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Diversity and distribution across a large environmental and spatial gradient: Evaluating the taxonomic and functional turnover, transitions and environmental drivers of benthic diatom communities

Virta, Leena

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1 **Diversity and distribution across a large environmental and spatial gradient: evaluating the**
2 **taxonomic and functional turnover, transitions and environmental drivers of benthic diatom**
3 **communities**

4 Leena Virta^{1,2*}, Janne Soininen¹ & Alf Norkko^{2,3}

5 ¹ Department of Geosciences and Geography, PO Box 64, FIN-00014 University of Helsinki,
6 Finland

7 ² Tvärminne Zoological Station, University of Helsinki, J.A. Palméns väg 260, FI-10900 Hangö,
8 Finland

9 ³ Baltic Sea Centre, Stockholm University, Stockholm, Sweden

10 * leena.virta@helsinki.fi

11 **Acknowledgements**

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16 of Finland (project ID 294853) for financial support.

17 **Biosketch**

18 Leena Virta is a doctoral student studying the functioning of marine ecosystems. Particular interests
19 include diversity and distribution of microphytobenthic organisms in the Baltic Sea ecosystem.

20 Janne Soininen is a professor of spatial environmental research and widely interested in causes and
21 consequences of aquatic biodiversity.

22 Alf Norkko is interested in the biodiversity of sea floor habitats and their importance for ecosystem
23 functioning across environmental gradients. He is particularly interested in how disturbance may
24 influence relationships between biodiversity and ecosystem functioning.

25 **Diversity and distribution across a large environmental and spatial gradient: evaluating the**
26 **taxonomic and functional turnover, transitions and environmental drivers of benthic diatom**
27 **communities**

28 **Running title: Diversity across a large gradient**

29 **Abstract**

30 **Aim:** Global biodiversity loss has raised interest in understanding variation in diversity at different
31 scales. Especially studies conducted across large spatial gradients are crucial, because they can
32 increase perspectives on how ecological patterns change relative to environmental factors, and
33 facilitate predictions of possible responses to environmental change. We explored the full extent of
34 a brackish sea to test the hypotheses that (i) benthic communities are defined by species' limited
35 ranges, controlled by varying drivers along a large environmental gradient, (ii) the responses of
36 taxonomic and functional community composition and turnover to the environmental gradient are
37 different, thus highlighting the need to include both measures in ecological studies, and (iii)
38 diversity reaches the minimum at intermediate salinities (Remane curve) due to the low adaptation
39 of freshwater and marine species.

40 **Location:** A large environmental and spatial gradient spanning the entire Swedish coastline (ca.
41 2300 km; salinity 1.2-27.6), the Baltic Sea

42 **Time period:** August 2018

43 **Major taxa studied:** Benthic diatoms

44 **Methods:** We assessed environmental drivers for the communities and calculated the taxonomic
45 and functional alpha and beta diversity along the gradient. We also compared the taxonomic and
46 functional composition and diversity of communities between areas with different salinity.

47 **Results:** We found support for the hypothesis of limited species ranges, as taxonomic beta diversity,
48 mainly induced by changes in salinity and climate, was high, whereas functional beta diversity
49 remained considerably lower, and the composition and diversity of communities, as well as
50 environmental drivers controlling the communities, differed between regions with different salinity.
51 The lowest taxonomic diversity was found at intermediate salinities of 5-6.

52 **Main conclusions:** These findings advance understanding of large-scale patterns of benthic
53 diversity, emphasize the importance of large gradient studies for a better understanding of general
54 ecological patterns, and highlight the vulnerability of brackish water ecosystems as ecologically
55 important tipping point realms.

56 **Keywords**

57 beta diversity, brackish, diatoms, diversity, functional, gradient, limited ranges, Remane curve,
58 salinity, tipping points

59 **Introduction**

60 The ongoing biodiversity crisis has increased the need for understanding the variation of diversity.
61 This, in turn, has raised interest and triggered substantial efforts for studying the different kinds of
62 gradients that often are associated with changing diversity patterns (Mittelbach et al., 2007).
63 However, our understanding of gradients underlying diversity patterns is hampered by different
64 obstacles: i) natural gradients are almost always complex, with several physical, chemical and
65 biological factors interacting and correlating with each other (Huston, 1994; Willig, Kaufman, &
66 Stevens, 2003), ii) diversity varies constantly along environmental, spatial and temporal gradients,
67 although the rate of this variation depends on the type of organisms (Willig et al., 2003), iii)
68 physical and chemical gradients are also constantly changing, and the ongoing climate change
69 accelerates this change (The BACC II Author Team, 2015).

