The Assessment of Phytoplankton Dynamics in Two Reservoirs in Southern Africa with Special Reference to Water Abstraction for Inter-Basin Transfers and Potable Water Production

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1. Introduction

Phytoplankton production and composition have been reported to be dynamic, vertically, and seasonally in aquatic ecosystems [1,2]. The dynamics could be exacerbated by elevation in water temperature, and nutrients due to changes in climatic conditions, plus anthropogenic activities such as agricultural runoff, and dysfunctional WWTPs [3–5]. In many subtropical eutrophic reservoirs used for portable water, toxic cyanobacteria have been reported to dominate the phytoplankton community and this phenomenon is becoming an increasing concern to many water utility managers [6–14]. The occurrence of potentially toxic cyanobacteria species in drinking water reservoirs leads to the abstraction of poor quality raw water for inter-basin and potable water provision, especially when the vertical and temporal dynamics are not known. The impact could be more severe in reservoirs found in a subtropical desert climate characterized by low rainfall, high evaporation, and spatially distributed populations, where water is transferred between dams to minimize evaporation losses.
Cyanobacteria with a tendency to dominate phytoplankton communities are known to tolerate a wide range of climatic and anthropogenic conditions, which lead to their proliferation as excessive masses in freshwater and marine ecosystems [5,15,16]. Under favorable climatic and anthropogenic induced environmental conditions, cyanobacteria form dense and sometimes toxic blooms in the freshwater and marine environment which threaten ecosystem functioning and reduce water quality for recreation and drinking [17–19]. However, when conditions are not favorable, cyanobacteria have the ability to store essential nutrients and metabolites within the cytoplasm to survive such conditions making them good competitors with other phytoplankton species. Previous studies reported that in many tropical and subtropical reservoirs phytoplankton composition shifts from diatom dominant systems toward high temperature tolerant species of cyanobacteria dominated by mainly *Microcystis* sp. [20–23] due to climate and anthropogenic induced changes in water temperature and nutrient availability.

Cyanobacteria species may gain dominance by using gas vesicles, which enable them to regulate their buoyancy, for vertical movement in the water column to track for light, nutrients, and favorable water temperature [24]. These gas vesicles have notable similarities in molecular structure amongst cyanobacterial genera, but they differ in shape, yield, and critical pressures, with *Microcystis* having a more stable gas vesicle compared to others [25]. It is reported that the optimal habitat for phytoplankton growth is at a depth of 3 m to 5 m within the water column [20]. Phytoplankton growth is lower near the water surface due to photo-inhibition and tends to increase with depth until the light becomes the limiting factor [20,24]. Zhang et al. [24] observed that maximum growth occurred at 0.3 m of the water column for diatoms, chlorophytes, and cyanobacteria which decreased as irradiance increased in Lake Taihu, China. Similarly, in Peri Lake, Brazil, a higher primary production rate of the toxic cyanobacteria species *Cylindrospermopsis* was found at the surface and decreased as a function of water column depth [25]. In addition, the thermal gradient and mixing which causes stratification in the water column is also reported to influence the seasonal composition of phytoplankton by controlling the nutrient distribution in the water column [21]. Chlorophyll-α (Chlα) is reported to vary with depths in many aquatic ecosystems, causing a shift in deep chlorophyll maximum (DCM) within the water column which is driven by light availability and an increase in cellular Chlα concentration [26,27].

In addition to vertical variations in the water column, phytoplankton assemblages also vary with seasons, governed mainly by associated changes in water, light, temperature, and nutrients. Cyanobacteria has been reported to dominate in all seasons in many subtropical lakes causing seasonal blooms [20]. While seasonal blooms may start in summer and last until autumn, some blooms occur throughout the seasons, whereas, episodic blooms which last for weeks or days, may also occur. For example, tropical Lake Ogelube, in Nigeria, reportedly had higher phytoplankton biomass in the rainy season, dominated by chlorophyceae followed by cyanobacteria [20]. Furthermore, tropical and subtropical African lakes including Kariba, in Zimbabwe, Malawi, in Malawi, Tanganyika, in Tanzania, and Victoria in Uganda are reportedly dominated by cyanobacteria in summer and diatoms in winter [20,28]. Touati et al. [27] and Rigosi et al. [29] reported an increase in Chlα in winter causing DCM to be shallower and a decrease in Chlα in summer resulting in an increased DCM depth.

Subtropical lakes found outside the desert climate region such as the Hartbeespoort and Vaal dams, in South Africa, are reportedly dominated by cyanobacteria (i.e., *Dolichospermum* and *Microcystis* sp.) during the warmer summer season [20,30–32]. Subtropical reservoirs, found in a desert climate like Lake Kinneret, Israel, were subjected to spring blooms of *Peridium gatunense* [33]. Lake Nasser, in southern Egypt and northern Sudan, situated in a desert climate, was found to be dominated by *Microcystis* in the spring months [22,34]. However, suspended Chlα concentrations were higher in both the autumn and spring seasons [34]. Karaoun Reservoir, Lebanon which is also located in a desert climate was found to be dominated by the bloom forming cyanobacteria *Aphanizomenon* in spring and autumn, and *Microcystis* in summer [23].
The Swakoppoort and Von Bach dams are important water sources in central Namibia [35]. They are located in a subtropical desert climate characterized by large differences in day and night-time temperature, low rainfall, low humidity, and high evapotranspiration [36]. The two dams are within an ephemeral river, which only flows sporadically during the rainy season [35]. Since the Swakoppoort Dam water is transferred to Von Bach Dam before treatment [35,37], the mixing of this water could cause treatment challenges in the future if the vertical and temporal dynamics of cyanobacteria as a function of water column depths and season are not well understood. Furthermore, the water in the two dams under study is abstracted selectively at different intake points [35], and the abstraction at these points is informed by water quality results of more than seven days on average from the time the water samples are collected to analyses in the laboratory. The water quality results do not take the vertical and temporal dynamics of possible toxic phytoplankton into consideration. Therefore, the combination of climate change and anthropogenic conditions could affect the water quality abstracted from dams, and if not properly treated could pose public health risks.

