Inter-Research Science Publisher

Marine Ecology Progress Series
Volume 785:meps15132

Published May 13, 2026
https://doi.org/10.3354/meps15132

Benthic biodiversity of drifting *Furcellaria lumbricalis* and *Fucus* spp. mats similar to seagrass meadows, despite low oxygen concentrations

Johan Severinson*, Per-Olav Moksnes

Department of Marine Sciences, University of Gothenburg, 405 30 Gothenburg, Sweden

ABSTRACT: Following seagrass decline, many shallow bays on the Swedish west coast are today instead occupied by large algal mats of perennial species (*Furcellaria lumbricalis* or *Fucus serratus*). This field study aims to elucidate how this shift in habitat-forming vegetation has affected the biodiversity of associated benthic fauna. This was done by measuring oxygen levels, collecting epifauna and infauna, and comparing these between 4 different habitats at 2 sites where these algal mats have replaced eelgrass meadows. The results revealed significantly lower oxygen concentrations within the drift algae habitats compared to concurrently measured unvegetated sediments. Despite this, species richness, abundance, and biomass of epifauna within the drift algae and seagrass were comparable and consistently significantly higher compared to unvegetated sediments. The infauna was mostly unaffected by the algal mats, as the drift algae supported similar species richness, abundance, and biomass as unvegetated sediments. However, the species composition of epifauna differed significantly across all habitats, and infauna differed between the drift algae and unvegetated sediments. While the shift from seagrass to drift algae has impacted species composition, it has not significantly reduced benthic biodiversity or abundance, indicating that these drifting algal mats of perennial species do not negatively affect infauna and provide important habitat functions for epifauna, comparable to seagrass meadows.

KEY WORDS: Biodiversity · Drift algae · *Zostera* · *Furcellaria* · *Fucus* · Oxygen · Epifauna · Infauna

1. INTRODUCTION

Marine biodiversity is under threat due to anthropogenic impacts, affecting ecosystem stability and limiting the provision of ecosystem services (Cardinale et al. 2012, Gamfeldt et al. 2015, Wernberg et al. 2024). Of great importance for the preservation of marine biodiversity are the habitat-forming ecosystem engineers, which sustain their associated fauna (Jones et al. 1994, Barbier et al. 2011). One such ecosystem engineer is seagrass, which in addition to promoting biodiversity (Unsworth et al. 2019, Duarte et al. 2025) also improves water quality by stabilizing sediments (van Katwijk & Hermus 2000, Moksnes et al. 2018), as well as through sequestration of carbon and nutrients (Duarte & Krause-Jensen 2017, Moksnes et al. 2021).

Seagrasses are globally declining ecosystems, with 19% of the known areal extent having perished during the 20th century (Dunic et al. 2021). In northern Europe, the dominant seagrass is eelgrass *Zostera marina* L., but other species such as widgeon grass *Ruppia maritima* L. and *Zostera noltii* are also present (Boström et al. 2003). In this region, seagrass extent declined heavily during the first half of the 20th century, due to eelgrass wasting disease *Labyrinthula zosterae* (Den Hartog 1987), but further losses have since been driven by anthropogenic pressures (Boström et al. 2014, Dunic et al. 2021). Along the Swedish NW coast, close to 50% of the area of eelgrass has disappeared since the 1980s due to anthropogenic pressures (Baden et al. 2003, Nyqvist et al. 2009, Moksnes et al. 2024). The losses have largely been attributed to the effects of coastal

*Corresponding author: johan.severinson@gu.se

Publisher: Inter-Research · www.int-res.com

eutrophication and overfishing of large predatory fish, causing a trophic cascade which has favoured competitors to eelgrass, such as fast-growing ephemeral macroalgae (Moksnes et al. 2008, Baden et al. 2010, 2012).

To recover ecosystem services and prevent further biodiversity losses, functional eelgrass restoration methods have been developed and used successfully in the last decade, both on the Swedish west coast and in the Baltic Sea (Moksnes et al. 2016, Eriander et al. 2025). However, efforts have also failed in many areas, particularly in the Kattegat–Skagerrak area, where sediment resuspension and disturbance from drifting algal mats of perennial species presently prevents natural recovery and restoration efforts (Moksnes et al. 2018, Steinfurth et al. 2024). In the Danish Odense fjord, field studies showed that drifting *Fucus* spp. attached to small stones explained 40% of eelgrass seedling mortality through uprooting and burial (Valdemarsen et al. 2010), and model studies suggest that up to 96% of the fjord area may be negatively impacted by macroalgal drift (Canal-Vergés et al. 2014). In addition, failure of a large-scale eelgrass restoration attempt in the fjord was largely attributed to disturbance from drifting algal mats (Steinfurth et al. 2024). In NW Sweden, disturbance from drifting algal mats of perennial species has also been shown to prevent restoration attempts in several areas. Here, it has been suggested that the drift algae constitute an important feedback mechanism that together with increased sediment resuspension, which follows the loss of the stabilizing effect of eelgrass, leads to a regime shift where the eelgrass is replaced by algal mats that can tolerate lower light levels than eelgrass (Moksnes et al. 2018). Although these algal accumulations can impede seagrass establishment, drift algae, such as perennial *Fucus vesiculosus* L. and ephemeral filamentous algae, can also play positive ecological roles in coastal ecosystems, often in conjunction with extant seagrass (Austin et al. 2021, Correia et al. 2022). This duality highlights the complex nature of algae–seagrass interactions, which can vary from facilitative to inhibitory (Richard & Quijón 2023).

Along the Swedish NW coast, these algal mats of perennial species are dominated by the red algae *Furcellaria lumbricalis* (Huds.) Lamour. (hereafter called *Furcellaria*) and the brown algae *Fucus serratus* L. (hereafter called *Fucus*). Both are perennial species typically attached to hard substrates, but *Furcellaria* can alter its morphology to a round form without holdfast, when drifting on soft-bottom sediments (Austin 1960). Drifting mats of *Furcellaria* were common in Danish waters during the middle of the 20th century (Austin 1960). However, they were since reportedly driven to local extinction by eutrophication and intense harvesting (Pedersén & Snoeijs 2001). Today, mats of *Furcellaria* are still harvested commercially in Estonia in the Baltic Sea (Weinberger et al. 2020), where the algae form large mats in moderately exposed areas at 4–10 m depth (Martin et al. 2013). The brown algae *F. vesiculosus* and *F. serratus* also display mat-forming, drifting morphs, and *F. vesiculosus* composes large mats in the Baltic Sea (Martin et al. 2013, Preston et al. 2022, 2025). In NW Sweden, these mats are typically found at 2–3 m depth covering large areas (10s of ha) of the soft sediment bays where they have replaced large eelgrass meadows that were found there in the 1980s (Moksnes et al. 2018, P. O. Moksnes unpubl. data). However, outside of the Baltic Sea, there is a general lack of studies on drifting *Furcellaria* and *Fucus* mats, and little is known about how they are formed, their population dynamics, their ecological function, and how this large-scale change from eelgrass to algal mats have affected the coastal ecosystems of NW Sweden.

One factor that may largely determine habitat suitability of drift algae for fauna is the oxygen concentration within the algal accumulation (Carstensen & Conley 2019). The algae constitute an organic enrichment which lowers the oxygen concentration through its decomposition by microbes, and given a large enough accumulation, the drift algae can also hinder oxygen diffusing from the water column from reaching the sediment below. This is a common occurrence for drifting filamentous algae associated with eutrophicated areas, which can completely deplete oxygen conditions as they decay (Norkko & Bonsdorff 1996a,b). Depending on the severity of anoxia, the epifauna and infauna communities may change rapidly, generally shifting to more tolerant species able to withstand the conditions (Norkko & Bonsdorff 1996a,b). In the Baltic Sea, drifting perennial *F. vesiculosus* has been shown to support diverse benthic communities, with positive effects for epifauna (Austin et al. 2021, D'Agata et al. 2025) and infauna (Preston et al. 2024). However, periodic hypoxia has also been observed in accumulations of *F. vesiculosus* detritus during periods of low wave action, with negative effects on the associated infauna and epifauna (Attard et al. 2023). For the NW coast of Sweden, it is presently not known if the drifting mats of *Furcellaria* and *Fucus* are perennial and persisting on the seafloor or are transient and decomposing or how they influence oxygen conditions and impact associated epifauna and infauna.

Because of the negative interaction between algal mats and eelgrass meadows, managers in NW Sweden are presently discussing limiting the algal extent

through preventative measures or through harvesting of the drifting perennial algae in the interest of eelgrass restoration and conservation (Moksnes et al. 2016). However, such biomanipulative methods warrant caution and ecological investigations prior to implementation in order to avoid potential risks to the ecosystem which may occur through unpredictable species interactions (Lindegren et al. 2010, Abelson et al. 2020). Therefore, there is a need to assess the ecological function of the drifting mats of *Furcellaria* and *Fucus* to evaluate how a shift from eelgrass to algal mats has affected the shallow soft-bottom ecosystems of NW Sweden. This will help inform management decisions regarding conservation of coastal ecosystems.

The aims of the present study were to investigate oxygen conditions, as well as the abundance and diversity of fauna, in drifting mats of *Furcellaria* and *Fucus*, seagrass meadows, and unvegetated sediments. Specifically, we sought to assess (1) if the mats are perennial or transient, (2) if they constitute an important habitat for epifauna, and (3) if they negatively impact infauna. The goal was to use the results to inform coastal management of NW Sweden.

2. MATERIALS AND METHODS

2.1. Study area

The southern part of the Swedish Skagerrak, in the Sälöfjord and Hakefjord, is an area targeted for eelgrass restoration (Moksnes et al. 2016, 2018). Mappings of eelgrass during the 1980s showed that this area contained more than 1050 ha of eelgrass, with the largest continuous meadow spanning over 200 ha. Since then, over 90% of these eelgrass meadows have been lost in this area (Moksnes et al. 2018, 2021). The area has estuarine conditions and experiences a freshwater outflow from the Nordre river which moves northward, creating a salinity gradient from around 6 PSU at the river mouth in the south, to around 18 PSU in the northern area.

This study investigates 2 areas, Nordön and Ryskärsfjorden in the Sälöfjord area, which have both experienced large losses of eelgrass (Fig. 1). At Nordön, there was an eelgrass meadow of approximately 146 ha in the 1980s where less than 1 ha remains today, consisting of a mix of eelgrass and *Ruppia maritima* (Moksnes et al. 2018). The dominating vegetation today is instead a mosaic of drifting algal mats, which accumulate mainly in the northern and eastern part of the bay, covering approximately 37 ha (J. Severinson unpubl. data; Fig. 1b). The drift algae consist mainly of separate mats of *Furcellaria* and *Fucus* (Fig. 2). At Ryskärsfjorden, eelgrass covered approximately 214 ha in the 1980s, and today none remain (Moksnes et al. 2018). Only small patches of *R. maritima* are found in the eastern part. The bay is instead dominated by a large (~70 ha) mostly continuous mat of *Furcellaria* that covers the central part of the bay. Small mats of drifting *F. vesiculosus* attached to pebbles or shell fragments are found in the southern part (J. Severinson unpubl. data; Fig. 1c). Both sites contain fine-grained sediments (~60% silt and clay) with a high content of organic material (4–8%; Moksnes et al. 2016). Nordön and Ryskärsfjorden have been the subject of several failed small-scale restoration attempts where eelgrass growth was mainly prevented by smothering from drifting algal mats of perennial species (Moksnes et al. 2018). These sites were selected as their dominant vegetation has shifted from eelgrass to drifting *Furcellaria* and *Fucus* and because field surveys showed they both contained all habitats of interest for this study, namely seagrass (*R. maritima* and/or *Zostera marina*), drifting *Furcellaria*, drifting *Fucus*, as well as unvegetated sediments.

