



Invertebrate Responses to Large- and Small-Scale Drivers in Coastal *Phragmites australis* Beds in the Northern Baltic Sea

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Abstract

Phragmites australis is a common helophyte, covering much of the sheltered and shallow soft bottoms along the coasts of the Baltic Sea. Despite the expansion of *P. australis* over the past decades, there is little information on aquatic macroinvertebrates within *P. australis* beds. In this study, we examined the effect of large-scale (wave exposure, nutrients) and small-scale (distance from the seaward edge, live and dead stalk density, epiphyte and rhizome biomass) drivers on the density, taxa richness, diversity, and community structure of epifauna and infauna in monospecific *P. australis* beds around the Åland Islands and the Archipelago Sea. We found that higher wave exposure and nutrient levels generally supported higher epi- and infauna abundance and taxa richness. The effects on Shannon–Wiener diversity were less evident apart from an increase of the infauna diversity in the Archipelago Sea with increasing nutrient levels. On a local scale, the distance from the seaward edge, live and dead stalk density, and epiphyte biomass had varying effects on both epi- and infauna communities in the different regions. Rhizome biomass had no effect on either the epi- or infauna abundance, taxa richness, or diversity. Furthermore, according to existing studies, other habitats, e.g., *Zostera marina* meadows, *Fucus vesiculosus* belts, and vegetated soft-bottomed shallow bays, are generally characterized by more abundant fauna, except for the infauna, which had a higher density in *P. australis* beds than in vegetated soft-bottomed shallow bays. *P. australis* are a widespread, expanding, and understudied habitat with an important role in supporting coastal biodiversity.

Keywords Marine macrofauna · Åland Islands · Archipelago Sea · Common reed · Wave exposure · Edge effects

Introduction

The common reed, *Phragmites australis*, is a cosmopolitan perennial helophyte, which can form large monotypic stands in fresh and brackish waters (Meyerson et al. 2016).

P. australis is able to rapidly colonize new shorelines, though very exposed shores with heavy wave action are mostly unfavorable (Coops and Van der Velde 1996; von Numers 2011). In addition to wave exposure, water depth is also a strong factor in the limitation of seaward expansion (Meriste et al. 2010). As the depth increases, the transport of oxygen to the root system becomes more difficult, hampering aeration pathways (Huhta 2009; Engloner and Major 2011), which limit the maximum growing depth of *P. australis* to ca. 2 m (Luther 1951). As a fast-growing and fast-spreading species, it can rapidly outcompete other vegetation and has expanded in many coastal areas (Chambers et al. 1999; Meyerson et al. 2016). As a result, *P. australis* beds make up a significant component of many brackish and estuarine ecosystems around the world and can strongly drive and/or alter local biodiversity and ecosystem functioning (Chambers et al. 1999; Wails et al. 2021). For example, the replacement of salt marsh cordgrasses by *P. australis* can lead to shifts in faunal abundance and biodiversity (Angradi et al. 2001), as well as changes in trophic functioning and ecosystem processes

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such as carbon and nitrogen cycling (Wainwright et al. 2000; Wails et al. 2021). As coastal wetlands are critical ecosystems that provide valuable ecosystem services, such as biodiversity provisioning, coastal protection, and carbon storage (Mitsch et al. 2015), these ecosystem shifts can have profound implications. *P. australis* also fulfills other ecological services by providing nesting habitats for birds as well as spawning and nursery areas for fish (Lappalainen et al. 2008; Kiviat 2019; Niemi et al. 2023).

In the Baltic Sea, *P. australis* is expanding at an annual rate of 1–8% (Altartouri et al. 2014), forming extensive beds. Due to their high aboveground (stalks and leaves) and belowground (rhizomes and roots) structure and biomass, *P. australis* beds can greatly increase structural habitat complexity in coastal areas. By providing a substrate for epiphytic algae (Müller 1995), *P. australis* stalks likely also increase secondary structural complexity (James et al. 1998), similar to seagrass shoots (Schneider and Mann 1991; Bologna and Heck 1999). Habitat complexity at different scales is a primary factor in determining associated faunal communities in vegetated marine and aquatic habitats (Bell et al. 2012). For example, plant cover and density, as well as habitat fragmentation and patch size, drive community structure and predator–prey dynamics in seagrass meadows and salt marshes (Irlandi 1994; Bowden et al. 2001; McFarlin et al. 2015). However, environmental factors, such as wave exposure, nutrient concentrations, or physical disturbances, can modify or mitigate the importance of habitat complexity (Hovel et al. 2002).

Despite slightly lower abundances than native cordgrasses, invertebrate densities of > 80 000 individuals m⁻² have been measured in *P. australis* stands of invaded salt marshes in North America (Angradi et al. 2001). In lakes, *P. australis* beds can also harbor high densities of invertebrates, though the dominant groups often vary. In Spain, salinity and nutrient status were important drivers of the invertebrate community composition (Sahuquillo et al. 2008), while in Polish lakes, the location within the *P. australis* bed was the main driver for the invertebrate community composition (Miler et al. 2018). In the Baltic Sea, *P. australis* beds are also potentially important habitats for coastal biodiversity and may support invertebrate biodiversity, which could compensate for the loss of invertebrate biodiversity in other, more vulnerable submerged habitats such as *Z. marina* meadows and *F. vesiculosus* belts. However, despite their high and expanding areal coverage, the importance of *P. australis* beds for invertebrate diversity is largely unknown. In the southern Baltic Sea, *P. australis* beds had high invertebrate densities, and the location within the bed was an important driver of species distribution (Pawlikowski et al. 2022). As that study only included a single site, the relative importance of large-scale vs. small-scale drivers in *P. australis* beds is largely

unknown compared to many other marine vegetated habitats such as seagrass meadows and macroalgal habitats in the Baltic Sea. For example, in *Z. marina* meadows and macroalgal beds, large-scale environmental drivers, such as exposure and eutrophication status (Korpinen et al. 2007a, b; Korpinen et al. 2010), facilitate or limit diversity and drive community structure. This also applies to small-scale variables within habitats, such as structural complexity and distance from the habitat edge (Wikström and Kautsky 2007; Boström and Bonsdorff 2000).

Here, we explored the role of *P. australis* beds in supporting coastal biodiversity and in particular the large-scale (wave exposure and nutrient levels) and small-scale (distance from the seaward edge, live and dead stalk density, epiphyte and rhizome biomass) drivers structuring epifaunal (animals living on the sediment or vegetation) and infaunal (animals living within the sediment) invertebrate diversity, abundance, taxa richness, and community structure. The study was conducted in two separate areas of the northern Baltic Sea to determine if the same patterns apply in two different regions. We hypothesized that (1) exposure and stalk density increase epi- and infauna abundance, taxa richness, and diversity, while (2) epiphyte biomass will increase epifauna abundance, that (3) high nutrient levels and distance from the seaward edge will decrease both epi- and infauna taxa richness and diversity, and that (4) rhizome biomass will decrease infauna abundance but increase infauna taxa richness. We further hypothesized that the effects would be similar in both regions.

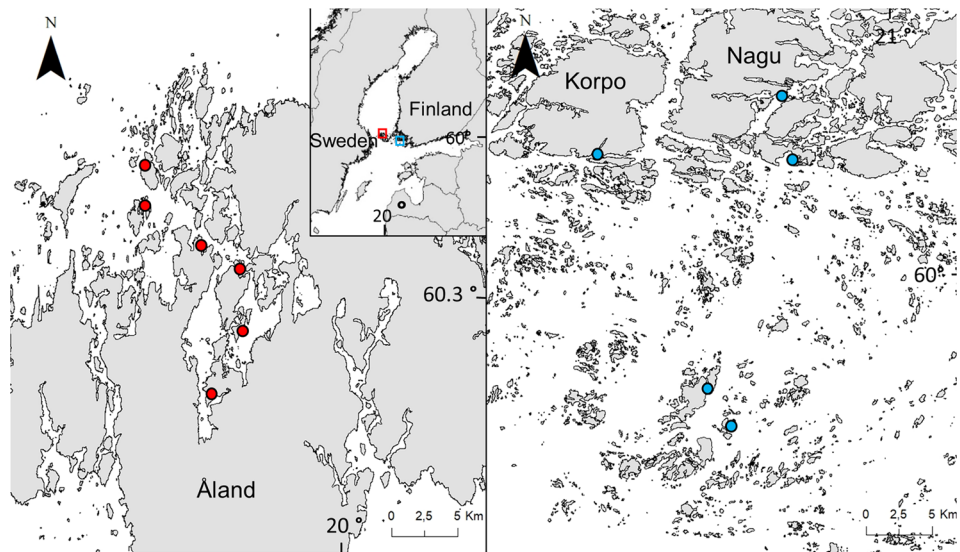
Materials and Methods

Study Area and Field Sampling

Our study area included eleven sites with *P. australis* beds along the southwestern coast of Finland: six sites from the outer to inner archipelago at the Åland Islands (hereafter ÅI) and five sites in the Archipelago Sea (hereafter AS) (Fig. 1). Before its expansion, *P. australis* was primarily found in inlets or around larger, sheltered islands, while today it grows along most soft-bottomed shores except the most exposed ones (von Numers 2011).

The invertebrates within *P. australis* beds were sampled in July–August 2018 in ÅI and in July–August 2021 in AS. Sites were selected according to similar patchiness, i.e., a similar distribution of different stalk densities ranging from 0 to 50 stalks/m², depth (0.8–1.7 m), and width of the *P. australis* bed (8–13 m, within the depth interval) (Fig. 2). Nine epifauna and twelve infauna samples were taken per site, evenly divided over gradients of stalk density and distance from the seaward edge of the *P. australis* bed.

