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# Spatial and temporal patterns of benthic diatom flora in Lake Stechlin, Germany

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**Abstract:** Phytoplankton and planktonic centric diatoms of Lake Stechlin have been extensively studied, while attached diatoms have received much less scientific interest. In the present study, the composition of benthic diatoms and their diversity metrics were determined and compared along the shoreline of the lake in spring 2013 and autumn 2014. Overall, 118 taxa classified in 52 genera were found, of which 15 species belonged to threat categories of the Red List for Central Europe. Species richness (33 ± 4), Shannon diversity (2.47 ± 0.23), and species composition did not show any differences between different basins. Besides the spatial homogeneity, considerable temporal differences were observed. In spring 2013, species number was significantly lower, while the proportion of Mediophyceae species was higher due to the high abundance of *Stephanodiscus rugosus* and *S. neoastraea*. Nonmetric multidimensional scaling (NMDS) showed significant differences between samples from the two years for the total and the Bacillariophyceae species composition. TP concentration of water samples suggested a mesotrophic status and most of the diatom taxa were considered eutraphentic and meso-eutraphentic.

**Key words:** Bacillariophyceae, Mediophyceae, algal biodiversity, indicator species, algal red list, Baltic Lake District

## 1. Introduction

The Baltic Lake District in northeastern Germany is composed of a multitude of lakes originated during the last glacial period (~12,000 years before). Some of the lakes are pristine and considered to represent high status in terms of the European Water Framework Directive. Lake Stechlin represents a highly valuable ecosystem. It belongs to the type of stratified lowland lakes with small catchment area and high content of calcite (Mathes et al., 2002). It is one of the most extensively studied lakes in northern Germany. Regular monitoring of its main limnological variables and biota was set in the 1950s in the context of the operation of a nuclear power plant (NPP) between 1966 and 1989. Through an external circulation system, the NPP's cooling water was taken from Lake Nehmitz, the heated water was pumped into Lake Stechlin, and diverted back to Lake Nehmitz (Casper, 1985; Koschel et al., 2002).

Phytoplankton of Lake Stechlin has been studied since 1959 (Casper, 1985), and water chemistry and primary production measurements using the $^{14}C$-technique started in 1970 (Koschel, 1974). Since 1994, a sampling program has been carried out to investigate the species composition and succession of phytoplankton (Padisák et al., 1998, 2010) and the occurrence of deep chlorophyll maxima (DCM) formed by cyanobacteria (Padisák et al., 1997, 2010; Selmeczy et al., 2016). In the last decade, an increasing abundance of cyanobacterial blooms indicated a change in water quality (Padisák et al., 2010; Üveges et al., 2012).

Diatom research in Lake Stechlin focused mainly on planktonic Centrales taxa. The population dynamics of two phycogeographically restricted unicellular diatom species were described (*Cyclotella tripartita* and *Stephanocostis chantaicus* - Scheffler and Padisák, 1997, 2000). In 1999, spatial and temporal changes in spring planktonic diatom populations were studied (Padisák et al., 2003). Scheffler et al. (2003, 2005) investigated the relationship between *Cyclotella comensis* and *Cyclotella pseudocomensis* with morphological, ecological, and molecular methods. Contrary to extensive and detailed phytoplankton studies, attached diatoms of the lake received much less scientific interest. In 1974 and 1975 (thermal load period), biomass and primary production of periphyton in the littoral zone were determined. Thereafter, a list of diatom taxa found in the probes was compiled and published in Casper's (1985) synthesis. Scheffler and Schönfelder (2004) reported the

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microflora of Lake Stechlin and their list contains the species number of benthic diatoms. Schönfelder et al. (2002) estimated the relationship between littoral diatom composition and environmental factors in northeastern German lakes including Lake Stechlin. In addition, Stechlin is included in the Water Framework Directive monitoring program of Brandenburg and related reports define reference conditions by means of analysis of diatoms (Schönfelder, 2002; Schönfelder et al., 2005). However, international publications concerning diversity and spatial and temporal distribution of benthic diatoms are lacking.

During a previous study focusing on phytoplankton communities in two basins of Lake Stechlin, no heterogeneous horizontal distribution was found (Fuchs et al., 2016). In the current research, we investigated whether (i) there is any spatial change in benthic diatom composition and diversity metrics along the shoreline of the lake at two different sampling dates or (ii) our observations are in accordance with the findings mentioned above.

## 2. Materials and methods

### 2.1. Study area

Lake Stechlin is located in northeastern Germany on the southern border of the Mecklenburg Lake District (53°10′/13°02′) (Figure 1). The lake is deep, dimictic (in some years warm monomictic) and only slightly affected by anthropogenic impacts. Its trophic status is originally oligotrophic, but in the early 2000s a change towards mesotrophic conditions was observed without specific local reasons. The lake has a surface area of 4.25 km$^2$, a calculated volume of 96.9 × 10$^6$ m$^3$, a maximum depth of 69.5 m located in the north basin, and the mean depth is 22.8 m. It is divided into four basins: north, west, south, and central. The basins have relative small surface areas (1.3, 1.1, 0.9, and 1.0 km$^2$) and belong to the category of deep lakes based on their relative depths (5.3%, 3.5%, 3.3%, and 5.2%). The lake has a temporary surface inflow from Lake Dagow and a surface runoff through the Polzow canal from the south basin of Lake Stechlin to the north basin of Lake Nehmitz. The shore of Lake Stechlin is

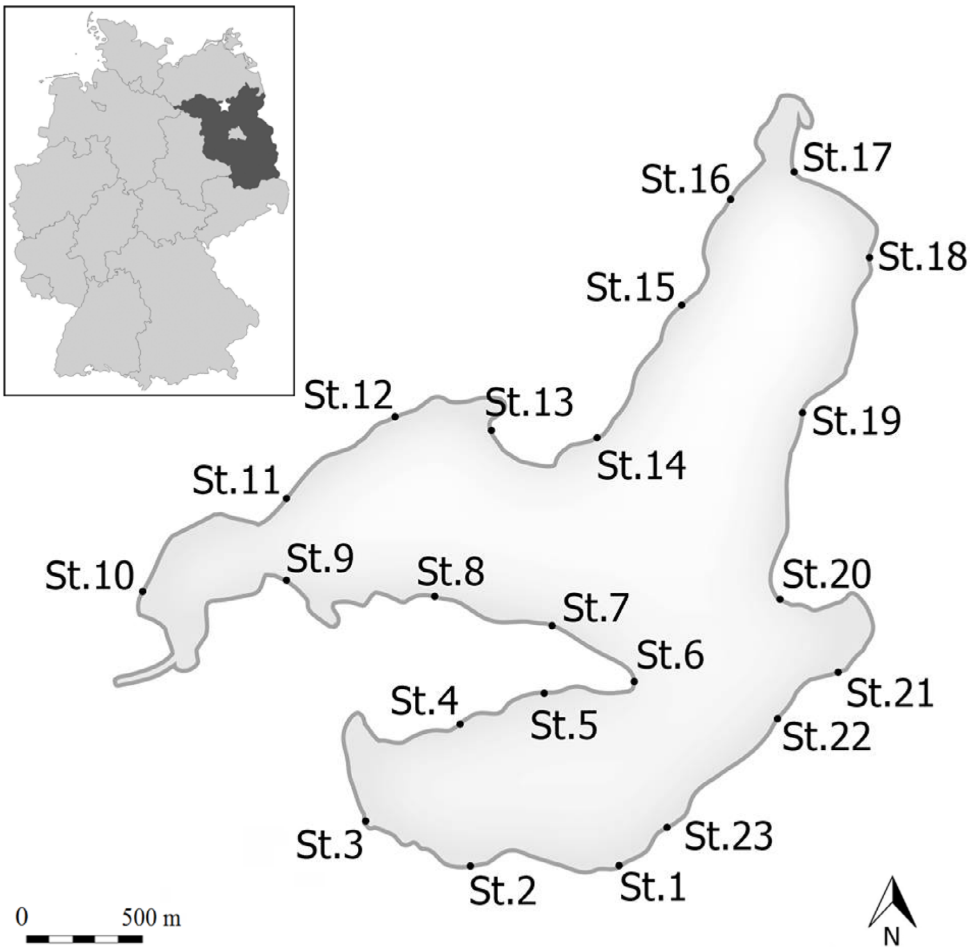



**Figure 1.** Lake Stechlin and its sampling sites.

vegetated by mixed forests consisting mainly of deciduous trees and almost 50% of their crowns hang over the water; the shoreline development factor is 2.1 (Casper, 1985). TP and TN concentrations and trophic level based on TP concentrations (OECD, 1982) of samples taken from the deepest point monthly between February 2013 and December 2014 are summarized in Table 1. Data represent the average of samples taken at 0-, 5-, and 10-m depths.

