Table S1. Covariates with their assumed relevance and expected relationships with structural and functional diversity

Covariate | Modalities or unit		Relevance	Expected relationships with:	
			Structural diversity	**Functional diversity**
Sediment properties	**Sediment type** (sand/mud)	It is commonly recognized that the structure of the macrofaunal communities depends largely on sediment parameters (Rousi et al. 2011). Sediment characteristics are often a significant explanatory factor in macrofaunal taxonomic and trait composition (Jacquot et al. 2018). The species distribution of the zoobenthos in and on the sediment of the northern Baltic Sea has been shown to be clearly affected by the nature of the sedimentary environment (Rousi et al. 2011, 2019).	**Sand (+):** ≠ Species composition (Rodil et al. 2009, Rousi et al. 2011) Abundance (+), Biomass (+), Species richness (+) (Jacquot et al. 2018, Rousi et al. 2019)	**Sand (+):** Feeding mode: pred (+), sdep (-), subdep (-), pfilt (+), afilt (+); Motility: swim (+), crawl (+) (Rodil et al. 2009, Rousi et al. 2011)
	Organic content	The amount of organic content in the sediment can serve as a proxy for food availability for macrofaunal organisms. The sediment-dwelling fauna is highly dependent on the energy produced in the photic zone, which is supplied to the soft-bottom as organic matter (Snoeijs-Leijonmalm et al. 2016).	**Organic content (+):** ≠ Species composition (Rodil et al. 2009, Rousi et al. 2011)	**Organic content (+):** Feeding mode: afilt (+), pfilt (+), sdep (+), subdep (+) (Rodil et al. 2009, Rousi et al. 2011)
Human ecosystem engineering factors	**Human presence** (HELCOM; "Disturbance of species due to human presence HOLAS")	This is an estimate of the human presence disturbance due to underwater sound creating acoustic pollution and visual disturbance is derived from three human activities occurring in the Åland archipelago: (1) recreational boating and sports, (2) bathing sites and (3) coastal urban land use (e.g. use of submarine power cables). Many invertebrates have been shown to be sound-sensitive, causing e.g. damage to sensory systems, stress, mortality, change in behavior (Solé et al. 2023).	?	?
	Physical disturbance (HELCOM; "Physical disturbance HOLAS")	Physical disturbances, such as dredging, has a direct physical impact on the benthic environment since it alters the sedimentary habitat structure and may harm the sediment-dwelling organisms by smothering (Snoeijs-Leijonmalm et al. 2016). The physical disturbance index included in this study combines all human activities occurring in the Baltic Sea and causing physical disturbance or damage to seabed: cables, dredging, extraction of sand and gravel, fishing intensity, pipelines, shipping density, etc. Such activities may cause erosion and resuspension of bottom sediments (Snoeijs-Leijonmalm et al. 2016).	**Physical disturbance (+):** ≠ Species composition (Krause et al. 2010)	**Physical disturbance (+):** Size: S (+), L (-); Feeding mode: scav (+), pfilt (-), afilt (-); Environmental position: deep (+); Motility: swim (+), crawl (+), tub (-), byss (-); Fragility: rob (-); Propagule dispersal: plankt (+), lecito (-); Reproductive method: spawn (+), brood (-) (Tillin et al. 2006, Krause et al. 2010)
	Proximity to fish farm (Distance from fish farm (m))	Bonsdorff et al. (1997) pinpointed fish farms as "local point sources" for nutrient inputs, having a significant impact in terms of eutrophication. The 35-40 operating fish farms contribute indeed to 15 times the load from municipal wastewater for phosphorus and 3 to 6 times the nitrogen input through treated wastewater (Bonsdorff et al. 1997). In the Åland Archipelago, fish farm effluents have been shown to have an impact on the water quality (due to input of nutrients, organic matter, hazardous substances, litter) (Nordvarg & Johansson 2002, HELCOM 2023) and macrofaunal communities (Kraufvelin et al. 2001, Villnäs