2.2. Oxygen concentrations

The near-bed dissolved oxygen conditions of each vegetated habitat were investigated by deploying a pair of dissolved oxygen concentration loggers with built-in temperature compensation (HOBO U26-001, Onset) during September to October 2023. The factory-specified accuracy of these loggers is ±6 µmol l^{-1} at 0 to 250 µmol l^{-1}, ±16 µmol l^{-1} at 250–625 µmol l^{-1}, with a resolution of 0.6 µmol l^{-1}, and 90% response time (T_{90}) < 2 min. Each logger was attached to a rod which was pushed into the sediment until the sensor was 5 cm above the sediment surface, to ensure that the sensors in the vegetated habitats were always within the >15 cm high canopy. For each vegetated habitat, one sensor was placed >20 m inside the mat or meadow while the other was placed at a nearby (distance ≈ 100 m) area devoid of vegetation (at least ~50 m from vegetation edge). *Furcellaria* was measured at Ryskärsfjorden while the seagrass and *Fucus* were measured at Nordön, as the largest area of each habitat was found there. The pair of sensors recorded every minute and were moved between habitats, recording for 4 d in the *Fucus*, followed by 14 d in *Furcellaria*, and lastly 14 d in the seagrass. Strong winds led to the loss of the unvegetated logger for seagrass at Nordön, meaning this habitat was not measured

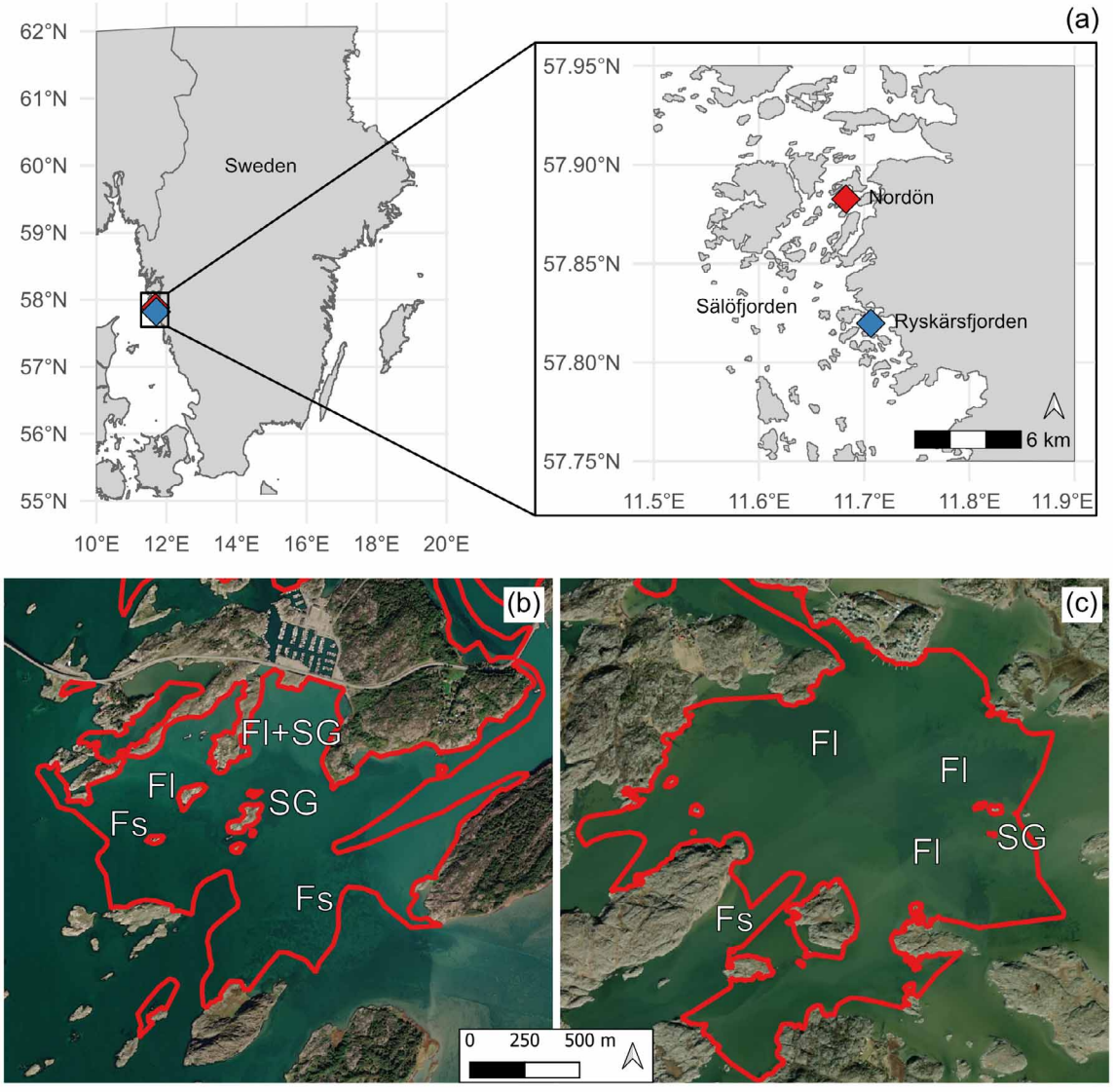

Fig. 1. (a) Two sampling locations (Nordön and Ryskärsfjorden) on the Swedish NW coast. Arial view of (b) Nordön and (c) Ryskärsfjorden, where mats of drift algae and seagrass (*Ruppia maritima* and *Zostera marina*) are seen as darker areas. Red lines mark the distribution of eelgrass in the 1980s, which covered 146 and 214 ha, respectively, of which only small patches remain today (Moksnes et al. 2018). Dominant habitats are marked: *Furcellaria* (Fl), *Fucus* (Fs), and seagrass (SG: *Z. marina* and/or *R. maritima*). At each site, the 3 vegetated habitats and bare sediments were sampled. Photos: Bing.com, retrieved April 5, 2025

concurrently with the nearby unvegetated sediments. No movements of the algal mats were detected during the measurement periods. Salinity was measured when loggers were deployed using a YSI ProDSS multiparameter digital water quality meter to correct measured oxygen concentrations for salinity.

2.3. Fauna sampling

To investigate how epifauna and infauna vary between the 2 types of drift algae (*Furcellaria* and *Fucus*), seagrass meadows (*Z. marina* and/or *R. maritima*) and unvegetated sediments, the habitats were sampled at multiple times in both bays to also capture seasonal and annual variation. For epifauna, 5 samples were collected in all 4 habitats in August 2022, July 2023, and September 2023. Infauna was only compared between the 2 types of drift algae and unvegetated sediments, where 5 samples were collected per habitat from the 2 sites in July and September 2023. Seagrass was excluded from this sampling as infauna in the study area have shown similar abundance and diversity in eelgrass and unvegetated sediments (Gagnon et al. 2023), and we were primarily interested to assess if algal mats could neg-

Fig. 2. Photo of drift algae at 2 m depth at Ryskärsfjorden, consisting mainly of *Furcellaria lumbricalis*, but *Fucus serratus* can also be seen towards the sides. Photo: J. Severinson, May 28, 2025

atively impact infauna compared to unvegetated sediments.

All samples were collected at 1.0–2.5 m depth, at random within the targeted habitat, while staying >2 m away from the edge of the seagrass meadows (as these were small), and >10 m from the edge of the algal mats to avoid edge effects on the faunal community. Fauna samples were collected by snorkelling. Epifauna was collected by pushing an open-ended plastic cylinder (Ø: 25.5 cm) into the sediment, thereby enclosing the habitat. The enclosed vegetation was then firstly collected by hand by carefully placing the material in fine-mesh (<0.5 mm) bags while staying within the cylinder walls. Seagrass was dislodged together with their roots. Secondly, a fine-mesh (<0.5 mm) hand-net was used to sweep across the enclosed area to catch any remaining epifauna. The same method was used for the unvegetated habitat. Infauna was collected using a polycarbonate corer (Ø: 10.5 cm, depth: 10 cm), which was pushed into the sediment, after which a lid was applied to create a vacuum, allowing the sediment to be extracted. All collected material of epifauna and infauna was placed in fine-mesh bags (mesh <0.5 mm), which were stored in a cooler for transport back to the lab, where they were immediately frozen at −20°C.

In the laboratory, fauna samples were sieved on a 0.5 mm sieve, and the fauna was collected and preserved in 95% ethanol (EtOH). Fauna was counted and identified to lowest possible taxonomic level (usually species level) using a stereomicroscope. Due to a very high abundance of amphipods in the epifauna samples, they were subsampled (~1/10 of sample wet weight) before counting. Fish (*Gobius niger*), pelagic mysids (*Praunus flexuosus*) and strictly infaunal species (infaunal polychaetes, oligochaetes, infaunal bivalves and amphipod *Corophium volutator*) were excluded from further epifauna analyses, while strictly epifaunal species (epifaunal isopods and gastropods) were excluded from the infauna analyses. This was done as the respective sampling methods are inappropriate for quantifying the excluded groups. Facultative epifaunal–infaunal species (isopod *Cyathura carinata*, gastropods *Hydrobia* sp. and *Tritia reticulata*, and bivalves *Mytilus edulis* and *Cerastoderma edule*) were included in both epifauna and infauna analyses. Species association to epifauna/infauna was determined using literature (Nygren & Pleijel 2015, Hayward & Ryland 2017, WoRMS 2024). Epifauna and infauna were dried at 60°C for 24 h and weighed to measure dry weight (DW) biomass. Prior to drying, epifauna was divided into the groups isopoda, amphipoda, decapoda, gastropoda, bivalvia, insecta, halacaridae, and echinodermata, while infauna was divided into fauna with or without shells. The biomass of gastropoda and bivalvia was measured with shells. Additionally, all vegetation within each epifauna sample was identified, dried at 60°C

for 48 h, and weighed to assess the vegetation species composition within each habitat.

2.4. Data analysis

To compare the dissolved oxygen concentrations between the vegetated habitats and the concurrently measured nearby unvegetated sediments, as well as between day and night, we used permutational multivariate analyses of variance (PERMANOVA; Anderson 2017), based on Euclidian dissimilarity matrices. For the 2 drift algae, we included habitat (vegetated/unvegetated) and time of day (day/night) as fixed factors in the model, while for the seagrass only time of day was included (as this habitat was not concurrently recorded with the nearby unvegetated sediment). Time of day was defined slightly differently for each habitat, as the days quickly got shorter throughout the measurement period. For *Fucus*, day was defined as between 06:00 and 18:59 h, and night as 19:00 and 05:59 h. For *Furcellaria*, day was defined as between 07:00 and 18:59 h, and night as 19:00 and 06:59 h. For seagrass, day was defined as between 07:00 and 17:59 h, and night as 18:00 and 06:59 h. These definitions were based on irradiance data during the measurement period from the Swedish Meteorological and Hydrological Institute (SMHI). The test assumption of homogeneity of dispersions was fulfilled, as tested using the 'betadisper' function, and the PERMANOVAS were performed using the 'adonis2' function, both from the *vegan* package (Oksanen et al. 2022). In case of significant results, pairwise comparisons with Holm-Bonferroni p-value adjustments were run as a post-hoc test, using the *pairwiseAdonis* package (Martinez Arbizu 2020).

Non-metric dimensional scaling (NMDS) with Bray-Curtis dissimilarities was used to investigate similarities in epifauna and infauna species composition between habitats. These were followed by PERMANOVAs based on Bray-Curtis dissimilarities testing for differences in epifauna and infauna species composition between habitats. To fulfil the assumption of homogeneity of dispersions, as tested using the 'betadisper' function from the *vegan* package (Oksanen et al. 2022), relative abundances were used for epifauna. Infauna abundances were fourth root-transformed to improve homogeneity of dispersions, but despite this, the assumption was unfulfilled (betadisper test, $F = 4.5$, $p = 0.015$). However, PERMANOVA is generally robust to variations in dispersions if the design is balanced (Anderson & Walsh 2013), so this test was run on the fourth root-transformed abundances using the 'adonis2' function from the *vegan* package (Oksanen et al. 2022). In case of significant results, pairwise comparisons with Holm-Bonferroni p-value adjustments were run as a post-hoc test, using the *pairwiseAdonis* package (Martinez Arbizu 2020). Contribution of each species to dissimilarities between habitats was investigated using a similarities percentage test (SIMPER; Clarke 1993), using the *vegan* package (Oksanen et al. 2022). An indicator species analysis was used in addition to find species closely associated to each habitat, using the package *indicspecies* (De Cáceres & Legendre 2009).

