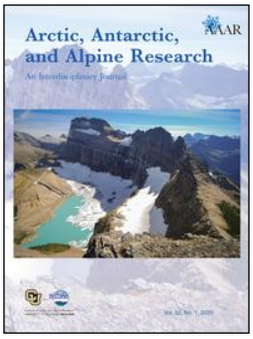

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Identification of the ecological preferences of *Cyclotella comensis* in mountain lakes of the northern European Alps

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ABSTRACT

Planktic diatom ecology in the mountain lakes of the northern European Alps has only been studied sparsely so far. To fill this knowledge gap, the driving parameters of planktic diatom assemblage composition in the euphotic zones of twenty lakes located between 955 and 2,060 m a.s.l. were assessed. The mean August water temperature, concentration of major ions, total phosphorous, and lake physical parameters explained significant amounts of variation within the diatom assemblages, as identified by redundancy analysis and consecutive backward selection. *Cyclotella comensis* was the most abundant taxon in these oligotrophic (<17 total phosphorus µg/L), phosphorous (P) limited, stratified study lakes, particularly when the calcium concentration was high (>35 mg/L). The results of generalized linear models and generalized additive models further revealed that August surface temperature, thermocline depth, and nitrate-N positively and significantly influenced *C. comensis* growth. These results shed light on the interplay between physical and chemical parameters as important drivers of *C. comensis* abundance in temperate mountain lakes. They may aid in the interpretation of past and the prediction of future climate-driven changes in planktic diatom composition in these lakes.

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Cyclotella comensis; mountain lakes; lake water temperature; phytoplankton

Introduction

Mountain lakes are often remote, and their catchments are therefore less affected by anthropogenic factors than the catchments of other lakes. This makes mountain lakes good sentinels for the study of environmental change (Catalan et al. 2013). Because long-term monitoring data on water properties are often lacking, temporal changes are usually inferred through abiotic and biotic remains in lake sediments (Smol, Birks, and Last 2002). In palaeolimnological studies, diatoms are well-established indicator organisms (Dixit et al. 1992; Scherer 2002) because their silica cell walls are preserved well in lake sediments and their characteristic cell structure allows for species identification by light microscopy (Scherer 2002). Diatoms have previously been used as indicators of pH, salinity, nutrient levels, mixing regimes, and light conditions (Flower and Battarbee 1983; Lotter et al. 1997, 1998; Curtis et al. 2009; Winder, Reuter, and Schladow 2009; Saros et al. 2016). However, interpretation of palaeolimnological results requires in-depth knowledge of the relationships between environmental factors and diatom distribution (Smol, Birks, and Last 2002).

A common approach to lake core analysis is the collection of training sets containing surface sediment samples with diatom assemblages representing the current state of lakes (e.g., Hall and Smol 1992). Though this approach has yielded valuable insights, it presents some limitations in terms of interpretation, because surface sediment samples commonly represent several years and many life cycles of diatoms, whereas chemical measurements are usually only taken once. Hence, the need for better integration of ecological information in paleoecology is increasingly acknowledged (Davidson et al. 2018).

Little is known about what controls the abundant planktic diatom *Cyclotella comensis* across ecological gradients (Saros and Anderson 2015). This species is an important component of many temperate lakes and shows pronounced reactions to climate change (Rühland, Paterson, and Smol 2008, 2015; Winder,

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Supplemental data for this article can be accessed here.

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Reuter, and Schladow 2009; Reavie et al. 2017). In terms of the distribution of this taxon, the interplay between environmental drivers such as lake temperature (Livingstone and Dokulil 2001), mixing patterns (Kraemer et al. 2015), nutrient composition, and turbidity (Whitehead et al. 2009) as well as competition with other planktic taxa (Jäger, Diehl, and Schmidt 2008; Stomp et al. 2011) are important.

Within the northern European Alps, only one comprehensive study investigating the ecology of planktic diatoms including *C. comensis* exists (Wunsam, Schmidt, and Klee 1995). The lakes sampled in that study were mostly located at elevations below 1,500 m a.s.l., although many lakes in the region are found at higher elevations. Therefore, the present study examined the ecological preferences of planktic diatom assemblages in twenty mountain lakes, with special emphasis on the ecology of *C. comensis*. This study was designed to survey lakes along an elevational gradient from 955 to 2,060 m a.s.l. Because the pH and total phosphorous (TP) gradients were short, it was hypothesized that changes in water temperature would influence planktic diatom assemblage composition along with concomitant changes in water chemistry (Reavie et al. 2017); that is, nitrate concentration and turbidity.

Study sites

The twenty study lakes are located in Bavaria (Germany) and Tyrol (Austria) along a longitudinal gradient of 220 km and a latitudinal gradient of 50 km (Figure 1).

Most of the lakes were formed by cirque glaciers. Typically, they are small (<7 ha) and shallow (<20 m; Table 1), consisting of one main basin. Two of the lakes are karstic; they are nearly round and have a smaller surface area–to-volume ratio than lakes of glacial origin.