**2.2. Sampling, preparation, and data analysis**

Phytobenthos samples were taken from natural stone substrates in the littoral zone at 23 different sites of Lake Stechlin (Figure 1) on 3 May 2013 and 26 September 2014. Epilithic diatom sampling followed the standard method (King et al., 2006). Diatom valves were cleaned by hot hydrogen-peroxide method (CEN, 2003) in order to remove the organic material and were embedded in Pleurax resin. A minimum of 400 valves was counted in each sample using a Zeiss Axio Imager A1 with a Planapochromat DIC lens at 1000× magnification. Accurate identification of centric species was conducted using a Hitachi S-4500 field emission scanning electron microscope (Hitachi Corporation, Tokyo, Japan). Species were identified according to the relevant taxonomic guides (Lange-Bertalot, 2001; Krammer, 2002; Levkov et al., 2010; Bey and Ector, 2013; Hofmann et al., 2013; Houk et al., 2014). The species were classified into two groups following Medlin and Kaczmarska (2004): Mediophyceae (polar centrics and radial Thalassiosirales) and Bacillariophyceae (pennates). The most frequent and abundant taxa were identified according to either of the following two criteria:

**Table 1.** Concentration of TP and TN (euphotic zone, 0–10 m; mean ± SD) and trophic status at the deepest point of Lake Stechlin. TL = trophic level based on TP concentration (OECD, 1982), O = oligotrophic, M = mesotrophic.

| Sampling date | TP [μg $L^{-1}$] | TN [μg $L^{-1}$] | TL |
|---|---|---|---|
| 05.02.2013 | 27.0 ± 0 | 424.0 ± 0 | M |
| 16.04.2013 | 17.0 ± 0 | 81.0 ± 0 | M |
| 07.05.2013 | 15.7 ± 1.5 | 82.0 ± 7.0 | M |
| 04.06.2013 | 15.7 ± 2.1 | 436.7 ± 8.4 | M |
| 09.07.2013 | 13.3 ± 1.2 | 476.0 ± 66.9 | M |
| 08.08.2013 | 12.7 ± 2.5 | 432.0 ± 15.0 | M |
| 18.09.2013 | 11.3 ± 0.6 | 526.7 ± 84.9 | M |
| 08.10.2013 | 9.3 ± 2.3 | 577.0 ± 70.1 | O |
| 14.11.2013 | 12.0 ± 1.0 | 469.3 ± 15.9 | M |
| 04.12.2013 | 10.3 ± 0.6 | 328.3 ± 50.8 | M |
| 15.01.2014 | 23.0 ± 0 | 392.0 ± 0 | M |
| 25.02.2014 | 22.0 ± 0 | 499.0 ± 0 | M |
| 18.03.2014 | 22.0 ± 0 | 478.0 ± 0 | M |
| 10.04.2014 | 16.0 ± 0 | 374.0 ± 0 | M |
| 13.05.2014 | 15.3 ± 1.5 | 432.7 ± 77.0 | M |
| 11.06.2014 | 16.3 ± 0.6 | 422.3 ± 86.4 | M |
| 09.07.2014 | 10.0 ± 0 | 469.7 ± 45.5 | M |
| 14.08.2014 | 12.0 ± 0 | 376.0 ± 0 | M |
| 08.09.2014 | 9.0 ± 0 | 397.0 ± 0 | O |
| 08.10.2014 | 12.0 ± 0 | 420.0 ± 0 | M |
| 06.11.2014 | 17.0 ± 0 | 575.0 ± 0 | M |
| 04.12.2014 | 12.0 ± 0 | 653.0 ± 0 | M |

(1) occurred in at least four samples and (2) reached a relative abundance of at least 5% in any of the samples.

In 2014, water temperature (°C), conductivity (µS $cm^{-1}$), and pH were measured in situ with an HI 9828 multiparameter probe (Hanna Instruments, Limena, Italy). Water samples for analysis of total nitrogen and total phosphorus were also collected at all sampling points (Figure 1) and analyzed by flow injection analysis (FIA-System, FOSS, Hillerød, Denmark) (APHA, 1998).

Preferences of the individual taxa with respect to pH and trophic status were determined according to van Dam et al. (1994). The German Red List was used to assess the conservational status of the species (Lange-Bertalot, 1996). Species richness and Shannon–Weaver diversity index were also calculated. We examined whether diversity metrics differ in the basins at the two sampling dates using repeated measures ANOVA (Type III) with a linear mixed-effect model. The t-test for unequal variances (Welch probe) was used to examine the differences in the relative abundance of centric and pennate diatom species between spring and autumn. Nonmetric multidimensional scaling (NMDS) was applied to study whether there is a difference between the epilithic diatom communities at the two sampling dates and in the three basins. Differences were tested statistically using analysis of similarities (ANOSIM). Since Mediophyceae species tend to be rather planktonic than members of the benthos, NMDS and ANOSIM were repeated to investigate the same differences retaining only diatoms belonging to the class Bacillariophyceae. Before performing NMDS, species abundance data were square root transformed and then submitted to Wisconsin double standardization. Statistical analyses were carried out in R statistical computing environment (R.3.02.) using the package Vegan.

## 3. Results

Conductivity values ranged from 251 to 265 µS $cm^{-1}$ and all sampling sites were alkaline, with average pH of 8.4 ± 0.1. Water temperature did not change considerably on the day of sampling: values varied between 16.4 and 17.1 °C (Table 2).

A total of 118 diatom taxa were identified, of which 41 species were reported in the species list published by Casper (1985) (Supplement). The species richness of the individual samples ranged from 23 to 41 and the Shannon diversity varied between 1.98 and 2.78. The species richness (Figure 2a) differed significantly between 2013 and 2014, while diversity (Figure 2b) did not show a significant difference at the two sampling dates (Table 3). Mean of species number was lower in May 2013 (31 ± 4) than in September 2014 (35 ± 2). The average diversity was 2.42 ± 0.22 in spring 2013, while that of the samples from autumn 2014 was 2.52 ± 0.23. No significant differences were found between the three basins based on species richness and Shannon diversity (Figures 2a and 2b; Table 3).