To assess how diversity, abundance and biomass of epifauna and infauna differed between habitats, sites and sampling occasion (time), a series of 3-way ANOVA models (type III) were used, testing species richness (SR), abundance (ind. m^{-2}), and DW biomass (g m^{-2}) as dependent variables and habitat (3–4 levels as described above), site (2 levels), and sampling occasion (2–3 levels) as fixed, independent variables. In addition, the abundance of specific groups was also tested in the same models to investigate whether the habitats differed in terms of supporting different functional groups. For epifauna, these groups were mobile crustaceans (amphipoda, isopoda, and decapoda), gastropods, and mesograzers (*Gammarus* sp. and *Idotea* sp.), while the infaunal groups were crustaceans (amphipoda and isopoda), bivalves, gastropods, and polychaetes. ANOVA test assumption checks were performed in R, with the assumption of normality tested with Shapiro-Wilk tests, using the 'shapiro.test' function, while the assumption of homogeneity of variances was tested with Levene's tests, using the 'leveneTest' function from the *car* package (Fox & Weisberg 2019). All abundance and biomass data, except for the abundance of polychaetes, was $\log(1 + x)$-transformed to fulfil the assumption of homogeneity of variances, while the species richness data fulfilled assumptions without transformations. In case of significant tests, *a posteriori* multiple comparisons were carried out with the Tukey's post-hoc test, using the *emmeans* package (Lenth 2024). Analyses were performed using R version 4.4.0 (R Core Team 2024) with $\alpha = 0.05$ for statistical tests. Permutational tests were run with 999 permutations.

3. RESULTS

3.1. Oxygen concentrations

The mean oxygen concentrations within the vegetated habitats, measured during the 3 habitat-

specific periods, were lowest in the *Fucus* mat, intermediate in the *Furcellaria* mat and highest in seagrass meadow (on average 4.98, 7.16, and 8.72 mg l^{-1}, respectively; Fig. 3). Oxygen concentrations were significantly lower in both drift algae habitats compared to the corresponding concurrently measured unvegetated sediments (Fig. 3; Table S1 in the Supplement at www.int-res.com/articles/suppl/meps15132_supp.pdf). In addition, time of day (day/night) significantly impacted the oxygen concentrations in the *Furcellaria* mat, with more oxygen during the day, but no such diurnal pattern was recorded above the unvegetated sediment, causing a significant interaction effect between habitat and time of day. There was also a significantly higher oxygen concentration in the seagrass during the day, compared to during the night. Contrastingly, oxygen concentration was not significantly higher during the day in the *Fucus* mat, similarly to the nearby unvegetated sediments (Fig. 3; Table S1). All vegetated habitats experienced periods of hypoxia ([O_2] <3 mg l^{-1}) and anoxia ([O_2] <1 mg l^{-1}). The percentage of hypoxic oxygen measurements within each vegetated habitat time-series was highest in the *Fucus*, followed by *Furcellaria* and lastly the seagrass habitat (26.2, 11.2, and 2.9% of measurements <3 mg l^{-1}, respectively), and the same pattern could be observed for anoxia (6.7, 4.7, and 1.1% of measurements <1 mg l^{-1}, respectively; Fig. 4).

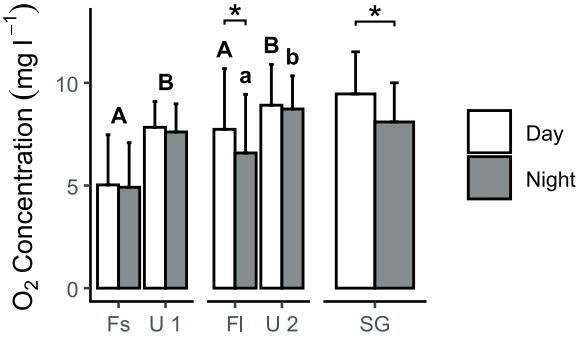

Fig. 3. Means (+SD) of dissolved oxygen concentrations during the day and night in the habitats *Fucus* (Fs), *Furcellaria* (Fl), seagrass (SG), and unvegetated sediments measured concurrently nearby the vegetated habitats, except for seagrass where the unvegetated logger was lost (U 1 concurrent with *Fucus* and U 2 concurrent with *Furcellaria*). Capital letters, lowercase letters, and asterisks above bars denote significance between a vegetated habitat and the concurrent unvegetated sediment (during daytime for Fl and U 2), between a vegetated habitat and the concurrent unvegetated sediment during nighttime, and within habitats between day/nighttime, respectively (PERMANOVA, $p < 0.05$)

3.2. Taxonomic diversity

3.2.1. Vegetation species composition

Analysis of the vegetation species composition in the epifauna samples revealed that the target vegetation all dominated within their habitat, where they constituted 95, 86, and 84% of the above-ground DW biomass in the *Furcellaria*, *Fucus*, and seagrass habitats, respectively. Within the algal mats, the remaining vegetation primarily consisted of the other algal species (*Furcellaria* in *Fucus* and vice versa) together with small amounts of filamentous red algae and *Gracilaria* sp., while remaining vegetation in the seagrass habitat was mainly constituted by *Furcellaria* and small amounts of filamentous red algae. Several of the collected *Fucus* thalli were observed to be in a late stage of decomposition, whereas this was never observed for *Furcellaria*.

3.2.2. Epifauna species composition

The NMDS and PERMANOVA analyses revealed that the community composition of epifauna differed significantly between the habitats. Pair-wise comparisons showed that the epifaunal composition was significantly different between all 4 habitats (Fig. 5a; Table S1). Most species were found in all vegetated habitats, but a few were found only in certain habitats. For epifauna, the invasive crab *Hemigrapsus* sp. and the mollusks *Tonicella* sp., *Crassostrea gigas*, and *Musculus subpictus* were only found in the *Fucus* habitat, while the shrimp *Crangon crangon* was only found in seagrass. Species unique to one habitat were always found in low abundances (see Table S2 for a summary of all collected epifauna). No epifauna species was unique to the *Furcellaria* habitat.

The SIMPER analysis revealed that dissimilarity in epifauna community composition between habitats was mainly driven by differences in the 2 most abundant groups, amphipods, and gastropods, which together explained >65% of the dissimilarity in all comparisons (Table S3). Unvegetated sediments were almost completely devoid of amphipods, but *Monocorophium insidiosum* was found in all vegetated habitats, while *Microdeutopus gryllotalpa* was mainly found in drift algae, and *Erichthonius difformis* was mainly common in seagrass. Dominant gastropod species in the unvegetated sediment were *Retusa obtusa, Hydrobia* sp., and *Bittium reticulatum,* while the drift algae was dominated by *Pusilina sarsii,* which together with

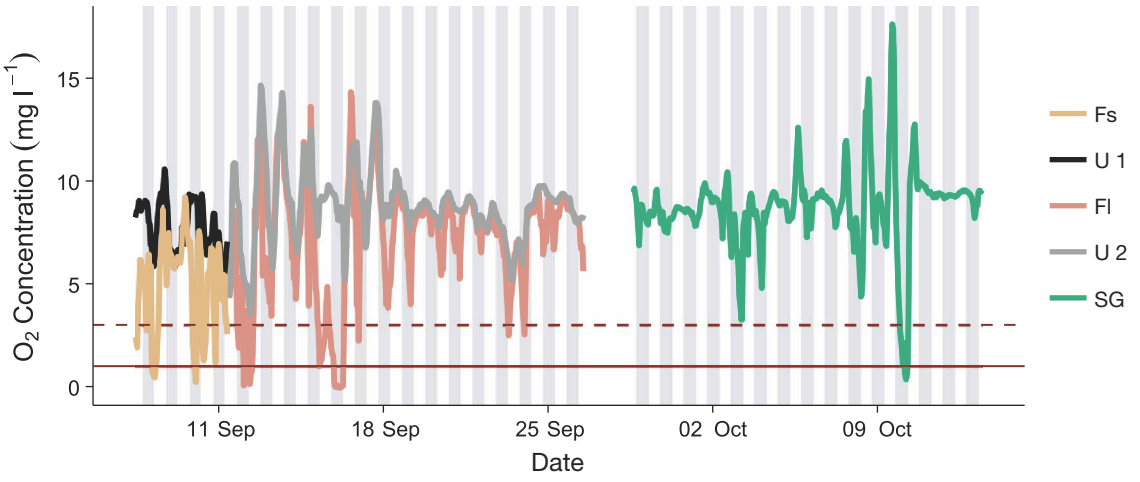

Fig. 4. Timeseries of dissolved O_2 concentration measured during 2023 in the habitats *Fucus* (Fs), *Furcellaria* (Fl), seagrass (SG), and unvegetated sediments concurrently measured nearby the vegetated habitats (U 1 and U 2), except for seagrass where the logger was lost. Horizontal dark red dashed and solid lines indicate limits for hypoxia (3 mg l^{-1}) and anoxia (1 mg l^{-1}), respectively. Background shading indicates nighttime

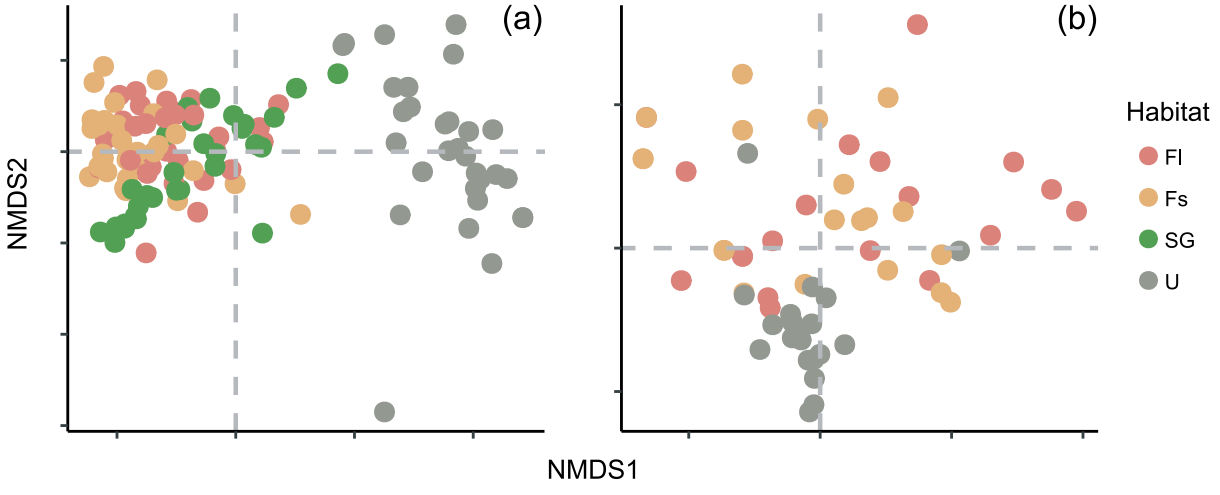

Fig. 5. Non-metric multi-dimensional scaling (NMDS) plots based on Bray-Curtis dissimilarity of (a) epifauna and (b) infauna species composition, in the habitats *Furcellaria* (Fl), *Fucus* (Fs), seagrass (SG, epifauna only), and unvegetated sediment (U). The NMDS stress levels of the epifauna and infauna plots are 0.15 and 0.14, respectively

Rissoa membranacea, also dominated in the seagrass (Table S2).

The subsequent multilevel pattern indicator species analysis of epifauna significantly associated the crustaceans *Gammarus* sp., *Stonothoe monoculoides, Idothea chelipes*, and *Jaera albifrons* with *Furcellaria*, while *Asterias rubens* and *C. gigas* were associated with *Fucus*, and *R. obtusa* was associated with the unvegetated sediments (Table S4). Seagrass, by itself, did not have any species significantly associated to it.

3.2.3. Infauna species composition

The NMDS and PERMANOVA analyses showed that the infauna community composition was significantly different between habitats. The infauna composition was similar between the *Furcellaria* and *Fucus* habitats, but they were both significantly different from the unvegetated sediment, as shown by pairwise comparisons (Fig. 5b; Table S1).

Some infauna species were unique to habitats, with the bivalve *Abra* sp. only found in unvegetated sed-

iments and the bivalve *Macoma balthica* unique to the *Fucus* habitat. Both these species were recorded in low abundances (see Table S5 for a summary of all collected infauna). No infauna species was unique to the *Furcellaria* habitat.

The SIMPER analysis showed that the dissimilarity in infauna community composition between the 2 drift algae and unvegetated sediments was mainly driven (>70%) by the high abundance of the amphipod *Corophium volutator* in both algal habitats and the high abundance of the gastropod *Hydrobia* sp., particulary in *Furcellaria*, but also by a higher abundance of the bivalve *Mya* sp. and the polychaete *Hediste diversicolor* in the unvegetated sediments (Tables S5 & S6). The subsequent multilevel pattern indicator species analysis did not significantly associate any infauna species to single habitats.

