

Phytoplankton communities in high alpine lakes of the National Park Hohe Tauern

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Abstract

Phytoplankton communities in high alpine lakes are a highly interesting topic. Located in extreme environment the species must be adapted to short growing phases in summer and long winters with ice covered surface. Expanding the time of growth in summer due to climate change can lead to differences in species composition. This change in vegetation period through earlier ice out can also influence mixing regimes, which can also change species composition (Rühland, et al., 2015). This study tried to document the species and their abundance in 18 lakes of the National Park Hohe Tauern located between 2000 and 2600 m a.s.l. over a period of three years (2018-2020) and compare these data to abiotic measurements over a period of six years(2017-2022). The presence of species seems to be determined to certain lakes although the abundance in different years alters a lot. The vegetation time between sampling and the melting of the ice cover of these lakes seem to be the driving force of species richness, which is low in general. Elevation and other abiotic factors like nitrogen are important for algae growth but don't have a strong effect on species composition.

Introduction

High alpine lakes are influenced through abiotic and biotic changes caused by climate change. These lakes are good sentinels to track climate change, since they are definitive and changes can be seen in abiotic measurements as well as in species composition, also lakes can be found around the globe, so data can be compared (Adrian, et al., 2009). Algae within these lakes are, due to their physiological characteristics, good indicator species (Tolotti, et al., 2003).

Through global warming, the ice-free periods may become longer. This causes higher primary production in the lakes and in the meadows around, which increases higher dissolved organic carbon rates, which leads to lower UV-light intensity (Sommaruga, et al., 1999). The meltwaters of glaciers can increase nitrogen delivery and weathering of the bare rock enhances phosphate inputs, which can lead to an additional eutrophication (Saros, et al., 2010) and higher primary production (Sommaruga, et al., 1999) This can cause a change in species composition enhanced by higher temperatures, differences in nutrients availability and altered mixing. This stratification change targets the shape of phytoplankton especially the weight to volume ratio (Rühland, et al., 2015). While some species have advantage to stay in the littoral zone others may sink to fast. With more mixing this shape advantage decreases. Lakes that have higher temperatures and less UV-exposure can be colonized by species that are more common in lower lakes and can outcompete the typical high alpine lake species. This can cause species loss, but it can also increase the biodiversity within these alpine lakes (Rosset, et al., 2010). As a consequence of climate warming, the pH in high alpine lakes is also assumed to increase (Koinig, et al., 1998), which would also affect species composition. In recent studies there was no species turnover associated with pH change, but difference in abundances (Koinig, et al., 1998). Despite the idea that earlier ice out will increase vegetation period there is evidence that the vegetation period starts even before ice out and that some phytoplankton can grow below an ice cover (Das, 2016).

This master thesis tries to explore the species composition in 18 lakes of the National Park Hohe Tauern and compare it to other findings. A similar sampling in the future would be useful to track changes in upcoming years.

Methods

In summer of 2018 and 2019 there were 18 Lakes in three different valleys of the National Park Hohe Tauern examined (Obersulzbachtal, Innergsschlöss and Seebachtal). In 2020 there were just 12 lakes in two valleys sampled (Innergsschlöß and Seebachtal), because of external circumstances. In each valley 6 lakes are located. In the first year the field work started on 25.07.2018 and ended on 08.08.2018 In the second year the field work started 24.07.2018 and ended 07.08.2018. In the last year 2020 there were some logistical problems leading to only two valleys sampled and the timeframe of 18.08-27.8.2020. In the summer of 2021, the temperature logger as well as the missing data of 2020 Obersulzbachtal could be collected.

The probes were collected by boat, to be able to take samples in the middle of the lake. If possible, in the depth of 2m with a hydrocast, if a chlorophyll maximum was detected, a second sample was taken. Some lakes were too small and shallow to use the boat, in this case the samples were taken from the shore. These samples were taken as deep as possible, without raising dust from the ground. The phytoplankton samples of 250ml were fixed in Lugol in 250ml glass bottles. The algae were detected and counted under the microscope (Nikon TE2000) in 10 ml Utermöhl-chambers. In the 10 ml chambers 20 fields in 200x magnification were randomly selected and counted. Then the cell number per ml were calculated. As the cells were observed under the microscope there was no need for a minimal abundance. Only cells above 15µm were detected as smaller cells would lead to errors with Lugol's fixation. Taxonomic resolution was done to genus level. Identification literature was "Das Leben im Wassertropfen Mikroflora und Mikrofauna des Süßwassers" by Heinz Streble, Dieter Krauter, Annegret Bäuerle, Heinz Streble, Wolfgang Lang and "The freshwater algal flora of the British Isles an identification guide to freshwater and terrestrial algae" by David Michael John and Brian Alan Whitton. Diversity was calculated as followed: Alpha diversity is the number of different species found in one lake over the period of all three years 2018-2020. Beta diversity is the number of different species between two lakes, similar to alpha diversity for all three years. Gamma diversity is the number of different species found in all three years in a specific valley. The probes were also counted with the Casy cell counter, to depict the small cells 3-25µm and count the total Biovolume 3-120µm. Here the sample volume was 400µl. This was done to improve the species counts of the microscope with a better biomass count method. The Casy cell counter is able to calculate the biovolume.

Chlorophyll a, temperature, pH, conductivity, NO₃ and Oxygen concentration were measured directly inside the lake with a YSI-EXO2 Multiparameter Water Quality Sonde. Also, the depth of the

chlorophyll maximum was examined. Since the summer of 2017 each lake was assembled with two temperature data loggers, measuring the temperature in 1m depth every 6 hours. This data was used to calculate the ice-free days. Ice-free days are the days between sampling and the time of fluctuating temperature above 2 C°. In 2018 none of the two dataloggers of lake 16 could be found. The datalogger of lake 7 and 11 were not recollected in 2019. In 2020 the loggers of lake 5 and 11 were missing. The floater could either be damaged or ripped off by ice and the datalogger sunk or the loggers were stolen.

In the lakes 5 and 6 fish were observed. The other lakes are without fish. In Table 1 you find precise information about the location of the lakes.

The statistical analysis and graphs were done in Excel and R Studio using the libraries tidyverse, readxl, ggplot2, gridExtra, lubridate.

Table 1: Overview of the lakes

| Lake Name | Lake Number | Valley | Altitude | Latitude | Longitude |
|------------------------|-------------|-----------------|----------|----------|-----------|
| Eisseele | 1 | InnergslöÙ | 2662 | 47.1237 | 12.39786 |
| In Loche | 2 | InnergslöÙ | 2628 | 47.12165 | 12.39774 |
| Gletscherplateau | 3 | InnergslöÙ | 2235 | 47.1162 | 12.41286 |
| Löbbensee | 4 | InnergslöÙ | 2139 | 47.11554 | 12.42593 |
| See nahe Löbbensee | 5 | InnergslöÙ | 2243 | 47.10368 | 12.47821 |
| Löbbensee | 6 | InnergslöÙ | 2230 | 47.10676 | 12.47731 |
| Kleiner Tauernsee | 7 | Seebachtal | 2308 | 47.03967 | 13.18216 |
| Grüneckersee | 8 | Seebachtal | 2442 | 47.03571 | 13.17559 |
| Schneefeldsee | 9 | Seebachtal | 2476 | 47.02962 | 13.15273 |
| Plattensee | 10 | Seebachtal | 2445 | 47.02641 | 13.1515 |
| Kleines Elend | 11 | Seebachtal | 2639 | 47.04191 | 13.25626 |
| GroÙes Elend | 12 | Seebachtal | 2517 | 47.03976 | 13.25272 |
| See neben Seebachsee | 13 | Obersulzbachtal | 2093 | 47.18023 | 12.22615 |
| Seebachsee | 14 | Obersulzbachtal | 2089 | 47.1809 | 12.22788 |
| FoiÙkarsee | 15 | Obersulzbachtal | 2143 | 47.17348 | 12.24235 |
| Sulzsee | 16 | Obersulzbachtal | 2213 | 47.11869 | 12.29514 |
| Obervorderjaidbachsee | 17 | Obersulzbachtal | 2396 | 47.14303 | 12.23676 |
| Untervorderjaidbachsee | 18 | Obersulzbachtal | 2269 | 47.15292 | 12.24128 |

Results

Summary of Results

The observed lakes are in general low in species richness. In the valley Seebachtal no bigger algae were found. The difference in species composition between lakes is high with no specific combination. *Synedra* sp. is very common and found in 6 lakes out of 8 that have bigger algae. *Asterionella* sp. and *Ankistrodesmus* sp. were only found in one lake. The species within a lake are quite stable and do not turn over between years. The deep chlorophyll maximum (DCM) has by far higher abundances in some species compared to the 2-meter sample, but not all species are present. Nitrogen levels decrease with depth and are not connected with DCM. No specific cell size dominates the biovolume in all lakes. The temperature cannot be explained by altitude. The year can be divided in two seasons. Winter were the lakes are covered with snow and temperatures are low and stable and summer with fluctuation and maximum temperatures between 8°C and 25°C. Ice-free days correlate positively with species richness.