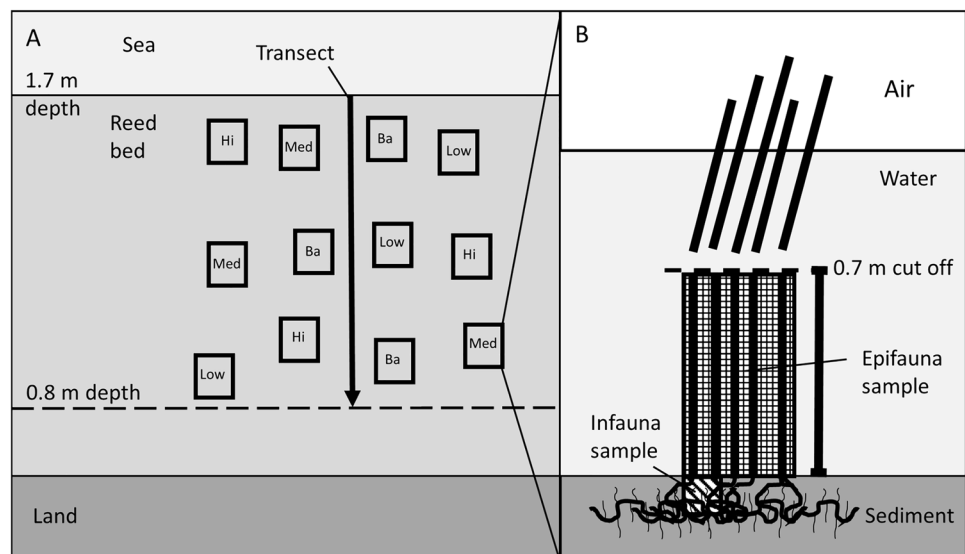
Fig. 1 Location of the eleven sampling sites in the Åland Islands (left) and the Archipelago Sea (right) in the northern Baltic Sea



The distance from the bed edge was measured by attaching a measuring tape to the first *P. australis* stalk on the seaward side of the bed and drawing it in a straight line perpendicular to the shore. Each sample was approached perpendicular from the transect line in order to minimize disturbance, and the position of each sample along the transect was noted to the nearest meter. Three epifauna and three infauna samples were sampled in three different stalk densities: high (mean 22.3 stalks m^{-2} , SE 1.4), medium (mean 13.3 stalks m^{-2} , SE 0.9), and low (mean 6.6 stalks m^{-2} , SE 0.9). In addition, three infauna samples were taken from unvegetated patches in three different distances within the *P. australis* bed from the seaward side (outer, 0–4 m from the edge; middle, 2–8 m from the edge; inner, 5–13 m from the edge, depending on the water depth and width of the

P. australis bed). Naturally, no epifauna could be sampled in the unvegetated sediment. The stalk density was measured by counting both live and standing dead stalks in a 0.5×0.5 m quadrat per sample. The epifauna was sampled by first cutting the stalks at a height of 0.7 m from the bottom, then placing a net bag (mesh size 0.5 mm) over the stalks in the quadrat, cutting the stalks just above the sediment level and preserved as one sample. On average, the epifauna samples from the higher stalk density consisted of 16.8 live and 5.3 dead stalks, the medium density contained 10.1 live and 4.8 dead stalks, and the low density contained 4.9 live and 2.4 dead stalks. The infauna was sampled by driving a steel corer with a vacuum lock ($\varnothing$ 11 cm) into the top 10 cm of the sediment immediately below the area sampled for epifauna. The content of the corer was sieved

Fig. 2 Drawing of the sampling setup. A Top-down view of site, visualizing the distribution of the different *P. australis* stalk densities high (Hi), medium (Med), low (Low), and bare sediment (Ba). B Side view of individual epi- and infauna sampling, showing first the cutting (0.7 m from the bottom) and sampling of stalks for epifauna (0–0.7 m above the sediment) and then the core sampling of sediment for infauna below



(0.5 mm) and preserved in 70% ethanol and stored individually. The epifauna was separated from the associated *P. australis* stalks and the infauna from the rhizomes, identified to the lowest practical taxonomic level, and counted under a dissecting microscope. From the separated *P. australis* stalks in the epifauna samples, epiphytes (consisting mainly of filamentous algae) were scraped off the stalks, while the infauna samples were separated and the rhizomes scraped clean. Both the epiphytes and rhizomes were dried at 60 °C for 48 h to calculate biomass.

Nutrient Levels and Wave Exposure

Water nutrient concentrations were measured by taking water samples at 1 m depth at each site; in ÅI, one sample was taken at each site three times between June and August 2018, while in AS one sample was taken at each site in August 2021. In AS, total phosphorous and nitrogen ($\mu\text{g/l}$) were analyzed using continuous flow analysis, while in ÅI, total phosphorous and nitrogen ($\mu\text{g/l}$) were analyzed by a manual discrete method (Koroleff 1977; Grasshoff et al. 1983) and the mean values per site were calculated. Total phosphorous was selected as a proxy value for nutrient level, as it is the limiting factor for primary production in coastal Baltic areas (Andersson et al. 1996). The wave exposure was estimated according to the WaveImpact 1.0 model where fetch is calculated as the refraction/diffraction for 25×25 m grids covering the sample area. Wave exposure values were obtained by multiplying the mean wind speed of 16 directions over a 5-year period by the adjusted fetch of the corresponding direction (Isæus 2004; Sundblad et al. 2014).

Statistical Analyses

Prior to analysis, the covariation between the environmental variables was analyzed by Spearman ranked correlation. Several variables were excluded (total phosphorous in ÅI) from the models to eliminate collinearity; in case of correlation, only the causal variable (wave exposure) was included. As the two regions were sampled in different years, they were analyzed separately. Taxa richness and Shannon–Wiener diversity for each site were calculated using the “specnumber” and “diversity” functions in the “vegan” package (Oksanen 2013) in R version 3.6.1. Prior to the application of the models, the response variables were examined for normal distribution with the Shapiro test, function: “shapiro.test.” In the case of normal distribution of the response variable, a Gaussian distribution was used in the model. In the case of non-normal distribution of the response variable, either a Poisson or negative binomial distribution was used, based on inspection of the quartile-quartile plots and residual plots. Generalized linear models were constructed with the “glm” and “glm.nb” functions (“mass”

package in R version 3.6.1) to examine the effects of the two site-specific variables: exposure and total phosphorus (i.e., variables that vary on a large scale between the *P. australis* beds). Additionally, the effects of several nested factors (i.e., that vary on a small scale within a *P. australis* bed): distance from the seaward edge, stalk density, proportion of live and dead stalks, epiphyte biomass, and rhizome biomass on both the epifauna and infauna total abundance, taxa richness, and Shannon–Wiener diversity, were tested.

To determine the relative importance of the environmental variables in shaping the invertebrate communities, a distance-based linear model (DistLM), based on a Bray–Curtis dissimilarity matrix, with the selection criterion corrected Akaike information criterion (AICc), and a specified selection procedure was used (Anderson et al. 2008). The DistLM was done using PRIMER7+ (Clarke and Gorley 2006). The non-metric multidimensional scaling (NMDS) was done using the function “metaMDS.” The NMDS was run until solutions with minimal stress were obtained (Oksanen et al. 2009). The “metaMDS” function auto-transformed (square root) the epifauna and infauna community data, from both regions, prior to calculating the Bray–Curtis dissimilarity matrix. The untransformed environmental variables were fitted to the unconstrained ordination to show the direction of the gradients and the relative strength of the correlation between the ordination and vectors of environmental variables with the “envfit” function.

Comparison to Other Habitats

To compare the invertebrate community within *P. australis* beds with the invertebrate communities in other vegetated Baltic Sea habitats, a literature study was done on the biodiversity in *F. vesiculosus* and *Z. marina* in the ÅI and AS region and in soft-bottomed shallow bays (vegetation consisting of *Stuckenia pectinata*, *Ceratophyllum demersum*, and *Chara tomentosa*) in ÅI. Epifauna and infauna densities from previous studies (1997–2020) were extracted. As these habitats differ widely in vegetation structure and biomass, all data were converted to invertebrate density m^{-2} . The lowest and highest densities from the different habitats were compared to the lowest and highest densities of the *P. australis* beds sampled in this study, to enable a general comparison of each habitat’s role in supporting marine invertebrates.

Results

Abundance, Richness, and Diversity

In this study, a total of 40 invertebrate taxa were found, of which 25 (62.5%) taxa occurred in both regions (Table 1). Twenty-five of these taxa were also found in both epifauna

Table 1 Epi- and infauna species/taxa within *P. australis* beds and total abundance m^{-2} (mean and SE) per species per region (ÅI & AS)

