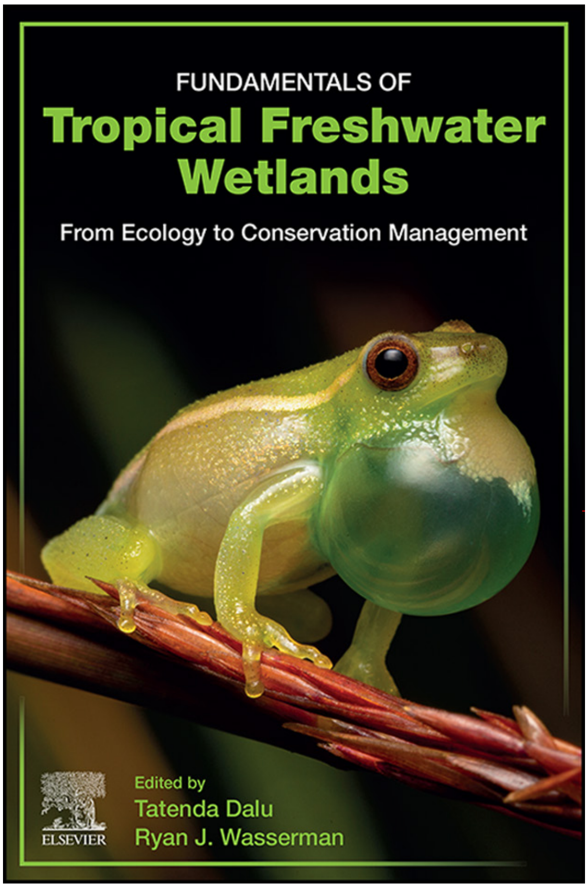

From Tatenda Dalu, Tongayi Mwedzi and Ryan J. Wasserman, Phytoplankton dynamics. In: Tatenda Dalu and Ryan J. Wasserman, editors, Fundamentals of Tropical Freshwater Wetlands. Chennai: Elsevier, 2022, pp. 189-220.
ISBN: 978-0-12-822362-8

Elsevier.

Chapter 8

Phytoplankton dynamics

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8.1 Introduction

Wetlands provide a wide array of essential ecological services (Srichandan et al., 2015; Lin et al., 2019; Wasserman and Dalu, 2022, Chapter 1). Freshwater wetlands are diverse in nature, with large wetland types having received much attention. Many tropical wetlands, however, constitute often small, understudied habitat types scattered across various landscape, harboring communities and meta-communities of aquatic fauna (see Gálvez et al., 2021, Chapter 18). These patchy environments can also act as evolutionary hotspots and provide natural laboratories to assess evolutionary, trophic, and other important ecological processes (Srichandan et al., 2015; Dalu et al., 2017b; An et al., 2019; Wasserman et al., 2018). The endemic ecological specialist species, restricted habitat size, and anthropogenic threats to small wetland ecosystems merit more intensive research focus as these systems may harbor unique taxa (Greenway, 2010; Chia et al., 2011). Primary productivity in these systems is driven by a combination of aquatic and semi-aquatic photosynthetically active groups (Bernard and Gorham, 1978). Wetlands are typically dominated by free-floating and rooted macrophytes which form a major component of carbon fixation. While macrophytes are extremely important primary producers in tropical wetlands, phytoplankton is also a major contributor and a crucial component for secondary aquatic productivity (Behrenfeld and Falkowski, 1997). Atmospheric, hydrological, geological, and biological dynamics all affect wetland phytoplankton productivity and communities, similar to other aquatic environments (Wetzel, 2001; Robertson et al., 2001).

However, unlike in marine and other freshwater ecosystems (i.e., rivers, lakes, reservoirs) where the ecology of phytoplankton communities are relatively well studied, systematic insights on phytoplankton community

Fundamentals of Tropical Freshwater Wetlands. DOI: https://doi.org/10.1016/B978-0-12-822362-8.00005-0

assemblages, functional qualities, and seasonal changes associated with environmental variables are largely lacking for many tropical wetland types. While there have been far more studies conducted on wetlands in temperate than in tropical and subtropical regions, recent studies have suggested that primary production rates are typically higher within the tropical regions than comparable temperate systems (Fig. 8.1; Davies et al., 2008). Relevant literature from the tropics has, however, increased with some work indicating that tropical aquatic ecosystems present distinct ecological patterns compared to other systems (Sarma et al., 2005; They et al., 2014; Iglesias et al., 2017; Clarke et al., 2017). This chapter provides an introductory overview of phytoplankton ecology in tropical wetlands, with an emphasis on small understudied wetland types. Further, given the importance of cyanobacterial blooms in both human and animal health, the chapter also gives an overview of cyanobacterial blooms and their toxins.

8.1.1 What is phytoplankton?

The term plankton was first coined by Victor Hensen in 1887 to include all organic matter particles which can float freely and involuntarily in open water, independent of shores and bottom, and excluded large vertebrates of

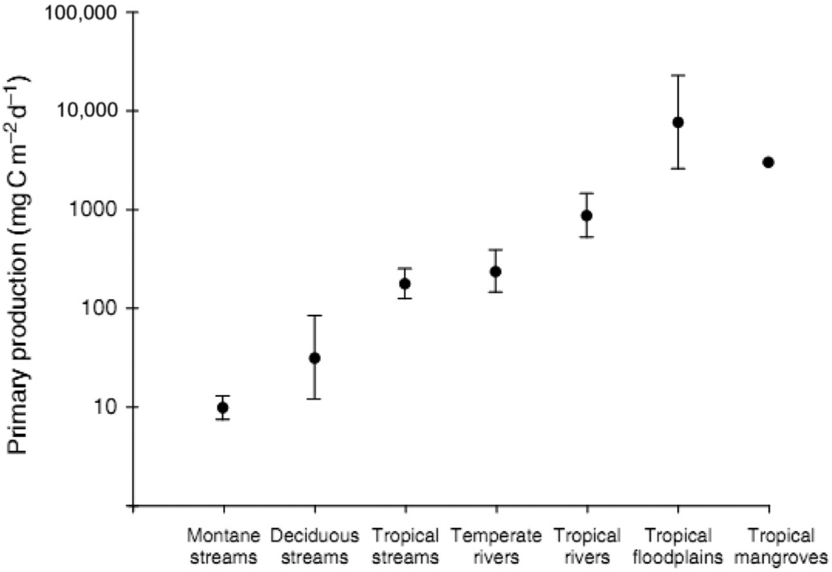


FIGURE 8.1 Primary production (mg C m^{-2} d^{-1}) rates for various ecosystems, outlining the relatively high levels of primary production in tropical aquatic environments. Reproduced with permission from *Davies Jr., P.M., Bunn Jr., S.E., Hamilton Jr., S.K., 2008. Primary production in tropical streams and rivers. In: Dudgeon, D. (Ed.), Tropical Stream Ecology. Academic Press, London.*

the open water which had the ability to swim (Reynolds, 1984). However, Hensen's definition included nonliving particles. Richard Kolkwitz in 1912 adopted the now commonly used definition which highlights that plankton are small and microscopic components found in all aquatic habitats (i.e., littoral, benthic, pelagic) and are mostly living organisms thereby excluding the nonliving components. Thus plankton were rudimentally divided into two groups, that is, plants (phytoplankton) and animals (zooplankton). Phytoplankton is generally considered the autotrophic (partial or complete) component of plankton. Autotrophy refers to the ability to synthesize food from inorganic substances using chemical or light energy (Quayle and Ferenci, 1978). Phytoplankton, typically employing light energy production through photosynthetic processes, includes several single-celled representative groups of algae and bacteria as well as infective stages of certain actinomycetes and fungi. Phytoplankton help purify waters by taking up nutrients and pollutants (regulating service) (Biggs and Kilroy, 2000). They also transform nutrients from inorganic to organic forms, such as Cyanophyta which converts atmospheric nitrogen (N_2) into ammonium (NH_3^+) (Lee et al., 2013). The various phytoplankton groups are well described in John et al. (2002) and include 15 common phyla: Bacillariophyta (diatoms), Chlorophyta (green algae), Chrysophyta (golden algae), Cryptophyta (cyptomonads), Cyanophyta (cyanobacteria), Euglenophyta (euglenoids), Eustigmatophyta, Glaucophyta, Haptophyta (Prymnesiophyta), Phaeophyta (brown algae), Prasinophyta, Pyrrophyta (dinoflagellates), Raphidophyta, Rhodophyta (red algae), and Xanthophyta (yellow-green algae), with the Chlorophyta and Bacillariophyta being the most diverse groups.