et al. 2011). In Åland Islands, fish farming has been shown to result in reduced oxygen content of bottom waters, anaerobic sediments, elevated nutrient concentrations in bottom waters, causing algal blooms and elevated chl-a values, organic enrichment, reduction in sediment redox potential (Villnäs et al. 2011). As a proxy for fish farm pollution, we estimated the distance to the nearest fish farm for each station. At the scale of the entire Åland Islands with the complex archipelago and associated hydrography, it was not possible to include water currents factoring into the level of impact at sites.	**Proximity to fish farm (+):** ≠ Species composition: *Monoporeia affinis* (-), *Macoma balthica* (-), Hydrobia spp. (+), Oligochaeta (+), Chironomidae (+), *Marenzelleria* spp. (+); Abundance (-), Biomass (-), Species richness (-) (Kraufvelin et al. 2001, Villnäs et al. 2011, Sanz-Lázaro & Marín 2011)	**Proximity to fish farm (+):** Feeding mode: sdep (+), subdep (+); Motility: burr (+), tub (+); Size: VS (-), S (-), L (+), VL (+); Environmental position: top (+); Longevity: short (+), long (-); Propagule dispersal: plankt (+), lecito (-); Reproductive method: spawn (+), brood (-) (Villnäs et al. 2011)
	Eutrophication (HELCOM; "Integrated eutrophication status assessment")	Coastal eutrophication caused by nutrient-rich runoff represents a major issue in most of the Baltic Sea and more specifically in the Archipelago Sea including Åland Islands (Cederwall & Elmgren 1990, Bonsdorff et al. 1997, Gustafsson et al. 2012, Bonsdorff 2021, HELCOM 2023), leading the area to be currently classified as "affected by eutrophication" (Andersen et al. 2011, 2017). Despite significant reductions of the nutrients inputs into the sea since the 1980s, low connectivity between the Baltic Sea and North Sea, inducing long retention times and stratification restricting ventilation of deep waters, has ensured that nutrient levels remain high to this day (Snoeijs-Leijonmalm et al. 2016, HELCOM 2023). Originating mainly from agriculture, riverine input, municipal wastewaters, aquaculture and airborne loading, nutrient inputs lead to increased primary production, decreased water clarity, increasing amounts of oxygen-consuming drift-algal mats and changes in zoobenthos and fish communities (Bonsdorff et al. 1997).	**Eutrophication (+):** Abundance (-), Biomass (-), Species richness (-) (Rönnberg & Bonsdorff 2004)	**Eutrophication (+):** Size: VS (+), S (+), L (-), VL (-); Environmental position: top (+), epi (+) (Rönnberg & Bonsdorff 2004)
	Hazardous substances (HELCOM; "Input of hazardous substances HOLAS")	Chemical substances can be considered hazardous if they are toxic, persistent and bioaccumulate or if they are highly persistent and bioaccumulate (Snoeijs-Leijonmalm et al. 2016). In the Baltic Sea, large amounts of hazardous chemicals have been used since the very beginning of the industrialization of the region. Chemical contamination by hazardous substances is identified as a pressure contributing to impoverished biodiversity in the Baltic Sea (HELCOM 2023). Macrofaunal bioturbation can also result in the release of these chemicals from the sediment to the water column (Hedman et al. 2011). The contamination ratio values of inputs of hazardous substances were calculated with CHASE Assessment tool for hazardous substances monitored in water, sediment and biota (i.e. heavy metals, radioactive substances, HBCDD, PBDE, PFOS, PCB, TBT, etc.).	**Hazardous substances (+):** Abundance (-), Diversity (-) (Ryu et al. 2011, Rabaoui et al. 2015)	**Hazardous substances (+):** Size: VS (+), S (+), M (-), L (-); Feeding mode: sdep (+), subdep (+), pred (-); Motility: crawl (-), swim (-) (Piló et al. 2016, Dong et al. 2021)