3.3. Species richness, abundance and biomass

3.3.1. Epifauna

This study recorded a total of 68 684 individuals of epifauna (after adjusting for the subsampling of amphipods), belonging to 32 different taxa (Table S2). Epifauna species richness, abundance, and biomass was always significantly higher in the vegetated habitats compared to the unvegetated sediments, while no consistent difference was found between the 3 vegetated habitats (Fig. 6, Table 1). The epifauna showed large variation between sites and sampling occasions, as seen by significant interaction effects between habitat and these factors, demonstrating high spatial and temporal dynamics.

Species richness of epifauna varied significantly across the habitats, sites, and the sampling occasions, as seen by 2 significant interactions effects (Table 1), but was consistently significantly lower in the unvegetated habitat (on average 3.4 species) compared to seagrass, *Fucus*, and *Furcellaria* habitats (on average 8.7, 10.2, and 11.4 species, respectively). The vegetated habitats were not significantly different during the first 2 sampling occasions, but species richness was significantly higher in *Furcellaria* compared to seagrass at both sites in the September 2023 sampling (Fig. 6a,b, Table 1).

Abundance of epifauna differed significantly between habitats and sampling occasions, as revealed by a significant interaction effect (Table 1). The abundance in seagrass, *Fucus*, and *Furcellaria* habitats was always significantly higher (on average 13 175, 14 065, and 15 406 ind. m^{-2}, respectively) compared to the unvegetated sediments (on average 685 ind. m^{-2}). The vegetated habitats did not significantly differ for the July 2023 sampling, but seagrass and *Furcellaria* differed significantly for the remaining 2 sampling occasions, with the abundance of seagrass being significantly higher in August 2022 but significantly lower in September 2023 compared to *Furcellaria* (Fig. 6c,d, Table 1). Epifauna abundance within the vegetated habitats was dominated by amphipods, followed by gastropods, which were the most abundant group on the unvegetated sediments (Fig. 7a; Table S2).

Biomass (DW) of epifauna was significantly higher in seagrass, *Fucus*, and *Furcellaria* (on average 11.4, 35.5, and 26.0 g m^{-2}, respectively) compared to the unvegetated sediments (on average 0.4 g m^{-2}) at both sites and on all sampling occasions, while within the vegetated habitats, the 2 drift algae habitats had a significantly higher biomass compared to the seagrass (Fig. 6e,f, Table 1). Epifauna biomass was dominated by gastropods, followed by bivalves (Fig. 7b).

Mobile crustacean abundance was significantly different across habitats and sampling occasions, as seen by a significant interaction between these factors (Table 2). The abundance of mobile crustaceans was always higher in the vegetated habitats compared to the unvegetated sediment. Within the vegetated habitats, the seagrass had a significantly higher abundance of mobile crustaceans in August 2022 compared to *Furcellaria* of the same sampling occasion, but this was not the case for the other sampling occasions where the abundance in seagrass was lower and at a similar level as the other vegetated habitats (Fig. 8a, Table 2).

Gastropod abundances also varied significantly between habitat and sampling occasion, with a significant interaction term (Table 2). During the two 2023 sampling occasions, the abundance of gastropods was significantly higher in the vegetated habitats compared to the unvegetated. However, in August 2022 only *Fucus* had a higher gastopod abundance than the unvegetated sediment, and in July 2023 *Fucus* had a significantly lower gastropod abundance compared to *Furcellaria*. Within habitats, the unvegetated sediments and *Fucus* had a higher epifaunal gastropod abundance in August 2022 compared to their July 2023 and September 2023 counterparts (Fig. 8b, Table 2).

Mesograzer (*Gammarus* sp. and *Idotea* sp.) abundance did not differ significantly between habitats (Table 2), but the p-value was marginally significant ($p = 0.053$), so a post-hoc test was carried out to investigate differences between habitats. This analysis indicated higher abundance of mesograzers in *Furcellaria* (on average 695 ind. m^{-2}) compared to the other

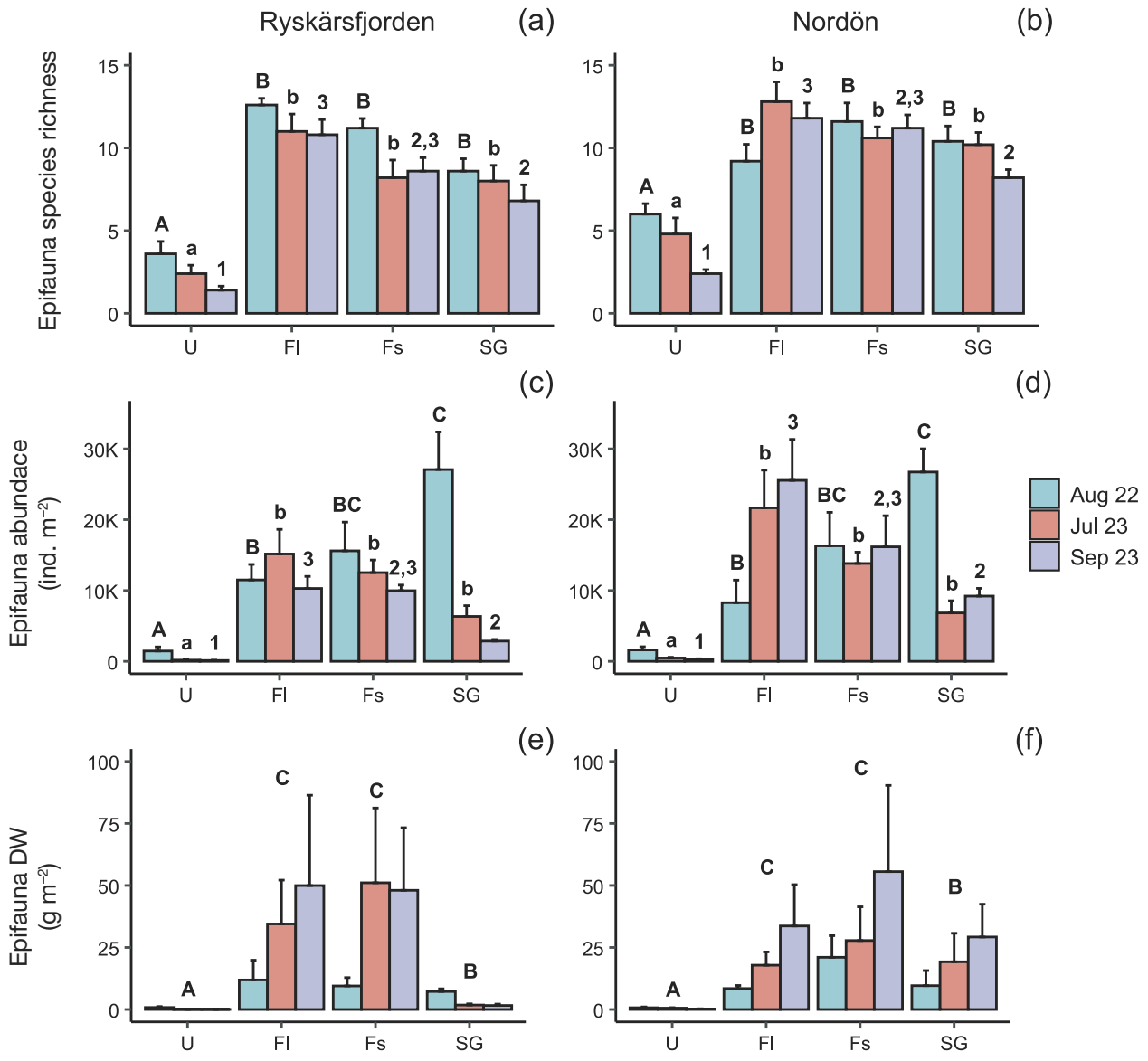

Fig. 6. Mean (+SE) epifauna species (a,b) richness, (c,d) abundance, and (e,f) dry weight (DW) biomass in the habitats: unvegetated sediments (U), *Furcellaria* (Fl), *Fucus* (Fs), and seagrass (SG). Data are divided between the sites (a,c,e) Ryskärsfjorden and (b,d,f) Nordön, and across sampling occasions (August 2022, July 2023, and September 2023). Capital letters, lowercase letters, and numbers above bars denote significance between habitats within sampling occasions and sites (Tukey's tests at $p < 0.05$). Differences between both sites and sampling occasions are not shown

habitats and higher abundance in *Fucus* (on average 101 ind. m^{-2}) compared to seagrass and unvegetated sediments (on average 15 and 1 ind. m^{-2}, respectively; Fig. 8c, Table 2).

3.3.2. Infauna

This study recorded 1312 individuals of infauna belonging to 12 different taxa (Table S5). In comparison to epifauna, the general effect of the algal mats on infauna was less clear, with species richness, abundance, and biomass either showing no significant differences between the habitats or by exhibiting patterns that changed between sampling occasions (Fig. 9, Table 3).

Species richness of infauna was significantly different between habitat, site, and sampling occasion, causing 2 significant interaction effects (Table 3). *Furcellaria* had a significantly lower species richness (on average 2.9 species) compared to *Fucus* and unvegetated sediments (on average 3.0 and 3.2 species, respectively) in July, but this pattern was partly reversed for the September sampling occasion, where

Table 1. Results of 3-way ANOVAs for differences in epifauna diversity metrics, considering the fixed factors habitat, time (sampling occasion), and site. ***p < 0.001; **p < 0.01; *p < 0.05; non-significant (ns), p > 0.05. DW: dry weight

Source of variation	df	Species richness			Abundance			Biomass (DW)		
		SS	*F*		SS	*F*		SS	*F*	
Habitat (A)	3	87	8.6	***	22.3	16.5	***	32.9	6.1	***
Time (B)	2	33.6	5.0	***	9.3	10.3	***	5.2	1.4	(ns)
Site (C)	1	14.4	4.3	*	0.5	1.1	(ns)	0.4	0.2	(ns)
A × B	6	69.9	3.4	**	17.4	6.4	***	9.8	0.9	(ns)
A × C	3	50.9	5.0	**	1.1	0.8	(ns)	1.5	0.3	(ns)
B × C	2	3.3	0.5	(ns)	0.7	0.8	(ns)	2.9	0.8	(ns)
A × B × C	6	32.2	1.6	(ns)	1.8	0.7	(ns)	11.5	1.1	(ns)
Residual	96	324.8			43.2			174		

Furcellaria supported a significantly higher species richness compared to its July counterpart and the unvegetated sediments (Fig. 9a,b, Table 3).

Abundance of infauna varied significantly between the habitats, sites, and sampling occasions, as seen by a significant 3-way interaction effect between factors (Table 3). Post-hoc tests did not identify any significant differences between habitats at Ryskärsfjorden, but at Nordön the unvegetated sediments was found to have a significantly higher abundance in July compared to *Furcellaria* and *Fucus*. However, in September, *Furcellaria* had a similar abundance to the unvegetated sediment and a significantly higher abundance than the *Fucus* habitat (Fig. 9c,d, Table 3). In July, polychaetes dominated the abundance in all habitats. However, in September they dominated only in unvegetated sediments, while amphipods and gastropods (only in *Furcellaria*) dominated the vegetated habitats (Fig. 10a).

In total, amphipods were the most abundant infaunal group, closely followed by polychaetes. Gastropods were generally not abundant, except for within the *Furcellaria* habitat during the September sampling occasion (Fig. 10a).

