Trait responses to direct drivers and effects on multiple macrofauna-mediated ecosystem functions

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ABSTRACT: As humans are facing challenges related to climate change, biodiversity loss and increasingly threatened ecosystems, there is a need to understand human-induced pressures, effects and feedback processes in the marine environment. Our study therefore aimed to identify environmental and anthropogenic drivers for coastal macrozoobenthic communities and the implications for macrofauna-mediated ecosystem functions. A large spatial—temporal data set combining environmental and macrofaunal data allowed us to highlight exposure and human-induced stressors as main drivers for the macrofaunal communities in the Åland archipelago (northern Baltic Sea). A eutrophication gradient from sheltered inner to exposed outer areas was associated with a change in species- and trait-composition, and a change in dominance from r- to K-strategists in the invertebrate community. Sediment properties were significant drivers in explaining macrofaunal structural diversity patterns. The decrease in abundance, biomass and species richness in muddy sediments was associated with a reduction in bioturbation and bioirrigation potential indices. Environmental and human-induced pressures reduced the availability of macrofauna as food resource for mesopredators (i.e. benthivorous fish). Our results provide a deeper understanding of environment—community relationships and the interplay between biotic and abiotic ecosystem components regarding human-induced pressures.

KEY WORDS: Trait-based diversity · Response and effect traits · Multiple environmental stressors · Zoobenthos · Spatial environment—ecological response relationships · Baltic Sea

1. INTRODUCTION

Numerous human socio-economic activities (such as agriculture, fish farming, traffic) correspond to cases where humans act as ecosystem engineers, modulating the flow of resources to other species by causing physical or chemical state changes in abiotic or biotic materials (Jones et al. 1994, Berke 2010). Today, as our efforts at ecosystem engineering are increasingly oriented towards ameliorating and counteracting anthropogenic environmental modifications, interest is growing in understanding the nature and consequences of the environmental impacts of human activities and managing these impacts to pro-

tect the well-being of humans and other life on Earth (Stenseth et al. 2020). Coastal ecosystems are highly sensitive to human ecosystem engineering and simultaneously highly valuable in terms of ecological functions, goods and benefits for human society (Barbier et al. 2011). At the interface between land and sea, coastal ecosystems are influenced by pressures coming from land, adjacent open waters, the local atmosphere, and human socio-economic activities, resulting in physical and biological restructuring (Brondizio et al. 2019). Ecosystem responses to environmental changes can lead to shifts in community dynamics as well as in the structure and function of coastal ecosystems (Frid et al. 2009, Capasso et al.

2010), e.g. affecting the ability of coastal ecosystems to form nurseries and feeding habitats for fish, to provide a nutrient-filtering function from land towards the open sea, to act as fishing grounds and to maintain benthic—pelagic coupling (Miller-Way & Twilley 1996, Griffiths et al. 2017).

Identification of inadvertent outcomes stemming from human ecosystem engineering within coastal ecosystems can be facilitated using bioindicators. Living in these ecosystems, macrobenthic organisms (>0.5 mm) are part of intricate ecological interplay with their surroundings, making them compelling bioindicators of environmental status (Perus et al. 2007). Given their constrained mobility, many infaunal organisms show a restricted capacity to avoid environmental and anthropogenic pressures. Consequently, the infaunal community is susceptible to pronounced effects of anthropogenic activities in coastal ecosystems, including topographical destruction of benthic habitats through dredging (Thrush & Dayton 2002), or nutrient inputs from agriculture and industry leading to eutrophication and organic enrichment (e.g. Bonsdorff 2021, HELCOM 2023). Human ecosystem engineering and environmental perturbations can exert notable impacts on macrofaunal communities, leading to reductions in abundance, biomass and/or diversity (Pearson & Rosenberg 1978, Dauer 1993). Linking changes in the environment to species-specific attributes is a widely employed practice, providing ecologically important insights into how environmental parameters influence individual species and entire community structures. Expanding our focus beyond taxonomic diversity to encompass trait-based characteristics of macrofaunal assemblages is valuable for evaluating potential ecosystem functions. The combination of both of these approaches is pivotal for understanding how ecosystem functions are affected by human ecosystem engineering and for identifying potential feedback to humans. Macrofaunal traits are intrinsically tied to their ecological processes and ecosystem functions (Cadotte et al. 2011) and can be rapidly responsive to multiple pressures (Mouillot et al. 2013, Voß & Schäfer 2017). Over the last 2 decades, multiple studies have demonstrated that the integration of taxonomic and trait-based diversity approaches is developing our understanding of ecosystem function on top of supporting efforts for better ecosystem management and conservation (Henseler et al. 2019, Villnäs et al. 2019, Jacquot et al. 2023).

In addition to their role as bioindicators, macrobenthic organisms are central to several ecosystem functions, e.g. enhancing the depth of oxygen penetration within sediments, facilitating the remineralization of organic matter (Aller & Aller 1998, Jovanovic et al. 2014) and playing a crucial part in energy transfer to higher trophic levels by serving as central food sources for epibenthic predators and demersal fish (Salvanes et al. 1992, Nilsen et al. 2006, Nordström et al. 2009). Several of the ecosystem services mediated by benthic infaunal communities are threatened by the impacts originating from human activities. Investigating the responsiveness of proxies for macrofauna-mediated ecosystem functions to anthropogenic activities allows us to gain insights into potential feedback for human society and economy. For instance, quantitative proxies for the bioturbation (community bioturbation potential, BP_c) (Queirós et al. 2013) and bioirrigation (community bioirrigation potential, BIP_c) (Renz et al. 2018) activity of communities were developed to evaluate effects of human engineering on physical structuring of sediment (Villnäs et al. 2012, 2013, Gogina et al. 2017, Tsikopoulou et al. 2021).

As one of the most extensively studied ecosystems in the world, the Baltic Sea represents a simplified ecosystem providing an 'ideal' study area (Reusch et al. 2018, Meier et al. 2022, Viitasalo & Bonsdorff 2022). The evolutionarily young age of this sea in combination with the predominant brackish conditions results in naturally low species diversity, which facilitates detailed analysis of community changes in response to human ecosystem engineering. Processes and patterns are expected to be easier to understand in this simplified system compared to more complex ones with higher species diversity. The ecological interest in the Baltic Sea has been fueled by anthropogenic pressures on the ecosystem structure and functioning exerted by socio-economic activities. Since the second half of the 20th century, human-induced environmental changes have had major effects on the Baltic Sea ecosystem, leading to most areas of the Baltic Sea to be classified as being in 'moderate', 'poor' or 'bad' ecosystem health according to the Holistic Assessment of Ecosystem Health Status (HOLAS) tool (Andersen et al. 2011, 2017, HELCOM 2023). The long-term influence of humans, including pressures as well as different governance measures, makes the Baltic Sea a model system because the pressures that the Baltic Sea faces already today comprise threats that many coastal and estuarine systems are, and will be, facing world-wide (Reusch et al. 2018). Using the coastal zoobenthos of this model system to understand taxonomic and functional variations in response to environmental variables contributes to a more complete and general

understanding of coastal communities in response to human ecosystem engineering and the resulting implications for coastal ecosystem functioning.

We studied zoobenthic communities around the Åland Islands (Finland), focusing on the time following a *Marenzelleria* spp. Mesnil, 1896 establishment-induced shift in community composition (Weigel et al. 2015). We aimed to identify environmental and human ecosystem engineering drivers of coastal macrobenthic communities and the implications for macrofauna-mediated ecosystem functions. The overall objective was to provide a deeper understanding of environment—community relationships and the interplay between biotic and abiotic ecosystem components regarding human ecosystem engineering. In particular, the objectives were (1) to understand how zoobenthic communities are structured in terms of species abundances and trait-based diversity depending on environmental variables and human ecosystem engineering, and (2) to disentangle the relative contributions of these environmental stressors to biologically mediated ecosystem processes (bioturbation and bioirrigation potential, as well as food availability for mesopredators) in coastal macroinvertebrate communities. To determine the spatial drivers of functional diversity, we compiled a large data set of macrofauna abundances covering the Åland Islands archipelago with corresponding descriptors to identify which environmental variables are driving macrofaunal communities.

2. MATERIALS AND METHODS

2.1. Study area and data collection

The Åland Islands are located at the junction of the northern Baltic Proper and the Bothnian Sea between Finland and Sweden (Fig. 1f). The coastal zone comprises over 6000 islands, forming a highly heterogeneous land- and seascape, with underwater habitats ranging from shallow, sheltered bays to exposed open-sea areas. Gradients in environmental drivers, such as water temperature, salinity, oxygen concentration and organic content, can be steep from the inner to the outer coastal zone. Consequently, the Åland archipelago reflects broad environment types and can hence be considered a model area for understanding community structure and function across environmental gradients.

