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Stable Seasonal and Annual Alpha Diversity of Benthic Diatom Communities Despite Changing Community Composition

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The global biodiversity loss has raised interest in the different facets of diversity, and the importance of diversity for ecosystem functions has been recognized. However, our knowledge on seasonal and inter-annual variation in the composition and diversity of communities is still poor. Here, we investigated the seasonal and inter-annual changes in taxonomic and functional community composition and diversity of benthic diatoms in a coastal habitat of the northern Baltic Sea, where seasonal and inter-annual variation of climate is pronounced. We found that the taxonomic and functional alpha diversity remained stable at seasonal and inter-annual level despite strong changes in community composition. However, alpha diversity decreased during an exceptionally warm winter possibly due to disturbances induced by the lack of ice. This may suggest that climate warming and consequently limited ice cover will affect the diversity of benthic communities.

Keywords: seasonal variation, annual variation, community composition, diversity, benthic diatoms, Baltic Sea, microphytobenthos

INTRODUCTION

The current global biodiversity crisis threatens all ecosystems and has increased interest in studying the diversity of different organisms on different scales. A great amount of research has resolved patterns of diversity and its effects on different aspects of ecosystem functioning and services, such as productivity (e.g., Smith, 2007; Cadotte et al., 2009) and nutrient cycling (e.g., Smetacek, 1999; Spilling et al., 2018). Some of these studies have presented snapshot results across spatial gradients (e.g., Virta et al., 2019) while others have included temporal variation (e.g., Morin et al., 2014), but most of them have neglected the strong seasonal and inter-annual variation that occurs across most parts of the globe (but see Hillebrand et al., 2010). Ignoring the seasonal and inter-annual changes in diversity undermines our ability to generalize biodiversity patterns, compromises inferences gained from monitoring programs and jeopardizes conservation efforts of valuable ecosystems.

The seasonal cycle of biotic communities is usually characterized by changes in taxonomic community composition induced by temporary species gain during favorable growing season and temporary species loss during more unfavorable conditions (Hobson and McQuoid, 1997). This results in seasonal changes in the functions of the community. However, this pattern can be altered by strong dispersal abilities and a large regional species pool that allow the replacement of temporarily transient species (Zobel, 1997), and thus, maintain steadily high local taxonomic diversity. Temporal changes in the taxonomy also affect the functional composition and diversity of the communities, which are often more effective than taxonomy in showing the relationship

between diversity and ecosystem functioning (Chapin et al., 2000). Furthermore, high taxonomic diversity supports functional redundancy (i.e., complementarity of species traits), which allows ecosystem stability throughout the year and also provides resilience against environmental change (Naeem et al., 2012). However, the temporal variation in functional diversity of communities in different ecosystems and habitats is still poorly known.

Diatoms are one of the most important groups of microorganisms in all aquatic ecosystems and account for as much as 20% of the total primary production on Earth (Nelson et al., 1995; Falkowski et al., 1998; Field et al., 1998). Different studies have agreed that the diversity of benthic diatom communities affects ecosystem productivity, although consensus on the direction of this effect has not been found. For example, Virta et al. (2019) showed that the diversity, especially functional alpha diversity, of benthic diatoms promotes ecosystem productivity, whereas Forster et al. (2006) found a negative relationship between diatom diversity and ecosystem productivity, which may be due to the dominance of a few highly productive species. However, considering the importance, high abundance and enormous diversity of benthic diatoms, it is surprising how little attention the temporal variation in their diversity has received.

To reduce these knowledge gaps, we present a study on the seasonal and inter-annual variation of the taxonomic and functional composition and diversity of benthic diatom communities. We conducted the study in the northern part of the Baltic Sea. The predominant climate zone in this area is a warm-summer humid continental climate with strong variations in air and water temperatures. Moreover, our sampling site was located in a generally shallow coastal archipelago area, which results in high seasonal and inter-annual variability in water temperature and annually occurring ice cover. Thus, biotic communities here experience strong temporal changes and are, thus, ideal for seasonal and inter-annual studies. Our specific research question and hypothesis was: *Does seasonal and inter-annual climatic variation affect the taxonomic and functional composition and alpha diversity of benthic diatom communities?* We hypothesized that the composition and diversity of communities would change significantly between seasons and climatically different years (Gilbert et al., 2010). We also predicted that we would find the lowest diversity during winter because of harsh conditions (Oberbeckmann et al., 2014).

