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2022-06-20

Virta , L & Teittinen , A 2022 , ' Threshold effects of climate change on benthic diatom communities: Evaluating impacts of salinity and wind disturbance on functional traits and benthic biomass ' , Science of the Total Environment , vol. 826 , 154130 . https://doi.org/10.1016/j.scitotenv.2022.15

http://hdl.handle.net/10138/341839
https://doi.org/10.1016/j.scitotenv.2022.154130

Science of the Total Environment 826 (2022) 154130

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Threshold effects of climate change on benthic diatom communities: Evaluating impacts of salinity and wind disturbance on functional traits and benthic biomass

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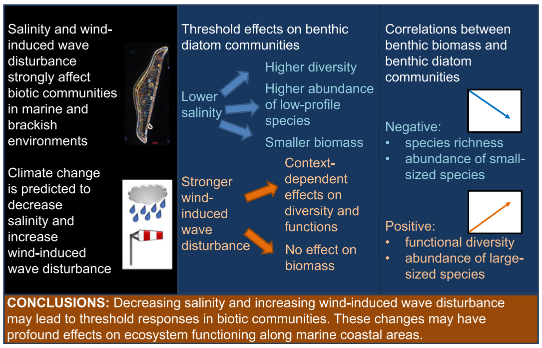
HIGHLIGHTS

- Climate change decreases salinity and increases wind disturbance in coastal areas.
- Decreasing salinity will increase diatom diversity but decrease productivity.
- Increasing wind disturbance will have context-dependent consequences.
- The abundance of the most resilient (low-profile) diatoms will change.
- Functional diversity and body size of diatoms affect benthic biomass.

GRAPHICAL ABSTRACT



CONCLUSIONS: Decreasing salinity and increasing wind-induced wave disturbance may lead to threshold responses in biotic communities. These changes may have profound effects on ecosystem functioning along marine coastal areas.

ARTICLE INFO

Article history:
Received 4 January 2022
Received in revised form 21 February 2022
Accepted 21 February 2022
Available online 25 February 2022

Editor: Sergi Sabater

Keywords:
Baltic Sea
Brackish
Ecosystem functioning
Low-profile guild
Rock pools
Coastal

ABSTRACT

The responses of biotic communities and ecosystems to climate change may be abrupt and non-linear. Thus, resolving ecological threshold mechanisms is crucial for understanding the consequences of climate change and for improving environmental management. Here, we present a study on the threshold responses of benthic diatom communities that are an important component of all aquatic environments and strongly contribute to global primary production. We reach beyond the taxonomic perspective by focusing on the diversity and functions of diatom communities and benthic biomass along gradients of salinity and wind disturbance, whose climate-change-induced changes have been predicted to strongly affect biotic communities in the marine and brackish systems in the future. To improve the generality of our results, we examine three self-collected datasets from different spatial scales (6–830 km) and ecosystem types. We collected samples from rock pools or from littoral stones and studied taxonomic thresholds using Threshold Indicator Taxa Analysis (TITAN2). We investigated threshold responses of community diversity, community functions, and benthic biomass using *t*-tests and regression analyses. Our results indicated that decreasing salinity may result in increasing diversity but decreasing biomass of brackish communities, while the effects of increasing wind disturbance were contradictory among spatial scales. Benthic biomass correlated with the taxonomic and functional diversity, as well as with the body size distribution of communities, highlighting the importance of considering community functions and organismal size when predicting ecosystem functions. The most pronounced effects of decreasing salinity and increasing wind disturbance on community functions were changes in the abundance of low-profile diatom species, which, due to the high resilience of low-profile diatoms, may lead to changes in ecosystem functioning and resilience. To conclude, decreasing salinity and increasing wind disturbance may lead to threshold responses of biotic communities, and these changes may have profound effects on ecosystem functioning along marine coastal areas.

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http://dx.doi.org/10.1016/j.scitotenv.2022.154130

1. Introduction

The rate and complexity of the human-induced climatic change, which is currently affecting all ecosystems, generate fundamental questions on how biological communities and ecosystems will respond to novel conditions. Due to the tendency of environmental change to push ecological systems across thresholds, the responses of communities and ecosystems may be non-linear, abrupt and unexpected (André et al., 2010). Thus, resolving ecological threshold mechanisms along gradients of climate-change-related environmental variables is crucial for improving our ability to predict changes, to manage the environments effectively, and to cope with the inevitable consequences of environmental change. Here, we aim at resolving the threshold responses of benthic diatom communities, their functions and benthic biomass along gradients of salinity and wind-induced disturbance in the Baltic Sea coastal regions.

Ecological thresholds can be described as abrupt changes in biological communities, which lead to the restructuring of the ecosystem, i.e., the system undergoing a regime shift between alternative states (Scheffer et al., 2001). Possible community changes underlying regime shifts include, e.g., modifications of species diversity (Chust et al., 2022), food web interactions (Banerjee et al., 2021) or foundation species' composition (Álvarez-Losada et al., 2020), or the loss of species or habitats. Consequently, the functioning and resilience of the ecosystems may fundamentally change (Delong et al., 2021), which may affect the services that the ecosystems provide to humans. Regime shifts can occur naturally, but are usually driven by anthropogenic disturbances, such as climate change or eutrophication. Shifts between alternative states can happen after stochastic events, such as weather extremes, but they can even occur when changes in the external driving forces are gradual, which impedes predicting the ecological thresholds (Scheffer et al., 2001; Kéfi et al., 2013).