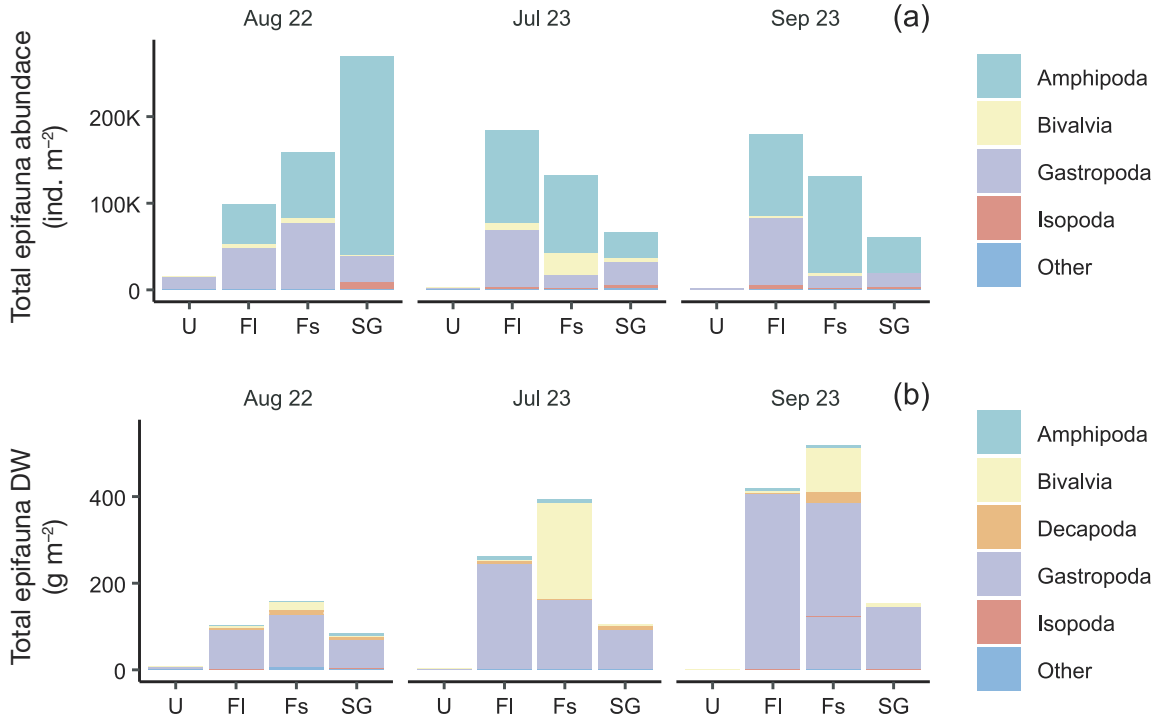

Fig. 7. (a) Total abundance and (b) dry weight (DW) biomass of different groups of epifauna across sampling occasions (August 2022, July 2023, and September 2023) for the habitats: unvegetated sediments (U), *Furcellaria* (Fl), *Fucus* (Fs), and seagrass (SG). The group 'Other' includes Echinodermata, Arachnida, Insecta, Tanaidae and Decapoda

Table 2. Results of 3-way ANOVAs for differences in abundance of epifauna groups, considering the fixed factors habitat, time (sampling occasion), and site. ***p < 0.001; **p < 0.01; *p < 0.05; non-significant (ns), p > 0.05

Source of variation	df	Mobile crustaceans SS	*F*		— Gastropods — SS	*F*		— Mesograzers — SS	*F*	
Habitat (A)	3	115.8	26.2	***	5.5	2.2	(ns)	32.6	2.7	(ns)
Time (B)	2	13.1	4.4	*	12.5	7.5	***	1.2	0.1	(ns)
Site (C)	1	4.7	3.2	(ns)	0.6	0.7	(ns)	0	0	(ns)
A × B	6	34.3	3.9	**	13.8	2.7	*	22.0	0.9	(ns)
A × C	3	8	1.8	(ns)	1.1	0.4	(ns)	25.6	2.1	(ns)
B × C	2	4.6	1.6	(ns)	1.2	0.7	(ns)	0	0	(ns)
A × B × C	6	11.1	1.3	(ns)	5.6	1.1	(ns)	9.8	0.4	(ns)
Residual	96	141.5			80.5			393.7		

The biomass (DW) of infauna did not significantly differ between factors, as there was large variation within the biomass, leading to standard deviations exceeding the means for all habitats (Fig. 9e,f, Table 3). There was also no clear pattern in terms of which fauna group dominated the biomass. In July, the fauna with shells (gastropods and bivalves) dominated the *Fucus* habitat but not the unvegetated sediments and the *Furcellaria*, but this pattern reversed for the September sampling occasion (Fig. 10b).

For the infaunal groups, crustacean abundance was significantly higher in the 2 algal habitats compared to the unvegetated sediments in September, but not in July, causing a significant interaction effect between site and time (Fig. 11a, Table 4). Infaunal bivalve abundance was significantly higher in the unvegetated sediments compared to *Furcellaria* in July, but there were no significant differences in September, causing a significant interaction between time and habitat (Fig. 11b, Table 4). The abundance of infaunal gastropods was significantly higher in the unvegetated sediments and *Furcellaria* compared to *Fucus* in September. However, there was no significant differences between habitats in September, causing a significant interaction between habitat and time (Fig. 11c, Table 4). Polychaete abundance was significantly higher in the unvegetated sediments compared to the 2 algal habitats at all sampling occasions (Fig. 11d, Table 4).

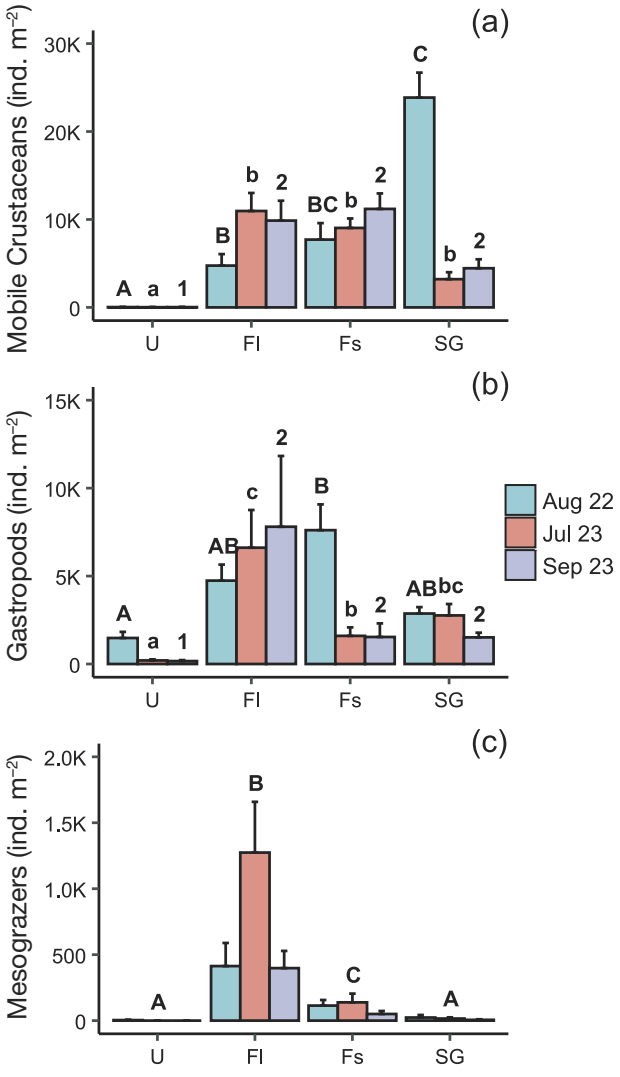

Fig. 8. Mean (+SE) abundance of (a) mobile crustaceans, (b) gastropods, and (c) mesograzers (*Gammarus* sp. and *Idotea* sp.) across sampling occasions (August 2022, July 2023, and September 2023) in the habitats: unvegetated sediments (U), *Furcellaria* (Fl), *Fucus* (Fs), and seagrass (SG). For (a) and (b), capital letters, lowercase letters, and numbers above bars denote significance between habitats within sampling occasions. For (c), capital letters above bars denote significant differences between habitats (Tukey's tests at p < 0.05)

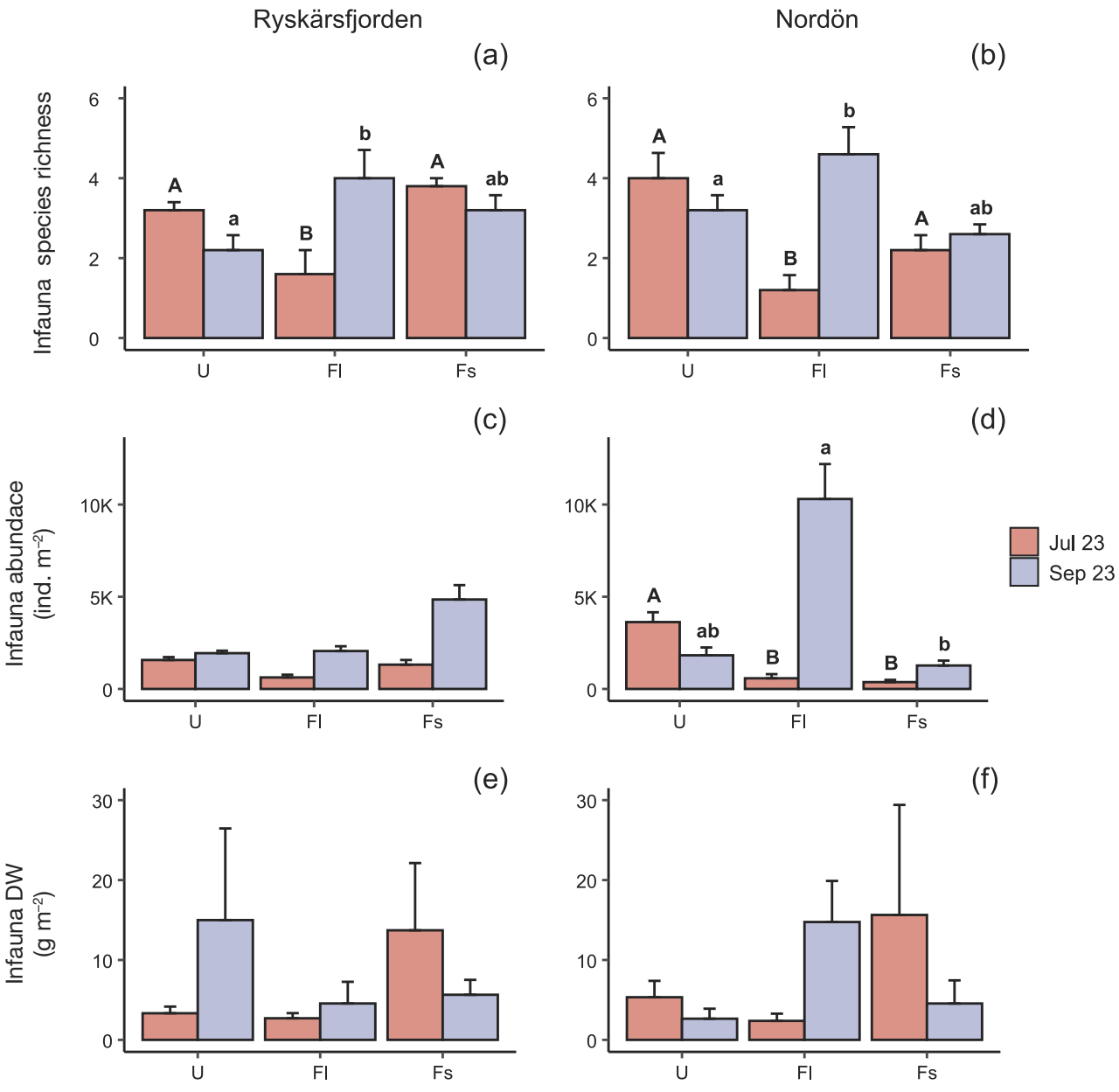

Fig. 9. Mean (+SE) infauna species (a,b) richness, (c,d) abundance, and (e,f) dry weight (DW) biomass in the habitats: unvegetated sediments (U), *Furcellaria* (Fl), and *Fucus* (Fs). Data are divided between the sites (a,c,e) Ryskärsfjorden and (b,d,f) Nordön, and across sampling occasions (July 2023 and September 2023). Capital letters and lowercase letters above bars denote significance between habitats within sampling occasions and sites (Tukey's tests at $p < 0.05$). Differences between both sites and sampling occasions are not shown

4. DISCUSSION

Along the Swedish NW coast, large drifting mats of *Furcellaria* and *Fucus* have replaced eelgrass meadows in many areas (Moksnes et al. 2018), but the impacts of this ecosystem shift on important ecosystem functions is unknown. This study showed that seagrasses and unvegetated sediments provided higher mean oxygen concentrations compared to drifting mats of *Fucus* and to a lesser degree mats of *Furcellaria*. Despite this, the epifauna diversity metrics of the drift algae was as high as those found in seagrass, and the vegetated habitats consistently supported a significantly higher abundance and biodiversity of epifauna compared to the unvegetated sediments. The drift algae habitats also did not negatively impact infauna, as they supported comparable diversity and abundances as the unvegetated sed-

Table 3. Results of 3-way ANOVAs for differences in infauna diversity metrics, considering the fixed factors habitat, time (sampling occasion), and site. ***p < 0.001; **p < 0.01; *p < 0.05; non-significant (ns), p > 0.05. DW: dry weight

Source of variation	df	Species richness			Abundance			Biomass (DW)		
		SS	*F*		SS	*F*		SS	*F*	
Habitat (A)	2	20.1	9.4	***	26	13.4	***	2.3	0.6	(ns)
Time (B)	1	1.6	1.5	(ns)	1.6	1.7	(ns)	1.8	1.0	(ns)
Site (C)	1	1.6	1.5	(ns)	1.7	1.7	(ns)	0.2	0.1	(ns)
A × B	2	23.4	11.0	***	29.7	15.3	***	8.4	2.2	(ns)
A × C	2	7.2	3.4	*	7.3	3.7	*	4.5	1.2	(ns)
B × C	1	0.1	0	(ns)	1.3	1.4	(ns)	2.5	1.4	(ns)
A × B × C	2	0.5	0.3	(ns)	9.2	4.7	*	6	1.6	(ns)
Residual	48	51.2			46.6			90.4		

iments. However, the species composition of epifauna and infauna differed significantly between habitats, suggesting that drift algae and seagrass may favor different species. As such, drifting mats of *Furcellaria* and *Fucus* provide important habitat functions for epifauna and infauna.