Certain phytoplankton can move independently, by means of flagella, or through various mechanisms that alter their buoyancy (Reynolds, 1984). They occur in benthic and pelagic environments, with their vertical distribution generally limited by light availability. While typically single-celled, some phytoplankton is capable of forming colonies and filaments. These seemingly inconspicuous primary producers are prevalent across marine and freshwater ecosystems, and form the base of aquatic food webs, on which almost all aquatic fauna directly or indirectly rely. In addition, as part of the photosynthetic process of converting light into energy, oxygen is released into the environment. It is thought that phytoplankton is responsible for more oxygen production than tropical rainforests such as the Amazon, which are often misleadingly referred to as the "lungs" of planet earth (Chavez et al., 2010). Given their basal role in aquatic food production and their importance in atmospheric processes, phytoplankton are among the most important and relevant groups, although their role is often overlooked by the general public (Fig. 8.2).

The cosmopolitan nature of phytoplankton has been highlighted in many scientific articles, books and reports. The Baas-Becking (1934) hypothesis which states that "everything is everywhere, but the environment selects" has dominated the view on phytoplankton distribution for over a century,

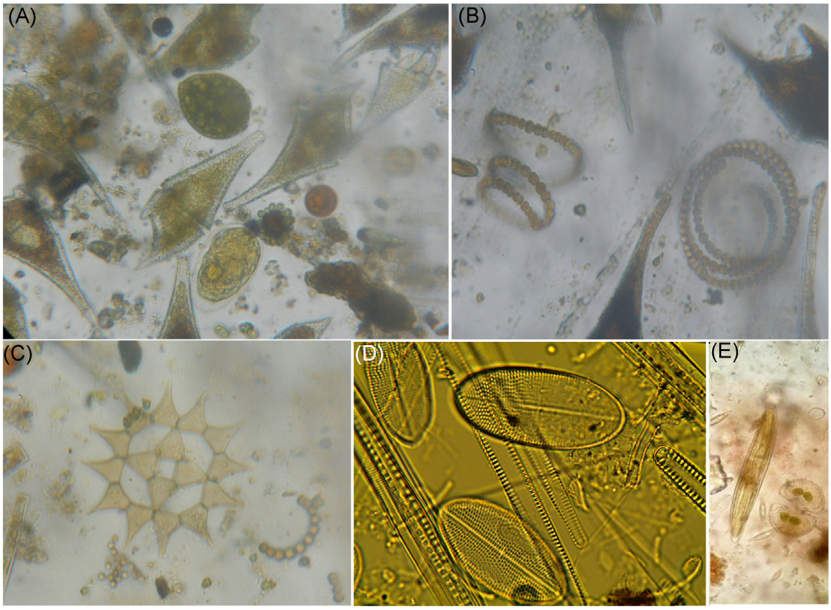


FIGURE 8.2 Various plankton taxa: (A) dinoflagellates (e.g., *Ceratium* sp.), cyanobacteria, and diatoms; (B) *Anabaena* sp. (cyanobacteria) and *Ceratium* sp. (dinoflagellate); (C) *Pediastrum* sp. (chlorophyte) and *Fragilaria* sp. (diatom); (D) diatoms, *Fragilaria* sp., and *Cocconeis* sp.; and (E) *Gyrosigma* sp. (diatom) and desmid from a water sample collected in a tropical African wetland. *Pictures by Tatenda Dalu.*

and has greatly contributed to the predominant notion that phytoplankton are cosmopolitan (Reynolds et al., 2002; Padisák et al., 2016; Mangadze et al., 2019). Thus it is true in a sense that they occur in almost each and every sufficiently irradiated aquatic habitat present on earth (Padisák et al., 2016). However, with increasing research knowledge on occurrence and distribution of phytoplankton species across different habitats and geographic regions, previously unrecorded taxa, reports on invasive species, phylogenetic assessment, and tracing of secondary metabolites (i.e., cyanotoxins) seem to contradict the Baas-Becking hypothesis (Incagnone et al., 2015; Padisák et al., 2016). Thus this suggests that all phytoplankton are neither cosmopolitan, nor ubiquitous (Padisák et al., 2016).

8.1.2 Phytoplankton reproduction and dispersal

A typical phytoplankton life cycle includes growth, reproduction, and death, but the life cycle of certain taxa can include a dormancy period (Reynolds, 1984). The golden algae, for example, can produce cysts and/or spores which can remain dormant for several months to years depending on prevailing conditions, and some diatoms and dinoflagellates form cysts during harsh periods such as wetland drying out (Timoney et al., 1997). Phytoplankton life cycles vary among the different species, and some species can produce small motile cells that keep growing and multiplying until nutrient levels decrease before forming colonies surrounded by sticky mucous coats containing nutrients that allow for continued growth and reproduction (Brand et al., 1981; Rojo, 2020).

Phytoplankton have efficient asexual and sexual reproductive strategies, and when growing conditions are suitable, they reproduce and grow quickly through various asexual reproduction means. For example, (1) fast-growing dinoflagellates divide through binary fission forming identical cells that will divide repetitively; (2) *Spirogyra* spp. (and other phytoplankton filament-forming groups) cells attach end to end, forming long filamentous chains which divide forming new filaments through simple mitosis and fragmentation (Fritsch and Rich, 1907); and (3) green algae and cyanobacteria may produce spores that continue dividing inside the parent cell, with mature endospores forming identical offspring. Sexual reproduction involves producing offspring with a unique genetic makeup and this genetic diversity enables the phytoplankton species to adapt to adverse environmental conditions. For example, (1) diatoms produce and release diploid male (spermatogonia) and female (oogonia) gametes which mate to form a zygote (auxospore) that can enter dormancy and only grow into diatoms under suitable conditions, and (2) *Volvox* spp. monecious colonies (and other green algae) produce both male and female gametes, while the diecious colonies produce either eggs or sperm (Nozaki, 1988). Thus in female *Volvox* spp. colonies, individual cells can grow to become oogametes which can enter a resting diploid zygote stage after syngamy.

Phytoplankton growth varies seasonally, and is regulated by temperature and nutrient availability (Reynolds, 1984). In many aquatic systems, winter mixing of the water column initiates spring/summer blooms by bringing nutrients from the bottom waters to the surface layers (Vincent, 1983; Vellidis et al., 2003). In shallow water wetland systems, however, nutrient availability is often less stratified than in deeper water bodies, with implications for its seasonal availability and uptake (Vellidis et al., 2003). In tropical regions, seasonal temperature effects are less prevalent than at higher latitudes, and as such, aquatic primary productivity is driven by other environmental factors, such as rainfall dynamics (Padisák et al., 2016). In both tropical and subtropical regions, seasonal rainfall is the primary driver of the freshwater wetland footprint. Many permanent wetland systems swell in size following the rains, converting adjacent terrestrial environments into wetlands. Many smaller systems are seasonal, temporary, or even ephemeral wetland environments, only becoming inundated following large rainfall events or replenishment of the water table. Further, systems of the region are often warm and characterized by large surface-area to volume ratios, with implications for evaporation rates. These factors drive variation in water volume and depth, as well as allochthonous nutrient availability, with implications for biota in freshwater wetlands of the region. Since phytoplankton vegetative forms only exist in inundated aquatic ecosystems, most phytoplankton in wetland systems have developed mechanisms (i.e., reproductive strategies and physiognomic characteristics) that make them well adapted to the variable conditions (Padial et al., 2014). Certain phytoplankton groups have specialized forms (i.e., spores, cysts, akinetes) that are resistant to the harsh terrestrial conditions (Padisák et al., 2016). For example, the cyanobacterial genus *Chroococcidiopsis* have adapted to desiccation by switching their metabolism on and off in response to environmental changes, making use of short periods of liquid water availability. Furthermore, they accumulate trehalose and sucrose in response to water stress which act as phospholipid bilayers and proteins stabilizer and then recover and resume photosynthesis when conditions are favorable (Potts, 1994; Caiola et al., 1996; Williams et al., 2014). Certain phytoplankton can survive in these habitats by not responding to rainfall during the dry season as extracellular polysaccharides regulate moisture penetration and thus protect cyanobacteria from premature "resurrection" (Williams et al., 2014).