Temporal variables	**Year**	Temporal changes in zoobenthos communities structure and functioning have been highlighted in Åland Islands (Weigel et al. 2015, 2016). The Baltic Sea environmental conditions have already contributed to the successful establishment of invasive species leading to a shift in species composition. This is what happened with the establishment of the spionid polychaete *Marenzelleria* spp. after 2000 (Weigel et al. 2015).	–	–
	Month	The Baltic Sea is subject to seasonal environmental fluctuations (e.g. ice cover in winter, spring algal blooms, seasonal fluctuations in temperature, salinity and oxygen levels), which might cause abundance and biomass variations (Rousi et al. 2013).	–	–

(Table S1 continued)

Covariate | Modalities or unit		Relevance	Expected relationships with:	
			Structural diversity	**Functional diversity**
Physical environment variables	**Wind-wave exposure** (EUNIS index)	The extent of exposure to waves and wind, depth, and proximity to land have been shown to be significant factors structuring biological communities (abundance, biomass, species composition) (Pihl 1986, Kilar & McLachlan 1989, Ricciardi & Bourget 1999). These structuring factors are included in an established exposure index for northern Baltic Sea coasts by Isæus (2004) and improved by Weigel et al. (2015, 2016). The exposure classification functions as a habitat proxy. Sheltered sites are generally shallower, closer to land and less influenced by wind and wave action compared to exposed sites. Weigel et al. (2015) showed that communities of the included sheltered and exposed habitats were clearly distinguishable in terms of macrofaunal species identity, temporal trends in biomass and their underlying environmental drivers.	**Exposure (+):** ≠ Species composition: *Monoporeia affinis* (+), *Marenzelleria* spp. (+), *Potamopyrgus antipodarum* (-), *Hydrobia* spp. (-), Oligochaeta (-), Chironomidae (-) (Weigel et al. 2015)	**Exposure (+):** Environmental position: deep (+), top (-); Feeding mode: sdep (+), subdep (+), min (-); Size: L (+); Fragility: frag (+); Longevity: vlong (+), long (+), short (-) (Weigel et al. 2016)
	Salinity (PSU)	Salinity and temperature are major driving variables for macrofaunal communities (Li et al. 2022). Salinity has been reported as the main environmental factor affecting benthic macrofauna community composition and structure in coastal and estuarine ecosystems (Conde et al. 2013, Verdelhos et al. 2015, Little et al. 2017). Climate effects (salinity and temperature) constitute one major vector of change in coastal ecosystems such as in the Baltic Sea. Coupled with an ongoing decrease in salinity, a higher increase in temperature has been highlighted in the Baltic Sea (>1 °C since the 1980s) compared with many other sea areas (<1 °C) (Belkin 2009, Philippart et al. 2011). In particular, marine heatwaves are increasing in frequency and intensity due to climate change (Kauppi & Villnäs 2022). Increased temperature and lower salinity induce biological effects including changed species distribution, composition and ecological patterns (Möllmann et al. 2009, Olsson et al. 2013).	**Salinity (-):** Biomass (-), Species richness (-) (Darr et al. 2014)	**Salinity (-):** Size: S (+), L (-); Longevity: short (+), long (-); Propagule dispersal: plankt (+), lecito (-) (Darr et al. 2014)
	Temperature (°C)		**Temperature (+) / Heatwaves:** ≠ Species composition (Pansch et al. 2018)	**Temperature (+) / Heatwaves:** Feeding mode: sdep (-), subdep (-), afilt (-), pfilt (-); Motility: burr (-) (Pansch et al. 2018, Kauppi et al. 2023)