The vertical and temporal dynamics of cyanobacteria in the Swakoppoort and Von Bach dams have not been established yet. However cyanobacteria cells were reported not to be reduced by phytoplankton control measures in the Swakoppoort Dam [38]. While the climate in which the dams are located is reported to be favorable for cyanobacteria growth, it remains unclear as to which depth ranges these species prefer to inhabit seasonally. The aim of the current study was to describe the vertical and temporal dynamics of phytoplankton communities during the wet (summer) and dry (autumn, winter and spring) seasons in the Swakoppoort and Von Bach dams and the resultant implications for water abstraction and inter-basin water transfers between the two dams as well as potable water provision. The objectives of the current study were (a) to define the vertical and temporal dynamics of potentially toxic phytoplankton species to prevent abstraction of those species for bulk water supply, and (b) to determine the depth ranges related to subtropical desert conditions for the inhabitation of possible toxic phytoplankton species in the Swakoppoort and Von Bach dams.

2. Materials and Methods

2.1. Characteristics of the Study Area and Field Sampling Sites

The Von Bach (21°59′59.27″ S—16°58′54.76″ E) and Swakoppoort dams (22°12′44.31″ S—16°31′44.97″ E) are located in a dry subtropical desert region in central Namibia. These impoundments are warm monomictic man-made dams that, are stratified throughout the year and only experiences overturn or mixing during the winter season due to cold conditions (Figure 1) [35]. The dams are used to supply water to the city of Windhoek, Okahandja Town, Karibib Town, Otjimbingwe Village, and Navahacb Mine [39,40].

Water from the Swakoppoort Dam is transferred through a pipeline to the Von Bach Dam due to its proximity to the treatment plant and the reduced water loss from evaporation due to its smaller surface area [35]. Water from the Von Bach Dam is then abstracted and transported via a pipeline to the Von Bach Treatment Plant for potable water production [40,41]. Swakoppoort Dam has the largest capacity (63.5 Mm$^3$), with a catchment area of 5480 km$^2$ and low annual rainfall of 350 mm/a (Table 1).

A single sampling site with existing historical datasets was selected per dam in the proximity of the dam wall (Figure 1b), as this is the deepest point in the dam, where water is abstracted for transfers and treatment. The selected sampling sites are standard sites established by the utility for continuous monitoring of the dams’ water quality. Depending on the water level in the selected dams, water samples were collected at different intake points. The current study is based on data collected at these sites from 2003 to 2019, on monthly basis in each season.
Figure 1. Maps indicating the (a) location of Namibia within Africa; (b) Swakoppoort and Von Bach dams located in central of Namibia, with sampling sites nearby the dam wall indicated; and (c) location of the Swakoppoort and Von Bach dams in the Swakop River. The maps were created with QGIS v 3.14 pi (Open Source Geospatial Foundation Project) using the Namibia Water Corporation dataset.

Table 1. The main features of the Swakoppoort and Von Bach dams.

| Feature                        | Von Bach Dam | Swakoppoort Dam |
|--------------------------------|--------------|-----------------|
| River                          | Swakop River | Swakop River    |
| Capacity (Mm³)                 | 48.56        | 63.48           |
| Max. depth (m)                 | 29           | 30              |
| Potential evaporation losses (mm/a) | 2254         | 2275            |
| Annual rainfall (mm/a)         | 370          | 350             |
| Surface area (FSC) (km²)       | 4.89         | 7.81            |
| Catchment area size (km²)      | 2920         | 5480            |
| Geology of the areas           | Schist and granite | Schists and granite |
| Year completed                 | 1970         | 1977            |
| Mean depth (m)                 | 10           | 8.1             |

FSC: Full supply capacity.

2.2. Analyses of Abiotic and Biotic Variables

The sampling was always performed between 09:30 a.m. and 2:00 p.m. using a designated boat in both dams. Water temperature (WT) was measured on-site using a digital thermometer (Yellow Springs Instrument, Model 54A, Yellow Springs, OH, USA) with a range of -5 °C to +45 °C, accuracy of ±0.7 °C, at 0.5 m intervals under the water column. Secchi depths (SD) were measured using the standard black and white Secchi disc, 20 cm diameter in size, at each sampling site. Water samples for chemical, phytoplankton identification, and suspended Chl a analyses were collected from the two sampling sites on a monthly basis from 2003–2019. To collect a representative sample at each sampling site, a dip sampling method was followed using a Von Dorn 5 L water sampler [42]. Water
samples were collected at the different depths ranging from the surface to the bottom at the sampling sites found nearby the dam wall, in both the Swakoppoort and Von Bach dams (Figure 1b). Three depth ranges were defined as (a) 0 to 5 m, (b) 5 to 10 m, and (c) 10 to 20 m in the two dams taking into consideration the different intake points where water is abstracted. In the Swakoppoort Dam, the different intake points 1, 2, 3, and 4 were classified under the depth range of 0 to 5 m, intake points 5, and 6 under 5 to 10 m, and intake 7, and 8 under 10 to 20 m. In Von Bach Dam, intake 1 was classified under depth range 0 to 5 m, intake 2, under 5 to 10 m, and intake 3 and 4 under 10 to 20 m respectively. The vertical variation of the biochemical and phytoplankton cells samples were established using the defined depth ranges. Taking into consideration the light penetration gradient of the two dams, the depth ranges of 0 to 5 m was in the photic zone, and both 5 to 10 m and 10 to 20 m were in the aphotic zone.

The collected water samples for biochemical and phytoplankton cells were transferred into 1 L labelled acid washed plastic and glass containers, which were kept in the dark in cooler boxes. The cooler boxes were transported to the laboratory where the phytoplankton were preserved and analyzed within 24 h.