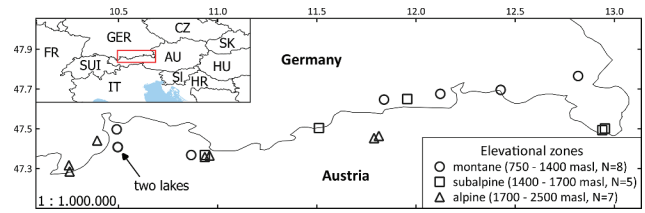

Figure 1. Geographical and zonal locations of the sampled lakes in the northern Alps in Austria and Germany. Background map based on Natural Earth data (2020).

The elevation of the twenty lakes ranges from 955 to 2,060 m.a.s.l. (Table 1). Eight of the lakes are located in montane forest (750–1,400 m a.s.l.), five are located in subalpine forest (1,400–1,700 m a.s.l.), and seven are located in alpine meadows and rock basins (1,700–2,500 m a.s.l.). In the study region, the montane forest is dominated by beech (*Fagus sylvatica*), spruce (*Picea abies*), and maple (*Acer pseudoplatanus*), whereas the subalpine forest mainly consists of spruce and—at the ecotone between forest and bare meadows—pine (*Pinus mugo* ssp. *mugo*). In alpine meadows, shrubs (e.g., *Rhododendron hirsutum*), sedge meadows (e.g., *Carex sempervirens*), and fellfields predominate.

Methods

Sampling and laboratory procedures

The twenty lakes were sampled twice during the ice-free period, once between June and the middle of August and once between August and November 2016. On the first sampling date, bathymetric measurements were taken with an echo sounder (Lawrence HDS8, Oslo, Norway), and a buoy fixed with a rope on a stone was subsequently installed at the deepest point of each lake. Temperature

Table 1. Descriptive metrics of the measured and calculated environmental variables of the twenty-lake set.

Parameter	Abbreviation	Minimum	Maximum	Mean	Median	Standard deviation
Elevation (m a.s.l.)	alt	955	2,060	1,491	1,537	373
Lake area (ha)	area	0.1	6.4	2.2	1.9	1.9
Maximum depth (m)	depth	1.5	20.7	9.3	7.4	6.4
Secchi depth (m)	secchi	1.5	11.3	5.3	4.6	2.91
Nitrate-N (mg/L)	NO3_N	0.03	0.93	0.39	0.41	0.27
Total phosphorous (µg/L)	TP	1.0	17.0	6.1	4.8	3.6
Silicate (mg/L)	Si	0.12	0.77	0.25	0.18	0.20
Ammonia-N (µg/L)	NH4_N	3.8	126.9	36.8	25.0	40.0
Calcium (mg/L)	Ca	14.97	49.24	31.62	30.53	9.29
Magnesium (mg/L)	Mg	1.42	18.40	6.90	5.20	4.60
pH value	pH	7.9	9.0	8.4	8.5	0.3
Conductivity (µS/cm)	cond	150.6	536.7	251.5	222.2	93.0
Ø August bottom temperature (°C)	T_B	4.5	18.4	9.4	8.8	4.0
Ø August surface temperature (°C)	T_S	8.8	22.6	15.1	14.5	3.8
Thermocline depth (m)	TCL	0.17	6.5	2.2	1.3	2.0
Ø Buoyancy frequency in epilimnion (s^{-1})	BFe_mean	0.0001	0.0067	0.0013	0.0008	0.00
Buoyancy frequency at thermocline (s^{-1})	BF_TCL	0.0001	0.0067	0.0017	0.0014	0.00
Atomic silica–to-nitrogen ratio	Si_N	0.07	4.30	0.58	0.27	0.93
Atomic nitrogen–to-phosphorous ratio	N_P	44.38	4,442.25	890.85	537.49	1,173.92

loggers (Onset Pendant UA-001-64 HOBO, Bourne, MA) were mounted on the rope 0.5 m above the sediment surface and 0.5 m below the water surface. Temperature data were recorded at 30-minute intervals between the first and second sampling dates. On both sampling dates, physical parameters (temperature, oxygen saturation, pH, and conductivity [at 25°C]) were measured with a multiprobe (WTW 350, Weilheim, Germany) at 1-m intervals from the deepest point of each lake.

After measuring the Secchi depth of each lake, 0.5 L of a mixed water sample was collected with a hose sampler from the euphotic zone (Z_{Euph}), which was defined as $Z_{Euph} = 5 \times Z_{Secchi}^{0.5}$ (DIN Technical Committee Water Analysis 2015). One half of the water sample was filtered (0.45 µm) on-site to analyze dissolved ions and the remaining sample was left unfiltered to analyze the concentration of TP. Both samples were stored at 4°C for further processing in the laboratory. Another liter of water was taken from the euphotic zone with the hose sampler and preserved with Lugol's solution to analyze planktic diatom communities (Throndsen 1978). At the end of the second sampling day, the temperature loggers, together with the stones, were retrieved from the lakes.