	Åland Islands	Archipelago Sea	Åland Islands	Archipelago Sea
	Epifauna		Infauna	
Gastropoda				
<i>Bithynia tentaculata</i>	9 (4.7)	0 (0)	224.6 (36.4)	31.6 (8)
<i>Hydrobia</i> sp.	15.1 (7.7)	0.8 (0.4)	2433.3 (652.1)	1617.5 (183.9)
<i>Lymnaea peregra</i>	0 (0)	0.4 (0.2)	0 (0)	63.2 (12.3)
<i>Lymnaea stagnalis</i>	0.1 (0.1)	0.1 (0.1)	0 (0)	8.8 (3.8)
<i>Physa fontinalis</i>	5.7 (3.8)	0 (0)	1.8 (1.5)	0 (0)
<i>Potamopyrgus antipodarum</i>	9.9 (4.6)	1.2 (0.6)	1192.9 (246.7)	578.9 (81.4)
<i>Radix balthica</i>	0.4 (0.3)	0 (0)	10.5 (6.2)	3.5 (2.5)
<i>Theodoxus fluviatilis</i>	43.9 (8.8)	6.1 (1.3)	129.8 (25.1)	157.9 (23.8)
<i>Valvata piscinalis</i>	0 (0)	0 (0)	3.5 (2.1)	0 (0)
Bivalvia				
<i>Cerastoderma glaucum</i>	3.6 (1.7)	5.6 (1.2)	80.7 (18.2)	435.1 (66.4)
<i>Macoma balthica</i>	0 (0)	0 (0)	368.4 (54.2)	770.2 (131.7)
<i>Mya arenaria</i>	0 (0)	0.1 (0.1)	17.5 (5.6)	49.1 (15.7)
<i>Mytilus edulis</i>	13.8 (10.8)	12.4 (3.3)	63.2 (14.9)	921 (175.1)
<i>Parvicardium hauniense</i>	0 (0)	0 (0)	21.1 (7.8)	0 (0)
Annelida				
<i>Hediste diversicolor</i>	1.2 (0.5)	0.3 (0.2)	124.6 (25.7)	368.4 (54.5)
<i>Marenzelleria</i> sp.	0.8 (0.3)	0.2 (0.1)	87.7 (16.4)	3.5 (2.5)
<i>Oligochaeta</i> sp.	2.8 (0.8)	0.1 (0.1)	128.1 (24.5)	738.6 (90.6)
Crustacea				
<i>Asellus aquaticus</i>	7.2 (3.8)	0 (0)	8.8 (19.4)	0 (0)
<i>Balanus improvisus</i>	23.6 (15.3)	7.7 (1.8)	3.5 (4.5)	336.8 (71.6)
<i>Bathyporeia pilosa</i>	0.1 (0.1)	0 (0)	0 (0)	0 (0)
<i>Corophium volutator</i>	0 (0)	0 (0)	5.3 (4.4)	0 (0)
<i>Gammarus</i> spp.	8.4 (2.1)	4.9 (1.2)	101.8 (20.9)	212.3 (74.5)
<i>Idotea balthica</i>	6.5 (3)	0.2 (0.2)	0 (0)	1.8 (1.8)
<i>Idotea chelipes</i>	0.8 (0.5)	0.4 (0.2)	1.8 (1.5)	5.3 (3.9)
<i>Isopoda</i> sp.	0 (0)	0 (0)	1.8 (1.5)	0 (0)
<i>Jaera</i> sp.	0.5 (0.3)	0.2 (0.1)	26.3 (16.3)	0 (0)
<i>Leptocheirus</i> sp.	0.3 (0.2)	0.2 (0.1)	0 (0)	7 (4.2)
<i>Mysis</i> sp.	0.2 (0.1)	0.1 (0.1)	0 (0)	0 (0)
<i>Palaemon elegans</i>	0.1 (0.1)	0 (0)	0 (0)	0 (0)
<i>Pontoporeia affinis</i>	0.1 (0.1)	0 (0)	0 (0)	0 (0)
<i>Sinelobus vanhaareni</i>	0 (0)	1.3 (0.4)	0 (0)	33.3 (11.9)
Insecta				
Chironomidae	19.4 (3.6)	50 (7.9)	778.9 (107.4)	531.6 (70.4)
<i>Donacia</i> sp.	0.1 (0.1)	0.3 (0.2)	0 (0)	0 (0)
<i>Macropoda mutica</i>	0 (0)	0 (0)	0 (0)	1.8 (1.8)
Odonata	1.7 (0.6)	0.6 (0.2)	17.5 (7.7)	33.3 (7.7)
Trichoptera	14.5 (3.3)	0 (0)	35.1 (15.4)	33.3 (7.7)
Other				
<i>Prostoma</i> sp.	0 (0)	0 (0)	0 (0)	3.5 (2.5)
Platyhelminthes sp.	0.1 (0.1)	1.1 (0.4)	0 (0)	0 (0)
<i>Halicryptus spinulosus</i>	0 (0)	0 (0)	0 (0)	1.8 (1.8)
Total abundance	10,264	4232	11,604	15,792
Total taxon richness	28	23	25	27

and infauna samples. Epifauna communities in both areas were characterized by high densities of gastropods (*Hydrobia* spp., *Potamopyrgus antipodarum*, *Theodoxus fluviatilis*), bivalves (*Cerastoderma glaucum*, *Mytilus edulis*), crustaceans (*Balanus improvisus*, *Gammarus* spp.), and insect larvae (Chironomidae, Trichoptera). Infauna communities included high densities of gastropods (*Bithynia tentaculata*, *Hydrobia* spp., *P. antipodarum*, *T. fluviatilis*), bivalves (*C. glaucum*, *Macoma balthica*, *Mya arenaria*, *M. edulis*), annelids (*Hediste diversicolor*, Oligochaeta), crustaceans (*Gammarus* spp.), and insect larvae (Chironomidae, Trichoptera) (Table 1).

Wave exposure had a positive effect on epifauna abundance ($p < 0.001$ for both ÅI and AS regions, $n = 54, 45$), taxa richness ($p < 0.001$, $n = 54, 45$), and diversity ($p = 0.049$, $p = 0.009$; $n = 54, 45$) in both ÅI and AS. Wave exposure also positively affected infauna abundance ($p < 0.001$ for both, $n = 56, 60$) in both ÅI and AS and taxa richness ($p < 0.001$, $n = 56$) in ÅI, while total phosphorus had positive effects on epifauna abundance ($p = 0.011$, $n = 45$), infauna abundance ($p < 0.001$, $n = 60$), taxa richness ($p = 0.015$, $n = 60$), and diversity ($p = 0.010$, $n = 60$) in AS (Table 2). Note that in ÅI wave exposure and total phosphorus were strongly correlated (Appendices Tables 5 and 6) and could not be treated separately. Instead, wave exposure should be considered as a proxy for total phosphorus for this region (Fig. 3). Within *P. australis* beds, the distance from the seaward edge negatively affected epifauna abundance ($p = 0.002$, $n = 45$) and diversity ($p = 0.015$, $n = 45$) in AS and infauna abundance ($p = 0.004$, $n = 60$) and taxa richness ($p = 0.037$, $n = 60$) in AS (Fig. 4). The density of live stalks negatively affected epifauna taxa richness ($p = 0.018$, $n = 54$) in ÅI, but positively affected epifauna abundance ($p < 0.001$, $n = 45$) and infauna abundance ($p < 0.001$, $n = 60$) in AS. The density of dead stalks had differing effects by region: it increased epifauna abundance ($p < 0.001$, $n = 54$) and taxa richness ($p = 0.006$, $n = 54$) but decreased infauna abundance ($p = 0.029$, $n = 56$) in ÅI and increased infauna abundance ($p < 0.001$, $n = 60$) in AS. Epiphyte biomass increased epifauna abundance ($p = 0.029$, $n = 54$) in ÅI as well as epifauna taxa richness ($p = 0.014$, $n = 45$) and diversity ($p = 0.026$, $n = 45$) in AS, but rhizome biomass had no effect in either region (Table 2). In general, increased wave exposure and total phosphorus were linked to higher invertebrate abundance and taxa richness in both regions (Fig. 3). The effects on Shannon–Wiener diversity were less evident apart from an increase of the infauna diversity in AS with increasing nutrient levels (Fig. 3).

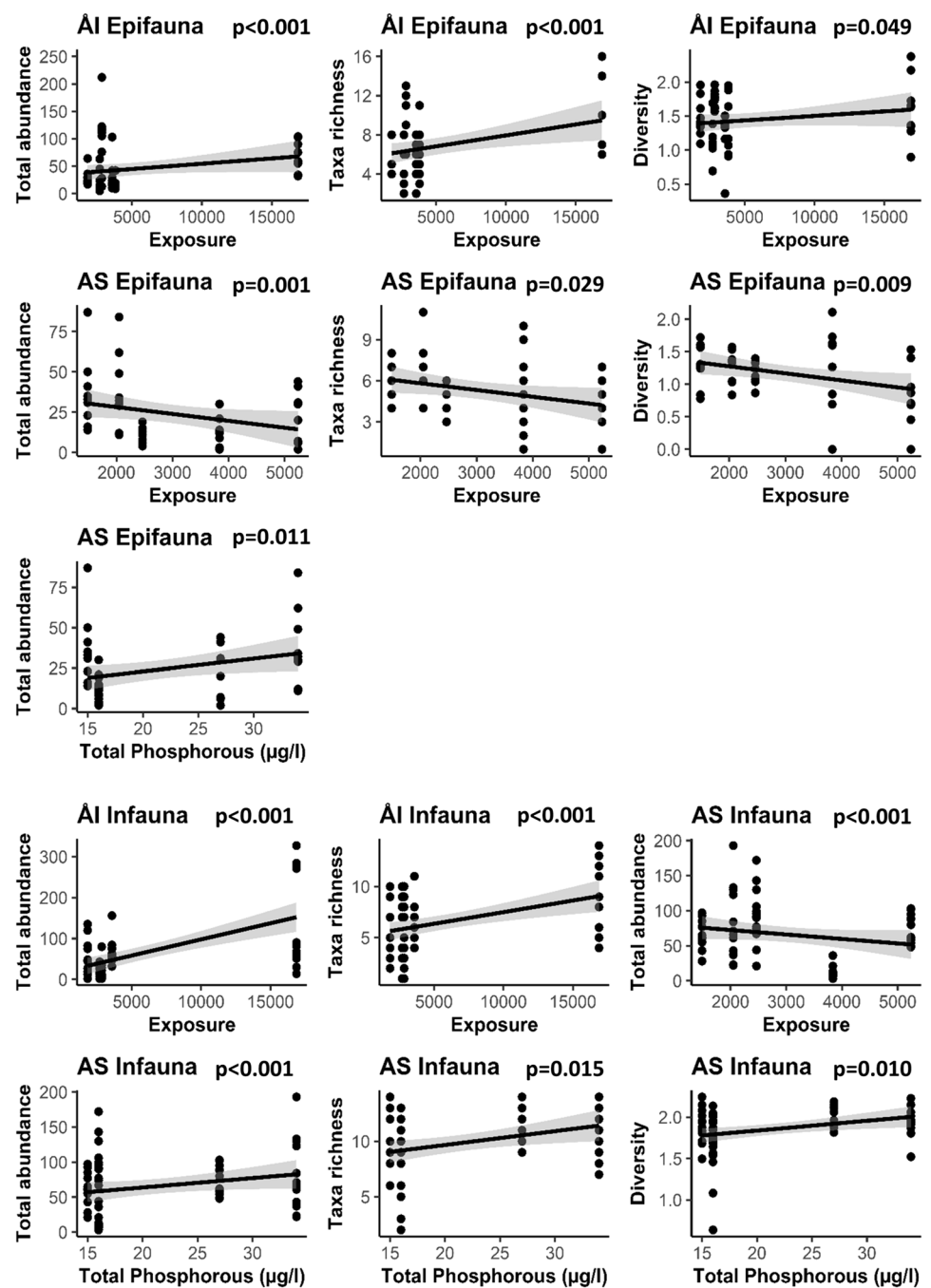
Community-Level Responses

According to the DistLMs, all the combined variables included in the GLMs explained 23–29% of the variation in the invertebrate community composition of the invertebrate