To identify phytoplankton, samples were sedimented in a Sedgewich–Rafter counting chamber and analyzed under an inverted microscope at 400× magnification using the strip-count method [43]. All phytoplankton were identified according to [44–47]. The OP and TP of the water samples were measured using the ascorbic acid method as described in American Public Health Association (APHA) (1998: part 4500 P E) using a spectrophotometer [48]. The total nitrogen of the water samples was measured using the cadmium reduction method as described in APHA (1998: part 4500 NO3-E) [48]. In the analysis of total nitrogen, a reduction column was used together with a spectrophotometer. The turbidity (NTU) of the water samples was measured using a turbidity meter following the nephelometric method (APHA, 1998: part 2130 B) in the laboratory [48]. Suspended Chl a contained in the water samples was measured using the spectrophotometric determination method as described in APHA (1998: part 10200 H) [48].

A blank sample without the analyte was used for quality control and assurance of the analytical processes for each analyzed biochemical sample to correct for potential background signals. The water samples were analysed in triplicate and the results of analysis were arranged in chronological order and sorted according to sampling sites, dates, seasons, and depths. A visual scan was performed to identify possible outliers that were re-analyzed, if necessary.

2.3. Statistical Analyses

The data from 2003–2019 did contain periods where data was missing in some months of the year due to issues of not sampling caused by the unavailability of the boat plus human resources and the timing of the sampling were also not always similar in both the dams. However, the long-term dataset analyses were sufficient to provide insights into the vertical and temporal dynamics of phytoplankton in the two dams. In the study, the summer season was defined as November, December, January, February, and March. Autumn was defined as the months April, and May, winter was defined as June, July, and August, and spring was defined as September and October. The wet season was summer, and the dry seasons were autumn, winter, and spring.

Variation in cyanobacteria abundance and water chemistry data within and among the two dams investigated were assessed using Repeated Measures Mixed Models (Variance Estimation and Precision Module, Statistica v13, Tibo Software, Palo Alto, CA, USA) [49,50]. Seasonal means per depth range per dam per year were used for the analyses. “Season” and “Year” were specified as random factors and applied as repeated measures, whereas, “Depth range” and “Dam” represented fixed effects. Pairwise differences were assessed through Fisher’s least significant difference (LSD) post hoc test. The normality of the datasets applied in mixed models was evaluated using normal probability plots of residu-
als. Cyanobacteria data that were not normally distributed were rank transformed before analysis, whilst, non-parametric chemistry data were boxcox transformed.

The phytoplankton species diversity of the Swakoppoort and Von Bach dams was calculated using Shannon’s diversity index (H) [51]. The TN: P molar ratio was used for the classification of the trophic status of the two dams during the study period using the nutrients index criteria [52–55].

Furthermore, a multivariate statistical analysis of surface water quality based on correlations and variations in the data set, i.e., principal component analysis (PCA) was performed. A PCA triplot was constructed using seasonal average cyanobacteria cell count and water chemistry data representing the 0 to 5 m, 5 to 10 m, and 10 to 20 m depth ranges for both dams investigated. The cyanobacteria data form the focal plot of the PCA triplot, whereas water quality parameters were treated as supplementary variables. Log transformed cyanobacteria data were centered and standardized before use in the PCA [56]. Canoco v5 (Microcomputer Power, Ithaca, NY, USA) was used for multivariate statistical analyses.

3. Results
3.1. Physicochemical Characteristic

During the study period from 2003–2019, the vertical and temporal dynamics of the water temperature was assessed. The summer months (November, December, January, February, and March) were warmer followed by autumn months (April, and May) and spring months (September and October) in both dams, which could be associated with thermal stratification (Table 2). However, winter months (June, July, and August) were found to be colder in both dams for the duration of the study, which could be associated with complete mixing (Table 2).

Vertically, both the Swakoppoort and Von Bach dams exhibited a thermal difference between the depth ranges, and water temperature decreased as a function of depth (Table 2a). Seasonally in the Swakoppoort Dam, the summer mean water temperature was at 23.2 °C reaching a maximum of 28.0 °C, 21.5 °C reaching a maximum of 28.0 °C in autumn, and 18.5 °C reaching a maximum of 28.0 °C in the spring season. Seasonally, the Von Bach Dam, summer mean water temperature was 21.2 °C reaching a maximum of 30.0 °C, 20.2 °C reaching a maximum of 26.0 °C in autumn, and 17.2 °C reaching a maximum of 26.5 °C in

| Dam          | Depth Ranges | Average Temp °C | Minum Temp °C | Maximum Temp °C |
|--------------|--------------|-----------------|---------------|-----------------|
| Swakoppoort Dam | 0 to 5 m     | 20.7 ± 3.8      | 14.0          | 27.0            |
|              | 5 to 10 m    | 19.8 ± 3.1      | 14.0          | 25.0            |
|              | 10 to 20 m   | 15.9 ± 2.1      | 13.0          | 23.0            |
| Von Bach Dam | 0 to 5 m     | 20.4 ± 4.1      | 12.0          | 27.0            |
|              | 5 to 10 m    | 18.6 ± 4.5      | 8.0           | 25.0            |
|              | 10 to 20 m   | 16.0 ± 2.4      | 12.0          | 21.0            |

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spring (Table 2b). Winter water temperatures in the Swakoppoort and Von Bach dams were 15.9 °C and 15.0 °C respectively, reaching a maximum of 21.0 °C, which is lower compared to the other seasons, but favorable for the growth of toxic cyanobacteria. The temperature depth profiles indicate that thermal stratification was experienced in all seasons except for the winter season in both dams. The favorable water temperature at all the depth ranges and seasons could be associated with the desert climate in which the dams are located (Table 2b).