Depending on the nature of the driving force and internal properties of the system, regime shifts can be either reversible or irreversible (Andersen et al., 2009). A shift caused by gradual external changes is bound to be a permanent shift between alternative states, whereas in a resilient system a regime shift caused by a stochastic event, such as a storm, may be temporary. However, gradual changes in external forces may decrease the resilience and, hence, make the system more fragile for permanent regime shifts also by stochastic events (Scheffer et al., 2001). In the marine and brackish realm, decreasing salinity and increasing wind and wave disturbance have been predicted to be among the most prominent gradual and stochastic effects of climate change on biotic communities (IPCC, 2021). In many coastal regions around the globe, salinity is predicted to gradually decrease due to increased precipitation (The BACC II Author Team, 2015). Wind-induced disturbance is expected to increase and affect coastal ecosystems via gradually increasing wind-speeds and higher waves, and more frequent and severe stochastic storm events (IPCC, 2021). However, so far studies on the threshold mechanisms have focused on, e.g., the effects of increasing temperature (Wilmking et al., 2004; Cavanaugh et al., 2014), pollution (Wooldridge, 2009), over exploitation (Mumby et al., 2007), and hypoxia (Conley et al., 2009), while the effects of changes in salinity and wind disturbance on ecosystem thresholds are still poorly known (but see Scherner et al., 2013; Isabel et al., 2021).

Ecosystems are particularly vulnerable to threshold responses and regime shifts in systems, where the foundation species are already close to environmental tipping points (Cavanaugh et al., 2014). The Baltic Sea is a good example of such a system, because the brackish salinity gradient of ~0 to ~9 limits the distribution of both freshwater and marine species and, thus, results in abrupt spatial changes in biotic communities along the gradient (Herlemann et al., 2011). In the Baltic Sea, as well as in other coastal ecosystems, diatoms are one of the most important components of microphytobenthic communities (Watermann et al., 1999) that are key players for all ecosystem functions. Microphytobenthic communities, including diatoms, drive biogeochemical processes that are responsible for element cycling, provide good-quality nutrition for higher trophic levels, and participate in habitat formation (Sundbäck et al., 2006; Fricke et al., 2017). Thus, climate-change-driven abrupt changes in benthic diatom communities would affect the entire Baltic Sea ecosystem.

While theories on threshold responses in ecosystems have gained increasing traction during the last decades (e.g. Liu et al., 2013; Nalley et al., 2021), empirical studies of community thresholds have often been executed on small spatial scales, or focused only on the taxonomic composition of communities. To improve the generality of our results on ecological thresholds, we analyze three self-collected datasets that cover different spatial scales (6–830 km) but have nearly identical salinity gradients. By using multiple spatial scales for testing the same drivers, we demonstrate possible temporal climate-change-induced threshold responses (Hillebrand et al., 2020). We also reach beyond the taxonomic composition of communities by focusing on thresholds in benthic biomass and functional traits that are robust indicators of environmental conditions (Westoby et al., 2002). Our specific hypotheses are: (H_1) salinity and wind disturbance significantly affect the composition of diatom communities, and diatom communities on different spatial scales exhibit taxonomic thresholds at similar values of salinity or wind disturbance; (H_2) taxonomic thresholds lead to similar regime shifts in community functions on different spatial scales; and (H_3) taxonomic thresholds lead to regime shifts in benthic biomass, and differences in biomass are connected to changes in community diversity or functions.

2. Methods

2.1. Study area and sampling

We collected samples from three different spatial scales with homologous salinity gradients of ca. 0–1 to 6–7. On the small spatial scale (ca. 6 km), samples were collected from rock pools in the archipelago of Hanko and Tammisaari, in south-western Finland (Fig. A.1). The rock pools were situated on 10 different islands, and on each island, the habitats formed a gradient from sheltered interior parts to exposed parts close to the sea. On the medium spatial scale (ca. 43 km), samples were collected from littoral rocks along a gradient from Pojo Bay estuary to Hanko archipelago and finally open sea in south-western Finland (Fig. A.1). Pojo Bay is a fjord-like estuary that transforms to a complex and shallow (< 40 m) archipelago, and finally to the open Gulf of Finland. Owing to the river Karjaanjoki discharging to Pojo Bay, the salinity in this area follows a north-south gradient. On the large spatial scale (ca. 830 km), samples were collected from littoral rocks along the Swedish coastline, from the area between northern Bothnian Bay and northern Baltic Proper (Fig. A.1). Due to restricted water exchange between the Baltic Sea and the North Sea, and rivers discharging to the northern Baltic Sea, salinity in this area follows a north-south gradient. On all three spatial scales, the salinity gradient leads to biotic communities transforming from freshwater-species-dominated to brackish/marine-species-dominated.

The small scale sampling was conducted on 16 September-2 October 2018. We collected diatom samples from 91 rock pools. We also measured salinity, water temperature and pH in situ, measured pool dimensions (length×width×depth) that were later used for calculating the volume of each pool, measured each pool's shortest distance to sea shore, and collected water samples for further nutrient analyses. The medium scale sampling was conducted on 26 June-4 July 2017. We collected diatom samples from 46 littoral sites, measured salinity, water temperature and pH in situ, measured the dimensions (length×width×height) of each sampling stone, and collected water samples for further nutrient analyses. We also collected chlorophyll *a* (Chl *a*) samples by scraping the surfaces (25 cm^2) of two sampling stones with a brush, and pooled the accumulated material into composite samples that were stored in filtered seawater in brown bottles and dark conditions. We used Chl *a* concentration as a measure of benthic biomass (Kromkamp and Peene, 2005). The large scale sampling was conducted on 9–24 August 2018. We collected 29 diatom samples from littoral stones, and also measured salinity, water temperature and pH in situ, measured the dimensions of each sampling stone, collected water samples for further nutrient analyses, and evaluated habitat characteristics by classifying the bottom type according to the amount of sediment (classes 1–3) and the amount of macroalgae or vegetation on stones (classes 1–3). We also collected Chl *a* samples following the same method as in medium scale sampling.

Along all spatial scales, diatom sampling followed the recommendations by Kelly et al. (1998). We collected ten samples from the submerged bedrock surface of the rock pools (small spatial scale) or ten (medium spatial scale)/20 (large spatial scale) samples from stones that were randomly collected from depths of 20–50 cm along the shoreline. The biofilm was collected by scraping the surfaces of rock or stones with a toothbrush or a sponge (100 cm^2 per spot on the small spatial scale sampling and 25 cm^2 per stone on the medium and large spatial scales). We pooled the accumulated suspensions into composite samples, which were stored in cold (+4 °C) and dark until further analyses. More detailed descriptions of study sites and sampling can be found in Teittinen & Virta (2021; small spatial scale), Virta et al. (2021; medium spatial scale), Virta et al. (2020a; large spatial scale), and Virta et al. (2020b; data for large spatial scale).