MATERIALS AND METHODS

Study Area and Sampling

The temporal sampling site was located in a small, sheltered and shallow (<2 m) bay on the Finnish coast of the Baltic Sea, at the Hanko-peninsula (**Figure 1**). The bottom of the bay is muddy, with cobble-sized stones close to shores. Due to the sheltered
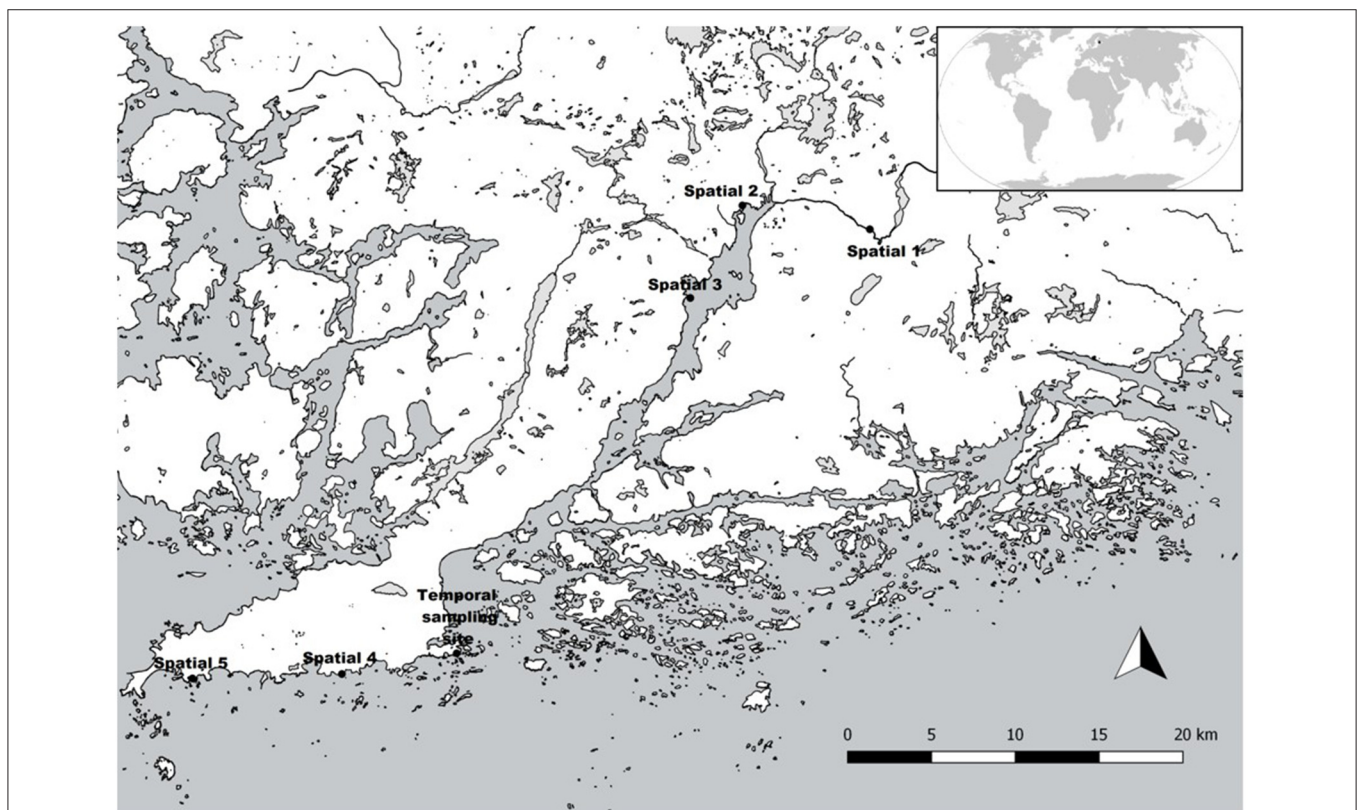
FIGURE 1 | Our temporal sampling site and five spatio-temporal sites along the Hanko Peninsula in southern Finland, Baltic Sea. Map layers derived from HELCOM (2019), European Environment Agency (2019), and SYKE (2019).