All chemical analyses were carried out in the laboratory of the Limnological Research Station in Iffeldorf. Standard colorimetric methods were applied using a Hitachi 150-200 photometer (Chiyoda, Japan) to determine the concentrations of TP (Murphy and Riley 1962), nitrate-N (Navone 1964), ammonia-N (Deutsches Institut für Normung e.V. 1983), and silica (Deutsches Institut für Normung e.V. 1983). The concentrations of major ions (calcium, magnesium, and sodium) were measured using a cation chromatograph (ICS-1100, Thermo Scientific, Waltham, MA).

Planktic diatom samples were concentrated with 0.45 µm syringe filters before further processing (Nixdorf et al. 2014). Diatoms were prepared according to van der Werff and Macan (1955). To analyze the composition of the diatom samples, 500 valves (including broken valves representing more than half of a complete valve) were identified in each case using a Leica DNM microscope at 1,000× magnification. Taxa were counted at the species level. Standard literature was used for identification (Krammer and Lange-Bertalot 1991a, 1991b, 1997a, 1997b; Krammer 2000, 2002; Lange-Bertalot 2001; Lange-Bertalot et al. 2017).

Data analysis

The atomic N/P ratios in lake water were calculated to determine pelagic nutrient limitation status by using the dissolved inorganic nitrogen–TP ratio (Bergström 2010; Kolzau et al. 2014). Our data set included only concentrations of nitrate-N and ammonia-N; nitrite-N was not measured. Therefore, the real dissolved inorganic nitrogen–TP ratio is probably higher than the results suggest. However, because nitrite occurs only at very low amounts under aerobic conditions and the conditions in the euphotic zones of the sampled lakes were mostly aerobic, this bias is probably negligible. Moreover, all lakes were found to be phosphorous (P) limited and integration of nitrite-N would have shifted the N/P ratio further in this direction. The lake mixing regime was assessed by calculating thermocline depth and buoyancy frequency at the thermocline and within the epilimnion based on temperature profiles using the R package rLakeAnalyzer (Winslow et al. 2019). Sodium was excluded from further analysis because it could only be detected in a few samples.

With the obtained set of nineteen abiotic parameters, a Pearson correlation matrix with Bonferroni-adjusted probabilities was computed (Haynes 2013) using the R package corrplot (Wei and Simko 2017). For significantly correlated parameters, coefficients of linear regression models were included. To identify relationships among environmental variables, principal component analysis (PCA) was carried out with the data sets of nineteen variables (Terbraak and Prentice 1988). Before analysis, all environmental variables except pH and elevation were log transformed to correct for nonnormal distribution (pH is a log scale and elevation showed a normal distribution). Further, the parameters were normalized by subtraction of the mean and dividing the result by the standard deviation for each variable (Oksanen et al. 2018).

The share of species with planktic life cycles was higher than 10 percent in all assemblages. For all calculations, benthic or tychoplanktic species were excluded and relative abundances were calculated based on the sum of obligate planktic species (Table S2). Before numerical analysis, the data set was Hellinger transformed (Prentice 1980) and the obtained Hellinger distance matrices were used for PCA (Legendre and Gallagher 2001). Prior to constrained analysis, variance inflation factors were calculated for the environmental data with the R package usdm (Naimi et al. 2014). To evaluate collinearity problems, the function "vifcor" of the usdm package was applied. According to the obtained results, no variable had collinearity problems. To evaluate whether diatom distribution followed a linear or unimodal trend, detrended correspondence analysis (DCA) was applied (Hill and Gauch 1980). For gradient lengths less than 3, linear constrained methods are considered appropriate; for gradient lengths between 3 and 4, linear or unimodal methods can fit; for higher gradient lengths, unimodal methods should be used (Terbraak and Prentice 1988). The DCA gradient length was 3.51 for the

first axis and 2.91 for the second axis. Based on the results of DCA and variance inflation factors, an initial redundancy analysis (RDA) with the fourteen initially measured variables was computed. The significance for the whole model and for the first and second RDA axes was assessed by means of a Monte Carlo permutation test with 999 permutations; all tests were significant ($p < .01$). For further evaluation of the importance of each single explanatory variable, backward selection was applied (Blanchet et al. 2008). With the selected variables, another RDA was performed. Because p values decrease and R^2 values increase with the number of explanatory variables, adjusted model values (R^2_{adj}) were obtained through Bonferroni–Holm correction (Haynes 2013). All models and each of the first two axes were significant as inferred by Monte Carlo permutation tests ($p < .01$). The explanatory potential and significance value of each single variable were obtained by setting the variable as the sole explanatory variable with all other variables as covariables in another round of Monte Carlo permutation tests. All multivariate analyses were carried out with the R package vegan (Oksanen et al. 2018).

To evaluate the correlation between environmental variables and *C. comensis*, generalized linear models (GLMs) were applied. For parameters with a significant influence on *C. comensis* based on GLM results and for further assumed important ecological drivers, generalized additive models (GAMs) were applied using the R package gam (Hastie 2019). GAMs were used instead of GLMs when the responses of *C. comensis* to interacting parameters were assumed to be nonlinear. All data analysis was carried out using the free statistics software R v3.6.3 (R Core Team 2013).