To spatially cover a broad range of environmental conditions and habitats and to identify major environmental drivers for macrofaunal communities (traits and species), data for a total of 168 stations located throughout the Åland archipelago (Fig. 1f) were compiled for a total of 708 samples. Species composition, abundance and biomass data for benthic macrofauna in addition to environmental data were collated from existing scientific surveys that together cover the Åland Islands marine area. The analysis was restricted to the period after 2000, as this year corresponds to a large-scale community shift in the zoobenthos in the region, shown to be mainly due to the establishment of *Marenzelleria* spp. (Weigel et al. 2016). The data sets were acquired from Husö Biological Station (Åbo Akademi University, Finland), and our selection comprises data from 2003 to 2022. As environmental descriptors, we used available data on temperature (°C), salinity and oxygen concentration (mg l^{-1}) of bottom water (measured with a YSI multi-parameter probe), sediment type (sand or mud) and sediment organic content (%), determined by loss on ignition (3 h at 500°C, dry weight). The extent of exposure to waves and wind, depth and proximity to land are significant factors structuring biological communities (abundance, biomass, species composition) (Pihl 1986, Kilar & McLachlan 1989, Ricciardi & Bourget 1999). Based on the established exposure index for the Northern Baltic Sea by Isæus (2004), the EUNIS index, we grouped the stations *a priori* into sheltered, semi-exposed and exposed sites. Fish-farm effluents have been shown to have an impact on both the water quality (Nordvarg & Johansson 2002) and macrofaunal communities (Kraufvelin et al. 2001, Nordström & Bonsdorff 2017) in the Åland archipelago. As a proxy for fish-farm pollution, we estimated the distance to the nearest fish farm for each station. Human ecosystem engineering was further explored based on the HELCOM metadata catalogue (https://metadata.helcom.fi/) (i.e. 'Disturbance of species due to human presence', 'Physical disturbance', 'Integrated eutrophication status assessment', and 'Input of hazardous substances') (for the full set of variables and complementary information, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m738p001_supp.pdf). Benthic samples included were all obtained in a standardized way, using an Ekman-Birge grab sampler (289 cm^2) and a 0.5 mm mesh sieve, and sampled material was preserved in 70% ethanol. Only stations with 3 to 5 replicate grab samples were included in the analysis. Taxonomic resolution was set at species level when possible and in accordance with the resolution of trait information available. A thorough taxonomic quality assurance included verification of taxonomy and scientific names following several databases: Marine Biodiversity and Ecosystem Func-
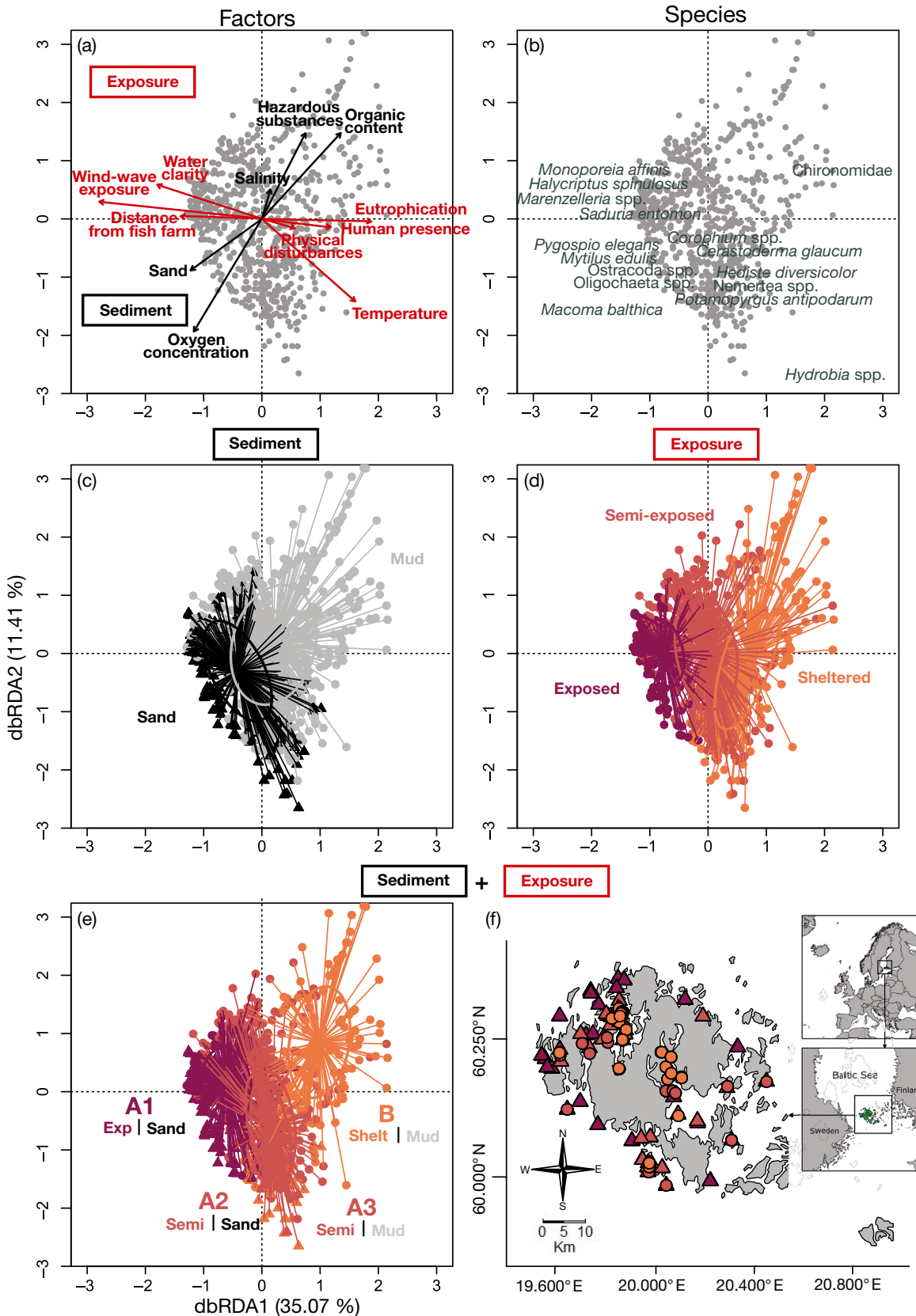
Fig. 1. Distance-based redundancy analysis (dbRDA) resulting from macrobenthos data based on Bray-Curtis similarities (ANOVA, p = 0.001). (a) Environmental variables with a significant influence on the distribution of sites (see Table S1 in the Supplement for additional information). (b) Macrofaunal species present at the different sites and showing a significant influence on the distribution of those sites in the analysis. Possible clusters are highlighted based on (c) sediment type, (d) exposure and (e) the combination of both sediment type and exposure, revealed by hierarchical clustering analysis. (f) Station characteristics in sediment and wave exposure in the archipelago. (c,e,f) Triangles: sand; circles: mud. (d,e,f) Dark, medium and light colours represent exposed, semi-exposed and sheltered environments. The first 2 axes (dbRDA1 and dbRDA2) summarize 45.48% of fitted and 44.17% of the total information

tioning (MarBEF) Data System - European Register of Marine Species (ERMS) (Costello et al. 2023), World Register of Marine Species (WoRMS Editorial Board 2023) and the Integrated Taxonomic Information System (ITIS 2023).

2.2. Trait selection

Traits reflect key components of functioning and are used as proxies for ecological processes (Törnroos & Bonsdorff 2012). We selected a set of fundamental traits reflecting key functions of zoobenthos communities within coastal ecosystems (Table 1; Table S2). With the selected traits, we focused on 2 main functional aspects within coastal systems, namely (1) the quality of zoobenthos as a food resource for higher trophic levels, with traits reflecting production, susceptibility to predation and palatability proxies; and (2) the role of zoobenthos as ecosystem engineers, including traits related to habitat modification, bioturbation, spatial resource dynamics and nutrient cycling. Information on these traits was collected for the lowest possible taxonomic level from a variety of published sources, namely literature (e.g. Törnroos & Bonsdorff 2012) and online databases, such as Polytraits (Faulwetter et al. 2014), the Biology Traits Information Catalogue (BIOTIC) (MarLIN 2006) and WoRMS (WoRMS Editorial Board 2023). As some species show plasticity in expression of certain trait categories, trait categories were scored using a fuzzy coding approach (Chevene et al. 1994), with a scoring range of 0 (no affinity) to 3 (total affinity towards trait category) (van der Linden et al. 2016, Hu et al. 2019, D'Alessandro et al. 2020). The fuzzy-coded species-trait matrix was then abundance-weighted using the average species abundances for each station.

2.3. Taxonomic and functional diversity

Macrofaunal taxonomic diversity was assessed using the following primary community variables and diversity indices (Gray & Elliott 2009): abundance (A), biomass (B), taxonomic richness (S), Shannon's diversity index (H'), Pielou's evenness (J') and Simpson's diversity index (1−D, hereafter D). Functional diversity was assessed with the following 3 multidimensional indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) (Villéger et al. 2008, Laliberté & Legendre 2010). These indices were built to be complementary

(Villéger et al. 2008) and identified as a relevant combination to fill the functional space of a community (Mouchet et al. 2010). FRic describes the amount of trait space occupied by the species within a community and therefore represents the number of trait categories expressed. FEve refers to how evenly species abundances are distributed between the expressed trait categories (low values indicating that some parts of niche space are under-utilized). FDiv defines the distribution of the abundance across the niche space, with a higher value indicating a high degree of niche differentiation (Mason et al. 2005).

2.4. Macrofauna-mediated ecosystem functions

2.4.1. Estimate of community quality as food resource for consumers (FP$_c$)

Macrofauna are found at the upper layers of the sediment and at the water—sediment interface and represent an important element of benthic—pelagic coupling (Griffiths et al. 2017). Macrofauna species act as food resources for larger benthic species, epifauna or demersal fish species (Rosenberg 1995). A species-specific energy content proxy (EC, J g^{-1}) was developed by Weigel & Bonsdorff (2018) as an estimation of production, susceptibility to predation, palatability and quality as a food resource (prey) for consumers (predators) in the ecosystem. Following optimal foraging theory, predators are likely to select prey that provide them with the highest energetic gain (EC$_i$) while losing minimal energy during the catching and handling process (expressed hereafter with Fr$_i$, Ep$_i$, Lp$_i$) (Pyke et al. 1977). Prey species with relatively high energy content should be preferred in cases where their abundances and accessibility are equal to those of lower-energy species. Consequently, areas where such high-energy prey species are easily accessible would present higher food resource potential.