Microscope

The lakes vary a lot in species composition as well as in abundance. All lakes observed are relatively low in phytoplankton diversity. Lakes have between 0-6 different phytoplankton species above 15µm. However, the diversity between the lakes is higher, with 9 different species found. There is no typical combination of species. In Table 2 the diversity is summarized. Lake 5 and 13 have the same species set. Lake 06 and 18 have the highest turnover of 6 species. In the valley Innerschlöß all 9 species were found, while in Obersulzbachtal it is only a subset of 6 species. In Seebachtal no phytoplankton bigger than 15µm was found. Another interesting finding is the determination of these species to a specific lake. The species found in a lake in 2018 are likely present in 2019 and 2020. 2018 shows less species compared to 2019. 2020 shows more species than 2019. This is true for lake 3-6. Lakes 2 and 14 and 18 show a different trend. The abundance differs a lot. Some species are not found in all years, maybe caused by lower abundance. Except of missing in one year the species pool of a lake does not change over the observed three years. The species composition seems to be stable in each lake. *Synedra* is the most common found in 6 different lakes, while *Ankistrodesmus* and *Asterionella* were only observed in one lake, *Ankistrodesmus* in 03

“Gletscherplateau” and *Asterionella* in 06 Löbbensee. Both are the dominant species of the lake. The species with the highest abundance are *Ankistrodesmus* belonging to Chlorophyceae and *Dinobryon* belonging to Chrysophyceae and *Asterionella* belonging to Bacillariophyta. The other observed algae belong to diatoms (Bacillariophyta). Deep chlorophyll maximum is slightly different from the measurement at 2 meters depth. The abundance of at least one species is higher, but not all species from 2 meters depth are present in the DCM. In 2018 lake 06 Löbbensee has a change in species composition with depth. *Amphora* (144 cells/ml) is only found in the 2-meter sample and replaced by *Epithemia* (86 cells/ml) in the DCM. The Abundance of *Cymbella* is slightly higher (144 to 258 cells/ml), while the abundance of *Asterionella* increases a lot more (1406 to 29274 cells/ml) in the DCM. In 2019 lake 06 Löbbensee *Asterionella* is the dominant species in the 2-meter sample but despite an increase in abundance it is not the dominant species in the DCM (2353 to 4334 cells/ml), where *Dinobryon* increases a lot more (115 to 11193 cells/ml). *Amphora* only occurs in the 2-meter sample (86 cells/ml) like in 2018. *Synedra* (315 to 57 cells/ml) and *Epithemia* (115 to 172) occur in the both 2-meter sample and in the DCM, but *Synedra* decreases while *Epithemia* increases in abundance. In 2020 lake 06 Löbbensee *Asterionella* has a high dominance in the DCM but very low abundance is the 2-meter sample compared to the other years (217 to 100421 cells/ml). *Dinobryon* is similar with high abundance in the DCM and rarely present at 2 meters (29 to 7032 cells/ml). *Amphora* is present in the DCM for the first time with reduces abundance (115 to 29 cells/ml). *Epithemia* has nearly equal abundance in both depths (172 to 201 cells/ml). *Synedra* has decreasing abundance in the DCM (230 to 29 cells/ml). Lake 13 “See neben Seebachsee” does only have a DCM in 2018, but not in 2019 same with the neighboring lake 14 “Seebachsee”. In Lake 13 “See neben Seebachsee” there is a species replacement of *Synedra* (1866 cells/ml) to *Fragilaria* (1550 cells/ml) in the DCM, while in lake 14 “Seebachsee” the species are the same in both depths *Dinobryon* (1922 to 6773 cells/ml) and *Synedra* (1119 to 2669 cells/ml). Despite the differences between 2 meters and DCM there were also differences in species occurrence between years in lakes without a DCM. Lake 2 “In Loche” has three species in 2018 *Amphora* (86 cells/ml), *Cymbella* (115 cells/ml) and *Synedra* (29 cells/ml). In 2019 there was a problem with the sample so no data available. In 2020 there only two species were found *Amphora* (29 cells/ml) and *Cymbella* (29 cells/ml). Lake 03 “Gletscherplateau” has three species in 2018 *Ankistrodesmus* (20320 cells/ml), *Peridinium* (3645 cells/ml) and *Synedra* (258 cells/ml). In 2019 the same species were found *Ankistrodesmus* (3013 cells/ml), *Peridinium* (832 cells/ml) and *Synedra* (201 cells/ml), but with decrease in abundance. In 2020 the abundance of *Ankistrodesmus* (631 cells/ml) decreased again, while *Peridinium* (1119 cells/ml) and *Synedra* (402 cells/ml) had slightly higher abundances. *Amphora* (29 cells/ml) was found in very low abundance for the first time in this lake. Lake 5 “See neben Löbbensee” was only populated by one species in 2018 *Epithemia* (172 cells/ml), this changes in 2019 to four different species. *Amphora* (57 cells/ml),

Epithemia (201 cells/ml), *Fragilaria* (144 cells/ml), and *Synedra* (287 cells/ml). In 2020 it decreased again to only two species *Amphora* (29 cells/ml) and *Epithemia* (373 cells/ml). In lake 17 “Untervorderjaidbachsee” two different species were found in 2018 *Dinobryon* (2613 cells/ml) and *Peridinium* (2583). One year later only *Dinobryon* (718 cells/ml) was found in decreased abundance. In 2020 this lake was not sampled.



Figure 1 Counts per ml of algae larger than 15µm. This was done manually under the microscope. The lakes missing bigger algae, lakes without larger algae are not shown. Lakes with DCM is the chlorophyll maximum of the lake.

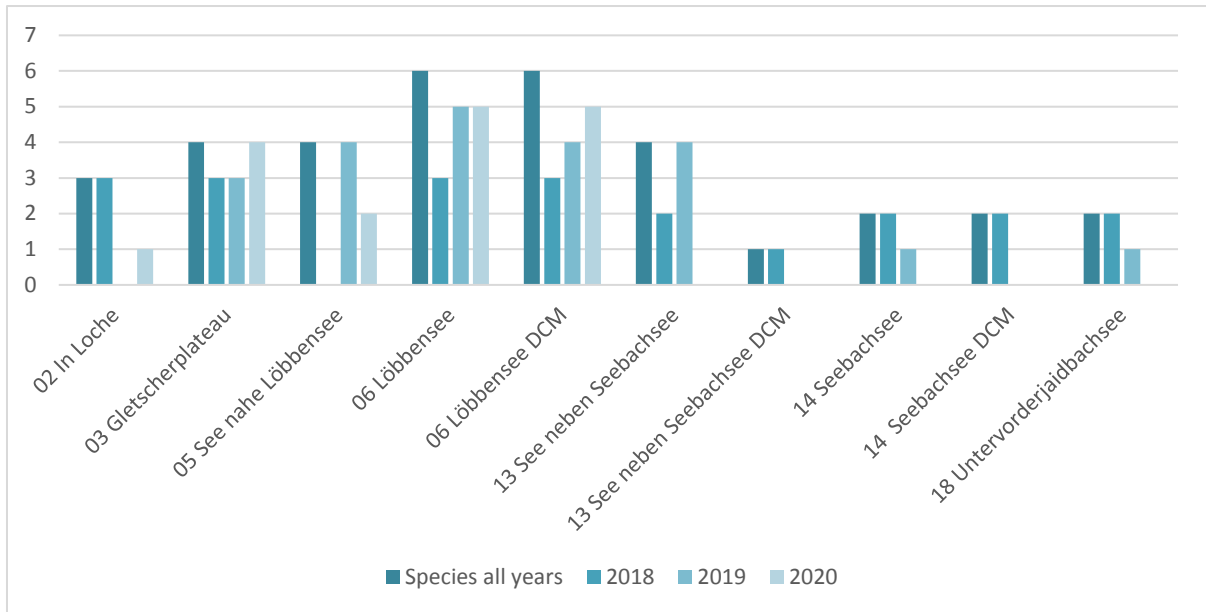


Figure 2 Sum of species bigger than 15µm in all years and in specific years per lake. Lakes without larger algae are not shown.

Table 2: Overview of Diversity

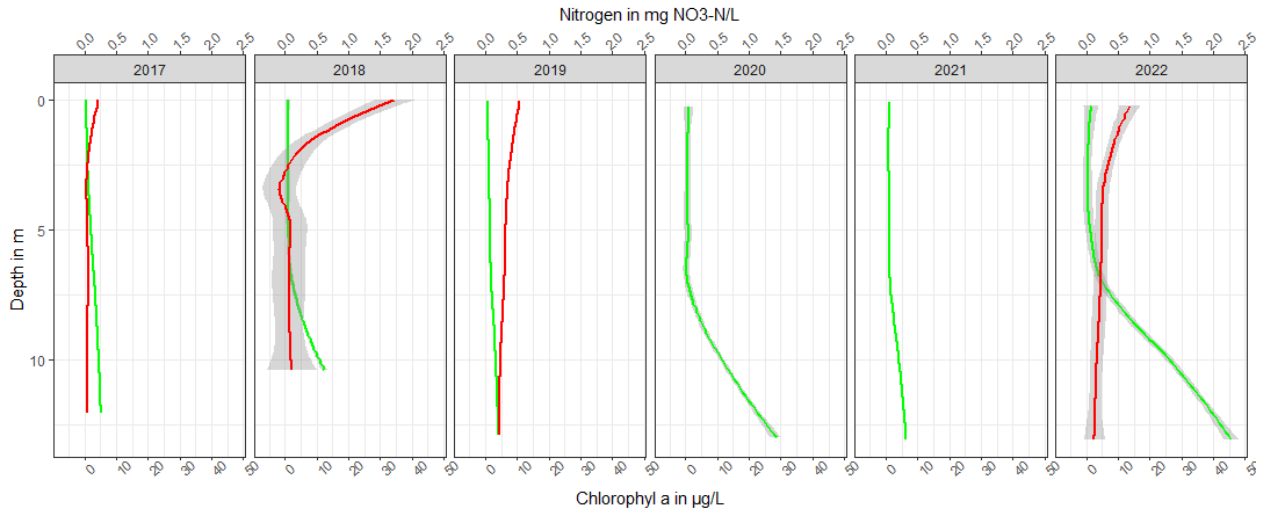
| Location | Alpha Diversity | Comparing Lakes | Beta Diversity |
|--------------------------------|-----------------|-----------------|----------------|
| Lake 02 In Loche | 3 | Lake 02 & 03 | 3 |
| Lake 03 gletscherplateau | 4 | Lake 02 & 05 | 3 |
| Lake 05 See nahe Löbbensee | 4 | Lake 02 & 06 | 3 |
| Lake 06 Löbbensee | 6 | Lake 02 & 13 | 3 |
| Lake 13 See neben Seebachsee | 4 | Lake 02 & 14 | 3 |
| Lake 14 Seebachsee | 2 | Lake 02 & 18 | 5 |
| Lake 18 Untervorderjaidbachsee | 2 | Lake 03 & 05 | 5 |
| | | Lake 03 & 06 | 6 |
| | | Lake 03 & 13 | 4 |
| Valley | Gamma Diversity | Lake 03 & 14 | 4 |
| Innerschlöß | 9 | Lake 03 & 18 | 4 |
| Seebachtal | 0 | Lake 05 & 06 | 4 |
| Obersulzbachtal | 6 | Lake 05 & 13 | 0 |
| Valleys Combined | 9 | Lake 05 & 14 | 4 |
| | | Lake 05 & 18 | 6 |
| | | Lake 06 & 13 | 4 |
| | | Lake 06 & 14 | 4 |
| | | Lake 06 & 18 | 6 |
| | | Lake 13 & 14 | 4 |
| | | Lake 13 & 18 | 6 |
| | | Lake 14 & 18 | 2 |