70 Despite the challenges listed above, studies conducted along gradients facilitate a better
71 understanding on how ecological patterns, such as variation in biodiversity, change relative to the
72 environment (Thrush et al., 2006). Spatial gradients, including gradients in latitude, have received
73 considerable attention as drivers of diversity (Willig et al., 2003). However, many environmental
74 variables vary in concert with spatial gradients and, hence, spatial gradients can act as surrogates for
75 primary environmental gradients, such as the ones of climate or productivity (Fuhrman et al., 2008).
76 Here we focus on the responses of benthic diatom communities to environmental factors along a
77 large-scale gradient of salinity, climate and space. For aquatic organisms, salinity is often a major
78 environmental driver that can vary along spatial gradients (Villnäs, & Norkko, 2011; Ji et al., 2019).
79 This applies for both freshwater and marine realms but is particularly pronounced in ecosystems
80 with strong salinity gradients, such as estuaries or semi-enclosed seas (Remane, 1934; Olli, Ptacnik,
81 Klais, & Tamminen, 2019).

82 As a study area, we used the Baltic Sea, which is a good example of a semi-enclosed, high-latitude
83 sea, where salinity forms a strong gradient but interacts and correlates with other environmental
84 factors, such as climatic and latitudinal forces. Due to several reasons, the Baltic Sea provides an
85 excellent platform for studying the responses of biotic communities to environmental factors across
86 gradients. First, the environmental gradient of the Baltic Sea is large, spanning from freshwater to
87 brackish and finally marine conditions. Studies conducted across such large gradients can be
88 particularly useful for increasing understanding and building predictions of possible community
89 responses to environmental change (Thrush et al., 2006). However, most of the studies in the Baltic
90 Sea, with consistently collected data have focused on regional or local areas, whereas only few have
91 utilized the whole salinity gradient (see Ulanova, Busse, & Snoeijs, 2009; Villnäs & Norkko, 2011;
92 Olli et al., 2019 for large gradient studies). Furthermore, sampling of large gradients is notoriously
93 time-consuming and arduous and, thus, large datasets have usually been collected in several parts
94 (but see Herlemann et al., 2011 for a large bacterial investigation). This may not cause a problem

95 while studying large organisms in stable climatic conditions, but may compromise the results of
96 studies conducted on quickly evolving communities, such as microphytobenthic communities, at
97 high latitudes, where strong seasonality leads to a seasonal succession of changing species
98 composition and diversity among short-lived organisms (Huston, 1994).

99 Secondly, across the Baltic Sea gradient, species typically have limited ranges that follow the
100 pattern suggested by the central-marginal hypothesis, i.e., lower and more variable abundances
101 towards the margins of their distribution dictated by environment, typically salinity (Gaston, 2009;
102 Westerbom, Mustonen, Jaatinen, Kilpi, & Norkko, 2019). Because the effects of environmental
103 change on biotic communities and their distributions can often first be detected at the edges of
104 distribution areas, studying gradients that include such marginal areas may further facilitate
105 understanding population responses to future environmental change (Sorte et al., 2017). In the
106 Baltic Sea, as well as other basins with strong salinity gradients, the limited ranges of species often
107 result in species richness minimum at intermediate salinities. This pattern is called the Remane
108 curve (Remane, 1934), and it is due to the inability of freshwater or marine species to tolerate such
109 salinities. Thirdly, the Baltic Sea has been predicted to respond strongly to climate change due to
110 increasing temperatures and river flow, thus lowering salinity and changing the salinity gradient
111 (The BACC II Author Team, 2015). And fourthly, the Baltic Sea has a long history of
112 eutrophication, and species are strongly affected by anthropogenic drivers (Gustafsson et al., 2012;
113 Andersen et al., 2017).

114 Diversity and distribution of species along gradients have most commonly been described using
115 taxonomic metrics, e.g., species richness and community composition. However, including the
116 functional characteristics, i.e. traits, of communities can provide a more effective way to describe
117 diversity and facilitate establishing links between environment and the community (Hooper et al.,
118 2005). Functional traits describe differences in resource acquisition, environmental preferences, and

119 tolerance to stressors and consumers (Passy, 2007), thus linking communities effectively to small-
120 and large-scale environmental gradients.

121 Here, while keeping in mind the theories of limited ranges of species, central-marginal hypotheses
122 and Remane curve (Remane, 1934), we sought to find new insights into the effects of environment
123 on communities and, thus, provide ideas of possible community responses to environmental change.

124 We did this by means of assessing the taxonomic and functional composition and diversity of
125 benthic diatoms in relation to environmental drivers along a large salinity, climatic and spatial
126 gradient in the Baltic Sea. Diatoms are eukaryotic microorganisms that have been estimated to
127 produce ~20% of oxygen in the atmosphere (Nelson, Treguer, Brzezinski, Leynaert, & Queguiner,
128 1995; Field, Behrenfeld, Randerson, & Falkowski, 1998). They are an integral part of the
129 microphytobenthos in all aquatic systems, and in regions with strong environmental gradients,
130 diatoms exhibit large variation in community composition and diversity (Passy, Pan, & Lowe,
131 1999) and, hence, provide an excellent model group for large gradient studies. We performed the
132 sampling during a short time period using consistent methods, and verified the results with re-
133 sampling of certain sites to control for temporal variance. We predicted that (i) despite continuous
134 water flow between sites and consequent free dispersal of organisms, differences in the environment
135 and consequent species' limited ranges would result in significant spatial variation in the
136 composition and diversity of communities (Busse & Snoeijs, 2003), thus identifying potential
137 tipping points that may indicate mechanisms and drivers of community change in response to
138 environmental change (Westerbom et al., 2019). We also hypothesized that different environmental
139 factors would structure the communities in the different parts of the gradient (Ulanova et al., 2009),
140 showing that studies conducted at large gradients are necessary for the understanding of general
141 ecosystem processes, and also possibly suggesting that climate change induced changes in physical
142 gradients may change environmental drivers and ultimately the communities in ways that we cannot
143 yet predict; (ii) the taxonomic and functional community composition would respond differently to