Statistically significant differences were found between 2013 and 2014 samples based on the relative abundance of species belonging to class Mediophyceae (Df = 22.393, $P < 0.001$) and Bacillariophyceae (Df = 22.438, $P < 0.001$) (Figure 3). In spring 2013, the mean contribution of Mediophyceae taxa to the total number of individuals reached 26.2%, due to dominance of *Stephanodiscus rugosus* and *Stephanodiscus neoastraea* (Figures 4–7). In the 2014 samples, the average proportion of Mediophyceae species was only 1.2%. NMDS projection displayed a clear separation according to the two sampling dates (ANOSIM R = 0.933, P = 0.001); however, the assemblages from the three basins (ANOSIM R = –0.023, P = 0.701) were not separated (Figure 8a). For only Bacillariophyceae taxa (Figure 8b) a similar result was found: structure of the diatom communities was different in the two years (ANOSIM R = 0.819, P = 0.001) and there was no separation according to the basins (ANOSIM R = –0.019, P = 0.678). The most frequent (counted in ≥4 samples) and abundant (maximum relative abundance ≥5%) species in both years were *Achnanthidium minutissimum*, *Amphora pediculus*, *Cocconeis placentula* var. *euglypta*, *Fragilaria capucina* var. *perminuta*, and *Gomphonema pumilum* var. *rigidum*. The most important Bacillariophyceae taxa with the same criteria in the 2013 samples were *Cymbella compacta*,

**Table 2.** Physical and chemical parameters measured in the littoral region of Lake Stechlin in September 2014.

| Variable | Unit | Mean ± SD | Min | Max |
|---|---|---|---|---|
| Conductivity | µS $cm^{-1}$ | 259 ± 2 | 251 | 265 |
| pH | | 8.4 ± 0.1 | 8.2 | 8.6 |
| Temperature | °C | 16.8 ± 0.2 | 16.4 | 17.1 |
| TP | µg $L^{-1}$ | 14.5 ± 4.7 | 11.0 | 29.0 |
| TN | µg $L^{-1}$ | 429.1 ± 54.3 | 281.0 | 542.0 |

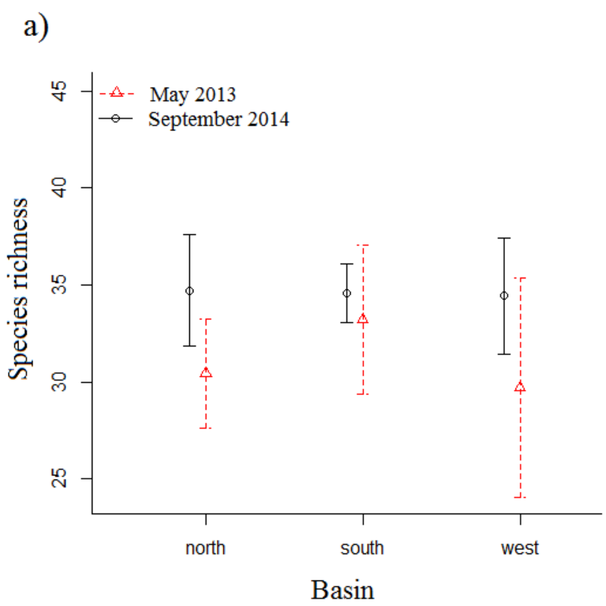



**Figure 2a.** Mean and standard deviation (SD) of species richness in the three basins in May 2013 and September 2014.

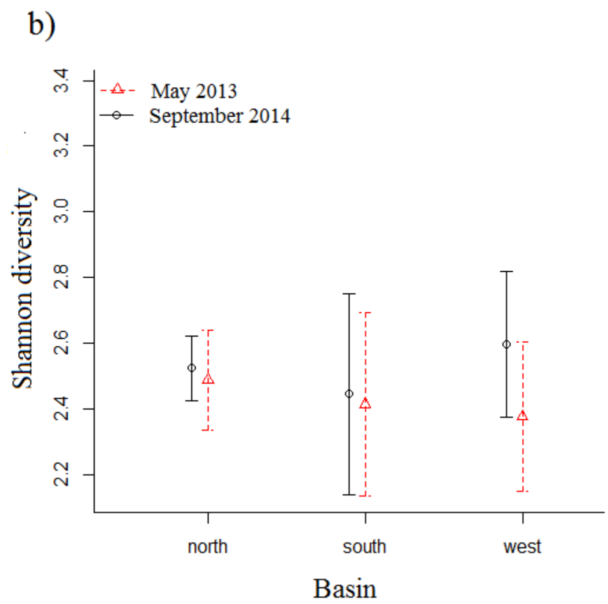



**Figure 2b.** Mean and standard deviation (SD) of Shannon diversity in the three basins in May 2013 and September 2014.

**Table 3.** Spatial and temporal effect on diversity metrics based on results of repeated measures ANOVA (Type III) with linear mixed-effect model (numDf = degrees of freedom in the numerator, denDf = degrees of freedom in the denominator, F = F-value, P = P-value).

| | | numDf | denDf | F | P |
|---|---|---|---|---|---|
| Species richness | Basin | 2 | 40 | 0.024 | 0.977 |
| | Sampling date | 1 | 40 | 5.379 | 0.026 |
| | Basin × sampling date | 2 | 40 | 1.163 | 0.323 |
| Shannon diversity | Basin | 2 | 40 | 0.829 | 0.783 |
| | Sampling date | 1 | 40 | 0.089 | 0.767 |
| | Basin × sampling date | 2 | 40 | 0.783 | 0.464 |

*Diatoma ehrenbergii*, *D. moniliformis*, *Fragilaria capucina* var. *vaucheriae*, *Gomphonema olivaceum*, *G. olivaceum* var. *olivaceoides*, *Nitzschia dissipata*, and *Rhoicosphenia tenuis*. In 2014, they were *Cocconeis neothumensis*, *Encyonopsis subminuta*, *Epithemia sorex*, *Fragilaria brevistriata*, *Karayevia clevei*, *K. laterostrata*, *Navicula cryptotenelloides*, *N. reichardtiana*, *N. tripunctata*, *Nitzschia dissipata* var. *media*, *N. lacuum*, *N. sociabilis*, and *Planothidium frequentissimum*. The most frequent and abundant taxa belonging to the class Bacillariophyceae are presented in Figures 9–34.

Preferences in pH of the water were available for 71% of the species (Supplement): 24% of these taxa were circumneutral, 59% alkaliphilous, and 17% alkalibiontic. With respect to trophic preferences, information was available for 79 taxa (Supplement). Most of the species (39%) belonged to the category eutraphentic and 29% were meso-eutraphentic. A considerable proportion (14%) of taxa were tolerant to oligo- to eutrophic environment. Altogether 13% of species belonged to categories 2 (oligo-mesotraphentic) and 3 (mesotraphentic) and 4% mainly occur in oligotrophic waters. Only one individual of a species was found in the category hypereutraphentic.

During this study 15 species were found that belong to threat categories of the Red List for Central Europe (Supplement, Figures 35–50). Five of them belong to category 3 ("endangered"): *Achnanthidium rosenstockii*, *Aneumastus stroesei*, and *Diploneis parma* were represented by only one individuum; *Planothidium joursacense* appeared with a small number of individuals;

