Biodiversity and Biomass of Algae in the Okavango Delta (Botswana), a Subtropical Flood-Pulsed Wetland

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by

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I, LUCA MARAZZI, confirm that the work presented in this thesis is my own.
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ABSTRACT

In freshwater bodies algae provide key ecosystem services such as food and water purification. This is the first systematic assessment of biodiversity, biomass and distribution patterns of these aquatic primary producers in the Okavango Delta (Botswana), a subtropical flood-pulsed wetland in semiarid Southern Africa.

This study delivers the first estimate of algal species and genera richness at the Delta scale; 496 species and 173 genera were observed in 132 samples. A new variety of desmid (Chlorophyta) was discovered, *Cosmarium pseudosulcatum var. okavangicum*, and species richness estimators suggest that a further few hundred unidentified species likely live in this wetland. Rare species represent 81% of species richness and 30% of total algal biovolume. Species composition is most similar within habitat types, thus varying more significantly at the Delta scale.

In seasonally inundated floodplains, algal species / genera richness and diversity are significantly higher than in permanently flooded open water habitats. The annual flood pulse has historically allowed more diverse algal communities to develop and persist in these shallower and warmer environments with higher mean nutrient levels and more substrata and more heterogenous habitats for benthic taxa. These results support the Intermediate Disturbance Hypothesis, Species-Energy Theory and Habitat Heterogeneity Diversity hypotheses. Higher algal biodiversity supports higher algal biomass in the floodplains, where species form three-dimensional communities of attached and periphytic algae requiring more nutrients than phytoplankton assemblages. Multivariate analyses demonstrate that habitat type, flooding frequency and conductivity most importantly influence the relative abundance of algal species, genera and phyla in the Okavango Delta.

This study's findings highlight how the preservation of water level fluctuations and habitat heterogeneity is crucial to maintaining biodiverse and thus resilient food webs in this unique ecosystem which faces increasing anthropogenic threats, such as global warming and upstream water abstraction plans.

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GLOSSARY OF KEY TERMS AND ABBREVIATIONS

Algal biomass: estimated by means of biovolume which is considered equivalent to wet algal biomass (1 $\mu m^3 L^{-1}$ = 1 $\mu g L^{-1}$ or $mm^3 L^{-1}$ = 1 mg L^{-1}) (Nauwerck, 1968)

Algal biovolume: proxy estimation of algal wet biomass obtained by identifying and measuring algae by means of an inverted microscope and calculating their cell volumes using approximated geometric formulas.

Benthic algae (or phytobenthos): algae attached to substrata such as sand (epipsammic), rocks (epilithic), sediment (epipelic) or plants (epiphytic).

Biodiversity (or biological diversity): "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (Convention on Biological Diversity, 2013). Here algal biodiversity is measured as taxon (species and genera) richness and diversity indices.

Campaign 1 and 2: Sampling campaigns conducted in 2006-2007 and 2009-2010

Chl *a*: Chlorophyll *a* concentrations ($\mu g L^{-1}$)

c.v.: coefficient of variation (%) = s.d. / mean * 100

Diversity: in this study species / genera diversity, measured by means of indices such as the Shannon Diversity.

DO: Dissolved Oxygen concentrations (mg L^{-1})

F: Floodplain; here Delta-scale habitat type, further divided into Open Water (OW) Sedgeland (S) and Grassland (G) for Campaign 2 data

Flood Class: categorical variable used to classify sampling sites into Permanently Flooded (PF), Seasonally Flooded (SF) and Occasionally Flooded (OF)

G: Grassland, i.e. the shallowest within-floodplain habitats characterised by grasses

Habitat: macrohabitats: Open Water, Marginal Vegetation and Floodplain at Delta scale; ii) Open Water, Sedgeland and Grassland within floodplains

HHH: Habitat Heterogeneity Hypothesis (MacArthur and MacArthur, 1961; see section 1.6.4)

IDH: Intermediate Disturbance Hypothesis (Connell, 1978; see section 1.6.1)

Intertropical convergence zone (ITCZ): an equatorial zonal belt of low pressure near the equator where the northeast trade winds meet the southeast trade winds. As these winds converge, moist air is forced upward, resulting in a band of heavy precipitation. This band moves seasonally.

K.W. test: Kruskal-Wallis test, used as a non-parametric test alternative to the O.W.A. test when data are not distributed normally and have unequal variance

K.S. test: Kolmogorov-Smirnov test, non-parametric test used to establish whether data are normally distributed or not

L. test: Levene test, used to establish whether data have equal or unequal variance

MV: Marginal Vegetation, habitat sampled in Campaign 1 near margins of river channels or lagoons

M.W. test: Mann-Whitney test, non-parametric test used as an alternative to the Tukey HSD post-hoc test, to find significant pair-wise differences

Other (taxonomic) group: algae not identified to genus or species level but identifies as *Chlorococcales*, *Oscillatoriales*, Pennate Diatoms etc.

OW: Open Water, i.e. deeper habitats in river channels, lagoons and floodplains (category used for both Delta-scale and within-floodplain habitats)

O.W.A. test: One-Way analysis of variance (ANOVA) test, parametric test used to determine whether there are any significant differences between the means of two or more independent (unrelated) groups

Periphyton: aggregation of diverse microorganisms (algae, bacteria, fungi, and invertebrates) and particles (mineral and detrital) embedded within an extracellular matrix (Hagerthey *et al.*, 2013); periphytic algae live on or ‘around plants’.

Phytobenthos: attached / benthic algae

Phytoplankton: free floating algae

Potamoplankton: river phytoplankton

Primary Production: gross primary production, has units of g C yr^{-1} for a lake, forest, field, ecosystem, biome, etc.

Primary Productivity: a measure of primary production per unit of time in terms of carbon fixed or oxygen produced by plants or algae / bacteria (e.g. g C m^{-2} yr^{-1}); gross primary productivity (GPP) = rate of conversion of CO_2 to organic carbon per unit surface area Units: g C m^{-2} yr^{-1}, or kJ m^{-2} yr^{-1}.

RDA: Redundancy analysis

RCT: Resource Competition Theory (Tilman, 1982; see section 1.6.2)

S: Sedgeland, i.e. within-floodplain habitats characterised by sedges

s.d.: standard deviation, a measure of spread of the data

S.D.: Shannon Diversity, index of diversity (see Equation 3.4 in section 3.7)

S.E.: Shannon Evenness, index of equitability (see Equation 3.5 in section 3.7)

SET: Species-Energy Theory (Wright, 1983; see section 1.6.3)

T. HSD test: Tukey Honest Significant Difference post-hoc test (parametric) to find significant pair-wise differences

Taxon richness: here it used as species / genera richness

TN: Total Nitrogen concentrations (mg L^{-1})
TP: Total Phosphorus concentrations (mg L^{-1})

VPA: Variation Partitioning Analysis

Wetland: area of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish, or salty including areas of marine water, the depth of which at low tide does not exceed 6 meters (Finlayson and Moser, 1991)

Chapter 1 – Wetlands and algae

1.1. OVERVIEW OF THESIS

This research aims to investigate and thus improve our understanding of the biodiversity, biomass and distribution patterns of algae, key primary producers in the food webs of the freshwater ecosystems of the Okavango Delta, a near-pristine subtropical wetland in North-Western Botswana.

The understanding of biological and ecological dynamics at the base of the food webs in aquatic ecosystems is of prominent importance to monitor the health of lakes, rivers and wetlands across the globe (Dudgeon *et al.*, 2006). In the Kalahari desert, the Okavango Delta is the only remaining vast reserve of freshwater and other resources for millions of animals and hundreds of thousands of people (Ramberg *et al.*, 2006). Therefore basic research on its ecology, starting from key aquatic producers such as algae, is ultimately of crucial importance to inform conservation and sustainable management strategies.

The results fill an important gap in the knowledge of algae in the semiarid Kalahari Basin, thus representing an original contribution to freshwater ecology of understudied organisms in a remote ecosystem of global importance. The aims, research questions and objectives are outlined in section 2.3.

Chapter 1 introduces the theoretical framework of this study, which concerns the importance of biodiversity assessments of small organisms, often overlooked, yet essential for ecosystems and human livelihoods. In Chapter 1 algae are described according to their main features, taxonomic groups, distribution and diversity. Chapter 2 summarises our basic knowledge on flood pulsed wetlands and discusses in detail the regional context of the Okavango River Basin and Delta. It also presents the aims, objectives and research questions of this study. Chapter 3 presents the methods used for sampling, microscope and laboratory analyses, biovolume estimation and data analysis. Chapter 4 presents descriptive results of the algal identification and counts and the Delta's limnology. Chapter 5 presents

and discusses the results of the estimation of the algal biovolume (wet algal biomass) and the spatiotemporal distribution patterns of the algae observed. Chapter 6 analyses the relationships between limnological and environmental variables and the distribution of algae in the Delta. Chapter 7 synthesises the principal findings and draws the conclusions.

1.2. WETLANDS

The broad definition of a wetland adopted by the Ramsar Convention, an international treaty established in 1971 to protect these ecosystems, is as follows:

> "*area of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters*" (The Ramsar Convention on Wetlands 2013)

Wetlands cover about 6% of the world surface: 8.2 to 10.1 million km^2 (Lehner and Doll, 2004), with 2.4 to 3.5 million km^2 are in polar/boreal regions, 0.7 to 1.1 million km^2 are in the temperate region, and 1.9 to 4.8 million km^2 are in the subtropics, according to different sources (Mitsch and Gosselink, 2000). Lehner and Doll (2004) classified wetlands in 12 categories (Figure 1.1): lakes; reservoirs; rivers; freshwater marshes and floodplains; swamp forests and flooded forests; coastal wetlands; pans and brackish/saline wetlands; bogs, fens and mires; intermittent wetlands/lakes; systems with 50-100% wetlands; systems with 25-50% wetlands; wetland complexes (0-25% wetland). Tropical and subtropical wetlands represent 30% of the world's wetlands (Mitsch *et al.*, 2011) and they contain some of the most pristine ecosystems left in the world, the Okavango Delta being one of the largest in Africa.

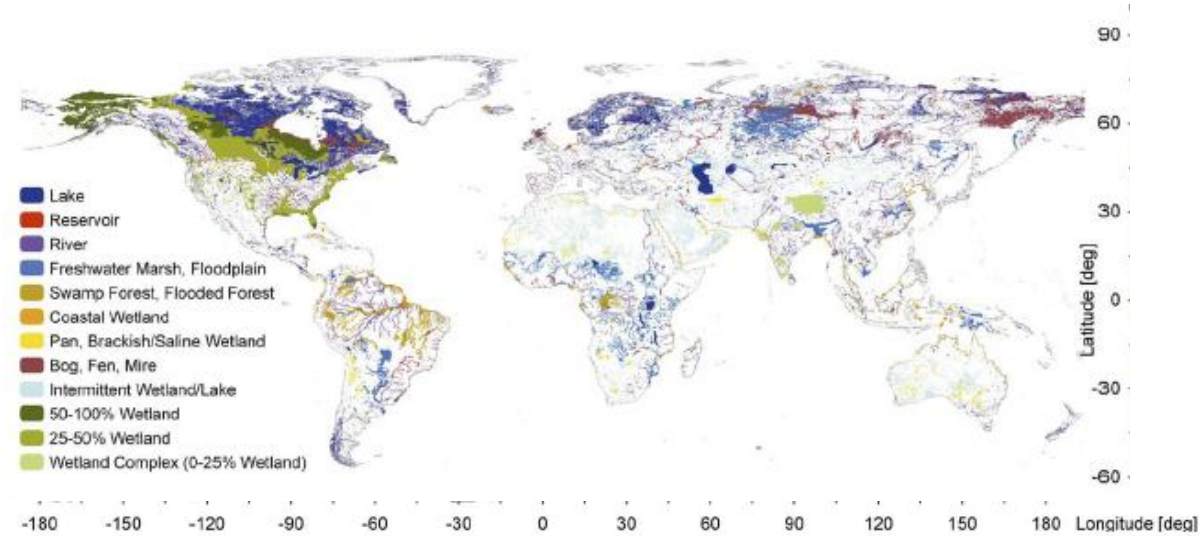


***Figure 1.1. Global wetlands map** (source: Luhner and Donn, 2004).*

Hydrology influences the level of biodiversity and biomass in wetlands, e.g. in India monsoon-induced hydrological changes create favourable conditions for high species richness (Gopal and Chauan, 2001), and primary production of plants is enhanced by faster nutrient cycling in these ecosystems (Junk, 2002). Moreover, morphological and physiological plasticity of traits of living organisms in many tropical species are high due to water level fluctuations (Junk, 2002). Other important factors include animals, particularly large mammals that can modify wetland hydrology when abundant and temperature regimes. Wetlands are systems with high primary production and complex food webs, based on detritus; microorganisms such as bacteria and algae form a “microbial loop” responsible for the decomposition and transfer of energy and matter to higher trophic levels (Mitsch and Gosselink, 2000).

Wetlands are both a sink of carbon (CO_2) and a source of carbon (CH_4) and CO_2 (e.g. Richey *et al.*, 2002); between 20 and 30% of carbon is estimated to be stored in wetlands (Lal, 2008) while 30% of methane emissions come from wetlands (Bergamaschi *et al.*, 2007). Richey *et al.* (2002) estimated that emissions of CO_2 from rivers and wetlands of the central Amazon basin amounted to 0.5 Gt C yr^{-1}, about ten times greater than fluvial export of organic carbon to the ocean. The sources of this carbon were organic matter accumulated from upland and flooded forests, then respired and outgassed downstream. Southern temperate and (sub)tropical wetlands have lower CH_4 / CO_2 ratios due to primary productivity being maintained during the winter months there; hence they can be considered as

carbon sinks on long timescales, e.g. a 500-year time horizon (Whiting and Chanton, 2001).

1.2.1. Wetland environments

The most important environmental forcing factor in wetlands is hydrology (Junk, 2002). Plants and animals living in these environments are adapted to changing dry and wet conditions; in fact wetlands are ecotones, areas of transition between terrestrial and aquatic environment. Junk *et al.* (2006) describe large wetlands as "*a complex of permanent aquatic, palustrine and terrestrial habitats, and in the case of river floodplains and tidal zones, of large Aquatic/Terrestrial Transition Zones (ATTZ) that periodically dry out*". Natural and anthropogenic flows of materials contribute to nutrient cycling between the terrestrial and aquatic phases. Water depth and flood duration and extent are key in creating ecological niches, habitat diversity and species richness in wetlands; the role of water level change in these systems can be compared to the role of fire occurrence for forests (Mitsch and Gosselink, 2000). For example, in floodplain forests in the Amazon trees have adapted to regular flooding in terms of seed germination after submersion, and the formation of adventitious roots to enhance oxygen uptake (Parolin *et al.*, 2004).
Flooding is important in wetlands as it creates an alternation of dry / wet conditions leading to the evolution of mixed assemblages of animals and plants with adaptive terrestrial and aquatic life stages (Junk *et al.*, 1989). Ramberg *et al.* (2010) argued that the combination of flooding and fire (considered distubances in ecosystems – see section 1.6) may be instrumental in maintaining high biological productivity and diversity in the floodplains of the Okavango Delta.

1.2.2. Ecosystem services and economic value

Wetlands provide important ecosystem services: water supply, groundwater recharge, water purification, nutrient cycling, flood protection and carbon storage (Mitsch and Gosselink, 2000); these ecosystems also support biodiversity and provide recreational and cultural services (Keddy, 2010). Fish populations living in wetlands around the world feed millions of people and a range of natural products are used to build shelters, clothes and tools. Human populations rely heavily and directly on wetlands, particularly in developing countries where subsistence farming

(e.g. flood recession agriculture), fishing and harvesting plant products are some of the main livelihood options (Mitchell, 2013). Moreover recreation and touristic activities in wetlands represent on one side an opportunity for local populations, but in many cases they can be a real threat to the same natural environment they rely on (Mbaiwa, 2003).

Climate regulation is a very important service that wetlands provide. In a globally warming planet, wetlands are important sinks of carbon, notably North American wetlands, in particular peatlands, though quantitiative estimates have large uncertainties (Bridgham *et al.*, 2006). However, wetlands can also contribute to global warming, as they can emit significant amounts of methane (CH_4), estimates at 92 and 237 million tonnes per year (House and Brovkin, 2005). Hence, overall wetlands contribute more to absorbing carbon rather than liberating it from the biosphere, but the net balance source / sink could change were wetland management to worsen (Mitra *et al.*, 2005).

The ecosystem goods and services coming from all inland waters and wetlands have been valued in US$ 4.9 trillion yr^{-1}, about 15% of the value of all ecosystems (Costanza *et al.*, 1997). The average values per unit area of rivers and wetlands (c. US$ 9,000-15,000 ha^{-1} yr^{-1}) are about two orders of magnitude higher than those of the most valuable terrestrial ecosystems, such as forests and grasslands (Costanza *et al.*, 1997). For the Okavango Delta a total value of ecosystem goods and services of 300 US$ million (in 1995) per year (surface area: 30,000 km^2; value: 10,000 US$ ha^{-1} yr^{-1}) value is quoted by Milzow *et al.* (2009).

1.2.3. Threats and conservation

A minimum of 100,000 species out of 1.8 million of all the species thus far described live in freshwater ecosystems (Dudgeon *et al.*, 2006); in particular, wetlands are sensitive hotspots of biodiversity hosting some 21,000 species of vertebrates (Lévêque *et al.*, 2005) and hundreds of plant species across, for example, a few key subtropical wetlands (Junk *et al.*, 2006).

These ecosystems face high anthropogenic pressures for two main reasons: the high economic value of their natural resources and because they are considered as land and water resources with free access. The global tragedy of the commons (Hardin, 1968) is still a present danger for many ecosystems which support the life of

billions of people and millions of species. Threats to freshwater ecosystems come from five main drivers of environmental change: overexploitation, water pollution and acidification, habitat degradation, species invasion (237 inland animal species introduced into 140 countries; Lévêque *et al.*, 2005) and flow modification (Figure 1.2; see also Mitchell, 2013).

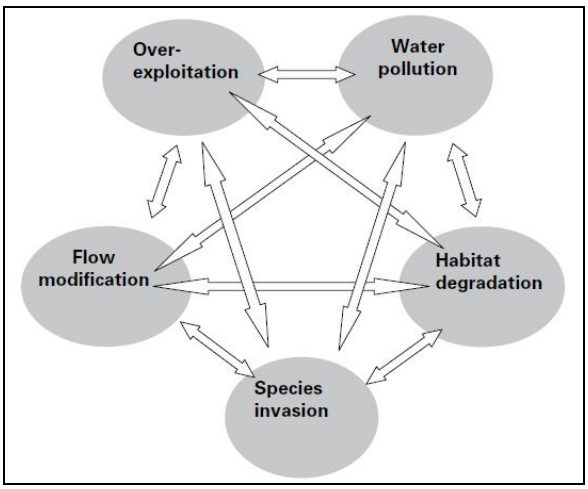


Figure 1.2. Five major threat categories and their interactive impacts on freshwater biodiversity (source: Dudgeon et al., 2006).

Pressures from human exploitation in lotic environments have often significantly reduced retention of water and organic material, disturbed flow regimes, fragmented habitats and damaged their biota (Malmqvist and Rundle, 2002). Eutrophication of freshwater ecosystems, including coastal wetlands and estuaries, is a global problem in which algae play a central role, as biomass and composition drastically change with nutrient enrichment (Smith, 2003). Flow modification, water quantity and quality are particularly severe problems in developing countries in Africa, both in the dry and wet tropics regions, and South America (Vörösmarty *et al.* 2000).

Large areas of the world's wetlands are to different degrees protected from such threats. A total of 2,186 wetlands of international importance are protected under the Ramsar Convention, covering an area of about 2.1 million km^2 (The Ramsar Convention on Wetlands, 2014). In the ranking of integrity of wetlands, South America has the most pristine ecosystems, Africa is second and Asian wetlands suffer the highest impacts (Junk, 2002). From a conservation and sustainable management viewpoint, debates on whether the protection of "flagship" species is the best approach in ecosystem protection, or whether the focus needs to be shifted to the preservation of key ecosystem functions, are very important, but not

appreciated by the public (Moss, 2000; Dudgeon, 2003). Junk (2002) suggest a combination of the two options to address people's various cultural and economic backgrounds.

1.2.4. Flood pulsed wetlands

The global surface of freshwater marsh and floodplains is about 2.5 million km^2 (Lehner and Doll, 2004). Flood pulsed wetlands are wetlands characterized by periodic inundation and drought, i.e. flood pulse of floodplains (Junk and Wantzen, 2004). In their seminal paper proposing the Flood Pulse Concept (FPC) Junk *et al.* (1989) define floodplains as:

> "*areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physicochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological and/or ethological adaptations, and produce characteristic community structures*".

According to Tockner and Stanford (2002) riverine floodplains globally occupy about 2 million km^2; the economic value of the ecosystem services provided by these environments is estimated in 3,920 billion US \$ yr^{-1} (over a half of the global wetlands' value - Costanza *et al.*, 1997). The most threatened of these ecosystems are in SE Asia, Sahelian Africa and North America (Tockner and Stanford, 2002). The FPC model maintains that the Aquatic-Terrestrial Transition Zones (ATTZ) and in particular the 'moving littoral' (the water from the shoreline to a few meters deep in the river) recycles nutrients and organic matter thus yielding high biological productivity; in riverine areas with long predictable pulses organisms adapt their life strategies to dynamic conditions of wetting and drying (Figure 1.3; Junk *et al.*, 1989). This concept works well in predicting nutrient and biota dynamics in river systems with lateral floodplains, particularly in high order streams.

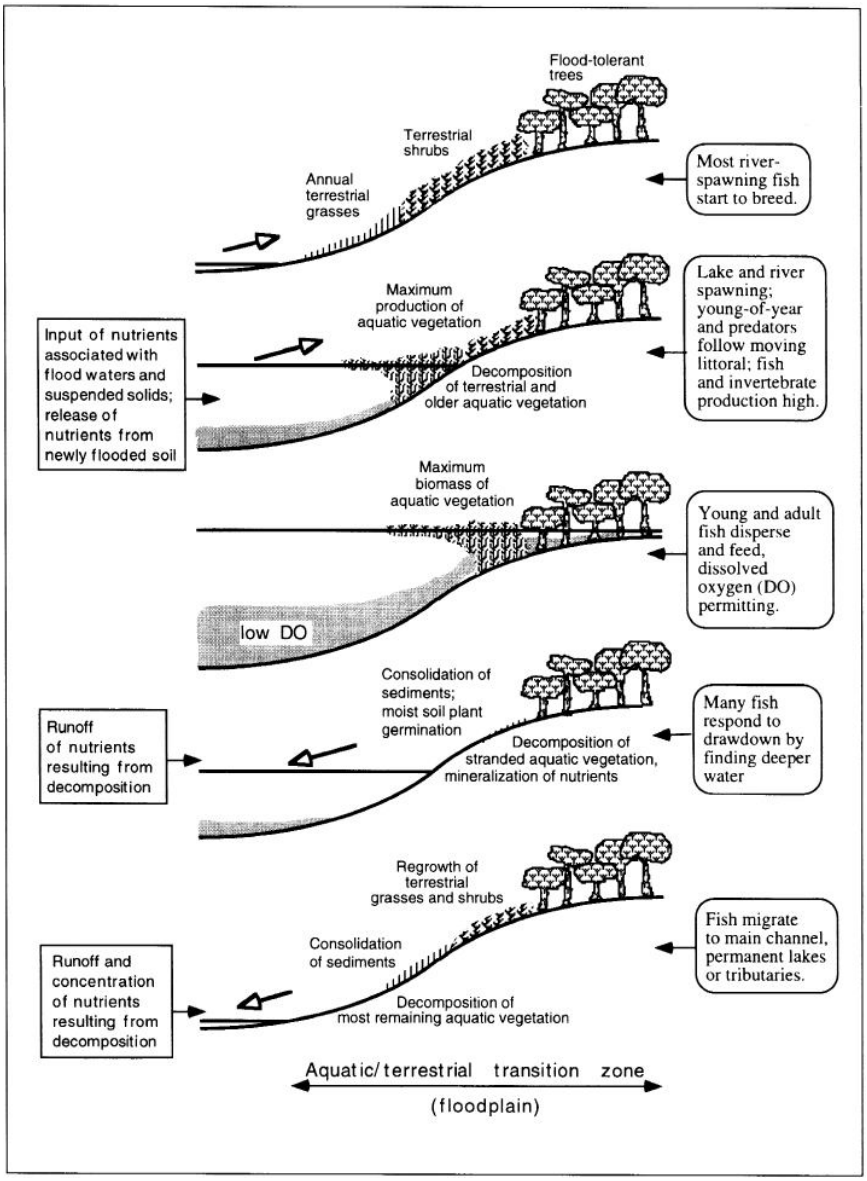


Figure 1.3. Schematic of the flood pulse concept with five snapshots of an annual hydrological cycle (source: Bayley, 1995 - derived from Junk et al., 1989).

An established general model about river ecosystems is the River Continuum Concept (RCC) (Vannote *et al.*, 1980). This predicts a prevalence of primary production in the middle reaches of rivers where shading effects from trees are smaller than in the upstream areas; both in these and in the lower course of rivers respiration is higher than primary production because of shading, high turbidity and depth (Vannote *et al.*, 1980). Two corollaries follow from the RCC, linked to other ideas. First, the resource-spiraling concept (Elwood *et al.*, 1983 in Johnson *et al.*, 1995), i.e. resources are stored periodically in organisms, detritus, and waste products rather than flowing continuously downstream. Second, the serial discontinuity concept, and its extension to floodplain rivers (Ward and Stanford, 1995), which predicts river ecosystem responses to stream regulation in the context

of recovery with distance downstream from the dam. Since Vannote *et al.* (1980), more advanced models of river ecosystems have been devised. For example, Thorp and Delong (1994) developed the Riverine Productivity Model (RPM) which included local instream primary production and riparian litterfall into a new framework to stress the contribution of the riparian zone in terms of local autochthonous production. The Flood Pulse Concept (FPC) was extended in various studies, in particular in Tockner *et al.* (2000) and further enhanced by Junk and Wantzen (2004) to include catchment, river channel and floodplain contributions to the productivity of the river-floodplain continuum.

All these concepts and models are valid to a certain extent and can be applied in different environments. In particular the RCC is mostly valid for small order streams and channels in temperate areas, the FPC for river-floodplain systems while the RPM works best for large rivers with constricted channels. Thorp *et al.* (2006) proposed the River Ecosystem Synthesis (RES) to integrate the contribution of these models and concepts in a flexible framework that recognizes the relative value of upstream/downstream, flood pulse and autochthonous production dynamics in various river systems, whilst stressing the importance of the geomorphology of river basins as well. Despite the flood pulse not being considered a disturbance *per se* (Junk *et al.*, 1989), several studies have proven that specific floods can be either a source of disturbance or a stimulus for phytoplankton development.

In flood-pulsed wetlands the ecotone between the terrestrial and the aquatic environment (i.e. the ATTZ) allows for microorganisms and small flora and fauna to be constantly subject to bidirectional water and nutrient flows (Junk *et al.*, 1989). Overlapping terrestrial and aquatic environments may provide reciprocal subsidies of inorganic and organic material and organisms (Nakano and Murakami, 2011).

1.2.5. Subtropical wetlands

The subtropical belt is the region between the Tropics of Cancer (23.45 ºN) and Capricorn (23.45 ºS) and 35 ºN and 35 ºS respectively. Large wetlands are situated in this region; in Africa alone there are about 2.1 million km^2 of wetlands, 9% of the continent's landmass (Mitchell, 2013). The seasonal movement of the Inter-Tropical Convergence Zone (ITCZ; see glossary) (Figure 1.4) is an important factor

influencing the location of subtropical wetlands, their seasonal pulses of water and hence river flows of great tropical rivers, as it controls rainfall (Mitsch *et al.*, 2011).

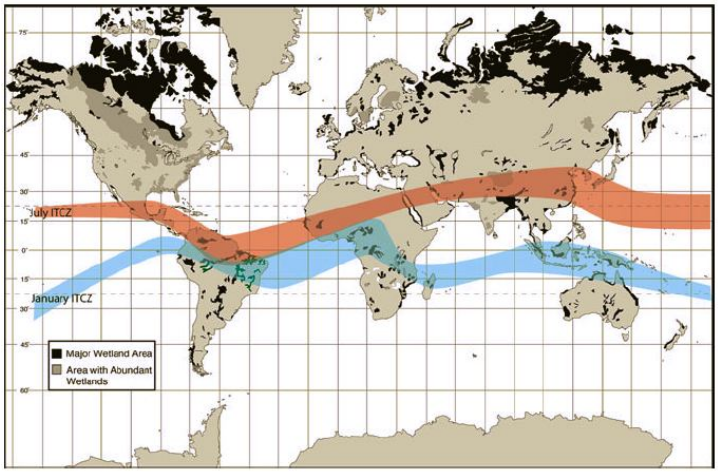


Figure 1.4. Seasons of the Inter-Tropical Convergence Zone (ITCZ) in January and July on map of major wetlands of the world (source: Mitsch et al., 2011).

The most prominent subtropical wetlands are the Everglades in the US State of Florida, the Pantanal in Brazil, the Okavango Delta in Botswana, the Sundarbans in Bangladesh and India, the Tonle Sap in Cambodia, and Kakadu in northern Australia. A comparative study of these six wetlands plus the Canadian Peatlands highlighted several points of interest for research, conservation and management: biodiversity levels are high due to relatively low nutrient statuts, endemic species are not numerous (apart from the Everglades), but some endangered and rare species concentrate here; their relatively low nutrient status helps maintain species diversity and hundreds of species of birds either live or migrate to these important habitats (Junk *et al.*, 2006). However, anthropogenic pressures are increasingly threatening these ecosystems: overpopulation; overexploitation of natural resources; pollution; water abstraction plans (e.g. new reservoirs and hydroelectric power stations); eutrophication; sediment load, among others (see Table 1.1).

Table 1.1. Direct and indirect threats to species diversity in different subtropical wetlands (information from Junk et al., 2006).

Wetland	**Major threats**
Everglades	Water exploitation, change of the flood pulse, dike and channel construction, land reclamation for civil construction and agriculture (now stopped), eutrophication, mercury intoxication.
Pantanal	Increase of sediment load by erosion in the catchment, release of mercury from gold mining, poaching, intensification of cattle ranching, deforestation. In the future: hydrological changes by reservoir construction, canalisation (hidrovia), dike and road construction, and pollution by industry (locally).
Okavango Delta	Water abstraction, channelling of water inside the delta, aerial spraying of insecticides against tsetse flies. In the future: hydrological changes by reservoir construction. Increased and intensified agriculture in the basin.
Sundarban	Alterations in freshwater flow regimes causing salinity changes, growth of human population, land reclamation for civil construction and agriculture, over-harvesting of natural resources.
Tonle Sap	Growth of human population, over-harvesting of natural resources, governance deficiencies. In the future: hydrological changes through reservoir construction along the Mekong River.
Kakadu National Park	Invasion of alien plants and animals, changed fire regime, water pollution from urban, tourism and mining activity, and salinisation and future climate change and sea level rise.

Some of these wetlands lie in arid and semi-arid regions, e.g. the Okavango Delta and the Kakadu National Park in Australia, which are crucially important areas for both animals and human beings during the dry seasons. For example, in the dry season large migrations of elephants, zebras, wildebeests, giraffes, buffalo, and tsessebes take place from the dry to the permanently wet areas of the Okavango Delta (Mbaiwa and Mbaiwa, 2006). Severe threats are faced by wetlands such as the Pantanal in Brazil due to agro-business and mining industry planning to canalise

the Paraguay River (Junk and Cunha, 2005) and the Okavango Delta due to water abstraction plans and climate change (Milzow *et al.*, 2010). In the African continent, water abstraction could increase to 337 km^3 yr^{-1} by 2025 (IUCN, 2000) and the Okavango River Basin and the Delta are expected to face higher pressures on their water resources (Pinheiro *et al.*, 2003).

Although knowledge about plant and animal biodiversity in these ecosystems is very substantial, research on algae, invertebrates, molluscs and crustaceans is patchy to not existent (Junk *et al.*, 2006). However, these small organisms are key for the food webs of tropical river-floodplains due to hydrological connections between the terrestrial and aquatic ecosystems (Junk *et al.* 1989) and between productive habitats like floodplains and less productive river habitats (Winemiller and Jepsen 1998). Algae have been shown to have a very important role in aquatic food webs, compared to other aquatic plants. In tropical rivers, aquatic macrophytes are key producers in inundated floodplains and wetlands, but only a few studies highlight their contribution to the aquatic metazoan food web (Hamilton *et al.*, 1992; Winemiller, 2004). While aquatic macrophytes, leaf litter and other organic matter provide biomass to the 'dead-end' microbial loop, algae (especially benthic ones) are the prevailing source of carbon at the base of food webs (Lewis *et al.* 2001; Douglas *et al.*, 2005). Numerous species of fish have been observed to rely on algae as a major food source in tropical river / wetland ecosystems, such as the Fly River in Papua New Guinea, and the Ord and the East Alligator rivers in Australia; however, macrophytes provide key habitats for aquatic invertebrates and fish, and a large surface substrate area for epiphytic algae (Douglas *et al.*, 2005). Seasonal changes in water levels see a shift in prevalent primary producers, from algae usually living in river channels and isolated water bodies during the dry periods, to emergent aquatic macrophytes in the wet season when flooding takes place (Pettit *et al.*, 2011 and references therein).

As compared to temperate rivers, where aquatic insects are major consumers, tropical rivers have more abundant and diverse fish and invertebrate (e.g. shrimps) populations which have a major influence on benthic sediments, detritus, nutrient demand, and significant top-down control of algal assemblages (Flecker and Taylor, 2004). This top-down control though tends to be influenced by seasonal hydrology,

as it is observed mainly with base-flow conditions (Douglas *et al.*, 2005). Tropical fish assemblages also tend to be more omnivorous than temperate ones due to food sources varying strongly over seasonal / hydrological cycles (Jepsen and Winemiller, 2002). Oligotrophic tropical river systems, e.g. in northern Australia, depend on carbon produced by algae. Here, due high light and temperature levels, even small changes in nutrient load or other relevant factors for algal community production and composition, such as turbidity, herbicides and some metals (e.g. Cu), can affect the productivity of fish and other consumers via increased primary production (Douglas *et al.*, 2005).

1.3. MAIN FEATURES OF ALGAE

This section introduces the organisms at the centre of this study, algae; their main distinguishing features, ie size and shape, their biology, ecology and general taxonomy are outlined.

1.3.1. Morphology and definitions

Algae can be broadly defined as "*aquatic, oxygen-evolving photosynthetic autotrophs that are unicellular, colonial or are constructed of filaments or composed of simple tissues*" (Guiry, 2012). Algae are mostly autotrophic and photosynthetic organisms, but some algae also take up complex organic molecules from the environment by organotrophy or heterotrophy, via absorption of organic compounds or active ingestion of particulate material (Bellinger and Sigee, 2010). Most algae are eukaryotic, but Cyanophyta (also called Cyanobacteria) are prokaryotic organisms, that is to say they are cells without a membrane-bound nucleus. Algae live as free floating or swimming forms in the open water (phytoplanktonic) or they are benthic, i.e. attached to vegetation or other algae (epiphytic), rocks (epilithic), sand (epipsammic) or mud (epipelic). Euplankton comprises fully adapted, truly planktonic algae while tychoplankton are algae present in the open water coming from adjacent habitats (Reynolds, 2006).

In streams and rivers, especially when water flow is fast, only a few planktonic species are present due to algae in suspension being washed downstream (Reynolds, 2000). Therefore benthic / attached algae tend to be the most important primary producers in streams (Law, 2013). As in lakes, large phytoplankton biomass is only

favoured by abundant nutrients in rivers, though fast water flow can induce turbulence and hence reduce light availability; however, low flow is not a sufficient condition for the establishment of high biomass algal populations, as inocula may be small, grazing rapid, sedimentary losses high and/or nutrients scarce (Reynolds, 2000).

The most commonly used classification of phytoplanktonic algae according to size range lists the following groups (Sieburth *et al.*, 1978 in Reynolds, 2006):

- picoplankton = 0.2-2 μm;
- nanoplankton: 2-20 μm;
- microplankton: 20-200 μm;
- macroplankton: >200 μm.

This study focuses on algae larger than 2 μm, picoplankton is excluded because of the identification limits of the inverted microscope technique (see Chapter 3). Algae exist as unicellular organisms, colonies, coenobia (singular coenobium), filaments and mucilaginous colonies (Reynolds, 2006). A coenobium is a colony with a fixed number of cells; a colony is typically formed by single cells in clumps; filamentous algae result from cell division in one plane (University of Hamburg, 2012). Therefore algae are typically enumerated as algal units, each algal unit being a cell, coenobium, colony or filament (see Chapter 3). Small round cells, elongated cells as well as filaments and coenobia evolved to maintain rather high S/V ratio that facilitates nutrient absorption and/or entrainment in the water medium (Lewis, 1976). Although mucilaginous colonies have a very low surface to volume ratio, the true function of mucilage is associated with buoyancy and resistance to grazers. Some typically mucilaginous taxa are very successful in eutrophic lakes, e.g., *Eudorina*, *Microcystis*, *Volvox* (Reynolds, 2006).

Between about 25,000 (Falkowski *et al.*, 2004) and 72,500 species of algae have been identified worldwide (43,918 described and about 28,500 still to be described; Guiry, 2012), but over a million more species are estimated to be undescribed only among the eukaryotic algae (i.e. excluding the prokaryotic Cyanophyta / Cyanobacteria; Andersen, 1992). Other estimates state that there could be between about 279,000 and 10,200,000 species of algae, of which as many as 100,000 to 10 million are diatoms (Andersen, 1992). The definition of species varies across algal

groups and is complicated by widespread asexual reproduction; for example, in diatoms many species likely contain reproductively isolated entities which should probably be recognised as species (Mann, 1999). Desmids are a very diverse group of green algae, and numerous infraspecific taxa are commonly defined as separate species despite them not being reproductively isolated (Kouwets, 2008). No single species concept is employed for all algae (Andersen, 1992); in this study algae are classified to species or genus level whenever possible, based on morphology (see section 3.3.3).

Diversity measures considering taxonomic divergence beyond species richness, e.g. phylogenetic distance, have also been used to investigate diversity in microorganisms, especially bacteria (Lozupone and Knight, 2008) and algae (Lewis and Lewis, 2005). However these require genetic analyses and go beyond the scope of this study (see section 2.5).

1.3.2. Algal cell structure, life and reproduction strategies

Most algae have eukaryotic cells, with various structures enclosed within the plasmalemma, a membrane in turn surrounded by a cell wall made of cellulose or pectin, a carbohydrate polymer; some groups of algae have cell walls made of silica e.g., diatoms, or carbonates e.g., Rhodophyta. The intracellular protoplasm (cytoplasm) is a suspension in which nucleus and plastids such as chloroplasts and mitochondria are located, alongside storage products (Reynolds, 2006). The key elements composing these algal organelles are hydrogen, oxygen and nitrogen; phosphorus, sulphur, potassium, sodium, calcium, magnesium and chlorine. Other trace elements useful to metabolic processes are: silicon, iron, manganese, molybdenum, copper, cobalt, zinc, barium and vanadium (Reynolds, 2006). All these elements must be soluble and diffusible to be assimilated by cells. In sediments, wetlands, macrophyte beds, and cyanobacterial mats, nitrogen fixation is better supported by higher availability of Mo in its reduced forms and Fe than in open water for planktonic organisms (Howarth *et al.*, 1988).

The key physical factors for algal life are the interception of sufficient light energy for carbon fixation, ambient temperature and a low rate of sinking, allowing them to remain in suspension in the upper parts of lakes and rivers (Reynolds, 2006). In water bodies, temperature is lower at greater depths and more variable close to the

surface, apart from with inverse stratification in winter temperate regions; shallow areas get warmer and change widely seasonally (Wetzel, 2001). Light availability is higher close to the surface, with rapid decrease within sediments, but usually moderate to high in the epiphyton (Wetzel, 2001). Nutrient uptake may be enhanced by diurnal migrations from the euphotic zone to nutrient rich sediments, for example in various epipelic algae – diatoms (Mitbavkar and Anil, 2004), flagellates (Flaim *et al.*, 2003) and cyanophyta (Round and Eaton, 1966). Cyanobacteria, chrysophytes, and cryptophytes produce toxins and allelochemicals that inhibit or stimulate the growth of other algae (Hagerthey *et al.*, 2013).

Algae may grow in seasonal cycles in lakes and rivers with the possibility of spring blooms of diatoms and summer blooms of cyanobacteria (Paerl *et al.*, 1998; John *et al.*, 2002, Xu *et al.*, 2010), respectively facilitated by water column mixing (Falkowski *et al.*, 2004) and warm temperatures (e.g. in shallow lakes; Kosten *et al.*, 2012). Algae, like terrestrial plants and animals, have different life strategies in relation to the amount of energy they 'invest' in reproduction and competition for resources. MacArthur and Wilson (1967) developed the concepts of r and K selection for animals (r refers to maximal intrinsic rate of natural increase and K to carrying capacity); these were subsequently developed in a broader framework to encompass plants by Grime (1977). In K-selected organisms the life expectancy of individuals is long and the proportion of the energy and other captured resources devoted to reproduction is small; on the other hand, r-selected organisms have a short life expectancy and large reproductive effort.

In plants and algae the competitive strategy (K selection) prevails in productive, relatively undisturbed environments, the stress-tolerant strategy (called S strategy, and characterized by strong K selection) is associated with continuously unproductive conditions, while the ruderal strategies (with r selection) is characteristic of severely disturbed, but potentially productive habitats (Grime, 1977; Reynolds *et al.*, 2006). Algal species may have a C strategy (competitors, opportunistic colonists), S (stress-tolerant) and R (disturbance-tolerant, or ruderal) strategy (Reynolds, 1988, 1997).

Phytoplankton are organised into assemblages according to light energy, nutrient supply and physical mixing, with the species having one of the three basic (C, S, R) strategies to fill their ecological niches in order to survive sub-optimal conditions

both in marine and freshwater environments (Smayda and Reynolds, 2003). From an evolutionary ecology viewpoint, diatoms are considered to be r-selected organisms as they tend to appear opportunistically in highly turbulent environments (Kilham and Kilham 1980), whereas flagellates such as Raphidophyta and Pyrrophyta tend to live in resource-limited environments (Harper 1977) and green algae such as desmids (Spijkerman *et al.*, 2004) are deemed to be prevalently K-selected organisms. The C-S-R framework developed by Grime (1977) was applied to phytoplankton by Reynolds (1997) and C, S, R comprise 'strategic adaptations'. C-strategists are small phytoplankton, with a high S/V ratio, growing rapidly and well adapted to both high light / energy and high nutrients; S-strategists are slow growing, large unicells or colonies, with a low S/V ratio, prevailing with high light / energy and low nutrients; R-strategists are usually large, elongated unicells and colonies or filaments, with a high S/V ratio and adapted to low light / energy (being tolerant of low insolation levels) and high nutrient conditions (Reynolds, 1997), a vital adaptation in deep, mixed and turbid waters (Reynolds, 2006). These strategies are referred to in the discussion sections in Chapters 4 and 5 to support the ecological interpretation of the distribution of algae in the Okavango Delta.

1.3.3. The role of algae in aquatic food webs

The biodiversity and biomass of autotrophic organisms are fundamental for all aquatic food webs. Algae are crucial primary producers for freshwater and marine environments; for example, marine diatoms account for 43% of global annual primary productivity, as estimated by Nelson *et al.* (1995) and about 40% of the net primary production in oceans (Falkowski *et al.*, 2004). Algae form the base of trophic networks (food webs) ending with fish and other consumers, including humans. As primary producers, they make sugars such as glucose by combining water and carbon dioxide into glucose via photosynthesis.

The decomposition of organic matter by organisms such as earthworms, snails, bacteria and fungi releases nutrients; plants, including algae, contribute to nutrient cycling (a supporting service; Table 1.2) (Cardinale, 2011), analogously to what soil organisms do in terrestrial ecosystems (Paine, 1980). Algae absorb carbon and macronutrients such as nitrogen and phosphorus to synthesise their vital structures and release oxygen to the atmosphere (Lee, 2008). Doing that, algae recycle

compounds that are toxic for humans, e.g., heavy metals, hence performing a water purification service (Paine, 1980). Algae are a significant source of food for invertebrates and fish in freshwater environments, ultimately having a role in the transfer of matter and energy to the top levels of the food webs (Paine, 1980), i.e., algae have a role in the provision of food to humans via, e.g., fish feeding on them. Consumers such as zooplankton and fish rely on primary producers like algae as sources of nutrients, e.g. carbon, nitrogen and phosphorus (Figure 1.5). While supporting services have indirect effects on people and can occur over a long period of time, they are necessary for all other ecosystem services (Russi *et al.*, 2013);

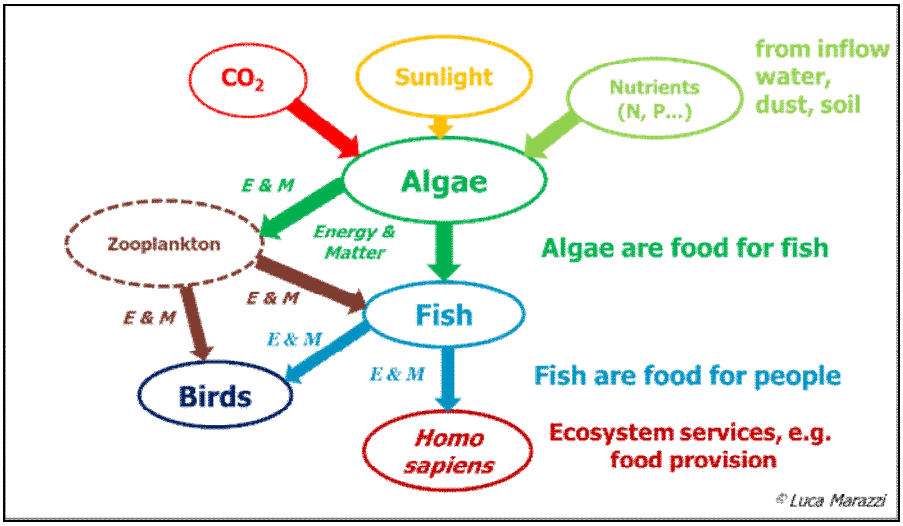


Figure 1.5. Conceptual scheme of the role of algae in food webs.

Algae play an important role as a food source in aquatic systems alongside other organisms such as macrophytes (Paine, 1980; Pettit *et al.*, 2011 and references therein) because of their higher nutrient content compared with plant coarse particulate matter (Hamilton *et al.*, 1992). These autotrophic microorganisms were shown to sustain a biomass of consumers of 300 kg ha^{-1} in the Orinoco floodplains (Lewis *et al.*, 2000). Accurate estimations of the global species richness of algae are very difficult due to the lack of sufficient systematics, dispersal and biogeography analyses (Sharma and Rai, 2010).

The conservation of threatened keystone species (e.g. birds, mammals) and the preservation of ecosystem health require the understanding and protection of the various levels of the food webs on which these consumer organisms rely for energy flows and matter cycles (Paine, 1980). In this respect the microbial loop in lotic (riverine) systems is of fundamental importance; the interlinked benthic and

planktonic microbial loops are a more direct food-web link in flowing (lotic) waters than in standing (lentic) waters or marine ecosystems. This is due to the presence of fewer direct trophic transfers (or a single one) between bacteria and top consumers given the abundance of macroscopic consumers such as and invertebrate grazers feeding directly on bacteria (Meyer, 1994).

Algae are key organisms in microbial loops because they excrete dissolved organic matter or as algal cells lyse when attacked by viruses or predators, which then constitute point sources of organic matter colonised by bacteria-feeding protozoa (Fenchel, 2008); much microbial activity in the water column takes place on these suspended particles on which copepods and other zooplankton feed (Grossart *et al.*, 2003). Thus, the water column is not a completely mixed system with random interactions between organisms; plankton is spatially organised with implications for biologically-mediated transfer of matter and energy (Fenchel, 2008). Bacterial diversity has been observed to have an impact on bacterial and algal biomasses (Naeem *et al.*, 2000). As algae are primary producers, they uptake nutrients from inorganic sources supplied by decomposers, whereas these, mostly fungi and bacteria, acquire carbon from organic sources produced by algae and plants. This creates a co-dependency between producers and decomposers which is relevant for ecosystem processes, implying that, when communities lose species of algae, fungi or bacteria, ecosystem functioning may be negatively affected (Naeem *et al.*, 2000).

Fenchel (2008) reviewed developments of studies on the microbial loop in the last 25 years. Despite most research in this field being conducted in the oceans, the microbial loop model has been used for freshwater ecosystems too (Meyer, 1994). Whereas the classical plankton food chain prevails with fresh supplies of mineral nutrients, e.g. during the spring bloom in temperate waters and in upwelling areas) the microbial loop dominates oligotrophic waters, with primary production favoured by dissolved mineral nutrients recycled taken up prevalently by small organisms (Chisholm, 1992). The presence of mixotrophic protists which use phagocytosis and phototrophy to generate energy and matter for their life was observed in many studies (e.g. on planktonic protists: Jones, 1994).

1.3.4. Algae's importance for biodiversity and ecosystem services

The ecologist E.O. Wilson first used the term biodiversity in the literature (Wilson, 1988), but the concept has been elaborated under the name 'biological diversity' since the nineteenth century. There are three levels of biological diversity: α-diversity, i.e. species richness (the number of species) at a site or habitat; ß diversity, the difference in species composition (or species turnover) between two or more sites (also called habitat diversity), and γ diversity, or the diversity of the landscape (Whittaker, 1960).

A comprehensive definition of biodiversity, i.e. biological diversity, at all three levels is contained in Article 2 of the Convention on Biological Diversity (2013):

> "*the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*."

According to the Millennium Ecosystem Assessment (2005) "*Biodiversity is the foundation of ecosystem services to which human well-being is intimately linked*". Numerous species of living organisms have positive or negative effects on both ecosystem health and human well-being. Despite the expression 'life support system' being more inclusive (see, e.g., Odum, 1989), more broadly accounting for the fact that species benefit one another and do not just provide services to human beings, the widely accepted term 'ecosystem services' will be used hereafter when referring to, e.g. water purification or primary production performed by algae. Ecosystem services themselves can be interpreted as natural services from ecosystems to humans with a narrow anthropocentric viewpoint or as natural services for life in general; this broader interpretation is closer to the 'life support systems' concept.

However, ecosystem services are more commonly defined as services to humankind, e.g. "*components of nature, directly enjoyed, consumed, or used to yield human well-being*" (Boyd and Banzhaf, 2007). There are four main categories of ecosystem services: provisioning services, regulating, cultural and supporting services (see Table 1.2). Ecosystem processes (or ecosystem functions) are biologically-induced changes in energy and matter over time and space, for example

production of carbon, respiration, and nutrient uptake (Reiss *et al.*, 2009). According to de Groot *et al.* (2002) ecosystem functions underlie ecosystem processes (Figure 1.6); for instance water regulation is an ecosystem function, whereas regulation of runoff and river discharge by land cover is the corresponding ecosystem process. The resulting drainage and natural irrigation are the ecosystem goods and services.

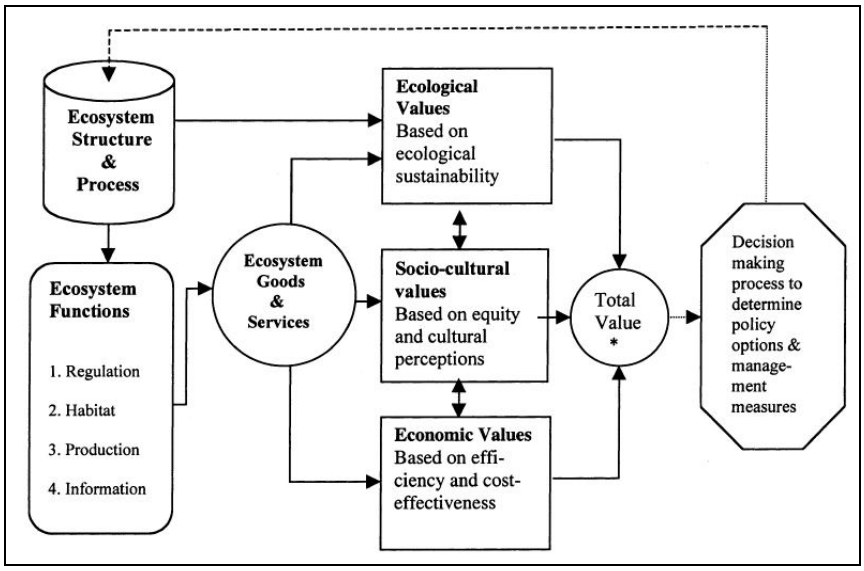


Figure 1.6. Framework for integrated assessment and valuation of ecosystem functions, goods and services (source: de Groot et al., 2002).

Ecosystem services encompass both use values (e.g. harvesting or tourism) and non-use values (e.g. the existence value of an ecosystem or a species). Higher biodiversity, e.g. species richness, is not necessarily associated with better ecosystem services provision. In a comprehensive review, Balvanera *et al.* (2006) accounted for positive effects of biodiversity on most ecosystem services; they showed evidence for neutral or negative relationships between biodiversity and ecosystem services, e.g. biodiversity does not seem to buffer influences of warming, drought or high environmental variance, but higher number of species are better able to resist nutrient level changes and invasive species.

Specific research on algae shows that more biodiverse algal assemblages contribute to better water purification in freshwater ecosystems, e.g., via niche partitioning increasing nitrate uptake and storage (Cardinale, 2011). Therefore assemblages with more species may be able to provide some ecosystem services more successfully than others with less species, i.e. these assemblages are more stable or vary less in, e.g., primary productivity due to a buffering effect (Yachi and Loreau, 1999) and

have a better 'performance', for example in terms plant productivity and CO_2 absorption (Naeem *et al.*, 1994; Yachi and Loreau, 1999). The insurance hypothesis states that biodiversity insures ecosystems against reduced functioning as the presence of numerous species in a certain environment means that some species will maintain, e.g. primary production, even if others fail (Yachi and Loreau, 1999). Plankton assemblages behave consistently with this hypothesis, i.e. species-rich assemblages with higher redundancy exhibit more reliable performances in terms of biomass and density measures (Naeem and Li, 1997). It is widely acknowledged that a larger number of species is probably critical for the stability of ecosystem processes in dynamic environments; moreover, the individual traits and interactions of certain species especially support ecosystem functioning and stability as well as biogeochemical cycles (Loreau and Hector, 2001).

Overall, algae (including macroalgae) underpin at least ten ecosystem services (Table 1.2). Various species are used for food, e.g., seaweeds and *Spirulina*, a member of the Cyanophyta, are used as dietary supplements (Belay *et al.*, 1993), alginate fibres from kelp, and fuel, e.g. some biofuels are produced by extracting oils from algae (provisioning services); marine planktonic algae contribute to climate regulation by producing dimethylsulphide then forming cloud-condensation nuclei made of sulphate aerosols (Charlson, 1987); also, algal crusts controls erosion by regulating soil moisture and thus giving shelter to seed plants (Booth, 1941). Moreover, algae help purify waters from nutrients and pollutants (regulating service) (Biggs and Kilroy, 2000) and they contribute to supporting services such as primary production liberating atmospheric oxygen and provision of habitats to other organisms (e.g. *Cladophora* mats hosting meiofauna and epiphytes; Dodds and Gudder, 1992). Benthic algae (phytobenthos) function as a 'chemical modulator' transforming nutrients from inorganic to organic forms, e.g. Cyanophyta convert atmospheric nitrogen (N_2) into ammonium (NH_3) (Law, 2013).

Table 1.2. Ecosystem services as per the Millennium Ecosystem Assessment (MEA, 2005; the services to which algae are thought to contribute are highlighted in bold).

Ecosystem Function	Ecosystem Services
Provisioning	**Food, fiber and fuel**
	Genetic resources
	Biochemicals
	Fresh water
Cultural	Spiritual and religious values
	Knowledge system
	Education and ispiration
	Recreation and aesthetic values
	Sense of place
Regulating	Invasion resistance
	Herbivory
	Pollination
	Seed dispersal
	Climate regulation
	Pest regulation
	Disease regulation
	Natural hazard protection
	Erosion regulation
	Water purification
Supporting	**Primary production**
	Provision of habitat
	Nutrient cycling
	Soil formation and retention
	Production of atmospheric oxygen
	Water cycling

The study of algae has made important contributions to ecological theories on trophic dynamics, biogeography and competition (e.g., Stevenson *et al.*, 1996; Chust *et al.*, 2012). The small size of algae (generally 10^{-2} to 10^{-7} m) and their short lifespan (generally $l0^4$ to $l0^7$ s, or 2.8 hours days to c. 3.9 months) allow scientists to thoroughly observe and experiment on their individuals, populations and assemblages (Reynolds *et al.*, 1993). Their position at the base of the food webs renders them good early indicators of modifications of hydrochemistry conditions, e.g. temperature, pH and salinity. Environmental change has been extensively investigated using diatoms (Battarbee *et al.*, 1986; 2001) and other algae, e.g. desmids (Coesel, 1983; 2001) due to algal assemblages being able to cost-effectively provide benchmarks on past and present water quality such as organic and inorganic pollution (Sladecek, 1986; Round, 1991). Other advantages of the use

algae in ecology are their ubiquity and ecological importance in most aquatic ecosystems, their sensitivity to many environmental stressors and their rapid response times to changes in environmental conditions (McCormick and Cairns, 1994). McCormick and Cairns (1994) effectively summarise the relevance of algae as ecological indicators: "*Because of their integral role in ecosystem energetics and biogeochemical cycling, algae provide a relatively unique composite picture of ecosystem condition*". However, when algae grow excessively or produce toxins, they hamper ecosystem service provision, e.g. drinking water, fisheries and recreational uses of water resources; hence the importance of monitoring algal species composition, biomass, metabolism and chemical byproducts in order to support the preservation and restoration of ecosystem services and human well-being (Stevenson, 2014).

Despite the importance of algae and other microorganisms sustaining aquatic food webs, their biodiversity and ecology are poorly understood and require more study (Stendera *et al.*, 2012). Though we do not know the conservation status of these microorganisms, apart from some groups of green algae like the charophytes, efforts to describe and monitor algal assemblages in understudied regions such as the tropics are ultimately useful for knowledge and heritage purposes (Guiry, 2012). The impact of reduction of algal productivity in the oceans due to pollution, and of loss of forests and coastal wetlands on the gas regulation function of ecosystems (based on, e.g., carbon and oxygen cycling, for maintaining air quality and regulating the climate) is large (de Groot *et al.*, 2002).

There is growing evidence that more diverse algal assemblages have a higher nutrient uptake; this contributes to a more effective removal of excess nitrates (Cardinale, 2011). A higher number of algal species in nutrient-rich environments enhances the resilience of the ecosystem to nutrient overloading reducing nutrient concentrations as, in such disturbed systems, species have faster rates of biomass accumulation when they are a part of species-rich assemblages (Cardinale *et al.*, 2005). Therefore both the study of patterns of algal productivity (the rate of biomass synthesis), biomass and biodiversity are important for an improved understanding of ecosystems. As productivity is seldom measured (Skácelová and Lepš, 2014), in this research the focus is on biomass, i.e., standing crops or instant community biomass, and taxon richness / diversity of microalgae (see Chapter 5).

This study undertakes an assessment of algal communities in a near-pristine subtropical wetland of global importance, the Okavango Delta, recently listed as UNESCO Heritage site (UNESCO, 2014). In December 2003, the United Nations General Assembly adopted resolution 58/217 which committed its member states to halve the proportion of people lacking access to safe drinking water and basic sanitation (Dudgeon *et al.,* 2006). The resolution included the proclamation of the International Decade for Action 'Water for Life' from 2005 to 2015 so as to mark the global importance of freshwater biodiversity as a priority for conservationists (Dudgeon *et al.,* 2006).

1.4. BIOGEOCHEMICAL CYCLES: THE ROLE OF ALGAE

Algae are fundamental for global primary production, one of the key ecosystem functions that living organisms contribute to (Andersen, 1992). Algal and plant photosynthesis have an important role in the carbon and phosphorus cycles of wetlands and other aquatic ecosystems, e.g. periphyton retains and deposits phosphorus loads (Dodds, 2003). Studying the biodiversity of algae in a remote near-pristine wetland in an arid subtropical region such as central Southern Africa, especially in the context of ongoing climatic changes (Wolski *et al.*, 2014), is thus particularly important.

Microscopic autotrophs such as diatoms (Bacillariophyta) are being increasingly used in studies of ecosystem functioning alongside, or alternatively to, terrestrial organisms, for example to investigate the relationships between diversity and primary production in shallow estuarine environments (Forster *et al.,* 2006). These organisms are involved in various stages of nutrient cycling for C, N, P and Si (Reynolds, 2006) as well as K, Mg, Na, Fe, Mn, Cl, Zn, Cu, and Se, important for biochemical enzyme-controlled reactions (Hagerthey et al., 2013). Despite the fundamental role that algae play in aquatic food webs in floodplain environments, insufficient attempts have been made to quantify biomass and rates of productivity of benthic and epiphytic algae (Davies *et al.*, 2008 in Pettit *et al.*, 2011); their contribution in terms of carbon source for consumers and the role of floodplains as possible sources or sinks of organic matter are also still poorly understood (Pettit *et al.*, 2011).

Photosynthesis controls oxidation-reduction potentials and heterotrophic metabolism and thus regulates biogeochemical processes, e.g., dissolved oxygen production and nutrient uptake (Hagerthey *et al.*, 2013). Algae uptake carbon by active or inactive processes, respectively using an H^+-ATPase or by diffuson; bicarbonate can either be transported into the cell via an anion channel or via an ATPase coupling (Spijkerman *et al.*, 2005). Many desmids use HCO_3^- rather than diffusive CO_2 to acquire inorganic carbon hence competing for HCO_3^- with other green algae (e.g. *Chlorella* and *Chlamydomonas*), but also with cyanobacteria (Spijkerman *et al.*, 2005). pH was shown to have an independent effect on the photosynthesis of desmids, regardless of CO_2 availability (Spijkerman *et al.* 2004), with species found in waters with low pH being considered CO_2 users, and species inhabiting alkaline sites are grouped as HCO_3^- users (Spijkerman *et al.*, 2005).

Algae contribute to nutrient cycling in wetlands and other freshwater and marine ecosystems. Wetlands are very important for cycles of nutrients (Boyer and Howarth, 2002) such as phosphorous (Tiessen, 1995). Diatoms also uptake dissolved silica (DSi) and deposit biogenic silica (BSi) alongside sponges, testate amoebae and plants - as phytoliths, i.e. inorganic plant remains (Struyf and Conley, 2012). However, silica is a neglected component of global biogeochemical cycles, despite the fact that herbaceous wetlands and other ecosystems such as various forests and grasslands act as ‘silica factories’; diatoms, sponges and chrysophytes work as ‘bioengineers’ recycling this nutrient in freshwater systems (Street-Perrott and Barker, 2008). Hydrology and vegetation were shown to control silica processing in wetlands, with human interference having impacts on both wetland Si biogeochemistry and climate change (Struyf and Conley, 2008); this is particularly relevant in the Okavango Delta, where scenarios of drying may become a reality due to climate change and water abstraction (see section 2.2.3; Milzow *et al.*, 2010). Diatoms are crucially important for the silica cycle (SiO_2), which occurs in the aqueous environment in only one dissolved form, the monomeric orthosilicic acid (H_2SiO_4), referred to as dissolved reactive silica (DSi). Diatoms incorporate DSi into their frustules and simple chemical dissolution of the diatom shells regenerates it in the water (Anderson, 1986).

1.5. ENVIRONMENTAL DRIVERS OF ALGAL DISTRIBUTION

This section introduces the factors and dynamics that significantly influence the distribution of algae in space and time at various scales, e.g., regional *vs* within-habitat types. Geography and space, limnology, seasonality and flood pulses and habitat structure are considered. The growth of algae in the benthos is influenced by several drivers such as temperature, substrata properties, nutrient and light availability and pH, as well as by competition, predation and immigration rates (Law, 2013). Light availability and low rate of sinking are also very important for phytoplankton (Reynolds, 2006). Geology, hydrology, human activities and climate factors (such as temperature) influence water quality and, in turn, algal assemblages (Stevenson *et al.*, 1996).

1.5.1. Geography and space

Wetland environments and communities of organisms living in them change according to geographical and spatial factors; latitude and altitude as well as distance from ocean influences climate, and hence water availability. Species composition is related to species richness and its relationship with habitat area; these are, at larger scales, influenced more by dispersal, speciation and extinction whereas disturbance, competition, and herbivory are the most important factors determining algal beta diversity at local scales (Passy and Blanchet, 2007). In general, living assemblages are controlled by external environmental factors such as climate, geology and water chemistry, and, on the other hand, by biological processes such as species interactions and neutral processes, e.g. ecological drift and dispersal (Hubbell, 2001). All these factors have an influence on spatial patterns; given that local deterministic structures and random noise (error) often are not spatially structured, each sampling site may show differences in, e.g., species composition, unrelated to trends taking place at higher scale (Borcard *et al.*, 2011). Over long time scales, local diversity does not have instantaneous effects on ecosystem processes; in fact, ß-diversity across entire meta-communities may maintain ecosystem functioning due to dispersal and disturbance, when these are interpreted as regional processes (Matthiessen and Hillebrand, 2006).

The scale at which algal assemblages are studied and spatial proximity of sampling sites play a role in determining their similarity or dissimilarity; sites close to one

another are more likely to have a more similar algal species composition than sites further apart, i.e. are spatially autocorrelated (Legendre, 1993; Borcard *et al.*, 2011). Spatial autocorrelation is defined as "*the tendency for random variables to covary as a function of their locations in space*" (Ver Hoef *et al.*, 2001) or, more straightforwardly, as the realization that "*everything is related to everything else but near things are more related than distant things*" (Tobler, 1970). In freshwater habitats larger organisms such as fish have shown higher spatial autocorrelation than smaller ones, e.g. plankton; the latter face fewer barriers to their passive dispersal than actively dispersing animals (Shurin *et al.*, 2009).

1.5.2. Limnology

The physical and chemical conditions of freshwaters are proven to contribute to determining the composition of the algal flora in rivers, lakes and wetlands. In particular, water depth and temperature, the concentration of nutrients such as nitrogen, phosphorus, silica and various cations and anions, dissolved oxygen, conductivity and pH levels and turbidity all influence which groups and species of algae live in freshwater ecosystems (Mitsch and Gosselink, 2000; Wetzel, 2001; Reynolds, 2006).

Temperature and light

Temperature has a profound influence on algal primary production in inland waters; species of, e.g., Cyanophyta, tolerate temperatures above 35 °C. However, studies on the distribution of algae in relation to this environmental variable are rare (e.g. Arctic Lapland lakes; Weckström and Korhola, 2001). Temperature has been shown to be a relevant factor for both algal growth / productivity (Raven and Geider, 1988) and ecology (Patrick, 1971) and was observed to have a strong positive relationship with periphyton biomass in rivers (Rosa *et al.*, 2013 in Mahdy, 2014) and lakes (Tarkowska-Kukuryk and Mieczan, 2012). At higher temperatures the performance of algae and other organisms increases, as kinetic energy and metabolic rates rise, but excessively high temperatures denature enzymes, reduce enzymatic function, slow metabolic rates, and alter biogeochemical rates (Hamilton, 2010). High temperatures, also due to low flow reducing water depth and enhancing warming effects of sunlight, also tend to cause increased consumption of nutrients (Larned,

2010). In most periphytic algae, optimal temperatures for growth are between 10 °C and 30 °C (Larned, 2010). Diatoms prevail between 5 and 20 °C, green algae between 15 and 30 °C and blue-green algae above 30 °C (DeNicola, 1996).

In nature, species are only rarely most abundant at their optima for specific growth rate, but experimental studies are rare (Talling, 2012). Moreover, temperature affects diatoms indirectly by changing water quality, microhabitat and various catchment factors, and hence can be used as a summary variable to describe potential climatic effects on diatoms (Weckström and Korhola, 2001 and references therein). Light is often correlated to temperature (Hill, 1996) and, together with nutrient availability and grazing determines species richness and diversity (Liess *et al.*, 2009); light has also been shown to increase algal biomass mostly when grazers are absent as very luminous conditions favour the growth of easily ingestable algae (Hillebrand, 2005). Light tends to be limiting in deep lakes, but less so in shallow wetlands, unless thick vegetation (e.g. duckweed) mats are present (Goldsborough, 1993) although other studies suggest that light limits the growth of periphytic and benthic algae more than (Lange *et al.*, 2011) or similarly to nutrients and grazing (Hillebrand, 2005).

Depth, conductivity and nutrients

Water depth is very important in determining the availability of light and nutrients. In a study of periphyton in the Everglades marshes, Gottlieb *et al.* (2006) showed that, where water levels were less variable over the course of a year, inundation was not the key determinant of species composition, while water depth had a higher influence on assemblages being desicatted annually. In the Everglades and other wetland types hydrology and water quality / chemistry have been found to be the dominant drivers of wetland structure and function (Gaiser, 2009; Mackay *et al.*, 2012). Periphytic algae respond rapidly to hydrological alterations such as moisture availability, substrate types available for colonization and supply of nutrients, in particular phosphorus, the limiting nutrient in many wetlands (Gaiser, 2009). For diatoms, temperature seems to be a less important factor than other variables such as water chemistry - pH, salinity / conductivity, nutrients and Dissolved Organic Carbon (DOC) (Anderson, 2000). Soil, vegetation, catchment and limnological processes determine their levels; turbulence, mixing, tolerance of physical

disturbance and light availability also play an important role in shaping algal assemblages (Anderson, 2000). Nutrient concentrations and hence availability are influenced by the spatial heterogeneity of resources in the substratum and water; this maintains the species diversity of periphytic algae (Pringle, 1990) as increases in surface heterogeneity at a certain nutrient level enhance species richness (Tilman, 1982). Processes such as nitrogen transformations in wetlands are mediated by microorganisms, e.g. bacteria and algae; for example, algae uptake nitrates from the water or they fix it directly from the atmosphere once N_2 is dissolved in water (Mitsch and Gosselink, 2000). Different groups of algae play various roles in the N, P as well as C cycle (see section 1.4); the availability and form in which key nutrients are taken up by algae is important for their distribution patterns and their biomass (Reynolds, 2006).

1.5.3. Seasonality and flood pulse

Distribution patterns of algae in aquatic ecosystems naturally vary across seasons given the temperature and flood gradients generated by natural climatic variability (Weckström and Korhola, 2001; Stendera *et al.*, 2012). In lakes in temperate regions spring blooms of diatoms and prevalence of green algae and cyanobacteria in the summer months are common (John *et al.*, 2002). In flood-pulsed wetlands lateral water movements play a major role in creating a 'hydroclimate' superimposed on the seasonal alternation of cold and warm months (Junk *et al.*, 1989). The flood pulse is a very important environmental process shaping assemblages of algae, plants, invertebrates and vertebrates in a number of tropical and subtropical wetlands (Junk *et al.*, 1989), such as the Okavango Delta (diatoms: Mackay *et al.*, 2012; invertebrates: Davidson *et al.*, 2012; plants: Tsheboeng *et al.*, 2014), the Pantanal in Brazil (algae: De-Lamonica-Freire and Heckman, 1996; Zalocar de Domitrovic, 2002), the Kakadu in Australia (from algae to vertebrates: Finlayson *et al.*, 2006) and wetlands in the Paraná river basin (macrophytes: Murphy *et al.*, 2003; phytoplankton: Train and Rodrigues, 1998; Izaguirre *et al.*, 2004). Seasonal variations in algal assemblages have been observed in numerous studies on flood-pulsed river systems such as the Pantanal with alternating abundance peaks of Euglenophyta and Cryptophyta (de Oliveira and Calheiros, 2000). Also, in the upper Paraná river Cyanophyta were observed to prevail during

periods of greater water column stability, while filamentous diatoms were more abundant during periods of high turbulence (Train and Rodrigues, 1998). Different flooding frequency and durations have been shown to create varying levels of species diversity (Connell, 1978; Reynolds *et al.*, 1993) and strongly influence water depth during flooding seasons. Optimal nutrient uptake rates may be advantageous in shallow nutrient rich environments, which may favor algal species with higher S/V ratios (e.g. Unrein, 2002; Izaguirre *et al.*, 2004). These dynamics have a major impacts on algal species composition and successions in wetland and other freshwater environments.

1.5.4. Habitat structure

Algae live in a variety of macro- and micro-habitats; variations in the environment at both landscape and patch scale, e.g. lagoon, channel or shallow floodplain (landscape scale) and open water, sedgeland and grassland (patch scale) are likely to be meaningful for species with different requirements in terms of water depths, temperature and light availability. Habitat availability and diversity are high, particularly among submersed macrophytes; attaching to these aquatic plants, algae often form a three-dimensional structures in biofilms (Wetzel, 2001) where, together with bacteria, fungi and protoza surrounded by a polysaccharid matrix, they play a significant role in ecosystem processes such as sediment / nutrient retention in aquatic environments (Battin *et al.*, 2003). High nutrient concentrations are usually present in the epipelon, coming from interstitial waters and sediments, where conditions are generally reducing; epilithic algae are exposed to higher oxygen levels with diurnal variations; whereas in the epiphyton oxygen concentrations tend to be low and variable (Wetzel, 2001). In shallow littoral regions, dynamic and productive submersed plant zone, microhabitat diversity is very large, most (80%) of freshwater species of algae and cyanobacteria are attached, sessile forms (Wetzel, 1996 in Wetzel, 2001). Water turbulence decreases rapidly with depth, submersed macrophytes attenuate flows in lakes and streams; loosely aggregated organic-rich sediments can serve as substrata for algae and cyanobacteria when they receive enough light. Modes of nutrition are also related to algal habitats; Wetzel (2001) summarised studies on algal heterotrophy, describing its occurrence as low to moderate in epipelon and low in the epiphyton; whereas

primary productivity tends to be low in the epipelon, but high in the epiphtyon. Symbiotic interactions tend to be moderate to high in epipelon, and high to very high in epiphyton. True phytoplankton may have limited access to nutrients such as nitrogen due to uptake by submersed macrophytes and epiphytic periphyton assemblages (Howard-Williams, 1981). The attached algae often dominate algal biomass in small streams and shallow lakes; probably > 90% of all algal species grow attached to a substratum - Coniugales, Cyanophyta, Euglenophyta, Xanthophyceae and Chrysophyceae and pennate diatoms being the major groups (Biggs, 1996; Lowe, 1996). Benthic algae have specific advantages over phytoplankton in terms of nutrient uptake, as Wetzel (2001) summarised: "*The immediate juxtaposition of attached algae to the metabolically active area of a living plant and bacterial concentrations can give them a distinct competitive advantage over their planktonic counterparts living in a habitat where nutrients are much more dispersed*". Whereas epilithic and epiphytic algae do interchange, epipelic algae live adnate to the sediments and are particularly motile. Epipsammic algae tend to be small diatoms and cyanobacteria "*attached to crevices in the surface of sand grains and rock surfaces*" (Wetzel, 2001). In floodplain wetlands, the regular flood pulse and high habitat heterogeneity favour a high biodiversity of terrestrial and aquatic plants and animals (Junk *et al.*, 1989). Evidence suggests that habitat availability plays a significant role in determining algal species distribution in tropical and subtropical aquatic environments (Rodrigues and Bicudo, 2001; Unrein, 2002). Macrophyte cover has also been shown to be a major factor in determining algal species distributions in shallow floodplain lake and oxbow lakes in the lower Paraná river (Izaguirre *et al.*, 2004). Furthermore, substrate composition may be important, as particle size and stability influence the composition, abundance and distribution of benthic algae and other organisms (Thomson *et al.*, 2001).

Habitats can be characterised by their environmental conditions. Heino and Soininen (2006) found that, in diatoms, niche position, or more generally habitat availability, was most important in determining their regional occupancy; this is in agreement with previous findings on multicellular organisms and supports the idea that everything is everywhere and the environment selects where species occur (Finlay *et al.*, 2002). Larger populations of small organisms with high dispersal

capabilities like algae show cosmopolitan distributions; however, habitats select better adapted species, for example, attached diatoms in stream riffles whereas non-attached diatoms are more successful in slow flowing freshwater habitats (Heino and Soininen, 2006). In the context of the Okavango Delta, spatial, temporal and physicochemical variations can be grouped in a framework whereby the algal populations, assemblages observed are determined by: the location in terms of both region of the Delta and type of habitat, e.g. deep lagoon vs shallow floodplain; the time of the year when algae were collected; limnological conditions, for example temperature and inorganic / organic content.

1.6. THEORETICAL FRAMEWORK FOR THE THESIS

The communities of higher plants and animals crucially depend on primary producers like algae and bacteria for energy and matter transfers, thus it is of utmost importance to investigate the algal assemblages at the base of the Delta's food webs. Several hundred species of algae are deemed to exist in the Delta (Ramberg *et al.*, 2006); Cholnoky (1966) observed a total of 327 species of diatoms in the Okavango River Basin with just a few sampling sites in the Delta. Cronberg *et al.* (1996b) found some 198 algal species, of which 50 were common in rivers, floodplains and isolated pools (Cronberg *et al.*, 1996a). Mackay et al. (2012) described 164 species (and 3 varieties) of periphytic diatoms following a sampling campaign which also yielded algal samples from open water habitats, used in this study (see Chapter 3). However, these studies either addressed specific groups of algae such as diatoms (Cholnoky, 1966a; Mackay *et al.*, 2012) and/or sampled areas beyond the Okavango Delta wetland, i.e. upstream sites in Botswana and Namibia (Cholnoky, 1966a; see section 4.1) or only the Boro region (Cronberg *et al.*, 1996a). This present study provides the first comprehensive estimates of the biomass and biodiversity of all algal groups in the Delta and interpretations of their distribution patterns in relation to limnology and other environmental factors (see Chapters 4, 5 and 6); it fills an important gap in the knowledge of biodiversity in this wetland of global importance.

The assemblages of algae in water analysed in this study are likely to be composed of mixed planktonic, benthic and periphytic species, especially in more shallow waters, e.g. floodplains. For example, in shallow lakes and wetlands it is common to

find abundant true planktonic algae in the epiphyton due to mixing processes and resuspension of sediments (Schallenberg and Burns 2004). In order to interpret the results of this study several theories are used, namely the Intermediate Disturbance Hypothesis (IDH - Grime, 1973; Connell, 1978; Reynolds *et al.*, 1993), Resource Competition Theory (RCT; Tilman, 1982; Tilman, 2004), Habitat Heterogeneity Hypothesis (HHH; MacArthur and MacArthur, 1961; Ricklefs, 1977; Tilman and Pacala, 1993), and the Species-Energy Theory (SET; Wright, 1983; Stevens and Carson, 2002). These are discussed in the following sections.

1.6.1. Intermediate Disturbance Hypothesis (IDH)

The Intermediate Disturbance Hypothesis (IDH) was developed by Connell (1978) who proposed that frequent changes / disturbances are responsible for high levels of biodiversity of, e.g. plants and corals, because they prevent the competitive exclusion of species. The highest diversity is recorded where the disturbance level, e.g. floods, storm waves or predators, is intermediate in terms of frequency, time lapse and magnitude; whereas at both ends of the spectrum, communities have low diversity (Connell, 1978) (Figure 1.7).

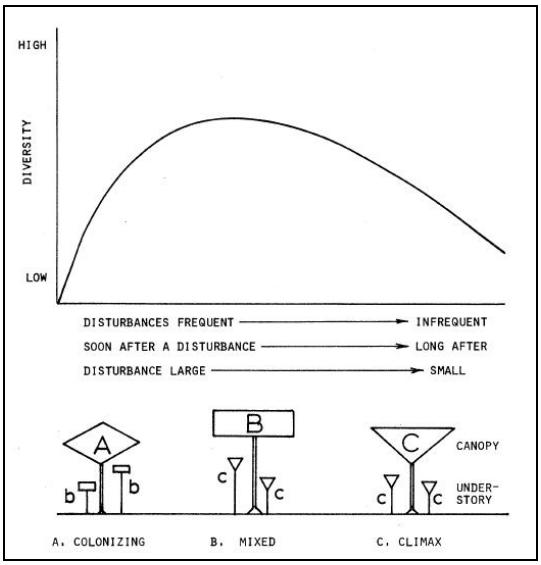


Figure 1.7. Schematic representation of the Intermediate Disturbance Hypothesis (source: Connell, 1978).

As Grime (1973) had already observed in grassland communities, rapid colonists (R-strategists) with high immigration rates are able to withstand high degrees of disturbance, as they are well adapted to frequent changes; on the other hand the best

competing species (C-strategists) with lower immigration rates are best adapted to low or no degree of disturbance (Biggs and Smith, 2002; see also section 1.2.2).

Reynolds *et al.* (1993) discussed the strengths and weaknesses of the IDH for research on phytoplankton. They defined disturbances as:

> "*Primarily non-biotic, stochastic events that result in distinct and abrupt changes in the composition and which interfere with internally-driven progress towards self-organization and ecological equilibrium; such events are understood to operate through the medium of (e.g.) weather and at the frequency scale of algal generation times*".

Various scholars have studied experimentally how algal diversity is influenced by flooding patterns in both freshwater (e.g. Reynolds *et al.*, 1993) and marine assemblages (e.g. Sommer, 1995). A total of 12-16 algal generations, i.e. periods of 35-60 days should allow undisturbed successions to approach competitive exclusion and ecological equilibrium in pelagic successions (Reynolds *et al.*, 1993). Reynolds *et al.* (1993) tested the effects of infrequent (2-8 times per year), more frequent (8-50 times per year) and high-frequency disturbances (50-365 times per year). They concluded that phytoplankton diversity increases with fast replacement rates (e.g. in warm waters with small sized algae) and declines in advanced successions and strongly selective environments, such as highly flushed or very oligotrophic systems (Reynolds *et al.*, 1993). However, in a natural river-floodplain ecosystem, an annual flooding is a predictable event (Junk *et al.*, 1989; Bayley, 1995; Junk and Wantzen, 2004).

The alternation of wet and dry years can lead to very different algal species richness. For example, in the semi-arid wetland Tablas de Daimiel National Park in central Spain (Àlvarez and Cobelas, 2003) observed highest algal species richness induced by hydrological perturbation. This wetland's hydrology leads to local spatial heterogeneity which enhances plankton species richness in the floodplain as compared to isolated water bodies, as hydrological connectivity enables dispersal (Rojo and Rodrigo, 2010 in Rojo *et al.*, 2012). In dry years species richness was higher than in wet years, unless droughts were severe, in which case species richness was reduced (Rojo *et al.*, 2012).

Hydrological connectivity and conditions have been shown to significantly influence the structure and productivity of planktonic communities in floodplain

lakes (Tockner *et al.*, 1999; de Melo and Huszar, 2000; Paidere *et al.*, 2007). Regular floods do not represent sudden disturbances and the seasonal development of phytoplankton under natural hydrological conditions, e.g. in the Central Amazon, is a progressive phenomenon (Huszar and Reynolds, 1997) analogous to gradual climate change, or in general, environmental changes happening at a longer time scale than algal generation times (Wilson, 1994). Given the short generation times of algae, periods of several months in plankton succession are analogous to decades in successions in grasslands and centuries in forests (Padisák, 1994). Rivers are highly kinetic and open systems in which fixed habitat structures are difficult to form; however, organisms such as algae are tolerant of these changing conditions hence perceiving them as uniform and undisturbed (Reynolds *et al.*, 1993). Indeed, even regular floods can be considered as a disturbance, e.g., in floodplain lakes of large European rivers that are temporally isolated, e.g. braided floodplains (Tocker *et al.*, 2000) and rivers with human impacts on flooding patterns (Roozen, 2005).

Many ecologists still refer to or use the IDH, however a recent paper by Fox (2012) suggests that this hypothesis should be abandoned because its arguments are logically flawed and empirical studies only seldom yield hump-shaped diversity curves like the one shown in Figure 2.12. In his seminal paper "*A general hypothesis on species diversity*" Huston (1979) described Connell's IDH as 'simply population reductions which prevent competitive equilibrium' and Sheil and Burslem (2013) consider the IDH as "*one potential explanation when unimodal patterns are observed*". This interpretation has been embraced by numerous scholars. The hump-shaped relationship is the predominant trend observed in plants, but linear positive relationships are most common amongst animal species (Groner and Novoplansky, 2003). Overall, <60% of empirical studies do not support the IDH, thus careful evaluations and accurate sampling of low and high levels of disturbance are required (Sheil and Burslem, 2013).

The discussion over the validity of the IDH and related developments and theories goes beyond the scope of this research, but this important hypothesis can be used to evaluate and interpret patterns in the Okavango Delta's algal assemblages. What is most important for this study is that the IDH can be qualitatively used as a reference point for the interpretation of taxon richness and observed diversity patterns. The extensive sampling of the complex landscape of the Delta allows for comparisons of riverine, lotic and floodplain environments, covering very different limnological conditions. Despite the fact that flood disturbance was not monitored at comparable

temporal resolutions as other works on wetlands (e.g. Paidere *et al.*, 2007), permanently, seasonally and occasionally flooded sites are very different environments with different flooding frequency for hundreds, if not thousands, of years (Wolski *et al.*, 2006).

In the Okavango Delta the frequency of flooding disturbance is once a year with a large flood pulse when rainfall reaches the region from the Angolan highlands; in addition to that local flooding due to rainfall events may take place (Wolski and Murray-Hudson, 2006). Therefore, in this study disturbance is interpreted mostly as long-term flooding frequency and duration, permanently flooded (PF) sites, seasonally flooded (SF) and occasionally flooded (OF) sites (see sections 3.1 and 5.3.1), assuming that environments such as floodplains in the lower Delta have, througout long timeframes, developed different algal assemblages than the Panhandle regions due to the effects of the flood pulse. Hence in this study the IDH is used in agreement with Reynolds *et al.* (1993): "*in spite of unresolved weaknesses, the concept of intermediate disturbance remains too useful in its potential to reject*". In particular, even though the Okavango Delta flooding patterns are in the domain of infrequent inundation events not representing a disturbance at algal generation time scale, the IDH is broadly tested to assess whether the long-term flooding frequency regimes in this wetland influence algal biodiversity and how (see Chapters 4 and 5).

1.6.2. Resource Competition Theory (RCT)

According to Hardin's competitive exclusion principle "*Competitors cannot coexist*", that is to say, out of two species occupying precisely the same ecological niche (i.e. the function performed by the species in the community of which it is a member; Elton, 1927) the one reproducing faster will outcompete the other (Hardin, 1960). All organisms compete for resources such as nutrients, light and habitat with other organisms of the same species (intraspecific competition) or of different species (interspecific competition); these resources may become limiting when their availability is not sufficient for organisms living in a specific environment (RCT; Tilman, 1982). The RCT predicts that a higher Number of Limiting Resources (NLR) has been shown to provide more opportunities for competitive trade-offs (Harpole and Tilman, 2007) and hence to increase species diversity (Tilman, 1982;

Interlandi and Kihlman, 2001; Grover and Chrzanowski, 2004). However, most studies supporting this pattern were on two-dimensional assemblages, e.g. grasslands and phytoplankton, where species have independent access to resources (Passy, 2008). In 3D-assemblages such as benthic algal assemblages, coexistence of species is promoted by tolerance to lower resource levels (McCormick and Stevenson, 1991), with understorey and overstorey species being able to coexist only if sufficiently abundant nutrients are available in the environment (Figure 1.8) (Passy, 2008).

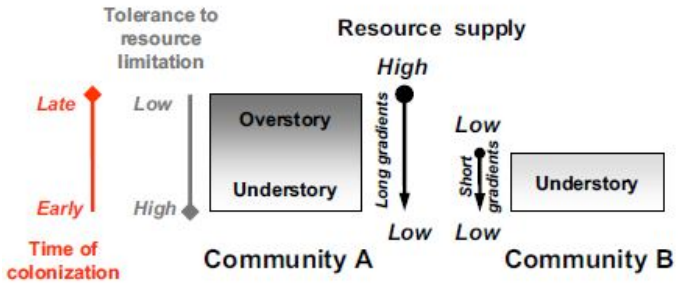


Figure 1.8. Conceptual model of the interaction between resource supply and biofilm composition in two hypothetical 3D assemblages growing on inert substrates under high (community A) and low (community B) resource supply (source: Passy, 2008).

Tilman's RCT (Tilman, 1982) has been mostly used as a heuristic basis for developing new conceptual models, as only 42 well designed tests were made since its publication (Miller *et al.*, 2005). Here RCT is also used as a conceptual reference point, as the quantification of specific limiting nutrient levels for algal taxa is beyond the scope of this study. One of the general paradigms in ecology is that areas that contain more microsite types or a wider spectrum of resource conditions should contain more species as more niche space is available (Lundholm, 2009).

However, neutral coexistence models of biodiversity attribute species richness to the size of the regional species pool; stochastic immigration and mortality, rather than niche differentiation, maintain species diversity (Hubbell, 2001). For example, regional species richness has been shown to influence local species pools and richness (Passy 2009) and Ricklefs (2004) suggested new research directions to account for the important relationships between local and regional species pools stating that "*What ecologists have called communities in the past should be thought of as point estimates of overlapping regional species distributions*". Tilman himself elaborated a new theory, the Stochastic Niche Theory (SNT) which resolves some

problems associated with neutral models not fitting observations of high correlations between species abundance and environmental conditions as well as using a more realistic model of resource partitioning (Tilman, 2004) than the widely used classic broken-stick model (MacArthur, 1957).

This study is a heuristic investigation which proposes plausible ecological interpretations of the results of our extensive survey on the biodiversity and biomass of algae living in the Okavango Delta; the theories outlined in this section are employed in Chapters 4, 5 and 6 to achieve this goal.

1.6.3. Species-Energy Theory (SET)

Habitat heterogeneity increases with larger areas and hence MacArthur and Wilson (1967) theorised that species diversity increased with island area and species immigration rates on islands or, more in general, habitat patches. The Species Area Relationship - SAR; $S=cA^z$, with S=number of species, A=area, c=a constant which depends on the unit used for area measurement, and z=the slope of the species area relationship in log-log space - entails a ß diversity component. The slope of the linearised SAR is an effective measure of ß diversity or the degree of compositional changes in microbial assemblages (Azovsky, 2002; Smith *et al.*, 2005), as well as macroorganisms, in a wide range of environments (Drakare *et al.*, 2006). Mechanisms generating SAR at large scales include dispersal, speciation, and extinction whereas at local scales disturbance, competition, and herbivory are important (Passy and Blanchet, 2007); also, dispersal mediated by disturbance determines ß-diversity (Matthiessen and Hillebrand, 2006). The species-area theory (MacArthur and Wilson, 1967) was elaborated further to include differences in the physical environment such as climate whereby the available energy in an ecosystem (directly proportional to its area) measures the total amount of available resource production, and provides better information on the variety of resource types present than area alone (Species-Energy Theory; Wright, 1983). Analysis of data on angisperms on land and freshwater birds on islands at different latitudes showed that 70–80% of variation in species number was explained by species-energy theory (Wright, 1983). Furthermore, experiments on plants which isolated the covariant nutrient distribution heterogeneity and average supply components, showed that mean resource levels or other correlates of productivity or ‘available energy’ were

better predictors of species richness patterns than resource heterogeneity (Stevens and Carson, 2002). Hence the importance of nutrient gradients at different spatial scales in terms of contributing to taxon richness and diversity patterns. In this study, habitat heterogeneity and nutrient gradients are dealt with as interconnected and also related to the annual flood pulse in the study region (see section 2.14). SET focusses on how the total availability of all limiting resources influence richness by reducing rates of stochastic extinction, while the emerging field of Biodiversity and Ecosystem Functioning (BEF) attributes a key role to the number of species in controlling how resources are taken up by competing taxa and transformed into biomass (Cardinale *et al.*, 2009b). This is highly relevant when looking at diversity-productivity relationships (see sections 5.1.4 and 5.2.6).

1.6.4. Habitat Heterogeneity Hypothesis (HHH)

Diversity of algae at a large scale can be linked to the size of the areas of investigation, e.g. larger areas of the same habitat will host more species. Habitat heterogeneity, which increases with area, has been identified as one of the major mechanisms generating both α-diversity, as per the Habitat Heterogeneity Hypothesis (HHH; MacArthur and MacArthur, 1961; Ricklefs, 1977; Tilman and Pacala, 1993), and ß-diversity (Connor and McCoy, 1979). More ecological space is available to species in areas supporting a greater range of microsite types or resource conditions (Lundholm, 2009).

In this study, habitat heterogeneity was not measured directly, but the assumption that floodplains contain more microhabitats is made due to the availability of multiple substrata for benthic algae to attach. In shallow wetlands, the availability of substrata such as plant stems and sand / sediments for the attachment of benthic algae is likely important for the establishment of productive and diverse algal communities. Higher algal and total plant (algal plus macrophyte) biomass were observed in wetland mesocosms with a greater richness of macrophyte species (Engelhardt and Richie, 2001). The HHH is used as a broader theoretical reference point to explain biodiversity patterns in relation to habitat heterogeneity in conjunction with the IDH and SET and the RCT in relation to the diversity-biomass relationships.

Chapter 2 – Study region: the Okavango Delta

2.1. THE OKAVANGO RIVER BASIN

The Okavango River Basin, lying between 12-21 ºC southern latitude, spans 725,000 km^2 across four countries: Angola (200,000 km^2), Namibia (165,000 km^2), Botswana (340,000 km^2) and a minor part of Zimbabwe (20,000 km^2) (Pinheiro *et al.*, 2003). Most of the water flow derives from a 120,000 km^2 area in the Cuando Cubango Province of Angola. A total of 11 rivers drain the basin: Cubango (known as Kavango in Namibia and Okavango in Botswana), Cutato, Cuchi, Cuelei, Cuebe, Cueio, Cuatir, Luassingua, Longa, Cuiriri and Cuito. The Cuito contributes 31% of total basin runoff, the Cubango 23% (OKACOM, 2011). The Okavango River is 1,500 km long, the third largest in southern Africa (UNESCO, 2014). Zimbabwe contributes water to the Makgadikgadi Pans where the Boteti river ends in the Ntwetwe basin (Figure 2.1), but it is not a member of OKACOM - The Permanent Okavango River Basin Water Commission (Mbaiwa *et al.*, 2004). This was established in 1994 through the signature of the "OKACOM agreements" by Angola, Namibia and Botswana and it has an operational secretariat in Maun.

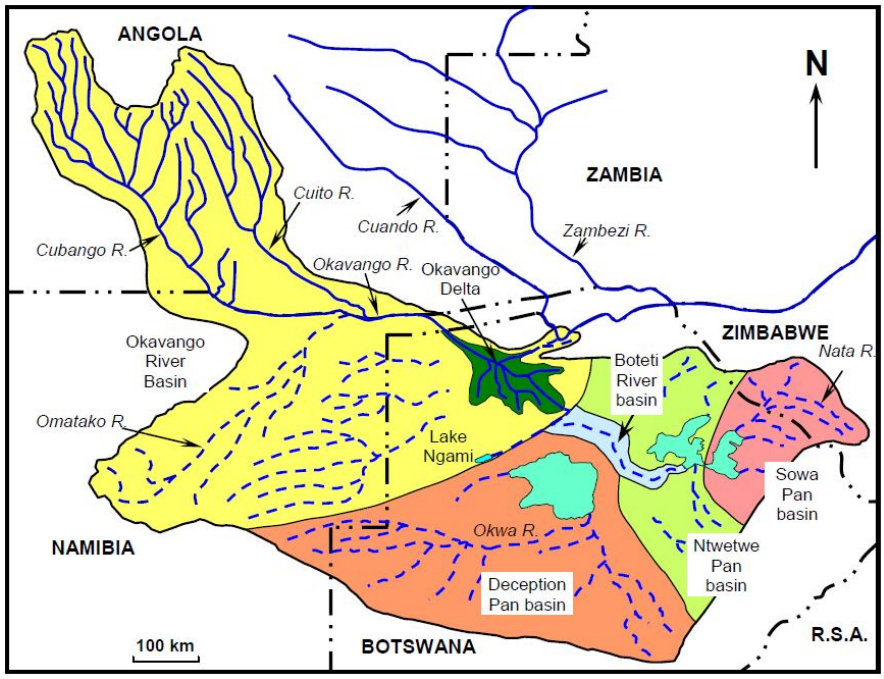


***Figure 2.1. Map of the Okavango River Basin** (source: Ashton and Neal, 2003; dotted line: ephemeral rivers; full line: rivers).*

The main objective of the Permanent Okavango River Basin Water Commission (OKACOM) is:

> "*to act as technical advisor to the Contracting Parties (the Governments of the three states) on matters relating to the conservation, development and utilisation of the resources of common interest to the Contracting Parties (basin member states)*".

The principles of equitable allocation, sustainable utilisation and environmental management and benefit sharing are sanctioned in the agreement (OKACOM Agreement, 1994). The Commission subsequently established three tasks force on Biodiversity, Hydrology, and Institutions and a Hydrological Data Sharing Protocol for the three countries (OKACOM, 2011).