Deep Chlorophyll maximum

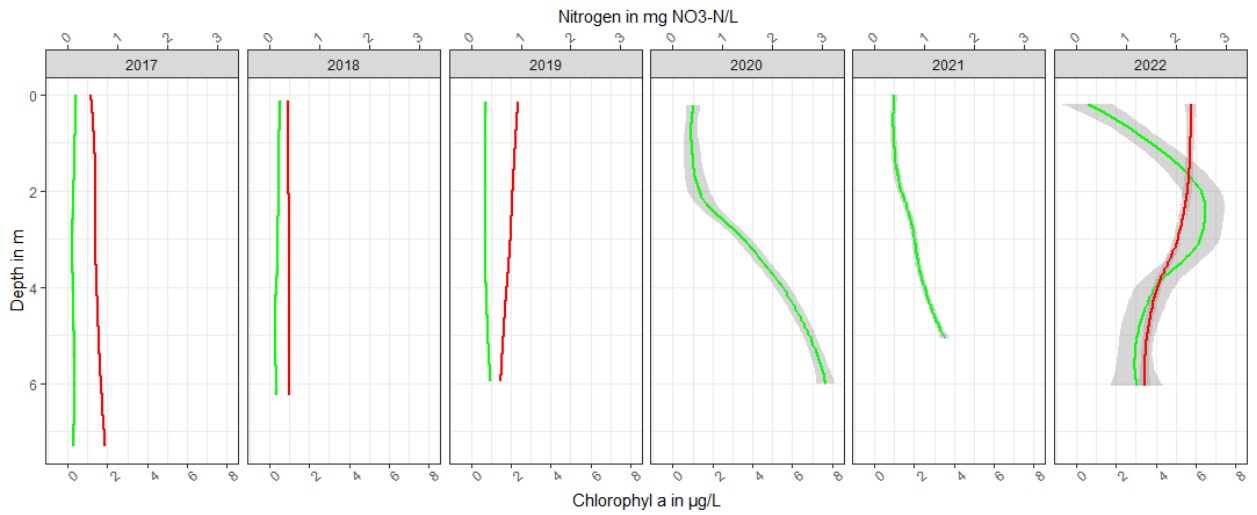
A Deep Chlorophyll maximum (DCM) occurs in 5 lakes 06 Löbbensee, 07 Kleiner Tauernsee, 13 "See neben Seebachsee", 14 Seebachsee and 17 "Obervorderjaidbachsee". Lake 01 "Eissele" does not have a clear DCM, but chlorophyll increases with depth. The Deep lakes 07 Kleiner Tauernsee and 08 Grüneckersee in Valley Seebachtal also have increasing chlorophyll a value with depth or even DCM but miss algae bigger 15µm to be counted under the microscope alike all the sampled lakes in valley Seebachtal. The DCM is 2-5 times higher compared to the 2-meter sample, except in lake 06 Löbbensee where Chlorophyll a values increase up to 40 times of the 2-meter sample value. In lake 16 Sulzsee Chlorophyll a does not change with depth. Lake Sulzsee has a short residence time, which hinders stratification. DCM were not found in all years in these lakes. 06 Löbbensee has a relatively stable DCM at 10 meters. The amount of chlorophyll measured ranging from 5-65µg/l with higher values every second year. The nitrogen profile does not show an explanation for this variation. 07 Kleiner Tauernsee has increased chlorophyll values only in the last three years of the sample period 2019-2022. At See neben Seebachsee" the years 2017, 2018 and 2021 and 2022 are similar in the rise of chlorophyll with depth, the years 2019 is different and no increase with depth occurs. The data of 2020 is missing, in this year Obersulzbachtal was not sampled. In lake 14 Seebachsee the DCM changes in depth. In 2019 it occurs at the deepest depth possible to measure. The lake is deeper than 15m so there could be higher chlorophyll values below this measured point. 2020 was not sampled. Lake 17 "Obervorderjaidbachsee" does have an increase in chlorophyll in 2017 and 2018 with depth, in other years there is no chlorophyll increase with depth. The measured chlorophyll values are by far lower compared to other lakes. With values of 1-2 µg per liter in "Obervorderjaidbachsee" to other lakes around 4-10µg per liter and even up to 65µg per liter in Löbbensee in 2022 which seems to be no artefact and no sediment.

Nitrogen (NO₃) is rather mirror- inverted or not interconnected to the chlorophyll a value, DCM does not follow nutrition availability. Nitrogen is decreasing with depth. The species found in the DCM are the same species as in the 2-meters below surface sample. In some cases, there are even less species in the DCM. The abundance is by far higher in the DCM compared to the 2 meters below surface sample, depending on the lake ranging between 2-3 times higher for *Amphora sp.* and *Dinobryon sp.* in lake 14 Seebachsee and 100-500 times higher for *Dinobryon sp.* and *Ankistrodesmus sp.* in lake 06 Löbbensee.