144 the environment (Virta et al., 2019), which would highlight the advantages of including both
145 community measures in ecological analyses; and (iii) lowest taxonomic diversity of communities
146 would be found at brackish water salinities of ca. 6 (Remane, 1934), thus emphasizing the
147 uniqueness and vulnerability of brackish water ecosystems.

148 **Materials and methods**

149 Study area and sampling

150 Our study area spanned the entire coastline of Sweden, in northern Europe. It extended from the
151 northern to southern Baltic Sea and finally to the transition zone from the Baltic Sea to the North
152 Sea (Fig. 1). The sampling gradient covered ca. 2300 km of coastline between latitudes 55.73°N
153 and 65.79°N and longitudes 11.17°E and 23.90°E. Environmental conditions in this area are highly
154 variable. Climate-related factors, such as air and water temperature, precipitation and the duration
155 of ice cover, follow a north-south gradient. Due to the restricted water exchange between the Baltic
156 Sea and the North Sea, and the abundance of rivers discharging into the Baltic Sea, salinity follows
157 a north-south and east-west gradient and increases from ~1 in the northeastern part of the sampling
158 gradient to ~28 in the western part of the gradient. Thus, biotic communities represent a transition
159 from freshwater to brackish and finally to marine species. Nutrient concentrations are also highly
160 variable but site-dependent without a clear gradient.

161 We conducted our sampling over a short time period in late summer, 9 - 24 August 2018, to
162 minimize the potential for temporal variability. We had a total of 46 study sites, focusing on areas
163 where the change in environment, such as salinity, is known to be most pronounced, and then re-
164 sampled the first six sites to explore the potential bias due to temporal variation. To minimize the
165 effect of terrestrial factors, such as the effect of land use, we chose sites at far ends of peninsulas or
166 islands, and avoided close proximities of river mouths. We conducted the sampling following the
167 modified recommendations by Kelly et al. (1998). At each site, we randomly selected twenty

168 cobble-sized stones along the shoreline from depths of 20-50 cm. We collected the biofilm by
169 scraping the surfaces of stones with a sponge (25 cm² per stone) and pooled the accumulated
170 suspension into a composite sample, which was then stored in cold (+4 °C) and dark conditions
171 until further processing. To account for the stability of the substrate, which may affect the growing
172 conditions of microphytobenthic organisms, we measured the volume (length × width × height) of
173 each sampling stone. We also measured salinity, pH and water temperature *in-situ*, and collected
174 water samples from each site. We froze the water samples immediately after sampling and later
175 analyzed them for nutrients, namely NO₂⁻ + NO₃⁻, NH₄⁺, PO₄³⁻, and Si. To evaluate habitat
176 characteristics, we classified the bottom type according to the amount of sediment (classes 1 to 3;
177 class 1 denotes a rocky bottom, class 2 a sedimentary or sandy bottom covered with stones, and
178 class 3 a sedimentary or sandy bottom with only a few stones) and the amount of macroalgae or
179 vegetation on stones (classes 1 to 3; class 1 denotes no macroalgae/vegetation, and class 3 stones
180 totally covered by macroalgae/vegetation) at each site.

181 Diatom and laboratory analyses, trait characteristics, wind exposure, and climatic variables

182 Diatom samples were boiled with hydrogen peroxide (30% H₂O₂) to remove organic material, and
183 the cleaned diatoms were mounted on slides using Naphrax (Brunel Microscopes Ltd, United
184 Kingdom). We used a phase contrast light microscope with a 1000× magnification to identify 500
185 valves per sample to the lowest possible taxonomic level (typically species level) following
186 Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Snoeijs (1993), Snoeijs and Vilbaste (1994),
187 Snoeijs and Potapova (1995), Snoeijs and Kasperovicienė (1996), and Witkowski (2000). After the
188 identification of diatoms, we transformed species counts into relative abundances and verified
189 taxonomic names according to AlgaeBase (Guiry, 2020).

190 To account for the functional composition of communities, we used the abundances of traits that are
191 robust indicators of ecological behavior (Westoby, Falster, Moles, Vesk, & Wright, 2002). We

classified diatom species according to their size (biovolume classes: large $> 1000\mu\text{m}^3$ / small $< 1000\mu\text{m}^3$), mobility (mobile / non-mobile), type of attachment (adnate / pedunculate [which was further divided to pad-attached / stalk-attached] / non-attached), colonization (colonial / non-colonial), guild (low-profile / high-profile / motile / planktonic) (Rimet & Bouchez, 2012), nitrogen-fixing abilities (nitrogen-fixer / non-nitrogen-fixer) (Passy, 2007), and salinity preference (freshwater / brackish / marine; each species may belong to 1-3 salinity categories depending on the breadth of distribution). Each species was classified according to all seven classifications, which resulted in numerous possible combinations for classifying a certain species. As the measure of trait composition, we used the combination of traits of all the species present in the community. To identify traits for each diatom species, we used, in addition to above mentioned species and trait literature, Snoeijs, Busse and Potapova (2002) and Diatoms of North America (2019). Traits used here indicate morphological characteristics of species and are related to ecosystem functioning. For example, grazers are dependent on high-profile diatom species, whereas low-profile species persist at low nutrient levels, where high-profile and motile species cannot survive (Passy, 2007).