2.1.1. Geography and climate

The Cubango-Okavango River Basin is formed by three catchment areas: i) the northern active catchment, in turn divided into the Cubango and Cuito sub catchments; ii) the Kavango-Okavango catchment, not contributing to surface runoff; iii) the Delta that collects the water generated by rainfalls in the Angolan highlands (Kgathi *et al.*, 2006). The Omatako River in Namibia (Figure 2.1) is

ephemeral and there is no other continuous water discharge to the Delta apart from the rivers starting in the Angolan uplands (Pinheiro *et al.*, 2003).

Kalahari sands and other sediments dating back to 65 to 2 million years ago underlie most of the Okavango River; old granite and gneiss quartz (2,500 - 1,800 million years) prevail in the Cubango highland catchment while younger coal shale and sandstone of the Karoo group (300 - 180 million years) are present in various areas of the basin including the southern Delta (OKACOM, 2011). Various savannah types occupy about 70% of the total land area in the river basin, with woodlands at 13% and marshes and swamps concentrated in the Delta only 0.5% (OKACOM, 2011).

The Southern Africa climate is semi-arid; 80% of the rainfall is concentrated in the summer months, from October to March (Tyson and Preston-Whyte, 2000). Annual temperatures in the Basin are on average 20 ºC, higher in its Southern part where the cloud cover is reduced (Mendelsohn and Obeid, 2004). Average daily temperatures are between 30 - 35 ºC from August to March in the Namibian and Botswana portions of the basin and 30 - 32 ºC in the Angolan part with minimum daily temperatures of 7 - 10 ºC and 3 - 8 ºC respectively (OKACOM, 2011).

In the Okavango River Basin rainfall reaches its highest levels in the North-West parts (1,300 mm yr^{-1}), it gradually decreases to an average of 500 to 600 mm yr^{-1} in the middle reaches and 469 mm yr^{-1} around Maun (Mitchell, 2013), the largest town to the South of the Delta (Mendelsohn *et al.*, 2010). In the Batswana part of the catchment mean rainfall is 400 mm yr^{-1} (Pinheiro *et al.*, 2003). The Inter-Tropical Convergence Zone (ITCZ) and the East African monsoon create a North-South and a West-East high to low rainfall gradient in the subcontinent (Kgathi *et al.*, 2006).

Climate projections

Given the lack of sufficiently long and coherent observational data across the River Basin, in particular in Angola, and the uncertainties and inherent variability of the climate system (e.g. due to the El Nino Southern Oscillation), climate modeling in this region is very challenging (Hughes *et al.*, 2010; Wolski *et al.*, 2012). However, regional simulations for the future account for a greater than global average warming on Southern Africa, a small increase in rainfall in the North of the basin and a small rainfall decrease in the South (Giorgi *et al.*, 2001). de Wit and

Stankiewicz (2006) estimated that a 10% decrease in precipitation in regions receiving 500 millimetres of rainfall per year, would entail a 50% lower surface drainage, with consequences for 25% of Africa by 2100. Most recently, Wolski *et al.* (2012) concluded that in the 21st century drier conditions will be more common in the Okavango Basin due to increasing temperatures enhancing evapotranspiration. However, multi-decadal oscillations may periodically offset or amplify the mean drying trend. According to climate simulations aimed to estimate the probability of occurrence of extreme flooding, the high flood events seen in the Delta in 2009-2011 are likely less frequent than they would have been in a climate without anthropogenic greenhouse gas emissions (Wolski *et al.*, 2014).

2.1.2. Socio-economic aspects

The population in the three basin countries is estimated in about 19.088 million in Angola, 2.156 million in Botswana and 2.198 million in Namibia (Central Intelligence Agency, 2014). The Gross Domestic Product (GDP) of Angola was over 52 billion US $, while Botswana and Namibia's are respectively 10.8 and 7.4 billion US $ (OKACOM, 2011). The total population of the Cubango-Okavango River Basin is estimated as 882,000 residents (57% in Angola, 25% in Namibia and 19% in Botswana) living in 195,000 households of which 62% are in rural areas. Projections suggest that in 2025 the basin population will be about 1.3 million with the largest increase concentrated in Angola (OKACOM, 2011).

The main economic activities are oil extraction (1st sector in Angola), mining (1st sector in Botswana - diamonds), tourism, government, commerce, banks and services. Agriculture is a significant activity in the Angolan uplands, while subsistence cropping and fishing prevail in Botswana and Namibia; the dominant crops are maize, manioc, millet and molapo and dry farming. Livestock numbers in the basin include about 940,000 cattle and 350,000 goats plus over 35,000 sheep, 70,000 donkeys and 25,000 pigs (OKACOM, 2011). The dependence of populations on the river / wetland portion of the basin varies considerably: whereas 19% Angolans and 32% Namibians rely on the Okavango River's resources, 45% of people living in Botswana depend on them, rather than on dryland resources (OKACOM, 2011). In particular, the inhabitants of the Okavango Delta crucially depend on the ecosystem services provided by the wetland (see section 2.2.6).

2.1.3. Threats

The Okavango River Basin faces several threats such as changes to precipitation and evaporation linked to future climate variability and pressures on water quality and quantity as human population increases (Mendelsohn *et al.*, 2010). Potentially unsustainable development from land use change, dams, abstractions and tourism is a risk for downstream near pristine areas of the Delta. In addition, over 4 million people had to flee their homes in the last 27 years of civil war (1976-2002) in Angola (Ellery and McCarthy, 1994).

Demand for goods and services is growing on a per-capita basis therefore water use (mainly for irrigation and hydropower) and water pollution, overgrazing, overhunting and overfishing are risks together with land use changes and fires. At present about 16,000 ha of crop fields are irrigated in the basin and a total of 270,000 ha of land are proposed for irrigation schemes in Angola and a further 186,323 ha are projected for 2025 (OKACOM, 2011). Although currently only one hydroelectric power station is being rehabilitated for use in Angola, 10 plants are considered feasible by the Angolan government and three are in the design phase; in Namibia the Popa Falls Hydropower Scheme was shelved for operational constraints (OKACOM, 2011). Due to these water abstraction plans and to climate change scenarios (Milzow *et al.*, 2010), according to Siziba *et al.* (2013), fishing in the Delta is under severe threat due to upstream water abstraction and, with the Southern Delta temporary floodplains facing possible reduced inundation. Furthermore, eutrophication and contamination with wastewaters (e.g. from mining operations) threaten the Delta's ecosystem (Milzow *et al.*, 2009).

The conditions for agriculture are not favorable across the Okavango River Basin: rainfall is too variable and soil is not fertile; pasture is also a problematic activity. Commercial production is low because of the remoteness from markets and large towns in the Southern African region and the low population in the basin does not attract investments (Mendelsohn *et al.*, 2010). Consequently poverty levels are high in the fourteen ethnic groups, in particular the San people, also marginalized as a cultural identity (Kgathi *et al.*, 2006).

Predictable hydrological patterns have been found to be a major influence on food web dynamics in the wet-dry tropics; hence, if hydrological cycles become less reliable, ecological impacts on food webs will be very significant (Douglas *et al.*,

2005). Climate change is a major threat to the Okavango River Basin and the wider Okavango-Kwando-Zambezi catchment. In southern Africa, mean annual precipitation has decreased, variability increased, and warm phase ENSO events were more frequent between 1950 and 2000 than in previous decades; rainfall is set to decrease further and the frequency of dry years to increase across the Okavango-Kwando-Zambezi (OKZ) catchment, with consequences for internationally important natural parks and reserves (Gaughan *et al.*, 2012). Conservation areas are totally absent in Angola, one very small area is protected in Namibia while large parts of the Delta and surrounding areas are under conservation management under the Batswana authority, notably the Moremi Game Reserve. Consequently tourism is much more developed in Botswana than in the other countries (Mendelsohn *et al.*, 2010); across the basin hunting and photographic concessions and community managed areas are numerous (OKACOM, 2011).

2.1.4. Scenarios

In the Okavango River Basin there is a contrast between Angola's and Namibia's demands for water for agricultural, domestic and energy purposes and Botswana's need to protect it as an asset for its crucial touristic sector. Namibia currently abstracts 20 million m^3 of water annually from the Okavango river and the fifth phase of the Eastern National Water Carrier, the construction of the 250 km pipeline Grootfontein – Rundu, is the last one to be completed to import water to the arid interior of the country (Pinheiro *et al.*, 2003). The Angolan section of the Okavango Basin is yet to effectively recover its infrastructure after the civil war and even basic agricultural activities are extremely hazardous due to large numbers of landmines still in the soil (Mitchell, 2013). However water needs are increasing and development plans might have severe consequences on the neighbouring countries (Pinheiro *et al.*, 2003).

According to Wolski and Murray-Hudson (2005a), damming would reduce peak flows and increase low flows, particularly during wet years when the size of permanent floodplains is expected to increase while seasonally inundated floodplains would become smaller causing drylands to get larger. Nonetheless the combined result of water abstraction, deforestation and new dams upstream would ultimately cause more regular flooding (Wolski and Murray-Hudson, 2005a). The

construction of all potential hydropower reservoirs in the Okavango River Basin may severely disrupt the monthly mean flow distribution, although with large impacts predicted only during wet years (Andersson *et al.*, 2006).

Scenarios developed by Murray-Hudson *et al.* (2006) show that upstream water abstraction and climate change may cause the Delta to dry significantly and the current limited impacts from water abstraction might grow substantially in the future (Pinheiro *et al.*, 2003), but modelling uncertainty remains high (Hughes *et al.*, 2010). Population increase in the basin is likely to drive water and energy demand increases, in line with the trend in the whole Africa where currently 25 countries produce more than 50% of their energy by means of hydroelectric plants; these have impacts on sediment transport, nutrient cycles and animal migration routes (Junk, 2002). Hence hydropower stations in Namibia and Angola, either run-of-river or with reservoirs would cause severe impacts to the Delta's economy and ecosystem. Changes are likely to happen in terms of floodplain water depth, duration and frequency of inundation, mainly due to deforestation and damming, rather than upstream abstractions with short-term effect (Murray-Hudson *et al.*, 2006). This, combined with the predicted climatic changes, i.e. decreased rainfall and higher evapotranspiration due to higher temperatures, may cause a significant drying of the delta (Mitchell, 2013) and a contraction of its vegetated areas (Milzow *et al.*, 2010).

A comprehensive Transboundary Diagnostic Analysis (TDA) was completed in 2011 (OKACOM, 2011) collating and bringing forward previous work in the Environmental Protection and Sustainable Management of the Okavango River Basin (EPSMO) Project, implemented by the United Nations Development Programme (UNDP) and executed by the Food and Agriculture Organization (FAO). Botswana's contribution mainly built on the Okavango Delta Management Plan (ODMP) (Botswana Department of Environmental Affairs, 2008). Four emerging areas of concern were identified: variation and reduction of hydrological flow, changes in sediment dynamics, changes in water quality and changes in the abundance and distribution of biota. Four driving forces responsible for these changes were: population dynamics, land use change, poverty and climate change (OKACOM, 2011). The Integrated Flow Assessment conducted in the TDA framework produced scenarios of low, medium and high water use. The

overarching trends predicted are that dry seasons would start earlier and last longer while the flood/wet season extent and duration would change less; ecosystem health indicators would decrease, particularly in the Delta and in the high water use scenario (all ten Angolan hydropower plants in place) livelihoods, national income and ecosystem services would significantly decrease with Botswana being the most affected country (OKACOM, 2011).

Although inherent uncertainty in climatic, socio-economic and ecosystem modelling must be taken into account, the scenarios discussed highlight the need for up to date and complex information on the state and trends of biodiversity and ecosystem services in the Okavango River Basin. This would allow scientists to promptly detect changes that can affect natural resources and local populations depending on them. The most pressing problems at the institutional level are the fact that transboundary Environmental Impact Assessment / Strategic Impact Assessment (EIA/SEA) procedures are still in the process of being adopted by Angola, Namibia or Botswana and there are issues in terms of a lack of skills, fragmentation of responsibilities and poor enforcement (OKACOM, 2011).

2.2. THE OKAVANGO DELTA

The Okavango Delta is one of WWF's 200 key eco-regions (Zambezian Flooded Savannahs Ecoregion) and the world's second largest inland delta after the Niger inner delta. It is the core of the largest Ramsar - protected Wetland of International Importance in the world. The Okavango Delta System was registered to Ramsar in 1997 when Botswana acceded to the Convention; it comprises an area of 68,640 km^2 including Lake Ngami, parts of the Kwando and Linyanti river systems and the Makgadikgadi Pans (see Figure 2.1) (The Ramsar Convention on Wetlands, 2014). In 2014 the Delta was listed as a UNESCO World's Heritage Site, extending to 20,236 km^2 with a buffer zone of 22,866 km^2 (UNESCO, 2014). The Delta is composed of three main types of aquatic environments: permanent swamps in the Panhandle in the North (UPH and LPH), seasonal flooplains and areas with occasional flooding proceeding towards the Southeastern reaches in Xakanaka (XAK), Boro (BOR) and Santantadibe (SAN). Permanent swamps have been flooded every year since 2004, with flood amplitude varying from 10 cm to 300 cm; seasonal floodplains have been inundated for 6 to 12 months every year since 2004

with an amplitude of 50 to 100 cm; occasionally flooded areas have been flooded for 3-4 years or less (see Table 3.6) for a duration of 3 to 6 months and an amplitude of 10 to 50 cm (see Figure 3.1).

The Upper Panhandle (UPH) in the north is a flat valley constrained by geological faults, subject to constant fluvial input from the Okavango River. Downstream from the UPH the lower Panhandle (LPH) region, characterized by river meanders across the floodplain. South of the LPH, river channels become smaller towards South and East. The main distributary (Nqoba / Maunachira / Khwai) continues the eastbound flow of the Okavango River, with many large, flow-through lagoons such as Xakanaxa (XAK). The principal of several secondary distributaries is the Jao / Boro (BOR) river system, flowing west of Chief's Island. Lake Ngami is situated at the end of the Xudum distributary (see Figure 2.3), and in recent decades it has been mainly dry, with floodwaters entering the lake in 2004, for the first time since 1998 (Mackay *et al.*, 2012).

2.2.1. Geology, topography and soil

The Okavango Delta is located at the centre of the Kalahari Basin (or Kalahari depression), a large arid / semiarid lowland area of 2.5 million km^2 covering most of Botswana and parts of Namibia, South Africa, Angola, Zambia, and Zimbabwe (Thomas and Shaw, 1991). The total surface of the Delta (dry and wet land) is 40,000 km^2 (Gumbricht *et al.*, 2005), its relief is of maximum 2 to 3 m (Gumbricht *et al.*, 2000). The mean surface gradient across the whole Delta is 0.00027, or 1 m : 3,700 m (McCarthy *et al.*, 2003); the gradient is much lower 0.00018 (1 m: 5,555 m) in the Panhandle and steeper, 0.00029 (1 m : 3,448 m) in the alluvial fan (Tooth and McCarthy, 2007). Sets of active faults cross the Okavango River Basin: in particular the Gumare fault separates the Panhandle from the alluvial fan and the Thamalakane and Kunyere faults stop the Delta's water from flowing south-eastwards. These faults were created an estimated 120 million years ago by tectonic movements of a South West extension of the East African Rift Valley which two million years ago "probably formed two sub-basins", where the Okavango Delta and the Makgadikadi Pans are located (Mendelsohn *et al.*, 2010).

A similar system to the present Delta probably developed only over the last 40,000 years (Junk *et al.*, 2006). Sediments deposited 65 million years ago are

superimposed onto complex bedrock, formed by fluvial, aeolian and volcanic rocks below which lie metamorphic rocks (Mendelsohn *et al.*, 2010). Future earthquake activities in the region might trigger the capture of the Okavango River, i.e. the diversion from its own bed, deemed to be "geologically imminent" (Gumbricht *et al.*, 2000).

The soils in the Delta are formed by silt, clay and fine sands and have accumulated organic matter and nutrients deposited by the periodic floods; these are the most fertile of the Okavango basin (OKACOM, 2011). In the permanent swamps, soil types are well-drained arenosols (sandy-textured soils) and organic histosols (low-density, acidic soils with a high proportion of organic material), while poorly drained fluvisols (typical in areas flooded periodically) and luvisols (with high nutrient content, and good drainage) characterize the seasonally flooded areas. Sand constitutes most of the river and channel bed material, but on riverine and island fringes, calcic luvisols and arenosols are formed (Sawula and Martins, 1991). The Okavango river transports three types of material to the Delta: fine sands transported as bedload (170,000 tonnes yr^{-1}); a suspended load of fine silt, clay and organic matter rich in nutrients; solutes (380,000 tonnes yr^{-1}) made of silica, calcium and magnesium carbonate, sodium and potassium bicarbonates (OKACOM, 2011).

2.2.2 Climate and hydrology

The mean annual temperature in the Okavango Delta is 26 °C. High evapotranspiration (on average 1,884 mm yr^{-1}; Mendehlson *et al.*, 2010) and low rainfall (c. 469 mm yr^{-1}; Mitchell, 2013) characterise this area. 95% of the annual rainfall in Botswana is concentrated between October and April (Wolski *et al.*, 2014). In the Delta only when local rainfall exceeds 700 mm yr^{-1} large areas get inundated; normally local water levels rise, but the predominant reason is the flood generated by rainfall in the basin (Wolski and Murray-Hudson, 2006).

The Okavango River meanders in the so called Panhandle, a flat valley, 15 km wide, bounded by a fault (Wolski and Murray Hudson, 2006) while the distal reaches form a broad and complex alluvial fan. The area covered by water in the Delta varies from 2,500 – 4,000 km^2 (6-10%) in February-March to its annual high

of 6,000 – 12,000 km^2 (15-30%) in August-September (McCarthy *et al.*, 2003) (see satellite images during sampling campaigns in Figure 2.2).

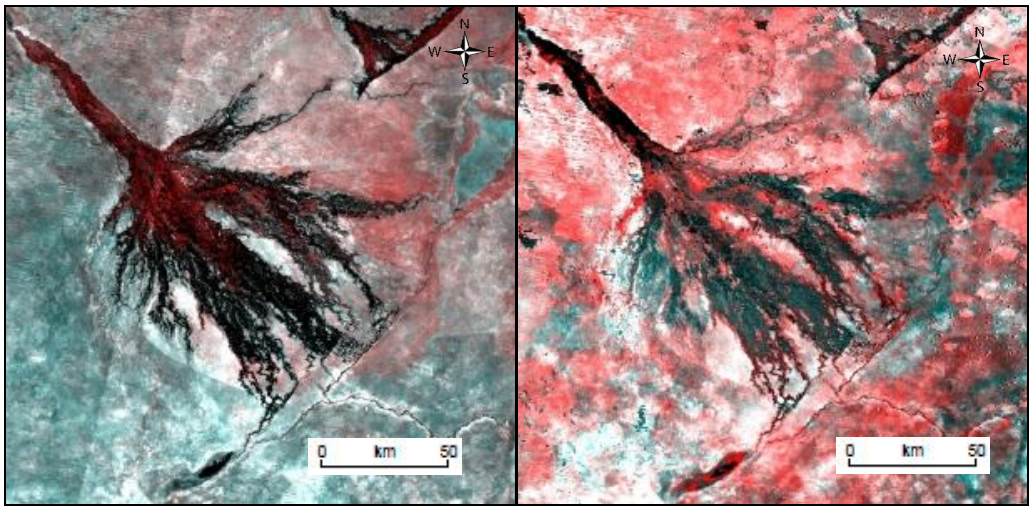


Figure 2.2. Map of the Okavango Delta at high flood (28th July 2009) and low flood (10th February 2010) (source: MODIS satellite images).

Thus, the Delta is maintained by the annual flooding of the Okavango River from precipitation that falls in the Angolan highlands, about 6 months earlier, on average 9 billion m^3 yr^{-1}, and by local summer rainfalls, on average 6 billion m^3 yr^{-1} (McCarthy *et al.*, 2003). The annual inflow at Mohembo, at the start of the Panhandle, varies from 6.0 to 16.4 billion m^3 with these extreme levels of rainfall recorded respectively in 1996 and 1963 (Tooth and McCarthy, 2007). Almost all the water (98%) though is lost by evaporation (74%) and transpiration (24%) in the Delta region (Mendelsohn *et al.*, 2010). South of the Panhandle the river starts flooding sideways in the Lower Panhandle (LPH) region (Figure 2.3); permanent swamps occupy areas around the central Chief Island; seasonal swamps characterise more distal part along the Island and towards Xakanaxa (XAK) eastwards and the Xudum channel westwards; occasional swamps occupy areas between Chief Island and the Thamalakane river collecting the small outflow of the Delta, i.e. 1-2% of the inflow and rainfall constituting the annual water input (Ramberg and Wolski, 2008; Wolski and Murray-Hudson, 2006). Of the major arms of the Delta the most westerly (Thaoge) is dormant, while the central channel (Jao-Boro) has the most pronounced seasonal variation and the easterly channel (Maunachira-Kwai) has a rather constant extension (McCarthy *et al.*, 2003) (Figure 2.3).

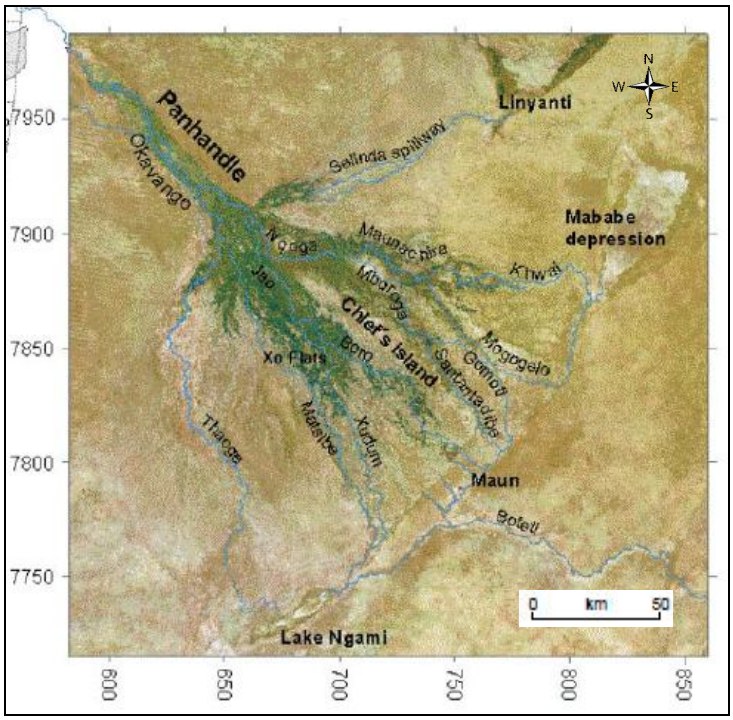


Figure 2.3. ***Map of the Okavango Delta channels*** ***(source: McCarthy et al., 2003).***

The Delta's flooded areas have shifted over the past 200 years, because of climatic changes and El Niño/Southern Oscillation (ENSO), sedimentation (sand accumulation), channel blockage by dead plants and avulsion (McCarthy *et al.*, 2003) as well as due to neotectonic activity developing new channels (Wolsky and Murray-Hudson, 2006). Historical trends in the Delta hydrology show seasonal, interannual and multidecadal variations (Figure 2.4).

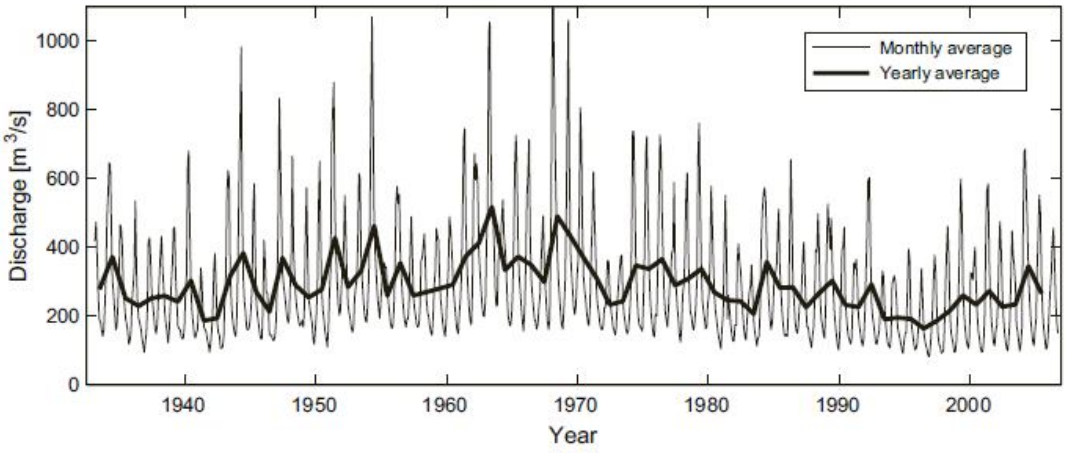


Figure 2.4. Monthly and annual average discharge measured at Mohembo, northern Panhandle ***(source: Milzow et al., 2009).***

In Mohembo, northern Panhandle, the flood typically lasts from January to May; in the Boro region it lasts between April and September, while further South near

Maun the flood is generally between June and September (see water discharge during the years when sampling was conducted - Figure 3.2).

2.2.3. Water chemistry and quality

The Delta maintains its freshwater and oligotrophic (low nutrients) character due to the fact that 94% of the solutes are retained in the landscape due to clastic sedimentation in the Panhandle region and chemical precipitation in the middle-lower reaches (Ramberg and Wolski, 2008 - but see Junk *et al.*, 2006 which define it a mesotrophic wetland). A total of 150,000 islands distributed across 13,500 km^2 have been formed by chemical precipitation whereby salts are removed from the shallow channels and floodplains and by termites building mounds which become islands (Ramberg and Wolski, 2008). This widespread phenomenon ultimately increases the salinity of the underlying groundwater where salts fall via density-driven flow; conductivity reaches extremely high maximum values of 10,000 to 30,000 μS cm^{-1} under islands in BOR (Bauer-Gottwein *et al.*, 2007) (Figure 2.5).

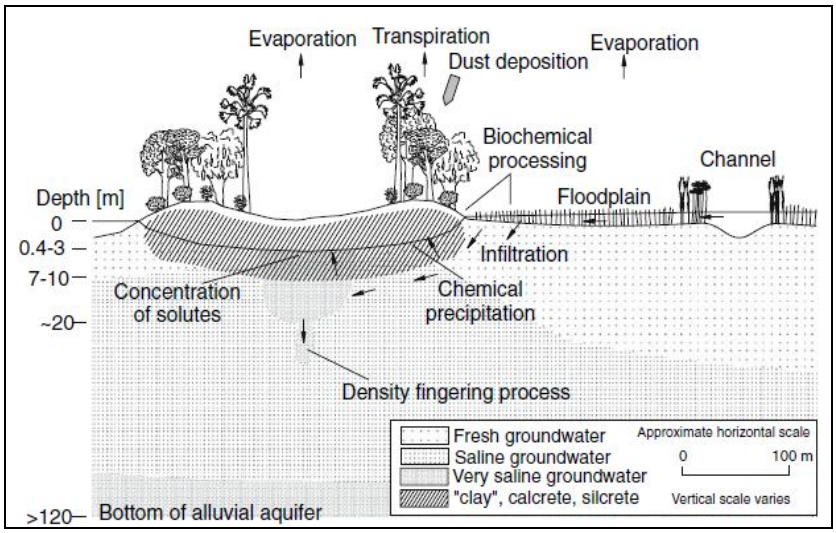


Figure 2.5. Main biogeochemical processes in water and islands in the Delta (source: Ramberg and Wolski, 2008).

According to Mladenov *et al.* (2008), Dissolved Organic Matter (DOM) accumulates in ground water as well, in particular beneath island centres. Carbonate and silicate systems selectively remove solutes in the swamps, islands, or floodplains, but not in the Boro River waters (Sawula and Martins, 1991). Islands occupy 5% of the total area of permanent swamps, while they cover 25% of the seasonal swamps and 50% in the occasional swamps (Gumbricht *et al.*, 2004).

This papyrus dominated wetland may be an important sink for silica as it accumulates large quantities of amorphous silica (ASi) (McCarthy *et al.*, 1989 in Struyf *et al.*, 2009). Many macrophytes such as *Cyperus papyrus* and *Phragmites australis* also absorb silica from the water to cope with various stresses such as attack by pathogens, drought and salinity (Schoelynck *et al.*, 2010). Akoko *et al.* (2013) assume that Dissolved Organic Carbon (DOC) respiration and/or photo-oxidation (Mladenov *et al.*, 2005; Cawley *et al.*, 2012) are occurring in the distributaries similarly to the Panhandle. The annual Okavango floodwaters accumulate clastic materials and phytolithic silica, together with fine-grained amorphous silica precipitated from groundwater induced by transpiration from aquatic grasses (McCarthy and Ellery, 1995 in Shaw and Nash, 1998). The flood-pulsed nature of the Okavango Delta means that carbon cycling is influenced by different levels of connectivity between the river channels and the floodplains; it depends more on local processes during the low water season and on river-floodplains exchanges in the high water season (Akoko *et al.*, 2013).

The Delta remains a freshwater body due to the process of salt removal / trapping under islands outlined above, described in detail by McCarthy *et al.* (1998), and Ramberg and Wolski (2008). Hence the water quality is usually good apart from some areas close to settlements such as Shakawe and Gumare in the Panhandle and along the Thamalakane river near Maun; touristic facilities (camps and lodges) also cause some localised pollution from solid wastes, waste waters (OKACOM, 2011). The monitoring system is not systematically in place in all locations and Botswana's government is still developing a Water Act on the basis of the Integrated Water Resources Management (IWRM) principles alongside a Water Resources Council with decision making powers in consultation with stakeholders (OKACOM, 2011).

2.2.4. Hydroecology

The Okavango Delta is an inland delta, a closed (endorheic) system, different from other large recharge wetlands such as the Everglades in Florida and the Pantanal in Brazil. Nevertheless, similar to the Pantanal the landscape is characterised by: "*shallow flooding with transparent water, little shading by trees and low salinity allow the growth of an extremely diverse aquatic and palustrine vegetation*" (Junk

et al., 2006). Freshwater swamps are treated as forested wetlands by Mitsch *et al.* (2000) so the Okavango Delta wetlands would be better defined as freshwater marshes that are characterized 'by graminoids such as *Typha* and *Phragmites*, the sedges *Cyperus* and *Carex* […] and floating plants such as *Nymphaea*'. The vegetation in this wetland is mainly formed by shrubs and grasses, while swamps are dominated by trees. The soil is high mineragenic in contrast with peatlands (bogs, fens, mires etc.) where it is organic. This is a relatively subtle terminology distinction and in many recent studies "freshwater swamp" is used when referring to the Okavango Delta. Swamp is more often used in the cited works on the Delta hence this term is used here, alongside the more specific floodplain.

In the Delta and other African wetlands, large C4 sedge papyrus is very abundant and 32 per cent of the inorganic fraction of the peat deposited in thick layers is composed of phytoliths, i.e. plant remains made of silica, especially in the Delta's Panhandle (McCarthy *et al.*, 1989). Abundant organic matter is retained by riparian vegetation, especially in the Panhandle; accumulation of peat in swamps is relevant across the whole Delta (McCarthy *et al.*, 1988). Swamp, floodplain and grassland plants have different preferred water depths, e.g. grasslands occupy shallower areas than permanent swamps and primary floodplains (Figure 2.6; Gumbricht *et al.*, 2005). Floodplains have a high primary productivity due to macrophytes, algae and bacteria and provide a shelter against predators; many fish species occur, particularly when the flood comes and expands (Lindholm *et al.*, 2007).

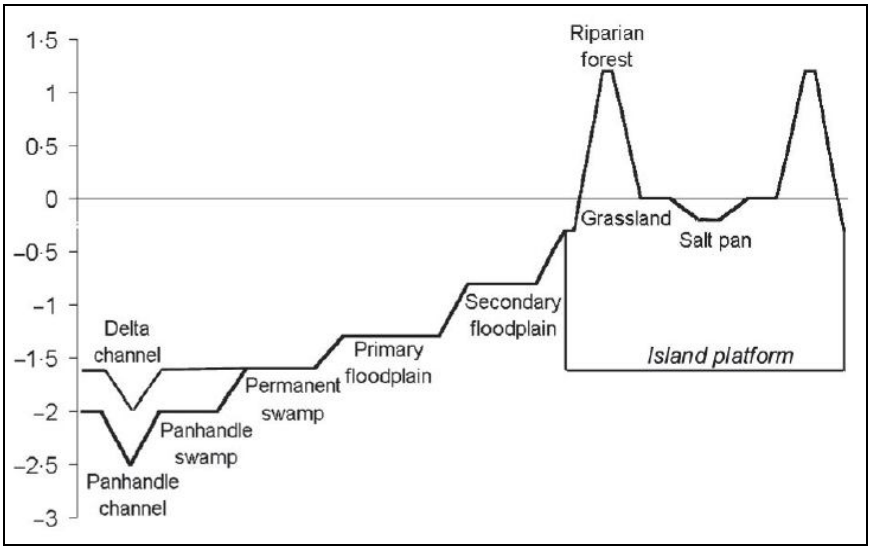


Figure 2.6. Diagram of the relationship between topography and vegetation classes in the Delta (*y axis: water level difference in meters; source: Gumbricht et al., 2005).

The Okavango Delta's annual flooding regime importantly contributes to the biodiversity and biomass of different organisms, which in turn influence water physicochemical conditions and in particular the distribution of micro- and macro-nutrients (Mackay *et al.*, 2011). Floodplains are crucial environments to assess the effect of the flooding regimes on biodiversity and ecological patterns. Krah *et al.* (2006) elaborated a conceptual model for a representative seasonal floodplain: the three major sources of ions and nutrients appear to be dust deposition (see also Garstang *et al.*, 1998), seasonal inflow and dissolution from the soil. They found that nitrogen and phosphorus had a local origin while chloride was mainly coming from long-range transport (Krah *et al.*, 2006). In the Delta, part of the nutrients dissolved from the soil come from dung left by elephants, buffalos, and antelopes that enrich the soil of organic matter up to a density of 500–700 kg dung per ha; decaying grasses and sedges release important amounts of nutrients as well (Lindholm *et al.*, 2007). As a consequence, Høberg *et al.* (2002) observed very high levels of primary productivity and zooplankton biomass at the onset of the flooding in a seasonal floodplain and key area for fish spawning.

2.2.5. Biodiversity

The Okavango Delta hosts a high biodiversity of organisms, habitats and landscapes due to the ever changing flood regimes shaping land and water environments; this diversity is comparable with that of other major subtropical wetlands, e.g. Pantanal in Brazil and Kakadu in Australia (Junk *et al.*, 2006). ß diversity, i.e. species turnover across different habitats and the number of species (α diversity) are high, while endemic species are relatively few due the Delta and the Zambezi system having been geographically well connected for long periods in the past 700,000 years (Ringrose *et al.*, 2005), particularly during wet climate phases (Ramberg *et al.*, 2006). In the Delta, 444 species of birds, 122 mammals, 71 fish species, 64 reptiles and 33 amphibians have been recorded (Mendelsohn *et al.*, 2010).

In wetlands diverse macrophyte assemblages sustain a higher periphytic algal biomass, which in turn contributes to increased phosphorus retention (Engelhardt and Ritchie, 2001; Mitsch *et al.*, 2005). Often wetlands are dominated by a few species of macrophytes, e.g., *Typha latifolia*, *Phragmites australis*, *Vallisneria americana*, *Hydrilla verticillata* and *Myriophyllum spicatum* (Ervin and Wetzel,

2002). However, in the Delta there are 208 species of aquatic and semi-aquatic plants (147 emergent, 21 submerged and 29 floating species), 689 herbs and 181 woody plants (Ramberg *et al.*, 2006). Mantlana *et al.* (2008) investigated three areas representative of perennial swamps, seasonal floodplains and rain-fed grasslands. In the perennial swamps common species are *Cyperus papyrus* and *Phragmites australis*; *Miscanthus junceus, Typha latifolia*, and *Imperata cylindrica*. In the seasonal floodplain sedges like *Schoenoplectus coryombosus* and *Cyperus articulatus* are dominant; *Panicum repens* and *I. cylindrica* are also present; in rain-fed rarely inundated sites annual and perennial grasses are typical, mainly *Urochloa trichopus*, *Cynodon dactylon*, and *Eragrostis lehmanniana*. Finally, islands are characterized by trees like *Phoenix reclinata* and others belonging to the genera *Lonchocarpus* and *Acacia* (Mantlana *et al.*, 2008). Figure 2.7 shows different vegetation types in areas of the Delta visited during this study (see also Table 3.6).

a) Panhandle vegetation with Papyrus

b) Lagoon with Nymphaea

c) Floodplain with various sedges and grasses.

Figure 2.7. Different vegetation types in three sites: a) Okavango river in the Panhandle; b) lagoon in Boro and c) occasionally flooded floodplain in Santantadibe (pictures taken in a. March 2010; b,c. April 2009).

Abundant and diverse macrophytes, especially in the Delta's floodplains; for example, the submergent *Utricularia* species, represent important substrata for attachment of desmids (Coesel and van Geest, 2008). Our sampling involved walking in vegetated floodplains (see section 3.2), most likely disturbed these benthic habitats sufficiently for a significant number of benthic taxa to be collected; hence the focus on algae in water rather than just phytoplanton. Murray-Hudson *et al.* (2014a) classified floodplain vegetation species according to their distribution in sites with varying flooding frequency and duration range; for example, *Cyonodon dactylon* and *Eragrostis cylindrifora* are associated with occasionally flooded savanna environments (flooded 1-2 years of 18; 1-3 months mean duration); *Panicum repens* and *Cyperus sphaerospermus* with seasonally inundated grassland (flooded 5-11 years of 18; 2-8 months mean duration); and *Nymphaea nuchali, Eleocharis dulcis* and *Cyperus articulatus* in seasonally flooded sedgeland (flooded 12 of 18 years; 7-10 months mean duration). These seasonally flooded floodplains are most frequent in the distal reaches of the Okavango Delta; here more diverse plant communities exist, i.e. 519 species in the seasonal swamps and 205 species in the permanent swamps (Ramberg *et al.*, 2006). This is relevant for the patterns of algal biodiversity investigated here (see section 1.6.4).

The most common large mammals are Impalas (140,000), Buffalos (60,000) and Red Lechwes (60,000) and elephants (35,000) (Bonyongo *et al.*, 2004). Some of these contribute to the formation of channels (in particular hippopotami) and to nutrient cycling as many of these mammals defecate in floodplains and lagoons (Lindholm *et al.*, 2007). Most mammal species though are rather small and elusive, including 31 species of *Rodentia*, 28 *Carnivora*, 26 *Chyroptera* and 22 species of *Artiodactyla* (Ramberg *et al.*, 2006). Of the 86 fish species found in the Okavango basin, 71 are recorded below the Popa Rapids of the Namibian East Caprivi Strip; 42 of these species belong to the *Cyprinidae* and *Cychlidae* families (Ramberg *et al.*, 2006). A total of 112 species of birds are aquatic, 275 species are terrestrial and 57 of the non aquatic species live in floodplain forests or reed beds (Ramberg *et al.*, 2006). Nevertheless, the state of knowledge on invertebrates remains very poor, exceptions being *Odonata* (99 species), the Delta being a hotspot of biodiversity for dragonflies and damselflies (Mendelsohn *et al.*, 2010), *Lepidoptera* (124 species) and *Mollusca* (22 species) (Ramberg *et al.*, 2006).

2.2.6. Ecosystem services and socio-economic aspects

The Okavango Delta provides vital resources for the livelihoods of the 150,000 residents of the area, 7% of the total population in Botswana (Central Intelligence Agency, 2014), as well as a considerable source of national income through tourism (Mendelsohn *et al.*, 2010). Many important economic activities depend on the flood pulse in the Delta: subsistence agriculture needs floods, domestic water for Maun needs recharge in the Delta's Panhandle and (eco)tourism needs the Delta's landscapes and wildlife. Traditional knowledge plays an important role in the Okavango Delta's subsistence economy. For example dug-out canoes (Mokoro) were brought to the resident Banoka by Bayeyi and Hambukushu-speaking people from contemporary Zambia and since used to navigate the Delta (Madzwamuse and Fabricius 2004 in Fabricius *et al.*, 2007).

Botswana's economy relies substantially on commercially exploitable diamonds, discovered one year after the 1966 independence; this allowed the country to become an African economic success story (World Travel Tourism Council, 2007). After the extraction of diamonds, tourism is the second most important sector of Botswana's economy which has recently been allowed to an extent in the Delta itself, with about 40 diamond mining licenses granted to several companies (Okavango Research Institute, 2014). 17% of Botswana's land-locked surface area is occupied by national parks and game reserves, and 22% by wildlife management areas (World Travel and Tourism Council, 2007). In 2006 this sector directly contributed about 8% of the country's Gross Domestic Product (GDP) and 10% in terms of employment (World Travel and Tourism Council, 2007). While in 1994 Botswana was visited by 620,000 people, in 2008 the number of tourists increased to *c.* 1.8 million (Botswana Department of Tourism, 2010) with an even higher peak a few years earlier, 1.9 million in 2005 (Mbaiwa, 2009). 80 hotels, camps and lodges with over 1,600 beds provide accommodation to this increasing number of tourists within the Okavango Delta Ramsar Site (OKACOM, 2011); between 2001 and 2005 11.5% of the tourists staying in Botswana visited Maun and the Delta (World Travel and Tourism Council, 2007).

The Delta is an important tourist attraction with its high revenue-low number of visitors formula (on average 120,000 tourists per year) chosen by the government of Botswana, i.e. expensive trips and stays in lodges across the wetland (Harry

Oppenheimer Okavango Research Centre, 2009). 95% of all 2006 national park entries were into the Okavango Delta and the Chobe National Park (World Travel and Tourism Council, 2007). This sector is very profitable for many foreign investors; 85% of the tourism-related companies operational in the Okavango region have direct foreign involvement (Mbaiwa, 2003), but only 10% of the households in the area of Ngamiland benefit directly from it (Arntzen *et al.*, 2005; Murray, 2005) so that relatively minor sums remain in the country to support workers' livelihoods. Interviews with local people in Ngamiland Mbaiwa (1999) revealed that "*there is a general assumption that the delta has been taken from them by government and given to foreign tour operators*". The tourism industry creates thousands of jobs in the Delta, but has some negative environmental impacts, e.g. poor waste management and noise pollution (Mbaiwa, 2003). Turpie *et al.* (2006) estimated that 81% of tourism value accrues to photographic tourism companies, 16% to hunting safari companies, and 4% goes to communities through CBNRM arrangements. Between 1995 and 2002 the average number of visitors to the Moremi Game Reserve, the largest conservation area in the Delta, was about 39,000 generating an income of 8.1 million Pulas, i.e. about 0.9 million $ (Murray, 2005). These telling statistics on the growing tourism industry suggest that the challenge of conciling economic development and sustainability is far from easy for Botswana's authorities. The international airport in Maun is being expanded because of the high attractiveness of the area for tourists, potentially increasing the impacts of more tourists in the Delta (Mbaiwa, 2009). However, policies that have been set out to foster the sector development in sustainable ways include the Tourism Master Plan (2000), the Ecotourism Strategy (2001) and the Community Based Natural Resources Management (CBNMR) policy (2007) (OKACOM, 2011).

Agriculture is mainly of a subsistence nature, with long-term grain yields of 142 kg ha^{-1}; droughts and the shift of flooding patterns from West to East forced farmers in Gumare (in the Panhandle region) and other villages to shift from rainfed to dryland cultivations (Murray, 2005). The surface of rainfed and floodplain cultivation is 8,000-10,000 ha; livestock is represented by over 625,000 cattle and 243,000 goats. The 2002 Botswana National Master Plan for Arable Agriculture and Dairy Development aims to enhance production and commercialization of agricultural outputs (OKACOM, 2011). In the Delta there is also considerable gathering of

medicinal plants and craft production (baskets, veld products etc.); whereas hunting was banned by the national government in late 2012 (National Geographic, 2012), but was a significant source of income for the tourism sector until this time. Fishing is mainly a subsistence activity, but it provides an essential source of animal protein; gill nets and hooks are used in deep waters while barrage traps and fishing baskets are more appropriate for shallow waters, particularly when the flood arrives or recedes (Mmopelwa *et al.*, 2009). Despite subsistence fishing being rather common, the lack of safe accessibility to many sites, due to the risk of hippopotamus attacks, limit catches. Therefore fish stock is very low in the Okavango Delta, the total yield of the fishery being 0.4 kg per Lundgren gillnet set compared with other freshwater environments in Africa (1.4 – 4.2 kg per fishing set) (Mosepele, 2000). In the Delta, local populations preferentially fish cichlids whose adults subtantially feed on algae (Mosepele, 2000); hence the crucial importance of algae as base of its food webs.

Other activities include grass and reed collection, e.g. for thatching, palm collection and beer brewing (Murray, 2005) and increasing portions of households' incomes derive from remittances (Mendelsohn *et al.*, 2010). Overall the dependence of people's livelihoods on ecosystem services in the Delta is high. An assessment of the direct economic use value in the Okavango Delta Ramsar site shows that the tourism sector accounts for 90%, agriculture for 7% and natural resource use (including fishing) for 3% (Turpie *et al.*, 2006). Commercial fishing is only practiced in the Panhandle with 65% of catches being bream and 28% catfish in 2004/2005 (FAO/ADB Cooperative Programme, 2007); in this region (northern Ngamiland) 65% of residents depend on fishing (OKACOM, 2011).

Local businesses and more equitable foreign / Batswana partnerships are present and represent an important way forward in improving people's lives in a country still facing large disparities despite Botswana's middle income status (based on average income, not considering resources distribution). Indigenous people actively participate in tourist activities, for example poling in mokoro canoes, taking tourists on game walks or cooking traditional food for them (Cassidy *et al.*, 2011). Policies and laws for land management stem from, among other sources, the National Strategy and Action Plan to Combat Desertification under the UNCCD (United Nations Convention to Combat Desertification) and the Okavango Delta

Management Plan (ODMP). Local communities and their authorities have an important role in allocating land (OKACOM, 2011).

Current specific threats facing the Delta (see section 2.1.3 for the basin-wide threats) are water abstraction, channelling of water inside the delta, aerial spraying of insecticides against tsetse flies while future ones include hydrological changes by reservoir construction and increased and intensified agriculture in the basin (Junk *et al.*, 2006). In order to tackle these threats the Okavango Delta Management Plan was coordinated by the National Conservation Strategy Agency to provide an integrated resource programme harmonizing sustainability and people well-being (Pinheiro *et al.*, 2003) and progress is being made towards full cooperation between Angola, Botswana and Namibia on the management of their natural resources (OKACOM, 2011). Conservation is a key issue for the Delta, its economy and future. Relevant legislation regarding the protection of the Delta's and the whole country's biodiversity in Botswana are the Wildlife Conservation and National Parks Act (1992) and the National Policy on Natural Resources Conservation and Development (1990) supported by the Botswana National Biodiversity Strategy and Action Plan (NBSAP) under the UN Convention on Biological Diversity (OKACOM, 2011).

Microscopic primary producers such as algae crucially sustain the Okavango Delta's food webs (Figure 1.5) and its charismatic wildlife, e.g. large mammals and colourful birds, which are in turn very important for tourism, as well as bearing intrinsic and spiritual value. Therefore, investigating the biodiversity, biomass and distribution of these aquatic plants is indirectly relevant for cultural services as well as for provisioning, regulating and supporting services (Table 1.2) and for the conservation of this wetland.

2.3. AIM, RESEARCH QUESTIONS AND OBJECTIVES

Algae are widely used as indicators of environmental conditions to detect environmental stress in a variety of ecosystems both in contemporary ecology and palaeoecological research (Williamson *et al.*, 2008). Globally, amongst freshwater ecology studies, small organisms such as benthic algae require a special attention as they have been neglected in favour of larger organisms, especially fish and plants (Stendera *et al.*, 2012). Wetlands support biodiversity, water purification, flood

abatement, and carbon storage and provide other essential functions, such as regulation of rainwater runoff and drought, seed dispersal and nutrient cycling (Zedler and Kercher, 2005). In studies on tropical rivers in North Australia with largely natural flow regimes food webs were shown to depend strongly on algal production; moreover the seasonal hydrology strongly influences ecosystem processes and food web structure (Douglas *et al.*, 2005). However, investigating microorganisms in pristine freshwater ecosystems constitutes an important challenge; various threats may hamper the discovery of numerous species and the understanding of how the base of the food webs of key ecosystems works, i.e. in terms of biodiversity and ecosystem functioning. The Okavango Delta is a near-pristine aquatic ecosystem, suitable for investigating the basic determinants of diversity, as habitat complexity and environmental fluctuations can be minimised in such systems (Huston, 1979). In the arid and semi-arid Kalahari Desert, the Okavango Delta wetland crucially provides water and food for wildlife, particularly during the dry season, and for local people who rely on fisheries as a primary or complementary source of livelihood (Mosepele, 2000). Thus basic research on biodiversity and biomass patterns of such an ecosystem is fundamental for describing reference conditions for future studies in the Delta and in other subtropical wetlands, which are increasingly threatened by overexploitation and global warming among other drivers of change (Dudgeon *et al.*, 2006).

Previous research on algae in the Okavango Delta and other subtropical wetlands

Identifying which and many species of algae living in near-pristine wetlands such as the Okavango Delta is important to set baselines for future comparative research. Other studies found between 80 and 690 species of algae in subtropical wetlands, respectively in the Sundarban in India (Sen *et al.*, 1999 in Ghopal and Chauan, 2006) and Kakadu (Northern Australia; Finlayson *et al.*, 2006). South American wetlands such as floodplain lakes along the Paranà river (Nabout *et al.*, 2006) and Araguaia river (Nabout *et al.*, 2006; 2007) respectively host 292 and 577 algal species. Several hundred species of algae are thought to exist in the Okavango Delta (Ramberg *et al.*, 2006) and previous studies about 200 species of algae, mainly from the distal reaches of the Delta Cronberg (1996 a/b); 327 diatom species were observed in the wider Okavango region, including areas upstream of the Panhandle

(Cholnoky, 1966). Biodiversity and Ecosystem Functioning (BEF) research showed that biodiversity frequently has a positive influence on ecosystem services, e.g. nutrient cycling (Balvanera *et al.*, 2006); in particular, more diverse algal communities improve water purification by means of better nutrient uptake (Cardinale, 2011).

Environmental drivers / controls of algal distribution, abundance / biomass and diversity include water depth, nutrient concentrations, habitat availability and heterogeneity and top-down control such as grazing. Water depth has been shown to be an important factor in determining species richness or diversity of algae, e.g. in the Vaal River, South Africa (Pieterse and van Zyl, 1988) and in the Paranà river floodplains (García de Emiliani, 1997).

This study builds on previous research on diatoms (Mackay *et al.*, 2012). Since 2006 the UCL Environmental Change Research Centre (ECRC) have been collaborating with the University of Botswana (ORI - Okavango Research Institute, formerly Harry Oppenheimer Okavango Research Centre) to study the relationships between aquatic organisms (diatoms, zooplankton and macroinvertebrates) and their environment, water chemistry/quality and hydrological parameters. This Ph.D. specifically focuses on the extension of baseline aquatic biological data provided by the Darwin Initiative project on periphytic diatoms (Mackay *et al.*, 2009); hence it fulfils the request for new ecological knowledge formulated in the Okavango Delta Management Plan (ODMP) Research Strategy (Botswana Department Environmental Affairs, 2008).

The main aim of this research is to further the knowledge and understanding of the occurrence and distribution of algae in the Okavango Delta as expressed in terms of biodiversity, biomass (estimated via biovolume) and relative abundance.

Four broad research questions are investigated:

1) What are the total species / genera richness and biomass of algae in the Okavango Delta?
2) How and why do biodiversity, biomass and relative abundance of algae vary in the Delta in relation to limnological variables, region, flooding frequency, habitat and seasonality?
3) Does species richness increase algal biomass in the Delta's floodplains?

4) How does the relative abundance of the most common individual algal taxa vary in relation to limnological conditions in the Delta?

The main objectives of this study are:

1. to assess taxon richness and diversity, estimate biomass, and describe distribution patterns of algae in water from five regions of the Okavango Delta with distinctive features (see section 3.1) in three seasons between September 2006 and July / August 2007 (Campaign 1);
2. to assess taxon richness and diversity and estimate biomass and describe distribution patterns of algae in water in eight floodplains in three habitats in four seasons between April 2009 and Febraury 2010 (Campaign 2);
3. to characterise the Delta's hydrology and limnological conditions on the basis of data collected in Campaign 1 and 2;
4. to analyse and interpret the relationships between: a) algal taxon richness, diversity, biomass and relative abundance and b) limnological variables, sampling region, season, flood class and habitat type.
5. to compare algal biodiversity, biomass and distribution patterns recorded in the Delta with those observed in other subtropical wetlands.

A secondary objective is to investigate the distribution of algal traits in the Okavango Delta in a descriptive / preliminary way in order to provide a baseline for further specific research (see section 4.8).

The experimental design was devised specifically to address the differences in diversity, biomass and distribution patterns across flooding, nutrient and habitat gradients. The research questions are answered by interpreting the results on the basis of the Intermediate Disturbance Hypothesis (IDH; Connell, 1978; Reynolds *et al.*, 1993), Habitat Heterogeneity Hypothesis (HHH; MacArthur and MacArthur, 1961; Hutchinson, 1961; Ricklefs, 1977; Tilman and Pacala, 1993) and Species-Energy Theory (SET; Wright, 1983; Stevens and Carson, 2002) (see sections 1.6.1 to 1.6.4). In particular, theory-derived expectations are that seasonally flooded sites / floodplain habitats are more diverse in algae than other areas due to the long-term intermediate flooding disturbance, habitat heterogeneity and mean nutrient concentrations. In turn, species richness is hypothesised to contribute to higher algal biomass in the shallow floodplains in BOR and SAN by means of niche differentiation / facilitation (Passy and Legendre, 2006a).

The main body of this thesis is structured to answer these questions and achieve the stated aim. In Chapter 3 the methods used to collect samples, enumerate and identify algae, those to measure limnological variables and for all data analyses are presented. Chapter 4 presents the results of exploratory analyses and systematic statistical tests to characterize both the Delta's algal assemblages and its limnology; comparisons of species lists in different studies in this wetland and upstream areas are also conducted. In Chapter 5 the assessment of algal biovolume (wet algal biomass) and of various measures of diversity is carried out; the species richness - algal biomass relationship is also invetsigated at different scales. In Chapter 6 the relationships between limnological variables / environmental factors and algal relative abundance (as well as overall species richness and biomass) are analysed.

Figure 2.8 illustrates how the main aim of the Thesis is achieved by analysing specific supporting data using different statistical techniques.

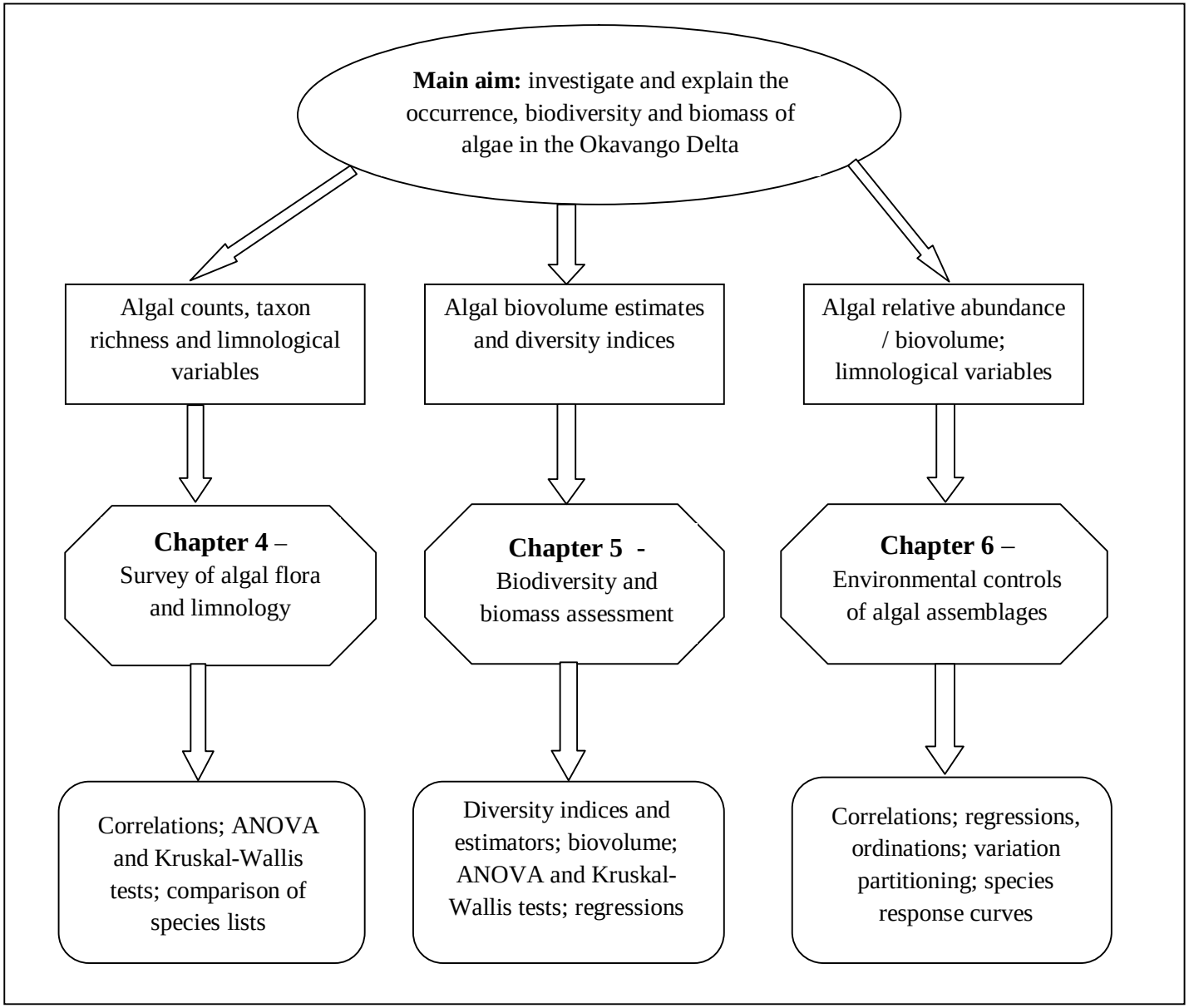


***Figure 2.8. Outline of the Thesis results chapters** (squares: main supporting data; octagons: chapter aim; smoothed octagons: analyses conducted).*

Chapter 3 – Study sites, field and laboratory methods

3.1. STUDY SITES AND SAMPLING CAMPAIGNS

The first aim of this chapter is to to detail the study sites visited in this Ph.D. during two campaigns, Campaign 1 (2006-2007) and Campaign 2 (2009-2010). The second aim is to describe in detail field and laboratory methods employed and the reasons they were chosen.

During Campaign 1 algal samples were collected from five regions - Upper Panhandle (UPH), Lower Panhandle (LPH), Xakanaxa (XAK), Boro (BOR) and Santantadibe (SAN) to provide a broad geographical characterisation of the distribution, biomass and diversity of algae across the Okavango Delta. These regions experience different flooding frequencies and durations; samples were collected in different habitats and in three seasons. Thus the aim of this extensive sampling was to provide a broad geographical representation of the algal assemblages in this wetland of global importance.

Campaign 2 sought to understand how the composition, biomass and diversity of algal assemblages varied in eight floodplains in the BOR and SAN regions and across habitat types in four seasons.

Figure 3.1 shows the map of the sampling points in Permanently (PF) - mainly in the Panhandle -, Seasonally (SF) and Occasionally Flooded (OF) areas - mostly in the distal reaches - in the five regions mentioned above, plus two other regions where two samples were taken in Campaign 1.

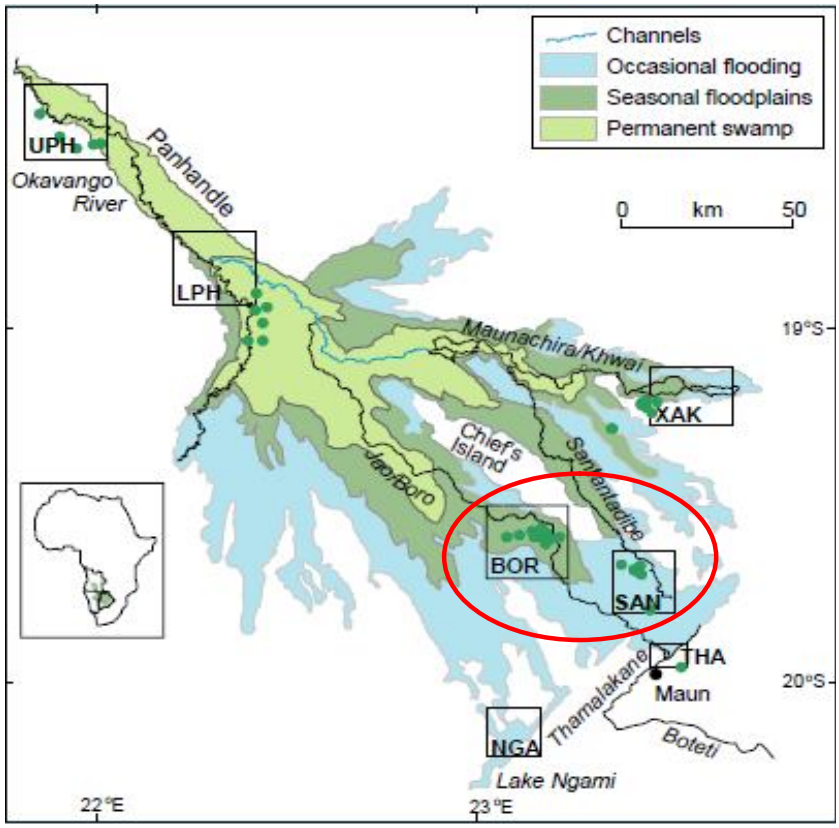


***Figure 3.1. Map of the sampling sites and regions in the Okavango Delta** (black boxes: Campaign 1; red box: Campaign 2; UPH= Upper Panhandle; LPH= Lower Panhandle; XAK= Xakanaxa; BOR= Boro; SAN= Santantadibe; NGA=Ngami; THA=Thamalakane).*

Sampling was undertaken over three 'flood years'; estimated average monthly discharges in the Okavango River at Mohembo (Northern Panhandle) were 394 m^3 s^{-1} in 2006-2007, 271 m^3 s^{-1} in 2007-2008 and 309 m^3 s^{-1} in 2009–2010 (Figure 3.2).

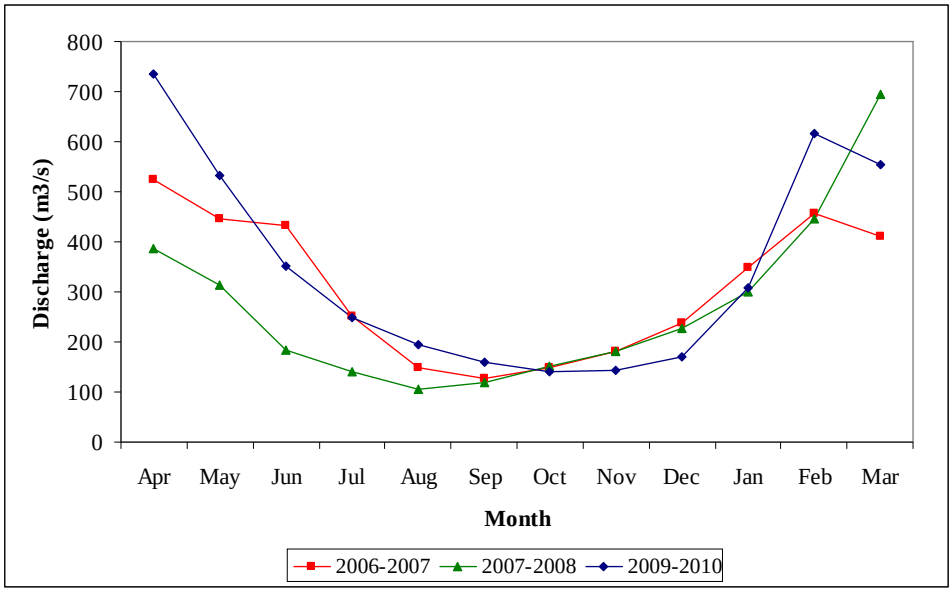


***Figure 3.2. Water discharge at Mohembo, Northern Panhandle, in the years of sampling** (source: Okavango Research Institute - http://168.167.30.198/ori/monitoring/water/).*

The first sampling campaign (Campaign 1) was conducted by Mackay *et al.* (2009; 2011; 2012) between September 2006 and August 2007 whereas Campaign 2 was run by myself, N. Siziba and ORI staff from April 2009 to February 2010. In Campaign 1, 93 algal samples were collected (Mackay *et al.*, 2009; 2011; 2012) whereas Campaign 2 yielded 69 samples (Figure 3.1 and Table 3.3). All sites were geo-referenced and accessed by boat, car and, in a few cases, by foot or by canoe. In order to account for variations in flooding frequency and duration, water temperatures, other physicochemical characteristics and seasonality, the Delta was visited during different seasons in 2006, 2007, 2009 and 2010. These two separate sampling campaigns were conducted across three flood cycles, named 'flood years' hereafter: 1) 2006-2007, i.e. April 2006 to March 2007; 2) 2007-2008, i.e. April 2007 to March 2008 and 3) 2009-2010, i.e. April 2009 to March 2010.

Campaign 1 (2006-2007):

Mackay *et al.* (2009; 2011; 2012) sampled water, periphytic diatoms and algae in water from 50 sites along an hydrological gradient from frequent to seasonal and occasional flooding, using previous research conducted in the Delta as reference point for site selection (Ashton *et al.*, 2003; Dallas and Mosepele, 2007). PF, SF and OF sites were sampled (see Table 3.4) to maximize the detection of diatom (and algae in general) responses to variation in the Delta's hydrology. Four sampling trips were conducted in 2006-2007: alongside periphytic diatom samples used in Mackay *et al.* (2011; 2012) and Davidson *et al.* (2012), Mackay and colleagues collected 93 samples of algae in water from 41 sites which were archived at UCL as part of this Ph.D. project (Mackay *et al.*, 2009). However, 30 samples obtained in November-December 2006 (low water phase) were lost during the storage phase; thus only 63 samples could be analysed for this study. The Ngami lake sample (NGA-2; September 2006) and one sample from Guma lagoon (LPH3-2; Lower Panhandle – LPH, December 2006) were included only in the analyses of algal counts and for the determination of the total species richness, as these, taken alone, were not representative of a region (the former) or a season (the latter). Hence data on 61 of these were used for statistical analyses.

Campaign 2 (2009-2010):

Sixty-nine algal samples were collected from different habitats in 10 sites during 2009-2010. Sites were selected in the lower reaches of the Delta (BOR and SAN), so as to represent primary, secondary and occasionally flooded floodplains experiencing different long-term flooding frequency (see Table 3.6); this was done to expand the dataset on algae and limnology on these regions, crucial for primary production and food web dynamics (Lindholm *et al.*, 2007). The rationale was to undertake a specific study of the floodplains and connected channels as compared to sampling of, mostly, Open Water (OW) and Marginal Vegetation (MV) environments in all regions in 2006-2007. This allowed the research to investigate a much larger spectrum of algae in the Delta, complementary to the extensive survey conducted on diatoms by Mackay *et al.* (2012).

The eight floodplains were chosen according to their flood class and accessibility providing three primary floodplains (ALD, HIP, POC); three secondary floodplains (LEC, WBE, WIL) and two occasionally inundated floodplains (BUF and DAU) (Siziba *et al.*, 2011a) (see Table 3.1, Figure 3.3).

Table 3.1. Campaign 2: floodplains sampled in 2009-2010 in floodplain type groups.

Primary Floodplains	Secondary Floodplains	Occasionally Flooded
Pool C (BOR)	Wildebeest pool (BOR)	Daunara (SAN)
Hippo pool (BOR)	Lechwe pool (BOR)	Buffalo fence (SAN)
Aldrovanda pool (BOR)	Water lily pool (BOR)	

Sites were coded according to location and season, with two separate systems for the two campaigns (Table 3.2).

Table 3.2. Coding system of sampling sites with information on region, season and habitat.

Site coding	**Campaign 1 (2006-2007)**
Region	UPH, LPH, XAK, BOR, SAN
Site	e.g. UPH1
Month and year	1=September ‘06; 2=November/December ‘06; 3=April/May ‘07; 4=Jul/August ‘07
Site coding	**Campaign 2 (2009-2010)**
Floodplain	e.g. ALD=Aldrovanda Pool
Habitat	1=Open Water; 2=Sedgeland; 3=Grassland
Month and year	6=April/May ‘09; 7=July/August ‘09; 8=October ‘09; 9=February ‘10

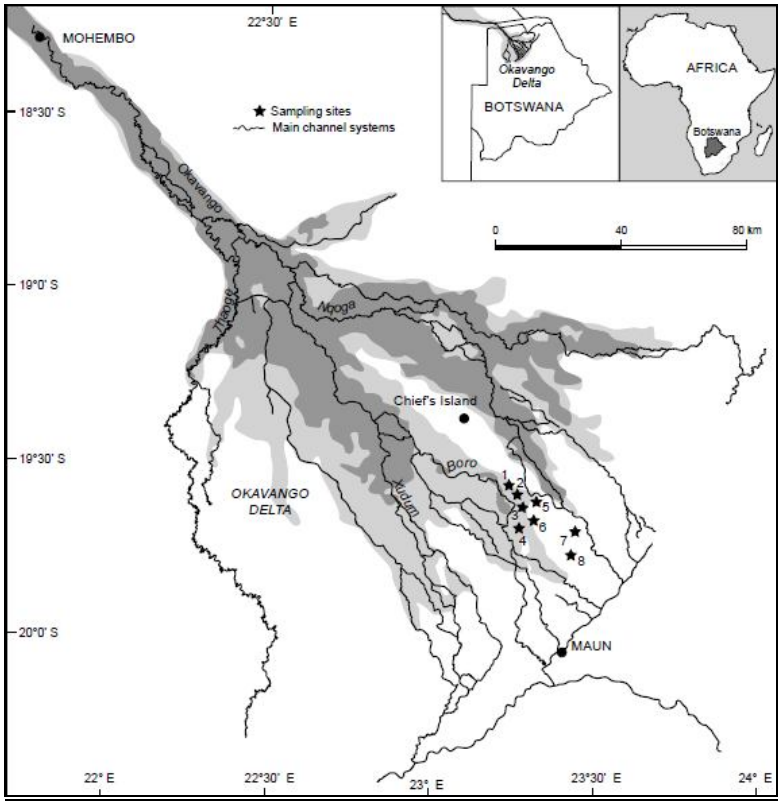


Figure 3.3. Map of the Okavango Delta showing the location of sampling points in Campaign 2 (source: Siziba et al., 2011b; 1 = Lechwe pool, 2 = Pool C; 3 = Hippo pool, 4 = Aldrovanda pool, 5 = Water lily pool, 6 = Wildebeest pool, 7 = Daunara, 8 = Buffalo fence).

The geographical coordinates of all the sampling points are shown in Table 3.3; several sites have the same coordinates because they were very close to one another (<20m) and / or were sampled in more than one occasion.

Table 3.3. Coordinates of sampling sites with information on location/floodplain, sample codes and dates, season, flood class and habitat (see Glossary on page 14 for Flood Class and Habitat codes; habitat codes in brackets = within-floodplain habitat type in Campaign 2).

N site	Location (region)	Samples	Date	Month	Flood Class	Habitat	Lat. (S)	Long. (E)
Campaign 1								
1	Upper Panhandle (UPH)	UPH1A-1 UPH1B-1 UPH1B-3 UPH1C-4	07/09/2006 07/09/2006 03/05/2007 05/08/2007	Sep. Sep. May. Aug.	PF PF PF PF	OW OW OW OW	18.409695	21.886945
2		UPH3A-1 UPH3A-3	06/09/2006 03/05/2007	Sep. May	PF PF	OW	18.410927	21.881083
3		UPH4A-1 UPH4B-1 UPH4B-3	06/09/2006 06/09/2006 03/05/2007	Sep. Sep. May	PF PF PF	OW OW OW	18.427485	21.981188
4		UPH5A-3 UPH5A-4	03/05/2007 05/08/2007	May Aug.	PF PF	OW OW	18.426972	21.971389
5		UPH6-3	03/05/2007	May	PF	OW	18.411833	21.889112
6		UPH7A-4	05/08/2007	Aug.	PF	OW	18.428403	21.919382
7		UPH8-3	03/05/2007	May.	PF	OW	19.175258	23.419887
8		UPH9A-3	05/05/2007	May	PF	OW	-	-
9	Lower Panhandle (LPH)	LPH1-1	04/09/2006	Sep.	PF	MV	18.879028	22.391055
10		LPH3-1 LPH3-2	04/09/2006 05/12/2006	Sep. Dec.	PF	MV MV	18.956098	22.377158
11		LPH4A-1	05/09/2006	Sep.	PF	MV	18.960190	22.382820
12		LPH5A-4	02/08/2007	Aug.	PF	MV	18.917593	22.409447
13		LPH6-4	03/08/2007	Aug.	SF	-	18.865341	22.419814
14		LPH8A-4	03/08/2007	Aug.	PF	MV	18.961050	22.406857
15		LPH9A-4	04/08/2007	Aug.	PF	MV	20.436227	22.830828
16	Xakanaxa (XAK)	XAK4A-3	29/04/2007	Apr.	PF	MV	19.187812	23.433718
17		XAK5A-4	30/07/2007	Jul.	PF	MV	19.188850	23.452418

Table 3.3. (continued from previous page).

N site	Location (region)	Samples	Date	Month	Flood Class	Habitat	Lat. (S)	Long. (E)
18	Xakanaxa (XAK)	XAK7A-4 XAK7B-4	30/07/2007	Jul.	SF	OW	19.201925	23.460653
19		XAK9-4	29/07/2007	Jul.	OF	OW	19.240080	23.356937
20		XAK12-3 XAK12-4	01/05/2007	May	PF PF	OW OW	19.191445	23.451972
21		XAK13-4	30/07/2007	Jul.	OF	F	19.183000	23.440861
22		XAK14-3	30/04/2007	Apr.	PF	F	19.177250	23.438028
23	Xakanaxa (XAK)	XAK15-3	30/04/2007	Apr.	PF	MV	19.172583	23.440806
24		XAK16-3 XAK18-4	30/04/2007 29/07/2007	Apr. Jul.	PF OF	MV F	19.196000	23.441000
25		XAK19-4	30/07/2007	Jul.	PF	F	18.187000	23.431000
26	Boro (BOR)	BOR2A-3	25/04/2007	Apr.	SF	MV	19.567102	23.204587
27		BOR2-4	26/07/2007	Jul.	SF	MV	19.538495	23.088402
28		BOR8A-3 BOR8A-4	26/04/2007 25/07/2007	Apr. Jul.	SF SF	F F	19.539652	23.089635
29		BOR8B-4	25/07/2007	Jul.	SF	MV	19.549053	23.177108
30		BOR9A-4	25/07/2007	Jul.	SF	MV	19.533420	23.183143
31		BOR10A-3 BOR10A-4	26/04/2007 17/04/2007	Apr. Apr.	SF SF	F F	19.526833	23.150667
32		BOR14-4	25/07/2007	Jul.	SF	F	19.538028	23.184139
33		BOR15-3	27/04/2007	Apr.	SF	OW	19.538711	23.114553
34		BOR17A-4	25/07/2007	Jul.	SF	OW	19.546492	23.186723
35		BOR19-4	26/07/2007	Jul.	SF	F	18.842305	22.403612
36	Santantadibe (SAN)	SAN1-1	12/09/2006	Sep.	OF	OW	19.627482	23.421058
37		SAN2-1	12/09/2006	Sep.	OF	OW	19.641405	23.424000
38		SAN3A-1 SAN3B-1	12/09/2006 12/09/2006	Sep. Sep.	OF OF	OW OW	19.622978	23.379247

Table 3.3. (continued from previous page).

N site	Location (region)	Samples	Date	Month	Flood Class	Habitat	Lat. (S)	Long. (E)
39	Santantadibe (SAN)	SAN4A-1	12/09/2006	Sep.	OF	F	19.633340	23.403977
40		SAN5-1	13/09/2006	Sep.	OF	F	19.638080	23.414852
41		SAN6-1	13/09/2006	Sep.	OF	F	18.339083	21.837138
42	L. Ngami (NGA)	NGA2-1	14/09/2006	Sep.	OF	OW	19.651743	23.429798
N site	**Floodplain (region)**	**Samples**	**Dates**	**Month**	**Flood Class**	**Habitat**	**Lat. (S)**	**Long. (E)**
Campaign 2								
43	Pool C (BOR)	POC1-6	06/05/2009	May	SF	OW	19.531517	23.182350
		POC1-7	30/07/2009	Jul.	SF	OW		
		POC1-8	21/10/2009	Oct.	SF	OW		
		POC1-9	10/02/2010	Feb.	SF	OW		
		POC2-6	06/05/2009	May	SF	F (S)		
		POC2-7	30/07/2009	Jul.	SF	F (S)		
		POC2-8	21/10/2009	Oct.	SF	F (S)		
		POC2-9	10/02/2010	Feb.	SF	F (S)		
		POC3-6	06/05/2009	May	SF	F (G)		
		POC3-7	30/07/2009	Jul.	SF	F (G)		
		POC3-8	21/10/2009	Oct.	SF	F (G)		
		POC3-9	10/02/2010	Feb.	SF	F (G)		
44	Water lily pool (BOR)	WLI1-6	06/05/2009	May	SF	OW	19.536667	23.192333
		WLI1-7	30/07/2009	Jul.	SF	OW		
		WLI2-6	06/05/2009	May	SF	F (S)		
		WLI2-7	30/07/2009	Jul.	SF	F (S)		
45/a	Hippo pool (BOR)	HIP1-6	06/05/2009	May	SF	OW	19.540850	23.180417
		HIP1-7	30/07/2009	Jul.	SF	OW		
		HIP1-8	21/10/2009	Oct.	SF	OW		
		HIP1-9	10/02/2010	Feb.	SF	OW		

Table 3.3. (continued from previous page).

N site	Floodplain (region)	Samples	Dates	Month	Flood Class	Habitat	Lat. (S)	Long. (E)
45/a	Hippo pool (BOR)	HIP2-6	06/05/2009	May	SF	F (S)	19.540850	23.180417
		HIP2-7	30/07/2009	Jul.	SF	F (S)		
		HIP2-8	21/10/2009	Oct.	SF	F (S)		
		HIP2-9	10/02/2010	Feb.	SF	F (S)		
45/b	Hippo pool (BOR)	HIP3-6	06/05/2009	May	SF	F (G)	19.544683	23.180417
		HIP3-7	30/07/2009	Jul.	SF	F (G)		
		HIP3-8	21/10/2009	Oct.	SF	F (G)		
		HIP3-9	10/02/2010	Feb.	SF	F (G)		
46	Lechwe pool (BOR)	LEC1-6	06/05/2009	May	SF	OW	19.542733	23.163267
		LEC2-7	31/07/2009	Jul.	SF	F (S)		
		LEC2-8	22/10/2009	Oct.	SF	F (S)		
		LEC3-6	06/05/2009	May	SF	F (G)		
		LEC3-7	31/07/2009	Jul.	SF	F (G)		
		LEC3-8	22/10/2009	Oct.	SF	F (G)		
47	Wildebeest pool (BOR)	WBE2-6	07/05/2009	May	SF	F (S)	19.54825	23.177783
		WBE2-7	31/07/2009	Jul.	SF	F (S)		
		WBE2-8	23/10/2009	Oct.	SF	F (S)		
		WBE3-6	07/05/2009	May	SF	F (G)		
		WBE3-7	31/07/2009	Jul.	SF	F (G)		
		WBE3-8	23/10/2009	Oct.	SF	F (G)		
		WBE3-9	10/02/2010	Feb.	SF	F (G)		
48/a	Aldrovanda pool (BOR)	ALD3-6	07/05/2009	May	SF	F (G)	19.550217	23.210500
		ALD3-7	30/07/2009	Jul.	SF	F (G)		
		ALD3-8	21/10/2009	Oct.	SF	F (G)		
		ALD3-9	10/02/2010	Feb.	SF	F (G)		
		ALD2-6	07/05/2009	May	SF	F (S)		
		ALD2-7	30/07/2009	Jul.	SF	F (S)		
		ALD2-8	21/10/2009	Oct.	SF	F (S)		

Table 3.3. (continued from previous page).

N	Floodplain (region)	Samples	Dates	Month	Flood Class	Habitat	Lat. (S)	Long. (E)
48/a	Aldrovanda pool (BOR)	ALD2-9	10/02/2010	Feb.	SF	F (S)	19.550217	23.210500
48/b	Aldrovanda pool (BOR)	ALD1-6	07/05/2009	May	SF	OW	19.551533	23.218183
		ALD1-7	30/07/2009	Jul.	SF	OW		
		ALD1-8	21/10/2009	Oct.	SF	OW		
		ALD1-9	10/02/2010	Feb.	SF	OW		
49	Daunara (SAN)	DAU1-6	08/05/2009	May	OF	OW	19.74720	23.456167
		DAU1-7	06/08/2009	Aug.	OF	OW		
		DAU1-8	27/10/2009	Oct.	OF	OW		
		DAU1-9	07/02/2010	Feb.	OF	OW		
		DAU3-6	08/05/2009	May	OF	F (G)		
		DAU3-7	06/08/2009	Aug.	OF	F (G)		
		DAU3-8	27/10/2009	Oct.	OF	F (G)		
		DAU3-9	06/02/2010	Feb.	OF	F (G)		
50	Buffalo fence (SAN)	BUF1-6	08/05/2009	May	OF	OW	19.90565	23.527650
		BUF1-7	06/08/2009	Aug.	OF	OW		
		BUF1-8	27/10/2009	Oct.	OF	OW		
		BUF1-9	08/02/2010	Feb.	OF	OW		
		BUF2-9	08/02/2010	Feb.	OF	F (S)		
		BUF3-6	08/05/2009	May	OF	F (G)		
		BUF3-7	06/08/2009	Aug.	OF	F (G)		
		BUF3-8	27/10/2009	Oct.	OF	F (G)		
		BUF3-9	08/02/2010	Feb.	OF	F (G)		

Table 3.4 shows sampling periods, number of algal samples collected per flooding phase in the two campaigns and the researcher leading each fieldtrip. The flooding phases in the Panhandle and in the lower Delta are not synchronous, but, broadly, there are four flood phases at a wetland scale: flood expansion in April-May; high flood in July-August; flood recession in September-October; and low flood in December-February.

Table 3.4. Algal samples collected in the two campaigns used for most of the analyses (apart from overall count and taxon richness results; LPH3-2 and NGA2-1 are excluded as they were the only samples taken respectively in December 2006 and in Ngami lake).

Campaign 1	**Sampling period**	**Region**	**N samples**	**Flood**	**Collection**
	September 2006	UPH	5	Recession	UCL (Mackay)
		LPH	4	Recession	UCL (Mackay)
		XAK	-	-	UCL (Mackay)
		BOR	-	-	UCL (Mackay)
		SAN	10	Recession	UCL (Mackay)
	April / May 2007	UPH	6	Expansion	UCL (Mackay)
		LPH	-	-	UCL (Mackay)
		XAK	5	Expansion	UCL (Mackay)
		BOR	4	Expansion	UCL (Mackay)
		SAN	-	-	UCL (Mackay)
	July / August 2007	UPH	4	High	UCL (Davidson)
		LPH	6	High	UCL (Davidson)
		XAK	8	High	UCL (Davidson)
		BOR	9	High	UCL (Davidson)
		SAN	-	-	UCL (Davidson)
Campaign 2	**Sampling period**	**Region**	**N samples**	**Flood**	**Collection**
	May 2009	BOR	14	Expansion	UCL (Marazzi)
		SAN	4	Expansion	UCL (Marazzi)
	July / August 2009	BOR	12	High	ORI (Siziba)
		SAN	4	High	ORI (Siziba)
	October 2009	BOR	13	Recession	ORI (Siziba)
		SAN	4	Recession	ORI (Siziba)
	February 2010	BOR	13	Low	UCL (Marazzi)
		SAN	5	Low	UCL (Marazzi)

Table 3.5 summarises the samples collected from sites with different flood class; a clear difference is evident between Northern and Eastern Delta (UPH, LPH and XAK) with mostly permanently flooded sites while the Southern Delta (BOR, SAN and NGA) is exclusively characterized by seasonally and occasionally flooded sites.

Table 3.5. Number of samples taken in sites with different flood class per region.

Flooding	**Permanently Flooded**		**Seasonally Flooded**		**Occasionally Flooded**		**Total**
Regions/ Year	**2006-2007**	**2009-2010**	**2006-2007**	**2009-2010**	**2006-2007**	**2009-2010**	**2006-2010**
UPH	15	0	0	0	0	0	**15**
LPH	10	0	1	0	0	0	**11**
XAK	8	0	2	0	3	0	**13**
BOR	0	0	13	52	0	0	**65**
SAN	0	0	0	0	10	17	**27**
NGA	0	0	0	0	1	0	**1**
Total	**33**	**0**	**16**	**52**	**14**	**17**	**132**

In Campaign 2, the eight floodplains visited for the joint sampling of algae and zooplankton (in particular microinvertebrates; Siziba *et al.*, 2012) were categorised into three specific groups: 1) primary floodplains which, being least elevated with respect to their tributary channels, receive water almost every year; 2) secondary floodplains which become inundated by water flowing from the primary floodplains once every 5 - 10 years; 3) occasionally (or rarely) flooded floodplains inundated by high floods happening every 18 - 30 years (Siziba *et al.*, 2011b; Wolski and Murray-Hudson, 2006). For the purpose of data analyses of the merged datasets, and to retain comparability between Campaigns 1 and 2, primary and secondary floodplains were assigned to the Seasonally Flooded site group (SF) and rarely flooded floodplains to the Occasionally Flooded (OF) sites group (Table 3.6) also used by Mackay *et al.* (2009; 2011; 2012).

Table 3.6. Vegetation and habitat features of the floodplains sampled in the lower Okavango Delta (modified from Siziba et al., 2011b).

Features	**Primary floodplains (*Pool C, Hippo pool, Aldrovanda pool*)**	**Secondary floodplains (*Wildebeest pool, Lechwe pool, Water lily pool*)**	**Rarely (Occasionally) flooded floodplains (*Daunara, Buffalo fence*)**
Terrestrial forests	Absent	Absent	Dominated by *Acacia* spp. and *Colophospermum mopane* forests
Aquatic vegetation	Dominated by sedges (*Cyperus articulatus*) and *Schoenoplectus corymbosus* and submerged macrophytes	Same as permanently flooded floodplains	Macrophytes were absent during the early phases of flooding and developed during the flood recession phase
Microhabitats	Three distinct microhabitats: open water, sedges and inundated grasses	Same as permanently flooded floodplains	Two microhabitats: open water and inundated grasses at the onset of flooding and macrophytes appeared during the flood recession phase
Inundated grasses	Dominated by *Sporobulus spicatus*, *Cynodon dactylon*, *Vetiveria nigratana* and *Panicum repens*	Same as permanently flooded floodplains	Dominated by grasses belonging to the *Poaceae*

Analogously to the habitat classifications, Siziba's floodplain type classification is also used for the analysis of Campaign 2 data (Siziba *et al.*, 2011b). The Campaign 1 floodplain sites are included in this "floodplain type" grouping, hence 14 floodplains from BOR, XAK, SAN and Ngami lake (NGA) sampled in 2006-2007 are also considered for specific floodplain dynamics. Therefore a total of 83 samples (64%) were collected from floodplains (see summary in Table 3.7), with the remaining 48 samples from river channels, lagoons, small pools and backwaters.

Table 3.7. Number of samples per floodplain type in all the samples.

Floodplain type	Campaign 1	Campaign 2	Total
Primary	4	33	37
Secondary	4	19	23
Occasionally flooded	6	17	23
Total	14	69	83

3.1.1. Habitat classifications

The sampling sites were classified according to two classification systems; one is specific to Campaign 2, the other describes the within-floodplain habitat types where algae were collected from; the second was generated in order to compare samples across Delta-scale habitat types in the two campaigns.

Within-floodplain habitats

In Campaign 2 sampling was conducted across three within-floodplain habitats: Open Water (OW), Sedgeland (S) and Grassland (G) (see Table 3.8). The rationale behind this choice was that nutrients tend to accumulate in the floodplain soils of the Delta, particularly in the (very) shallow grasslands (Lindholm *et al.*, 2007). Algal populations are hypothesised to be influenced by this nutrient gradient and availability of benthic microhabitats in terms of biodiversity and biomass.

Table 3.8. Number of samples from within-floodplain habitats in Campaign 2.

Region	BOR	SAN	Total
Open Water (OW)	11	8	19
Sedgeland (S)	20	1	21
Grassland (G)	21	8	29
Total	**52**	**17**	**69**

Delta-scale habitats

In order to assess the influence of macrohabitat types on algal populations across the Delta sites visited in Campaign 1 (2006-2007) were classified into three groups: OW, Marginal Vegetation (MV) and Floodplain (F). This was done using fieldwork notes provided by Mackay and colleagues (Mackay *et al.*, 2012). The algal samples collected in Campaign 1 in UPH are from both MV (off the main channel) and areas with floating vegetation in OW; LPH was sampled both in OW and MV habitats. XAK was sampled in F and OW. Samples taken in the BOR and SAN were collected from F or main channel (OW); OW habitats in the distal reaches are shallower than in UPH and XAK.

The sites sampled in Campaign 2 (2009-2010) were either from OW or Floodplain F; the within floodplain habitat types 'Sedgeland' and 'Grassland' were pooled into the Floodplain habitat group to compare samples in the whole dataset. Overall, across the two campaigns a total of 41 samples were taken from river channels and lagoons, sites classified as OW of which 22 from Campaign 1 and 19 from Campaign 2; 18 samples came from areas with MV, all from Campaign 1, while 70 samples were collected in F of which 20 in Campaign 1 and 50 in Campaign 2. One sample from LPH was not classified because its habitat was not recorded. Approximately a third of the 41 OW samples were collected in respectively PF, SF and OF sites; 14 out of 18 MV samples were taken in PF and 4 in SF areas; 48 out 70 floodplain samples come from SF, 18 from OF and 4 from PF sites (Table 3.9).

Table 3.9. Number of samples taken from different habitats in the two campaigns.

Region	Open Water (OW)		Marginal Vegetation (MV)	Floodplain (= S+G)		Total
	2006-2007	2009-2010	2006-2007	2006-2007	2009-2010	2006-2010
UPH	9	0	4	2	0	15
LPH	3	0	6	0	0	9
XAK	4	0	4	5	0	13
BOR	2	11	4	7	41	65
SAN	4	8	0	6	9	27
Total	**22**	**19**	**18**	**20**	**50**	**129**

Using these separate habitat classifications makes it possible to compare sites across the two sampling campaigns for a broader understanding of the ecological patterns in the Delta, e.g. all the floodplain sites are recognized as such. On the other hand these allow to investigate specific floodplain dynamics of, e.g. algal biomass and biodiversity across the three floodplain habitats abovementioned (OW, S and G) in the Campaign 2 database, specifically created for this Ph.D. research.

3.2. SAMPLING OF ALGAE

During Campaign 1, Mackay and colleagues (Mackay *et al.*, 2009) collected samples of algae in water using 1.5 L PVC bottles filled with water at elbow depth. In Campaign 2, since both inundated grasses and sedges are habitats with dense vegetation, water samples for limnological and algal analyses were collected following the tube sampling method (Graves and Morrow, 1998). A plexiglass tube (6 cm in diameter, 0.5 m in length) was pushed through the macrophytes or water column; in the floodplains, water was taken from about 10 cm above sediments not to excessively disturb the sediment (Figure 3.4a). In Campaign 2 water samples were collected from about 20 randomly selected points about 10 m apart to fill a 20 L container to minimise the effects potential local heterogeneity. A 275 mL bottle was used to obtain algal samples representative of the area from which 20 L of water were collected. Siziba *et al.* (2011b, 2012) analysed zooplankton samples (e.g. microinvertebrates such as copepoda and cladocera) collected during the same campaign (Figure 3.4b).

a) *b)*

Figure 3.4. a) Field assistant Ponde Kauheva sampling from a canoe in an occasionally flooded floodplain in Boro; b) Nqobizitha Siziba and myself filtering a composite sample for zooplankton analysis.

In both campaigns, a few drops of acidified Lugol's iodine was added straight after sampling as a preservative. This solution was prepared using 100 g I, 200 g KI, 200 mL glacial acetic acid, and 2000 mL of distilled water Willén (1962). The samples were stored at the Okavango Research Institute in the dark and then 30 mL (Campaign 1) and 50 mL subsamples (Campaign 2) were placed in Sterilins® (hereafter referred to as tubes). Campaign 2 samples were concentrated, i.e. supernatant was taken from the 0.275 mL sampling bottles, whereas this step was not not undertaken on Campaign 1 samples. As the water sample volumes taken were not the same during the two campaigns, different formulas for biovolume estimation were used (see section 3.4). All samples from both campaigns were transported back to the UK for long term storage and analysis.

3.3. ALGAL ANALYSES

Samples of algae from Campaign 1 were stored in the dark at ambient temperature while the samples collected in Campaign 2 were placed in a coldstore at approximately 5 °C according to modified protocols published after the first campaign (European Standard, 2005). These different procedures were followed to avoid potential preservation problems in the most recently collected samples. Campaign 1 samples were analysed respectively about three to five years after

collection while Campaign 2 samples were studied two to three years after sampling. Evidence of degradation was scarce in either set of samples.

3.3.1. Sub-sample preparation

Prior to microsopy, sedimentation chambers, pipettes and other equipment were allowed to acclimatise to the research microscope room temperature for at least 24 hours. This was done to promote a random distribution of algae in the sedimentation chamber thus preventing the formation of convection currents due to thermal differences (European Standard, 2005). Identification and enumeration of algae were performed using an inverted microscope according to the Utermöhl technique (Utermöhl, 1958), suitable for investigation of the abundance, composition and biovolume (see Chapter 4) of phytoplankton in rivers and lakes. Chlorophyta, Bacillariophyta and other phyla can be jointly studied with this method.

During sample storage, suspended particles settle out and (small) algae tend to become indistinguishable because they are either incorporated in detritus aggregates or they adhere to other large algal cells (European Standard, 2005). Samples were re-suspended and separated by gentle shaking to avoid any breakage. The mixing of the subsamples was done manually and standardised using a combination of alternating horizontal rolling and vertical tumbling (turning upside down) of the sample bottle for 2 minutes. After the 30 mL (2006-2007) or 50 mL samples (2009-2010) were thoroughly mixed, sedimentation chambers were filled with 5/10/15 mL subsamples. A simple counting chamber consists of three parts: (1) a bottom part, which is a piece of Plexiglas (area 40 mm^2 and 6 mm thick), (2) a cylinder to contain the subsamples and (3) a glass coverslip glued over the bottom of the hole. Sedimentation chambers similar to the recommended Hydro-Bios of approximately 5, 10 and 15 mL capacity were used (Figure 3.5).

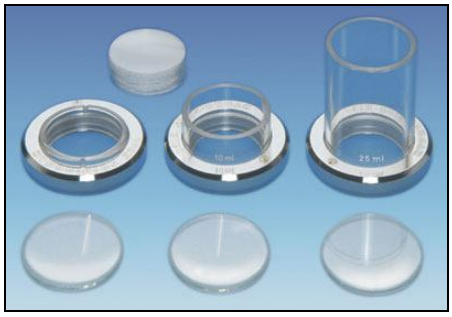


Figure 3.5. Sedimentation chambers: 5, 10, 15 mL
(source: http://www.hydrobios.de).

The measurement of the exact volume of these chamber allowed for the most accurate biovolume estimates possible (see section 3.4); the sedimentation chambers and lids were weighed whilst empty, then filled with distilled water and re-weighed three times to record the average value. The weight in grams is equivalent to volume in mL; chamber volumes recorded were: 4.85 mL; 9.97 mL and 14.52 mL. Care was taken to fill the chamber so to achieve a random distribution of algal cells; the chamber was filled in one addition, gently pouring the water directly from the sample tube, allowing a little water to over-spill the chamber when sliding the thick cover slip across to avoid the formation of air bubbles (European Standard, 2005). According to the algal density observed in the sample tube, 1 sample was counted using a 5 mL sedimentation chamber, 26 with a 10 mL chamber and 22 samples with a 15 mL chamber (n=49). For 13 samples a pre-concentration step was necessary: 30 mL subsamples were left to settle overnight and the 20ml supernatant was siphoned off so that the concentrated 10ml subsample was used for counting; the total number of 2006-2007 samples was 63 (1 missing). The 2009-2010 samples, stored in 50 mL tube, were all counted in 10 mL subsamples (n= 69) because algal density was sufficient for enumeration.