For each sample, we multiplied the species-specific energy content (EC$_i$, J g^{-1}) by the mean individual biomass (expressed by the relation B_i/A_i, where B_i is a dry weight in g m^{-2}, and A_i is abundance in ind. m^{-2}) of each species within a sample and with standardized scores for prey vulnerability to predation based on its living position (Lp$_i$), standardized scores for the ability of the species to escape based on its motility (Ep$_i$) and standardized scores regarding the ease of being ingested by the predator based on the body fragility (Fr$_i$). The following index gives an estimate of food resource potential for each species (FP$_i$, J m^{-2}) and for

Table 1. Traits and functional categories included in this study. See Table S2 in the Supplement for additional information regarding trait descriptions, relevance and hypothesized relationships with environmental factors

Trait	Category	Label	Definition	Key mechanisms and functions
Feeding mode Response trait (Resistance) Effect trait (Bioturbation)	Scavenger Predator Parasite Miner	scav pred par min	Feeding on carcasses. Feeding on living animals Obtaining food from another animal (host) Obtaining food through mining in e.g. woody material	Food acquisition, productivity, turnover, proxy for energy transfer, strength of benthic— pelagic coupling, prey accessibility
	Scraper/grazer Surface deposit feeder	graz sdep	Feeding on leaves or other plant parts Feeding on phytoplankton, litter and organic matter in the sediment and water column	
	Sub-surface deposit feeder	subdep	Feeding on phytoplankton, litter and organic matter in the sediment and water column	
	Passive suspension/ filter feeder Active suspension/ filter feeder	pfilt afilt	Feeding on suspended matter or food particles in the water column Feeding on suspended matter or food particles in the water column	
Motility Response trait (Resistance, Recovery potential) Effect trait (Food resource, Bioturbation)	Motile swimmer Motile rafter/drifter Motile crawler Motile burrower Semi-mobile tube Sessile byssus	swim raft crawl burr tub byss	Free-swimming Rafting on e.g. drifting algal mats Moving on the sediment surface Living in burrows within the sediment Living in a tube Attached to the surface of a hard substrate	Mobility, dispersal, susceptibility to cropping/predation and environmental pressures
Environmental position Response trait (Resistance) Effect trait (Food resource, Bioturbation)	Infauna deep Infauna middle Infauna top Epibenthic Bentho-pelagic	deep midd top epi benp	Living within the substrate, deeper than 5 cm Living within the substrate between 2 and 5 cm Living within the top 2 cm of the substrate Living on the surface of the substrate Living in the water column and feeding on the bottom	Prey accessibility, susceptibility to cropping and predation, productivity, elemental cycling, space resource dynamics
Maximum adult body size Response trait (Resistance, Recovery potential) Effect trait (Food resource, Bioturbation)	Very small Small Medium Large	VS S M L	0—0.01 g 0.01—0.1 g 0.1—1 g >1 g	Growth rate, productivity, elemental cycling, metabolism, feeding interactions
Fragility Response trait (Resistance) Effect trait (Food resource)	Fragile Intermediate Robust	frag inter rob	Likely to crack as a result of physical impact Liable to suffer minor damage Unlikely to be damaged by physical impact (e.g. hard, leathery)	Prey accessibility, protection against predation and physical pressures, proxy for palatability, productivity, proxy for litter quality, ease of ingestion and decomposition
Longevity Response trait (Recovery potential) Effect trait (Food resource)	Very short Short Long Very long	vshort short long vlong	<1 yr 1—2 yr 2—5 yr 5—10 yr	Life cycle/lifespan, turnover rate, productivity, energy fixation
Reproductive method Response trait (Recovery potential)	Asexual-fragmentation Sexual broadcast spawner Sexual brooder	asex spawn brood	Asexual, both fragmentation and budding Fertilized eggs laid or spawned Egg layer/brooder	Reproduction, turnover, productivity
Propagule dispersal Response trait (Recovery potential)	Pelagic planktotrophic Pelagic lecithotrophic Benthic direct development	plankt lecito direct	Feeding on material captured from the plankton Nourished on internal resources, yolk Direct development of mini adults	Movement of resources, decomposition, productivity, proxy for recruitment success, elemental transport
Degree of contagion Effect trait (Food resource)	Solitary Patchy Highly aggregated	sol patch aggr	Living alone Living in groups (aggregated together) occasionally (e.g. mussels) Living in groups, growing in clusters, schooling	Consumption rate, elemental cycling, decomposition

the community (FP_c, J m^{-2}) at each station as follows (Eq. 1):

$$FP_c = \sum_{i=1}^{n} FP_i =$$
$$\sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times A_i \times EC_i \times Fr_i \times Ep_i \times Lp_i \quad (1)$$

For the energy estimations (EC_i), we followed established biometric conversion factors from existing literature (Brey 2001, Brey et al. 2010). Information on Fr_i, Ep_i and Lp_i was coded following our previous trait selection. In cases where no species-specific data were available, we applied the values of the closest taxonomic level.

2.4.2. Estimate of the community bioturbation potential (BP_c)

A frequently used approach to assess the ecosystem function related to the sediment reworking activity of macrofauna is the community bioturbation potential (BP_c) (Solan et al. 2004, Queirós et al. 2013). This index is used as a proxy for organic matter mineralization, as it provides indirect information on the oxygen penetration within the sediment. The community bioturbation potential was also linked to sediment chlorophyll a (Josefson et al. 2012) and total organic carbon (Solan et al. 2012), sediment reworking (Morys et al. 2017), redox metrics (Birchenough et al. 2012), biogeochemical cycling (Braeckman et al. 2014) and chemical pollution (Mazik & Elliott 2000).

This index includes quantitative measures of species biomass (B_i) and abundance (A_i), as well as qualitative considerations for mobility (M_i) and functional sediment reworking (R_i), 2 traits known to regulate biological sediment mixing, a key component of bioturbation (Solan et al. 2004). Information on mobility and sediment reworking mode was coded following Queirós et al. (2013) and Gogina et al. (2017). These data were used to estimate the species (BP_i) and community (BP_c) bioturbation potential, using the equation in Solan et al. (2004):

$$BP_c = \sum_{i=1}^{n} BP_i =$$
$$\sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times A_i \times M_i \times R_i \quad (2)$$

2.4.3. Estimate of the community bioirrigation potential (BIP_c)

To quantify the potential for solute exchange at the sediment−water interface, community bioirrigation potential (BIP_c) (Renz et al. 2018) was calculated. In order to account for different underlying physical processes in mud and sand, BIP_c applies different scores for advective systems (corresponding to medium sand and coarser sediment types), and for diffusive benthic systems (very fine and fine sand sediments, all other muddy and less permeable sediment types). Considering the sampling method adopted in this study, which restricts the collection to only muddy to fine sand sediments, the scores corresponding to diffusive benthic systems were assigned to all taxa. To calculate BIP_c, the mean individual biomass (expressed by the relation B_i/A_i, where B_i is a dry weight in g m^{-2}, and O_i is abundance in ind. m^{-2}) of each species within a sample is multiplied by the relevant scores for the trait categories feeding type (FT_i), burrow type (BT_i) and depth (L_i), and they are weighted in turn by species abundance as given in the following equation. Afterwards, the results are summed up across all species present in the sample at a particular station:

$$BIP_c = \sum_{i=1}^{n} BIP_i =$$
$$\sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times A_i \times BT_i \times FT_i \times L_i \quad (3)$$

In the cases where trait categories were deemed irrelevant or negligible regarding solute exchange across the sediment−water interface (e.g. epifauna), a score of 'zero' was assigned. Information on BT_i modes, FT_i types and L_i (cm) were obtained from the literature (e.g. Renz et al. 2018) and databases (e.g. MarLIN 2006, Faulwetter et al. 2014).

2.5. Statistical analysis

Known as a robust approach to identify the relative influence of different ecological factors in driving community assembly (Jupke & Schäfer 2020), a distance-based redundancy analysis (dbRDA) was performed. This method is used for carrying out constrained ordinations on data using Bray-Curtis distances (Legendre & Gallagher 2001). dbRDA synthesizes the complete data set of taxa abundances at different sites with a triplot projection (sites, stations and explaining factors) on 2 axes. This analysis assessed the influence of the following variables on taxa abundances across samples: sampling year and month, bottom-water oxygen concentration, depth, temperature, salinity, sediment type, sediment organic content, wind-wave exposure index, water clarity, distance from fish farm, integrated eutrophication status, physical disturbances, human presence and inputs of hazardous

substances (Table S1). To ensure the significance of the dbRDA, an ANOVA was conducted on the model (Legendre & Anderson 1999). Hierarchical cluster analysis was applied to abundance data to identify similarities among sites and build clusters on dbRDA plots. Following $\log_{10}(x + 1)$ transformation of macrofauna counts, cluster analysis (group-average linkage) was performed on a resemblance matrix of the transformed data based on Bray-Curtis distances.

Identified cluster groups were further described with boxplots for environmental variables. Boxplots for univariate data were also computed with samples pooled in testing groups based on the hierarchical cluster analysis results to assess macrofaunal taxonomic and functional diversity. Before performing statistical tests on univariate characteristics of macrofaunal α diversity (A, B, S, H', J', D), functional diversity (FRic, FEve, FDiv) and macrofauna-mediated ecosystem functions (FP_c, BP_c, BIP_c), all faunal and environmental variables were checked for normality (graphically and using an Agostino test), and fourth-root, $\log(x+1)$ or arcsine transformed if necessary. If data did not meet the assumptions for one-way ANOVA, a Kruskal-Wallis 1-way ANOVA by ranks was used. If significant differences were detected by the main test ($p < 0.05$), post hoc tests for pairwise multiple comparisons (Nemenyi's test) were used to identify differences between pairs of stations.

