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Seaweed cultivation and its impacts on biodiversity: a study from the Faroe Islands

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Abstract

Seaweeds are said to be ecosystem engineers, supporting biodiversity with habitat creation. This study assessed how large-scale seaweed cultivation by the company in the Faroe Islands - using three-year cultivation cycle and partial harvesting – affects local marine biodiversity. Methods included (a) comparing cultivation site organisms to biodiversity in natural seaweed beds (b) fish stomach content analysis and (c) eDNA samples taken in a transect, gradually distancing from the cultivation site. The dropper line sampling results from the three-year cultivation cycle practice from the seaweed cultivation site showed a significant increase in biodiversity enrichment over time. While single-season seaweed cultivations often provide temporary habitat, our results indicate that long-term cultivation combined with only partially harvesting - leaving holdfast, stem and part of the blade - offer greater ecological advantages. It was further concluded that cultivated *Saccharina latissima* supports a subset of the taxa also found in near natural seaweed habitats formed in part by *S. latissima*, indicating that the cultivation does not create entirely novel communities. The key difference is the lack in cultivations of benthic organisms inhabiting natural seaweed forests. Overlap of organisms found within fish stomachs and associated with natural and cultivated seaweed indicates that fish might find their prey also in cultivated seaweed structures. Comparison of results obtained by morphology- and eDNA-based analysis highlights biases of both methods, concluding to a complementary approach. Standardized biodiversity assessment protocols for seaweed cultivations are lacking; questions remain on their impact and to what extent it can be influenced.

247 words

Keywords: marine biodiversity, successive species, natural seaweed forest, eDNA, metabarcoding, marine ecosystem services

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Declaration of conflict of interests

No conflict of interests has been declared.

Availability of data and material

The dataset on invertebrate sampling in this publication is available in the Zenodo repository under a CC BY 4.0 license (Koch & Alberg, 2026).

Author contributions

Sophie J I Koch: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review and editing, Validation; **Jóhanna Alberg:** Investigation, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review and editing, Validation; **Urd Grandorf-Bak:** Conceptualization, Investigation, Data curation, Methodology, Writing – review and editing, Validation; **Eirikur Danielsen:** Data curation, Validation; **Amanada Vang:** Investigation, Validation; **Ása Jacobson:** Investigation, Writing – review and editing, Validation; **Ása Johannesen:** Formal analysis,, Validation; **Agnes Mols-Mortensen:** Investigation, Writing – review and editing, Validation; **Sólvá Jacobsen:** Investigation, Writing - review and editing, Validation; **Sander van den Burg:** Project administration , Funding Acquisition, Writing – review and editing, Validation; **Sven Künzel:** Data curation, Formal analysis, Validation; **Florian Weinberger:** Supervision, Methodology, Data curation, Formal analysis, Writing – review and editing, Validation.

1. Introduction

Ecosystems are complex networks of interacting species and their abiotic environment, and ecosystem services (ES) represent the benefits humans derive from healthy ecosystems (CICES V5.2; European Environment Agency (EEA), 2025). Biodiversity is classified as a *supporting ecosystem service* because it maintains habitat structure and sustains species diversity. Biodiversity encompasses the variety of species and individuals present at a given location, with dynamic and constantly changing interactions (World Resources Institute, 2003), and is essential for the functioning of marine ecosystems (IPBES, 2019). Seaweed is often described as an “ecosystem engineer” or habitat-forming species (Smale et al., 2013), as both natural and cultivated seaweed beds create habitats that enhance local biodiversity (Pereira et al., 2021; Radulovich et al., 2015; Teagle et al., 2017; Walls et al., 2016). These habitats provide food resources (Hehre & Meeuwig, 2016; Theuerkauf et al., 2021) and support reproduction and recruitment of associated species (Theuerkauf et al., 2021). Seaweed farms host a diverse assemblage of organisms, including invertebrates such as shellfish, crustaceans, and polychaete worms, as well as various fish species.

Quantitative studies highlight the biodiversity potential of seaweed habitats; a single kelp forest may support over 7,000 benthic organism individuals encompassing multiple species (Bernard et al., 2019). However, other evidence suggests that cultivated seaweed systems are unlikely to achieve equivalent biodiversity levels (Forbes et al., 2022). Management practices can strongly influence these outcomes; for example, longer cultivation times have shown to increase taxa richness (Corrigan et al., 2023b, 2023a; Walls et al. 2016). However, no study yet assessed developments during three-years of cultivation and with partially harvested seaweed lines. The objective of this study was to assess the impact this particular cultivation technique on the local marine biodiversity. The objective was addressed via the following research questions:

- 1) Which species (very common, rare or invasive) and how many species can be found within these cultivation units?
- 2) How does the abundance and richness of organisms within the cultivation differ within the seasons, over the years, with different exposures?
- 3) Are organisms found, and biodiversity developed, closer to natural seaweed beds than with one seasonal cultivation systems?

The investigated seaweed company from the Faroe Islands uses a three-dimensional cultivation system, practices partial harvesting and a three-year cultivation cycle. It presents thus a unique case, different to conventional one seasonal seaweed cultivations and was thus used as a case study. Results can be used to inform management practices oriented towards biodiversity benefits. No standard methods for biodiversity assessments in seaweed farms exist, for this reason we compared

approaches based on morphological identification of farm-associated organisms with an eDNA-based approach.

2. Methodology

2.1. Study site

2.1.1. Funningsfjørður for cultivated seaweed

The study site of the cultivated seaweed is located in the Faroe Islands in the fjord Funningsfjørður. A semi-exposed farm site Funning (62° 26'38.5", -6° 9'59.076") is located in the central part of the fjord and a nearshore exposed site Barmur (62° 28'35.94", -6° 9'28.520") is located in the outer part of the fjord (Figure 1, green).

The semi-exposed site has a water depth of 20-30 m, little to no current and maximal wave heights of 2 m. The exposed site has a depth of 50 to 70 m, water currents of up to 15-25 cm s⁻¹ and wave heights of up to 4 m (Bruntse et al., 1999; Norði & Patursson, 2012). Muddy substrate was below the cultivation sites. The annual water temperature surrounding the farms was between 7 to 11 °C and the salinity at around 35 ppt (Bruntse et al., 1999; Larsen et al., 2008). According to the exposure scale from Bruntse et al. (1999), ranging from sheltered (9) to exposed (0), the semi-exposed site was a 3.5 and

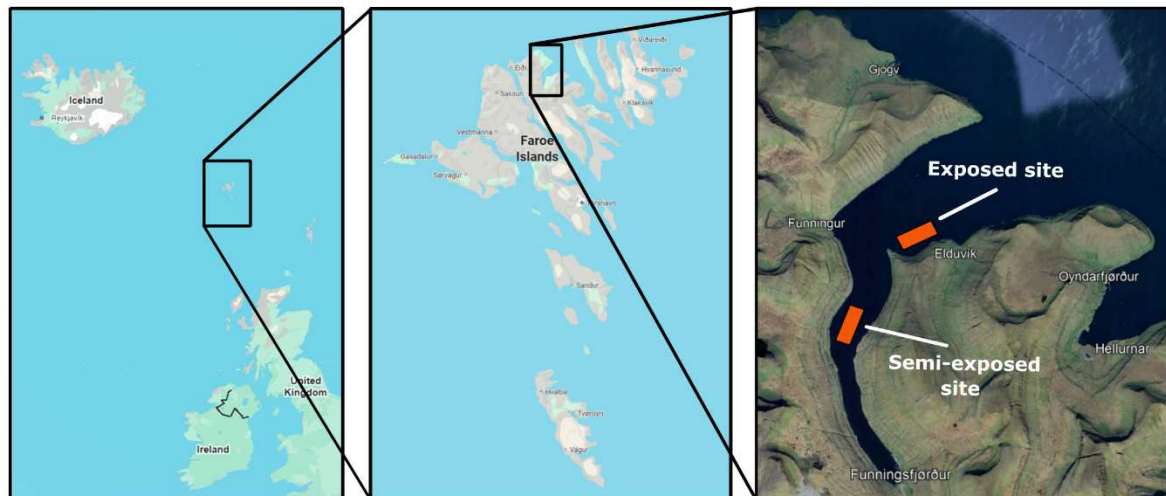


Figure 1: Geographical location of the investigated cultivated seaweed sites in the Faroe Islands.

the exposed site a 2.8.

The seaweed species cultivated was *Saccharina latissima* (Linnaeus) C.E. Lane, C.Mayers, Druehl & G.W. Saunders, a seaweed species naturally found within the fjord. It was cultivated using a unique 3D structure with vertical dropper lines of 10 meters length shown in Figure 2. The lines were left in the water for 3 years with a partial harvest once or twice a year from April to October.

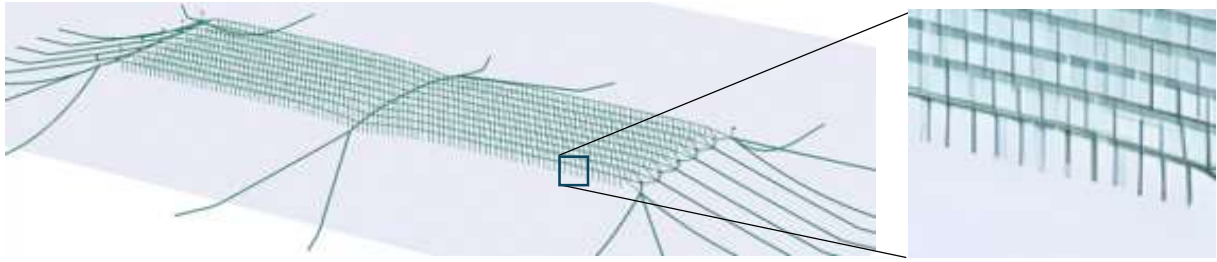


Figure 2: Seaweed cultivation structure showing the vertical dropper lines.

2.1.2. Kaldbaksfjørður for natural seaweed forests

The study of natural seaweed took place in 2022-2023 in Kaldbaksfjørður, located in a distance of roughly 30 km from our sampled cultivation facility in Funningsfjørður. The sampled site is called Mógvanes (Fig. 3), and according to Bruntse et al. (1999) it is categorized as a semi-exposed site ($62^{\circ} 0601'$, $-6^{\circ} 8227'$). The fjord faces out towards Tangafjørður and is exposed to the open ocean from southeast direction. The fjord is 6.6 km long, maximum 60 m deep and about 1700 m wide at the entrance, which has a sill at about 40 m depth. The sampling was performed in three transects from the shore and 30 m outwards at a maximum depth of approximately 15 m.

