
Praunus flexuosus	0	0	0	0	1	0
CLASS INSECTA						
ORDER DIPTERA						
Fam. Chironomidae	0	0	0	57	0	0
PHYLUM BRYOZOA	0	894	0	0	0	50
PHYLUM ECHINODERMATA						
CLASS ASTEROIDEA						
ORDER FORCIPULATIDA						
Asterias rubens	0	2	0	0	0	16
PHYLUM MOLLUSCA						
CLASS GASTRAPODA						
Fam. Patellidae	0	2	0	0	0	18
ORDER NEOGASTROPODA						
*Buccinum undatum (*Juv)	0	31	0	0	0	0
Nucella lapillus	0	1	0	0	0	0
ORDER NUDIBRANCHIA						
Clade. Nudibranchia	0	0	0	0	0	1
Fam. Onchidorididae	0	0	0	0	0	1
ORDER LITTORINIMORPHA						

Littorina obtusata	78	156	0	0	0	0
Littorina spp.	3	72	501	2428	152	96
Peringia ulvae	22	12	498	1219	321	76
Pusillina inconspicua	0	58	0	0	0	135
CLASS BIVALVIA						
ORDER CARDIIDA						
Cerastoderma edule	1	0	0	1	0	0
ORDER MYIDA						
Mya arenaria	1	5	13	10	3	0
ORDER MYTILOIDA						
Mytilus edulis	56	99	16	107	24	91
PHYLUM NEMERTEA	0	0	0	3	0	0
PHYLUM PLATYHELMINTES						
CLASS TURBELLARIA	0	0	0	12	0	0

Fucus subsample, epifauna

Table ii. The contribution of *Fucus* subsamples to the total epifauna abundance. No individuals were recorded on the subsamples from Valnesfjorden, and are thus not presented here.

Location	Habitat	Specie	Abundance subsamples	Abundance samples
Røvika	*Fucus*	*Spirorbis spirorbis*	5420	63 253
Røvika	*Fucus*	Phylum Bryozoa	66	895
Røvika	*Fucus*	*Mytilus edulis*	5	53
Juvika	*Fucus*	*Spirorbis spirorbis*	853	13 574
Juvika	*Fucus*	*Mytilus edulis*	3	50
Juvika	*Fucus*	Phylum Bryozoa	3	50
Juvika	*Fucus*	*Spirobranchus triqueter*	2	31

Epifauna samples biomass

Table iii. Mean weights (g) of *Z. marina* and *Fucus* spp. samples

	Røvika	Valnesfjorden	Juvika
Fucus spp. total sample	359.6	288.3	300.3
Fucus spp. subsample	33.6	9.3	17.9
Z. marina	29.1	99.6	19.2

Infauna

Table iv. Species list infauna

	RØVIKA			VALNESFJORDEN			JUVIKA		
	Zostera	*Fucus*	**Bare sed.**	*Zostera*	*Fucus*	**Bare sed.**	*Zostera*	*Fucus*	**Bare sed.**
PHYLUM ANNELIDA									
CLASS POLYCHAETA									
ORDER CAPITELLIDAE									
Arenicola marina	2	1	3	0	1	0	1	1	0
Capitella spp.	0	0	0	3	21	1	0	0	0
ORDER PHYLLODOCIDA									
Eteone longa	2	0	0	0	0	0	4	3	1
Harmothoe spp.	1	0	0	0	0	0	2	1	0
Hediste diversicolor	0	0	0	4	0	6	0	0	0
Nephtys (juvenile)	1	0	0	0	0	0	0	0	0
Pholoe spp.	0	0	0	0	0	0	0	0	1
ORDER OPHELIIDA									
Ophelia limacina	1	0	0	0	0	0	0	0	0
ORDER ORBINIIDA									
Orbinia latreillii	1	0	0	0	0	0	0	0	0
Scoloplos armiger	7	17	7	0	0	0	57	36	63
ORDER SPIONIDA									
Pygospio elegans	3	6	0	78	123	7	0	0	1
Scolelepis foliosa	1	1	3	0	0	0	1	0	0
Malacoceros spp.	0	0	0	0	0	0	0	2	0
CLASS CLITELLATA									
ORDER HAPLOTAXIA									
Subclass Oligochaeta	3	24	0	161	202	67	44	8	5
Genus Tubificoides	38	38	14	156	386	2	5	20	67
PHYLUM ARTHROPODA									
CLASS INSECTA									
ORDER DIPTERA									
Fam. Chironomidae	2	0	0	33	43	8	0	0	0
CLASS MALACOSTRACA									
ORDER AMPHIPODA									
Gammarus oceanicus	1	0	0	11	10	0	0	0	0
ORDER ISOPODA									
Idotea balthica	6	0	0	0	0	0	0	0	0
Jaera albifrons	0	0	0	0	1	0	0	0	0
ORDER MYSIDA									
Praunus flexuosus	0	2	0	0	0	0	0	0	0
PHYLUM MOLLUSCA									
CLASS BIVALVIA									
ORDER MYIDA									
Mya arenaria	9	1	2	17	6	29	6	0	8
ORDER CARDIIDA									
Cerastoderma edule	0	0	0	1	0	1	1	0	0
ORDER MYTILOIDA									
Mytilus edulis	4	0	0	2	5	0	0	0	0
CLASS GASTROPODA									
ORDER LITTORINIMORPHA									
Littorina obtusata	7	0	0	0	0	0	0	0	0
Littorina spp.	0	0	0	3	92	1	0	0	0
Peringia ulvae	1	0	0	114	124	29	4	1	4
PHYLUM NEMERTEA	1	0	0	0	7	0	0	1	0