	Dissolved oxygen concentration (DO) (mg L^{-1})	Most organisms require oxygen to serve as the terminal electron acceptor in energy production (respiration) and to drive many redox reactions. Different taxa have specific tolerance ranges and, as a consequence, oxygen (normoxia, hypoxia, anoxia) is a strong predictor for species diversity and occurrence in the zoobenthic assemblage in general and more specifically in our study area (Weigel et al. 2015, Rousi et al. 2019). The oxygenation status of the environment can be estimated by measuring dissolved oxygen. Hypoxia (<3.5 mg O_2 L^{-1}, level recommended by Steckbauer et al. (2011) to designate hypoxic water masses) and anoxia (0 mg O_2 L^{-1}) are two of the most important structuring factors for the zoobenthic communities of the Baltic Sea, leading to an impoverishment or complete loss of benthic macrofauna (Pearson & Rosenberg 1978, Rousi et al. 2019).	**DO (-):** ≠ Species composition: *Monoporeia affinis* (-), *Pontoporeia femorata* (-), Oligochaeta (+), Chironomidae (+), *Marenzelleria* spp. (+) (Karlson et al. 2005, Rousi et al. 2019), Biomass (-) (Weigel et al. 2015), Species richness (-) (Rousi et al. 2019)	**DO (-):** Feeding mode: sdep (-), afilt (-), pfilt (-), graz (-); Motility: burr (-) (Villnäs et al. 2012)
	Water clarity (Secchi Depth (m))	Light attenuation and thus water clarity was quantified as the Secchi depth: the murkier and less clear the water, the lower the Secchi depth (Fleming-Lehtinen 2016). Substances reducing the clarity of natural seawater include chlorophyll a (as a proxy of phytoplankton biomass), coloured dissolved organic matter (CDOM), and suspended particles such as clay and silt. For example, the decrease in Secchi depth can be associated with increase in chlorophyll-a concentration due to eutrophication, with resuspension of bottom sediments due to climate events (e.g. storm) or to physical disturbances (e.g. dredging, installation of submarine power cables), or with increase in CDOM (e.g. caused by fish farming)… Being a composite indicator, Secchi depth was found suitable for expressing eutrophication together with other indicators; relying on Secchi depth alone would introduce a risk of misinterpretations but it also turned out to be valuable in reflecting signals not currently captured by other indicators (Fleming-Lehtinen 2016).	–	**Water clarity (-):** Feeding mode: sdep (+), subdep (+), pfilt (-), afilt (-) (Riemann et al. 2016)

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Table S2. Traits description, relevance and their hypothesized relationships with factors responsible for spatial patterns in infaunal assemblages including traits helping to distinguish between natural and human-induced changes.

Traits	Description and relevance	Hypothesized relationships with environment
Feeding mode RESPONSE TRAIT (Resistance) EFFECT TRAIT (Bioturbation)	Feeding interactions have long been considered a central factor structuring macrobenthic communities (Pearson & Rosenberg 1987). Feeding types contribute to production and trophic support, and play a role in nutrient uptake and recycling (Norling et al. 2007). It provides insights into the interactions between different species and their food sources. A diverse set of feeding modes indicates diverse food sources available in an area (Pacheco et al. 2011). The feeding mode is considered to be a proxy for energy fixation/transfer and ecosystem production (Törnroos & Bonsdorff 2012). It has important implications for the transfer of carbon between the sediment and the water column and within the sediment. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg 1995).	Predators and scavengers will be associated with areas with high availability of prey (Dolbeth et al. 2007). Scavengers are attracted to areas where physical disturbances occur and are expected to be more common in areas of high fishing or fish farming intensity. Organic enrichment caused by fish farming is expected to favor large deposit-feeders (Donadi et al. 2015). Scrapers and grazers are more abundant in areas with high levels of primary producers, usually found in areas with low depth (Dolbeth et al. 2007) and potentially low hydrodynamics. Surface feeders are obtaining food from the surface of the substratum so they transport energy from the pelagos. They act on the pelagos-benthos elemental cycling. Sub-surface feeders obtain food within the sediment so energy transport stays within benthos.