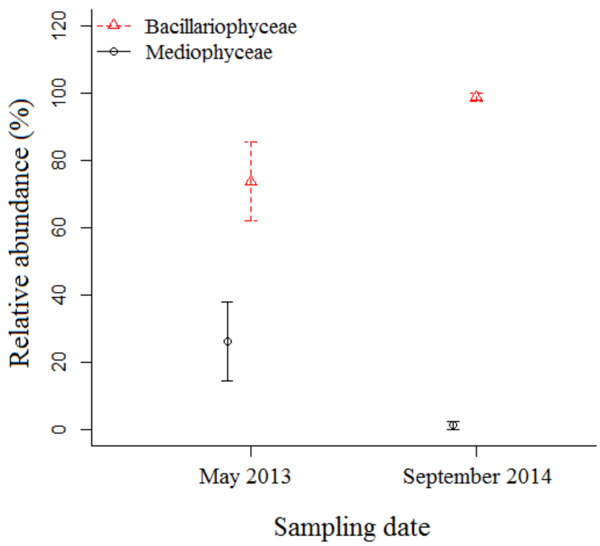
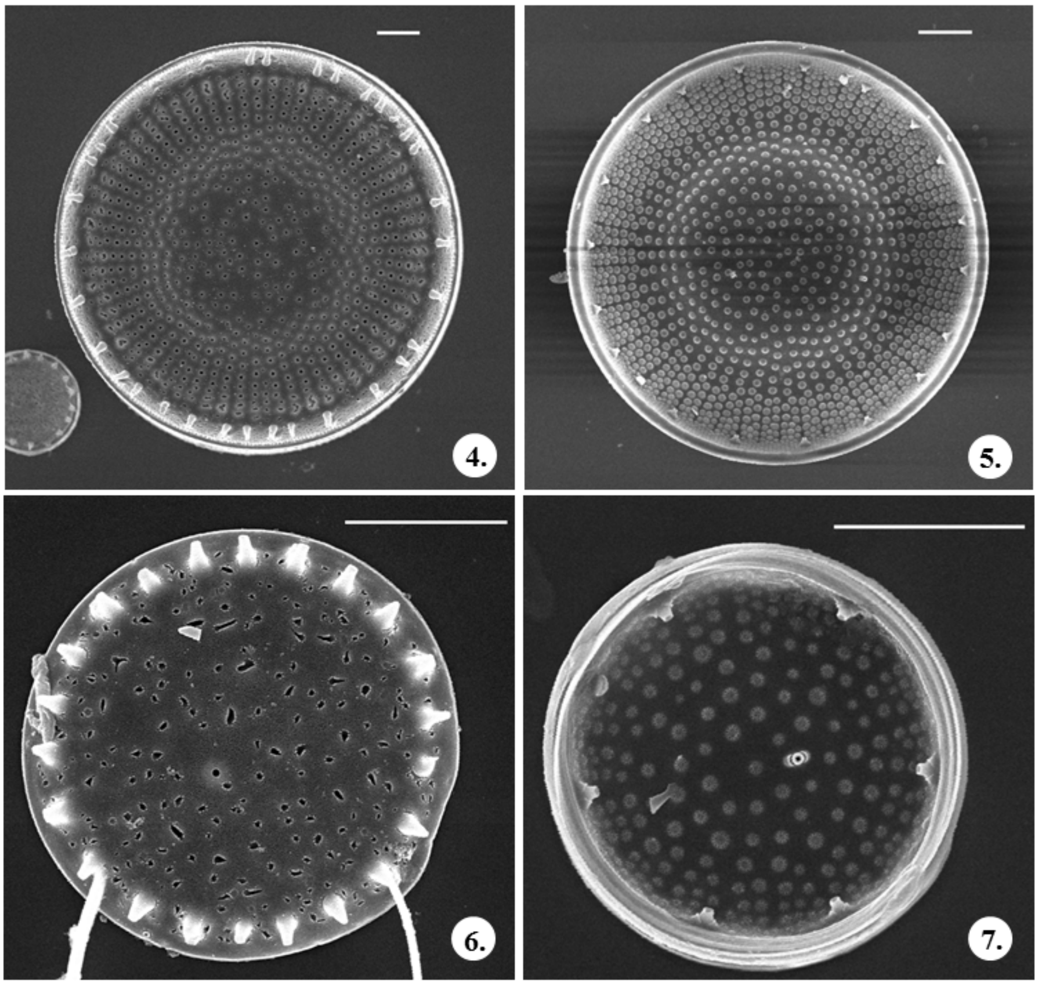



**Figure 3.** Mean and standard deviation (SD) of the relative abundance of Mediophyceae and Bacillariophyceae diatom species in May 2013 and September 2014.




**Figures 4–7.** SEM pictures of two dominant Mediophyceae species in spring. 4–5. *Stephanodiscus neoastraea*; 6–7. *Stephanodiscus rugosus*. Scale bar = 3 µm.

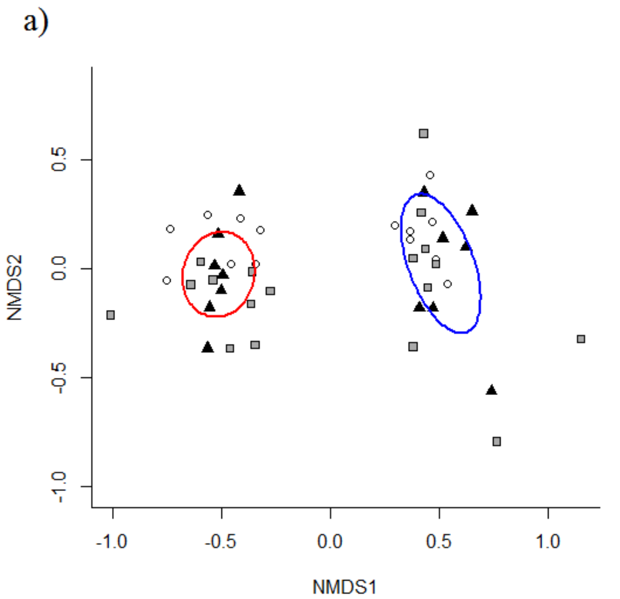



**Figure 8a.** NMDS (Bray–Curtis distance, stress 0.134) projection of phytobenthos samples based on transformed and standardized relative abundance data of total diatom species (open circle = north basin, grey square = south basin, black triangle = west basin). Red and blue ellipses are drawn around centroid of 2013 and 2014 classes.