Table 2 Effects of environmental (Tot. P and exposure) and site parameters (distance, live stalks, dead stalks, epiphyte biomass, and rhizome biomass) on epi- and infauna total abundance (A), taxa richness (S), and Shannon–Wiener diversity (H) according to generalized linear models, including distributions, in the Åland and Archipelago Sea regions. Statistically significant factors ($p < 0.05$) indicated by an asterisk. Tot. P = total phosphorus. Distance = distance from the seaward edge of *P. australis* bed

	Region	Family	Link	Tot. P	Exposure	Distance	Live stalks	Dead stalks	Epiphyte biomass/stalk	Rhizome biomass
Epifauna A	Åland	Negative binomial	–	N.A	<0.001*	0.446	0.510	<0.001*	0.029*	N.A
Epifauna S	Åland	Poisson	Log	N.A	<0.001*	0.386	0.018*	0.006*	0.388	N.A
Epifauna H	Åland	Gaussian	Identity	N.A	0.049*	0.814	0.107	0.594	0.765	N.A
Epifauna A	Archipelago Sea	Negative binomial	–	0.011*	0.001*	0.002*	<0.001*	0.870	0.084	N.A
Epifauna S	Archipelago Sea	Poisson	Log	0.142	0.029*	0.080	0.278	0.183	0.014*	N.A
Epifauna H	Archipelago Sea	Gaussian	Identity	0.911	0.009*	0.015*	0.337	0.105	0.026*	N.A
Infauna A	Åland	Negative binomial	–	N.A	<0.001*	0.004*	0.070	0.029*	N.A	0.655
Infauna S	Åland	Gaussian	Identity	N.A	<0.001*	0.037*	0.130	0.006*	N.A	0.277
Infauna H	Åland	Gaussian	Identity	N.A	0.963	0.422	0.553	0.856	N.A	0.399
Infauna A	Archipelago Sea	Poisson	Log	<0.001*	<0.001*	0.167	<0.001*	<0.001*	N.A	0.134
Infauna S	Archipelago Sea	Gaussian	Identity	0.015*	0.176	0.192	0.203	0.545	N.A	0.509
Infauna H	Archipelago Sea	Gaussian	Identity	0.010*	0.290	0.285	0.143	0.653	N.A	0.634

Fig. 3 Scatterplots of the epi- and infauna total abundance (A), taxa richness (S), and Shannon–Wiener diversity (H) vs. wave exposure and total phosphorous with GLM smoother in both AI and AS



community except for the infauna in AI, where they accounted for 48% of the variation (Table 3).

Additionally, the DistLM revealed that the large-scale factors of total phosphorus and wave exposure had the largest effect in determining epi- and infauna communities in both regions (accounting for 5–30% and 7–12% of total variation in AI and AS, respectively), while small-scale factors (distance from the seaward edge 3%, live stalks

3–5%, dead stalks 2%) had minor effects (Appendix 3, Table 7). Based on the envfit analysis, wave exposure was among the important drivers in both regions and epi- and infaunal communities, while epiphyte biomass also played a role in shaping the epifauna community composition (Fig. 5). The ordination of the infauna community in both regions was affected by exposure, total phosphorous, the density of dead stalks, and the epiphyte biomass (Fig. 5).

Fig. 4 Scatterplots of the epi- and infauna total abundance (A), taxa richness (S), and Shannon–Wiener diversity (H) vs. distance from the seaward edge of the bed with GLM smoother in both ÅI and AS

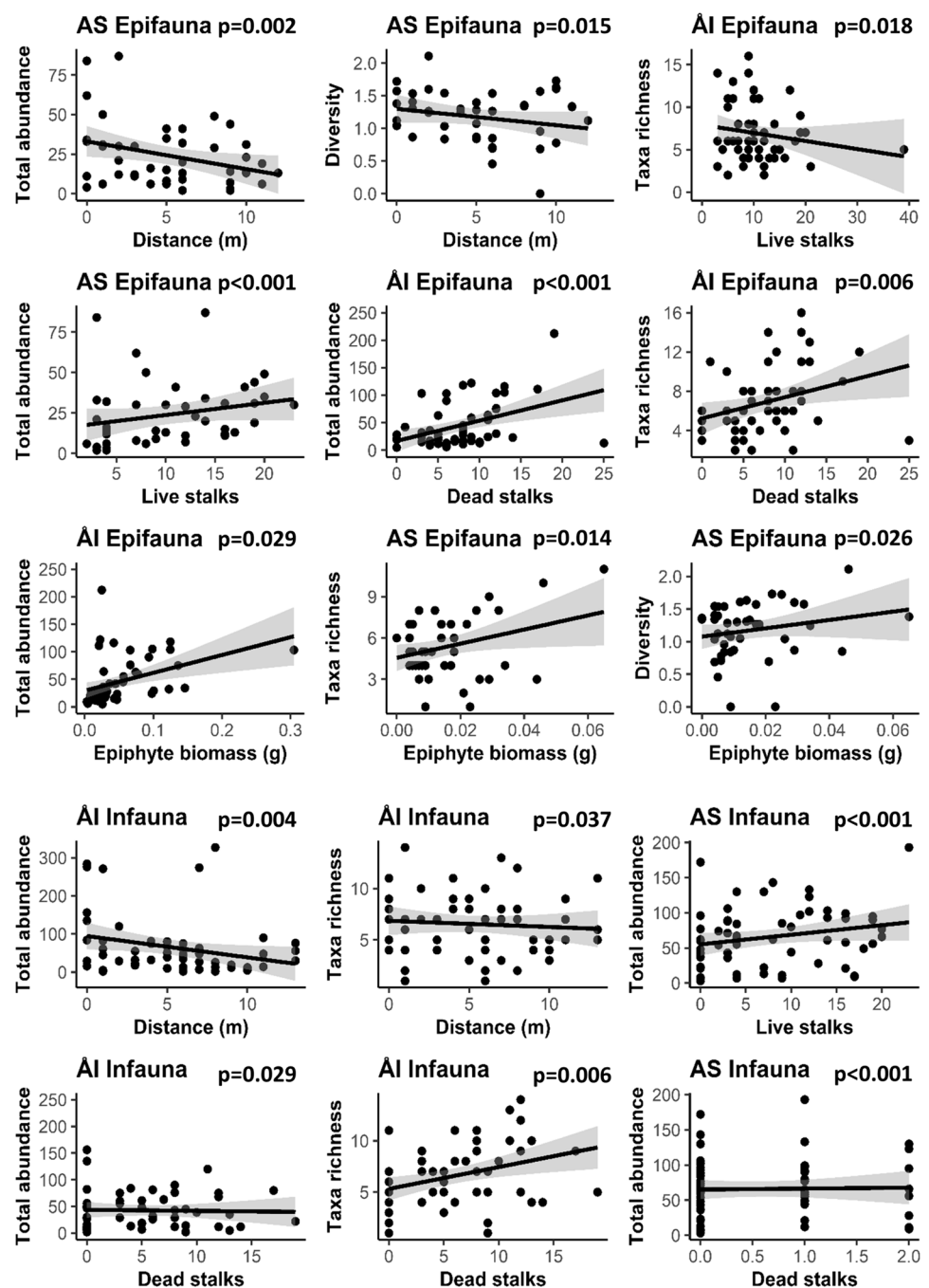


Table 3 The proportion of variation of epi- and infauna communities around the Åland and Archipelago Sea regions explained by the included variables through distance-based linear modeling (DistLM).

Region—community	Selected model	R ²
Åland epifauna	Tot. P + wave exposure + distance + live stalks + dead stalks + epiphyte biomass/stalk	0.28
Archipelago Sea epifauna	Tot. P + wave exposure + distance + live stalks + dead stalks + epiphyte biomass/stalk	0.29
Åland infauna	Tot. P + wave exposure + distance + live stalks + dead stalks + rhizome biomass	0.48
Archipelago Sea infauna	Tot. P + wave exposure + distance + live stalks + dead stalks + rhizome biomass	0.23

Tot. P = total phosphorus. Distance = distance from the seaward edge of the *P. australis* bed