Mesopredators

Table v. Species list mobile mesopredators

	RØVIKA			VALNESFJORDEN			JUVIKA		
	Zostera	Fucus	Bare sed.	Zostera	Fucus	Bare sed.	Zostera	Fucus	Bare sed.
PHYLUM ARTHROPODA									
CLASS MALACOSTRACA									
ORDER DECAPODA									
Crangon crangon	2	7	6	5	3	4	1	1	0
Palaemon elegans	1	0	0	0	0	0	0	0	1
PHYLUM CHORDATA									
CLASS ACTINOPTERI									
ORDER GADIFORMES									
Gadus morhua	7	6	0	0	0	0	0	1	0
ORDER GASTEROSTEIFORMES									
Gasterosteus aculeatus	0	0	0	65	87	127	0	0	0
ORDER SCORPAENIFORMES									
Myoxocephalus scorpius	12	14	1	0	0	0	1	2	0
ORDER PERCIFORMES									
Pholis gunnellus	0	0	0	0	0	0	0	0	1
Pomatoschistus minutus	1	0	0	0	1	0	0	0	0
Zoarces viviparus	8	4	0	13	4	4	1	0	1
ORDER PLEURONECTIFORMES									
Pleuronectes platessa	2	4	1	1	1	2	0	3	0

Appendix B – Keys for species identification

An overview of keys utilized in the species identifications. The sources are also listed in the reference list above.

- *British marine amphipoda: Gammaridea* (Lincoln, 1979)
- *Handbook of the marine fauna of North-West Europe* (Hayward & Ryland, 1995)
- *Molluscs: Prosobranchs and Pyramidellid Gastropods: Keys and Notes for the Identification of the Species* (Graham, 1988)
- *Ecology and systematics of the north European species of Rissoa and Pusillina (Prosobranchia: Rissoidae)* (Warén, 1996)
- *Molluscs: benthic opisthobranchs: Mollusca, Gastropoda: keys and notes for the identification of the species* (Thompson, 1988)
- *Polychaetes from Scottish waters. A guide to identification. Part 3.* (Chambers & Garwood, 1992)
- *Introduction to: Key to the families of polychaeta* (Eibye Jacobsen, 2003)
- *Havbørsteorme I. Errantia. Danmarks Fauna* (Kirkegaard, 1992)

Appendix C – Univariate analysis

Table vi. Post-hoc results, comparing abundance (ind. m^{-2}) and species richness between each habitat at each location, as well as habitats across locations. Significant results are highlighted ($p<0.05$).