The Secchi depth (SD) was on average 0.6 m reaching a maximum of 4.1 m in the Swakoppoort Dam and was 0.9 m reaching a maximum of 3.6 m in the Von Bach Dam. In the Swakoppoort Dam, the average water turbidity was higher at the depth ranges of 0 to 5 m being 32.62 NTU, compared to deeper depth ranges of 5 to 10 m and 10 to 20 m, although only significantly so relative to the 10 to 20 m range (p = 0.04) (Table 3a). Seasonally, the water turbidity was higher during the dry season of autumn (24.50 NTU), spring (22.87 NTU), and rainy season of summer (18.48 NTU) (Table 3b) which could be related to cyanobacteria blooms during the dry seasons and inflow of suspended solids during the rainy season in the Swakoppoort Dam.

Table 3. The average ± standard deviation of the physiochemical characteristics of the Swakoppoort and Von Bach dams at (a) the different depth ranges; and (b) among seasons.

(a) | Dams                  | Depth Ranges (m) | Total Phosphorus (mg/L) | Total Nitrogen (mg/L) | Ortho-Phosphate (mg/L) | Turbidity (NTU) | Chlorophyll a (µg/L) |
---|----------------------|------------------|-------------------------|-----------------------|------------------------|-----------------|---------------------|
| Swakoppoort Dam       | 0 to 5 m          | 0.35 ± 0.45       | 2.01 ± 0.99             | 0.10 ± 0.10           | 32.62 ± 49.76       | 102.35 ± 117.20  |
|                       | 5 to 10 m         | 0.38 ± 1.38       | 1.98 ± 0.96             | 0.11 ± 0.11           | 15.01 ± 13.38       | 51.88 ± 38.85     |
|                       | 10 to 20 m        | 0.29 ± 0.22       | 2.18 ± 1.10             | 0.15 ± 0.12           | 12.27 ± 8.96        | 24.71 ± 23.17     |
| Von Bach Dam           | 0 to 5 m          | 0.28 ± 0.62       | 1.43 ± 1.02             | 0.03 ± 0.06           | 14.08 ± 35.39       | 45.19 ± 114.14    |
|                       | 5 to 10 m         | 0.18 ± 0.28       | 1.34 ± 0.83             | 0.03 ± 0.07           | 13.75 ± 33.64       | 20.04 ± 29.20     |
|                       | 10 to 20 m        | 0.18 ± 0.22       | 1.61 ± 0.84             | 0.05 ± 0.05           | 17.57 ± 32.91       | 7.18 ± 10.02      |

(b) | Dams                  | Seasons          | Total Phosphorus (mg/L) | Total Nitrogen (mg/L) | Ortho-Phosphate (mg/L) | Turbidity (NTU) | Chlorophyll a (µg/L) |
---|----------------------|------------------|-------------------------|-----------------------|------------------------|-----------------|---------------------|
| Swakoppoort Dam       | Summer            | 0.37 ± 1.34       | 2.23 ± 1.12             | 0.12 ± 0.12           | 18.48 ± 17.92       | 46.42 ± 39.53    |
|                       | Autumn             | 0.30 ± 0.34       | 2.07 ± 0.88             | 0.16 ± 0.12           | 24.50 ± 38.35       | 83.98 ± 121.28   |
|                       | Winter             | 0.37 ± 0.50       | 2.03 ± 0.99             | 0.10 ± 0.08           | 17.21 ± 27.22       | 65.94 ± 98.90    |
|                       | Spring             | 0.27 ± 0.24       | 1.77 ± 0.89             | 0.13 ± 0.13           | 22.87 ± 29.82       | 57.10 ± 57.73    |
| Von Bach Dam           | Summer             | 0.22 ± 0.50       | 1.56 ± 0.97             | 0.05 ± 0.09           | 24.45 ± 51.43       | 14.67 ± 25.65    |
|                       | Autumn             | 0.18 ± 0.23       | 1.48 ± 0.93             | 0.04 ± 0.04           | 13.60 ± 16.62       | 24.10 ± 65.53    |
|                       | Winter             | 0.19 ± 0.29       | 1.32 ± 0.80             | 0.03 ± 0.02           | 7.80 ± 8.65         | 19.06 ± 43.75    |
|                       | Spring             | 0.25 ± 0.44       | 1.55 ± 0.85             | 0.03 ± 0.03           | 11.10 ± 18.08       | 39.32 ± 121.51   |

However, the opposite was observed in the Von Bach Dam, where the average turbidity was generally higher at the deeper depth ranges of 10 to 20 m (17.57 NTU) relative to 0 to 5 m and 5 to 10 m depth ranges (Table 3a). This could be attributed to the inflow of rainfall water carrying suspended solids from the catchment area, as the turbidity was higher in the wet season of summer compared to the dry season of autumn, spring, and winter (Table 3b). The only significant difference in turbidity was, however, between the 5 to 10 m and 10 to 20 m categories (p = 0.02) in the Von Bach Dam. When the seasons were considered collectively, turbidity was significantly higher in the Swakoppoort Dam than the Von Bach Dam (F1,290 = 147.71, p < 0.001).

Throughout the study period from 2003 to 2019, the Swakoppoort Dam was eutrophic with a low N:P ratio of 17.2, while the Von Bach Dam was mesotrophic with a high N:P ratio of 26.7. In the Swakoppoort Dam, there was a high concentration of TP at the upper depth ranges of 0 to 5 m (0.35 mg/L) and 5 to 10 m (0.38 mg/L) compared to the deeper depth range of 10 to 20 m (0.29 mg/L) (Table 3a). Seasonally, summer and winter seasons were observed with a higher concentration of TP followed by autumn and spring (Table 3b). However, there was no significant difference in TP between the different depth ranges (F2,111 = 0.79, p = 0.46). In addition, pH varied significantly among
depth ranges ($F_{2.111} = 24.91, p < 0.001$), although, the only significant pairwise difference was among the 0 to 5 m and the 10 to 20 m ranges ($p < 0.001$). Unlike TP, OP concentration was, however, higher at the depth range of 10 to 20 m (0.15 mg/L) compared to the upper depth ranges (Table 3a). Seasonally, OP concentration was higher in autumn followed by spring and summer (Table 3b). However, there was no significant difference in OP between the different depth ranges ($F_{2.108} = 0.21, p = 0.81$).