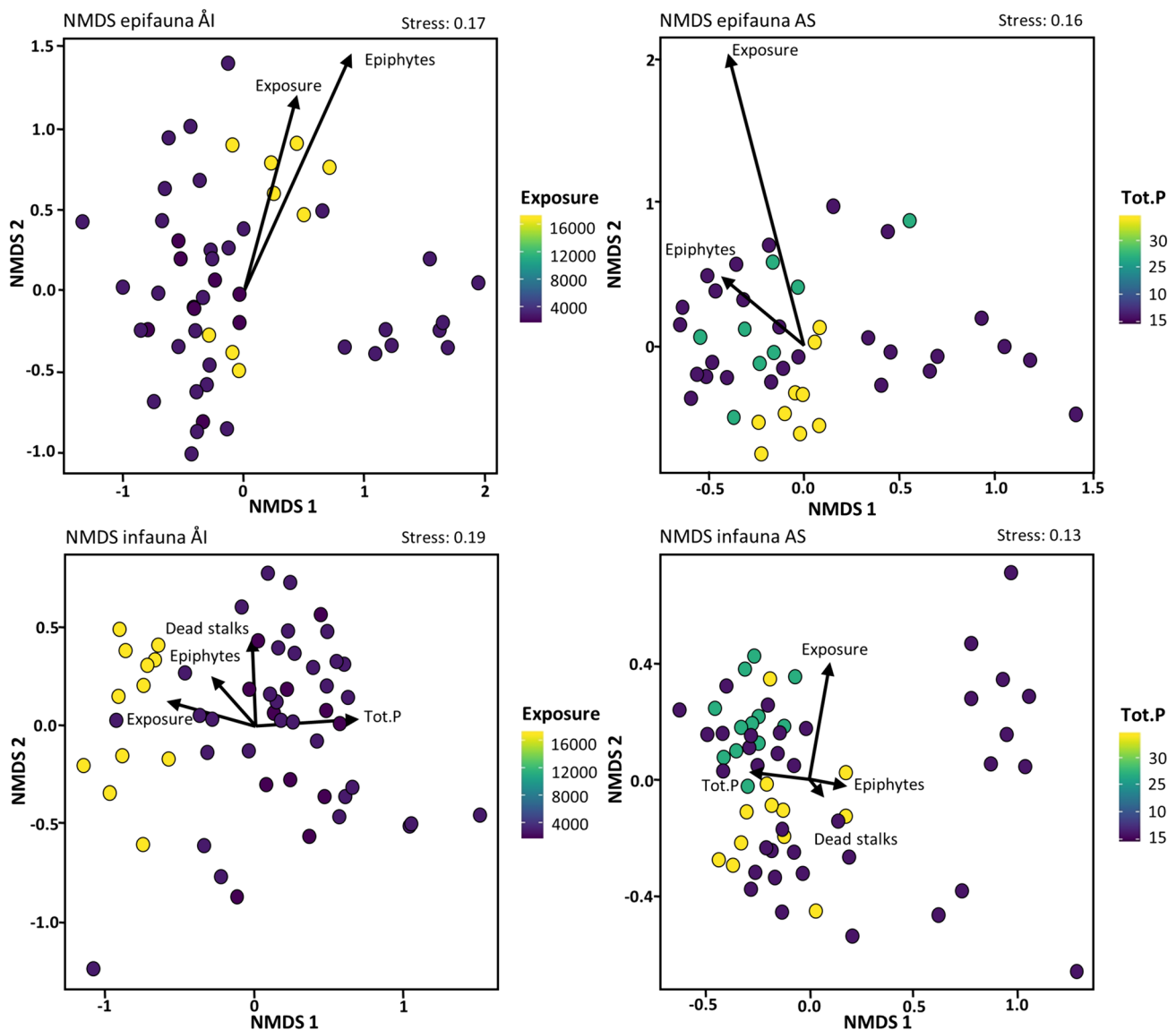


Fig. 5 NMDS ordination of epifauna (top) and infauna (bottom) communities in the Åland Islands (left) and Archipelago Sea (right). The arrows indicate the most important environmental variables according to the envfit analysis, with line length proportional to variable importance

Comparison to Other Habitats

P. australis beds generally host a lower density (on an areal basis, m^{-2}) of both epi- and infauna than eelgrass (*Z. marina*) and bladderwrack (*F. vesiculosus*) habitats. Overall, the epifauna densities were 13–94 times higher in both other habitats than in *P. australis*, while infauna densities were 3–8 times higher in *Z. marina* than in *P. australis*. In shallow, soft-bottomed bays, epifauna densities were 13–17 times higher than in *P. australis*, whereas infauna densities were 4 times higher in *P. australis* than in soft-bottomed shallow bays (Table 4).

Discussion

In this study, we showed that *P. australis* beds provide habitat for a substantial number of epifauna and infauna invertebrate taxa, of terrestrial, freshwater, and marine origin. As shown in James et al. (1998) and Pawlikowski and Kornijów (2023), the taxa in this study cover a range of trophic roles, including mesopredators, herbivores, and detritivores as well as functional roles, including sediment-dwelling, free-swimming, crawling, and tube-dwelling species. Together these findings indicate that *P. australis* beds are important in supporting coastal biodiversity and in maintaining links between marine

Table 4 Comparison of epi- and infauna density in *P. australis* beds with eelgrass meadows (*Z. marina*) and bladderwrack beds (*F. vesiculosus*) and vegetation from soft-bottomed shallow bays

	Mean invertebrate density (ind m ⁻²)		References
Habitat	Åland Islands	Archipelago Sea	
Epifauna			
<i>Phragmites australis</i>	56–392	39–170	<i>This study</i>
<i>Zostera marina</i>	1500–10,000	750–19,000	(Boström and Bonsdorff 1997; Baden and Boström 2001; Gustafsson and Boström 2009; Gustafsson and Salo 2012; Reynolds et al. 2018; Gagnon et al. 2019, 2021; Henseler et al. 2019)
<i>Fucus vesiculosus</i>	2300–10,400	1000–16,000	(Kraufvelin and Salovius 2004; Gagnon and Boström 2016; Saarinen et al. 2018; Gagnon et al. 2019; Henseler et al. 2019)
Shallow, soft-bottomed bays	934–5453	–	According to data gathered in (Eveleens Maarse et al. 2021)
Infauna			
<i>Phragmites australis</i>	2600–17,000	1300–12,000	<i>This study</i>
<i>Zostera marina</i>	23,000–55,000	10,000–75,000	(Boström and Bonsdorff 1997; Boström et al. 2006; Gustafsson and Boström 2011; Henseler et al. 2019; Meysick et al. 2020)
Shallow, soft-bottomed bays	660–4442	–	According to data gathered in (Eveleens Maarse et al. 2021)

and terrestrial ecosystems by providing habitat for terrestrial, aquatic insect larvae. We observed a considerable overlap (more than 50%) of taxa, which occurred as both epifauna and infauna. The sediment within *P. australis* beds is often covered and intermixed with old stalks broken off from previous years' growth as well as detritus, which likely provide both food and shelter for invertebrates. Likewise, the hollow structure of dead *P. australis* stalks may provide suitable habitats for many species, which typically occur as infauna. Thus, *P. australis* beds likely provide multiple physical habitat niches for associated fauna with varying trophic and functional roles, by adding both above- and belowground habitat complexity (Kovalenko et al. 2012).

We found that wave exposure and nutrients (here represented by total phosphorous) are the main drivers of the invertebrate community. Wave exposure positively affected epi- and infauna abundance and taxa richness, as well as epifauna Shannon–Wiener diversity in ÅI. In AS, wave exposure had a negative effect on epi- and infauna abundance, epifauna taxa richness, and epifauna diversity (Table 2, Figs. 3 and 5), thus supporting the hypothesis (1) on the effects of wave exposure in ÅI, but rejecting it in AS. Wave exposure is known to also be a strong large-scale driver of invertebrate communities in soft-bottomed shallow bays (Eveleens Maarse et al. 2021), *Z. marina* meadows (Boström and Bonsdorff 2000), and macroalgal beds (Korpinen et al. 2007a, b; Rinne et al. 2022). The effects of wave exposure on the invertebrate community can be either direct, e.g., reduced water flow, which affect filter feeding organisms negatively (Lenihan et al. 1996), or indirect, e.g., by driving variations in nutrient levels and salinity (Hansen et al. 2008). Nutrient levels had a positive effect on epi- and infauna abundance, infauna taxa richness, and infauna diversity,

rejecting the hypothesis (3) that high nutrient levels would decrease both epi- and infauna taxa richness and diversity. Nutrient levels are also known to affect invertebrate communities in other vegetated habitats, although their effects can vary. In *F. vesiculosus* belts, moderately increased nutrient levels had no clear effect on epifauna number of taxa and diversity, while in areas with lower nutrient levels there were generally lower abundances (Rinne et al. 2022), and in *Z. marina* meadows, the effects of nutrients seem to be more context-dependent (Meysick et al. 2020). Both wave exposure and nutrient enrichment can, either separately or together, also indirectly shape invertebrate communities in shallow coastal habitats by modifying biotic and trophic interactions (Korpinen et al. 2007a, b; Moksnes et al. 2008).

At a smaller spatial scale (i.e., within a site), the density of both live and dead stalks had varied effect of the invertebrate communities, which was not in line with hypothesis (1). The higher stalk density increased both the structural complexity and thus the potential shelter from predation and the available substrate, although this did not always increase diversity metrics. However, the effects of stalk densities may vary depending on season. At the end of winter, ice scouring may remove a large part of the above ground biomass of the *P. australis* beds and thereby reduce the overall structural complexity. After ice-scour, new stalks are regenerated from the rhizomes, increasing complexity from April until October (Pawlikowski and Kornijów 2022), while the scoured stalks are deposited on the seafloor. In *P. australis* beds with low exposure, the limited water movement enhances the deposition of finer material with high organic content, which further increases decomposition. Similarly as in seagrass beds, this material is rapidly mineralized by the microbial community in the rhizosphere, and the decaying

organic material is consumed by bioturbating detritivores (Pawlikowski and Kornijów 2019). Furthermore, in *P. australis* beds, the stalks suppress the kinetic energy of the wave action (Pawlikowski and Kornijów 2019), reducing the hydrodynamic stress on epifauna and stabilizing the habitat. The facilitating properties (e.g., food availability, shelter from predation, and hydraulic stress) of submerged vegetation have been well documented in different habitats, such as hard substrates, exposed sandy bottoms, and soft-bottomed shallow bays (e.g., Boström and Bonsdorff 2000; Wikström and Kautsky 2007; Hansen et al. 2010). For example, the exact role of small-scale structural complexity in seagrass meadows (due to, e.g., variation in patch size, shoot density, or shoot length) is known to be highly context- and species-dependent (Boström et al. 2006; Moore and Hovel 2010), and the same is likely true in *P. australis* beds.