	Epifauna		Infauna	
	Abundance	Species richness	Abundance	Species richness
Juvika bare sediment - Røvika bare sediment			**0.0290**	0.9068
Juvika bare sediment - Valnesfjorden bare sediment			1.0000	0.4701
Røvika bare sediment - Valnesfjorden bare sediment			**0.0111**	**0.0315**
Juvika *Fucus* - Røvika *Fucus*	0.3288	0.2471	0.9421	1.0000
Juvika *Fucus* - Valnesfjorden *Fucus*	0.4271	0.7710	**<.0001**	**0.0004**
Røvika *Fucus* - Valnesfjorden *Fucus*	**0.0065**	**0.0156**	**<.0001**	**0.0001**
Juvika *Zostera* - Røvika *Zostera*	0.5284	0.2471	0.7958	0.4109
Juvika *Zostera* - Valnesfjorden *Zostera*	0.8073	0.7710	**0.0004**	**0.0091**
Røvika *Zostera* - Valnesfjorden *Zostera*	0.0637	**0.0156**	**<.0001**	0.7235
Juvika *Fucus* - Juvika *Zostera*	**<.0001**	**<.0001**	0.3471	0.9433
Røvika *Fucus* - Røvika *Zostera*	**<.0001**	**<.0001**	0.9999	**0.0308**
Valnesfjorden *Fucus* - Valnesfjorden *Zostera*	0.1271	**<.0001**	0.6843	0.9433
Røvika bare sediment - Røvika *Fucus*			**0.0263**	0.9895
Juvika bare sediment - Juvika *Fucus*			0.7947	1.0000
Valnesfjorden bare sediment - Valnesfjorden *Fucus*			**0.0019**	0.0681
Røvika bare sediment - Røvika *Zostera*			0.0590	**0.0010**
Juvika bare sediment - Juvika *Zostera*			1.0000	0.9267
Valnesfjorden bare sediment - Valnesfjorden *Zostera*			0.0547	0.3290

Appendix D – Similarity percentage (SIMPER) analysis

Epifauna

Table vii. Main contributing species to the dissimilarities between the habitats *Fucus* and *Zostera* at each location from the similarity percentage (SIMPER) analysis. Cut-off percentage was set to 90%, and only species contributing to more than 5% of the dissimilarity is included in this table.

Fucus-Zostera	**Average dissimilarity(%)**	**Species**	**Av.Abund *Fucus***	**Av.Abund *Zostera***	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Juvika	84.69	*Spirorbis spirorbis*	49.75	0.00	50.58	6.74	59.73	59.73
		Peringia ulvae	1.74	7.82	7.84	1.88	9.25	68.98
		Pusillina inconspicua	4.02	0.00	5.46	1.14	6.45	75.43
Røvika	83.21	*Spirorbis spirorbis*	101.93	0.63	61.12	4.74	73.44	73.44
		Bryozoa	10.34	0.00	5.37	1.40	6.45	79.89
Valnesfjorden	42.16	*Littorina* spp.	21.89	9.77	15.06	3.32	35.73	35.73
		Peringia ulvae	15.32	9.09	8.64	1.36	20.48	56.21
		Gammarus oceanicus	5.28	3.07	3.63	1.34	8.60	64.81
		Chironomidae	2.84	0.00	3.56	1.49	8.43	73.25
		Mytilus edulis	4.60	1.78	3.47	5.66	8.24	81.48
		Jaera albifrons	1.92	0.00	2.36	1.54	5.59	87.07

Table viii. Main contributing species to the dissimilarities between the habitats across locations from the similarity percentage (SIMPER) analysis. Cut-off percentage was set to 90%, and only species contributing to more than 5% of the dissimilarity is included in this table.

a) *Fucus*	Average dissimilarity	Species	Av.Abund Loc 1	Av.Abund Loc 2	Av.Diss	Diss/SD	Contrib%	Cum.%
Juvika-Røvika	50.69	*Spirorbis spirorbis*	49.75	101.93	29.17	2.19	57.54	57.54
		Bryozoa	1.41	10.34	3.93	1.32	7.75	65.30
		Littorina obtusata	0.00	5.37	3.06	1.38	6.03	71.33
Juvika - Valnesfjorden	89.29	*Spirorbis spirorbis*	49.75	0.00	35.96	4.91	40.28	40.28
		Littorina spp.	3.95	21.89	14.00	3.60	15.67	55.95
		Peringia ulvae	1.74	15.32	10.94	2.29	12.26	68.21
Røvika - Valnesfjorden	89.64	*Spirorbis spirorbis*	101.93	0.00	47.56	3.25	53.05	53.05
		Littorina spp.	3.58	21.89	11.02	1.91	12.29	65.35
		Peringia ulvae	0.69	15.32	8.81	1.78	9.83	75.17