Motility RESPONSE TRAIT (Resistance, Recovery potential) EFFECT TRAIT (Food resource, Bioturbation)	Despite the generally restricted motility of benthic infauna, the small-scale motility of these organisms is crucial for the ecology of benthic communities. Not only motility provides insights into the ability to avoid physical disturbance (Hinchey et al. 2006) but also into the predatory-prey activities or the creation of biological structures. Mobility also affects the ability for adult recolonisation of disturbed areas. In addition, mobility may increase prey vulnerability or decrease it in case of strong escape response.	Sessile organisms are more subject to changes in the abiotic environment than motile species Sarà (1986). Motile species are expected to have a better ability to avoid stressors (e.g. fish farming, hypoxia events, eutrophication, physical disturbance…) and to be able to recolonize areas by migration (Krause et al. 2010, Pacheco et al. 2011, Gogina et al. 2014). Faster moving species (particularly swimmers) are more likely to evade local physical pressure, while those capable of movement within the sediment may regain sediment position following burial (Bolam 2011). Burrow-dwellers and tubicolous are potentially less vulnerable to strong hydrodynamic disturbance, anoxic conditions and water pollution as opposed to free-living species because they can hide in their fixed tubes or burrow (Reise 2002).
Environmental position RESPONSE TRAIT (Resistance) EFFECT TRAIT (Food resource, Bioturbation)	Environmental position refers to the typical living position in the sediment profile. Because species need to re-establish their sediment vertical position following a physical disturbance to undertake their biological processes (e.g., feeding), the deeper infaunal taxa are living the less likely they are affected by pressures.	Infauna is expected to be less affected by wave exposure and to be found in higher proportions in deeper areas. Spatial overlap of predator and prey niches increases prey vulnerability. Indeed, infauna living in the top layer of the sediment, epibenthos and bentho-pelagic individuals are more accessible to cropping and predation than infauna living deeper in the sediment. If infauna is living deeper in the sediment, it suggests that there is a potential for water penetration into the sediment surface which may provide organic matter to lower sediment layers where it can be decomposed and also incorporate oxygen in the sediment (Pacheco et al. 2011).
Maximum adult body size RESPONSE TRAIT (Resistance, Recovery potential) EFFECT TRAIT (Food resource, Bioturbation)	The organism body size has a crucial relevance in the functioning and dynamics of aquatic systems (Woodward et al. 2005). Body size is correlated with many life-history traits and influences a wide range of biological and ecological functions (Warwick & Clarke 1984, LaBarbera 1989, Bourassa & Morin 1995, Saiz-Salinas & Ramos 1999, Macdonald et al. 2012). This biometric parameter can be more responsible for the trophic structure than taxonomic identity itself (Jennings et al. 2001). Body size has implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small bodied species (high turnover) (Pearson & Rosenberg 1978).	Small-bodied species may characterize environments with high instability, the result of environmental/anthropogenic disturbances imposed on the organisms (Mouillot et al. 2006). We expect small-sized species to be prevalent in high hydrodynamic areas (Donadi et al. 2015) and to have higher P/B ratios (Schwinghamer 1981) with higher metabolic rates (Gillooly et al. 2001). Increases in organic matter in the sediment, e.g. due to fish farming, would favor large individuals (Donadi et al. 2015). Hypoxia is also expected to act on the body size, sometimes favoring medium/large individuals (Gogina et al. 2014) and sometimes small size ones (Pacheco et al. 2011). Smaller prey body size increases prey vulnerability.
Fragility RESPONSE TRAIT (Resistance) EFFECT TRAIT (Food resource)	Different morphologies vary in their relative susceptibility to damage from physical pressure (e.g., dredging).	Fragile individuals are likely to crack as a result of physical impact (e.g. dredging, submarine power cables installation) (Krause et al. 2010). Individuals with intermediate fragility are liable to suffer minor damage and robust individuals are unlikely to be damaged by physical impact (e.g. hard, leathery). Fragile individuals are expected to have a higher palatibility and to decompose faster (Törnroos & Bonsdorff 2012).