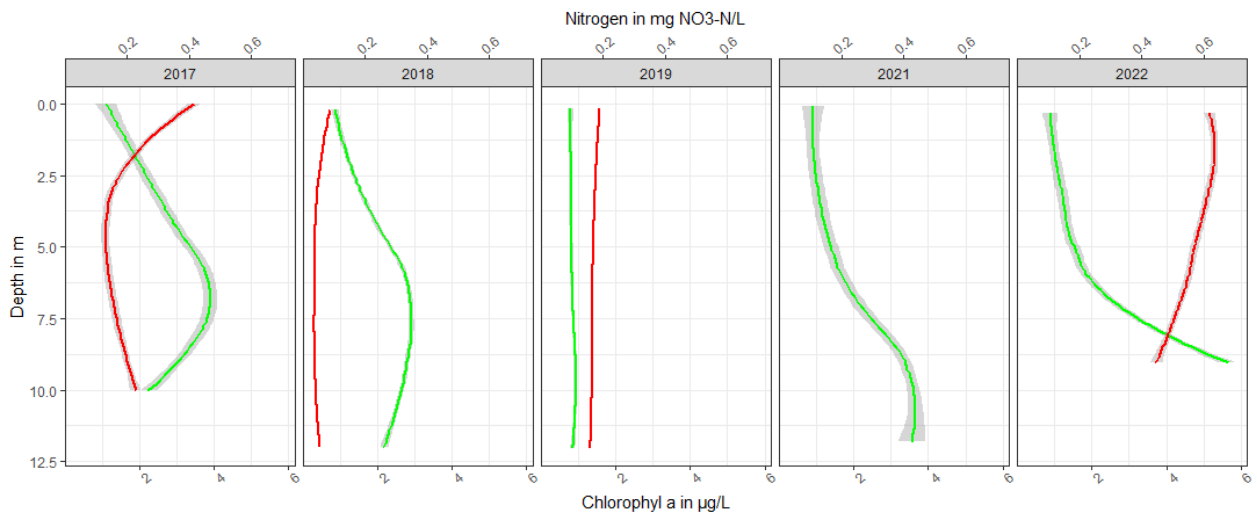
06 Löbbensee



07 Kleiner Tauersee



13 See neben Seebachsee



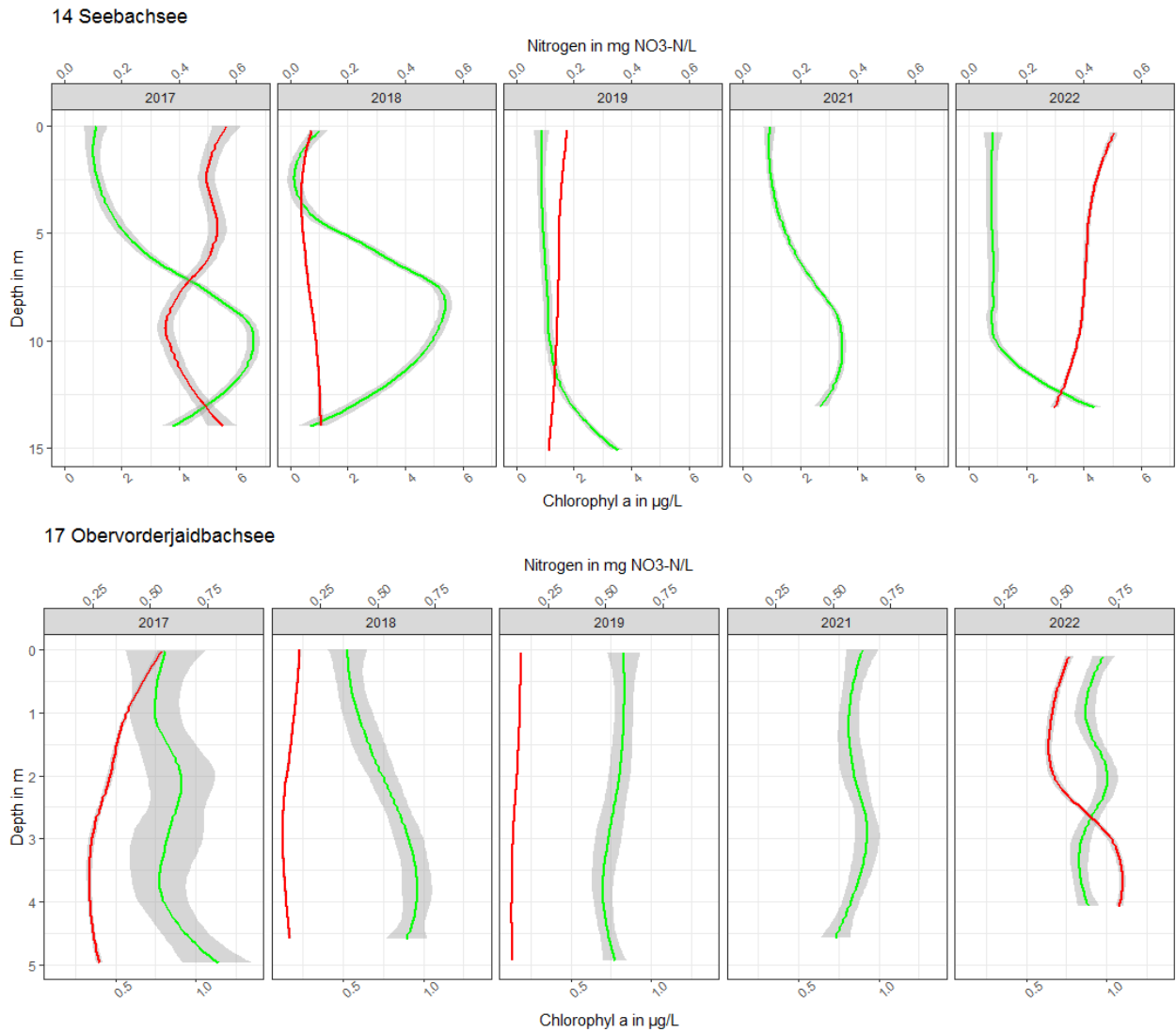
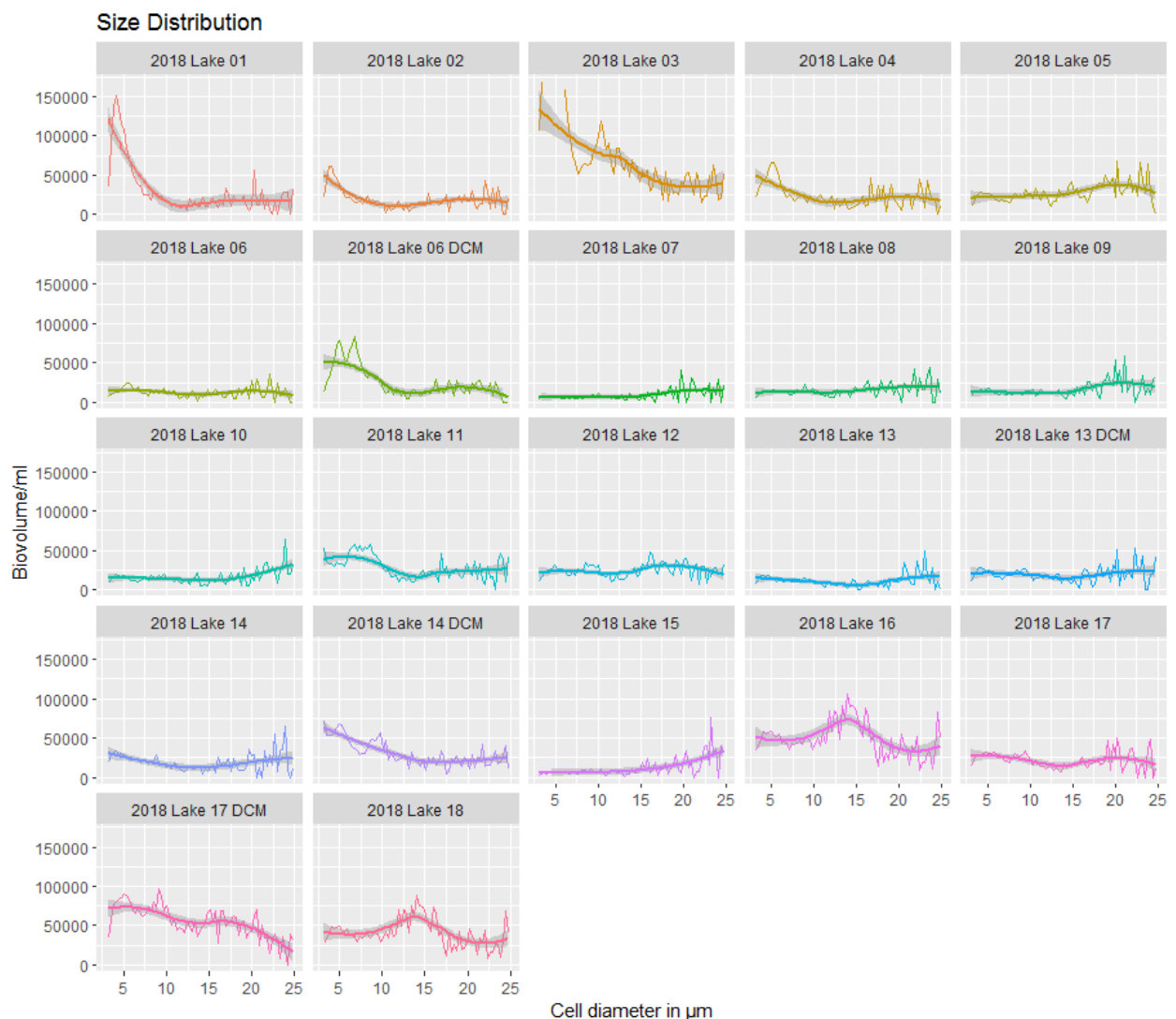


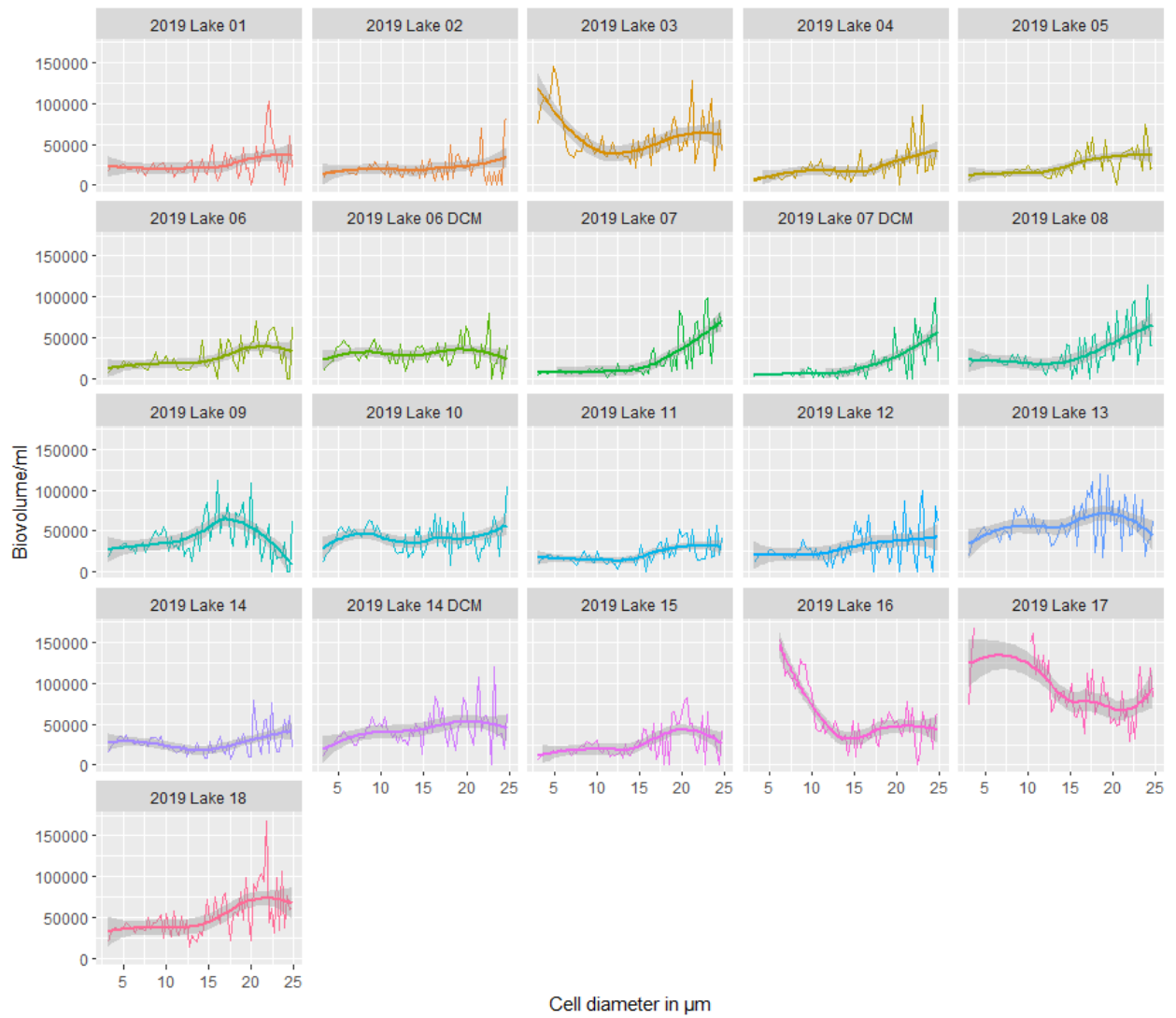
Figure 3 Chlorophyll a (green) and Nitrogen (red) profiles. The year 2020 has missing data for lakes located in Obersulzbachtal. In 2020 and 2021 there were problems with the nitrogen sensor, so this data is not included. The lines were made with a LOESS Fit.

Biovolume

Similar to the species abundance of the microscopical data the biomass varies a lot between lakes and between years. There is no size category that contributes most of the biomass in all lakes, for each lake the contribution of the different size categories to the absolute biomass is disparate. In Lake 01 "Eisseele" 2018 has the highest volume contribution in very small cells below 5µm. in 2019 there is no peak but more abundance in cells between 20-25µm. 2020 there us again a high peak in this very small cell size. In Lake 02 "In Loche" the cell sizes that contribute the most to biovolume is very different in each year. 2018 there is a little peak in very small cells around 5 µm, while in 2019 the cells of 20-25µm contribute more to the biovolume. In 2020 the biovolume is in general higher but with a medium peak around 20-25µm and a strong peak in the very small cells of 5µm. In 2018 in lake 03 "Gletscherplateau" the biovolume is in general high but increasing the smaller the cells get with a cut at 10 µm this is similar in 2019 but not in 2020, where the biovolume is higher in all cell sizes. In lake 4 Salzbodensee 2018 smaller cells of 5µm contribute more to the biomass, while 2019 bigger cells of 20 µm are more present. In 2020 the distribution is equalized. Lake 05 "See nahe Löbbensee" has more biovolume in the bigger cells in 2018 and 2019 and very low biovolume in 2020. Lake 06 Löbbensee shows the highest biovolume in 2019 in the bigger cells of 20µm 2018 and 2019 is lower in biovolume. The DCM in 2018 is dominated by smaller cells of 5-10µm. In 2019 the size distribution is not dominated by a specific size category. In 2020 the biovolume has the highest values between 5-20µm and very high biovolume in general. Lake 07 Kleiner Tauernsee has low biovolume values in general in all years except in 2019 cells between 20-25µm have more abundance. 2019 the DCM is equally dominated by this cell size, in 2020 the DCM does not show a dominance for a specific cell size but has slightly higher values for 20-25µm as well as for 5µm. Lake 08 Grüneckersee show low contribution to biovolume in all cell sizes except in 2018 there is a similar shift to cells of 20-25µm. Lake 09 has higher biovolume around 20µm in 2018. In 2019 the biovolume is generally increased and dominated by cells 15-20µm in size. 2020 has increased biovolume in small cells of 5-10µm. Lake 10 "Plattensee" has low biovolume in 2018, which increases in the years 2019 and 2020 no cell size dominating. In 2018 the lake 11 "Kleines Elend" is dominated by cells of 10µm, in 2019 and 2020 bigger cells contribute more to the biovolume. "Kleines Elend" was sampled later than the other lakes of this valley in 2019, because it was still frozen at the regular date of sampling. Lake 12 "Großes Elend" has increased biovolume in 2019 compared to the years 2018 and 2020 with equal size distribution in all years. In Lake 13 "See neben Seebachsee" the biovolume measurements of 2018 at 2 meters and at the DCM are low in general with cells of 20-25µm slightly more contributing to the biovolume. In 2019 there was no DCM, but the biovolume in 2 meters increased