b) *Zostera*	Average dissimilarity	Species	Av.Abund Loc 1	Av.Abund Loc 2	Av.Diss	Diss/SD	Contrib%	Cum.%
Juvika-Røvika	62.65	*Peringia ulvae*	7.82	1.99	17.80	4.02	28.41	28.41
		Littorina spp.	5.39	0.60	14.76	4.51	23.56	51.97
		Littorina obtusata	0.00	3.90	12.29	4.84	19.62	71.59
		Idotea balthica	2.18	2.24	4.84	1.25	7.73	79.32
		Mytilus edulis	2.09	3.12	4.20	1.10	6.70	86.02
Juvika - Valnesfjorden	36.61	*Littorina* spp.	5.39	9.77	10.16	1.73	27.76	27.76
		Peringia ulvae	7.82	9.09	8.93	1.66	24.39	52.15
		Gammarus oceanicus	0.00	3.07	7.32	1.45	20.00	72.15
		Idotea balthica	2.18	0.00	4.82	1.47	13.18	85.33
		Mya arenaria	0.60	1.24	2.54	1.70	6.93	92.27
Røvika - Valnesfjorden	75.50	*Littorina* spp.	0.60	9.77	23.64	4.97	31.31	31.31
		Peringia ulvae	1.99	9.09	17.06	2.04	22.59	53.90
		Littorina obtusata	3.90	0.00	10.23	4.71	13.55	67.45
		Gammarus oceanicus	0.20	3.07	7.83	1.47	10.37	77.82
		Idotea balthica	2.24	0.00	5.87	1.92	7.78	85.60

Infauna

Table ix. Main contributing species to the dissimilarities between the habitats at a) Røvika, b) Valnesfjorden and c) Juvika from the similarity percentage (SIMPER) analysis. Cut-off percentage was set to 90%, and only species contributing to more than 5% of the dissimilarity is included in this table.

a) Røvika	Average dissimilarity	Species	Av.Abund hab 1	Av.Abund Hab 2	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare sediment - *Fucus*	63.71	Tubificoides	1.60	2.42	15.73	1.48	24.69	24.69
		Scoloplos armiger	0.69	1.59	13.70	1.49	21.50	46.19
		Oligochaeta	0.00	1.38	11.89	0.78	18.66	64.86
		Pygospio elegans	0.00	0.83	7.36	1.09	11.56	76.41
		Scolelepis foliosa	0.48	0.20	4.86	0.85	7.63	84.04
		Arenicola marina	0.35	0.20	4.29	0.71	6.73	90.77
Bare sediment - *Zostera*	77.58	Tubificoides	1.60	1.95	12.47	1.51	16.08	42.96
		Idotea balthica	0.00	1.08	8.90	2.70	11.48	27.55
		Mya arenaria	0.40	1.01	8.01	1.01	10.32	37.87
		Scoloplos armiger	0.69	0.69	6.97	0.99	8.99	46.86
		Littorina obtusata	0.00	0.85	6.51	1.10	8.39	55.25
		Mytilus edulis	0.00	0.57	5.01	0.78	6.46	61.71
		Oligochaeta	0.00	0.60	4.81	1.13	6.20	67.91
		Arenicola marina	0.35	0.40	4.43	0.92	5.71	73.62
		Scolelepis foliosa	0.48	0.20	4.04	0.85	5.21	78.83
Fucus - Zostera	73.55	Tubificoides	2.42	1.95	12.28	1.38	16.69	16.69
		Oligochaeta	1.38	0.60	8.78	1.25	11.94	28.64
		Scoloplos armiger	1.59	0.69	8.55	1.48	11.63	40.26
		Idotea balthica	0.00	1.08	6.76	3.36	9.19	49.45
		Mya arenaria	0.20	1.01	6.25	1.05	8.50	57.95
		Littorina obtusata	0.00	0.85	5.02	1.09	6.83	64.78
		Pygospio elegans	0.83	0.35	4.95	1.12	6.72	71.50
		Mytilus edulis	0.00	0.57	3.76	0.79	5.11	76.61