Longevity RESPONSE TRAIT (Recovery potential) EFFECT TRAIT (Food resource)	Longevity represents the maximum lifespan of the adult stage (years). It indicates the relative investment of energy in somatic rather than reproductive growth and the relative age of sexual maturity, i.e. a proxy for relative r- and k- strategy (Pearson & Rosenberg 1978).	Longer-lived species (k-strategy) are expected to be found in deeper waters where light, food availability, temperature and disturbance intensity drive highly predictable distributions (Montero-Serra et al. 2018). As long-living species are more common in undisturbed habitats, we further expect such species, particularly those of a larger body size, to be rarer in disturbed areas (Pacheco et al. 2011, Gogina et al. 2014). Long-living species have lower relative production due to slow growth and turnover rates (Ridgway et al. 2011, Moss et al. 2016).
Reproductive Method RESPONSE TRAIT (Recovery potential)	Species can reproduce asexually (fragmentation, budding), or eggs can be released into the water column (pelagic) or onto/into the bed either free or maintained by mucous (benthic) or eggs are maintained by adult for protection, either within parental tube or within body cavity (brood). These different mechanisms vary in their potential susceptibility to damage from physical pressures (Bolam et al. 2020).	Brooders (k-strategy) have fewer offspring but invest more time and resources in ensuring survival, both in gestation and rearing. Broadcast spawners (r-strategy) have numerous offspring to overwhelm the odds. This means that few resources and minimal energy are invested in the survival of each individual. We expect broadcast spawners to decrease with depth and an increase in species with other reproductive methods (Mileikovsky 1971). Asexual reproduction may be an adaptation to unfavorable environmental conditions and for species where sexual reproduction is uncertain and/or infrequent (Foster et al. 2013, Wangensteen et al. 2016). We expect that asexual reproduction will dominate in areas that have been disturbed by anthropogenic pressures over a long period of time.
Propagule dispersal RESPONSE TRAIT (Recovery potential)	This trait indicates the potential for dispersal of the larval stage prior to settlement from direct (no larval stage), lecithotrophic (larvae with yolk sac, pelagic for short periods) to planktotrophic (larvae feed and grow in water column). Dispersal is a fundamental ecological process that affects the organization of biological diversity at multiple temporal and spatial scales (Bohonak & Jenkins 2003). Dispersal strongly influences metapopulation and metacommunity dynamics through the movement of individuals and species, respectively (Heino et al. 2015). This trait is heavily associated with the export of carbon and energy (under the form of offspring) out of the system (i.e. source/sink concept) and represents a critical factor in the effect of the community on ecosystem stability (e.g. temporal variation, resilience *sensu* Loreau (1994)).	Direct developing larvae look like adults and they have typically very low dispersal potential because they crawl away from their egg after hatching (i.e. slow benthic dispersion, k-strategy). Planktotrophic larvae (i.e. r-strategy) are associated with long pelagic duration and high dispersal capacity while lecithotrophic larvae developing from large eggs, containing a high quantity of yolk, correlate with a short pelagic duration and settlement close to parents (Foster et al. 2013). Therefore, we expect that planktotrophic species can recolonize more easily areas that have been disturbed by anthropogenic pressures over a long period of time (e.g. physical disturbances, eutrophication, human presence, hazardous substances) (Krause et al. 2010, Pacheco et al. 2011, Gogina et al. 2014). Additionally, we expect an increase of species with lecithotrophic or direct developing larvae with depth.
Degree of contagion EFFECT TRAIT (Food resource)	Macrofauna species act as food resources for larger benthic species, epifauna, or demersal fish species (Rosenberg 1995). Therefore, the macrofaunal degree of contagion traits gives insights on food distribution for consumers (Ding et al. 2020).	Large-sized species that form aggregations are expected to create habitat for other species and large spatial scales and thereby increase biodiversity.