in all cell sizes. Lakes 13-18 were not sampled in 2020. In 2018 and 2019 in Lake 14 “Seebachsee” small cells of 5µm and bigger cells 20-25µm contribute more than mid-sized cells to biovolume. In the DCM of 2018 smaller cells are dominant, while in 2019 20µm cells have higher values. In lake 15 Föiðkarsee biovolume is increases with cell size. In 2019 cells of 20µm are more dominant. Lake 16 Sulzsee has high biovolume values with a peak at 15µm in 2018. The year after in 2019 it is dominated by much smaller cells of 5-10µm. Lake 17 “Obervorderjaidbachsee” show big variance between the year 2018 and 2019. In 2018 it has medium Biovolume with lower values around 15µm. In 2019 the cells of 5-10mm and 25mm have very high values. This biovolume contribution is similar to the DCM of 2018. While the lake 18 “Untervorderjaidbachsee” is dominated by 15µm cells this changes 2019 to cells of 20µm size.





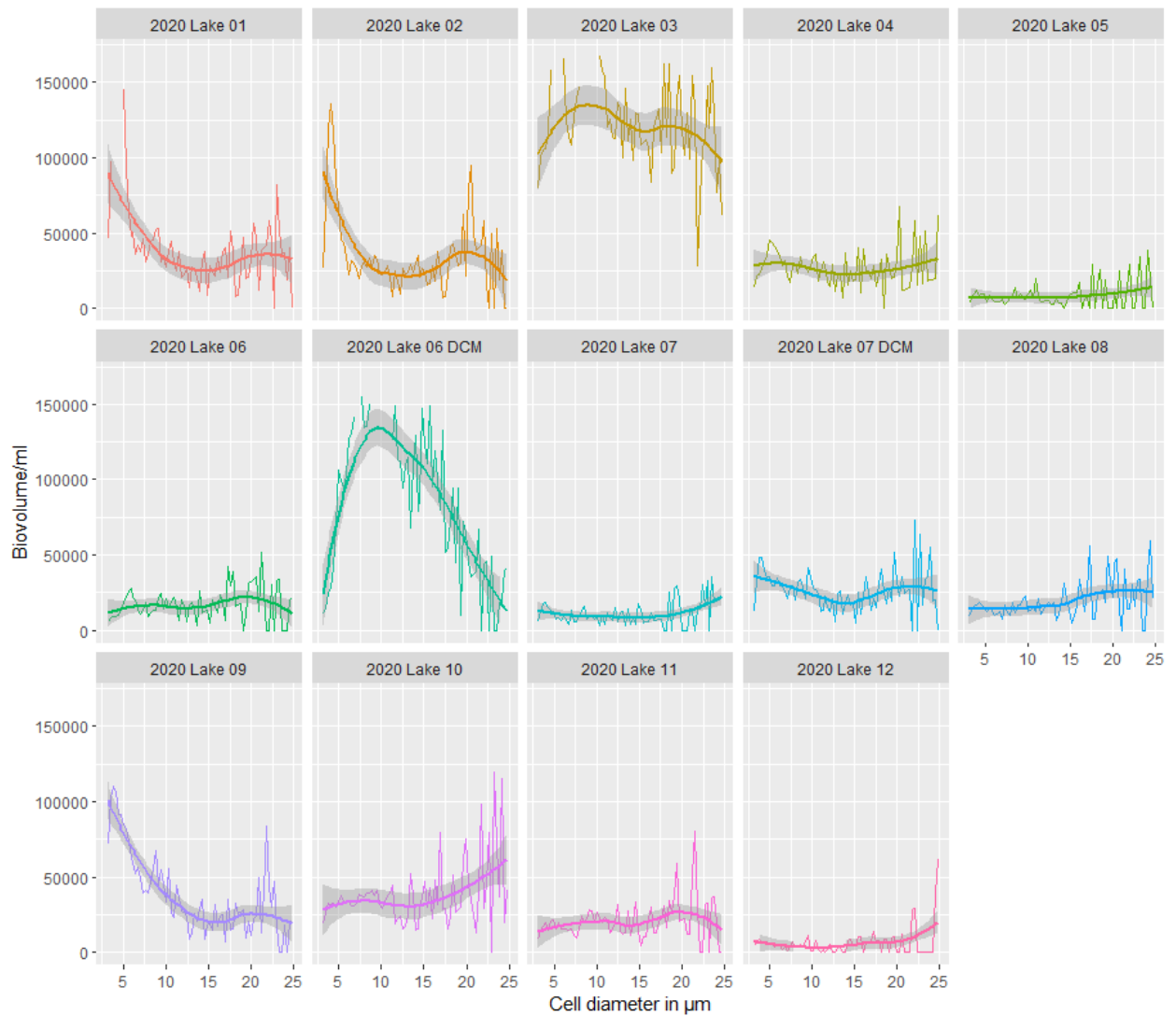


Figure 4 Size distribution of the lakes. Biovolume per Cell diameter in μm . Counted with Casy cell counter the size of 3-25 μm was chosen because the measurements start at 3 μm . above 25 μm the cells counted are below 10 per category so the statistical error and volume transformation is high in error. The lines were made with a LOESS Fit.

Abiotic measurements

Temperature loggers

In general, Innerschlöß is the warmest and Seebachtal the coldest of the three valleys. This does not fit to the different mean altitudes of the lakes. In Innerschlöß the mean altitude is 2320, in Seebachtal the mean altitude is 2440 and in Obersulzbachtal the mean altitude is 2200. The Year can be divided in Winter and Summer. Winter is the period where the lakes are ice covered, therefore there is no fluctuation in temperature and Summer with fluctuation in temperature. The Winter begins in November and ends in May. Some lakes have ice covers and low temperatures till July. These timespans vary between years depending on the weather particularly on the amount of snow in winter. Especially if the lakes are not exposed to the sun and are in a cirque, where the snow accumulates. As soon as the ice cover melts the temperature increases rapidly. The temperature of the lakes shows relatively similar maximum temperature every year with 2018 and 2021 slightly warmer and 2019 and 2021 slightly colder. Lake 16 Sulzsee is the coldest lake with a maximum of 8 °C. It has also the most stable temperature most likely because of the buffering effect of the glacier next to it. Smaller lakes have higher maximum temperatures up to 25 °C.

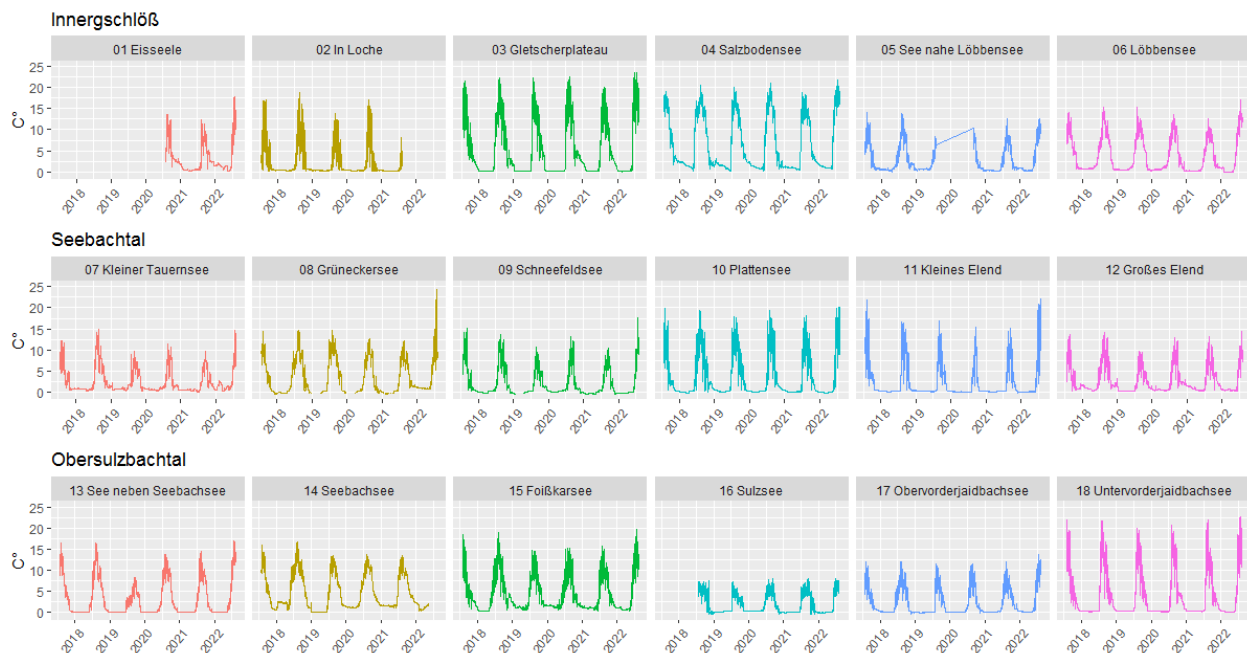


Figure 5 Temperature of each lake sorted by valley. Lake 01 "Eisseele" is missing data before 2020. This is because of ice drift or other reasons the loggers could not be found in the years before. Same problem is in lake 02 "In Loche" in 2022, 05 "See nahe Löbbensee" in 2020 and 16 Sulzsee before 2018.