The water subsamples were allowed to settle undisturbed for at least 8 to 12 hours, following the recommended 4 hours per cm height of chamber (Nauwerck, 1963 in European Standard, 2005). This procedure allows algae to evenly settle onto the bottom of the chambers so that they can be observed under the microscope. A Leitz® Diavert inverted microscope with phase contrast was used, 10x binocular eyepieces and 10x, 40x and 100x objectives. Hereafter 100x, 400x and 1000x magnification will be referred to as composite magnifications (eyepiece + objective). The microscope was fitted with a digital camera so that micrographs of specimens could be taken. A mechanical stage was placed onto the microscope so that sedimentation chambers could be moved precisely during the counting and without causing any undesirable movement in the subsample observed. All eyepiece/graticule and objective combinations were calibrated with a stage micrometer (e.g. 100 μm x 10 μm divisions) and the dimensions and areas of counting fields, transects and the total chamber area were calculated and recorded in an Excel® workbook for each of the magnifications used.

3.3.2. Counting technique and strategies

When the algae had settled at the bottom of the chamber, keeping the microscope on a flat surface, they were counted and identified. Algal cells both with and without cell content (e.g. chloroplasts) were counted; both planktonic and benthic algae were observed and counted as the scope of this study is on all algae found in water samples whether free-floating or resuspended.

The counting procedure involved recording the taxa observed and the number of algal units (cells, coenobia, colonies and filaments) for each taxon in a known area of the counting chamber. Algae are counted as cells when they are unicellular or coenobium and as colonies or filaments when in groups of cells. As the volume of sample added was recorded and the area of the whole chamber measured with a micrometer, the concentration of each individual taxon and their biovolume could be calculated (see section 3.4).

The algal counts were carried out via scanning the chamber in random fields of view or transects (with a random distribution of cells, a set of field of views is *de facto* equivalent to a random transect) observed at a low magnification, 100x, to pick up large taxa, followed by high magnification count (400x) to record the small taxa. Random fields of view counted at 100x were not counted at 400x so that chances of double counting error were minimised. Random fields of view were selected by means of random number generator software (Randomgen®); the mechanical stage was positioned at the selected coordinates before starting the counting of each subsample and checked regularly.

A tally of the number of fields counted was recorded in a notebook with the counts of individual algal units and number of cells identified; the data were then input into an Excel® spreadsheet. At least 400 algal units per sample were enumerated when possible (in most cases) to ensure that the count was representative of the sample, thus recording the great majority of the species present; the recommended 4 algal units / field view average concentration standard was adhered to (European Standard, 2005). About 200 algal units were counted at 100x and 200 units at 400x in order not to underestimate smaller or larger species; larger algal taxa are observed more frequently at 100x, but they were identified at 400x when necessary, by simply ‘zooming-in’ on the specimen under observation. This standard counting method was used to ensure comparability of results between all algal samples from

the start. In this study, algae smaller than 15 μm were mostly ignored at 100x, unless clearly identifiable, and counted at 400x so to reduce the overestimation of small cells.

3.3.3. Identification of algae

Algae were identified with reference to John *et al.* (2002) and, for diatoms, Cox (1996), studies on diatoms in the Okavango Delta (Cholnoky, 1966a; Cronberg *et al.*, 1996a) and Southern Africa (Cholnoky, 1966b); research articles in the Delta were used to aid identification of desmids (Coesel and Van Geest, 2008; 2009). Other useful taxonomic references included Ramberg *et al.* (1986) and Carter (2011) and studies of the phytoplankton of West and East Africa (Thomasson 1957, 1960 and 1965; Gerrath, 1988; Ricci *et al.*, 1990). Finally a number of websites containing micrographs, species descriptions and keys were used: http://protist.i.hosei.ac.jp, http://westerndiatoms.colorado.edu, www.desmids.nl, www.algaebase.org (see References, p. 401). To aid taxonomic identification an introductory course was undertaken in February 2009 at the University of Milano Bicocca; later an advanced course was also attended, at the University of Durham (July 2011). Taxa were identified to genus or species level wherever possible. Identification at other taxonomic levels other than species and genera were made when the very small dimension of algal cells (< 12-15 μm) and the effect of the preservative (Lugol's) on features and colours led to identification difficulties, e.g. Cyanophyta were frequently identified at genus or class level (e.g. *Oscillatoriales*, *Chroococcales*, *Nostocales*) and Cryptophyta and Pyrrophyta at genus level.

3.3.4. Algal traits

Recent work has recommended that ecologists, in particular community ecologists, to refocus their research towards trait analysis in order to answer questions beyond how many species there are in different environments and why, to encompass variations in traits and environmental gradients (McGill *et al.*, 2006). In phytoplanktonic algal species, functional traits mediate their growth, sedimentation, grazing losses and nutrient acquisition, as shape, size and motility, among other characteristics, influence species performances (Weithoff, 2003). Most of the algal functional traits considered by Weithoff (2003) for phytoplankton were employed in

this study to investigate their frequency of occurrence in different environments in the Delta. Algal taxa were classified according to their cell size (Greatest Axial Linear Dimension – GALD, i.e. most frequently length; Reynolds, 1997), algae being unicellular or multicellular (in filaments, coenobia, colonies), motile (with or without flagella) or non motile, and their metabolic features (nitrogen fixation, phagotrophy and demand for silica).

Cell length classes were generated so that each group represented about a third of the observed values in the algal counts, i.e. between about 14,500 and 16,000 algal units per group. The categories "Structure", "Motility" ("Motile" algae are non flagellated, but move by oscillation or using a raphe) and "Metabolism" shown in Table 3.10 were generated for the data, on the basis of several sources: John *et al.* (2002), Van Dam *et al.* (1994) and Porter (1988).

Table 3.10. Functional groups in which algae are classified according to their traits.

Structure	Cell length	Motility	Metabolism
Unicellular	<25 μm	Non motile	Siliceous exoskeleton
Coenobium	25-50 μm	Flagellated	Nitrogen-fixing
Colony	> 50 μm	Motile	Phagotrophic
Filament	-	-	-
Unicellular / Colony	-	-	-
Filament / Colony	-	-	-

The relative abundance (%) of algal units identified is used to visualise specific trends, e.g. smaller / larger algae prevailing in a given region, flood class or habitat. Data on average length of algal cells, corresponding to their GALD were analysed to provide a measure of algal cell growth. Average cell length influences biovolume estimates (i.e. wet algal biomass; see section 3.1), a concentration value for algae (mg L^{-1}) or 'standing crop'. Biomass differs from productivity, measured as the rate of carbon production per time unit (e.g., g C m^{-2} yr^{-1}), but is often used in research on diversity-biomass relationships as a surrogate of productivity (Mittelbach *et al.*, 2001). Hence the descriptive analyses undertaken on average cell length provides complementary information to algal taxon abundance as the size of cells observed and their abundance are the basis for the estimation of algal biomass.

3.4. ESTIMATION OF ALGAL BIOVOLUME (WET BIOMASS)

Cell counts were converted to wet-weight biomass by calculating approximated cell volumes. Estimates of cell volume for each species were obtained by routine measurements of the algal cells observed and application of the geometric formula best fitted to the shape of the cell (European Standard, 2005; Brierley *et al.*, 2007; Table 3.11). A specific gravity of 1 (μg / μm^3 or mg / mm^3) is assumed for cellular biomass so that biovolume corresponds to wet algal biomass (Nauwerck, 1968); hence 1 $\mu m^3 L^{-1}$ = 1 μg L^{-1}. Biovolume was estimated for all algal taxa: simple geometric shapes were assigned to each cell, filament, coenobium or colony. The appropriate dimensions, typically length and width, were measured for the majority of algal cells showing large size variations (e.g. numerous desmid and diatom genera and species) and for at least 20-30 cells for algae with minimal size variation (e.g. *Rhodomonas* spp.). From these total algal biovolume in each sample was estimated (see Equations 3.1 and 3.2).

Table 3.11 summarises the range of shapes and formulas used to estimate the biovolume of the stated genera, species and other groups of algae such as class (by using a representative taxon).

Table 3.11. Geometric shapes and formulas for the estimation of algal biovolume (sources: European Standard, 2005; Brierley et al., 2007).

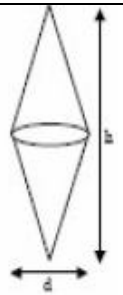
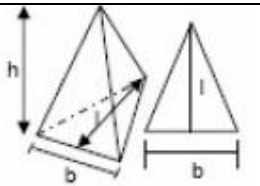
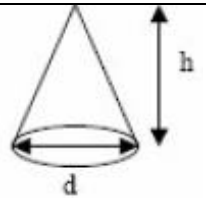
Shape	**Drawing**	**Formula volume**	**Genera**
2 Cones		$V= 1/12*\pi*d^2*h$	*Ankistrodesmus, Ankyra, Closteriopsis, Closterium, Elakatothrix, Kirchneriella, Koliella, Monoraphidium* (approximated), *Schroederia, Selenastrum*
2 Tetrahedrons		$V=1/6*\sqrt{2}*b^3$	*Staurastrum, Xanthidium*
Cone		$V= 1/12*\pi*d^2*h$	*Euglena, Euglenales, Peronema*
Cone + half sphere		$V=1/12* \pi*d^2*(h+d/2)$	*Peridinium, Rhodomonas, Synura*

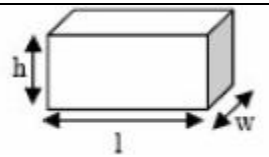
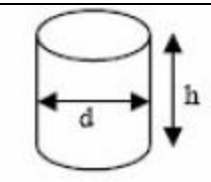
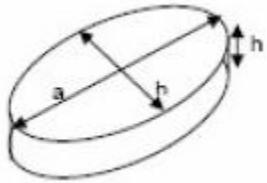
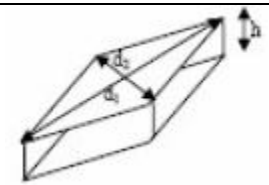
Table 3.11. (continued from previous page).			
Shape	**Drawing**	**Formula volume**	**Genera**
Cuboid		V=l*w*h	*Achnanthes, Asterionella, Eunotia, Frustulia, Gomphonema, Hantzschia, Navicula, Nitzschia, Pennate Diatoms, Pinnularia, Rhopalodia, Synedra, Tabellaria*
Cylinder		V= ¼*π*d^2*h	*Aulacoseira, Bambusina, Bulbochaete, Centritractus, Cladophora, Cyclotella, Docidium, Gonatozygon, Haplotaenium, Lyngbya, Melosira, Microspora, Mougeotia, Nostocales, Oedogonium, Ophyocitium, Oscillatoria, Oscillatoriales, Pediastrum, Pleurotaenium, Schizothrix, Scytonema, Spirogyra, Spirulina, Stigonematales, Tolypothrix, Tribonema, Ulothrix, Zygnema, Zygnematales*
Elliptic cylinder		V= ¼*π*d_1*d_2*h	*Achanthidium, Amphora, Caloneis, Cocconeis, Craticula, Cymatopleura, Diploneis, Eunotia arcus, E. faba, E. minor, E. pectinalis, Neidium, Placoneis, Stauroneis, Surirella, Synedra*
Rhomboid prism		V= ½*d_1*d_2*h	*Fragilaria, Gyrosigma*

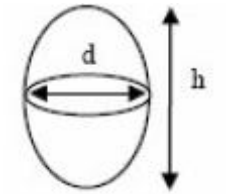
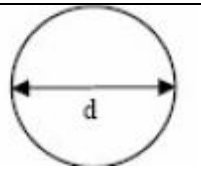
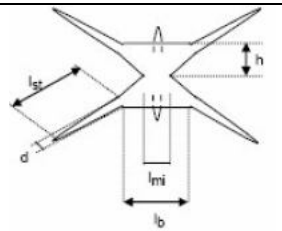
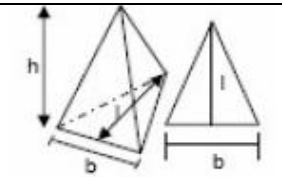
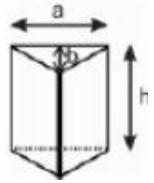
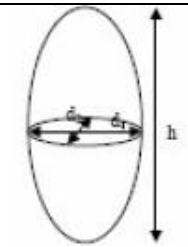
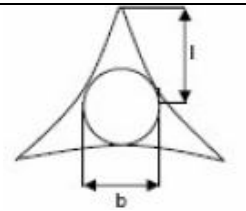
Table 3.11. (continued from previous page).			
Shape	**Drawing**	**Formula volume**	**Genera**
Rotational ellipsoid		$V= 1/6*\pi*d^2*h$	*Bitrichia, Chlamydomonas, Chromulina, Coccomixa, Cystodinium, Dictyosphaerium, Dimorphococcus, Dinobryon, Eremosphaera, Euglena limnophila, E. proxima, Gomphosphaeria, Kephryon, Lepocinclis, Mallomonas, Netrium, Onychonema, Oocystis, Penium, Scenedesmus, Strombomonas, Tetraselmis, Trachelomonas, Woronichinia*
Sphere		$V= 1/6*\pi*d^3$	*Anabaena, Centric Diatom, Chlorella, Chlorococcales, Chlorococcum, Chroococcales, Chroococcus, Coelastrum, Coelosphaerium, Colony, Eudorina, Gloeocapsa, Golenkinia, Golenkiniopsis, Merismopedia, Microcystis, Planktosphaeria, Snowella, Sphaerocystis, Synechococcus, Tetrastrum, Uroglena*
Staurastrum shape		Approximated to 2 Tetrahedrons: $V=1/6*\sqrt{2}*b^3$	*Staurastrum, Staurodesmus*
Tetrahedron		$V=1/12*\sqrt{2}*b^3$	*Tetraedron*
Triangular prism		$V=1/2*a*b*h$	*Cymbella, Fragilaria, Nitzschia*

Table 3.11. (continued from previous page).			
Shape	**Drawing**	**Formula volume**	**Genera**
Triaxial ellipsoid		$V= 1/6*\pi*d_1*d_2*h$	*Amphidinium, Botryococcus, Chroomonas, Cosmarium, Crucigenia, Cryptomonas, Euastrum, Euglena, Gymnodinium, Micrasterias, Peridiniopsis, Phacotus, Phacus, Pteromonas, Spondylosium, Teilingia, Tetmemorus, Woloszynskia*
Trident		$V=1/6*\pi*b^3+1/16*\pi*b^2*l$	*Goniochloris*

Once the biovolume of all algal units was calculated, estimations of the total biovolume of different taxon in each sample was derived following Equation 3.1.; Equations 3.2a for Campaign 1 and 3.2b for Campaign 2 were employed to calculate Total Algal Biovolume accounting for the different water volumes collected, i.e. 1.5 L in Campaign 1 and 0.275 L in Campaign 2.

Equation 3.1:

$$\textbf{Biovolume}_i = \textbf{Biovolume algal units counted} * \frac{\textbf{Area sedimentation chamber}}{\textbf{Total area fields of view counted}}$$

The sedimentation chambers used (5, 10 and 15 mL) all have an area of 452.16 mm^2 (circle with radius=12 mm). The areas of fields of view at different magnifications are respectively: 100x field=2,543 mm^2 and 400x=0.142 mm^2, calculated from measurements of radiuses made by means of a micrometer (respectively 0.9 mm and 0.2125 mm). Hence the Total area of fields of view counted was calculated by multiplying the number of fields of view screened by their respective area.

Equation 3.2a:

$$\textbf{Total Algal Biovolume (Campaign 1)} = \sum_{i}^{n} \frac{\textbf{Biovolume}_i * 10^3 \left[\frac{mL}{L}\right]}{V_{ss} * 10^9 \left[\frac{\mu m^3}{mg}\right]}$$

Equation 3.2b:

$$\textbf{Total Algal Biovolume (Campaign 2)} = \sum_{i}^{n} \frac{\textbf{Biovolume}_i * 10^3 \left[\frac{mL}{L}\right]}{\frac{V_t}{(V_{ss} * V_b)} * 10^9 \left[\frac{\mu m^3}{mg}\right]}$$

where

- i= species / taxon
- V_t= volume of tube (50 mL)
- $V_{ss=}$ volume of subsample (most frequently used: *c.* 10 mL)
- $V_{b=}$ volume of sampling bottle

*Biovolume = Biomass in wet weight: 1 mg = 1 mm^3

In Campaign 1 a 1.5 L sampling bottle was used, but the samples were not pre-concentrated while in Campaign 2 the 275 mL sampling volumes were concentrated into 50 mL tubes. Thus Equation 3.2b takes into account a concentration factor of

5.5 (275 mL /50 mL); thus it can also be written as follows: Total Algal Biovolume = (Biovolume$_i$*1,000 [ml/L] / V_{ss}) / (5.5 *1,000,000,000 [mm^3=mg]).

3.5. LIMNOLOGICAL VARIABLES

In this section the methods and instruments used to measure and / or analyse limnological variables are outlined for the two sampling campaigns. Respectively, Okavango Research Institute technicians and Nqobizitha Siziba undertook water chemistry analyses of Campaign 1 and Campaign 2 samples, the latter limited to TP and Chlorophyll *a*.

Campaign 1

Methods used to measure physical variables (and pH) are summarized below after Mackay *et al.* (2011):

- pH (pH units) and conductivity (µS cm^{-1}): *in situ* measurement with a portable *Fisher Scientific Accumet* AP85 waterproof pH/conductivity meter;
- Water depth (m) was measured using a *Plastimo Echotest II* handheld depth sounder in 2006-2007;
- Velocity of water flow (m s^{-1}) was measured by means of a *OTT Nautilus C 2000 Electromagnetic Flow Sensor*;
- Water temperature (°C) and Dissolved Oxygen (DO) (mg L^{-1}) were measured by means of a YSI 550 instrument;
- Total Suspended Solids (TSS) (mg L^{-1}) was measured by filtering water (at least 1 L) in the field after sampling and weighing the residue on GF/C filter papers after drying at 105 °C for 24 hours (mg L^{-1}).

Water samples for laboratory analyses of chemical variables known to be important for algal growth, including nutrients (e.g. nitrogen and phosphorus), cations such as Ca^{2+}, and anions like HCO_3^- and SiO_2 (silica) were collected in Campaign 1. Apart from Total Phosphorus (TP), surface water chemistry variables were only available during December 2006, May 2007 and July 2007 (Mackay *et al.*, 2011). Field equipment was calibrated before each trip. A brief summary of the chemistry analyses methods used in their project is reported below (Mackay *et al.*, 2011):

- Mg^{2+} (mg L^{-1}) by flame atomic absorption spectrometry using a *Varion Spectra 220* instrument;
- Na^{+} (mg L^{-1}) and K (mg L^{-1}) by flame photometry using a *Sherwood Flame Photometer 410* instrument;
- HCO_3^- (mg L^{-1}) using an auto-titrator (Mettler Toledo model DL 50);
- Cl^- (mg L^{-1}) and SO_4 (mg L^{-1}) by ion chromatography using a *DX-120* ion chromatograph;
- Dissolved Organic Carbon (DOC) (mg L^{-1}) by measuring the absorbance of the water samples at 280 nm using a *Perkin Elmer Lamda 20* UV/Vis spectrophotometer;
- TP (mg L^{-1}) and TN (mg L^{-1}) using an air segmented flow analyser (*Bran* C *Luebbe* AA3) after persulphate digestion;
- SiO_2 (mg L^{-1}) by means of the heteropoly blue method at 815 nm.

Campaign 2

In the 2009-2010 sampling fieldtrips the following instruments for *in situ* measurements of physical variables were employed:

- Water depth (m): wooden pole with 10 cm interval marks;
- Water temperature (ºC): Oxi 330i/set meter;
- Turbidity (NTU): Eutech turbidimeter TN-100 calibrated using 800, 100, 20, 0.02 NTU standards;
- Conductivity (µS cm^{-1}): Hanna Hi 9033 multi-range conductivity meter calibrated using 1416 standard;
- pH (pH units): 330i/set calibrated using 4 and 7 buffer solutions;
- Dissolved Oxygen (mg L^{-1}): Oxi 330i / set calibrated in water vapour saturated air vessel.

Unfortunately data on pH and water depth were not collected as planned by ORI staff during the July 2009 and October 2009 fieldtrips and, despite arrangements made with the laboratory at ORI in Botswana, the water chemistry analyses of the samples specifically collected for the Ph.D. were not conducted. However, data on

Chlorophyll *a* (Chl *a*) and TP were made available by Siziba who conducted these analyses for his Ph.D. (Siziba *et al.*, 2011a,b; 2012).

Water samples for Chl *a* and TP determination were taken as subsamples from the composite macrosamples used for the collection of algae (20 L container – see section 3.4). Standard laboratory procedures were applied (APHA 1998); water samples for Chl *a* were filtered using GF/C filters (47 mm) and the filtrates were stored in the dark, at low temperature (<4 °C). Chl *a* concentration was determined spectrophotometrically at wavelength 663 nm in acetone extracts, using a Perkin Elmer, Lambda 20 UV/VS spectrophotometer, and expressed as μg L^{-1} (APHA, 1998; Siziba *et al.*, 2011b). Algal biomass is a frequently measured in limnological studies in terms of Chl *a*, assuming that the great part of chlorophyll content in the water is that present in algae. Kruskopf and Flynn (2006) criticised its unquestioned use (alongside fluorescence measurements), as Chl *a* is not equivalent to biomass of algae and proposed more sophisticated methods to precisely associate Chl *a* and algal photosynthetic activity. However, this variable is still a relevant and valuable a proxy measure of algal biomass in marine (Jesus *et al.*, 2006) and freshwater environments (McNair and Chow-Fraser, 2003; Kruskopf and Flynn, 2006). Hence Chl *a* concentrations are used as a term of comparison with algal biomass estimates (biovolume) and with other studies on freshwater ecosystems in the tropics.

Table 3.12 summarises the limnological data available from Campaign 1 and 2.

Table 3.12. Number of samples for which limnological data are available.

Variables	Campaign 1	Campaign 2	Total
Conductivity	62	68	130
Depth	62	40	102
Dissolved Oxygen (DO)	62	69	131
pH	62	34	96
Temperature	62	69	131
Velocity	27		27
Ca^{2+}	41		41
Chlorophyll *a* (Chl *a*)		67	67
Cl^{-}	41		41
Dissolved Organic Carbon (DOC)	41		41
HCO_3^{-}	41		41
K^{+}	41		41
Mg^{2+}	41		41
Na^{+}	41		41
PO_4^{2-}	15		15
SiO_2	41		41
SO_4^{2-}	41		41
Total Nitrogen (TN)	41		41
Total Phosphorus (TP)	41	60	101
Total Suspended Solids (TSS)	41		41
Turbidity		72	72

A One-Way ANOVA tests were carried out on algal species richness and biovolume to look for systematic differences for data from Boro (BOR) and Santantadibe (SAN), where sampling took place in both campaigns. This was done to decide whether it was appropriate to jointly analyse the data from the two campaigns despite the different sampling methods used, i.e. 1.5 L bottle at elbow depth (Campaign 1) and 20 L composed sample (Campaign 2). Species richness (N species) is normally distributed (Kolmogorov-Smirnov / K.S. test: $Z=0.096$; $p>0.01$) and does not vary significantly between the two datasets (L. test: $p>0.01$; O.W.A. test: $F=1.562$; $p>0.01$). Total biovolume is also normally distributed when log-transformed (K.S. test: $Z=0.070$; $p>0.01$) and does not vary significantly between the two datasets (L. test: $p>0.01$; O.W.A. test: $F=0.070$; $p>0.01$). As the different sampling methods do not yield systematic differences, Campaign 1 and Campaign 2 data were analysed jointly. However, the data were also analysed separately due to their different rationales: a broader biogeographical survey for Campaign 1 and a more specific study of the Southern Delta's floodplains for Campaign 2.

3.6. PARAMETRIC AND NON PARAMETRIC STATISTICAL TESTS

The descriptive analyses illustrated in Tables and Figures in sections 4.4 and 4.5 were generated in Excel®. Statistical tests and boxplots were produced using SPSS® (version 22). Suspected outliers are highlighted as asterisks and very suspected outliers by circles in the boxplots (SPSS Inc., 2008).

Species richness and algal biomass estimates were analysed by means of parametric and non-parametric tests, depending on whether these variables were normally distributed with homogenous variances across regions, flood class, seasons, floodplain type and habitat types, i.e. the criteria by which sampling sites were classified. Tests of normality distribution, i.e. Kolmogorov-Smirnov (hereafter K.S. test) and Levene test (L. test) for homogeneity of variance (or heteroscedasticity) were performed to decide whether to undertake parametric or non-parametric tests. The parametric O.W.A. test (O.W.A. test) and Tukey HSD Honest Significant Difference post-hoc test (T. HSD test), and non-parametric options, e.g. Kruskal-Wallis and Mann-Whitney U tests (respectively K.W. test and M.W.U test), were used to determine the significant differences between explanatory and response variables. The more robust p-value of 0.01, rather than 0.05, was chosen in order to highlight the most significant changes in a very large dataset of algal taxon richness, diversity and biomass and limnological variables so as to explain broad patterns across the Delta, habitats, flood class and seasons more confidently.

Linear regression

The relationships between the response variable algal biovolume and limnological variables as well as species richness as predictor were modelled using simple linear regressions (see section 5.2.6). These were run both on total biovolume and species richness and on phylum-specific data. Linear regressions were conducted by means of SPSS® (version 22); the $AdJR^2$ is used to show the percentage of variation explained by only those independent variables that truly affect the dependent variables (Dytham, 2011).

3.7. DIVERSITY MEASURES

Biodiversity is a complex concept, entailing biological diversity at genes, species and ecosystem, habitat and landscape levels (see section 1.1). Diversity is both a

function of richness, i.e. the number of species, and evenness or equitability, i.e. how similar the species abundances are in a certain assemblage (Magurran and McGill, 2004). For a simple description of species richness the total number of species was used in Chapter 4. A range of different diversity measures accounting for species relative abundance are discussed and suitable indices are chosen.

α, ß and γ diversity components are frequently used (after Whittaker, 1972). α diversity, or within-community diversity component (Magurran and McGill, 2004), is richness in species, measured as the number of species in a sample of standard size. By contrast, the extent of differentiation of assemblages along habitat gradients is ß diversity. According to Whittaker (1972) the product of the α diversity of its assemblages and the degree of differentiation among them (ß diversity) is the γ diversity of a landscape or geographic area, whereas other scholars consider γ diversity as the sum of α and ß diversity components, i.e. additive partitioning (Lande, 1996). Given that diversity is an evolutionary product, "*no single measurement serves all purposes*" (Whittaker, 1972), there is a need to consider various components of diversity. ß diversity is a more difficult, albeit key, concept than α and γ diversity, if not an 'abstruse' one, as many scientists do not agree on the best way to measure it (Novotny and Weiblen, 2005). Whereas α diversity (species richness, Shannon and Simpson Indices) and γ diversity are respectively the number of local and regional species, i.e. inventory diversity measures, ß diversity is a differentiation diversity measure of compositional similarity between samples (Whittaker, 1977; Jurasinski *et al.*, 2009). Numerous approaches for ß-diversity assessments have been developed, also using dissimilarity matrices to study similarity / dissimilarity patterns thus introducing methodological and definition problems (Tuomisto, 2010). In this study, algal diversity is investigated at different spatial scales using α, ß and γ diversity measures. α-diversity is Local Species Richness (LSR) whereas γ and ß diversity are respectively the regional diversity (e.g. Delta scale or sampling region-scale) and the γ diversity divided by α-diversity according to site classifications (e.g. ß diversity for region, flood class or habitat).

α-diversity

Diversity indices allow a more in-depth examination of species and taxon diversity as they measure both richness and evenness (Magurran and McGill, 2004). The Shannon index (Equation 3.3; Shannon, 1948) is probably the most common measure of diversity that combines species richness with relative abundance (Magurran and McGill, 2004).

Equation 3.3:

$$\mathbf{D_{Shannon}} = -\sum \mathbf{p_i} \ln(\mathbf{p_i})$$

where *pi* = the number of specimen i / total specimens. However, in order to transform this diversity index into a true diversity increasing with higher number of species with similar abundance (Jost, 2006), the exponential formula is used (Equation 3.4).

Equation 3.4:

$$\mathbf{D_{Shannon(exp)}} = \mathbf{exp}\left(-\sum \mathbf{p_i} \ln(\mathbf{p_i})\right)$$

The Simpon index (Simpson, 1949), another commonly used measure of α-diversity, measures the probability that two individuals randomly selected from a sample will belong to the same species or another defined category. The Simpson Index is a measure of dominance; whereas species richness is particularly sensitive to rare species and the Simpson Index favours common (including dominant) species, $D_{Shannon}$ is a measure of diversity that weighs all species proportionately to their frequencies in the sample (Jost, 2006). Hence Shannon measures are intermediate between species richness which gives more importance to rare species and the Simpson Index, instead focussed more on dominant species. In this chapter only the Shannon Index in its exponential form (Equation 3.4) is employed for α-diversity. This index is extensively used as a measure of diversity in terms of uncertainty / information (e.g. about the identity of the specimen sampled) not only in biology, but in physics, mathematics (Jost, 2006) and information theory (Shannon, 1948). In order to include a measure of equitability or evenness, the

Shannon Evenness is also calculated (Equation 3.5), an index of similarity between the relative abundance of species (here also used for genera).

Equation 3.5:

$$\textbf{Shannon Eveness} = \frac{\mathbf{D_{Shannon}}}{\ln(\textbf{Species Richness})}$$

The Shannon Diversity (ShD) and Shannon Evenness (ShE) indices of diversity in the merged datasets (species richness changes within campaigns are shown in section 5.2.1) were calculated with the software EstimateS (Colwell, 2000) using raw counts of all algae identified at species and genus level. The Chao 1 species richness estimator was calculated by means of EstimateS (Colwell, 2000) as per Equations 3.6, 3.7 and 3.8 and the resulting graphs plotted using Excel® (version 2010).

The results of the index calcuations for species and genera are compared across regions, flood class, seasons and habitats to highlight differences in diversity patterns in relation to the precision of taxon identification; boxplots and histograms are generated in SPSS (version 22.0) or in Excel® (version 2010) (e.g. Figure 5.28 and results on richness estimators) and statistical tests are undertaken in SPSS (version 22.0). Values that are suspected outliers are indicated by asterisks and very suspected outliers by circles in the boxplots (SPSS Inc., 2008). Appendix D lists sample codes shown in boxplots in Chapters 4 and 5. Standard deviation (s.d.) and coefficient of variation (c.v.) are used to compare the variations in algal diversity and algal biovolume observed. It should be noted that species richness includes the algae identified to species level and those identified to genus counted as a species, albeit unidentified, e.g. *Mougeotia* spp. or *Cryptomonas* spp. were counted as two genera and two species. Here the diversity at species and genus level are analysed in detail and hence only the counts of algae identified to respectively species and genus level are considered; thus the number of identified species and genera are lower than species and genera richness (see section 5.2.1). Both Shannon Diversity and Shannon Evenness indices are calculated so as to fully account for rare species and evenness, i.e. equitability or similarity between species and genera relative abundance.

Estimated taxon richness

The results on algal species richness and diversity presented in section 5.3 stem from enumeration and identification of algae in water samples and are an estimation of the number of taxa actually living in the Delta. Estimating the diversity of microorganims such as (micro)algae is of interest to understanding factors and processes influencing it and the ways in which microbial, e.g. algal, assemblages influence ecosystem functioning (Hughes *et al.*, 2001). To estimate the 'true' diversity of algae including the species not collected or present in the sample, especially rare species (less likely to be sampled), several estimators have been developed (Colwell and Coddington, 1994). Non-parametric estimators, adapted from mark-release-recapture (MRR) statistics for estimating the size of animal populations (Krebs, 1989), are most promising for analysis of microorganisms, for example the Chao1 estimator (Chao, 1984). This is designed for estimations of total species richness from single samples and hence is appropriate for this study; it adds a correction factor to the observed number of species (Hughes *et al.*, 2001).

Parametric estimators use models of relative species abundance such as the lognormal curves, but require well-sampled assemblages, often difficult to obtain for microorganisms (Hughes *et al.*, 2001). Rarefaction is best suited for comparing observed richness among sites sampled in an unequal way, e.g. when sampling effort differs across sites. However, this is not the case in this study, therefore non-parametric estimators such as Chao 1 are used in this section. Algal samples only represent the empirical samples and not the ecological samples (Magurran and McGill, 2004); certainly more species than those observed in this study live in the Delta. Hence, estimators of the total number of species of algae in the locations and times of sampling, i.e. the species richness of ecological samples, are also employed so as to provide an estimate of the unknown algal biodiversity (Magurran and McGill, 2004) in terms of species and genera.

Log-linear 95% confidence intervals suggested by Chao (1987) are used. The lower bound of these asymmetrical confidence intervals, based on the assumption that log (S_{Chao} - S_{obs}) is normally distributed, is lower than the observed number of species in all samples pooled, S_{obs}. The Chao 1 (Equation 3.6) estimator in its refined version (EstimateS, 2013) is used to calculate the mean total species richness:

Equation 3.6:

$$S_{Chao1} = S_{obs} + \left(\frac{n-1}{n}\right)\frac{F_1(F_1-1)}{2(F_2+1)}$$

F_i is the number of species that have exactly *i* individuals when all samples are pooled; i=1, 2; F_1 (singletons or uniques) and F_2 (doubletons or duplicates).
The Lower and Upper Bounds for Chao 1 estimators with 95% confidence intervals are estimated by means of Equation 3.7 and 3.8.

Equation 3.7:

$$\text{Lower 95\% Bound} = S_{obs} + \frac{T}{K}$$

Equation 3.8:

$$\text{Upper 95\% Bound} = S_{obs} + TK$$

where

$$T = Chao_1 - S_{obs}, \text{ and } K = \exp\left\{1.96\left[\log\left(1 + \frac{\text{var}[(S]_{Chao_1})}{T^2}\right)\right]^{\frac{1}{2}}\right\}$$

These techniques are species-based qualitative measures, taking into account only presence/absence data, in particular of species with singletons and doubletons, whereas the Shannon and Simpson indices are quantitative, as they include relative abundance. The Chao 1 species richness estimator was calculated as per Equations 3.6-3.8 by means of EstimateS (Colwell, 2000) and the resulting graphs plotted using Excel® (version 2010).

ß and γ diversity

ß diversity has been defined and used in many different ways creating confusion and obstacles to comparisons between different studies, but it can be simply defined as the variation in community composition (Tuomisto, 2010). α and ß diversity decompose regional diversity into a measure of average single-location (or single-community) diversity and a measure of the relative change in species composition between locations (or assemblages) (Jost, 2007). It is possible to partition γ

diversity into its α and ß components, by summing (additioning partitioning) or multiplying (multiplicative partitioning; Equation 3.9) α and ß diversity. Algal assemblages in the Delta have varying population densities, which influences biovolume (e.g. in XAK algal biomass is significantly lower than in other regions; see section 5.2.5), resulting in unequal statistical weights for different samples or assemblages / communities; hence the only logically consistent measure of ß diversity is the true ß diversity (Equation 3.9) (Jost, 2007; Tuomisto, 2010):

Equation 3.9:

$$\beta_{\text{diversity}} = \frac{\exp(\text{Shannon } \gamma)}{\exp(\text{Shannon } \alpha)}$$

Shannon γ and Shannon α are calculated using Equation 3.3 using respectively relative abundance in the entire dataset and relative abundance of algal taxa within each region, flood class, habitat and season. True ß-diversity (here the Shannon Index is used as per Equation 3.9) is the effective number of distinct assemblages or samples in the region - or the number of compositional units in the dataset (Tuomisto, 2010).

In section 5.2.4, ß diversity was calculated by means of Equation 3.9 using Shannon γ diversity at the numerator. Both results were obtained in Excel®.

Species composition similarity

The similarity in species composition between samples, according to the Bray-Curtis distance, called 'quantitative Sørensen' index (Bray and Curtis, 1957), was calculated via Equation 3.10.

Equation 3.10:

$$BC_{ij} = \frac{2C_{ij}}{S_i + S_j}$$

Where C_{ij} is the sum of the lesser value for only those species in common between both sites. S_i and S_j are the total number of specimens counted at both sites. This measure takes values between 0 (samples completely disjoint) and 1 (samples identical); it is regarded as being robust to non-linear species responses (Gauch and

Whittaker, 1972), more so than other measures such as Chord distances, Chi-squared and Euclidean distances (Faith *et al.*, 1987).

Both the additive (γ diversity as the sum of α and ß diversity) and multiplicative partitioning approaches belong to the proportional diversity domain alongside the calculation of the slope of the species-area curve (Jurasinski *et al.*, 2009). Beyond proportional diversity, the other two categories of ß diversity measures proposed by Jurasinski *et al.* (2009) to clarify hypotheses made in this field are differentiation - resemblance and sum of squares of species matrix - and turnover – gradient length ordination and slope of distance decay relationship / halving distance. The focus of this study is a snapshot assessment of taxon richness and diversity, biomass and distribution of algae; here an ecological interpretation as to why certain ß-diversity and similarity levels are observed is attempted, also referring to results presented in sections 5.2.1, 5.2.2 and 5.2.3.

3.8. UNIVARIATE AND MULTIVARIATE STATISTICAL ANALYSES

Firstly, correlation coefficients give an indication of associations between environmental variables and between these and response variables such as algal biomass and species richness; in Chapter 4 these are supplemented by Principal Component Analysis (PCA). Secondly, ordination analyses such as Redundancy Analysis (RDA) are appropriate to explain species distribution patterns from multivariate datasets of, e.g., algal counts and biovolume estimates, as opposed to the Multivariate Regression Trees (MRT) (De'Ath *et al.*, 2002) which focus more on prediction (Borcard and Legendre, 2002) (Chapter 6).

Correlation analyses were undertaken using SPSS® (version 22.0). Kolmogorov-Smirnov tests (K-S) are performed to establish which variables are normally distributed. Pearson product-moment correlation (PPMC) coefficients are calculated between normally distributed variables whereas Spearman Rank correlation coefficients are used for not normally distributed variables (Dytham, 2011). Water temperature, depth, conductivity, DO, pH, TP data were collected for the great majority of samples whereas water chemistry was available only for Campaign 1, apart from Chl *a* (available only in Campaign 2) and TP (available in both campaigns) (see Table 3.12). Hence, separate correlation tables are shown so as to best describe the environmental variations. PCA, RDA, VPA and species response

curve analyses were all performed in R (R Core Team, 2013) with packages 'vegan' (Oksanen *et al.*, 2013) and 'eHOF' (Jansen and Oksanen, 2013).

Multivariate (multiresponse) analyses such as ordination techniques (Principal Components Analaysis and Redundancy Analysis, hereafter respectively PCA and RDA) are used to model how the measured environmental variables influence algal species, genera, other groups and phyla distribution in terms of taxon relative abundance (%) and biomass share (as estimated by biovolume) (%).
The data used for this analysis at whole Delta scale were limited to six environmental variables (conductivity, depth, DO, pH, temperature and TP), several categorical factors (region, habitat types, flood class, floodplain type, season and flood year) and the geographical coordinates of the sampling points taken by means of a GPS, important to account for spatial autocorrelation (Legendre, 1993; see subsection "*Variation Partitioning Analysis*"). For Campaign 1, water chemistry data allow for a more in-depth investigation regarding which nutrients (TN, TP, SiO_2, anions – Cl^-, HCO_3^-, $PO4^{2-}$, $SO4^{2-}$ - and cations – Na^+, Ca^{2+}, K^+, Mg^{2+}) may be more important in determining community composition, biomass and diversity. For Campaign 2 only TP concentrations could be measured and evaluated.

All non normally distributed variables were log-transformed for inclusion in PCA and RDA. PCA is a classical ordination method, whereas RDA combines multiple regression with classical ordination (Borcard *et al.*, 2011). The statistical significance of the ordination axes was tested with permutation tests (max permutations = 999). Variation Partitioning Analysis (VPA; Borcard *et al.*, 1992) was used to establish which proportions of the variation in the relative abundance and biovolume of algal taxa, as well as species richness and total biovolume, are explained by limnological variables and environmental factors (e.g. habitat type), spatial component (coordinates of sampling points) due to spatial autocorrelation (i.e. more similar community composition, richness or biomass may be due to spatial proximity) and a combination of spatial and environmental components.

Principal Component Analysis (PCA)

In Chapter 4, PCA is used to describe and explore the environmental variations in the Delta, in particular in relation to its limnological features. The first two major

components (PCA axes 1 and 2) are analysed to highlight significant gradients created by the interplay of environmental variables highly correlated to them. In PCA, species or environmental variables can be modelled in unconstrained form, with the major axes representing supercomponents of variation in environmental gradients; the eigenvalues of the first two axes are compared to the ones generated by a broken-stick model (MacArthur, 1957) to test their significance (Jolliffe, 1986). The broken-stick is a null model of community structure which predicts the distribution of the relative abundances of species (i.e. dominance/diversity relations) when resources are partitioned into niches at random (Wilson, 1993).

Redundancy Analysis (RDA)

In Chapter 6, a sequence of RDAs are undertaken to investigate the distribution of algal taxa (species, genera, phyla and other groups) across the environmental gradients identified. In RDA ordination axes are created by means of linear combinations of known environmental variables so that community variations can be related to environmental changes. Algal species, genera, other groups and phyla are assumed to have Gaussian shaped (unimodal) response surfaces in relation to linearly compound environmental gradients which constrain the main axes of variation, i.e. this model assumes the same response model for all species (ter Braak, 1986). RDA truly explains the variation of the dependent matrix of transformed count data via the use of linear combinations of environmental (explanatory) variables which constrain the axes and best explain the variation of the response matrix; the unexplained variation is expressed by the unconstrained PCA eigenvalues (Borcard *et al.*, 2011).

In this study, the abundance of algal taxa in relation to single environmental variables has a rather linear or unimodal distribution, but with a few high abundance points hence RDA on transformed data is an appropriate method. Hellinger transformation was performed on raw counts and biovolume estimates, as it is adequate for RDA and related variation partitioning and for datasets with numerous zero-values (Legendre and Gallagher, 2001; Borcard and Legendre, 2002). In community composition datasets species usually have unimodal distributions along environmental gradients; hence, many species (and taxa more in general) are absent in sites far from their optimal living conditions, generating a large number of zero

values (ter Braak and Prentice, 1988). Due to the fact that algal abundance data were strongly skewed with many rare species present (see Figure 4.2, section 4.4) and that log transformations on count data has been recently shown to perform poorly (O'Hara and Kotze, 2010), these were transformed using the Hellinger distance transformation (Rao, 1995). This first requires the raw count data to be pre-transformed taking the square root of the relative abundance per site (Equation 3.11) and then calculate the euclidean distance as per Equation 3.12 (Legendre and Gallagher, 2001).

Equation 3.11:

$$y_{ij}' = \sqrt{\frac{yi_j}{yi+}}$$

where y1+ and y+ are the total algal abundances at each site (i to p).

Equation 3.12:

$$D_{Hellinger}(x1, x2) = \sqrt{\sum_{j=1}^{p}\left[\sqrt{\frac{y1_j}{y1+}} - \sqrt{\frac{y2_j}{y2+}}\right]^2}$$

The Hellinger transformation represents a better compromise between linearity and resolution than chi-square metric and chi-square distance, especially in datasets with many zero-values in the algal abundance and biovolume datasets (Legendre and Gallagher, 2001).

RDA was conducted using this transformed raw abundance and biovolume data and the continuous environmental variables available for the two datasets (temperature, depth, conductivity, DO, pH, and TP), as well as the water chemistry data collected for Campaign 1. Redundant variables were removed through a step-wise selection procedure implemented by the R function "ordistep" which runs a combination of backward and forward selection by means of the "vegan" package, with which all the ordination analyses were conducted (Oksanen *et al.*, 2013). This ensures that a minimum number of variables that significantly explain variation in the algal data are used in the RDA analyses; F-statistics and, if F is equal, the Akaike Information

Criterion (AIC) values was used to choose the most significant variables for inclusion in the RDA (Borcard *et al.*, 2011). The p-value was set to 0.01, analogously to the other analyses in this study. RDA was run on a correlation matrix, i.e. centering and standardising the variables (Borcard *et al.*, 2011). Permutation tests to assess the significance of the canonical axes were performed in order to counter widespread problems of non-normal distributions in ecological data; these allow to establish to what extent the constrained (canonical) axes of the RDA better explain the variation in the response variables than random factors represented in the residual unconstrained axes (Borcard *et al.*, 2011).

Variation Partitioning Analysis (VPA)

In Chapter 6, VPA (Borcard *et al.*, 1992; Borcard and Legendre, 2002) was used to evaluate what portions of the algal taxa variations can be attributed to spatial (location of sampling points) and environmental factors and their joint effects. VPA was applied to community data, environmental data and spatial predictors. As spatially heterogeneous ecological structures can originate from physical forcing of environmental variables or from processes within assemblages, ecological models must be spatially explicit, i.e. take into account how ecosystems are spatially structured (Borcard and Legendre, 2002). This overcomes the problem of spatially autocorrelated data; in fact most statistical testing techniques assume independence of observations (Legendre, 1993). Site proximity may be responsible for community trends attributed to environmental variables, hence over-interpreting the latter can be avoided by partialling out the spatial component, i.e. geographical location of sampling sites (Legendre, 1993). Here, Principal Coordinate Analysis (PCoA) was performed on Euclidean distances between the geographical GPS coordinates of the sampling points, following Borcard and Legendre (2002). This yielded spatial predictors for partial RDA analysis (pRDA), i.e. VPA (Borcard *et al.*, 1992) which were used to explain abundance and biovolume data alongside the environmental variables which constrain the variation in data on algal species, genera and phyla. Partial ordination (pRDA) was employed so that conditioning variables are analysed together with constraints, after selection of non multicollinear explanatory variables within the environmental variable dataset by means of step-wise selection using the R function “ordistep” with 499 permutations (Oksanen *et al.*, 2013). In such partial

ordination techniques, conditioning variables are analysed together with constraints; all the environmental variables were analysed together as the environmental component of variation as well as single constraints. The statistical significance of the variation partitioning was tested with RDA and embedded permutation tests (max permutations = 999).

Only the step-wise selected variables were used in order to account for multicollinearity; moreover, $AdjR^2$ values can be negative in which case they are considered null for the ecological interpretation, as random factors are more important than the variables considered (Oksanen *et al.*, 2011). Multicollinear variables were discarded using the Variance Inflation Factor (VIF), if not already excluded by step-wise selection; variables with a VIF higher than 10, indicating redundant constraints, were eliminated from the RDAs (Oksanen *et al.*, 2013).

Species Response Curves

The relative abundance of the most important algal taxa (i.e. abundant and common, hence species present in numerous sites thus having high total abundance in the Delta) is analysed in relation to limnological variables. The distribution of the most common species and genera is analysed by means of hierarchical logistical regression models, a type of species response curve approach, the Huisman–Olff–Fresco models (HOF) which fits the observations by means of logistic and non-linear regression techniques (Huisman *et al.*, 1993). These models were chosen because they can be applied to positive data with an upper bound, i.e. maximum abundance or 100%, such as the relative abundance / frequency of algal taxa in different sites (%).

HOF models are able to analyse the niche widths of species along the observed gradient; bootstrapping these models makes the model selection more reliable, especially for unbalanced samples and rare species (Jansen and Oksanen, 2013). Furthermore they have been shown to perform better than Generalised Linear Models (GLMs) (Oksanen and Minchin, 2002) and their non-parametric extension, Generalised Additive Models (GAMs) (Jansen and Oksanen, 2013) based on smoothers (Yee and Mitchell, 1991). The most frequent model type of the bootstrapped random data sets was chosen if it was different from the originally estimated model type selected on the basis of the AIC criterion. In the random runs

original occurrences were re-sampled with replacement until the original number of occurrences was reached (Jansen and Oksanen, 2013).

The R package "eHOF" (Jansen and Oksanen, 2013), which extended the set of models from five to seven (Huisman *et al.*, 1993), was employed to analyse species and genera responses for the six limnological variables, i.e. water depth, temperature, conductivity, DO, pH and TP – which, overall, were available for almost all samples in this study (see Table 3.12). The features of the seven models are as follows. Model type number I is a flat response, with no significant trend along the gradient for that species. It represents a null hypothesis so that only species with a clear response are modelled with one of the further model types. Shape II is monotone sigmoid with a top at one end of the gradient, III is a monotone sigmoid which plateaus below the maximum abundance value. Model type IV is the canonical form of species response, a unimodal symmetric model, V is a unimodal skewed model. The two additional models (VI and VII) represent bimodal responses with two optima, VI with tops being equal; these can appropriately account for extremes of the ecological gradients, usually not captured by the other models (Jansen and Oksanen, 2013), but usually important for numerous taxa due to intense competition at intermediate values of a given environmental variable (Hardin, 1960). Figure 3.6 shows examples of all the seven models from Jansen and Oksanen (2013).

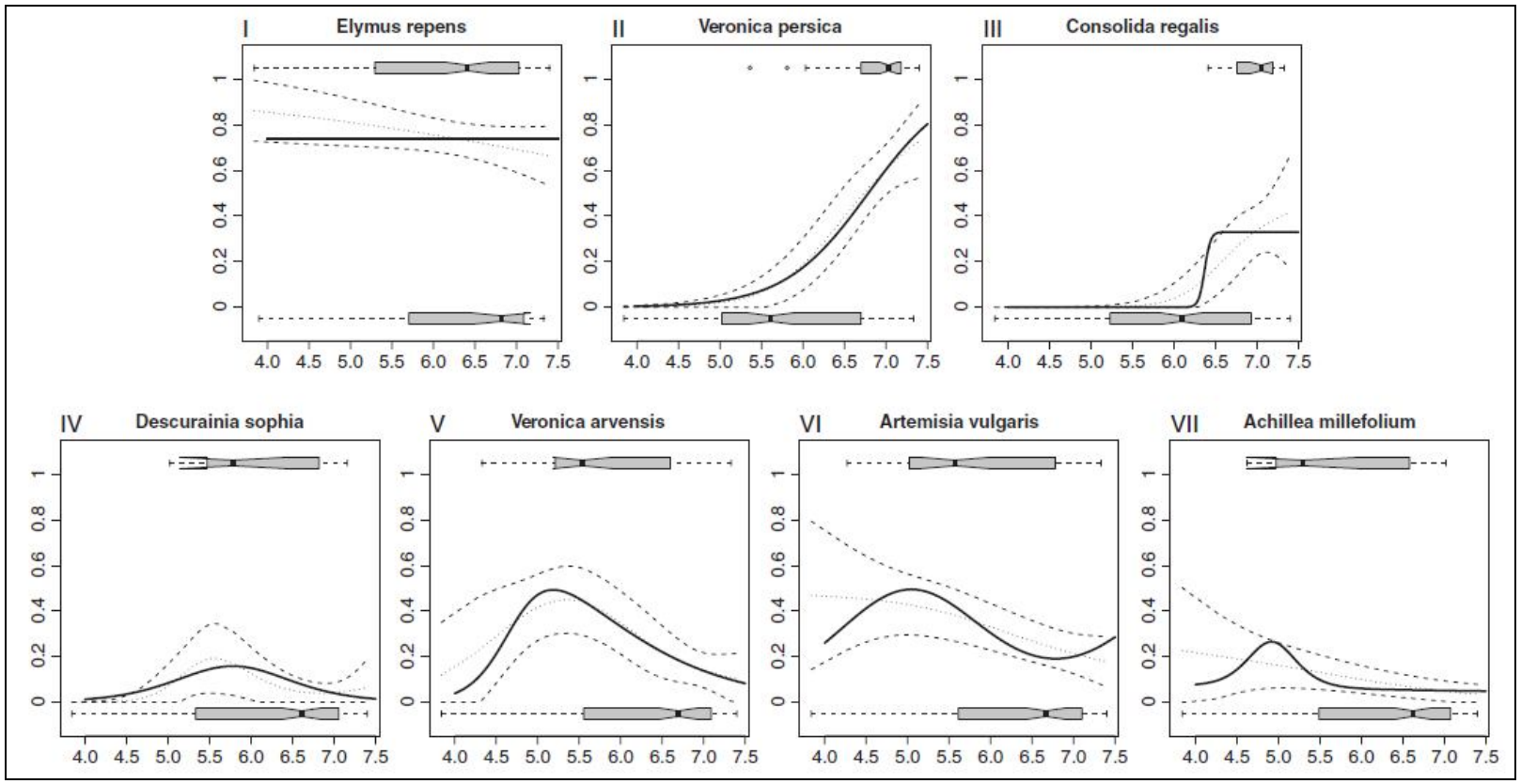


Figure 3.6. Examples of HOF models for a pH gradient

(horizontal boxplots represent absences (y = 0), respective occurrences (y = 1) of the respective species along the gradient. Source: Jansen and Oksanen, 2013).

Chapter 4 – Algal flora and limnology of the Okavango Delta

4.1. PREVIOUS RESEARCH IN THE DELTA

Algae, as discussed in Chapter 1, are primary producers at the base of aquatic food-webs on which numerous species of fish rely, and provide important ecosystem services such as food and habitat provision, water purification (Cardinale, 2011). These microorganisms are particularly relevant as producers for the largely pristine Okavango Delta where many village communities rely on fisheries as one of their sources of livelihood (see section 1.1). The generation of new knowledge on algal assemblages in un-impacted freshwater ecosystems and the understanding of food web structure and functioning is crucial (Stendera *et al.*, 2012), especially in semi-arid regions such as Southern Africa. In order to provide original insight into the algal assemblages of the Delta, systematic analyses of data on the presence and abundance of different taxa and the limnological, flooding and habitat characteristics of the sampling sites were undertaken (see Chapter 3). This chapter fulfils objective 4 to characterise the Delta's limnology which is essential to understand how algae are distributed in the sites sampled; the algal count results are also illustrated.

The results of previous works on the Delta's limnology and algae are summarised here. Prior to the start of this Ph.D. extensive studies of the hydrochemistry of the Delta (Mackay *et al.*, 2011), its diatoms (Mackay *et al.*, 2012) and macroinvertebrates (Davidson *et al.* 2012) were conducted as part of a Darwin Initiative project (Mackay *et al.*, 2009). Mackay *et al.* (2012) investigated periphytic diatom samples from 53 sites taking 5-cm sections of dominant macrophyte species, cutting them *c.* 20 cm below the water surface (avoiding dead stems, new shoots and recently wetter sections resulting from rising water level). These are not only epiphytic algae as water from the sampling points was used to

obtain a good representation of diatoms living attached to or around plants (Mackay, personal communication).

Earlier research activities on algae in the Okavango Delta included a specific diatom survey (Cholnoky, 1966a) and an investigation of water chemistry, bacteria and phytoplankton (Cronberg *et al.*, 1996a). Cholnoky (1966) found 327 species of diatoms belonging to 32 different genera in the Okavango Delta and numerous upstream areas in Namibia, such as the Omatako river and the ancient Omuramba river, and downstream sites on Ngami Lake and the Thamalakane river. Genera with 10 or more species include: *Navicula* (101 spp.), *Nitzschia* (41 spp.), *Pinnularia* (29 spp.), *Eunotia* (25 spp.), *Stauroneis* (20 spp.), *Cymbella* (19 spp.), *Gomphonema* (14 spp.), *Achnanthes* (10 spp.) and *Fragilaria* (10 spp.) (Cholnoky, 1966a). Cronberg observed over 198 species of algae (Cronberg *et al.*, 1996a/b) of which 50 were common in the Jao/Boro region during a study on water chemistry and algal populations. 58 samples were collected from river channels, 118 from swamps and 37 samples from isolated pools in four seasons: November 1991, March 1992, June 1992 and October-November 1992; river channel samples contained about half the number of taxa (*c.* 25 genera and species) compared to swamps and floodplains (*c.* 52 taxa), while 37 taxa were found in isolated pools (Cronberg *et al.*, 1996a). In lagoons, desmids, e.g., *Staurastrum*, and other green algae such as *Mougeotia*, *Spirogyra* and *Botryococcus* were abundant with lower numbers of *Synedra* spp., cryptomonads and *Peridinium* spp. (dinoflagellates).

Algal biomass levels reached a maximum 45 mg L^{-1} in swamps, much higher than the usually lower than 1 mg L^{-1} biomass found in the river channels (Cronberg *et al.*, 1996a). The site with the highest algal biomass (65 mg L^{-1}) was in the isolated pools though; Euglenophyta and Cyanophyta were observed (in high abundance) almost only in these sites, supported by high levels of nitrogen and phosphorus, and accompanied by desmids and diatoms (*Cyclotella*, *Synedra* and *Melosira* being the most abundant) (Cronberg *et al.*, 1996a). Benthic and periphytic algal assemblages developed in the swamps and isolated pools, while true phytoplankton was present only in deep lagoons and isolated water bodies. The species found in Cronberg's research were widely distributed in tropical freshwater environments, such as Zambian Lakes Shiva and Bangwelu (Thomasson 1957), the Amazon River (Foster 1969a; 1969b; Thomasson, 1971) and the Alligator River in Australia (Ling and

Tyler, 1986). Cronberg *et al.* (1996a) concluded that desmids, overall the most abundant group of very frequently benthic algae, diatoms and chrysophytes are able to survive and reproduce due to their ability to produce resting cysts. However, the studies above mentioned were not very extensive; Cholnoky (1966) analysed only a few samples from the Shakawe (UPH), Maun and Ngami lake areas, while Cronberg *et al.* (1996a/b) sampled in the Boro region and was more focussed on water chemistry than phytoplankton analyses.

Much more recently, Mackay *et al.* (2012) found 164 species (167 taxa including varieties) of periphytic diatoms in the Delta in 100 sample points and demonstrated the sensitivity of diatoms to TN and SiO_2 concentrations, variables in turn influenced by the hydrological cycle. Mackay *et al.* (2011) highlighted significant changes in the chemical variables monitored across regions and flood phases. They confirmed what had emerged in earlier works about hydrochemistry in the Delta: conductivity is low, bicarbonates of Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}, SiO_2, DOC and NO_3^{2-} increase towards the distal reaches of BOR and SAN (Dinçer et al, 1978 in Mackay *et al.*, 2011; McCarthy and Ellery, 1994; Cronberg *et al.*, 1996a). Akoko *et al.* (2013) demonstrated that seasonally inundated floodplains have higher dissolved inorganic carbon (DIC) concentrations - by respectively 70% and 331% in the low and high water phase - than the Panhandle permanently flooded areas. This is due to the fact that the Delta's distal reaches experience higher evapotranspiration due to longer hydraulic residence times (Akoko *et al.*, 2013). As observed by Cronberg *et al.* (1996a), HCO_3^{-} showed the highest concentrations (over 90%) among anions throughout the Delta.

Macronutrients such as TN and TP showed a higher TN/TP ratio by mass (20.4) in the Boro region (BOR) than in the Panhandle (UPH and LPH) and Xakanaka (XAK) (on average 13.7); this suggests potential P limitation in BOR (Mackay *et al.*, 2011) and co-limitation of Nitrogen and Phosphorus in the other regions (Abell *et al.* 2010). The trends of nutrient concentrations and TN:TP ratio recorded in this study are presented in section 4.9 and discussed in section 6.4 in relation to algal distribution and other environmental variables and factors. The oligotrophic character of the Delta (Mitsch and Gosselink, 2000; Ramberg and Wolski, 2008) and the long-term survival of its ecosystem are also due to the low amounts of allochthonous mineral matter, as uptake of soluble ions by the peat is key to off-

setting the high levels of metals due to evaporative concentration (McCarthy *et al.*, 1989). The formation of islands in this wetland also permanently removes large amounts of salts from the surface waters hence contributing to its generally agreed oligotrophic status (Ramberg and Wolski, 2008; see section 2.8). However, Junk *et al.* (2006) define this wetland as mesotrophic, presumably on the basis of the high productivity of its floodplains.

In the Okavango Delta, conductivity has been shown to vary significantly between the permanent (perennial) and seasonal swamps, with higher values in the latter environments; Cronberg *et al.* (1996a) measured values of between 105 and 114 μS cm^{-1} in seasonally flooded channels and swamps as compared to 39-69 μS cm^{-1} in perennial swamps, with higher conductivity in swamps than channel habitats. Mackay *et al.* (2011) observed average conductivity values of about 80 μS cm^{-1} in BOR as compared to c. 40 μS cm^{-1} in UPH and LPH (a subset of their data was used for this study - Campaign 1).

4.2. AIMS AND RATIONALE

The aims of this chapter are to (i) present the overall results of algal analyses in terms of abundance (section 4.4 and 4.5) and total species / genera richness and phylum species richness (section 4.6); ii) compare this study's species list (Appendix B) with previous surveys on algae conducted between 1966 and 2012 in the Okavango Delta and Okavango River Basin (section 4.7); iii) investigate distribution patterns of ecologically important traits of algae, such as motility, nitrogen fixation and silica requirements (section 4.8); iv) provide insight into the significant limnological variations across the Okavango Delta (section 4.9). The Thesis objective 1, 2 are addressed, in particular in relation to the assessment of taxon (species and genera) richness in both Campaign 1 and Campaign 2; objective 3 is also dealt with, i.e. to characterise the Delta's hydrology and limnological conditions (section 2.3).

Physical measurements such as water depth, pH and temperature (available for most of the samples) and concentrations of anions and cations (e.g. Ca^{2+} and HCO_3^-) are essential to characterise the sampling sites and explain variations of response variables such as algal relative abundance, species richness and biomass. Limnological data (see section 4.9) are first analysed separately in Campaign 1 and

Campaign 2 as different algal sampling methods were used and the limnological data available are different (see Table 3.12). Once the datasets are merged patterns are either confirmed or change according to, for example, spatial scale issues, i.e. Campaign 1 was conducted over the whole Delta, while Campaign 2 was focussed on the floodplains of the distal reaches (BOR and SAN regions). The methods used to produce the data are discussed in sections 3.1 to 3.3 (sampling and microscopy), 3.5 (limnological variables) and those for statistical analyses in section 3.6.

4.3. RESULTS: ALGAL COUNTS

In this section the general results of counts of algae are shown, first in the merged datasets to give an overview, then describing differences between the two campaigns. A total of 49,970 algal units were counted from 132 samples collected in Campaign 1 and Campaign 2. Chlorophyta and Bacillariophyta (diatoms) constitute 38.9% and 43.3% of the total algal units respectively, Cyanophyta 6.9%, Cryptophyta 5.6% and Euglenophyta 3.2% (Figure 4.1).

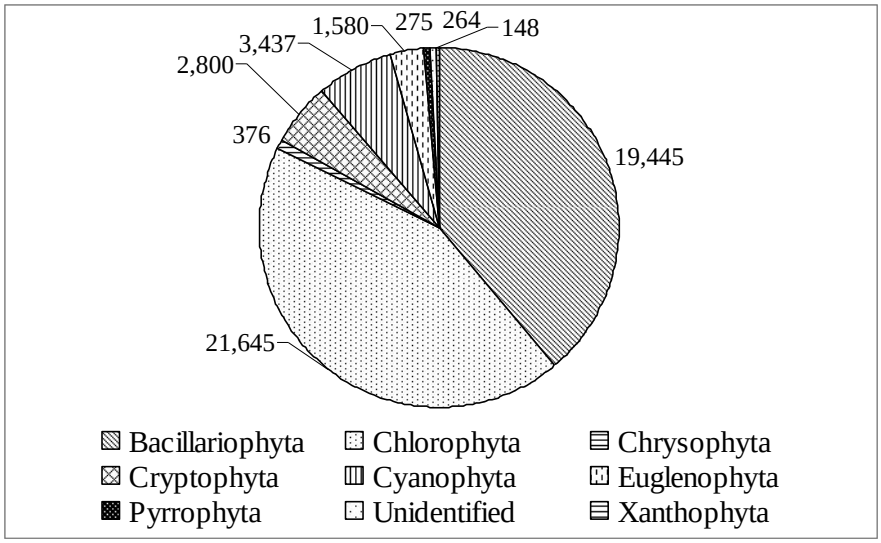


Figure 4.1. Number of algal units counted in all the samples.

Overall, Bacillariophyta (diatoms) are the most abundant algal phylum in Upper Panhandle (UPH), Lower Panhandle (LPH), and Xakanaxa (XAK) while Chlorophyta (green algae) are the most abundant phylum in Boro (BOR) and, to a lesser extent, Santantadibe (SAN). Cryptophyta (Cry), Cyanophyta (Cya), Euglenophyta (Eug), Pyrrophyta (Pyr) and Xanthophyta (Xan) are much more abundant in BOR and SAN than in UPH and LPH (also due to more numerous

samples collected in the former regions); Chrysophyta (Chr) are most abundant in XAK (see summary in Table 4.1).

Table 4.1. Number of algal units counted per phylum in the regions sampled [Bac= Bacillariophyta; Chl=Chlorophyta; Chr=Chrysophyta; Cry=Cryptophyta; Eug= Euglenophyta; Pra= Prasinophyta; Pyr=Pyrrophyta; Uni=Unidentified; Xan=Xanthophyta].

Regions	**Bac**	**Chl**	**Chr**	**Cry**	**Cya**	**Eug**	**Pra**	**Pyr**	**Uni**	**Xan**	**Total**
UPH	4,407	1,095	14	133	214	36	0	12	13	7	5,931
LPH	2,560	839	30	281	132	34	0	9	8	6	3,899
XAK	2,196	1,108	230	365	192	102	0	67	1	11	4,272
BOR	6,190	14,068	81	1,404	2,277	762	0	115	182	95	25,177
SAN	3,918	4,311	21	617	605	647	1	72	60	28	10,282
NGA	179	217	0	0	17	0	0	0	0	1	414
Total	**19,450**	**21,638**	**376**	**2,800**	**3,437**	**1,581**	**1**	**275**	**264**	**148**	**49,975**

A total of 15,203 individual algae (30.5%) were identified at species level; 29,682 (59.6%) at genus level, and 4,647 (9.3%) at the level of order or phylum or generic group (e.g. Pennate Diatom). A total of 496 species belonging to 173 genera of algae were observed. The majority of the taxa identified belong to Chlorophyta and Bacillariophyta: 396 species (80%) and 126 genera (72%). Respectively 97 species and 48 genera belong to the other phyla (Table 4.2). 30.1% of Bacillariophyta and 37.4% of Chlorophyta were identified at species level. Appendix B and Appendix C respectively show the full list of species observed and of other genera identified not included in the species list, i.e. a significant number of algae could not be reliably identified to species level due to their small size or to the limits of using 400x magnification, notably for diatoms, or to the turbidity of samples. Of the 496 algal species found in the samples 423 species were identified to species level (Appendix B) and 73 species identified to genus level (Appendix C) (Table 4.2).

Table 4.2. Number of species and genera identified per algal phylum in all the samples.

Phylum	**N Species**	**%**	**N Genera**	**%**
Bacillariophyta	113	22.6	37	21.4
Chlorophyta	283	57.1	86	49.7
Chrysophyta	8	1.6	7	4.0
Cryptophyta	11	2.2	3	1.7
Cyanophyta	28	5.6	22	12.7
Euglenophyta	37	7.5	6	3.5
Prasinophyta	1	0.2	1	0.6
Pyrrophyta	8	1.6	7	4.0
Xanthophyta	7	1.4	4	2.3
Total	**496**	**100.0**	**173**	**100.0**

Regional Species Richness (RSR), i.e., the total number of species identified in the samples per region, is 92 and 84 in UPH and LPH, 89 in XAK, 331 and 261 in BOR and SAN. Also, in UPH, LPH and XAK 84, 83 and 87 genera were observed, whereas BOR and SAN host 139 and 109 algal genera respectively. These total figures are used to calculate the average number of species per region for comparison with taxon richness estimators (see section 5.2.3) and are relevant for the discussion of richness and diversity patterns at different spatial scales (see section 5.3.1). Moreover, 60 species and one genus (*Phymatodocis*) of desmids were identified in a few Campaign 2 samples by David Williamson beyond those observed in this study (unpublished data; see Appendix H).

Clear differences emerge between the two datasets (Figure 4.2), connected to the different proportion of samples taken in the five regions in the two campaigns. The 63 samples taken across the whole Delta (Campaign 1) show a much higher proportion of diatoms (54%) than green algae (29%); in the 69 samples collected in Campaign 2 green algae largely prevail (55%) over diatoms (26%). Three algal phyla have significantly different species richness between the two campaigns. Bacillariophyta had a higher species richness in Campaign 1 (L. test: $p>0.01$; O.W.A. test: $F= 16.255$; $p<0.001^{**}$; M.W.U test: $p<0.001^{**}$), whereas Chlorophyta species richness was higher in Campaign 2 (K.W.: $\chi^2= 56.771$; $p<0.001^{**}$; M.W.U test: $p<0.001^{**}$) and Cyanophyta showed a similar trend to Chlorophyta (K.W. test: $\chi^2= 21.298$; $p<0.001^{**}$; M.W.U test: $p<0.001^{**}$).

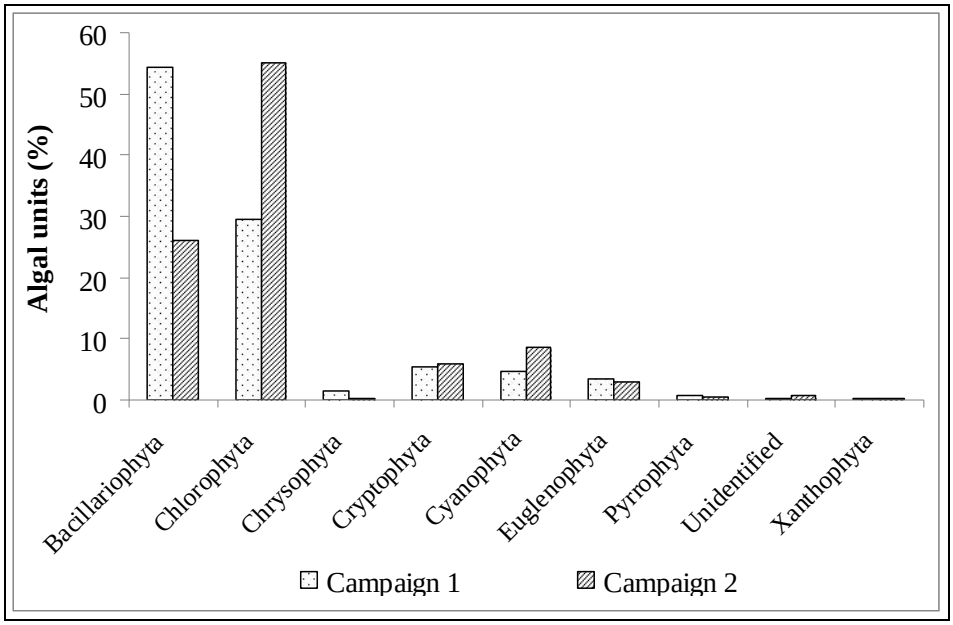


Figure 4.2. Percentage of algal units per phyla in the two datasets.

A total of 291 species belonging to 142 genera were identified in samples collected in Campaign 1 (Table 4.3).

Table 4.3. Number of species and genera identified per algal phylum in Campaign 1.

Phylum	**N Species**	**%**	**N Genera**	**%**
Bacillariophyta	72	24.7	33	23.2
Chlorophyta	154	52.9	65	45.8
Chrysophyta	4	1.4	5	3.5
Cryptophyta	6	2.1	3	2.1
Cyanophyta	16	5.5	18	12.7
Euglenophyta	26	8.9	6	4.2
Prasinophyta	1	0.3	1	0.7
Pyrrophyta	6	2.1	7	4.9
Xanthophyta	6	2.1	4	2.8
Total	**291**	**100.0**	**142**	**100.0**

Algae identified in Campaign 2 belong to a higher number of species, 442, but to a rather similar number of genera, 152 (Table 4.4).

Table 4.4. Number of species and genera identified per algal phylum in Campaign 2.

Phylum	**N Species**	**%**	**N Genera**	**%**
Bacillariophyta	88	19.9	30	19.7
Chlorophyta	270	61.1	81	53.3
Chrysophyta	6	1.4	3	2.0
Cryptophyta	10	2.3	3	2.0
Cyanophyta	25	5.7	18	11.8
Euglenophyta	29	6.6	5	3.3
Prasinophyta	0	0.0	1	0.7
Pyrrophyta	8	1.8	7	4.6
Xanthophyta	6	1.4	4	2.6
Total	**442**	**100.0**	**152**	**100.0**

Species accumulation curves, i.e. plots of the number of observed species as a function of the sampling effort required to find and identify them (Colwell *et al.*, 2004), allow the description of the results of taxonomic work in a way that highlights how many new species (or genera) are found in the sequence of samples analysed. Figure 4.3 shows the number of species and genera as they were observed from the first to the last sample counted. The number of genera increases more gradually than does the number of species; whereas in samples 1-64 (Campaign 1) the number of species and genera identified follows a gradually increasing trend, in samples 65-132 the number of species increases following a much steeper curve. Figure 4.3 shows how algal species richness is substantially higher in Campaign 2 samples, i.e. from sample 64 onwards (see also Tables 4.4 and 4.5); this is mainly due to many more desmid species observed than in Campaign 1 samples.

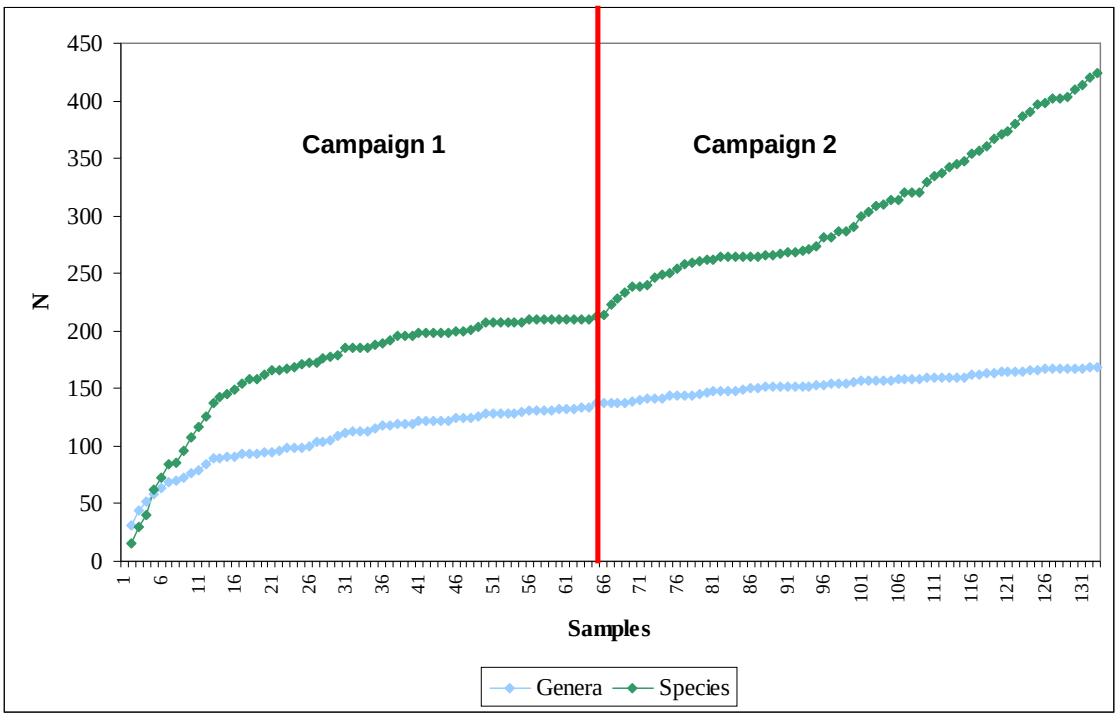


Figure 4.3. Accumulation curve of genera and species identified in the samples analysed (sample 1-63: Campaign 1; sample 64-132: Campaign 2).

4.4. RESULTS: ABUNDANT AND RARE TAXA

The abundance of the 20 most abundant algal taxa in the Delta are shown in Figure 4.4. The thirteen most abundant genera identified in the 132 samples collected are: *Eunotia*, *Mougeotia*, *Cosmarium*, *Gomphonema*, *Synedra*, *Scenedesmus*, *Cryptomonas*, *Nitzschia*, *Aulacoseira*, *Staurastrum*, *Chroomonas*, *Navicula* and *Oedogonium*. The five most abundant algae identified to species level are: *Synedra ulna*, *Monoraphidium arcuatum*, *Monoraphidium griffithii*, *Eunotia pectinalis* and *Eunotia rhomboidea*. Hence six genera and three species of diatoms and five genera and two species of green algae are the most abundant taxa in the Delta; *Cryptomonas* and *Chroomonas* are the only algal genera belonging to another phylum, the Cryptophyta, in the list of the top 20 most abundant taxa. Numerous pennate diatoms and Chroococcales are also very abundant algae which could not be identified to genus or species level (Figure 4.4).

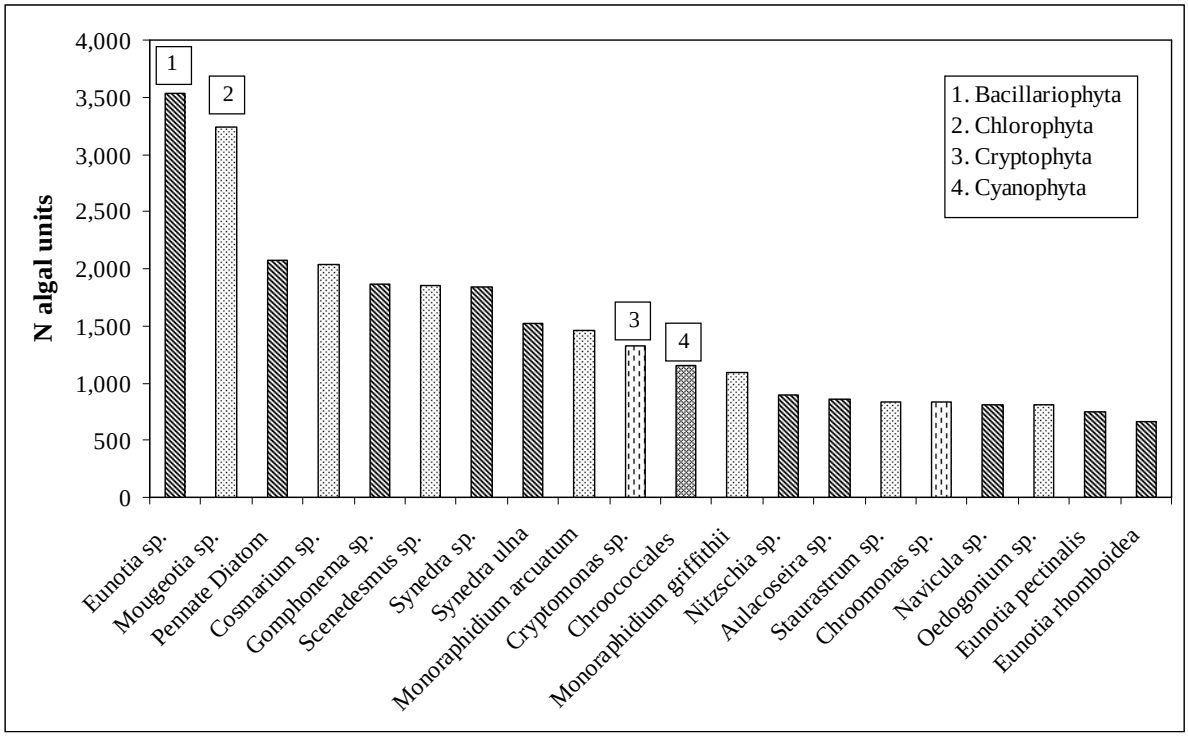


Figure 4.4. The 20 most abundant algal taxa / groups observed in this study (numbers indicating pattern fills corresponding to the relative phylum).

In terms of frequency of occurrence, 5 taxa were observed in at least 120 samples, i.e. *Cosmarium spp.*, *Scenedesmus spp.*, *Monoraphidium griffithii*, *Synedra spp.* and *Monoraphidium arcuatum*; another 11 taxa were found in at least 100 samples in the Delta, of which 5 were green algae, 4 diatoms and 2 cryptomonads (see section 6.3.6 on Species Response Curves).

Overall, most species, and taxa in general, were found in a few sites and in small numbers. Figure 4.5 illustrates how many algal units were identified in four abundance classes (1-10; 10-100; 100-1,000; > 1,000).

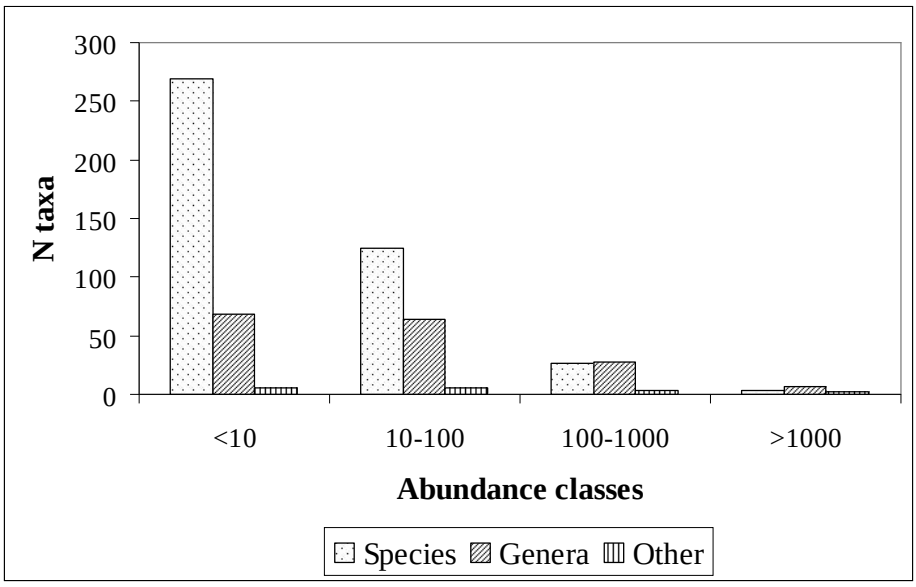


Figure 4.5. Number of species and genera in relation to their occurrence frequency.

Figure 4.6 shows how common algal taxa were in the 132 samples collected from the Delta (1-10 samples; 11-20; 21-50; 51-100 and 101-132 samples).

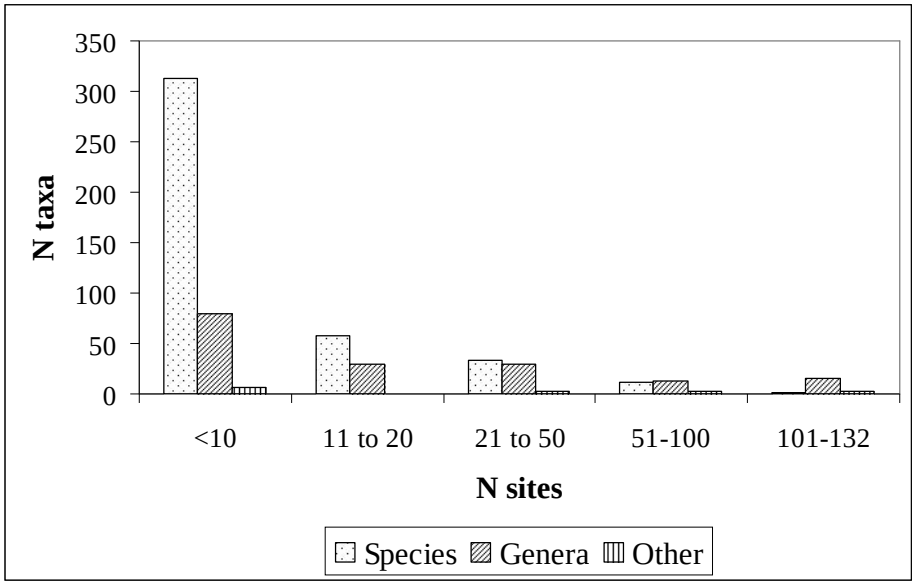


Figure 4.6. Number of algal species, genera and other taxonomic groups found in each occurrence frequency class.

Overall, 374 species were rare, i.e. here defined as present in less than 20 samples, and represented 75.4% of the total number of species observed. Amongst these rare species, 116 were only found once in one sample and 278 species were found in less than 5 samples. Just a few rare species have high local abundance, i.e. *Aulacoseira granulata*, *Rhodomonas lacustris*, *Lyngbya contorta*, *Aulacoseira ambigua*, *Micrasterias foliacea*, *Bambusina borreri*, and *Cryptomonas ovata*; the others are present in low numbers in the (<20) samples in which they were found.

4.5. RESULTS: ALGAL FLORAS IN THE OKAVANGO REGION

In order to place this study in the context of other research on algae in this region, here the species and genera observed in this study (Appendix B) are compared with previous studies on the algal flora of the Okavango Delta. Here, comparisons of algal species lists are made between different studies in the Delta (Cronberg *et al.*, 1996a; Coesel and van Geest, 2008, 2009; Mackay *et al.*, 2012) and between these and investigations including upstream areas of the Okavango River Basin (Cholnoky, 1966a; Grönblad and Croasdale, 1971). Only occurrences of algal species are evaluated as presence/absence data, as a preliminary assessment of similarity of algal communities.

Comparisons between studies in the Delta

In the 1960s Cholnoky observed 327 species of diatoms (32 genera) in the Okavango region, although only a few sites were situated in the Delta with most locations visited being upstream (Cholnoky, 1966). 52 of those species (26% of the total) belonging to 17 genera were also observed in this study. Another five diatom genera were found in this study which could not be identified to species level and also observed by Cholnoky (1966): *Cymatopleura*, *Diploneis*, *Epithemia*, *Melosira* and *Stenopterobia*. Mackay *et al.* (2012) observed 164 species of periphytic diatoms in an extensive Delta-scale study (167 taxa including varieties); 48 of these species (29%), belonging to 17 genera, were also found in this study on algae sampled in water, (phytoplanktonic or benthic ones likely resuspended). Moreover, a total of 29 species, over 50% of those observed by Cholnoky (1966) were also found in this study and by Mackay *et al.* (2012).

In a study on the Delta's ion chemistry, bacteria and phytoplankton, Cronberg *et al.* (1996a/b) found 51 species and 66 genera which were also observed in this study, respectively 10% and 38% of those observed here, i.e. 496 and 173, of which 423 identified as species and 73 only at genus level. In total Cronberg *et al.* (1996b) identified 198 species and 109 genera; the most species-rich phyla in their study were Chlorophyta (55 species), Cyanophyta (26) and Bacillariophyta (8 species).

Desmids, Cholorophyta belonging to the Mesotaeniaceae family (John *et al.*, 2002), were recently studied in the Delta by Coesel and van Geest (2008) which observed 25 species in four sites across the wetland. 9 of these species (belonging to 4

genera), which Coesel and van Geest (2008) found around Chief Island (BOR) were also observed in this study, mostly in BOR and SAN: *Penium gonatozygiforme* (also in LPH), *Tetmemorus euastroides* (only in UPH), *Euastrum truncatiforme*, *Euastrum africanum*, *Euastrum spinulosum*, *Euastrum divergens* (only a few specimens in Ngami lake and Xakanaxa), *Euastrum sphyroides* (also in UPH), *Euastrum attenuatum*, *Micrasterias tropica* (this species was also found in UPH) (Coesel and van Geest, 2008). A further 6 species were observed by Coesel and van Geest (2009) – who found 23 taxa in total - in the Boro region and in this study: *Cosmarium geminatum*, *Cosmarium haynaldii* and *Cosmarium okavangicum, Cosmarium pseudotus*, *Staurastrum rzoskae* (in BOR) and *Cosmarium pseudosulcatum* (in SAN). In this study 184 species of desmids (65% of the green algal species) were observed belonging to 23 genera (Marazzi, 2013; see Appendix H). Williamson and Marazzi (2013; see Appendix I) discovered and described a new variety, *Cosmarium pseudosulcatum var. okavangicum* from a site in Lechwe Pool (Boro region) (see Figure 3.3).

In addition to the 496 species of algae found, 113 species of diatoms and 60 species of desmids (see section 6.4) were found respectively by Mackay *et al.* (2012) and by David Williamson in a subset of samples (unpublished data; see Appendix H). Thus in the last few years a total of 669 algal species have been found in the Delta in this research and connected projects / collaborations. These data recorded in recent years and can be used as a compound estimate of algal biodiversity in the Okavango Delta. A very similar number of species, over 690, were observed in another subtropical wetland, Kakadu in Australia (Thomas, 1983; Ling and Tyler, 1986; Finlayson *et al.*, 2006; see section 4.10.1).

4.6. RESULTS: ALGAL TRAITS

Here the frequency of algal traits observed in the Delta is considered, i.e. cell size, motility and metabolic features. The relative abundance of algae with each given trait varies across regions, flood classes and habitats, as shown by the statistical analyses, i.e. One-Way ANOVA (O.W.A) and Kruskall-Wallis tests (K.W.).

4.6.1. Cell arrangement

Here relative abundance of algae with given cell structure, size and traits are illustrated (Figures 4.7 to 4.10) and analysed. PF and OF areas have higher abundance of unicellular algae, while filamentous algae were found more commonly in OF sites. Figure 4.7c shows these differences according to habitats. UPH and XAK contain higher abundances of filamentous algae, while algae found in colonies and coenobia are below 10% in every region (Figure 4.7a).

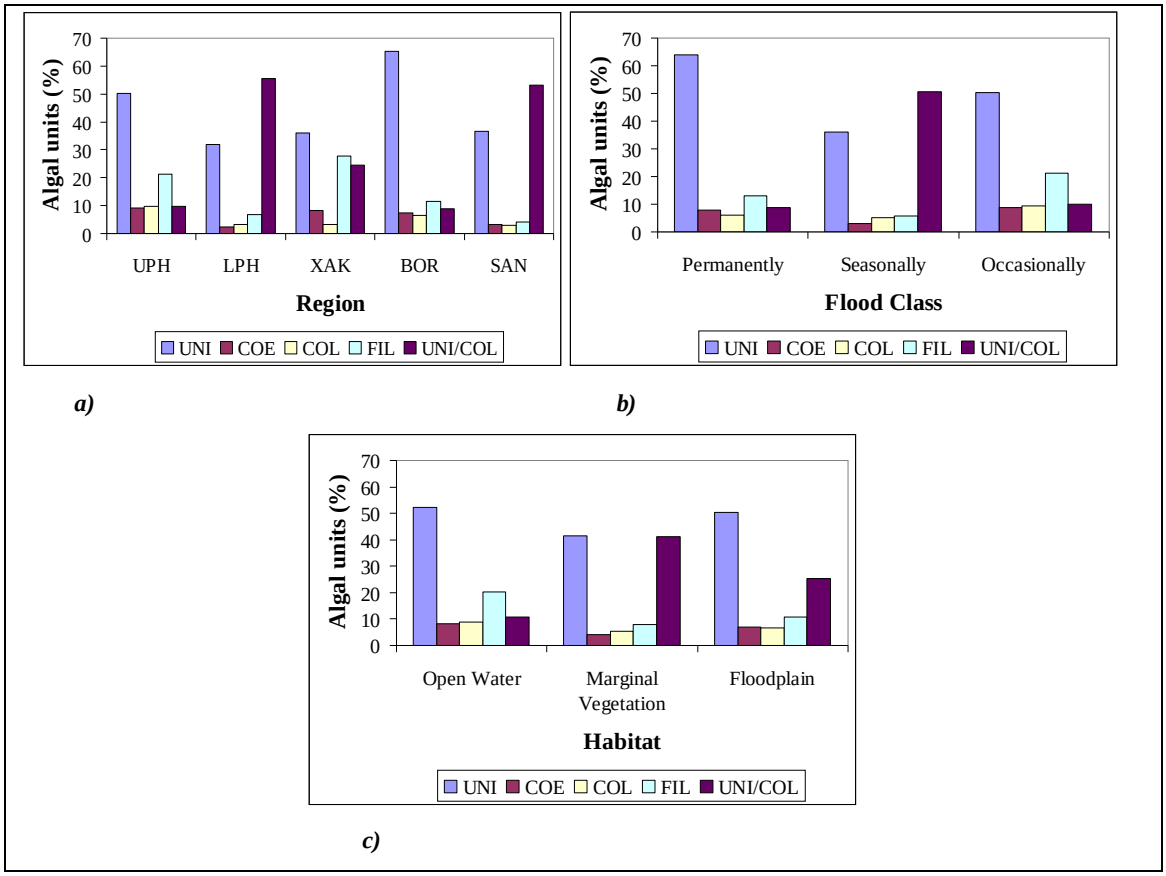


Figure 4.7. Frequency of algal cell arrangement types across: a)regions; b) flood class; c)habitat (UNI=Unicellular; COE=Coenobium; COL=Colony; FIL=Filament; UNI/COL=taxon with Unicellular or Colony forms; n.a. information on site habitat not available).

4.6.2. Cell length

The average cell length of algae is higher in the Panhandle regions than in the distal reaches; smaller algae are more abundant in SF and OF sites, while larger ones are present in higher numbers in PF sites. OW and F sites have higher abundance of small algae than MV. The relative abundance of cell length classes varies significantly across regions (<25 µm: O.W.A.: $F=22.011$, $p<0.001^{**}$; 25-50 µm: KW: $\chi^2=37.920$; >50 µm: $\chi^2=23.596$, $p<0.001$ for both): small-sized algae (<25 µm) are more abundant in BOR and SAN than UPH and LPH ($p<0.001^{**}$); medium-

sized algae are more abundant in UPH and LPH than BOR ($p<0.001^{**}$ and $p<0.01^{*}$) and in SAN than BOR ($p<0.01^{*}$), large algae (> 50 µm) are more abundant in UPH than XAK ($p<0.001^{**}$) and in LPH and BOR than in SAN ($p<0.001$ and $p<0.01$) (Figure 4.8a). The frequency of cell length classes also varies across flood classes (O.W.A.: <25 µm: $F=8.473$, $p<0.001^{**}$; >50 µm: $F=14.836$, $p<0.001^{**}$ for both; < 25 µm: OF > PF: $p<0.001^{**}$; PF > OF and SF > OF $p<0.01^{*}$) (Figure 4.8b) and habitats (L. test: $p<0.01^{*}$; K.W.: $\chi^2=17.632$, $p<0.001^{**}$; < 25 µm: OW > MV: $p<0.01^{*}$; F > MV: $p<0.001^{**}$; 25-50 µm: MV > F: $p<0.01^{*}$) (Figure 4.8c).

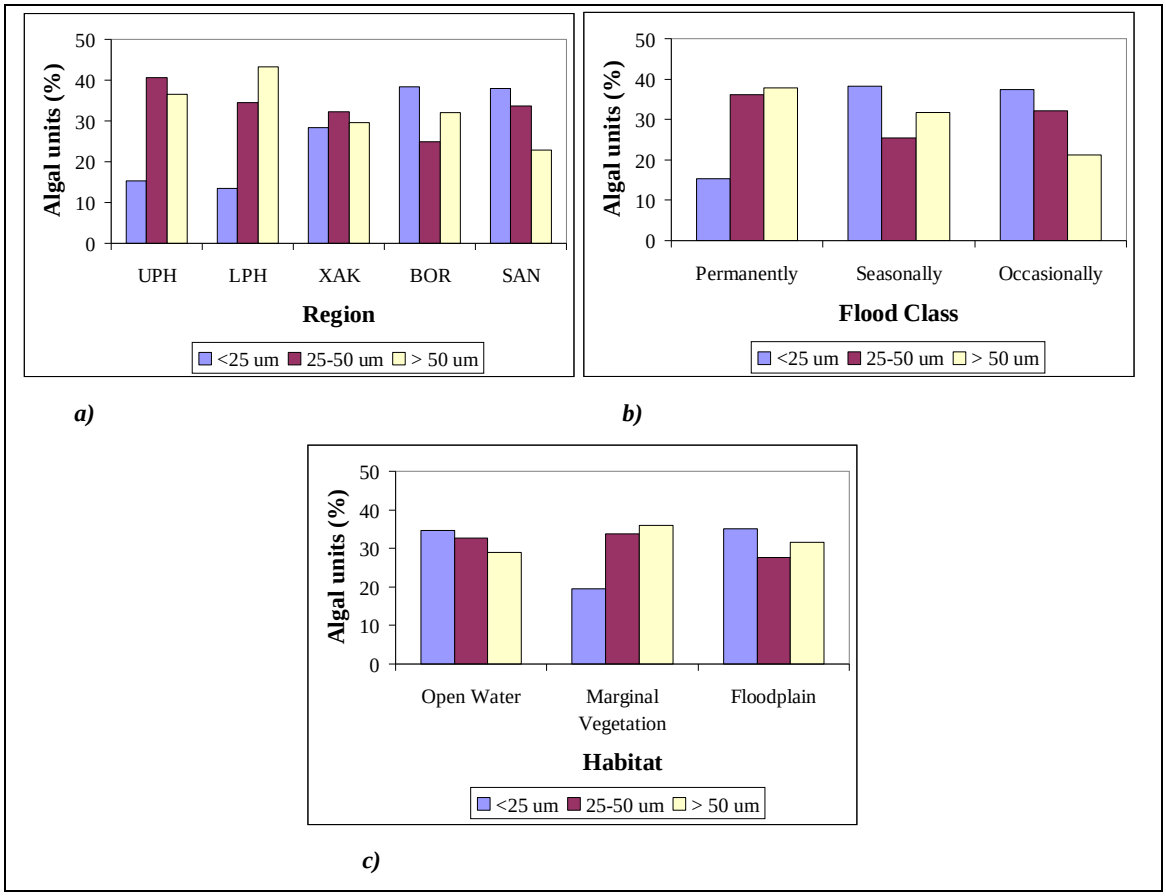


Figure 4.8. Frequency of average cell length classes across: a)regions; b) flood classes; c)habitat.