2.2. Diatom species and trait analyses, laboratory analyses, and wind exposure calculations

To investigate the taxonomic composition of diatom communities, we boiled the samples with hydrogen peroxide (30% H_2O_2) to remove organic material, mounted cleaned diatoms on slides using Naphrax (Brunel Microscopes, Chippenham, UK), and used a phase contrast light microscope with ×1000 magnification to identify ~500 valves per sample to the lowest possible taxonomic level (typically species level). Species identification followed Krammer & Lange-Bertalot (1986, 1988, 1991a, and 1991b), Snoeijs (1993), Snoeijs and Kasperovicienè (1996), Snoeijs and Potapova (1995), Snoeijs and Vilbaste (1994), Witkowski (2000), and Lange-Bertalot et al. (2017). Taxonomic names were verified according to AlgaeBase (Guiry and Guiry, 2021).

We investigated the functional composition of communities by using abundances of traits that indicate morphological characteristics of species and are related to ecosystem functioning. Each diatom species was classified according to their size (biovolume classes: large >1000 μm^3/small <1000 μm^3), mobility (mobile [species with raphe]/non-mobile [species without raphe]), type of attachment (non-attached/adnate/pedunculate, which was further divided to pad-attached/stalk-attached), ability to form colonies (colonial/non-colonial), guild (low-profile/high-profile/motile/planktonic, Rimet and Bouchez, 2012), and nitrogen-fixing abilities (nitrogen-fixer/non-nitrogen-fixer, Passy, 2007). For diatom trait identification, we used above-mentioned species literature, and Diatoms of North America (2021), and Snoeijs et al. (2002).

In the laboratory, water samples collected from the small spatial scale were used for the analyses of total phosphorus (TP) and total nitrogen (TN), and analyzed according to SFS-EN ISO 6878 (TP) and SFS-EN ISO 11 905-1 (TN) with Hach-Lange DR 5000 spectrometer. Water samples from the medium spatial scale were used for the analyses of TP, TN, $NO_2^- + NO_3^-$, NH_4^+, PO_4^{3-}, and Si, and water samples from the large spatial scale for the analyses of $NO_2^- + NO_3^-$, NH_4^+, PO_4^{3-}, and Si. Analyses of the medium and large spatial scale samples were conducted with an automated photometric analyzer (Thermo Scientific Aquakem 250; Thermo Fisher Scientific Oy, Vantaa, Finland; TP, $NO_2^- + NO_3^-$, PO_4^{3-}, and Si) or manually (TN, NH_4^+). Chl *a* samples (medium and large spatial scales) were filtered on Whatman GF/F filters and analyzed with a fluorescence spectrophotometer.

In the sea, wind-induced waves constitute a major disturbance to biotic communities. As a proxy for the wave disturbance, we used wind exposure, which was calculated as fetch, i.e., the distance over which wind can travel over open water. We calculated fetch for each sampling site on the medium and large spatial scales. The fetch was measured as the average of distances from the exact study site to the closest shore, island or islet along 36 (large spatial scale) or 40 (medium spatial scale) lines that were 9° (medium spatial scale) or 10° (large spatial scale) apart from each other (Mason et al., 2018). The calculations were conducted with a transparent circular disc and sea charts (medium spatial scale) or the ruler tool in Google Earth (Google; large spatial scale). The small spatial scale sites were excluded from fetch calculations, because the sampled rock pools were not connected to the sea by permanent watercourses and, hence, the effect of wind on biotic communities was different and not directly comparable to the effect of wind on medium and large spatial scales.

2.3. Statistical analyses

Before statistical analyses, we assessed the statistical dependence between salinity and wind exposure on medium and large spatial scales using Spearman's rank correlations (r_s). Both correlations were low ($<|0.7|$) and, thus, both variables were included in further analyses.

To investigate if salinity and wind exposure significantly affect the community composition on different spatial scales, we used distance-based redundancy analyses (dbRDAs) with Bray-Curtis distance (Bray and Curtis, 1957). We constructed three different models, one for each spatial scale, and included all measured environmental variables, except highly correlated ($r_s > |0.7|$) variables (small spatial scale: TN that correlated with TP; medium spatial scale: temperature that correlated with salinity, and TP that correlated with TN and PO_4^{3-}; large spatial scale: Si that correlated with salinity). Prior to the dbRDAs, we $\log_{10}$-transformed several environmental variables (small spatial scale: salinity, TP, pool volume, distance to sea; medium spatial scale: salinity, wind exposure, TN, $NO_2^- + NO_3^-$, NH_4^+, PO_4^{3-}, and Si; large spatial scale: salinity, wind exposure, $NO_2^- + NO_3^-$, NH_4^+, PO_4^{3-} and stone volume) to reduce their skewed distributions, and Hellinger-transformed the taxonomic data. We performed the dbRDAs with R package vegan using function *capscale* (Oksanen et al., 2020).

Next, we analyzed taxonomic threshold points along gradients of salinity and wind exposure using Threshold Indicator Taxa Analysis with R package TITAN2 using function *titan*() (Baker et al., 2020). The functioning of TITAN2 package is illustrated in Fig. 1. Shortly, this method examines all species that are present at ≥3 sites and detects ecological threshold values for entire biotic communities and individual species along a gradient of a single environmental variable, in our case salinity or wind exposure. The method calculates IndVal scores (Dufrêne and Legendre, 1997) for individual species based on their abundance and frequency, and then finds the optimal change point for the species by partitioning the dataset and calculating two IndVal values, one for samples below the potential splitpoint and the other for samples above the splitpoint. The relative strength of the IndVal scores on different sides of the potential change point indicates either a negative or a positive species response to the environmental gradient. We ran the analysis separately for each spatial scale, the salinity analysis on all three spatial scales and the wind exposure analysis on medium and large spatial scales.