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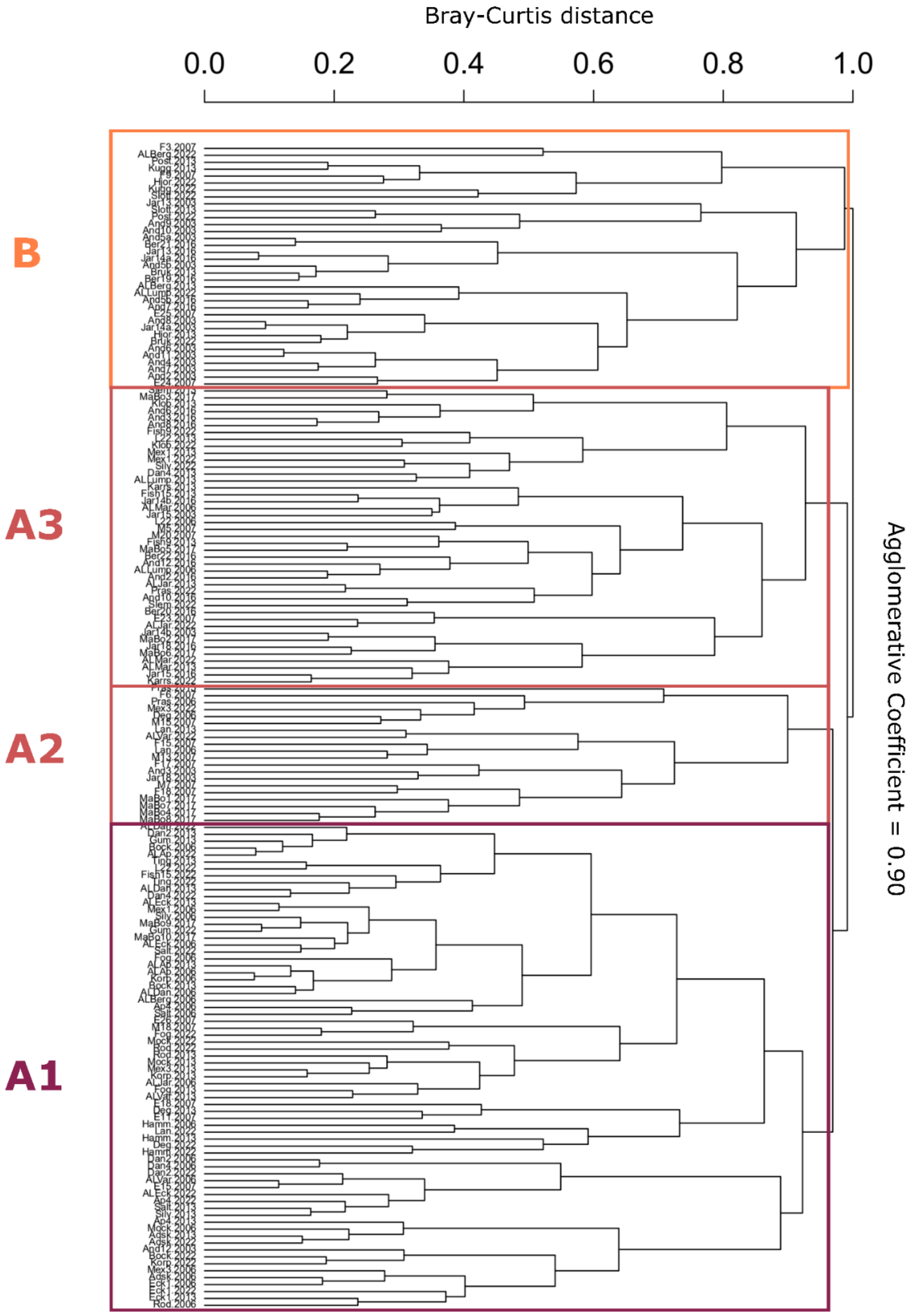

Fig. S1. Dendrogram from group-averaged hierarchical cluster analysis based on Bray-Curtis distances, produced using log10(1 + x) transformed macrofaunal abundances (data at 168 stations in the Åland archipelago).