Results

Physical and chemical features

The lakes were shallow (maximum depth 20.7 m, median depth 7.4 m) and small (<6.4 ha). Though most of the lakes can be assumed to stratify during summer (the sampling period), at least four of the lakes probably mix irregularly because they are very shallow (<4 m). All lakes are P limited and well buffered, as reflected by pH values between 8 and 9 and high concentrations of major ions (Table 1). The Secchi depths of the lakes ranged from 1.5 m to 11.3 m (median = 4.6 m). At seven sites, the Secchi depth was equal to the maximum lake depth; that is, light reached the bottom of the lake. Concentrations of alkaline earth ions reached 49.2 mg/L for Ca^{2+} and 18.4 mg/L for Mg^{2+}. Accordingly, electrical conductivity averaged 251.5 µS/cm (reference temperature = 25°C). The maximum conductivity level, which was more than 500 µS/cm, was recorded in one of the karstic lakes (Sieglsee groß; see Table S1), which was strongly influenced by groundwater. Nitrate-N and TP concentrations were generally low, with a mean of 0.39 mg/L and 6 µg/L, respectively, classifying most lakes as oligotrophic according to Vollenweider (1968). Based on N/P ratios, all lakes were P limited (N/P > 43; sensu Klausmeier et al. 2004) and all but two lakes (Engeratsgundsee and Rappensee; see Table S1) were co-limited by silica (Si/N < 1.12; sensu Brzezinski 1985). The ammonia-N concentration was low in most lakes (median 26.7 µg/L), but showed a wide range (3.8–126.9 µg/L), possibly due to oxygen depletion in the hypolimnion of a few lakes. The means of the average August surface and bottom water temperatures were 15.1°C and 9.4°C, respectively.

The chemical parameters of the twenty study lakes mainly varied along the elevation gradient, which was correlated with PCA axis 1 (λ = 4.59, 24.17 percent; Figure 2). Elevation was negatively correlated with conductivity, ammonia-N, nitrate-N, N/P ratio, August surface temperature, and Ca and Mg concentrations. It was positively correlated with pH and the Si/N ratio (Figure S1, Figure S2). The second PCA axis (λ = 3.97, 20.91 percent) was positively correlated with lake depth and Secchi depth but negatively correlated with August surface and bottom temperatures, thermocline depth, and buoyancy frequency. The positive correlation between lake depth and Secchi depth was highly significant and can be explained by seven lakes that had equal Secchi depths and maximum depths (Table S1).

Bottom water temperature decreased significantly with maximum lake depth and Secchi depth and was positively correlated with surface water temperature. Buoyancy frequency at the thermocline and within the epilimnion were negatively correlated with Secchi depth, whereas thermocline depth was not correlated with any of the measured variables. Correlations among nutrients were significant for nitrate-N and ammonia-N (positive), nitrate-N and TP (negative), ammonia-N and Ca (positive), and nitrate-N and Ca (positive; Figure S1).

Diatom assemblages

Obligate planktic taxa occurred with relative abundances of 10.4 to 100 percent (median = 79.8 percent, n = 20; Table S2). Of the fourteen identified planktic taxa, *Cyclotella comensis* was the most abundant (33 percent of all planktic taxa, present in ten lakes, abundance range = 0.4–100 percent, median = 19 percent). Also abundant were *Fragilaria nanana* (21 percent), *Fragilaria delicatissima* (12 percent), *Discostella woltereckii* (10 percent), *Fragilaria gracilis* (8 percent), and *Discostella stelligeroides* (7 percent; Table S2).