A higher concentration of TP was observed at the upper depth ranges of 0 to 5 m (0.28 mg/L) compared to the two lower depth ranges in the Von Bach Dam (Table 3a). The TP concentration was higher in the spring (0.25 mg/L), and summer (0.22 mg/L) compared to the other seasons (Table 3b). However, there was no significant difference in TP among the depth ranges ($p > 0.05$). Moreover, TP varied significantly among the two dams when the seasons were considered collectively, being significantly higher in the Swakoppoort Dam ($F_{1.285} = 41.96, p < 0.001$). Unlike TP, OP concentration was higher at the deeper depth range (0.05 mg/L) compared to the upper depth ranges (Table 3a). Seasonally, summer (0.05 mg/L) and autumn (0.04 mg/L) recorded a higher concentration of OP compared to the other seasons (Table 3b). The concentration of OP was, however, not significantly different between the depth ranges in Von Bach Dam ($F_{2.144} = 0.61, p = 0.55$) or among the two dams ($F_{1.278} = 3.47, p = 0.06$).

3.2. Phytoplankton Community

Throughout the study period from 2003 to 2019, in the Swakoppoort Dam, the phytoplankton community consisted of seven taxonomic groups and 62 species. The taxonomic groups were cyanobacteria (blue-green algae), chrysophyceae (brown algae), bacillariophyceae (diatoms), cryptophyceae (cryptomonads), dinophyceae (dinophyta), euglenophyceae (euglenoids), and chlorophyceae (green algae). Chlorophyceae was the most diverse group, with 39 species, which comprised 63% of the total species richness, followed by bacillariophyceae with 10 species, which were 16% of the total species richness. The latter was followed by cyanobacteria with five species, which were 8% of the total species richness. Chlorophyceae was the most diverse group but only accounted for 13% of the total cell counts. Among the phytoplankton, cyanobacteria dominated the community at 85% of the total cell counts.

In the Swakoppoort Dam, the phytoplankton community was found to vary vertically among depth ranges. Cyanobacteria cell numbers were dominating followed by chlorophyceae at all the depth ranges, but more concentrated at the 5 to 10 m depth range (Table 4a, Figure 2a). Cyanobacteria cell numbers were significantly different between the depth ranges ($F_{2.392} = 10.69, p < 0.001$) in the Swakoppoort Dam. Similarly, Chl a varied significantly as function of depth ($F_{2.101} = 30.89, p < 0.001$), being lower at the 5 to 10 m compared to both the 0 to 5 m and 10 to 20 m depth ranges ($p < 0.001$) (Table 3a).

### Table 4.
The average ± standard deviation of the phytoplankton communities of the Swakoppoort and Von Bach Dams at (a) different depths and (b) among seasons.

| Dams          | Depth Ranges (m) | Cyanobacteria (Cells/mL) | Chrysophyceae (Cells/mL) | Bacillariophyceae (Cells/mL) | Euglenophyceae (Cells/mL) | Dinophyceae (Cells/mL) | Cryptophyceae (Cells/mL) | Chlorophyceae (Cells/mL) |
|---------------|-----------------|--------------------------|--------------------------|-------------------------------|--------------------------|-----------------------|--------------------------|--------------------------|
| Swakoppoort Dam | 0 to 5 m        | 99,270 ± 173,371         | 4 ± 38                  | 1047 ± 1580                  | 37 ± 218                 | 17 ± 156              | 599 ± 1742              | 14,885 ± 40,087          |
|               | 5 to 10 m       | 123,823 ± 136,905        | 6 ± 56                  | 1684 ± 3599                  | 48 ± 279               | 24 ± 177              | 603 ± 999              | 21,900 ± 61,762          |
|               | 10 to 20 m      | 69,661 ± 106,762         | 1 ± 6                   | 1688 ± 2731                  | 60 ± 347               | 41 ± 323              | 283 ± 459              | 8506 ± 28,820            |
| Von Bach Dam  | 0 to 5 m        | 26,691 ± 146,972         | 10 ± 45                 | 379 ± 683                    | 40 ± 116               | 314 ± 802             | 240 ± 602              | 3661 ± 6760              |
|               | 5 to 10 m       | 6702 ± 16,018            | 3 ± 10                  | 391 ± 946                    | 36 ± 101               | 107 ± 222             | 140 ± 409              | 2403 ± 3541              |
|               | 10 to 20 m      | 4406 ± 14,861            | 48 ± 484                | 195 ± 458                    | 15 ± 26               | 27 ± 61               | 32 ± 73                | 1818 ± 4613              |
Temporal variation with seasons were also observed and cyanobacteria dominated the phytoplankton community at the depth ranges of 5 to 10 m during the dry autumn (165,897 cells/mL) and, spring (147,299 cells/mL), and winter (116,338 cells/mL) seasons.
compared to the wet summer season (90,401 cells/mL) in the Swakoppoort Dam (Table 4b, Figure 2a). In the aforementioned depth ranges and seasons, *Microcystis* dominated the cyanobacteria followed by *Dolichospermum* (Table 4a, Figure 2b). Significant variation associated with water depth was observed in the abundance of *Dolichospermum* ($F_{2.392} = 7.29$, $p < 0.001$) and *Microcystis* ($F_{2.392} = 8.74$, $p < 0.001$), whereas *Merismopedia* abundance did not vary among the depth ranges ($F_{2.392} = 0.50$, $p = 0.61$). Applying the seasonal means, cyanobacteria were found to be dominant at all the depth ranges in Swakoppoort Dam but were more concentrated at the 5 to 10 m depth range over the 17-year study period (Figure 3a).

![Figure 3](image-url)  
**Figure 3.** Yearly mean of cyanobacteria species cell counts in, (a) the Swakoppoort Dam and (b) the Von Bach Dam at different depths ranges from 2003–2019. Error bars indicate standard deviations.