To move from one water body to another, phytoplankton propagules have to travel over the terrestrial environment exposed to desiccation risk. Thus the phytoplankton dispersal requires some dispersal agent (i.e., air, animals, humans, water), with species transport tolerances for travel distances and conditions varying. Several phytoplankton taxa produce mucilage, and have cell walls that can act as defences, allowing for short-distance dispersal (see Genitsaris et al., 2011; Incagnone et al., 2015). Some phytoplankton (i.e., chlorophytes, cyanobacteria, cryptophytes, diatoms, euglenophytes) have cryptic dispersal methods such as the vegetative cells which are dispersed from water by bubble-burst processes for short distances generated by wind action on water surfaces (Hamilton and Lenton, 1998; Vanormelingen et al., 2008; Padisák et al., 2016). While specialized forms are common in many taxa in tropical wetland systems, most phytoplankton groups do not show such adaptation (Padisák et al., 2016). So, given the hydrologically dynamic nature of tropical, and in particular subtropical wetlands, the role of specialist life-history strategies in driving phytoplankton community assemblages and phenologies is likely much more important than in larger aquatic ecosystems.

8.2 Distribution patterns

There are no known key phytoplankton taxa that occur exclusively in tropical wetlands, although some taxa may occur in high abundances or specific forms within these systems as discussed below. Due to their long evolutionary history, cyanobacteria dominate and have adapted to all freshwater environments. *Chroococcus*, *Aphanocapsa*, *Microcystis*, *Merismopedia*, and *Synechocystis* are some of the most dominant wetland species (Muzaffar and Ahmed, 2007a,b; Anusa et al., 2012). The ability of cyanobacteria to outcompete other freshwater phytoplankton has been attributed to several factors such as (1) optimum growth at high temperatures; (2) low light, high pH:CO_2 concentrations, and nitrogen: phosphorus ratio tolerances; (3) depth regulation by buoyancy; (4) zooplankton grazing resistance; and (5) aerobic bacteria symbiotic relationships (Bellinger and Sigee, 2015). Another key advantage associated with cyanobacteria is the ability of some species to fix atmospheric N_2 in nitrogen-limited environments.

Bacillariophyta (diatoms) are a distinct group of algae with a typically thick silica cell wall. They occur mostly as nonflagellated single cells, simple colonies, or chains of cells with a very wide distribution in the planktonic and benthic freshwater environments. Diatoms have a ubiquitous freshwater distribution occurring as benthic, planktonic, epiphytic, and epizoic organisms with *Achnanthidium*, *Amphora*, *Gomphonema*, *Eunotia*, *Encyonema*, and *Nitzschia* dominating (Nhiwatiwa et al., 2019). They have distinct ecological preferences such as fast growth rates, sensitivity to environmental change and/or disturbances such as eutrophication, acidification, land use, and pollution, and short generation times, making them useful biological indicators (Mangadze et al., 2019).

Chlorophyta (green algae) are mostly microscopic unicellular organisms capable of forming large colonies and filaments. Among others, the flagellate *Haematococcus* is dominant in many small wetland systems and normally colors these systems bright red if present. Small unicellular phytoplankton, *Chlorella*, *Selanastrum*, *Chlamydomonas*, *Monoraphidium*, *Spirogyra*, *Mougeotia*, and Desmids (e.g., *Cosmarium*, *Closterium*, *Staurastrum*) can also dominate wetland green algae communities (Silva, 2007; Anusa et al., 2012; Dunck et al., 2013; Bellinger and Sigee, 2015).

Euglenoids are generally found in environments where there is an abundance of decaying organic matter in line with their autotrophic and heterotrophic nature. Some *Euglena*, *Trachelomonas*, and *Phacus* have the ability to grow in very low pH waters and are typically found in metal-contaminated wetland ponds (Silva, 2007). Xanthophyta are nonmotile, single-celled, or colonial algae with a distinctive pigmentation that gives cells a yellow or green appearance. Xanthophyta are rather limited in their exploitation of aquatic habitats, tending to occur on damp mud at the edge of wetland ponds. Where planktonic Xanthophyta occur, they tend to occur in small ditches and ponds. *Characiopsis*, *Tribonema*, *Chlamydomyxa*, and *Botrydiopsis* are some of the common wetland taxa (Silva, 2007; Dunck et al., 2013; Bellinger and Sigee, 2015).

Dinoflagellates are mostly biflagellate unicellular algae, with a few being without flagella. Dinoflagellates are meroplanktonic algae and can be present in wetlands, with *Ceratium*, *Peridinium*, and *Peridiniopsis* being common taxa. Dinoflagellates can survive in sediments as resistant cysts. Cryptophyta are generally small- to medium-sized unicellular taxa forming a small component in terms of taxa, abundance, and biomass of water bodies. Chrysophyta exhibit considerable diversity in their organizational structure, ranging from unicellular (e.g., *Synura*) to spherical and branching colonial types (e.g., *Dinobryon*). They are potentially useful as environmental indicator species (e.g., *Chromulina*, *Dinobryon*, *Lagynium*, *Synura*, *Mallomonas*) in temporary wetland systems and in paleoecology (Dunck et al., 2013; Bellinger and Sigee, 2015). Rhodophyta are predominantly marine taxa with about 3% being found in true freshwater habitats such as *Batrachospermum*, *Lemanea*, and *Hildenbandia*. Similarly, Phaeophyta are also mostly marine with about 1% being freshwater species and mostly benthic in nature. Freshwater brown algae include taxa such as *Pleurocladia* and *Heribaudiella* and can be considered the least diverse of all freshwater phytoplankton. Rhodophyta and Phaeophyta have been poorly studied in freshwater habitats, and hence their ecological characteristics are poorly known (Bellinger and Sigee, 2015).

Within Africa and Australia, there are relatively few and often limited published studies on phytoplankton community assemblages from tropical wetlands (e.g., Anusa et al., 2012; Riato et al., 2014; Mowe et al., 2015; McGregor and Sendall, 2017a,b; McGregor, 2018 and references therein). The initial comprehensive study of wetlands in southern Africa was conducted in the Highveld area by Hutchinson et al. (1932) who carried out an ecological survey of a variety of temporary and permanent wetland pans. In the southern African subtropical highveld region (as defined by Kottek et al., 2006), temporary wetland pans were found to be dominated by diatom taxa that are slightly acidic to circumneutral, dystrophic, and nutrient-poor water species (e.g., *Nitzschia acidoclinata*, *Gomphonema gracile*, and *Eunotia bilunaris*; Riato et al., 2014). Other diverse aerophilic taxa assemblages such as *Luticola mutica*, *Hantzschia amphioxys*, *Pinnularia borealis*, and *Pinnularia subcapitata* were also observed, with studies by Lowe and Collins (1973) suggesting that the taxa can grow in, or endure drought-prone, low-moisture environments. *Gomphonema parvulum* and *Nitzschia palea*, eutrophic indicator taxa, were prevalent in some Highveld wetland pans due to high nutrient and organic matter inputs as a result of agricultural practices (Riato et al., 2014).