In addition to looking at species composition, community-level weighted means (CWMs) of trait values, representing the expressed trait categories weighted by abundances, were computed for each replicate and used to compare the trait composition between groups identified in the hierarchical cluster analysis. A similarity percentage (SIMPER) analysis was applied to examine the dissimilarity between the cluster groups concerning species and trait composition.

To further explore the relationship between the ecological traits of macrobenthos and environmental variables, a combination of RLQ (Dolédec et al. 1996) and fourth-corner analysis (Legendre et al. 1997) according to Dray et al. (2014) was applied. For the RLQ analysis, tables for environmental variables (R), species abundance (L) and traits (Q) were analyzed using Hill-Smith analysis, correspondence analysis (CA) and principal component analysis (PCA), respectively (Dray et al. 2014). The overall significance of this relationship was assessed using a global Monte Carlo test with 49 999 random permutations of models 2 and 4 (Dray & Legendre 2008, Dray et al. 2014). Model 2 tests whether the distribution of species with fixed traits is influenced by the environmental conditions, while model 4 tests whether traits influence

the composition of species assemblages found in samples, keeping environmental conditions fixed (Dray et al. 2014). In addition, because RLQ analysis cannot determine which traits are affected by specific environmental variables, fourth-corner analysis, with an adjusted p-value (false discovery rate method, FDR) (Benjamini & Hochberg 1995) for multiple testing, was applied. Furthermore, by combining both RLQ and fourth-corner analysis, the significance of the association between environmental variables or traits and the RLQ axes was investigated (Dray et al. 2014).

An automatic stepwise model building for constrained ordination methods was used to determine important predictors of the macrofaunal communities and to determine how much of the variation can be explained by predictor variables (Legendre & Anderson 1999, Anderson 2008). Resemblance matrices for the multivariate community $\log_{10}(x + 1)$ transformed abundance, biomass, traits (CWMs) and macrofauna-mediated ecosystem functions (FP_i, BP_i, BIP_i) were based on Bray-Curtis similarities between samples. Predictors included in the analysis were sampling month and year, bottom-water oxygen concentration, depth, temperature, salinity, sediment type, organic content, water clarity, wind-wave exposure index and the distance from fish farms.

Variance partitioning analysis (VPA) was performed to evaluate the contribution of human ecosystem engineering and abiotic factors to the variance in structural and functional diversity. The variables in VPA were selected using the 'ordistep' function in the dbRDA, and only the variables that explained significant variation ($p < 0.05$) were retained. Before VPA, covariates were divided into 4 groups, one of which was human ecosystem engineering (i.e. human presence, proximity to fish farm, integrated eutrophication status, physical disturbances, inputs of hazardous substances), another group included variables related to the physical environment (i.e. depth, temperature, salinity, bottom-water oxygen concentration, wind-wave exposure index and water clarity), the third group comprised sediment properties (i.e. sediment type, organic content), and the last group was temporal variability (i.e. year, month). The response variables of the structural and functional diversity and the quantitative variables were $\log_2(x + 1)$ transformed.

All analyses were performed using the R Statistical Software v.4.2.2 (R Core Team 2022). The functional diversity indices (FRic, FEve and FDiv) were calculated using the 'FD' package (Laliberté & Legendre 2010) in R based on the fuzzy coding matrix of the traits and the abundance of species. RLQ and fourth-

corner analyses were performed in the 'ade4' R package (Dray & Dufour 2007). Both the dbRDA and VPA analyses were performed using the 'vegan' package (Oksanen et al. 2011).

3. RESULTS

3.1. Species and trait composition in relation to exposure and sediment properties

Among 168 stations and 708 samples collected between 2003 and 2022 in the Åland archipelago, a total of 83 982 macrofauna individuals were identified belonging to 44 different taxa. The hierarchical clustering analysis conducted on abundance data grouped sites with similar abundances and species compositions and identified 4 groups depending on their exposure (exposed [Exp], semi-exposed [Semi] or sheltered [Shelt]) and sediment type (sandy [Sand] or muddy [Mud]): A1 (Exp/Sand), A2 (Semi/Sand), A3 (Semi/Mud) and B (Shelt/Mud). Clusters identified with the hierarchical cluster analysis (Fig. S1) were clearly highlighted in the dbRDA (Fig. 1) and showed the major influence of the combination of both sediment characteristics of stations and their locations in the archipelago, more specifically their exposure to wind and waves and to human ecosystem engineering factors (i.e. human presence, proxies for fish farm pollution, eutrophication, hazardous substances and physical disturbance). Oxygen concentrations also appeared as an important structuring factor for the macrofaunal communities. Sandy stations grouped together and formed 2 clusters split by wave exposure, namely A1 (Exp/Sand) and A2 (Semi/Sand). Cluster A3 (Semi/Mud) grouped muddy and semi-exposed stations and cluster B (Shelt/Mud) represented muddy and sheltered stations (ANOVA on the dbRDA: p < 0.001).

Each variable presented significant differences between the previously identified cluster groups (Fig. S2). The EUNIS index highlighted the gradient in terms of wind-wave exposure, from the most exposed (A1 [Exp/Sand]) to the most sheltered (B [Shelt/Mud]) (Fig. S2a). The most exposed group (A1 [Exp/Sand]) regrouped stations with the lowest temperatures, the highest salinities and the lowest exposure to human ecosystem engineering (i.e. the highest Secchi depth and distance from fish farms, the lowest eutrophication levels and lower human presence and physical disturbances). Water clarity followed the exposure gradient, with the lowest levels found in the last group (B [Shelt/Mud]) (Fig. S2b). This group was also the

one presenting the highest organic content levels (Fig. S2i). The highest temperatures were measured in group A3 (Semi/Mud) (Fig. S2g). In contrast to A3 and B being exclusively muddy, A1 and A2 presented sand content (Fig. S2h). Muddy stations (A3 and B) presented higher levels of hazardous substances compared to sandy ones (A1 and A2) (Fig. S2j). Dissolved oxygen concentrations were higher in sandy groups than in muddy ones, with the lowest concentrations found in group B (Shelt/Mud) (Fig. S2k). With scores higher than 1, eutrophication status classifications are qualified as 'not good' for all groups, with the highest levels found in B (Shelt/Mud) (Fig. S2c). Human presence was higher in A1 (Exp/Sand) and A3 (Semi/Mud) (Fig. S2e), while A2 (Semi/Sand) was subject to the highest levels of physical disturbance (Fig. S2f).

Species composition was different in relation to exposure and sediment type (Fig. 1b) with a dissimilarity higher than 70% between each group based on the SIMPER analysis (Fig. 2). Exposed and sandy stations (A1) were dominated by 50% *Marenzelleria* spp., 15% *Monoporeia affinis* (Lindström, 1855), 15% *Macoma balthica* (Linnaeus, 1758) and 5% *Mytilus edulis* Linnaeus, 1758 (Fig. 2). Mollusks were particularly abundant (60% of the total species composition) in semi-exposed and sandy stations (A2), with mainly *M. balthica* and *Hydrobia* spp. W. Hartmann, 1821. Semi-exposed and muddy stations (A3) were dominated by 40% *M. balthica*, 30% *Hydrobia* spp., 15% Oligochaeta spp. Grube, 1850 and 15% Ostracoda spp. Latreille, 1802. Sheltered and muddy stations (B) showed a different set of species, with 58% Chironomidae spp. and 15% Oligochaeta spp. Species composition was mostly influenced by exposure, with exposed stations characterized by the high presence of *M. affinis* and *Marenzelleria* spp. and sheltered stations by high proportions of Chironomidae spp. Semi-exposed groups (A2 [Semi/Sand] and A3 [Semi/Mud]) were characterized by high proportions of mollusks (*M. balthica* and *Hydrobia* spp.). *Potamopyrgus antipodarum* (J. E. Gray, 1843) was absent from highly exposed and sandy stations.