Consistent with the results discussed above, the average algal cell length varies significantly across regions and flood classes, with larger algae more abundant in the Panhandle than in the distal reaches. Region (L.: p>0.01): KW: $\chi^2=23.178$; $p<0.001^{**}$; UPH and LPH > SAN ($p<0.001^{**}$); BOR > SAN ($p<0.01^{*}$). Flood class (L. test: p>0.01): $F=14.176$; $p<0.001^{**}$): PF > OF ($p<0.001^{**}$), SF > OF ($p<0.01^{*}$). Average cell length varies significantly across flood years (L. test: p>0.01): O.W.A. test: $F=4.842$, $p<0.01^{*}$, but with no pair-wise changes. Finally, no significant differences are recorded across seasons, habitats or campaigns.

4.6.3. Motility

Abundance trends show that the majority of algae are non motile. Motile algae - with raphe, flagellum/flagella or other movement type, e.g. some *Oscillatoriales* – are more abundant in XAK, BOR and SAN than in the other regions (Figure 4.9a). Motile algae are slightly more abundant in OF sites than PF and SF areas (Figures 4.9b) whereas differences across habitats are very small (Figure 4.9c).

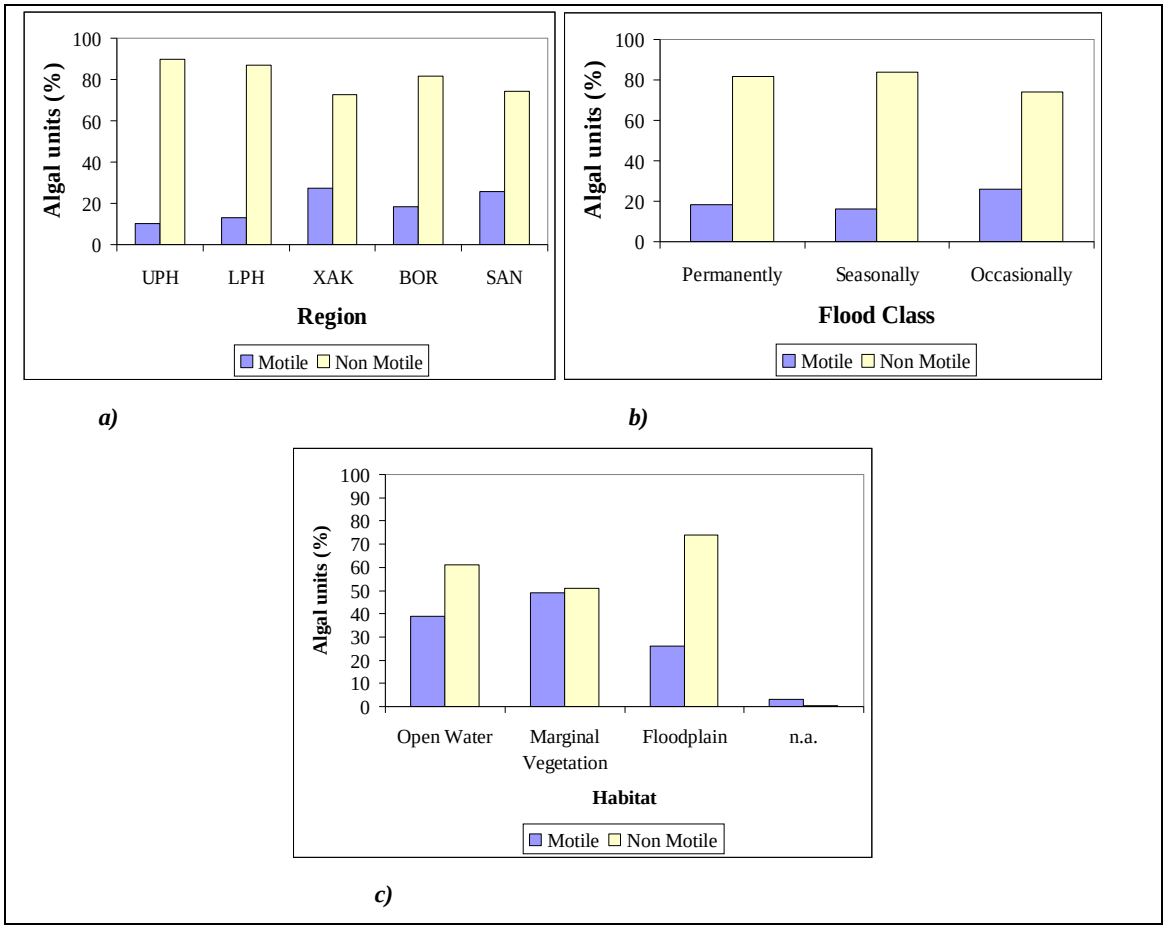


Figure 4.9. Frequency of motility traits across: a) regions; b) flood class; c) habitat.

The differences displayed in Figure 4.9 are statistically significant only across regions. The abundance of both motile and non motile algae varies across regions (KW: χ^2=26.496, $p<0.001^{**}$); motile algae are more abundant in UPH than XAK ($p<0.001^{**}$), in BOR and SAN than UPH ($p<0.001^{**}$), in XAK than BOR ($p<0.01^{*}$) and SAN than BOR ($p<0.01^{*}$).

4.6.4. Metabolic traits

Nitrogen-fixers, e.g. Nostocales and some diatoms, and algae with silica demand (in diatoms and some chrysophytes) are more frequent in PF and SF sites. Phagotrophy is a slightly more common trait in SF sites than in the other areas sampled. The

abundance of siliceous algae is high across flood classes (Figure 4.10 a and b). The distribution of metabolic traits does not vary greatly across habitats; nitrogen fixers is slightly higher in OW and MV, phagotrophy in MV and silica demand in F habitats (Figure 4.10c).

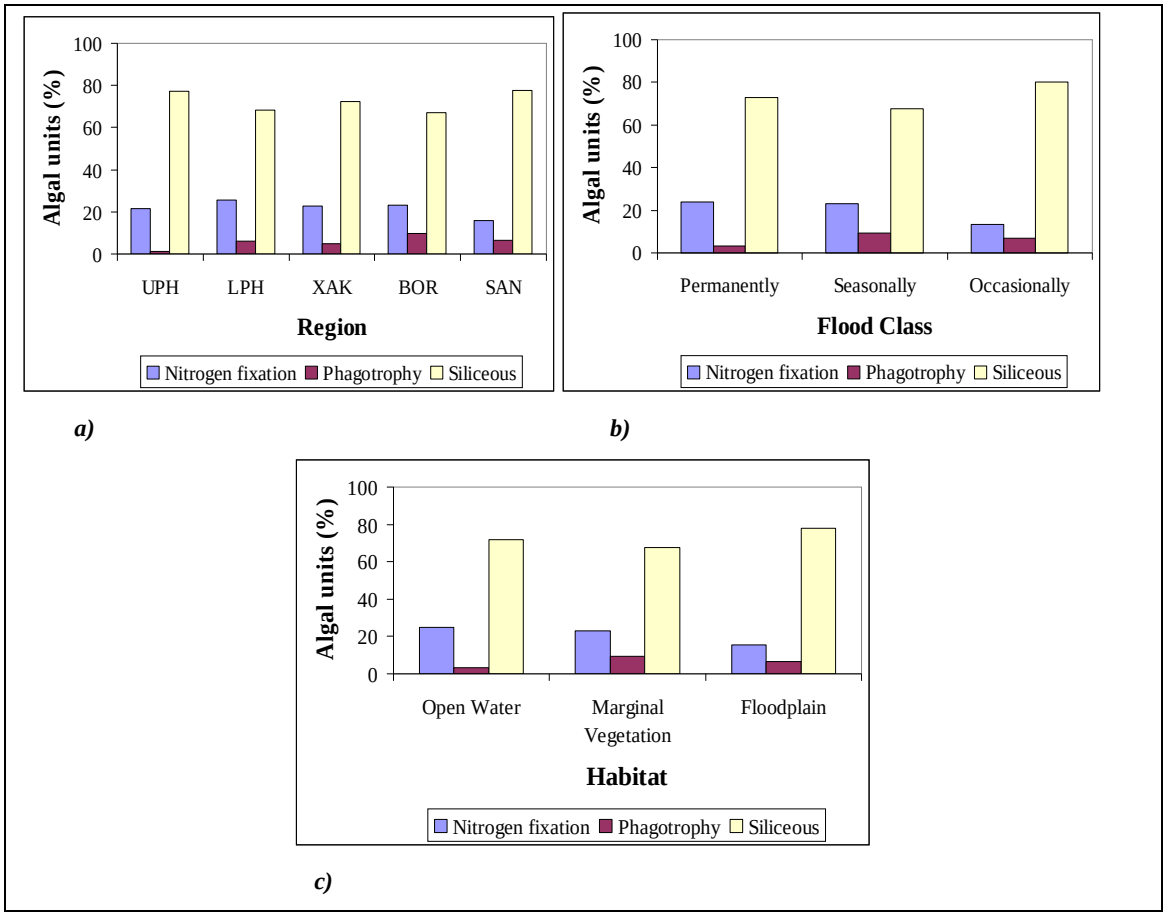


Figure 4.10. Frequency of metabolic traits across: a) regions; b) flood classes; c) habitats.

Metabolic trait frequency varies significantly across regions (nitrogen fixation: $F=3.804$, $p<0.01$; phagotrophy: KW: $\chi^2=17.434$, $p<0.01^{*}$; silica demand: $F=6.045$, $p<0.001^{**}$). Phagotrophic algae are more abundant in LPH ($p<0.01^{*}$), BOR ($p<0.001^{**}$) and SAN than UPH ($p<0.01^{*}$); silica demand is a more common feature in SAN than BOR ($p<0.01^{*}$). The percentages of nitrogen fixers (O.W.A.: $F=9.470$, $p<0.001^{**}$) and of algae with silica demand vary across flood classes (O.W.A.: $F=7.158$, $p<0.01^{*}$). Nitrogen fixers is more common in PF and SF than OF sites ($p<0.01^{*}$), while silica demand is more frequent in OF than PF ($p<0.001^{**}$). No differences emerge across habitats.

4.7. RESULTS: LIMNOLOGICAL VARIABLES

A summary of the limnological field and laboratory data, the latter conducted at the Okavango Research Institute, is shown in Table 4.5. Analyses are presented for the two Campaigns separately first and secondly in the merged dataset.

***Table 4.5. Summary of the limnological data measured** (x=mean; s.d.=standard deviation; c.v.=coefficient of variation; *NTU=Nephelometric Turbidity Units).*

Campaign	Variable	N	Min	Max	x	s.d.	c.v. (%)
1	Conductivity (μs cm^{-1})	61	19.3	162	66.9	41.8	66.9
2		62	75.9	175	108	24.7	22.8
1	Depth (m)	61	0.00	5.30	1.63	1.18	72.3
2		39	0.10	1.60	0.57	0.46	81.8
1	DO (mg L^{-1})	61	0.41	7.87	4.06	1.86	45.7
2		66	0.08	7.12	2.03	1.62	80.2
1	pH (pH units)	61	4.68	7.69	6.68	0.45	6.81
2		31	6.04	7.70	6.72	0.40	6.55
1	Temperature (°C)	61	13.6	30.1	20.5	3.78	18.5
2		65	15.0	38.1	26.1	4.82	18.6
1	Velocity (m s^{-1})	42	0.00	1.56	0.16	0.29	180
1	Ca^{2+} (mg L^{-1})	41	3.46	9.29	5.87	1.55	26.3
2	Chlorophyll *a* (μg L^{-1})	62	10.0	75.1	26.8	15.1	56.1
1	Cl^{-} (mg L^{-1})	41	0.11	2.74	0.62	0.59	95.7
1	DOC (mg L^{-1})	41	2.73	19.1	7.27	3.85	52.9
1	HCO_3^{-} (mg L^{-1})	41	3.97	117	52.2	19.6	37.5
1	K^{+} (mg L^{-1})	41	0.33	5.10	1.81	1.36	75.2
1	Mg^{2+} (mg L^{-1})	41	0.38	1.91	0.95	0.32	34.0
1	Na^{+} (mg L^{-1})	41	0.82	4.09	2.03	1.03	50.6
1	PO_4^{2-} (mg L^{-1})	41	0.00	0.07	0.01	0.02	200
1	SiO_2 (mg L^{-1})	41	3.07	29.8	11.8	6.79	57.6
1	SO_4^{2-} (mg L^{-1})	41	0.02	2.58	0.25	0.41	160
1	TN (mg L^{-1})	41	0.16	1.60	0.65	0.30	46.5
1	TP (mg L^{-1})	41	0.015	0.11	0.04	0.02	55.1
2		57	0.004	0.17	0.05	0.03	65.4
1	TSS (mg L^{-1})	41	0.70	10.0	3.33	2.35	70.6
2	Turbidity (NTU)	64	0.57	77.8	7.77	13.1	167

The most noticeable differences between average values in the two datasets were: in Campaign 2 water depth was much lower than in Campaign 1 (mean 0.6 m vs 1.6 m); mean water temperatures is about six degrees higher in the shallower water sites sampled in Campaign 2 (mean 26.1 ºC vs 20.5 ºC); mean Dissolved Oxygen

concentration was higher in Campaign 1 (4.1 mg L^{-1} *vs* 2.0 mg L^{-1}) and the mean conductivity in Campaign 2 much higher (107.6 µs cm^{-1}) as compared to in Campaign 1 (60.9 µs cm^{-1}). Variations across flood years are not shown in graphs as they reflect the predominance of floodplain samples in 2009-2010.

4.7.1. Correlations between limnological variables

Table 4.6 shows the results of K.S. tests to determine normality of variables in each dataset and in the aggregate dataset. 10 out of 21 variables are normally distributed in Campaign 1 and 3 out of 8 variables are normally distributed in Campaign 2; in the merged dataset 2 out of 6 variables are normally distributed (Table 4.6).

Table 4.6. Kolmogorov-Smirnov normality test on limnological variables (p-values > 0.01 for normally distributed variables in bold; Z is the test statistics to assess if the difference between the observed distribution and a normal distribution is small enough to be just due to chance).

	Campaign 1			Campaign 2			All samples		
Variable	**N**	**Z**	**p-value**	**N**	**Z**	**p-value**	**N**	**Z**	**p-value**
Conductivity	61	0.180	0.000	63	0.214	0.000	124	0.101	0.003
Depth	61	0.215	0.000	39	0.196	0.001	100	0.189	0.000
DO	61	0.078	**0.200**	67	0.157	0.000	128	0.096	0.005
pH	61	0.115	**0.045**	49	0.092	**0.200**	110	0.091	**0.024**
Temperature	61	0.145	0.003	66	0.066	**0.200**	127	0.105	0.002
Chlorophyll a				62	0.163	0.000			
Velocity	42	0.290	0.000						
Ca^{2+}	26	0.104	**0.200**						
Cl^{-}	41	0.249	0.000						
DOC	41	0.172	0.004						
HCO_3^{-}	41	0.134	**0.063**						
K^{+}	41	0.153	**0.017**						
Mg^{2+}	41	0.166	0.006						
Na^{+}	41	0.242	0.000						
PO_4^{2-}	41	0.325	0.000						
SiO_2	41	0.108	**0.200**						
SO_4^{2-}	41	0.328	0.000						
TN	41	0.145	**0.030**						
TP	41	0.157	**0.013**	58	0.130	**0.016**	99	0.102	**0.013**
TSS	41	0.205	0.000						
Turbidity				65	0.303	0.000			
Anions	41	0.138	**0.049**						
Cations	41	0.114	**0.200**						

Pearson product-moment correlation (PPMC) tests on not normally distributed variables yield different results to the Spearman rank correlation coefficientss and correlations vary between campaigns; hence the results are reported in separate

tables according to normality / non normality and sampling campaign. Tables 4.8 and 4.11 show the coefficients (PPMC) between normally distributed variables in Campaigns 1 and 2; Spearman correlation coefficients for not normally distributed variables are reported in Table 4.8 (Campaign 1) and Table 4.12 (Campaign 2) and in Tables 4.10, 4.13 and 4.14 for normally *vs* not normally distributed variables in Campaigns 1 and 2. A total of 47 statistically significant correlations (35%) were found between limnological variables measured in Campaign 1 (5 in Table 4.7, 14 in Table 4.8 and 28 in Table 4.9) as compared to 8 significant correlations (29%) in Campaign 2 - none in Table 4.10, 3 in Table 4.11, and 5 in Table 4.12. Numerous significant positive correlations are observed between cation, anion concentrations and SiO_2, Cl^-, HCO_3^-, DOC and conductivity (some also with temperature), which are negatively correlated with water depth (Table 4.8). Water velocity, TN, TP, TSS, PO_4 and SO_4 concentrations are significantly correlated with fewer variables, if any, than the limnological variables above mentioned (Tables 4.8-4.10).

Table 4.7. Correlation coefficients between variables normally distributed in Campaign 1 (*=0.01, significant at 99% confidence level).

Pearson Correlation	**DO**	**pH**	**Ca^{2+}**	**HCO_3^-**	**K^+**	**SiO_2**	**TN**	**TP**
DO	1	**0.338***	-0.186	-0.194	-0.293	**-0.433***	0.173	-0.149
pH		1	0.374	-0.285	-0.139	-0.292	-0.384	0.026
Ca^{2+}			1	0.480	**0.645***	**0.739***	-0.089	-0.163
HCO_3^-				1	**0.646***	**0.700***	0.389	-0.109
K^+					1	**0.841***	0.096	-0.141
SiO_2						1	0.241	-0.131
TN							1	-0.211
TP								1

Table 4.8. Correlation coefficients between variables not normally distributed in Campaign 1 (*=0.01, significant at 99% confidence level).

Spearman Correlation	**Conductivity**	**Depth**	**Temperature**	**Velocity**	**Cl^-**	**DOC**	**Mg^{2+}**	**Na^+**	**PO_4^{2-}**	**SO_4^{2-}**	**TSS**
Conductivity	1	**-0.533***	0.157	-0.022	0.355	**0.870***	**0.712***	**0.728***	-0.139	0.173	-0118
Depth		1	-0.121	0.232	-0.234	**-0.631***	**-0.460***	**-0.633***	-0.062	-0.079	0.45
Temperature			1	0.129	**0.464***	0.242	0.321	-0.309	**0.738***	0.173	-0.257
Velocity				1	0.168	-0.037	-0.003	-0.221	0.167	-0.143	-0.091
Cl^-					1	**0.429***	0.365	0.100	0.389	0.187	0.164
DOC						1	**0.869***	**0.756***	0.073	0.240	-0.197
Mg^{2+}							1	**0.565***	0.254	0.140	-0.191
Na^+								1	**-0.434***	0.083	0.037
PO_4^{2-}									1	-0.129	-0.171
SO_4^{2-}										1	-0.045
TSS											1

Table 4.9. Correlation coefficients between variables normally and not normally distributed in Campaign 1 (*=0.01, significant at 99% confidence level).

Spearman correlation	DO	pH	Ca^{2+}	HCO_3^-	K^+	SiO_2	TN	TP
Conductivity	-0.286	0.252	**0.718***	**0.644***	**0.579***	**0.651***	0.306	-0.082
Depth	-0.167	**-0.330***	**-0.599***	**-0.563***	**-0.680***	**-0.743***	-0.061	-0.057
Temperature	-0.283	**0.340***	0.246	-0.019	0.207	0.269	-0.383	-0.169
Velocity	0.001	-0.029	0.195	-0.059	-0.055	-0.158	0.040	-0.062
Cl^-	-0.158	0.016	0.360	**0.447***	**0.407***	**0.401***	0.008	**-0.429***
DOC	-0.318	0.058	**0.831***	**0.761***	**0.763***	**0.863***	0.194	-0.198
Mg^{2+}	-0.376	0.139	**0.691***	**0.724***	**0.700***	**0.754***	0.140	-0.040
Na^+	0.086	0.151	**0.714***	**0.618***	**0.598***	**0.633***	0.265	-0.028
PO_4^{2-}	-0.382	0.283	-	0.053	0.329	0.243	**-0.460***	-0.108
SO_4^{2-}	0.004	-0.253	0.019	0.126	0.016	0.245	0.301	**-0.430***
TSS	0.314	0.104	-0.253	0.061	-0.087	-0.240	-0.045	0.012

Table 4.10. Correlation coefficients between variables normally distributed in Campaign 2 (*=0.01, significant at 99% confidence level).

Pearson Correlation	pH	Temperature	TP
pH	1	-0.114	-0.014
Temperature		1	0.325
TP			1

Table 4.11. Correlation coefficients between variables not normally distributed in Campaign 2 (*=0.01, significant at 99% confidence level).

Spearman Correlation	Conductivity	Depth	DO	Chlorophyll *a*	Turbidity
Conductivity	1	-0.057	0.118	**0.383***	0.284
Depth		1	-0.102	**-0.454***	-0.279
DO			1	-0.189	**0.394***
Chlorophyll *a*				1	0.211
Turbidity					1

Table 4.12. Correlation coefficients between variables normally and not normally distributed in Campaign 2 (*: p=0.01, significant at 99% confidence level).

Spearman Correlation	pH	Temperature	TP
Conductivity	0.224	0.058	0.198
Depth	-0.052	-0.249	-0.384
DO	**0.483***	-0.295	-0.102
Chlorophyll a	0.079	0.211	0.114
Turbidity	0.188	0.267	0.191

In the merged dataset temperature and TP are the only normally distributed variables, but they are not significantly correlated with one another. However, the other five environmental variables measured in both campaigns show several statistically significant correlations (Table 4.13).

Table 4.13. Correlation coefficients between variables normally and not normally distributed in all the samples (*:=0.01, significant at 99% confidence level).

Spearman Correlation	Conductivity	Depth	DO	pH	Temperature	TP
Conductivity	1	**-0.589***	**-0.353***	0.178	**0.430***	0.123
Depth		1	0.153	-0.079	**-0.449***	-0.213
DO			1	**0.355***	**-0.472***	-0.143
pH				1	0.708	0.930
Temperature					1	0.209
TP						1

4.7.2. PCA: environmental gradients in the Delta

In this section algal relative abundance and relative biovolume (% of the total biovolume contributed by each taxon) data are analysed in relation to environmental variables using multivariate ordination techniques.

The results of the PCA analysis show that the first two axes explain about 53.7% (Table 4.14) of the total variance in water depth, temperature, conductivity, DO, pH, TP, as well as the dummy variables 'flood class' and 'habitat'. For these categorical variables only two are used, i.e. SF, OF and OW, F as the variance-covariance matrix of dummy variables is singular and cannot be inverted (Legendre and Birks, 2012). The two main PCA components (PC axis 1 and 2) have higher

eigenvalues than the eigenvalues simulated by the random broken stick, as shown in the screeplot (Table 4.14 and Figure 4.11), which means they significantly explain the environmental variables better than the random model.

Table 4.14. Results of PCA on the environmental data in all the samples.

Eigen values	**PCA axes**				**Inertia**
	1	**2**	**3**	**4**	
Eigenvalues	0.327	0.210	0.139	0.097	1
Cum. % var. spp. data		53.7%			
Broken stick	0.293	0.193	0.143	0.110	

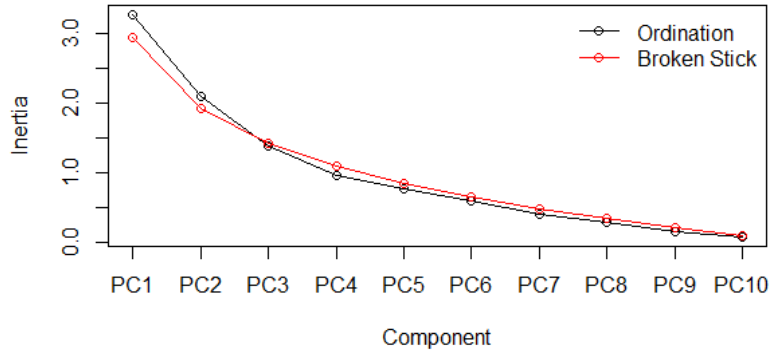


Figure 4.11. Screeplot of PCA axes (red) and broken stick (black) axes in all the samples ("Inertia" represents the total unstandardised inertia=variance).

In the merged dataset PC axis 1 is most highly positively correlated with depth (score=1.542) and DO (score=1.172) and negatively with F (score=-1.524) and conductivity (score=-1.376). These results are not shown in a biplot graph due to the very large number of sites.

In Campaign 1 the first two axes account for 53.0% of the total variance and better explain the variation of environmental variables than the unconstrained axis (Table 4.15 and Figure 4.12).

Table 4.15. Results of PCA of environmental data in Campaign 1.

Eigen values	**PCA axes**				**Inertia**
	1	**2**	**3**	**4**	
Eigenvalues	0.389	0.141	0.088	0.073	1
Cumulative % variance		53.0%			
Broken stick	0.162	0.119	0.097	0.083	

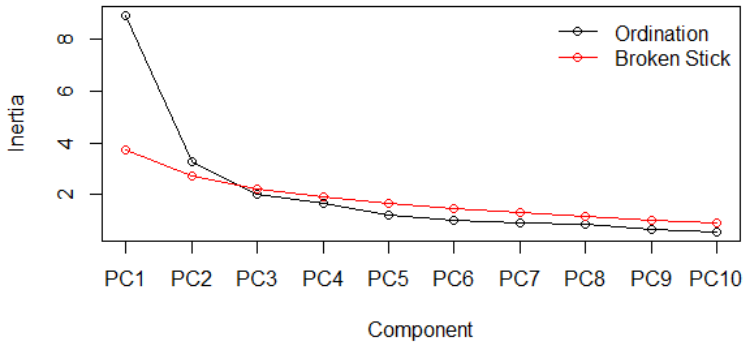


Figure 4.12. Screeplot of PCA axes (red) and broken stick (black) axes in Campaign 1 ("Inertia" represents the total unstandardised inertia=variance).

PC axis 1 is most strongly negatively correlated with the categorical variable OF linked to occasional flooding (followed by pH which is higher in OF sites) and positively with DOC (and also with most ion and nutrient concentrations) while the secondary gradient (PC axis 2) is negatively associated with depth which is higher in Open Water (OW) sites than in Floodplains at the other end of the gradient (Figure 4.13). Figure 6.5 also shows how in, Campaign 1, conductivity and temperature are higher in BOR, XAK SAN sites, but also in some UPH sites (e.g. U4B-1 and UP7A-4 on the left) whereas in a number of UPH and LPH sites water depth is deeper and DO higher (e.g. U3-1, U1C-4 and L3A-4).

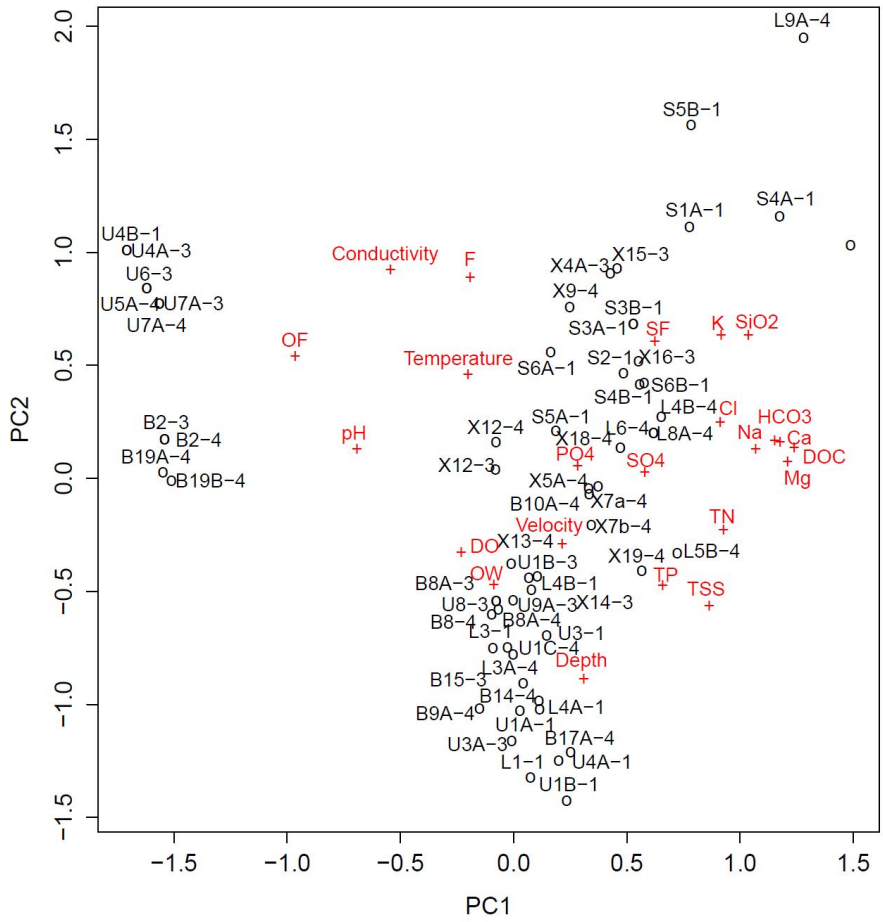


Figure 4.13. PCA biplot of environmental variables in Campaign 1 (eigenvalues: PC1= 38.9%; PC2= 14.1%; B=BOR; L=LPH; S=SAN; U=UPH; X=XAK).

In Campaign 2 the portion of variance explained by the two main axes is 55.4%, but only PC axis 2 has a higher eigenvalue than the broken stick model, i.e. better explains the variation than an unconstrained axis (Table 4.16 and Figure 4.14).

Table 4.16. Results of PCA of environmental data in Campaign 2.

Eigen values	**PCA axes**				**Inertia**
	1	**2**	**3**	**4**	
Eigenvalues	0.299	0.255	0.148	0.104	1
Cumulative % variance		55.4%			
Broken stick	0.340	0.215	0.152	0.111	

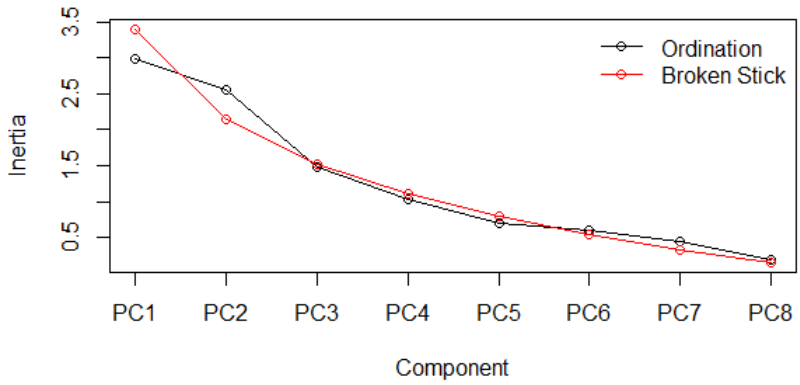


Figure 4.14. Screeplot of PCA axes (red) and broken stick (black) axes in Campaign 2 ("Inertia" represents the total unstandardised inertia=variance).

In Campaign 2 OF is most strongly correlated and F negatively with axis 1 (Figure 4.15); conductivity and temperature are higher in floodpain (F) habitats (suffices '2' and '3' in sample codes) whereas in OW sites water depth is deeper and DO higher. However, axis 2 is the only one with a higher explanatory power than the unconstrained axis; respectively TP and temperature are most positively correlated with it and depth negatively (Figure 4.15).

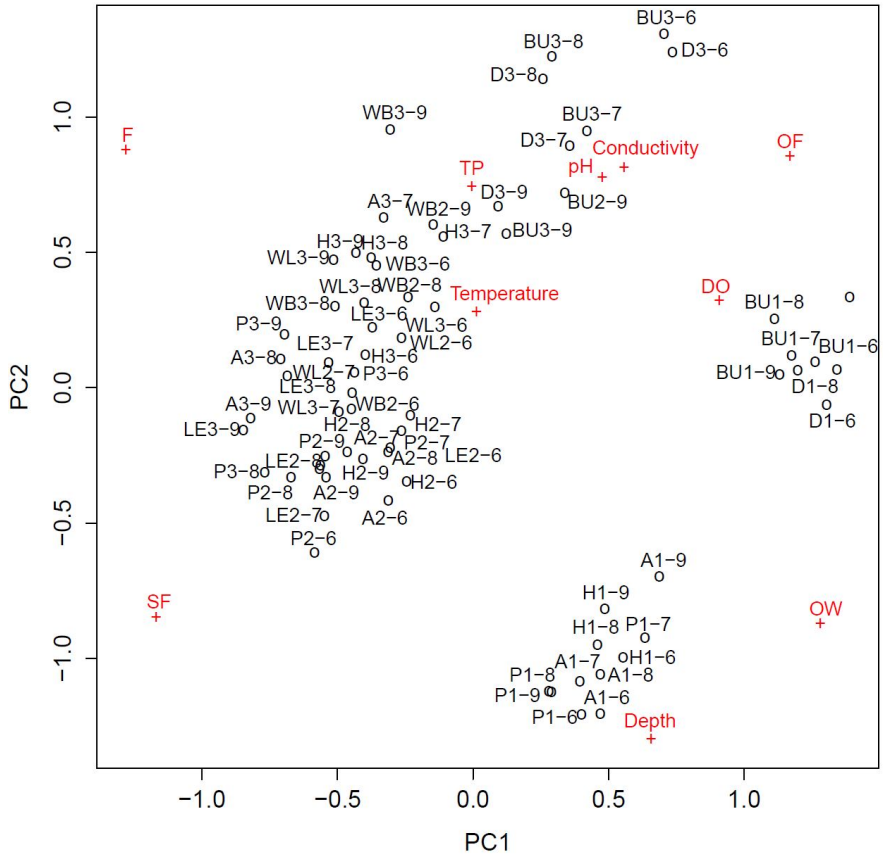


Figure 4.15. PCA biplot of environmental variables in Campaign 2 (% explained variance: PC1= 29.9%; PC2= 25.5%; A=ALD; BU=BUF; D=DAU; H=HIP; LE=LEC; P=POC; WB=WBE; WL=WLI).

4.7.3. Statistical tests on variables measured in both campaigns

A summary of all these significant differences between limnological variables measured across regions, seasons, flood class and habitat categories is presented in Table 4.17. Conductivity and DO show most numerous significant variations in the data from separate campaigns than the other variables measured in both campaigns; DOC and cations are the variables showing more numerous significant variations among the water chemistry data in Campaign 1. Sites in UPH, LPH are overall characterised by deeper and colder waters than BOR, SAN with higher DO concentrations; samples taken in XAK have conductivity and micronutrient concentrations (cations and anions) intermediate between the Panhandle and BOR / SAN, but temperature and DO values more similar to UPH and LPH, due to these areas being either permanently or occasionally flooded and with different habitats (see section 3.1).

Table 4.17. Significant statistical differences in limnological variables (x=significant difference; -=no significant difference; n.a.= not available).

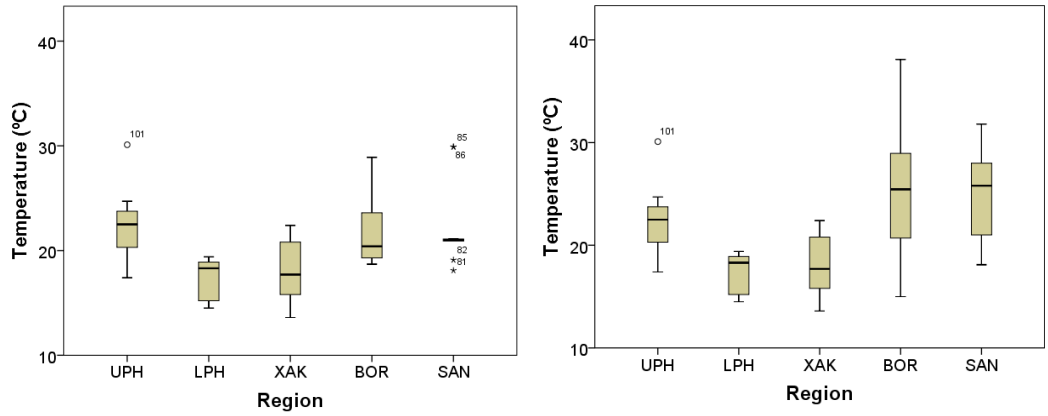
Variable	Campaign 1				Campaign 2						Merged dataset				
	Region	Season	Flood class	Habitat	Region	Season	Flood Class	Habitat	Habitat Floodplain	Floodplain Type	Region	Season	Flood Class	Habitat	Floodplain Type
Temp.	x	x	-	-	-	x	-	-	-	-	x	x	x	x	-
Depth	x	-	x	-	-	-	-	-	-	-	x	x	x	x	-
Cond.	x	-	x	x	x	-	x	-	-	-	x	x	x	x	x
DO	x	-	x	-	-	x	x	x	-	-	x	x	x	x	-
pH	x	x	-	-	-	x	x	-	-	-	x	x	x	-	x
Velocity	-	-	-	-	n.a.	n.a.	n.a.	n.a.	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
TSS	-	-	-	-	-	-	-	-	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
DOC	x	-	x	x	-	-	-	-	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
SiO_2	x	-	x	-	n.a.	n.a.	n.a.	n.a.	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
TN	-	-	-	-	n.a.	n.a.	n.a.	n.a.	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
TP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cations	x	x	x	-	n.a.	n.a.	n.a.	n.a.	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
Anions	x	-	-	-	n.a.	n.a.	n.a.	n.a.	-	-	n.a.	n.a.	n.a.	n.a.	n.a.
Chl *a*	n.a.	n.a.	n.a.	n.a.	-	-	-	x	x	-	n.a.	n.a.	n.a.	n.a.	n.a.
Turbidity	n.a.	n.a.	n.a.	n.a.	-	-	x	-	-	x	n.a.	n.a.	n.a.	n.a.	n.a.

In Campaign 1 regional variations are most common (followed by those across flood classes), while in Campaign 2 environmental variables vary the most across samples taken in sites with different flood class and in different seasons (Table 4.17). Overall, significant variations of limnological variables measured represented 33% (20/60) of the regional, seasonal, flood class and habitat changes in Campaign 1, 20% (11/55) in Campaign 2 and 68% (19/28) in all the samples pooled together (Table 4.17). Greater changes were observed, e.g., in conductivity levels of up to 100 μS cm^{-1} between PF and OF sites in Campaign 1 (Figure 4.24a) as compared to Campaign 2, with water samples on average between 90 μS cm^{-1} and 125 μS cm^{-1} (Figure 4.24b). No significant change was observed between water depths in Campaign 2; Boro (BOR) sites were on average 0.62 m deep and Santantadibe (SAN) sites 0.40 m deep, whereas in Campaign 1 much deeper sites were sampled in the Panhandle than in BOR and SAN (see Figure 4.20). Sections 4.7.3 and 4.7.4 present all the statistical tests and relative graphs on the Delta's limnology.

In this section the results on variables measured in both campaigns are shown via box-plots and statistical tests to detect significant differences (significance levels: $p=0.01^{*}$; $p=0.001^{**}$, respectively 99% and 99.9% confidence); comparisons are also made between Campaign 1 and 2 and the merged dataset.

Water temperature

Water temperature varies significantly between regions in Campaign 1 (L. test: $p>0.01$; O.W.A. test: $F=6.887$, $p<0.001^{**}$); with these pair-wise differences (M-W U): UPH higher than LPH and XAK ($p<0.01^{*}$) (Figure 4.16a). No significant differences were observed in Campaign 2. However in the merged dataset, higher average temperatures were recorded in BOR and SAN than elsewhere. In particular, temperatures are higher in UPH than LPH ($p<0.001^{**}$) and XAK ($p<0.01^{*}$); in BOR than LPH ($p<0.001^{**}$) and XAK ($p<0.001^{**}$); in SAN than LPH ($p<0.001^{**}$) and XAK ($p<0.001^{**}$) (Figure 4.16b).



a) ***b)***

Figure 4.16. Water temperatures across regions in a) Campaign 1; b) all the samples.

Temperatures do not vary significantly according to flood class or habitat type in Campaign 1 or 2. However, seasonal variations are evident in both Campaign 1 (L. test: $p>0.01$; O.W.A. test: $F=28.645$, $p<0.001^{**}$) and Campaign 2 (L. test: $p>0.01$; O.W.A. test: $F=45.035$, $p<0.001^{**}$). As per T. HSD tests, in 2007 April temperatures are higher than July (winter; $p<0.001^{**}$) (Figure 4.17a). In February 2010 (summer) water temperatures were higher than April/May 2007/2009 and July/August 2007/2009 ($p<0.001^{**}$); in April/May temperatures are significantly warmer than in July/August and October ($p<0.001^{**}$), when water is warmer than in the winter (July/August; $p<0.001^{**}$) (Figure 4.17b). Hence a seasonal temperature change emerges in the joint dataset too; in the water recession phase (September 2006 and October 2009) temperatures are higher than during the water expansion and high water phases (April/May and July/August 2007/2009) (Table 4.18).

Table 4.18. Tukey HSD tests on seasonal temperature changes.

p-values	**Apr/May**	**Jul/Aug**	**Sep**
Apr/May		$<0.001^{**}$	$<0.01^{*}$
Oct	$<0.001^{**}$	$<0.001^{**}$	$<0.001^{**}$
Feb	$<0.001^{**}$	$<0.001^{**}$	$<0.001^{**}$

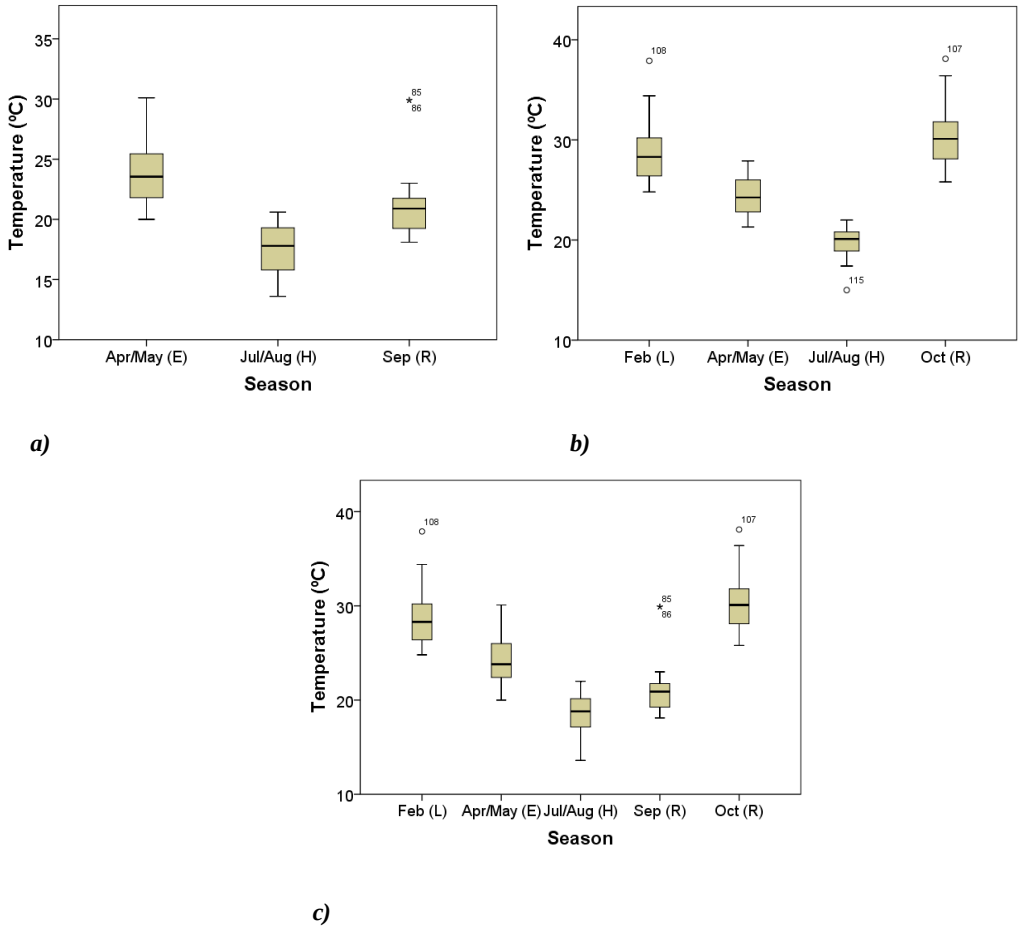


Figure 4.17. Water temperature across seasons in a) Campaign 1; b) Campaign 2; c) all the samples (flood phase: E=Expansion; H=High; R=Recession).

Water samples collected in the 2009-2010 flood year are overall significantly warmer than in 2006-2007 and 2007-2008 (T. HSD test: $p<0.001^{**}$) (L. test: $p>0.01$: O.W.A. test: $F=28.364$; $p<0.001^{**}$). The water temperature is significantly warmer in Campaign 2 than Campaign 1 (average 26.0 ºC vs 20.5 ºC) (L. test: $p>0.01$; O.W.A. test: $F=53.585$, $p<0.001^{**}$). Temperatures vary across flood class only in the merged dataset (L. test: $p<0.01^{*}$): K.W.: $\chi^2=18.063$; $p<0.001^{**}$, with warmer sites in SF and OF than PF areas ($p<0.001^{**}$ and $p<0.01^{*}$) (Figure 4.18).

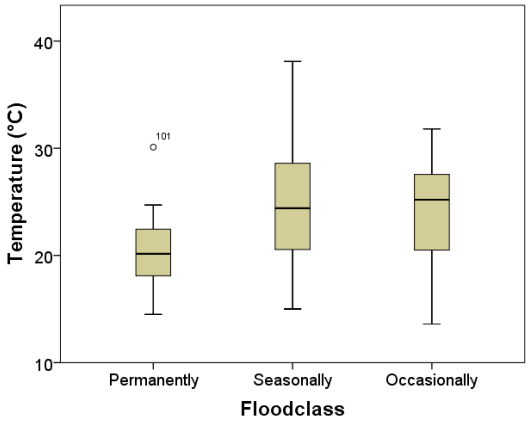


Figure 4.18. Water temperatures across flood classes in all the samples.

Habitat-wise, floodplains have warmer waters than marginal vegetation sites (L. test: $p>0.01$; O.W.A. test: $F=7.387$, T. HSD test: $p<0.01^{*}$) across all the samples taken between September 2006 and February 2010 (Figure 4.19).

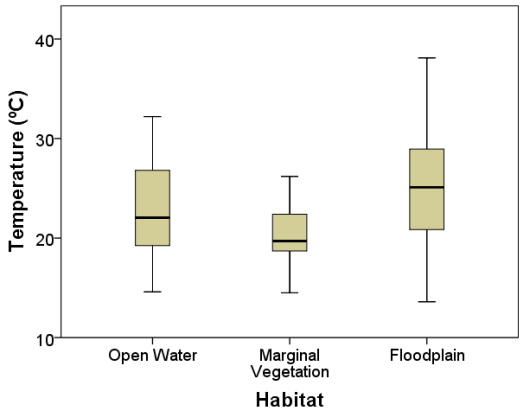
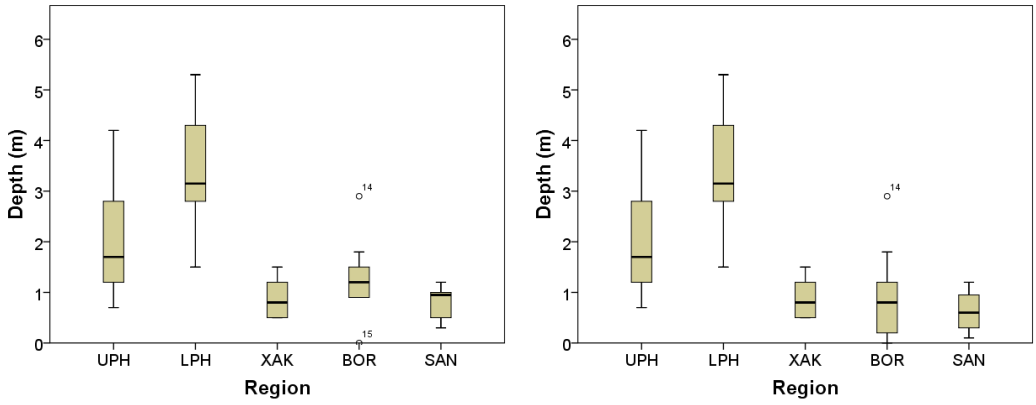


Figure 4.19. Water temperatures across habitats in all the samples.

Water depth

Water depths vary significantly between the five regions sampled in 2006-2007 (O.W.A. test on log-transformed depths: $F=18.162$, $p<0.001^{**}$). Pair-wise differences are as follows (T. HSD test): sites are deeper in UPH than XAK ($p<0.01^{*}$) and than SAN ($p<0.001^{**}$); also LPH sites were deeper than the in other regions ($p<0.001^{**}$) except UPH and in XAK than SAN ($p<0.001^{**}$) (Figure 4.20a). In the joint dataset water depth is significantly different across regions with deeper waters in the Panhandle sites (K.W. test: $\chi^2=41.813$; $p<0.001^{**}$) (Figure 4.20b).



a) ***b)***

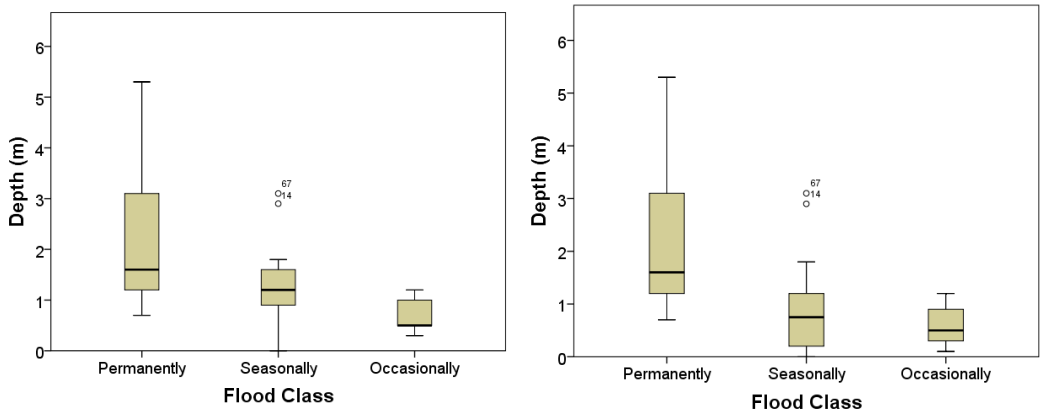
Figure 4.20. Water depth across regions in a) Campaign 1 and 2) all the samples.

Table 4.19 shows the post-hoc test results, highlighting pair-wise comparisons.

Table 4.19. Mann-Whitney tests on water depth across regions.

p-values	UPH	LPH
LPH	<0.001**	
XAK	<0.01*	<0.001**
BOR	<0.001**	<0.001**
SAN	<0.001**	<0.001**

Depth varies significantly between the flood class categories in Campaign 1 (O.W.A. test: F= 19.953, p<0.001**); water was deepest in PF sites followed by SF and OF (M.W. U tests: PF > OF and SF > OF, p<0.001**) (Figure 4.21a). Water depth does not vary significantly across flood classes or habitat types in the shallower sites sampled in Campaign 2 and it does not show a significant seasonal variation in either campaign when analysed separately. Water depth is significantly higher in Campaign 1 (L. test: p<0.001**; K.W. test: χ^2=28.913; p<0.001**), with an average of 1.6 m as compared to 0.6 m in Campaign 2. In the merged dataset, water depth across the Delta is significantly higher in PF sites than SF and OF (L. test: p<0.001**; K.W.: χ^2=37.437, p<0.001**; M.W.U test:both p<0.001**; see Figure 4.21b). No significant difference is observed across floodplain types at p=0.01.



a) ***b)***

Figure 4.21. Water depth across flood classes in a) Campaign 1 and b) all the samples.

Water depth varies significantly across seasons in the merged dataset (K.W. test: χ^2=20.134, p<0.001) with significantly lower levels in February than in Apr/May (p<0.01*), July/August (p<0.001**) and September (p<0.01*) (Figure 4.22).

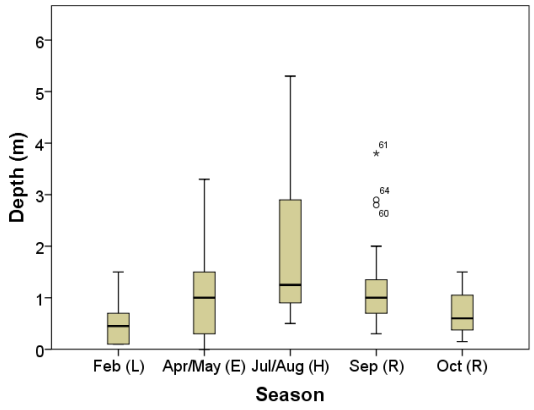


Figure 4.22. Water depth across seasons in all the samples.

Water levels are lower in 2009-2010, as compared to the other flood years (L. test: $p<0.001^{**}$; O.W.A. test: $F=31.190$, $p<0.001^{**}$; M.W.U: $p=0.001$ for 2006-2007 and $p<0.001^{**}$ for 2007-2008), but this is influenced by the heavy sampling of shallower floodplain sites in Campaign 2 than at whole-Delta scale. In the merged dataset water depth varies significantly across habitats (K.W. test: $\chi^2=45.595$, $p<0.001^{**}$), with deeper sites in OW and MV than F ($p<0.001^{**}$ for both) (Figure 4.23).

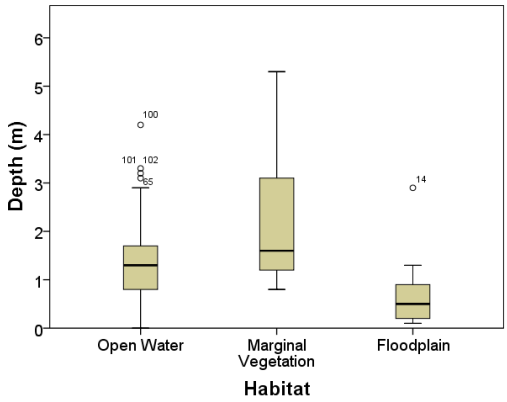


Figure 4.23. Water depth across habitats in all the samples.

Conductivity

Conductivity changes significantly between sites of different regions in Campaign 1 (L. test: $p<0.001^{**}$; K.W. test: $\chi^2= 41.854$, $p<0.001^{**}$) (Figure 4.24a). Conductivity also significantly varies regionally in Campaign 2 (M.W.U test: BOR < SAN: $p<0.01^{*}$) (Figure 4.24b) and in the merged dataset (L. test: $p>0.01$; K.W.: $\chi^2=83.433$); BOR and SAN show higher conductivity than UPH ($p<0.001^{*}$); XAK, BOR and SAN have higher values than LPH; and BOR shows higher conductivity than XAK ($p<0.001^{*}$) (Figure 4.24c).

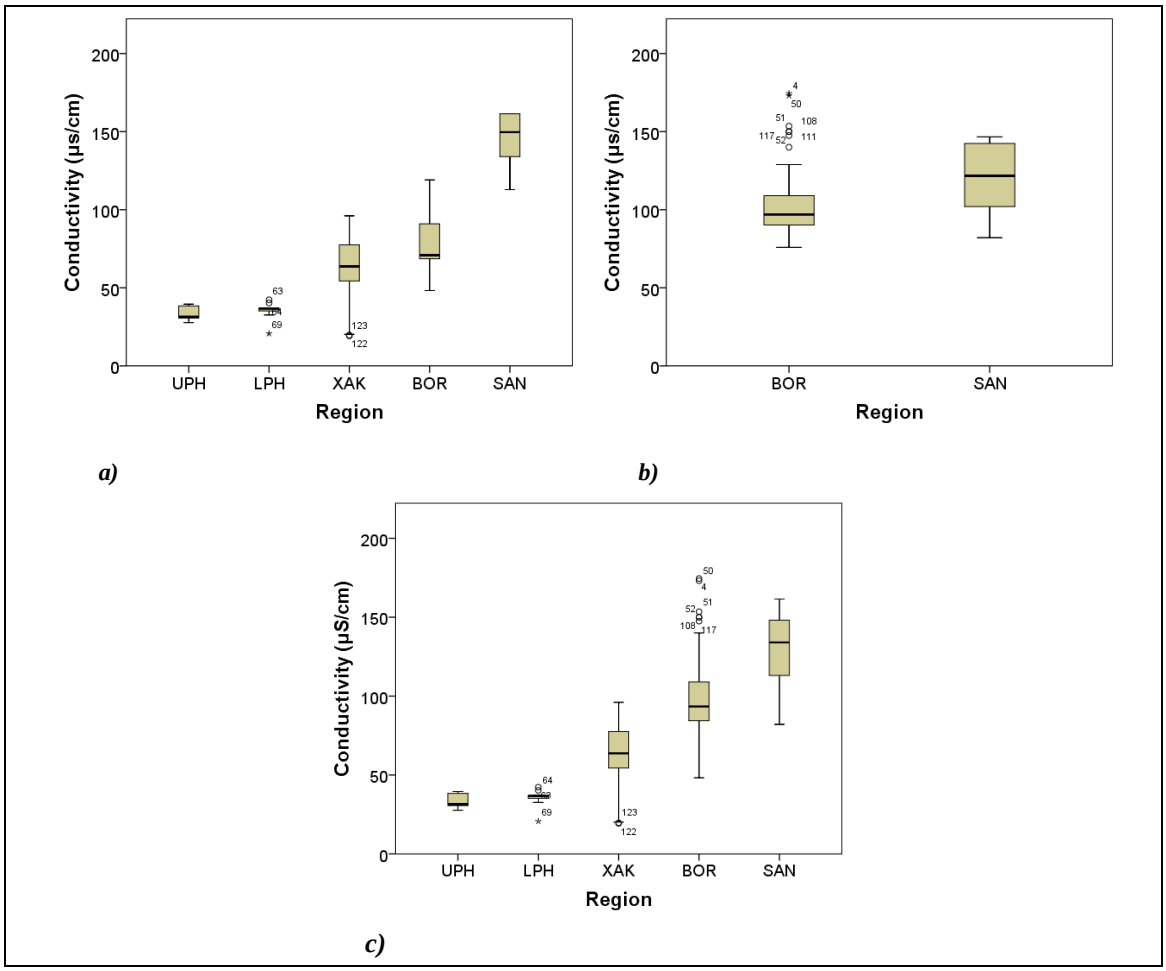


Figure 4.24. Conductivity across regions in a) Campaign 1; b) Campaign 2; c) all the samples.

Table 4.20 shows the significant differences in conductivity across regions in Campaign 1.

Table 4.20. Mann-Whitney tests on conductivity across regions in Campaign 1.

p-values	UPH	LPH
XAK		$<0.001^{**}$
BOR	$<0.001^{**}$	$<0.001^{**}$
SAN	$<0.001^{**}$	$<0.001^{**}$

Conductivity varies between sites of different flood class in Campaign 1 (K.W. test: $\chi^2=43.958$; $p<0.001^{**}$). However, in Campaign 2 SF sites has higher conductivity than PF sites (MW-U test: $p<0.001^{**}$) and OF sites shows higher conductivity than both PF and SF ($p<0.001^{**}$) (see Figure 4.25a). Conductivity does not vary across flood classes in Campaign 2, but it changes with flood class in the merged dataset (L. test: $p<0.01$; K.W.: $\chi^2=78.133$; $p<0.001^{**}$). SF and OF have higher conductivity than PF sites and OF higher than SF (all $p<0.001^{**}$) (Figure 4.25b).

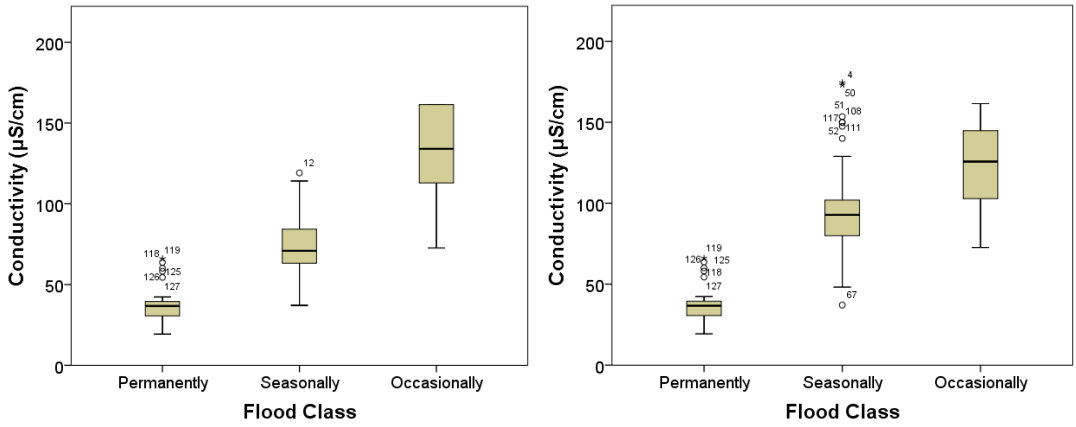


Figure 4.25. Conductivity across flood classes in a) Campaign 1; b) all the samples.

Conductivity does not vary significantly between flooding phases / seasons in either dataset; however it varies across seasons in the merged dataset (L.test: $p>0.01$; $\chi^2=19.258$; $p<0.01^{*}$), with February showing higher values than in April/May ($p<0.01^{*}$) and July/August ($p<0.001^{**}$); conductivity was also significantly higher in October than in July/August ($p<0.001^{**}$) (Figure 4.26).

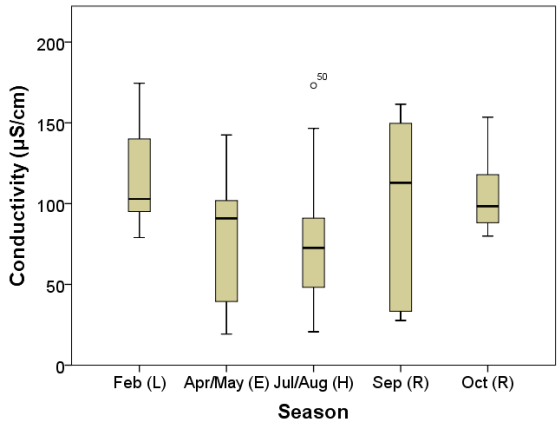
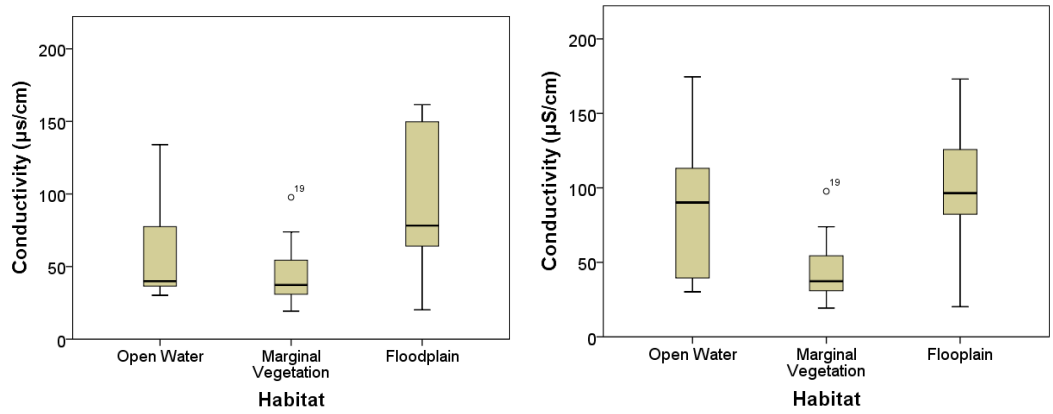


Figure 4.26. Conductivity across seasons in all the samples.

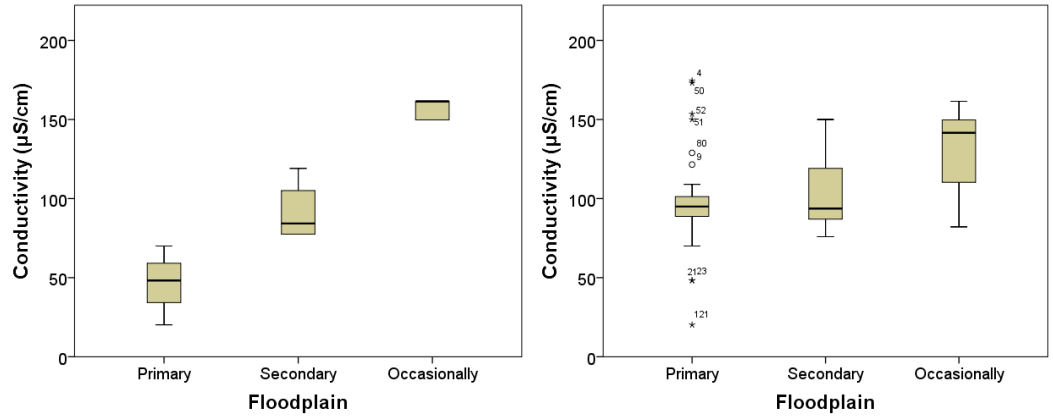
In Campaign 1 conductivity varies significantly between different habitats (L. test: $p<0.01^{*}$; K.W. test: $\chi^2=13.682$, $p<0.01^{*}$). According to M.W.U tests, conductivity is higher in F than MV habitats ($p<0.001^{**}$) (Figure 4.27a). In the merged dataset, habitats show higher conductivity in OW and F than MV: K.W. test: $\chi^2=30.820$, $p<0.001^{**}$ (M-W U test: $p<0.001^{**}$) (Figure 4.27b). No significant variations were recorded across either Delta-scale habitat and within-floodplain habitats (Open Water, Sedgeland and Grassland) in Campaign 2.



a) ***b)***

Figure 4.27. Conductivity across habitats in a) Campaign 1; b) all the samples.

Conductivity is overall higher in Campaign 2 than Campaign 1 (L. test: $p<0.001^{**}$; K.W. test: $\chi^2=36.154$; $p<0.001^{**}$). This variable also differs across flood years (L. test: $p<0.001^{**}$: K.W.: $\chi^2=47.082$), higher levels in 2009-2010 than 2007-2008 ($p<0.001^{**}$); and across floodplain types (L. test: $p>0.01$; O.W.A: $F=65.636$ in Campaign 1; $F=10.444$ in the merged dataset; $p<0.001^{**}$). Higher values recorded in OF than primary ($p<0.01^{*}$ and $p<0.001^{**}$) and secondary floodplains ($p<0.001^{**}$ and $p<0.01^{*}$) and in secondary than primary floodplains ($p<0.01^{*}$) (Figure 4.28 a and b).



a) ***b)***

Figure 4.28. Conductivity across floodplain types in a) Campaign 1; b) all the samples.

Dissolved Oxygen (DO)

DO concentrations are higher in Campaign 1 than Campaign 2 (L. test: $p>0.01$; O.W.A. test: $F=43.380$; $p<0.001^{**}$). In Campaign 1 DO varies between sites of different regions (L. test: $p>0.01$; O.W.A. test: $F=3.896$, $p<0.01^{*}$), but with no pair-wise differences (Figure 4.29a). In Campaign 2 DO does not vary regionally, but it does in the merged dataset (L. test: $p>0.01$; O.W.A. test: $F=16.661$; $p<0.001^{**}$); higher values in UPH, XAK and SAN than BOR ($p<0.01^{*}$) (Figure 4.29b).

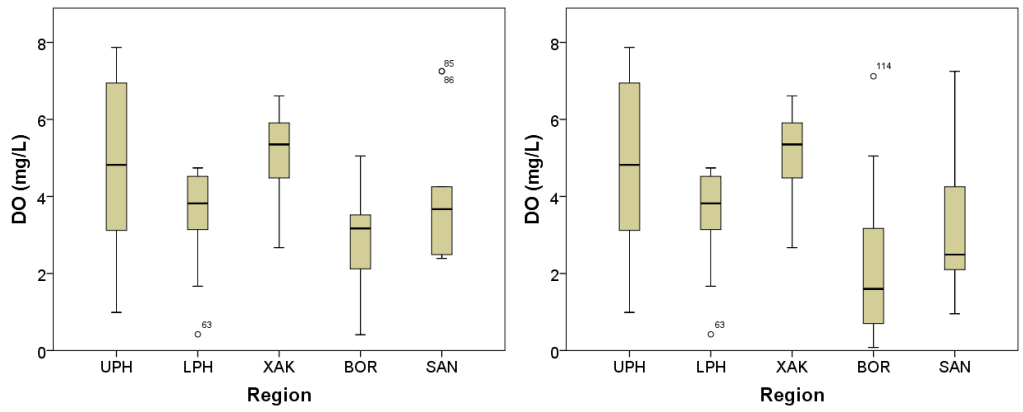


Figure 4.29. Dissolved Oxygen across regions in a) Campaign 1; b) all the samples.

In Campaign 1 DO varies significantly across flood classes (L. test: p>0.01; O.W.A. test: F=5.201, p<0.01*), but with no pair-wise differences (Figure 4.30a). In Campaign 2 (L. test: p>0.01; O.W.A. test: F=7.997, p<0.01*), the post-hoc test between SF and OF is not significant (p=0.012) (Figure 4.30b). The aggregate data (L. test: p>0.01; O.W.A. test: F=22.245, p<0.001**) show higher levels in PF and OF than SF sites (T. HSD test: p<0.001* and p<0.01*) (Figure 4.30c).

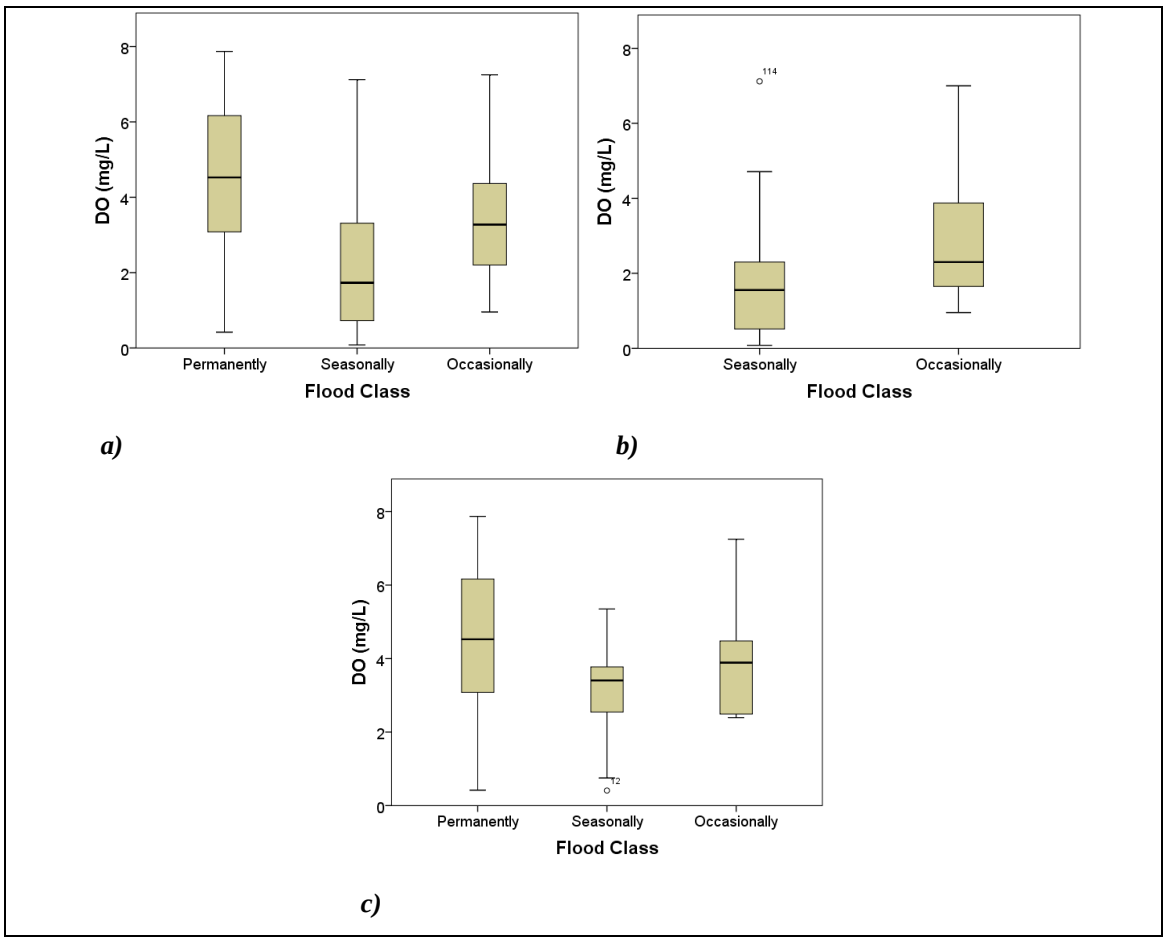
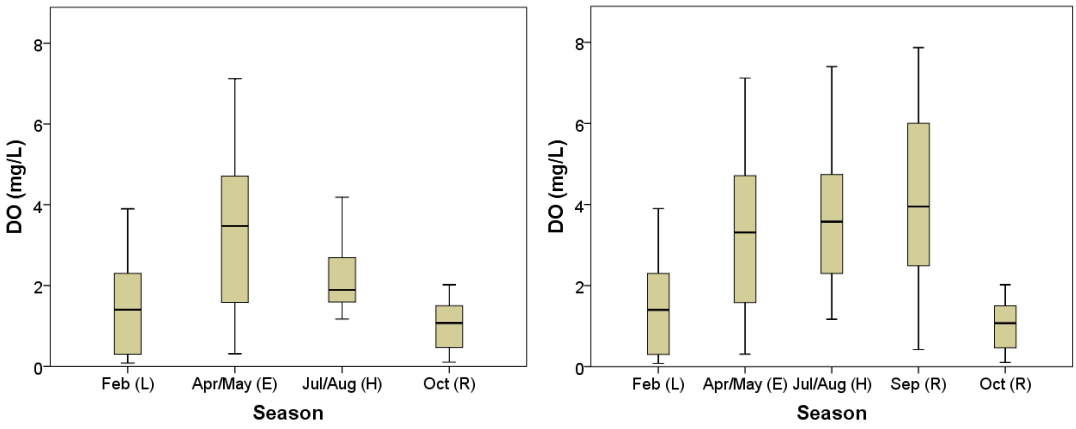


Figure 4.30. Dissolved Oxygen across flood classes in: a) Campaign 1; b) Campaign 2; c) all the samples.

DO concentrations change significantly between seasons in Campaign 2 (L. test: $p<0.01^{*}$; $\chi^2=21.178$; $p<0.001^{**}$), with higher values in the flood Expansion phase (Apr/May) than during Low Water (February) and Recession (October) (MW-U tests: $p<0.01$; $p<0.001^{**}$) and in the High Water (Jul/Aug) than Recession phases ($p<0.001^{**}$) (Figure 4.31a). In the merged dataset DO levels vary across seasons (K.W. test: $\chi^2= 49.500$; $p<0.001^{**}$) with significantly higher values April/May, July/August and September than in October and February (Figure 4.31b).



a) ***b)***

Figure 4.31. Dissolved Oxygen across seasons in a) Campaign 2; b) all the samples.

Interseasonal pair-wise differences in DO levels are highlighted in Table 4.21.

Table 4.21. Mann-Whitney tests on DO concentrations across seasons in all the samples.

p-values	**October**	**February**
April/May	$<0.001^{**}$	$<0.01^{*}$
July/August	$<0.001^{**}$	$<0.001^{**}$
September	$<0.001^{**}$	$<0.001^{**}$

DO concentrations do not vary significantly across habitat types in either campaign. DO values vary significantly across flooding years (L. test: $p>0.01$; O.W.A. test: $F=22.385$, $p<0.001^{**}$): 2006-2007 and 2007-2008 samples have higher DO than 2009-2010 (both $p<0.001^{**}$), as more OW samples were taken in those years. Dissolved Oxygen levels do not vary across floodplain types. Overall, the concentrations of DO vary across habitats (L. test: $p>0.01$; O.W.A. test: $F=5.159$; $p<0.01^{*}$); however the difference MV *vs* F is not significant (Figure 4.32).

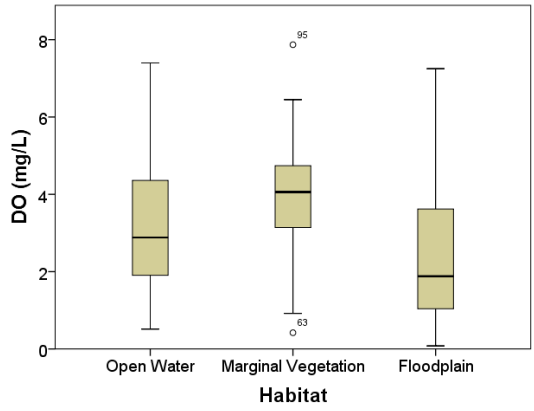


Figure 4.32. Dissolved Oxygen across habitats in all the samples.

DO concentrations also vary significantly across floodplain type (L. test: p>0.01; O.W.A.: F=5.732, p<0.01*) with Occasionally Flooded floodplains having higher values than Primary Floodplains (p<0.01*) (Figure 4.33).

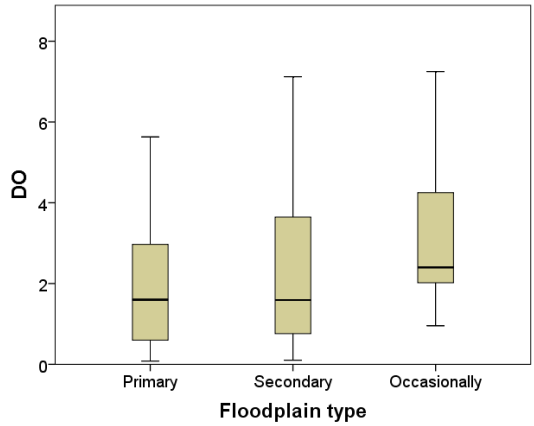


Figure 4.33. Dissolved Oxygen across floodplain types in all the samples.

pH

In Campaign 1 pH varies significantly between sites of different regions (L. test: p>0.01; O.W.A. test: F=5.656, p<0.01*). T.HSD tests show that SAN had higher water pH than LPH and BOR (p<0.01*) (Figure 4.34a). The same differences were recorded across regions in the joint dataset (L. test: p>0.01; O.W.A. test: F=5.833; p<0.001**), i.e. pH was also significantly higher in SAN than in LPH and BOR (p<0.01* and p<0.001**) (Figure 4.34b).

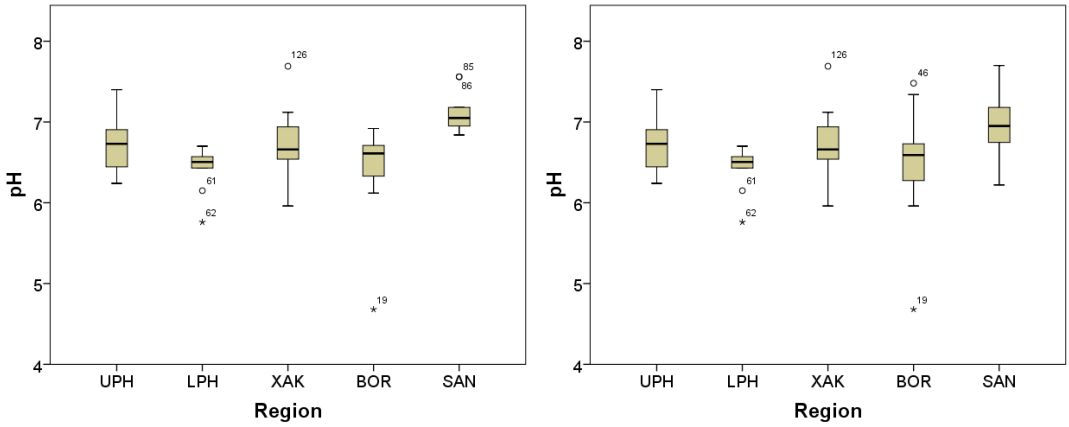


Figure 4.34. pH across regions in a) Campaign 1; b) all the samples.

In Campaign 2 there is no significant variation in pH across regions or flood classes. pH values do not change across habitat in either datasets. pH does vary significantly across the stages of the floods in 2006-2007 (L. test: $p<0.01^{*}$; K.W.: $\chi^2=12.204$; $p<0.01^{*}$). In particular sites sampled in High Water phase had lower values than those in the Expansion phase ($p<0.001^{**}$) (Figure 4.35). pH values do not change significantly over the three flood years or between Campaign 1 and 2.

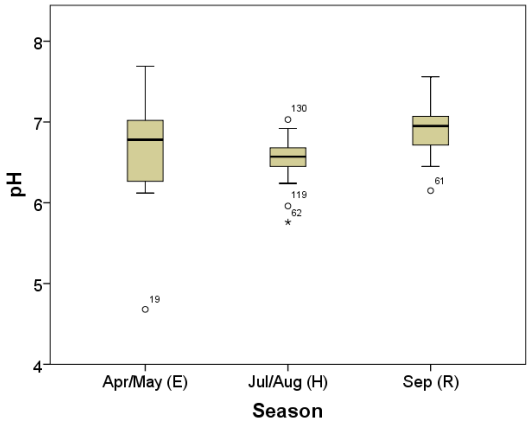


Figure 4.35. pH across seasons in Campaign 1.

Sites with different flood class show significant changes of pH (L. test: $p>0.01$; O.W.A. test: $F=9.074$; $p<0.001^{**}$) with higher values in occasionally floodes sites than seasonally inundated floodplains ($p<0.001^{**}$) (Figure 4.36).

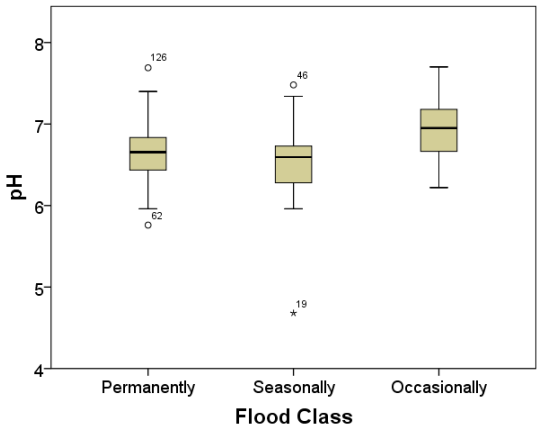


Figure 4.36. pH across flood classes in all the samples.

pH varies significantly across floodplain types both in Campaign 1 and in the whole dataset (L. test: p>0.01; O.W.A.: F=7.327 and F=8.053, p<0.01*); occasionally flooded sites have higher pH values than primary floodplains (p<0.01*) (Figure 4.37) in the overall dataset, but no significant post-hoc pair-wise differences recorded in Campaign 1. pH does not vary across seasons or habitats.

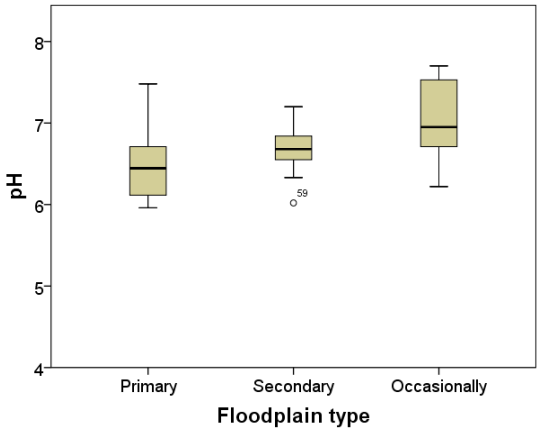


Figure 4.37. pH across floodplain types in all the samples.

Total Nitrogen (TN) and Total Phosphorus (TP)

The concentrations of TN and TP do not vary significantly across regions, flood class, habitats or floodplain type. However, TP levels are slightly higher in LPH, BOR and SAN than UPH and in OF than SF and PF sites. TP, but not TN, concentrations vary across seasons (L. test: p>0.01: O.W.A: F=5.811; p<0.01*), with higher values in February (Low water phase) than in Apr/May (Expansion phase) and July/August (High water phase) (p<0.01*) (Figure 4.38).

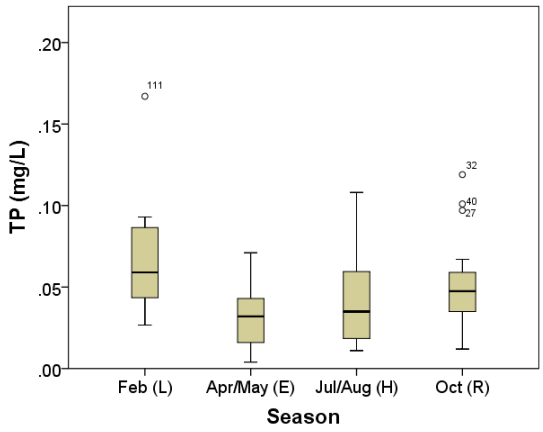


Figure 4.38. Total Phosphorus across seasons in Campaign 2.

Samples used in this study show that in UPH, LPH and XAK the TN:TP ratio was 19.6 as compared to 30.8 in BOR (no chemistry data were available for SAN) (see sections 4.7.3 and 4.8.3).

4.7.4. Statistical tests on variables measured only in Campaign 1

In this subsection the results on limnological variables only available for Campaign 1 (Mackay *et al.*, 2011, 2012) are presented. The data relative to the algal samples collected have been re-analysed for this study. The presence or absence of significant variations of water velocity, cation and anion concentrations and TSS are illustrated.

Water velocity

Water velocity does not show any significant changes across regions, seasons / flooding phases, flood classes, but it is higher in permanently flooded (0.26 m s^{-1}) than in seasonally inundated sites (0.06 m s^{-1}) and in Open Water (0.35 m s^{-1}) than in Marginal Vegetation (MV) (0.24 m s^{-1}) and Floodplain (F) sites (0.07 m s^{-1}).

Dissolved Organic Carbon (DOC)

Dissolved Organic Carbon concentrations (DOC) vary across regions (L. test: $p<0.001^{**}$): K.W. test: $\chi^2=30.549$, $p<0.001^{**}$. Higher DOC levels were recorded in XAK than UPH and LPH ($p<0.001^{**}$ and $p<0.01^{*}$) and in BOR as compared to UPH and LPH ($p<0.001^{**}$ and $p<0.01^{*}$) (Figure 4.39).

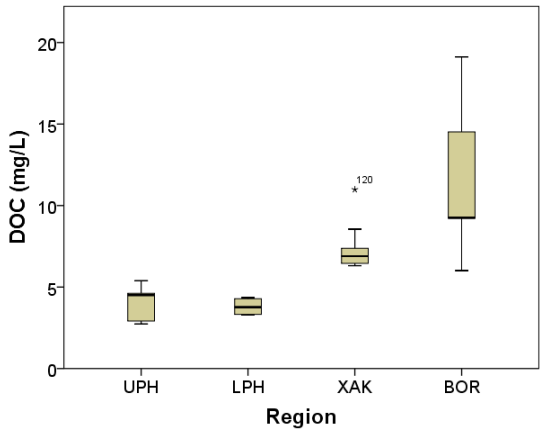


Figure 4.39. Dissolved Organic Carbon across regions in Campaign 1.

DOC levels do not vary across seasons, but they do change across sites with different flood class (L. test: $p<0.01$; K.W. test: $\chi^2=21.231$, $p<0.001^{**}$); SF and OF sites showed higher values than PF sites ($p<0.001^{**}$ and $p<0.01^{*}$) (Figure 4.40). DOC values do not vary across different habitats at p=0.01.

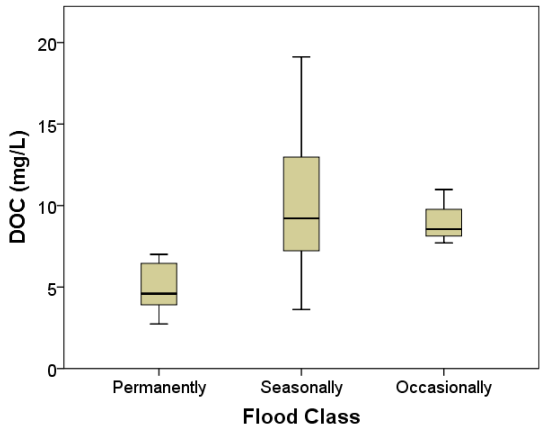


Figure 4.40. Dissolved Organic Carbon across flood classes in Campaign 1.

Silica concentrations (SiO_2)

Silica concentrations (SiO_2) measured in Campaign 1 are significantly different across regions (L. test: $p<0.001^{**}$; K.W. test: $\chi^2=28.357$; $p<0.001^{**}$); UPH and XAK have higher concentrations of SiO_2 than LPH ($p<0.001^{**}$) (Figure 4.41).

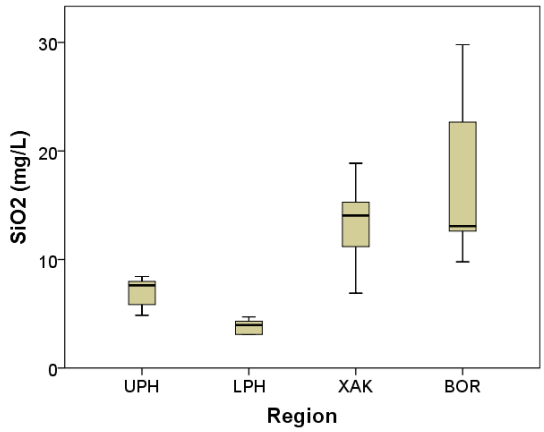


Figure 4.41. SiO_2 across regions in Campaign 1.

SiO_2 also varies between sites with varying flood class (O.W.A.: F=10.331, $p<0.001^{**}$) with seasonally flooded areas having higher SiO_2 values than permanently flooded sites (T. HSD test: $p<0.001^{**}$) (Figure 4.42). No statistically significant changes are detected between different seasons (data were available only for April / May and July / August 2007) or across habitats.

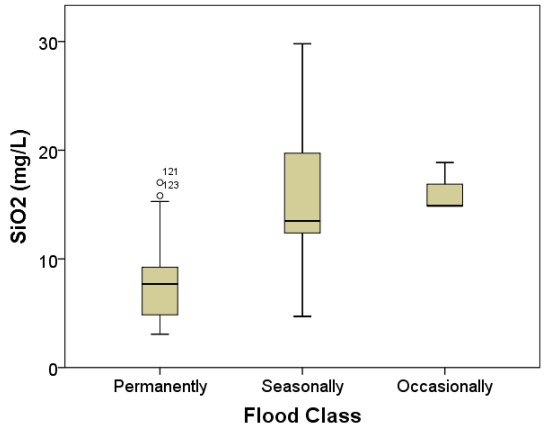


Figure 4.42. SiO_2 across flood classes in Campaign 1.

Cation and anion concentrations

Statistical analyses were conducted on the total concentrations of cations (Ca^{2+}, K^{+}, Mg^{2+}, Na^{+}) and anions (Cl^{-}, PO_4^{2-}, SO_4^{2-}) so as to provide a synthetic 'picture' of how the concentrations of these ions varied in the environment. Cations vary significantly across regions (L. test: $p<0.01^{*}$; K.W. test: $\chi^2=23.021$, $p<0.001^{**}$); LPH, XAK and BOR have higher cation concentrations than UPH ($p<0.001^{**}$) and BOR than LPH ($p<0.001^{**}$) (Figure 4.43).

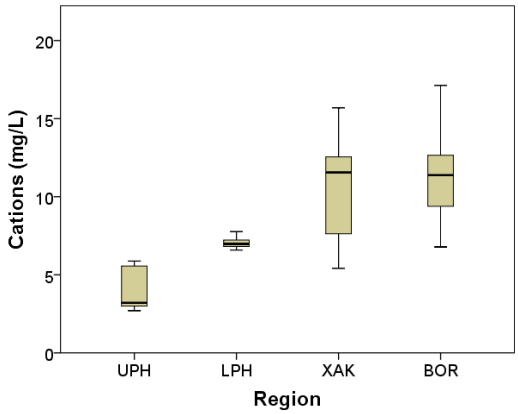


Figure 4.43. Cations across regions in Campaign 1.

Anion levels also vary significantly across the Delta's regions (L. test: p>0.01; O.W.A. test: F=6.792, p<0.01*); BOR and XAK show significantly higher anion concentrations than UPH (p<0.01* for both) (Figure 4.44).

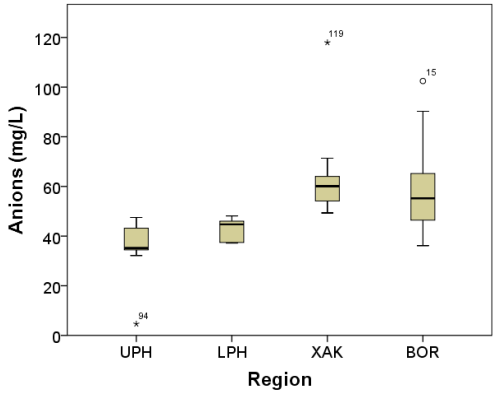


Figure 4.44. Anions across regions in Campaign 1.

Cations vary across seasons (L. test: p>0.01; O.W.A. test: F=24.843, p<0.001**); in the high water phase values were higher than in the flood expansion stage (p<0.001**) (Figure 4.45). Anions do not vary significantly with season.

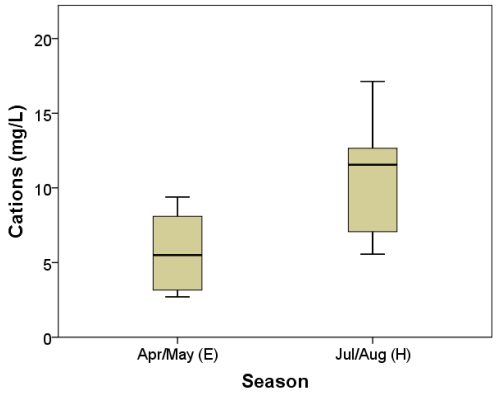


Figure 4.45. Cations across seasons in Campaign 1.

Cation concentrations also vary with flood class (L. test: p>0.01; O.W.A. test: F=21.736, p<0.001**); SF and OF sites have higher concentrations than PF sites (MW-U test: p<0.001**) (Figure 4.46). Anion concentrations do not change significantly across flood class and neither cations or anions vary across habitats.

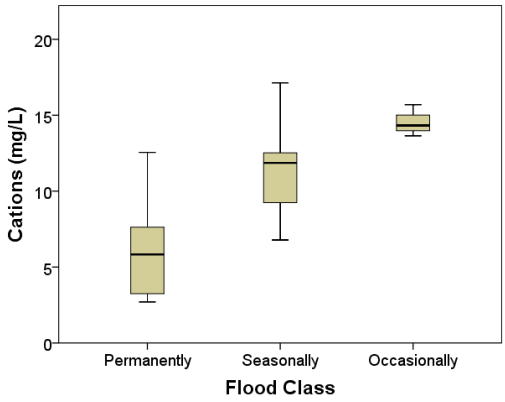


Figure 4.46. Cations across flood classes in Campaign 1.

These differences reflect variations in the concentrations of individual ions. In particular, Ca^{2+}, K^{+}, Mg^{2+}, Na^{+} all contribute to the overall variation across regions (Tables 4.23 and 4.24). BOR and XAK have significantly higher concentrations of most ions than UPH and LPH. The cation concentrations variations are mainly due to Mg^{2+} and Na^{+}, the only two ions showing a regional variation, as per O.W.A. tests: F=6.953 for Mg^{2+} and F=26.024 for Na^{+} (L. test: p>0.01*) (Table 4.22).

Table 4.22. Statistical tests on individual ion concentration changes across regions (*=p<0.01; **=p<0.001; L. test: p>0.01 for O.W.A tests and p<0.01 for K.W. tests).

Ion	Region	Flood Class
Ca^{2+}	$F=13.323^{**}$	
K^{+}	$\chi^2=28.537^{**}$	
Mg^{2+}	$\chi^2=16.472^{*}$	$F=6.953^{*}$
Na^{+}	$\chi^2=28.243^{**}$	$F=26.024^{**}$
HCO_3^{-}	$F=6.728^{*}$	

Mg^{2+} and Na^{+} concentrations are higher in seasonally flooded sites than permanently flooded ones, whereas Na^{+} is also significantly higher in occasionally flooded sites than in permanently inundated ones.

Table 4.23. Post-hoc statistical tests of individual ion concentration changes across regions (Tukey H.S.D. for O.W.A test; M.W.U for K.W. test).