Along the environmental gradient, the Threshold Indicator Taxa Analysis calculates taxonomic threshold points separately with species with a negative response (sumz-) and species with a positive response (sumz+) to the current environmental variable. In order to investigate possible changes in community diversity and functions or benthic biomass on different sides of the taxonomic threshold point, we divided the sampling sites to two groups by using the average value of sumz- and sumz+. For this, we used the filtered versions (fsumz- and fsumz+), because filtering computes the sum(z) scores using only taxa that are determined to be pure and reliable indicators (Baker and King, 2010). Cut-off values that defined what were considered as a pure response direction and a reliable response magnitude were 0.95.

We then computed *t*-tests to investigate, whether the community diversity (species richness, taxonomic Shannon's diversity, functional Shannon's diversity, taxonomic Pielou's evenness, functional Pielou's evenness), community functions (diatom functional traits: small-sized, large-sized, mobile, colonial, nitrogen-fixer, high-profile, low-profile, motile), or benthic biomass (Chl *a*) were different on different sides of the taxonomic threshold points along different spatial scales. *t*-tests with *p*-values <0.05 were considered to indicate significant differences.

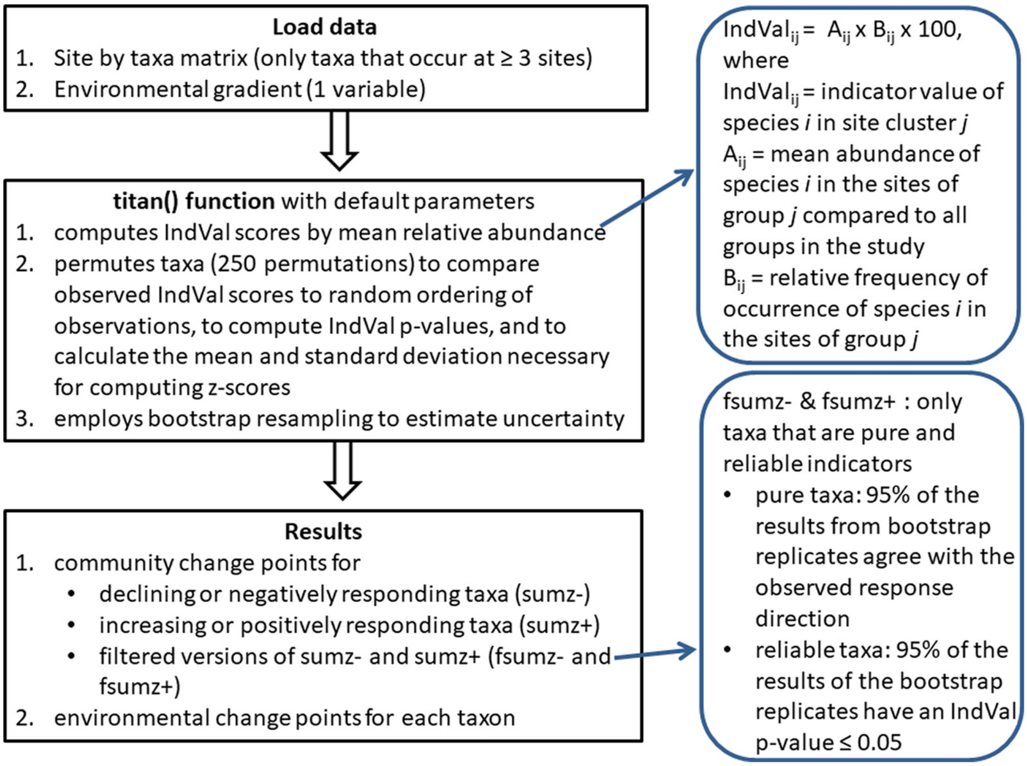

Fig. 1. Illustration of the functioning of TITAN2 package to analyze taxonomic threshold points. Black boxes represent the required steps from loading the appropriate data to using the *titan*() function and interpreting the results. Blue boxes contain explanations of terms used in the package.

On the salinity gradient of the medium spatial scale, Chl *a* concentrations were found to significantly differ between different sides of the taxonomic threshold point. To find possible connections between benthic biomass and diatom communities below and above the taxonomic threshold point, we studied correlations between Chl *a* and community diversity (species richness, taxonomic Shannon's diversity, functional Shannon's diversity, taxonomic Pielou's evenness, functional Pielou's evenness) and community functions (diatom functional traits: small-sized, large-sized, mobile, colonial, nitrogen-fixer, high-profile, low-profile, motile) using Spearman's rank correlations (r_s). Significant correlations ($p < 0.05$) were visualized with R package ggplot2 (Wickham et al., 2021) using functions *geom_point* and *geom_smooth*.

All statistical analyses were conducted using R version 4.1.1 (R Core Team, 2021).

3. Results

Salinity varied between 0.01 and 6.96 on the small spatial scale, between 0.1 and 6.1 on the medium spatial scale, and between 1.23 and 6.12 on the large spatial scale (Table 1). Wind exposure varied between 0 and 47,427 on the medium spatial scale, and between 20 and 35,442 (with one exceptionally high value 1,214,603 on one study site) on the large spatial scale.

Salinity was the most significant environmental variable for explaining taxonomic community composition on all spatial scales (Table A.1). Wind exposure was also significant on medium and large spatial scales. On the small spatial scale, other significant ($p < 0.05$) environmental variables were distance to sea, water temperature, pH and total P. On the medium spatial scale, other significant ($p < 0.05$) environmental variables were total N and $NO_2^- + NO_3^-$. On the large spatial scale, other significant ($p < 0.05$) environmental variables were $NO_2^- + NO_3^-$, NH_4^+ and PO_4^{3-}. All measured environmental variables together explained 25.15%, 46.85% and 62.75% of variation in taxonomic community composition on small, medium and large spatial scales, respectively.