Stations grouped together by exposure and sediment type also showed different trait compositions, with a dissimilarity higher than 51% between each group based on the SIMPER analysis (Fig. 3). Groups A1 (Exp/Sand) and B (Shelt/Mud) presented the highest dissimilarity in their trait composition (67.73%). Exposed and sandy stations (A1) were dominated by large, fragile individuals with high and very high longevity, brooders, pelagic lecithotrophic larvae, subsurface and surface deposit feeders and predators,
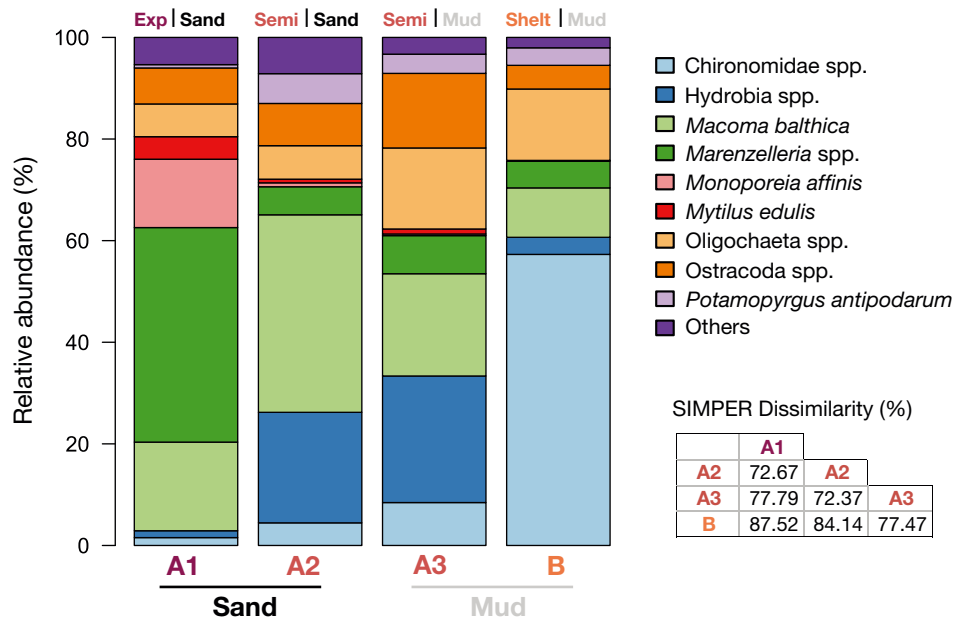
Fig. 2. Relative abundance of species from pooled data from each group identified with hierarchical cluster analysis. Species not contributing to the upper 95% of the composition were combined into the category 'Others'. Exp, Semi and Shelt: exposed, semi-exposed and sheltered environments. The matrix on the right bottom displays average between-group dissimilarities in species composition (%) between cluster groups as result of the SIMPER analysis

burrowers, infauna (middle, deep and top) and patchily distributed organisms. Sheltered and muddy stations (B) were dominated by medium-sized individuals with intermediate fragility, short longevity, spawners, benthic direct development, passive filter-feeders and miners, crawlers, tube builders and rafters/drifters, top infauna and epifauna and solitary organisms. Groups A2 (Semi/Sand) and A3 (Semi/Mud) showed a higher similar trait composition with an intermediate trait composition, halfway between A1 (Exp/Sand) and B (Shelt/Mud).

This trend is further highlighted with the RLQ analysis (Fig. 4). Deeper stations presenting higher wind-wave exposure, higher water clarity, greater distance from fish farms and lower temperatures were associated with large-sized, long-lived, fragile organisms, predators and sub-surface deposit feeders, motile burrowers, with pelagic lecithotrophic propagule dispersal and living deeper than 5 cm within the sediment; whereas stations at the opposite side of this spectrum were characterized by epibenthic, robust, medium-sized organisms, sexual broadcast spawners, motile crawlers and rafters, with pelagic planktotrophic propagule dispersal (Fig. 4a,b). Muddy stations with higher organic content, closer to fish farms and subject to eutrophication were significantly positively associated with miners (Fig. 4c). Stations with higher oxygen concentrations were characterized by

higher levels of brooders and patchy degree of contagion and presented a significant negative association with solitary degree of contagion and the miner feeding mode (Fig. 4c).

3.2. Diversity patterns and macrofauna-mediated ecosystem functions

Total abundance ranged from 69 to 21 142 ind. m^{-2} (4013.76 ± 139.96; mean ± SE) and total biomass from 0.03 to 1038.05 gDW m^{-2} (13.78 ± 28.47). Species richness ranged from 1 to 18 species at individual stations (6.70 ± 0.11). The sand content influenced macrofaunal abundance, biomass and species richness, with significantly higher levels in sandy stations (A1 [Exp/Sand] and A2 [Semi/Sand]) (Fig. 5a−c). The highest taxonomic diversity (*H'*, *J'* and *D*) was highlighted in the semi-exposed muddy group (A3), and these diversity indices were significantly lowest in the sheltered muddy group (B) (Fig. 5d,f). The highest functional richness (FRic) was found in the semi-exposed and sandy group (A2) (Fig. 5g). Functional evenness (FEve) was significantly higher in mud (A3 [Semi/Mud] and B [Shelt/Mud]) than in sand (A1 [Exp/Sand] and A2 [Semi/Sand]) (Fig. 5h). Compared to all other groups, A3 (Semi/Mud) presented the lowest func-
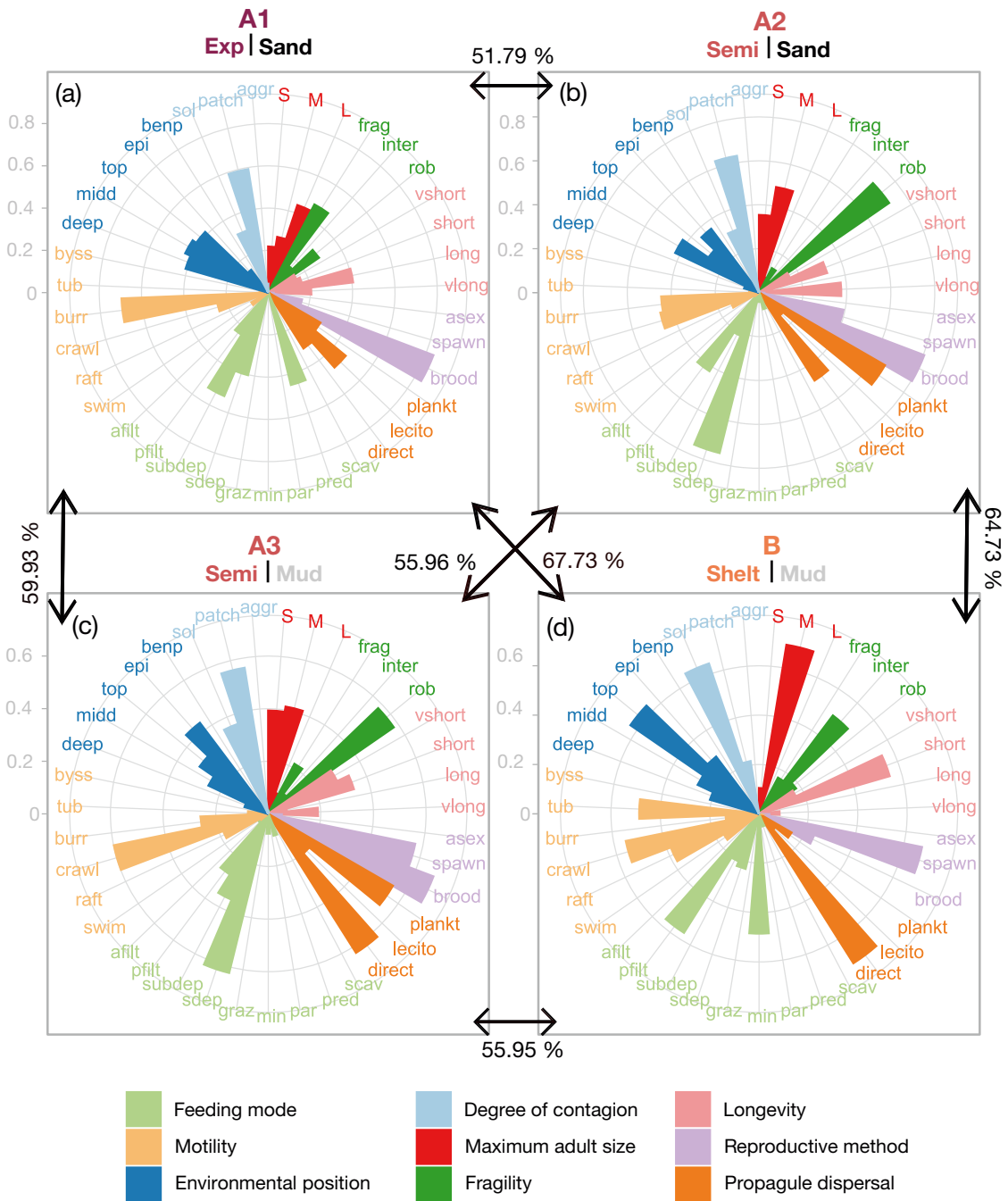
Fig. 3. Community-level weighted means of trait values per groups: (a) exposed and sandy (Exp/Sand, A1), (b) semi-exposed and sandy (Semi/Sand, A2), (c) semi-exposed and muddy (Semi/Mud, A3) and sheltered and muddy (Shelt/Mud, B) for the invertebrate community. Colors differentiate between the traits (see legend). For label descriptions, see Table 1. Black arrows show average between-group dissimilarities in trait composition (%) between cluster groups as result of the SIMPER analysis

tional divergence (FDiv) (Fig. 5i). Every macrofauna-related ecosystem function (food resource, bioturbation and bioirrigation) was higher in sandy stations than in mud (Fig. 5j,k,l). A3 (Semi/Mud) presented the lowest food resource potential for consumers (Fig. 5j).