Regions	Ca^{2+}	K^{+}	Mg^{2+}	Na^{+}	HCO_3^{-}
XAK > UPH	<0.01*	<0.001**	<0.01*	<0.001**	<0.01*
XAK > LPH	<0.01*	<0.001**	<0.01*	0.001**	
BOR > UPH	<0.01*	<0.001**	<0.01*	<0.001**	<0.01*
BOR > LPH	<0.01*	0.001**		0.001**	

Total Suspended Solids (TSS)

According to O.W.A. and K.W. tests, the concentrations of TSS do not vary significantly across regions, seasons, flood class or habitats; however on average Open Water (OW) environments slightly higher TSS concentrations than Floodplains (F) (p-value <0.05).

4.7.5. Statistical tests on variables measured only in Campaign 2

Chl *a* and turbidity were measured only in 2009-2010; their patterns of variation are presented below.

Chlorophyll a (Chl a)

In Campaign 2, Chl *a* concentrations do not vary significantly across regions, seasons or flood class, but it changes across sites with different floodplain habitats (L. test: p>0.01: O.W.A. test: F=8.484, p<0.01*), Grasslands and Sedgelands show higher Chl *a* than Open Water sites (p<0.01* for both) (see Figure 4.47).

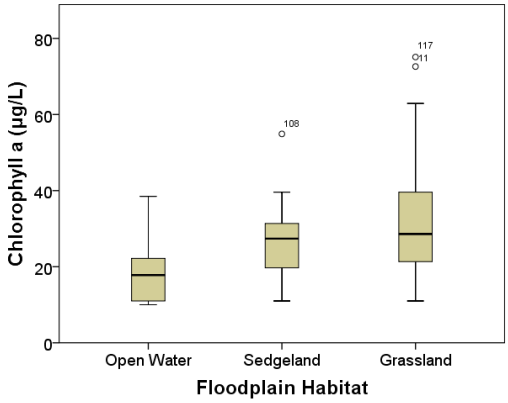


Figure 4.47. Chlorophyll a across within-floodplain habitats in Campaign 2.

Turbidity

Turbidity does not vary significantly between regions, seasons or habitats; however it changes with flood class (L. test: $p<0.001^{**}$; K.W. test: $\chi^2=27.065$, $p<0.001^{**}$): OF sites have higher turbidity levels than SF areas ($p<0.001^{**}$) (Figure 4.48).

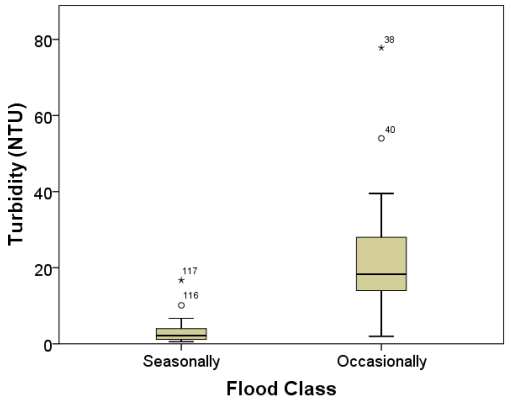


Figure 4.48. Turbidity across flood classes in Campaign 2.

Similarly, turbidity changes significantly according to floodplain type (L. test: $p<0.001^{**}$; K.W. test: $\chi^2=29.616$, $p<0.001^{**}$), with higher turbidity in occasionally inundated than primary and secondary floodplains ($p<0.001^{**}$) (Figure 4.49).

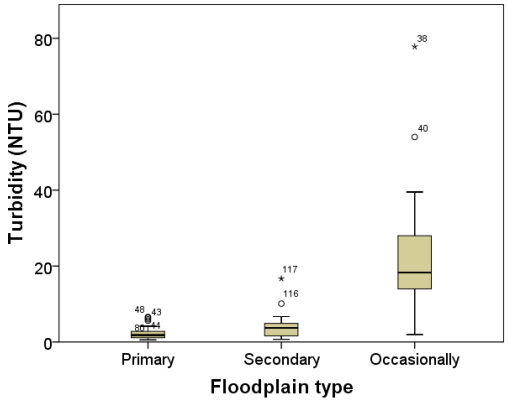


Figure 4.49. Turbidity across floodplain types in Campaign 2.

The results presented in sections 4.7.3 to 4.7.5 indicate that there are numerous significant differences between limnological characteristics of the water sampled in the five regions, three flood class categories, four flooding phases in different years. The investigation of how the hydrology and water characteristics of the Delta influenced algal assemblages and were influenced by them will be undertaken in Chapter 5. Table 4.24 shows a summary of the average variation of limnological variables within regions, flood classes, habitats and seasons. Most frequently coefficients of variation are higher between samples taken in the same habitat and season, whereas samples within a region or flood class show lower changes; this is

linked to the fact that the three Delta-scale habitat were sampled in the whole wetland and data grouped by seasons also represent samples taken in the five regions, whereas regional data and those grouped by flood class show smaller variations as they are clustered geographically, e.g. PF in UPH and LPH.

Table 4.24. Average coefficients of variation of limnological variables within region, flood class, habitat and season (the highest c.v. is underlined for each variable).

Average c.v. (%)	Region	Flood Class	Habitat	Season
Conductivity	23.2	42.6	27.1	40.1
Depth	53.0	71.0	65.3	82.1
DO	48.9	57.6	61.0	58.5
pH	5.7	6.2	7.1	6.3
Temperature	15.8	19.9	19.6	12.0
TP	54.5	60.6	65.4	58.2
SiO_2 (C1)	26.3	37.0	56.5	53.2
TN (C1)	46.8	33.5	43.8	49.1
Velocity (C1)	149.3	161.1	165.3	158.5
DOC (C1)	23.1	30.3	50.1	52.4
Chlorophyll a (C2)	47.1	47.1	48.9	47.9
Turbidity (C2)	85.4	85.4	144.4	144.0
Anions (C1)	27.2	27.4	35.5	37.6
Cations (C1)	24.5	25.4	26.2	38.2

4.8. DISCUSSION

In this section, first the results of the algal counts on phyla abundance, and on species and genera richness are discussed in relation to previous studies on the Delta and literature on other wetlands; secondly, the results of the field measurements and chemistry analyses are used to characterise the environments of the Delta. These results are used as reference point for the interpretations of the results presented in Chapters 5 and 6.

4.8.1. Algal counts and floras

This study produced a large dataset of algal counts from the Okavango Delta, an understudied near-pristine wetland in the semiarid Kalahari desert. Green algae (Chlorophyta) and diatoms (Bacillariophyta) are by far the most abundant algal phyla, together representing 82% of the total specimens. Chlorophyta are more

abundant than diatoms (55% *vs* 26%) in Campaign 2, which was focussed on the distal (Southern) reaches of the Delta whereas Bacillariophyta dominate over Chlorophyta (54% *vs* 29%) in Campaign 1 samples, collected from across the whole wetland, including the Panhandle. Five other phyla are present in significant abundance: Cyanophyta, Cryptophyta and Euglenophyta (together about 16% of the total algal counts), and Chrysophyta, Pyrrophyta and Xanthophyta (0.9% of the total); only one alga belonging to the Prasinophyta was identified (Table 4.2 and Appendix B). Bacillariophyta and Chlorophyta are also the most important phyla in the Delta in terms of species and genera richness; together they represent 80% (396) of the 496 species and 71% (123) of the 173 genera found (Table 4.1).

Here some important characteristics of the most abundant algal taxa are outlined. The most abundant genera of diatoms (Bacillariophyta) observed are:

a) Eunotia (Ehrenberg, 1837): essentially a freshwater diatom genus comprising around 200 species (Van Landingham, 1969 in Sala *et al.*, 2002). Cells may be single, or form long ribbon-like colonies, free, or attached by mucilaginous stalks; *Eunotia* species are widespread and diverse in acidic and dystrophic habitats (Furey, 2010). The genus is distributed world-wide; numerous species are restricted to tropical areas, due to the fact that they prefer environments with low pH and conductivity (Sala *et al.*, 2002). Overall, diatoms of the genus *Eunotia* are benthic non motile and "*a strong indicator for acid, fresh, oligotrophic water, which is rich in oxygen and poor in organic nitrogen compounds*" (Van Dam *et al.*, 1994). *Eunotia pectinalis*, *Eunotia flexuosa* and *Eunotia spp.* are shown in Figure 4.50.

b) Gomphonema (Ehrenberg, 1832): a relatively common genus in freshwater diatom assemblages with circumneutral pH (Spaulding and Eldlund, 2009); these diatoms form mucilaginous stalks attached to solid substrata and are amongst the algae responsible for transforming the structure of benthic assemblages from two to three dimensional (Round *et al.*, 1990). *Gomphonema gracile* is shown in Figure 4.4; this species has been observed in stagnant waters in East African lakes (Gasse, 1986), but it does not tolerate high nutrient concentrations (Van Dam *et al.*, 1994) instead preferring intermediate phosphorus levels (Cooper *et al.*, 1999).

c) Synedra (Ehrenberg, 1830; renamed *Ulnaria*; Compère, 2001, here the old genus name is kept to draw comparisons with other studies): frustules are robust and

typically needle-like; cells typically form radiate colonies with cells attached by mucilage pads (Spaulding and Edlund, 2008c). This is a genus of mostly planktonic (but can grow attached to plants) diatoms much longer than wide, that was shown to be very good competitor for (and usually limited by) P, but a poor competitor for Si hence they grow best at high Si:P ratios (Tilman, 1981; Kilham, 1984); *Synedra ulna* tends to grow fast in overstorey rosette-like colonies and with P and N enrichment (Pan and Lowe, 1994) (Figure 4.50).

d) *Nitzschia* (Hassall, 1845): a genus of raphid, motile diatoms; species of this genus occur in benthic (and rarely planktonic) habitats in many lentic and lotic systems. *Nitzschia* is a very common genus with a large number of species often difficult to identify, some species reach high abundance in waters high in organic pollution (Spaulding and Edlund, 2008b).

e) *Aulacoseira* (Twhaites, 1848): one of the most successful freshwater centric diatoms, particularly abundant in plankton of lakes and large rivers; a very similar genus, *Melosira*, is primarily marine (Spaulding and Edlund, 2008a). This diatom's requirements for light and P are defined as 'intermediate' by Kilham *et al.* (1986). This diatom genus is also characterized by the formation of resting spores which can survive up to hundreds of years in the sediments (Spaulding and Edlund, 2008a). A common species is *Aulacoseira granulata* (Figure 4.50).

The most abundant genera of green algae (Chlorophyta) observed are:

a) *Mougeotia* (Agardh, 1824; Figure 4.50): a cylindrical-shaped filamentous green alga characterized by sexual reproduction; algae of this genus are cosmopolitan, living at the margins of ponds, but also in streams and on moist soil, often entangled around macrophytes and toleratant of reduced light and increasing mixing depth (Happey-Wood, 1988 in de Melo and Huszar, 2000). About 140 species are estimated to live worldwide, however identification to species level is limited by the need for rarely visible sexual structures to be analysed (John *et al.*, 2002). These algae are well adapted to warm temperatures and low pH, they can photosynthesize with low light levels, i.e. are shade-tolerant (Graham *et al.*, 1996) and prefer mesotrophic and eutrophic conditions (Hagerthey *et al.*, 2013).

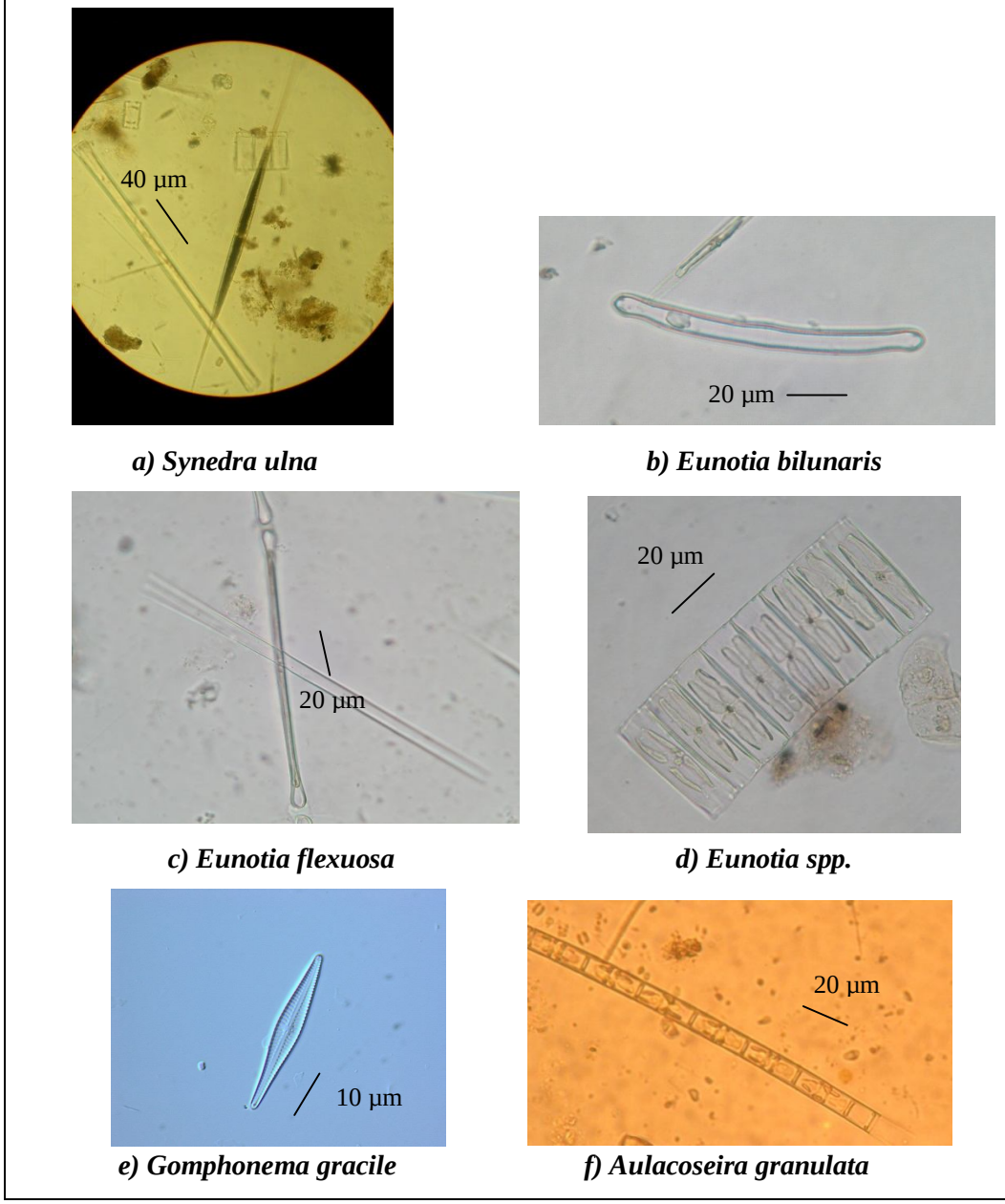
b) *Cosmarium* (Corda ex Ralfs, 1848): a unicellular green alga, belonging to the Desmidiales, composed of 2 semicells joined by a central isthmus; very common in

acid bogs and pools in association with *Sphagnum* and *Utricularia* and in margins of ponds and lakes, sometimes common in the plankton (John *et al.*, 2002) (Figure 4.50).

c) *Scenedesmus* (Meyen, 1829): a very common genus of Chlorococcalean algae; they forms coenobia of 2, most frequently 4 or 8 cells, typically disposed in parallel rows. These algae are cosmopolitan, planktonic or associated with sediments or aquatic vegetation, normally in standing and slow-flowing water. About 200 species have been described (John *et al.*, 2002) (Figure 4.50).

b) *Monoraphidium* (Komarkova-Legnerova, 1969): a small free living unicellular green alga, more or less spindle-shaped, probably cosmopolitan, planktonic or associated with macrophytes or submerged surfaces in still or slow-flowing water (John *et al.*, 2002) (Figure 4.50).

The most common genus of Cryptophyta is *Cryptomonas* (Ehrenberg, 1838), a cosmopolitan flagellate alga, widespread in aquatic habitats; about 200 species have been recognized, 100 occurring in freshwater habitats (John *et al.*, 2002) (Figure 4.50). Micrographs of some of the common taxa of diatoms and other algae are respectively shown in Figure 4.50 and Figure 4.51. More species of diatoms and green algae are shown in Appendix E1 and E2.



a) Synedra ulna

b) Eunotia bilunaris

c) Eunotia flexuosa

d) Eunotia spp.

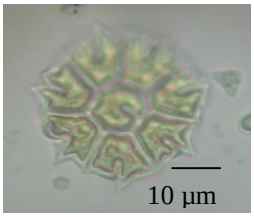
e) Gomphonema gracile

f) Aulacoseira granulata

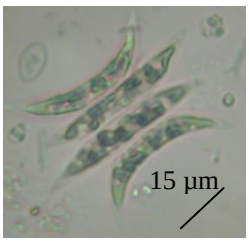
Figure 4.50. Micrographs of some of the common taxa of diatoms observed in the Delta.

a) Mougeotia spp.

b) Cosmarium spp.



c) Pediastrum tetras



d) Scenedesmus spp.

e) Cryptomonas spp.

Figure 4.51. Micrographs of some of the common species of green algae and of one Cryptophyta genus observed in the Delta.

Comparisons between studies in the Delta and in the River Basin

This is the first comprehensive and systematic research project investigating all the algal groups in the Okavango Delta; it adds important new knowledge to previous work on planktonic algae (Cronberg *et al.*, 1996a), diatoms (Cholnoky, 1966a; Mackay *et al.*, 2012) and desmids (Coesel and Van Geest, 2008; 2009) in this subtropical wetland. 496 species and 173 genera were observed, which is the first estimate of algal taxon richness in the Delta, confirming the expectation that several hundred algal species live there (Ramberg *et al.*, 2006). 139 of diatom species (28% of the total) were also found by Mackay *et al.* (2012).

The detailed cross-study comparisons presented in section 4.7 demonstrated that the algal flora of the Delta shares on average 11% (range: 0.9-46%) of the species with a section of the Okavango River in Namibia (Grönblad and Croasdale, 1971) and Namibia / Botswana (Cholnoky, 1966a), fewer than the species found in the Delta itself in multiple works (Cronberg *et al.*, 1996a; Coesel and van Geest, 2008; 2009; Mackay *et al.*, 2012) and in this study, i.e. on average 16% (range: 0.2-43%) (Table 4.25). Grönblad and Croasdale (1971) found 185 desmid taxa in a Namibian section

of the Okavango River near Nkure-Nkuru (the great majority of more than 200 species identified); among these, 24 species of the genera *Cosmarium*, *Euastrum*, *Micrasterias*, *Onychonema* and *Staurastrum* were also observed in this study in the Okavango Delta wetland, which begins about 400 km downstream (South-East direction). Hence, 13% (24 out 185) of the desmid species were found in this study and in the Okavango river's Namibian section (Grönblad and Croasdale, 1971); 8% (15 out of 185) of the desmid species found by Coesel and van Geest (2008; 2009) in the Delta were also observed in this study. Finally, 5 species of *Euastrum* and 1 of *Cosmarium* were observed by Grönblad and Croasdale (1971) and by Coesel and van Geest (2008; 2009). Cronberg *et al.* (1996a) and Grönblad and Croasdale (1971) found only two species (*Closterium kuetzingii* and *Desmidium bailey*) and four genera in common (4%) – *Closterium*, *Cosmarium*, *Euastrum* and *Staurastrum*. Similarly, only five species (10%) of two genera were found by Grönblad and Croasdale (1971) and Coesel and van Geest (2008; 2009): *Cosmarium taxichondrum*, *Euastrum attenuatum*, *E. divergens*, *E. mononcylum*, *E. spinulosum*. Appendix F lists all the algal taxa in common between the main studies used for these comparisons, i.e. Cholnoky (1966), Croberg *et al.* (1996a/b), Mackay *et al.* (2012) and this study.

Table 4.25 shows a summary of the number and percentage of the algal species observed in studies conducted between 1966 and 2014. An average of 11% of species were observed in studies on algae beyond the Okavango Delta wetland (e.g. in riverine upstream areas in Namibia and Botswana) and in those which surveyed algae only in the Delta. On average, 16% of the species were found in this study and in the other ones undertaken in the Okavango Delta wetland (Cronberg *et al.*, 1996a/b; Coesel and van Geest, 2008; 2009). Thus the algal flora of the Okavango River upstream of the Panhandle differs *c.* 50% more (16% *vs* 11%) from this study's flora than previous works in the Delta compared to this study do. This comparison of six studies of algal floras in the Delta and upstream areas spanning about 40 years (made on the basis of species lists) is a significant stepping stone for possible biogeographic research in the Okavango River Basin (see section 7.3).

Table 4.25. Number of algal species observed in this and previous studies in the Delta (Lead authors: 1966: Cholnoky; 1971: Grönblad and Croasdale; 1996: Cronberg; 2008-2009: Coesel and van Geest; 2012: Mackay; 2014: Marazzi).

Studies	**1966**	**1971**	**1996** ***a/b***	**2008-2009**	**2012**	**2014**
Okavango Delta Basin						
1966 (diatoms)	-	0	1 (0.9%)	n.a.	29 (8.9%)	52 (46%)
1971 (desmids)		-	2 (1.1%)	5 (2.7%)	n.a.	24 (13%)
Okavango Delta						
1996 (all algae)			-	0	1 (0.2%)	52 (11%)
2008-2009 (desmids)				-	n.a.	15 (8.1%)
2012 (diatoms)					-	48 (43%)
2014 (all algae)						-

Hillebrand *et al.* (2001) demonstrated that species composition of microorganisms becomes more dissimilar as geographic distance increases, both for diatoms and ciliates. Consistently with that, this study suggests that the algal assemblages living in the Delta are more dissimilar than those found in upstream areas of the Okavango River Basin, than assemblages observed in the Delta in different sampling years. To the author's knowledge, this is the first evidence of the differences in occurrence of algal species in the Delta (studies conducted between 1996 and 2008-2009) and upstream areas in the Okavango River Basin differ. Spatial, environmental and limnological conditions are likely to influence these differences in species presence / absence; further work could tackle this issue by systematically sampling algae in the river basin so as to establish the degree to which algae are cosmopolitan in this region and how strongly they are influenced by environmental conditions affecting their niche space.

Both this study and Mackay *et al.* (2012) observed a higher number of species of diatoms in PF areas in UPH and LPH. However, in 2007, periphytic diatom taxon richness decreased significantly at the height of the flood (July; Davidson *et al.*, 2012). By contrast, here the lowest diatom species richness in water was observed earlier, i.e. in Apr/May 2007-2009, during the flood expansion phase (see Figure 4.17) with a significant increase during flood recession (September 2006 and October 2009) and low water phase (February 2010). This is likely due to the higher water temperatures and micronutrient concentrations and conductivity, in these seasons (see Figures 4.12 and 4.38), i.e. more energy and nutrients allow for the coexistence of more species as per Species-Energy-Theory (Wright, 1983).

4.8.2. Algal traits

Here the patterns in cell arrangement and size (length), motility and metabolism are discussed in relation to previous studies on wetlands and freshwater environments. Cell arrangements more complex than unicellular, i.e. colonies and filaments, are more frequent in BOR than the other regions and in floodplains than other habitats, whereas unicellular algae are relatively more abundant in SAN than other cell arrangements (see section 4.6.1). This reflects the fact that higher nutrient levels favour Chlorophyta and Cyanophyta which are algal phyla with more frequent colonial and filamentous algal forms.

In the Delta, average algal cell length is significantly smaller in the distal reaches (BOR and SAN regions) (see section 4.6.2). Small green algae, in this study *Monoraphidium arcuatum* and various species of *Scenedesmus*, are more common in the shallow floodplains (see also section 6.4), as observed in other subtropical shallow wetlands, e.g. in the Lower Paraná River in Argentina (Unrein, 2002; Izaguirre *et al.*, 2004). These small green algae algae with high S/V ratio have the advantage of rapidly uptaking nutrients (Reynolds, 1997). Algal cell size was shown to change across nutrient gradients in other wetlands too. In the Everglades an increase in abundance of coccoid blue-green algae was observed with higher phosphorus concentrations (Pan *et al.*, 2000). In the Paraná river floodplain, García de Emiliani (1993) recorded a higher biomass of smaller algae during nutrient inflows. Smaller algae with higher S/V ratios tend to be r-strategists with short reproduction cycles and high reproductive rates; in the Okavango Delta plants with r-strategy were also shown to be common in flooded grasslands inundated for less than 5 months per year (Junk and Piedade, 1993 in Murray-Hudson *et al.*, 2014b).

In this study, TP concentrations are only marginally higher in BOR than UPH, but conductivity levels, linked to micronutrient concentrations (e.g. Ca^{2+} and HCO_3^-) (Potapova and Charles, 2003) are markedly higher in the distal reaches of the Delta (see section 4.7.3). Hence, in the Okavango Delta, in the Everglades (Pan *et al.*, 2000) and in the Paraná river floodplain (García de Emiliani, 1993) there is evidence that a higher abundance of small algae are observed in waters with higher macro- or micro-nutrient levels. This may be due to the fact that smaller r-selected algae have higher production / biomass (P/B) ratios and prevail at early successional stages, but are less energy-efficient than larger ones (K-selected) which are

dominant in mature ecosystems where nutrient cycling is more efficient and diversity as well as stability are higher (Odum, 1971; Reynolds, 2006). Flooding disturbance interrupts algal successions (Reynolds *et al.*, 1993) and hence may favour smaller algae with faster nutrient uptake in seasonally flooded areas (Figure 4.8b). Small algae are significantly more abundant in OW and F than MV habitats whereas large algae prevail in MV, but these differences are rather small (Figure 4.8c). Also, taxon-specific cell dimensions of the most abundant algae did not show significant changes. However, this study does not have sufficient data for a detailed investigation of seasonality and successions, as sampling algae every several months equates to studying long term succession in forests without sufficient samples to describe community / assemblage developments (Padisák, 1994). Furthermore, the direct effect of flooding on algal communities could be tested only by means of field experiments with enclosures / microcosms to measure changes at fine temporal and spatial resolution (see section 7.3), whereas here flooding disturbance is defined as frequency of inundation, i.e. permanent, seasonal or occasional, over the past 30 years (see section 3.1; Siziba *et al.*, 2011b).

Non motile algae are by far the prevalent group in all regions, flood classes and habitats (see section 4.6.3). A higher proportion of motile algae are present in the OF sites of the Delta (Figure 4.9), e.g., diatoms such as *Navicula* and *Nitzschia* (Round, 1991). Motile diatoms, benthic cyanobacteria and Euglenophyta are present in higher abundance in these areas with sediments, which can be explained by motility being a key adaptation to prevent burial by siltation (Fore and Grafe, 2002). In terms of metabolic traits, phagotrophy is more frequently present in the SF floodplains of BOR (and to a lesser extent SAN), which also contains about 30% of the N-fixing algae observed, with PF areas hosting 40% and a slightly higher frequency in OF sites (see section 4.8.4, Figure 4.10b). In the Lower Paraná, potamoplanktonic species such as *Aulacoseira granulata*, typical of turbid environments, dominate the channels while mixotrophic phytoflagellates, facultative N-heterotrophic diatoms and small-sized green algae prevail in the swamps (Unrein, 2002). In this study, *A. granulata* also shows higher abundance in turbid environments in BOR and SAN than in the other regions alongide small green algae such as several species of *Monoraphidium* and *Scenedesmus.*

4.8.3. Limnology of the Okavango Delta

Overall, 21 of the significant correlations between limnological variables are weak (r=0.25 - 0.50), 29 are of moderate strength (r=0.50 - 0.75) and only 7 are strong correlations (r> 0.75). Deeper waters are colder and have lower conductivity and dissolved ion content, whereas shallower sites, such as floodplains have warmer and more nutrient-rich waters. The associations between the six variables measured in both campaigns vary to an extent between Campaign 1 and Campaign 2, notably depth and conductivity are negatively correlated only in the Delta-scale survey, i.e. Campaign 1 (see Tables 4.9 and Table 4.11).

In the floodplains, the water is shallower than in river channels and lagoons. Hence higher evapotranspiration takes place here than in the Panhandle region (see section 4.7.3; Mackay *et al.*, 2011; Akoko *et al.*, 2013) which causes the conductivity and concentration of dissolved ions to be significantly higher in these environments in BOR and SAN compared to the Panhandle. Moreover, the shallow floodplain waters experience substantial microbial decomposition, likely caused by both high availability of organic matter from vascular plants (Mladenov *et al.*, 2007) and animal dung (Lindholm *et al.*, 2007) and enhanced by light availability stimulating UV degradation of organic matter (Mladenov *et al.*, 2007). This also increases concentrations of cations and anions in these habitats located mostly in BOR and SAN (Figure 4.43 and 4.44).

In Campaign 1, conductivity, ion concentrations, SiO_2 and DOC are higher where water depth is lower, as larger water volumes dilute these (see also section 4.7.3). DO decreases as temperature increases due to lower oxygen solubility in warmer waters and to higher microbial decomposition activity (and hence respiration which reduces oxygen levels) taking place in shallow floodplain waters than in the Panhandle (Mladenov *et al.*, 2007). This trend was also observed by Mackay *et al.* (2011) on a larger water chemistry dataset including data used in this study (see section 3.5). pH increases with DO as higher photosysthesis consumes CO_2 in turn increasing both DO and pH, e.g. in the floodplains of SAN; on the other hand, the lower DO levels recorded in the seasonally inundated sites of BOR, where microbial decomposition tends to be high (Mackay *et al.*, 2011), are associated with slightly lower pH values (Figure 4.34 and Tables 4.7).

The data analyses on limnological variables confirmed that the Okavango Delta is characterized by higher conductivity, DOC, concentrations of cations, anions and SiO_2 in the distal reaches occupied by seasonally and occasionally flooded sites (BOR and SAN) than in the Upper and Lower Panhandle (UPH and LPH) (see section 4.7.3) (Sawula and Martins, 1991; Mackay *et al.*, 2011). In fact, a decreasing trend in dissolved solute concentrations with higher water levels (see Figure 4.60) was observed by Mackay *et al.* (2011) for K^+, Cl^-, Ca^{2+}, as well as by Cronberg *et al.* (1996b). Mladenov *et al.* (2005) observed lower concentrations of Dissolved Organic Carbon (DOC) with higher water levels, but they did not decrease in this study or in Mackay *et al.* (2011). However, in habitats classified as wet or wet/dry in Mackay *et al.* (2011) conductivity and concentrations of most anions, cations and DOC were significantly lower in permanently wet sites than in areas subject to drying. This corresponds to this study's results. "Wet" habitats correspond to permanently flooded sites and "wet/dry" habitats to SF and OF ones, the latter having higher DOC (Figure 4.40).

Overall, floodplain sites have higher conductivity and concentrations of ions in the lower Delta than the Panhandle sampling points (see section 4.7.3) due to the mobilisation of dissolved salts from dry soil surfaces coming from river flow (Cronberg *et al.*, 1996a), accumulations in sediments over thousands of years (Mendelsohn *et al.*, 2010), wind-blown dust (Garstang *et al.*, 1998) and animal faeces (Lindholm *et al.*, 2007). Mean DOC levels in Campaign 1, i.e. 7.3 mg L^{-1}, are within the range observed in undisturbed wetlands and fluctuate significantly during the year (Figures 4.39 and 4.40) due to the flood pulse (Mladenov *et al.*, 2007). In the Delta, there is a North-West / South-East gradient of these variables due to evaporative processes, especially for cations (e.g. Ca^{2+}, Na^+, K^+, Mg^{2+}) and the increase in area of seasonally inundated floodplains (see also Krah *et al.*, 2006; Mackay *et al.*, 2011).

In Campaign 1, mean SiO_2 and HCO_3^- concentrations in BOR are 17 mg L^{-1} and 59 mg L^{-1} (see Figures 4.40 and 4.43), respectively lower and higher than those measured by Sawula and Martins (1991) in 1989-1990, i.e. 38 mg L^{-1} and 27 mg L^{-1}.

In Campaign 1 water velocity does not vary significantly across regions, flood class or habitats, but it is slightly higher in UPH than in the other regions, in PF sites and OW habitats (see section 4.7.4).

Mackay *et al.* (2011) found significantly higher TN concentrations during the high flood period, which may be linked to the slightly higher nitrogen concentrations in the floodwaters than in wetland soils (Cronberg *et al.*, 1996a; Mubyana *et al.*, 2003). In this work, TN concentrations do not exhibit any significant differences in space or time; however, TP concentrations do change significantly across flood phases, with highest concentrations in the recession stage of the flood across the Delta (Figure 4.38), as already observed by Mackay *et al.* (2011). TP levels detected in the Pool C floodplain in BOR, on average similar to other studies, i.e. 0.04 mg L^{-1} (Krah *et al.*, 2006; Lindholm *et al.*, 2007), were highest during the initial flood stage and decreasing in later phases. When flooding takes place in the Delta phosphorus is usually released at the moist soil pH values due to lower cation levels (Mubyana *et al.*, 2003); however in this study cation levels (Figure 4.43) are higher in high flood season hence they may still be able to bind some phosphorous. In this study TN:TP ratios were higher in BOR (on average 30.8) and UPH, LPH and XAK (19.6) (see section 4.7.3) than in Mackay *et al.* (2011), respectively 20.4 and 13.7, who concluded that N and P co-limitation may take place in the latter regions and P limitation in BOR (TN:TP ratios higher than 15; Abell *et al.*, 2010). In the samples used here, P appears to be limiting in four regions, as no chemistry data are available for SAN (see section 3.1).

Seasonal temperature variations are much higher than those recorded in a shallow tropical lake, the Coqueiro Lake in Northern Brazil, i.e. 26.8 ± 0.4 °C in the autumn and 28.6 ± 0.2 °C in the spring (Loverde-Oliveira *et al.*, 2009). In Campaign 2, mean temperatures were respectively 24.3 ± 2.1 °C in April/May (autumn) and 27.0 ± 5.4 °C in July to February (winter to summer). Other freshwater ecosystems in the subtropics, such as the Lower Paraná River, experience an absolute temperature excursion between winter and summer, i.e. mean temperatures of 9.5 °C and 22 °C (Izaguirre *et al.*, 2004), which is similar to that observed in the Delta, i.e. 18 °C in winter (Jul/Aug 2007/2009) and 29 °C in summer (February 2010) (see Figure 4.17). Conductivity and the concentrations of some of the ions show lowest values during the high water season (see section 4.7.3, though cations and anions don't show this trend), which is likely due to dilution, as also observed in other wetlands (e.g. Kinross, Michigan; Kadlec and Bevis, 1990). Regional and floodplain-scale gradients have both been studies in subtropical wetland ecology literature. In the

Lower Paraná floodplain (Argentina) depth, pH, dissolved oxygen, suspended solids and nitrates decreased from channel to swamp habitats whereas Chl *a* increased (Unrein, 2002). In this study, water depth and DO also decrease from channel to swamp, but no significant trends were detected in pH, nitrogen concentrations (here measured as TN), suspended solids (TSS); Chl *a* did increase from OW to Grasslands (see Figure 4.47 and section 4.7.5).

pH varies less than the above mentioned variables in the Delta, with the highest values in OF sites in SAN (Figures 4.34 and 4.36). TN and TP concentrations do not show significant changes, but TP levels tend to be higher in the flood recession phases (Figure 4.38). DOC, SiO_2, cation and anion concentrations are higher in the distal reaches where sites are seasonally or occasionally flooded (see section 4.7.4).

Despite the rather high nutrient levels, the Delta is deemed to maintain oligotrophic status due to the processes of nutrient uptake by the vegetation in the Panhandle (McCarthy and Ellery, 1994) and chemical precipitation under the very numerous islands scattered in the distal reaches (Gumbricht *et al.*, 2004; Ramberg and Wolski, 2008). However, as discussed in section 6.5, chemical (TN and TP concentrations) and biological (e.g. Chl *a*) criteria used to classify freshwater ecosystems in trophic levels yield different results. In a comparative assessment of the biodiversity of globally important wetlands Junk *et al.* (2006) defined the Okavango Delta as mesotrophic. Many tropical lakes are classified as eutrophic due to the lack of obvious light limitation and the small variations of the photoperiod and temperature through the year (Esteves, 1988 in Huszar *et al.*, 1998). Furthermore, benthic algae are crucial for primary production and TP absorption in subtropical wetlands, but increased nutrient levels may not be detected in the water samples due to nutrients being stored in periphyton as observed in the Everglades (Gaiser *et al.*, 2004). Therefore, investigating phytobenthos and periphyton as well as phytoplankton in terms of the nutrients they absorb (Gaiser *et al.*, 2004) allow a more complete and thorough estimation of wetland water quality.

The Delta faces anthropogenic pressures such as increased tourism and population growth and hence more comprehensive water quality assessments are advisable (sections 2.2.3 and 7.3) alongside improved water chemistry analyses (Mmualefe and Torto, 2011). Filamentous algae have been observed most recently in July 2014 (before the delayed onset of the floods) in the Sexaxa region, along the

Thamalakane river south of the Boro region; here nutrients are likely to have higher concentrations due to activities such as cattle rearing (Murray-Hudson, personal communication). Studying specifically algal blooms may help support informed decisions on management of the Delta's waters and ecosystems.

4.9. SUMMARY

This chapter provided the results of algal identification and counting, the detailed description of the overall trends in species and genera richness and a full characterisation of the limnological conditions across the Okavango Delta. The great majority of algal units counted (82%) and species identified (80%) belong to Bacillariophyta and Chlorophyta, the former prevailing in the Panhandle (UPH and LPH) and the latter in the distal reaches (especially in BOR). In total 496 species of algae (173 genera) were observed, intermediate species richness between that recorded in the Pantanal in Brazil (337 spp.; De-Lamonica-Freire and Heckman, 1996) and the Kakadu region in Australia (690 spp.; Finlayson *et al.*, 2006). Desmids, more common than diatoms in tropical regions (Rojo *et al.*, 1994), are the most diverse group with 184 species. The number of species identified in the Delta by this and connected studies (Mackay *et al.*, 2012; Williamson, unpublished data) amounts to a total of 672.

Overall, less frequently flooded sites in BOR and SAN host more species and genera than permanently flooded areas in UPH and LPH; floodplain habitats show higher taxon richness than the other habitats. Significant differences in water depth, temperature, conductivity and ion concentrations between the Panhandle region and the lower Delta areas confirm previous research (e.g. Mackay *et al.*, 2011); UPH and LPH sites are characterized by deeper, colder and faster flowing waters whereas BOR and SAN sites are shallower, warmer and more nutrient-rich. These results support the Intermediate Disturbance Hypothesis (IDH; Connell, 1978; Reynolds *et al.*, 1993), the Habitat Heterogeneity Hypothesis (HHH; MacArthur and MacArthur, 1961; Ricklefs, 1977) and the Species-Energy Theory (SET; Wright, 1983; Stevens and Carson, 2002), as flood disturbance and evapoconcentration of solutes in the distal reaches allow for algal assemblages with more species and genera to develop than in homogeneous environments in the Panhandle river channels and lagoons. In Chapter 5 further evidence of these trends is provided by means of diversity measures (e.g. Shannon Diversity and Evenness Index) to support this interpretation, estimates of algal biomass are presented and the species richness – biomass relationship is investigated.

Chapter 5 – Algal biodiversity and biomass patterns and controls

5.1. INTRODUCTION

Algae are at the base of aquatic food webs and hence underpin freshwater ecosystem and biodiversity (Paine, 1980); yet the world's algal species richness is likely to be considerably underestimated (John and Maggs, 1997). 72,000 species, including an estimate of those still to be described, are thought to exist (Guiry, 2012). This is specifically addressed in this study by estimating the number of unknown species and genera of algae that may exist in Okavango Delta, but which haven't been found or identified (see section 5.2.3). The lack of knowledge on algal diversity and ecology and their relationship with primary production and ecosystem functions and services highlights the need for studies in both pristine and impacted / constructed wetlands. In particular, largely pristine wetlands such as the Okavango Delta are crucial sites for scientific investigations on the structure and functioning of ecosystems, as human impacts are, at present, very low (Murray-Hudson *et al.*, 2006), but could increase substantially due to water abstraction plans and climate change (Andersson *et al.*, 2006). Diversity indices are used to further assess biodiversity of algae in the Delta in addition to species and genera richness.

Here Thesis objective 4 is addressed by analysing and interpreting the relationships between algal diversity and biomass and limnological variables, sampling region, season, flood class and habitat type. Objective 5 is also undertaken, i.e. comparisons are drawn between this study's results and other research on subtropical wetlands. Finally, a specific focus is placed on research question 4 on whether the species richness-biomass relationship is scale dependent in the Delta (section 2.3).

5.1.1. Taxon richness and diversity of algae

Algae are distributed globally, but they are subject to natural selection pressures and preferentially occupy the ecological niches they are well adapted to (Hutchinson, 1961) and show endemisms (Tyler, 1996). Also, assemblages of various groups of microorganisms resemble one another more if they live in the same habitat in distant locations rather than in different habitats in geographically adjacent areas (Patterson and Lee, 2000 in Finlay *et al.*, 2002). Criticism has been put forward on the relevance of the "endemism" concept when applied to diatoms, and to all microscopic eukaryotes; their high concentrations in the environment (10^3-10^{10} m^{-2}) and lack of physical barriers to their dispersal may allow them to be globally ubiquitous (Finlay *et al.*, 2002; Finlay, 2002). Remarkably, Finlay and Clarke (1999) observed 80% of the global known species of the flagellate genus *Paraphysomonas* in a <0.1 cm^2 sample of sediment from a freshwater pond in England (by means of more than 700 hours of observation with an electron microscope). This meets the prediction of the "*Everything is everywhere, the environment selects*" paradigm, also known as the Baas–Becking hypothesis (Chust *et al.*, 2012) and often erroneously attributed to Bjereinck (Quispel, 2010). Environmental conditions do select which of these 'ubiquitously dispersed' species of various organisms actually live where they do and with what 'success', i.e. at what abundance levels (Schoener, 1974). Fenchel (1993) concluded that smaller organisms are more widely distributed, or are even cosmopolitan; they disperse more efficiently, speciate and get extinct at a lower rate than do larger organisms. This is a more prudent view than the one expressed by other scholars that all microorganisms are distributed globally (Finlay, 2002; Lachance, 2004). It is practically impossible to prove the extent of both true endemisms and cosmopolitanism, especially for microorganisms; this debate is ongoing, especially amongst molecular ecologists (Šlapeta *et al.*, 2005), but goes beyond the scope of this study.

In this study algae are studied across environmental gradients in a largely pristine wetland; here communities are compared across regions and sites with different flood class, i.e. a geographic scale of a few hundred kilometers (see Figure 3.1), as well as across habitats, approximately at a scale of a few meters to max 30 meters, i.e. the distance between open water and the grassland portion in, e.g., a floodplain

at each site (see section 3.1). Diversity of algae at large scales can be linked to the size of the areas of investigation, e.g. larger areas of the same habitat will host more species. Habitat heterogeneity enhances both α-diversity, as per Habitat Heterogeneity Hypothesis (MacArthur and MacArthur, 1961; Ricklefs, 1977), and ß-diversity (Connor and McCoy, 1979). Habitat heterogeneity though increases with larger areas (MacArthur and Wilson, 1967). The Species Area Relationship (SAR) is expressed as: $S=cA^z$, S=number of species, A=area, c=a constant which depends on the unit used for area measurement, z=the slope of the species area relationship in log-log space. Thus the slope of the linearised SAR is an effective measure of ß diversity or the degree of compositional changes in microbial assemblages (Azovsky, 2002; Smith *et al.*, 2005), as well as macroorganisms in a wide range of environments (Drakare *et al.*, 2006). Mechanisms generating SAR at large scales include dispersal, speciation, and extinction whereas at local scales disturbance, competition, and herbivory (Passy and Blanchet, 2007) and dispersal mediated by disturbance are more important (Matthiessen and Hillebrand, 2006). Globally, the relationship between number of taxa and habitat area of aquatic and terrestrial microbial eukaryotes has been shown to be rather flat (Finlay, 2002; Azovsky, 2002), suggesting that microorganisms may have a high local diversity, but be only moderately diverse at a regional scale (Green *et al.*, 2004). Here, this will be used as a theoretical background for analyses comparing algal diversity at different spatial scales (see sections 5.2.1 and 5.2.2).

5.1.2. Factors determining biodiversity of algae

In general, regional diversity of various freshwater organisms can be predicted by several key factors: dispersal ability and biotic interactions and physical disturbance (Moss *et al.*, 2009). Evidence from experimental studies suggests that diversity of algae peaks after approximately 3 generations after disturbance or (depending on temperature) between 5 and 15 days after the stimulus is applied (Reynolds, 1993). Sommer (1993) defined disturbance as any factor which prevents phytoplankton biomass from reaching carrying capacity (K); diversity was shown to decline with long undisturbed periods without wind mixing events.

In streams, nitrogen (N) enrichment has been shown to enhance phytobenthic diversity (Peterson and Grimm, 1992); very abundant stress-tolerant species in low-nutrient

understories and eutrophic species in the overstory form highly diverse algal communities (Pringle, 1990; Larned, 2010).

Proulx and Mazumder (1998) proposed that plant species richness (including algae) is reduced by high grazing in nutrient-poor ecosystems due to a limitation of available resources for species regrowth after grazing. Other covariates contribute to these varying patterns, e.g. disturbance frequency and abundance and activity of grazers (Peterson and Grimm, 1992). More recent work concluded that productivity (linked to resource supply), consumers and physical disturbances all co-determine species richness at different trophic levels (Worm *et al.,* 2002). Grazing tends to have a negative effect on algal species richness (Mulholland *et al.,* 1991), but less so in lotic systems than in other ecosystems due to unidirectional water flow replacing species lost and to phytobenthic species reproducing rapidly and surviving in resting growth forms (Steinman *et al.*, 1992). In an experimental study on periphytic diatoms, Liess *et al.* (2009) found that light and nutrients increased species richness, productivity and nutrient content. Phytobenthos recycles nutrients more efficiently when these are in low concentrations (Paul *et al.*, 1991) so that the communities can maintain their diversity levels (Mulholland *et al.*, 1995). Spatial scale also needs to be considered when studying diversity patterns; micronutrient supply and watershed features in streams have been found to influence both local and regional species richness of diatoms (Passy, 2009).

In this study possible environmental and biological / ecological factors determining taxon richness (number of species / genera), diversity and biomass are analysed (see sections 5.3 and 6.3) in relation to the limnological variables measured (see section 4.7.3) and relevant literature on other wetlands in the tropics are considered.

5.1.3. Total algal biovolume and its controls

In this thesis, algal biomass is estimated by means of algal biovolume calculation (see section 3.4), which works as a proxy for algal wet biomass (1 mm^3 = 1 mg L^{-1}) (Nauwerck, 1968). Chl *a* is also used as a proxy for algal biomass (Reynolds, 2006). Despite the fact that algal cell volume calculation likely overestimates the size of larger cells with a higher relative vacuole volume (Smayda, 1978 in Hillebrand, 1999), biovolume calculations have been used extensively and are a reliable method for algal biomass estimation (Hillebrand *et al.*, 1999).

Algal biomass has been shown to be controlled by interacting resource (nutrients, light) and factors such as grazing, interpreted as a physical disturbance (Passy, 2007). Hillebrand (2005) found that light availability is a factor as important as other resources such as nutrients for benthic algal biomass, which increases with both grazer removal and light enhancement. The majority of investigations on the combination of nutrient and light limitations agree that light is more of a limiting factor for the growth of benthic algae than nutrients or herbivory (Lange *et al.*, 2011). Overall, for phytoplankton there are usually no more than three limiting nutrients, i.e. N, P and Si, given that micronutrients such as anions and cations very rarely limit algal growth (Padisák *et al.*, 2003; but see Sterner, 2008 on iron limitation in lake phytoplankton).

In freshwater systems, ecologists place a stronger focus on macronutrients, e.g., N, P, than on micronutrients such as cations and anions (Padisák *et al.*, 2003; Passy, 2009). Algal nutrient content is also influenced by light availability. A substantial body of evidence supports the light : nutrient hypothesis (LNH) (Fanta *et al.*, 2010); this posits that primary producers in high light conditions are nutrient poor relative to water column nutrients, whereas algae are nutrient-rich with lower light availability and nutrients (Sterner *et al.*, 1997). Algal cells store more intracellular carbon, as they fix surplus amounts during photosynthesis at higher irradiances (Sterner and Elser, 2002), which in turn dilutes intracellular P levels. On the other hand, more P seems to be needed by green algae, e.g. *Selenastrum capricornutum* when they need to adapt to low irradiances and related self-shading issues (Hessen *et al.*, 2002).

In wetlands epiphytic biomass is principally determined by the presence of macrophytes and by water level decreases allowing for the development of larger algal assemblages (Gosselain *et al.*, 2005). Grazing by microcrustacea (e.g. cladocerans, copepods and rotifera) and other organisms such as oligochaetes, chironomids (Hann, 1991; Norlin *et al.*, 2005; Keckeis *et al.*, 2003) and snails (Carlsson *et al.*, 2004) is an important top-down control of algal biomass in wetlands (Goldsborough and Robinson, 1996), including the Okavango Delta (Hart *et al.*, 2003). Water depth has been argued to be the most important variable defining a wetland and hence its algae (Kadlec, 1979); in the Delta its fluctuations induced by the annual flood pulse are superimposed on seasonal temperature

changes and linked nutrient mobilisation, with implications for algal biomass variations, e.g. water dilution may decrease biomass of algae in the high water season which coincides with lowest temperatures (see Figure 5.43).

5.1.4. Species richness – biovolume relationship

Debates over the nature and direction of the relationship between diversity and productivity or surrogate measures of instant community biomass (e.g. standing crop/biomass) in algae, plants and other organisms have taken place in ecology research over the last decades (Grime, 1973; Tilman, 1982; Abrams, 1995; Waide *et al.*, 1999; Schmid, 2002; Cardinale *et al.*, 2009a; Skácelová and Lepš, 2014). Both the direction of causality and the shape of the relationship between different measures of diversity and biomass have been investigated (Mittelbach *et al.*, 2001; Schmid, 2002; Cardinale *et al.*, 2009a).

Waide *et al.* (1999) reviewed about 200 relationships, of which 30% were unimodal, 26% were positive linear, 12% were negative linear, and 32% were not significant. Mittelbach *et al.* (2001) analysed 171 studies (including 6 on algae), finding that positive linear or hump-shaped relationships were particularly common in both plants and animals, even more so in aquatic environments and in studies in which plant biomass was the surrogate measure of productivity. Tilman *et al.* (2001) showed that experimental plots with higher plant diversity and niche complementarity had greater biomass than monocultures over 7 years, via "*stable multispecies coexistence*". Whereas unimodal diversity-productivity relationships are more frequent in plant studies (including algae; see, e.g., Passy and Legendre, 2006a), positively linear relationships are more common in animal studies (Groner and Novoplansky, 2003). Research projects on terrestrial plants and animals continue to be prevalent (Skácelová and Lepš, 2014), with some notable exceptions, e.g. experiments on marine microalgal successions (Matthiessen *et al.*, 2010). In Skácelová and Lepš (2014) analysed over 400 phytoplankton samples from stagnant waters (e.g. lakes, ponds and reservoirs) in the Czech Republic; algal diversity and biomass showed an asymmetric unimodal relationship, but decreasingly so when indices accounting for species proportions (Shannon and Simpson) were used rather than species richness. While low nutrients reduced diversity when algal biomass was low, competition for light caused the extinction of some species hence limiting

diversity at high biomass (Skácelová and Lepš, 2014). Passy and Legendre (2006a) observed a consistent unimodal relationship between algal species richness and biovolume across hundreds of streams in the USA and in various habitats, with particular reference to phytoplankton and phytobenthos.

The focus of ecological investigations has seen a shift from the concept, based on numerous studies, that diversity is a function of productivity due to the extinction of species when resource supply diminishes (e.g. Currie, 1991) to the idea that diversity enhances productivity (Naeem *et al.*, 2009) and ecosystem functioning, e.g. water purification (Cardinale *et al.*, 2005). Feedback mechanisms between biodiversity changes, ecosystem functions and environmental factors also take place (Loreau and Hector, 2001) so that the diversity-productivity relationship is not one of clear directional causality, i.e. diversity increases productivity or viceversa, but rather a more complex two-way relationship. Also, the mechanisms generating diversity-productivity relationship vary across spatial scales, with local (growth and species interactions) and regional processes (dispersal and disturbance) contributing to such trends (Chase and Leibold, 2002; Cardinale *et al.*, 2004). This study contributes relevant evidence on species richness – biomass relationships in algae in the Okavango Delta across, e.g. regions and habitats. Increasing evidence supporting the idea that biodiversity affects resource capture and productivity (Naeem *et al.*, 2009) has balanced previous works viewing biodiversity as a function of productivity (e.g. Currie, 1991). Biodiversity influences ecosystem functioning not as much via unidirectional causality between diversity and productivity, but with feedbacks among biodiversity changes, ecosystem functioning, and environmental factors, and taking into account local, landscape and regional scales (Loreau and Hector, 2001).

Various theories are relevant for debates over the shape of diversity-productivity curves. The Productivity Hypothesis (PH; Rosenzweig and Abramsky, 1993), a concept linked to the IDH, predicts that species richness is a unimodal function of the availability of resources limiting production. Successive flooding of sufficient length allows the development of assemblages of microorganisms before the next major disturbance occurs so that the algal productivity can be high; however, with frequent and intense flooding, productivity of, e.g. periphyton, can be much reduced (Wetzel, 2001). Thus, disturbance and productivity can be seen as co-factors

contributing to the diversity of assemblages. Diversity-productivity trends in periphyton for 85 streams in the mid-Atlantic USA (Cardinale *et al.*, 2006) supported Successional Diversity Theory (SDT) (Kondoh, 2001), which combines the IDH and the PH. SDT predicts that species richness is influenced by periodic disturbances creating new niche opportunities and by biomass increase accelerating the displacement of inferior competitors by better adapted organisms (Kondoh, 2001). Another prediction of this model is that higher productivity favours superior competitors, e.g. overstorey stalked and filamentous algae, while higher disturbance levels favour inferior competitors, i.e. faster colonisers (Kondoh, 2001). These multivariate predictions of species richness have arguably overcome the limits of the previous theories, e.g. IDH and PH (Cardinale *et al.*, 2006). The Multivariate Productivity Diversity hypothesis (MPD) combines these different lines of reasoning, adding experimental evidence to show that algal biomass increases with both nutrient supply and local richness, hence confirming the bidirectionality of the diversity-productivity relationship (Cardinale *et al.*, 2009b).

Diversity-productivity patterns recorded may be due to scales of investigation (Soininen *et al.*, 2009) and the type of measure, especially when productivity is estimated by means of proxies such as average annual temperatures, altitude or latitude (Groner and Novoplansky, 2003). This relationship changes across different scales as well. The widely observed unimodal curve was shown to shift to a linear pattern from smaller to larger scales (Mittelbach *et al.* 2001; Chase and Leibold 2002), but in other works unimodal curves for herbaceous plants appear at large scale too (e.g., Gross *et al.* 2000). According to a modelling study conducted by Cardinale *et al.* (2004), the shape of the diversity-productivity relationship is independent of spatial scale; however, the mechanisms generating the relationship differ between scales of observation. Both local (growth and interspecific interactions) and regional processes (dispersal and disturbance) can determine the diversity-productivity relationship in natural ecosystems (Cardinale *et al.*, 2004). This study contributes a term of comparison in the real world of the issue whether the diversity-productivity relationship (here measured as species richness-biomass) is scale-dependent or not for algae in the Okavango Delta.

Species richness – biovolume relationships in algae

Despite being crucial in providing habitats for microorganisms and purifying water from pollutants, among other ecosystem services (Cardinale, 2011), diversity-productivity relationships in algae have not been studied as much as vascular plants and animals (Mittelbach *et al.*, 2001). Ecological dynamics are different in phytoplankton and phytobenthos; environmental gradients (in resources and disturbance regimes) in well-mixed planktonic assemblages are shorter than in the heterogeneous benthos, where nutrient depletion, light attenuation, current velocity and grazer disturbance show multiple and steep gradients (Stevenson *et al*., 1996). Unimodal relationships have been observed between diversity and productivity in algal assemblages (diatoms - Passy and Legendre, 2006a; phytoplankton - Skácelová and Lepš, 2014). Passy and Legendre (2006a) explained how benthic assemblages reach higher species richness than planktonic ones due to longer environmental gradients than in open water; also, the highest biomass levels are reached at higher species richness in three-dimensional biofilms in the phytobenthos than in two-dimensional open water environments. Competitive exclusion tends to limit diversity in the plankton due to the more homogeneous open water environments, i.e. shorter environmental gradients, whereas in the benthos facilitation mechanisms take place between species (Passy and Legendre, 2006a). Furthermore, species richness increases in the phytobenthos are attributable to congeneric species rather than species belonging to different higher groups like in the phytoplankton, which poses a new paradox of the plankton: "*the homogeneous environment of open running waters promotes the greatest biodiversity at higher taxonomic levels compared to the heterogeneous benthic habitats*" (Passy and Legendre, 2006b).

The main aims of this chapter are to describe and interpret patterns of algal diversity and biomass in the Okavango Delta as well as species richness-biovolume relationships and identify what factors determine their variation. The methods used on biovolume estimations, statistical tests, diversity measures and linear regressions are respectively illustrated in sections 3.4, 3.6 and 3.7 and 3.8. The main hypotheses tested here are that algal species richness and biomass are higher in the seasonally flooded floodplains in BOR and SAN and that algal species richness and algal biomass are scale-dependent in the Delta.

5.2. RESULTS

In this section results on algal diversity, species richness estimators and algal biovolume estimates are presented by means of statistical tests, tables and boxplots highlighting the significant differences observed in these variables. A less strict p-value of 0.05 was used in Chapter 5 and to respectively investigate important changes in total algal biovolume and species-richness – biovolume relationships (see section 5.2.5 and 5.2.6) which were not significant at p=0.01.

5.2.1. Species and genera richness

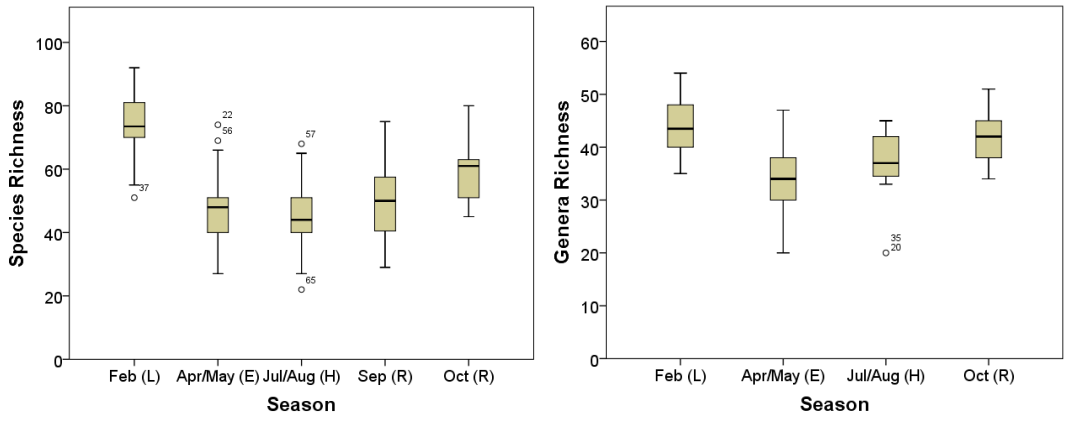
As shown in section 4.4, 496 species were observed in 132 samples throughout the Okavango Delta. However, 495 species belonging to 172 genera were found in the 130 samples that are fully analysed here with parametric and non parametric statistical to identify important differences (section 4.3) and linear regression to investigate the links between algal species richness and biomass (section 5.5). One genus and hence 1 species were only found in the Ngami lake sample excluded from the following analyses - alongside a sample from December 2006 in LPH. Detailed results on species richness (including those species identified only at genus level) are presented in section 4.3.

Here patterns of species and genera richness and limnological data are analysed across regions, flood class, seasons / flooding phases, flood year, floodplain type and habitat types. First, Campaign 1 and Campaign 2 are investigated separately. The combined mean algal species richness is 53 per sample (s.d.=14.3 and c.v.=27.2%) ranging from 22 to 92 per sample; the mean genera richness is 37 (s.d=7.5 and c.v.=20.4%) ranging from 17 to 54 per sample. The coefficient of variations of species richness within each region, flood class, habitat and season are shown in Table 5.1. Both species and genera richness vary the least within seasons and the most within habitat types, the coefficients of variation (c.v.) for other categories are at most 20% higher than for seasons.

Table 5.1. Coefficients of variation (c.v.) of species and genera richness.

Species Richness							
Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	16.7	PF	19.5	OW	27.1	Feb	14.6
LPH	21.6	SF	26.4	MV	21.2	Apr / May	21.9
XAN	22.7	OF	26.9	F	25.4	Jul / Aug	23.4
BOR	26.3	-	-	-	-	Sep	24.2
SAN	25.0	-	-	-	-	Oct	17.7
Average	**22.5**	-	**24.3**	-	**24.6**	-	**20.4**
Genera richness							
Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	17.9	PF	20.3	OW	23.6	Feb	13.7
LPH	21.4	SF	18.3	MV	21.4	Apr / May	19.5
XAN	18.9	OF	19.9	F	15.8	Jul / Aug	20.3
BOR	18.1	-	-	-	-	Sep	20.5
SAN	19.9	-	-	-	-	Oct	11.2
Average	**19.2**	-	**19.5**	-	**20.3**	-	**17.0**

In Campaign 1 the number of species does not vary significantly between regions, seasons, flood year, flood class, floodplain types or habitat types. In Campaign 2 species richness varies significantly according to seasons, with sites during flood recession showing higher numbers of species (K.S. test: Z=0.835; p>0.01; L. test: p>0.01; O.W.A. test: F=20.661; p<0.001**) (Figure 5.1, Table 5.2 and Table 5.3).



a) ***b)***

Figure 5.1. Species (a) and genera (b) richness across seasons in Campaign 2 (flood phases: L=Low; E=Expansion; H=High water; R=Recession).

Table 5.2. Tukey HSD test results on species richness across seasons in Campaign 2.

p-value	April/May '07/'09	July/August '07/'09	October '09
October '09	<0.01*		
February '10	<0.001**	<0.001**	<0.01*

Genera richness also varies significantly across seasons (K.S. test: Z=0.066; p>0.01; L.: p>0.01; O-W: F=11.016, p<0.001**), with highest values in February 2010 and lowest in Apr/May 2006/2007.

Table 5.3. Tukey HSD test results on genera richness across seasons in Campaign 2.

p-value	April/May '07/'09	July/August '07/'09	October '09
October '09	<0.01*		
February '10	<0.001**	<0.01*	<0.01*

Species richness (but not genera richness) varies significantly across flood years (L. test: p<0.01*): K.W. test: χ^2 =21.554, p<0.001**. Sites sampled in 2009-2010 have higher algal species richness than 2007-2008 (M-W U test: p<0.001**) (Figure 5.2), due to samples from floodplains being mostly collected in this flood year.

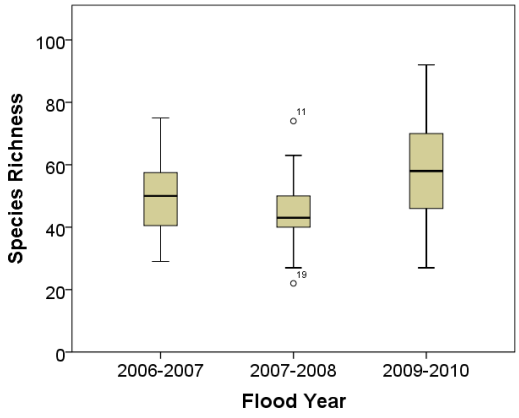
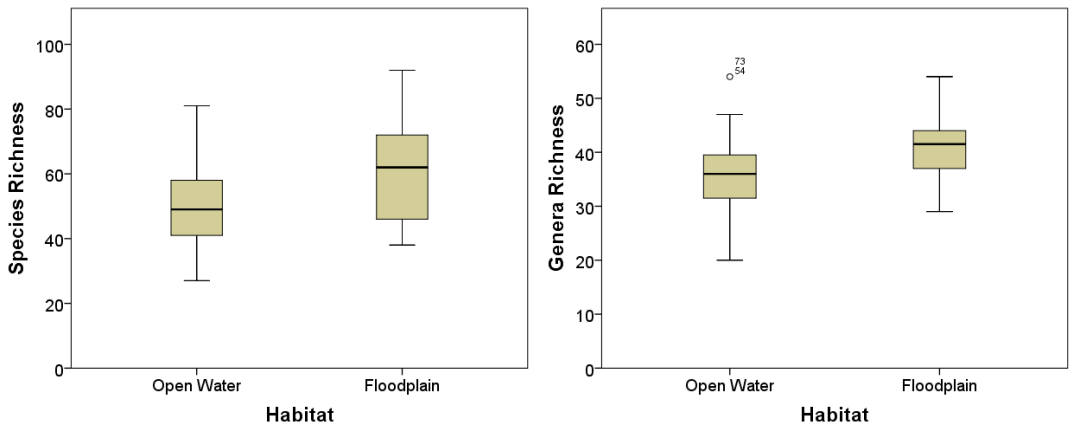


Figure 5.2. Species richness across flood years in all the samples.

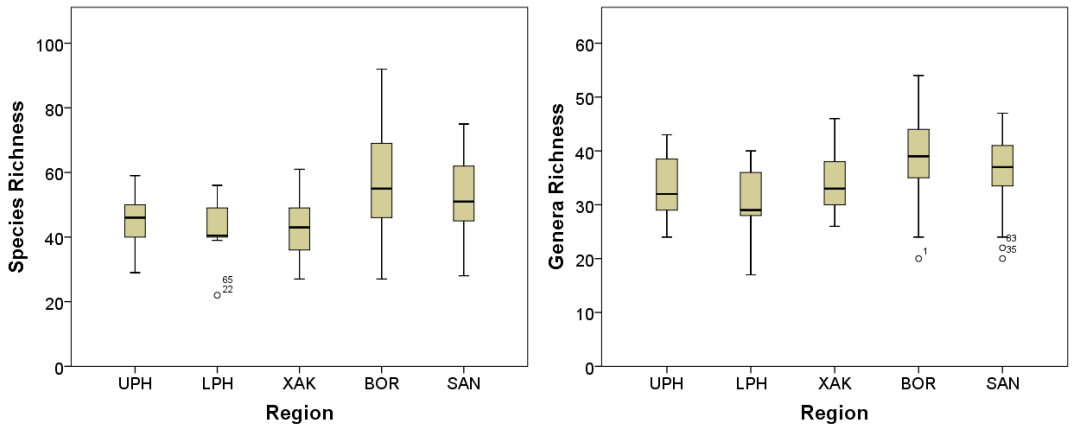
Species and genera richness are significantly different between different habitat types in Campaign 2 (L. test: p>0.01; O.W.A. test species: F=7.426; p<0.01*; F=7.583, p<0.01*). However, the post-hoc T. HSD tests do not yield significant results (Figure 5.3) similarly to what recorded for within-floodplain habitat and floodplain type categories.



a) ***b)***

Figure 5.3. Species richness (a) and genera richness (b) across habitats in Campaign 2.

When the datasets are merged, the results do change quite substantially. Species richness is distributed normally (K.S. test: Z=1.262; p>0.01), but variances are not homogeneous (L. test: $p<0.01^{*}$). The number of species per region varies overall, as per K.W. test: $\chi^2=22.062$; $p<0.001^{**}$. BOR has significantly higher species richness than UPH and LPH or XAK ($p<0.01^{*}$ for all comparisons) (Figure 5.4a). Genera richness shows similar changes (L. test: p>0.01; O.W.A: F=6.503; $p<0.001^{*}$) (Figure 5.4b).



a) ***b)***

Figure 5.4. Species (a) and genera (b) richness across regions in all the samples.

Species richness varies significantly across flood classes in the pooled data (L. test: $p<0.01^{*}$): K.W. test: $\chi^2=15.691$; $p<0.001^{**}$. In particular, Seasonally Flooded (SF) sites have a higher number of species than Permanently Flooded (PF) sites ($p<0.01^{*}$) (Figure 5.5a). Genera richness also varies (L. test: p>0.01; O.W.A.: F=9.673; $p<0.001^{*}$) with SF sites having higher values than PF sites ($p<0.001^{**}$) (Figure 5.5b).

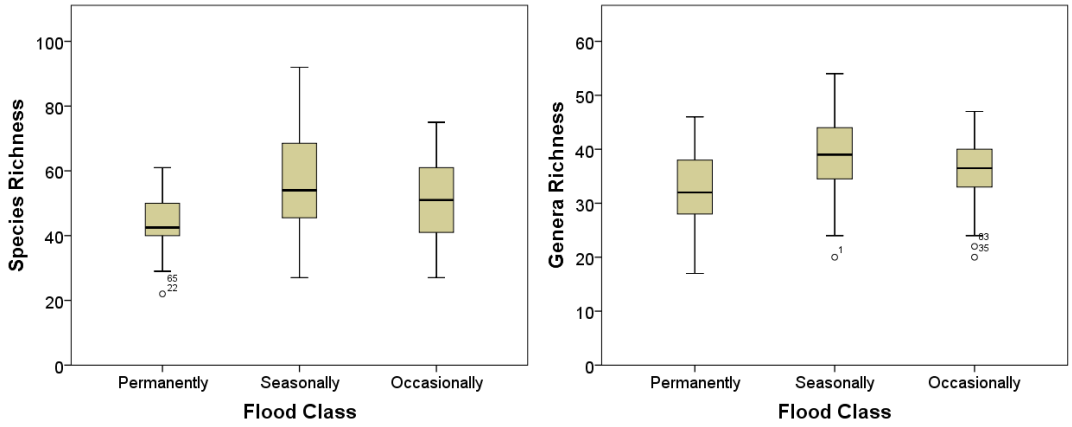


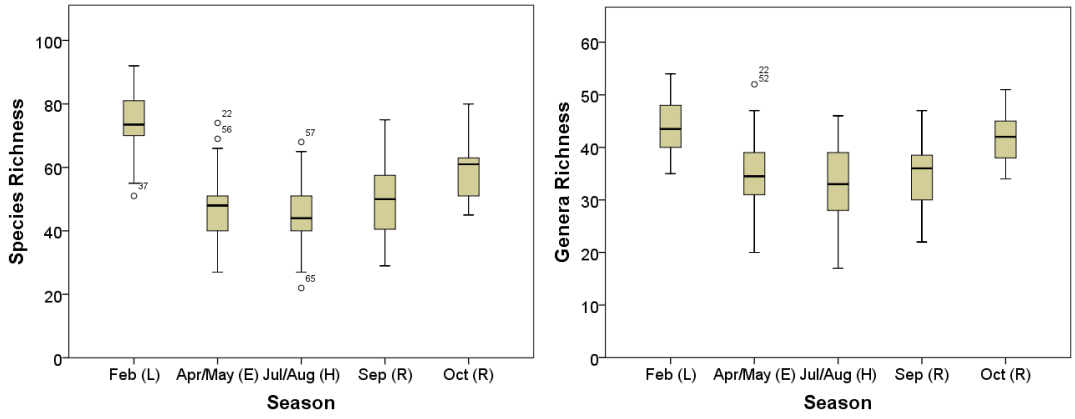
Figure 5.5. Species (a) and genera (b) richness across flood classes in all the samples.

Species richness varies significantly across seasons in the merged dataset. In February 2010 and, to an extent October 2009, sampling sites showed higher species richness than the other seasons (Table 5.4 and Figure 5.6a).

Table 5.4. Tukey HSD test results on species richness differences across seasons (L. test: p>0.01; O.W.A. test: F=24.966; p<0.001**).

p-value	April/May	July/August	September	October
October '09	<0.001**	<0.001**		
February '10	<0.001**	<0.001**	<0.001**	<0.01*

Genera richness is also significantly different across seasons (L.: p>0.01; O-W: F=11.016, p<0.001**) with these pair-wise differences: Feb > Apr (p<0.001**), Feb > Jul and Oct > Apr (p<0.01*) (Figure 5.6b).



a) ***b)***

Figure 5.6. Species (a) and genera richness (b) across seasons in all the samples (flood phases: L=Low; E=Expansion; H=High; R=Recession).

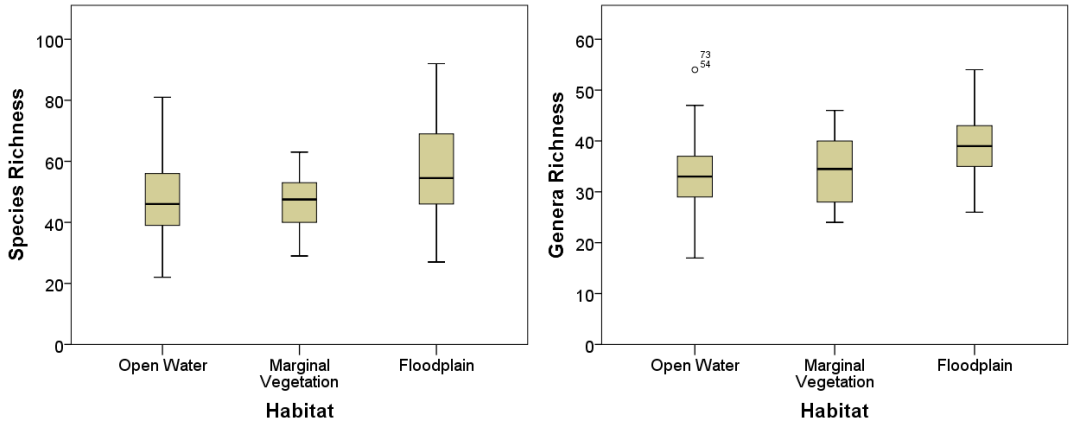
The flooding phases in the merged datasets do not coincide with the sampling seasons, as both September 2006 and October 2009 are classified in the flood

'Recession' phase. Hence the seasonal differences do not entirely coincide with changes across flooding phases: during the Low Water phase species and genera richness are higher than in the other flooding phases; also more species are present during the Recession phase (Sep 2006 and Oct 2009) than the High Water phase (Table 5.5).

Table 5.5. Tukey HSD test results on species and genera richness across flooding phases (L. test: p>0.01; O.W.A. test: F=29.104; p<0.001**).

p-value	Expansion	High Water	Recession
Recession (species)		<0.01*	
Low Water (species and genera)	<0.001**	<0.001**	<0.001**

Species richness varies significantly across habitats (L. test: p>0.01; O.W.A. test: F=9.073, p<0.001**). Floodplains (F) host significantly more species than Open Water (OW) (p<0.01*) (Figure 5.7a). Overall, genera richness shows a change across habitats (L. test: p>0.01; O-W: F=7.583), but with no pair-wise differences (Figure 5.7b).



a) ***b)***

Figure 5.7. Species (a) and genera richness (b) across habitats in all the samples.

The coefficients of variation of species richness within regions, habitats and seasons are, on average, rather similar 22.5%, 20.4% and 24.6%; similarly, the coefficients of variations genera richness are respectively, on average, 19.2%, 20.3% and 17.0% within regions, habitats and seasons (Table 5.1).

Species richness of different algal phyla

Here results on algal species richness of various phyla and statistical tests to highlight significant changes are presented. Given the general similarity of the

results on species richness and genera richness, only species richness data (including unidentified species belonging to known genera) were analysed. Figures 5.8, 5.10, 5.12, 5.13 and 5.16 can be referred to visualise the overall trends, but not the statistically significant differences, which can be appreciated in specific graphs.

Regions

The species richness of algal phyla across regions is shown in Figure 5.8. A higher mean number of Chlorophyta species is present in BOR and SAN, while diatoms are more species-rich in UPH, LPH and XAK (Figure 5.9).

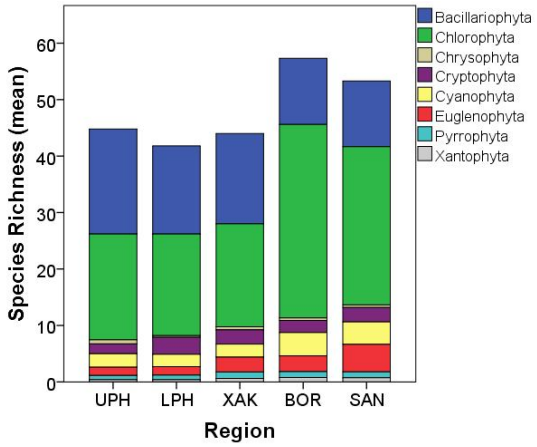
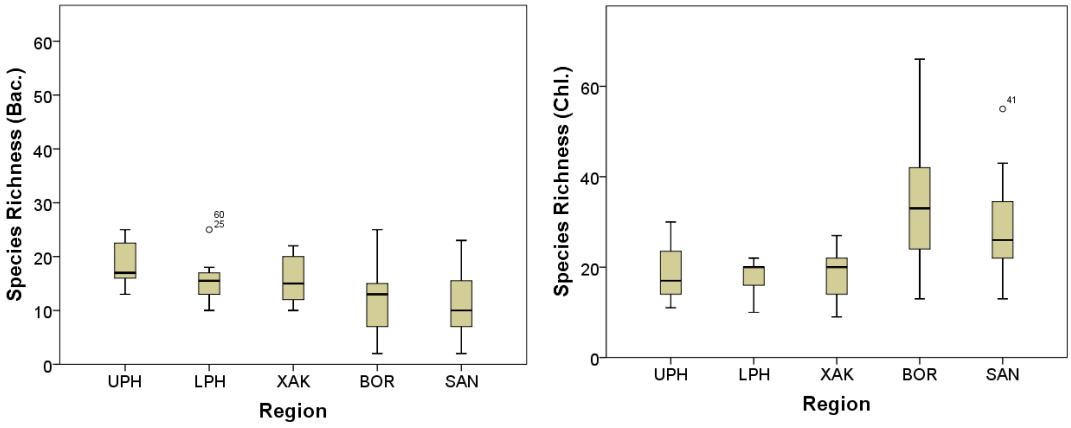


Figure 5.8. Species richness of algal phyla across regions.

The species richness of Bacillariophyta varies across regions in the Delta (L. test: $p>0.01$): O.W.A. test: $F=6.776$, $p<0.001^{**}$. The same is true for Chlorophyta (L. test: $p<0.01^{*}$); K.W. test: $\chi^2=48.659$ ($p<0.001^{**}$). The species richness of Cyanophyta and Euglenophyta also vary; the results are respectively: Cyanophyta (L. test: $p>0.01$): O.W.A. test: $F=7.550$ ($p<0.001^{**}$) and K.W.: $\chi^2=21.305$ ($p<0.001^{**}$). Only the differences for the first two phyla are shown in Figure 5.9 a and b, as patterns for other two phyla are not as clearly noticeable in a boxplot.



a) *b)*

Figure 5.9. Species richness of: a) Bacillariophyta (Bac.), b) Chlorophyta (Chl.) across regions.

The details of post-hoc tests on the regional variations of algal species richness for those phyla with significant changes are illustrated in Table 5.6.

Table 5.6. P-values of post-hoc tests of regional variations of phylum species richness (T. HSD test for Bacillariophyta and Cyanophyta; M.W. U test for Chlorophyta and Euglenophyta).

Phylum	Region	BOR	SAN
Bacillariophyta	UPH	<0.001**	<0.01*
Chlorophyta	UPH	<0.001**	<0.01*
	LPH	<0.001**	<0.01*
	XAK	<0.001**	<0.01*
Cyanophyta	UPH	<0.01*	
	LPH	<0.01*	
	XAK	<0.01*	
Euglenophyta	UPH		<0.001**
	LPH		<0.01*
	BOR		<0.01*

Seasons

Average species richness across seasons is shown in Figure 5.10, with higher values in the flood recession and low water phases (October 2009 and February 2010).

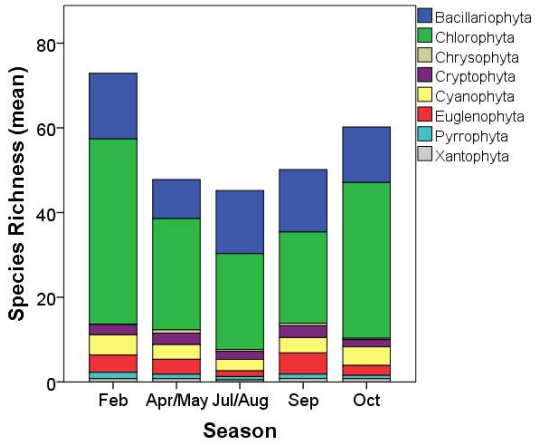


Figure 5.10. Species richness of algal phyla across seasons in all the samples.

Chlorophyta, Cyanophyta (Table 5.7), Bacillariophyta, Chrysophyta, Cryptophyta, and Euglenophyta have different species richness across seasons (Table 5.8).

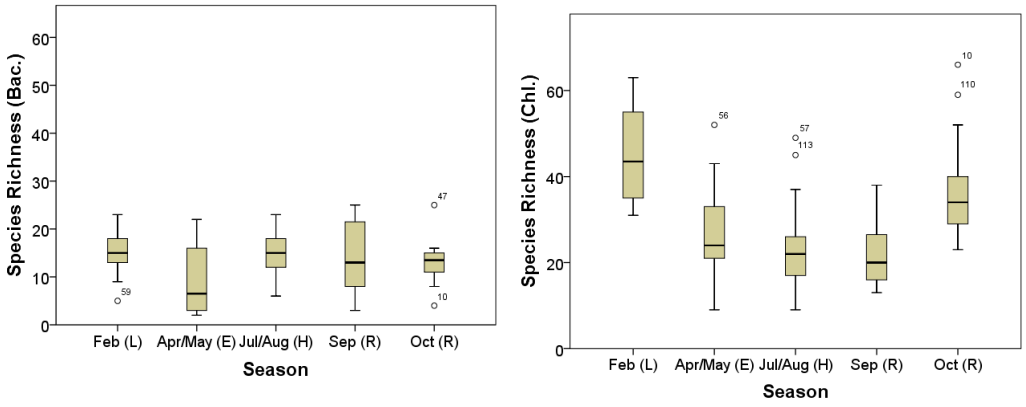
Table 5.7. O.W. A. test results on phylum species richness seasonal variations (L. test: p>0.01*).

O.W.A. test	Chlorophyta	Cyanophyta
F	22.240	5.485
p-value	<0.001**	<0.001**

Table 5.8. K.W. test results on phylum species richness seasonal variations (L. test: p<0.01*).

K.W.	Bacillariophyta	Chrysophyta	Euglenophyta
χ^2	16.967	17.855	40.131
p-value	<0.01*	<0.01*	<0.001**

Figure 5.11 shows the seasonal changes in species richness of the two most abundant and diverse phyla, Bacillariophyta and Chlorophyta. Diatoms have highest number of species during the Recession and High water phases (respectively in Feb. 2010 / Sep. 2006 / Oct. 2009 and Jul/Aug. 2006-2007) and green algae are most diverse during the recession phases in Oct. 2009 and Feb. 2010.



a) ***b)***

Figure 5.11. Species richness of: a) Bacillariophyta, b) Chlorophyta across seasons.

Table 5.9 outlines the post-hoc test results, i.e. all the pair-wise comparisons between seasonal species richness of the different algal phyla across the Delta. Overall, sampling sites in the Low water and Recession phases host more species of the different algal phyla.

Table 5.9. P-values of post-hoc tests on seasonal changes in species richness (T. HSD for Chlorophyta and Cyanophyta; M.W. U test for other phyla).

Phylum	Season (flooding phase)	Apr/May	Jul/Aug	Sep	Oct
Bacillariophyta	Feb (Low water)	$<0.01^{*}$			
	Apr/May (Expansion)		$<0.001^{**}$	$<0.01^{*}$	$<0.01^{*}$
	Jul/Aug (High water)				$<0.01^{*}$
Chlorophyta	Feb (Low water)	$<0.001^{**}$	$<0.001^{**}$	$<0.01^{*}$	
	Apr/May (Expansion)				$<0.01^{*}$
	Jul/Aug (High water)				$<0.01^{*}$
Chysophyta	Feb (Low water)	$<0.001^{**}$	$<0.01^{*}$	$<0.01^{*}$	
Cryptophyta	Apr/May (Expansion)		$<0.01^{*}$		$<0.01^{*}$
Cyanophyta	Feb (Low water)		$<0.01^{*}$		
Euglenophyta	Feb (Low water)		$<0.001^{**}$		
	Apr/May (Expansion)		$<0.001^{**}$		
	Jul/Aug (High water)			$<0.001^{**}$	$<0.01^{*}$

Flood year

Species richness of Chlorophyta and Bacillariophyta have different trends across the three 'flood years'; whereas green algae have higher number of species in 2009-2010 (L.: $p<0.01$): K.W.: $\chi^2=57.065$, $p<0.001^{**}$; diatoms have higher number of species in 2007-2008 than 2009-2010 (L.: $p<0.01$): K.W.: $\chi^2=15.310$, $p<0.001^{**}$. Cyanophyta (L. test: $p>0.01$: O.W.A.: $F=12.530$, $p<0.001^{**}$) and Euglenophyta (L.

test: $p<0.001^{**}$: K.W.: $\chi^2=9.390$, $p<0.01^{*}$) also have different number of species across flooding years. Cyanophyta have more algal species in 2009-2010 than 2007-2008 ($p<0.001^{**}$). Euglenophyta host more diverse assemblages in 2006-2007 than 2007-2008 ($p<0.01^{*}$). These trends are summarised in Figure 5.12.

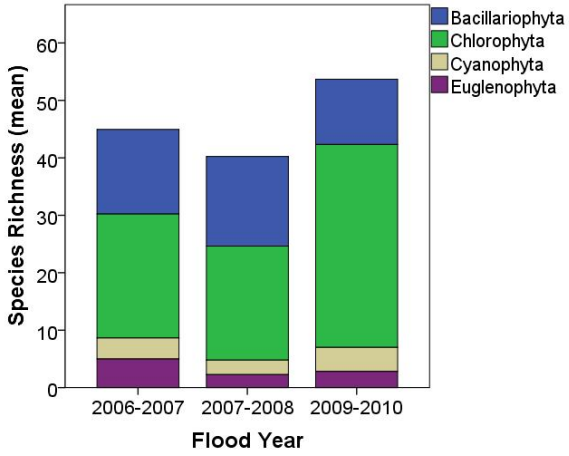


Figure 5.12. Species richness of phyla across flood years.

The difference in species richness across flood years reflect the fact that the great majority of floodplain sites were sampled in 2009-2010, where more species of green algae were observed than of diatoms.

Flood class

The higher species and genera richness in the seasonally than in permanently and occasionally flooded sites, is due to the species richness of different phyla varying across different flood classes (Figures 5.13 and 5.14).

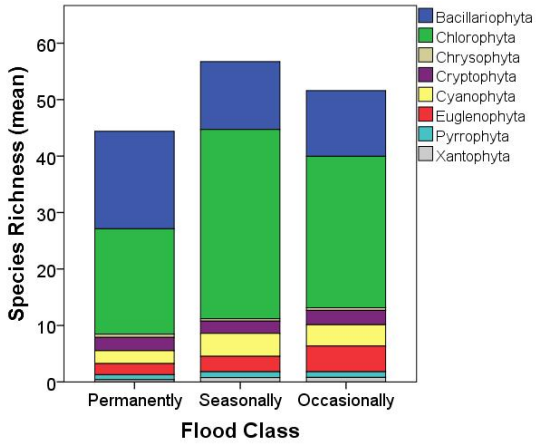
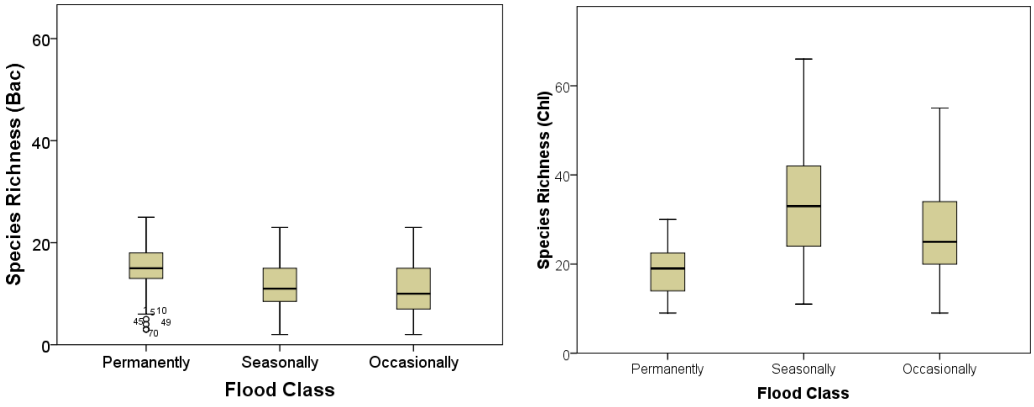


Figure 5.13. Species richness of algal phyla across flood classes.

Species richness of Bacillariophyta (L. test: $p>0.01$: O.W.A. test: $F=11.682$, $p<0.001^{**}$) and Chlorophyta (L. test: $p<0.001^{**}$: $\chi^2=38.315$, $p<0.001^{**}$) change

significantly according to flood class. The number of diatom species is higher in PF areas than in SF ones ($p<0.001^{**}$) and OF sites ($p<0.001^{**}$) (Figure 5.14a), while species richness of green algae is higher in both SF and OF than PF ($p<0.001^{**}$ for both) (Figure 5.14b). Cyanophyta (L. test: $p>0.01$) has different number of species in these groups of sites: O.W.A. test: $F=12.602$ ($p<0.001^{**}$) SF and OF > PF ($p<0.001^{**}$ and $p<0.01^{*}$). Euglenophyta (L. tests: $p<0.001^{**}$) show a variation in species richness (K.W. test: $\chi^2=12.917$, $p<0.01^{*}$), with OF sites hosting more species than PF ($p<0.001^{**}$) and SF ($p<0.01^{*}$). Only the variations for the two main phyla are shown in Figure 5.14.



a) *b)*

Figure 5.14. Species Richness of: a) Bacillariophyta, b) Chlorophyta across flood classes.

Floodplain type

Species richness does not vary across floodplain type (primary, secondary and occasionally flooded) for any phyla, apart from Euglenophyta (K.W.: $\chi^2=14.056$; $p<0.01^{*}$), with primary floodplains having more species than secondary floodplains ($p<0.01^{*}$) and occasionally flooded floodplains having more species-rich Euglenophyta than secondary ones ($p<0.01^{*}$) (Figure 5.15).

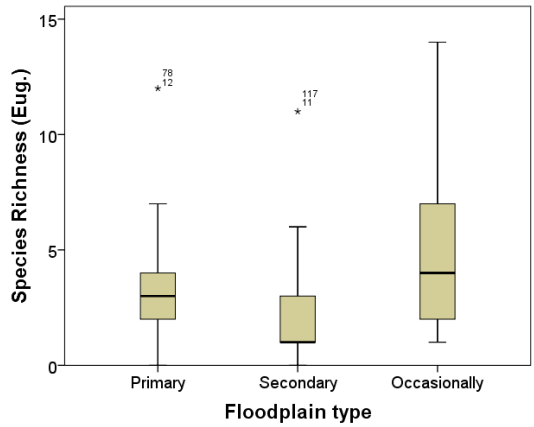


Figure 5.15. Species richness of Euglenophyta across flooplain types.

Habitat types

As per Delta-scale habitat, mean species richness are presented in Figure 5.16. Green algae (Chlorophyta) substantially contribute to a higher total species richness in the floodplains, whereas diatoms (Bacillariophyta) are less species-rich there.

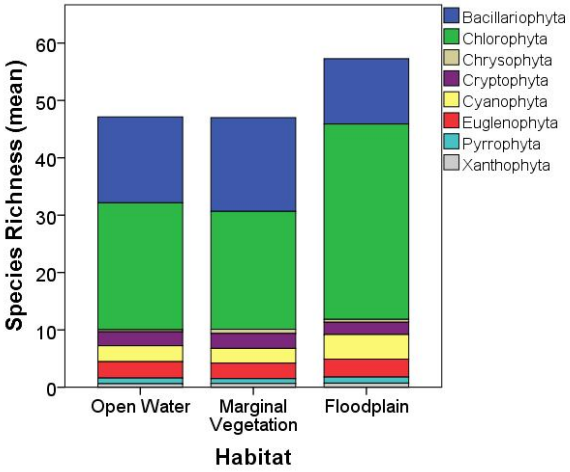
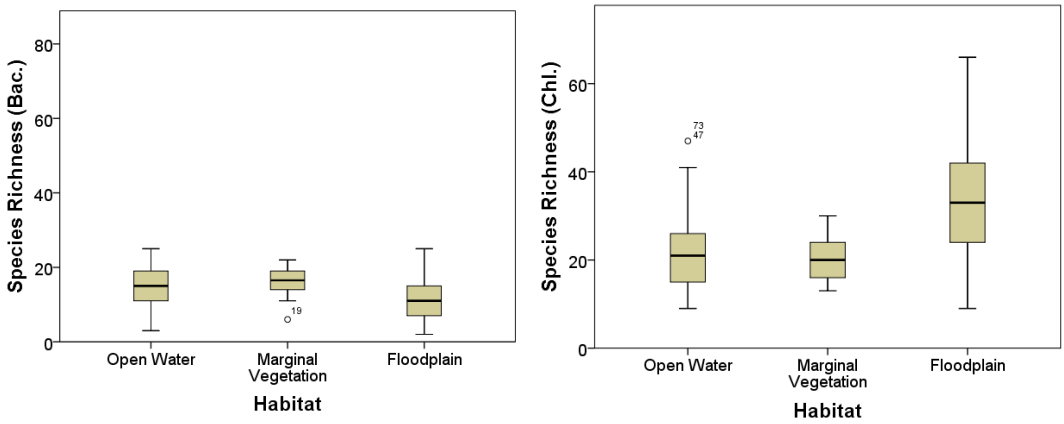


Figure 5.16. Species richness of algal phyla across habitats.

Bacillariophyta have more species in OW and MV than in F habitats across the Delta (L. test: $p>0.01$): O.W.A. test: $F=8.558$, $p<0.001^{**}$; T. HSD test: $p<0.01^{*}$ and $p<0.01^{*}$ (Figure 5.17a). Chlorophyta shows the opposite trend (L. test: $p<0.01^{*}$); K.W. test: $\chi^2=36.337$ ($p<0.001^{**}$); F > OW ($p<0.001^{**}$) and F > MV ($p<0.001^{**}$) (Figure 5.17b). Cyanophyta also shows differences (L. test: $p>0.01$): O.W.A. test: $F=14.317$, $p<0.001^{**}$; F have more Cyanophyta species than both OW and MV ($p<0.001^{**}$ for both). The other five phyla do not change significantly.



a) ***b)***

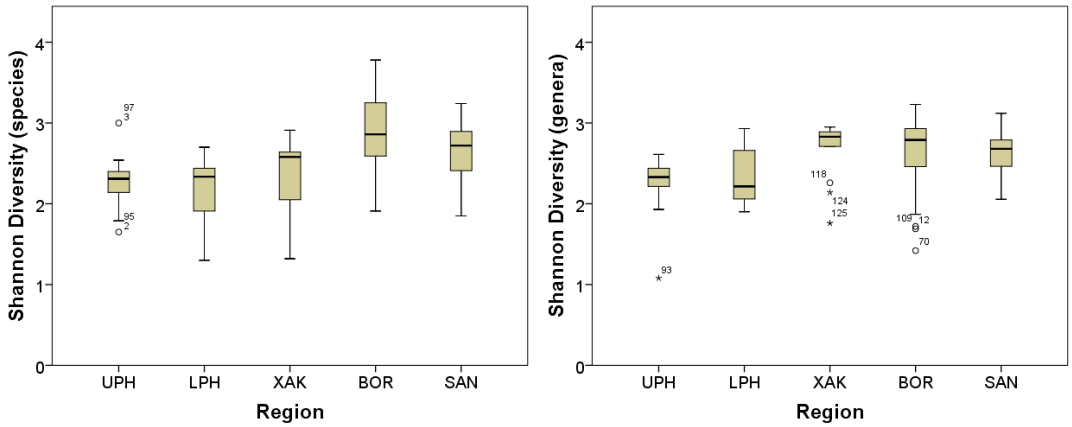
Figure 5.17. Species richness of: a) Bacillariophyta, b) Chlorophyta across habitats.

5.2.2. Diversity indices

The results of the calculations of Shannon Diversity (hereafter ShD) and Shannon Evenness (hereafter ShE) indices performed in EstimateS (Colwell, 2000) are presented and statistically compared in SPSS® (version 22) across regions, flood class, seasons and habitats.