b) Valnesfjorden	**Average dissimilarity**	**Species**	**Av.Abund Hab 1**	**Av.Abund Hab 2**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Bare sediment - *Fucus*	65.09	Tubificoides	0.28	8.28	16.90	2.80	25.97	25.97
		Littorina spp.	0.20	3.98	7.93	2.02	12.18	38.15
		Pygospio elegans	0.85	4.53	7.52	2.02	11.56	49.71
		Oligochaeta	3.31	5.93	7.14	1.44	10.96	60.67
		Peringia ulvae	2.27	4.80	5.40	1.69	8.29	68.97
		Chironomidae	0.98	2.86	3.96	1.85	6.09	75.06
		Mya arenaria	2.40	0.65	3.87	1.93	5.95	81.01
Bare sediment - *Zostera*	47.27	Tubificoides	0.28	4.17	9.95	1.12	21.04	42.84
		Pygospio elegans	0.85	3.49	7.62	1.39	16.12	37.16
		Peringia ulvae	2.27	4.68	6.86	1.69	14.51	51.67
		Oligochaeta	3.31	5.47	6.76	1.57	14.30	65.97
		Chironomidae	0.98	2.46	4.46	1.82	9.43	75.40
		Gammarus oceanicus	0.00	1.12	3.01	1.12	6.37	81.76
Fucus - Zostera	36.54	Tubificoides	8.28	4.17	8.97	1.62	24.56	24.56
		Littorina spp.	3.98	0.48	5.74	1.96	15.72	40.28
		Oligochaeta	5.93	5.47	4.00	1.31	10.95	51.23
		Pygospio elegans	4.53	3.49	3.90	1.46	10.67	61.89
		Capitella spp.	1.49	0.35	2.31	1.16	6.31	68.21
		Mya arenaria	0.65	1.78	2.21	1.84	6.05	74.26
		Peringia ulvae	4.80	4.68	2.07	1.25	5.67	79.94

c) Juvika	Average dissimilarity	Species	Av.Abund Hab 1	Av.Abund Hab 2	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare sediment - *Fucus*	61.36	*Scoloplos armiger*	3.46	1.93	14.19	1.69	23.13	23.13
		Tubificoides	2.57	1.53	14.07	1.24	22.93	46.06
		Oligochaeta	0.77	1.44	7.24	1.25	11.80	57.86
		Mya arenaria	0.98	0.00	6.97	1.09	11.36	69.22
		Peringia ulvae	0.40	0.20	3.76	0.61	6.12	75.34
		Eteone longa	0.20	0.48	3.25	0.81	5.30	80.64
Bare sediment - *Zostera*	54.69	Tubificoides	2.57	0.75	12.11	1.31	22.13	22.13
		Oligochaeta	0.77	2.36	11.42	1.38	20.89	43.02
		Scoloplos armiger	3.46	2.77	10.69	1.38	19.55	62.58
		Mya arenaria	0.98	0.95	4.70	1.40	8.60	71.18
		Peringia ulvae	0.40	0.57	4.48	0.90	8.19	79.36
		Eteone longa	0.20	0.68	3.84	1.03	7.03	86.39
Fucus - Zostera	61.26	*Scoloplos armiger*	1.93	2.77	14.69	1.46	23.97	23.97
		Oligochaeta	1.44	2.36	10.67	1.20	17.41	41.39
		Tubificoides	1.53	0.75	8.60	1.55	14.03	55.42
		Mya arenaria	0.00	0.95	6.05	1.60	9.88	65.30
		Eteone longa	0.48	0.68	4.30	1.06	7.02	72.32
		Peringia ulvae	0.20	0.57	3.93	0.88	6.42	78.74

Table x. Main contributing species to the dissimilarities between the location in a) Bare sediment, b) *Fucus* and c) *Zostera* from the similarity percentage (SIMPER) analysis. Cut-off percentage was set to 90%, and only species contributing to more than 5% of the dissimilarity is included in this table.

a) Bare sediment	**Average dissimilarity**	**Species**	**Av.Abund Loc 1**	**Av.Abund Loc 2**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Juvika-Røvika	70.86	*Scoloplos armiger*	3.46	0.69	24.29	1.86	34.28	34.28
		Tubificoides	2.57	1.60	17.22	1.79	24.30	58.59
		Mya arenaria	0.98	0.40	8.51	1.08	12.00	70.59
		Oligochaeta	0.77	0.00	5.87	1.10	8.28	78.87
		Peringia ulvae	0.40	0.00	4.19	0.48	5.92	84.79
		Scolelepis foliosa	0.00	0.48	3.95	0.72	5.57	90.36
Juvika - Valnesfjorden	76.91	*Scoloplos armiger*	3.46	0.00	17.03	4.15	22.14	22.14
		Oligochaeta	0.77	3.31	13.45	1.44	17.49	39.64
		Tubificoides	2.57	0.28	10.77	1.07	14.00	53.64
		Peringia ulvae	0.40	2.27	9.37	1.87	12.19	65.83
		Mya arenaria	0.98	2.40	6.88	1.70	8.95	74.78
		Hediste diversicolor	0.00	1.08	5.46	3.86	7.10	81.88
		Chironomidae	0.00	0.98	4.97	1.09	6.46	88.34
		Pygospio elegans	0.20	0.85	3.92	0.94	5.10	93.44
Røvika - Valnesfjorden	92.69	Oligochaeta	0.00	3.31	22.41	1.90	24.18	24.18
		Peringia ulvae	0.00	2.27	14.92	2.99	16.09	40.27
		Mya arenaria	0.40	2.40	13.70	2.75	14.78	55.05
		Tubificoides	1.60	0.28	9.37	2.24	10.11	65.15
		Hediste diversicolor	0.00	1.08	7.34	4.14	7.92	73.08
		Chironomidae	0.00	0.98	6.73	1.09	7.26	80.34
		Pygospio elegans	0.00	0.85	5.30	0.94	5.72	86.06