Although wetland biota constitute a significant portion of biodiversity in both tropical Asia and America, studies of phytoplankton assemblages of wetland ecosystems are also limited in these regions (e.g., Gopal and Chauhan, 2001; de Graaf and Marttin, 2003; Kumar and Oommen, 2011). It has, however, been observed that the distribution of phytoplankton in tropical Asian and American wetlands is dependent on water quality and seasonality (Kumar and Oommen, 2011). For instance, Kumar and Oommen (2011) observed that the postmonsoon months were dominated by the Chlorophytes, whereas Bacillariophytes (*Achnanthes*, *Cyclotella*, *Cymbella*, *Fragillaria*, *Navicula*, *Mastogloia*, *Gomphonema*, and *Nitzschia*) dominated the winter months of the wetland phytoplankton community in Kanewal, India. This was easily explained by the high DO and low nutrient condition of waters in winter. Other studies in India have also recorded these and other genera belonging to Cyanophyceae, Euglenophyceae, Dinophyceae, and Chrysophyceae (Brraich and Kaur, 2015; Muzaffar and Ahmed, 2007a,b; Kumar and Oommen, 2011). In the study by Muzaffar and Ahmed (2007a,b), Cyanophyceae dominated throughout the study period, but particularly in the high water period. Subsequently, as the water levels started to subside, the Cyanophyceae declined.

8.3 Important community drivers

Phytoplankton assemblages are structured by physicochemical and biological variables within aquatic ecosystems. These variables influence rates of primary productivity and adaptive strategies of phytoplankton to cope with water movements and nutrient availability. Literature suggests that several environmental factors, together with site-specific factors, strongly correlate with variations in phytoplankton community composition in most tropical wetlands. Environmental changes in aquatic ecosystems affect phytoplankton biomass and diversity (Geethu and Balamurali, 2018). Traditionally, studies on the phytoplankton abundance, diversity, dominance, and seasonality of wetlands have emphasized the role of local environmental factors such as hydroperiod (i.e., flooding cycles), area, nutrients (nitrogen, phosphorus), altitude, and ionic composition (i.e., pH, conductivity, hardness, calcium) of water in regulating the community structure (Deemy et al., 2022a, Chapter 4; Cuthbert et al., 2022, Chapter 17). In other parts of the world, studies have highlighted that hydroperiod and nutrient concentration loads are important in phytoplankton community structuring (Wetzel, 2001; Incagnone et al., 2015; Nhiwatiwa et al., 2017, 2019; Dalu et al., 2020). Phytoplankton communities in wetland environments have been highlighted to change according to geographical and spatial factors, latitude and altitude, water availability, and distance from ocean buffering climates (Hubbell, 2001). Wetland depth and area can be important predictors of phytoplankton community structure and nutrient concentrations in wetland habitats. Large wetlands have been shown to have more diverse phytoplankton communities when compared with small wetlands, with the controlling effect not being only the area, but habitat diversity as microhabitat types generally increase with area (see Box 8.1; Browne, 1981; Anusa et al., 2012). Overall, this emphasizes that resource components might exert a strong selection pressure on wetland phytoplankton communities, with high potential for these phytoplankton communities to respond to changes in nutrient and habitat resources.

The level of availability of water has been identified as a factor driving phytoplankton diversity in wetlands. In wetlands in Nigeria, Chia et al. (2011) demonstrated that phytoplankton diversity is high during the dry months (i.e., low water level) when water levels are reduced and nutrients

BOX 8.1 Influence of pool size and hydroperiod on physicochemical water properties and phytoplankton diversity in temporary rock pools in Zimbabwe (Anusa et al., 2012).

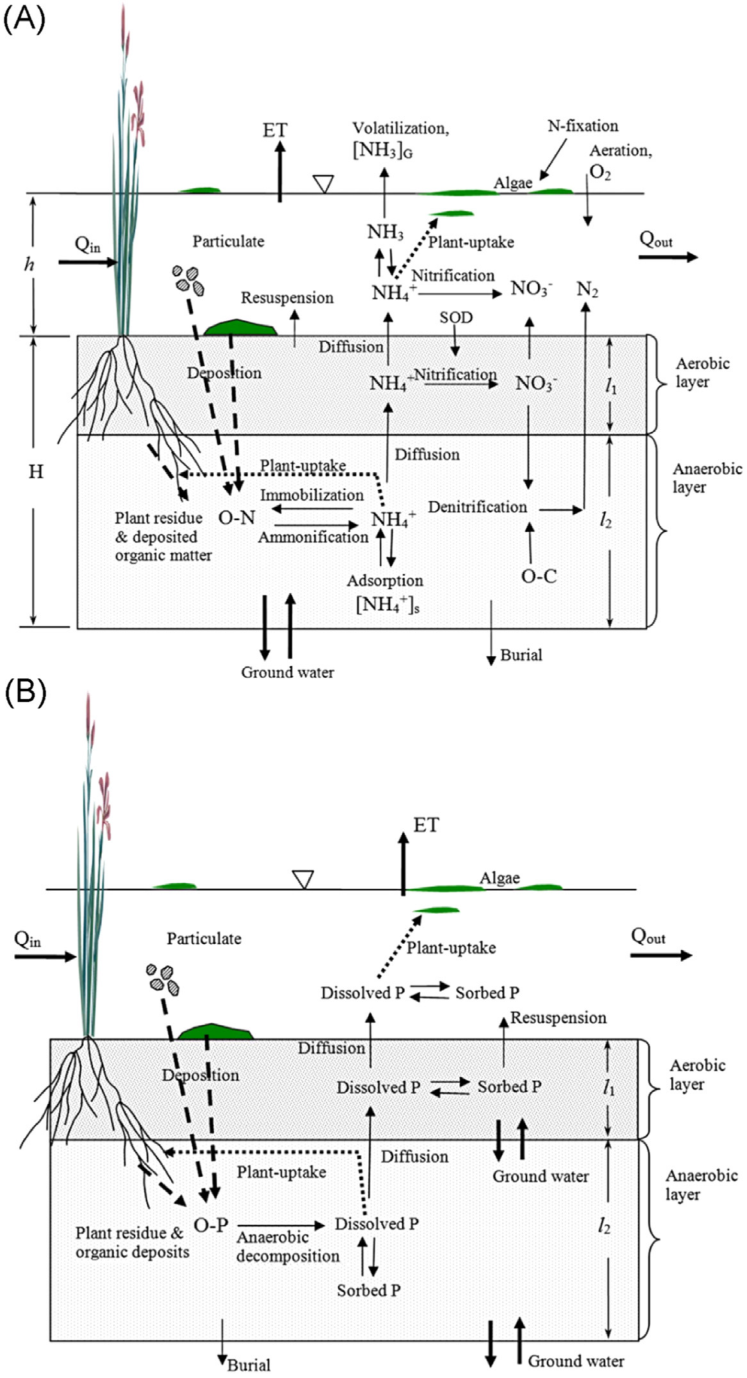
The water temperature in the temporary rock pools ranged between 20°C and 35°C, with low conductivity immediately after filling fluctuating between 6 and 50 $\mu S\ cm^{-1}$. The rock pool pH ranged from 6 (acidic) to 10 (alkaline). Rock pool systems were classified as oligotrophic open to significant nutrient inputs and outputs. The high nutrient (nitrogen and phosphorus) concentration loads in large deep pools compared to small shallow pools was observed, with these nutrient concentrations varying throughout the hydroperiod cycle, and was dependent on rock pool size which also had an effect on phytoplankton biomass in large pools. Using depth as a proxy for disturbance, phytoplankton species composition was influenced by inundation (i.e., hydroperiod) duration. Green algae (i.e., *Spirogyra rhizobrachiales, Tabellaria flocculosa, Ulothrix zonata*) and cyanobacteria (i.e., *Microcystis aeruginosa, Synechocystis aquatilis*) occurred abundantly in small rock pools. The initial phytoplankton community composition was dominated by short-residence green algae (*S. rhizobrachiales, T. flocculosa, U. zonata*), which were later replaced by cyanobacteria (*M. aeruginosa, S. aquatilis*) in large rock pools which were also driven by high nutrient concentration loads. The persistence of the cyanobacteria in large rock pools was mainly due to the long hydroperiod and stable environmental condition, compared to the small rock pools. The number of species present in pools tended to increase as pool area increased. Phytoplankton composition in long- and short-lived rock pools followed a similar trend of 70 and 105 days after filling.