3.3. Environmental drivers

Permutation tests highlighted 2 main driving factors for macrofaunal communities (abundance, biomass, traits) and for macrofauna-mediated ecosystem functions related to BP_i and BIP_i: the wind-wave expo-
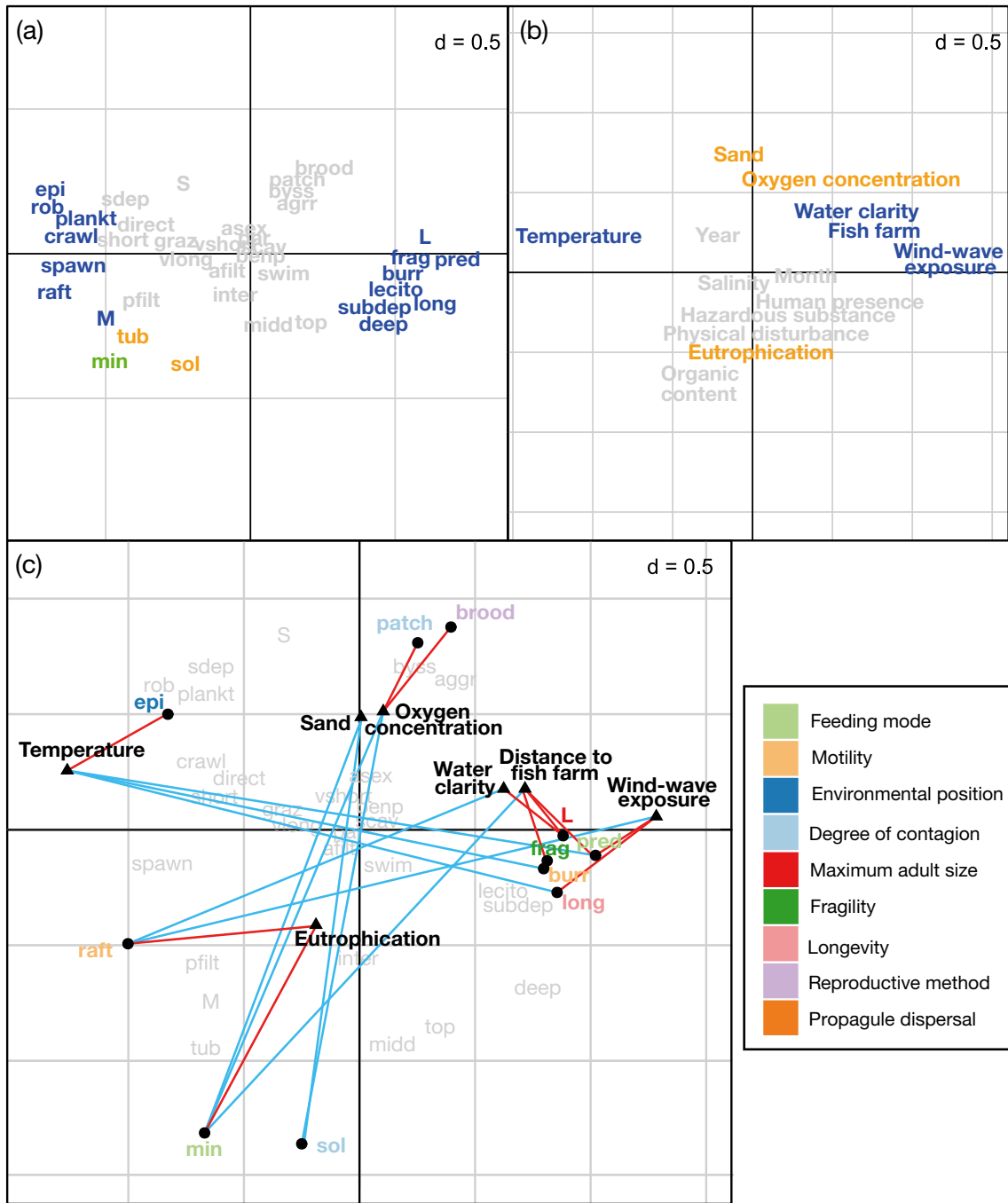
Fig. 4. Combination of fourth-corner and RLQ results. Ordination biplot of significant (p < 0.05) associations identified by the fourth-corner method on the factorial map of RLQ analysis with (a) traits and (b) environmental variables. In (a) and (b), significant associations with the first axis are represented in blue, with the second axis in orange and with both in green. In (c), positive (negative) significant associations are represented by red (blue) lines. Traits are in **bold** type and are represented by circles; environmental variables are in lighter type and are represented by triangles. Variables with no significant associations are shown in light gray. p-values were adjusted for multiple comparisons using the FDR procedure. The d-values indicate the grid size. Codes for traits are explained in Table 1, and more information on environmental variables can be found in Table S1

sure and sediment type (Fig. 6a). Regarding the eco-system function related to FP_i, sediment type appeared as the main driver (Fig. 6a). Oxygen levels were also significantly one of the main drivers contributing to explaining traits (Fig. 6a). The combination of the significant variables (p < 0.05) (Fig. 6) explained more
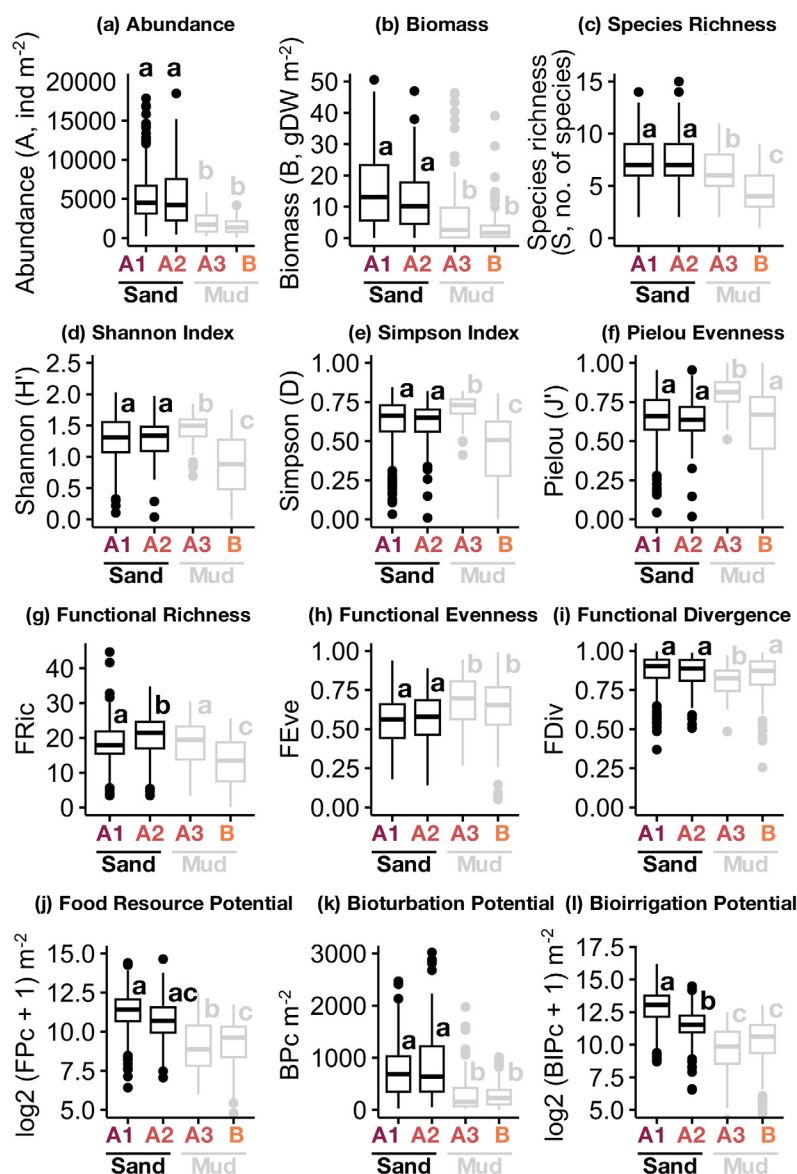
Fig. 5. Macrofaunal (a) total abundance, (b) total biomass, (c) species richness, (d) Shannon's diversity index, (e) Simpson's diversity index, (f) Pielou's evenness, (g) functional richness (FRic), (h) functional evenness (FEve), (i) functional divergence (FDiv), (j) community food resource potential for consumers (FP_c), (k) community bioturbation potential (BP_c), (l) community bioirrigation potential (BIP_c). Stations (n = 168) were grouped based on the hierarchical cluster analysis results. The lower and upper box boundaries indicate 1st and 3rd quartiles, respectively. Bold horizontal lines inside boxes are medians. Whiskers represent minimal and maximal values (1.5× the interquartile range below the 1st quartile or above the 3rd quartile) and outliers are indicated by dots. Different lowercase letters above boxplots show significant differences (p < 0.05) (Kruskal-Wallis tests with Nemenyi's post hoc tests)

ral variation through VPA, the physical environment and human activities were highlighted as explaining the main variation in macrofaunal communities (abundance, biomass, traits) and in macrofauna-mediated ecosystem functions (BP_i, BIP_i, FP_i) (Fig. 6b). Sediment properties and temporal variations also contributed to explaining variations in abundance, traits, bioturbation and bioirrigation potentials (Fig. 6b).

4. DISCUSSION

The present study identified significant environmental and human ecosystem engineering drivers for macrobenthic community structure and functioning. This large data set allowed us to go deeper than previous studies in the area in disentangling the relative contributions of environmental stressors to biologically mediated ecosystem processes related to sediment reworking and food availability for mesopredators.