Nutrient analyses of the water were conducted with an automated photometric analyzer (Thermo Scientific Aquakem 250 [Thermo Fisher Scientific Oy, Vantaa, Finland]) ($\text{NO}_2^- + \text{NO}_3^-$, PO_4^{3-} , and Si), except for NH_4^+ , which was analyzed manually. To account for the wind exposure of our sampling sites, we calculated fetch, i.e., the distance over which wind can travel across open water. We did this using the ruler tool in Google Earth (Google). We placed the beginning of the ruler at the exact study site and measured the distance to next shore, island or islet along 36 lines, which were 10° apart from each other. Thus, we obtained 36 values for each site, and used the sum of these values as the measure of the fetch of the sampling site (Mason, Riseng, Layman, & Jensen, 2018). To account for climate, we extracted the average annual temperature and average annual precipitation (representative of 1950-2000, spatial resolution $\sim 1\text{km}^2$) from WorldClim database

216 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and calculated climatic values for sampling sites
217 with the ArcGIS 10.2.1, Arcmap-application.

218 Statistical analyses

219 Prior to statistical analyses, we log10-transformed environmental variables $\text{NO}_2^- + \text{NO}_3^-$, NH_4^+ ,
220 PO_4^{3-} , Si, salinity, stone volume and fetch to reduce their skewed distributions. We assessed
221 statistical dependence between explanatory variables using Spearman's rank correlation
222 coefficients. Si, air temperature, precipitation, latitude and longitude were highly correlated (> 0.7)
223 with salinity. Thus, these variables were excluded from analyses, and salinity was used as a proxy
224 for climatic and spatial variables, reflecting the joint effect of these factors for biotic communities.
225 To validate the results of the spatial sampling, we calculated the degree of temporal beta diversity at
226 the six sites that had been visited twice. Our aim was to see whether the communities changed
227 significantly during our sampling project. This was done using temporal beta diversity indices (TBI)
228 (Winegardner, Legendre, Beisner, & Gregory-Eaves, 2017). TBI computes the total temporal beta
229 diversity and its components (species gain or species loss) at each sampling site. We calculated the
230 TBI for taxonomic composition using binary data and Sørensen dissimilarities, and computed
231 significances with a parametric paired t-test with 9999 permutations. TBI was done with the R
232 package adespatial (Dray et al., 2019).

233 To study the spatial beta diversity of communities, we calculated all pairwise dissimilarities in
234 taxonomic and functional community composition using abundance data and the Bray-Curtis
235 dissimilarity index (Bray, & Curtis, 1957). Then, we examined the relationship between
236 dissimilarities and the salinity gradient, which was identified by generalized dissimilarity models
237 (GDM) as the only environmental variable to significantly affect the communities (see below),
238 using linear models. The significance of the relationship was determined using Mantel tests with
239 Pearson's correlation and 999 permutations.

240 We studied the effects of individual environmental variables on taxonomic and functional beta
241 diversity with generalized dissimilarity modelling (GDM) (Ferrier, Manion, Elith, & Richardson,
242 2007). GDM is a technique for studying spatial variation in biodiversity between pairs of
243 geographical locations, and for defining the importance of predictor variables for beta diversity. We
244 performed GDMs with taxonomic and functional abundance data and Bray-Curtis distance, and
245 used function *gdm.varImp* with 50 permutations to estimate p-values for the whole model and each
246 of the predictor variables. We constructed GDMs using R package *gdm* (Manion et al., 2018).

247 To study the variation in communities along the environmental gradient, we classified our sampling
248 sites according to salinity, which was indicated by GDM as the only environmental variable to
249 significantly explain taxonomic and functional beta diversity. The classification of samples was
250 conducted, because it enabled us to visualize the taxonomic and functional community composition
251 at different salinities, and also enabled us to indicate, which environmental variables control the
252 communities at areas with different salinities. This is important for, e.g., conservation perspectives,
253 because if different factors affect the communities at different salinities, conservation measures,
254 such as nutrient reductions, need to be modified accordingly. No consensus of common salinity
255 categories has been reached in literature (Snoeijs, & Weckström, 2019), but we used salinity
256 categories of > 20 to indicate brackish to marine water with high salinity (11 samples), 10-20 to
257 indicate brackish water with higher salinity (6 samples), 4-10 to indicate brackish water with lower
258 salinity (21 samples), and 0-4 to indicate fresh to brackish water with low salinity (14 samples)
259 (modified from Snoeijs, 1993 and Snoeijs, & Weckström, 2010). We then used pie charts to
260 illustrate diatom species assigned to major taxonomic groups, i.e., genus, and functional traits in
261 different salinity categories. For the pie charts, we used the R package *ggplot2* (Wickham, 2019).