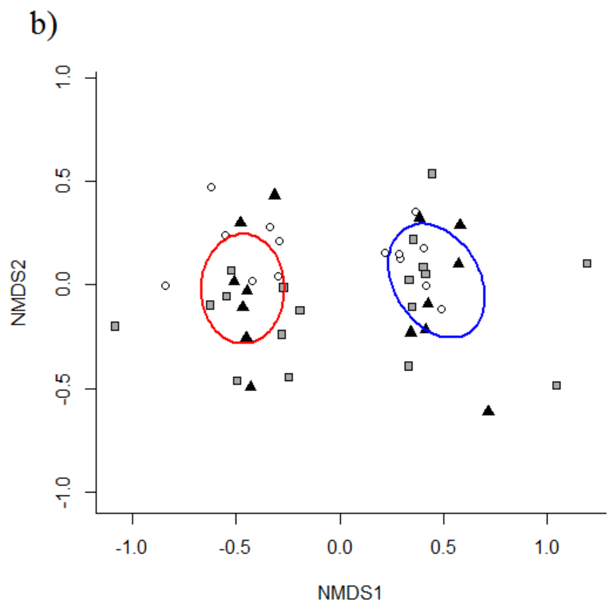
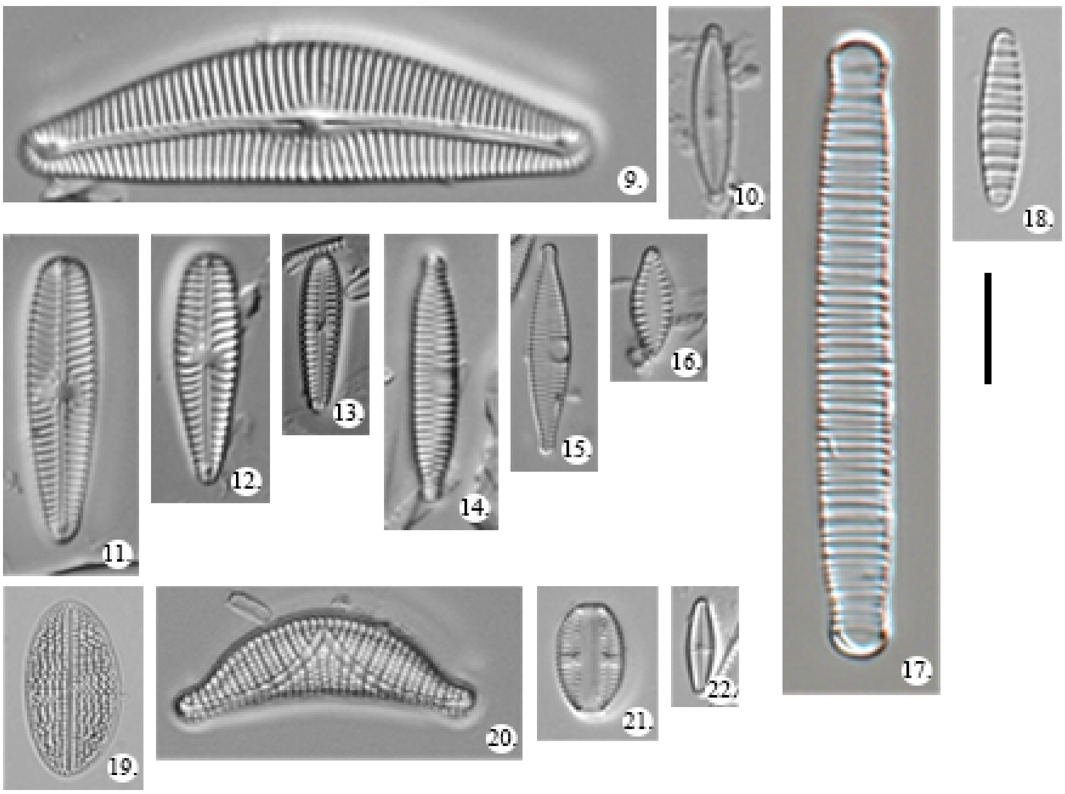
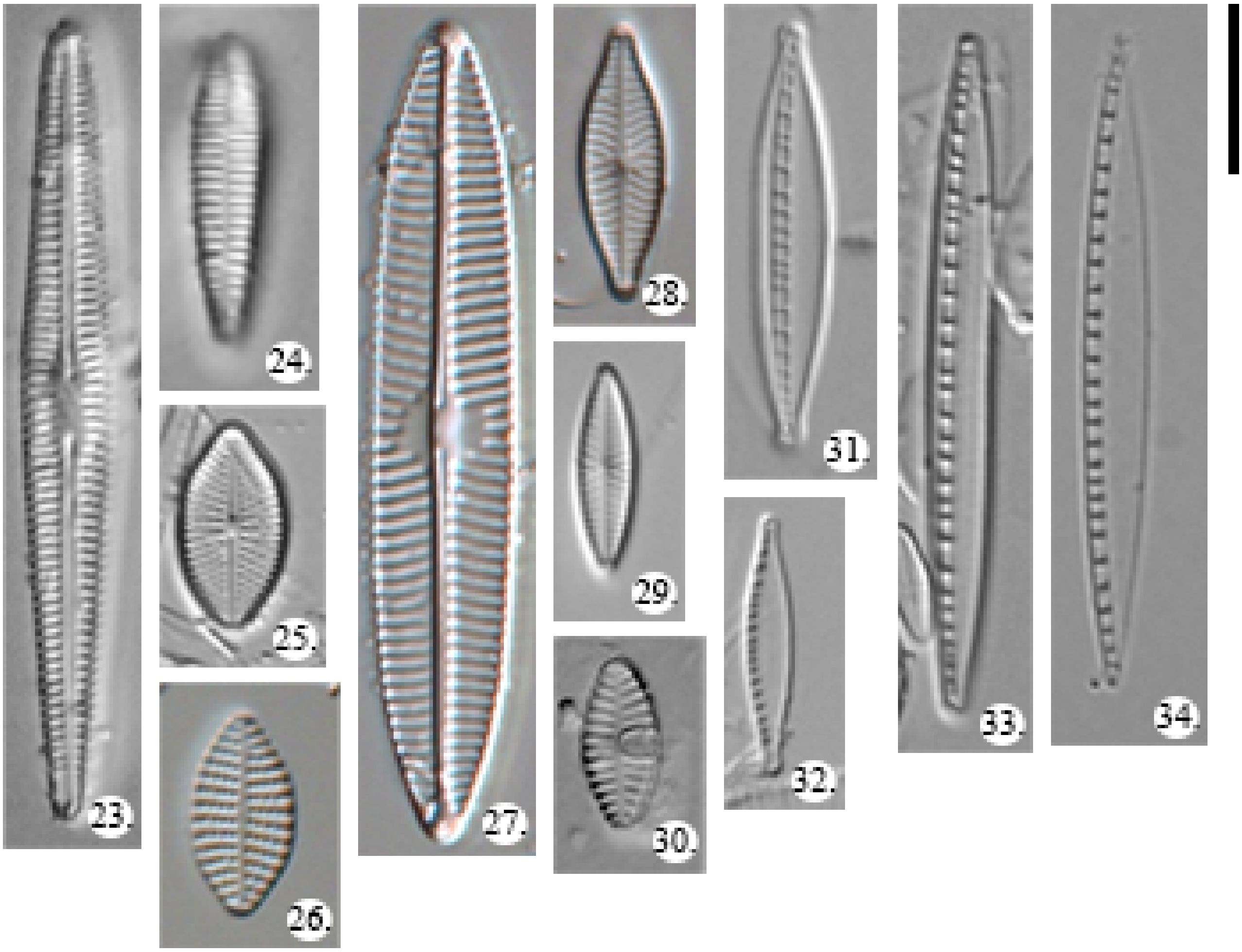



**Figure 8b.** NMDS (Bray–Curtis distance, stress 0.150) projection of phytobenthos samples based on transformed and standardized relative abundance data of Bacillariophyceae diatom species (open circle = north basin, grey square = south basin, black triangle = west basin). Red and blue ellipses are drawn around centroid of 2013 and 2014 classes.




**Figures 9–22.** Most frequent and abundant Bacillariophyceae species in Lake Stechlin. 9. *Cymbella compacta*; 10. *Encyonopsis subminuta*; 11. *Gomphonema olivaceum* var. *olivaceoides*; 12. *Gomphonema olivaceum*; 13. *Gomphonema pumilum* var. *rigidum*; 14. *Fragilaria capucina* var. *vaucheriae*; 15. *Fragilaria capucina* var. *perminuta*; 16. *Fragilaria brevistriata*; 17. *Diatoma ehrenbergii*; 18. *Diatoma moniliformis*; 19. *Cocconeis placentula* var. *euglypta*; 20. *Epithemia sorex*; 21. *Amphora pediculus*; 22. *Achnanthidium minutissimum*. Scale bar = 10 µm.