In the Von Bach Dam, the phytoplankton community did consist of seven taxonomic groups and 78 species. The taxonomic groups were cyanobacteria (blue-green algae), chrysophyceae (brown algae), bacillariophyceae (diatoms), cryptophyceae (cryptomonads), dinophyceae (dinophyta), euglenophyceae (euglenoids), and chlorophyceae (green algae). Chlorophyceae was the most diverse group, with 48 species (62% of the total species richness), followed by bacillariophyceae with 13 species (17%), followed by cyanobacteria with 5 species (6%). Chlorophyceae was the most diverse group, but they only accounted for 17% of the total cell counts during the study period. Cyanobacteria dominated the phytoplankton community in most of the study period representing 79% of the total cell counts.

The phytoplankton community was found to vary vertically, being dominated by cyanobacteria at the depth ranges of 0 to 5 m in Von Bach Dam (Table 4a, Figure 2a). Total cyanobacteria abundance varied significantly among the different depth ranges ($F_{2.538} = 27.11$, $p < 0.001$). Chl$\alpha$ also varied significantly as a function of depth ($F_{2.147} = 37.06$, $p < 0.001$), and was found to be higher at the 0 to 5 m depth range compared to the 5 to 10 m ($p = 0.002$) and 10 to 20 m ($p < 0.001$) depth ranges (Table 3a).
Temporal variations with seasons were also found and cyanobacteria dominated the phytoplankton community during the dry season of spring (25,416 cells/mL) compared to the summer rainy season (9714 cells/mL) in the Von Bach Dam (Table 4b, Figure 2a). In the depth ranges of 0 to 5 m and spring season, Microcystis dominated the cyanobacteria followed by Dolichospermum (Figure 2b). Significant variation associated with water depth was observed in the abundance of both Dolichospermum ($F_{2,538} = 27.11, p < 0.001$) and Microcystis ($F_{2,538} = 11.43, p < 0.001$), whereas Merismopedia abundance did not vary among the depth ranges ($F_{2,538} = 1.35, p = 0.26$). Applying the seasonal means, yearly cyanobacteria cells in the Von Bach Dam dominated at all the depth categories but were more concentrated at the 0 to 5 m depth range throughout the 17 year study period (Figure 3b).

Cyanobacteria cell numbers were significantly higher in the Swakoppoort Dam relative to Von Bach Dam ($F_{1,949} = 875.43, p < 0.001$) (Table 4a,b, Figure 2a). Moreover, significantly higher cell counts of Dolichospermum ($F_{1,949} = 155.84, p < 0.001$), Microcystis ($F_{1,949} = 829.64, p < 0.001$) and Merismopedia ($F_{1,949} = 75.10, p < 0.001$) were observed in the Swakoppoort Dam relative to the Von Bach Dam (Table 5a,b, Figure 2b).

**Table 5.** The average ± standard deviation of the abundance of cyanobacteria species observed in Swakoppoort and Von Bach dams at (a) different depth ranges and (b) among seasons.

| Dams          | Depth Ranges | Dolichospermum (Cells/mL) | Cylindrospermopsis (Cell/mL) | Merismopedia (Cell/mL) | Microcystis (Cell/mL) | Oscillatoria (Cells/mL) |
|---------------|--------------|----------------------------|----------------------------|------------------------|-----------------------|-------------------------|
| **Swakoppoort** | 0 to 5 m     | 16,655 ± 67,699            | 321 ± 1615                 | 5356 ± 18,437          | 67,921 ± 145,498      | 12 ± 140                |
|               | 5 to 10 m    | 15,916 ± 39,976            | 520 ± 2150                 | 4347 ± 15,279          | 86,576 ± 126,867      | 702 ± 8515              |
|               | 10 to 20 m   | 7442 ± 12,149              | 308 ± 1457                 | 7109 ± 18,199          | 50,546 ± 105,331      | 2 ± 21                  |
| **Von Bach**  | 0 to 5 m     | 5104 ± 13,612              | 127 ± 931                  | 372 ± 1514             | 20631 ± 146,475       | 19 ± 181                |
|               | 5 to 10 m    | 2437 ± 6986               | 97 ± 981                   | 258 ± 1122             | 3524 ± 13,388         | 124 ± 1376              |
|               | 10 to 20 m   | 756 ± 2674                | 81 ± 1106                  | 1599 ± 12,118          | 1528 ± 6809           | 3 ± 46                  |

| Dams          | Seasons      | Dolichospermum (Cells/mL) | Cylindrospermopsis (Cell/mL) | Merismopedia (Cell/mL) | Microcystis (Cell/mL) | Oscillatoria (Cells/mL) |
|---------------|--------------|----------------------------|----------------------------|------------------------|-----------------------|-------------------------|
| **Swakoppoort** | Autum       | 2743 ± 4266               | 442 ± 2235                 | 12,996 ± 2235          | 96,267 ± 156,646      | -                       |
|               | Spring       | 22,890 ± 85,142           | 333 ± 1484                 | 2,608 ± 18,559         | 97,370 ± 133,018      | -                       |
|               | Summer       | 21,681 ± 49,748           | 390 ± 1492                 | 5502 ± 11,827          | 33,945 ± 57,724       | 719 ± 8603              |
|               | Winter       | 5683 ± 9229              | 380 ± 1937                 | 1855 ± 9192            | 76,527 ± 156,657      | 15 ± 160                |
| **Von Bach**  | Autum       | 3458 ± 7363              | 396 ± 2249                 | 1389 ± 2800            | 2049 ± 4796           | 20 ± 145                |
|               | Spring       | 1817 ± 6484              | -                          | 11 ± 63                | 23,533 ± 183,298      | 10 ± 100                |
|               | Summer       | 3819 ± 12,634            | 62 ± 476                   | 1407 ± 12,384          | 3993 ± 22,366         | 100 ± 1214              |
|               | Winter       | 934 ± 1939              | 15 ± 113                   | 145 ± 581              | 8297 ± 58,085         | -                       |

Using the Shannon’s Diversity Index (H), the species richness of the phytoplankton community considering the dominant taxonomic group, which is cyanobacteria, was calculated for the two dams. The Von Bach Dam was characterized by low species diversity as indicated by Shannon’s Diversity Index $H = 0.4$. Similarly, Swakoppoort Dam did also have a low species diversity of $H = 0.3$.