Edge effects are highly important in aquatic vegetated habitats (Moore and Hovel 2010; Yarnall et al. 2022), and we found that increased distance from the seaward edge decreased epifauna abundance and diversity in the Archipelago Sea as well as infauna abundance and taxa richness in the Åland Islands (Table 2, Fig. 4), supporting the hypothesis (3) that distance from the seaward edge would decrease both epi- and infauna taxa richness and diversity. This corresponds to some extent with the results from Pawlikowski and Kornijów (2022), where the distance from the seaward edge had a strong effect on both the infauna total abundance and the species richness, with the highest numbers of both generally occurring at 20–30 m from the seaward edge. This was attributed to higher oxygen levels due to better water circulation compared to the innermost parts (50–60 m from the seaward edge in that study) of the *P. australis* bed. Another study from Polish lakes also demonstrated large differences between the invertebrate communities in the outer (1 m from the seaward edge) and inner (~25 m from the seaward edge) parts of the *P. australis* beds where the inner part hosted more Gastropoda, Hydrachnidia, and Coleoptera, while the outer part hosted higher abundances of Bivalvia and Diptera (Miler et al. 2018). Likewise, similar large difference has been found between infauna abundance sampled from the interior compared to the edge of *Z. marina* patches, where the edges of the patches hosted lower densities of infauna (Meysick et al. 2019). In *Z. marina* meadows, these differences are explained by lower recruitment along the edges (Carroll et al. 2012) or differences in predator distribution between the edges and interior of the meadows (Macreadie et al. 2010). However, more research is needed to confirm if the same applies to *P. australis* beds. At an even smaller scale, epiphyte (filamentous algae) biomass increased epifauna abundance in ÅI, thus supporting the hypothesis (2), and additionally increased species richness and diversity in AS. These effects could be the result of the additional structural complexity and shelter, which epiphytes provide to

mobile epifauna species (Hall and Bell 1988; Martin-Smith 1993; Pihl et al. 1995). Epiphytes also provide an additional food source for especially grazing epifauna species (Bologna and Heck 1999; Orav-Kotta and Kotta 2004) such as gastropods, which were abundant in this study. The biomass of *P. australis* rhizomes had no effect on the associated infauna community, contradicting hypothesis (4) and indicating that the rhizomes themselves play a relatively small role in structuring the infaunal community in *P. australis* beds. This supports studies on the more delicate rhizomes in *Z. marina* meadows, which have also been found to have little effect on the infauna community (Webster et al. 1998). However, *P. australis* rhizomes are dense and may therefore impair the movements of infauna (Pawlikowski and Kornijów 2023). In *Z. marina* beds, the infauna community is driven by sediment characteristics such as grain size and organic content (Boström et al. 2006). Though we did not consider sediment characteristics, this is potentially the case for *P. australis* beds as well.

The role of the root systems on infauna has experimentally been studied using a mesh, mimicking the root system (González-Ortiz et al. 2016), and by studying *P. australis* rhizomes in the southern Baltic Sea (Pawlikowski and Kornijów 2023). These studies found that small-sized and burrowing species had high abundances within the rhizomes and that increased belowground macrophyte structure (either roots or a mesh) may have impeded larger burrowing organisms and thus affected the infauna community. The lack of larger burrowing organisms such as crabs, which would be most impeded by more *P. australis* rhizomes in the northern Baltic Sea (e.g., Fowler 2013), may explain why increased rhizome biomass did not affect the infauna community in this study.

A potential reason for varying invertebrate community responses to the different drivers in the two regions included in this study is the difference in geography. The ÅI sites were located along the shore of an inlet whereas the AS sites were located along the shores of both inlets and islands. This could cause the hydrography of the AS sites to be more complex and unpredictable compared to the ÅI sites, potentially complicating the interpretation of the effects of environmental drivers.

The epifauna invertebrate densities (individuals m⁻²) in the *P. australis* beds were up to 94 times lower than in *Z. marina* and *F. vesiculosus* habitats, while infauna densities were up to 8 times lower. Epifauna densities in *P. australis* beds were 13–17 times lower compared to macrophytes in soft-bottomed shallow bays. The infauna densities in *P. australis* beds were, on the contrary, higher than those occurring in macrophyte covered soft-bottomed shallow bays. While *P. australis* likely hosts lower densities of invertebrates compared to well-established foundation species like *F. vesiculosus* and *Z. marina*, it provides a structured habitat for a variety of taxa in shallow soft-bottomed areas.

Conclusions

In shallow waters of the Baltic Sea, *P. australis* provides habitats for a large number of epifauna and infauna invertebrate taxa. In *P. australis* habitats, there is a considerable overlap of taxa, which occur as both epi- and infauna. Wave exposure and nutrient concentrations are the main drivers for the *P. australis*-associated epi- and infauna community composition. Within sites, the distance from the seaward edge, live and dead stalk density, and epiphyte biomass have variable effects on epi- and infauna abundance, taxa richness, and diversity. The rhizome

biomass does not affect infaunal communities. There are likely additional environmental drivers causing regional differences in, e.g., hydrography, caused by geography, which were not included in this study. *P. australis* beds host low invertebrate densities compared to other foundation species (*F. vesiculosus* belts and *Z. marina* meadows) and lower densities of epifauna, but higher abundances of infauna than macrophytes in soft-bottomed shallow bays. *P. australis* beds provide a habitat for invertebrates in shallow waters of the Baltic Sea, but further research on this understudied habitat in the Baltic Sea is essential to increase the understanding of its role in the ecosystem.

Appendix 1

Table 5 Epifauna Spearman rank correlation coefficients (upper part) and *p* values (lower part) of environmental (Tot. P and exposure) and site parameters (distance, live stalks, dead stalks, epiphyte biomass and rhizome biomass)

Åland	Tot. P	Exposure	Distance from seaward edge	Live stalks	Dead stalks	Epiphyte biomass/stalk
Tot. P		−0.82	−0.05	−0.01	0.13	−0.24
Exposure	< 0.0001		0.04	0.02	−0.03	0.46
Distance from seaward edge	0.7245	0.7603		0.13	0.25	−0.03
Live stalks	0.9244	0.8911	0.3713		0.3	−0.34
Dead stalks	0.3465	0.8252	0.0665	0.0274		0.09
Epiphyte biomass/stalk	0.0791	0.0005	0.838	0.0126	0.499	
Archipelago Sea	Tot. P	Exposure	Distance from seaward edge	Live stalks	Dead stalks	Epiphyte biomass/stalk
Tot. P		0.36	−0.15	0.02	−0.09	−0.29
Exposure	0.015		0.11	−0.05	−0.11	0.02
Distance from seaward edge	0.310	0.476		0.26	0.43	−0.24
Live stalks	0.887	0.745	0.084		0.65	−0.63
Dead stalks	0.561	0.471	0.003	< 0.0001		−0.49
Epiphyte biomass/stalk	0.052	0.884	0.116	< 0.0001	0.001	

Values in bold indicate that $p < 0.05$

Appendix 2

Table 6 Infauna Spearman rank correlation coefficients (upper part) and *p* values (lower part) of environmental (Tot. P and exposure) and site parameters (distance, live stalks, dead stalks, epiphyte biomass and rhizome biomass)

Åland	Tot. P	Exposure	Distance from seaward edge	Live stalk	Dead stalks	Epiphyte biomass/stalk	Rhizome dw
Tot. P		−0.78	0.01	0.1	0.09	−0.31	−0.17
Exposure	< 0.0001		0.01	0.01	0.02	0.44	0.34
Distance from seaward edge	0.9562	0.9195		0.08	0.11	0.01	−0.15
Live stalks	0.4438	0.9493	0.5671		0.76	0.5	0.37
Dead stalks	0.4907	0.9079	0.4322	< 0.0001		0.61	0.4
Epiphyte biomass/stalk	0.0194	0.0007	0.9355	< 0.0001	< 0.0001		0.44
Rhizome dw	0.1983	0.0114	0.2751	0.0049	0.0022	0.0007	
Archipelago Sea	Tot. P	Exposure	Distance from seaward edge	Live stalks	Dead stalks	Epiphyte biomass/stalk	Rhizome dw
Tot. P		0.32	−0.17	−0.03	−0.07	−0.19	−0.29
Exposure	0.0131		0.08	−0.1	−0.11	0	−0.25
Distance from seaward edge	0.1982	0.5652		0.22	0.35	−0.07	0.42
Live stalks	0.8413	0.4524	0.0936		0.73	0.22	0.45
Dead stalks	0.5931	0.4102	0.0055	< 0.0001		0.03	0.39
Epiphyte biomass/stalk	0.1531	0.9815	0.571	0.0846	0.8226		0.3
Rhizome dw	0.0266	0.0497	0.0008	0.0003	0.0022	0.0179	

Values in bold indicate that $p < 0.05$

Appendix 3

Table 7 Distance-based linear model output for the epi- and infauna from the Åland Islands and Archipelago Sea regions of environmental (Tot. P and exposure) and site parameters (distance, live stalks, dead stalks, epiphyte biomass and rhizome biomass)

	Variable	AICc	SS (trace)	Pseudo-F	<i>p</i>	Prop	Cumul	res.df	<i>R</i> ²
Åland epifauna	Tot. P	421.41	8067.8	29,623	0.01	0.055	0.055	51	0.26548
	Exposure	416.39	17,810	73,542	0.001	0.121	0.176	50	
	Distance from seaward edge	417.53	2713.9	11,234	0.338	0.018	0.195	49	
	Live stalks	418.28	3732	15,626	0.143	0.025	0.220	48	
	Dead stalks	418.67	4576.3	19,542	0.078	0.031	0.251	47	
	Epiphyte biomass/stalk	420.3	2116.5	0.9019	0.466	0.014	0.265	46	
Archipelago Sea epifauna	Tot. P	336.98	3884.3	22,844	0.05	0.050	0.050	43	0.29112
	Exposure	333.39	8958	58,644	0.001	0.116	0.167	42	
	Distance from seaward edge	334.28	2145.4	14,185	0.177	0.028	0.195	41	
	Live stalks	333.72	4123	2849	0.024	0.054	0.248	40	
	Dead stalks	335.67	924.33	0.63285	0.701	0.012	0.260	39	
	Epiphyte biomass/stalk	336.56	2380.5	16,573	0.14	0.031	0.291	38	
Åland epifauna	Tot. P	418.73	40,627	23,901	0.001	0.307	0.307	54	0.47783
	Exposure	414.44	10,098	65,516	0.001	0.076	0.383	53	
	Distance from seaward edge	414.26	3567.6	23,746	0.02	0.027	0.410	52	
	Live stalks	413.57	4222.4	29,139	0.012	0.032	0.442	51	
	Dead stalks	413.82	2920.3	20,571	0.038	0.022	0.464	50	
	Rhizome biomass	414.97	1837.5	13,022	0.226	0.014	0.478	49	
Archipelago Sea epifauna	Tot. P	434.41	4689.3	34,872	0.007	0.057	0.057	58	0.22502
	Exposure	430.51	7567.9	61,251	0.001	0.092	0.148	57	
	Distance from seaward edge	430.49	2670.7	22,073	0.055	0.032	0.181	56	
	Live stalks	431.54	1491	12,375	0.257	0.018	0.199	55	
	Dead stalks	432.98	1123.2	0.93105	0.435	0.014	0.212	54	
	Rhizome dw	434.57	1063.1	0.87932	0.438	0.013	0.225	53	

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Data Availability Data available upon request.