Region

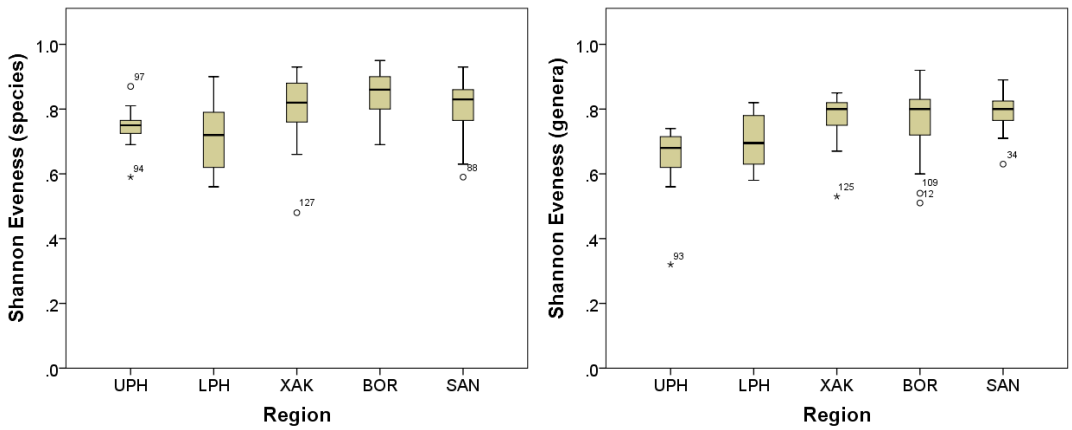
ShD for species and genera is significantly different across regions, with higher diversity in the distal reaches than in the Panhandle. ShD for species varies across regions (Levene test, hereafter L. test: $p>0.01$): One-Way ANOVA (hereafter O.W.A.) test: $F=11.172$, $p<0.001^{**}$; BOR > UPH, LPH and XAK ($p<0.01^{*}$). The same variation is shown for ShD for genera (L. test: $p>0.01$): O.W.A. test: $F=5.933$ ($p<0.01^{*}$); BOR > UPH ($p<0.001^{**}$) and SAN > UPH ($p<0.01^{*}$) (Figure 5.18).



a) ***b)***

Figure 5.18. Shannon Diversity for a) species and b) genera across regions.

ShE for species also shows significant variations (L. test: $p>0.01$): O.W.A. test: $F=7.961$, $p<0.001^{**}$; BOR > UPH and LPH ($p<0.01^{**}$) (Figure 5.19a), for genera as well (L-test: $p>0.01$): O.W.A. test: $F=9.988$, $p<0.001^{**}$; XAK and SAN > UPH ($p<0.01^{*}$), BOR > UPH ($p<0.01^{**}$) (Figure 5.19b).



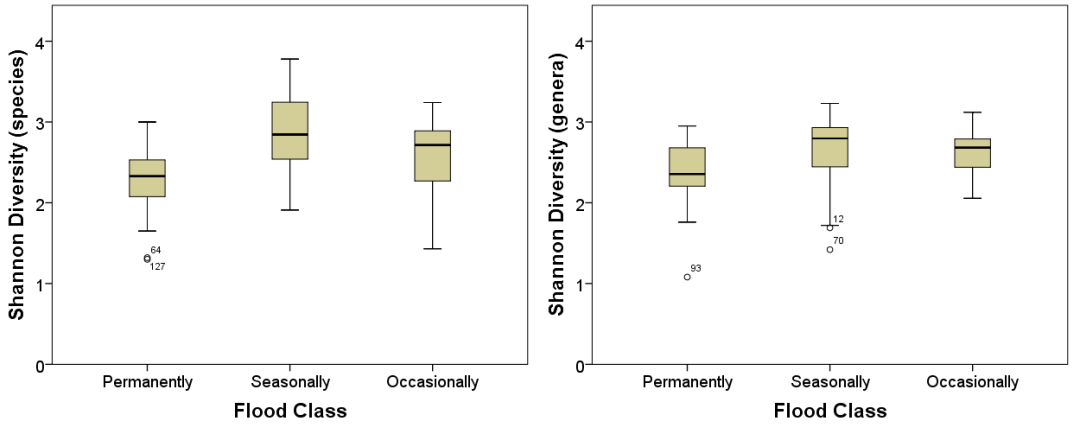
a) ***b)***

Figure 5.19. Shannon Evenness Index for a) species and b) genera across regions.

Flood class

Significant differences in diversity indices are also recorded among sites with different flood class.

Less frequently inundated areas, i.e. Seasonally Flooded (SF) and Occasionally Flooded (OF) host more diverse algal assemblages than Permanently Flooded areas (PF) both at species and genera level. ShD for species (L. test: $p>0.01$); O.W.A. test: $F=20.733$, $p<0.001^{**}$; SF > PF ($p<0.001^{**}$) (Figure 5.20a); ShD for genera (L. test: $p>0.01$): O.W.A. test: $F=6.596$ ($p<0.01^{*}$); SF > PF ($p<0.001^{**}$) (Figure 5.20b).



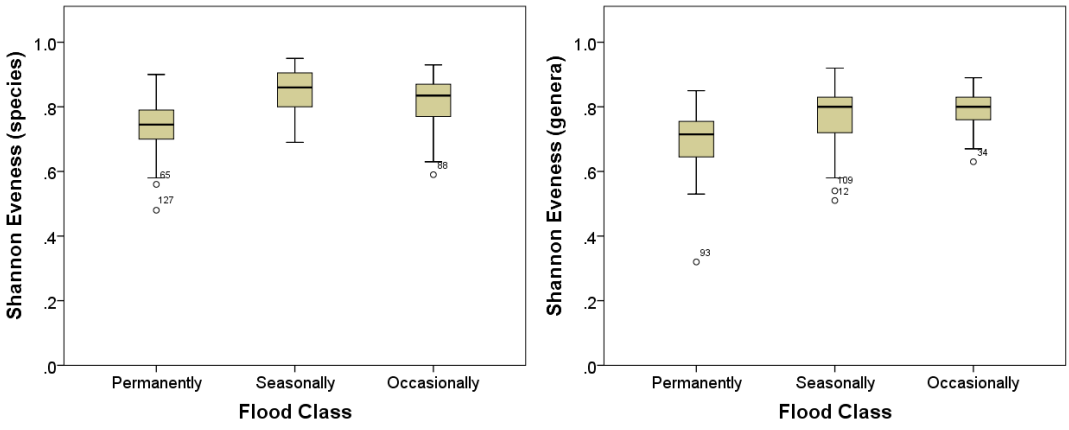
a) ***b)***

Figure 5.20. Shannon Diversity for a) species and b) genera across flood classes.

However, ShD for species and genera do not show any significant variations across floodplain types, i.e. primary, secondary and occasionally flooded floodplains.

ShE for species shows similar significant variations to ShD (L-test: $p>0.01$): O.W.A. test: $F=20.179$, $p<0.001^{**}$; SF and OF > PF ($p<0.001^{**}$) (Figure 5.21a). This

applies to ShE for genera as well (L-test: p>0.01): O.W.A. test: F=12.048, p<0.001**; SF > PF (p<0.01*) and OF > PF (p<0.001**) (Figure 5.21b).



a) *b)*

Figure 5.21. Shannon Evenness for a) species and b) genera across flood classes.

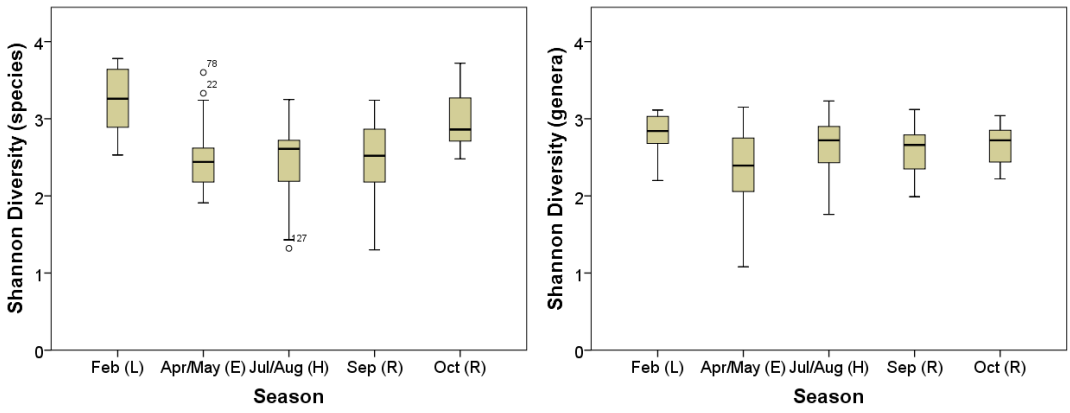
Season and flood year

Overall, across the Delta ShD for species and genera (L-test: p>0.01) are highest in February 2010 in the summer and flood recession phases. Species: O.W.A. test: F=14.431; p<0.001**; genera: F=5.107, p<0.01*. T. HSD tests on ShD for species show the differences summarised in Table 5.10 and Figure 5.22a.

Table 5.10. Tukey HSD test on ShD (species) across seasons.

Seasons	Apr/May (E)	Jul/Aug (H)	Sep (R)
Feb (Low Water)	<0.001**	<0.001**	<0.001**
Oct (Recession)	<0.01*	<0.001**	<0.01*

ShD for genera is higher in Feb (L) than Apr/May (E) (L-test: p<0.01): K.W. test: χ^2 =14.457, p<0.01* (Figure 5.22b); Feb (L) > Apr/May (E).



a) *b)*

Figure 5.22. Shannon Diversity for a) species; b) genera across seasons.

ShD for species varies significantly across flood years (L. test: p>0.01): O.W.A. test: F=15.442, p<0.001**. In particular, 2009-2010 samples have higher algal diversity values than 2006-2007 (p<0.01*) and 2007-2008 (p<0.001**) (Figure 5.23). However, this diversity index at genus level does not vary across the three year; furthermore, no significant differences are recorded in taxon richness or diversity indices across habitats. This reflects the floodplain samples having been collected mostly in 2009-2010 (see section 3.1).

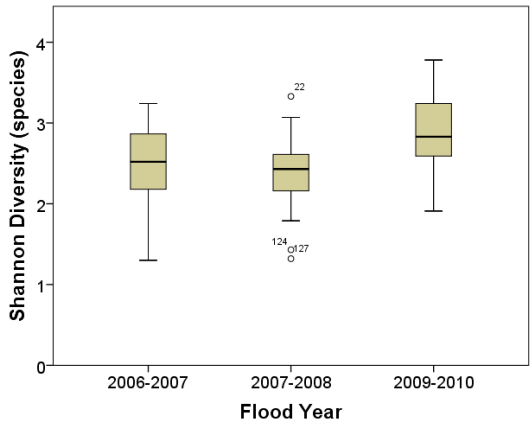
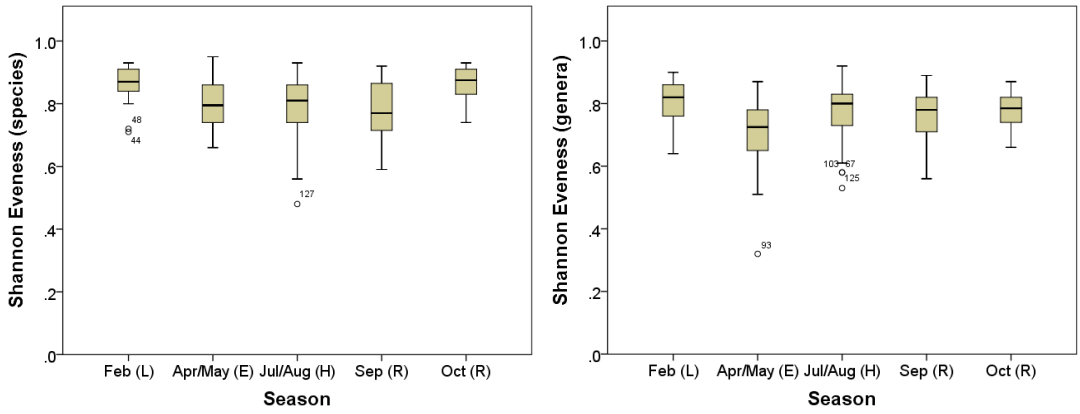


Figure 5.23. Shannon Diversity for species across flood years.

ShE for species varies significantly across seasons (L-test: p>0.01): O.W.A. test: F=3.810, p<0.01*, but no pair-wise significant differences are detected (Figure 5.24a). These changes are also present at genus level (L-test: p>0.01): O.W.A. test: F=4.296, p<0.01*, with Feb (L) > Apr/May (E) (p<0.01*) (Figure 5.24b).



a) ***b)***

Figure 5.24. Shannon Evenness for a) species; b) genera across seasons.

This measure of species equitability is significantly higher in the 2009-2010 flood year than in 2007-2008. (L-test: p>0.01): O.W.A. test: F=6.505, p<0.01*, M.W.U test (p<0.01*) (Figure 5.25), but no correspondent statistically significant variations were observed at genus level.

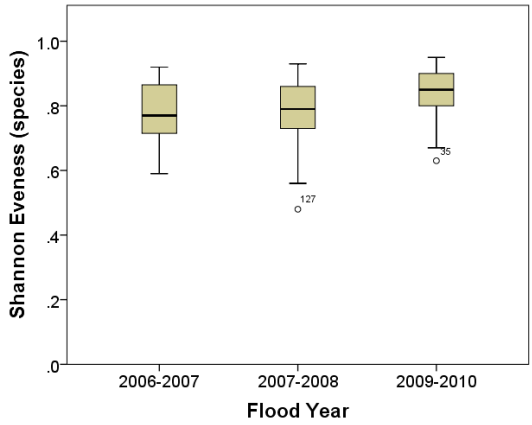
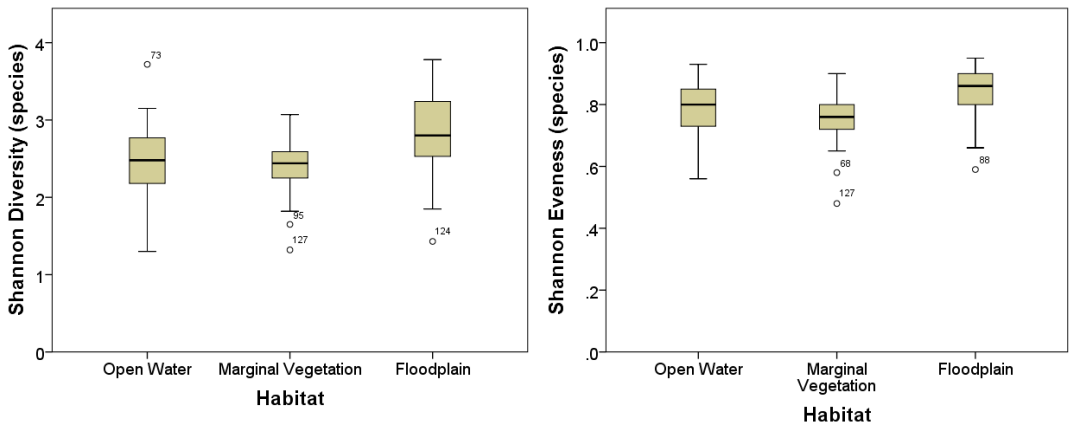


Figure 5.25. Shannon Evenness for species across flood years.

However, when data are analysed within each season these significant differences are not maintained, i.e. during the flood expansion and high water phases ShD and ShE do not vary significantly between 2006-2007, 2007-2008 and 2009-2010. Therefore, Figure 5.25 reflects the fact that ShE, like other diversity indices, is higher in Campaign 2 when samples were all collected from floodplains.

Habitat

Diversity at species level varies significantly across habitat categories. ShD for species is higher in Floodplains (F) than in the other Delta-scale habitats, i.e. Open Water (OW) and Marginal Vegetation (MV). Species: L-test: $p>0.01$; O.W.A.: $F=10.523$; $p<0.001^{**}$. T. HSD tests are as follows: Species: F > OW and MV ($p<0.01^{*}$) (Figure 5.26a). No significant differences were recorded in ShD for genera. ShE for species varies significantly across Delta-scale habitat type (L-test: $p>0.01$): O.W.A. test: $F=8.694$, $p<0.001^{*}$ with algal assemblages in F being more diverse than in both Open Water and Marginal Vegetation ($p<0.01^{*}$) (Figure 5.26b), whereas this index does not change significantly at genus level. No significant differences in ShD and ShE at species or genus level are detected across floodplain types.



a) ***b)***

Figure 5.26. a) Shannon Diversity and b) Shannon Evenness for species across habitats.

ShD for species is significantly higher in the within-floodplain habitats Grasslands (G) than OW (O.W.A.: F=5.357, $p<0.01^{*}$, T.H.S.D.: $p<0.01^{*}$) (Figure 5.27).

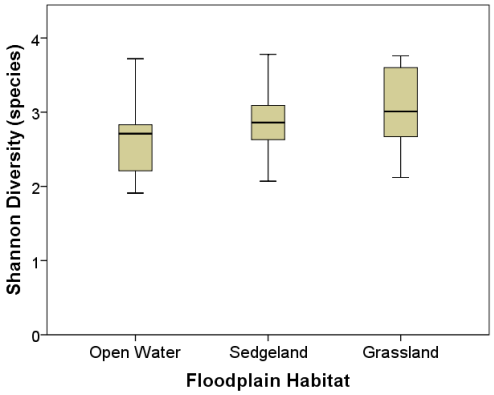


Figure 5.27. Shannon Diversity for species across within-floodplain habitats.

The coefficient of variations of ShD and ShE for species and genera are shown in Table 5.11. The values of these diversity indices vary the least within season and the most within habitat types, c.v. for other categories are at most 20% higher than for seasons. Overall, this is a similar result to that obtained for species and genera richness, including the fact that c.v. varies rather substantially in each region, flood class, habitat and season, which is also the case for taxon richness (see Table 5.1).

Table 5.11. Coefficients of variation of Shannon Diversity and Evenness (species and genera).

Shannon Diversity – Species							
Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	13.9	PF	16.8	OW	18.6	February	12.5
LPH	19.5	SF	17.8	MV	18.4	April / May	16.6
XAN	22.0	OF	16.7	F	18.8	July / August	18.4
BOR	18.0	-	-	-	-	September	21.6
SAN	14.0	-	-	-	-	October	15.0
Average	**17.5**	-	**17.1**	-	**18.6**	-	**16.8**
Shannon Diversity – Genera							
Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	16.3		17.0		16.6	February	8.6
LPH	17.1		15.0		14.1	April / May	20.2
XAN	14.4		10.6		14.0	July / August	14.1
BOR	14.7	-	-	-	-	September	11.6
SAN	10.4	-	-	-	-	October	9.3
Average	**14.6**	-	**14.2**	-	**14.9**	-	**12.8**
Shannon Evenness – Species							
Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	8.2	PF	13.1	OW	11.4	February	7.6
LPH	16.4	SF	8.2	MV	14.5	April / May	10.4
XAN	15.2	OF	10.7	F	9.4	July / August	13.3
BOR	8.2	-	-	-	-	September	12.7
SAN	11.1	-	-	-	-	October	6.9
Average	**11.8**	-	**10.7**	-	**11.8**	-	**10.2**
Shannon Evenness – Genera							
Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	16.4		15.2		13.3	February	8.9
LPH	12.2		11.4		12.1	April / May	15.7
XAN	11.6		7.4		11.6	July / August	11.8
BOR	11.1	-	-	-	-	September	10.6
SAN	7.1	-	-	-	-	October	7.8
Average	**11.7**	-	**11.3**	-	**12.3**	-	**11.0**

Summary of diversity indices variations

Table 5.12 shows all the significant variations of diversity indices and species richness across regions, flood class, seasons and Delta-scale habitat types recorded in the two datasets and the pair-wise comparisons. Significant variations in species richness are described in section 5.2.1 and summarised here. Whereas in Campaign 1 there are significant variations in taxon (species and genera) richness across regions and flood classes, in Campaign 2 these variables change across seasons and habitats due to, for example, spatial scale differences, i.e. Campaign 1 samples were taken from the whole Delta in sites of varying flooding frequency while only BOR and SAN sites - only in seasonally and occasionally flooded areas - were sampled in Campaign 2. Habitat differences appear to matter more at this scale, i.e. in the distal reaches of the Delta, than in the whole wetland.

Table 5.12. Summary of the significant differences in diversity and evenness (x=significant differences detected; - =no significant difference).

Diversity measure		**Region**			**Flood Class**			**Season**			**Habitat**		
Campaign		1	2	all	1	2	all	1	2	all	1	2	all
Species richness		-	-	x	-	-	x	x	x	x	-	x	x
Genera richness		-	-	x	-	-	x	-	x	x	-	x	x
Shannon Diversity	Species	-	-	x	x	-	x	-	x	x	-	x	x
	Genera	x	-	x	x	-	x	-	x	x	-	-	-
Shannon Evenness	Species	-	-	x	x	-	x	-	-	x	-	-	x
	Genera	x	-	x	x	-	x	-	x	x	-	-	-

The significant variations of diversity indices in the two separate datasets are outlined below (for the pair-wise comparisons of species richness, see section 4.3.1). Table 5.13 illustrates the significant changes in algal diversity and evenness across regions and flood class in Campaign 1; no significant differences were observed across seasons, habitats and floodplain types.

Table 5.13. Summary of the significant differences in diversity and evenness in Campaign 1 (F refers to O.W.A. test; χ^2 to K.W. test; post-hoc tests: T. HSD for ANOVA and M.W. U test for K.W.).

Test results		Region	Flood class
Shannon Diversity	**species**	no significant differences	F=5.300; $p<0.01^{*}$; SF > PF ($p<0.01^{*}$)
	genera	F=6.310, $p<0.001^{**}$; BOR and SAN > UPH ($p<0.01^{*}$)	F=6.074; $p<0.01^{*}$; no significant pair-wise differences
Shannon Evenness	**species**	no significant differences	F=9.718; $p<0.01^{*}$; SF > PF ($p<0.001^{**}$)
	genera	F=7.034, $p<0.001^{**}$; XAK, BOR, SAN > UPH ($p<0.01^{*}$)	F=6.846; $p<0.01^{*}$; OF > PF ($p<0.01^{*}$)

In Campaign 2 a seasonal variation in algal diversity and some changes across habitats are observed (Table 5.14), but no variations across regions, flood classes or floodplain types.

Table 5.14. Summary of the significant differences in diversity and evenness in Campaign 2 (F refers to O.W.A. test; χ^2 to K.W. test; post-hoc tests: T. HSD for ANOVA and M.W. U test for K.W.).

Test results		Season	Habitat
Shannon Diversity	**species**	F=9.987; $p<0.001^{**}$; Feb (L) > Apr/May (E) ($p<0.001^{**}$) and Jul/Aug (H) ($p<0.01^{*}$)	F=9.249, $p<0.01^{*}$, F > OW ($p<0.01^{*}$); F=5.357, G > OW ($p<0.01^{*}$)
	genera	F=9.376; $p<0.001^{**}$; Feb (L), Jul/Aug (H), Oct (R) > Apr/May (E) ($p<0.001^{**}$; $p<0.01^{*}$)	no significant differences
Shannon Evenness	**species**	no significant differences	no significant differences
	genera	F=6.084; $p<0.01^{*}$ Feb (L), Jul/Aug (H) > Apr/May (E) ($p<0.01^{*}$)	no significant differences

5.2.3. Taxon richness estimators

The results of the Chao 1 species and genera richness estimates are shown in Tables 5.6 and 5.7 across regions. The number of unknown species and genera are calculated by substracting the number of identified species or genera (species and genera richness) from the Chao 1 mean value (obtained by means of Equation 3.6) by using Chao 1 mean. Lower (LB) and Upper Bounds (UB) (95% Confidence

Interval) are also shown to include the uncertainty of the estimate. Table 5.15 and Figure 5.28 show that in the Panhandle regions (UPH and LPH) and in Xakanaxa (XAK) the average estimated number of unknown species per sample is lower than in the distal reaches of the Delta (BOR) and (SAN), respectively 32% and 23% of the species are estimated to have not been found in UPH and LPH as compared to 40%, 39% and 37% in XAK, BOR and SAN (100 - "% True richness").

Table 5.15. Average observed species richness, Chao 1 estimates of species richness across regions, species not found and true species richness.

Region	Average species richness	Chao 1 Mean	Chao 1 95% CI LB	Chao 1 95% CI UB	Species not found (per sample) [range]	% True species richness
UPH	22	32	24	65	10 [2-43]	68
LPH	22	29	23	54	7 [1-32]	77
XAK	20	33	23	71	13 [3-51]	60
BOR	34	55	41	102	21 [7-68]	61
SAN	33	52	39	98	19 [6-65]	63

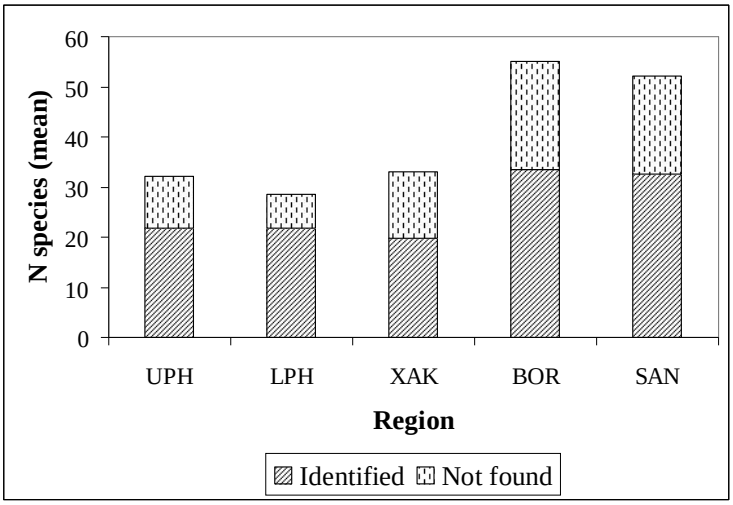


Figure 5.28. Average number of species identified and not found across regions (see Table 5.15 Chao 1 mean and "Species not found").

Chao 1 estimates of genera richness are shown in Table 5.16 and Figure 5.29. The estimated number of genera not found was rather similar across regions, between 11 and 14, but with upper bound ranges of between 44 and 52 genera not found. The % true genera richness is higher than the % true species richness in all regions apart from LPH (see Table 5.15).

Table 5.16. Average observed genera richness, Chao 1 estimates of genera richness across regions, genera not found and true genera richness.

Region	Average genera richness	Chao 1 Mean	Chao 1 95% CI LB	Chao 1 95% CI UB	Genera not found (per sample) [range]	True genera Richness
UPH	31	43	34	75	12 [3-44]	72%
LPH	29	42	33	79	13 [4-50]	68%
XAK	32	44	36	76	12 [4-44]	73%
BOR	33	48	38	86	14 [4-52]	71%
SAN	31	42	34	75	11 [3-44]	74%

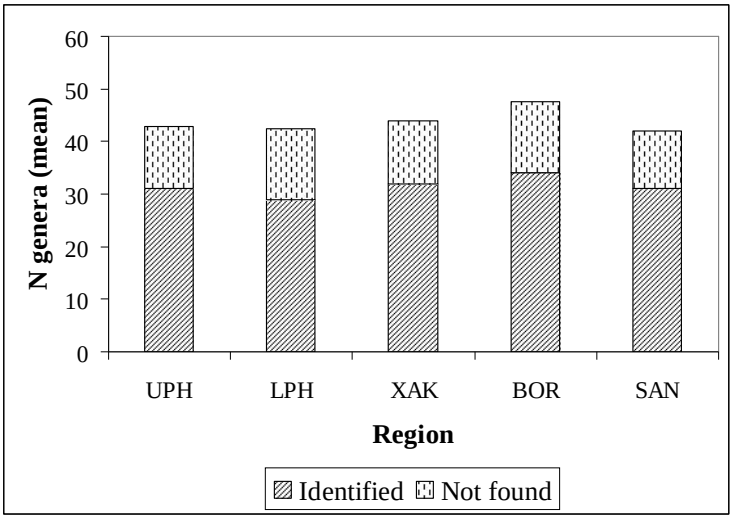


Figure 5.29. Average number of genera identified and not found across regions (see Table 5.16 Chao 1 mean and "Genera not found").

Therefore the regions likely to host highest number of species of algae not found in this study are the more diverse regions in the distal reaches, BOR and SAN, while the number of genera still to be found is more similar across regions.

5.2.4. β-diversity and species composition similarity

β-diversity was first calculated as the ratio between the exponential forms of the Shannon Diversity at Delta scale (γ-diversity) and sample scale (α-diversity). Secondly, the similarity in species composition calculated by means of the Bray-Curtis distance between samples are presented alongside the average number of shared species. β-diversity varies significantly across regions, flood classes and habitats. BOR has a significantly higher values than UPH, LPH and XAK (L. test: $p>0.01$; O.W.A.: $F=8.590$, $p<0.001^{**}$; T.H.S.D.: $p<0.01^{*}$) (Figure 5.30a). Samples collected in SF and OF sites showed significantly higher algal β-diversity than those taken in PF areas (L. test: $p>0.01$; O.W.A.: $F=15.342$, $p<0.001^{**}$; T.H.S.D.:

p<0.001** and p<0.01*) (Figure 5.30b). F habitats have higher β-diversity levels than OW and MV (L. test: p>0.01; O.W.A.: F=9.358, p<0.001**; T.H.S.D.: both p<0.01*) (Figure 5.30c). Finally, β-diversity is significantly higher in Feb than Apr/May, Jul/Aug and Sep (L. test: p>0.01; O.W.A.: F=15.790, p<0.001**; T.H.S.D.: p<0.001**) and in Oct than Jul/Aug (p<0.001**; Figure 5.30d).

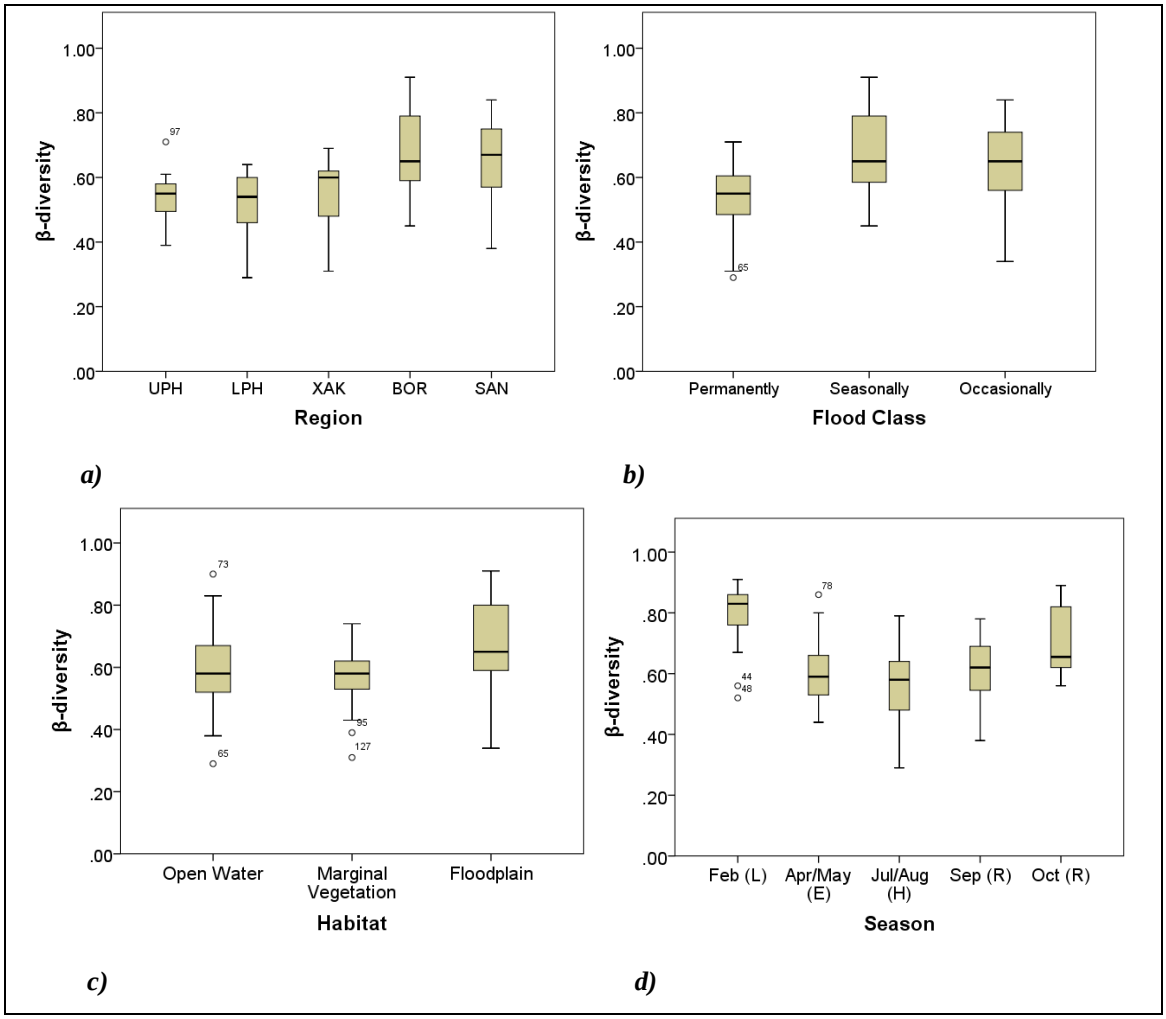


Figure 5.30. β-diversity within a) region, b) flood class, c) habitat and d) season.

Bray-Curtis similarity within regions overall varies from 0.213 to 0.291, with the lowest overall average value (0.248) (Table 5.17), as compared to similarity within flood classes (0.266; range 0.189-0.357) (Table 5.18) and habitats, which showed the highest overall similarity between samples (0.370; range: 0.318-0.444) (Table 5.19). Similarity between samples taken in different regions range from 0.161 (LPH-SAN) to 0.376 (UPH-LPH) with average values (0.226) intermediate between those recorded for similarity between samples collected in different flood classes (0.199; range: 0.179-0.203) and habitats (0.308; range: 0.281-0.315) (Tables 5.17 to 5.19). UPH samples have an average similarity of 0.276 with samples taken from

other regions, as compared to 0.241 for LPH, 0.217 for XAK, 0.204 for BOR and 0.194 for SAN (Table 5.17). Hence the variation of similarity in species composition (measureable as % change in similarity) is higher across regions than across flood classes and habitats, whereas the average similarity itself is highest across habitats.

Table 5.17. Average Bray-Curtis similarity between samples within and across regions (underlined the within-region similarity values).

Region	UPH	LPH	XAK	BOR	SAN
UPH	0.291	0.376	0.265	0.234	0.229
LPH		0.256	0.248	0.178	0.161
XAK			0.233	0.186	0.170
BOR				0.247	0.216
SAN					0.213

Table 5.18. Average Bray-Curtis similarity between samples within and across flood classes (underlined the within-region similarity values).

Flood Class	PF	SF	OF
PF	0.357	0.216	0.179
SF		0.251	0.203
OF			0.189

Table 5.19. Average Bray-Curtis similarity between samples within and across habitats (underlined the within-region similarity values).

Habitat	OW	MV	F
OW	0.349	0.315	0.328
MV		0.444	0.281
F			0.318

The similarity between samples within each region is highest in UPH and lowest in SAN (37% higher in UPH than in SAN); however, the average Bray-Curtis similarity is relatively similar, i.e. between 0.2 and 0.3, in the five regions sampled. Samples from BOR contain, on average, about 10 species in common (shared) with other BOR samples, whereas in XAK about 7.5 species are shared between samples and around 8 within the other regions (Figure 5.31).

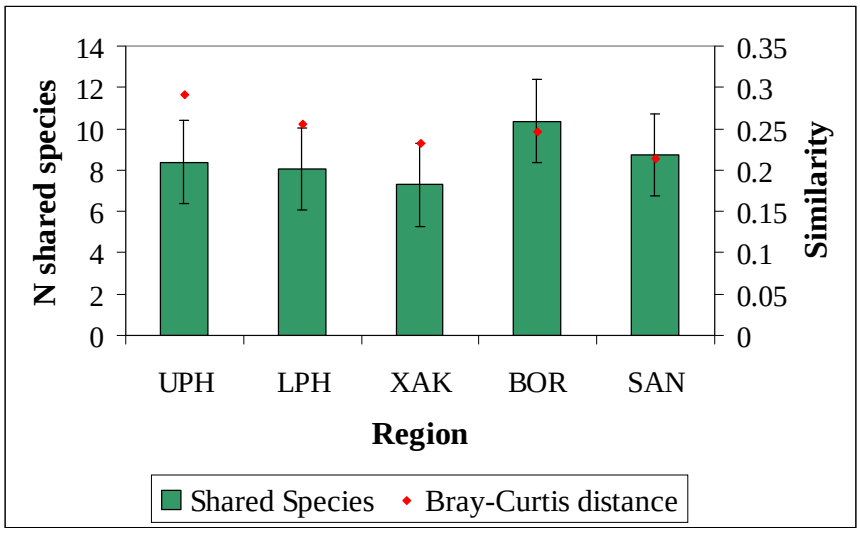


Figure 5.31. Mean number of shared species and similarity (Bray-Curtis distance) between samples within the same region.

Figure 5.32 illustrates the Bray-Curtis similarity and the number of shared species between different regions. Samples in UPH are most similar in algal species composition to LPH sites and have the highest number of species in common. UPH samples share fewer species with XAK and BOR samples. LPH samples have a 54% and 11% higher similarity to XAK and BOR than SAN. XAK samples share an average of between 7 and 7.5 species with the other regions and are most similar to UPH and least similar to SAN samples. BOR samples are most dissimilar to XAK and most similar to SAN. Overall, UPH has a higher average algal species composition similarity with other regions across the Delta (see Table 5.17).

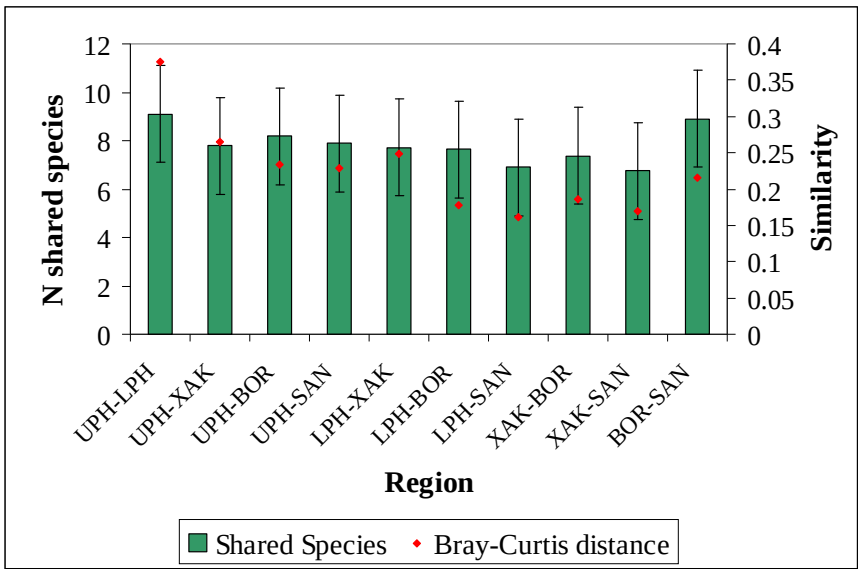


Figure 5.32. Mean number of shared species and similarity (Bray-Curtis distance) between samples in different regions.

Analysing the data within each flood class category reveals that the least similar samples are those within OF sites (they also have the lowest number of shared species), whereas within PF areas algal community composition is most similar and SF sites host algal communities with intermediate similarity from site to site, but most shared species (Figure 5.33).

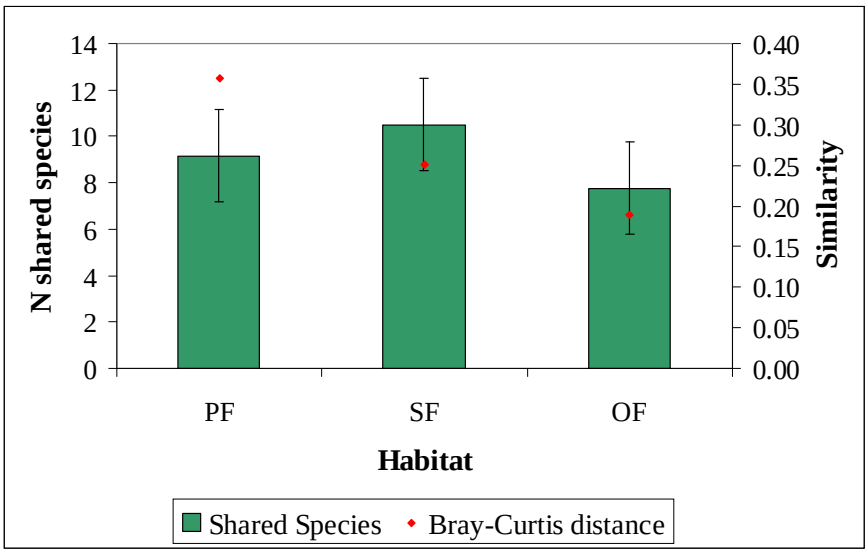


Figure 5.33. Mean number of shared species and similarity (Bray-Curtis distance) between samples within the same flood class (PF= Permanently Flooded; SF= Seasonally Flooded Flooded; OF= Occasionally Flooded).

Algal samples taken from PF sites are least similar to (and share the least number of species with) OF samples and are most similar to SF samples (Figure 5.34).

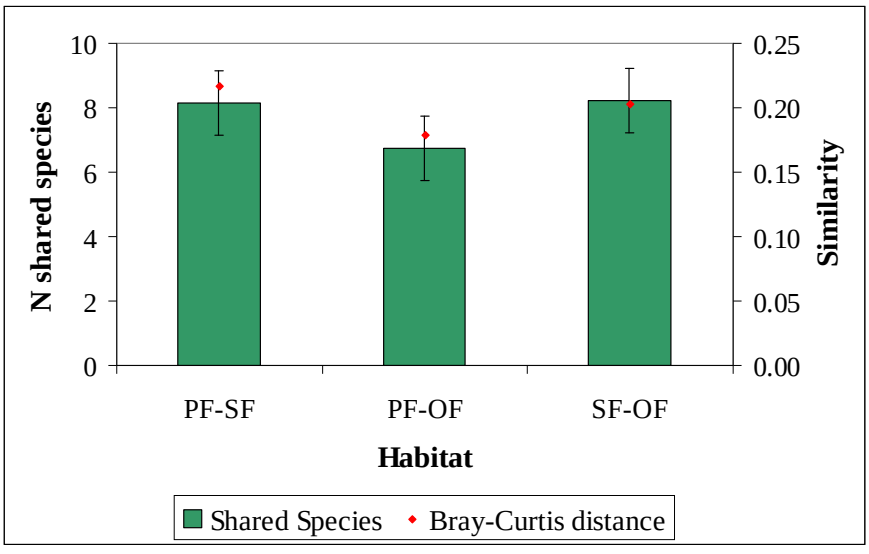


Figure 5.34. Mean number of shared species and similarity (Bray-Curtis distance) between samples in different flood classes (PF= Permanently Flooded; SF= Seasonally Flooded Flooded; OF= Occasionally Flooded).

F algal samples are more different from one another than OW and MV; these share an average of about 10 species with other F samples as compared to about 8 species which samples in OW and MV share with same-habitat sites (Figure 5.35).

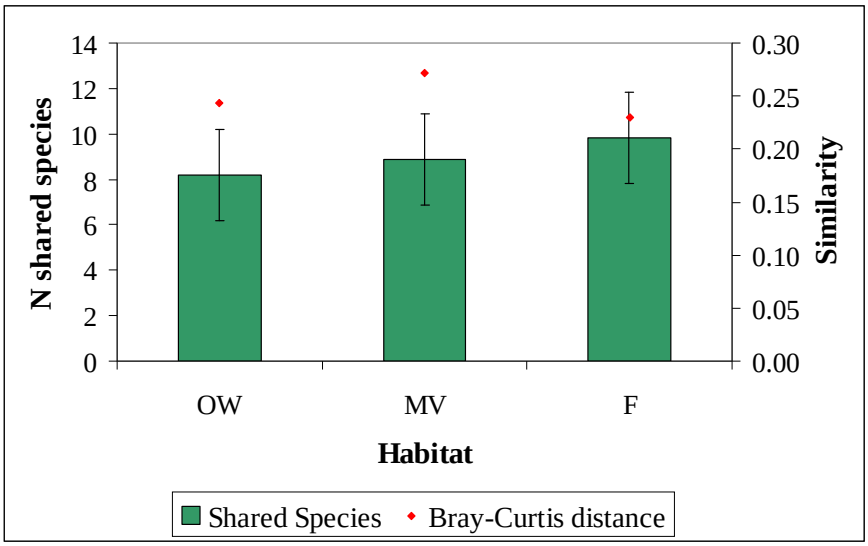


Figure 5.35. Mean number of shared species and similarity (Bray-Curtis distance) between samples within the same habitat (OW= Open Water; MV= Marginal Vegetation; F= Floodplain).

Samples in OW and F habitats are on average most similar (Bray-Curtis distance is 17% higher than between MV and F) and share almost 10 species (on average) as compared to the *c.* 8 species respectively shared by OW-MV and MV-F habitats which are more dissimilar in species composition (Figure 5.36).

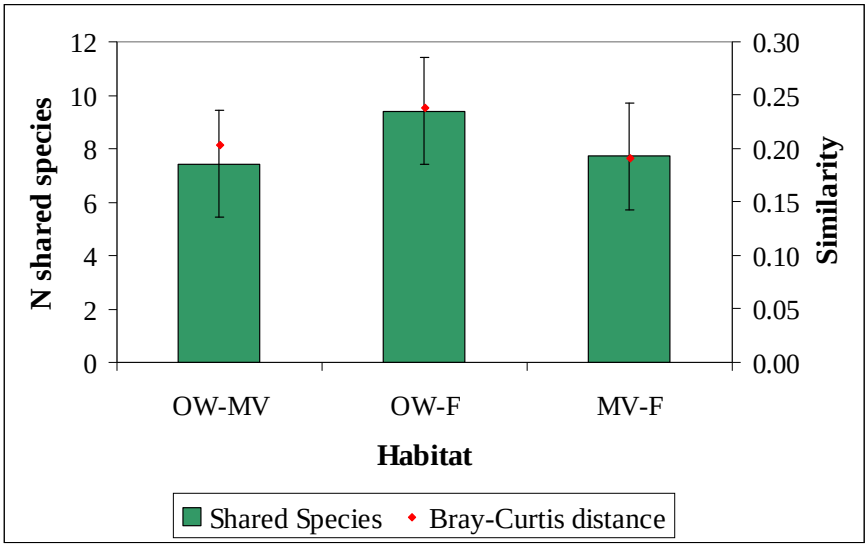


Figure 5.36. Mean number of shared species and similarity (Bray-Curtis distance) between samples in different habitats (OW= Open Water; MV= Marginal Vegetation; F= Floodplain).

Summarising, consistent with results on α-diversity, algal samples showed higher β-diversity in BOR, SAN, in seasonally and occasionally inundated sites and

floodplain habitats in these distal regions. Samples have a more similar species composition within the same habitat type, i.e. samples taken in the same habitat are on average more similar to one another, regardless of where they were collected in the Delta, than samples in the same region or belonging to the same flood class category. Moreover, similarity in algal species composition and number of shared species were compared within and across region, flood class and habitats. Average similarity in species composition is higher between samples collected within BOR, SF sites and floodplain habitats (Figure 5.31); however the number of shared species is higher in UPH, in Permanently Flooded (PF) sites and Marginal Vegetation (MV) sites. This is likely due to the Bray-Curtis similarity index being derived from relative abundance data rather than just presence / absence data. Samples from UPH-LPH and BOR-SAN show higher similarity than other pairs of regions (Figure 5.32). PF areas have least similar algal species composition to Occasionally Flooded sites (Figure 5.34); the latter have the lowest within-flood class similarity (Figure 5.33). OW and F have higher species similarity than other pairs of habitats; this is likely related to OW sites in Campaign 2 being very different environments, e.g. shallower and more nutrient-rich, than OW in Campaign 1. Thus, overall OW to MV are rather dissimilar (Figure 5.36), whereas within-habitat similarity and number of shared species show less clear trends (Figure 5.35).

5.2.5. Total algal biovolume

In this section, results of the estimates of algal biovolume, i.e. algal wet biomass, are presented. Firstly, total biovolume estimates across regions, flood class, habitat and seasons are presented; secondly, patterns of algal phylum biovolume are shown.

Total biovolume trends

Total biovolume shows significant variations both within sampling campaigns and across the whole study. The median algal biovolume, i.e. wet biomass, was 4.64 mg L^{-1} (s.d.=12.63), ranging from 0.176 to 90.41 mg L^{-1}. Detailed results of statistical tests and graphs corresponding to significant changes are presented below.

Campaign 1

In the five regions visited in 2006-2007, estimates of biovolume (=algal wet biomass) yield values between 0.202 mg L^{-1} and 47.97 mg L^{-1}; median 5.54 mg L^{-1} (s.d.=10.89 and c.v.=109.0%). Biovolume estimates from 2006-2007 are not normally distributed (K.S. test test: Z=1.514; p>0.01); hence, after verification of the homogeneity of variances (L. test), parametric statistical tests are used on log-transformed data to highlight significant differences. According to O.W.A., log-transformed biovolume are significantly lower in XAK than in UPH (L. test: p>0.01; F=6.694; p<0.001**; Tukey-HSD: UPH > XAK (p<0.001**) (Figure 5.37). Total algal biovolume does not vary significantly between sites of different flood class, floodplain type and habitats; no general or within-region seasonal changes are recorded at p=0.01.

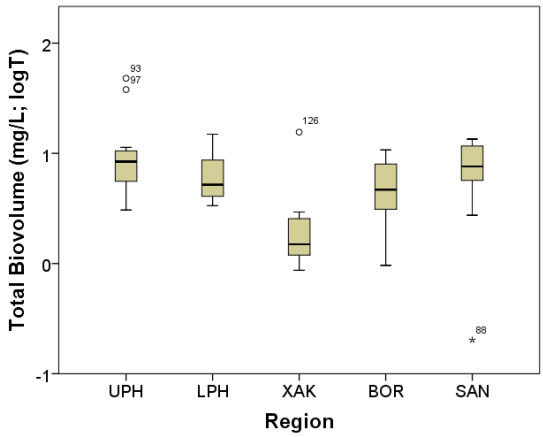


Figure 5.37. Total biovolume across regions in Campaign 1.

Campaign 2

In the two regions sampled in 2009-2010, estimates of biovolume yield values between 0.176 mg L^{-1} and 90.41 mg L^{-1}, with median 4.22 mg L^{-1}. Total biovolume estimates are not normally distributed (K.S. test: Z=2.566; p<0.001**). Biovolume does not vary significantly across BOR and SAN and it does not change with flood class or season. It varies significantly across Delta-scale habitats (L. test: p>0.01; O.W.A. test: F= 27.899; p<0.001**), with Floodplain (comprising sedgelands and grasslands) having higher biovolume than Open Water habitats (M.W. U test: p<0.001**) (Figure 5.38).

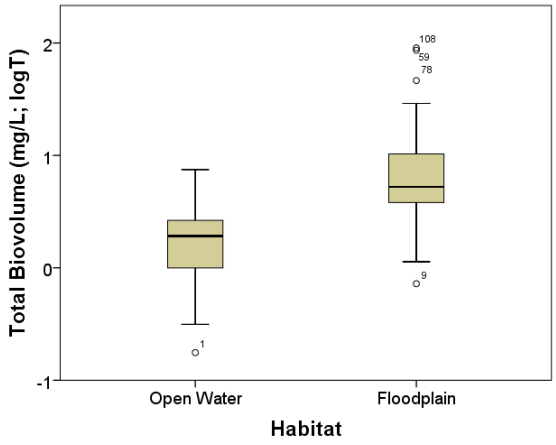


Figure 5.38. Total biovolume across habitats in Campaign 2.

It follows that total biovolume varies across different within-floodplain habitats (L. test: p=0.811; O.W.A. test: F=13.764; p<0.001**), with lower values in OW sites than both Sedgeland and Grassland areas (M.W. U test: p<0.001**) (Figure 5.39).

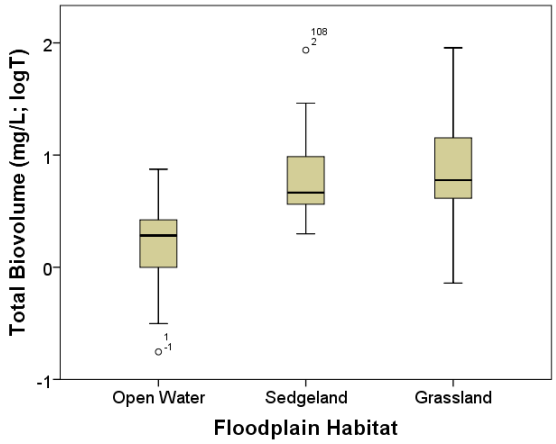


Figure 5.39. Total biovolume across within-floodplain habitats in Campaign 2.

Merged dataset

In the merged dataset total algal biovolume has a highest median value in UPH (8.41 mg L^{-1}) and lowest across regions in XAK (1.50 mg L^{-1}); OW has the lowest total biovolume (2.93 mg L^{-1}) among habitats. Other regions, flood classes and habitats show median total biovolume of about 4 to 5 mg L^{-1}, with LPH reaching 5.75 mg L^{-1} (Table 5.20).

Table 5.20. Total biovolume (median) across regions, flood classes and habitats.

Region	**Biovolume (median)**	**s.d.**
UPH	8.41	12.88
LPH	5.75	3.630
XAK	1.50	3.920
BOR	4.58	16.05
SAN	4.47	4.650
Flood Class	**Biovolume (median)**	**s.d.**
PF	5.68	9.876
SF	4.37	15.75
OF	4.21	4.612
Habitat	**Biovolume (median)**	**s.d.**
OW	2.93	7.740
MV	5.15	3.840
F	4.95	15.82

Total algal biovolume varies significantly across regions; L. test: p>0.01; O.W.A. test: F=4.323; p<0.01*; the only statistically significant pair-wise difference is that UPH has higher values than XAK (p<0.01*) (Figure 5.40). However, it does not change significantly across seasons, flood class or flood year or habitat at p=0.01.

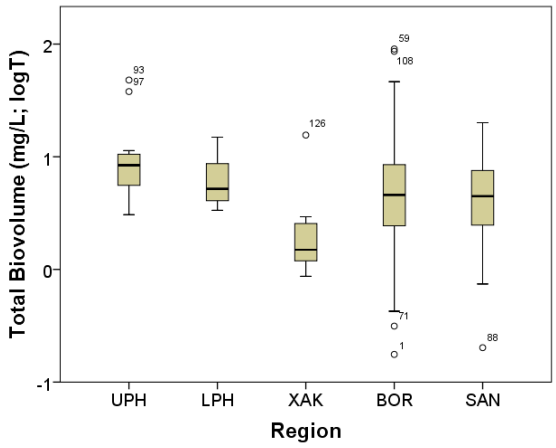


Figure 5.40. Total biovolume across regions in all the samples.

Figure 5.41 shows the total biovolume variations across habitats; they are not significant at p=0.01, but they are at p=0.05 (L. test: p>0.01; O.W.A: F=3.659; p=0.29). Variations across flood classes are not shown as not significant at p=0.05, whereas biovolume changes across seasons are illustrated in Figure 5.43 as they are significant at p=0.05 (L. test: p>0.01; O.W.A: F=2.961; p=0.22).

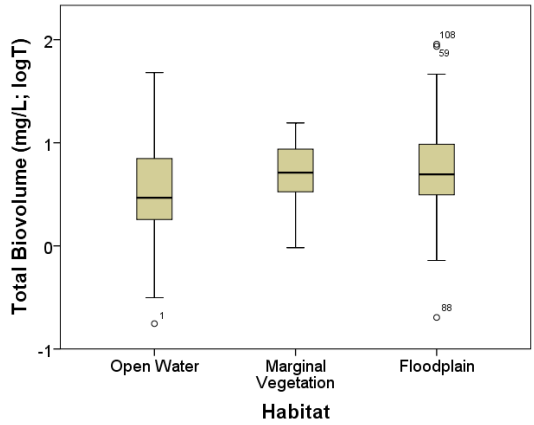


Figure 5.41. Total biovolume across habitats in all the samples (differences significant at p=0.05).

Table 5.21 illustrates all the coefficients of variation within region, flood class, habitat and season. BOR and XAK, seasonally flooded sites and floodplains are the areas with the highest coefficient of variation and February 2010 is the season in which total algal biovolume varies the most, i.e. more than twice than most of the other seasons. The average coefficients of variation of total algal biovolume are rather similar, i.e. respectively, on average, 110.5%, 119.3%, 124.9% and 119.6% within region, flood class, habitat and season. Despite the different coefficients of variation in different areas and seasons, the average variability of total biovolume is comparable across these categories, even though average c.v. within regions is about 10% lower than for the other categories. This reflects the fact that flood class, habitat and season groupings contain samples from different regions of the Delta. Thus algal biomass may be linked to spatial location (see section 6.3.2).

Table 5.21. Coefficients of variation of total biovolume across regions, flood classes, habitats and seasons.

Region	**c.v. (%)**	**Flood Class**	**c.v. (%)**	**Habitat**	**c.v. (%)**	**Season**	**c.v. (%)**
UPH	106.2	PF	116.2	OW	138.7	Feb	214.4
LPH	53.3	SF	172.8	MV	63.5	Apr / May	115.0
XAN	142.6	OF	85.7	F	155.6	Jul / Aug	107.4
BOR	170.6	-		-		Sep	79.7
SAN	79.7	-		-		Oct	81.5
Average	**110.5**	-	**119.3**	-	**124.9**	-	**119.6**

Biovolume of different phyla

Of the nine algal phyla observed, biovolume estimates are produced for eight of them, as only one specimen of Prasinophyta was found in the samples (see Table 4.2). Five phyla have biovolume estimates for over 100 samples (Bacillariophyta, Chlorophyta, Cryptophyta, Cyanophyta and Euglenophyta), with green algae showing the highest median (1.79 mg L^{-1}) and Pyrrophyta the lowest (0.04 mg L^{-1}). Standard deviations are higher than mean and median values in the great majority of cases (Table 5.22).

Table 5.22. Summary statistics of biovolume per algal phylum (c.v.= s.d / median * 100).

Biovolume (mg L^{-1})	**N**	**Range**	**Mean**	**Median**	**s.d.**	**c.v. (%)**
Bacillariophyta	130	0.017-29.72	0.379	0.942	3.933	163.3
Chlorophyta	130	0.051-82.17	3.405	1.792	9.127	203.7
Chrysophyta	49	0.000-0.534	0.043	0.040	0.121	151.5
Cryptophyta	118	0.000-1.250	0.064	0.034	0.177	193.6
Cyanophyta	129	0.000-59.21	0.563	0.029	5.209	877.7
Euglenophyta	119	0.000-4.946	0.163	0.076	0.807	232.6
Pyrrophyta	72	0.000-0.576	0.038	0.017	0.092	185.6
Xanthophyta	50	0.000-2.968	0.086	0.007	0.404	338.8
Total	**130**	**0.176-90.41**	**8.103**	**4.638**	**12.625**	**155.8**

71.3% of the total algal biovolume across the Delta is represented by 108 taxa (species and genera) relatively more common, i.e. present in at least 20 out of 132 samples and 80.3% of the total algal units identified. These are mostly green algae (69) and diatoms (25). *Mougeotia* spp. is the taxon with the highest total biovolume, i.e. 203.2 mg L^{-1} in 118 samples. The 374 species (88.4%) and 108 genera (62.4%) which are relatively rare (found in less than 20 samples), account for 29.7% of the biovolume and 19.7% of the total algal units. Hence rare taxa are very important in the Delta in terms of, abundance, taxon richness and biomass.

Region

Figure 5.42a shows the significant variations for Bacillariophyta across regions (L. test: $p<0.01^{*}$; K.W. test: $\chi^2=48.959$, $p<0.001^{**}$). UPH, LPH (M.W. U test: $p<0.001^{**}$), BOR and SAN ($p<0.001^{*}$) all have higher algal biovolume than XAK; UPH has higher diatom biovolume than both BOR and SAN ($p<0.001^{*}$); and LPH

higher than BOR and SAN ($p<0.001^{*}$). Chlorophyta's biovolume vary across regions (L-test: $p>0.01$; O.W.A. test: $F=5.514$, $p<0.001^{**}$) with higher values in BOR than XAK ($p<0.001^{**}$) (Figure 5.42b). Cyanophyta (L-test: $p>0.01$; O-W A.: $F=12.723$, $p<0.001^{**}$) have higher biovolume in BOR than UPH and XAK ($p<0.001^{**}$) and in SAN than XAK ($p<0.01^{*}$) (Figure 5.42c). Biovolume of Euglenophyta (L-test: $p>0.01$; O-W A.: $F=4.851$, $p<0.01^{*}$) are higher in SAN than UPH and XAK ($p<0.01^{*}$) (Figure 5.42d). Xanthophyta (L-test: $p>0.01$; O-W A.: $F=6.612$, $p<0.001^{**}$) show higher biovolume in BOR than XAK ($p<0.01^{*}$) (Figure 5.42e).

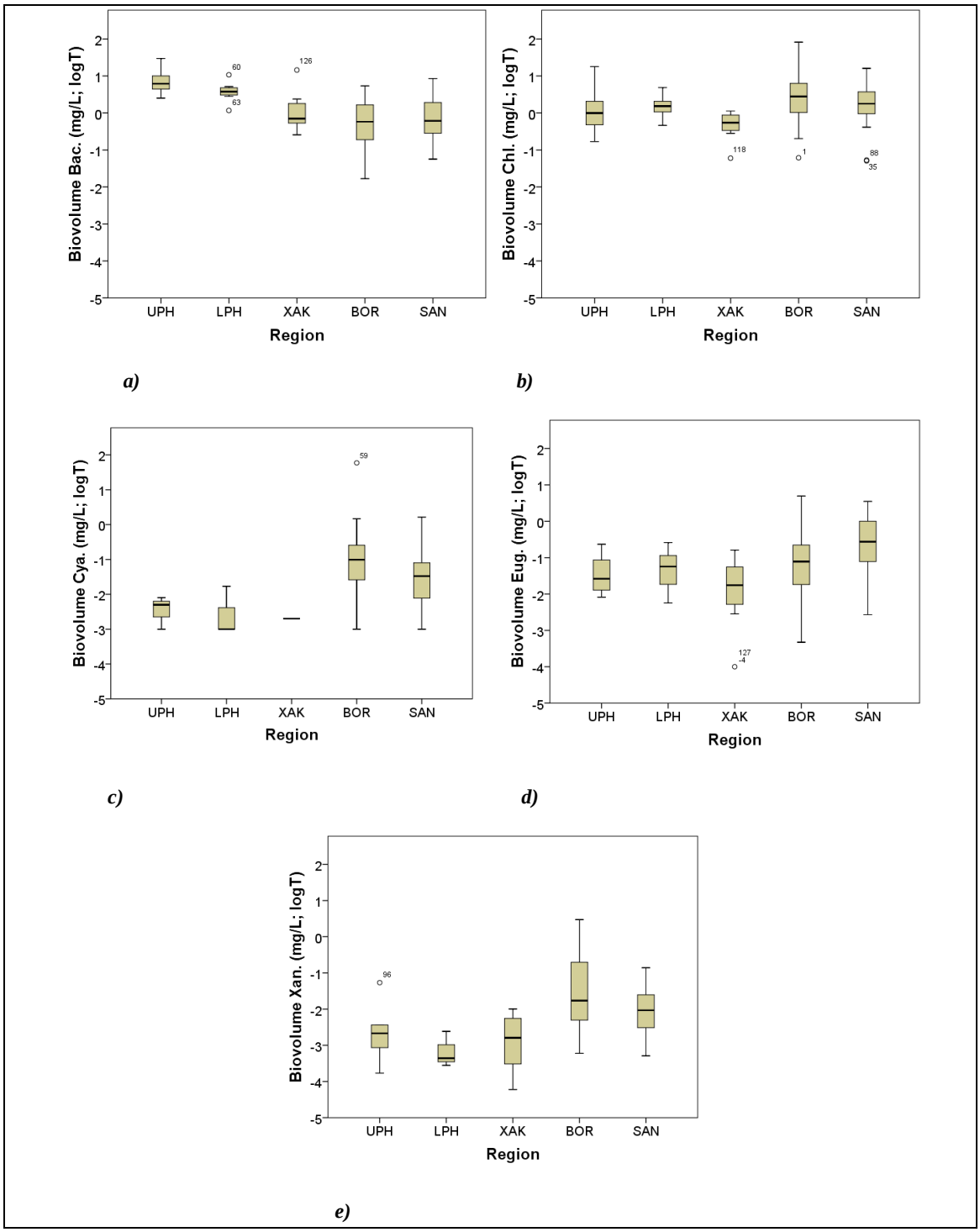


Figure 5.42. Total biovolume of a) Bacillariophyta; b) Chlorophyta; c) Cyanophya; d) Euglenophyta and e) Xanthophyta across regions.

Season

Despite the seasonal variations of total algal biovolume are not statistically significant at p=0.01, but they are at p=0.05 (L. test: p>0.01; O.W.A: F=2.961; p=0.22; Figure 5.43).

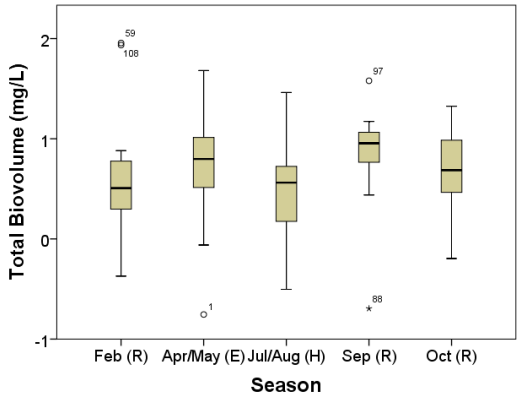


Figure 5.43. Total biovolume across seasons in all the samples (differences significant at p=0.05).

The significant biovolume changes are shown in Figure 5.44 for five phyla. The biovolume of Bacillariophyta varies significantly across seasons in all the samples (L. test: $p>0.01$; K.W. test: $\chi^2=29.793$, $p<0.001^{**}$) (Figure 5.44a and Table 5.23).

Table 5.23. Summary of the significant differences in Bacillariophyta biovolume in all the samples (M.W. U test).

Seasons (flooding phase)	**Jul/Aug (High water)**	**Sep (Recession)**
Feb (Low water)	$p<0.001^{**}$	$p<0.001^{**}$
Apr/May (Expansion)		$p<0.01^{*}$
Jul/Aug (High water)		$p<0.001^{**}$
Oct (Recession)	$p<0.01^{*}$	$p<0.001^{**}$

- The biovolume of Chrysophyta also varies significantly (L. test: $p>0.01$, O.W.A. test: $F=4.497$, $p=0.01^{*}$), with higher biovolume in Apr/May (E) than Jul/Aug (H) ($p<0.01^{*}$) (Figure 5.44b).
- Cyanophyta also have variations in biovolume (L-test: $p<0.01^{*}$; K.W. test: $\chi^2=22.680$, $p<0.001^{**}$) with higher values in Feb (R) than Jul/Aug (H) ($p<0.001^{**}$), Apr/May and Sep (R) ($p<0.01^{*}$); and in Oct (R) than Jul/Aug (H) ($p<0.01^{*}$) (Figure 5.44c).
- Euglenophyta (L-test: $p>0.01$; O-W A.: $F=11.802$, $p<0.001^{**}$) have higher biovolume in Feb (L), Apr/May (E) and Sep (R) than Jul/Aug (H) ($p<0.001^{**}$) (Figure 5.44d).
- Xanthophyta's biovolume vary across seasons (L. test: $p>0.01$): O.W.A. test: $F=10.917$, $p<0.001^{**}$; Feb (L) higher than Jul/Aug ($p<0.001^{**}$) and than Sep (R) ($p<0.01^{*}$); Oct (R) higher than Jul/Aug ($p<0.001^{**}$) and than Sep (R) ($p<0.01^{*}$) (Figure 5.44e).

Four out of eight phyla have lowest biomass in the winter season (July / August), while Bacillariophyta have lowest biomass in the warmer seasons (October and February) which correspond to the flood recession phase (Figure 5.44a); Chlorophyta, Cryptophyta and Pyrrophyta do not show significant seasonal differences across the Delta.

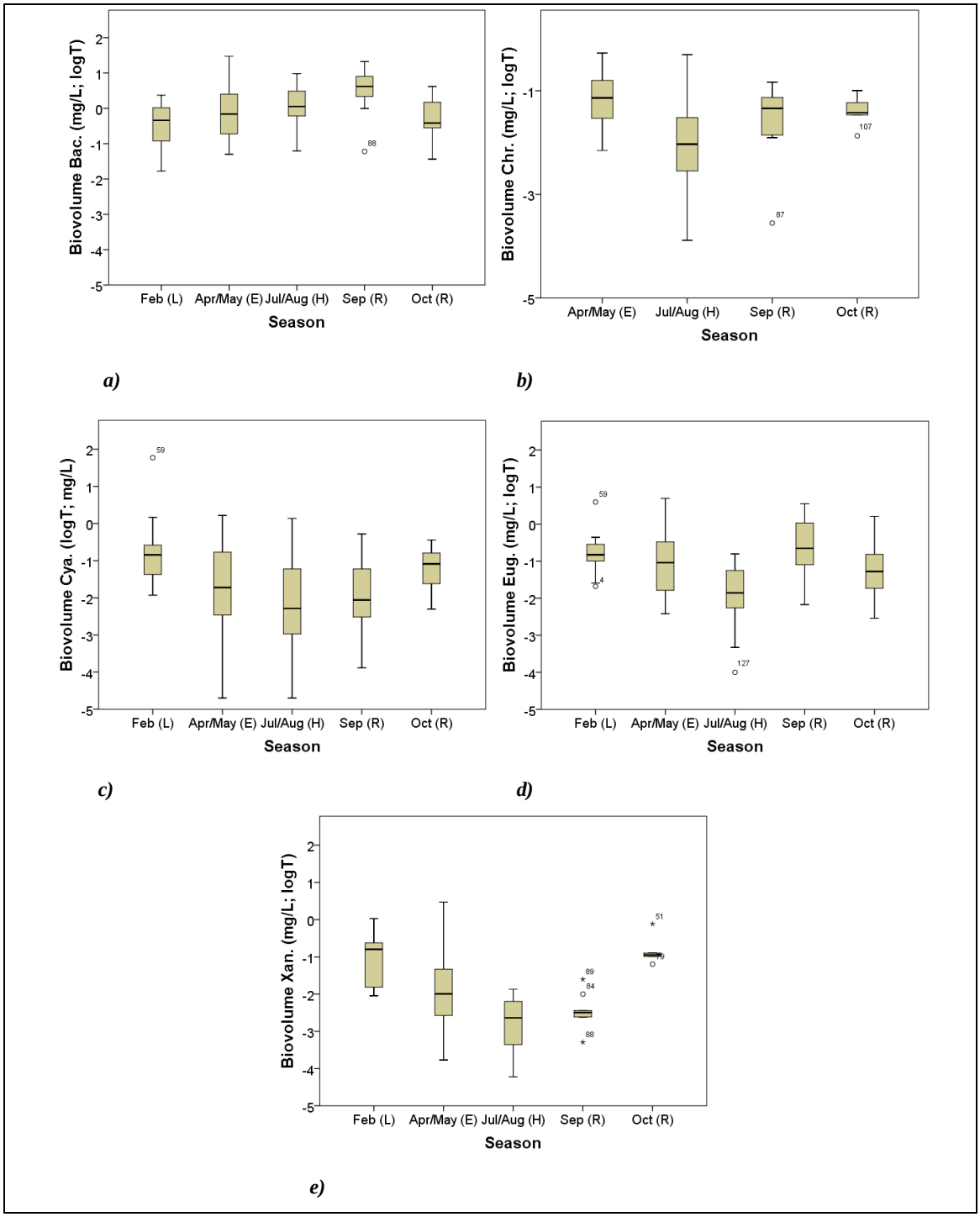


Figure 5.44. Biovolume of a) Bacillariophyta; b) Chrysophyta; c) Cyanophyta; d) Euglenophyta; e) Xanthophyta across seasons.

Flood class

Total algal biovolume does not vary significantly across flood classes. However, significant differences among biovolume of some algal phyla were recorded in relation to flood class of the sites sampled. The most relevant variation is in the biovolume of Bacillariophyta and Chlorophyta; the former prevail in the Permanently Flooded (PF) areas, the latter in the Seasonally Flooded (SF) sites.

Four out of eight phyla have higher biomass in SF and OF sites apart from Bacillariophyta which have higher biomass in PF sites and Chrysophyta, Cryptophyta and Pyrrophyta which do not have significant differences. Bacillariophyta (L-test: $p>0.01$; O.W.A. test: $F=25.050$, $p<0.001^{**}$) have higher biovolume in PF sites than SF and OF sites ($p<0.001^{**}$) (Figure 5.45a). Chlorophyta (L-test: $p>0.01$; O-W A.: $F=5.363$, $p<0.01^{*}$) show higher biovolume in SF than PF sites ($p<0.01^{*}$) (Figure 5.45b); the same applies to Cyanophyta (L-test: $p>0.01$; O-W A.: $F=15.484$, $p<0.001^{**}$; SF > PF, $p<0.001^{**}$) (Figure 5.45c). Euglenophyta (L-test: $p>0.01$; O-W A.: $F=4.909$, $p<0.01^{*}$) have higher biovolume in OF than PF sites ($p<0.01^{*}$) (Figure 5.45d). Finally, Xanthophyta (L. test: $p>0.01$; K.W.: $\chi^2=15.339$, $p<0.001^{**}$) have higher biovolume in SF than PF areas ($p<0.001^{**}$) (Figure 5.45e).

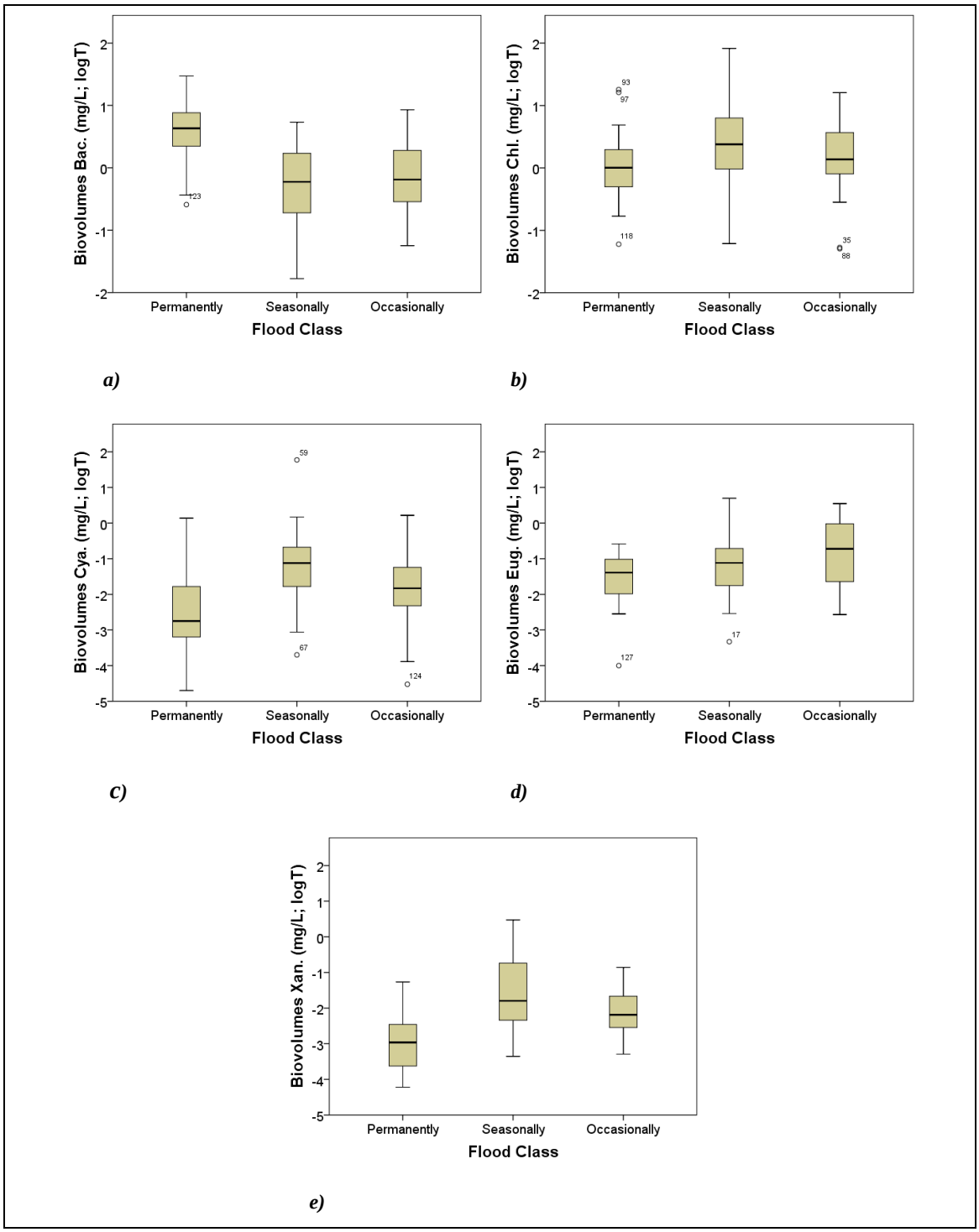


Figure 5.45. Biovolume of a) Bacillariophyta; b) Chlorophyta; c) Cyanophyta; d) Euglenophyta; e) Xanthophyta across flood classes.

Habitat

Total algal biovolume varies across habitat types in the merged datasets. K.W. tests show that Bacillariophyta (L-test: $p<0.01^{*}$; $\chi^2=17.423$, $p<0.001^{**}$) have higher biovolume in MV than F ($p<0.001^{**}$) (Figure 5.46a). Chlorophyta have a similar pattern (O.W.A. test: L. test: $p>0.01$; $F=16.642$, $p<0.001^{**}$), i.e. higher biovolume in F than OW ($p<0.001^{**}$) and MV ($p<0.01^{*}$) (Figure 5.46b). Cyanophyta (L-test:

p>0.01; O-W A.: F=16.099, p<0.001**), also have higher total biovolume in F than OW (p<0.001**) (Figure 5.46c).

Only three phyla show significant variation in biovolume across habitats; Bacillariophyta – higher biomass in OW and MV; Chlorophyta and Cyanophyta have higher biomass in F than OW and MV (with lower Cyanophyta biomass in MV as compared to Chlorophyta).

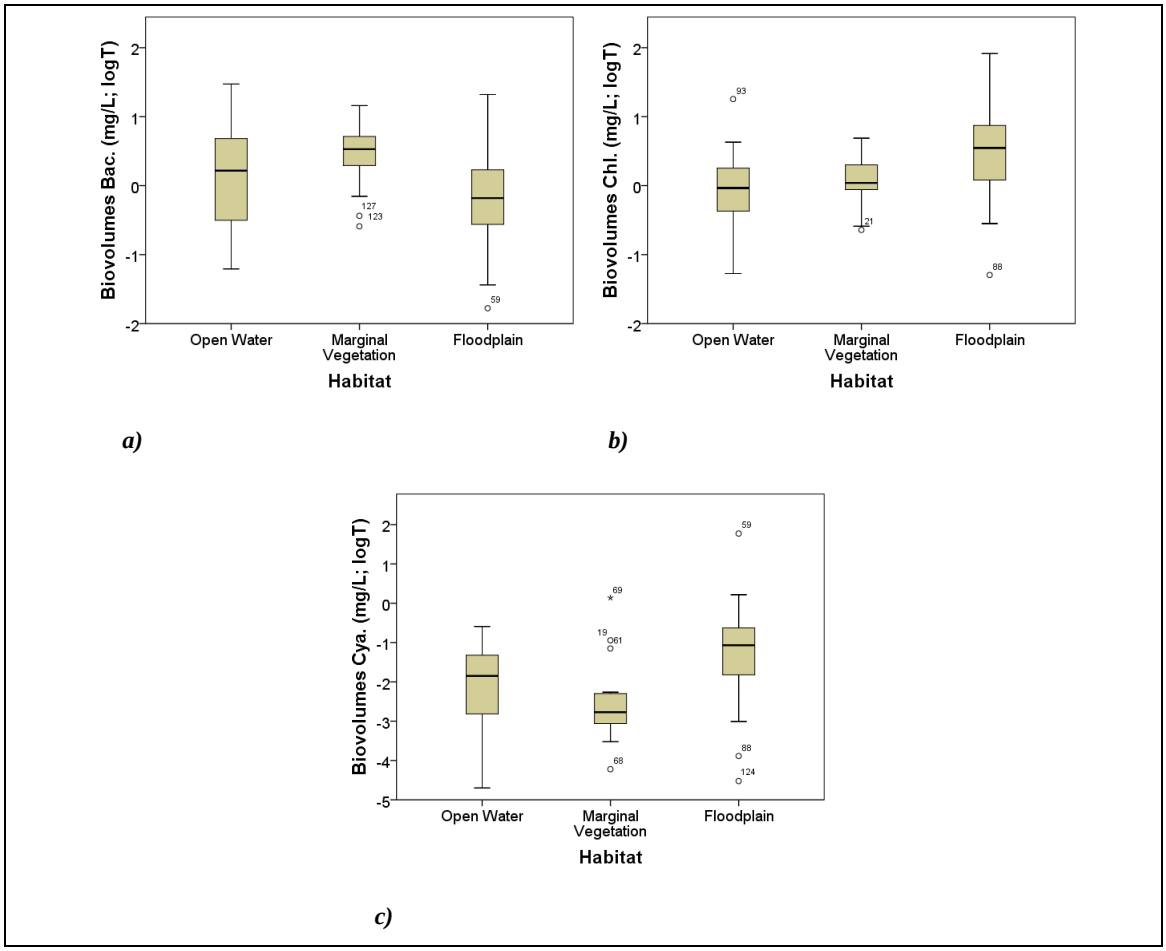


Figure 5.46. Biovolume of a) Bacillariophyta; b) Chlorophyta; c) Cyanophyta across habitats.

5.2.6. Algal species richness – biovolume relationship

In this section algal biomass (estimated via biovolume) and diversity (species richness) are analysed to examine the extent to which algal species richness is a significant predictor of biomass, i.e. biovolume (see section 3.4), as well as to investigate the shape of the diversity-biomass curve across different classifications of sampling sites (region, flood class, habitat and floodplain type).

Below, differences in the shape and strength of the relationship between species richness and estimated algal biomass are analysed at Delta-scale, by region, flood class, season and habitat.

Here, the relationship between total algal biovolume and species richness is analysed at a much more local/regional scale in a subtropical wetland. No significant regression was found at p=0.01. Hence significant models at p=0.05 (95% confidence) were investigated in order to highlight possible undetected trends, albeit less significant. The linear model was the only significant model at p=0.05 (Figure 5.47; adj R^2=0.030, F=4.955, p=0.027), hence highlighting a very weak relationship.

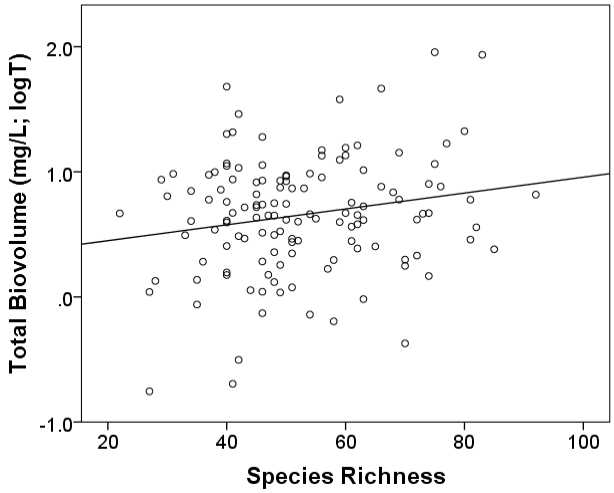


Figure 5.47. Total biovolume vs species richness in all the samples.

The parameters of the linear regression in all the samples are shown in Table 5.24.

Table 5.24. Regression parameters for total biovolume vs species richness in all the samples.

Variables	**AdjR^2**	**β (standardised)**	**t**	**p-value**
Intercept	0.030	-	-1.104	0.027
Species		0.195	2.246	0.026*

Regional scale patterns

The only significant linear regression within regions is in XAK (Figure 5.48) with a positive trend and an AdjR^2 of 0.262 (Table 5.25).

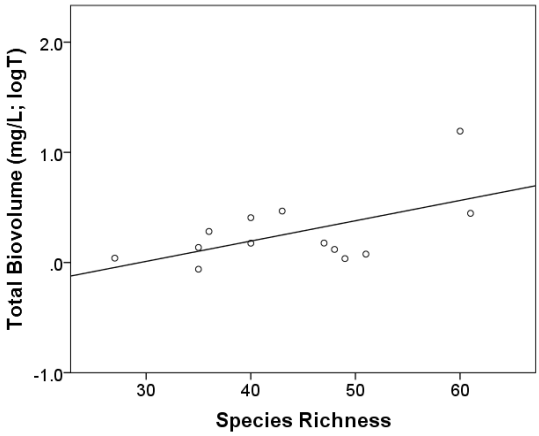


Figure 5.48. Total biovolume vs species richness in XAK samples.

Table 5.25. Regression parameters for total biovolume vs species richness in XAK.

Variables	**AdjR^2**	**β (standardised)**	**t**	**p-value**
Intercept	0.262	-	-1.498	0.043*
Species		0.568	2.292	0.027*

The shape of the relationship between species richness and biomass in the other regions is analysed qualitatively with scatterplot and loess smoothers. Total algal biovolume and species richness trends vary in the different regions, both in terms of maximum number of species, i.e. about 60 in UPH, LPH and XAK as compared to 80-90 in BOR and SAN, and in relation to the relationship between these variables, i.e. increasing more markedly in the first two regions than in BOR and SAN However, the number of samples is higher and thus the patterns more robust in the distal reaches (Figure 5.49 c and d).

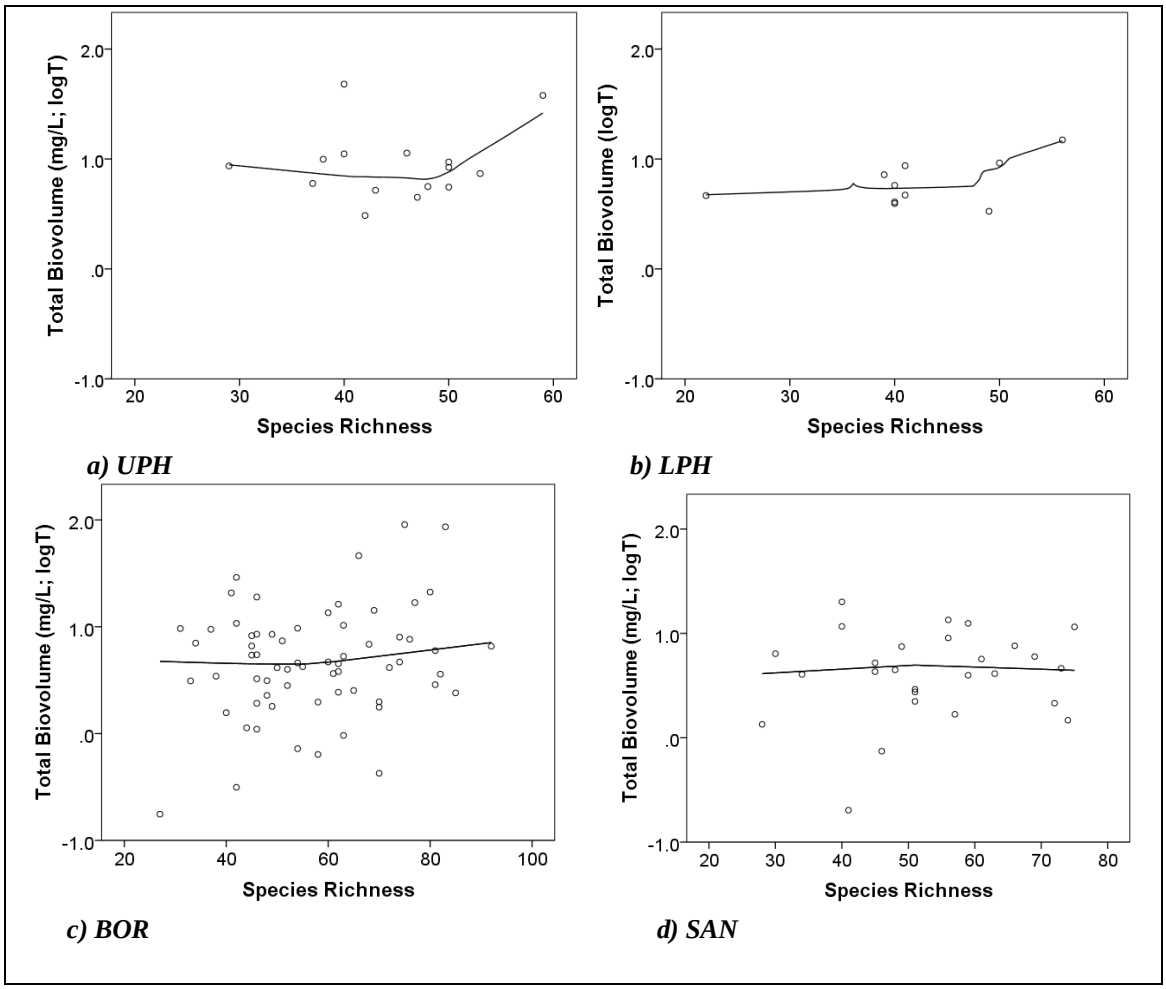


Figure 5.49. Total biovolume vs species richness across regions (logT=log-transformed; a loess smoother fitting 99% of the points interpolates the data).

No significant linear regression is observed in samples analysed by flood class (Figure 5.50). However, an increasing trend in algal biovolume is visible in PF, SF and OF sites. In PF (only in UPH, LPH and XAK) the increase is more marked than in SF (mainly in BOR) and even more than OF sites (mainly in SAN).

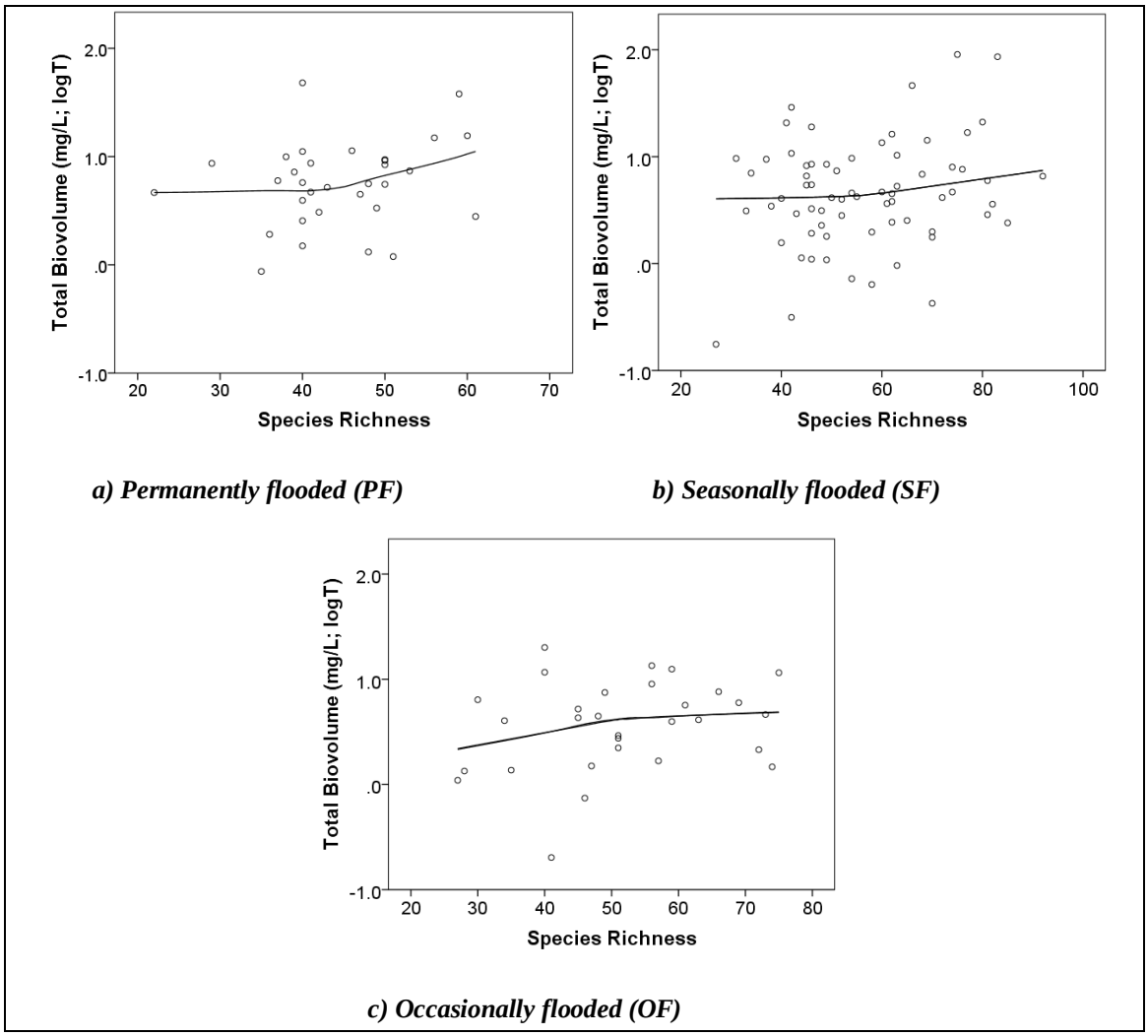


Figure 5.50. Total biovolume vs species richness across flood classes (logT=log-transformed; a loess smoother fitting 99% of the points interpolates the data).

Seasonal patterns

Linear regression is significant only for Apr/May data (Figure 5.51) with a positive trend and an AdjR^2 of 0.112 (Table 5.26).

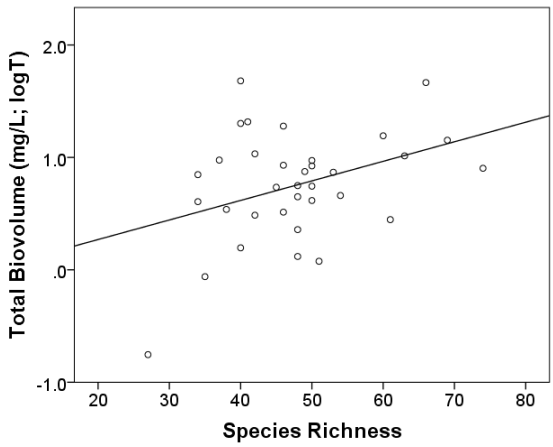


Figure 5.51. Total biovolume vs species richness in Apr/May.

Table 5.26. Regression parameters for total biovolume vs species richness in Apr/May.

Variables	AdjR^2	β (standardised)	t	p-value
Intercept	0.112	-	-0.209	0.836
Species		0.372	2.270	0.030*

Other seasonal patterns analysed are also different. In the low water phase (Feb) and flood recession phase (Sep and Oct), total algal biovolume increases, especially with species richness above 50-60 (Figure 5.52 a and d); whereas in the high water phase (Jul/Aug) algal biomass estimates are on average rather stable (Figure 5.52c).