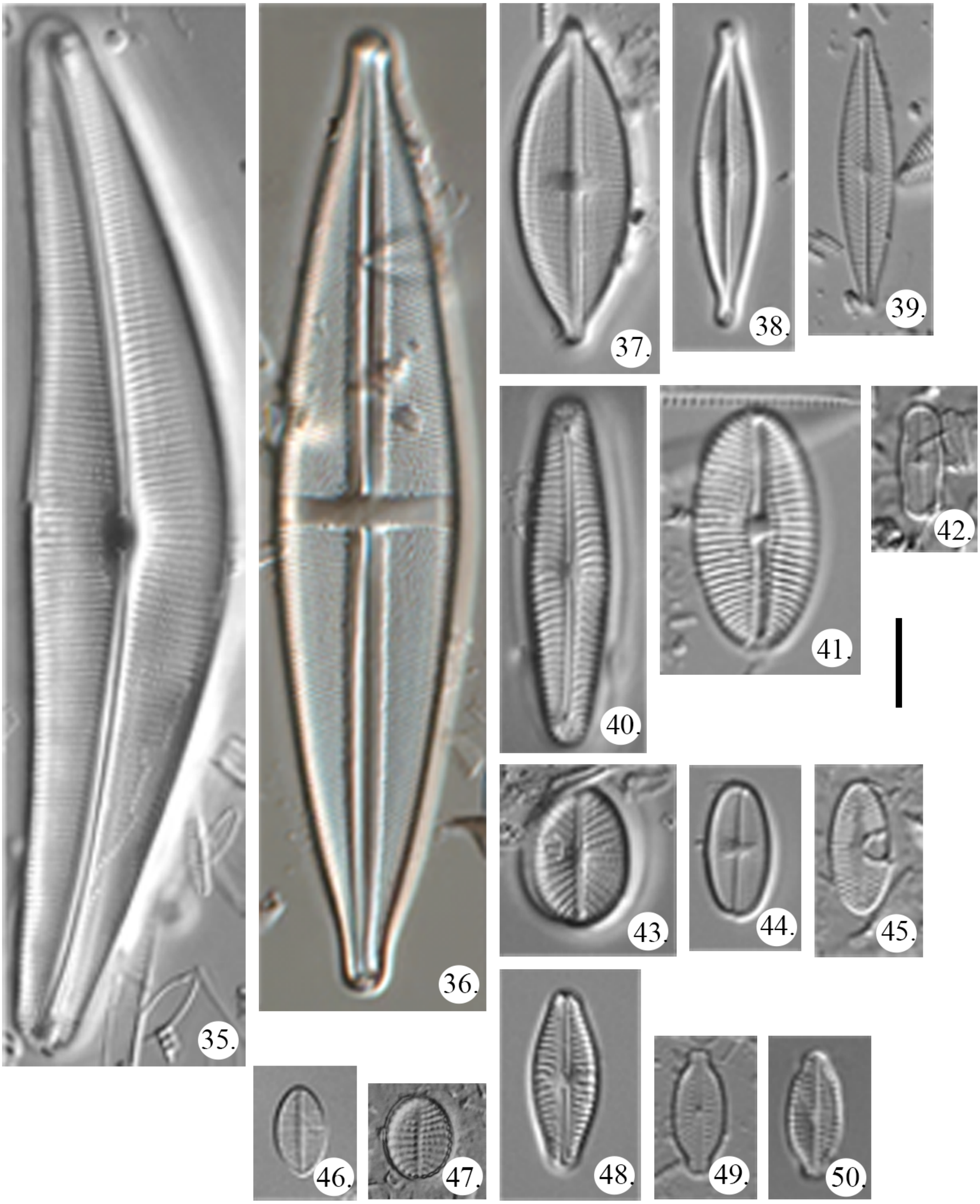



**Figures 23–34.** Most frequent and abundant Bacillariophyceae species in Lake Stechlin. 23–24. *Rhoicosphenia tenuis* (raphe and rapheless valve); 25–26. *Karayevia clevei* (raphe and rapheless valve); 27. *Navicula tripunctata*; 28. *Navicula reichardtiana*; 29. *Navicula cryptotenelloides*; 30. *Planothidium frequentissimum*; 31. *Nitzschia dissipata*; 32. *Nitzschia lacuum*; 33. *Nitzschia dissipata* var. *media*; 34. *Nitzschia sociabilis*. Scale bar = 10 µm.

and *Karayevia laterostrata* was characteristic in the 2014 samples. Two taxa were "extremely rare": *Cocconeis neodiminuta* and *Navicula hofmanniae*, which appeared only occasionally in some samples. Some species were found that are not endangered but are in regression (listed by decreasing number of occurrences): *Cocconeis neothumensis*, *Navicula subalpina*, *Cymbella lanceolata*, *Psammothidium bioretii*, *Cymbellafalsa diluviana*, *Cavinula scutelloides*, *Encyonema lacustre*, and *Stauroneis gracilis*.

## 4. Discussion

Rimet et al. (2015) supposed that the homogeneous or heterogeneous manner of benthic diatom communities can be affected by the size of the lake. In large lakes like Lake Balaton and Lake Geneva (Crossetti et al., 2013; Rimet et al., 2016) heterogeneity of littoral benthic assemblages was reported, which can be attributed to human impact, shore morphology (Snell and Irvine, 2015), or river inlets (i.e. point source of contaminants) (King et al., 2006; Rimet et al., 2016). On the other hand, waves can play an important role in the development of benthic communities in the wind-exposed littoral zone and makes them much more heterogeneous (Cantonati and Lowe, 2014). In contrast, since Lake Stechlin has a relatively small surface area and the anthropogenic impact is negligible, our results confirm previous observations by King et al. (2002, 2006) that assemblages in smaller lakes are quite homogeneous: species richness and diversity did not show any differences between the sampling sites and the basins, and the diatom composition showed uniform appearance along the littoral region of the lake. These results confirm our hypothesis that distribution of diatom communities is as homogeneous in the littoral region as phytoplankton communities in the pelagic zone (Fuchs et al., 2016). According to the standard




**Figures 35–50.** Red List species found in Lake Stechlin. 35. *Cymbella lanceolata*; 36. *Stauroneis gracilis*; 37. *Aneumastus stroesei*; 38. *Navicula hofmanniae*; 39. *Navicula subalpina*; 40. *Encyonema lacustre*; 41. *Diploneis parma*; 42. *Achnanthidium rosenstockii*; 43. *Cavinula scutelloides*; 44. *Psammothidium bioretii*; 45. *Planothidium joursacense*; 46. *Cocconeis neothumensis*; 47. *Cocconeis neodiminuta*; 48. *Cymbellafalsa diluviana*; 49–50. *Karayevia laterostrata* (raphe and rapheless valve). Scale bar = 10 µm.

methods, for financial and practical reasons, sampling of benthic diatoms from the littoral region in a single site per lake is recommended (King et al., 2006). Due to the spatial homogeneity of assemblages observed in Lake Stechlin, we confirm this suggestion for national monitoring surveys concerning benthic diatoms.

Besides spatial uniformity, temporal differences in species richness and species composition were found in Lake Stechlin. We assumed that the difference is due to the distinct sampling season (spring and autumn). Seasonal succession of phytoplankton in freshwater ecosystems (e.g., Padisák et al., 2006) is typically characterized by a spring diatom bloom and a less intense autumn bloom (e.g., Hinder et al., 1999; Simona et al., 1999). In Lake Stechlin, an explicit spring maximum and a moderate summer maximum of phytoplankton biomass can be observed. In addition to the autotrophic picoplankton, centric diatoms are prominent in the spring phytoplankton maximum, which starts to develop in early March and reaches a peak early in May. When water column stratification begins, biomass rapidly declines because diatoms sink to the hypolimnion (Scheffler and Padisák, 1997; Padisák et al., 1998). At the beginning of May 2013, a considerable proportion of Mediophyceae taxa were observed in the epilithic diatom samples due to the dominance of *Stephanodiscus rugosus* and *Stephanodiscus neoastraea. Stephanodiscus* species are considered to be among the most frequent diatoms in the spring phytoplankton bloom in Lake Stechlin (Padisák et al., 1998, 2003, 2010; Selmeczy et al., 2016). *Stephanodiscus minutulus* was commonly observed in the phytoplankton of Lake Stechlin (Padisák et al., 1998, 2003). Its variable outline of areolae (often slit-like) and in many cases flat valve face surface was described in previous studies (e.g., Scheffler and Morabito, 2003; Cruces et al., 2010), whose features correspond to the morphological characteristics of *Stephanodiscus rugosus* described in 1979 (Sieminska and Chudybowa). Even nowadays, the differentiation between *S. minutulus* and *S. rugosus* is disputed. However, according to some taxonomists (e.g., Casper et al., 1988) *S. minutulus* and *S. rugosus* are considered identical, while Houk et al. (2014) regarded them as two different species. Moreover, molecular evidence does not prove the difference, thus not solving the confusion in the literature concerning these species.

Seasonal dynamics of littoral benthic diatoms are poorly described (Cantonati and Lowe, 2014); the results have quite dissimilar patterns. Several studies proved clear seasonal patterns of diatom assemblages (Barbiero, 2000; Rimet et al., 2015), while others did not find any explicit seasonal succession (Jones and Flower, 1986; Nygaard, 1994). In turn, biomass of benthic diatoms in Lake Erken varied seasonally and variation in species composition was strongly related to nutrient conditions and wind (Kahlert et al., 2002). In temperate lakes where temporal changes in littoral benthic diatoms are typical, the appropriate sampling frequency representative for the whole lake must be carefully chosen. In Germany, the Water Framework Directive guideline for monitoring phytobenthos calls attention to a potentially high percentage of planktonic diatoms and suggests excluding these species from counting (Schaumburg et al., 2014). Since our samples taken in spring 2013 contained a considerable amount of planktonic diatoms, we do not suggest sampling from Lake Stechlin for ecological quality assessment in this season.