Taxonomic threshold points were effectively found along all considered gradients, i.e., salinity gradients on small, medium and large spatial scales, and wind exposure gradients on medium and large spatial scales. Along the salinity gradient, the taxonomic threshold points of declining or negatively responding filtered taxa (fsumz-) occurred at salinities 2.17, 3.35 and 3.98, and the taxonomic threshold points of increasing or positively responding filtered taxa (fsumz+) at salinities 2.98, 3.35 and 3.98 on the small, medium and large spatial scales, respectively. Average taxonomic threshold points, calculated as the average of fsumz- and fsumz+, occurred at salinities 2.57, 3.35 and 3.98 on small, medium and large spatial scales, respectively. Along the wind exposure gradient, the taxonomic threshold points of declining or negatively responding filtered taxa (fsumz-) occurred at wind exposure indices 1072.50 and 210.69, and the taxonomic threshold points of increasing or positively responding filtered taxa (fsumz+) at wind exposure indices 1233.75 and 3074.86 on the medium and large spatial scales, respectively. Average taxonomic threshold points occurred at wind exposure indices 1153.13 and 1642.78 on medium and large spatial scales, respectively.

Table. 1
Mean, minimum and maximum values of salinity at the sampling sites of all spatial scales, and mean, minimum and maximum values of fetch (wind exposure) at the sampling sites of medium and large spatial scales.

	Small spatial scale	Medium spatial scale	Large spatial scale
	Mean (min - max)	Mean (min - max)	Mean (min - max)
Salinity (psu)	4.24 (0.01–6.96)	3.9 (0.1–6.1)	3.88 (1.23–6.12)
Fetch (index)	NA	3024.1 (0–47,426.8)	48,005.3 (20.6–1,214,602.8)

Along salinity gradients, 30, 46, and 36 species were found as pure and reliable indicator species on the small, medium and large spatial scales, respectively (Fig. A.2). Along wind exposure gradients, 33 and 15 species were found as pure and reliable indicator species on medium and large spatial scales, respectively. Taxa that were found as common indicator species for two or three different spatial scales are listed in Table 2. Other indicator species were different among spatial scales.

t-tests indicated that several measures of community diversity and functions were significantly different on different sides of taxonomic threshold points along gradients of salinity and wind exposure on different spatial scales (Table 3). Species richness was higher in low salinity and low wind exposure on several different gradients. Other diversity measures (Shannon's diversity and Pielou's evenness) were also often higher in low salinity and low wind exposure, except on large spatial scale, where functional diversity and evenness were higher in high wind exposure. Low-profile diatoms were more abundant in low salinity and low wind exposure, except on the large spatial scale, where they were more abundant in high wind exposure. Several traits were significantly different on different sides of the taxonomic threshold point along the salinity gradient of the small spatial scale. Benthic biomass (Chl *a*) was higher in high salinity on the medium spatial scale.

The *t*-test showed that Chl *a* concentration was significantly different on different sides of the taxonomic threshold point along the salinity gradient of the medium spatial scale. Along this spatial scale, Chl *a* correlated significantly negatively with species richness at sites with lower salinity, significantly positively with functional Shannon's diversity and the abundance of large-sized diatoms at sites with higher salinity, and significantly negatively with the abundance of small-sized diatoms at sites with higher salinity (Fig. 2). Correlations between Chl *a* and other variables of community diversity or community functions were non-significant.

4. Discussion

We investigated the threshold responses of benthic diatom communities and benthic biomass to changes in salinity and wind disturbance that have been predicted to change in marine and brackish systems along the climatic change. To the best of our knowledge, this is one of the first studies to investigate ecosystem thresholds along gradients of salinity or wind disturbance, or to examine several spatial scales in an attempt to find general patterns in community thresholds.

4.1. Community thresholds along gradients of salinity and wind disturbance on different spatial scales (H_1)

As hypothesized (Westerbom et al., 2019a), salinity was the most important environmental variable to explain the composition of communities on all spatial scales. Salinity is an environmental master factor, because organisms' reproduction, behavior, recruitment and, hence, geographical distribution are dictated by salinity (Smyth and Elliot, 2016). The effect of salinity is particularly pronounced in nearshore marine areas, like the Baltic Sea, which experience spatial and temporal salinity variations. In our datasets, communities changed from freshwater-dominated to brackish-dominated species at salinities of 2.6–4.0, depending on the spatial scale. Thus, the taxonomic threshold points along salinity gradients were fairly similar on different spatial scales, which confirmed our hypothesis. This result agrees with Herlemann et al. (2011), who found freshwater bacterial species inhabiting salinities 0–3, but somewhat differs from some other investigations on the biotic communities of the Baltic Sea that have found salinities 4.5–6.5 to be cut-off values for the distribution and turnover of different macro-organisms (Westerbom et al., 2002; Avellan et al., 2013). Thus, taxonomic thresholds along the salinity gradient may be dependent on the size and type of organisms.

Table 2

Taxa that were found as common indicator species among spatial scales.

Salinity gradient

	Small spatial scale	Medium spatial scale	Large spatial scale
Negatively responding taxa			
Achnanthes oblongella Østrup		x	x
Achnantidium minutissimum (Kützing) Czarnecki	x	x	x
Amphora pediculus (Kützing) Grunow		x	x
Cocconeis placentula Ehrenberg	x	x	
Encyonema silesiacum (Bleisch) D.G.Mann		x	x
Fragilaria capucina Desmazières		x	x
Fragilaria exigua Grunow	x		x
Fragilaria vaucheriae (Kützing) J.B.Petersen		x	x
Gomphonema parvulum (Kützing) Kützing	x	x	
Navicula gregaria Donkin	x	x	x
Nitzschia valdestriata Aleem & Hustedt		x	x
Planothidium delicatulum (Kützing) Round & Bukhtiyarova		x	x
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot		x	x
Pseudostaurosira brevistriata (Grunow) D.M.Williams & Round		x	x
Positively responding taxa			
Amphora micrometra M.H.Giffen	x	x	
Cyclotella choctawhatcheeana Prasad	x		x
Halamphora cf. *tenerrima* (Aleem & Hustedt) Levkov	x	x	
Navicula perminuta Grunow	x	x	x
Tabularia fasciculata (C.Agardh) D.M.Williams & Round	x	x	