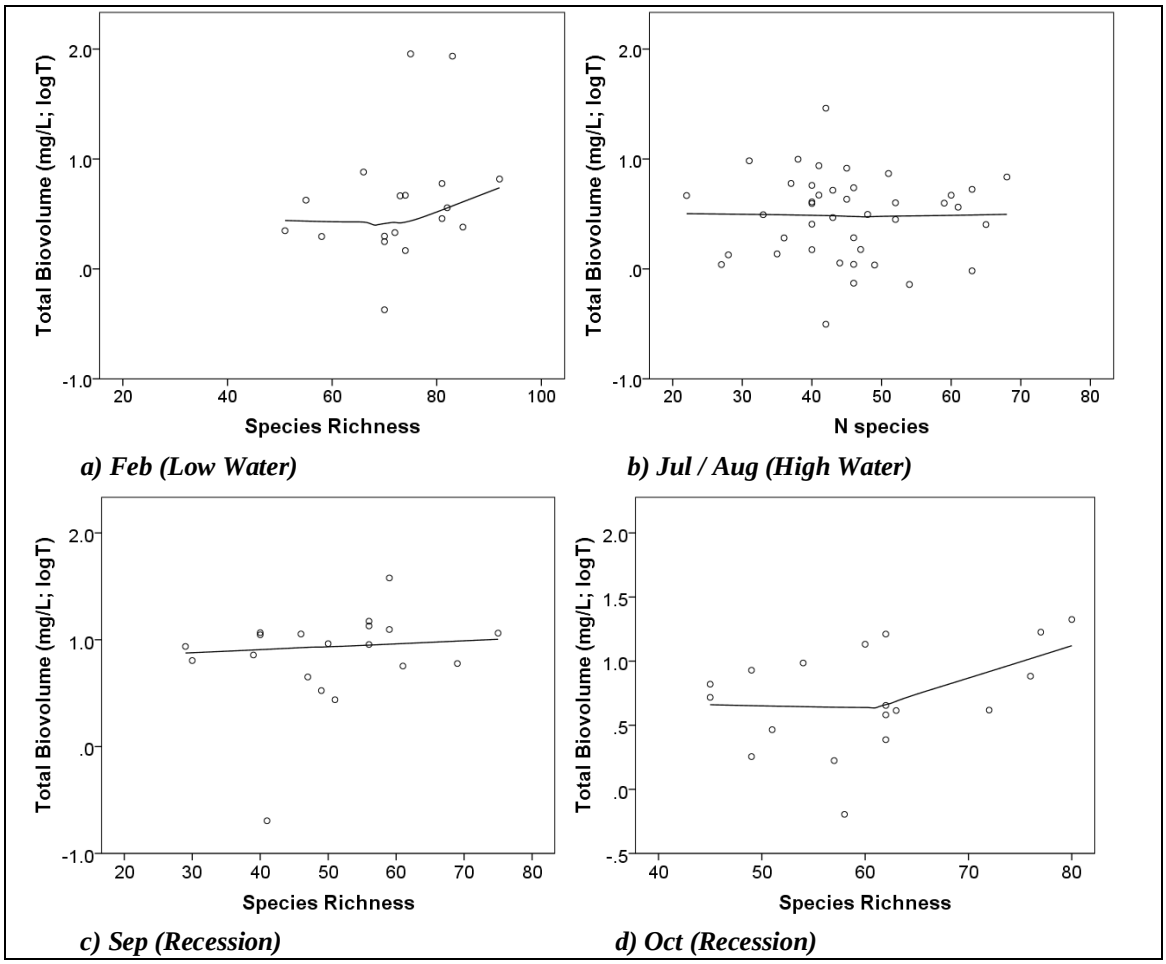


Figure 5.52. Total biovolume vs species richness across seasons (logT=log-transformed; a loess smoother fitting 99% of the points interpolates the data).

Habitat scale patterns

Figure 5.53 illustrates the higher species richness observed in F as compared to OW and MV habitats; floodplains tend to have significantly higher total algal biovolume than other habitats in the Campaign 2 dataset (see Figure 5.55).

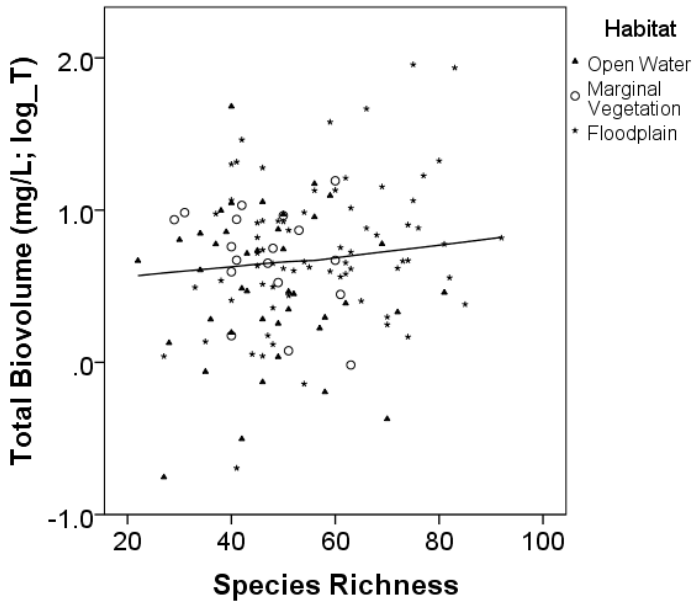


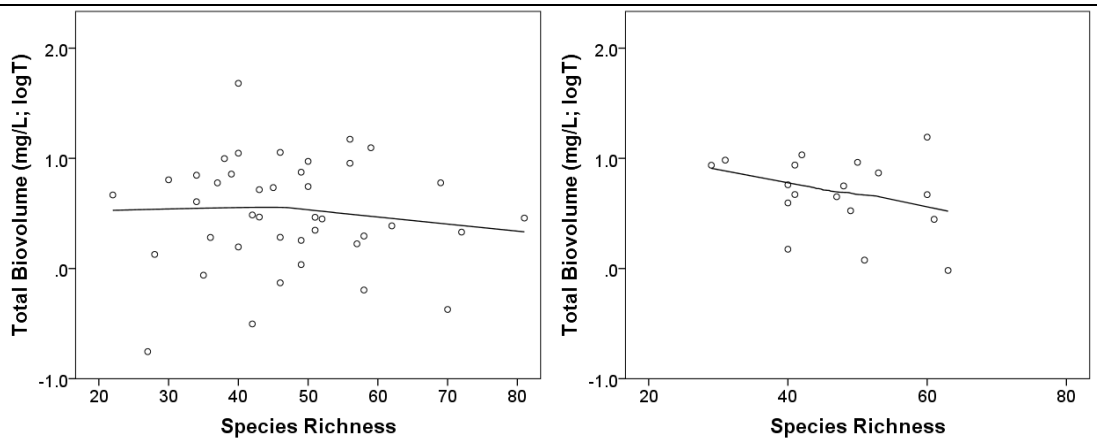
Figure 5.53. Total biovolume vs species richness across all habitats (logT=log-transformed; a loess smoother fitting 99% of the points interpolates the data).

Linear regression suggests a weak significant positive species richness - total biovolume linear relationship for floodplain samples (Table 5.27), supported by a much larger number of observations than the other two habitats.

Table 5.27. Regression parameters for total biovolume vs species richness in floodplains.

Variables	**AdjR^2**	**β (standardised)**	**t**	**p-value**
Intercept	0.062	-	1.081	0.284
Species Richness		0.275	2.359	0.021*

Data on OW and MV indicate a non-significant negative relationship between species richness and algal biomass (Figure 5.54).



a) Open Water ***b) Marginal Vegetation***

Figure 5.54. Total biovolume vs species richness in a) OW and b) MV habitats (logT=log-transformed; a loess smoother fitting 99% of the points interpolates the data).

Figure 5.55 illustrates the different relationships observed in each of the eight floodplains in BOR (a to f) and SAN (g and h); there is no consistent pattern in primary, secondary and occasionally floodded floodplains. Therefore these relationships are not scale-invariant, i.e. they do not follow the same pattern as at Delta scale (Figure 5.47); in fact at local scale algal biovolume increases (e.g. Figure 5.55 a and d) or decreases (see Figure 5.55h) or fluctuate less (Figure 5.55b and c) with increasing species richness. When genera richness is used, rather than species richness, the trends are rather similar and hence these are not shown.

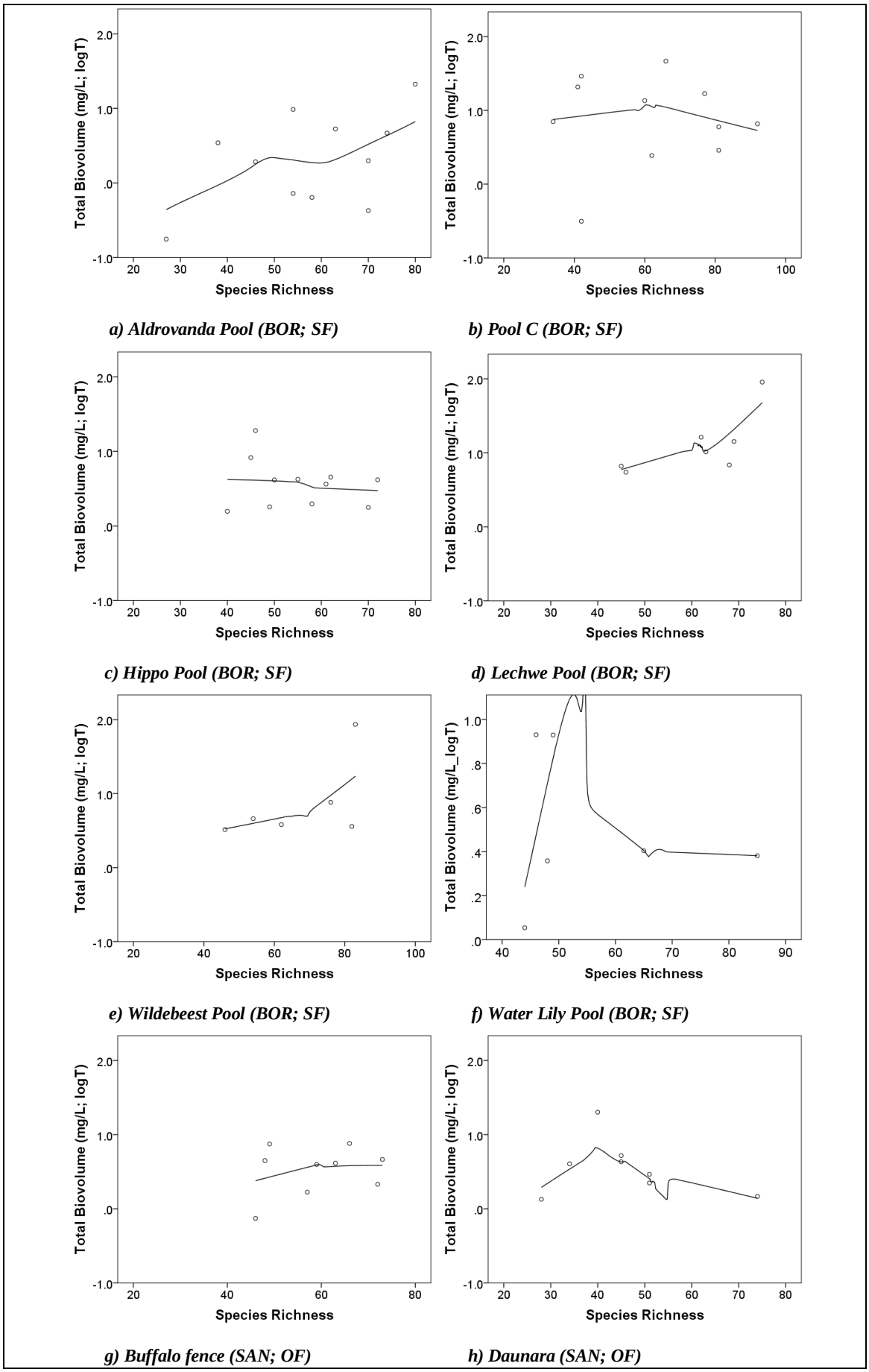


Figure 5.55. Total biovolume vs species richness in floodplains in Campaign 2.

Table 5.28 shows the detailed results of significant regression equations with total biovolume and biovolume of each phylum as predictands and relative species richness as predictors. All biovolume estimates of algal phyla, apart from Xanthophyta, are significantly predicted by species richness, with higher $AdjR^2$ than when total biovolume is analysed (see Tables 5.24 to 5.27).

Table 5.28. Results of linear regressions of algal biovolume vs species richness (log-transformed) across phyla.

Phylum	**$AdjR^2$**	**F**	**p-value**	**β (standardised)**
Bacillariophyta	0.237	41.104	<0.001**	0.493
Chlorophyta	0.279	51.019	<0.001**	0.534
Cryptophyta	0.325	57.358	<0.001**	0.575
Cyanophyta	0.384	79.682	<0.001**	0.622
Euglenophyta	0.429	87.317	<0.001**	0.659
Pyrrophyta	0.348	37.287	<0.001**	0.590

These results are illustrated in Figure 5.56 for the two major algal phyla, Bacillariophyta and Chlorophyta; diatoms reach a similar biovolume of 10 mg L^{-1} (equal to 1 in the log-scale graph) with much fewer species (between 15 and 25) than green algae (between 15 and 50 species).

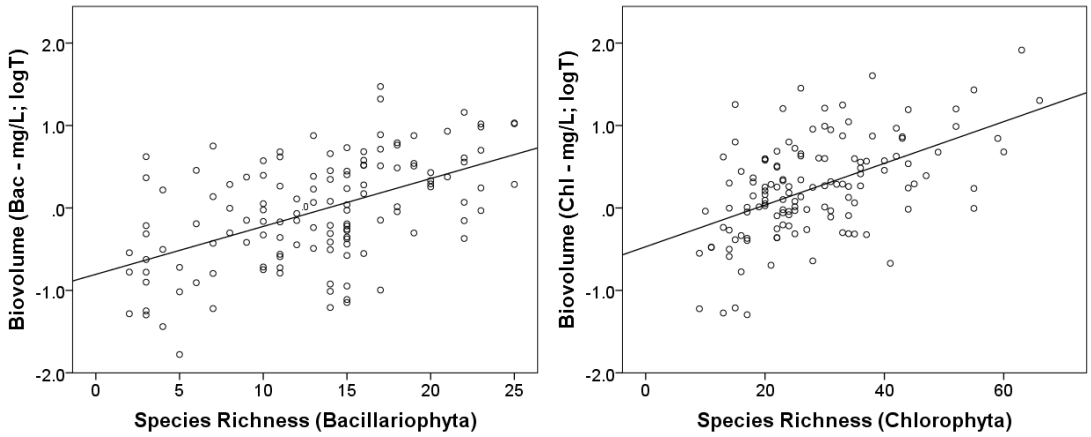


Figure 5.56. Biovolume and species richness of: a) Bacillariophyta and b) Chlorophyta.

5.3. DISCUSSION

Investigating patterns of algal biodiversity and biomass at whole-Delta scale as well as within and between regions, flood classes, habitats and seasons is important to understanding the ecological dynamics of this near-pristine wetland, e.g. developing hypotheses as to where the more diverse species assemblages and the ones where higher biomass are found and why. This study allows us to evaluate and quantify the contribution of algal biodiversity to algal biomass alongside interrelated environmental variables and factors such as flood pulse, habitat and nutrient availability.

Considerable variations in algal diversity and biomass occur across the Delta regions sampled, sampling seasons, flood classes (linked to long term flooding frequency) and habitat types. This is reflected in the shape of the relationships between algal species richness (used instead of diversity indices to avoid underestimating the role of rare species) and biomass. In fact, the most significant difference between the shape of the richness-biomass curve is observed when sites are compared across habitats (Figures 5.36 and 5.37). As the linear regression results show, the species richness of algae partially controls their total biomass, especially in habitats with reduced water velocity, higher temperature and nutrient levels as well as abundant substrata for benthic algae to attach to, i.e. floodplains (F), algal biovolume tends to be significantly higher than in the more homogeneous OW habitats, especially in Campaign 2 (see Figures 5.21 and 5.37). However, on average, UPH and LPH sites show similar algal biomass to BOR and SAN. Fewer species of algae, such as large diatoms (e.g. *Eunotia pectinalis* and *Synedra* spp.) are very abundant and hence represent a significant share of algal biomass in the Panhandle; by contrast, in the distal reaches algae are on average smaller, with green algae (e.g. *Cosmarium* spp. and *Monoraphidium arcuatum*) being particularly abundant (see also section 4.6.2).

The following sections propose plausible evidence-based ecological interpretations of the taxon richness and diversity of algae (5.3.1), their biomass (5.3.2) and species richness – biomass relationships (5.3.3).

5.3.1. Interpretation of algal taxon richness and diversity

Significant differences in species and genera richness emerge across space and time, particularly in the merged dataset which allowed us to produce the first systematic description of this wetland's algal assemblages in relation to the Delta's geography and environment. The total number of species in the different regions is defined as Regional Species Richness (RSR); this is substantially higher in the distal reaches (BOR and SAN) than in the Panhandle (UPH and LPH) and XAK. 331 and 261 species were identified in BOR and SAN. This is due to the average species and genera richness at the sampling points (Local Species Richness; LSR) being higher than in the Panhandle (see section 4.4), but also to the higher sampling effort made in the Delta's distal reaches, which augments the effect of local LSR on RSR.

The BOR and SAN regions host a higher total number of species and genera than UPH, LPH and XAK (Figure 5.4), SF sites have higher taxon richness than PF ones (Figure 5.5) and F habitats are more diverse than OW (Figure 5.7). From a seasonal / flood phase viewpoint, species and genera richness are higher during the flood recession phases (Figure 5.6). Therefore the shallow environments in the distal reaches (BOR and SAN) host higher numbers of species and genera; here floodplains are a prominent feature of the landscape and flooding is less frequent than in the deeper Panhandle sites (see Figure 3.1). Shallower waters are also associated with higher species and genera richness from a seasonal viewpoint as during flood recession more algal taxa are observed.

Moreover, in this study, Campaign 2 samples were shown to have species richness increasing at a much faster rate than Campaign 1 samples, whereas genera richness showed a more gradual increase (see Figure 4.3). This supports the interpretation reached by Passy and Legendre (2006b) using an extensive dataset on diatoms in streams from 50 watershed in the USA, i.e. the species richness of benthic algae tends to be due to congeneric species rather than to differentiation at higher taxonomic levels (see section 5.3.3).

Results from Campaign 1 do not show significant differences in total or phylum species and genera richness across regions, seasons, flood class and habitat types. Green algae (Chlorophyta) have significantly higher species richness during the low water and recession phases, whereas diatoms (Bacillariophyta) show smaller changes, with slightly higher species richness in the flood expansion (April/May

2007-2009) and one of the recession phases (September 2006) (Figure 5.X). Habitat-wise, in Campaign 2 diatoms are present in a significantly higher number of species in OW and MV sites; conversely, green algae have a higher species / genera richness in F than in OW (Figure 5.Y).

Spatial scale may play a role in determining algal diversity trends in the Okavango Delta. This is likely due to a combination of higher long-term flooding disturbance in seasonally inundated and occasionally inundated areas, greater benthic microhabitat availability in these habitats (due to lower flow velocity and shallower waters), intensively sampled in the 2009-2010 Campaign 2, higher temperature and nutrient availability. In fact, it is assumed that the availability of sediment and vegetation surfaces allows the growth of more algal species in the phytobenthos, e.g. periphytic and epiphytic taxa (living around or attached to plants), than in the phytoplankton growing in the more homogeneous river channel environments (Figure 5.7). This is in agreement with theories on biodiversity of algae and other primary producers, e.g. plants, in relation to habitat heterogeneity (e.g. Hutchinson, 1961; Ricklefs, 1977). Therefore, the higher nutrient concentrations, conductivity and temperatures recorded in the floodplains in BOR and SAN likely enhance taxon richness in these environments by creating broader / more numerous ecological niches; the annual flood pulse (and its long-term disturbance effect) is the phenomenon generating the underlying environmental differences between the Panhandle and the distal reaches.

According to species-energy theory higher 'available energy' associated with climatic factors and resource availability allow more diverse communities of primary producers and consumers (such as zooplankton) to form in various ecosystems (Wright, 1983). Higher mean nutrient levels have been experimentally shown to determine higher diversity in plants, rather than their resource heterogeneity in the environment (Stevens and Carson, 2002). Here it is proposed that higher cation, conductivity and temperature levels facilitate the development of more diverse algal communities in the Okavango Delta, likely in conjunction with habitat heterogeneity.

The key differences between the most abundant algal phyla in this study are as follows. Whereas diatoms are more abundant and diverse in PF sites in UPH and LPH, green algae are present in higher numbers and with more species in SF sites in

BOR (Figures 4.15 and 4.19, 4.20). Hence, a higher number of diatom species was found in Campaign 1 due to the sampling sites being distributed in the whole Delta (including UPH, LPH and XAK where these algae were more abundant), as compared to Campaign 2 focussed in the BOR and SAN regions where many more species of Chlorophyta were identified (Tables 4.4 and 4.5). This broadly reflects the general ecological preferences of planktonic diatoms for better mixed aquatic environments (e.g. Tozzi *et al.*, 2004) such as the deeper river channels and lagoons in the Panhandle sampled only in 2006-2007 (Campaign 1). Green algae are significantly more abundant in Campaign 2 samples collected in floodplain environments in BOR and SAN (see Table 4.2). Desmids are a prominent algal group in the Delta and are known to preferentially live in sites with substrata for loose or close attachment to macrophytes and sediments and with higher spatial and temporal heterogeneity (Coesel, 1983; Borics *et al.*, 2003). This heterogeneity is due to the three dimensional assemblages which develop frequently in the phytobenthos, e.g. biofilms. In this study their relative abundance is higher in floodplains than river channels and lagoons; in the former habitats spatial heterogenity is assumed to be higher, but was not measured in the Delta.

In this study only very few endemic species were observed, for example *Eunotia okawangoi* and *Cosmarium pseudosulcatum var. okavangicum* (Williamson and Marazzi, 2013; see Appendix H). Algal assemblages appear to form regional species pools (see also section 4.7), but the full characterisation of these and the detailed analysis of the degree of cosmopolitanism and endemism of the algae living in the Delta are beyond the scope of this study. This study's large dataset and these lines of evidence followed may allow further work and relevant comparisons with phycological and biogeographical literature to be made (see section 7.3).

Rare species have been found to be a significant proportion of algal assemblages in this (>75%) and other studies. Rojo *et al.* (1994) found that over 50% of the taxa were observed sporadically (not defined by the authors) in the 67 studies on freshwater ecosystems globally. Padisák (1992) found that the great majority of 417 algal species in Lake Balaton (Hungary) were extremely rare, with just a few dominant ones.

Species richness comparisons with other studies

Almost two decades ago, Cronberg *et al.* (1996a) found 50 common species in the Boro region, with river channels hosting a much lower number of taxa (25 genera and species) than swamps and floodplains (52 taxa), and isolated pools (37 taxa); this study also found a higher numbers of species in floodplains (Figure 5.7). In comprehensive studies in other subtropical wetlands algal species richness was of the same order of magnitude, e.g. 337 algal species in the Pantanal (Brazil; De-Lamonica-Freire and Heckman, 1996) and 690 species in the Kakadu region (Northern Australia; Finlayson *et al.*, 2006), including 160 diatom species (Thomas, 1983) and over 530 species of other algae (Ling and Tyler, 1986). Nabout and co-workers observed respectively 292 algal species (106 of green algae; Nabout *et al.*, 2006) and 577 species in floodplain lakes along the Araguaia river in Brazil with green algae being the most diverse group (Nabout *et al.*, 2006; 2007). 80 species of planktonic and benthic species were observed in the Indian Sundarban (32 cyanobacteria, 27 green algae and 7 diatoms) (Sen *et al.*, 1999 in Ghopal and Chauan, 2006); 48 species of diatoms were found in the Hooghly-Matla estuary alone by Banerjee and Santra (1999; in Gopal and Chauan, 2006) while Naskar *et al.* (2004; in Gopal and Chauan, 2006) identified 150 species of algae. In the floodplain lake Tonle Sap (Cambodia) a total of 123 species of algae were identified, including 37 species of Bacillariophyta, 34 of Chlorophyta, 34 of Cyanophyta and 14 of Euglenophyta (Tran Truong Luu and Bun Ny, 1993 in Campbell *et al.*, 2006). In the Paraguay river Zalocar de Domitrovic (2002) found 332 algal taxa: 298 in the upper section (Pantanal) and 143 in the middle and lower sections. In the Florida Everglades a total of about 1,700 periphytic algal taxa have been identified, the majority being Cyanophyta, Bacillariophyta and Chlorophyta (Hagerthey, unpublished data, 2010 in Hagerthey *et al.*, 2013).

Looking at lower taxonomic level (higher taxonomic resolution), in this study 18 out 113 species of diatoms belong to the *Eunotia* genus (16%), which is in line with a comprehensive analysis of tropical species: species richness of the *Eunotia* genus represented 26% (27 out of 103) of the number of diatom species in creeks and lakes in the Colombian Amazon (Sala *et al.*, 2002) and 20% in a study on various South American tropical aquatic environments (Metzeltin and Lange-Bertalot, 1998

in Sala *et al.*, 2002). Other diverse diatom genera in this study are *Gomphonema* (13 spp.), *Pinnularia* (12), *Nitzschia* (10) and *Navicula* (8 spp.) (see Appendix B).

Among green algae, desmids are the group with the highest number of species; the following genera are particularly species-rich: *Cosmarium* (46 spp.), *Staurastrum* (32), *Closterium* (25), *Euastrum* (15), *Staurodesmus* (14), *Micrasterias* (10 spp.); another green algal genus is also diverse, *Scenedesmus* (19 spp.). The total number of species in these seven genera combined (161) contribute to 56.9% of the species richness of green algae observed in the Okavango Delta in this study. Species-rich genera of other phyla are the Euglenophyta *Euglena* (15 spp.) and *Phacus* (14 spp.). These genera of Chlorophyta, Bacillariophyta and Euglenophyta genera considered here (overall 14 genera or 8% of the total genera found) represent 47% (a total of 233) of the 496 total species identified. The majority of the rest of the species (192 out of 263) are other Chlorophyta and Bacillariophyta; thus algal species richness is predominantly (79.7 %) comprised of green algae and diatoms (Table 4.2).

In a study on the Pantanal of Mato Grosso wetlands De-Lamonica-Freire and Heckam (1996) found similar species richness of the desmid genera *Cosmarium* (39 spp.), *Staurastrum* (24), *Closterium* (26), *Euastrum* (13), *Micrasterias* (16) and *Staurodesmus* (10 spp.); 10 species of *Scenedesmus* were also found. Among Euglenophyta 15 species of *Euglena* and 14 species of *Phacus* were recorded by De-Lamonica-Freire and Heckam (1996), but diatom genera were found in lower diversity than in the Okavango Delta, i.e. *Eunotia* had 4 species and *Gomphonema, Navicula* and *Pinnularia* were all present with just 3 species. For most of these genera an average of about a third of the species found in the Pantanal (De-Lamonica-Freire and Heckman, 1996) were also observed in this study, e.g. 10/39 species of *Cosmarium*, 9 out of 26 *Closterium* and 4/12 of *Phacus* species. This comparison can be used as a basis for further biogeographical research on the biodiversity patterns of algae in tropical wetlands (see section 7.3).

According to Rojo *et al.* (1994) respectively diatoms and desmids tend to dominate in temperate and tropical systems in terms of number of species; diatoms' longer photoinhibition effects or lower tolerance to higher water temperatures might cause these differences. In tropical rivers, the number of desmid species is higher than that of diatoms or other green algae (Rojo *et al.*, 1994), e.g. in the Amazon and Uruguay river basins (Uherkovich, 1976; O'Farrell and Izaguirre, 1994 in Rojo *et al.*, 1994).

This was also the case in this study, as 185 species of desmids were identified as compared to 113 species of diatoms and 99 of other green algae (see section 4.3). However, in studies in the Paraná River floodplain desmids were found in low abundance and diversity (Zalocar de Domitrovic, 2003).

The flood pulse contributes to the creation of resource gradients shaping biological communities and their diversity in the Delta. Here, large dry areas are submerged as the annual flood arrives, which makes nutrients and ions on dry surfaces newly available to the biota (Krah *et al.*, 2006). Once the Delta is inundated, its water chemistry is influenced directly by dust deposition (atmospheric inputs are 6-60% of the total annual deposition; Garstang *et al.*, 1998) and flood pulse, with no disturbing effects caused by rainfall as the flooding coincides with the dry season (Krah *et al.*, 2006). The annual floods were shown to support the development of highly diverse aquatic assemblages of diatoms (Mackay *et al.*, 2012), invertebrates (Siziba *et al.*, 2011b; Davidson *et al.*, 2012) and fish (Siziba *et al.*, 2011a), e.g., by mobilising nutrients from sediments in the seasonally inundated floodplains (Lindholm *et al.*, 2007) then uptaken up by the biota (Mubyana *et al.*, 2003).

These environmental conditions also create the best opportunities for diverse algal assemblages to grow and persist in the Delta. The results on ShD and ShE indices indicate that BOR and SAN are the regions with the highest local diversity of algae in the Delta (Figures 5.8 and 5.9); SF sites with long-term intermediate frequency flooding (Figures 5.20 and 5.21) and F are the most diverse sites (Figures 5.26, 5.27), consistent with the results on taxon richness (see section 5.2.1). Moreover, ShD for species (Figure 5.22a) and species richness (Figure 5.10) have very similar seasonal patterns, i.e. higher diversity in February 2010 and October 2009 than Apr/May 2007/2009 and September 2006, whereas ShD for genera shows similar, but less pronounced changes (Figure 5.22b). Therefore species richness generally reflects the broad temporal variations of algal diversity, as measured with ShD and ShE indices.

Overall, these results support established knowledge that in benthic environments (such as the Delta's floodplains) higher nutrient levels and greater micro-habitat availability (e.g. substrates such as plant leaves and stems and sand grains) facilitate the coexistence of more algal species than in open water habitats (Hutchinson, 1961; Stevenson *et al.*, 1996). Heterogeneous habitats and higher nutrient

concentrations are known to support higher diversity of algae, as per the Habitat Heterogeneity Hypothesis (HHH; MacArthur and MacArthur, 1961; Hutchinson, 1961; Passy and Legendre, 2006a) and higher plants (Ricklefs, 1977) and Species-Energy Theory (SET; Wright, 1983; Stevens and Carson, 2002) (see section 1.6). Furthermore, plant diversity is substantially higher in the distal reaches of BOR and SAN, i.e. 519 *vs* 205 species in permanent swamps (Ramberg *et al.*, 2006) which most likely increases the spectrum of substrata available in terms of types of stems and leaves that algae may attach to.

The detailed interpretation of the results on algal taxon richness, diversity and biomass is made by using the theories and hypotheses outlined in section 1.6.1, i.e. Intermediate Disturbance Hypothesis (IDH), Resource Competition Theory (RCT), SET and HHH. Other ecological mechanisms such as niche overlap / competition and niche differentiation / complementarity (Passy and Legendre, 2006a) are used here and in Chapter 6 to explain the differences in species richness observed across habitats, considering the varying ecology of phytoplankton and phytobenthos.

Intermediate Disturbance Hypothesis (IDH)

In the Delta, shallower seasonally flooded areas show statistically significantly higher diversity both in terms of species richness and ShD / ShE indices (see sections 5.2.1 and 5.2.2) than permanently and occasionally inundated sites, consistently with the availability of more nutrients (see section 5.8.1), and the IDH. Here disturbance is broadly interpreted as long-term alternation of periodical flooding; permanently and, to a lower extent, occasionally inundated sites have lower algal diversity than seasonally flooded areas (see Figures 5.3 and 5.4). Nutrient levels and flooding disturbance are interrelated as the water level fluctuations influence the concentrations of solutes as well as phytoplankton biomass, as observed, e.g., in an Amazonian floodplain lake (Huszar and Reynolds, 1997), in the Paraná river floodplain (Zalocar de Domitrovic, 2003) and in Coqueiro Lake (Brazil; Loverde-Oliveira *et al.*, 2009) (see subsection “Species-Energy theory”).

Here flooding disturbance and ecohydrological dynamics are discussed and comparisons are drawn with other works on freshwater ecosystems in the subtropics as well as temperate areas when relevant to the research questions, in particular on

what are the main drivers of algal diversity in the Delta. The IDH (Connell, 1978) and its applications to phytoplankton (Reynolds *et al.*, 1993) can be invoked to explain and interpret the observed patterns in algal diversity in the Delta, complementarily to the theories on resource competion, habitat heterogeneity and species-energy theories (see section 1.6).

Reynolds (1993) defined 'infrequent disturbance' as flooding occurring 2-8 times per year, intermediate disturbance 8-50 times per year and frequent disturbance as 50-365 flood events per year. In the Okavango Delta, the predictable flood pulse can be likened to an infrequent regional disturbance which creates the heterogenous landscape in the Seasonally (SF) and Occasionally Flooded (OF) floodplains. In this wetland there is a major annual flood event and, usually earlier, a smaller flooding caused by local rainfall; flooding infrequently yields a major expansion of inundated area coincident with this rainfall events, i.e. when this exceeds 700 mm yr^{-1} (only 3 times between 1976 and 2005), or flooding of small, isolated depressions (Wolski and Murray-Hudson, 2006). During average and low rainfall years, precipitation only makes local water level rise within the already flooded area; the total inundated area continues to decline during the rainy season, which corresponds to the flood recession phase between November and February (Wolski and Murray-Hudson, 2006). Even though the annual predictable flood does not represent a strong physical disturbance for algae with very short generation times, at landscape and perhaps evolutionary time scales, seasonally flooded floodplains can arguably be seen as more disturbed habitats than permanently flooded river channels and swamps. Hence, the recurrent annual flooding may have allowed for the development of more diverse regional species pools of algae than in the more homogeneous lagoons, channels and permanent swamps in the Panhandle, i.e. isotropic open water environments (see section 4.4). Recent studies on benthic algae in streams in the mid-Atlantic USA (Cardinale *et al.*, 2006) and long established knowledge (Stevenson *et al.*, 1996 and references therein) also highlight how in benthic environments the coexistence of numerous algal species is favoured by periodic disturbance of moderate intensity.

Hydrology was shown to influence the distribution of both diatoms and other algae in periphyton mats in the Everglades (Florida, USA); short hydroperiod (sites inundated for < 300 days) sites had higher taxon richness of diatoms and long

hydroperiod sites (inundated for > 300 days) hosted more species of soft algae, i.e. algae either without cell wall or with cellulosic cell wall (as opposed to siliceous cell wall in diatoms; Gottlieb *et al.*, 2006). The data collected here show the opposite trend, i.e. a higher number of species of soft algae, in particular Chlorophyta, in less frequently flooded areas while Bacillariophyta prevail and are more diverse in more frequently inundated sites (Table 4.2; Figure 5.14). However, water discharge is also an important factor in determining phytoplankton diversity in lotic environments, e.g. in the Vaal River, South Africa (Pieterse and van Zyl, 1988) and in the River Danube in Hungary (Ács and Kiss, 1993) where higher diversity was found at low water. García de Emiliani (1997) found water level to be the prime driver of phytoplankton species diversity and evenness, as well as biomass, in the Paraná river-floodplain lake system, with El Tigre Lake showing higher algal diversity than the deeper Correntoso River. This is in line with this study's results on higher species richness in the shallow waters of BOR and SAN (Figure 5.4).

Periodic disturbance was shown to increase diversity and species richness (e.g., Reynolds *et al.*, 1993); this is particularly true in oligotrophic phytoplankton assemblages with low algal cell / colony abundance and hence weak interactions between them (Siegel, 1998). As hypothesised by Siegel's modelling study (1998) for aquatic systems with low nutrient levels, episodic nutrient inputs (e.g. due to flood pulses), diel cycles, and specialization of the grazer assemblage may be the prevailing determinants of phytoplankton species composition in the Okavango Delta as well. Huszar and Reynolds (1997) observed how periodic disturbances resist the maturation of planktonic successions in Lago Batata (Brazil); hence competitive interactions are weak and diversity is high, as other phytoplankton studies also concluded (e.g. Reynolds, 1993; Padisák, 1994; Hambright and Zohary, 2000). The results presented support this interpretation, as the predictable slow-flowing flood pulse in the Delta's floodplains at least partially contributes to higher algal taxon richness and diversity (sections 4.6.1 and 5.3.1). For example, in the less frequently inundated floodplains flooding increases habitat heterogeneity and mobilises nutrients much more than in nutrient-poor and homogenous river habitats in the Panhandle (see subsection 'Habitat heterogeneity'). The results of this study support the IDH (Connell, 1978), analogously to other works on phytoplankton and

zooplankton in subtropical freshwater bodies, such as the Barra Bonita reservoir in Brazil (Matsumura-Tundisi and Tundisi, 2005) and the Paraná river floodplain (García de Emiliani, 1997; Zalocar de Domitrovic, 2003).

Another interpretation of hydrological disturbance is associated with water velocity. In the Delta, water velocity was hypothesised to contribute to determine algal diversity of Bacillariophyta in terms of species richness (Mackay *et al.*, 2012) similarly to observations made by Passy (2007) on the diversity of diatoms in terms of functional guilds in two extensively studied streams in Bulgaria and USA. However, Mackay *et al.* (2012) found that the diversity of periphytic diatoms was higher in UPH than LPH and BOR, possibly due to sufficient physical disturbance due to faster water flow (as per IDH) and more limiting resources (as per RCT; Tilman, 1982). In the latter studies, faster flowing waters (e.g. in UPH) were shown to host more diverse diatom assemblages, i.e. diatoms tend to occupy available niches quickly (Mackay *et al.*, 2012). However, Mackay *et al.* (2012) sampled periphytic diatoms from stems and leaves of aquatic plants whereas in this study algae were sampled in water; this suggests that water velocity may enhance the diversity of diatoms attached to or close to the vegetation (periphytic) as well as that of diatoms living in water, but not the taxon richness (Figure 5.4) or diversity of all algae (Figure 5.18) in the Panhandle. In general riverine (lotic) conditions were also shown to favour diatoms in this study both in terms of species richness (see Figure 5.9) and biomass (Figure 5.44).

Physical short-term distubance caused by high flow velocity must be distinguished from long-term landscape scale flooding disturbance causing periodic water-level fluctuations and drying / re-wetting of sediments. In the Delta, during the low-flood season occasionally flooded sites such as Buffalo Fence and Daunara (Figure 3.3) have historically been either completely dry or inundated by small water volumes; their flooding frequency is once every 18-30 years (Siziba *et al.*, 2011a). However these floodplains they were inundated both during the 2009 and 2010 flooding seasons. Here algae form more diverse assemblages than where the aquatic habitat is more homogeneous, i.e. permanently wet, as in the upstream channels and lagoons in UPH and LPH; species richness and Shannon diversity in OF sites in SAN is slightly lower than in SF areas of BOR (Figure 5.Z and 5.3). Thus changes from dry to wet conditions, albeit infrequent, might constitute a sufficient

disturbance for the development of more diverse algal assemblages than in the Panhandle PF sites (Figures 4.13, 5.3 and 5.4). Despite similar water level fluctuations (Figure 4.20) and nutrient concentrations in XAK to those in BOR and SAN (e.g. SiO_2 and cations; Figures 4.41, 4.43), the former shows lower species and (to a lesser extent) genera richness and diversity (Figures 5.1 and 5.8) and total biomass (Figure 5.40). This may be due to 8 XAK sites being permanently flooded, 3 occasionally and 2 seasonally inundated so that in this regions algal biodiversity is higher than in UPH and LPH (see sections 5.2.1 and 5.2.2).

One last interpretation of disturbance is that it is associated with the amplitude of the floods. The floods in 2009-2011 were the largest seen in the Delta in the last 20 years, with exceptional total annual discharge of respectively 10,860 and 12,730 $Mm^3\ yr^{-1}$ in 2009 and 2010, corresponding to 78^{th} and 92^{nd} percentile of the observed range of discharges between 1934–2011 (Wolski *et al.*, 2014). Hence, in addition to constituting the first comprehensive research on all the algae of this wetland, this study made it possible to gather comprehensive data on the floodplains during an extreme hydrological phase. Abnormal floods and droughts constitute a disturbance for aquatic biota (Sparks and Spink, 1998), hence in the Delta disturbance can also be seen as the deviation from a mean annual predictable flood. In this study, whereas algal taxon (species and genera) richness do not show significantly differences across flood years, ShD and ShE were slightly higher in 2009-2010 (large flood) than 2006-2007 (smaller flood) (Figures 5.6 and 5.8). This is most likely a reflection of the much higher number of samples taken from floodplains in Campaign 2, which was limited to 2009-2010 (see sections 3.1); no significant differences were found in taxon richness or diversity when OW, MV and F data are analysed separately (see section 5.3.1). Therefore, this study does not provide evidence that large floods have an impact on the diversity of algae in the Okavango Delta; water discharge at sampling locations were not available, but would be useful additional data support a better understanding of algal population and diversity changes.

Other organisms at higher trophic levels than primary producers show contrasting trends in different studies. Amongst zooplankton, Lindholm *et al.* (2009) observed the highest species richness of cladocera in the Delta's seasonal floodplains and attributed it to the annual flood pulse causing intermediate disturbance levels in

these environments so that r- and K-strategist species coexist. However, Davidson *et al.* (2012) found that regions with short hydroperiod, i.e. less frequently flooded and/or inundated for shorter periods, showed lower invertebrate taxon richness than permanently flooded sites, partially confirming previous findings on these consumers (Dallas and Mosepele, 2007).

Food web interactions are also important in determining aquatic biota population dynamics; for example, high grazing by zooplankton and macroinvertebrates was shown to play a major role in determining periphytic abundance and biomass in shallow lakes (Jones and Sayer, 2003). Abundance and biomass are connected to taxon richness and diversity. Hence, the contrasting findings outlined above about the Okavango Delta may be due to complex top-down and bottom-up controls on the diversity of both primary producers and consumers. Other research that demonstrated how consumers can influence the biodiversity-productivity linkages inferred from the primary producer level alone; for example, species-rich consumer assemblages can reduce resource abundance through complementary feeding preferences and facilitation (Worm and Duffy, 2003). Seasonal variations in diversity show that the ShD of both algae (Figure 5.22) and periphytic diatoms decreased in the Delta in the high water phase (Davidson *et al.*, 2012 and Mackay *et al.*, 2012). The lower diversity levels in the cold season (July/August) characterised by high water can be interpreted as a response to lower 'energy' available (Wright, 1983) due to lower temperatures (Figure 4.17) and TP concentrations (Figure 4.38) and/or higher grazing pressure which can be plausibly inferred from the higher abundance of invertebrates after flood peak in that period (Davidson *et al.*, 2012), but this phenomenon was not directly measured. Hence more work is needed to strengthen findings within the primary producer and consumer food web levels and across them.

Resource Competition Theory (RCT)

In the Delta's Panhandle region, Mackay *et al.* (2012) observed higher diversity of periphytic algae which seems to be consistent with classical RCT. This predicts that diversity is directly proportional to the number of resources at limiting levels within a system and that the highest diversity of competing species will occur at an intermediate ratio of the availabilities of two resources (Tilman, 1982; Miller *et al.*,

2005). Higher numbers of species are usually observed in the plankton than expected using the RCT model (Tilman, 1982) due to competitive exclusion not taking place at low algal density (Hutchinson, 1961; Siegel, 1998). The RCT prediction that species richness and diversity in the Delta is higher where intermediate nutrient ratios, here TN/TP, are observed is not met in this study. The water chemistry analyses indicate that the lower / intermediate levels of TN:TP found in the Panhandle sites (UPH and LPH) do not produce significantly higher algal diversity compared to the distal reaches (BOR and SAN; see Table 5.3). However, the degree of variation of resources in the environment may also play a role in determining algal diversity.

In previous studies, algal diversity (e.g. of diatoms) in freshwater environments has been attributed to limiting resources such as nutrients (Passy, 2008) and light (Liess *et al.*, 2009). However, results of these studies diverge and our results on the Okavango Delta algal assemblages are in agreement with Passy (2008). Interlandi and Kilham (2001) studied phytoplankton assemblages in three lakes in the Yellowstone region (Wyoming, USA) in relation to N, P, Si and light, finding a strong positive correlation between diversity and number of limiting resources, i.e. higher diversity where more resources were limiting. By contrast, in this study diversity of algae is lower in the Panhandle region (Figure 5.4 and 5.18) where more numerous resources are likely to be at limiting concentrations given their lower levels, e.g. cations, anions, silica and DOC. A lack of nutrients (*likely implying more numerous limiting nutrients*), was shown to decrease benthic diversity, but enhance planktonic diversity in diatoms in hundreds of streams across the USA (Passy, 2008). In the Delta waters, as in the USA streams, in the benthos only high nutrient levels allow algal species to survive in the understorey hence maintaining high diversity; in fact, different levels of tolerance to stress among benthic diatoms may allow substantial overgrowth hence reducing nutrient transport to the biofilm (Passy, 2008). Thus only high resource levels in the aquatic environment can support a high algal biodiversity in the phytobenthos. Instead planktonic diatoms have higher diversity with more numerous limiting nutrients due to enhanced competition for them (Passy, 2008), in line with Resource Competition Theory in terrestrial ecosystems (Tilman, 1982). A high degree of variation in environmental conditions is associated with the available niche space; in the

benthos multiple environmental gradients are present, e.g. vertical and horizontal nutrient gradients (Passy and Legendre, 2006a). Hence RCT and the relationships between habitat heterogeneity and diversity (HHH; MacArthur and MacArthur, 1961) are interlinked (Tilman 1982; Lundholm, 2009). However, taxon specific competition dynamics for nutrients and light are beyond the scope of this study, hence a need for further research (see section 7.3).

Another important resource for autotrophic algae is light (Reynolds, 2006), which was not measured in the Delta; however previous data support possible interpretations of its role. The euphotic depth - depth in which 1% of the Photosynthetically Active Radiation (PAR; 400–700 nm) remains in the water – can be usually estimated to be 2-3 times the Secchi Disc depth (Lake Access, 2014). The Delta's waters are very trasparent, Secchi Disc depths of 1.7 - 3.4 m were recorded in previous studies (Alonso and Nordin, 2003; Mackay *et al.*, 2011); thus the euphotic depth is likely to extend to the water bottom even in the deepest sites, i.e. > 4m. In fact, most of the sampling sites in the Delta have water depths below 2 m (84 out of 102 sites where the exact depth was measured), and the depth of about 20 shallow floodplain sites with no recorded value was most probably similar to the average water depth of sampling points in Campaign 2, i.e. about 0.6 m (see section 4.7.3). Therefore light availability is unlikely to be a limiting factor for algae and their diversity in the Delta's waters, also due to its subtropical climate and hence high insolation throughout the year (Huszar and Reynolds, 1997). The higher turbidity in floodplains is likely outweighed by their low depth so that the light climate supports high algal taxon richness (Figure 5.7) and biomass (Figure 5.40), as observed in other shallow floodplain systems in the tropics (Talling, 1992).

Species-Energy Theory (SET)

Nutrients, light and habitat conditions are propitious for algae in the distal reaches of BOR and SAN. The seasonal flooding mobilises nutrients such as phosphorus and nitrogen from the sandy sediments of the Delta hence boosting phytoplankton production in the floodplains, as observed by Hart *et al.* (2003). Light conditions are favourable in these environments, as shading by trees is very limited, waters are shallow and nutrients are concentrated there by evaporation (see section 4.7.3). Therefore a higher number of species are able to thrive in these environments with

enough light and resources available; higher mean nutrient levels mean that numerous algal taxa with varying environmental requirements can occupy multiple ecological niches (Stevens and Carson, 2002). This is consistent with the species-energy theory, which was developed predict species richness of angiosperms and of land and freshwater bird on islands (Wright, 1983; see section 1.6.3). In contrast with long-held views, an experimental study on terrestrial plants demonstrated that resource heterogeneity (deemed of utmost importance in RCT) had almost no effect on diversity, while average supply rate of light maintained plant diversity (Stevens and Carson, 2002). This seems a plausible explanation for algae systematically showing higher taxon richness and diversity in the Delta's mesotrophic floodplains, mainly in BOR and SAN, than in oligotrophic river channels in the Panhandle (UPH and LPH) (see sections 5.2.1 and 5.2.2).

In the wetland under study, other organisms show similar patterns meeting the species-energy theory predictions in the Delta. Invertebrates were found in high diversity (and abundance) levels in the three-dimensionally structured sedgeland and grassland habitats of the Delta (Siziba *et al.*, 2012) and in inundated floodplains, floating vegetation and marginal vegetation in backwaters (Dallas and Mosepele, 2007). This is also consistent with species-energy theory, which used zooplankton as test basis alongside higher plants and birds (Wright, 1983), as nutrient supply is significantly higher in these than in permanently flooded environments (see section 4.7.3). Furthermore, temperature is higher in these shallow environments (Figure 4.18) which enhances energy levels as compared to deeper colder open water sites.

In a study on the Paraná river floodplain, total species richness of planktonic algae was higher in the high water warm season, i.e. February onwards (Train and Rodrigues, 1998); in this study the number of species was also higher in the warm season, i.e. February, which coincides with low water levels in the Delta (Figure 5.6). Temperature is one of the climatic variables measuring the amount of 'available energy' (higher in the Southern Hemisphere summer, i.e. December to March). Higher species richness in this season in the Delta is likely to be, at least partially, due to this factor; in fact, more algal species with broader temperature ranges may coexist then than at temperatures <10 $^{\circ}$C and >20 $^{\circ}$C which select against, respectively some green algae and diatoms (Butterwick *et al.*, 2005).

Other climatic factors (related to 'available energy') have been shown to influence algal diversity in subtropical wetlands. Nabout *et al.* (2006) observed a reduction in biodiversity in the high flood rainy season due to mechanical shock and reduction of water transparency, which in turn limited Photosynthetic Active Reaction (PAR). Such a phenomenon is however not observed in the Delta, where winter local rainfalls usually do not have an impact on flood area extent (Wolski and Murray-Hudson, 2006). In the Okavango the high flood season does not coincide with the rainy season, occurring during the recession/low flood phase; hence comparisons must take into account the different flooding mechanisms in different ecosystems.

Habitat Heterogeneity Hypothesis (HHH)

This chapter helps address research questions 2 and 3, respectively on the patterns and reasons of biodiversity and biomass variations in the Delta and on the species richness – algal biovolume relationship, especially in the floodplains. The presence of diverse habitats, i.e. environmental heterogeneity, has been shown to be an important factor for species richness and diversity in phytoplanktonic assemblages (Hutchinson, 1961), as per the diversity-heterogeneity hypothesis later developed by Ricklefs studying plants (1977) and here applied to the algae of the Okavango Delta. The Habitat Heterogeneity Hypothesis (HHH) predicts positive habitat-diversity relationships for coarse-grained heterogeneity (Tilman 1982; Tilman and Pacala 1993), i.e. when the size of the habitat patch is larger than individuals. This is certainly the case for this study's data, as habitat categories represent an area of several square meters as compared to the microscopic dimensions of algae.

On one side, environmental heterogeneity provides the basis for resource partitioning and coexistence of competing species (Ricklefs, 1977); on the other hand, nutrient provision from the sediment as well as from the water likely supports the creation of thick multi-storey biofilms (see Figure 1.8; Passy, 2009). Here it is assumed that more microhabitats are available to algae given the presence of abundant and diverse aquatic plants in the Delta's floodplains (350 species; Junk *et al.*, 2006), where water velocity is slower than in the Panhandle; hence conditions are more suitable for three-dimensional phytobenthic communities to develop and persist. Like in other subtropical wetlands, such as the Pantanal, in the Okavango shallow flooding with clear water, little shading by trees and low conductivity allow

the growth of very diverse aquatic vegetation (Junk *et al.*, 2006). This most likely favours the abundance and diversity of attached algae, especially epiphytic ones, observed in the floodplains in BOR and SAN (Figures 4.12, 4.15, 5.9 and 5.10).

The literature on diversity–heterogeneity relationships proposes a positive relationship between habitat heterogeneity and species diversity (Ricklefs, 1977; Tilman and Pacala, 1993). In this study, the higher algal diversity found in shallow floodplains with abundant substrata for benthic species to attach to, e.g. macrophyte stems and leaves and sand grains, fulfils the prediction of this model. The flood pulse creates the conditions for these environments to be heterogeneous across space and time; periodical flooding disturbance and habitat diversity are strongly interlinked in the Delta. In an article on phytoplankton succession in the Paraná river floodplain, García de Emiliani (1993) suggested that seasonal changes of phytoplankton in floodplain lakes are best interpreted as true successional development and intermediate disturbance. However, more research at finer spatial scales is needed to better identify the ecological mechnisms at play as here habitat types, e.g. open water and floodplain, are intended as macrohabitats. The majority of taxa found in the Delta are benthic / periphytic, e.g. desmids and motile diatoms such as *Navicula* and *Nitzschia*, while Chlorococcales and centric diatoms are much less common, as also observed in a wetland system in the Lower Paraná River (Izaguirre *et al.*, 2004). Future work could focus on specifically sampling algae on different substrates in order to obtain a detailed characterisation of planktonic, epiphytic, epipsammic and/or periphytic character (see section 7.3).

β-diversity and species composition similarity

Floodplains have high α, β, and γ diversity due to habitat complexity and hydrological connectivity gradients, e.g., disconnection / isolation of channels and floodplains *vs* transport / flood phase between river and floodplain (Amoros and Bornette, 2002). In this study β diversity was also shown to be significantly higher in the seasonally flooded floodplains in BOR and SAN, where α diversity was higher (see section 5.3.1). The analysis of species composition similarity within regions, flood class and habitats shows that the areas of the Delta with higher average similarity from sample to sample are BOR, SF sites and F habitats, e.g. samples in BOR are more similar to one other than samples in other regions.

This supports the interpretation proposed by Passy and Legendre (2006b), i.e. that algal species richness increases due to more species belonging to the same higher taxon, e.g. genus, living in these environments as opposed to species of different higher taxonomic groups in open waters (Passy and Legendre, 2006b). In the Delta algal species richness is particularly high in floodplain sites where samples have more species in common with one another, with many belonging to the same genera, for example species-rich desmids such as *Cosmarium* and *Staurastrum* (see Appendix B and the species accumulation curve in Figure 4.3). Hence these congeneric algae have similar requirements and different ecological niches (niche facilitation or complementarity) which do not overlap like in nutrient poor sites as hypothesised by Passy and Legendre (2006a) for streams in the USA. For example these desmid taxa may have (slightly) different tolerances to higher TP or pH values in the Delta's distal floodplain sites (see section 6.3.6), rather than competing for low nutrient levels like in the Panhandle region river channel / lagoon sites.

Average Bray-Curtis similarity is on average higher when samples are classified according to their habitat rather than flood class and region (Tables 5.8 to 5.10). Hence species composition is more homogeneous, i.e. it varies less between samples taken from the same habitat regardless of the sampling region than between samples in the same region taken from different habitats; thus habitat-specific assemblages are more similar to one another than regional species pools are across the Delta. This relates to environmental variables and factors, as floodplain habitats have significantly higher conductivity, ion concentrations and temperatures and lower water depths than other habitats (see sections 4.7.3). Variations in species composition across regions, flood classes and habitats indicate that in UPH samples the composition of species tends to be more similar to that of other regions than species composition of samples in the other regions (Table 5.17). UPH / LPH and BOR / SAN are regions close to one another hence they unsurprisingly show rather high similarity values, whereas XAK has a species similarity index closer to UPH and LPH than to BOR and SAN (Table 5.17). This is not too surprising as a number of XAK sites are similar environments to the Panhandle's sites, e.g. lagoons and PF areas. These results suggest that spatial proximity increases similarity of algal assemblages as per spatial autocorrelation (Legendre, 1993), i.e. "*everything is*

related to everything else but near things are more related than distant things" (Tobler, 1970) (see also section 6.3.5).

Other studies on wetland environments have shed some light on the most important factors enhancing β-diversity; qualitative comparisons are attempted using the available literature. For example, in floodplain lakes, high spatial environmental heterogeneity such as differences in morphology, geology, limnology, and degree of human impact cause high β-diversity (Nabout *et al.*, 2007). In this study, seasonally and occasionally inundated floodplains, and hence the regions where these are predominant in the landscape (BOR and SAN), show higher β-diversity (Figure 5.30 a-c). High water seasons were observed to have decreased β-diversity in the Rio Paraná floodplains due to the homogeneization of the aquatic environment (Thomaz *et al.*, 1997 in Nabout *et al.*, 2007). However, in the Araguaia River tropical floodplain lakes local rainfalls were shown to enhance β-diversity in the high water phase (measured as species turnover), as these increased spatial heterogeneity (Nabout *et al.*, 2007). In this study, β-diversity is significantly higher in the low water phase and, to a lesser extent, in the recession phase than during high water phases (Jul/Aug) (Figure 5.30d), when the river channel and floodplains are more connected and hence have lower β-diversity, in agreement with Thomaz *et al.* (1997; in Nabout *et al.*, 2007). Local rainfalls were not monitored so that their role in increasing spatial heterogeneity cannot be evaluated.

5.3.2. Interpretation of algal biovolume patterns

This chapter provided answers to questions over biomass variations in the Okavango Delta in relation to limnology, region, habitat, flooding patterns and biodiversity among other factors (see section 2.3). Algal biomass estimates (biovolume) across the regions sampled range between 0.176 and 90.41 mg L^{-1} (median 4.64 mg L^{-1}; see Table 5.11), on average higher than biovolume estimated by Cronberg *et al.* (1996a) in the Boro region, i.e. < 1 mg L^{-1}. Cronberg *et al.* (1996a) collected samples mainly in channels; in fast running waters phytoplankton was practically absent, whereas high biovolume of filamentous green algae (32 mg L^{-1}), *Spirogyra* spp. (45 mg L^{-1}) and *Mougeotia* spp. (6.5 mg L^{-1}) were recorded in swamp sites (Cronberg *et al.*, 1996a). In this study, sites in the PF region of UPH have a statistically significantly higher algal biomass than XAK, i.e., sites with

permanent water but low flood amplitude or rarely flooded sites, while SF sites in BOR and SAN show respectively marginally lower than and similar biovolume to UPH and LPH (Figure 5.40). The fact that seasonal water level fluctuations are smaller in XAK than in some other regions may create a smaller disturbance with a negative effect on algal biomass; on the other hand taxon richness and diversity in XAK tend not to be significantly lower than elsewhere (see Figures 5.1, 5.2 and section 5.3.1). As species richness and nutrient levels are rather high in this region, the lower algal biomass in XAK may be due to grazing linked to rather high invertebrate abundances (Davidson *et al.*, 2012).

Algal biovolume in other freshwater ecosystems

Lake and river phytoplankton total algal biomass tend to differ, with a broader range in lakes (0.02 - 100 mg L^{-1}; Smith, 1990 in Rojo *et al.*, 1994) than in rivers (0.06 - 25 mg L^{-1}) (Rojo *et al.*, 1994). The algal biomass estimated in this study reaches higher maximum levels, i.e. 90.41 mg L^{-1} than in rivers, closer to values observed in lakes (Smith, 1990 in Rojo *et al.*, 1994); this is not surprising as the Okavango Delta is a complex wetland with lagoons and pools, e.g. Xakanaxa lagoon, which resembles a shallow lake which were sampled in this study. For example in the floodplain site 'Pool C' in BOR (see Figure 3.3), total algal biovolume is higher than 10 mg L^{-1} in 5 out of 11 samples whereas in the river channels in UPH and LPH algal biomass estimates are lower, i.e. 5 out of 15 sites higher than 10 mg L^{-1} in UPH and a maximum of 15 mg L^{-1} in LPH (see Figure 5.40). Townsend *et al.* (2012) estimated substantial algal growth and hence biomass in the Daly River (Northern Australia) even in fast flowing channels (~ 4 m s^{-1}); in the Delta algal biomass reaches similar levels in the Panhandle riverine sites to the productive floodplains of BOR and SAN (Figure 5.40), though waters flow much more slowly in our study site (average and maximum velocity respectively: 0.2 m s^{-1}, 1.6 m s^{-1}; Table 4.5) than in the Daly River. Therefore, algal populations reach similar biomass in the Okavango Delta despite the considerable differences in nutrient concentrations (see section 4.7.3); this is due to the different algal cell size (see section 4.6.2).

Dilution and temperature effects on algal biovolume / biomass

In the Delta, the similar algal biomass levels observed between the very different UPH and BOR/SAN regions (Figure 5.40) may also be due to the high water transparency in the Delta (1.7 - 3.4 m; Alonso and Nordin, 2003) which supports primary production. By contrast, in equally shallow, but more turbid and nutrient-rich subtropical freshwater bodies, such as Lake Okeechobee in Florida, algal growth is limited by lower transparency (Phlips *et al.*, 1997). Even turbidity may not limit the growth of benthic algae (but see Domingues *et al.*, 2011); for example, in African shallow lakes and wetlands, surficial sediments often disturbed and resuspended by wind-induced currents were sufficiently well-illuminated to support benthic growth of algae, which in turn has an effect on turbidity (Talling, 1992). In the Delta, the most turbid environments are the occasionally inundated floodplains in BOR and SAN (Figure 4.48), likely both due to higher dissolved nutrients and algal biomass (Figure 5.40), which itself increases turbidity.

Algal biovolume estimates showed that the Delta supports higher algal biomass levels than observed in other tropical rivers and lakes (Rojo *et al.*, 1994; Zalocar de Domitrovic, 2002; 2003). Values beyond 4 mg L^{-1}, infrequent in the review by Rojo *et al.* (1994), and higher than the average values estimated by Zalocar de Domitrovic (2002; 2003) were reached in 77 out of 130 samples (59%) (see also section 5.2.5). In BOR Cronberg *et al.* (1996a) estimated biovolume lower than 1 mg L^{-1} in channels and lagoons and significantly higher (up to 45 mg L^{-1}) in swamp / floodplain areas. In this study, total algal biovolume is also higher in F than OW and MV, though these differences (on log-transformed data) are significant only in Campaign 2 (Figure 5.38). Despite total biovolume is not statistically significantly different across habitats at p=0.01, the mean absolute biovolume in all the samples is higher, i.e. 10.1 mg L^{-1}, in F habitats as compared to, respectively 5.6 mg L^{-1} and 6.0 mg L^{-1} in OW and MV (see section 5.2.5). Therefore habitat heterogeneity and micronutrient concentrations may have a direct or indirect (via taxon richness / diversity) relationship with algal biomass.

In this work, seasonal variations of algal biomass (estimated via biovolume) are not significant at p=0.01, and the within-season coefficients of variation are rather similar across regions, habitats and seasons (see section 5.2.5). However, total algal biovolume (data pooled across regions) is slightly higher at the flood onset and

early recession, i.e. in April/May and September than in July/August 2006-2007 and in February 2010 (Figure 5.43). Only one other study provided algal biomass estimates in this wetland to the author's knowledge. Cronberg *et al.* (1996a) estimated higher biovolume in the Delta in June 1992 (0.004 - 45 mg L^{-1}) and October-November 1992 (0.011 - 27.17 mg L^{-1}) than November-December 1991 (0.001 - 1.462 mg L^{-1}) and March 1992 (0.003 - 1.06 mg L^{-1}). Hence this study's results are in agreement with Cronberg *et al.* (1996a), as the recession and low water phases (September / October 2009 and February 2010; Figure 5.43) have higher biomass than other seasons (October-December 1992 in Cronberg *et al.*, 1996a). In the expansion and recession phases of the annual flood respectively nutrient mobilisation and macrophytes and animal dung decomposition facilitate algal growth (Bayley, 1995 in Siziba *et al.*, 2013). This was also observed in shallow lake systems, e.g. in 39 eutrophic lakes in UK and Denmark (Sayer *et al.*, 2010), where algae form blooms shortly after plant senescence episodes and in tropical streams in Northern Australia where, with low tree cover, benthic algae are the major source of organic carbon for consumers (Pettit *et al.*, 2012). In the Delta decomposition may in turn be facilitated by higher temperatures, especially in October 2009 (Figure 4.17), which can support algal communities.

Floodplain lakes have been more extensively studied in South America than in Africa and thus are used as main point of comparison with the Okavango Delta for ecological research on phytoplankton (and algae in general). Their hydrosedimentological regime induces significant temporal fluctuations in phytoplankton assemblages. In the Paraguay river Zalocar de Domitrovic (2002) estimated phytoplankton biomass of 0.215 to 0.372 mg L^{-1} in the winter high water phase and 0.586 to 1.223 mg L^{-1} in the summer low water phase. Similarly, in the Paraná river floodplain, mean higher phytoplankton biomass is lower in the low water limnophase (2.03 mg L^{-1}) than in high water potamophase (0.86 mg L^{-1}) (Zalocar de Domitrovic, 2003). Average algal biomass estimated in the Delta was 0.176 mg L^{-1}, rather similar to the minima above mentioned; however, the maximum biomass is much higher, i.e. over 90 mg L^{-1} (see section 5.2.5) and 45 mg L^{-1} (Cronberg *et al.*, 1996a).

The low algal biomass observed in winter (July/August 2007-2009) may be due to lower solar radiation (and hence temperature) as observed in other shallow

freshwater ecosystems (e.g. the Paraná river floodplains; Zalocar de Domitrovic, 2002). However, dilution plays a role in reducing algal biomass levels in numerous studies in which high water and cold temperatures coincide, hence masking the separate effect of each of these factos. In a review of studies on temperate and tropical rivers (the latter were limited to a small dataset from Ivory Coast) over 60% of the biovolume estimates were below 0.2 mg L^{-1} (Rojo *et al.*, 1994). In a floodplain lake in the Pantanal Loverde-Oliveira *et al.* (2007) recorded highest algal biomass in the low water season (average: 5.5 mg L^{-1}; as compared to 12.8 mg L^{-1} in this study's February samples), but they also observed high values during high water periods (11.6 mg L^{-1}) attributed to resuspension processes liberating diatoms from the sediments. In this study, only one sample taken in the high water period had a biovolume higher than 10 mg L^{-1} (see Figure 5.43). Train and Rodrigues (2004; in Bovo-Scomparin and Train, 2008) found that the Argentinian Paraná River floodplain lakes tend to have low values of phytoplankton biovolume during periods of high water (potamophase); this was also the case in the Upper Paraná in Southern Brazil (Rodrigues *et al.*, 2009) and in a floodplain wetland in Oregon (Weilhoefer *et al.*, 2008). In these sites and in the Delta, dilution due to higher water depths in this season contribute to the lower algal biomass recorded in, e.g., flood expansion phase, as observed in other water bodies in which the concentration of pollutants, Chl *a* and algae were reduced by artificially increasing water volumes e.g. in Moses Lake, Western-USA (Welch *et al.*, 1992) or by natural flooding processes, e.g. Zeekoevlei lake in South Africa (Harding, 1992) in Lake Batata, Brazil (de Melo and Huszar, 2000).

The flood-induced dilution effect is superimposed on decreasing temperatures which may limit algal growth in terms of biomass, density or Chl *a* in the cold season, as observed in other studies in the Paraná and Pantanal floodplains (Izaguirre *et al.*, 2001; Unrein, 2002; Zalocar de Domitrovic, 2002; 2003). Izaguirre *et al.* (2001), concluded that in the Paraná river low algal biomass in winter, measured as Chl *a*, was due to both dilution and colder temperatures. In most of these studies apart from Unrein (2002), the cold and high water seasons coincide. Other works on tropical wetlands showed increasing biovolume corresponding to higher water levels in the colder season (June-July), e.g. in a tropical floodplain lake in the Mary River (Australia; Townsend, 2006) and in the Upper Paraná River

where Train and Rodrigues (1998) found high biovolume in the cold (June 1993), but also in the warm season (February 1994). Rojo *et al.* (1994) concluded that tropical rivers (in Africa, India and South America) have their highest phytoplankton biomass in April/May, corresponding approximately to the autumn season in the Southern hemisphere, as compared to July-October (summer) in temperate rivers in the Northern hemisphere (see also Rojo *et al.*, 2010). In the Delta during the flood recession (October 2009 and February 2010, but less so in September 2006) higher water temperatures are recorded. Also, the lowest water temperatures, i.e. on average 19 °C in July (Figure 4.17), are associated with reduced algal biomass levels in five phyla (see Figure 5.44), which is also linked to lowest water levels in these seasons (Figure 4.22). Hence both dilution and temperature play a role in driving algal biomass levels in various freshwater ecosystems.

However, the dilution effect on algal biomass is not mirrorred on all nutrient-related variables. Conductivity, TP are also lower in the high water phase in July and August (Figures 4.28 and 4.38), but TN and cations (Figure 4.45) do not have their lowest concentrations when the water depth is highest. Thus dilution takes place, but not consistently on all water solutes (see section 4.7.3), while algal taxon richness, diversity and biomass are lowest mostly during the high water phase (Figure 5.11, 5.22 and 5.24). This is most likely related with both temperature and dilution, as not only lower biovolume, but also fewer algal taxa may be found in larger volumes of water dispersing algal cells, filaments and colonies (Proulx and Mazumder, 1998). The contributions of temperature and water depth in determining algal biomass are difficult to separate; evidence that autotrophic processes such as primary production are less influenced by temperature than heterotrophic processes such as respiration (Tilzer *et al.*, 1986 in Sommer and Lengfellner, 2008) suggests that flooding-induced dilution may be more important in reducing the algal biovolume of these phyla in the Delta during the high water season (but see discrepancy in cation levels; Figure 4.59).

Seasonal flooding and temperature fluctuations are interlinked. Seasonal variation in day length and heat income is lower in the tropics than in temperate areas, but higher than equatorial locations (Huszar and Reynolds, 1997; Train and Rodrigues, 1998); thus subtropical wetlands may be more subject temperature control of

biomass than equatorial ones. In this study, total algal biovolume are highest in April/May (and September; Figure 5.43), which is in agreement with Rojo *et al.* (1994). However, these seasonal fluctuations and flushing / mixing events tend to be subordinate to large fluctuations in water levels (Huszar and Reynolds, 1997). Analogously to this study's results on algal biomass (see Figure 5.43), in the Pantanal the rising water period, i.e. when the limnological changes are most marked as the river water first enters into contact with the floodplain, was characterised by higher phytoplanktonic population densities (de Oliveira and Calheiros, 2000). The asynchronous effect of the flood pulse, i.e. with flooding starting when temperature starts decreasing, complicates the interpretation of seasonal patterns on algal populations. A definitive conclusion on whether a temperature or a dilution effect prevail on algal growth and biomass is further hampered by the fact that algal biomass (standing crop as estimated via biovolume) may also be decoupled from primary production rates (g C m^{-2} yr^{-1}), i.e. high productivity may not coincide with high biomass, as algae may grow very rapidly and then be grazed rapidly too. Thus, in the Delta temperature somehow limits algal biovolume together with flooding which dilutes it in the high water season, coinciding with the colder season (July/August).

Nutrient effects on algal biovolume / biomass

Other studies in the subtropics highlight the influence of nutrient concentrations on algal biomass. In the Everglades periphyton biomass metrics of wet biovolume all decline with increasing water depth and hydroperiod as well as with increasing available amounts of phosphorus (Gaiser *et al.*, 2006). In three South African lakes (Soetendalsvlei South, Voëlvlei and Waskraalsvlei), phytoplankton biomass was associated with higher conductivity in the autumn (in May 2007) (Gordon *et al.*, 2011). In this work, low conductivity and TP levels in July/August (Figures 4.26 and 4.38) coincide with the lowest total algal biovolume (Figure 5.43). However, cation concentrations are highest during this high water 'colder' season (Figure 4.45) which may be due to river transport of these solutes. Therefore, the influence of lower concentrations of phosphorus, lower temperature and dilution, may override the availability of other micronutrients, such as cations (Ca^{2+}, Na^{+}, K^{+}, Mg^{2+}), anions (HCO_3^{-}, SO_4^{2-} and PO_4^{2-}) and TN, which are slightly higher in the

colder high water season (July/August) than in the flood expansion phase (April/May) and thus reduce total biovolume of algae (Figure 5.43).

In shallow wetlands on the Agulhas Plain (South Africa) Gordon *et al.* (2011) observed higher phytoplankton biomass in May when conductivity was higher. In this study algal biomass was higher during the flood recession phase (Figure 5.43) when conductivity also increased (Figure 4.26). Therefore higher algal biomass in this period is likely due to the availability of more micronutrients (positively correlated with conductivity, as ion concentrations could not be measured during flood recession phases) and perhaps by the increased habitat availability in these early-wetting and early-drying periods, especially in the floodplains of BOR and SAN. Therefore, higher algal biomass (as estimated by biovolume) is likely increased by nutrients while temperature and dilution, which, to an extent, decreases nutrient levels, reduce algal biovolume in the winter.

Temperature and nutrient concentrations may also be related to one another like other research showed. Higher sediment temperatures likely increase mineralisation rates, in turn enhancing nutrient release into the water, as observed in shallow lakes (Søndergaard *et al.*, 2002). In this study TP concentrations are significantly higher in the summer (February 2010; Figure 4.38), but this is not associated with higher biovolume in the warmer season (see section 5.2.5). Hence this study does not support such indirect temperature effect on algal biomass by means of higher nutrient supply, but TP may be uptaken by algae directly from the sediment due to the nutrient storage function of floodplains in the Delta (Lindholm *et al.*, 2007).

Grazing effects on algal biomass and food-web dynamics

Grazing is also likely to influence algal biomass and species richness in the Delta. Algae are eaten by macroinvertebrates and hence represent not only a direct, but also an indirect source of food for fish (Covich *et al.*, 1999). High invertebrate abundance in the flood expansion and high water phases (April/May and July/August) (Davidson *et al.*, 2012) and consequent plausible higher grazing levels may reduce algal biomass in (some of) these periods. The highest total algal biovolume was observed in September 2006, slightly higher than April/May (aggregate 2007 and 2009 data) while invertebrate abundance is highest at the peak of the flood (July 2007; Davidson *et al.*, 2012), when algal biomass is lowest

(Figure 5.43). Siziba *et al.* (2012) also found higher abundance of microinvertebrates such as rotifera, cladocera, copepoda and ostracoda in the flooding peak and flood recession phases. Therefore, grazing is likely to be higher during these wetting and drying periods, in turn influencing algal biomass, alongside nutrient concentrations, temperature and dilution (water level).

Grazing is likely to be higher during the high water phase, as invertebrate abundance was highest in this period in the Delta (Davidson *et al.*, 2012) which may contribute to the lower algal biomass levels (Figure 5.43) and, to an extent, taxon richness (Figure 5.10), as was also observed by Proulx and Mazumder (1998) in an experimental study in nutrient-poor ecosystems. The significant lower biomass may be due to high grazing, which can be inferred by high invertebrate abundance in these sites (Davidson *et al.*, 2012). The widespread use of pesticide spraying to control tse-tse flies in the Delta does not seem to have induced toxicity on algae, e.g. *Scenedesmus*, a genus which showed sensitivity to organochlorine compounds (Stadnyk *et al.*, 1971), was found in relatively high abundaces in XAK and other regions.

Algae are a significant food source for various consumers including fish. In the Delta, during the warm low-flood season, old macrophytes break apart and decompose hence offering substrates for algal assemblages to grow on; this detritus and algae represent food sources for mayfly larvae, especially in marginal vegetation habitats (Mazebedi, 2009). Siziba *et al.* (2013) found that algae represented 10% of the gut content of all fish (larger proportions in tilapia's diet), with microcrustaceans being the most important food source (71%) and the rest being detritus, macroinvertebrates, small fishes and plant materials. In particular, adult topminnow diet is known to be based on small-sized invertebrates (Skelton, 2001) whereas adult cichlids feed largely on terrestrial detritus and algae (Winemiller and Kelso-Winemiller, 2003), which were abundant in the productive rarely flooded wetlands of the Delta (Siziba *et al.*, 2011a).

Siziba *et al.* (2013) also observed that during larger floods fish populations use occasionally (rarely) inundated floodplains as living habitat. However, algal biomass was not significantly different across the three flood years in this study (2006-2007; 2007-2008 and 2009-2010) (section 5.2.5). Hence OF floodplains offer more space for fish to live and reproduce, but algae are not available in larger

quantities in these sites during large floods. More research could quantify the transfer of energy and matter between algae and other primary producers, e.g. macrophytes (Winemiller, 2004) and bacteria and their invertebrate and vertebrate consumers (see section 7.3), especially important during the large floods of 2009 and 2010.

5.3.3. Interpretation of the species richness-biovolume relationship

The most important result is that the algal species richness – total biovolume relationship is scale-dependent in the Okavango Delta. In particular, at habitat and floodplain (local) scale biovolume tend to increase or decrease likely depending on factors such as nutrient availability, e.g. overall floodplains show a significant (with 95% confidence) linear positive relationship with species richness. However, this is the result obtained by analysing all the data, while the relationship in each floodplain site changes perhaps in relation to stochasticity; low numbers of samples yield different trends while at larger geographical scale algal assemblages tend to have higher biomass when more species are present.

As the algal taxon richness, diversity and biomass estimates showed (see section 5.2), the Okavango Delta's floodplains (heavily sampled in this study, see section 3.1) are suitable environments for diverse and productive algal assemblages to develop. These environments are likely to allow the formation of biofilms and diverse phytobenthic assemblages due to the abundance and diversity of macrophytes (Gosselain *et al.,* 2005; Douglas *et al.,* 2005) and other substrata such as sand and sediments. Here the observed relationships between species richness and biomass (section 5.2.6) are discussed in the context of resource availability (e.g. nutrients), habitat and spatial scale.

Phytobenthos and phytoplankton habitats

In studies on three dimensional benthic habitats, consumption by diatoms in the overstorey (at the top of the biofilm, or algal 'canopy') was shown to substantially reduce the resources reaching the understorey, including micronutrients, carbon, ammonia, phosphate, nitrate, silica, and light (e.g. Passy, 2008; see also Figure 1.8). Thus longer environmental gradients are observed in these habitats than in open water where phytoplankton live (Passy, 2008). The Delta's phosphorus-rich

sediments (Wolski *et al.*, 2005b) likely subsidise benthic algae in these shallow water assemblages (including diatoms), especially during smaller floods (Mubyana *et al.*, 2003; Lindholm *et al.*, 2007). This allows the formation of productive and diverse algal assemblages in the floodplains in BOR and SAN. Here it is more likely that competitive displacement is reduced, i.e., the likelihood that many species are limited by resource scarcity is lower, given the higher levels of such resources in the water, e.g. cations, SiO_2 and DOC and in the sediments. By contrast in the Panhandle regions (UPH and LPH) SiO_2, cation, DOC concentrations are lower; here the reduced nutrient availability may force stronger competition for such resources thus reducing algal species richness in these upstream areas.

Passy and Legendre (2006a) showed that algal biodiversity controls algal biomass in streams across the USA; the data available in the Delta are here used to verify whether this may also be the case in the Okavango Delta as well. Patterns of biomass in relation to species richness vary across habitats in this wetland. Whereas Floodplain (F) samples show a significant linear positive relationship species richness-biomass (Table 5.27), in Open Water (OW) and Marginal Vegetation (MV) sites (less intensively sampled) there is no significant relationship (see section 5.4). This study highlights how in areas of the Okavango Delta with deeper aquatic habitats and permanent flooding, fewer species and genera compose the algal assemblages than in the shallow floodplains with seasonal and occasional flooding (Figure 5.5); diversity indices accouting for relative abundance are also significantly lower in PF sites (see section 5.3.1). However, total algal biomass reaches similar levels across regions (apart from XAK) and flood classes (see section 5.2.5). Algal biomass in the Panhandle (UPH and LPH) is represented by fewer species of rather dominant diatoms, e.g. *Eunotia* spp., which may better compete for scarce nutrients than other algae. By contrast, in the lower Delta reaches environmental gradients are longer and nutrient levels higher which increases the ecological niches available so that a higher number of species coexist (see section 4.7.3).

The relationship between algal species richness and biomass varies at different scales, e.g. from local to regional and between different habitats. Hence the research question has been addressed finding the scale-dependency of species richness – biovolume in algae in the Delta. This was done by means of a qualitative

comparison of our results with those produced by Passy and Legendre (2006a) allows to highlight similar patterns. In the Delta, 60 species contribute to the maximum algal biomass in planktonic habitats (OW) as compared to 80 species in benthic habitats (F). By contrast, in US streams, 16 species of phytoplankton contribute to the highest algal biomass as compared to 50 in benthic habitats (Figure 2 in Passy and Legendre, 2006a). However, in this study the overall relationship between species richness and algal biomass is linear (see section 5.6), not unimodal, as concluded by Passy and Legendre (2006a) in their large scale study, i.e. across the continental USA, over about ten years (1993-2003). This could represent only the increasing arm of a unimodal curve, below the peak in species richness and be linked to shorter environmental gradients, i.e. near pristine oligotrophic sites in the Delta *vs* numerous impacted sites in US streams, and the smaller scale of the study, i.e., a single wetland *vs* a continental-scale study (Passy and Legendre, 2006a).

Numerous authors stressed the relevance of floodplains for biodiversity and its conservation (Bunn and Arthington, 2002), particularly in Africa (Gordon, 2002; Høberg *et al.*, 2002), South America (Agostinho *et al.*, 2005) and Australia (Kingsford, 2000); algae are particularly important as primary producers at the base of the food webs in these ecosystems (Lewis *et al.*, 2000). F habitats are the most important environments in the Delta in terms of maintaining its algal biodiversity and primary production (Figures 4.15 and 5.9). This higher biodiversity, facilitated by higher 'energy' levels (Wright, 1983), i.e. nutrient concentrations and temperatures, microhabitat availability and ultimately long-term flooding disturbance causes algal biomass to be higher in floodplains (Figure 5.41), in particular of Chlorophyta and Cyanophyta (Figure 5.46).

This study adds new knowledge of the relationships between species richness and biomass of algae, previously studied in rather few works (at least seven: 6 reviewed by Mittelbach *et al.*, 2001 and Skácelová and Lepš, 2014). Some ecological studies on both producers and consumers show that unimodal patterns at local scales become linear at larger scale (Mittelbach *et al.*, 2001; Korhonen *et al.*, 2011; Chase and Leibold, 2002) whereas others conclude that the reverse is true for herbaceous plant communities, i.e. unimodal relationship at field-scale (within biomes or biogeographic regions) and negative linear relationship within a community type at the scale of fields (Gross *et al.*, 2000). Passy and Legendre (2006a) found a

consistent unimodal relationship in three stream habitats: i) richest targeted habitats (RTH) including epilithon and epiphyton; ii) depositional-targeted habitats (DTH), i.e. epipelic and epipsammic habitats; and iii) phytoplankton. In this study's much smaller dataset in the Delta's river channels, lagoons and floodplains an approximately unimodal relationship is only observed in OW sites, but supported by a limited number of observations (Figure 5.54a). A positive linear relationship prevails in data within each region, flood class and season (Figures 5.32 to 5.35) whereas at local (floodplain) scale negative relationships are also present, but on less than 15 samples (Figure 5.38). This confirms what Korhonen *et al.* (2011) observed relationships on phytoplankton and zooplankton in 100 small Boreal lakes, i.e. variable patterns at local scale ranging from positive linear and unimodal to negative linear.

Furthermore, human impact is very low in the Delta (Mladenov *et al.*, 2005) and this may contribute to the fact that the overall shape of the biomass-species richness relationship is different from unimodal, e.g. pollution-sensitive algal species are not eliminated from the species pool (see Passy and Legendre, 2006a). These species may be lost due to human impacts and an excessive number of species may also take place; these phenomena contribute to the emergence of the unimodal relationship on streams in the USA (Passy and Legendre, 2006a).

The Multivariate Productivity Hypothesis (MPD) (Cardinale *et al.*, 2009b) help further explain the cause-effect links between nutrients and species richness and biomass (see section 5.3): 1) resource supply directly limits the standing biomass and/or rate of primary production, (2) the richness of species locally competing for resources directly influences producer biomass, and (3) producer biomass is indirectly affected by resource supply rate because this influences the fraction of species from a colonist pool that coexist locally. In the Delta, resources limit algal species richness, but not biomass in the Panhandle, while they facilitate high species richness in BOR and SAN. It is not clear whether higher nutrients allow for higher productivity which boosts species richness or whether it is the availability of more resources and microhabitats to increase species richness which in turn supports higher algal biomass than in open waters (at least in Campaign 2; Figure 5.38).

One aim of this study was to determine what relationship there is between algal species richness and biomass across the Delta (see section 2.3). At local scale only

floodplain sites from Campaign 2 were compared as these were sampled more systematically across seasons than in Campaign 1 (see Table 3.3 in section 3.1). The relative low number of observations in each of the eight floodplain sites sampled most likely contributes to the variability observed in the species richness-biomass relationships. The varying trends in algal biomass *vs* species richness in different habitats (Figure 5.53) and floodplain sites (Figure 5.55) suggest that: i) higher resource and habitat availability in the floodplains allow for more species to coexist hence driving biomass to increase without it appearing to reach a peak and decline afterwards; ii) stochastic fluctuations in algal assemblages likely contribute to different shapes of the species richness-biomass in different locations and times of sampling. The qualitative analysis conducted in this study on the species richness-biomass relationships, i.e. loess smoothers used to visualise the trends observed (see Figures 5.49 to 5.55), contribute to the intepretation that niche overlap and niche facilitation respectively prevail in OW and F (Passy and Legendre, 2006a) hence explaining the different diversity levels in these habitats in the Delta. In benthic environments such as shallow floodplains, facilitation is a key ecological mechanism, as algal communities establish themselves also due to preconditioning of the substrate by pioneer species (Korte and Blinn 1983). Thus both the use of resources by algae and their survival under stressful conditions are improved in turn elevating ecosystem productivity (Loreau and Hector 2001), for example by increasing the probability of positive species interactions in biophysically complex habitats at different scales (Cardinale *et al.* 2002). In the Delta's shallow floodplains, and in channels with slow-flowing water, more diverse communities of algae develop; this may improve resource use efficiency in these environments, with impacts on higher trophic levels (Worm and Duffy, 2003).

This study's results are the first evidence-base on the relationships between species richness and algal biomass (via biovolume estimates) in the Okavango Delta; positive interactions (niche facilitation) and negative ones (e.g. competition) are likely to prevail in floodplains due to higher availability of resources and substrata for three dimensional assemblages to form and persist. Further work aimed to disentangle in full the algal diversity - biomass / productivity relationships in the Delta using diversity indices (see Skácelová and Lepš, 2014) and direct measures of

primary productivity can usefully build on these findings and preliminary explanations (see section 7.3).

Methodological limitations

This research has a few methodological limitations in relation to sampling methods, data aggregation / disaggregation and taxonomic resolution of algal identifications. The 496 species and 173 genera of algae observed in the Okavango Delta represent an underestimation (see sections 4.3 and 7.3). In fact, a number of very small algae (e.g. *Chlorococcales*) and of diatoms could not be identified at species level at 400x magnification; also, 400 algal units were counted in each sample as recommended by international protocols (European Standard, 2005). Obviously, the number of species actually contained in each sample is most likely higher as not all algal cells can be counted and identified, especially with a limited magnification. The taxon richness estimators allowed to conclude that, on average, about 66% and 72% of species and genera have been found in the samples collected, hence about 30% of taxa are likely to exist in the Delta that have not been sampled and/or identified.

In this study, samples were taken with low temporal frequency, typically at intervals of several months and in Campaign 1 local environmental heterogeneities may influence our observations as replicate samples were not collected. This issue was solved in Campaign 2 by collecting composite samples, i.e. 20 L of water taken with plastic tubes from several meters around the sampling point (see section 3.2); subsamples were taken from these 20 L composite samples, to minimise possible local heterogeneities, e.g., algal blooms or aggregations of algae.

Another issue faced was the necessity to bring together two separate sets of samples and hence methodological approaches to generate a coherent body of new research. Campaign 1 was a first endeavour conducted by Mackay *et al.* (2009) to collect algal samples from multiple regions of the Okavango Delta between September 2006 and July 2007. Campaign 2 was a specifically designed research activity to investigate algal assemblages in the Delta's floodplain along a habitat gradient from Open Water (OW) to Grasslands (G) via Sedgeland (S), under the hypothesis that higher nutrients in the shallower S and G habitats results in higher algal richness and diversity (see section 2.3). To address this difference, firstly a classification of macrohabitats applicable to the merged dataset was adopted: OW, Marginal

Vegetation (MV) (Mackay *et al.*, 2012) and Floodplains (F); sites classified as seasonally inundated pools and floodplains in Mackay *et al.* (2012) were considered F for simplification purposes to represent shallower water bodies isolated to different extent from the main channels and their margins (OW and MV). Secondly, data on algae and limnology were analysed separately in Chapter 4 and 5 to account for the different sampling methods (see section 3.2) and to obtain a full picture of the results over the four sampling years.

Whereas in Chapters 4 and 5 the ecological response variables analysed were species and genera richness, taxon richness estimators and diversity indices, in Chapters 6 individual algal taxa responses to the environmental conditions measured in the Okavango Delta sampling sites between 2006 and 2010.

5.4. SUMMARY

In this chapter, detailed evidence was presented on the patterns of algal taxon richness and Shannon Diversity and Shannon Evenness; these are all higher in shallow floodplains, in particular in BOR and SAN. Species richness drives algal biomass to higher levels as a significant positive linear relationship is observed between these response variables in the Delta, particularly in Floodplains (F; Table 5.27). By contrast, biomass decreases with higher species richness in OW and MV habitats (see section 5.2.5) while at floodplain scale the shape of this relationship changes (Figure 5.55).

Algal diversity is higher in shallow habitats than in deeper open waters due to higher microhabitat availability, and higher 'available energy', i.e. higher nutrient levels and temperature (species-energy theory) which allow stronger niche differentiation. This suggests that niche facilitation prevails in phytobenthic habitats (F) whereas niche overlap or complementarity with enhanced competition may take place in planktonic environments (OW and, to an extent, MV) (Passy and Legendre, 2006a). In turn high species richness increases algal biomass which tends to be higher and reach a maximum where more species are present in floodplains than in the other habitats.

On average, taxon richness indicators indicate that 66% of the algal species and 72% of the genera likely existing have been found in this study (see Tables 5.12 and 5.13). ß diversity analyses confirm that the most biodiverse regions of the Delta are BOR and SAN, due to higher ratios between exponential γ and α diversity.

Chapter 6 – Environmental controls of algal taxon distribution in the Delta

6.1. INTRODUCTION

This extensive study on the algae of the Okavango Delta represents a substantial and original contribution to the description of the poorly known algal flora of a remote and largely pristine subtropical wetland and to the ecological interpretation of the distribution, biodiversity and biomass patterns of the taxa living there. Whereas the previous chapter focussed on questions over the biodiversity and biomass of algae, here the distribution of taxa is investigated in relation to limnological variables, e.g. water depth and conductivity, and environmental factors such as habitat type (e.g. OW, MV, F) and flooding frequency (flood class). In order to determine the main causes of variation in algal assemblages at different taxonomic levels, i.e. species, genus, phylum and other group, various analyses are conducted. Correlation between limnological variables and between these and species richness and biomass are calculated in order to highlight (similar or opposing) trends of variation; ordination and variation partitioning analyses respectively aim to establish the main gradients of variation in algal assemblages and the relative role of environmental variables and spatial location of samples in determining such variations (see Figure 2.8). Here Thesis objective 4 is addressed with further supporting evidence to that produced in Chapter 5, i.e. analyse and interpret the relationships between: a) relative abundance and b) limnological variables, sampling region, season, flood class and habitat type (section 2.3).

6.1.1. Factors influencing the distribution of algae

Environmental factors have varying impact on algal distribution, as stochastic processes and the presence of few obstacles to dispersal allow many species to be cosmopolitan (e.g. Finlay, 2002; Finlay *et al.*, 2002; Lachance, 2004). However, abundance levels in relation to environmental conditions and the presence of endemisms are influenced by environmental conditions (Vanormelingen *et al.*, 2008). The predictions of the Unified Neutral Theory of Biodiversity and Biogeography (Hubbell, 2001) are generally met by a global study on marine diatoms, in particular partial niche assembly and partial dispersal and drift assembly with similarity decreasing with geographical distance (Chust *et al.*, 2012). Thus both habitat filtering and dispersal limitation both strongly influence phytoplankton community structure (Chust *et al.*, 2012). Potential for community structuring of diatoms related to dispersal as well as local environmental factors has been also observed in lakes (Verleyen *et al.*, 2009). Similarly, in river diatom communities, both at the regional (Soininen *et al.*, 2004, Soininen 2007) and continental scale (Potapova and Charles 2002) dispersal related variables explain species distribution. Also, in inland water environments, regional richness relationships depend on regional habitat availability, i.e. dispersal does limit diatom distribution as it is slow enough to allow metacommunities to form (Telford *et al.*, 2006). In freshwater ecosystems, algal biodiversity is determined by local factors such as dispersal ability, lake area, water chemistry, trophy level as well as regional factors, e.g., geology, history and climate (Stendera *et al.*, 2012). Hydroperiod (time of presence of standing water in a location) is one of the strongest factors affecting species in ponds, shallow lakes and wetlands (Mackay *et al.*, 2012; Stendera *et al.*, 2012; Lee *et al.*, 2013). In ecotonal waters in Arctic Lapland, Weckström and Korhola (2001) showed that distribution, composition and species diversity of diatoms are significantly regulated by temperature and other climate-related factors. However, algal growth rates in relation to temperature vary considerably according to species, with diatoms, green algae and cyanobacteria being best adapted to, respectively colder, intermediate and warmer temperatures (Patrick, 1969 in Moss, 1973). For example, maximum growth rates for desmid taxa were frequently recorded in the range 20-25 °C (Moss, 1973).

The spatial distribution of algae, particularly planktonic species, is influenced by physical mixing processes and associated light availability (Huisman *et al.*, 2004 and references therein), nutrients, competition, grazing and climatic factors (Reynolds, 2006). Nutrient enrichment usually increases diversity in stream phytobenthos (Peterson and Grimm, 1992), for example due to P enrichment at the scale of periphytic mats (Biggs and Smith, 2002).

Here, analyses of algal data in relation to limnological conditions, e.g. depth and conductivity, and environmental factors such as flood class and habitat, are carried out to contribute to the understanding of the patterns of algal distribution in the Okavango Delta, including the geographical coordinates of sampling points.

6.1.2. Chapter aims

In this chapter, the distribution of algae is investigated across regions, flood class and habitats in the wetland under study. The geographical scales go from over one hundred km distance between two sampling regions such as UPH and BOR, to a much shorter distance of several meters between open water, sedgeland and grassland habitats in the Delta's floodplains. The main aim of this chapter is to investigate how the distribution of algae is influenced by limnological variables (e.g. depth and nutrients) and environmental factors (flooding frequency and habitat type) at different taxonomic levels, i.e. species, genera, phylum and 'Other' taxonomic groups. This category includes algae that were not identified at species or genus level, but named as 'colony', 'branched filament', 'filament', 'centric diatoms' and pennate diatom or identified as *Chlorococcales*, *Chlorophyceae*, *Chroococcales*, *Euglenales*, *Gymnodiniales*, *Nostocales*, *Oscillatoriales*, *Stigonematales* or *Zygnematales*. Limnological variables, regions, flood class and habitat type are used to interpret the distribution of algae (in terms of % abundance and biomass).

In a study on periphytic diatoms in the Okavango Delta, Mackay *et al.* (2012) concluded that flooding frequency and duration, flow velocity and nutrients SiO_2 and TN were the key factors influencing the distribution. This study expands the evidence base to test whether similar or different ecological dynamics take place for other algae. Spatial location of sampling points (i.e. geographical coordinates) is also used to investigate its influence on the distribution of algae in conjunction with

or independently from limnological variables. The key response variables analysed in Chapter 5, i.e. species richness and total algal biovolume, are used here to test how environmental variables affect them by means of Variation Partitioning Analysis (VPA; see section 6.2.3), and the distribution patterns of the most common taxa are analysed via species response curves (section 6.2.4). Figure 6.1 outlines the univariate (Correlation analysis and Species Response Curves) and multivariate analyses (PCA and RDA), their purpose and the relative software used.

Overall these analyses contribute to an improved understanding of the factors governing algal biodiversity, biomass and distribution in the Okavango Delta. The methods are discussed in sections 3.8 (univariate and multivariate statistical analyses) and 3.9 (species response curves).

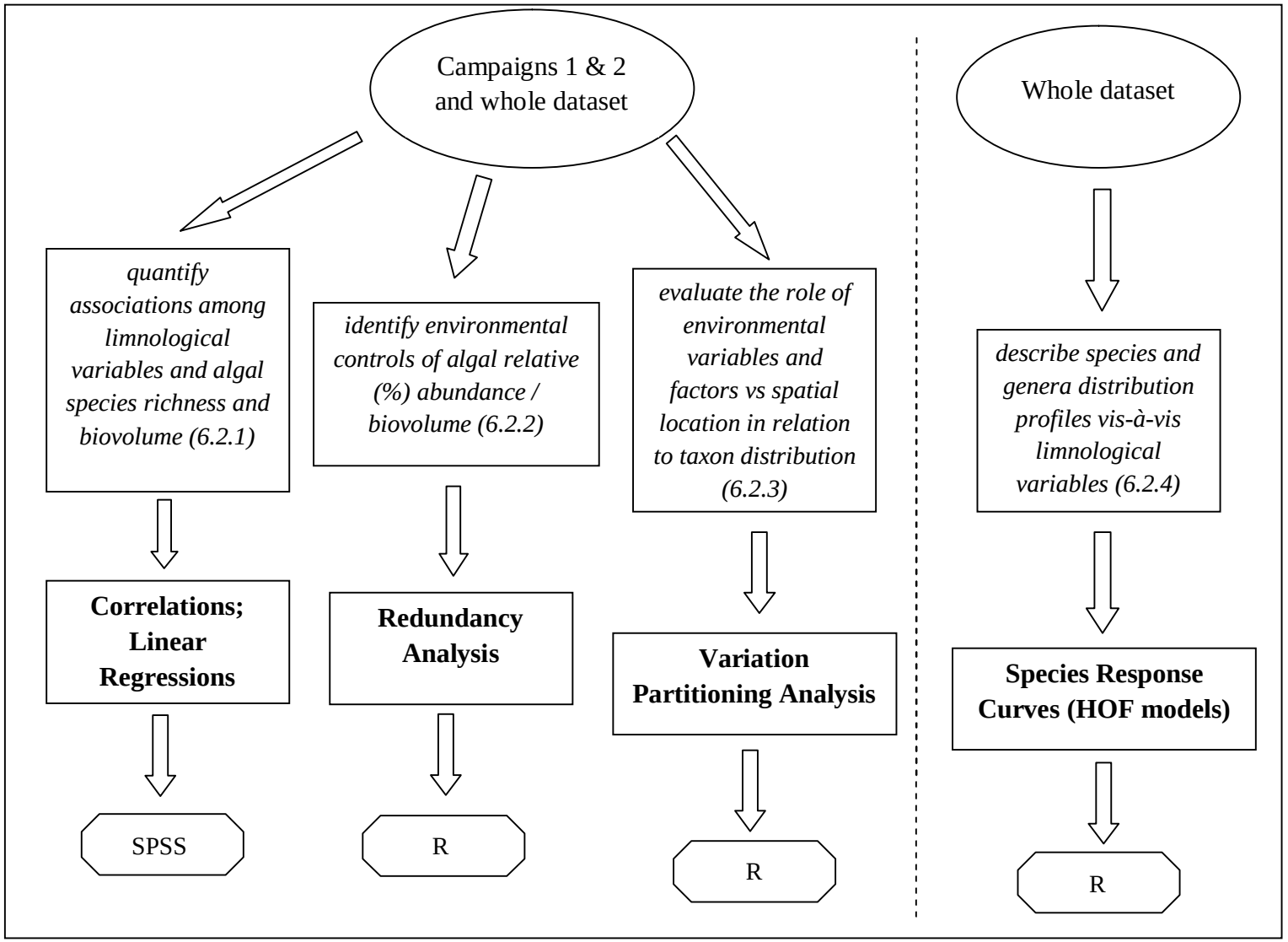


Figure 6.1. Outline of the analyses conducted in this chapter, their purpose and data sources utilised.