262 We also used distance-based redundancy analyses (dbRDA) with Hellinger-transformed data to
263 examine the influence of environmental variables on the taxonomic and functional community
264 composition within different salinity groups (Legendre, & Gallagher, 2001). We used Bray-Curtis

265 distance for species composition and Gower's distance for trait composition (Legendre, &
266 Anderson, 1999). To ensure an adequate number of samples in each salinity group, salinities 10-20
267 and > 20 were combined in dbRDA analyses. We used the R package vegan for the dbRDA
268 analyses (Oksanen, 2019).

269 We studied the relationship between taxonomic and functional community composition and species
270 richness and salinity using regression models. Taxonomic and functional community composition
271 was described as multidimensional scaling (nMDS) 1 scores, and the nMDS were calculated with
272 Bray-Curtis similarity index and two dimensions. To visualize the relationships, we used the R
273 package ggplot2 (Wickham, 2019).

274 All statistical analyses were calculated using R version 3.6.1 (R Development Core Team, 2019).

275 All data used in the analyses are available through the Dryad Repository
276 (<https://doi.org/10.5061/dryad.bvq83bk6p>).

277 **Results**

278 Community composition did not change significantly at any of the twice-visited six sites between
279 the first sampling at the beginning of August and the second sampling at the end of August
280 (Appendix, table 1).

281 Across the broad-scale spatial gradients, communities were taxonomically highly different at
282 different parts of the sampling gradient (Fig. 2). Pairwise mean taxonomic dissimilarity was 0.732
283 (max 0.990, min 0.206). Functional dissimilarities were considerably lower, as pairwise mean
284 functional dissimilarity was 0.230 (max 0.577, min 0.032). Taxonomic and functional
285 dissimilarities changed significantly (p : 0.001) along the salinity gradient, and the relationships
286 between community similarity and the salinity gradient were statistically significant (taxonomic
287 dissimilarity: R : 0.549, p : 0.001; functional dissimilarity: R : 0.403, p : 0.001) (Fig. 2).

288 Environment explained taxonomic and functional spatial beta diversity significantly ($p < 0.001$),
289 although the deviance of taxonomic beta diversity was explained more efficiently than the deviance
290 of functional beta diversity (Table 1). Salinity was the only significant variable for both taxonomic
291 and functional beta diversity. However, this may indicate the combined influence of salinity,
292 climate and spatial factors, because climatic and spatial variables were excluded from analyses due
293 to high correlation with salinity.

294 The genus *Navicula* and *Nitzschia* were the dominant taxonomic groups along the environmental
295 gradient (Appendix, fig. 1) and formed 16.9% and 28.5% of the communities, respectively, when all
296 salinity categories were considered. The contribution of different taxonomic groups varied between
297 salinity categories, with salinity category < 4 featuring the most even distribution of groups with no
298 clear dominance. Many functional traits showed a gradient from high to low salinity (Fig. 3). The
299 relative proportion of large versus small diatoms increased towards low salinity, as well as the
300 relative proportion of pedunculate versus mobile diatoms, high-profile versus motile diatoms, and
301 colonial versus non-colonial diatoms. The relative proportions of diatoms with preference for
302 freshwater, brackish or marine environment did not show a clear pattern.

303 Taxonomic and functional community composition was significantly explained by environmental
304 variables in all salinity groups (Table 2). Nutrients were among the significant environmental
305 variables in all salinity groups for taxonomic composition and in two of three salinity groups for
306 functional composition. Wind exposure, i.e. fetch, and stone volume were significant in almost all
307 the groups, and water temperature, pH, salinity, vegetation amount, and sediment amount were
308 significant in at least one of the salinity groups for either taxonomic or functional community
309 composition.

310 The relationships between salinity and taxonomic/functional community composition or species
311 richness were non-linear (Fig. 4, Fig. 5). Lowest species richness (26, 28 and 29 species per sample)
312 was found in brackish water with intermediate salinity (5.4, 5.2 and 5.3, respectively), whereas

313 highest species richness (109, 98 and 83 species per sample) was found in marine water with high
314 salinity (26.0, 26.6 and 26.7, respectively).

315 **Discussion**

316 We investigated the general hypotheses that benthic communities along a large environmental
317 gradient are defined by species' limited ranges (Gaston, 2009), controlled by varying drivers along
318 a large environmental gradient, and that diversity reaches the minimum at intermediate salinities
319 due to the low adaptation of freshwater and marine species (Remane, 1934). To our best knowledge,
320 this is one of the first studies to investigate aquatic microorganismal communities on an
321 environmentally and spatially large gradient (across ca. 2300 km) with a coherent sampling project
322 that minimized the influence of temporal variability on the communities.

323 As suggested by the theories of limited species ranges and the central-marginal hypothesis (Gaston,
324 2009), we found an almost complete spatial taxonomic beta diversity, i.e. turnover of communities
325 from one end of the gradient to the other end, in other words, only a few same species were found at
326 both ends. Due to the strong gradient in environment, especially salinity, this was expected.