b) *Fucus*	Average dissimilarity	Species	Av.Abund Loc 1	Av.Abund Loc 2	Av.Diss	Diss/SD	Contrib%	Cum.%
Juvika-Røvika	62.31	Tubificoides	1.53	2.42	13.07	1.03	20.98	20.98
		Oligochaeta	1.44	1.38	11.91	1.49	19.12	40.09
		Scoloplos armiger	1.93	1.59	11.60	1.59	18.62	58.71
		Pygospio elegans	0.00	0.83	5.68	1.08	9.12	67.83
		Malacoceros spp.	0.40	0.00	3.33	0.75	5.34	73.17
		Eteone longa	0.48	0.00	3.25	0.75	5.21	78.39
Juvika - Valnesfjorden	84.59	Tubificoides	1.53	8.28	15.94	2.11	18.85	18.85
		Oligochaeta	1.44	5.93	10.98	1.54	12.98	31.82
		Peringia ulvae	0.20	4.80	10.94	3.32	12.93	44.75
		Pygospio elegans	0.00	4.53	10.14	2.85	11.99	56.74
		Littorina spp.	0.00	3.98	9.28	2.17	10.98	67.72
		Chironomidae	0.00	2.86	6.78	4.59	8.01	75.73
		Scoloplos armiger	1.93	0.00	4.57	1.03	5.41	81.14
Røvika - Valnesfjorden	78.10	Tubificoides	2.42	8.28	13.53	1.91	17.33	17.33
		Oligochaeta	1.38	5.93	11.54	1.61	14.77	32.10
		Peringia ulvae	0.00	4.80	11.33	3.77	14.50	46.60
		Littorina spp.	0.00	3.98	9.23	2.18	11.82	58.42
		Pygospio elegans	0.83	4.53	8.23	1.99	10.53	68.95
		Chironomidae	0.00	2.86	6.74	4.74	8.63	77.58

c) *Zostera*	Average dissimilarity	Species	Av.Abund Loc 1	Av.Abund Loc 2	Av.Diss	Diss/SD	Contrib%	Cum.%
Juvika-Røvika	75.80	*Scoloplos armiger*	2.77	0.69	13.61	1.37	17.96	17.96
		Oligochaeta	2.36	0.60	11.01	1.59	14.53	32.49
		Tubificoides	0.75	1.95	9.33	1.27	12.31	44.79
		Idotea balthica	0.00	1.08	6.05	3.68	7.98	52.77
		Mya arenaria	0.95	1.01	4.94	1.38	6.52	59.29
		Littorina obtusata	0.00	0.85	4.52	1.09	5.96	65.25
		Eteone longa	0.68	0.28	3.82	1.12	5.04	70.29
Juvika - Valnesfjorden	73.08	*Peringia ulvae*	0.57	4.68	12.43	2.84	17.00	17.00
		Pygospio elegans	0.00	3.49	10.46	1.85	14.31	31.31
		Tubificoides	0.75	4.17	9.39	0.99	12.84	44.16
		Oligochaeta	2.36	5.47	9.16	1.75	12.53	56.69
		Scoloplos armiger	2.77	0.00	8.20	1.39	11.22	67.91
		Chironomidae	0.00	2.46	7.28	3.03	9.96	77.87
Røvika - Valnesfjorden	77.61	Oligochaeta	0.60	5.47	13.78	3.80	17.76	17.76
		Peringia ulvae	0.20	4.68	13.34	3.10	17.19	34.95
		Tubificoides	1.95	4.17	9.71	1.21	12.51	47.46
		Pygospio elegans	0.35	3.49	9.49	1.63	12.23	59.68
		Chironomidae	0.40	2.46	6.00	2.13	7.73	67.41