Declarations

Competing Interests The authors declare no competing interests.

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References

- Altartouri, A., L. Nurminen, and A. Jolma. 2014. Modeling the role of the close-range effect and environmental variables in the occurrence and spread of *Phragmites australis* in four sites on the Finnish coast of the Gulf of Finland and the Archipelago Sea. *Ecology and Evolution* 4: 987–1005 Wiley Online Library.
- Anderson, M., R. N. Gorley, and R. K. Clarke. 2008. Permanova+ for primer: Guide to software and statistical methods. *Primer-E Limited*.
- Andersson, A., S. Hajdu, P. Haecky, J. Kuparinen, and J. Wikner. 1996. Succession and growth limitation of phytoplankton in the Gulf of Bothnia (Baltic Sea). *Marine Biology* 126: 791–801. <https://doi.org/10.1007/BF00351346>.
- Angradi, T.R., S.M. Hagan, and K.W. Able. 2001. Vegetation type and the intertidal macroinvertebrate fauna of a brackish marsh: *Phragmites* vs. *Spartina*. *Wetlands* 21: 75–92.
- Baden, S.P., and C. Boström. 2021. The leaf canopy of seagrass beds: Faunal community structure and function in a salinity gradient along the Swedish coast. In *In Ecological Comparisons of Sedimentary Shores*, ed. K. Reise. Ecological Studies, 213–236. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-56557-1_11.
- Bell, S.S., E.D. McCoy, and H.R. Mushinsky. 2012. *Habitat structure The physical arrangement of objects in space* Vol. 8. Springer Science & Business Media, Dordrecht.
- Bologna, P.A., and K.L. Heck Jr. 1999. Macrofaunal associations with seagrass epiphytes: Relative importance of trophic and structural characteristics. *Journal of experimental marine biology and ecology* 242: 21–39 Elsevier.
- Boström, C., and E. Bonsdorff. 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *Journal of Sea Research* 37: 153–166. [https://doi.org/10.1016/S1385-1101\(96\)00007-X](https://doi.org/10.1016/S1385-1101(96)00007-X).
- Boström, C., and E. Bonsdorff. 2000. Zoobenthic community establishment and habitat complexity the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series* 205: 123–138.
- Boström, C., E.L. Jackson, and C.A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: A review. *Estuarine, Coastal and Shelf Science* 68: 383–403. <https://doi.org/10.1016/j.ecss.2006.01.026>. Ecological and Management Implications on Seagrass Landscapes.
- Bowden, D.A., A.A. Rowden, and M.J. Attrill. 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *Journal of Experimental Marine Biology and Ecology*. 259: 133–154 Elsevier.
- Carroll, J.M., B.T. Furman, S.T. Tettelbach, and B.J. Peterson. 2012. Balancing the edge effects budget: Bay scallop settlement and loss along a seagrass edge. *Ecology* 93: 1637–1647. <https://doi.org/10.1890/11-1904.1>.
- Chambers, R.M., L.A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic botany* 64: 261–273 Elsevier.
- Clarke, K.R., and R.N. Gorley. 2006. PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research). *PRIMER-E, Plymouth*.
- Coops, H., and G. Van der Velde. 1996. Effects of waves on helophyte stands: Mechanical characteristics of stems of *Phragmites australis* and *Scirpus lacustris*. *Aquatic Botany* 53: 175–185. [https://doi.org/10.1016/0304-3770\(96\)01026-1](https://doi.org/10.1016/0304-3770(96)01026-1).
- Engloner, A.I., and Á. Major. 2011. Clonal diversity of *Phragmites australis* propagating along water depth gradient. *Aquatic Botany* 94: 172–176. <https://doi.org/10.1016/j.aquabot.2011.02.007>.
- Eveleens Maarse, F., S. Salovius-Laurén, and M. Snickars. 2021. Physical drivers of epi- and infauna communities related to dominating macrophytes in shallow bays in the Northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 262: 107600. <https://doi.org/10.1016/j.ecss.2021.107600>.
- Fowler, A., E. Forsström, T. M. von Numers, and O. Vesakoski. 2013. The North American mud crab *Rhithropanopeus harrisi* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. *Aquatic Invasions* 8(1).
- Gagnon, K., and C. Boström. 2016. Habitat expansion of the Harris mud crab *Rhithropanopeus harrisi* (Gould, 1841) in the northern Baltic Sea: Potential consequences for the eelgrass food web. *BioInvasions Records* 5: 101–106. <https://doi.org/10.3391/bir.2016.5.2.07>.
- Gagnon, K., M. Gräfnings, and C. Boström. 2019. Trophic role of the mesopredatory three-spined stickleback in habitats of varying complexity. *Journal of Experimental Marine Biology and Ecology* 510: 46–53. <https://doi.org/10.1016/j.jembe.2018.10.003>.
- Gagnon, K., C. Gustafsson, T. Salo, F. Rossi, S. Gunell, J.P. Richardson, P.L. Reynolds, J.E. Duffy, and C. Boström. 2021. Role of food web interactions in promoting resilience to nutrient enrichment in a brackish water eelgrass (*Zostera marina*) ecosystem. *Limnology and Oceanography* 66: 2810–2826. <https://doi.org/10.1002/lno.11792>.
- González-Ortiz, V., L.G. Egea, R. Jiménez-Ramos, F. Moreno-Marín, J.L. Pérez-Lloréns, T. Bouma, and F. Brun. 2016. Submerged vegetation complexity modifies benthic infauna communities: The hidden role of the belowground system. *Marine Ecology* 37: 543–552. <https://doi.org/10.1111/maec.12292>.
- Grasshoff, P. 1983. Methods of seawater analysis. *Verlag Chemie* 419: 61–72.
- Gustafsson, C., and C. Boström. 2009. Effects of plant species richness and composition on epifaunal colonization in brackish water