Image 1 An example of temporary rock pool wetland habitat. *Photo by Tatenda Dalu.*

loads concentrated through evaporation and other factors such as excessive agricultural activities. A low diatom diversity and abundance during the summer wet months could be attributed to high dilution levels, which results in reduced nutrient concentrations available for diatoms in the small wetlands, or even reduced encounter rates. Recently, more emphasis has been placed on regional processes in studies directly addressing the spatial configuration of ponds (Nhiwatiwa et al., 2019), and in studies examining the roles of connectivity and dispersal capacity of phytoplankton *per se*, with spatial phytoplankton community patterns across wetlands having been largely ignored (Vanormelingen et al., 2008). Wetland water connectivity has been highlighted as not having a significant influence on phytoplankton community composition or diversity, although some evidence suggests occurrence of mass effects at the scale of neighboring wetland ponds (Vanormelingen et al., 2008; Nhiwatiwa et al., 2019). For example, phytoplankton cells are more easily dispersed among isolated wetland systems via air and animal vectors due to their smaller size (Kristiansen, 1996). da Silva et al. (2020) highlighted that wetland pond isolation did not influence the phytoplankton species composition, although a high stochastic distribution was observed. An interaction among local structuring (i.e., light limitation, water depth, wetland size) and spatial (dispersal) variables appears to best explain phytoplankton distribution and community structure in freshwater wetlands.

8.3.1 Nutrients

Nutrient availability and stoichiometry are key determinants of aquatic primary production (Deemy et al., 2022b, Chapter 6). Productivity in wetlands ecosystems is particularly limited by nitrogen and phosphorus (Sterner, 2008). For instance, phytoplankton changes seasonally due to phosphorus and nitrogen limitation in central Amazon floodplain wetlands depending on the suspended inorganic material concentrations that carry readily available phosphorus (Davies et al., 2008). In general, phytoplankton is phosphorus-limited in temperate wetlands and nitrogen-limited in tropical regions (Vitousek and Howarth, 1991; Poxleitner et al., 2016). Despite the abundance of nitrogen in the atmosphere, its relative inertness restricts photoautotrophic exploitation to nitrogen compounds. Therefore the principal forms of nitrogen that photoautotrophs can use are the ions nitrate, nitrite, and ammonium (Reynolds, 2006). Furthermore, nitrogen is readily lost through leaching or volatilization and denitrification to the atmosphere (Vitousek and Howarth, 1991). In tropical regions, there is increased denitrification (due to higher temperatures compared to the temperate regions) that further raises nitrogen losses (They et al., 2014). Consequently, phytoplankton species in the tropics are conditioned by physiological and morphological adaptations under nitrogen deficiency. This therefore favors dominance by nitrogen-fixing phytoplankton, for example, the cyanobacterial group Nostocales (Vitousek and Howarth, 1991; They et al., 2014). Fig. 8.3 depicts a conceptual biogeochemical pathway model for mineralization of wetland organic matter to ammonium and phosphate, and subsequent transport, retention, uptake, and removal (i.e., denitrification, volatilization, burial) across the


(A)
ET
Volatilization,
$[NH_3]_G$
N-fixation
Aeration,
O_2
Algae
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h
Particulate
NH_3
Plant-uptake
Q_{out}
Nitrification
NH_4^+
NO_3^-
N_2
Resuspension
SOD
Diffusion
Deposition
NH_4^+
Nitrification
NO_3^-
l_1
Aerobic layer
H
Diffusion
Anaerobic layer
Plant-uptake
Immobilization
Plant residue & deposited organic matter
O-N
NH_4^+
Denitrification
l_2
Ammonification
Adsorption
$[NH_4^+]_s$
O-C
Ground water
Burial
(B)
ET
Algae
Q_{in}
Particulate
Plant-uptake
Q_{out}
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Sorbed P
Resuspension
Diffusion
Deposition
Dissolved P
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l_1
Aerobic layer
Diffusion
Ground water
Anaerobic layer
Plant-uptake
O-P
Dissolved P
Plant residue & organic deposits
Anaerobic decomposition
l_2
Sorbed P
Burial
Ground water

water column (pelagic), wetland soil layer, and plant biomass according to Hantush et al. (2013).

A study by Dalu et al. (2020) in a tropical South African wetland observed that when nutrient concentrations were low, especially during summer, phytoplankton was dominated by small-sized, pico- and nanophytoplankton, whereas the large-sized cell fractions increased as nutrients increased in winter. These contrasting phytoplankton community structures also relate to different ecosystem functioning modes. Under nutrient limitation, an ecosystem will maximize nutrient recycling, while new primary production based on inputs from allochthonous sources generally supports highly productive ecosystems resulting in dominance of numerous large-celled phytoplankton, that is, microphytoplankton (Cózar et al., 2018). Another important means of overcoming nutrient limitation is mixotrophy. Mixotrophy, a strategy adopted by several, phylogenetically distinct, phytoplankton groups across different aquatic ecosystems, involves a combination of photosynthesis and direct access to organic carbon sources through mainly osmotrophy or phagotrophy (Nhiwatiwa et al., 2019).

8.3.2 Water temperature

Temperature has been identified as a major selective factor restricting phytoplankton species occurrence within and across tropical latitudinal bands (Padisák et al., 2016), through both direct physiological effects and indirect effects through changes in hydrological and physicochemical processes (Murulidharand and Murthy, 2015). Several studies have demonstrated the critical role of water temperature as an environmental driver of phytoplankton succession in the tropics. Gogoi et al. (2019) observed a positive correlation between temperature and phytoplankton abundance in Indian wetlands. Euglenophyceae, Xanthophyceae, and Mediophyceae were positively correlated with the water temperature (Gogoi et al., 2019). Similarly, in Argentina, elevated dominance of Cyanobacteria (particularly *Synechocystis salina*) was associated with the highest temperatures recorded (Cony et al., 2017). Murulidharand and Murthy (2015) reported that long duration of photoperiod coupled with high temperatures favored growth in different phytoplankton groups. Temperature plays an important role in controlling the

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FIGURE 8.3 (A) Nitrogen and (B) phosphate processes in wetlands across the water column, aerobic, and reduced lower soil layers. *Abbreviations*: *C*, carbon; *ET*, evapotranspiration; *h*, water column; *H*, sediment; *N*, nitrogen; NH_3, ammonia; NH_4^+, ammonium; N_2, nitrogen; NO_3^-, nitrate; *O*, oxygen; *P*, phosphate; *Q*, flow/discharge rate; *SOD*, root biomass and tillering zone. *Detailed model explanation is provided in Hantush, M.M., Kalin, L., Isik, S., Yucekaya, A., 2013. Nutrient dynamics in flooded wetlands. I: model development. Journal of Hydrologic Engineering 18, 1709–1723 (Reproduced with permission from American Society of Civil Engineers,* Journal of Hydrologic Engineering*).*

species richness, abundance, diversity, and productivity of phytoplankton in tropical wetlands (Laskar and Gupta, 2009).

Temperature also regulates biogeochemical activities in the wetland environment. For instance, oxygen solubility in water increases with reduction in temperature (Nagar, 2011). Murulidharand and Murthy (2015) reported that dissolved oxygen was negatively correlated with phytoplankton in Teetha Wetland (India) as temperatures increased. An increase in temperature also enhances the rate of decomposition and evaporation. Subsequently, there is an increase in nutrient concentration which increases the phytoplankton density (Brraich and Kaur, 2015).

8.3.3 Light

Given that light is the source of energy in photosynthetically active autotrophs, the amount and depth of light penetration through the water column is central for primary productivity levels. Low phytoplankton productivity can be a result of low light penetration. Globally, turbidity is a fundamental determinant of phytoplankton growth. Turbidity is a measure of light scatter as a result of particles in the water that hinder light penetration through the water column and availability for phytoplankton. Therefore without vertical mixing of the water column, there are limits upon the phytoplankton cell concentration that can be supported by the light energy available. Many tropical freshwater wetlands, however, are shallow and, as such, depth-associated light limitation is less of a hindrance for primary production than in larger water bodies. Indeed, given the shallow nature of many systems of the region, much of the phytoplankton community is composed of taxa that are often associated with the benthic environment, but also occur in the water column, given high levels of bentho−pelagic coupling (Threlkeld, 1994; Zapperi et al., 2016). In addition, the high angle of the sun and solar intensity results in greater inputs of light into the water column in the tropics compared to temperate regions. As a result of these light effects, in combination with temperature effects, rates of primary production are characteristically higher in tropical (lower latitude) aquatic ecosystems.