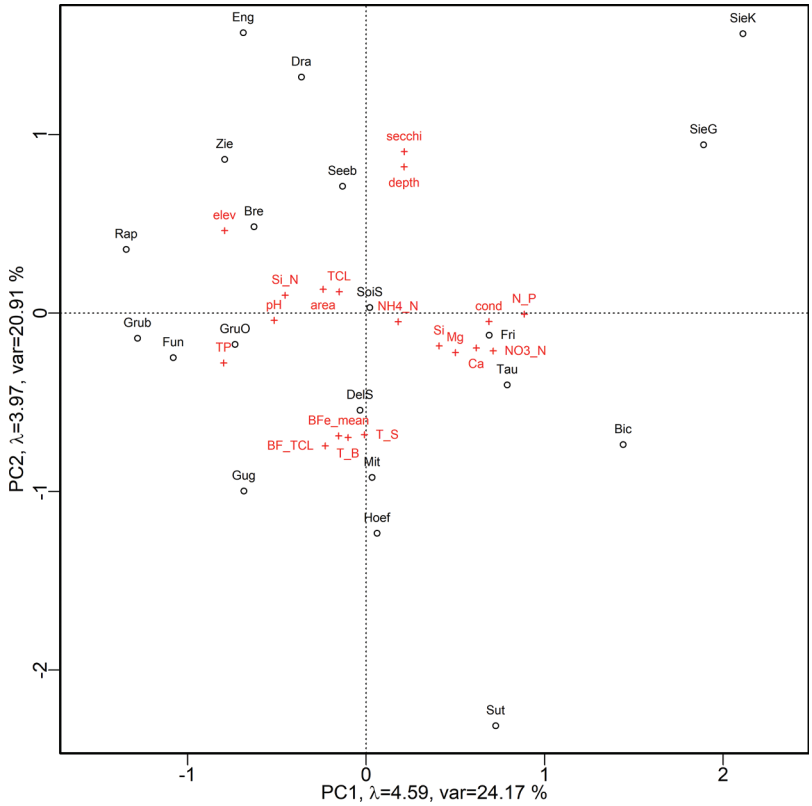

Figure 2. Principal component analysis correlation biplot for nineteen environmental variables measured in twenty mountain lakes in the northern European Alps. Principal components 1 and 2 (PC1, PC2) are plotted. λ indicates eigenvalues, var indicates percentage of explained variance. For variable and lake abbreviations, see Table S1.

Diatom–environment relationships

Variation in planktic taxa distribution was significantly influenced by the August surface temperature, lake area, Ca concentration, Secchi depth, Mg concentration, August bottom temperature, and TP, which explained 11.6, 7.6, 6.6, 5.3, 5.2, 5.1, and 4.6 percent of variation, respectively. The adjusted R^2 value of the full RDA model was 37.8 percent (Table 2).

For the planktic diatom data set, the first constrained RDA axis (λ = 0.172, variance = 29.99 percent, p = .001) was negatively correlated with August surface and bottom temperatures and TP. The second axis (λ = 0.079, variance = 11.26 percent, p = .001) was negatively correlated with Mg concentration and positively correlated with Secchi depth and lake area (Figure 3). The RDA biplot revealed a preference of *C. comensis* for warm, calcium-rich lakes, whereas *Fragilaria nanana* showed the opposite preference. *Discostella woltereckii* was abundant in lakes with high Secchi depths, whereas *Fragilaria delicatissima* showed a preference for magnesium-rich waters (Figure 3).

The results of the GLMs confirmed the tight coupling of *C. comensis* abundance and August surface temperature (p = .025, R^2 = 0.66) and further revealed a significant positive correlation of thermocline depth on *C. comensis* abundance (p = .047, R^2 = 0.41; Figure 4). None of the models including the other parameters significantly predicted *C. comensis* abundance; however, high relative abundances of *C. comensis* were found in samples with Ca values above 35 mg/L, Secchi depths of 4 to 5 m, and nitrogen-N levels of 0.5 to 1 mg/L. GLMs were also applied to all other taxa in the data set; however, no model identified a significant correlation between these taxa and any of the measured variables.

According to the GLM analysis, the relative abundance of *C. comensis* was significantly correlated with August surface temperature and thermocline depth. The GAMs also included nitrate-N because it was deemed to have an effect on *C. comensis* based on literature. For all three parameters, a significant GAM was found, with thermocline depth having the lowest Akaike information criterion (AIC) score and highest R^2_{adj} (Table 3). All combinations of parameters produced higher AIC scores, with August surface temperature and nitrate-N scoring lowest among all model combinations. The models suggested a pronounced increase in *C. comensis* abundance at lake surface temperatures above 18°C and nitrate-N values above 0.8 mg/L (Figure 5). *Cyclotella comensis* was also particularly dominant in the planktic diatom assemblages