Multi Probe Data

Dissolved nitrogen is generally low but increases in 2019. In 2020 and 2021 there were problems with the sensors. 2022 the Nitrogen levels are higher in general, in Seebachtal the increase is by far the strongest. Lake 7 Kleiner Tauernsee and lake 08 Grüneckersee have nitrogen levels of 2.5 mg NO₃-N/L. Dissolved oxygen differs little from year to year and between the lakes, with values of 65-85% for most lakes. In 2019 there were lakes with lower values of only 60%. Conductivity has a lot of variation between the lakes and between years. With values below 60 µS/cm they are relatively low. In Seebachtal the conductivity in all lakes is below 20 µS/cm, the lakes of other two valleys have variation of 20-60 µS/cm. Low conductivity does not explain the absence of bigger algae in Seebachtal. Chlorophyll mean values are quite stable of about 1 µg/l with a lot of variance in the outliers. Lake temperature is very variable both in years but even more between lakes. Ranging from slightly below 0 °C to 18 °C.

The temperature of 2020 is relatively low as the missing valley decrease the temperature median. Also, the samples were taken later in summer compared to the other years by one month. But this might already be the time where lake temperature is already decreasing. Between the years there is a very high variance but also between the lakes. Ice-free Days were calculated as the days between sampling and the lake temperature being above 2 °C and fluctuating, because an ice cover would inhibit fluctuation. The timespan in vary from over 80 days to just a few days before sampling (6 days at "Schneefeldsee"). In 2019 the lake 11 "kleines Elend" had to be revisited later because on the regular date it was still covered with ice. The data of 2020 fits the later sampling time well, compared to 2019. In 2018 there is a lot of variance. This variance might be caused by the amount of snow in the winter before, which would not have great impact on exposed lakes, but would highly impact lakes in narrow cirques filled with snow.

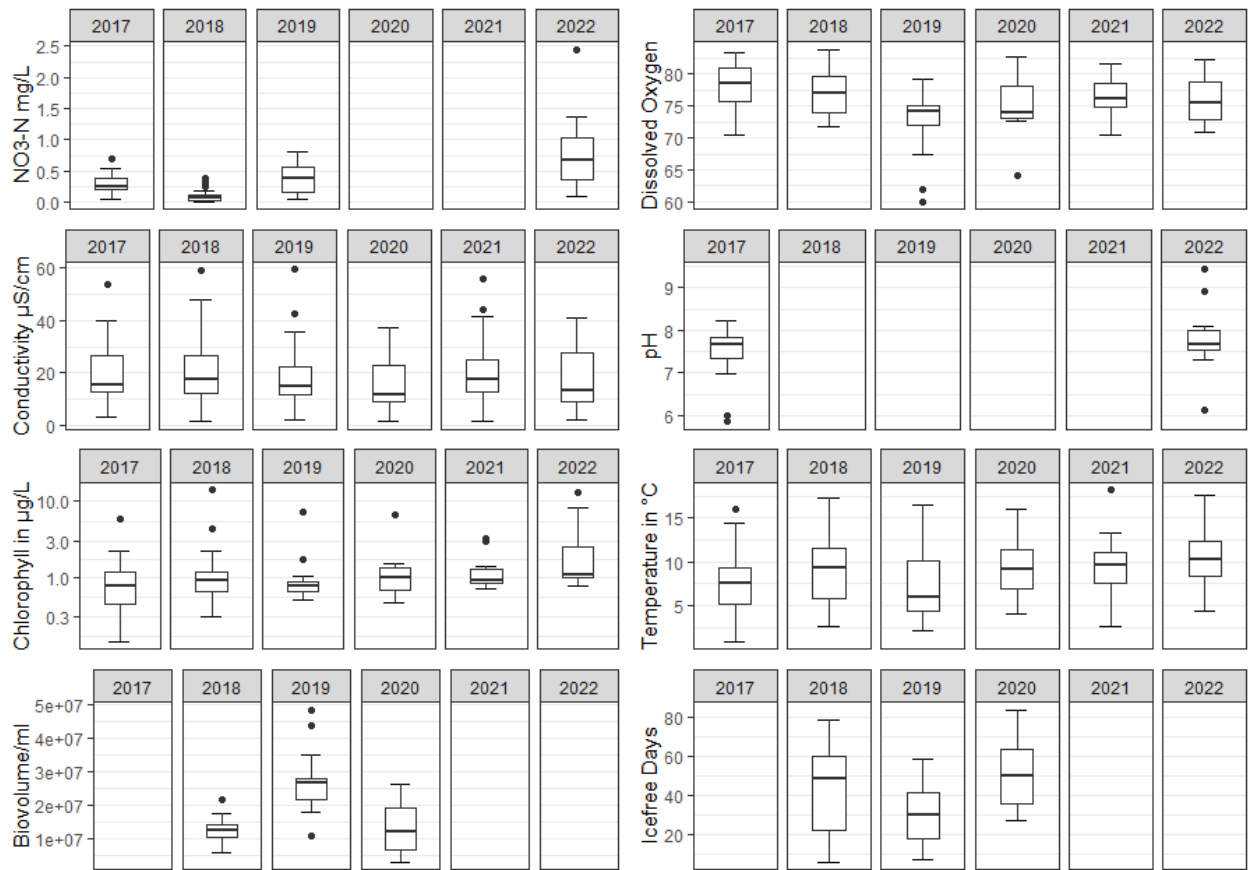


Figure 6 Mean 2-meter values of all 18 lakes except 2020 where only 12 lakes could be sampled. Biovolume was not evaluated in 2017 and the biovolume data of lake 2 in 2019 is missing. PH is missing in 2018-2021 and Nitrogen is missing in 2020 and 2021 due to problems with the sensor. Ice-free Days were calculated as the days between sampling and the lake temperature being above 2 °C and fluctuating. 2017 were no samples taken and no temperature logger data available. The lake "kleines Elend" was revisited in 2018 because on the regular date it was still covered in ice.



Figure 7 Shows the mean 2-meter values of the lakes. Biovolume was not evaluated in 2017 and the biovolume data of lake 2 in 2019 is missing. PH is missing in 2018-2021 and Nitrogen is missing in 2020 and 2021 due to problems with the sensor. Ice-free Days were calculated as the days between sampling and the lake temperature being above 2 °C and fluctuating. 2017 were no samples taken and no temperature logger data available. The lake "kleines Elend" was revisited in 2018 because on the regular date it was still covered in ice.

Combining Abiotic and Biotic Measurements

Similarities Between Lakes

In addition to the species composition difference, the abiotic factors taken with a multi probe vary a lot between lakes and years. The mean of the abiotic factor data shown in Figure 6 and 7 can be combined into a PCA diagram. Lakes that share similar characteristics are closer together. Lake 16 Sulzsee and lake 17 "Obervorderjaidbachsee" are both in Obersulzbachtal a few Kilometers apart from each other but both are directly fed by an icefield. Lake 6 and 14 are very deep and huge lakes and are potted closely. Lakes with algae are with some exceptions plotted closer together as well as lakes without algae.

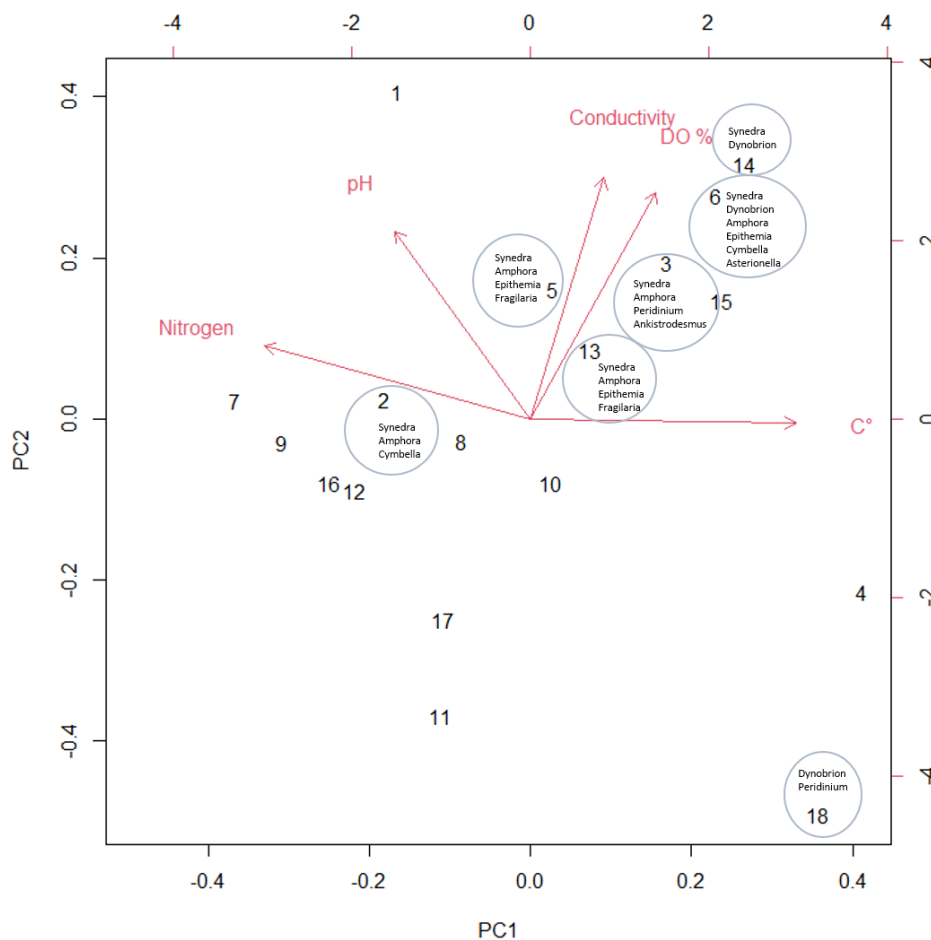


Figure 8 This PCA shows the different abiotic factors which were tested with the multi probe. The numbers refer to the number of the lakes shown in table 1. Inside the ellipses the species found in the lake are combined with the lake number. The abiotic factors are mean values of the 2-meter vales (or 1 meter for shallow lakes) of all years sampled. The red arrows indicate the contribution of the abiotic factors to the PCA axes.

Ice-free Days

There is a positive correlation between ice-free days and number of species. The correlation has one outlier lake 14 “Seebachsee” that has less species, the other lakes fit. Ice free days could be a limiting factor for species richness. Excluding this lake leads to a significant correlation between ice-free days and species richness.