8.3.4 Hydrological effect

Given that phytoplankton populations live in suspension, they are largely dependent on the movement of water masses. It has been observed that the relationship between phytoplankton and physicochemical and biological variables is strongly controlled by the hydrological regime in the tropical regions (Martinet et al., 2014). The hydrology (due to flood pulse) induces changes in phytoplankton communities responding to nutrient concentration (due to receding waters) and dilution (flooding) (see Box 8.2; also see Deemy et al., 2022c, Chapter 4). In floodplain wetlands, phytoplankton communities are

BOX 8.2 Effects of flooding cycle on the phytoplankton community diversity in a Ramsar wetland in Bangladesh (Muzaffar and Ahmed, 2007a,b).

Freshwater wetlands in tropical Asia are strongly influenced by monsoons, and the annual flood cycle has measurable impact on the abiotic and biotic variables. The north-eastern Bangladesh Haor Basin is particularly rich in seasonal floodplain wetlands that support a wide diversity of fauna and flora. Water levels gradually rise from June to August, before receding in September. Over the course of the flood cycle, 107 phytoplankton taxa representing five classes were recorded in the system. Ammonia-N, pH, dissolved oxygen, hardness, and chloride were found to be important in structuring phytoplankton communities. Cyanophyta accounted for more than 97% of all taxa recorded. *Microcystis* dominated and were particularly high during the early high water period phase in June, before gradual declining to low abundances in December. Cyanophyta genera such as *Anabaena*, *Aphanocapsa*, *Chroococcus*, *Coelosphaerium*, *Gloeocapsa*, and *Lyngbia* were also abundant but showed varied trends. *Lyngbia* declined to low densities in December, whereas *Anabaena*, *Aphanocapsa*, and *Coelosphaerium* increased significantly, causing the overall shifts in phytoplankton communities. *Melosira* was also a dominant taxon, reaching bloom proportions early on during the high water period. Other abundance of the Cyanophyta to increase in December cycling phase and nutrient availability seemed to be important in controlling phytoplankton dynamics.

mainly associated with water level fluctuations, hydrological connectivity, and habitat diversity (Muzaffar and Ahmed, 2007a,b; Laskar et al., 2013). The influence of habitat heterogeneity on phytoplankton communities has been reported previously for tropical Brazilian floodplain wetlands, where the degree of connectivity with the mainstem river was seen to influence phytoplankton abundances and diversities, with the most distant and disconnected systems having the highest abundances and diversities (García de Emiliani, 1990). Additionally, recent studies highlight the importance of habitat fragmentation during low water periods in promoting phytoplankton diversity, because it acts as a key regulator of the occurrence of different phytoplankton functional groups within wetland systems (Devercelli, 2006; Laskar and Gupta, 2009). As in other plankton communities, phytoplankton abundance and diversity in floodplain wetlands is mostly driven by flood pulse-induced forces, interacting with climate and biotic processes such as competition. Thus in addition to the alpha diversity (site species richness), more studies are required to assess the phytoplankton gamma diversity (total species pool) and beta diversity (species turnover between and within systems), which have been rarely evaluated in floodplain and other tropical wetland types.

8.3.5 Macrophytes

Aquatic macrophytes are important elements in structuring freshwater ecosystems and are frequently used as indicators of their ecological quality (Søndergaard et al., 2010; Piedade et al., 2022, Chapter 7). There is increasing concern about the effects of free-floating macrophytes on aquatic biota given their increase through invasions, and potential shifts in their geographical range due to eutrophication and increasing winter temperatures (de Tezanos Pinto and O'Farrell, 2014). Many free-floating macrophytes are native to South America and their sensitivity to low air temperature and freezing is reflected in their predominantly tropical distribution (O'Farrell et al., 2009). Increases in free-floating macrophytes can lead to changes in chemical and physical conditions of the water, generating mosaics of environmental conditions in small water bodies (They et al., 2014). These changes have consequences for the entire food web, but their impact is easily observed on phytoplankton biomass.

Free-floating macrophytes are known to attenuate incoming light (through shading), immobilize nutrients in their biomass, enhance suspended solids sedimentation, and release allelopathic substances (de Tezanos Pinto and O'Farrell, 2014). In Argentina, O'Farrell et al. (2009) observed that the persistence of a floating macrophyte cover caused a stressful phytoplankton environment, due to the low light penetration and intensity that impaired photosynthesis and growth. The low light availability causes a shift in the algal community to mixotrophic species (species that the use autotrophy and heterotrophy) with low light requirements (de Tezanos Pinto and O'Farrell, 2014).

8.4 Tropical cyanobacterial blooms

Cyanobacterial blooms pose a health issue in freshwater systems (Paerl et al., 2020) principally because some species are able to produce toxins which are dangerous to humans and animals (Box 8.3). Although freshwater cyanobacterial blooms are a worldwide occurrence, there are variations in the typical cyanobacteria species and toxins found within the temperate and tropical regions. *Microcystis* is the most prevalent cyanobacteria bloom-causing genus in Africa, Asia, and America, followed by *Cylindrospermopsis* (Fig. 8.4A) and four toxins have been detected across Africa, Asia, Australia, and America (Fig. 8.4B; Mowe et al., 2015).

Cyanobacteria toxin poisonings are the main cause of concern over harmful algal blooms (HABs) (Carmichael et al., 2001). Among the worst reported incidents of human poisoning attributed to cyanotoxins for tropical America were from Brazil in 1988 in which 2000 gastroenteritis cases were recorded and 88 of these resulted in death (Carmichael et al., 2001). Following these incidents, there has been a lot of research on toxins in South

BOX 8.3 Cyanotoxins which are specifically harmful to people.

There are currently two kinds of cyanotoxins which are specifically known to be harmful to people: hepatotoxins (cyclic peptides) and neurotoxins (alkaloids). The cyclic peptides represent the greatest concern to human health due to their potential risk of long-term exposure to relatively low toxin concentrations in drinking water supplies. Cyclic peptides, microcystins and nodularins, cause liver poisoning in animals, particularly mammals, and can even cause death due to liver hemorrhage and failure. The cyclic peptides may also promote liver growth and tumors following chronic low-dose exposure. The alkaloid neurotoxins (i.e., anatoxins, asaxitoxins/paralytic shellfish poisoning toxins) have been shown to have only acute effects in mammals. However, some of the alkaloid toxins are known to accumulate to high concentrations in freshwater and marine animals. They therefore pose a risk in many areas of the world where local populations consume aquatic animals from contaminated water bodies with toxic cyanobacteria.

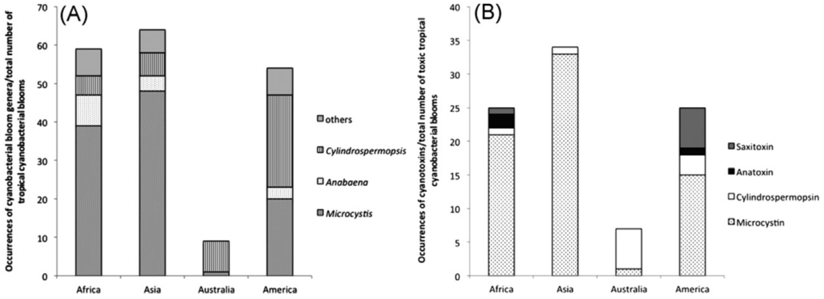

FIGURE 8.4 Proportion of tropical (A) cyanobacteria genera and (B) cyanobacterial toxins found within the different regions. *Mowe, M.A., Mitrovic, S.M., Lim, R.P., Furey, A., Yeo, D.C., 2015. Tropical cyanobacterial blooms: a review of prevalence, problem taxa, toxins and influencing environmental factors. Journal of Limnology 74, 205–224 and reproduced with permission from PAGEPress Srl.*

American wetlands aiming to document cyanobacterial blooms and progenitor species (Mowe et al., 2015).