4.1. Dissolved oxygen concentration as a predictor of species composition and algal mat persistence

Dissolved oxygen concentrations were significantly lower in both mats of drift algae compared to the corresponding concurrently measured nearby unvegetated sediments. Overall, mean oxygen concentrations were lower and the occurrence of hypoxia and anoxia higher in the 2 drift algae habitats compared to seagrass and unvegetated sediments, particularly in the *Fucus* mat which showed no clear sign of photosynthesis and oxygen production during the day. It is, however, important to note that the oxygen recordings of the vegetated habitats differed spatially and temporally, as these habitats were recorded one at a time across 2 bays. The apparent differences between the vegetated habitats should, therefore, be interpreted with caution. Despite the negative impact on

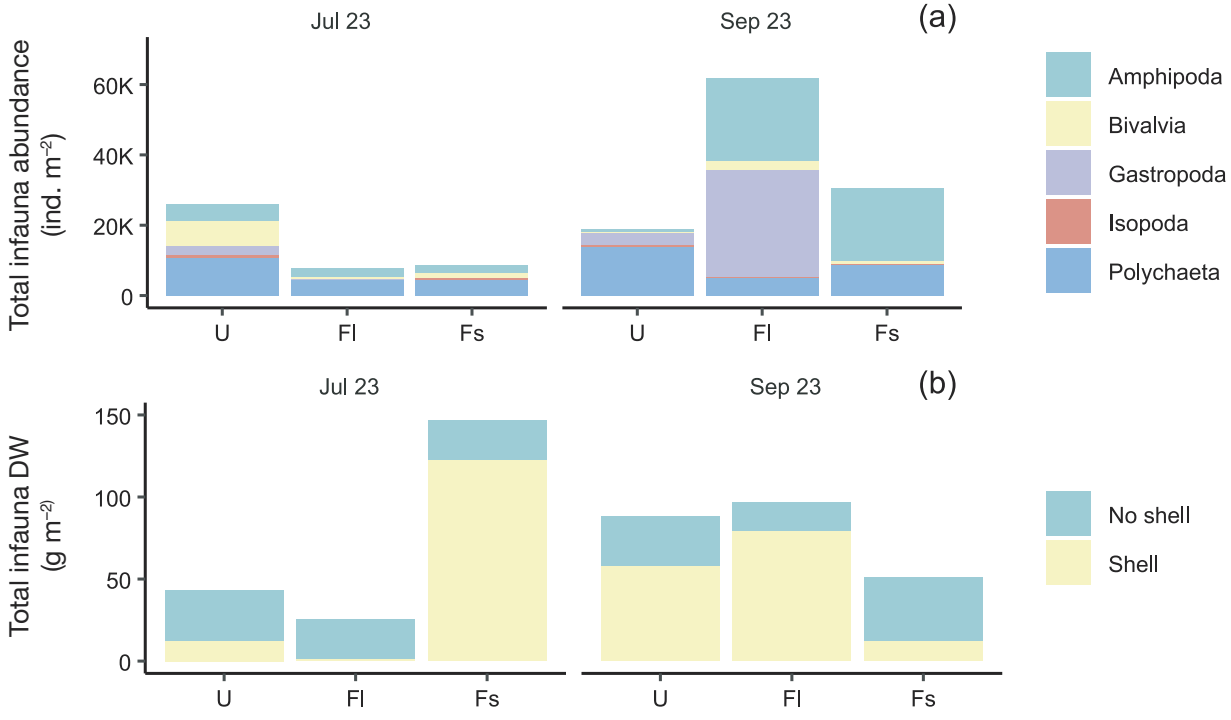

Fig. 10. (a) Total abundance and (b) dry weight (DW) biomass of different groups of infauna across sampling occasions (July 2023 and September 2023), for the habitats: unvegetated sediments (U), *Furcellaria* (Fl), and *Fucus* (Fs). Biomass is divided into fauna with shells (Bivalvia and Gastropoda) and fauna without shells (Amphipoda, Isopoda and Polychaeta)

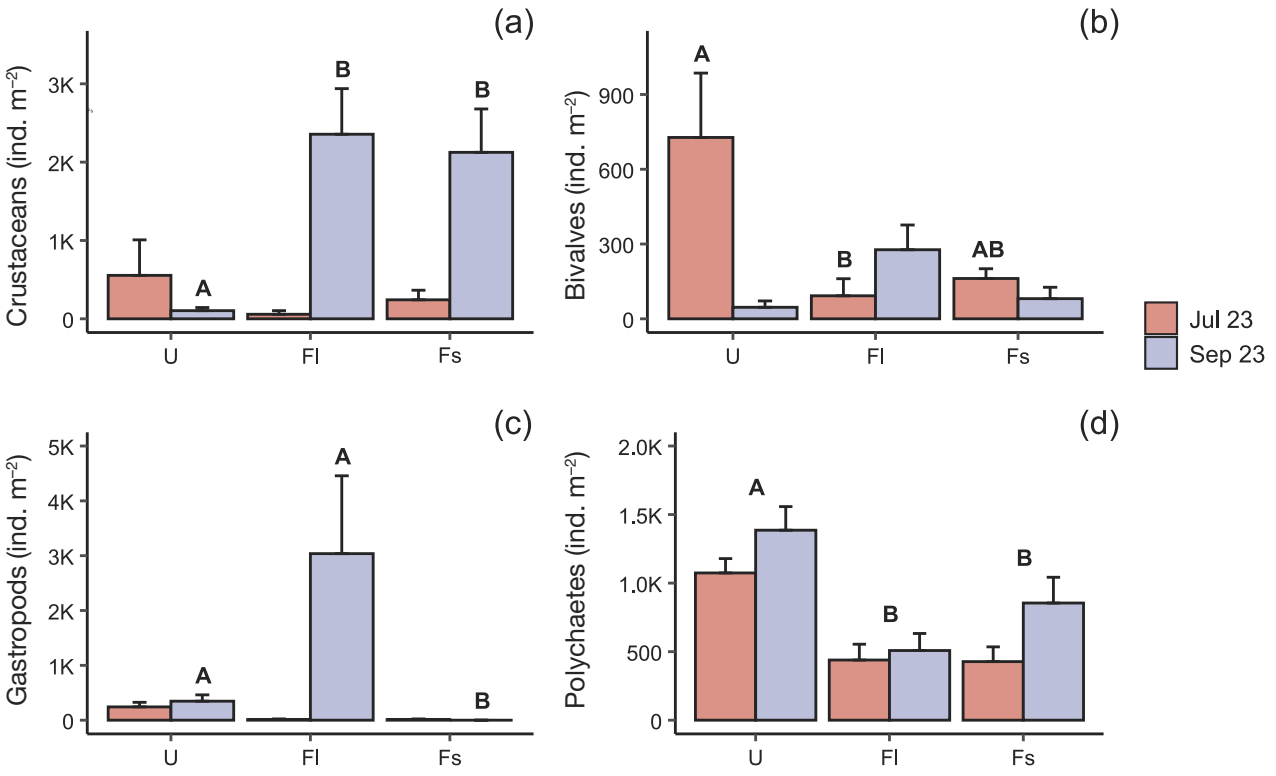

Fig. 11. Mean (+SE) abundance of (a) infaunal crustaceans, (b) bivalves, (c) gastropods, and (d) polychaetes, across sampling occasions (July 2023 and September 2023) in the habitats: unvegetated sediments (U), *Furcellaria* (Fl), and *Fucus* (Fs). For (a–c), capital letters above bars denote significant differences between habitats within sampling occasions. For (d), capital letters above bars denote significant differences between habitats (Tukey's tests at $p < 0.05$)

oxygen levels in the algal mats, they supported similar species richness and abundances of epifauna compared to seagrass and similar infauna compared to unvegetated habitats. Differences were found in terms of epifauna species composition between vegetated habitats, but if oxygen played a large role in driving these dissimilarities, we would expect a lack of species sensitive to hypoxia, such as amphipods, and a dominance of tolerant species, such as gastropods (Vaquer-Sunyer & Duarte 2008). However, these groups were present in all the vegetated habitats and often in similar abundances. It is possible, as these are mobile fauna, that they can avoid the hypoxia by climbing to the top of the algal canopy, especially as low oxygen concentrations were mainly recorded during the night, during which some groups increase their activity (Weckström & Salovius-Laurén 2023) and the threat of predation from visual predators is lower (Diehl 1988).

An important difference was detected between the algal mats, where *Furcellaria* and seagrass showed a significantly higher oxygen concentration during

Table 4. Results of 3-way ANOVAs for differences in abundance of infauna groups, considering the fixed factors habitat, time (sampling occasion), and site. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; non-significant (ns), $p > 0.05$

Source of variation	df	Crustaceans			Bivalves			Gastropods			Polychaetes		
		SS	*F*		SS	*F*		SS	*F*		SS	*F*	
Habitat (A)	2	15.9	1.6	(ns)	35.9	2.6	(ns)	34.8	3.2	*	2 701 227	8.7	***
Time (B)	1	0.3	0.1	(ns)	37.9	5.5	*	9.6	1.8	(ns)	12 003	0.1	(ns)
Site (C)	1	5.4	1.1	(ns)	5.2	0.8	(ns)	0	0	(ns)	33 343	0.2	(ns)
A × B	2	52.5	5.3	***	55.2	4.0	*	76.5	7.1	**	59 573	0.2	(ns)
A × C	2	29.3	2.9	(ns)	26.6	1.9	(ns)	4.5	0.4	(ns)	523 707	1.7	(ns)
B × C	1	2.6	0.5	(ns)	0.5	0.1	(ns)	0.9	0.2	(ns)	294 085	1.9	(ns)
A × B × C	2	0.3	0	(ns)	5.5	0.4	(ns)	16.5	1.5	(ns)	217 396	0.7	(ns)
Residual	48	239			331.4			259.9			7 474 164		

the day, likely produced by photosynthetic activity, whereas *Fucus* did not. This could indicate a lack of photosynthesis, meaning *Fucus* may be less stable than *Furcellaria* mats, and more likely to slowly deteriorate rather than grow. This was supported by regular observations of decomposed *Fucus* thalli in the epifauna samples, which was never observed for collected *Furcellaria*. Examples of this can be seen in shed *Laminaria* kelp detritus, where the biomass is able to partly sustain itself through limited photosynthesis, but not to a level where the biomass increases or is kept stable (Frontier et al. 2021), and thereby act as a temporary habitat for fauna (de Bettignies et al. 2020). Field experiments with individually marked pieces of *Furcellaria* and *Fucus* support this notion, as the *Furcellaria* remained fresh and healthy over a 5 mo growing season while the *Fucus* deteriorated over the same period (J. Severinson unpubl. data). Thus, the *Fucus* habitat may not be perennial and may, in contrast to the free-living form of *Furcellaria*, rely on continuous supply of shed biomass or detached individuals from nearby attached conspecifics. This is further supported by remote sensing data over a 7 yr period showing that the large *Fucus* mat at Nordön displayed substantial variation in areal extent between years whereas the large *Furcellaria* mat in Ryskärsfjorden was much more stable (J. Severinson unpubl. data). The ecological implications of this are that *Fucus* mats may be transient and therefore a less suitable habitat, as low-mobility fauna may be unable to find alternative shelter as the habitat withers away, possibly making the *Fucus* an ecological sink. However, this will depend on the rate of degradation and whether the continuous resupply of algae biomass outweighs the losses, as the mat may persist despite the degradation of individual thalli. More studies are needed to address this notion, as this study found similar epifaunal abundance and biodiversity between the vegetated habitats. Further investigations into the dispersal, growth and permanence of the 2 species of drifting algal mats are needed to understand their population dynamics and to which degree they can sustain themselves.