location, waves do not roll the stones, which form, thus, stable substrata for benthic diatoms. Climate in this area is a mixture of continental and oceanic climates, with strong seasonal and inter-annual variations. The average annual air temperature is ca. 6.8°C, and ice cover forms annually (Finnish Meteorological Institute, 2019). Water in the area is brackish with a salinity of 5–7. Thus, biotic communities are a mixture of brackish and freshwater species.

To provide more generality and context to the results from our intensively sampled site, we also collected spatio-temporal samples from five sites at three occasions (see below), hence 15 spatio-temporal samples altogether, and compared the temporal changes in diversity between these sites and our temporally intensive sampling site. These five sites were located at a distance of ca. 60 kilometers from the temporally intensive sampling site (**Figure 1**), and represent a gradient from a freshwater river Karjaanjoki, through its estuary Pojo Bay, to the brackish archipelago area at the coast of the Hanko-peninsula. Thus, biotic communities at these sites represent highly different environmental conditions in terms of salinity, nutrients, and exposure to wave action.

We conducted temporal sampling at two-week-intervals over a ca. two-year-period, 20 April 2017–29 May 2019, covering altogether a period of 111 weeks (**Supplementary Table 1**). We collected a total of 56 samples from natural stones following the recommendations of Kelly et al. (1998). We randomly selected 10 cobble-sized stones from depths of 20–50 cm, and avoided using the same stones again for at least eight following weeks, because of the required re-colonization time of benthic microalgae (Hillebrand and Sommer, 2000). We collected the biofilm by brushing the surfaces of stones with a toothbrush (25 cm²/stone) and pooled the accumulated suspension into a composite sample. After sampling, we stored the samples in cold (+4°C) and dark conditions until further analyses. Our spatial samples for validation purposes were collected three times, June 2017, September 2017, and May 2019, following the same procedure.

Laboratory Analyses, Trait Analyses, and Temperature Calculations

We boiled the diatom samples in hydrogen peroxide (30% H_2O_2) to remove organic material, and mounted cleaned diatoms on slides using Naphrax (Brunel Microscopes Ltd., United Kingdom). We identified the diatoms (500 valves/sample) with a phase contrast light microscope with a 1,000× magnification to the lowest possible taxonomic level (typically species level). The identification followed Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Snoeijs (1993), Snoeijs and Vilbaste (1994), Snoeijs and Potapova (1995), and Snoeijs and Kasperovicienè (1996). After identification, we transformed species counts into relative abundances.

To account for functional composition and diversity of diatom communities, we divided species to traits that are robust indicators of ecological behavior (Hodapp et al., 2016). We categorized species according to different classifications: size (biovolume classes: small < 1,000

µm/large > 1,000 µm), mobility (mobile/non-mobile), type of attachment [adnate/pedunculate (which was further divided to pad-attached/stalk-attached)/non-attached], colonization (colonial/non-colonial), guilds (low-profile/high-profile/motile/planktonic) (Rimet and Bouchez, 2012), and nitrogen-fixing abilities (nitrogen-fixer/non-nitrogen-fixer) (Passy, 2017). Each species was categorized according to all six classifications, which resulted in numerous possible combinations for classifying a certain species. For example, one of the common species, *Bacillaria paxillifera* (O.F. Müller) T.Marsson, was classified as large/mobile/non-attached/non-colonial/motile/non-nitrogen-fixer. As the measure of trait composition, we used the combination of traits of all the species present in the community. For the identification of traits, we used above mentioned species and trait literature, and Snoeijs et al. (2002) and Diatoms of North America (2019).

We derived average seasonal air temperatures of the study area from a weather station located in close proximity of our temporal sampling site, at Tvärminne Zoological Station (Finnish Meteorological Institute, 2019). Average seasonal water temperatures were derived from permanent loggers located close to the sampling site (Monicoast, 2019). These loggers by Finnish Meteorological Institute and later by Tvärminne Zoological Station have measured water temperature since the beginning of 1900.