4.1. Macrobenthos response to direct drivers

Species and trait compositions were very similar to the results of Weigel et al. (2015, 2016) after the *Marenzelleria* spp.-induced shift in the communities. Also consistent with other previous studies (Bonsdorff 2006, Laine et al. 2007, Rousi et al. 2019), both spatial and temporal variables accounted for the distribution of macrobenthos, with the spatial variables (i.e. physical environment, sediment properties and human ecosystem engineering) being more important than the temporal dynamics (sampling year and month). One important temporal event to mention is the introduction of the sabellid polychaete *Laonome xeprovala* Bick & Bastrop, in Bick et al., 2018, appearing in our data set in 2022 (Pykäri 2022), which could potentially become invasive as seen in Luga Bay, in the Gulf of Finland (Tamulyonis et al. 2020).
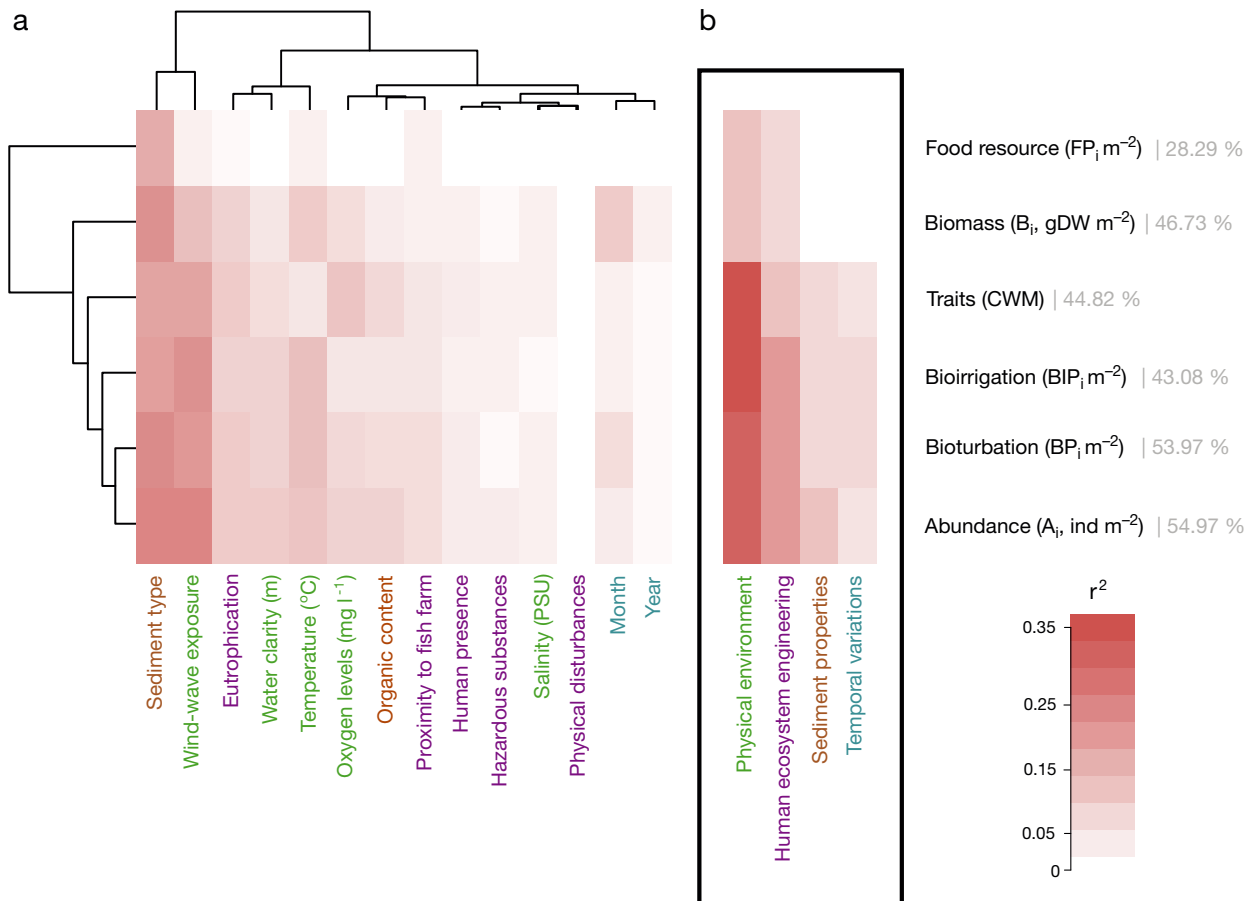
than 40% of the variability in abundances, biomass, traits, bioturbation and bioirrigation potential, and 28.29% of the variability in food resource potential.

When significant factors were combined into physical environmental descriptors, sediment properties, human ecosystem engineering and tempo-

Fig. 6. Environmental drivers for macrofaunal communities (abundance, biomass, traits) and for macrofauna-mediated ecosystem functions (FP_i, BP_i, BIP_i, see Fig. 5 for definitions) after *Marenzelleria* spp. establishment. (a) r^2 results from the automatic stepwise model building for constrained ordination methods. Total variation in each community descriptor explained by the combined variables is indicated with percentages in grey. (b) r^2 results from the variance partitioning analysis of the structural and functional diversity and of the macrofauna-mediated ecosystem functions explained by physical environment (i.e. wind-wave exposure, temperature, oxygen concentrations, salinity and water clarity), sediment properties (i.e. sediment type and organic content), human ecosystem engineering activities (i.e. proximity to fish farms, eutrophication, human presence, hazardous substances and physical disturbances), and temporal variation (i.e. year and month). Additional information on environmental variables is available in Table S1

The exposure to wind-waves and to human ecosystem engineering was one of the main drivers highlighted for the macrofaunal communities in the Åland archipelago (Fig. 7). In this archipelago, the coastal zone comprises over 6000 islands, forming a highly heterogeneous land- and seascape, ranging from shallow, sheltered bays to exposed open-sea areas (Bonsdorff et al. 1996, Weigel et al. 2015). Gradients in environmental drivers, such as exposure to wind-waves, water temperature, salinity and oxygen concentration, can therefore be steep from the inner/sheltered to the outer/exposed coastal zone. Alongside this environmental gradient, a gradient in human ecosystem engineering is also noticeable where physical disturbance, human presence and inputs of hazardous substances change from the coast to the open sea. Higher eutrophication levels were evident in sheltered areas based on the HELCOM integrated eutrophication status index in addition to several environmental parameters known to jointly describe eutrophication (i.e. Secchi depth, organic content and bottom water oxygen). Human activities can further be context-related, e.g. following different degrees of coastal exposure and targeting specific activities to areas with sandy beaches, suitable locations for boat harbors, or depth and water quality needed for fish farming. Disentangling the relative effects of the physical environment from human-induced disturbances on macrofaunal communities is challenging. Repeated sampling may give insight into how changes in anthropogenic pressures shift the macrofaunal community ecotone along the environmental gradient (Weigel et al. 2015). In our study, data may
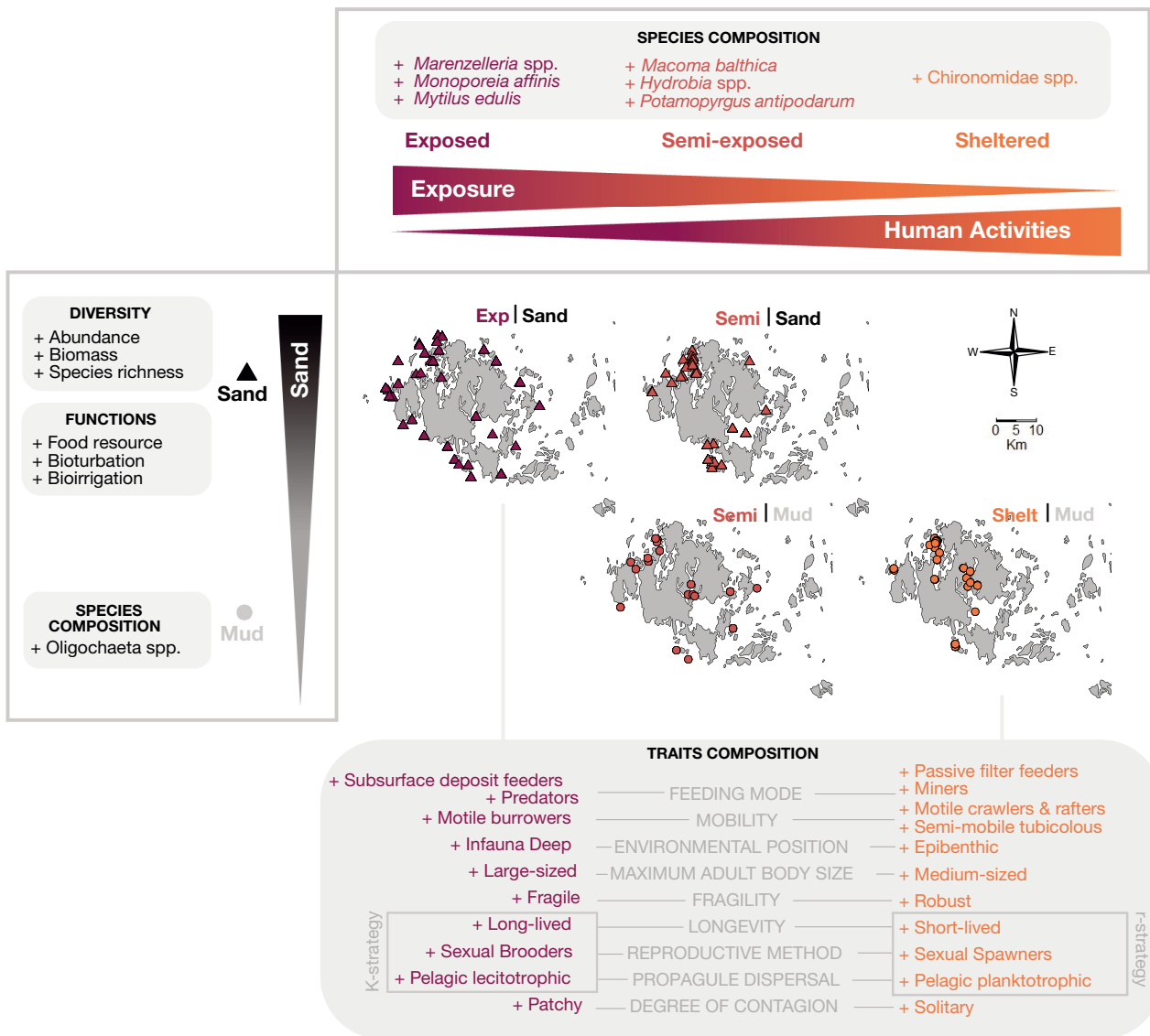
Fig. 7. Conceptual model of the effects of exposure to wind-waves and to human ecosystem engineering (ranging from exposed to sheltered) and sediment type (sandy to muddy) highlighted by distance-based redundancy analysis on macrobenthic communities, more specifically on their structural and functional diversity, species and traits composition and on their mediated ecosystem functions (i.e. their potential as food resource for consumers [FP_c] and their bioturbation [BP_c] and bioirrigation potential [BIP_c])

furthermore be lacking regarding human disturbances or pressures at deeper, more exposed sites, potentially skewing human impact estimates for part of the gradient. Consequently, it is crucial to recognize that the impacts, both direct and indirect, of human ecosystem engineering as described in this study, are likely underestimated, particularly in light of factors such as climate change.