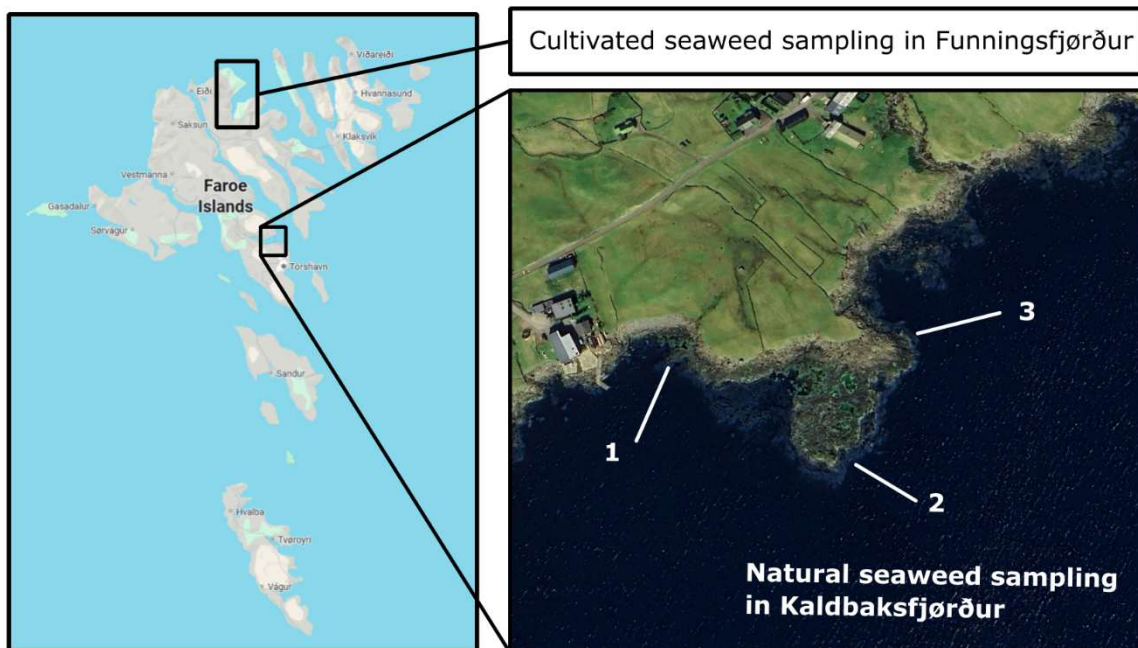


Figure 3: Sampling site of natural kelp in Kaldbaksfjørður. 5, 10, 15, 20, 25 and 30 m bottom depth contours are indicated. Gillnets were deployed along sections 1, 2 and 3.

2.2. Sampling

2.2.1. Funningsfjörður for cultivated seaweed

Dropper line sampling

Two series of sampling were realized to allow for a seasonal comparison of the associated organisms. The first sampling was carried out in early spring (April 2024) at the beginning of the growth period, and a 2nd sampling in summer (July 2024) when the seaweed was fully grown. Periods of expected low biodiversity in the spring and high biodiversity in the summer could thus be captured. At each sampling three replicate dropper lines were taken from 1st-, 2nd- and 3rd year horizontal lines at the exposed site to capture the full life cycle of the seaweed. In addition, 3rd year dropper lines at the semi-exposed site were sampled in order to compare the effect of exposure on biodiversity. To collect a dropper line, a net (opening diameter 1.5 m, length 2 m and mesh size 1 cm) was lowered below the 10 m vertical line, positioned below the line with help of an anchor and pulled up. The net containing the entire single vertical line and the organisms living in and on it (Fig. 4, left) was then brought onboard and weighed, before the line was placed into a fish box full of seawater (Fig. 4, middle). The net was rinsed thoroughly above the fish box so as to not lose any organisms bigger than 1 cm (Fig. 4, right).

The growth line was carefully washed in the fish box and removed in segments to release as many attached mobile organisms as possible into the fish tub. Then, segments of 30 cm length were taken at the 4th and 7th meter of the line and placed separately in bags for further analysis (sessile samples). The water and organisms in the fish box were rinsed through sieves (1 mm mesh size) to catch all the detached (mostly

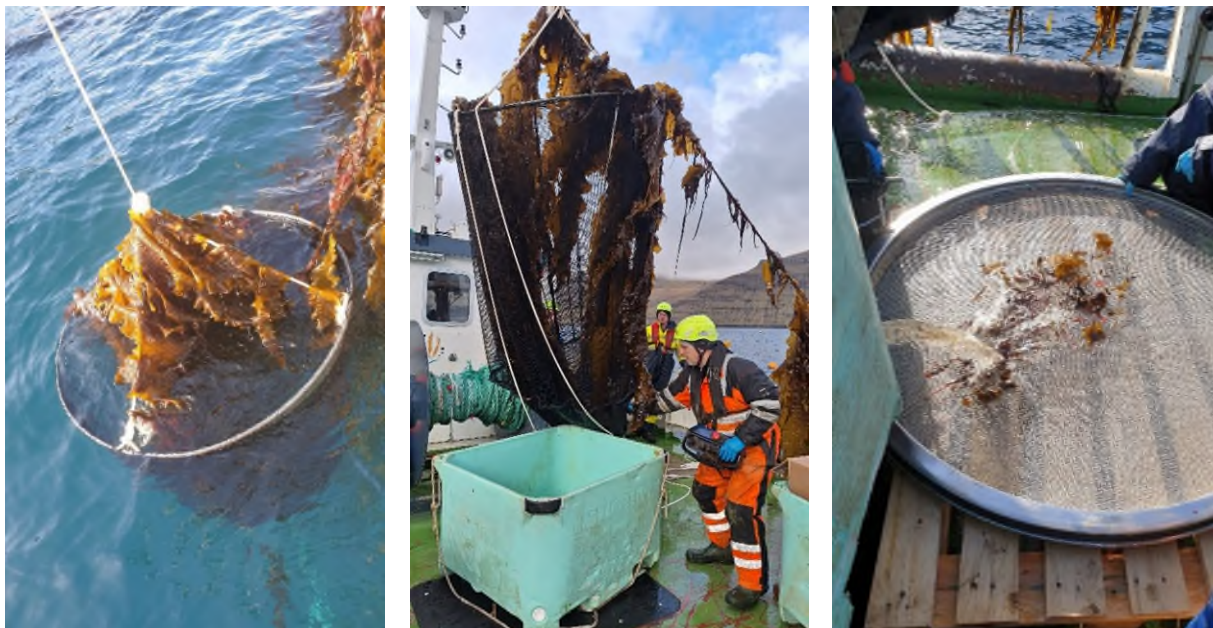


Figure 4: Sampling process. Left: Vertical line being lifted out of the water. Middle: vertical line being placed in the fish tub. Right: mobile organisms being filtered out.

mobile) organisms (Fig. 4, right), which were placed in bags for further analysis (mobile samples). This was done for all 12 lines, in both sampling events.

The bags with the samples were brought to shore, kept at 10 °C and sorted the day after sampling. For the sessile samples, all organisms visible with the bare eye were picked off the seaweed blades and holdfast and the line itself and placed in a jar with 70% ethanol for further analysis. For the mobile samples, all individuals larger than 1cm were also placed in a jar with 70% ethanol. Bryozoans, Hydrozoa and Porifera were recorded as present, but not quantified. All jars were stored in a cool room (10 °C) until organisms present in the samples were identified to the lowest taxonomic level possible and counted (July and September 2024). Since organisms smaller than 1 cm could have been washed out of the net, we did not quantify them but took a small sub-sample of each organism for identification.

Environmental DNA sampling

Water samples were taken for eDNA analysis of organisms in the area. 1.5l bottles of store-bought mineral water were emptied, opened beneath the water surface and once full of seawater, closed under the water surface. This was done for both the semi-exposed and the exposed site with three replicates at each sampling point. The sampling points were going further away from the cultivation in a transect: in the middle of the seaweed cultivation unit (in results referred to as 'middle'), at one meter outside the unit (edge), at 100 meters away (100 m) and at 500-1000 meters away (away). In July additional samples of water were collected at two natural kelp sites in Funningsfjørður (n=3), thereof one close to the exposed site and one further inside the fjord, rather sheltered (also n = 3).

In the laboratory all the water from each sample was pressed portion wise through filter cartridges (0.45 µm sterivex-HV filter, Millipore) using sterile plastic syringes of 50 mL, one filter and multiple syringes for each sample. The cartridges were then filled up with 100% ethanol, sealed with parafilm and kept at -18 °C. The content of two previously unopened bottles of mineral water was filtered in the same way to pick up any DNA that might stem from the mineral water ("filtration controls"). This was done for both seasons.

To confirm the organism identification based on morphology genetically, subsamples containing one individual of each of the organisms found in each dropper line sample were stored in a 50mL centrifuge tube containing 70% Ethanol and stored for metabarcoding in a freezer.

2.2.2. Kaldbaksfjørður for natural seaweed forests

Invertebrate sampling

Preliminary macroalgal assessments were conducted using a remotely operated vehicle (ROV) to gain a visual overview. Based on ROV footage, biological sampling was

carried out at 4 m and 8 m depths at three transects. At each depth, quadrats of 0.25 m² were placed on the seafloor, and all biomass within the frame was collected, weighed, and identified. The sampling took place in July 2022.

Sampling of fish stomachs

To catch the fish for the stomach content analysis, a total of 11 trips were conducted between 22 April 2022 and 19 April 2023. Sampling equipment consisted of floating and bottom gillnets, as well as traps. Initially, Minnow Traps were used but were later replaced with eel traps. Nets were generally set at around 9 a.m. and retrieved at approximately 2 p.m. to minimize crab bycatch associated with night-time hauls. Captured fish were measured, weighed, sexed, and sampled for gonad and stomach content analyses.

The stomachs of 10 Saithe were analyzed. Fish stomachs were collected and stored individually in labelled plastic bags at –20 °C until analysis. Prior to processing, samples were thawed in cold to lukewarm water. Each stomach was inspected to ensure it was intact and then gently cleaned of adhering tissue and debris.

Stomachs were blotted dry, weighed (full stomach weight), and the degree of fullness was visually estimated using a five-point fullness index (1 = empty, 5 = distended). Stomachs were then transferred to Petri dishes and cut open longitudinally. All contents were carefully removed, including by rinsing with distilled water if necessary, and transferred to the dish. The empty stomach was dried on tissue paper and reweighed (empty stomach weight).

Stomach contents were diluted with distilled water as required and examined under a stereomicroscope using a counting chamber equipped with an ocular micrometer. Prey items were identified to the lowest feasible taxonomic level, and their state of digestion was categorized using a five-point digestion index (1 = undigested, 5 = fully digested). Large prey items (e.g. fish and large isopods) were also weighed separately.

For each prey category, both the number of items recorded, and the number of individuals represented were noted. Fragmented organisms were handled consistently: if only one body part was present and no whole individuals, it was counted as one individual; otherwise, body parts were tallied separately but not assigned to individuals. Non-food items (e.g. stones, plastic fibers) were recorded but excluded from prey counts.

A report served as basis for some of the data on fish gut content and invertebrate biodiversity in natural seaweed forests, written by four of the co-authors (Jacobsen et al., 2025).

2.3. Data analysis for cultivated seaweed

Quantifying dropper line samples

Organisms present in all samples were identified based on morphological traits, using Hayward (1998) and Hayward & Ryland (2017), and counted. Identifications were verified by comparison with metabarcoding results obtained for subsamples of these samples (see below) and in some cases corrected accordingly.