Statistical Analyses

We divided our data into seasons according to thermal seasons (Finnish Meteorological Institute, 2019). Thermal seasons are characteristic to each location and each year. They are categorized as follows: thermal summer begins when daily average temperature rises permanently above +10°C, thermal fall when average daily temperature decreases below +10°C, thermal winter when average daily temperature decreases below 0°C, and thermal spring when average daily temperature rises permanently above 0°C.

To test if the diatom communities are significantly different between adjacent seasons and years, we ran analysis of similarities (ANOSIM), with Bray-Curtis distance (Clarke, 1993). ANOSIM is a distribution-free analog of one-way ANOVA, where values range between −1 and 1, 1 indicating total dissimilarity between groups and −1 greater dissimilarities within groups than between groups.

To illustrate season-specific patterns in taxonomic and functional community composition, we used Nonmetric Multidimensional Scaling (NMDS) with Bray-Curtis distance, and three dimensions for taxonomic composition and two dimensions for functional composition. We also calculated a centroid for the samples of each sampling season. We ran NMDS with the R packages vegan (Oksanen, 2019) and ggplot2 (Wickham, 2019).

To compare the taxonomic and functional alpha diversity in diatom communities between seasons, we used Shannon diversity index with logarithm base of b = 2 (Shannon and Weaver, 1962), which is a commonly used measure of diversity. Due to its sensitivity to rare species (Nagendra, 2002), it is a suitable index for studies concerning diatom communities, where

the majority of species is usually rare. Although species richness is the most commonly used measure of diversity, we decided not to include it as a parameter in this study. This decision was due to the large variation in species richness between samples and the fixed amount (500) of frustules identified per sample, which may have underestimated the number of species in speciose samples.

To test the significance of differences in taxonomic and functional diversity between seasons, we first computed one-way ANOVA test with season as a categorical factor. Then, we calculated pairwise significances between diversities of all seasons with Tukey Honest Significant Differences. We considered adjusted $p < 0.05$ to denote significant differences.

To validate the results of our temporal samples, we compared the degree of temporal beta diversity of our temporal sampling site with five other sites, which were sampled three times, using temporal beta diversity indices (TBI) (Winegardner et al., 2017). Our aim was to see whether the direction of change in diversity at our temporal site coincides with other five sites and, thus, to make our results more general. TBI is based on the Podani family of beta diversity and computes total temporal beta diversity as well as different components (species loss or species gain) of that beta diversity by forming pairs observed at time 1 (T1) and time 2 (T2). It computes species loss (bj) from T1 to T2 with the equation: $bj = (y1j–y2j)$ if $y1j > y2j$, and species gain (cj) from T1 to T2 with the equation: $cj = (y2j–y1j)$ if $y2j > y1j$. We ran the TBI for taxonomic temporal beta diversity with binary data using Bray-Curtis dissimilarities. The significances were computed using a parametric paired t-test with 9999 permutations. We ran the TBI with the R package adespatial (Dray et al., 2019).

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

RESULTS

Total species richness in our temporal samples was 272, and species richness per sample varied between 31 and 70 (**Supplementary Table 1**). In general, all traits were present in all the samples, except planktonic guild, which was absent from nine samples and the nitrogen-fixing trait that was absent from 11 samples. Species abundances at sampling sites are presented in **Supplementary Table 2**, and trait classifications for all the species in **Supplementary Table 3**.

Thermal summer at our temporal site began on 19 May in 2017, 8 May in 2018 and 16 May in 2019, thermal fall on 6 October in 2017 and 24 September in 2018, thermal winter on 10 January in 2017–2018 (hereafter referred to as winter 2018) and 13 December in 2018–2019 (hereafter referred to as winter 2019), and thermal spring on 4 April in 2018 and 14 March in 2019 (Finnish Meteorological Institute, 2019). ANOSIM showed that the diatom communities were taxonomically and functionally different between most of the seasons (**Table 1**). Communities were also significantly different between the first and the second sampling year.