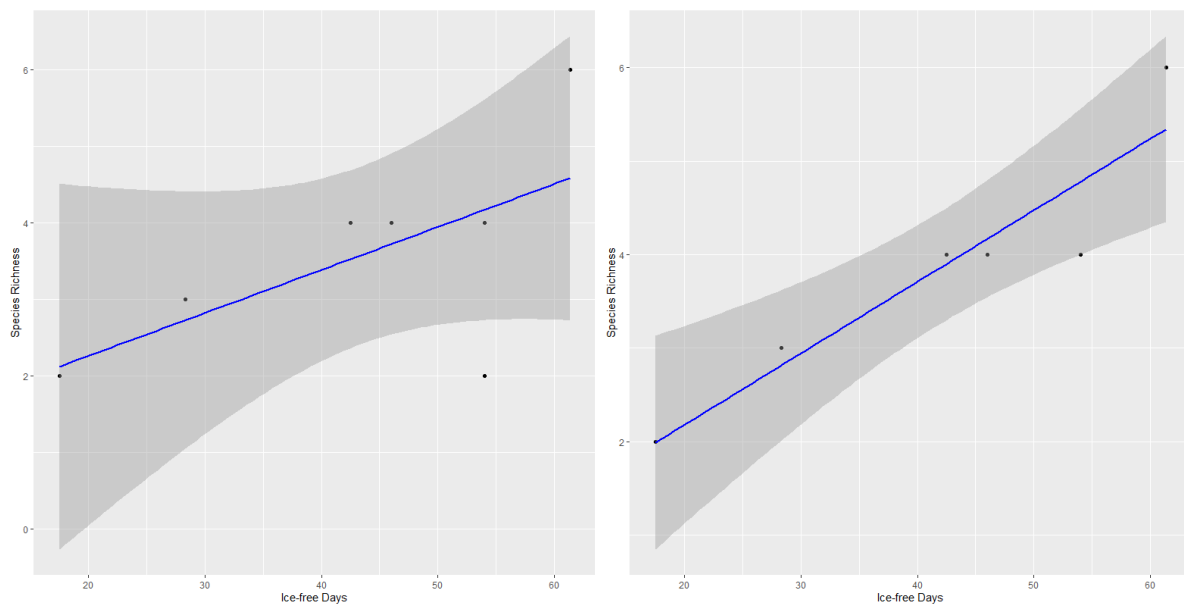


Figure 9 Number of species plotted against mean ice-free days. Ice-free days are the number of days between the lake reaching a defined threshold and the date of sampling. The threshold is temperature above 2 C° and fluctuating temperature as indication of wind and mixing. Only lakes with more than 1 species were considered. The number of ice-free days is the mean value of the years 2018-2020. On the left side $R^2=0.3904$ p -value= 0.1336. On the right side the outlier of lake 14 is removed. $R^2=0.8738$ and p -value= 0.006242**.

Discussion

Species composition

The aim of this study is to identify the species composition in the observed lakes, which abiotic factors influence species composition and to discuss which possible changes could occur if the mean temperature of the year increases. The phytoplankton in these lakes consist of Bacillariophyceae, Chrysophyceae and Dinophyceae and small coccal algae smaller than 15 μ m, that were not classified further. Bacillariophyceae, Chrysophyceae and Dinophyceae were classified further to *Synedra sp.*, *Fragilaria sp.*, *Asterionella sp.*, *Ankistrodesmus sp.*, *Amphora sp.*, *Epithemia sp.*, *Cymbella sp.*, *Dinobryon sp.* and *Peridinium sp.* In most lakes if found diatoms are dominants in the waterbodies of these ecosystems, which seems to be comparable to other studies (Tsarenko, et al., 2019). The lakes often show very little species richness in this size category. Algae bigger than 15 μ m are shown in Figure 1. Often 2-6 different species were found, also lakes without any bigger species were found. Alpine lakes are often dominated by small unicellular flagellates (Tolotti, et al., 2006), which can be seen in Figure 4 in some lakes there is a high peak in Biovolume at 10 μ m sized cells. High alpine lakes are characterized by the relative long winter phase between November and May and the changing light conditions between winter and summer as well as the low nutrient levels (Pechlaner, 1971). Only few species are capable to grow and survive in these harsh conditions, these are mostly not endemic but a selection of low lake species (Tolotti, et al., 2006).

Another point of interest is in comparing the different years. While some lakes only have few different algae species in some years. It seems determined which algae species are in the same lakes with few variances. Lakes that do not have big algae do not get them the next year. Lakes that have big algae also have them in following years. If the abundance is very low, they might not be detected in one year but can be found in the following again.

Higher temperatures favor species with higher surface area to volume ratio (Weckström, et al., 2018). Like *Synedra*, *Fragilaria*, *Asterionella* and *Ankistrodesmus* which are found in higher abundance in 2018 which was warmer compared to 2019, where the abundance is generally lower. Warmer years are also accompanied by longer vegetation periods in these lakes, which can also favor higher abundances. But these differences in abundances are not that strong in other species like *Amphora*, *Epithemia* or *Cymbella*, which only have slightly higher abundances in 2018 compared to 2019. In 2020, which is not so easy to compare as one valley could not be sampled, the abundance is higher in *Amphora*, *Epithemia* and *Cymbella*. For *Synedra*, *Fragilaria*, *Asterionella* and

Ankistrodesmus there is not such a clear trend. In three lakes the abundance is the lowest of all three years, with an exception of lake 06 Löbbensee where the 2 meter abundance is lower and the DCM is exceptionally high (sum of the abundances per ml of *Synedra*, *Fragilaria*, *Asterionella* and *Ankistrodesmus* in 2018 = 29300, 2019 = 4400, 2020 = 100450 cells/ml). *Asterionella* contributes the most. *Dinobryon* does not seem to be affected by colder or warmer years as the abundance does not follow a trend. This means higher temperatures would affect species composition in the epilimnion in these lakes to more needle like species maybe caused by a difference in mixing and stratification as seen in other studies (Rühland, et al., 2015). The presence of *Asterionella* seems to be a marker for strong mixing (Wang, et al., 2012). *Asterionella* is described to bloom in spring or autumn (Rühland, et al., 2015), which might also explain the high peak in 2020 as the sampling time was a few weeks later (27.08.2020), then in the years before (02.08.2018 and 01.08.2019).

Deep Chlorophyll maximum

A Deep Chlorophyll maximum is a very common feature of deeper oligotrophic alpine lakes with stratification (Sawatzky, et al., 2006). In 5 out of 18 lakes a DCM occurs. 8 lakes are very shallow and not deeper than 5 meters. Lake 16 Sulzsee is deep but has a short residence time. The other lakes without a DCM might be too unproductive like lake 01 "Eissele" which show a slight increase in chlorophyll with depth but not enough for a DCM. It is still unclear if the formation of a DCM is due to UV avoidance or a greater nutrient availability (Saros, et al., 2005). In the observed lakes nitrogen is decreasing with depth. The main source seems to be air deposited nitrogen, similar to other studies (Hundey, et al., 2016) (KopciCek, et al., 1995), with maximum concentration on the surface. This suggests no indication for greater nutrient availability with depth and favors the UV avoidance hypothesis. Nitrogen levels could also be low through higher biomass using the available nitrogen as it seems commonly limited in layers of DCM (Sawatzky, et al., 2006). The species found in the DCM do not differ from the 2 meters sample. This is different to other studies like (Latasa, et al., 2016). Where they found separation of species even within the DCM. As the observed lakes only have few larger species there might be no need for this separation within the DCM. The Casy data show differences in cell size distribution between DCM and 2-meter measurements (see figure 4). The DCM has slightly higher biovolume in general but the lower sized cells in all observed DCM contribute the most to the higher biovolume. Additional to differences in species composition (Latasa, et al., 2016) also found an increase in chlorophyll a within deeper layers of the DCM without an increase in cell size, similar to the findings of (Felip & Catalan, 2000) who found an allometric relationship between

phytoplankton biomass and chlorophyll a levels fluctuating seasonally depending on species dominance. There were no measurements within different depths of the DCM but in general there were greater abundance in cells compared to the 2 meters sample not only in pigmentation. The DCM also changes in depth through different years. As the measurements are only once per year it is not possible to tell if they also change throughout the year but it is suggested that the DCM is not constant (Abott, et al., 1984). As already pointed out earlier mixing has a big influence in species composition (Rühland, et al., 2015), outside of alpine lakes mixing was found to influence DCM through changes in sinking rates but also in nutrition supply from below (Huisman, et al., 2006). This might be a different explanation to the UV avoidance hypothesis and to the focus on only nutrient availability. Phytoplankton as well as zooplankton in these alpine lakes are adapted to high UV radiation through pigments (Sommaruga, 2001), this might explain the biomass in shallow depth of 2 meters and indicates an alternative explanation than UV avoidance for the DCM. The differences in DCM depth can be explained by different mixing. Another influence of DCM is zooplankton grazing (Sawatzky, et al., 2006). This could also explain the differences between years as the time of sampling and the time between sampling and ice out varies slightly. The exceptional high DCM values of Lake 06 Löbbensee can be explained by the removal of large zooplankton as this lake has fish in it.

Abiotic factors

The lakes show some variety in abiotic factors between years, but the variety between different lakes is much larger. Abiotic measurements alternate from year to year but do not follow a specific trend like a continuous warming or a continuous increase or decrease in any other measured value. 2022 being the year with the warmest logger maximum temperature, so whole year data one can argue for an increase in temperature, but 2021 is slightly below average. The multi probe data also show higher temperature on the day of sampling for both years 2021 and 2022 but this is just one day in the year so an indication for warming but not enough to see a trend, also it contradicts the trend of the logger data. The glaciers within the valleys Obersulzbachtal and Innerschlöß are getting visible smaller each year. Ice fields can have a buffering effect that changes the trend of warming (Chen, et al., 2014). This could explain the stable temperature in these lakes. In Seebachtal the dominance of the glacier is lower as it is smaller and not in the middle of the valley like in Innerschlöß, lake 08 Grüneckersee which is situated with very much distance to any icefield show a very high increase in maximum temperature (logger data) from 15 °C to 25°. In lake 09 "Schneefeldsee" there is also increase in temperature visible. This lake is named after the ice field reaching inside the lake, the ice

field cools down the lake but as its size decreased very much the buffering effect might also be less effective.

Comparing the biovolume temperature and chlorophyll a in Figure 6 there is a negative correlation between temperature and biovolume as well as temperature and chlorophyll a. So higher summer temperature leads to fewer algae. This is similar to the findings of other studies (Parker, et al., 2008). Although it seems a bit counter intuitive that summers with higher temperatures come with less biovolume, but longer ice-free days periods seem to increase species richness. One possible answer is that the summer temperature is the temperature of the sampling event and is a smaller window. Ice-free days on the other hand are more dependent on spring and autumn temperatures and snowpack of the winter.