The PCA and associated triplot indicates that phytoplankton abundance and water quality parameters varied among the two dams investigated—based on the segregation in ordinal space (Figure 4). The chemistry parameters Chla, pH, TN, and OP were positively correlated with phytoplankton indicators including total phytoplankton cells, total cyanobacteria, and the abundance scores of various phytoplankton groups investigated (Figure 4). In addition, TN, OP, and suspended Chla as well as the majority of phytoplankton groups studied associated positively with the Swakoppoort data points representing both seasons and depth classes except for the wet season 5–10 m class (Figure 4).
The PCA and associated triplot indicates that phytoplankton abundance and water quality parameters varied among the two dams investigated—based on the segregation in ordinal space (Figure 4). The chemistry parameters Chl$_a$, pH, TN, and OP were positively correlated with phytoplankton indicators including total phytoplankton cells, total cyanobacteria, and the abundance scores of various phytoplankton groups investigated (Figure 4). In addition, TN, OP, and suspended Chl$_a$ as well as the majority of phytoplankton groups studied associated positively with the Swakoppoort data points representing both seasons and depth classes except for the wet season 5–10 m class (Figure 4).

**Figure 4.** Principal component analysis (PCA) triplot indicating the associations between selected phytoplankton classes and genera, total phytoplankton cell number, and selected water quality parameters at different depth range in the Swakoppoort and Von Bach dams.

**4. Discussion**

Aquatic ecosystems exhibit spatial and temporal variability in the phytoplankton community. The dominance of a particular species is related to changing environmental conditions. In the current study, the phytoplankton community was dominated by cyanobacteria and, in particular, mainly the species of *Microcystis* followed by *Dolichospermum* in both dams, at all the studied depth ranges and seasons. Vertical variation as a function of depth was found in both dams, and cyanobacteria was the dominant phytoplankton species at all depth ranges. However, temporal variations with dry and wet seasons was only found in the Swakoppoort Dam, and not in the Von Bach Dam. The high cell numbers of cyanobacteria in the Swakoppoort Dam could be due to its eutrophic status as compared to the mesotrophic status of the Von Bach Dam during the study period.

The results of the current study are similar to other reports in the literature which justify the dominance of *Microcystis* in subtropical lakes with favorable water temperature and elevated nutrient levels caused by partially treated sewage and industrial effluent [1,22,34,57]. The dominance of cyanobacteria in the subtropical Lake Chivero, in Zimbabwe and Hartbeespoort Dam in South Africa, has previously been reported [20,21,32,58,59], corresponding to the results of the present study featuring two water bodies which are also located in a subtropical region although also semi-arid. A study by Kassem et al. [34] on the subtropical semi-arid Lake Nasser in Egypt revealed similar findings of the dominance of the phytoplankton community by cyanobacteria species of *Microcystis*. In addition, Ballot et al. [32], reported that cyanobacteria species of *Microcystis* dominates the Hartbeespoort Dam in South African, surface water. In fact, the dominance of the phytoplankton community by cyanobacteria species of *Microcystis* is common in subtropical lakes, but less common in tropical lakes where other species like *Cylindrospermopsis* are present [1,20,60,61]. Throughout the study, both dams exhibited thermal variation in the water temperature at the three...
depth ranges and seasons, which could be due to the desert climate conditions in the region. This could have contributed toward the depth profiles and seasonal dynamics of the phytoplankton communities, and the concentration of phytoplankton cell numbers at favorable depth ranges.

Cyanobacteria species are reported to dominate other phytoplankton species due to elevated water temperature of >15 °C [62,63]. The two dams’ water temperatures were above 15 °C at all the depth ranges, and across seasons. Ndebele-Murisa et al. [20] states that the increase in water temperature due to climate warming will shift the phytoplankton species composition from Chlorophyceae to Cyanophyceae. Haakonsson et al. [64] reported the dominance by *Microcystis*, which was caused by the increase in water temperature in subtropical lentic systems. The increase in water temperature causes thermal stratification in lakes, which influences the quality of water in the water column. Noori et al. [65] reported the strongest thermal stratification occurred during summer in Karkheh Dam Reservoir, when the water temperature difference between the surface and bottom in the reservoirs exceed 18 °C. The thermal stratifications were reported to cause the spatial temporal variation in ammonium and nitrate in Karkheh Dam Reservoir [65].

At the preferred depth ranges for the habitation of toxic phytoplankton, the water turbidity was slightly lowered compared to the other depth ranges in both dams. These findings support the observations by Jeppesen et al. [22], on the occurrence of major toxic cyanobacteria blooms of *Microcystis* during the decline in turbidity in subtropical and tropical lakes. The nutrient concentrations in the two dams were suitable for cyanobacteria growths at all the depth ranges and seasons. This was similar to conditions of the nutrient-enriched subtropical lakes of Chivero, in Zimbabwe, and the South African dams of Hartbeespoort, Erfenis, and Allemanasraal [20]. Noori et al. [66] reported a rapid transition from oligotrophic to eutrophic causing water deterioration of the Sabalan Reservoir, Iran, due to external pollution loads (natural and anthropogenic activities), internal pollutant cycling from the sediments, reduced inflows, and reservoir operations strategy. Similar causes may have resulted in water quality deterioration in the two dams presently studied, which are also used for domestic water supply.