In the NMDS, compositions during most of the individual seasons formed clear clusters (**Figure 2**). These clusters showed cyclic annual variation in taxonomic and functional community

TABLE 1 | Results of the ANOSIM to analyze the differences in taxonomic and functional community composition between **(A)** seasons and **(B)** years.

	Taxonomic		Functional	
	R	**p**	**R**	**p**
(A)				
Summer 2017–fall 2017	**0.857**	**0.002**	**0.926**	**0.001**
Fall 2017–winter 2018	0.183	0.073	0.024	0.361
Winter 2018–spring 2018	0.219	0.151	0.281	0.142
Spring 2018–summer 2018	**0.602**	**0.040**	0.377	0.122
Summer 2018–fall 2018	**0.337**	**0.013**	**0.312**	**0.039**
Fall 2018–winter 2019	**0.504**	**0.012**	**0.550**	**0.014**
Winter 2019–spring 2019	**0.466**	**0.025**	**0.611**	**0.007**
(B)				
2017/2018–2018/2019	**0.421**	**0.001**	0.055	**0.043**

Significant ($p < 0.05$) differences are bolded. Spring 2017 and summer 2019 were excluded from the analyses, because our sampling period only covered a part of them.
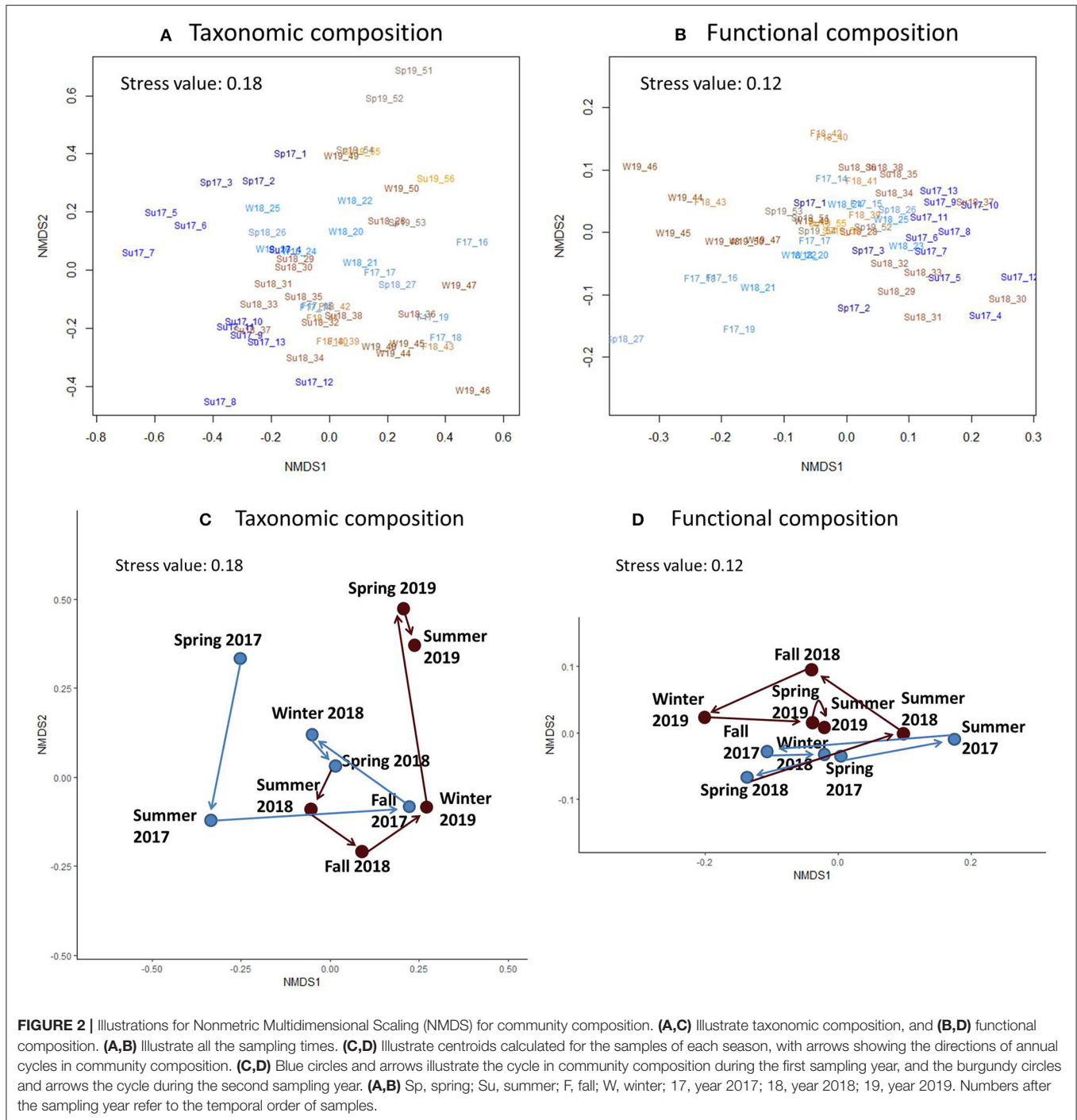
composition. Taxonomic composition cycles showed clear differences between years, whereas functional composition cycles remained more similar between years.