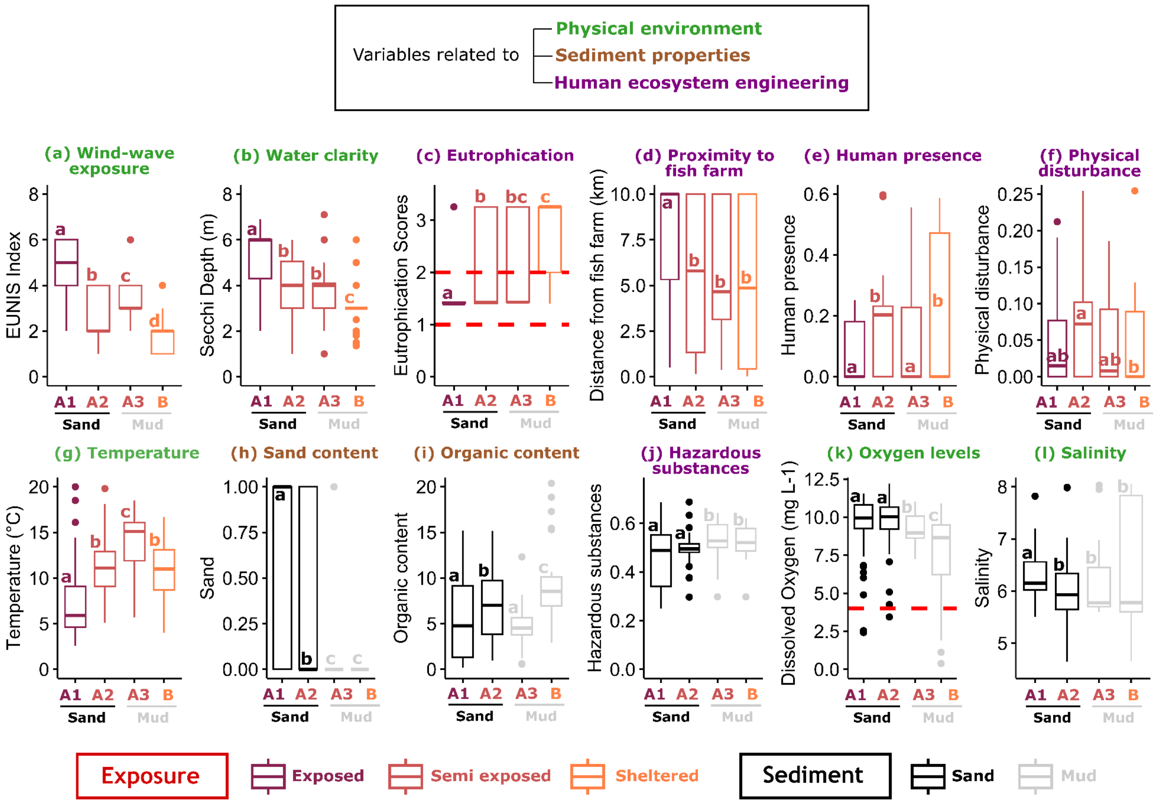

Fig. S2. Boxplots of variables with a significant influence on the distribution of sites with (a) wind-wave exposure, (b) water clarity, (c) eutrophication, (d) proximity to fish farm, (e) human presence, (f) physical disturbance, (g) temperature, (h) sand content, (i) organic content, (j) hazardous substances, (k) oxygen levels, (l) salinity. 168 stations were grouped based on the hierarchical cluster analysis results. Different lowercase letters above boxplots show significant differences ($p < 0.05$) (Kruskal-Wallis tests with Nemenyir's post-hoc tests). Dashed red lines indicate important thresholds for macrofaunal communities based on literature.