- angiosperm communities. *Journal of Experimental Marine Biology and Ecology* 382: 8–17. <https://doi.org/10.1016/j.jembe.2009.10.013>.
- Gustafsson, C., and C. Boström. 2011. Biodiversity influences ecosystem functioning in aquatic angiosperm communities. *Oikos* 120: 1037–1046. <https://doi.org/10.1111/j.1600-0706.2010.19008.x>.
- Gustafsson, C., and T. Salo. 2012. The effect of patch isolation on epifaunal colonization in two different seagrass ecosystems. *Marine Biology* 159: 1497–1507. <https://doi.org/10.1007/s00227-012-1932-7>.
- Hall, M., and S. Bell. 1988. Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. *Journal of Marine Research* 46: 613–630. <https://doi.org/10.1357/002224088785113531>.
- Hansen, J.P., J. Sagerman, and S.A. Wikström. 2010. Effects of plant morphology on small-scale distribution of invertebrates. *Marine Biology* 157: 2143–2155. <https://doi.org/10.1007/s00227-010-1479-4>.
- Hansen, J.P., S.A. Wikström, and L. Kautsky. 2008. Effects of water exchange and vegetation on the macroinvertebrate fauna composition of shallow land-uplift bays in the Baltic Sea. *Estuarine, Coastal and Shelf Science* 77: 535–547 Elsevier.
- Henseler, C., M.C. Nordström, A. Törnroos, M. Snickars, L. Pecuchet, M. Lindegren, and E. Bonsdorff. 2019. Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach. *Estuarine, Coastal and Shelf Science* 226: 106272. <https://doi.org/10.1016/j.ecss.2019.106272>.
- Hovel, K.A., M.S. Fonseca, D.L. Myer, W.J. Kenworthy, and P.E. Whitfield. 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. *Marine Ecology Progress Series* 243: 11–24.
- Huhta, A. 2009. Decorative or outrageous—the significance of the common reed (*Phragmites australis*) on water quality. *Comments from Turku University of Applied Sciences* 48: 1–33.
- Irlandi, E.A. 1994. Large- and small-scale effects of habitat structure on rates of predation: How percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98: 176–183 Springer.
- Isæus, M. 2004. Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. PhD thesis, Department of Botany, Stockholm University.
- James, M.R., M. Weatherhead, C. Stanger, and E. Graynoth. 1998. Macroinvertebrate distribution in the littoral zone of Lake Coleridge, South Island, New Zealand—effects of habitat stability, wind exposure, and macrophytes. *New Zealand Journal of Marine and Freshwater Research* 32: 287–305. <https://doi.org/10.1080/00288330.1998.9516826>. Taylor & Francis.
- Kiviat, E. 2019. Organisms using *Phragmites australis* are diverse and similar on three continents. *Journal of Natural History* 53: 1975–2010. <https://doi.org/10.1080/00222933.2019.1676478>. Taylor & Francis.
- Koroleff, F. 1977. Simultaneous persulphate oxidation of phosphorus and nitrogen compounds in water. In *Methods of Seawater Analysis*, eds. Grasshoff, K., K. Kremling, M. Erhardt, and C. Osterroth, 29–31. Report Baltic Intercal. Workshop, Annex Compiler. Kiel.
- Korpinen, S., V. Jormalainen, and T. Honkanen. 2007b. Bottom-up and cascading top-down control of macroalgae along a depth gradient. *Journal of Experimental Marine Biology and Ecology* 343: 52–63. <https://doi.org/10.1016/j.jembe.2006.11.012>.
- Korpinen, S., V. Jormalainen, and T. Honkanen. 2007. Effects of nutrients, herbivory, and depth on the macroalgal community in the rocky sublittoral. *Ecology* 88: 839–852 Wiley Online Library.
- Korpinen, S., V. Jormalainen, and E. Pettay. 2010. Nutrient availability modifies species abundance and community structure of *Fucus*-associated littoral benthic fauna. *Marine environmental research* 70: 283–292 Elsevier.
- Kovalenko, K.E., S.M. Thomaz, and D.M. Warfe. 2012. Habitat complexity: Approaches and future directions. *Hydrobiologia* 685: 1–17. <https://doi.org/10.1007/s10750-011-0974-z>.
- Kraufvelin, P., and S. Salovius. 2004. Animal diversity in Baltic rocky shore macroalgae: Can *Cladophora glomerata* compensate for lost *Fucus vesiculosus*? *Estuarine, Coastal and Shelf Science* 61: 369–378. <https://doi.org/10.1016/j.ecss.2004.06.006>.
- Lappalainen, A., M. Härmä, S. Kuningas, and L. Urho. 2008. *Reproduction of pike (Esox lucius) in reed belt shores of the SW coast of Finland*. Baltic Sea: A new survey approach. Boreal Environment Research Publishing Board.
- Lenihan, H.S., C.H. Peterson, and J.M. Allen. 1996. Does flow speed also have a direct effect on growth of active suspension-feeders: An experimental test on oysters. *Limnology and Oceanography* 41: 1359–1366. <https://doi.org/10.4319/lo.1996.41.6.1359>.
- Luther, H. 1951. *Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinland II spezieller Teil*. Societas pro fauna et flora Fennica: University of Helsinki (UH-Viikki).
- Macreadie, P.I., J.S. Hindell, M.J. Keough, G.P. Jenkins, and R.M. Connolly. 2010. Resource distribution influences positive edge effects in a seagrass fish. *Ecology* 91: 2013–2021. <https://doi.org/10.1890/08-1890.1>.
- Martin-Smith, K.M. 1993. Abundance of mobile epifauna: The role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* 174: 243–260. [https://doi.org/10.1016/0022-0981\(93\)90020-O](https://doi.org/10.1016/0022-0981(93)90020-O).
- McFarlin, C.R., T.D. Bishop, M.W. Hester, and M. Alber. 2015. Context-dependent effects of the loss of *Spartina alterniflora* on salt marsh invertebrate communities. *Estuarine, Coastal and Shelf Science* 163: 218–230 Elsevier.
- Meriste, M., K. Kirsimäe, and L. Freiberg. 2010. Relative sea-level changes at shallow coasts inferred from reed bed distribution over the last 50 years in Matsalu Bay, the Baltic Sea. *Journal of Coastal Research* 28: 1–10. <https://doi.org/10.2112/JCOASTRES-D-10-00049.1>.
- Meyerson, L.A., J.T. Cronin, and P. Pyšek. 2016. *Phragmites australis* as a model organism for studying plant invasions. *Biological Invasions* 18: 2421–2431 Springer.
- Meysick, L., E. Infantes, and C. Boström. 2019. The influence of hydrodynamics and ecosystem engineers on eelgrass seed trapping. *Edited by Frank Melzner. PLOS ONE* 14: e0222020. <https://doi.org/10.1371/journal.pone.0222020>.
- Meysick, L., A. Norkko, K. Gagnon, M. Gräfnings, and C. Boström. 2020. Context-dependency of eelgrass-clam interactions: Implications for coastal restoration. *Marine Ecology Progress Series* 647: 93–108. <https://doi.org/10.3354/meps13408>.
- Miler, O., M. Czarnecka, X.-F. Garcia, A. Jäger, and M. Pusch. 2018. Across-shore differences in lake benthic invertebrate communities within reed stands (*Phragmites australis* (Cav.) Trin. ex Steud.). *International Review of Hydrobiology* 103: 99–112 Wiley Online Library.
- Mitsch, W.J., B. Bernal, and M.E. Hernandez. 2015. Ecosystem services of wetlands. *International Journal of Biodiversity Science, Ecosystem Services & Management* 11 (1): 1–4. <https://doi.org/10.1080/21513732.2015.1006250>.
- Moksnes, P.-O., M. Gullström, K. Tryman, and S. Baden. 2008. Trophic cascades in a temperate seagrass community. *Oikos* 117: 763–777. <https://doi.org/10.1111/j.0030-1299.2008.16521.x>.
- Moore, E.C., and K.A. Hovel. 2010. Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. *Oikos* 119 (8): 1299–1311.

- Müller, U. 1995. Vertical zonation and production rates of epiphytic algae on *Phragmites australis*. *Freshwater Biology* 34: 69–80 Wiley Online Library.
- Niemi, N., J.P. Hansen, J.S. Eklöf, B.K. Eriksson, H.C. Andersson, U. Bergström, and Ö. Östman. 2023. Influence of reed beds (*Phragmites australis*) and submerged vegetation on pike (*Esox lucius*). *Fisheries Research* 261: 106621. <https://doi.org/10.1016/j.fishres.2023.106621>.
- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. Simpson, P. Solymos, M. Stevens, and H. Wagner. 2009. Vegan: Community ecology package.
- Oksanen, J. 2013. Multivariate analysis of ecological communities in R: vegan tutorial. *R Package Version 1* (7): 1–43.
- Orav-Kotta, H., and J. Kotta. 2004. Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia* 514: 79–85. <https://doi.org/10.1023/B:hydr.0000018208.72394.09>.
- Pawlikowski, K., and R. Kornijów. 2019. Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea). *Oceanologia* 61: 26–37. <https://doi.org/10.1016/j.oceano.2018.05.003>.
- Pawlikowski, K., and R. Kornijów. 2022. Distribution of benthic macroinvertebrates across a reed stand in a brackish Baltic lagoon. *Oceanologia* 64: 433–444. <https://doi.org/10.1016/j.oceano.2022.02.004>.
- Pawlikowski, K., and R. Kornijów. 2023. Above- and belowground habitat complexity created by emergent and submerged vegetation drives the structure of benthic assemblages. *Oceanologia* 65: 358–370. <https://doi.org/10.1016/j.oceano.2022.10.002>.
- Pihl, L., I. Isaksson, H. Wennhage, and P.-O. Moksnes. 1995. Recent increase of filamentous algae in shallow Swedish bays: Effects on the community structure of epibenthic fauna and fish. *Netherlands Journal of Aquatic Ecology* 29: 349–358. <https://doi.org/10.1007/BF02084234>.
- Reynolds, P.L., J.J. Stachowicz, K. Hovel, C. Boström, K. Boyer, M. Cusson, J.S. Eklöf, et al. 2018. Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. *Ecology* 99: 29–35. <https://doi.org/10.1002/ecy.2064>.
- Rinne, H., J.-F. Blanc, T. Salo, M.C. Nordström, N. Salmela, and S. Salovius-Laurén. 2022. Variation in *Fucus vesiculosus* associated fauna along a eutrophication gradient. *Estuarine, Coastal and Shelf Science* 275: 107976. <https://doi.org/10.1016/j.ecss.2022.107976>.
- Saarinen, A., S. Salovius-Laurén, and J. Mattila. 2018. Epifaunal community composition in five macroalgal species – what are the consequences if some algal species are lost? *Estuarine, Coastal and Shelf Science* 207: 402–413. <https://doi.org/10.1016/j.ecss.2017.08.009>.
- Sahuquillo, M., M.R. Miracle Solé, M. Rieradevall i Sant, and R. Kornijów. 2008. Macroinvertebrate assemblages on reed beds, with special attention to Chironomidae (Diptera), in Mediterranean shallow lakes. *Limnetica* 27 (2): 239–250 Asociación Ibérica de Limnología.
- Schneider, F.I., and K.H. Mann. 1991. Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *Journal of Experimental Marine Biology and Ecology* 145: 119–139 Elsevier.
- Sundblad, G., T. Bekkby, M. Isæus, A. Nikolopoulos, K.M. Norderhaug, and E. Rinde. 2014. Comparing the ecological relevance of four wave exposure models. *Estuarine, Coastal and Shelf Science* 140: 7–13 Elsevier.
- von Numers, M. 2011. Sea shore plants of the SW archipelago of Finland — distribution patterns and long-term changes during the 20th century. *Annales Botanici Fennici* 48: 1–46 Finnish Zoological and Botanical Publishing Board.
- Wails, C.N., K. Baker, R. Blackburn, A. Del Vallé, J. Heise, H. Herakovich, W.A. Holthuijzen, M.P. Nissenbaum, L. Rankin, and K. Savage. 2021. Assessing changes to ecosystem structure and function following invasion by *Spartina alterniflora* and *Phragmites australis*: A meta-analysis. *Biological Invasions* 23: 2695–2709 Springer.
- Wainright, S.C., M.P. Weinstein, K.W. Able, and C.A. Currin. 2000. Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. *Marine Ecology Progress Series* 200: 77–91.
- Webster, P.J., A.A. Rowden, and M.J. Attrill. 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. *Estuarine, Coastal and Shelf Science* 47: 351–357. <https://doi.org/10.1006/ecss.1998.0358>.
- Wikström, S.A., and L. Kautsky. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science* 72: 168–176. <https://doi.org/10.1016/j.ecss.2006.10.009>.
- Yarnall, A.H., J.E. Byers, L.A. Yeager, and F.J. Fodrie. 2022. Comparing edge and fragmentation effects within seagrass communities: A meta-analysis. *Ecology* 103 (3): e3603.