Despite considerable seasonal variation in air temperature (average seasonal temperature $-4.0°C$ to $16.6°C$) and water temperature (average seasonal temperature $0.6°C$ to $15.1°C$), average seasonal diversity in our samples remained stable throughout the sampling period (**Table 2A**). Seasonal taxonomic diversity (Shannon diversity index) varied between 1.209 and 1.358, and seasonal functional diversity (Shannon diversity index) between 2.932 and 3.272. Season also appeared as a significant factor for both the taxonomic and functional diversity in the ANOVA (**Table 2B**). Taxonomic diversity was highest during winter 2018, which was a cold winter (average air temperature $-4.0°C$ and solid ice cover at the sampling site for five consecutive sampling times), and lowest during winter 2019, which was a warm winter (average air temperature $-1.5°C$ and solid ice cover at the sampling site for only two consecutive sampling times). Tukey multiple pairwise comparisons confirmed that the diversity of diatom communities was significantly different during the warm winter 2019 than during other seasons (**Table 2C**).

Our TBI analysis showed that temporal beta diversity was non-significant at the temporal sampling site and four of the spatio-temporal sites from June 2017 to September 2017, and from September 2017 to May 2019 (**Table 3**). The only significant temporal beta diversity occurred at the spatio-temporal sampling site 4, where the change was significant and negative from June 2017 to September 2017.

DISCUSSION

We studied the seasonal and inter-annual variation in the taxonomic and functional structure and diversity of littoral benthic diatom communities in the Baltic Sea, where seasons and years are climatically highly variable. Despite the importance

FIGURE 2 | Illustrations for Nonmetric Multidimensional Scaling (NMDS) for community composition. **(A,C)** Illustrate taxonomic composition, and **(B,D)** functional composition. **(A,B)** Illustrate all the sampling times. **(C,D)** Illustrate centroids calculated for the samples of each season, with arrows showing the directions of annual cycles in community composition. **(C,D)** Blue circles and arrows illustrate the cycle in community composition during the first sampling year, and the burgundy circles and arrows the cycle during the second sampling year. **(A,B)** Sp, spring; Su, summer; F, fall; W, winter; 17, year 2017; 18, year 2018; 19, year 2019. Numbers after the sampling year refer to the temporal order of samples.

of benthic communities for ecosystem functioning and services, seasonal and inter-annual changes are often overlooked, which compromises the effectiveness of monitoring and conservation efforts of these valuable ecosystems.

We collected samples at two-week-intervals for two consecutive years, from spring 2017 to summer 2019. There was considerable variation in air and water temperatures between seasons and years, year 2017–2018 featuring a cool summer and a cold winter, whereas 2018–2019 featuring

the warmest ever recorded summer (Monicoast, 2019) and a mild winter. Due to the northern and continental/marine location of our sampling area, such strong seasonal and annual changes in climate are typical. Along with the climatic temperature changes, other factors that have previously been shown to affect diatom communities in the Baltic Sea and elsewhere, such as nutrient concentrations (Svensson et al., 2014), daytime length and light intensity (Yang and Flower, 2012), also vary seasonally in this area and may have had

TABLE 2 | (A) Mean and standard deviation for taxonomic and functional diversity (Shannon diversity index), water temperature and air temperature during seasons; **(B)** Results of the one-way ANOVA test to analyze the significance of the season for taxonomic and functional diversity; **(C)** Results of the Tukey Honest Significant Differences test to analyze pairwise differences between diversities of all seasons.