Wind exposure gradient

	Small spatial scale	Medium spatial scale	Large spatial scale
Negatively responding taxa			
Bacillaria paxillifera (O.F.Müller) T.Marsson	NA	x	x
Karayevia ploenensis (Hustedt) Bukhtiyarova	NA	x	x
Pseudostaurosira elliptica (Schumann) Edlund, Morales & Spaulding	NA	x	x
Positively responding taxa			
Diatoma moniliformis (Kützing) D.M.Williams	NA	x	x
Encyonema silesiacum (Bleisch) D.G.Mann	NA	x	x
Gomphonema olivaceum (Hornemann) Ehrenberg	NA	x	x

Table 3

Results of *t*-tests to compare community diversity, community functions, and benthic biomass on different sides of the taxonomic threshold points along gradients of salinity and wind exposure on different spatial scales. Significant ($p < 0.05$) results are bolded. Positive values indicate higher average values below the taxonomic threshold point, i.e. in low salinity or low wind exposure, and negative values indicate higher average values above the taxonomic threshold point, i.e. in high salinity or high wind exposure.

	Salinity			Wind exposure	
	Small spatial scale	Medium spatial scale	Large spatial scale	Medium spatial scale	Large spatial scale
Community diversity					
Species richness	1.172	**3.437**	**6.127**	**7.193**	−0.783
Taxonomic Shannon's diversity	0.163	2.012	**3.461**	**4.833**	−0.496
Functional Shannon's diversity	−0.973	1.759	1.722	**2.924**	**−2.413**
Taxonomic Pielou's evenness	0.041	1.515	1.676	**3.685**	−0.078
Functional Pielou's evenness	−0.665	1.373	1.986	**2.264**	**−2.563**
Community functions (traits)					
Small-sized	−1.057	1.812	0.215	0.679	−0.077
Large-sized	1.057	−1.678	−0.105	−0.784	−0.116
Mobile	**4.606**	0.626	0.085	0.738	−0.914
Colonial	**−4.283**	1.481	0.664	1.698	0.567
Nitrogen-fixer	0.156	−1.753	−1.793	1.070	−1.668
High-profile	**−2.241**	−1.478	1.068	−1.455	0.204
Low-profile	**3.292**	**3.590**	**2.898**	**3.829**	**−2.452**
Motile	−0.531	−1.063	**−2.586**	−0.442	1.126
Benthic biomass					
Chl *a*	NA	**−2.287**	0.122	−0.785	0.928

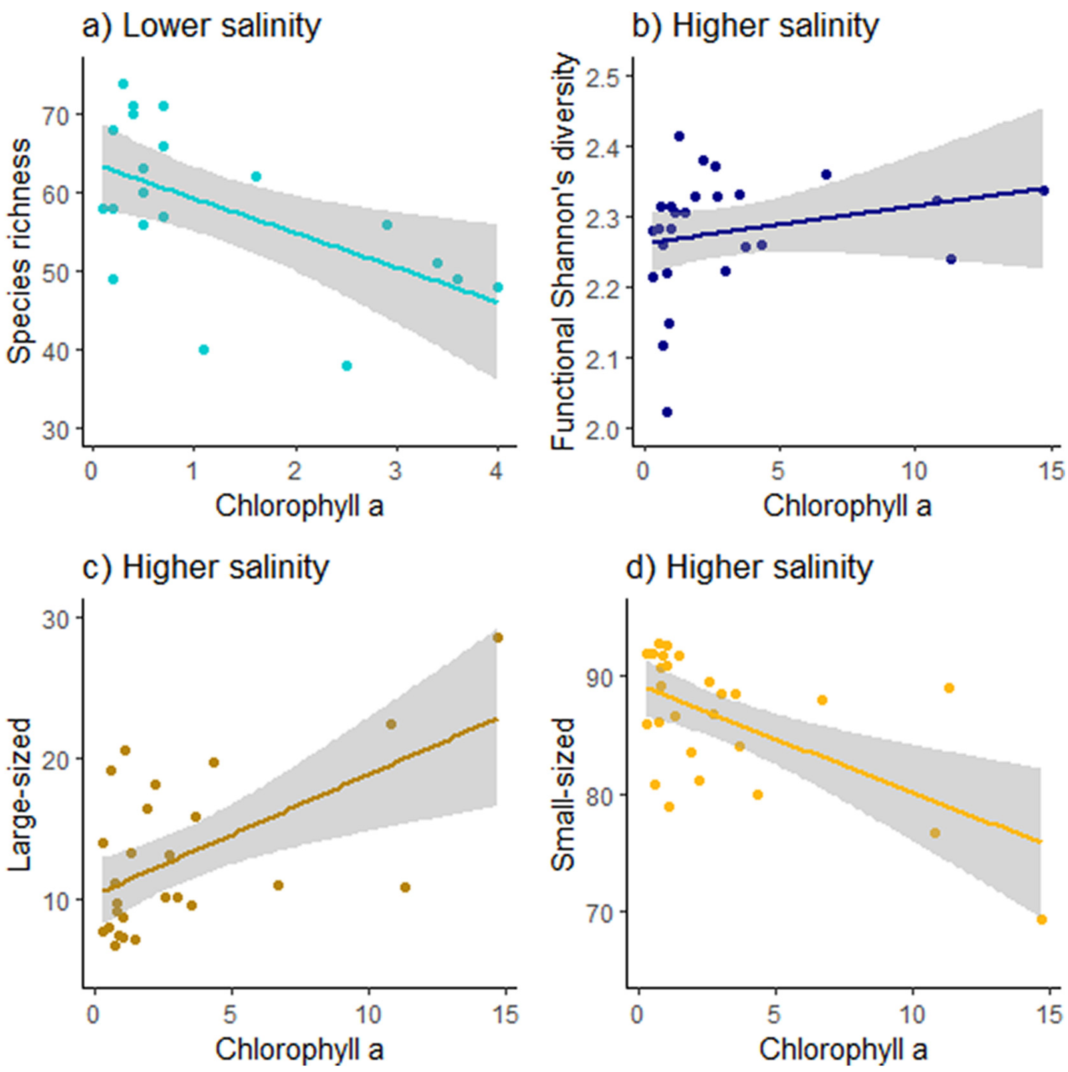

Fig. 2. Significant correlations between Chl *a* and different variables of community diversity and community functions below (panel a) and above (panels b–d) the taxonomic threshold point along the salinity gradient of the medium spatial scale.