To combine the data obtained for line and mobile samples, the following steps were conducted: Mobile organisms in the mobile samples and sessile organisms in sessile samples were counted, but sessile organisms found in the mobile samples, (i.e. fallen off shells and clams), and mobile organisms that were smaller than the mesh size of the sampling net) were ignored (Table S1 supplementary material: 'not considered'). Mobile organisms attached to the line found within sessile samples were counted, resulting in five taxa being considered both in mobile (only larger than one cm) and sessile samples (all sizes): *Hyas coarctatus*, *Caprella mutica*, *Galathea nexa*, *Dendronotus frondosus* and *Polychaeta* (Table S2 supplementary material). Correspondingly, individuals of all sizes (found in the line samples) and individuals >1 cm² (found in the mobile samples) were considered separately for these taxa. Data obtained from sessile samples representing 30 cm in the 4 m and 7 m ranges of the same vertical growth line were pooled and extrapolated from 60 cm to 10 m, the length of a dropper line. Finally, sessile samples and mobile samples were added together to represent one sample for one dropper line.

Analysis of eDNA

The water samples and subsamples of dropper lines were transported to GEOMAR Helmholtz Center at Kiel, Germany. Prior to DNA extraction ethanol was evaporated from the cartridges in a lyophilizer. The dropper line samples were freed of ethanol using an evaporator, freeze-dried to remove traces of water and pulverized in a bead beater before subsamples were taken for extraction. DNA was extracted from organism samples by incubation for one h at 56 °C on a shaker in Tris buffer (1 mL; 100 mM, pH 8.1) containing cetyltrimethylammonium bromide (CTAB, 2%), EDTA (20 mM) and proteinase K (20 µg µL⁻¹, 1 µL mL⁻¹) (Doyle & Doyle, 1987). The cartridges were extracted for 4 h at 56°C in a hybridization oven, using the same buffer. All extracts were subsequently purified as described in Doyle & Doyle (1987). AccuStart PCR ToughMix polymerase and the COI minibarcoding primers nsCOIFo and mlCOLintK were applied in the first PCR step, following the protocol described in Günther et al. (2018). The resulting PCR products were multiplexed using Kapa HiFi Polymerase (Roche) with the buffer provided by the producer. In PCR2 as described in Gohl et al. (2016) and subsequently separated by agarose gel (2 %) electrophoresis. The target amplicon content of the individual samples was standardized, based on the intensity of gel green (Merck Millipore) stained DNA band fluorescence on photos obtained in the UV illuminator. The intensity was analyzed and quantified using the ImageJ software package (Rueden et al., 2017). Mixed samples with approximately equimolar target amplicon contents of all individual samples were then prepared. The resulting pooled

sample was separated from excess primers and DNA fragments by gel electrophoresis and the band with the length of the desired amplicon was cut out of the gel and purified with a gel extraction kit (Zymo Clean Gel DNA Recovery from Zymo Research). The resulting DNA library was sequenced on an Illumina MiSeq sequencer at the Max-Planck-Institute for Evolutionary Biology.

Demultiplexed reads were processed unpaired, using the qiime2 software package (Bolyen et al., 2019). The reads underwent a quality filter using the DADA2 plugin (Callahan et al., 2016) and chimeras were removed as implemented in qiime2. Amplicon sequence variants (ASVs) detected in the control water bottles were considered as contaminants and eliminated from the data set. For annotation of the remaining 11632 ASVs three different data bases were used. The MetaZooGene (MZG) database (Bucklin et al., 2021) was downloaded in its entirety for this purpose. The COI databases in GeneBank (Benson et al., 2013) and in the Barcode of Life (BOLD) database (Ratnasingham & Hebert, 2007) were downloaded excluding all insect genes except those of dipterans. Sequences containing any ambiguous bases (3.6 % of all sequences in the case of MZG, slightly more in the other two cases) or representing unidentified taxa were removed from the data sets prior to use. Taxonomies linked with the remaining sequences were obtained using the “accessiontoTaxa” procedure implemented within the “taxonomizr” package for R (R Core Team, 2025). Annotations were then conducted in qiime2 using the vsearch algorithm. Only reference sequences were admitted in this procedure that exhibited complete overlap with reads to be annotated and at least 80% sequence identity. After repeatedly annotating the COI reads with the three different databases, the result with the highest percentage identity between read and reference read was accepted as the best. Species identification was only considered as correct if a read and a reference sequence matched by at least 97%. A few ASVs representing non-marine mammals (humans, sheep and cat) were not considered in subsequent analyses.

Statistical analyses

For multivariate statistics PRIMER v7 with the PERMANOVA add-on was used. For directly counted abundances of organisms Bray-Curtis similarity ordination was used, PERMANOVA was conducted with up to 99 999 permutations under an unrestricted model and dummy organisms were added to better differentiate samples with zero or just one organism. Distributions of ASVs among water samples were analysed using Jaccard distance ordination and PERMANOVA was conducted with up to 999 999 permutations. When a factor showed a significant effect ($p < 0.05$), pairwise comparisons of levels were conducted. For calculation of Shannon indices and generation of cluster graphs PRIMER v7 was used, while the bar diagrams were made using the GraphPad Prism 11 software. To identify which organisms contribute most to differences between samples, Canonical Analysis of Principal Coordinates (CAP) based on Bray-Curtis similarities was performed.

A project report written by four of the co-authors, including the first author, served as a basis for the results from dropper line sampling and analysis (Koch et al., 2025). The

dataset supporting the project report is publication is available in the Zenodo repository under a CC BY 4.0 license (Koch & Alberg, 2026).

3. Results

3.1. Results from cultivated seaweed in Funningsfjørður

3.1.1. Organisms present in the cultivation unit

Dropper line samples

Our dropper line results differentiated between 21 quantified taxa (Table 1) and three unquantified taxa (*Porifera*, *Bryozoa* and *Hydrozoa*, S1 cf supplementary material). Our quantified dropper line results represented five phyla, of which we identified eight classes, 11 Orders, 14 Families, 13 Genera and 10 Species.

As previously mentioned in Koch et al. (2025) the saltwater clams (*Anomiidae*) were the most dominant organisms found overall, followed by the amphipods and sea snails (*Lacuna vincta*). However, bivalves only started to appear from the 2nd year onwards, thus the most dominant species in the 1st year were the amphipods, followed by snails *L. vincta* and Skeleton shrimp *Caprella mutica*. In the samples from April saltwater clams (*Anomiidae*) were by far the most dominant organisms, followed by brittle worms (*Polychaeta*) and amphipods. Despite the decrease in total numbers of saltwater clams, *Anomiidae*, from April to July, they were still the most dominant in July, followed by amphipods, and *L. vincta*, whose abundances were now in the same range of magnitude (Table 1).

Differences become visible, such as the role the seasons can play in organism abundance, but also the years, as the 1st year samples distinguish themselves from the 2nd and 3rd year samples by their limited number of organisms.

Many organisms appeared or increased in abundance in July (Table 1), when *S. latissima* was fully grown. For example, *L. vincta* multiplied by factor 586, barnacles (*Balanus sp.*) by factor 27 and amphipods by factor 12.5 (Table 1). However few organisms were more present in the springtime, such as saltwater clams (*Anomiidae*), squat lobster (*G. nexa*) or brittle worms (*Polychaeta*).

Water eDNA samples

The most frequent organisms detected in six or more water samples were compiled and compared to the organisms identified morphologically in the dropper line samples (Fig. 5). Taxa not identified to the species level in the dropper line samples, such as Cnidaria,

Porifera, Bryozoa, Rhodophyta or Phaeophyceae, were for this comparison also not considered in the water samples, even though the eDNA method detected them (Fig. 5).

Both methods detected many of the same taxonomic groups, mainly within the classes of Gastropoda, Malacostraca, Thecostraca and Polychaeta. Several species of Polychaeta were frequently detected in the eDNA samples, but not differentiated in the dropper line samples. However, in the dropper line subsamples analysed by metabarcoding many of these species were also detected, as indicated by * in the eDNA list. On the other hand, a few species detected in the dropper line samples were not or only rarely detected with the eDNA approach. The eDNA method did not detect organisms of the class Echinoidea and those of the phylum Chordata, the order Decapoda and the class Bivalvia only rarely, while the phylum Rotifera and the class Copepoda were not detected in dropper line samples.

Table 1: Quantity and list of identified organisms from dropper line samples within the seaweed cultivation site. The list is confirmed and adjusted with eDNA samples from dropper lines. Indet. stands for organisms that were not possible to identify to a higher taxonomic level. Shades of green represent quantities, with darker shades being higher and lighter green being lower.

						Site	Exposed						Semi exposed		Both sites			Both sites		To	
						Season	April			July			April	July	Both seasons			April	July		
Phylum	Class	Order	Family	Genus	Species	Year	1	2	3	1	2	3	3	3	1	2	3				
Mollusca	Bivalvia	Mytilida	Mytilidae	Mytilus sp.			0	67	17	0	350	217	300	367	0	417	900	383	934		
		Adapedonta	Hiatellidae	Hiatella sp.			0	1867	900	0	2450	1500	683	3384	0	4318	6468	3451	7335	1	
		Pectinida	Pectinidae	Aequipecten	<i>Aequipecten opercularis</i>		0	17	0	0	0	0	17	0	0	17	17	33	0		
			Anomiidae				0	35307	34957	0	16487	8835	6151	6518	0	51794	56461	76415	31840	10	
	Patellogastropoda	Lottiidae	Tectura	<i>Tectura virginea</i>		0	0	0	0	0	0	17	0	0	0	17	17	0			
	Gastropoda	Nudibranchia	Dendronotidae	Dendronotus	frondosus (>1 cm2)	0	0	0	3	3	1	1	0	3	3	2	1	4			
				Dendronotus	frondosus	0	0	0	0	0	17	0	50	0	0	67	0	67			
	Mesogastropoda	Littorinidae	Lacuna	<i>Lacuna vincta</i>		0	17	0	2284	6035	5568	17	7918	2284	6051	13503	33	19521	2		
		Oregoniidae	Hyas	<i>Hyas Coarctatus</i>		0	7	10	0	5	6	2	14	0	12	32	19	25			
	Arthropoda	Decapoda				<i>Hyas Coarctatus</i>		0	117	50	67	1867	305	0	217	67	1984	572	167	2389	
					<i>Galathea nexa</i> (>1 cm2)		0	9	6	0	1	1	1	2	0	10	10	16	4		
					<i>Galathea nexa</i>		0	83	17	0	50	0	0	0	0	133	17	100	50		
			Caridea	Hippolyte	<i>Hippolyte varians</i>		0	1	2	0	1	0	8	3	0	2	13	11	4		
Amphipoda		Caprellidae	Caprella	<i>Caprella mutica</i>		0	0	0	2	0	0	0	0	0	2	0	0	0	0		
					<i>Caprella mutica</i>		0	17	0	283	367	1327	0	918	283	383	2245	17	2612		
Amphipoda indet.						0	467	567	3234	5301	15736	667	317	3234	5768	17287	1700	21354	2		
Isopoda		Idoteidae	Idotea	<i>Idotea balthica</i>		0	0	0	0	0	0	0	2	0	0	2	0	2	0	2	
			Idotea indet.			1	2	3	1	0	0	0	2	2	2	2	7	8	2		
Thecostraca		Balanomorpha	Balanidae	Balanus sp.		0	167	217	67	1434	984	150	11769	67	1600	13119	533	14186	1		
Actinopterygii					0	1	0	1	1	4	4	2	1	2	10	5	7				
Chordata	Asciidiacea	Phlebobranchia	Asciidiidae	Asciidiella	<i>Asciidiella scabra</i>	0	0	0	0	0	33	0	550	0	0	583	0	583			
			Asciidiella sp. indet.		0	67	33	0	50	0	50	333	0	117	417	150	383				
Annelida	Polychaeta (>1 cm2)				0	108	29	5	15	16	77	75	5	123	197	214	106				
	Polychaeta				0	2417	583	17	567	1184	1250	1934	17	2984	4951	4251	3684				
Echinodermata	Echinoidea				0	0	0	0	1	0	0	0	0	1	0	0	1				
Ichthyoplankton (>1 cm2)					0	0	0	0	3	0	0	0	0	3	0	0	3				
Ichthyoplankton					0	0	0	1	3	0	0	1	1	3	1	0	4				