	Taxonomic diversity (Shannon diversity index)	Functional diversity (Shannon diversity index)	Water temperature (°C)	Air temperature (°C)	
(A)					
Season	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	
Summer 2017	1.289 (0.051)	3.195 (0.051)	13.6 (2.2)	14.0 (2.6)	
Fall 2017	1.243 (0.082)	3.089 (0.144)	6.8 (2.7)	4.1 (2.8)	
Winter 2018	1.358 (0.028)	3.217 (0.060)	0.6 (0.7)	−4.0 (4.3)	
Spring 2018	1.224 (0.173)	2.932 (0.356)	4.6 (1.6)	4.8 (2.2)	
Summer 2018	1.311 (0.031)	3.238 (0.071)	15.1 (4.7)	16.6 (3.6)	
Fall 2018	1.272 (0.041)	3.238 (0.107)	7.8 (2.2)	5.9 (4.0)	
Winter 2019	1.209 (0.056)	2.948 (0.132)	0.6 (0.7)	−1.5 (3.4)	
Spring 2019	1.315 (0.026)	3.272 (0.028)	4.0 (2.3)	4.8 (3.1)	
(B)					
	Df	Sum of Squares	Mean Square	F value	Pr(>F)
Season (taxonomic diversity)	9	0.056	0.006	2.176	0.041*
Season (functional diversity)	9	0.324	0.036	3.468	0.002**
(C)					
Taxonomic diversity	**Difference between means**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**Adjusted p**	
Winter 2018 - winter 2019	−0.103	−0.202	−0.004	0.036*	
Functional diversity	**Difference between means**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**Adjusted p**	
Summer 2017–winter 2019	−0.171	−0.338	−0.004	0.041*	
Summer 2018–winter 2019	−0.201	−0.365	−0.038	0.006**	
Fall 2018–winter 2019	−0.201	−0.399	−0.003	0.045*	
Winter 2019–spring 2019	0.225	0.013	0.437	0.030*	

*Only significant results are shown 0.001 ***, < 0.01 **, < 0.05 *. Spring 2017 and summer 2019 were excluded from the table, because our sampling period only covered a part of them.*

TABLE 3 | Temporal beta diversity according to temporal beta diversity indices (TBI) at our temporal sampling site and five spatial sites between **(A)** June 2017 and September 2017, and **(B)** September 2017 and May 2019.

	Temporal sampling site	Spatial sampling site 1	Spatial sampling site 2	Spatial sampling site 3	Spatial sampling site 4	Spatial sampling site 5
(A)						
TBI	0.504	0.487	0.443	0.392	**0.585**	0.293
p-value	0.1351	0.2336	0.5903	0.9212	**0.0015**	0.9999
Change	−	+	+	−	−	+
(B)						
TBI	0.525	0.544	0.517	0.491	0.545	0.386
p-value	0.3523	0.2108	0.4299	0.6488	0.2011	0.9966
Change	+	−	−	+	−	−

Significant values (p < 0.05) are bolded. TBI denotes total temporal beta diversity, + species gain, and − species loss.

an impact on the communities. In contrast, salinity, which often is the strongest driver of benthic diatom communities (Ulanova et al., 2009), remains highly similar throughout the year and was, thus, not likely to affect the communities in our study.

As we expected, this variation in environment led to highly variable taxonomic composition of communities between seasons and years, and also highly variable functional composition between seasons. Similar results of strong temporal variation have been found with different organisms in different

ecosystems, such as soil microbes (Waldrop and Firestone, 2006), bacterioplankton (Van der Gucht et al., 2001), and fishes (Lazzari et al., 1999). However, our results disagree with several previous studies in the Baltic Sea, which have shown temporally stable community composition of benthic diatoms (Sabbe, 1993; Vilbaste et al., 2000). However, the duration of these studies has been remarkably shorter than ours, and they have been conducted on sedimentary soft bottoms, which may provide a more stable environment for the microphytobenthic organisms than stones.