While cyanobacterial blooms have been characteristic of eutrophic systems, there have been increasing reports of their recent occurrence in wetlands ranging from oligotrophic to eutrophic trophic states (Cottingham et al., 2015; Carey et al., 2008; Carey et al., 2014). Of concern, recent studies have observed that cyanobacterial blooms can actually induce eutrophication in water bodies by altering the nitrogen and phosphorus cycles (Cottingham et al., 2015; Carey et al., 2014). Through nitrogen fixation, cyanobacteria transforms dissolved nitrogen into biologically active forms making nitrogen that would have been inaccessible to other phytoplankton available. Further to this, many cyanobacteria taxa produce extracellular polyphosphatase enzymes which enable them to access phosphorus stored in sediments (Cottingham et al., 2015). They also have the capacity for uptake and storage of phosphorus in excess of immediate demand. This phosphorus is subsequently released into the water column through zooplankton grazing, senescence, or leakage stimulating growth of phytoplankton and starting a cycle of eutrophication (Carey et al., 2014). These observations are critical in the wake of climate change where temperatures are likely to become more favorable for cyanobacterial dominance (Kosten et al., 2012; Paerl and Otten, 2013). A more recent example of how cyanobacteria may be increasingly emerging as problem associated with climate change is that of the mass elephant mortality events that occurred in Botswana between March and June 2020 (Azeem et al., 2020). Reports suggest that "sending test samples to specialized laboratories...the deaths were caused by neurotoxins ...from a species of cyanobacteria" (York, 2020). Although at the time of the writing of this chapter, specific details were yet to be published, this unprecedented event suggests that shifting environmental conditions may be having implications for phytoplankton communities in wetlands used by elephants and other wildlife as watering points.

Many techniques have been proposed, employed, and evaluated for managing cyanobacterial HABS in different wetland systems. These approaches are varied, ranging from physical, chemical to biological. Physical manipulations include activities such as rechanneling water through affected systems to promote flushing; removal of buoyant surface blooms by skimming; deployment of surface mixers/fountains and ultrasonic emission devices aimed at disrupting blooms; withdrawal of bottom waters; and dredging or excavation (Paerl et al., 2016). The success of these physical approaches has been mainly reported in relatively small ecosystems (Paerl and Otten, 2013). For instance, dredging works in shallow wetlands where sediment-derived nutrients are possibly the most important source of nutrients to the water body (Burford et al., 2019). Chemical techniques, on the other hand, encompass precipitation and immobilization of phosphorus in bottom sediments (coagulation and flocculation) and application of algaecides (e.g., copper sulfate, tetra-chlorobenzoquionone, sodium penta-chlorophenate, potassium permanganate, chlorine) (Sharma et al., 2011). Biological means of bloom control include biomanipulation of the aquatic food web to increase grazing pressure on cyanobacteria; use of aquatic plants (which compete with cyanobacterial HABS and shade the water body inhibiting bloom formation); and use of floating treatment wetlands and riparian vegetation (which filter and trap nutrients) (Paerl et al., 2016; Burford et al., 2019). However, it is important to emphasize here that most of these techniques (physical, chemical, and biological) provide short-term solutions and do not compensate for excessive nutrient loading—the root cause of cyanobacterial HABS expansion and persistence. Therefore all these approaches do not substitute and must be coupled with comprehensive nutrient input reductions in the watershed.

8.5 Phytoplankton use in water quality assessments

The ability of phytoplankton to incorporate environmental changes within a short period of time makes them ideal for biomonitoring and have been widely used as such (Geethu and Balamurali, 2018; Greenfield, 2022, Chapter 20). Inadequate and limited reference information, which is useful as a means of establishing aquatic community expectations following restoration initiatives, is a major hindrance to development of tropical region wetland health indices (Riato et al., 2017a,b, 2018; Mangadze et al., 2019). Despite the general recognition of phytoplankton as a valuable biological indicator tool in wetland assessments (Gaiser and Rühland, 2010), research on phytoplankton used to assess the biological condition of tropical wetlands is limited (Rountree et al., 2013; Riato et al., 2017a). However, the usefulness of phytoplankton, particularly diatoms, as a wetland biological assessment tool has been demonstrated in temperate and arid regional studies (e.g., John, 1993; Gaiser et al., 2004; Tibby et al., 2007). Thus recent studies (e.g., Gaiser et al., 2004; Owen et al., 2004; Tibby et al., 2007; Riato et al., 2017a, 2018) have demonstrated the effectiveness of diatoms as biological indicators of changing tropical freshwater wetland environmental conditions. Therefore monitoring of diatom community assemblages may present an important alternative in wetland assessments within the tropical regions, where the use of other biological indicator types such as fish, macroinvertebrates, and macrophytes have proven to be less effective.

Until recently, no diatom multimetric indices developed for tropical freshwater wetlands had accounted for natural variation effects on the obtained index values, where natural variability of environmental factors among sites (i.e., variables least affected by anthropogenic disturbances) could reduce diatom index accuracy (Cao et al., 2007; Hawkins et al., 2010). This was found to be particularly important for wetland habitats which are characteristically highly variable systems, even within and across wetland types, which can vary considerably over small spatial scales (Riato et al., 2017a). Thus most diatom-based multimetric indices used to assess freshwater wetland condition have mostly been developed to quantify salinity, nutrient loading, and pH changes (e.g., Lane and Brown, 2007; Miller et al., 2016; Riato et al., 2017a), but no tropical wetland condition diatom index had been developed to quantify mining impacts such as acid mine drainage (AMD). Riato et al. (2018) developed a diatom-based multimetric index for subtropical Highveld wetlands sensitive to coal mining impairment by assessing AMD impacts, and this metric was found to be suitable for optimizing wetland conservation across the region in the context of environmental management, protection, and rehabilitation, but could also be transferable to other regions, although this might require further testing (see Box 8.4). However, caution should be taken when extending diatom-based bioassessments to frequently inundated floodplain wetlands as diatom community

BOX 8.4 Diatom-based wetland multimetric index for acid mine drainage (Riato et al., 2018).

Acid mine drainage (AMD) causes severe chemical and biological degradation of aquatic habitats, specifically tropical depressional wetlands, as mines use these systems for AMD storage. Diatom-based multimetric indices (MMIs) to assess wetland condition have mostly been developed to assess agricultural and urban land-use impacts. Previous approaches to wetland diatom-based MMI development have not accounted for natural variability. Thus natural variability among wetlands may influence diatom MMIs accuracy. Epiphytic diatom MMIs sensitive to AMD were developed for a variety of Highveld depressional wetland types to account for natural variation within the metrics. For this, Riato et al. (2018) classified wetland types based on diatom typologies assigned to four categories (diversity, functional group, similarity to reference sites, taxonomic composition). Four final metrics were selected from a pool of 154 candidate metrics to develop the MMIs based on precision, responsiveness, sensitivity, and relevancy, and their broad range, high separation power, and low correlation among metrics (Table 8.1). Thus final metrics were selected from three categories: functional groups, similarity to reference sites, and taxonomic composition, which represent different aspects of diatom assemblage structure and function. The MMI performances were evaluated according to their precision in distinguishing reference sites, responsiveness to discriminate reference and disturbed sites, sensitivity to human disturbances, and relevancy to AMD-related stressors. Each MMI showed excellent discriminatory power, whether or not it accounted for natural variation. However, accounting for variation by grouping sites based on diatom typologies improved overall performance of MMIs.

assemblages may reflect the influence of both the wetland condition and floodwaters (Weilhoefer et al., 2008).