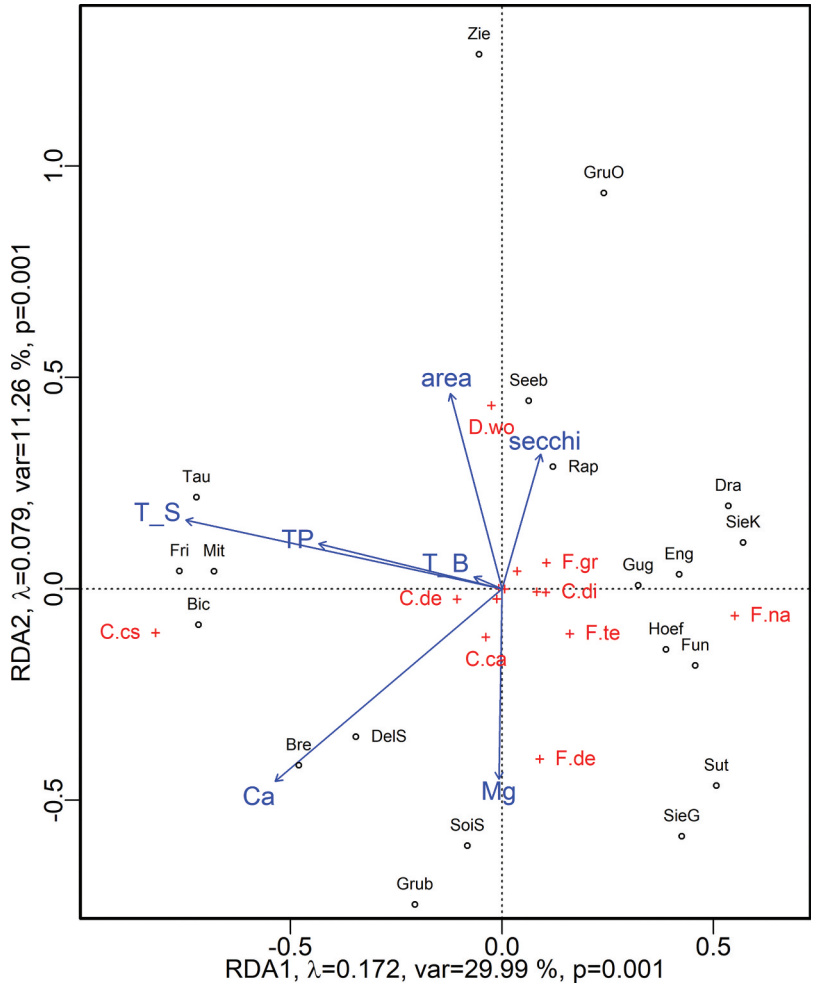

Figure 3. RDA correlation biplot of species scores and environmental parameters that significantly and independently influenced diatom taxon composition as determined by backward selection applied to RDA models for planktic diatom assemblages of twenty lakes. For variable, species, and lake abbreviations, see Table S1 and Table S2.

Table 2. Adjusted R^2 values for a planktic diatom RDA model with backward selected variables. Explained variance and *p* values were inferred from Monte Carlo permutation test.

Dataset	Variable	var. (%)	p
Plankton	T_S	11.6	0.001
n=20	area	7.6	0.007
R^2= 60.7 %	Ca	6.6	0.009
R^2_{adj} = 37.8 %	secchi	5.3	0.025
	Mg	5.2	0.026
	T_B	5.1	0.027
	TP	4.6	0.052

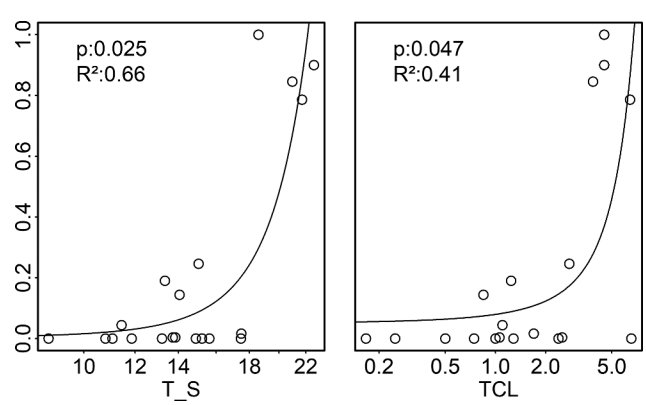

Figure 4. Relative abundances of *Cyclotella comensis* plotted against nineteen environmental variables. August surface temperature and thermocline depth. R^2 values and *p* values are given for generalized linear models; model prediction curves are plotted for significant models ($p < .05$). For abbreviations and units, see Table 1.

when August surface water temperatures and nitrate-N concentrations were high (Figure 6).

Discussion

Cyclotella comensis occurred at high abundance in the plankton communities of alkaline montane lakes with high August surface temperatures (>18°C) and thermocline depths of 4 to 5 m. The lakes were P limited but rich in nitrogen (>0.8 mg/L), giving high N/P ratios. Further, most of the lakes had intermediate Secchi

Table 3. Model coefficients for generalized additive models for abundance of cyclotella comensis in response to environmental variabels that proved to be important for *Cyclotella comensis* abundance based on GLM results and are known to be ecologically important factors influencing the taxon. For abbreviations see Table 1.

Model	F value	p	R^2_{adj}	AIC
T_S	34.27	< 0.001	0.941	215.3
TCL	55.15	< 0.001	0.963	206.3
NO3_N	4.854	0.013	0.421	257.9
log(NO3_N)	3.946	0.017	0.507	256.0
Secchi	1.655	0.201	0.210	264.7
T_S + TCL			0.864	230.0
T_S	6.082	0.020		
TCL	6.570	0.002		
T_S + NO3_N			0.930	218.6
T_S	17.619	< 0.001		
NO3_N	4.793	0.018		
TCL + NO3_N			0.88	228.7
TCL	20.221	< 0.001		
NO3_N	6.774	0.021		

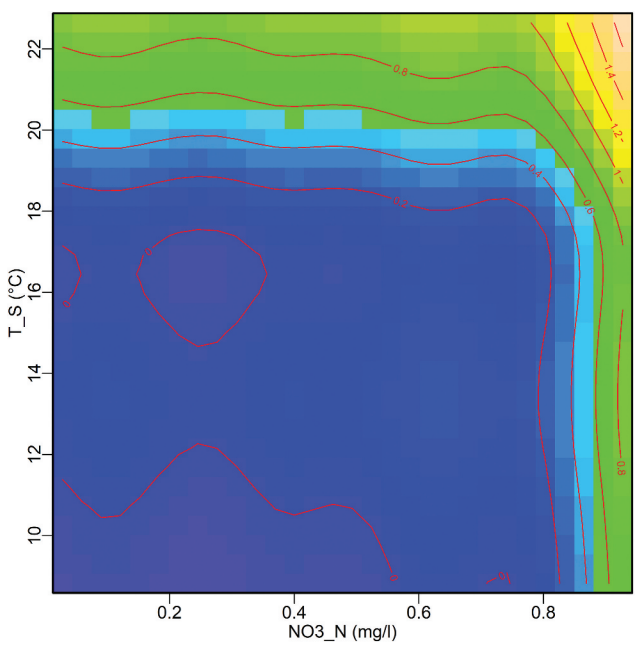

Figure 5. Generalized additive model results for the relative abundance of *Cyclotella comensis* and its interaction with August surface temperature and nitrogen-N. For model scores, see Table 3.