As hypothesized (Busse and Snoeijs, 2003; Westerbom et al., 2019b), the effect of wind disturbance was also very significant on the community composition on medium and large spatial scales, where samples were collected from littoral stones. The communities changed from species favoring sheltered conditions to species favoring exposed conditions at fairly similar wind exposure of 1153–1643, which confirmed our hypotheses. Sampling sites below the threshold were typically sheltered by peninsulas, islands or breakwaters and had very little or no direct access for waves from the open sea, whereas sampling sites above the threshold were exposed shores with direct access for open sea waves. Wind disturbance thresholds at intermediate wind disturbance have also been found for the distribution of other aquatic organisms, such as flounder (Florin et al., 2009).

4.2. The effect of taxonomic threshold points on the taxonomic, functional and diversity regimes of communities (H_2)

4.2.1. Taxonomic regimes

Indicator species for salinity gradients were more abundant, 30–46 per spatial scale, than indicator species for wind disturbance gradients, 15–33 per spatial scale, which reflects the stronger effect of salinity for the composition of diatom communities. Only a small percentage of indicator species were common to different spatial scales. This may be because species compositions in different sampling areas were different due to limited dispersal (Hajek et al., 2011) or other underlying environmental factors such as nutrients (Kafouris et al., 2019), or because species respond to environmental factors, such as salinity and wind disturbance, in different ways depending on the environment (Potapova and Charles, 2002). For investigating the taxonomic composition of communities, we used microscopy, which is a traditional, accurate (Rivera et al., 2018) and still widely used method for analyzing benthic diatom samples. However, molecular approaches, especially DNA metabarcoding, are already gaining ground in benthic diatom studies and are likely to be the dominating method for diatom identification in the future. Such molecular approaches, provided that the DNA reference libraries are encompassing, will make diatom identification considerably less time-consuming and, in the case of cryptic diatom taxa, more accurate. Thus, molecular approaches may also have an impact on the results of studies concerning the diversity of diatoms.

4.2.2. Diversity regimes

Our hypothesis was partly confirmed, as different spatial scales shared some differences in diversity regimes. On medium and large spatial scales, diversity of communities was higher in low salinity, which suggests that the diversity of communities may increase with climate-change-induced decreasing salinity. This agrees with the so-called Remane curve (Remane, 1934) that suggests minimal species richness at intermediate salinities of ca. 5–8, because neither freshwater nor marine species are able to tolerate such salinities. During the last decades, the Remane concept has been repeatedly revisited by different studies, some of which have found support for the Remane curve (e.g. Olli et al., 2019 with phytoplankton; Virta et al., 2020a with benthic diatoms), while others have found opposite results (e.g. Telesh et al., 2011 and Telesh et al., 2013 with phyto- and zooplankton; Schubert et al., 2011 with macroalgae). Thus, it seems that the diversity distribution of different organisms along the salinity gradient from freshwater to marine water is variable and context-dependent. On the small spatial scale where samples were collected from rock pools, the taxonomic threshold point on the salinity gradient failed to lead to a regime shift in diversity. This may be due to other factors, such as dispersal barriers, controlling diversity in these systems (Teittinen et al., 2021). Wind disturbance had controversial effects on the diversity of communities. On the medium spatial scale, communities were taxonomically and functionally more diverse on sampling sites with lower wind disturbance, whereas on the large spatial scale, higher wind disturbance led to higher functional diversity. Such a controversial effect of wind may be due to versatile effects of wind and waves on communities. In the fetch-limited and practically tideless coastal archipelago of the Baltic Sea, local wind is the main cause for waves and sea level fluctuations (Suursaar et al., 2012), and waves induced by wind can have a strong effect on biotic communities. Thus, because waves can decrease the diversity of communities of sessile or slow-moving organisms, such as diatoms, by detaching them from the substratum, wind can have an indirect negative effect on diversity. However, in the strongly stratified Baltic Sea, local winds are also the primary source for surface currents (Delpeche-Ellmann et al., 2021) that can re-distribute slow-moving organisms, such as benthic diatoms. Hence, wind can also positively affect diversity by facilitating distribution (Bowman and Deming, 2017). Furthermore, the direct impact of wind and waves on diatoms can be mitigated by the facilitating effect of other organisms, such as macroalgae (Westerbom et al., 2019b). Thus, the effects of climate-change-induced increased wind disturbance on communities may be context-dependent and, hence, difficult to predict.

4.2.3. Functional regimes

In the light of previous research (Snoeijs et al., 2002; Passy, 2007), surprisingly few functional traits showed regime shifts at the taxonomic threshold points along gradients of salinity or wind disturbance. However, our hypothesis of similar functional regimes across spatial scales was confirmed, as the abundance of low-profile diatoms showed a significant regime shift at the taxonomic threshold point along all salinity and wind disturbance gradients. To our knowledge, this is the first study to show such regime shifts for low-profile diatoms along environmental gradients. It is an important finding, because due to low-profile diatoms' ability to cope in high-disturbance and nutrient-poor environments where other benthic diatoms fail to survive (Passy, 2007), variation in the abundance of low-profile diatoms can affect the resilience and stability of the ecosystem. The small spatial scale, i.e. rock pools, showed functional regime shifts also in the abundance of colonial, high-profile and mobile diatoms and, thus, differed from the functional regime shifts of medium and large spatial scales. Such functional regime shifts on the small spatial scale may be due to restricted dispersal among rock pools, differing dispersal abilities of different functional groups, and the harsh and varying environmental conditions that rock pool organisms encounter (Passy, 2007; Altermatt et al., 2009; Neustupa et al., 2013).