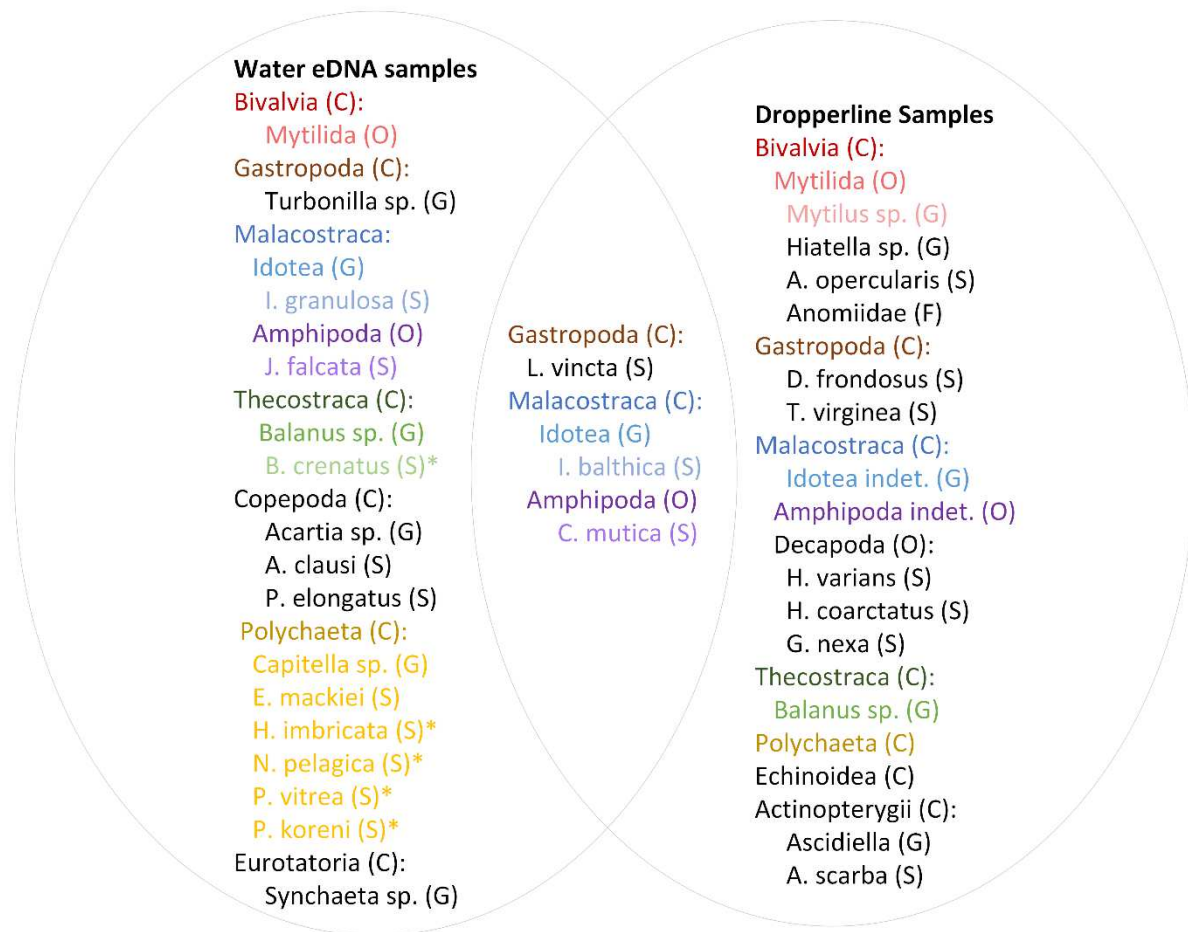


Figure 5: Comparison of organism lists from both biodiversity identification methods: water eDNA results versus morphologically identified organisms from dropper lines. Same colours represent the same taxon, even though potentially different species were identified.

*Signify that these species were also detected by metabarcoding of biomass samples results from the subsamples of the dropper lines, used for organism confirmation, but are not detailed in the organism list, as they were not distinguished morphologically by the researchers.

3.1.2. Statistical testing of biodiversity development

PERMANOVA was used to test compositional differences among levels of the four factors 'year' (only for dropper line samples), 'season', 'exposure' and 'distance' (only for water samples) statistically and their interactions, when possible (Table 2). One-way-tests showed statistical significance for 'year' and 'season', but not for 'exposure' and 'distance'. Within July, cultivated and natural sites also differed significantly. Within the dropper line samples the two significant factors 'season' and 'year' also exhibited a significant interaction, when tested in a two-way-design. Further, because results obtained with eDNA-samples differed seasonally, the two factors 'exposure' and 'distance' were also tested separately for April and July samples, which revealed a significant effect of 'distance' and of 'exposure' in April only.

Table 2: P values of PERMANOVA for different factors for morphologically identified results as well as for eDNA water results.

PERMA NOVA	Factors	Dropper line		eDNA Water	
				April	July
One- way	Year	$F_{2,22} = 8.96$; $P = 1 \times 10^{-5}$		N.A.	N.A.
	Season	$F_{1,23} = 5.78$; $P = 5 \times 10^{-5}$		$F_{1,41} = 4.49$; $P = 1 \times 10^{-5+}$	
	Exposure	$F_{1,11} = 1.82^{++}$; $P = 0.12^{++}$		$F_{1,41} = 0.997$; $P = 0.36^{+}$	
	Distance	N.A.		$F_{3,36} = 0.93$; $P = 0.84^{+}$	
	Farmed vs. natural sites	N.A.		N.A.	$F_{1,23} = 1.56$; $P = 1 \times 10^{-6}$
Two- way	<u>Season x year</u>				
	Factor season	$F_{1,17} = 11.196$; $P = 4 \times 10^{-5+++}$		N.A.	
	Factor year	$F_{2,16} = 9.62$; $P = 1 \times 10^{-5+++}$		N.A.	
	Interaction season and year	$F_{2,16} = 3.72$; $P = 0.002^{+++}$		N.A.	
	<u>Exposure x distance</u>				
	Factor exposure	N.A.	N.A.	$F_{1,14} = 1.14$; $P = 0.03^{+}$	$F_{1,12} = 1.003$; $P = 0.43$
	Factor distance	N.A.	N.A.	$F_{3,14} = 1.09$; $P = 0.02^{+}$	$F_{3,12} = 1.02$; $P = 0.24$
	Interaction exposure and distance	N.A.	N.A.	$F_{2,14} = 1.04$; $P = 0.17^{+}$	$F_{2,12} = 0.99$; $P = 0.56$

*Without natural seaweed samples

**Only 3rd year line samples, as the semi-exposed site did not have samples from 1st and 2nd year lines 3rd year

+++Only the exposed site was tested in interaction with year, as the semi-exposed site had only 3rd year samples

3.1.3. Biodiversity development over time

Year

Pairwise PERMANOVA showed that 1st and 3rd year dropper line samples were compositionally most different ($P=1 \times 10^{-6}$), 1st and 2nd year line samples were also significantly different ($P=1 \times 10^{-5}$), while 2nd and 3rd year line samples were not ($P=0.5692$), as previously mentioned in Koch et al. (2025). These tests included the 3rd year samples from the semi exposed site, since the sites were not statistically different.

Using CAP, we identified organisms that play a main role in the difference among samples from different years. CAP clearly separated the 1st year line samples from those of the following years (supplementary material Fig. S1). The absence of six taxa contributed particularly strongly to this contrast, as they were all underrepresented in samples collected in year 1. These taxa were *Anomiidae*, *Hiatella sp.*, *G. nexa*, *Polychaeta*, *H. coarctatus* (>1cm²) and *H. coarctatus*. PERMANOVA, including a Monte Carlo test, statistically confirmed that *Polychaeta* ($P=0.017$) contributed most to this

separation of groups, with a very low number of individuals in the 1st year compared to the two other years (circled in Fig. 6).

Other organisms significantly creating a difference among samples of year 1 and other years were *Anomiidae* (P=0.0242) and *Hiatella* sp. (P=0.0175), both marked in Figure 6 by circles and also mentioned in Koch et al. (2025).