327 However, functional beta diversity remained low, i.e., species were replaced by taxonomically new
328 but functionally similar species along the gradient. Similar results of low functional despite high
329 taxonomic beta diversity have been found before across short spatial gradients in estuaries
330 (Villéger, Miranda, Hernandez, & Mouillot, 2012 in a tropical estuary; authors' unpublished data in
331 a Baltic Sea estuary), but our large spatial gradient makes the result interesting. It seems that the
332 functional characteristics of microphytobenthos needed for efficient benthic ecosystem functioning
333 are very similar in very different environments. In our study, the number of species per site (54 on
334 average) was considerably higher than the number of traits (7 per site), and this confounding effect
335 may affect the notable difference between taxonomic and functional beta diversity. However, due to
336 our method of categorizing each species according to seven different classifications, the number of
337 possible functional combinations per site was high and closely comparable to the species number.

338 Salinity was the only environmental variable that significantly explained taxonomic and functional
339 beta diversity of the communities. Due to the large range of salinity (1.2-27.6) in our sampling area,
340 the effect of salinity was to be expected, as salinity has regularly been found as a major driver for
341 biotic communities in aquatic systems (Cognetti, & Maltagliati, 2000; Villnäs, & Norkko, 2011),
342 even in studies with considerably smaller range (Svensson, Norberg, & Snoeijs, 2014 on a salinity
343 gradient of 0.5-7.8). However, salinity was also used as a proxy for highly correlated climatic and
344 spatial variables, and hence, climate and spatial distance probably also contributed to beta diversity.
345 There are a number of climatic variables that can affect aquatic communities at high latitudes, such
346 as air temperature (Chu, Jones, Mandrak, Piggott, & Minns, 2008), precipitation (Primo, Azeiteiro,
347 Marques, Martinho, & Pardal, 2009), day-time length, and ice cover duration (Virta, Soininen, &
348 Norkko, 2020). These variables are usually highly inter-correlated, which supports the use of only
349 one or two of them to represent climate, which we did. Our finding of climate as an important factor
350 for determining species distribution is supported by several previous studies at the regional scale
351 (Pearson, Dawson, & Liu, 2004; Pajunen, Luoto, & Soininen, 2016). Although spatial variables
352 (latitude and longitude) were also correlated with salinity and climate, we think that they are not a
353 major driver for the communities in this study, because there is a continuous water flow and, thus,
354 free dispersal of species between sites.

355 Our classification of sites according to salinity divided the sampling area to four different areas: 1.
356 the western area of Kattegat and the North Sea, with salinity of > 20 ; 2. the southwestern area of the
357 Belt Sea, with salinity of 10-20; 3. the eastern area of the Bornholm Basin, the Western Gotland
358 Basin, the Åland Sea and the Bothnian Sea, with salinity of 4-10; and 4. the northernmost area of
359 the Bothnian Bay, with salinity of < 4 . As was hypothesized following the ideas of limited species
360 ranges and the central-marginal hypothesis (Gaston, 2009), the taxonomic composition of
361 communities differed between these areas. All the main taxonomic groups were present in all
362 salinity areas, but their relative proportions varied across areas, and the area with the lowest salinity

363 differed from the other areas by having the most even distribution of taxonomic groups. Thus, it
364 seems that marine and brackish waters share characteristics of taxonomic groups, whereas there is a
365 clear distinction and a threshold between brackish and fresh waters. This may indicate potential
366 changes in the benthic communities at the transition zone between brackish and freshwater
367 conditions, if future climate change decreases salinity in the Baltic Sea as has been predicted.

368 Many functional characteristics also showed a gradient along salinity areas. The general trend was
369 the increase of large and high-growing species or colonies (traits large, pedunculate, high-profile
370 and colonial) towards low salinities. This was surprising, because other organisms, such as benthic
371 macrofauna, grow in size from the low salinities of the Baltic Sea to the higher salinities of the
372 North Sea (Furman, Pihlajamäki, Välipakka, & Myrberg, 2014). The different behavior of diatoms
373 in relation to other organisms may be due to several abiotic factors, such as different responses to
374 salinity and other environmental factors by small and large diatom species (Snøeijls et al., 2002),
375 varying nutrient conditions along the gradient, or increasing disturbance by wind exposure towards
376 marine conditions (Passy, 2007). We also speculate that, due to the increase of the species richness
377 and abundance of benthic fauna towards marine conditions (Norkko et al., 2015), biotic
378 disturbances, i.e., grazers, may have played a key role in shaping the functional characteristics of
379 diatom communities along the salinity gradient and in favoring smaller species with better
380 resistance to grazers at high salinities. The distribution of species with preference to fresh, brackish
381 or marine water was surprisingly constant across salinity areas. This may be due to a high number
382 of species that were included in two or three preference groups because of their large geographical
383 distribution areas.