4.2. Habitat function of drifting *Furcellaria* and *Fucus* mats

Although oxygen conditions appeared lower in the algal mats, we did not find any negative effects on the infauna. Compared to unvegetated sediments, the abundance and species richness of epifauna was an order of magnitude higher in the algal mats, similarly to those measured in the seagrass habitat, suggesting that the positive effects of a structurally complex habitat outweighed any potentially negative effects of variable oxygen conditions in the algal habitats. The difference between the drift algae and the unvegetated sediments was clear across all epifauna diversity metrics. Within sampling occasions, epifauna species richness was between ~2 and 6 times higher in the algae habitats compared to unvegetated sediments, while the epifauna abundance was ~6 and 90 times higher. For infauna, the unvegetated sediments generally supported similar diversity and abundances compared to the drift algae, with the corresponding numbers equalling 0.8–1.6 for species richness and 0.2–3.3 for abundance. As such, compared to unvegetated sediments, these drift algae fulfil an important ecological role by promoting epifauna biodiversity and abundance at a similar level as seagrasses.

Because of recent large-scale eelgrass losses in the study area (Moksnes et al. 2021), the small size of the sampled seagrass meadows, the lack of eelgrass at Ryskärsfjorden, and the relatively low salinity in this estuarine environment, we were concerned that the epifauna abundance and diversity in the sampled seagrass habitats may not be representative for eelgrass meadows in NW Sweden. However, in comparison to earlier studies of the Kattegat–Skagerrak area, the present study found similar abundances and species diversity of epifauna associated with both eelgrass (Thormar et al. 2016, Riera et al. 2020, Gagnon et al. 2023, Kindeberg et al. 2024) and perennial brown algae attached to rocky shores (Armitage & Sjøtun 2016). Epifauna metrics were also comparable to transient mats of shed *Laminaria* detritus in France, where they found that epifauna species richness increased as the algae biomass decomposed, while abundance first decreased, but later returned to initial numbers (de Bettignies et al. 2020). This supports our findings, as the shed detritus of perennial algal species did not give rise to negative trends for associated epifauna metrics, despite decomposing in the *Fucus* habitat. Contrastingly, our epifauna results differ greatly from those measured in drifting mats of perennial *F. vesiculosus* in the Baltic Sea (Attard et al. 2023), where they recorded poor oxygen conditions within the algal canopy and epifauna species richness and abundances ~2 and ~30 times lower, respectively, compared to this study, despite other nearby habitats like attached *F. vesiculosus* and *Zostera marina* supporting comparable metrics to the present study. In addition, lower abundances of associated macrobenthos compared to unvegetated sediments was also found for drifting *F. vesiculosus* and *Furcellaria* in

Estonian waters (Kotta & Orav 2001), with reported abundances ~3 times lower compared to this study. Both studies also observed that abundances within the algae were dominated by mollusks, which are generally tolerant to hypoxia (Vaquer-Sunyer & Duarte 2008), unlike our results where crustaceans often dominated total abundances. Thus, the impact of low oxygen levels in drifting algal mats of perennial species on epifauna appears to vary between regions and algal species. The present results suggest that these algal mats constitute a valuable habitat for epifauna, where low oxygen concentrations do not necessarily translate to low associated epifauna diversity and abundance.

For infauna, values measured in this study are, however, on the lower end compared to the studies above. A contributor to this is the low number of polychaete species identified which, together with the lower polychaete abundance in the drift algae compared to the unvegetated sediments, implies that this group may disfavor drifting *Furcellaria* and *Fucus*.

Although species diversity and abundance were similar between the vegetated habitats in the present study, the species composition of epifauna differed between all habitats while infauna differed between unvegetated sediments and the 2 drift algae. However, the assumption of homogeneity of dispersions in the analysis was unfulfilled for infauna so this result should be interpreted with caution. Main contributors to dissimilarity were amphipods and gastropods, where the dominating species drove epifauna dissimilarity while abundances of specific species drove infauna dissimilarity. As such, the observed shift from seagrass to drift algae has impacted the abundance of certain species. This can be seen for the gastropods, where the drift algae had a higher abundance of *Pusilina sarsii* and *Hydrobia* sp. but a lower abundance of *Rissoa membranacea* compared to seagrass. This is in line with previous studies showing a high affinity of *R. membranacea* to seagrass (Riera et al. 2020, Gagnon et al. 2023). However, although different species of amphipods and gastropods dominated in different vegetated habitats, they share similar functional roles as grazers on ephemeral macro- and microalgae (e.g. Moksnes et al. 2008). Thus, differences in species composition between the algal and seagrass habitats likely have not impacted functional diversity. In contrast, the abundance of infaunal polychaetes was higher in unvegetated sediments compared to algal mats. The factors behind these differences are unclear, but it is possibly associated with different physical conditions (e.g. oxygen), food and larval supply, as well as substrates for foraging and shelter in the different habitats. However, it could also be due to differences in terms of within-bay sediment heterogeneity. Of note is that the crustacean mesograzers were more abundant in the drift algae compared to seagrass, with *Gammarus* sp. and *Idothea chelipes* found in ~100 and ~8 times higher abundances in *Furcellaria*, respectively, while only *Gammarus* sp. was more abundant (~17 times) in the *Fucus* compared to seagrass. These species are highly effective herbivores on filamentous algae growing in eelgrass meadows but have largely been lost from eelgrass meadows on the Swedish west coast due to overfishing of large predators, causing a trophic cascade that increased the number of mesopredators, thus releasing ephemeral algae from grazer control (Moksnes et al. 2008, Baden et al. 2010, 2012, Riera et al. 2020). The much higher abundance in *Furcellaria* could be due to increased food supply, either through a higher biomass of periphyton or through the possibility of using the algae itself as a food source, although a previous study showed that while *Furcellaria* can be grazed by *Idothea baltica*, it was not preferred (Kotta et al. 2000). Since these grazer species are large (10–30 mm) and very sensitive to fish predation (Moksnes et al. 2008, Baden et al. 2010), a more likely explanation is that *Furcellaria*, being finely branched and a very structurally complex habitat (Fig. 2), provides better protection against predation in comparison to the other habitats.

This study exemplifies the importance of sampling at multiples times and sites to obtain a representative sample of how benthic invertebrate fauna differ between habitats. Both abundances and species richness of the epifauna showed high spatial and temporal variation within the vegetated habitats, which was mainly driven by the amphipods and gastropods. This is in line with other studies proposing that between-year and within-year variation in species abundances can change drastically due to a range of factors, such as temperature or vegetation dynamics (Gagnon et al. 2023, Steinfurth et al. 2024).

4.3. Implications for management

The loss of approximately 1000 ha of eelgrass meadows in the study area, where recovery and restoration are hindered by decreased water quality and disturbance from drifting mats of perennial algae, has coastal managers concerned because of the potential loss of biodiversity and other valuable ecosystem services provided by eelgrass (Cole & Moksnes 2016, Moksnes et al. 2018, 2021). Coastal man-

agers in NW Sweden are therefore presently considering measures to remove these algal mats to facilitate the recovery of eelgrass (Moksnes et al. 2016). However, the results of this study highlight that drifting algal mats constituted of *Furcellaria* and *Fucus* support biodiversity and abundance of epifauna that were an order of magnitude higher than unvegetated sediments and similar to seagrass habitats, while supporting infauna at a similar level to unvegetated sediments.

Thus, the observed regime shift from a clear water, eelgrass state to a turbid state dominated by mats of perennial algae species (Moksnes et al. 2018) may not have large direct negative effects on the invertebrate faunal community. These algae mats appear to provide an important habitat function for a diverse community of epifauna, without causing any measurable negative effects on infauna. This may particularly be the case for *Furcellaria* mats that appear to be perennial and photosynthesize and grow on the bottom, providing a stable habitat for several years. *Furcellaria* also had the highest densities of mesograzer crustaceans, which are important in controlling growth of ephemeral algae in seagrass habitats (Moksnes et al. 2008). The algae mats may, therefore, also function as a spatial refuge from high predation rates in other habitats. A shallow, soft sediment bay with algal mats may, consequently, have higher values in terms of ecosystem function and services than one without. It is, therefore, not advisable to remove mats of perennial algae, unless they can be replaced with a habitat of higher function.

Although these algal mats had similar diversity and abundance of epifauna as nearby seagrass meadows, eelgrass provides additional, important ecosystem functions and services (Cole & Moksnes 2016, Moksnes et al. 2021) that algal mats likely do not. For example, an important ecosystem function of eelgrass meadows is dampening of waves and currents by the canopy, and sediment stabilization by the roots and rhizomes, increasing sedimentation and decreasing resuspension. This function results in clearer water and facilitates sequestration of carbon and nutrients, mitigating both climate change and eutrophication (Duarte et al. 2005, Moksnes et al. 2018, 2021, Röhr et al. 2018). In the Sälöfjord–Hakefjord area, the eelgrass losses have decreased secchi depth by up to 2 m in affected areas (Moksnes et al. 2018) and released carbon and nutrients, resulting in costs to society equivalent to ~150 million US $ (Moksnes et al. 2021). Drifting mats of *Furcellaria* and *Fucus* lack this stabilizing effect as evident by the lower water clarity in areas where they dominate (Moksnes et al. 2018), and studies have shown that drifting algae can increase the resuspension of sediment through physical abrasion (Canal-Vergés et al. 2010).

Another important ecosystem function and service that eelgrass in Sweden provides is fish production, by constituting an important nursery habitat for several juvenile fish species, including commercially important cod fishes that receive shelter and food in the meadows (Pihl et al. 2006, Rönnbäck et al. 2007). This function may be less supported by the drift algae, as the low profile (~15 cm canopy height) and highly complex structure of the algae, particularly the *Furcellaria* mats, likely offer juvenile fish less shelter and may hinder the fish's ability to forage in comparison to eelgrass meadows or perennial algae on hard substrate. In addition, the higher turbidity in the bays dominated by algal mats (Moksnes et al. 2018) may also present suboptimal conditions for visual fish predators. In support of this suggestion, very few fish were observed around the algal mats during sampling, in comparison to the abundant and diverse fish fauna viewed with snorkeling in eelgrass meadows in the study area during daytime sampling (Castro-Fernández et al. 2025). The high abundance of large amphipods and isopods in the *Furcellaria* mat, as discussed above, may also indicate suboptimal forage conditions for fish, as these species are highly vulnerable to fish predation (Moksnes et al. 2008).

In summary, although drifting mats of *Furcellaria* and *Fucus* may not provide all the ecosystem function and services as eelgrass meadows, they still constitute an important habitat for epifauna in the study area without negative effects on the infauna. In particular, the *Furcellaria* mats which appear to grow and persist for many years, should be viewed as a natural perennial habitat with important roles for the coastal ecosystem. Removal of these algal mats is, therefore, likely not the best conservation option for managers. Studies assessing how the shift from eelgrass to drifting algal mats has impacted sediment resuspension, sequestration of organic matter, and fish production would be valuable contributions to improve management of these areas.

Acknowledgements. We sincerely thank Patrik Magnestam, Louise Eriander, Karl Karlsson, Maru Bernal, Henrik Möller, and Matilda Rasmussen for their assistance with field work. We also thank Anders Olsson and Niclas Åberg for their input and feedback at the project start. We thank Johan Persson for assistance with infauna counting and Susanne Pihl Baden for help with amphipod identification. Lastly, we thank 3 anonymous reviewers who provided very helpful comments that improved an earlier version of the manuscript. Funding of this research was provided by the Västra Götaland county administrative board (LOVA project 5186) and Gothenburg University.