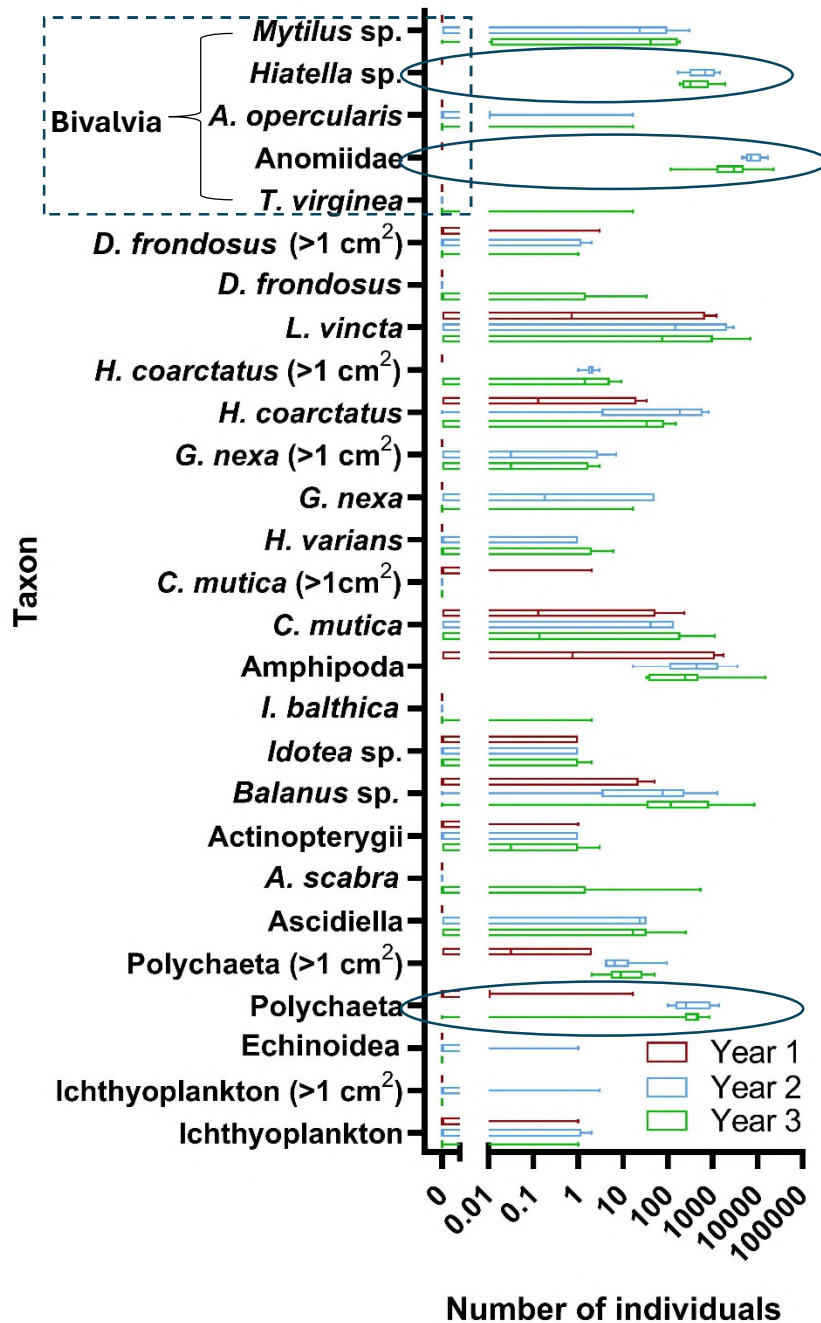


Figure 6: Bar diagram of data from both seasons comparing the years with the with the Median and interquartile ranges. Circles show the organisms responsible for creating the biggest difference in the samples. Bivalvia are framed (dotted line).

Season

Concerning the dropper line samples, Pearson regressions showed that *L. vincta* ($r=0.571$), *C. mutica* ($r=0.470$), *Hyas coarctatus* ($r=0.468$), *Ichthyoplankton* ($r=0.4181$) and *D. frondosus* ($r=0.354$) correlated most with the difference in the seasons. PERMANOVA, including the Monte Carlo tests showed that *L. vincta* (MC=0.0035), *Caprella mutica* (MC=0.0205), *H. coarctatus* (MC=0.0212) and *Ichthyoplankton* (MC=0.0422) were significantly responsible for the distinction of samples between seasons (circled in Fig. 7).

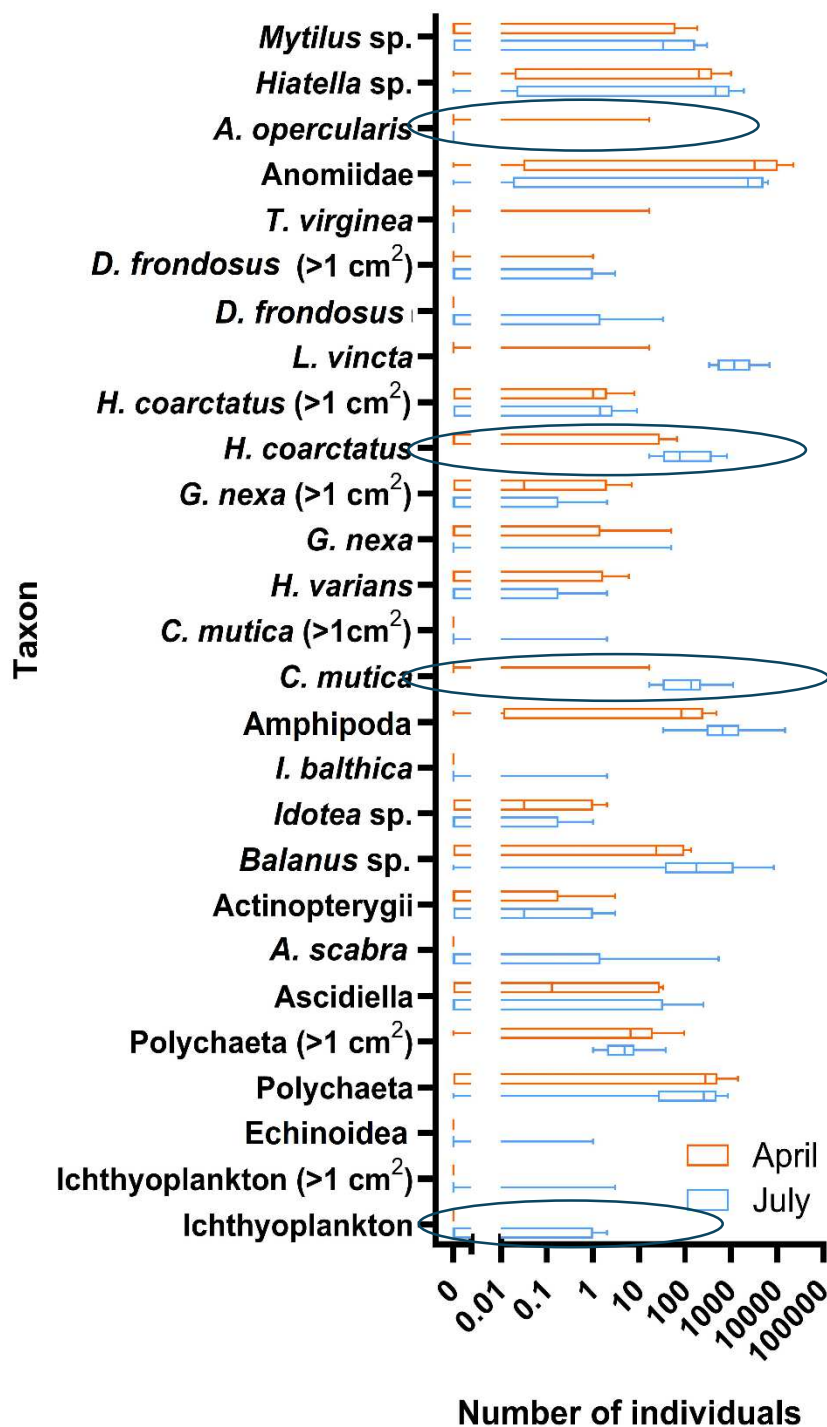


Figure 7: Bar diagram of data from all three years comparing the seasons (April and July), with the Median and interquartile ranges. Circles show the organisms responsible for creating the biggest difference in the samples.

Interaction of Season and Year

When looking at the interaction of the factors 'season and year' of the dropper line samples, statistically there was only a difference in seasons within the 3rd year samples ($P=0.0117$), in the 1st and 2nd year line samples there was no statistical difference (respectively $P=0.0998$ and $P=0.1$).

When looking at how the years changed within the season, only 1st and 3rd year line samples were statistically different ($P=0.0048$ in April and $P=0.0226$ in July), see Table 3. In general years were more different in April than they are in July; the similarity within the samples grew from April to July. To obtain further information, levels of the two factors ‘year’ and ‘season’ were pairwise compared in all possible combinations (Table 3), to test how and when the development in biodiversity changed.

Table 3: P-values obtained by post hoc PERMANOVA for different level combinations within the two factors ‘year’ and ‘season’.

		Year	1st year	2nd year		3rd year	
		Month	July	April	July	April	July
Year	Month	Time [month]	7	16	19	27	31
1st year	April	4	0.0998	0.0997	0.1004	0.0048	0.0179
	July	7		0.1	0.1005	0.0037	0.0226
2nd year	April	16			0.1	0.5698	0.0474
	July	19				0.076	0.8787
3rd year	April	27					0.0117

Significant differences were only detected for sample sets collected after the 2nd year. The consecutive interactions start being more significant and then statistically different within the 3rd year. Thus, the consecutive development in biodiversity is limited in the beginning, not being statistically different within the time steps of 4-9 months, but in the 3rd year changes are significant and statistically relevant, even within a 4-month step. These findings are in line with PERMANOVA results on the interaction of ‘season and year’ showing that statistically significant differences between the seasons only start in the 3rd year. The absence of significant differences between samples collected in year 1 and 2 in these pairwise tests contrasts with the significant differences between these years when PERMANOVA was conducted for the factor ‘year’ only. This can be explained by the lower number of samples and for this reason lower statistical power in tests of interactions.

Shannon index

The Shannon index, assessing the richness and evenness, was determined for each sub sample set, in order to compare the biodiversity development within the three factors ‘season’, ‘year’ and ‘exposure’, view Table 4. As previously mentioned in Koch et al. (2025) the Shannon index was 0 for the 1st year line April samples, as only one taxon was quantified (*Idotea sp.*). Samples collected in July had in general a higher index value than those collected in April and the 3rd year line July samples in the semi-exposed site had the biggest index value ($H=1.57$), followed by the 2nd year line July samples in the exposed site ($H=1.52$).

These results confirm prior results on higher biodiversity development in the 3rd year compared to the 1st year, and that 2nd and 3rd year are closer together, but differ from

prior results by showing a higher biodiversity in the 2nd than in the 3rd year. Since Shannon index calculates a combination of evenness and richness, while PERMANOVAS only consider richness, the organisms' richness index was calculated, confirming the PERMANOVA results on organism richness being the highest in the 3rd year (Table S2 cf. Supplementary material).

Table 4: Shannon index of averages of replicates.

	Exposed site				Semi-exposed site	Both sites
	All years	1 st year	2 nd year	3 rd year	3 rd year	3 rd year
April	0.32	0	0.54	0.43	1.24	0.83
July	1.24	0.95	1.52	1.24	1.57	1.40
Both seasons	0.78	0.48	1.03	0.83	1.40	1.12

3.1.4. Biodiversity differences over space

The Shannon index for all eDNA water samples was 4.6, while it was 4.9 for natural seaweed samples. An MDS graph (Fig. 8) of samples visually demonstrates the seasonal difference between the samples and a difference between samples collected in cultivations and natural habitats.