384 Our hypothesis of different environmental drivers for community composition at different salinity
385 areas was partly confirmed, because many of the variables appeared as significant at only one or
386 two salinity areas. This emphasizes the importance of large gradient studies for the understanding of
387 ecosystem processes. However, certain environmental drivers seemed to affect communities

388 everywhere. Wind exposure and stone volume, both describing physical disturbance, were
389 important in almost all areas. Physical disturbance has been shown to affect all kinds of benthic
390 communities, such as diatoms (Passy, 2007), macroalgae (Underwood, 1998), and macrofauna (Cai,
391 Gong, & Qin, 2012), and this effect may increase in the future with intensifying winds and more
392 severe storms (The BACC II Author Team, 2015). Nutrients were also important for the
393 communities in all salinity groups, but with varying contributions. The areas with lowest (< 4) and
394 highest (> 10) salinity were limited by both nitrogen and phosphorus, and the brackish waters
395 (salinity 4-10) by phosphorus. These results disagree with several other studies that have shown
396 phosphorus limitation in freshwater realms and in the northern parts of the Baltic Sea and nitrogen
397 limitation in brackish and marine waters (Tamminen, & Andersen, 2007). This disagreement may
398 possibly be due to the seasonally varying nutrient compositions in the Baltic Sea, or the effect of
399 eutrophication, as suggested by Tamminen and Andersen (2007).

400 All the relationships between community metrics (taxonomic and functional community
401 composition, and species richness) and salinity were non-linear but considerably different from
402 each other. Change in the taxonomic and functional community composition remained quite even
403 through salinities 0-ca. 20 before levelling off at salinities >20 . This seems to indicate that even
404 small changes in salinity have strong effects on communities in fresh and brackish waters, which
405 may lead to considerable changes in communities if climate change alters the salinity, as has been
406 expected. The relationship between species richness and salinity indicated high diversity in samples
407 with low and high salinity, whereas diversity in the brackish water samples was lower. This agrees
408 with the ideas of Remane (1934) and many other studies after him that have described the lowest
409 diversity of organisms at intermediate salinities of ca. 5-8 (e.g. Olli et al., 2019). The species
410 richness is at its lowest at these salinities probably because estuaries and brackish water seas are
411 universally small, ephemeral and isolated from each other, which has prevented the development
412 and speciation of actual brackish-water species (Olli et al., 2019).

413 To conclude, resolving patterns in biotic communities and their drivers along large environmental
414 gradients is important for understanding variation in biodiversity, especially given concerns over
415 environmental change and consequent biodiversity loss. Large gradients can reveal patterns that
416 remain hidden in smaller areas. We showed that, across a large environmental and spatial gradient,
417 benthic diatom communities can exhibit a total taxonomic turnover and be controlled by different
418 environmental factors in different parts of the gradient, thus supporting the hypotheses of species'
419 limited ranges and central-marginal theory. Functional turnover remained considerably lower,
420 suggesting that functional characteristics needed for stable ecosystem functioning are fairly similar
421 in very different environments. The minimum diversity occurred at intermediate salinities, which
422 confirmed the validity of the Remane curve and suggested that areas with intermediate salinities are
423 a threshold and a tipping point for biotic communities. This emphasizes the vulnerability and
424 uniqueness of brackish water areas and the need to apply measures to preserve biodiversity in these
425 ecosystems in the course of human-induced climate change.

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602 **Figures**

603 Fig. 1. Our sampling sites and the salinity along the coastline of Sweden, in the Baltic Sea. Salinity
 604 values have been obtained by interpolation from field data. Source of the European coastline
 605 shapefile: European Environmental Agency

606 Fig. 2. Pairwise relationships between taxonomic and functional similarities (Bray-Curtis
 607 dissimilarity index, abundance data) and the salinity gradient. The dashed line denotes linear model
 608 fitted to data.

609 Fig. 3. Relative proportions of functional traits in different salinity categories. Towards low salinity,
610 there was an increase in the relative proportion of large versus small, pedunculate versus mobile,
611 high-profile versus motile, and colonial versus non-colonial diatoms. The relative proportions in
612 salinity preference did not show a clear pattern.

613 Fig. 4. The relationship between taxonomic and functional community composition (described as
614 NMDS1 scores) and salinity.

615 Fig. 5. Species richness of diatom communities along the salinity gradient.

616 Appendix, fig. 1. Relative proportions of diatom species assigned to major taxonomic groups in
617 different salinity categories. Groups that had less than hundred frustules in the whole data, are
618 featured in the combined group of Other.

619 **Data accessibility statement**

620 The data (diatom species table, diatom trait table, environmental data, and R code) supporting the
621 results of this article are available in Dryad Repository (<https://doi.org/10.5061/dryad.bvq83bk6p>).

622 **Tables**

623 Table 1. Results of generalized dissimilarity models (GDM) to explain taxonomic and functional
624 spatial beta diversity. Fetch denotes wind exposure. 0.001 ***, < 0.01 **, < 0.05 *, < 0.1 .