According to Hobbs (Hobbs, et al., 2010) et al 2010 *Asterionella* is associated with higher nitrogen levels. In lake 06 Löbbensee there is an *Asterionella* bloom, but nitrogen levels are not exceptionally high compared with other lakes of the three valleys, they are well in the midfield. In 2020 the nitrogen levels could not be correctly measured due to problems with the sensor, so the high *Asterionella* bloom cannot be compared. In 2018 and 2019 there is a difference between *Asterionella* abundance that could be explained by different levels of nitrogen as 2018 has high *Asterionella* abundance and higher nitrogen levels compared to 2019 where there was less *Asterionella* and lower nitrogen levels.

As already discussed in 2019 the biovolume is higher than in 2018 and 2020 with a decrease in temperature on the sampling day. Nitrogen levels in 2019 are also very high compared to other years. This indicates that nitrogen is a limiting factor for algae growth in these lakes. In 2022 the nitrogen levels are even higher with a similar increase in measured chlorophyll. Oligotrophic alpine lakes are often limited in nitrogen (Camacho, et al., 2003), lakes that are influenced by deposition of high levels of atmospheric nitrogen of urban and agricultural sources can be limited by phosphor instead of nitrogen, at least at surface levels (Gardner, et al., 2008). In the observed lakes the main nitrogen source is atmospheric deposition as nitrogen levels decline quickly with depth (Figure 3). However the surface nitrogen levels are relatively high in some lakes especially in 2022 in the lakes 07 Kleiner Tauernsee and 08 Grüneckersee compared with oligotrophic lakes (Bergström, 2010) (Wang, et al., 2019). Phosphor could be a limiting factor in surface water while deep chlorophyll layers are possibly limited in in both nutrients.

Conductivity has variety between the lakes and in different years but no clear increase over this five year time period can be seen like in other alpine lakes the mean conductivity is also slightly lower in

comparison to (Rogora, et al., 2020). Conductivity was not able to explain phytoplankton differences between lakes.

According to (Gnjato, et al., 2022) pH showed a big role in diatom species assemblage in the observed lakes. The pH could only be reliably measured in 2017 and 2022 and does not show continuous values so it is suboptimal to compare the phytoplankton data of 2018-2020 with the years 2017 and 2022. The values vary more between these two years than between the lakes of one year.

Ice-free days

The Species richness correlates positively with Ice-free days. $R^2 = 0.3904$, $p\text{-value} = 0.1336$ for all lakes and $R^2 = 0.8738$, and $p\text{-values} = 0.006242^{**}$ if the outliers lake 14 is removed. The number of species is not just determined by the days without an ice cover of the lakes, as there are a lot of lakes without algae. Concentrating on the ones with algae there is a clear pattern that more species richness comes with more ice-free days, except one lake that has only 2 species instead of 4 which would be the perfect fit. This might be caused by other limitations. This strong effect of ice cover difference on diatom species communities was also observed by (Keatley, et al., 2008) who found two very similar lake in abiotic factors next to each other with very different community response which can be explained by ice cover differences.

This is also interesting in the case of climate change. Ice-free days do not only depend on temperature in summer that leads to faster melting but also on the amount of snow on the lakes and surrounding, which could increase with climate change. But if there are more ice-free days then this could lead to a higher species richness. The number of Ice-free days differs each year. The number of species is better associated with the mean number of ice-free days than with a single year, as changes in species composition are rather slow and seems to be relatively stable.

The correlation between ice-free days and biomass is weak. Which is an interesting finding since species richness is linked to ice-free days, but biomass is not. Biomass takes the small phytoplankton into account and this might be growing so fast that other parameters like Nitrogen and temperature in the last weeks before measurements is more important. Also, the Zooplankton feeding on these might be of greater importance, as bigger algae have a size advantage against feeding pressure from zooplankton in these high alpine lakes. The number of species increases with longer vegetation periods, but the species are not related to a specific vegetation period, except *Peridinium and*

Asterionella. Peridinium was found at the lake with the shortest period of 18 days that has bigger algae as well as in another lake with longer vegetation period. *Asterionella* is only found in the lake with the longest vegetation period that has bigger algae. *Asterionella* is associated with high mixing rates (Wang, et al., 2012) which can be affected by more ice-free days. Ice out does not only affect the growing season timewise but can also alternate stratification and mixing regimes that changes nutrient supplies and sinking rates (Rühland, et al., 2015).

Comparison of neighboring lakes

Lakes that are located close to each other could show similarities in species composition as well as in abiotic factors as they are more likely to share microclimate similarities and watershed (Keatley, et al., 2008). Microclimate is an important factor for vegetation period (Oliver & Corbet, 1966). Vegetation period before sampling seems to have the most influence on species composition (Figure 9). The lake pairs that are close to each other are lake 01 "Eisseele" & lake 02 "In Loche", 05 "See nahe Löbbensee" & 06 Löbbensee in Innerschlöß, lake 11 "Kleines Elend" & lake 12 "Großes Elend" in Seebachtal and lake 13 "See neben Seebachsee" & lake 14 Seebachsee as well as lake 17 "Obervorderjaidbachsee" & lake 18 "Untervorderjaidbachsee" in Obersulzbachtal. These similarities could be in abiotic factors and in species occurrence. In Figure 8 the neighboring lakes are not closer together so no similarity in abiotic factors. Lakes with bigger species occurrence are close together. In Innerschlöß lake 01 "Eisseele" and 02 "In Loche" and 17 "Obervorderjaidbachsee" & 18 "Untervorderjaidbachsee" have bigger sized algae in one of the lakes, but the lake nearby does not have any at all. Both lakes 05 "See nahe Löbbensee" & 06 Löbbensee have bigger algae and in both lakes 11 "Kleines Elend" & 12 "Großes Elend" no bigger algae were observed. The abiotic factors between these neighboring lakes are not similar. Lake 05 "See nahe Löbbensee" & 06 Löbbensee are connected by a river. Except of the appearance of *Fragilaria* in 2019 in lake 05 "See nahe Löbbensee" and not in lake 06 Löbbensee, the community of lake 05 "See nahe Löbbensee" can be described as subset of lake 06 Löbbensee. The absence of *Fragilaria* in lake 06 Löbbensee is an interesting finding as the dispersal could be possible via the river connecting both lakes and the distance between both lakes is short. There might be a predator or a competitor hindering the appearance of *Fragilaria* in this lake. Another explanation is the depth and size of the lakes which might result in different mixing leading to the sinking of *Fragilaria*. This difference in depth also explains the DCM of Lake 06 Löbbensee with very high abundances, lake 05 "See neben Löbbensee" is only about 6 meters deep while the lake 06 Löbbensee is deeper than 15 meters. Both lakes are the only ones which have fish in them (Schabetsberger, et al., 1997), except of the appearance of *Asterionella* this does not seem to

affect or limit the species. The pair of lake 13 “See neben Seebachsee” & lake 14 Seebachsee has a high species turnover of 4 species . While in both lakes *Synedra sp.* occurs, *Dynobrion sp.* was only found in 14 Seebachsee. In lake 13 “See neben Seebachsee” *Amphora*, *Epithemia* and *Fragilaria* occurs. Similar to the pair of Lake 05 “See nahe Löbbensee” & 06 Löbbensee the first lake has *Fragilaria* but not the second. Here there are even more species that would be able to be dispersed to the second lake but somehow are not found in the second lake. Both lakes are connected by a river and the distance between both lakes is below 20 meters. In 2020 there were no measurements in Obersulzbachtal so it cannot be assured if these species occur again as 2019 *Epithemia* and *Fragilaria* had very low abundances. Nitrogen levels were higher in 2019 in both lakes as in 2018. As all three species are common in other lakes with low nitrogen levels it might not be limiting in 2018. To conclude this, neighboring lakes are not similar in abiotic factors or in species composition. There is even species turnover between connected lakes.

Absence of bigger algae in Seebachtal

The lack of bigger algae and diatoms in the Valley Seebachtal cannot clearly be explained by the rock or lack of silica as it is similar to that of the other valleys. The lakes of Seebachtal are all located at very high elevation of 2300-2600 meters. In Innergschlöß there were big algae present at elevations of 2500 meters which contradicts this idea.

In lake 7 kleiner Tauernsee there was a DCM in two of the three sampled years. However, the phytoplankton responsible for this DCM is small in size (about 10 µm see Figure 4) therefore it was not identified further. Different mixing and stratification of the lakes in Seebachtal compared to the other valleys can be an explanation for the absence of bigger algae. As different shapes and volume to surface ratios in combination with different stratification can be a driver of species shifts in planktic diatoms. (Rühland, et al., 2015).

The prescribed shift to small diatoms like *Cyclotella* and *Discostella* is likely to fall into the black box of algae smaller 15µm with *Cyclotella* cell size between 5-54µm (Spaulding & Edlund, 2008) and *Discostella* slightly smaller 2-31µm (Spaulding & Edlund, 2009). No algae bigger 15µm of these genera were found but as some species are well below this size, they would be only visible in the Casy count data.

Conclusion

High alpine Lakes of the National Park Hohe Tauern are not species rich in phytoplankton bigger than 15µm. The species seem to be determined to the specific lake and do not shift through the years except in lake 13 "See neben Seebachsee" there was a species turnover with very low abundances. The variation in species between lakes is greater than the variation between years. Lakes with a longer vegetation period are more likely to have a higher number of different species. No species patterns of cooccurrence were observed. The biovolume as well as the abundance in different size categories show great differences between lakes and years and is often dominated by cells between 5-10µm. Biovolume cannot be explained by vegetation period. Abiotic measurements have great variety on a year to year and on a lake to lake scale. Higher nitrogen levels are associated with higher chlorophyll values but do not explain deep chlorophyll maxima. DCM can be explained by mixing and sinking rates as species are similar to 2-meter samples. Lakes with the occurrence of bigger algae are more similar in abiotic measurements. The absence of bigger algae in Seebachtal cannot clearly be explained. Lakes that are close together do show differences in species composition. While some species compositions in some lakes can be seen as subsets of neighboring lakes, there is also some species turnover even between connected lakes. The species composition can change in the future through climate change, but microclimate of the lake through buffering effects of ice fields will have the biggest influence on length of the vegetation period. It is more likely with longer summer periods that species richness is increasing as lakes with longer vegetation period are more species rich than lakes with shorter vegetation period.

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