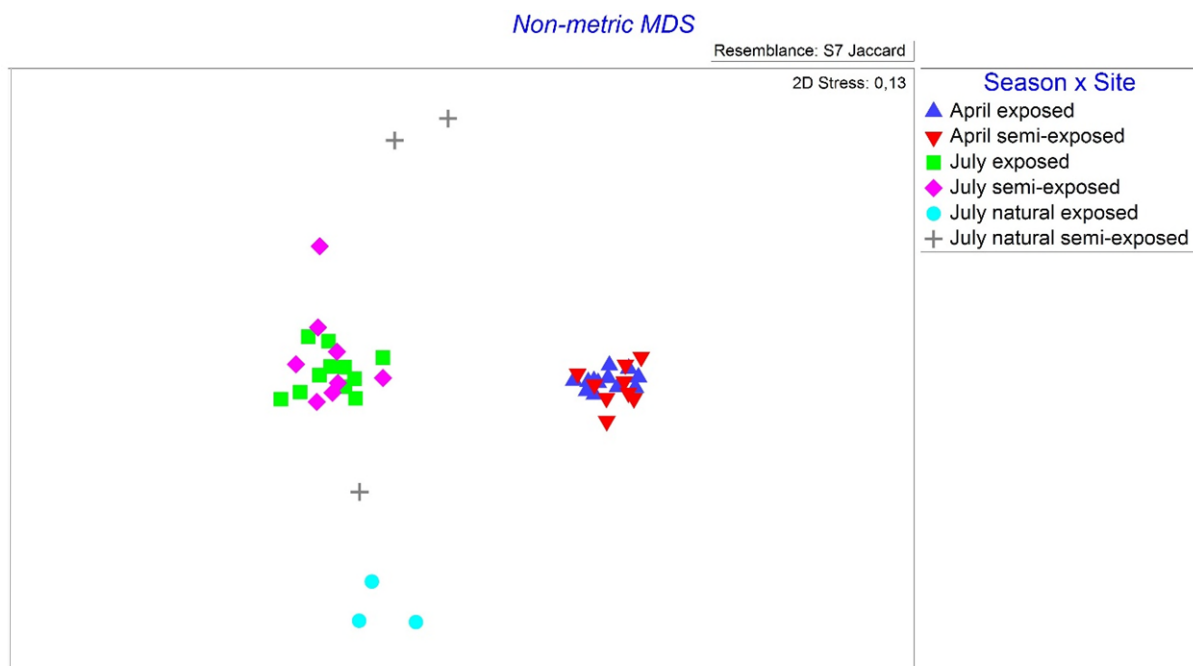


Figure 8: Non-metric MDS graph showing proximity of specific groups of water eDNA samples.

In April, pairwise PERMANOVA tests of the factor 'distance' revealed that water samples collected 500 to 1000 m away from the cultivation ("Away") differed significantly from samples collected within ("middle") or at the edge ("edge") of the cultivation and weakly significantly from those collected in a distance of only 100 m ("100 m", Table 5).

Table 5: Differences among levels of factor “distance” between eDNA water samples collected in July. Given are P-values of pairwise tests of levels of the factor as obtained by two-way-PERMANOVA, the second factor was ‘exposure’ (see Tab.2).

Distance	Edge	100 m	Away
Middle	0.1793	0.3765	0.0084
Edge		0.8773	0.0098
100 m			0.0799

3.2. Results from natural seaweed in Kaldbaksfjørður

3.2.1. Invertebrate abundance

Fifteen different invertebrate taxa, belonging to 6 different phyla, were detected in the six quadrat samples from the seaweed forest in Kaldbaksfjørður (Table 6).

Table 6: invertebrates identified in natural seaweed in Kaldbaksfjørður

Phylum	Class	Order	Family	Genus	Species
Porifera					
Cnidaria	Hydrozoa				
Mollusca	Bivalvia	Adapedonta	Hiattellidae	Hiattella sp.	
	Gastropoda	Mesogastropoda	Littorinidae	Lacuna	<i>Lacuna vincta</i>
		Patellogastropoda	Patellidae	Patella sp.	
		Trochida	Trochidae	Steromphala	<i>Steromphala cineraria</i>
Annalida	Polychaeta				
Arthropoda	Malacostraca	Amphipoda	Gammaridae		
			Caprellidae	Caprella sp.	
		Decapoda	Paguridae		
			Oregoniidae	Hyas sp.	
	Thecostraca	Balanomorpha	Balanidae	Balanus sp.	
Echinodermata	Ophiuroidea	Ophiurida	Ophiuridae	Ophiura	<i>Ophiura ophiura</i>
	Asteroidea	Forcipulatida	Asteriidae	Asterias sp.	
	Holothuroidea	Dendrochirotida	Cucumariidae	Cucumaria	<i>Cucumaria frondosa</i>
	Echinoidea				

3.2.2. Fish stomach content

Most of the ten saithe stomachs analyzed exhibited a medium fullness index, indicating they were neither empty nor completely full. Stomach fullness was generally higher between May and September compared to January. Eighteen different invertebrate organisms, belonging to five phyla, were found within these stomachs (Table 7).

Table 7: List of organisms found in fish stomach

Phylum	Class	Order	Family	Genus	Species
--------	-------	-------	--------	-------	---------

Nematoda					
	Gastropoda				
Mollusca	Bivalvia				
		Isopoda indet.			
			Idoteidae	Idotea sp. indet.	
		Isopoda		Idotea	<i>Idotea neglecta</i> <i>Idotea emarginata</i>
		Euphausiacea			
		Amphipoda indet.			
			Gammaridae indet.		
		Amphipoda	Gammaridae	Gammarus	<i>Gammarus locusta</i>
	Malacostraca		Caprellidae	Caprella sp.	
		Siphonostomatoida	Caligadae		
			Temoridae	Temora	<i>Temora longicornis</i>
		Calanoida	Calanidae	Calanus	<i>Calanus finmarchicus</i>
	Copepoda				
	Copepoda indet.				
Chordata	Actinopterygii				
Annelida	N.A.	Phyllodocida	Aphroditidae	Aphrodita	<i>Aphrodita aculeata</i>

*indet. stands for organisms that were not able to be further identified to a lower taxonomic level.

4. Discussion

4.1. Comparison of organisms found in natural- and cultivated seaweed

A key question is whether seaweed cultivations can act as habitats and support biodiversity (Bekkby et al., 2023; Forbes et al., 2022; Walls et al., 2016). Forbes et al., (2022) state, that seaweed cultivations typically create novel habitats that support distinct communities different to the ones in natural seaweed stands. Bekkby et al., (2023) further conclude that the habitat created by cultivated seaweed is not distinct from natural seaweed, but rather acts as a receiver for whatever communities species it is surrounded by. However, these studies did not measure biodiversity development beyond the 1st year, and our comparison of a three-year cultivation site to wild seaweed is the first of its kind.

In Figure 9 we compared our results on cultivated seaweed (section 3.1)(excluding the fish organisms found), to the results from natural seaweed (section 3.2) and a study done in 1999 assessing invertebrates in holdfasts and stipes of *Laminaria hyperborea* (Gunnerus) Foslie around the Faroe Islands in July to late August, see Table 9 and 10 in Bruntse et al. (1999). Bruntse et al. (1999) identified species from 2 holdfasts (age seven

and 11 years) and at stipes from 16 stations around the Faroe Islands. The Bruntse et al., (1999) study included samples from both soft and hard-substrate and also in the supralittoral, littoral and sublittoral stations. To compare their data to ours, we focused on the hard substrate sublittoral data.

Similarities

Yet, many of the taxa overlap in all three studies, indicating that our identified organisms in the cultivated seaweed are also found in natural seaweed around the Faroe Islands and that this seaweed cultivation does not create a completely novel and distinct habitat. Community composition and abundance would, however, further have to be assessed to make a meaningful statement about the similarity of the ecosystem created by cultivated seaweed to the one of natural seaweed.

Bruntse et al., (1999) state that amphipods (Crustaceans) made up almost half of the total number of specimens. Polychaeta, Nematoda, Isopoda, Copepoda, Prosobranchia(belongs to Gastropoda) and Bivalvia were also very common. Our results from the cultivated seaweed showed a similar pattern, also with Bivalvia (*Anomiidae* and *Hiatella* sp.), as well as *Amphipods*, *Gastropoda* and *Polychaeta* being the most abundant taxa. Other studies from Norway comparing cultivated seaweed to natural seaweed forests also found *Amphipods* and *Gastropoda* in both ecosystems (Bekkby et al., 2023; Christie et al., 2003).

Differences

eDNA results from Funningsfjørður show a growing difference in biodiversity with growing distance from the cultivation site. The main differences between cultivated and natural seaweed are:

- a seaweed cultivation of *S. latissima* of shorter duration (usually a few months, in the studied case 3 years) explaining why organisms such as *Nemertinea* and *Pygnogonida* were not found in cultivated seaweed, as they are associated with older holdfasts (11-year-old), going beyond the life cycle of cultivated seaweed (Bruntse et al., 1999).
- seaweed cultivations are located at the ocean surface instead of anchored in the seabed, where *S. latissima* would usually grow (Bekkby et al., 2023), explaining some of the differences seen in our comparison (Fig. 9): *Holothuroidea* (sea cucumber), *Asteroidea* (sea stars) and *Ophiuroidea* (brittle stars) are benthic organisms, and therefore not commonly found in seaweed cultivations structures located at the sea surface. *Asteroidea* and *Ophiuroidea* also appear rather in deeper water, 15- 20m (Bruntse et al., 1999), which would be below the depth of our seaweed cultivation and the sampling of natural seaweed from 2023.

Another interesting difference in the taxa identified is *C. mutica*, an invasive species from Japan, likely imported as fouling organism on ship hulls (Ashton et al., 2007) in the 90s into the Faroese Ecoregion and first registered in 2008 (Pers. comment Jan Sørensen; Ashton et al., 2006). Our results, and another study on seaweed cultivation in Norway (Andrews et al., 2025), detected this species only in cultivated seaweed, while a related native species of the genus *Caprella* sp. were found in both natural seaweed studies, in ours and in Bruntse et al (1999) (Fig. 9). *C. mutica* is frequently seen around fish farms, which are present in Funningsfjørður, but not in Kaldbaksfjørður. This could be one reason why it was not seen in natural seaweed samples. It was, however, spotted in seaweed cultivation also in Kaldbaksfjørður, but only once the lines were left in the water for longer than usual (Koester, 2022). Researchers suggest that the reason why *C. mutica* is commonly found on artificial structures, such as aquaculture

structures and not in natural seaweed, might be due to high competition with native species in natural seaweed (Adams et al., 2014; Koester, 2022; Willis et al., 2004).

Our results are from two different fjords of the Faroe Islands, but it can be argued that there will not be a big ecological difference between the fjords, since the Faroe Islands are relatively small- Kaldbaksfjørður and Funningsfjørður have a distance of roughly 30 km - and the exposure was assessed to be similar with a 3 for Kaldbaksfjørður and 2,8 – 3,5 for Funningsfjørður on Bruntse et al (1999) exposure scale, ranging from 0 (exposed) to 9 (sheltered).