	Diatom species			Diatom traits	
Deviance explained	52.50 %			28.24 %	
Model p-value	< 0.001 ***			< 0.001 ***	
	Importance	p-value		Importance	p-value
Salinity	74.31	< 0.001 ***		73.96	< 0.001 ***
PO ₄ ³⁻	3.12	0.08		1.10	0.40
Fetch	1.13	0.14		0.84	0.30
NO ₂ ⁻ + NO ₃ ⁻	0.89	0.16		0.00	0.98
Water temperature	0.48	0.36		6.46	0.14
Sediment amount	0.41	0.20		2.93E-07	1.00
Vegetation amount	0.20	0.22		0.00	0.92
Stone volume	0.11	0.64		0.74	0.44
Ammonium	0.00	0.98		1.27	0.36
pH	0.00	1.00		0.00	1.00

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Table 2. Results of the distance-based redundancy analyses (dbRDA) to examine the effect of environmental variables on taxonomic and functional community composition in different salinity groups. Only significant variables indicated by the dbRDA are listed. Fetch denotes wind exposure. < 0.001 ***, < 0.01 **, < 0.05 *, < 0.1 .

Salinity < 4							
Taxonomic composition				Functional composition			
Eigenvalues: CAP1: 10.378, CAP2: 0.344				Eigenvalues: CAP1: 0.308, CAP2: 0.238			
Proportion explained: CAP1: 0.187, CAP2: 0.170				Proportion explained: CAP1: 0.359, CAP2: 0.2770			
Model p: 0.001 ***				Model p: 0.011 *			
	<i>SumOfSqs</i>	<i>F</i>	<i>p-value</i>		<i>SumOfSqs</i>	<i>F</i>	<i>p-value</i>
PO ₄ ³⁻	0.284	3.191	0.001 ***	Fetch	0.216	7.416	0.001 ***
NO ₂ ⁻ + NO ₃ ⁻	0.282	3.163	0.001 ***	Stone volume	0.131	4.523	0.007 **
Salinity	0.198	2.227	0.003 **	pH	0.125	4.3	0.009 **
NH ₄ ⁺	0.162	1.813	0.029 *	NO ₂ ⁻ + NO ₃ ⁻	0.07	2.421	0.067 .
Water temperature	0.161	1.805	0.029 *	PO ₄ ³⁻	0.064	2.202	0.087 .
pH	0.141	1.584	0.062 .				
Vegetation amount	0.15	1.685	0.053 .				
Salinity 4-10							
Taxonomic composition				Functional composition			
Eigenvalues: CAP1: 0.533, CAP2: 0.395				Eigenvalues: CAP1: 0.561, CAP2: 0.150			
Proportion explained: CAP1: 0.194, CAP2: 0.144				Proportion explained: CAP1: 0.612, CAP2: 0.163			
Model p: 0.001 ***				Model p: 0.014 *			
	<i>SumOfSqs</i>	<i>F</i>	<i>p-value</i>		<i>SumOfSqs</i>	<i>F</i>	<i>p-value</i>
Fetch	0.329	3.422	0.002 **	PO ₄ ³⁻	0.321	7.311	0.002 **
PO ₄ ³⁻	0.275	2.857	0.002 **	Fetch	0.169	3.856	0.017 *
Sediment amount	0.247	2.576	0.005 **	pH	0.099	2.259	0.083 .
Salinity	0.207	2.151	0.013 *	Salinity	0.098	2.242	0.091 .
Stone volume	0.145	1.506	0.091 .				
Salinity > 10							
Taxonomic composition				Functional composition			
Eigenvalues: CAP1: 0.769, CAP2: 0.517				Eigenvalues: CAP1: 0.760, CAP2: 0.096			
Proportion explained: CAP1: 0.253, CAP2: 0.170				Proportion explained: CAP1: 0.641, CAP2: 0.081			
Model p: 0.001 ***				Model p: 0.025 *			
	<i>SumOfSqs</i>	<i>F</i>	<i>p-value</i>		<i>SumOfSqs</i>	<i>F</i>	<i>p-value</i>
NH ₄ ⁺	0.457	4.27	0.001 ***	Fetch	0.478	13.483	0.001 ***
Water temperature	0.37	3.458	0.001 ***	Stone volume	0.098	2.777	0.096 .
Salinity	0.358	3.352	0.001 ***				
Fetch	0.239	2.24	0.017 *				
Stone volume	0.226	2.116	0.020 *				
NO ₂ ⁻ + NO ₃ ⁻	0.222	2.074	0.023 *				
PO ₄ ³⁻	0.196	1.832	0.050 *				

631   **Appendices**

632   Appendix, table. 1. Results of the temporal beta diversity indices (TBI). TBI denotes the level of
633   change in community composition between two sampling occasions, p-value the significance of the
634   change (values of < 0.05 are considered significant), Change species gain (+) or species loss (-)
635   from the first sampling occasion to the second, SR1 species richness during the first sampling, and
636   SR2 species richness during the second sampling.

	<i>Site 1</i>	<i>Site 2</i>	<i>Site 3</i>	<i>Site 4</i>	<i>Site 5</i>	<i>Site 6</i>
TBI	0.447	0.495	0.558	0.506	0.548	0.425
p-value	0.851	0.489	0.075	0.392	0.120	0.939
Change	+	+	+	-	-	-
SR1	29	35	26	53	49	47
SR2	40	35	28	51	56	65

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