Many of our most frequent and abundant species earlier not listed by Casper (1985) are common in lakes of the Baltic Lake District (e.g., *Navicula cryptotenelloides*, *Planothidium frequentissimum*) or in water bodies of the alpine regions (e.g., *Diatoma ehrenbergii*), or in both areas (e.g., *Encyonopsis subminuta*, *Gomphonema olivaceum* var. *olivaceoides*, *G. pumilum* var. *rigidum*). Others are rather characteristic for large rivers (e.g., *Cymbella compacta*, *Nitzschia sociabilis*) (Hofmann et al., 2013). Among our Red List species absent from Casper's synthesis, there were some indicators of excellent ecological quality. These species can be found mainly in the alpine regions but rarely in the North German lakes (e.g., *Achnanthidium rosenstockii*, *Navicula subalpina*) and some are common in the latter area (e.g., *Cocconeis neothumensis*, *Cymbellafalsa diluviana*, *Planothidium joursacense*) (Hofmann et al., 2013).

In accordance with the slightly alkaline environment determined in the littoral region of the lake, most of the species found in the phytobenthos were alkaliphilous or alkalibiontic, while others preferred circumneutral waters. Except two sampling dates, the trophic status of the pelagic zone judged by the OECD criteria for TP (1982, Table 1) was mesotrophic in 2013 and 2014, which is in accordance with our results found in the littoral region (Table 2). Schönfelder et al. (2002) determined a low nutrient content and low trophic state based on benthic diatom community of Lake Stechlin between 1992 and 1999. Using the same samples, Schönfelder et al. (2005) calculated three diatom indices and they gave distinct results: diatom index for planktonic (DI-PROF) and benthic (DI-BENT) taxa in the profundal zone indicated oligotrophic and weakly mesotrophic while index for littoral samples (DI-LIT) showed a strongly mesotrophic state. Their mean referred to a weakly mesotrophic state. Our results support the previous conclusions (Koschel et al., 2002; Padisák et al., 2010) that the trophic status of the lake changed from oligotrophic to mesotrophic in the last several years, as most of the taxa identified in the epilithon were meso-eutraphentic, eutraphentic, or tolerate a wide range of trophic levels.

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**Supplement.** List of diatom taxa found in Lake Stechlin in 2013 spring and 2014 autumn. RL = Red List species (Lange-Bertalot, 1996), 3 = endangered, V = decreasing, R = extremely rare, D = data scarce, * = at present not considered threatened, ** = surely not threatened. B = Basin where the taxon was counted, n = north basin, s = south basin, w = west basin. S = season, SP = spring, A = autumn. Ecological preferences according to van Dam et al. (1994), pH = pH preferences. 3 = circumneutral, 4 = alkaliphilous, 5 = alkalibiontic. T = trophic preferences, 1 = oligotraphentic, 2 = oligo-mesotraphentic, 3 = mesotraphentic, 4 = meso-eutraphentic, 5 = eutraphentic, 6 = hypereutraphentic, 7 = oligo to eutraphentic (hypereutraphentic). + = species listed by Casper (1985).