4.3. The effect of taxonomic threshold points on regimes of benthic biomass, and relationships between benthic biomass and community characteristics (H_3)

Benthic biomass showed a regime shift, i.e. larger biomass in higher salinity, at the taxonomic threshold point along the salinity gradient of the medium spatial scale. As the climate change has been predicted to decrease salinity in coastal areas, this may possibly indicate smaller microphytobenthic biomass in the future. Salinity can affect biomass directly by affecting, for example, nutrient concentrations in the water. For example, sulfate, which is a major component of marine salt, increases phosphorus in the water column by mitigating iron sequestering and, thus, by weakening the removal of phosphorus (Blomqvist et al., 2004). Salinity can also affect biomass indirectly via, for example, biotic interactions. Along the salinity gradient of our sampling areas, the species richness and abundance of grazers were likely greater in low salinity areas (Remane, 1934), which may have resulted in larger diatom biomass towards higher salinity.

Below the taxonomic threshold point of the salinity gradient along the medium spatial scale, benthic biomass correlated negatively with species richness, i.e., communities with lowest number of diatom species contained the highest amount of Chl *a*. Possible reasons for such a negative diversity-ecosystem functioning relationship include, e.g., highly productive species in species-poor communities (Aarssen, 1997), negative biotic interactions, such as growth inhibition which is a common mechanism in aquatic systems and reduces the performance of keystone species (Leflaive and Ten-Hage, 2007), or low genetic diversity of dominant species in species-rich communities (Crawford and Rudgers, 2012). Although diatoms often dominate in cold and temperate waters (Watermann et al., 1999), other autotrophic organisms, such as cyanobacteria and green algae, may also contribute to the negative relationship between diatom species richness and benthic biomass.

Above the taxonomic threshold point along the salinity gradient of the medium spatial scale, benthic biomass correlated positively with the functional diversity of communities. Although marine diatoms are highly important for the global primary production of carbon (Nelson et al., 1995), and benthic diatoms strongly contribute to benthic productivity and biomass (Karsten et al., 2021; Kuriyama et al., 2021), studies on the diversity-biomass relationship on marine or brackish benthic diatoms are rare. Thus, generalizing or comparing our result of the positive relationship between functional diversity and benthic biomass or the productivity of benthic ecosystems to other regions is difficult, but this finding agrees with our previous study where we showed a positive relationship between functional diversity of soft bottom benthic diatoms and benthic biomass in a brackish archipelago (Virta et al., 2019). Thus, it seems that the functional diversity of benthic diatoms supports high biomass in brackish waters. This could be due to, e.g., niche complementarity, i.e. different trait groups occupying different niches and using resources in a complementary way (Kahmen et al., 2006), or environmental effect, such as resource availability (Gross and Cardinale, 2007).

Above the taxonomic threshold point along the salinity gradient of the medium spatial scale, benthic biomass also correlated positively with the size of diatoms. Communities with higher number of individuals of large species contained the largest amount of biomass. Despite the size of an organism being a master trait that affects, for example, species' dispersal ability (Passy, 2012) and metabolic rates (Okie et al., 2013), the importance of body size (or cell size) for biomass or ecosystem productivity has rarely been studied. However, some studies have also shown the importance of body size and large individuals on ecosystem functioning (Reiss et al., 2011; Norkko et al., 2013; Teittinen et al., 2022). Thus, it would be useful to further consider the interspecific and intraspecific size of organisms when explaining ecosystem biomass or productivity.

5. Conclusions

In this study, we showed that combining studies of different spatial scales can effectively reveal threshold responses of biotic communities and ecosystems to temporal climate-change-induced environmental change. Our results indicated that salinity and wind exposure, which indirectly affects the communities of benthic diatoms by inducing wave action, significantly affected the composition of benthic diatom communities. Taxonomic threshold points of communities were effectively found along the gradients of salinity and wind exposure, and regime shifts in community diversity, community functions and benthic biomass were found between communities below and above the taxonomic threshold points. The diversity of communities was higher in low salinity, which suggests higher diversity of benthic diatom communities if the climate change decreases the salinity of the Baltic Sea, as has been predicted. The effect of wind exposure on diversity was context-dependent, thus, predicting the effects of climate-change-induced changes in wind disturbance on benthic communities may be difficult. The most pronounced regime shift in community functions along the salinity and wind exposure gradients was the difference in the abundance of low-profile diatoms, i.e., the most resilient type of benthic diatoms. Hence, the resilience of benthic diatom communities may change along the climatic change. Benthic biomass showed a regime shift along the salinity gradient, i.e., communities contained more biomass in higher salinity. This may indicate decreasing benthic biomass, if climate change leads to lowering salinity in the coastal Baltic Sea. All in all, our results indicated that climate-change-induced modifications in the environment may lead to threshold responses in biotic communities, and these community changes may have profound effects on ecosystem functioning and services.

CRediT authorship contribution statement

Leena Virta: Conceptualization, investigation, formal analyses, writing – original draft, visualization, project administration, funding acquisition.

Anette Teittinen: Conceptualization, investigation, writing – review & editing, funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are thankful for Mervi Sjöblom and Jaana Koistinen at Tvärminne Zoological Station, University of Helsinki, and for Hanna Reijola and Tuija Vaahtojärvi at the Department of Geosciences and Geography, University of Helsinki, for the nutrient analyses. We also thank Prof. Alf Norkko for assistance in designing and conducting the field work.

Funding: This work was supported by the Walter and Andrée de Nottbeck Foundation, Societas pro Fauna et Flora Fennica, the Finnish Society of Sciences and Letters, the Ella and Georg Ehrnrooth Foundation, and the Emil Aaltonen Foundation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.154130.

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