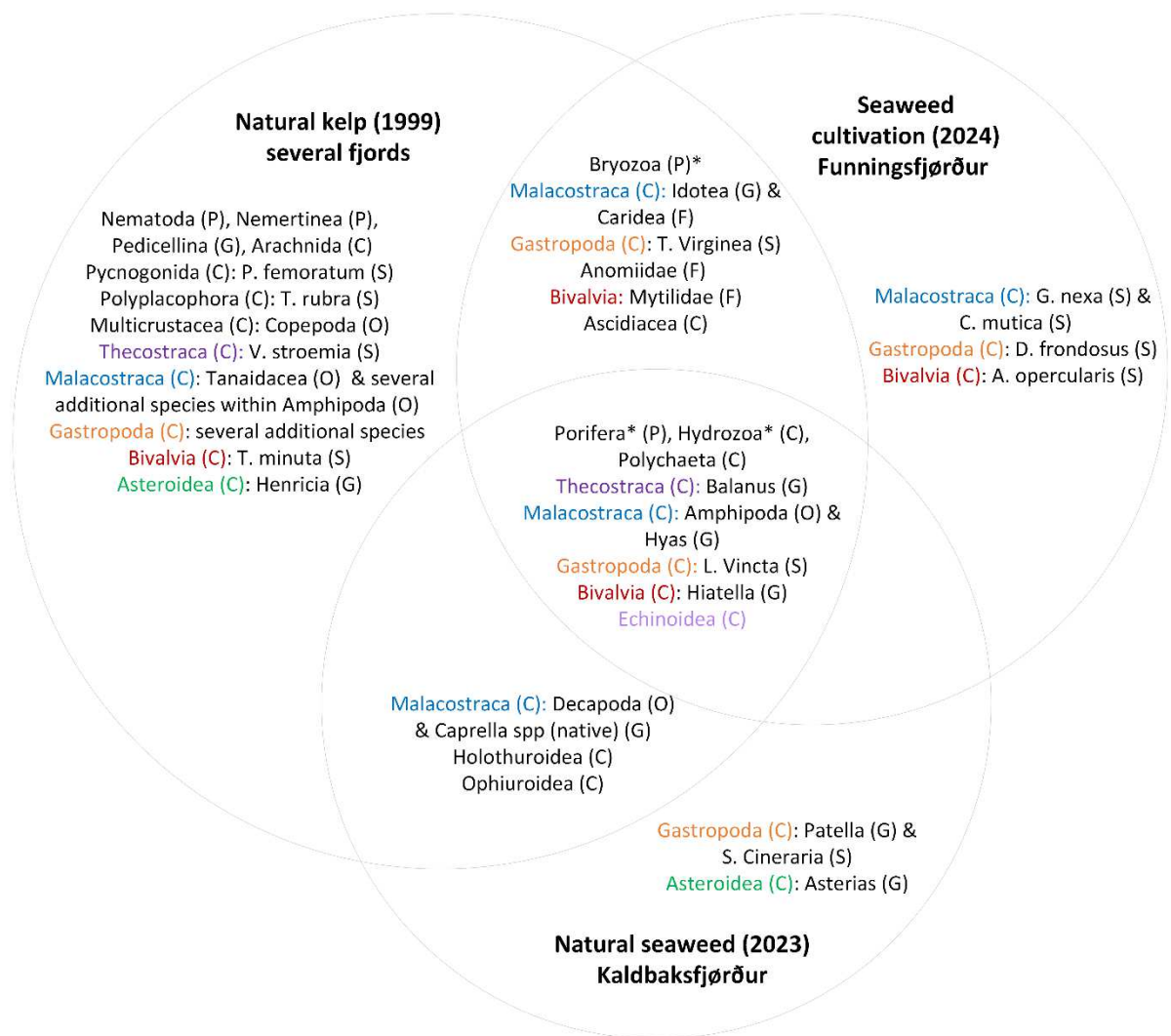


Figure 9: Comparison of invertebrates (excluding fish from cultivated seaweed samples) of three distinct studies in invertebrates around kelp around the Faroe Islands. The colours represent same classes that can be found in the different samples. Organisms are listed separately if there are different organisms of the same taxonomic level identified, if one of the studies had not identified further down the taxonomic level, organisms are presented at this level.

*Organisms not quantified in cultivated seaweed and therefore don't show up in Table S1 and not searched for in natural seaweed samples from Kaldbaksfjørður.

There is not a lot of literature available on these specific geographical ecosystems, and none on the fjords where our sampling events were conducted. We acknowledge that the sampling methods in both fjords were different, and it was not the same group of researchers identifying the organisms in both sites, potentially leading to different taxonomic errors. The higher taxa richness within Bruntse et al., (1999), might be due to the more elaborate set up and extent of their study and does not mean species richness has declined.

Bias was similarly observed across identical study sites but among distinct methodological approaches. Our comparative analysis revealed that morphological identification of organisms from dropper lines enabled the detection of certain taxa that eDNA analysis failed to identify, including specific bivalves and decapods. Notably, certain taxa, such as *Aequipecten opercularis*, *Anomiidae*, and *T. virginea* - all bivalves - were entirely absent from eDNA results, even when applying a lower confidence threshold. Conversely, the eDNA method facilitated the identification of species at a finer taxonomic resolution, which may be challenging to distinguish morphologically, as well as the detection of small planktonic organisms such as copepods and rotifers, which are imperceptible to the naked eye. Interestingly, in another study from Norway concluding, that eDNA did not detect differences in community composition the way traditional sampling can, had not found *C. mutica* in their eDNA results, but in their traditional sampling results (Andrews et al., 2025). Our eDNA results however detected *C. mutica*, showing another bias within the eDNA method carried out in different locations and labs.

Furthermore, to compare our two methods of biodiversity analysis, we established a threshold requiring taxa to be present in six or more water samples; however, expanding this threshold to include lower occurrence frequencies would broaden the list of detected organisms in the water eDNA results by a factor of approximately five.

4.2. The development of biodiversity over time

Our statistical tests confirm that the biggest difference in sample biodiversity is generated by the factors 'year' and 'season'. When looking at the interaction of 'year' and 'season', the increase in biodiversity is limited in the beginning, not being statistically different within 4–9-month segments, but in the 3rd year changes are significant and statistically relevant, even within the same year. This increase in biodiversity over the years is also seen in the Shannon index, being bigger in the 2nd and 3rd year than the 1st year for our samples, which only have mobile organisms present.

We compared these results to other studies which quantified species diversity in *S. latissima* cultivation sites. Our results from 1st year samples may be compared to one seasonal cultivation, such as in a study conducted in the Gulf of Maine with *S. latissima* and *S. angustissima*, which found the most dominant invertebrates to be amphipods

(*Lembos websteri*), copepods (*Paracalanus sp.*) and the skeleton shrimp (*Caprella linearis*) (Schutt et al., 2023). In the UK a study on *S. latissima* found amphipods, primarily *Jassa falcata*, to be most dominant - just as in our study - together with bivalves and bryozoans (Corrigan et al., 2023a). A study in Norway found isopods (*Idotea pelagica*) as a dominant species in the younger cultivation (3 months after seeding) and amphipods (*Caprella*) as a dominant species in the older cultivation (7 months after seeding) (Bekkby et al., 2023). We found those species also rather in the April than in the July samples, even though these animals were not dominant in our samples. Thus, when analyzing just the 1st year samples, the impacts from the cultivation system studied by us are still comparable to other one seasonal cultivation systems.

As soon as it goes beyond the 1st year samples, the overall composition of taxa is not comparable to other studied *S. latissima* cultivations anymore. *Anomiidae* bivalves, as well as other sessile fauna such as *Balanus sp.* and *Ascidella* become most abundant, indicating that the studied Faroese cultivation process provides enough time for successional species, not only pioneer species, to settle, which contrasts with the shorter time most other seaweed cultivation structures are in the water. Andrews et al. (2025) concluded in a study of one-season cultivation, that a key difference in biodiversity between cultivated and natural *S. latissima* habitats was the lack of *Lacuna* snails in the cultivation. *Lacuna*, however, is present in the seaweed cultivation with a three-year cycle.

These results hint at increasing similarity of cultivated *L. saccharina* habitats with natural habitats if cultivation times are prolonged and are in line with Corrigan et al., (2023b, 2023a) who observed that epibiont abundance, biomass, and richness only peaked after the usual harvest, quantified in three months post usual harvest samples. Walls et al (2016) even found that species richness in *L. digitata* farms was higher than in natural seaweed habitats when the alga was cultivated longer. Forbes et al., (2022) and Bekkby et al., (2023) also assume that a longer growth period for cultivated seaweed would increase its size and complexity. However, no study yet assessed three-year developments during cultivation. Taxa richness on *S. latissima* cultivation has shown to be higher after partial harvest (Corrigan et al., 2023a, 2024), this could be explained by the holdfast usually being the part of the seaweed with particularly high abundance and diversity of invertebrates, which grows older with the partial harvest methods (Bruntse et al., 1999; Corrigan et al., 2023a; Katharoyan et al., 2024). Corrigan et al., (2023a) thus even suggested that partial harvest could retain habitat provisioning and other associated ecosystem services.

4.3. The impact of harvest

Forbes et al., (2022) state, that seaweed cultivation is usually too short to create a meaningful habitat comparable to natural seaweed forests and cultivation thus

generally has lower and different biodiversity than natural seaweed forests (Andrews et al., 2025; Bekkby et al., 2023; Forbes et al., 2022). Wild seaweed lives for many years, *S. latissima* for example commonly lives up to 2-4 years (Bunker et al., 2017), creating longer lasting habitats. A study on wild seaweed restoration states that it takes 4-5 years for the seaweed associated species to return after trawling (Bekkby et al., 2023; Christie et al., 2003).

It has been questioned what the effect on biodiversity would be after harvest, when the created habitat, as well as some of the marine life within, is harvested and thereby abruptly removed (Corrigan et al., 2022, 2024). Cultivation structure is suggested to be an important factor for increasing biodiversity (Forbes et al., 2022; Schutt et al., 2023), which would also be removed in most cultivation practices from temperate waters. Thus, harvest might even be a trap for all animals not capable of surviving the cycles of commercial harvesting and replanting. Corrigan et al. (2024) showed that fish abundance and richness decline after harvest, confirming that seaweed cultivation facilities are only a temporary habitat, when they are fully harvested and the whole cultivation structure is removed (Corrigan et al., 2024). Schutt et al., (2023) even conclude it to be a positive thing, that their temporary cultivation did not provide habitat, and thus no harm was done due to harvest. It was therefore of value to study the impact a year-round cultivation has on biodiversity.

4.4. The impact we want – or rather no impact at all?

The impact on biodiversity varies with factors such as scale and size of cultivation, species and the management practice (Forbes et al., 2022). So far, many conclusions from our results support the argument of more biodiversity developing on the studied Faroese seaweed cultivation due to their unique cultivation technique:

- The 3 year-long deployment cycles allow to leave most of the habitat of the organisms intact, as many of them reside in the holdfast or are mobile species. This permits not only pioneer species but also successional species to settle.
- With a rotating system of only adding newly seeded 1st year lines in places where 3rd year lines had been harvested, results in having year-round roughly two thirds of the cultivation structure with partially harvested seaweed in place. This allows to sustain habitat at least for mobile species (Theuerkauf et al., 2021).
- Furthermore, the cultivation unit design provides a 3D habitat provision while typical longline cultivation designs provide a 2D structure (Bak et al., 2020).

A critical question in the development of seaweed aquaculture concerns its ecological objectives: should cultivation systems be designed to emulate the ecological functions of natural seaweed beds, thereby providing habitat structure, biodiversity support, and ecosystem services, or should they instead minimize ecological interactions altogether, favouring short cultivation cycles and complete removal of structures to reduce local

impacts? This debate aligns with the broader discourse on *built environments*, which addresses how human-made structures in marine systems (e.g., aquaculture installations, artificial reefs, offshore wind farms) alter community composition, trophic interactions, and biogeochemical processes (Bishop et al., 2017; Bulleri & Chapman, 2010).