LITERATURE CITED

Abelson A, Reed DC, Edgar GJ, Smith CS and others (2020) Challenges for restoration of coastal marine ecosystems in the Anthropocene. Front Mar Sci 7:544105

Anderson MJ (2017) Permutational multivariate analysis of variance (PERMANOVA). In: Balakrishnan N, Colton T, Everitt B, Piegorsch W, Ruggeri F, Teugels JL (eds) Wiley StatsRef: statistics reference online. Wiley, p 1–15

Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr 83:557–574

Armitage CS, Sjøtun K (2016) Epiphytic macroalgae mediate the impact of a non-native alga on associated fauna. Hydrobiologia 776:35–49

Attard KM, Lyssenko A, Rodil IF (2023) High metabolism and periodic hypoxia associated with drifting macrophyte detritus in the shallow subtidal Baltic Sea. Biogeosciences 20:1713–1724

Austin AP (1960) Observations on *Furcellaria fastigiata* (L.) Lam. forma *aegagropila* Reinke in Danish waters together with a note on other unattached algal forms. Hydrobiologia 14:255–277

Austin Å, Hansen J, Donadi S, Bergström U, Eriksson B, Sundblad G, Eklöf J (2021) Synergistic effects of rooted aquatic vegetation and drift wrack on ecosystem multifunctionality. Ecosystems 24:1670–1686

Baden S, Gullström M, Lundén B, Pihl L, Rosenberg R (2003) Vanishing seagrass *(Zostera marina*, L.) in Swedish coastal waters. Ambio 32:374–377

Baden S, Boström C, Tobiasson S, Arponen H, Moksnes PO (2010) Relative importance of trophic interactions and nutrient enrichment in seagrass ecosystems: a broad-scale field experiment in the Baltic–Skagerrak area. Limnol Oceanogr 55:1435–1448

Baden S, Emanuelsson A, Pihl L, Svensson CJ, Åberg P (2012) Shift in seagrass food web structure over decades is linked to overfishing. Mar Ecol Prog Ser 451:61–73

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193

Boström C, Baden SP, Krause-Jensen D (2003) The seagrasses of Scandinavia and the Baltic Sea. In: Green EP, Short FT, Spalding MD (eds) World atlas of seagrasses. University of California Press, Berkeley, CA, p 27–37

Boström C, Baden S, Bockelmann A, Dromph K and others (2014) Distribution, structure and function of Nordic eelgrass *(Zostera marina)* ecosystems: implications for coastal management and conservation. Aquat Conserv 24: 410–434

Canal-Vergés P, Vedel M, Valdemarsen T, Kristensen E, Flindt MR (2010) Resuspension created by bedload transport of macroalgae: implications for ecosystem functioning. Hydrobiologia 649:69–76

Canal-Vergés P, Potthoff M, Hansen FT, Holmboe N, Rasmussen EK, Flindt MR (2014) Eelgrass re-establishment in shallow estuaries is affected by drifting macroalgae — evaluated by agent-based modeling. Ecol Modell 272: 116–128

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU and others (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Carstensen J, Conley DJ (2019) Baltic Sea hypoxia takes many shapes and sizes. Limnol Oceanogr Bull 28:125–129

Castro-Fernández J, Terrados J, Hinz H, Castejón-Silvo I, Moksnes PO, Infantes E (2025) Fish community structure and habitat complexity in restored and natural eelgrass meadows. Aquat Conserv 35:e70092

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Cole SG, Moksnes PO (2016) Valuing multiple eelgrass ecosystem services in Sweden: fish production and uptake of carbon and nitrogen. Front Mar Sci 2:121

Correia KM, Alford SB, Belgrad BA, Darnell KM and others (2022) Drift macroalgae positively influence seagrass-associated nekton communities of the northern Gulf of Mexico. Front Environ Sci 10:939296

D'Agata C, Staveley T, Eklöf J, Lefcheck J, Rosenqvist G, Nordlund L (2025) Submersed aquatic vegetation enhances density and diversity of epifaunal invertebrates compared to filamentous mats in the central Baltic Sea. Ecol Evol 15:e71498

de Bettignies F, Dauby P, Lepoint G, Riera P and others (2020) Temporal succession of a macrofaunal community associated with kelp fragment accumulations in an *in situ* experiment. Mar Ecol Prog Ser 656:109–121

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574

Den Hartog C (1987) 'Wasting disease' and other dynamic phenomena in *Zostera* beds. Aquat Bot 27:3–14

Diehl S (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53:207

Duarte CM, Krause-Jensen D (2017) Export from seagrass meadows contributes to marine carbon sequestration. Front Mar Sci 4:13

Duarte CM, Middelburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2:1–8

Duarte CM, Apostolaki ET, Serrano O, Steckbauer A, Unsworth RKF (2025) Conserving seagrass ecosystems to meet global biodiversity and climate goals. Nat Rev Biodiver 1:150–165

Dunic JC, Brown CJ, Connolly RM, Turschwell MP, Côté IM (2021) Long-term declines and recovery of meadow area across the world's seagrass bioregions. Glob Chang Biol 27:4096–4109

Eriander L, Alenius B, Infantes E, Olsson A, Moksnes PO (2025) Handbok för restaurering av ålgräs i Sverige — Uppdatering av kunskapsläget 2016–2024. Report 2025: 13. Swedish Agency for Marine and Water Management, Gothenburg (in Swedish)

Fox J, Weisberg S (2019) An R companion to applied regression. Sage, Thousand Oaks, CA

Frontier N, de Bettignies F, Foggo A, Davoult D (2021) Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: detached or broken, but not dead. Mar Environ Res 166:105277

Gagnon K, Bocoum E, Chen CY, Baden SP, Moksnes PO, Infantes E (2023) Rapid faunal colonization and recovery of biodiversity and functional diversity following eelgrass restoration. Restor Ecol 31:e13887

Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN (2015) Marine biodiversity and ecosystem functioning: What's known and what's next? Oikos 124: 252–265

Hayward PJ, Ryland JS (eds) (2017) Handbook of the marine fauna of north-west Europe, 2nd edn. Oxford University Press, Oxford

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373

Kindeberg T, Attard KM, Hüller J, Müller J, Quintana CO, Infantes E (2024) Structural complexity and benthic

metabolism: resolving the links between carbon cycling and biodiversity in restored seagrass meadows. Biogeosciences 21:1685–1705

Kotta J, Orav H (2001) Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea). Ann Zool Fenn 38:163–171

Kotta J, Paalme T, Martin G, Mäkinen A (2000) Major changes in macroalgae community composition affect the food and habitat preference of *Idotea baltica*. Int Rev Hydrobiol 85:697–705

Lenth R (2024) Emmeans: estimated marginal means, aka least-squares means. R package version 1.10.2. https://rvlenth.github.io/emmeans/

Lindegren M, Möllmann C, Hansson LA (2010) Biomanipulation: a tool in marine ecosystem management and restoration? Ecol Appl 20:2237–2248

Martin G, Kotta J, Möller T, Herkül K (2013) Spatial distribution of marine benthic habitats in the Estonian coastal sea, northeastern Baltic Sea. Estonian J Ecol 62:165

Martinez Arbizu P (2020) PairwiseAdonis: pairwise multilevel comparison using adonis. R package version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis

Moksnes PO, Gullström M, Tryman K, Baden S (2008) Trophic cascades in a temperate seagrass community. Oikos 117:763–777

Moksnes PO, Gipperth L, Eriander L, Laas K, Cole S, Infantes E (2016) Handbook for restoration of eelgrass in Sweden — national guideline. Report number 2021:5. Swedish Agency for Marine and Water Management, Gothenburg

Moksnes PO, Eriander L, Infantes E, Holmer M (2018) Local regime shifts prevent natural recovery and restoration of lost eelgrass beds along the Swedish west coast. Estuaries Coasts 41:1712–1731

Moksnes PO, Röhr ME, Holmer M, Eklöf JS, Eriander L, Infantes E, Boström C (2021) Major impacts and societal costs of seagrass loss on sediment carbon and nitrogen stocks. Ecosphere 12:e03658

Moksnes PO, Svensson R, Bergström P, Lindegarth M (2024) Statusklassificering av ålgräs i Västerhavet. Report number 2024:17. Swedish Agency for Marine and Water Management, Gothenburg (in Swedish)

Norkko A, Bonsdorff E (1996a) Population responses of coastal zoobenthos to stress induced by drifting algal mats. Mar Ecol Prog Ser 140:141–151

Norkko A, Bonsdorff E (1996b) Rapid zoobenthic community responses to accumulations of drifting algae. Mar Ecol Prog Ser 131:143–157

Nygren A, Pleijel F (2015) Ringmaskar: Havsborstmaskar, Annelida: Polychaeta. Artdatabanken SLU, Uppsala (in Swedish)

Nyqvist A, André C, Gullström M, Baden SP, Åberg P (2009) Dynamics of seagrass meadows on the Swedish Skagerrak coast. Ambio 38:85–88

Oksanen J, Simpson G, Blanchet F, Kindt R and others (2022) Vegan: community ecology package R. R package version 2.6-4. https://vegandevs.github.io/vegan/

Pedersén M, Snoeijs P (2001) Patterns of macroalgal diversity, community composition and long-term changes along the Swedish west coast. Hydrobiologia 459: 83–102

Pihl L, Baden S, Kautsky N, Rönnbäck P, Söderqvist T, Troell M, Wennhage H (2006) Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuar Coast Shelf Sci 67:123–132

Preston R, Blomster J, Schagerström E, Seppä P (2022) Clonality, polyploidy and spatial population structure in Baltic Sea *Fucus vesiculosus*. Ecol Evol 12:e9336

Preston R, Blomster J, Schagerström E, Seppä P (2024) Different approaches to estimate benthic metazoan diversity associated with free-living macroalgae (*Fucus vesiculosus*) on shallow soft sediments. Estuar Coast Shelf Sci 301:108731

Preston R, Blomster J, Kautsy L, Salovius-Lauren S, Schagerström E (2025) Untangling the literature on unattached *Fucus* (Phaeophyceae): an overview of current knowledge. Eur J Phycol 60:389–413

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Richard M, Quijón PA (2023) Seagrass-macroalgal interactions in a changing ocean. Front Clim 5:1283305

Riera R, Vasconcelos J, Baden S, Gerhardt L, Sousa R, Infantes E (2020) Severe shifts of *Zostera marina* epifauna: comparative study between 1997 and 2018 on the Swedish Skagerrak coast. Mar Pollut Bull 158:111434

Röhr ME, Holmer M, Baum JK, Björk M and others (2018) Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. Global Biogeochem Cycles 32: 1457–1475

Rönnbäck P, Kautsky N, Pihl L, Troell M, Söderqvist T, Wennhage H (2007) Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. Ambio 36:534–544

Steinfurth RC, Nielsen B, Elsberg LF, Lange T and others (2024) Macrofaunal colonization after large-scale sandcap and *Zostera marina* restoration of organic enriched sediments in a Danish fjord. Mar Ecol Prog Ser 729:63–79

Thormar J, Hasler-Sheetal H, Baden S, Boström C and others (2016) Eelgrass (*Zostera marina*) food web structure in different environmental settings. PLOS ONE 11:e0146479

Unsworth RKF, Nordlund LM, Cullen-Unsworth LC (2019) Seagrass meadows support global fisheries production. Conserv Lett 12:e12566

Valdemarsen T, Canal-Vergés P, Kristensen E, Holmer M, Kristiansen MD, Flindt MR (2010) Vulnerability of *Zostera marina* seedlings to physical stress. Mar Ecol Prog Ser 418:119–130

van Katwijk MM, Hermus DCR (2000) Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. Mar Ecol Prog Ser 208:107–118

Vaquer-Sunyer R, Duarte CM (2008) Thresholds of hypoxia for marine biodiversity. Proc Natl Acad Sci USA 105: 15452–15457

Weckström K, Salovius-Laurén S (2023) Diel activity patterns of rocky shore macroinvertebrates in the northern Baltic Sea. J Sea Res 193:102376

Weinberger F, Paalme T, Wikström SA (2020) Seaweed resources of the Baltic Sea, Kattegat and German and Danish North Sea coasts. Bot Mar 63:61–72

Wernberg T, Thomsen MS, Baum JK, Bishop MJ and others (2024) Impacts of climate change on marine foundation species. Annu Rev Mar Sci 16:247–282

WoRMS (2024) World Register of Marine Species (WoRMS). www.marinespecies.org (accessed 15 Nov 2024)

Editorial responsibility: Mirta Teichberg, Woods Hole, Massachusetts, USA
Reviewed by: R. Preston and 2 anonymous referees
Submitted: July 2, 2025; Accepted: February 5, 2026
Proofs received from author(s): May 9, 2026