depths (4–5 m, range = 1.5–11.3 m). The ecology of *C. comensis* has been the subject of numerous studies involving the combination of palaeolimnological lake data and recent observations (Lotter and Bigler 2000), the compilation of training sets (Hall and Smol 1992; Wunsam, Schmidt, and Klee 1995; Werner and Smol 2006; Catalan et al. 2009; Curtis et al. 2009), investigations of in situ growth (Williamson et al. 2010a), and mesocosm experiments (Jäger, Diehl, and Schmidt 2008).

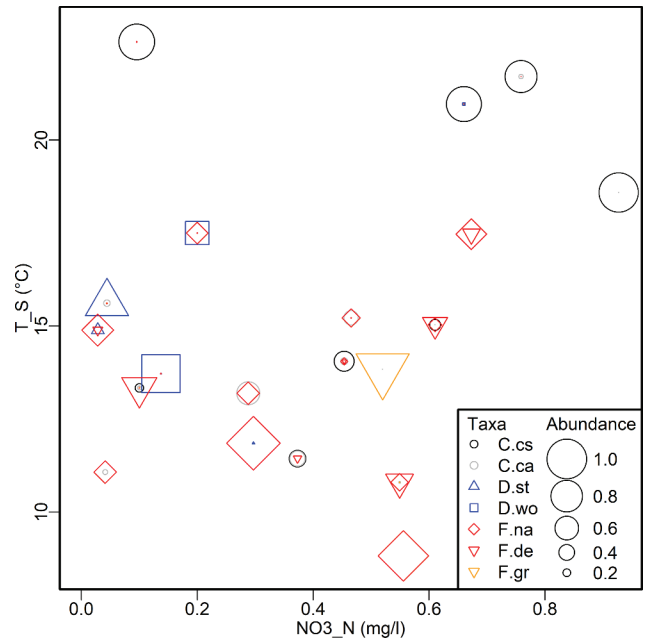

Figure 6. Scatterplot depicting relative abundances of the most frequent taxa in the data along the nitrate-N gradient and the August surface temperature gradient. The plotted taxa represent 93 percent of all counts. For species abbreviations, see Table S2.

Apart from one study that found *C. comensis* under slightly acidic conditions (Battarbee 1984), this taxon prefers alkaline conditions with an optimum pH between 8 and 9 (Scheffler, Nicklisch, and Schonfelder 2005; Werner and Smol 2006; Saros and Anderson 2015). In line with this, all study lakes were alkaline in the present study (pH range = 7.9–9.0, median = 8.5), and *C. comensis* was especially abundant at the higher end of the Ca^{2+} gradient (35–49 mg/L; range = 15–49 mg/L, median = 27 mg/L).

Cyclotella comensis is generally rare at TP concentrations above ca. 10 µg/L (Hall and Smol 1992; Wunsam, Schmidt, and Klee 1995; Ramstack et al. 2003; Werner and Smol 2006; Saros et al. 2012; Saros and Anderson 2015). In the present study, the taxon occurred only in one lake with a TP concentration above 10 µg/L (range = 1–17 µg/L, median = 5 µg/L). The results are in line with those of the only other comprehensive study on lake diatom ecology within the study region, which identified a TP optimum of <15 µg/L for *C. comensis* (range = 2–266 µg TP/L; Wunsam, Schmidt, and Klee 1995).

Despite the insights into *C. comensis* ecology that the present results provide, the responses of this taxon to environmental changes remain unclear in some respects. In particular, the interaction of epilimnetic water temperature with *C. comensis* (and the *Cyclotella sensu lato* complex in general) remains controversial, because there are various examples of increasing abundances of these taxa

with higher temperatures (e.g., the present study; Pienitz, Smol, and Birks 1995; Catalan, Pla, et al. 2002; Koinig et al. 2002), though there is also evidence for the opposite pattern (Weckstrom, Korhola, and Blom 1997). Various studies have noted that increases in *C. comensis* abundance with increasing water temperature may reflect indirect limnological factors, such as interactive effects between water temperature and thermocline depth (Catalan and Fee 1994; Huisman and Weissing 1995; Huisman, Van Oostveen, and Weissing 1999; Catalan, Pla et al. 2002). The results of the present study demonstrate that thermocline depth has a significant effect on the abundance of *C. comensis* (Figure 4; GLM: $p = .047$, $R^2 = 0.41$; GAM: $p < .001$, $R^2_{adj} = 0.963$, lowest AIC among all significant parameters). The thermocline depth in small lakes in turn depends on several factors, including water temperature (Catalan, Ventura, et al. 2002), turbidity (Sadro and Melack 2012; Strock et al. 2017), and fetch (France 1997). In our data set, none of the assessed variables, including mean August water temperature, were significantly correlated with thermocline depth (Figure S1). This finding indicates that multiple drivers may be relevant and that a single dominating driver of *C. comensis* abundance seems unlikely. However, turbidity and fetch were not assessed in the present study. Therefore, further research in these lakes should consider the importance of factors that control thermocline depth separately.