The question, whether aquaculture should mimic or avoid ecological functions cannot be generalized and needs to balance in each case the benefits to biodiversity against the risks of unintended ecological change. This requires empirical assessments of how different cultivation strategies (e.g., year-round vs. seasonal deployment, partial vs. full harvest, structural removal) influence local and regional ecosystem processes.

4.5. Potential link to commercially valuable fish species

It is argued that seaweed cultivation sites could provide habitat, spawning grounds, or shelter for commercially or ecologically important fish (Bergman et al., 2001; Corrigan et al., 2024; Kelly et al., 2020; Theuerkauf et al., 2021). A recent study from the UK on *S. latissima*, showed that more fish were observed in the cultivation than in the reference site and that low trophic level fish having high proportions of amphipods in their stomachs, the most dominant species found within their seaweed study site (Corrigan et al., 2024). The researchers also analyzed stomach contents of higher level species fish and concluded that seaweed cultivation provide new foraging grounds and support secondary and tertiary production (Corrigan et al., 2024).

In the Faroe Islands, commercially valuable fish species such as cod (*Gadus morhua*) and saithe (*Pollachius virens*) inhabit nearshore areas in their juvenile life stages (Jacobsen et al., 2025). The organism found in the stomachs of saithe are compared to the identified organisms inhabiting natural and cultivated *S. latissima* in Figure 10. Malacostraca, a group of organisms with high abundance within seaweed, is represented in all samples. Interestingly, only the native kind of *Caprella* was found in fish stomachs.

Earlier studies on cod stomachs, stated that early-stage cod are highly adaptable to variation in prey abundance, species and composition (Heath & Lough, 2007). Late juvenile cod prefer Malacostracans (Heath & Lough, 2007), which were abundant in our different sampling events.

These results might indicate that seaweed cultivation could potentially provide additional food sources for the declining cod and saithe stock and contribute to its regeneration, but more data needs to be collected to draw this conclusion. Fish consume selectively and further studies are needed to quantify the changes of catch per unit effort and stable isotopes or biomarkers, to confirm prey sources and trophic linkages.

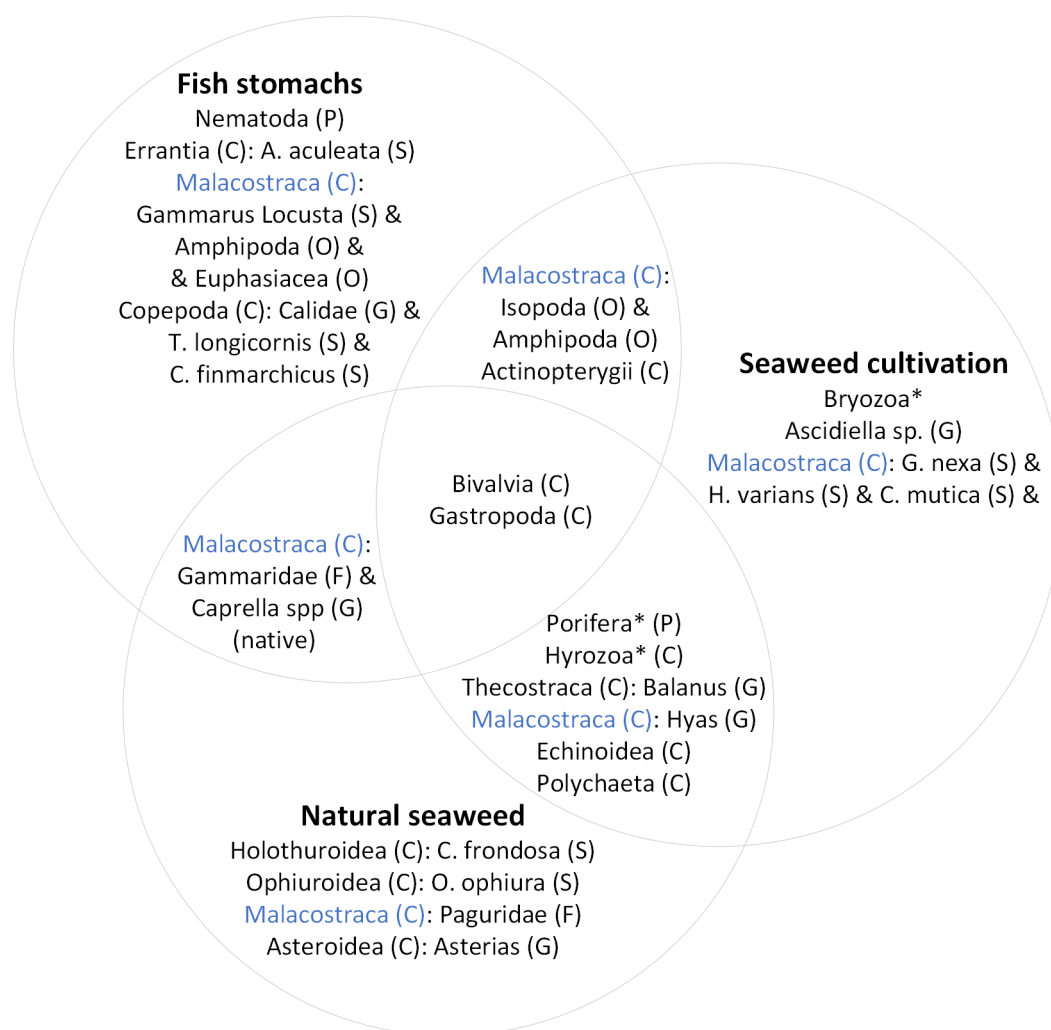


Figure 10: Overlap of organisms sampled in the natural seaweed forest, seaweed cultivation and found in fish stomachs. Note that identified fish, such as lumpfish, were not sampled for in the natural seaweed samples. The colours represent same classes that can be found in the different samples.

*Organisms not quantified and therefore don't show up in Table S1

4.6. Potential negative impacts

More fish or invertebrates are not always inherently positive. The impact that the organisms finding habitat within the seaweed aquaculture have on the ecosystem function needs to be assessed (Corrigan et al., 2022), as the created new habitats may differ to natural seaweed (Corrigan et al., 2024; Forbes et al., 2022). Furthermore, depending on the perspective and context, seaweed cultivation units can also be seen as 'ecological traps' where the fish are more vulnerable to capture or natural predators like seals (Alleway et al., 2018; Kelly et al., 2020; Theuerkauf et al., 2021).

In shallow water seaweed cultivation may also compete with seagrass and other natural ecosystems, through mechanisms such as shading or physical disturbance caused by farming activities, potentially leading to reduced seagrass biomass and slower growth rates (Eklöf et al., 2005; Kelly et al., 2020). Over the long term, establishing seaweed

cultivations on seagrass beds can negatively affect fish populations habituated to seagrass, thereby impacting fisheries (de la Torre-Castro & Rönnbäck, 2004; Kelly et al., 2020). In addition, seaweed farming can modify hydrodynamic conditions, increased sedimentation, organic enrichment, and affect microbial processes (Campbell et al., 2019; Corrigan et al., 2022; Hasselström et al., 2018; Wood et al., 2017). In general, it has been shown that effects on the benthic ecosystem are less severe in temperate ecosystems with suspended cultivation (Visch et al., 2020; Walls et al., 2017). Negative impacts on the benthic community structure would need to be studied for the investigated cultivation on the Faroe Island, however they might be limited as the water depth is at least 20 m, also excluding other photosynthesis dependent ecosystems such as wild seaweed (Wegeberg et al., 2024).

Like other artificial structures introduced into marine environments, seaweed cultivations may contribute to habitat degradation, declines in biodiversity and ecosystem productivity, and even pose entanglement risks for large marine mammals (Bizzaro et al., 2022; Grebe et al., 2019), as well as for other wildlife such as seabirds (Corrigan et al., 2022). Fricke et al. (2024) also highlight broader ecosystem impacts of seaweed farming, for example potential effects on microbial communities. Moreover, large-scale seaweed cultivation can lead to the introduction of non-native or invasive species, or disrupt native genetic diversity, even when local genetic material is used (Banach et al., 2022; Campbell et al., 2019; Fricke et al., 2024; Kelly et al., 2020; Koch et al., 2026; Pereira et al., 2021). The cultivations in the Faroe Islands are thus far considered small scale, therefore such impact are not expected (Wegeberg et al., 2024).

The intensity and management of the cultivation play an important role in the magnitude of these potential impacts (Campbell et al., 2019; Grebe et al., 2019), when impacts start becoming negative and when negative impacts are beyond the limit of acceptance (carrying capacity), need to be researched and quantified to avoid harm to the ecosystem. (Byron et al., 2024; Koch et al., 2026).

4.7. Research needs

Further data collection is still needed to confirm if the habitat created under these specific cultivation conditions, is the same or similar as the one of natural seaweed and supports a similar functional biodiversity.

More research is needed to better understand the impact harvest or partial harvest can have on the biodiversity in and around cultivation to confirm the benefits seen on this site.

Questions remain, and more studies are needed to quantify the impact of seaweed cultivation on the surrounding biodiversity.

Questions on the additionality of habitat created need to be investigated: Does seaweed cultivation only serve as a biodiversity aggregation or really create additional habitat and richness in species (Gentry et al., 2020; Hasselström et al., 2018; Radulovich et al., 2015; Theuerkauf et al., 2021)?

It is important not to neglect that seaweed cultivation can also have other negative impacts and thus pose risks to the environment, see previous paragraph.

To accurately assess biodiversity gains around seaweed cultivations, robust methods for quantifying increases in commercially valuable species must be developed and refined.

5. Conclusion

Our results suggest that cultivated *S. latissima* supports a subset of the taxa found in natural seaweed habitats, indicating that these cultivations do not create entirely novel communities. Yet eDNA results confirm a remaining difference to natural seaweed, even with a three-year cultivation cycle. The organisms identified to benefit of seaweed cultivation habitat are also potentially prey organisms for commercially interesting fish, as comparison to digested organisms in fish stomachs showed.

We further found that biodiversity in *S. latissima* cultivation increases significantly over multiple years, with the most pronounced changes observed in the 2nd and 3rd years. Early-stage samples are dominated by mobile organisms, comparable to one-season cultivations reported in other studies, whereas longer-term cultivation supports sessile and successional organisms, including bivalves, thecostracan, and ascidians. This suggests that extended growth periods and partial-harvest practices enhance habitat complexity and taxa richness, potentially maximizing associated ecosystem services. To our knowledge, this study provides the first assessment of biodiversity development over a three-year cultivation cycle, highlighting the importance of temporal scale in evaluating the ecological contributions of seaweed cultivations.

These findings highlight that the ecological role of seaweed aquaculture depends on management practices, cultivation design, and deployment duration. Consequently, whether cultivation should emulate natural seaweed beds to support biodiversity or minimize ecological interactions requires careful, site-specific assessment, balancing ecological benefits against potential unintended impacts.

Our results further confirm that there is a complementarity in the biodiversity assessment methods such as morphologically identifying organisms in and around seaweed cultivations and water eDNA sampling.

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