| Taxa | RL | B | S | pH | T | Casper (1985) |
|---|---|---|---|---|---|---|
| *Achnanthidium minutissimum* (Kützing) Czarnecki | ** | n, s, w | SP, A | 3 | 7 | + |
| *Achnanthidium rosenstockii* (Lange-Bertalot) Lange-Bertalot | 3 | n | A | 4 | 2 | |
| *Amphipleura pellucida* (Kützing) Kützing | * | s | SP | 4 | 2 | + |
| *Amphora aequalis* Krammer | * | w | A | | | |
| *Amphora indistincta* Levkov | | n, s | A | | | |
| *Amphora pediculus* (Kützing) Grunow ex A.Schmidt | ** | n, s, w | SP, A | 4 | 5 | + |
| *Amphora stechlinensis* Levkov & Metzeltin | | s | A | | | |
| *Aneumastus minor* Lange-Bertalot | | n, s, w | SP, A | 5 | | |
| *Aneumastus stroesei* (Østrup) D.G.Mann | 3 | s | A | 5 | 4 | |
| *Asterionella formosa* Hassall | ** | n, s | A | 4 | 4 | + |
| *Caloneis lancettula* (Schulz) Lange-Bertalot & Witkowski | | w | SP, A | | | |
| *Cavinula scutelloides* (W.Smith) Lange-Bertalot | V | n, w | SP, A | 5 | 5 | + |
| *Cocconeis neodiminuta* Krammer | R | s, w | SP, A | | | + |
| *Cocconeis neothumensis* Krammer | V | n, s, w | A | 5 | | |
| *Cocconeis pediculus* Ehrenberg | ** | n, s, w | SP, A | 4 | 5 | |
| *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow | ** | n, s, w | SP, A | 4 | 5 | + |
| *Cocconeis placentula* var. *lineata* (Ehrenberg) van Heurck | ** | n, s, w | A | 4 | 5 | + |
| *Cocconeis pseudolineata* (Geitler) Lange-Bertalot | D | n, s, w | A | 4 | | |
| *Craticula cuspidata* (Kützing) D.G.Mann | ** | n | SP | 4 | 5 | + |
| *Cyclotella ocellata* Pantocsek | * | n, s, w | SP, A | 4 | 4 | + |
| *Cyclotella radiosa* (Grunow) Lemmermann | * | n, s | A | 4 | 5 | |
| *Cyclotella stelligera* Cleve & Grunow | * | n | A | | | |
| *Cymbella compacta* Østrup | * | n, s | SP, A | | | |
| *Cymbella excisa* Kützing | | n, s, w | SP, A | 4 | 5 | |
| *Cymbella lanceolata* (C.Agardh) C.Agardh | V | n, s, w | SP | | | + |
| *Cymbella neocistula* Krammer | | s, w | SP | 4 | 5 | |
| *Cymbellafalsa diluviana* (Krasske) Lange-Bertalot & Metzeltin | V | s, w | SP, A | | | |
| *Cymbopleura inaequalis* (Ehrenberg) Krammer | | w | A | | | |
| *Denticula kuetzingii* Grunow | * | n | A | 4 | 3 | + |
| *Diatoma ehrenbergii* Kützing | ** | n, s, w | SP, A | 5 | 4 | |
| *Diatoma moniliformis* (Kützing) D.M.Williams | ** | n, s, w | SP | 5 | 5 | |
| *Diatoma tenuis* C.Agardh | ** | n, s, w | SP | 4 | 5 | + |
| *Diploneis oculata* (Brébisson) Cleve | * | s | A | 3 | | |
| *Diploneis parma* Cleve | 3 | s | A | | | |
| *Encyonema caespitosum* Kützing | ** | n, s, w | SP, A | | 7 | |
| *Encyonema lacustre* (C.Agardh) F.W.Mills | V | s | A | 4 | 4 | |
| *Encyonema prostratum* (Berkeley) Kützing | ** | n, s, w | SP, A | 4 | 5 | + |
| *Encyonema reichardtii* (Krammer) D.G.Mann | * | s | A | | | |
| *Encyonema silesiacum* (Bleisch) D.G.Mann | * | n, s, w | SP, A | 3 | 7 | |
| *Encyonopsis subminuta* Krammer & E.Reichardt | | n, s, w | SP, A | 3 | 1 | |
| *Epithemia adnata* (Kützing) Brébisson | ** | s, w | A | 5 | 4 | + |
| *Epithemia frickei* Krammer | | n, s, w | SP, A | 4 | | |
| *Epithemia sorex* Kützing | ** | n, s, w | SP, A | 5 | 5 | + |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Epithemia turgida* (Ehrenberg) Kützing | * | n, s, w | SP, A | 5 | 4 | + |
| *Eucocconeis laevis* (Østrup) Lange-Bertalot | * | s, w | SP | 3 | 1 | |
| *Fallacia subhamulata* (Grunow) D.G.Mann | * | s | A | 3 | 4 | |
| *Fragilaria acus* (Kützing) Lange-Bertalot | * | s | SP | 4 | 5 | + |
| *Fragilaria brevistriata* Grunow | ** | n, s, w | SP, A | 4 | 7 | + |
| *Fragilaria capucina* var. *mesolepta* (Rabenhorst) Rabenhorst | ** | n, s, w | SP | 4 | | + |
| *Fragilaria capucina* var. *perminuta* (Grunow) Lange-Bertalot | * | n, s, w | SP, A | 3 | | |
| *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot | ** | n, s, w | SP, A | 4 | 5 | + |
| *Fragilaria construens* (Ehrenberg) Grunow | ** | n, s, w | A | 4 | 4 | + |
| *Fragilaria parasitica* var. *subconstricta* Grunow | ** | n, w | SP, A | 4 | 4 | |
| *Geissleria decussis* (Østrup) Lange-Bertalot & Metzeltin | ** | n, s, w | SP, A | 4 | 4 | |
| *Gomphoneis* sp. | | s, w | SP | | | |
| *Gomphonema acuminatum* Ehrenberg | ** | n, s, w | SP, A | 4 | 5 | + |
| *Gomphonema angusticephalum* E.Reichardt & Lange-Bertalot | | s, w | SP, A | | | |
| *Gomphonema italicum* Kützing | | n, w | SP | | | |
| *Gomphonema olivaceum* (Hornemann) Brébisson | ** | n, s, w | SP, A | 5 | 5 | + |
| *Gomphonema olivaceum* var. *olivaceoides* (Hustedt) Lange-Bertalot | * | n, s, w | SP | 3 | 3 | |
| *Gomphonema olivaceum* var. *olivaceolacuum* Lange-Bertalot & Reichardt | * | n, s | SP | | | |
| *Gomphonema pala* E.Reichardt | | n, s, w | SP, A | | | |
| *Gomphonema parvulum* (Kützing) Kützing | ** | n, s, w | SP, A | 3 | 5 | + |
| *Gomphonema pumilum* var. *rigidum* E.Reichardt & Lange-Bertalot | | n, s, w | SP, A | | | |
| *Gomphonema truncatum* Ehrenberg | * | s | SP | 4 | 4 | |
| *Gyrosigma sciotoense* (W.S.Sullivant) Cleve | | s, w | SP | 4 | 5 | |
| *Halamphora thumensis* (A.Mayer) Levkov | * | s | A | 5 | | |
| *Hippodonta capitata* (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski | * | n, s | SP, A | 4 | 4 | |
| *Hippodonta lueneburgensis* (Grunow) Lange-Bertalot, Metzeltin & Witkowski | | w | SP | | | |
| *Karayevia clevei* (Grunow) Round & Bukhtiyarova | * | n, s, w | SP, A | 4 | 4 | + |
| *Karayevia laterostrata* (Hustedt) Round & Bukhtiyarova | 3 | n, s, w | A | 3 | 1 | |
| *Kolbesia gessneri* (Hustedt) M.Aboal | | s, w | SP, A | 4 | 4 | |
| *Lemnicola hungarica* (Grunow) F.E.Round & P.W.Basson | ** | s | A | 4 | 6 | |
| *Martyana martyi* (Héribaud-Joseph) Round | * | s | A | 4 | 4 | + |
| *Navicula antonii* Lange-Bertalot | | n, s, w | SP, A | 4 | 5 | |
| *Navicula capitatoradiata* Germain | ** | n, s, w | SP, A | 4 | 5 | |
| *Navicula cari* Ehrenberg | ** | s | A | | 7 | + |
| *Navicula cryptotenella* Lange-Bertalot | ** | n, s, w | SP, A | 4 | 7 | |
| *Navicula cryptotenelloides* Lange-Bertalot | * | n, s, w | SP, A | 4 | 7 | |
| *Navicula hofmanniae* Lange-Bertalot | R | n, s, w | A | | | |
| *Navicula jakovljevicii* Hustedt | | n, s, w | SP, A | | | |
| *Navicula radiosa* Kützing | ** | n, s, w | SP, A | 3 | 4 | + |
| *Navicula reichardtiana* Lange-Bertalot | ** | n, s, w | SP, A | 4 | | |
| *Navicula reinhardtii* (Grunow) Grunow in Cl. & Möller | | n, s, w | SP, A | 5 | 5 | + |
| *Navicula subalpina* Reichardt | V | n, s, w | SP, A | | | |
| *Navicula tripunctata* (O.F.Müller) Bory de Saint-Vincent | ** | n, s, w | SP, A | 4 | 5 | |
| *Navicula utermoehlii* Hustedt | * | s | A | 3 | 3 | |
| *Neidium dubium* (Ehrenberg) Cleve | * | s, w | SP, A | 3 | 4 | |
| *Nitzschia archibaldii* Lange-Bertalot | * | n, s, w | A | 3 | 5 | |
| *Nitzschia dissipata* (Kützing) Rabenhorst | ** | n, s, w | SP, A | 4 | 4 | + |
| *Nitzschia dissipata* var. *media* (Hantzsch) Grunow | D | n, s, w | SP, A | 4 | | |
| *Nitzschia lacuum* Lange-Bertalot | * | n, s, w | SP, A | 4 | 3 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Nitzschia sociabilis* Hustedt | ** | n, s, w | A | 3 | 5 | |
| *Nitzschia sublinearis* Hustedt | * | n, s, w | SP, A | | | |
| *Placoneis clementis* (Grunow) E.J.Cox | * | s | SP | | | |
| *Placoneis minor* (Grunow) Lange-Bertalot | | n | SP | | | |
| *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot | ** | n, s, w | SP, A | 4 | 7 | |
| *Planothidium joursacense* (Héribaud-Joseph) Lange-Bertalot | 3 | n, s | A | 4 | 2 | |
| *Planothidium lanceolatum* (Brébisson ex Kützing) Bukhtiyarova | ** | w | SP | 4 | 5 | + |
| *Planothidium rostratum* (Østrup) Lange-Bertalot | D | n, s, w | SP, A | 4 | 5 | + |
| *Platessa conspicua* (A.Mayer) Lange-Bertalot | ** | n, s, w | SP, A | 3 | 7 | + |
| *Platessa ziegleri* (Lange-Bertalot) Lange-Bertalot | * | s, w | SP, A | | | |
| *Psammothidium bioretii* (Germain) Bukhtiyarova & Round | V | n, s | SP, A | 3 | 3 | |
| *Reimeria sinuata* (Gregory) Kociolek & Stoermer | ** | n, s, w | SP, A | 3 | 3 | |
| *Rhoicosphenia tenuis* Z.Levkov & T.Nakov | ** | n, s, w | SP, A | | | |
| *Rhopalodia gibba* (Ehrenberg) Otto Müller | * | n, s, w | A | 5 | 5 | + |
| *Sellaphora pupula* (Kützing) Mereschkovsky | ** | s, w | SP, A | 3 | 4 | + |
| *Simonsenia delognei* (Grunow) Lange-Bertalot | ** | s | A | | 5 | |
| *Stauroneis gracilis* Ehrenberg | V | w | A | | | |
| *Staurosira construens* var. *binodis* (Ehrenberg) P.B.Hamilton | * | s, w | A | 4 | 4 | + |
| *Staurosira venter* (Ehrenberg) Cleve & Moeller | ** | n, s, w | SP, A | 4 | 4 | + |
| *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round | ** | n, s, w | SP, A | 4 | 7 | + |
| *Stephanodiscus binatus* H.Håkansson & H.J.Kling | | n, s, w | SP | | | |
| *Stephanodiscus neoastraea* Håkansson & Hickel | ** | n, s, w | SP, A | 5 | 5 | |
| *Stephanodiscus rugosus* J.Sieminska & D.Chudybowa | | n, s, w | SP, A | | | |
| *Tabularia fasciculata* (C.Agardh) D.M.Williams & Round | | s | SP | | | |
| *Tryblionella angustata* W.Smith | * | s | SP | 3 | 3 | |
| *Ulnaria ulna* (Nitzsch) P.Compère | * | n, s, w | SP | 4 | 7 | + |