However, the functional composition showed only low variation between years, and the alpha diversity of communities remained fairly stable between seasons and years. Such stable diversity patterns were discovered not only on our temporal sampling site but also on our five spatial sites, where we collected three samples during different seasons to validate our temporal results. This disagrees with studies conducted in other ecosystems, such as deep sea (Ramalho et al., 2014) and pelagic waters (Sabanci and Koray, 2011), but is in line with other benthic diatom studies in the Baltic Sea (Sabbe, 1993; Vilbaste et al., 2000). Reasons for the temporally stable diversity may include effective dispersal and large regional species pool, and consequent high functional redundancy of benthic microalgal communities. In other words, changing environmental conditions, such as water temperature, nutrients and light intensity, led to the disappearance of some species, but the seed bank, i.e., locally occurring resting stages of some species, the effective dispersal, and large regional species pool allowed them to be replaced by species that were favored by the new predominant conditions (Zobel, 1997). Hence, the communities were able to preserve high taxonomic diversity, which supported functional redundancy, i.e., complementarity of species traits that allows ecosystem stability throughout the year and also provides resilience against environmental change (Naeem et al., 2012).

Despite the similar result of temporally stable diversity in our study and other studies on benthic diatoms in the Baltic Sea, the diversity measured with Shannon's diversity index was remarkably lower in our study than in other studies in the same area. Our seasonal taxonomic mean diversity varied between 1.2 and 1.4, and seasonal functional mean diversity between 2.9 and 3.3, whereas, e.g., Vilbaste et al. (2000) found values of 2.8–5.2 for the taxonomic diversity of benthic diatom communities in the Gulf of Riga, Baltic Sea. Low diversity in our communities is astonishing, considering the fairly highly species richness, but we speculate that the low diversity is due to the dominance of a few species and, thus, low evenness of the communities.

Although the diversity of communities remained temporally fairly stable throughout our 2-year sampling period, we found the highest diversity of all seasons during the cold winter 2018 and the lowest diversity during the mild winter 2019. Taxonomic and functional diversity during the warm winter 2019 differed also significantly from several other seasons. Furthermore, the functional compositions of communities were different between winters, the cold winter 2018 featuring proportionally large amounts of large and high-growing species (traits: large-sized, pedunculate, pad-attached, colonial, and high-profile) and the warm winter 2019 small and mobile species (traits: small-sized, mobile, non-colonial, and motile). This finding of different response of small and large diatom species to environmental conditions is in agreement with Busse and Snoeijs (2002), who showed that small species were mostly affected by exposure to wave action and large species by salinity.

We speculate that the difference between winters in our study was due to differences in the duration of ice cover. Solid ice cover at the sampling site lasted for ca. 10 weeks during winter 2018 but only ca. 4 weeks during winter 2019. Microalgal studies in winter have concentrated on pelagic and sea-ice algae (e.g., Edgar et al., 2016; Enberg et al., 2018), which prevents comparing our results, but we speculate that low water temperature that always occurs during winter and wind-induced waves due to the lack of ice are cumulative stressors (Morin et al., 2015) that make species more vulnerable during ice-free winters. Thus, ice cover seems to be needed to protect high benthic diversity in winter. However, we only compared two consecutive years, and for broader conclusions on the effects of ice-cover or climate in general, studies covering longer time series are needed.

CONCLUSIONS

We showed that the diversity of benthic diatom communities is seasonally and inter-annually highly stable despite strong climatic variation and consequent changes in community composition. However, diversity seems to decrease during exceptionally warm winters possibly due to disturbances induced by the lack of ice. This may suggest that climate warming with smaller extent and shorter duration of ice cover will affect the diversity of benthic communities.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

LV, JS, and AN designed the study. LV conducted the field work, identified species, defined traits, conducted statistical analyses, and drafted the manuscript. All authors commented on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00088/full#supplementary-material

Supplementary Table 1 | Sampling details.

Supplementary Table 2 | Species abundance table.

Supplementary Table 3 | Trait table.

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