Macrofaunal species composition was conditioned by gradients from sheltered sites, characterized by e.g. higher temperatures, lower oxygen levels and higher eutrophication levels, to exposed areas being deeper

and presenting higher water clarity and exposure to wind-waves, and the lowest exposure to human ecosystem engineering. Exposed areas were dominated by *Marenzelleria* spp., *Monoporeia affinis*, *Macoma balthica* and *Mytilus edulis*; semi-exposed areas were dominated by mollusks (*M. balthica*, *Hydrobia* spp. and *Potamopyrgus antipodarum*); and sheltered areas were dominated by pollution-tolerant insect larvae (Chironomidae spp.) (Leppäkoski 1975) (Fig. 7). Described as not sensitive to nutrient enrichment (Leppäkoski 1975) or hypoxia (Gamenick et al. 1996), Oligochaeta spp. were found in higher proportions in muddy

sediments with higher levels of de-oxygenation, eutrophication, fish farm proximity and hazardous substances. Particularly sensitive to pollution, species such as *M. affinis* and *Halicryptus spinulosus* von Siebold, 1849 were only present in outer stations, farther from eutrophication and hazardous substances.

In addition to the exposure gradient, sediment properties were highlighted as a significant driver in explaining macrofaunal structural diversity patterns (Fig. 7). Higher abundances, biomass and species richness were indeed detected in sandy sediments compared to muddy ones. This is consistent with results from the Finnish coast of the Gulf of Finland in the Baltic Sea, highlighting that the sediment type accounted for most of the variation in macrofaunal abundances (Rousi et al. 2019).

4.2. Effects on macrozoobenthos traits

Completely different sets of traits were prominent in exposed versus sheltered areas (Fig. 7). Exposed areas were dominated by large, fragile individuals with high longevity, brooders, pelagic lecithotrophic larvae, sub-surface and surface deposit feeders and predators, burrowers, infauna (middle, deep and top) and patchily distributed organisms, whereas sheltered areas were dominated by medium-sized individuals with intermediate fragility, low longevity, spawners, benthic direct development, passive filter-feeders and miners, crawlers, tube builders and rafters/drifters, top infauna and epifauna, and solitary organisms. Semi-exposed areas showed an intermediate trait composition between sheltered and exposed areas, highlighting a switch in the macrofaunal trait composition from sheltered to exposed areas, occurring gradually along the exposure gradient related to wind-waves and to human ecosystem engineering. Combining traits from both sheltered and exposed areas, functional richness was the highest in this transition area with intermediate exposure to wind-waves and human-induced pressures, which is consistent with the intermediate disturbance hypothesis (Wilkinson 1999). This change in the trait composition corresponds to a switch from an r-strategy in sheltered areas affected by eutrophication, to a K-strategy in exposed areas presenting a more stable environment. r-selected species with fast reproduction (planktotrophic larvae), short life cycle, numerous offspring (spawners) and smaller body size can indeed be at an advantage when an ecosystem faces severe or frequent disturbance, such as eutrophication or prolonged hypoxia, while K-selected species with lecithotrophic larvae, late sexual maturity and fewer offspring (brooders) will decrease in relative abundance (Pearson & Rosenberg 1978, Jeschke et al. 2008). For example, higher proximity to fish farms was associated with a decrease in body size and an increase in robustness. Eutrophication also specifically affected traits associated with motility and feeding mode, resulting in higher proportions of motile rafters/drifters as well as miners. Our results are consistent with those of Shi et al. (2023), highlighting the effects of eutrophication on trait composition of macrobenthic fauna, especially on motility and body size, and concluding that macrobenthic fauna exhibited opportunistic traits in eutrophic areas.

4.3. Effects on macrofauna-mediated ecosystem functions

4.3.1. Effects on food availability for mesopredators

Community reorganizations due to environmental pressures and human ecosystem engineering not only reshuffle species and trait compositions as observed in this study, but also affect species interactions and trophic dynamics (Tylianakis et al. 2008). What makes prey species suitable and/or favorable for their predators is a central question in ecology especially in regard to accelerating rates of changing communities and shifting interactions (Harley et al. 2006, Both et al. 2009, Schmitz & Barton 2014). In this study, we applied a novel index to estimate the macrofaunal community quality as a food resource for consumers, such as benthic-feeding fish. The use of a trait-based approach was relevant, knowing that predators select their prey irrespective of taxonomic identities but based on a multitude of phenotypic characteristics, such as morphological, behavioral and life history traits (Green & Côté 2014, Spitz et al. 2014, Rodríguez-Lozano et al. 2016). Based on the relevant functional traits, this approach applied to our results succeeded in reflecting the optimal foraging theory: the highest index levels were indeed found in areas where predators are likely to find prey that provide them with highest energetic gain while losing minimal energy during the catching and handling process. The combination of both the energy content and the accessibility of the prey was determinant in calculated FP_c: the highest values were associated with higher abundances and biomass in addition to large-sized, easily ingested, fragile individuals (e.g. *Marenzelleria* spp.) in exposed sandy areas, whereas the lowest FP_c values were found in areas with lower abundances and biomass in addition to smaller

and more robust individuals (e.g. *Hydrobia* spp.) in semi-exposed muddy areas. FP_c values did not differ between areas with higher abundance and biomass with robust individuals and areas with lower abundance and biomass including individuals with higher energy content (i.e. insect larvae) and higher accessibility (epifauna). Disparities in the availability of macrofaunal food resources across the Åland Island archipelago may lead to reduced secondary production and food provision for benthic mesopredators in muddy semi-exposed areas, processes known to link to provisioning services for humans (Rodrigues-Filho et al. 2023, Jacquot 2024).

4.3.2. Effects on sediment reworking

Additional important ecosystem processes associated with macrofaunal communities are linked to their sediment bioturbation and bioirrigation capacities. The differences in species and trait composition and in community structure highlighted in this study have the potential to affect bioturbation and bioirrigation potentials and in so doing to also impact ecosystem functioning (e.g. influencing sediment chlorophyll *a*) (Josefson et al. 2012), total organic carbon (Solan et al. 2012), sediment reworking (Morys et al. 2017), redox metrics (Birchenough et al. 2012) and biogeochemical cycling (Braeckman et al. 2014). Our results showed that a reduction in bioturbation and bioirrigation potential indices was associated with a decrease in abundance, biomass and macrofaunal species richness. This is in line with previous studies showing that macrozoobenthic community structure influences bioturbation processes (Biles et al. 2002, Nasi et al. 2020). Differences in macrofaunal bioturbation attributes were likely due to sediment properties. Several other studies also highlighted sediment characteristics (i.e. grain size, organic matter content) as the main drivers of different bioturbation attribute patterns (Nasi et al. 2020, Gogina et al. 2022). In particular, the highest bioirrigation levels were related to invertebrates with high burrowing depths, such as *Marenzelleria* spp. found in high abundances at the most exposed sandy stations. Nasi et al. (2020) showed that such taxa enhance bioirrigation, and Hedman et al. (2011) highlighted *Marenzelleria* spp. to be a more efficient bioirrigator compared to other species such as the polychaete *Hediste diversicolor* (O.F. Müller, 1776). Reduced bioturbation (BP_c) and bioirrigation (BIP_c) potentials found in muddy sediments and inner, more fluctuating environments, closer to human activities in the Åland archipelago, in contrast to sandy

outer areas, which are farther from human ecosystem engineering, suggest spatial variation in biogeochemical processes connected to supporting services (Rodrigues-Filho et al. 2023, Jacquot 2024).

5. CONCLUSIONS

Based on a large data set spanning 2 decades and communities across the Åland archipelago, the present study (1) identified significant relationships between environmental descriptors and macrofaunal community structure and functioning, and (2) disentangled the relative contributions of those environmental stressors to biologically mediated ecosystem processes related to sediment reworking and food availability for mesopredators. Both spatial and temporal variables accounted for the distribution of macrobenthos, with the main 2 drivers identified as the exposure to wind-waves and to human-induced pressures and the sediment properties. A gradient from inner sheltered, highly eutrophied sites to outer exposed areas was linked to a change in species and trait compositions, leading to a switch from r- to K-strategists, also affecting the availability of macrofauna as a food resource for mesopredators. Our results also highlighted a decrease in abundance, biomass and macrofaunal species richness in muddy sediments compared to sandy ones, which was associated with a reduction in bioturbation and bioirrigation potential indices. In the context of the socio-ecological crisis humanity is currently facing, our results provide a deeper understanding of environment—community relationships and the interplay between biotic and abiotic ecosystem components regarding human ecosystem engineering.

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