The preferred depth range of cyanobacteria in the Von Bach Dam was in the photic zone, and that of the Swakoppoort Dam was in the aphotic zone. The findings of the occurrence of increased phytoplankton abundance in the photic and aphotic zones of the two study areas correspond to the observations by Moura et al. [1], in the Caprina Reservoir, Brazil. However, the assemblages were dominated by multi-species of cyanobacteria unlike in the Swakoppoort and Von Bach dams with one dominant species of cyanobacteria. The findings of Moura et al. [1] revealed that vertical variation was less pronounced than seasonal variation in the cyanobacteria population, while in the current study both vertical and seasonal variations were pronounced in the Swakoppoort Dam and only vertical variation in the Von Bach Dam. A limitation of the study by Moura et al. [1], is however duration as it features only two years of observations.

Bittencourt-Oliveira et al. [61] reported the dominance of cyanobacteria by *Cylindrospermopsis* during the dry and rainy seasons due to stratification and de-stratification in the Arcoverde Reservoir in Brazil. In the current study, *Microcystis* was found to dominate during both the dry and rainy seasons. These findings support the observations by Kassem et al. [34], in the Khor Ramla and Khor Abu-Simbel of Lake Nasser where more phytoplankton was reported in the dry season, with spring blooms of *Microcystis*. The observations of the current study corresponds to those of Kassem et al. [34] under desert climate conditions, with spring blooms observed in both dams with higher numbers of cyanobacteria cells, compared to the other seasons. Blooms were also observed during the dry autumn and winter season in the two dams. In Lake George in the United States of America, dry periods are characterized by dense cyanobacteria blooms [22]. Lake Nasser in southern Egypt and northern Sudan, and Lake George in the USA are also subtropical and tropical lakes with similar desert climates like that of the Swakoppoort and Von Bach dams.
Graham et al. [67] state that cyanobacteria maintain the position in the photic zone despite the mixing, and may migrate to different locations within the same zone using buoyancy regulation. The authors further mentioned that the cyanobacteria population distribution was in the proximity of the surface at night, and early morning, followed by movement to deeper water later in the day. This movement is dominated mainly by Microcystis [67]. The findings of the present study support the theory of Graham et al. [67] as Microcystis was found to dominate in the upper water column, although some depths were aphotic. In Hartbeespoort Dam, South Africa, Microcystis was reported to dominate at the depth of 5 m, which was a layer with minimal light due to hyperscum covering the water surface [59]. Oberholster and Botha, [59] further state that the concentration of Microcystis at the low light strata results in no reverse buoyancy. Reynolds et al. [68] stated that Microcystis generally dominate subtropical systems. This is due to diel alteration of thermal stratification and mixing conditions [68,69]. Therefore, the abstraction of water with potentially higher toxic cyanobacteria abundance could pose challenges to water transfers between dams and potable water production due to the buoyancy regulation of Microcystis.

Chemical pollution is a further factor to account for as part of water extraction management practices. Aradpour et al. [70] reported concentrations of arsenic in the water column and sediment of the Sabalan Dam Reservoir, Iran. A scenario-based risk assessment indicated that water extracted below 10 m can pose a human health risk due to higher concentrations of arsenic at depths exceeding 10 m [70]. The results of Aradpour et al. [70] and the present findings suggest that water extraction strategies should account for both hazardous chemical and potentially harmful phytoplankton depth profiles in waterbodies known to be polluted.

The findings in this study on the vertical and temporal dynamics of possible toxic phytoplankton could enhance the traditional selective withdrawal of water from the two dams to ensure that good water quality is abstracted for treatment and transfers at preferred depth ranges in different seasons.

5. Conclusions

In conclusion, the phytoplankton communities in the two dams were dominated by toxic cyanobacteria, mainly by Microcystis, followed by Dolichospermum at all the depth ranges and seasons. The dry seasons of autumn, spring, and winter were characterized by increased phytoplankton cell numbers compared to the wet summer season. Spring and autumn cyanobacterial blooms were observed in the two dams with more phytoplankton cell numbers compared to the dry winter and autumn. In the Swakoppoort Dam, the preferred depth ranges by the potentially toxic phytoplankton was at 5 to 10 m, and in Von Bach Dam the preferred depth was shallower, being 0 to 5 m. The depth ranges preferred by cyanobacteria corresponded to the depths at which favorable water temperature and nutrient concentrations for phytoplankton growth was observed.

Given the vertical and temporal dynamics in the phytoplankton community of the dams, we recommend the following: firstly, the traditional selective withdrawal at varied depths to be enhanced with consideration of vertical and temporal dynamics of possible toxic cyanobacteria to ensure the abstraction of good quality water with minimal numbers of potentially toxic phytoplankton species from both dams. The 5 to 10 m depth range should be avoided in the Swakoppoort Dam during the dry seasons. The depth range 0 to 5 m should be considered in all the seasons and if possible also the depth range of 10 to 20 m. While in the Von Bach Dam, the depth range of 0 to 5 m can be considered for
abstraction in all the seasons except in the spring season. The other Von Bach Dam depth ranges of 5 to 10 m and 10 to 20 m should be considered throughout the year.

Secondly, the utility manager may consider preparing for a possible eruption of toxins from the dominant toxic cyanobacteria species such as *Microcystis* and *Dolichospermum*. Because the water extracted from Swakoppoort Dam is mixed with Von Bach Dam water before treatment, consideration for continuous cyanotoxin testing during the dry seasons of autumn, spring, and winter could ensure the safety of water produced at the Von Bach Dam treatment plant for the capital city of Windhoek, Namibia.

Thirdly, the transfer of nutrient rich and salt water from Swakoppoort Dam to Von Bach Dam needs to be monitored over time.

Fourthly, during water transfer from Swakoppoort Dam to Von Bach Dam, the operation strategy should consider for sufficient water for dilutions of pollutants emanating from internal cycling from the sediment bottom of the Swakoppoort Dam.

Fifthly, future studies are required to further research (a) the variation of cyanobacteria toxin at the different depth ranges of the two dams, (b) water withdrawal influence on internal nutrients cycling from the bottom of the sediments.

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