Landscape-scale models can become important tools in wetlands because diatom community assemblage patterns are constant across wetland types. Therefore spatially explicit visualizations of these diatoms models are useful for evaluating the performance of diatom-based inferences over large wetland areas around the world with high hydrologic connectivity. Since hydrology has been identified as an important driver of ecosystem change, hydrologic alterations due to restoration efforts could significantly modify phytoplankton responses. In freshwater wetlands, phytoplankton (i.e., diatoms) is an important component of mat-forming calcareous periphyton (i.e., biofilms attached on rock surfaces) assemblages that contribute to the structural organization and function of the entire periphyton matrix (Lee et al., 2013). Thus specific diatom community assemblages inhabiting periphyton mats can be used to infer past and present conditions and inform environmental management decisions based on how community assemblages are changing or have changed. Therefore there is a need for sound ecologically

TABLE 8.1 Final metric variables used for developing composite metrics within each metric category.

Category/final metric	MMI-1	MMI-2	MMI-3	MMI-4	Response
Similarity to reference sites					
%Reference taxa	x	x	x	x	−
%Tolerant taxa	x	x	x	x	+
%Similarity to reference sites	x	x	x		−
%Reference taxa found in reference sites that occurred in impaired sites			x	x	−
%Reference individuals found in reference sites that occurred in impaired sites	x				−
No. of distinct reference taxa		x	x	x	−
Functional group					
Mobile % taxa	x				−
Adnate % Lisa			x		−
Pad (attached to substrate) % taxa	x		x		+
Noncolonial			x		−
Ribbon % taxa			x		+
Ribbon % individuals	x				+
High profile guild. % taxa			x		+
Taxonomic composition					
%Encyonopsis taxa			x		+
%Cocconeis taxa			x		+
%Craticula taxa			x		−
%Ctenophora taxa	x		x		+
%Comphone taxa			x	x	v
%Nittschia individuals k				x	−

Abbreviations: *x*, metrics selected for each multimetric index best discriminated between references and disturbed sites; + *or* − , increase or decrease to disturbance direction of metric response to disturbance; *v*, a variable response.
Source: Adapted from Riato, L., Leira, M., Della Bella, V., Oberholster, P.J., 2018. Development of a diatom-based multimetric index for acid mine drainage impacted depressional wetlands. Science of the Total Environment 612, 214−222.

based tropical wetland assessments that require an understanding of how community assemblages respond to ecosystem parameters to make interpretations about past and present conditions, develop future targets, and aid in important wetland assessments (Lee et al., 2013; Riato et al., 2017a, 2018). Thus wetland environmental management programs should incorporate the obtained information from assessments to infer landscape-scale biological responses to hydrologic and community changes and to inform tropical wetland restoration targets, especially where hydroperiod regimes no longer follow natural spatiotemporal patterns. Diatom composition seems to follow a predictable relationship with two important habitat wetland characteristics, that is, hydroperiod and periphyton biovolume. Thus phytoplankton autecological information in tropical wetlands should be further utilized to investigate the poorly described flora distribution patterns (La Hée and Gaiser, 2012). Thus the potential of molecular approach to phytoplankton biomonitoring has developed over the past decades (see de Bruin et al., 2003; Keck et al., 2017) and this has lessened the dependency of qualified taxonomical expertise, which is often a stumbling block in biomonitoring efforts.

8.6 Future direction

In terms of phytoplankton tolerances, ecophysiology, and ecological preferences, much work still needs to be carried out (Dalu and Froneman, 2016). Accruing more data on autecology and taxonomy of a large number of biological indicators (i.e., phytoplankton species) will improve diatom-based biological indices, making them more powerful tools for monitoring wetland health. In particular, more information is needed on taxa that dominate in tropical systems. The array of inland wetland types in the tropics (see Wasserman and Dalu, 2022, Chapter 1; Job et al., 2022, Chapter 2 for details) also needs to be considered as many studies do not identify and outline wetland type, making comparisons across system types difficult. But perhaps the most important point of consideration for driving the field forward is the lack of human capacity in tropical regions. Most tropical regions overlay developing countries with limited capacity to train phytoplankton specialists. As a result, studies in tropical countries are often conducted by investigators from the developed world, employing a "parachute science" approach (de Vos 2020), whereby local training and collaboration is not prioritized. Given that most of the developed world lies in temperate regions, it is not surprising that temperature system paradigms pervade in tropical system investigations.

While the lack of human capacity and baseline phytoplankton information on community composition, structuring, and ecological requirements represent significant challenges, phytoplankton biomonitoring potentially holds much promise for understanding wetland ecological functioning and informing management of these unique aquatic ecosystems in the tropical regions. Therefore there is a compelling need for wetland phytoplankton systematics research to be undertaken within multiinterdisciplinary research projects, rather than focusing on species taxonomic identification, as such an approach will help in addressing the current challenging ecological problems. Thus further studies are urgently required to assess seasonal and yearly phytoplankton variation in wetland systems that experience extensive flooding.

Low-profile phytoplankton guilds dominated by pioneer life-forms have been shown to have a strong relationship with high disturbance levels such as increasing sodium (Na^+), alkalinity, and a decrease in depth (Riato et al., 2017b). Similarly, it has been observed that the phytoplanktonic guild and tube-living, rosette, and adnate life-forms dominate at high disturbance levels whereas the high-profile diatoms display an opposite trend (Riato et al., 2017b). Thus the strong ecological responses of phytoplankton life-forms and guilds to changing environmental conditions suggest that with further research, wetland phytoplankton functional groups may be used in wetland biological assessments and monitoring, where wetland phytoplankton species taxonomy are poorly described and studied. The use of phytoplankton functional groups may also be beneficial where budgets are limited, because a reliable wetland ecological status is still required, and the use of functional groups rather than species is a time- and cost-effective approach. Thus although most tropical wetlands have received inadequate and limited attention to date, advancements made by assessment, monitoring, and restoration efforts can guide newly developing wetland protection programs. Field and laboratory studies must be carried out to test for allelochemicals presence from macrophytes in water and how they impact on phytoplankton community structuring (Chia et al., 2011). The identification of specific macrophyte allelochemicals will provide an estimation of the amount of allelochemicals leached that could potentially impact on the phytoplankton community, and an understanding of the chemical transformations and mechanism of action of these allelochemicals in situ within the water column have on community structuring. More studies focusing on benthic phytoplankton production of extracellular polymeric substances as a sediment stabilization and substrate for microbial communities (see Dalu et al., 2020) are also lacking in tropical freshwater wetland literature, as well as research of potentially toxic and alien invasive phytoplankton species.

With limited studies providing a checklist of phytoplankton across the varied wetland types across tropical regions, there is a need for more studies that will contribute to a better knowledge of the phytoplankton community structuring, richness, and composition for management purposes. This is particularly vital in tropical regions where wetlands are under serious threat from environmental modifications and land-cover conversion due to anthropogenic activities (Dalu et al., 2017a). Future research is also required to identify phytoplankton indicators as well as species-specific responses to human impacts (e.g., agriculture, mining, tourism, urbanization) on freshwater wetlands as it will go a long way in providing guidance on the management of aquatic ecosystems used for multiple socio-economic purposes. This is particularly relevant for phytoplankton species that can cause direct harm to humans and animals, such as those species that produce toxins, or are implicated in eutrophication events. In addition, there is much scope for bioprospecting from species that produce secondary metabolites such as toxins as such compounds can have biomedical applications.

It is important to note that failure to recognize, understand, and manage temporary and ephemeral wetlands can lead to serious aquatic ecosystem degradation accompanied by negative impacts to the societies that depend upon them (Dalu et al., 2017a). Thus the legal status of temporary and ephemeral wetlands in comparison to permanent wetlands is different and the extent to which they are incorporated into policy, management, and regulatory decisions vary widely across the tropical region countries depending on how these systems are defined by the authorities, as well as what kinds of protection are given to some extent size of the temporary and ephemeral wetlands. For policies to be consistent across the region with current science, naturally, temporary wetland systems should be legally defined as part of the larger permanent wetland systems, and to implement these policies, we need improved mapping of all wetland systems in general (Acuña et al., 2014; Irvine et al., 2022, Chapter 21). In conclusion, it is important to maximize ecological resilience, maintain biodiversity, and ecosystem services for future generations within these wetland systems.

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