Interestingly, the results of the GAMs indicate interactive effects between thermocline depth, nutrients and *C. comensis* abundance ($F_{TCL} = 20.221$, $F_{NO3} = 6.774$, $p_{TCL} < .001$, $p_{NO3} = .021$, $R^2_{adj} = 0.88$, AIC = 228.7). The positive interactive effect of thermocline depth and nitrogen on *C. comensis* growth may be attributed to weaker phosphorous upcycling from the hypolimnion (Jager, Diehl, and Emans 2010); phosphorus is mostly released through internal hypolimnetic processes. Nitrogen input, in contrast, mainly comes from external sources (Rogora et al. 2018; Schwefel et al. 2019). It was found that an increase in the N/P ratio can select for small centrics that have competitive advantages due to more effective nutrient uptake mechanisms (Tolotti et al. 2007, 2012; Malik, Northington, and Saros 2017). In experiments in which light and nutrient concentrations were varied, *Cyclotella bodanica* and *C. radiosa* showed especially high growth rates under P limitation and moderate to low light conditions but required sufficient nitrogen; that is, their growth declined under co-limitation of nitrogen (Malik, Northington, and Saros 2017). This can be explained by the fact that nitrogen is an important component of the light-harvesting apparatus of these taxa, which supports sustained growth even under P limitation. An increase in phosphorous can even be detrimental because it increases susceptibility to photoinhibition (Litchman 2003). Hence, it is likely that increased thermocline depths offer superior nutrient conditions for *C. comensis*, leading to competitive advantages within the phytoplankton assemblage (Catalan, Pla et al. 2002a; Huisman et al. 2004; Jäger, Diehl, and Schmidt 2008; Jager, Diehl, and Emans 2010; Williamson et al. 2010b; Cantin et al. 2011). Under climate change, extreme precipitation events will become more frequent (Gobiet et al. 2014) and thus external input of nitrogen compounds into the study lakes will likely increase. Furthermore, the input of atmospheric nitrogen into high-altitude lakes is increasing and it is likely that this trend will continue (Catalan et al. 2013). As a result, *C. comensis* may become more abundant in lakes at higher elevations within the study region.

This study further demonstrated a significant positive correlation between August surface water temperature and the relative abundance of *C. comensis* (Figure 4; GLM: $p = .025$, $R^2 = 0.66$; GAM: $F_{T_S} = 34.27$, $p < .001$, $R^2_{adj} = 0.941$, AIC = 215.3). Epilimnetic water temperature was found to be correlated with various parameters that may in turn be relevant to *C. comensis* growth. These include the duration of ice cover (Catalan, Pla, et al. 2002; Koinig et al. 2002; Sorvari et al. 2002), the strength of summer stratification (Catalan et al. 2013; Korhola et al. 2002; Reavie et al. 2017; Rühland, Paterson, and Smol 2008, 2015; Saros et al. 2016; Thompson, Kamenik, and Schmidt 2005), elevation and consequently catchment characteristics (e.g., Kamenik et al. 2001; Livingstone, Lotter, and Walker 1999), as well as light availability (Winder, Reuter, and Schladow 2009; Tolotti et al. 2012; Saros and Anderson 2015; Malik, Northington, and Saros 2017). All of these parameters in turn influence lake biogeochemical cycling (Catalan, Pla et al. 2002; Catalan, Ventura et al. 2002). Based on the data of the present study, buoyancy frequency within the epilimnion (which corresponds to the strength of summer stratification) did not significantly influence *C. comensis* growth. However, August surface water temperature was negatively correlated with elevation, implicating possible interactions with variables that were not assessed, such as the duration of ice cover, which in turn depends on catchment characteristics and can influence light availability. Further research should integrate these possible secondary effects to further specify the influence of epilimnetic temperature on *C. comensis*.

Conclusions

The present study underscores the potential of the diatom *C. comensis* to be used as an indicator of rising lake

temperatures under elevated nitrate concentrations. *C. comensis* abundance is indicative of relatively deep thermoclines, whereas the strength of summer stratification was not an important driver of *C. comensis* abundance within the sampled lakes. At present, the conditions in montane lakes of the northern European Alps are especially favorable for *C. comensis*. As temperatures rise, the tree line will shift upwards, catchment vegetation and soil formation will be enhanced, and extreme precipitation events will become more frequent. All of these consequences of climate change will lead to higher input of organic compounds, including nitrate, into mountain lakes. Therefore, it is possible that *C. comensis* will also increase in abundance and possibly dominate lake plankton in subalpine or even alpine lakes in the future, if thermoclines are sufficiently deep and epilimnetic water temperatures continue to rise.

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