6.2. RESULTS

Here the relationships between the explanatory limnological variables and total species richness, biovolume as well as relative abundance / biovolume of individual taxa are analysed in order to establish what controls these response variables.

6.2.1. Limonological controls of algal phyla species richness and biovolume

Correlations between environmental data and algal species richness and biovolume are illustrated. Species richness is normally distributed (K.S. test: Z=1.080; p=0.193), but Spearman correlation coefficients are used because some of the environmental variables are not normally distributed (see Table 4.6). In the merged dataset species richness is weakly significantly positively correlated with temperature, TP and conductivity and weakly negatively correlated with TN, DO and depth (Table 6.1).

Table 6.1. Significant correlations between species and genera richness and limnological variables (*<0.01).

Variables	Species Richness (Pearson r)	Species Richness (Spearman r)	Genera Richness (Pearson r)	Genera Richness (Spearman r)
Temp.	-	0.506*	-	0.383*
Depth	-	-0.393*	-	-
Cond.	-	0.268*	-	-
DO	-	-0.424*	-	-
Ca^{2+}	-	-	-0.846*	-
TN	-0.441*	-	-	-
TP	0.319*	-	0.411*	-

Total algal biovolume is not normally distributed (K.S. test: Z=1.446; p=0.030) therefore Spearman correlation coefficients are used. This response variable exhibits a significantly weak negative correlation with Na^+ and with the sum of cation concentrations (cations) (Table 6.2).

Table 6.2. Significant correlations between total biovolume and limnological variables (*: <0.01).

Variables	Biovolume (Spearman r)
Na^+	-0.486*
Cations	-0.477*

In Campaign 1 data species richness shows a weak negative correlation with TN (Pearson r=-0.441) and total biovolume has a weak significant positive correlation with temperature (Spearman r=0.384*) and negative correlation with Na^{+} (Spearman r=-0.486*). Species richness is correlated with temperature and TN in the merged dataset (Table 6.1). In Campaign 2, species richness is significantly negatively correlated with depth (Spearman r=-0.425*) and positively with temperature (Spearman r=0.476) whereas total biovolume does not exhibit any significant correlations with limnological variables. Overall, the associations between species richness and total biovolume are weak, but suggest a positive effect of temperature and a negative one of TN on species richness (but with much fewer observations). Genera richness is more strongly negatively associated with Ca^{2+}, and more weakly positively with TP. Total biovolume does not exhibit very meaningful associations with limnological variables as the only significant correlations are found in the merged dataset, but with variables that were only measured in Campaign 1 and are not seen in the separate dataset.

Algal phyla species richness and biovolume

Here algal biomass and species richness are analysed in relation to each limnological variable one by one measured in the field or laboratory in all the samples (see section 4.7.3) in order to highlight the most relevant factors influencing these response variables. This is done by means of simple linear regressions for total biomass and species richness as well as for species richness and biomass of each phylum.

Linear regression analysis

According to linear regression analysis, the significant positive predictors of algal species richness are conductivity, temperature and TP and the negative predictors are depth, DO and TN (Table 6.3).

Table 6.3. Significant predictors of total species richness as per linear regression (*=p<0.01; **=p<0.001; logT=log-transformed).

Variable	**R^2**	**β (standardised)**
Conductivity (logT)	R^2=0.076	β=0.276*
Depth (logT)	R^2=0.208	β=-0.456**
DO (logT)	R^2=0.168	β=-0.410**
Temperature (logT)	R^2=0.264	β=0.513**
Total Nitrogen (TN)	R^2=0.220	β=-0.469*
Total Phosphorus (TP)	R^2=0.100	β=0.316*

By contrast, total algal biovolume has overall only two significant negative predictors, i.e. Na^+ concentrations (R^2=0.262; standardised β=-0.516*) and cation concentrations (sum of Ca^{2+}, K^+, Mg^{2+}, Na^+) (R^2=0.256; standardised β=-0.506*). Chl *a* concentrations (available for 67 samples), which can be used as a proxy for algal biomass, are significantly positively predicted by conductivity (AdjR^2=0.099; F=7.287, p<0.01*, β=0.339) and turbidity (AdjR^2=0.121; F=9.364; p<0.01*, β=0.367) and negatively by depth (AdjR^2=0.193; F=9.634; p<0.01*, β=-0.465).

The results of the simple linear regressions on species richness and biovolume for each phylum (log-transformed) are summarised in Tables 6.4 and 6.5.

***Table 6.4. Significant predictors of phylum species richness as per linear regression** (standardised β coefficients shown, *=p<0.01; **=p<0.001; the most significant relationships for each phylum are underlined. No statistically significant regression was found for Chrysophyta and Pyrrophyta).*

Variable	Phylum					
	Bacillariophyta	**Chlorophyta**	**Cryptophyta**	**Cyanophyta**	**Euglenophyta**	**Xanthophyta**
Conductivity	R^2=0.154; β=-0.392**	R^2=0.184; β=0.429**		R^2=0.139; β=0.372**	R^2=0.107; β=0.327**	
Depth	R^2=0.130; β=0.360**	R^2=0.312; β=-0.558**		R^2=0.180; β=-0.424**		
DO				R^2=0.146; β=-0.383**		
Temperature		R^2=0.349; β=0.591**		R^2=0.156; β=0.395**	R^2=0.067; β=0.260*	
Velocity	R^2=0.387; β=0.622*					R^2=0.698; β=-0.835*
Ca^{2+}	R^2=0.307; β=-0.554*					
DOC	R^2=0.347; β=-0.589**				R^2=0.215; β=0.463*	
HCO_3^-	R^2=0.243; β=-0.493*				R^2=0.255; β=0.505*	
K^+	R^2=0.206; β=-0.454*				R^2=0.435; β=0.659**	
Mg^{2+}	R^2=0.384; β=-0.620*				R^2=0.241; β=0.491*	
SiO_2	R^2=0.373; β=-0.611**				R^2=0.394; β=0.628**	
TN	R^2=0.167; β=-0.409*		R^2=0.235; β=-0.485*			
TP		R^2=0.078; β=0.280*		R^2=0.177; β=0.278*		
Anions	R^2=0.239; β=-0.489*				R^2=0.263; β=0.513*	

***Table 6.5. Significant predictors of phylum biovolume as per linear regression** (standardised β coefficients shown, *=p<0.01; **=p<0.001; the most significant relationships are underlined. No statistically significant regression was found for Cryptophyta and Pyrrophyta).*

Variable	Phylum					
	Bacillariophyta	**Chlorophyta**	**Chrysophyta**	**Cyanophyta**	**Euglenophyta**	**Xanthophyta**
Cond.	R^2=0.211; β=-0.460**			R^2=0.158; β=0.397**	R^2=0.097; β=0.311*	R^2=0.141; β=0.376*
Depth	R^2=0.273; β=0.522**	R^2=0.098; β=-0.314*		$\underline{R^2=0.242; \beta=-0.492^{**}}$		R^2=0.134; β=-0.365*
DO	R^2=0.070; β=0.265*	R^2=0.103; β=-0.321**		R^2=0.165; β=-0.406**		R^2=0.186; β=-0.432*
Temp.	R^2=0.083; β=-0.288*	$\underline{R^2=0.144; \beta=0.379^{**}}$		R^2=0.230; β=0.479**	R^2=0.120; β=0.347**	$\underline{R^2=0.380; \beta=0.616^{**}}$
Ca^{2+}	$\underline{R^2=0.374; \beta=-0.612^{**}}$					
DOC	R^2=0.229; β=-0.478*					
HCO_3^-	R^2=0.195; β=-0.441*					
K^+	R^2=0.188; β=-0.433*				R^2=0.266; β=0.516**	
Na^+	R^2=0.305; β=-0.552**		R^2=0.380; β=-0.616*			
SiO_2	R^2=0.215; β=-0.464*				$\underline{R^2=0.277; \beta=0.526^{*}}$	
Anions	R^2=0.193; β=-0.439**					
Cations	R^2=0.314; β=-0.560**					

6.2.2. RDA: environmental controls of algal taxon distribution

The environmental variables were selected by means of the function “ordistep” in R (Oksanen *et al.*, 2013) to eliminate multicollinear variables before their inclusion into ordination analysis (see section 6.1.3). The RDA models with variables selected via step-wise selection procedure are shown in Table 6.6 with details on to taxonomic level and dataset; the explanatory power of the chosen models are illustrated in Table 6.7. Temperature is selected in 9 out of 24 cases, pH in 8, conductivity and TP in 7 occasions, DO in 5, depth in 4, PO_4^{2-} in 3, SiO_2 and SO_4^{2-} in 2 cases; the dummy variable SF is selected in 17 cases, OW in 13, F in 4, OF in 3 (Table 6.6).

Table 6.6. Variables selected by 'ordistep' backward and forward selection for RDA (p-value: 0.01; 0.001 underlined; C1=Campaign 1; C2=Campaign 2; F=Floodplain; OW=Open Water; SF=Seasonally Flooded; OF=Occasionally Flooded).

Type of data	Dataset	Species	Genera	Phyla	Other
Abundance (%)	C1	SF, SO_4^{2-}, OW, SiO_2	OW, SF, PO_4^{2-}	SF, OW, PO_4^{2-}	OW
	C2	SF, pH, OW	OW, SF, DO	OW, OF	TP
	All	depth, conductivity, temperature, SF, pH, OF, TP	SF, F, OF, depth, conductivity, pH, temperature, DO	conductivity, SF, F, temperature, pH	SF, temperature, TP
Biovolume (%)	C1	SO_4^{2-}, SF, OW	OW, SF, PO_4^{2-}	SiO_2, OW, SF	OW, DO
	C2	DO, SF, depth, temperature, TP	OW, pH	OW, conductivity	TP
	All	conductivity, SF, temperature, pH, TP, depth	F, SF, pH, temperature	conductivity, F, temperature, SF, pH	conductivity, temperature, SF, TP, DO

After the step-wise variable selection no variable showed multicollinearity: the Variance Inflation Factor (VIF) applied to the RDA models chosen by step-wise were all lower than 10 and hence were kept in the analysis (Oksanen *et al.*, 2013). This confirms the effective selection of non multicollinear variables by means of the 'ordistep' function. In the merged dataset the constrained axes explain 17.8% of species relative abundance variation (12.9% of species share of total biovolume) and 23.9% of genera abundance changes (21.7% for biovolume). RDA conducted on phyla abundance reveal that the constrained axes explain 39.4% of the total variance (35.8% with biovolume data). Respectively 15.5% and 27.6% of the abundance and biovolume of other taxonomic groups is explained by the selected environmental variables.

Table 6.7 presents the RDA results in terms of explanatory power of the variables selected via step-wise method in the merged dataset. These are higher than in the separate datasets (Table 6.8) due to more variables being available in Campaign 1 which helps better explain variations in the overall dataset. However, the results are not illustrated in a graph as the number of algal taxon and sites is very high and hence does not allow to convey the information clearly.

Table 6.7. Explanatory power of RDA axes 1 and 2 in all the samples (constrained by variables shown in Table 6.6).

Taxa	**Abundance**	**Biovolume**
Species	17.8%	12.9%
Genera	23.9%	21.7%
Phyla	39.4%	35.7%
Other groups	15.5%	27.6%
Average	*24.2%*	*24.5%*

Table 6.8 shows the results of the RDA analysis on separate datasets. Some differences, e.g., genera and other groups in Campaign 2, are present, but, on average, between 8.1% and 12.2% of the variations are explained by the selected environmental variables (Table 6.6).

Table 6.8. Explanatory power of RDA axes 1 and 2 in Campaign 1 and Campaign 2 (constrained by variables shown in Table 6.6).

Taxonomic level	Campaign 1		Campaign 2		Average
	Abundance	Biovolume	Abundance	Biovolume	
Species	13.6%	9.7%	8.2%	12.0%	*10.9%*
Genera	10.4%	10.6%	14.7%	8.0%	*10.9%*
Phyla	14.1%	18.9%	12.4%	8.5%	*13.5%*
Other groups	7.3%	9.6%	10.0%	3.8%	*7.7%*
Average	*11.4%*	*12.2%*	*10.8%*	*8.1%*	*10.7%*

Table 6.9 outlines the RDA 1 and RDA 2 highest axis scores; habitat type OW and flood class SF and OF are particularly important in determining the variation in algal taxon relative abundance in relation to, respectively, the first and second axis.

Table 6.9. Variables with the highest scores in relation to RDA axes 1 and 2 (RDA conducted using taxon abundance data).

RDA 1	Species	Genera	Phyla	Other
Campaign 1	SF: -0.851	OW: -0.623	OW: -0.575	OW: -1
Campaign 2	OW: -0.719	OW: -0.974	OW: -0.820	TP: 0.930
All the samples	Cond.: -0.924	Cond.: -0.782	Cond.: -0.773	SF: -0.829
RDA 2	**Species**	**Genera**	**Phyla**	**Other**
Campaign 1	SO_4^{2-}: 0.789	SF: -0.942	PO_4^{2-}: -0.796	-
Campaign 2	SF: -0.744	SF: -0.765	OF: -0.651	pH: -0.900
All the samples	OF: -0.536	OF: -0.584	pH: -0.443	TP: 0.909

Drivers of species richness and total biovolume

According to RDA analysis, only a small part of the variation in total algal species richness and biovolume in the Delta is determined by measured variables and factors, using each continuous environmental variable as a single constraint and the other ones as covariates. Temperature, DO and depth account for *c.* 5.1%, 3.5% and 3.1% respectively of the total variance in species richness. Conductivity, TP and temperature explain *c.* 5.6%, 3.4%, 3.0% respectively of the total variance in algal biovolume estimates (see full results in Table 6.10).

Table 6.10. Single constrained RDA results: variance of algal species richness and total biovolume explained (%) by the main environmental variables (in bold the most important ones).

Variable	Species Richness	Total Biovolume
Conductivity	0.16	**5.59**
Depth	3.09	0.94
DO	3.45	0.06
pH	0.02	0.03
Temperature	**5.13**	2.95
TP	1.36	3.40
Average	*2.16*	*2.20*

In order to pinpoint any temperature effects within the same season and to compare it with the influence of other factors which also fluctuate seasonally, e.g. depth (see also section 4.8), RDA analyses were conducted on data within each season. The influence of temperature on species richness and, to a less extent, on total biovolume varies across seasons, highest being in February for species richness and in July/August for total biovolume (Table 6.11). Water depth has a higher influence on these response variables in October 2009 (recession phase) for both variables (14.8% for species richness and 26.6% for biovolume) (Table 6.11).

Table 6.11. Single constrained RDA results: variance of algal species richness and total biovolume explained (%) by temperature and depth (in bold the most important ones).

Season	Species Richness		Total Biovolume	
	Temperature	***Depth***	***Temperature***	***Depth***
February	**3.50**	3.47	1.21	0.24
April/May	0.34	5.97	3.37	0.10
July/August	1.56	4.25	**3.39**	2.52
September	0.05	0.80	1.84	2.19
October	0.81	**14.8**	1.68	**26.6**
Average	*1.25*	*5.86*	*2.30*	*6.33*

Conductivity best explains algal species richness in October 2009 whereas TP does so in September; both explanatory variables explain the highest share of variation in total biovolume in the high water phase (July/August 2007/2009) (Table 6.12).

Table 6.12. Single constrained RDA results: variance of algal species richness and total biovolume (%) explained by conductivity and TP (in bold the most important ones).

Season	**Species Richness**		**Total Biovolume**	
	Conductivity	***TP***	***Conductivity***	***TP***
February	10.5	0.27	4.41	0.02
April/May	8.93	0.46	1.49	0.36
July/August	4.56	0.06	**16.0**	**9.05**
September	15.7	**5.38**	5.81	1.29
October	**21.5**	0.69	2.44	2.71
Average	*12.2*	*1.37*	*6.03*	*2.69*

In terms of DO and pH the highest contributions on species richness are respectively in July/August 2007/2009 and February 2010 and their most important influence on algal biovolume across the Delta was in February 2010 (Table 6.13).

Table 6.13. Single constrained RDA results: variance of algal species richness and total biovolume (%) explained by DO and pH (in bold the most important ones).

Season	**Species Richness**		**Total Biovolume**	
	DO	***pH***	***DO***	***pH***
February	0.19	**6.09**	**6.25**	**4.61**
April/May	1.23	0.68	0.5	0.06
July/August	**1.62**	2.05	4.34	0.25
September	0.26	0.79	0.18	0.1
October	0.51	2.06	5.9	0.04
Average	*0.76*	*2.33*	*3.43*	*1.01*

Finally, the contribution of algal species richness to total biovolume and vice versa in the different seasons are shown in Table 6.14, with stronger reciprocal influence in September 2006 (recession phase) and April/May 2007/2009 (expansion phase).

Table 6.14. Single constrained RDA results: variance of algal species richness and total biovolume explained by total biovolume and species richness (in bold the most important ones).

Season	**Species Richness**	**Total Biovolume**
	Total Biovolume	***Species Richness***
February	2.90	2.49
April/May	13.9	12.0
July/August	0.22	0.20
September	**16.6**	**16.2**
October	0.90	3.10
Average	*6.90*	*6.80*

These analyses have shown that different environmental variables explain a varying proportion of the variance in total species richness and biovolume, which is on average small, i.e. range 0.76% to 12.2% as average contribution of each variable to variations of species richness or total biovolume within each season.

6.2.3. VPA results: environment and spatial location

Here VPA analysis is undertaken in order to determine what proportions of the variations in algal assemblages and of taxon richness and total biovolume are due to continuous environmental (limnological) variables, spatial location of the sampling points and a combination of environment and space. Multicollinear variables were eliminated from the dataset of limnological variables by means of step-wise selection (Oksanen *et al.*, 2011). The Venn Diagrams (Figures 6.2 to 6.7) are not drawn to scale (Borcard *et al.*, 2011) and only show the results for either abundance or biovolume data, on the basis of which of these variables has the higher $AdjR^2$. All the VPA models created were tested for significance of the environmental and spatial component by means of RDA (Borcard and Legendre, 2002) - see asterisks in Figures 6.2 to 6.7. Figure 6.2 to 6.4 show results for relative abundance, as opposed to share of total biovolume in Figure 6.5 as the $AdjR^2$ was higher on these data for 'other groups'.

Species and genera relative abundance and biovolume

For species abundance the $AdjR^2$ of the environmental variables is 0.08 (0.06 for biovolume) and 0.05 for spatial and environmental variables (0.03 for biovolume), with no variation due to the location of sampling points (0.01 for biovolume) (Figure 6.2 on species abundance).

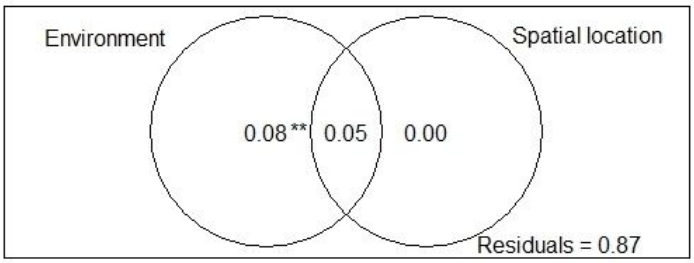


Figure 6.2. Variation partitioning results for species abundance in terms of $AdjR^2$ (total $AdjR^2$=0.13; *: p<0.01).

The variance in genera abundance explained by environmental variables equates to 0.12 (0.08 with biovolume); spatial and environmental factors explain an $AdjR^2$ of 0.07 (0.05 with biovolume), and 0.01 is exclusively due to spatial location of samples (0.02 with biovolume); the total $AdjR^2$ is 0.20 (0.15 with biovolume) (Figure 6.3 on genera abundance).

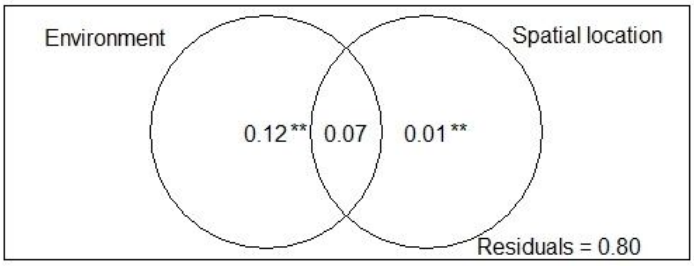


Figure 6.3. Variation partitioning results for genus abundance in terms of $AdjR^2$ (total $AdjR^2$=0.20; **: p<0.01).

Environmental variables explain 0.22 of 0.38 variance ($AdjR^2$) of abundance (0.16 with biovolume), 0.15 by spatial and environmental factors (0.16 for biovolume), and 0.01 of exclusively spatial variation (0.03 with biovolume) (Figure 6.4).

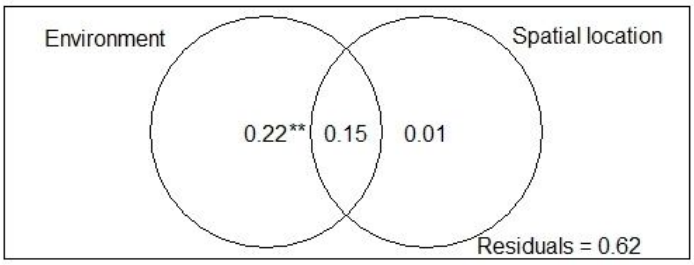


Figure 6.4. Variation partitioning results for phylum abundance in terms of $AdjR^2$ (total $AdjR^2$=0.38; **: p=0.01).

A 0.12 $AdjR^2$ portion of the variance of total biovolume of other taxonomic groups (algae identified as, e.g., *Chlorococcales* or *Chroococcales*) is explained by environmental factors, 0.13 by joint spatial and environmental variables and 0.02 (approximated figures may add up to more than 1) (Figure 6.5). With abundance 0.10 of the 0.13 $AdjR^2$ is explained by the environmental variables, 0.03 by the joint data spatial and environmental components and none by spatial location.

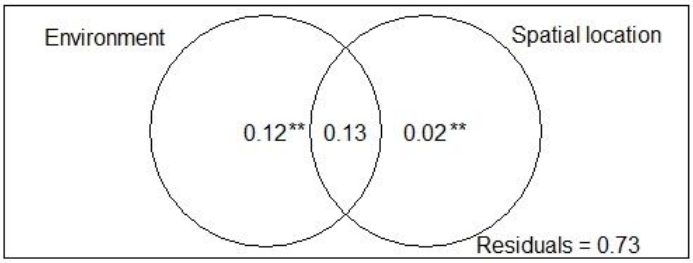


Figure 6.5. Variation partitioning results for biovolume of other taxonomic groups in terms of AdjR^2 (total AdjR^2=0.27; **: p=0.01).

Table 6.15 shows all the AdjR^2 values for the variation partitioning conducted on the separate datasets, with relative significant p-values highlighted.

Table 6.15. VPA results: AdjR^2 for algal taxon abundance and biovolume explained by environmental and spatial components (**: p<0.001).

Campaign	Variables	Data	Species	Genera	Phyla	Other
Campaign 1	**Environment**	Abundance	0.06**	0.03**	0.07**	0.05**
		Biovolume	0.02*	0.04**	0.10**	0.04*
	Spatial + Environment	Abundance	0.01	0.02	0.03	-
		Biovolume	0.02	0.02	0.05	0.02
	Spatial	Abundance	0.02**	0.04*	0.05*	-
		Biovolume	-	0.02	0.03	0.01
	Total Adj R^2	**Abundance**	**0.10**	**0.10**	**0.15**	**0.05**
		Biovolume	**0.05**	**0.08**	**0.17**	**0.08**
Campaign 2	**Environment**	Abundance	0.02**	0.06**	0.04*	0.07**
		Biovolume	0.03**	0.05**	0.04*	0.03*
	Spatial + Environment	Abundance	0.02	0.03	0.06	-0.01
		Biovolume	0.01	0.01	0.01	-0.01
	Spatial	Abundance	-	-	-	-
		Biovolume	-	0.01	0.01	-
	Total Adj R^2	**Abundance**	**0.04**	**0.09**	**0.09**	**0.06**
		Biovolume	**0.04**	**0.07**	**0.07**	**0.01**

Hence the explanation power of algal distribution is approximately three times higher for Campaign 1 with water chemistry data in comparison to the more reduced dataset of limnological variables for Campaign 2; these results highlight that the explanatory power of limnological variables measured in the field (e.g. conductivity and pH) is substantially increased by additional water chemistry data obtained by laboratory analyses (e.g. anion and cation concentrations).

Total species richness and biovolume

VPA analysis also showed that a rather large proportion of species richness variation is explained by environmental variables (0.28 / 0.35 total $AdjR^2$), while about a $AdjR^2$ of 0.07 is interpretable as a combination of space and environment and no exclusively spatial variation (negative $AdjR^2$) (Figure 6.6).

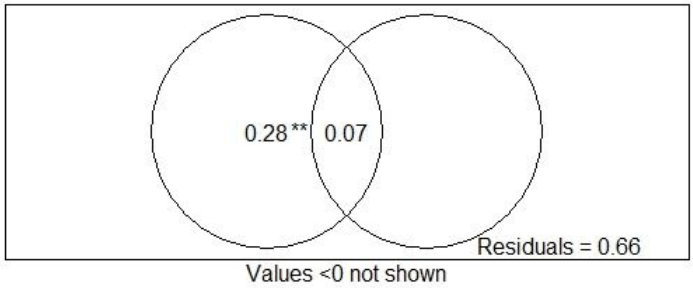


Figure 6.6. Variation partitioning results for species richness in terms of $AdjR^2$.

A much smaller proportion of total algal biovolume is explained by environmental variables (0.10 / 0.21 $AdjR^2$) than species richness; the exclusively spatial variation amounts to 0.14 of the variation in biovolume, but there is no joint meaningful contribution of space and environment (negative values; Figure 6.7). This means that the effect of the environmental variables on total algal biovolume are independent of the location of sampling points in the Delta, i.e. total biovolume is controlled more significantly by the stochastic fluctuations than by broader scale limnological variations.

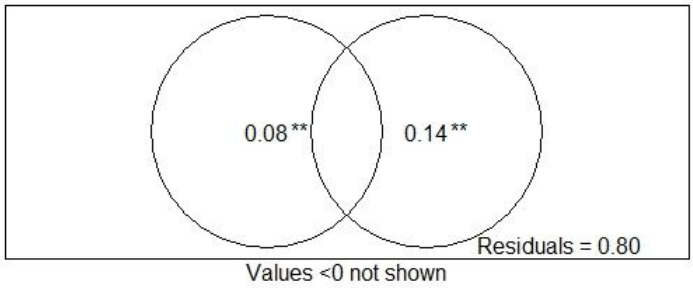


Figure 6.7. Variation partitioning results for total biovolume in terms of $AdjR^2$.

6.2.4. Species Response Curves

In section 6.3.3 ordination techniques were used to evaluate the broad relationship of algae with multiple variables and factors by means of very simple response

models, such as the weighted average used for RDA (ter Braak and Prentice, 1988). Here the focus is on specific responses of common species and genera to the measured limnological variables. The results of the most frequent Huisman–Olff–Fresco model (HOF) (Huisman *et al.*, 1993) selected by bootstrapping are presented for three algal genera found in more than 100 sites and with a total abundance higher than 1,000 algal units in relation to the six environmental variables measured in most sites: temperature, depth, conductivity, DO, pH and TP (Figures 6.8 to 6.12). This choice was made to detect defined trends in relative abundance in order to draw comparisons between typical responses of, e.g., abundant Bacillariophyta and Chlorophyta. In fact, the relative abundance of different taxa can be compared across graphs on a scale 0-100, analogously to Jansen and Oksanen (2013) which used a scale 0-1.

Therefore only the results for three very common species and six genera are discussed and the patterns of taxa with clearer associations to the limnological variables are illustrated in graphs. Algae of the genera *Scenedesmus*, *Staurastrum*, *Oedogonium* and *Closterium* (Chlorophyta), *Gomphonema*, *Synedra*, *Navicula* and *Pinnularia* (Bacillariophyta), *Cryptomonas* and *Chroomonas* (Cryptophyta) have also been observed in more than 100 sites in the Okavango Delta. Among these genera, *Gomphonema*, *Scenedesmus*, *Synedra* and *Cryptomonas* have a total abundance of over 1,000 algal units.

However, the results for only six taxa are shown here as these have clearer trends in relation to the measured environmental variables, i.e. *Eunotia*, *Mougeotia*, *Cosmarium*, *Monoraphidium arcuatum*, *Pedsiatrum tetras* and *Synedra ulna*. The relative abundance of *Eunotia* spp. show a positive relationship with depth and DO and a negative curvilinear response conductivity, temperature and TP, whereas a rather flat relationship appears with pH (Figures 6.8 and 6.9). On the contrary, *Mougeotia* and *Cosmarium* have a negative curvilinear relationship with water depth and DO concentrations. *Mougeotia* shows highest abundance with conductivity around 100 μS cm^{-1}, temperature of about 28 °C and DO lower than 4 mg L^{-1}, as well as a slight preference for pH lower than 6.5 and TP between 0.05 and 0.10 mg L^{-1}. *Cosmarium* is more abundant in warmer waters (above 30 °C) with higher conductivity and TP levels, but has rather flat trends with respect to DO and pH (Figures 6.8 and 6.9).

In Figures 6.8 to 6.12 horizontal boxplots represent absences (y=0), maximum relative abundance (100%; y=100) of the respective species along the gradient. Given that these analyses are simply used to illustrate different types of algal species responses and hence are rather descriptive, here fitted cubic spline Generalised Additive Models (GAM) with cubic regression splines and confidence intervals are not shown, differently from Jansen and Oksanen (2013; Figure 3.6).

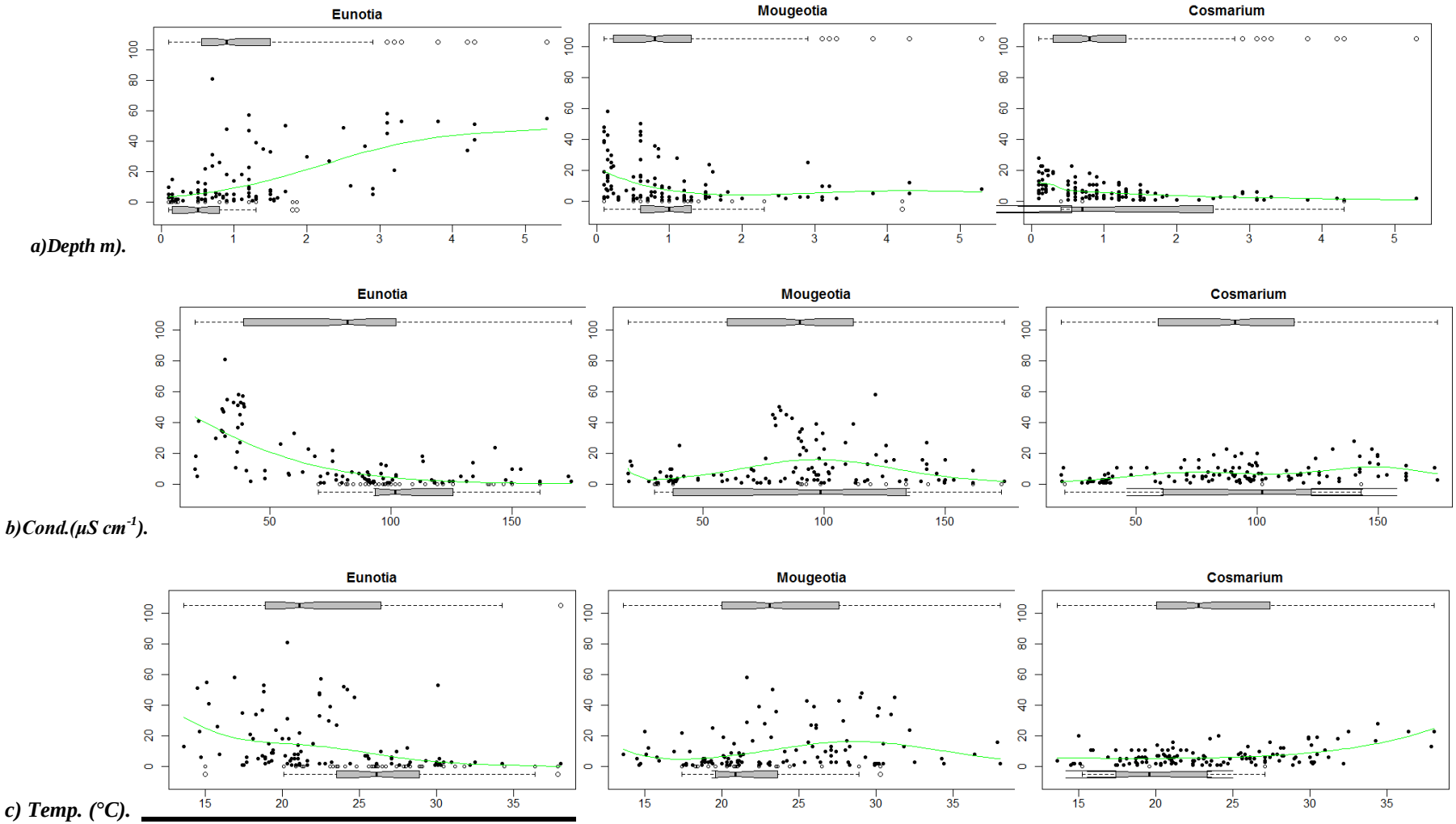
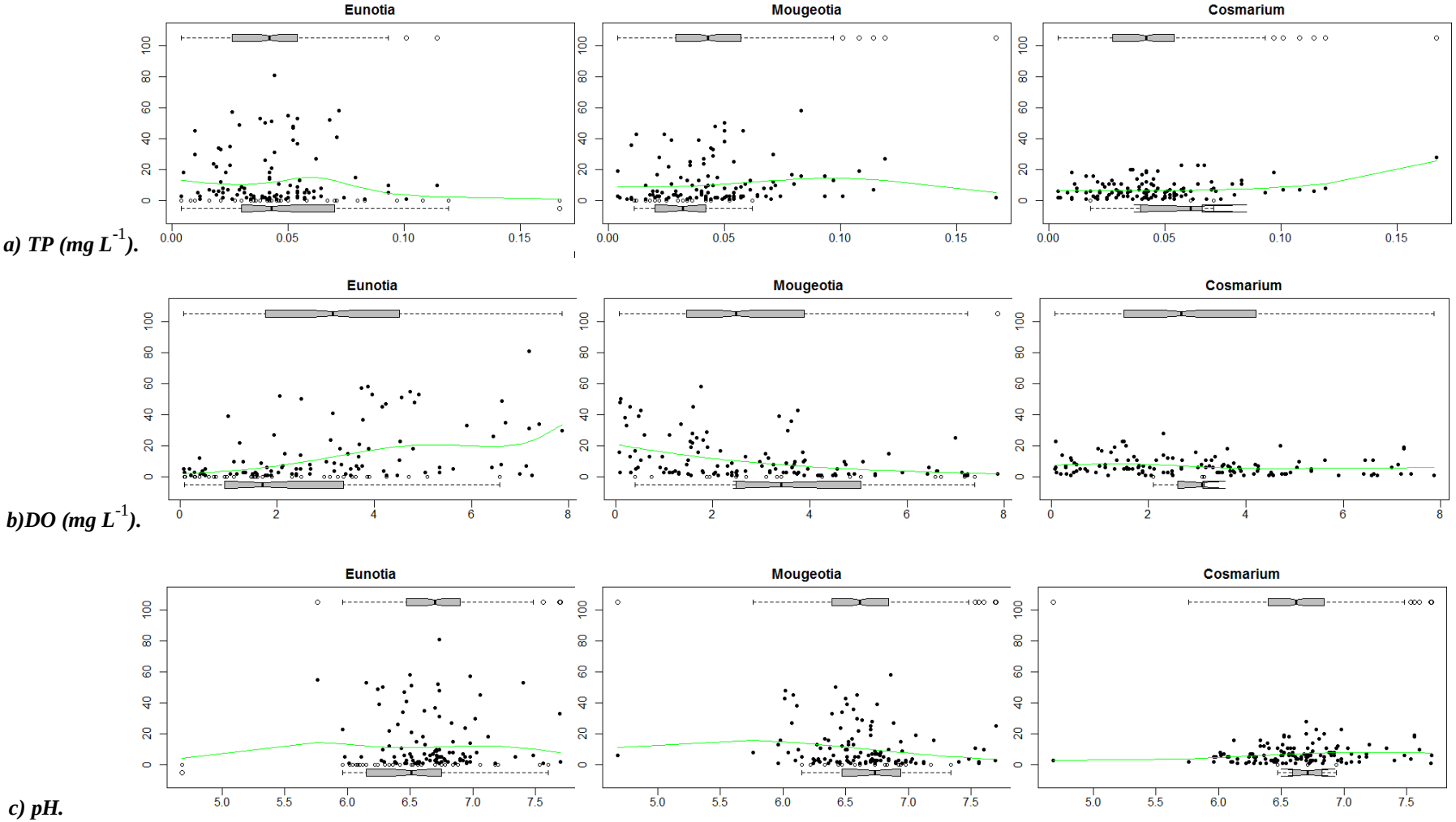


Figure 6.8. Species response curves of Eunotia, Mougeotia, Cosmarium in relation to: a) depth, b) conductivity and c) temperature (model VII, apart from model VI for Eunotia-conductivity and model III for Eunotia-depth).



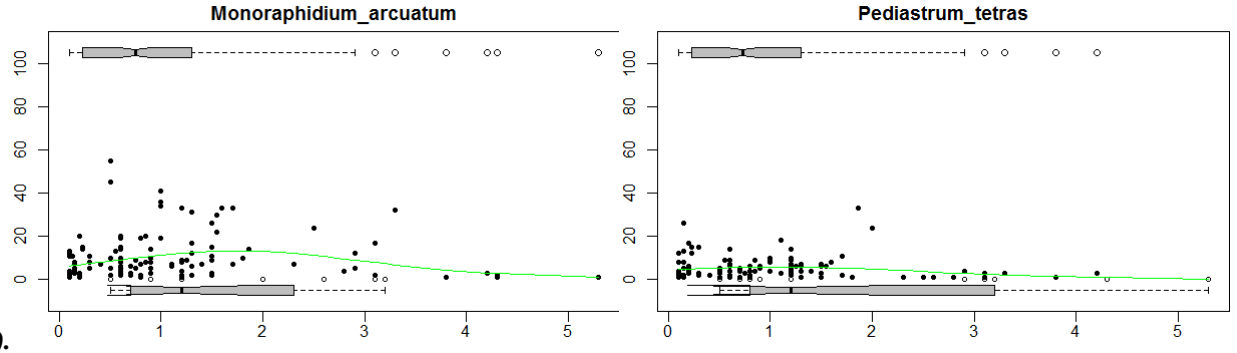
a) TP (mg L^{-1}).

b)DO (mg L^{-1}).

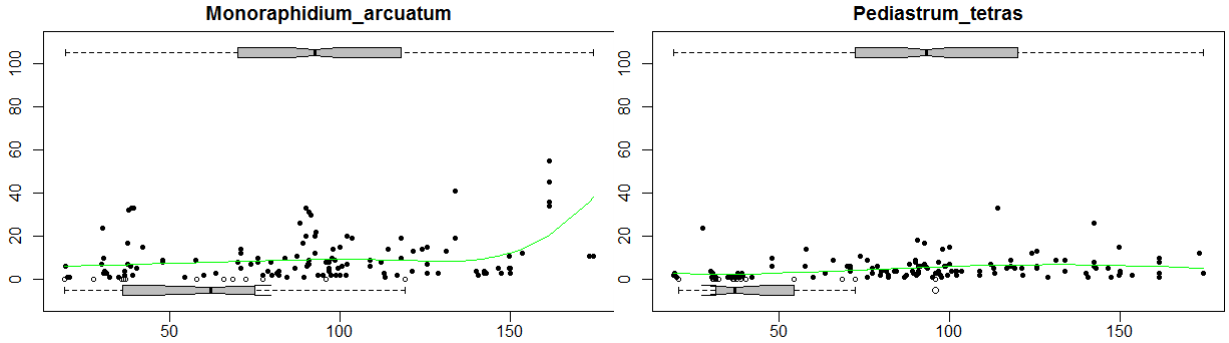
c) pH.

Figure 6.9. Species response curves of Eunotia, Mougeotia, Cosmarium in relation to: a) TP, b) DO and c) pH (model VII for all trends).

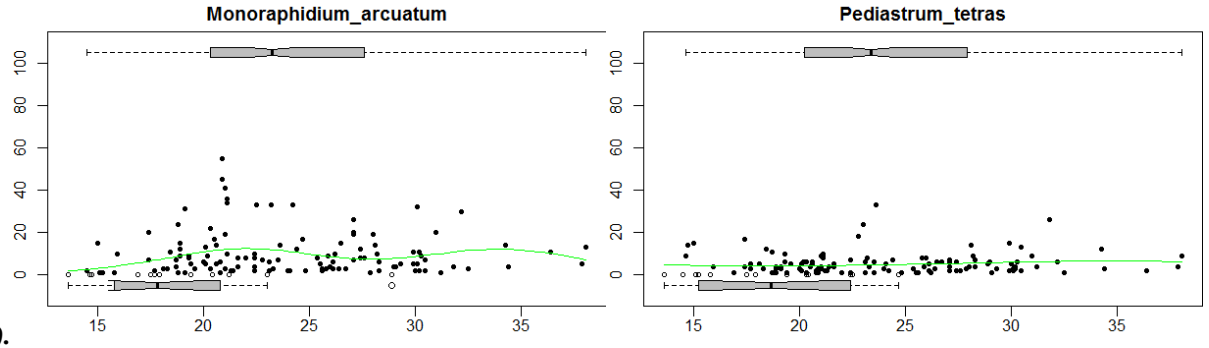
The results of species response curves are also shown for three species, i.e. *Monoraphidium arcuatum*, *Pediastrum tetras* and *Synedra ulna*, selected from a group of eight species which were present in at least 75 sites, all with total abundance higher than 250 across the Delta (Figures 6.10 to 6.12). *M. arcuatum* shows a negative abundance trend in relation to water depth and less clearly with TP, with a slightly increasing trend in response to conductivity (especially above 150 μS cm^{-1}) and temperature; this species has rather flat responses to DO and pH, with higher abundance between 7 and 7.5, though supported by a few samples (Figure 6.11). *P. tetras* has rather flat responses to all the environmental variables considered here (perhaps also due to low relative abundance), and also is cosmopolitan in the Delta, i.e. present in 119, similarly to *M. arcuatum* which was observed in 121 samples. The HOF models chosen by bootstrapping were: V for *M. arcuatum* in relation to depth, VI for *M. arcuatum* with temperature and TP and for *P. tetras* with DO, pH and TP and model VII for all the other species.



a) Depth (m).

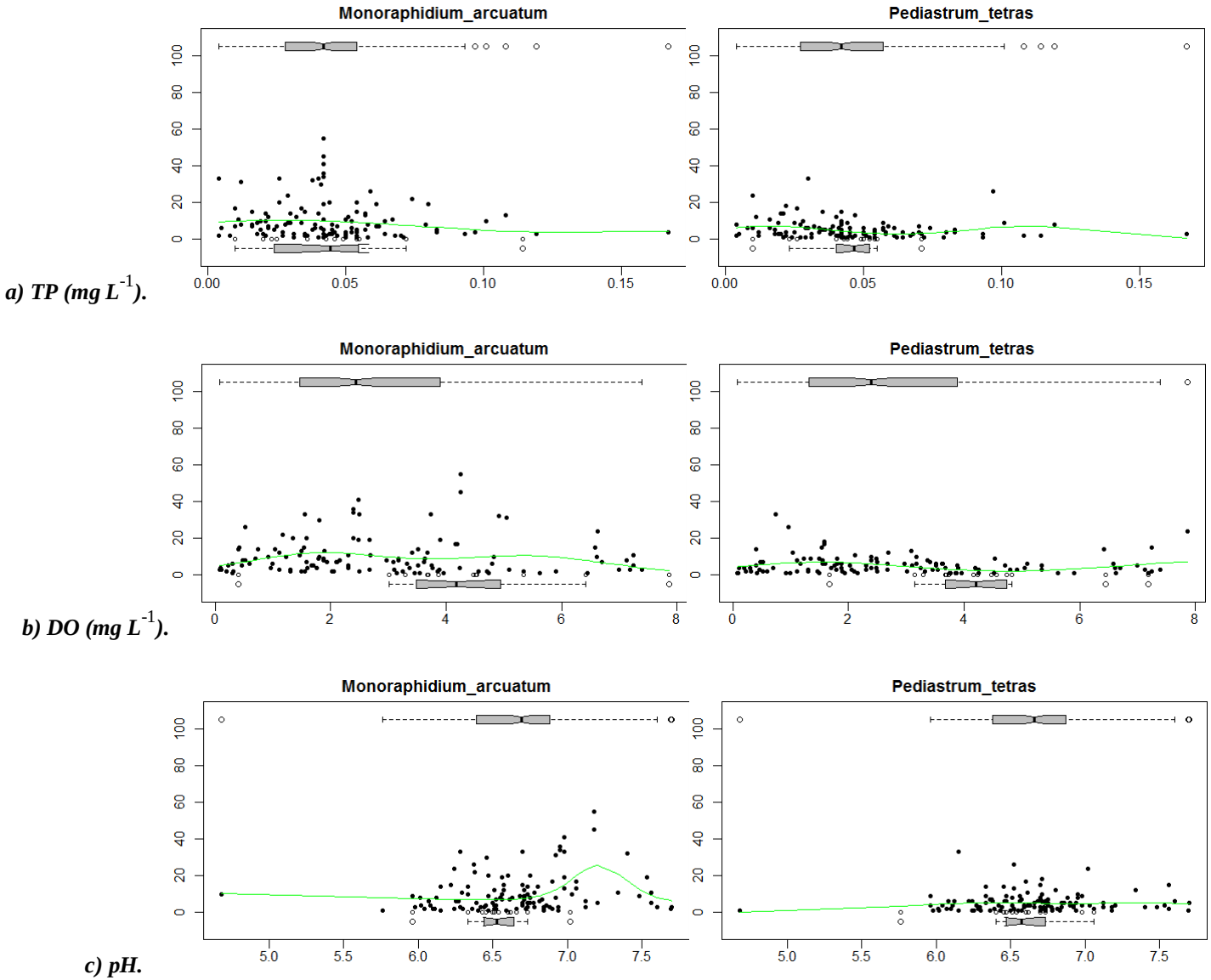


b) Cond. ($\mu S\ cm^{-1}$).



c) Temp. (°C).

Figure 6.10. Species response curves of Monoraphidium arcuatum and Pediastrum tetras in relation to a) depth, b)conductivity and c) temperature (model V for M. arcuatum vs depth and model VII for all the other graphs).



a) TP (mg L^{-1}).

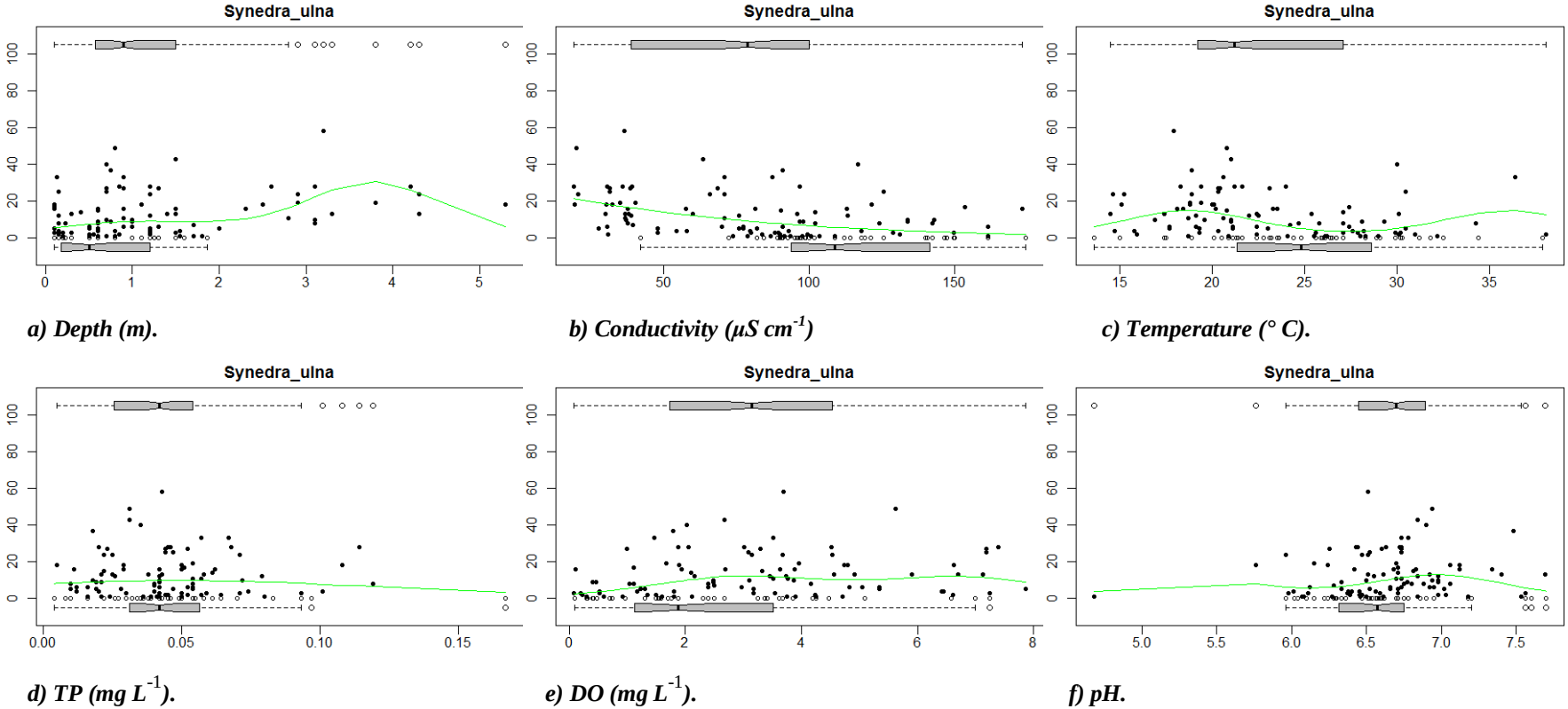
b) DO (mg L^{-1}).

c) pH.

Figure 6.11. Species response curves of Monoraphidium arcuatum and Pediastrum tetras in relation to a) TP, b) DO and c) pH (model VI for M. arcuatum with TP and for P. tetras with DO, pH and TP and model VII for M.arcuatum vs DO and pH).

According to the HOF models, *Synedra ulna* has a positive curvilinear relationship with water depth (particularly in sites deeper than 2m) and DO; by contrast, as conductivity and TP increase this species occurrs in lower numbers (less clear trend) (Figure 6.12). High abundance levels are reached at 18 °C and above 30 °C (supported by few observations) and at pH of around 7 (Figure 6.12). Model VII was chosen by bootstrapping for all the response curves for this species apart from temperature, for which model VI was a better option.

Therefore, species and genera of Bacillariophyta and Chlorophyta broadly show respectively increasing and decreasing trends in relative abundance in relation to water depth (Figures 6.8, 6.10 and 6.12). Diatom taxa have decreasing abundance levels with temperature increases which instead favour green algal taxa such as *Mougeotia* spp. and *Cosmarium* spp. (Figure 6.8), but less clearly *Monoraphidium arcuatum* and *Pediastrum tetras* which reach lower relative abundance in the wetland studied (Figure 6.10). The diatom taxa considered also show declining abundance levels with conductivity increases whereas green algae taxa have higher relative abundance at intermediate (c. 100 μS cm^{-1} for *Mougeotia* spp.; Figure 6.8) or high conductivity levels (> 120 μS cm^{-1} for *Monoraphidium arcuatum*; Figure 6.10). *Eunotia* spp. has increasing relative abundance with higher DO concentrations whereas the abundance of *Mougeotia* spp. decreases with increasing DO levels. *Monoraphidium arcuatum* and *Synedra ulna* show fluctuating abundance with highest values at intermediate DO (c. 4 mg L^{-1}) (Figure 6.11 and 6.12) while *Cosmarium* spp. and *Pediastrum tetras* do not have clear trends, also due to their low relative abundance (Figure 6.9 and 6.11). The pH optimum (indicated by the upper boxplot) is about 6.5 for all taxa, with *Synedra ulna* reaching highest abundance at pH of 7 (Figure 6.12). Relative abundance of all the algal taxa considered in this section tend to be highest with optimum TP concentrations of about 0.05 mg L^{-1}; however, *Eunotia* spp. shows decreasing abundance with increasing TP levels whereas *Cosmarium* spp. and, to an extent, *Mougeotia* spp. have higher abundance with higher TP values (Figure 6.9).



a) Depth (m). *b) Conductivity ($\mu S\ cm^{-1}$)* *c) Temperature (° C).*

d) TP ($mg\ L^{-1}$). *e) DO ($mg\ L^{-1}$).* *f) pH.*

Figure 6.12. Species response curves of Synedra ulna in relation to: a) depth, b) conductivity, c) temperature, d) TP, e) DO and f) pH.

6.3. DISCUSSION

Here the results of the multivariate analyses undertaken to explain algal taxon relative abundance and biovolume by means of measured environmental variables, and factors are discussed, alongside the results of species response curves detailing the responses of abundant, individual taxa to the Delta's environmental conditions. Firstly, the correlation analyses are briefly summarised and the trophic status of the Delta discussed; secondly, the results of redundancy analysis (RDA) and variation partitioning analysis (VPA) are discussed and comparisons are drawn with other studies, including on the role of spatial location in the variation of relative abundance and biovolume; thirdly, the results of species response curve analysis are discussed in relation to relevant literature on algal studies in tropical and subtropical freshwater ecosystems. In Chapter 5 the results on algal biomass and diversity estimates are presented and explanations of their trends in relation to environmental variables and between them were proposed. Here the focus shifts on the investigation of the drivers / controls of individual taxa and their relative abundance and biomass (see Figure 6.1).

6.3.1. Environmental controls of species richness and total biovolume

Algal species richness is significantly positively correlated with temperature, TP and conductivity and negatively with TN, DO and depth. Genera richness is also positively associated with temperature and TP and negatively with the concentrations of Ca^{2+} (Table 6.1). Total algal biovolume is significantly negatively correlated with Na^{+} and total cation concentrations (Table 6.2). This further supports the interpretation that higher 'available energy' alongside microhabitat availability favours the establishment of diverse algal assemblages in the Delta's floodplains (as per Species-Energy Theory; Wright, 1983; Stevens and Carson, 2002; see sections 5.3.1 and 5.3.2).

Environment and space as controls of species richness and total biovolume

VPA shows that overall, species richness is better explained by environmental (limnological) variables ($AdjR^2$=0.28) (total $AdjR^2$=0.35; 'Environment' in Figure 6.6) than total algal biovolume is ($AdjR^2$=0.08; Figure 6.7), with spatial location exerting a combined influence with limnology for species richness and on its own

for biovolume. The stronger dependence of total biovolume on spatial location than environmental variables (Figure 6.7) suggests that local factors, independently from the environmental conditions, e.g. stochastic fluctuations in algal populations (Huisman *et al*., 2001) contribute to determine our estimates of algal biomass in the Delta. As a consequence, the shape of the species richness-biomass relationship likely varies due to both regional processes such as flooding, which determines the nutrient gradient from the Panhandle to the distal reaches, and local factors and dynamics associated with the location of the sampling points in the Delta (see section 5.3.3), perhaps influenced by the highly stochastic nature of algal population dynamics (Huisman *et al*., 2001).

Limnological controls of total species richness and biovolume within seasons

According to single constrained RDA, temperature is an important factor influencing total algal biovolume, alongside conductivity (the variable explaining most of the variance) and TP (Table 6.10). The most important variables influencing algal species richness are temperature, DO and depth (see Table 6.10). Other studies on subtropical freshwater ecosystems, e.g. in the Lower Paraná Basin, found that water temperature also explains algal distribution patterns (Izaguirre *et al*., 2001) as well as species richness and biomass (Zalocar de Domitrovic, 2002). Water temperature exerts a reduced influence on biovolume and species richness within each sampling season than in the complete dataset. This however does not seem to be due to stronger seasonal fluctuations of water temperature than other variables (see coefficients of variations; Table 4.24), but rather to the reduced numbers of observations at the basis of these patterns. In general, the seasons in which temperature and other limnological conditions influence more strongly species richness and total biovolume are July/August 2006/2007, September 2006 and/or October 2009 (see section 5.3.2). However, these environmental variables explain a small proportion of variance in species richness and total biovolume (on average 3.8%; Tables 6.22 to 6.24).

According to single constrained RDA, species richness explains best total biovolume (and vice versa) during the early recession phase (September 2006) and, on average, better (*c.* 7%) than the environmental variables above mentioned do (Table 6.25). This suggests the importance of algal biodiversity in determining total

algal biomass in the Delta, as per ecological interpretations proposed in section 5.3.3 and other studies. For example, Passy and Legendre (2006a) Skácelová and Lepš (2014) demonstrated that algal diversity has a unimodal relationship with biomass respectively in streams across the USA and in stagnant waters in the Czech Republic. Although a weak positive linear relationship between species richness and biomass is observed (significant only at p=0.05), the maximum total algal biomass in Open Water and Marginal Vegetation habitats is lower than that estimated in Floodplains (see Figure 5.53). This may be due to the lower nutrient concentrations in these sites which likely have a direct influence on the algal biomass and on species richness, i.e. species have less 'available energy' or ecological space, which in turn has an effect on the total biomass. The Multivariate Productivity-Diversity hypothesis (MPD) put forward by Cardinale *et al.* (2009b) explains how both resource supply and species richness independently influence biomass and/or productivity; resource supply also has an indirect impact on the biomass of producers by influencing the fraction of species from a colonist pool that locally coexist (see Figure 1 in Cardinale *et al.*, 2009b).

In aquatic environments, an increasing number of individuals can be related to higher total abundance of organisms and productivity itself can have a positive effect on species richness, as hypothesised by Šímová *et al.* (2013), even though productivity is more strongly linked to species richness than abundance. Cardinale *et al.* (2009b) and Skácelová and Lepš (2014) argue that resource supply controls species richness and biomass and the former also indirectly influences algal biomass, but that there is no plausible mechanism by which the number of individuals or the total biomass has an effect on the number of species coexisting in the environment under study.

Limnological controls of algal phylum species richness and biovolume

The results of the linear regressions on limnological predictors of phylum biomass indicate these main relationships: i) Bacillariophyta biomass is negatively predicted by conductivity and ion concentrations and positively by DO concentrations; ii) biovolume of Chlorophyta and Cyanophyta is positively predicted by temperatures and negatively by water depth; iii) the biomass of Cyanophyta is also favoured by higher conductivity; the same applies to Euglenophyta whose biovolume is also

increased by higher K and SiO_2 concentrations (Table 6.5). Overall, in 21 cases out of 84 (25%) significant predictors of phylum biovolume also predict species richness with the same positive / negative trend, e.g. high temperature increases both species richness and biovolume of Chlorophyta (see Tables 6.12 and 6.13). This suggests that a relationship between species richness and biomass of algae is present in the Delta across phyla hence strengthening the interpretations proposed in section 5.3. For example, total biovolume was shown to have a significant linear increase with increasing species richness for both the major algal phyla, Chlorophyta and Bacillariophyta (Figure 5.39).

Bacillariophyta

The biovolume of Bacillariophyta is higher in deeper faster flowing waters with higher DO and lower concentrations of nutrients in the Panhandle as shown here by Table 6.5 (see also section 5.2.5). This may contribute to the lower levels of dissolved silica (SiO_2) observed there, i.e. < 10 mg L^{-1} as compared to *c.* 12 mg L^{-1} in XAK and BOR (see Figure 4.41), which may be due to diatom uptake and consistently with past findings (McCarthy *et al.*, 1994). Silica depletion due to diatom growth has been observed in other aquatic environments (e.g. Anderson, 1986). Research in the Mary River (Australia) concluded that SiO_2 concentrations of about 3-4 mg L^{-1} are not likely to limit diatom growth (Townsend, 2006) and the similar / higher levels of this nutrient in this study indicate that Bacillariophyta are not limited by SiO_2 in the Delta. Our results are in line with established knowledge that diatoms are well adapted to the turbulent conditions in freshwater environments (Sommer, 1989 in Rojo *et al.*, 1994) characterised by nutrient pulses (Falkowski *et al.*, 2004). Diatoms maintain their viability in cold dark waters or on the sediment surface during their life histories (Smetacek, 1985); the river channels have a higher and colder temperatures and higher water velocity than the distal reaches hence are more tubulent, in agreement with the above mentioned works.

Chlorophyta, Cyanophyta and Euglenophyta

Temperature is the strongest significant positive predictor of Chlorophyta (in terms of R^2) and the second strongest for Cyanophyta biovolume (Table 6.5). Water temperatures are significantly higher in BOR and SAN than in UPH and LPH (see Figure 4.16); this contributes to the higher abundance and biomass reached by

Chlorophyta, notably desmids, as well as Cyanophyta in the distal reaches (Figures 4.2 and 5.25 b/c) as observed in other works (Coesel, 1996; Schwaderer *et al.*, 2011; Kosten *et al.*, 2012). Higher temperature and micronutrients such as Ca^{+} and Mg^{+} in these shallow environments facilitate the coexistence of more numerous and diverse algae. This is due to higher mean resource supply increasing algal species richness (as per Species-Energy Theory, Wright, 1983; Steven and Carson, 2002), which in turn contributes to higher total biovolume, especially in floodplain habitats (Figure 5.41). Negative predictors of biovolume for the above mentioned phyla are DO and water depth (Table 6.5), as deeper sites have colder waters with higher DO (Figure 4.29).

Cyanophyta, though never dominant, were more abundant in shallow water regions (BOR and SAN) and during low water phases as shown by linear regression on biovolume (Table 6.5). Previous studies highlighted the development of nitrogen fixing Cyanophyta in nutrient-poor lagoons such as Xaxanaxa (as well as nutrient rich ones, e.g. Gadikwe), in the form of "*small to large gelatinous balls*" that are attached to the submerged stems and leaves of aquatic plants (Alonso and Nordin, 2003). However, nitrogen-fixing algae were observed in similar numbers across regions and habitats (see section 4.8.4) and this research does not include an assessment of algal blooms and periphyton mats in which Cyanophyta are usually abundant in other subtropical wetlands (Gaiser *et al.*, 2011). The species richness of and biovolume of Cyanophyta are also significantly predicted by conductivity (Table 6.4 and 6.5). Other studies showed that these algae are well adapted to floodplain high nutrient conditions, especially during the potamophase, i.e. high water, though Cyanophyta were in general not very frequent (e.g. in the Paraná River floodplain - García de Emiliani, 1993, Zalocar de Domitrovic, 2003).

Euglenophyta are also better adapted to the warmer lower Delta SF and OF floodplains in BOR and SAN (Table 4.2); their species richness and biovolume are significantly predicted by temperature, conductivity and, especially species richness by dissolved nutrients such as ion concentrations (Table 6.4), while SiO_2 is a positive predictor of their biovolume (Table 6.5).

Cryptophyta

The species richness of Cryptophyta, well known for their cosmopolitan character (John *et al.*, 2002) have only one negative predictor, TN (Table 6.4). They were

observed in low abundance in numerous locations across the Delta and they are overall more abundant than Cyanophyta in LPH and XAK (Table 4.2). In three lakes of the Paranà river floodplain, Cryptophyta were frequently found in higher abundances during high water phases (García de Emiliani, 1993; Zalocar de Domitrovic, 1993), but this trend was not observed in 1995-1996, i.e. (Zalocar de Domitrovic, 2003). In this study, no significant seasonal changes in the biovolume of this phylum were recorded (see section 5.2.5).

Other phyla

The biovolume of Chrysophyta only show significant changes across seasons, with lowest values in July and August (2007 and 2009), the coldest high water season; Na^+ is the only negative predictor of biovolume for this phyla. One sample in XAK (XAK19-4) showed a particularly high abundance of *Dinobryon*, hence influencing the overall results. These algal group is represented by cosmopolitan, but also more restricted regional distribution (Kristiansen, 2008). The uncommon Xanthophyta show a significant linear regression relationship between their species richness and velocity (Table 6.4) and a positive trend between biovolume and temperature and conductivity (Table 6.5) which highlights their better adaptation to the Delta's shallow floodplain habitats. Pyrrophyta do not have any significant linear regression predictors for either species richness or total biovolume.

6.3.2. Environmental controls of the distribution of algae in the Delta

RDA allows to select the variables which are important for structuring biological communities along environmental gradients (Lepš and Šmilauer, 2003). This study has focussed especially on limnological and habitat variables. Overall, environmental variables explain similar amounts of variation in both Campaign 1 and 2, regardless of relative abundance and biovolume of species, genera, phyla and other taxonomic groups, particularly in Campaign 1 (Table 6.8) and in the merged dataset (Table 6.7). Hence, abundance data may be most efficiently used for the study of distribution patterns of algae, as the estimation of biovolume is time consuming and subject to various sources of errors (Hillebrand *et al.*, 1999; Rott *et al.*, 2007). This is particularly true if a larger number of observations is available (merged dataset), as a higher explanatory power of RDA is recorded than on the separate datasets (Table 6.8) and less sensitive to the type of data used, i.e. relative

abundance or biovolume (Table 6.7). Respectively, habitat type OW in Campaign 1, flood class SF and OF in Campaign 2, and conductivity in the merged dataset are particularly important variables for the distribution of algae in the Delta, i.e. they are most strongly correlated with the RDA axes (Table 6.20).

Environmental and spatial components of algal taxon variation

According to VPA, the environmental (limnological) variables and spatial location explain a small part of the variation in algal taxa relative abundance and biovolume of species, genera, phyla and other taxonomic groups, higher in Campaign 1 (due to the availability of more variables) than Campaign 2 (Table 6.26). The spatial location is shown to have a combined influence with the limnological variables in controlling the relative abundance / biovolume (%) of the algal taxa observed in the Delta; on average 40.5% of the explained variance, i.e. AdjR^2 is due to the 'Environment + Spatial location' effect (e.g. 0.05 / 0.13 for species abundance; Figures 6.2 to 6.9). This means that the environmental variations, i.e. here limnological conditions, vary significantly in relation to the geographical position of the sampling points in the Delta, as was shown in section 4.7.3; most of the remaining explained variation is due to the limnological variables independently of the spatial location of sampling points. For example, conductivity shows variations within each region (see Figure 4.24) determined by local heterogeneity in the concentration of dissolved cations and anions influencing (and correlated with) its value (see Figure 4.43). These are not due to the geographical distance between Panhandle and distal reaches at which scale the nutrient gradient takes place and hence are explained as 'environmental component' of variation by VPA.

In the merged dataset, the variable most highly correlated with the primary RDA axis is conductivity. Conductivity was shown to significantly influence algal distribution in other subtropical wetlands and freshwater bodies, e.g. alongside water depth in epiphytic algae in the Paraná River Basin (Natural Reserve Otamendi) in Argentina (Rodríguez *et al.*, 2011). Also in lotic systems facing high anthropogenic impacts (e.g pollution) such as the Vaal River in South Africa conductivity was one of the most important variables influencing phytoplankton composition, together with turbidity, temperature and SiO_2 (van Vuuren and Pieterse, 2005). The flood cycle and associated nutrient concentrations were shown

to influence algal distribution and diversity on periphytic diatoms in the Delta (Mackay *et al.*, 2012), periphyton in the Everglades (Lee *et al.*, 2013) and phytoplankton in the Tanguar Haor, a Ramsar wetland in Bangladesh (Muzaffar and Ahmed, 2007). Therefore this study provides new evidence of the importance of conductivity, flooding frequency and habitat - all connected with spatial scale in the Okavango Delta - for the distribution of algae in tropical freshwater environments.

The portion of variation in taxon relative abundance explained by VPA as environmental (limnological) data and spatial location of sampling points is small, i.e. 10% in Campaign 1 and 6% in Campaign 2 (see Table 6.8). Other studies, such as Nabout *et al.* (2009) did not find any significant effect of environmental or spatial processes on phytoplankton communities in the Araguaia River floodplain in Central Brazil, also using VPA. This study supports the conclusion that collecting more explanatory variables, notably biological ones such as grazing, may well allow for better results (Nabout *et al.*, 2009).

6.3.3. Individual algal taxon responses to limnological conditions

Given the findings above that environmental variables are important in controlling species richness at regional-scale across the Delta, here the nature of this relationship with respect the most common taxa is further explored. This is done using response curve analyses on common species and genera. The results on algal genera found in more than 100 sites and with a total abundance higher than 1,000 algal units (4 species and 11 genera) were chosen to highlight patterns which can be detected and visible in HOF model graphs with relative abundance (%) (Figures 6.8 to 6.12). Six algal taxa showing a clearer trend in relation to the measured limnological variables are chosen and the relative graphs of the HOF model selected shown; these are *Eunotia*, *Mougeotia*, *Cosmarium*, *Monoraphidium arcuatum*, *Pediastrum tetras* and *Synedra ulna* (see Figures 6.8 to 6.12).

Chlorophyta

Desmids, the most diverse group of algae in this study, are abundant (thus having higher biovolume) in environments with higher nutrient concentrations, i.e. the shallow floodplains. This is consistent with established knowledge that the majority of desmidiaceous taxa prefer mesotrophic environments (Kovask, 1973 in Coesel, 1975) and are not planktonic, but live in protected spaces among submerged aquatic

vegetation (Brook, 1959) and are favoured by structurally stable and diverse habitats (Coesel, 1975). The abundant and diverse plants in the Delta's floodplains offer the optimal conditions for these and other green algae to thrive, in particular the submergent *Utricularia* species (Coesel and van Geest, 2008). Our sampling methodology which involved walking in vegetated floodplains most likely disturbed these benthic habitats so that many desmids were collected. In the Delta shallow floodplain habitats are characterised by abundant macrophytes, higher water temperature and nutrient concentrations than the Panhandle (see section 4.7.3).

Mougeotia was shown to prefer higher temperatures (Figures 6.8), consistently with other studies (Graham *et al.*, 1996), but no clear trend with pH and light availability was observed in this study (Figure 6.9). Together with other filamentous green algae, *Mougeotia* spp. are typical of mesotrophic and eutrophic conditions (Hagerthey *et al.*, 2013). The optimum conditions for growth of this algal genus is low to medium nutrient levels, i.e. oligo-mesotrophy (Salmaso, 2002); consistent with that, this study found that intermediate conductivity and TP levels correspond to higher relative abundance of *Mougeotia* (Figure 6.9).

Cosmarium shows relative abundance that tend to be higher with higher conductivity levels, but without a clear preference for, e.g. high TP concentrations (only a few samples have higher abundance with high phosphorus levels; Figure 6.9). Despite the largely pristine status of the Delta, these desmids show low abundance, i.e. 5.2% of all green algae. By contrast, *Cosmarium*, *Closterium* and *Staurastrum*, which were shown to dominate in eutrophic sites in Dutch wetlands (Coesel, 1982), represent a relevant part, about 21.2%, of the total abundance of green algae in this study. In the most recent study conducted on all algal groups in the Delta, Cronberg *et al.* (1996a) also found three desmid genera out of five which are usually associated with high nutrient levels: *Closterium*, *Cosmarium* and *Staurastrum* (Coesel, 1982). Hence the Delta's aquatic environments, especially the floodplains in BOR and SAN, are better environments for desmid taxa preferring mesotrophic if not eutrophic conditions than for less abundant more strictly oligotrophic taxa, e.g. *Desmidium* and *Micrasterias*, present in low abundance. These data and interpretation on the desmids living in the Okavango Delta are in agreement with the water chemistry evidence provided (see section 4.9) to suggest

that this subtropical wetland's floodplains are mesotrophic, due to its Chl *a* and TP levels.

Bacillariophyta

Bacillariophyta e.g., *Eunotia* spp. and *Synedra ulna*, are particularly abundant in the Panhandle where nutrient concentrations are significantly lower than in the Delta's distal reaches. *Eunotia* spp. show very different distribution patterns to desmids, i.e. they are most abundant in colder deeper waters with higher DO concentrations and lower conductivity and ion concentrations (Figures 6.8 and 6.9). *Synedra ulna* shows higher abundance with lower conductivity (Figure 6.12b), but a less clear association with colder temperatures and high DO levels than *Eunotia* spp. (Figure 6.8). Trends of *Eunotia* spp. abundance are in agreement with their affinity for low conductivity (Sala *et al.*, 2002) and high DO concentrations (Van Dam *et al.*, 1994). In an experimental study, Pan and Lowe (1994) found *Synedra ulna* to be associated with high phosphorus concentrations (25 μg L^{-1} or 0.25 mg L^{-1}); in this study this diatom species reaches its highest abundance levels with concentrations above 0.3 mg L^{-1} (Figure 6.12d). *Synedra ulna* was associated with eutrophic and alkaline conditions in lakes in Florida and related literature (Whitmore, 1989); this species does have a somewhat higher relative abundance with higher pH in the Delta (Figure 6.12f).

6.4. SUMMARY

This chapter has furthered our understanding on the relationships between algal taxa and limnological variables (e.g. water depth and nutrient concentrations) and environmental factors in the Okavango Delta. VPA attributes most of the variation in algal taxon distribution to limnological variables ('Environment' in Figures 6.2 to 6.7), spatial location of sampling points and the interplay / combination of these, i.e. nutrient gradient over a large geographical scale. However, whereas species richness is also largely explained by the limnological variables measured ('Environment'; Figure 6.6), total algal biovolume varies more with the spatial location of sampling points (Figure 6.7). Single constrained RDA suggests that species richness and total biovolume influence one another more strongly during the flood recession (September 2006) and flood expansion phases (Apr/May) (Table 6.25), which stresses the importance of (re)wetting and drying phases in enhancing species richness and biomass (see Figure 5.43). Linear regressions indicate that a number of significant predictors of algal phyla species richness also significantly predict total algal biovolume, for example water depth for Bacillariophyta and temperature for Chlorophyta. This reinforces the conclusion that algal species richness and biovolume are closely interconnected and directly or indirectly influenced by the same environmental factors.

Relative taxon abundance and biovolume (%) are on average explained by environmental variables in similar proportions, especially in Campaign 1, which supports the use of abundance data as most efficient to detect environmental drivers of algal distribution. RDA is rather robust to the use of relative abundance or biovolume data to explain algal taxon distribution.

Species Response Curves (SRC) show that the very common diatoms *Eunotia* spp. have an increasing relative abundance with increasing water depth and DO and decreasing conductivity whereas the green algae *Mougeotia* spp. and *Cosmarium* spp. are found in higher abundance with increasing temperatures, conductivity and nutrient concentrations. Other very common taxa such as *Synedra ulna*, *Pediastrum tetras*, *Monoraphidium arcuatum* exhibit less clear patterns in their relative abundance in relation to environmental conditions (Figures 6.10 to 6.12).

Chapter 7 – Conclusions

This study is the first systematic assessment of all algae in the Okavango Delta, a near-pristine subtropical wetland in semiarid Kalahari desert; hence it provides a significant contribution to filling the gap of knowledge about these important primary producers in the second largest inland Delta in Africa (The Ramsar Convention on Wetlands, 2014). It represents a comprehensive assessment of the algae living in the Okavango Delta waters, their taxon richness, diversity and biomass as well as the relationships with environmental variables. Thus it provides detailed new knowledge on broad geographical patterns of diversity and biomass across vast areas of the Delta in several years and seasons, flood class, and floodplain and habitat types. This study explored pressing questions for ecological theory, such as diversity-productivity relationships (here investigated as species-richness biomass), and produced results and plausible explanations which further research can be built on.

The main aim to increase the knowledge of occurrence and distribution of algae in this wetland has been achieved by means of a series of exploratory, univariate and multivariate analyses. The first general research question on how many algal taxa live in the Delta has been addressed by systematically studying all algal groups for the first time from over 50 sites across 5 regions. 496 species (173 genera) belonging to eight of the fifteen phyla (John *et al.*, 2002) were recorded (423 species identified and 73 genera of which the species is unknown). This is a major improvement on previous estimates, e.g. Cronberg *et al.* (1996b) who observed 198 species (96 genera) in the Boro (BOR) region alone. Better taxonomic resolution in the analysis of these samples and the collection of more samples can lead to discovering the presence of undetected taxa or species and varieties new to science, such as *Cosmarium pseudosulcatum var. okavangicum* (Williamson and Marazzi, 2013; Appendix I). Thus there may be hundreds more species to be found in this wetland, both known and unknown to science as the species accumulation curve shows, especially in the shallow floodplains in BOR and SAN (Figure 4.3).

The second research question on the modes and reasons for distribution patterns of algae in the Delta in relation to environmental variables and factors has been addressed by means of exploratory analyses and statistical tests in Chapter 4, univariate analyses in Chapter 5 and multivariate analyses in Chapter 6. The results obtained highlight the following broad trends on algal taxon richness and diversity, biomass and distribution:

- less frequently flooded floodplain sites in the distal reaches of BOR and SAN host significantly more diverse algal assemblages in terms of species and genera richness as well as Shannon Diversity and Shannon Evenness (section 5.3.1);
- the total algal biomass in the Delta is on average rather comparable across the five regions sampled, apart from XAK, where it is significantly lower (more research is needed to explain this difference; section 5.2.5);
- long-term flooding disturbance, higher nutrient concentrations and temperature, and more microhabitats are the most important factors enhancing the biodiversity of algae in the shallow floodplains of the Delta, as per the Intermediate Disturbance Hypothesis (Connell, 1978; Reynolds *et al.*, 1993), Species-Energy Theory (Wright, 1983) and Habitat Diversity Hypotheses (Ricklefs, 1977) (section 5.3.1);
- taxon richness estimators suggest that about 66% of the algal species and 72% of the genera existing in this wetland have been found, hence a further few hundred unidentified species may live in the Delta (section 5.2.3);
- the algal species composition is more similar between samples collected from closer regions in the Delta and within the same habitat types (see section 5.2.4);
- conductivity and the Open Water - Floodplain habitat gradient, were shown to be the most important factors in explaining the variation of taxon relative abundance / biovolume (see section 6.3.4), however most of these changes (71-83%) remain unexplained by the variables and factors considered.

The third research question, i.e. whether or not algal species richness - biomass relationship vary at different spatial scales in the Delta, has been addressed by means of univariate analyses and qualitative comparisons with other studies in

Chapter 5. The overall shape of the species richness-biomass curve is positive linear (see section 5.2.6), determined most importantly by the more numerous samples taken from the Delta's floodplains where niche differentiation / facilitation likely prevails over niche overlap / complementarity as was observed in an extensive survey of streams in the USA (Passy and Legendre, 2006a). This is due to the different spatial structure of algal communities in the phytoplankton and phytobenthos with respectively homogeneous / isotropic (plankton) and heterogeneous three dimensional environments (benthic) for algae. The shallow floodplains mostly located in BOR and SAN host more numerous benthic algal taxa due to the availability of larger surfaces with macrophytes, sediments and sands available for attachment in these environments with slow-flowing waters. Hence in these areas biofilms can form in which three dimensional communities develop that are able to exploit nutrients coming from both the water and sediments; competition is more limited as ecological niches are more numerous and environmental gradients longer than in open water habitats (Passy and Legendre, 2006a). However, more research on specific phytobenthic such as epiphyton is needed in order to confirm and strengthen this finding on algae found in water (phytoplankton and resuspended benthic taxa).

The fourth research question on the ways in which the relative abundance of the most common algal taxa varies in relation to limnological conditions in the Delta, has been addressed descriptively by means of species response curves. Whereas common diatom taxa such as *Eunotia* spp. are more abundant in deeper colder waters with lower nutrient concentrations in the Panhandle, green algae such as *Mougeotia* spp. and the desmid *Cosmarium* show increasing relative abundance in shallower and warmer floodplains with higher nutrient concentrations (see section 6.3.6). These taxa importantly contribute to the phylum-specific biovolume patterns observed in Bacillariophyta and Chlorophyta (see section 5.2.5).

Water quality

This study's results confirm previous water chemistry analyses in the Delta, e.g. the maximum concentrations of TN and TP were 1.6 mg L^{-1} and 0.17 µg L^{-1} (Table 4.5). In a review of water quality studies Mmualefe and Torto (2011) concluded that these parameters were just within the range of potable water standards, i.e.

maximum levels of 1.7 mg L^{-1} and 1.6 mg L^{-1} respectively. However, according to Mmualefe and Torto (2011) other pollutants such as organochlorine pesticides, such as dichlorodiphenyltrichloroethane (DDT) and endosulfan, need to be monitored, e.g. in XAK where they were air-sprayed from the 1940s to the late 1990s in order to control the vectors of malaria and other diseases, e.g. tse-tse fly. This study highligths the possibility that the lower algal biomass recorded in XAK in this study (Figure 5.40) may be connected to the concentrations of these substances in the water; organochlorine insecticides were shown to limit carbon fixation and production in *Scenedesmus* (Stadnyk *et al.*, 1971), a very common alga in the Delta. However, in this study's dataset the relative abundance of *Scenedesmus* spp. was very similar to BOR and SAN and higher than UPH and LPH. Recent data on high concentrations of pesticides in the Delta gives some first evidence to corroborate this hypothesis; between September 2005 and September 2006 Mmualefe *et al.* (2009) measured the concentrations in water of hexachlorobenzene, trans-chlordane, 4,4′-DDD and 4,4′-DDE in various sites including Xakanaxa (XAK), Chief's Island, Guma Lagoon (LPH), Shakawe (UPH). In general, these were much higher than the recommended EU levels for drinking water (Mmualefe *et al.*, 2009), which may have had an impact on the viability of algae in XAK, where total algal biomass was much lower than in the other regions (Figure 5.40). Although concentrations of these pollutants were higher than the established limits in other regions as well, algal biomass was higher in UPH, LPH and BOR and SAN than in XAK, which may mean that other specific unmeasured / unknwon factors limit algal growth there.

Other variables relevant for water quality were monitored by Cronberg *et al.* (1996b) at the outflow near the town of Maun (the most populated in the Delta), finding them of poor quality, with bacterial counts of 0.07 to 3.89 * 10^9 cells L^{-1}. However, Ramberg *et al.* (2000; in Wolski *et al.*, 2005b) observed much lower values of bacterial counts at water table depth in a floodplain island, i.e. between 4.0 * 10^5 and 4.8 * 10^8. Overall, more data are needed to determine the possible factors causing the specific differences in biomass XAK and regular monitoring of the Delta's water quality (Mmualefe and Torto, 2011).

Trophic status of the Okavango Delta

The high abundance of desmid taxa well adapted to mesotrophic habitats, such as *Cosmarium* spp. and *Staurastrum* spp., supports the classification of the Delta as mesotrophic, in particular its floodplains (see section 6.3.4). The definition of trophic status of a freshwater body depends on the environmental and/or biological criteria chosen. The Delta's Chl *a* levels measured in the BOR and SAN regions are relatively high, on average 28 μg L^{-1} (see Table 4.5) which is higher than the 20 μg L^{-1} threshold between mesotrophic and eutrophic conditions, as defined by the South African Trophic Status Assessment for impoundments (SATSA; Van Ginkel, 2002). On this basis these productive habitats can be considered naturally eutrophic, as human impacts are very low in this wetland (Mladenov *et al.*, 2005); if TP concentrations are used, half of LPH samples are also classified as eutrophic, whereas samples in the other regions have mean TP concentrations of 41 to 46 μg L^{-1} (0.041 to 0.046 mg L^{-1}) (see Table 4.5), just below the 47 μg L^{-1} (0.047 mg L^{-1}) threshold and thus are mesotrophic (Van Ginkel, 2002). TN values are on average below the 0.700 mg L^{-1} limit between oligotrophic and mesotrophic conditions Dodds *et al.* (1998) (i.e. 0.65 mg L^{-1}; see Table 4.5); however, while LPH and XAK have TN lower concentrations than 0.6 mg L^{-1}, BOR sites reach a 0.715 mg L^{-1} level. This limit was used as SATSA does not have a specific TN threshold (Van Ginkel, 2002).

These results are in contrast with the commonly held view that the Okavango Delta is an oligotrophic wetland, but are in agreement with its definition as a mesotrophic ecosystem by Junk *et al.* (2006) in a comparative assessment of wetlands of global importance. The mesotrophic nutrient status of this wetland is not too surprising, as numerous tropical lakes are classified as eutrophic due to the lack of obvious light limitation and the small fluctuations of photoperiod and temperature through the year (Esteves, 1988 in Huszar *et al.*, 1998). However, the nutrient and Chl *a* criteria for the classification of freshwater ecosystems in relation to their trophic status have been developed for deep, temperate lakes; by this standard, many shallow tropical lakes would be considered eutrophic (Huszar *et al.*, 1998). Therefore, caution should be paid to apply such approaches to subtropical wetlands, very different (and distant) freshwater bodies from deep lentic systems at temperate latitudes.

Use of data for the elaboration of ecological scenarios

The results produced in this study are an important baseline for future studies on algae in the Okavango Delta and as a potential pristine-state benchmark for subtropical wetlands, in terms of representing 'natural' conditions without significant anthropogenic impacts (Stoddard *et al.*, 2006). If upstream hydropower and reservoir plans are implemented upstream, the water discharge in the Delta is likely to be impacted, with global warming representing an additional threat, e.g. in terms of overall drier conditions (Wolski *et al.*, 2012). The large database produced and its results on algal taxa distribution, diversity and biomass are a useful basis for possible modelling exercises on the impacts of future hydrological and environmental changes on algal communities. Alongside data from other studies on invertebrates (Siziba *et al.*, 2011b) and fish (Mosepele *et al.*, 2012), predictions could also be made on food web dynamics and ecosystem services in this wetland.

Global warming and water abstraction plans may modify the hydroecology of this currently largely pristine wetland (Wolski *et al.*, 2014). Thus, taxa associated with shallower waters such as many small green algae (e.g. desmids) may see their ecological space reduced in the future as a consequence of the lower water availability predicted by scenario analysis of climate change and water abstraction plans upstream (Andersson *et al.*, 2006; Wolski *et al.*, 2014). Recent large floods in the Delta have produced vast impacts on the local populations and their economic activities, i.e. housing, transportations and power supply (Wolski *et al.*, 2014). On the other hand, drier conditions may damage flood recession farming in the Delta's distal reaches, which is important source of food and income for rural people (Murray-Hudson *et al.*, 2006). A reduced water discharge is already apparent, especially after the 1980s (see Figure 2.4) Thus the importance of describing baseline ecological conditions from the base of the food webs to fish populations and fisheries. However, accurate predictions on water availability in this region are difficult to make as the uncertainty in both Global Climate Models (GCMs) and in the magnitude of future global warming are considerable (Hughes *et al.*, 2010).

The knowledge-base on the algae of the Okavango Delta has been enriched by this study and it can contribute to assessing its present and future ecosystem health. It could also be one of the triggers for medium to long term monitoring programmes of shallow wetlands, still less developed than for lakes and rivers (Hamilton, 2010).

Furthermore, macroecology research addressing key questions on the relationships between biodiversity and biomass and ecosystem resilience / stability could be undertaken in more and less impacted (sub)tropical wetlands; this could help identify what are the effects of, e.g. lower water quality and quantity, on the algal assemblages and diversity of, e.g., the Okavango Delta, the Everglades and Kakadu.

Future research directions

Given the lack of comprehensive data on these microorganisms in this remote wetland, the biological, geographical and hydrochemistry data available has allowed a systematic heuristic investigation which is relevant for algal biogeography and wetland ecology in the Okavango Delta. Future research activities could also measure more quantitatively flooding frequency and duration. The flooding frequency and duration of the broadly defined Permanently, Seasonally and Occasionally Flooded sites (PF, SF, and OF) could be quantified, e.g. by using the semi-quantitative variable 'hydroperiod class' (values 1-7 with increasing flooding frequency and duration; Mackay *et al.*, 2012), which was not available for this study's Campaign 2 sites. Rigorously testing the Intermediate Disturbance Hypothesis (IDH) on algae in the Delta would require a more frequent sampling activity to gather data finer temporal resolution patterns. Flooding influences algal assemblages at microscale hence a finer spatial resolution study of the microhabitats during the wetting of the sediments, e.g. in the floodplains, would allow to measure the physical disturbance and its effects on algae. The habitat categories (Open Water, Marginal Vegetation and Floodplain - OW, MV and F and, within F, OW, Sedgeland (S) and Grassland (G) - could be used as a preliminary sampling framework for a specific sampling of benthic and periphytic algae, e.g. by scraping plant stems and collecting sediments.

More frequent sampling and the inclusion of multiple environmental criteria can improve ecological understanding of these systems (Weilhoefer and Pan, 2007), and would allow us to better account for their natural heterogeneity hence helping a more thorough bioassessment of human impacts in this wetland. This would further the scientific findings obtained by snapshot assessments of the biodiversity, biomass and distribution of algae, like the one undertaken in this study. As is the case for other important wetlands, from the Everglades in Florida (Gaiser *et al.*,

2011) to the Great Lakes Coastal wetlands in Ontario (McNair and Chow-Fraser, 2003), more quantitative and qualitative data on phytoplankton and zooplankton in the Okavango Delta (Siziba *et al.*, 2012) are needed for enhanced understanding of their role in these ecosystems. Other ongoing research on the Delta's fish populations and stable isotope analyses can further shed light on food webs and their components and dynamics, ultimately relevant for the ecosystem services on which the local populations of this wetland heavily rely (e.g., Mosepele *et al.*, 2009, Mosepele *et al.*, 2012). Microcosm (and mesocosm) experiments could also be devised in collaboration with the Okavango Research Institute in order to study biodiversity and biomass patterns of algae and invertebrate consumers such as cladocera and copepoda (see Siziba *et al.*, 2013) under controlled flood disturbance, nutrient levels and temperature. A combination of contemporary ecology and paleoecology approaches could help use algae such as diatoms to infer past wetland conditions (Lee *et al.*, 2013) in the Okavango Delta (Mackay *et al.*, 2012) and elsewhere to provide further baselines of pristine conditions or warmer / colder and drier / wetter climates. Finally, the Okavango Research Institute (University of Botswana) hosts an herbarium with numerous and diverse plant specimens; these could be used to investigate past environmental conditions in the Delta by studying diatoms and other preserved algae. In fact, herbaria have been already used to infer past 'reference conditions' free from human impacts in UK river sites with Europe-wide scope for application (Yallop *et al.*, 2009). In the case of the Okavango Delta, near-pristine conditions are still present and monitored (Davidson *et al.*, 2012; Mackay *et al.*, 2012; Siziba *et al.*, 2011b), but working on recently collected plants could support future comparative studies, should undesirable impacts materialise.

Implications for management and conservation

The Okavango River Basin faces risks of changes in sediment dynamics, water quality and changes in the abundance and distribution of biota (OKACOM, 2011). These threats may limit water quantity in its less frequently flooded distal reaches in the future, with potential harmful effects on the local economy in terms of reduced fisheries and tourism. Ecosystem services such as water purification are mediated by algae and other microorganisms (Cardinale, 2011). The conservation of aquatic landscapes and of the ecosystem services they provide is most effective with an

integrated landscape-based approach (Sayer, 2014); the Permanent Okavango River Basin Water Commission is already pursuing such a strategy to find sustainable compromises between people's needs and the integrity of the Okavango river and the Delta's floodplain ecosystems (OKACOM, 2011).

However, more long-term research needs to be undertaken. The importance of algae for ecosystem services in the Delta and their increasing use to monitor freshwater ecosystem health - for example under the European Union Water Framework Directive (WFD) (EC Parliament and Council, 2000) for lakes and rivers (Padisák *et al.*, 2006; Kelly *et al.*, 2009) - suggests undertaking such monitoring exercises in remote and still largely pristine Okavango Delta. This would be beneficial for generations to come in Botswana. Mmualefe and Torto (2011) called for government departments such as Water Affairs to run an organised water monitoring programme on dissolved nutrients such as TN, TP and ions as well as pesticides, e.g. DDT, dichlorodiphenyltrichloroethane. Due to their negative impacts on algae and other biota (Stadnyk *et al.*, 1971), the sources of pesticide contamination, e.g. disease control programmes, need to be continuously monitored and taken under control to prevent further contamination of the Okavango Delta waters (Mmualefe *et al.*, 2009).

In order to assess possible future changes in the Delta ecosystem it is of paramount importance to better understand which algae, invertebrates and fish species live where and what their biodiversity and biomass is. Relevant authorities in Botswana can use the new valuable knowledge produced by this and other studies (e.g., Mackay *et al.*, 2012; Siziba *et al.*, 2011b) as an inspiration to establish and maintain long-term monitoring activities on small organisms at the base of this wetland's food webs and on limnological parameters influencing their ecology. This research highlights the need to preserve habitat heterogeneity and water level fluctuations as key elements of a dynamic, highly biodiverse and hence resilient Okavango Delta.

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APPENDIX A. Descriptions of algal phyla

A background on all the algal phyla described is provided here. Fourteen phyla of algae are known to live in freshwater and marine environments: Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanophyta, Euglenophyta, Eustigmatophyta, Glaucophyta, Haptophyta, Phaeophyta, Prasinophyta, Pyrrophyta, Raphidophyta, Rhodophyta and Xanthophyta. Synthetic descriptions of the existing phyla of algae are reported below mainly drawing from three sources: Bellinger and Sigee (2010), John *et al.* (2002) and Lee (2008).

Bacillariophyta (diatoms)

Bacillariophyta have cells encased within a cell wall made of silica (hydrated silicon dioxide) called a frustule, which usually consist of two asymmetrical valves, the hypovalve and the epivalve, separated by a cingulum with girdle bands. Two major subgroups exist with characteristic shape: centric (radially symmetric, e.g. *Cyclotella*) and pennate diatoms (bilaterally symmetric); the latter is composed of species with a raphe (raphid) or without it (araphid). The raphe is a groove or channel able to allow the cell's movement along a substrate by secretion of mucilaginous material - carbohydrate-rich extracellular polymeric substances, EPS which are used by bacteria, meiofauna, and macrofauna as a carbon source; Underwood *et al.* (2004). Thus raphid diatoms are motile; they have either two raphes like in *Navicula* (biraphid) or just one like in *Achnanthes* (monoraphid) while araphid diatoms are non-motile (e.g. *Synedra*). Truly planktonic diatoms usually are non-motile. Sexual reproduction is an obligate stage in most diatom species, which have a unique life cycle and size-dependent control of sexuality (Chepurnov *et al.*, 2004).

Diatoms are responsible for approximately 40% of the net aquatic primary production and more than 50% of the organic carbon that is exported to the ocean interior (Falkowski *et al.*, 2004) and use a fucoxanthin chlorophyll *a/c* complex to undertake photosynthesis. Benthic diatoms may undertake diurnal migrations, e.g., in estuarine intertidal zones (Consalvey *et al.*, 2004); irradiance has been shown to be more important than other factors, such as tides, in triggering vertical migration in diatoms in tropical intertidal flats in India (Mitbavkar, 2004).

Diatom distribution patterns in rivers are determined by nutrients, flow rate, turbidity, light, temperature, acidity, and salinity (Dixit *et al.*, 1992) and not just by random dispersal. Bacillariophyta possess specific characteristics in different environments. For example, planktonic diatoms have evolved a nutrient storage vacuole that retains high

concentrations of nitrate and phosphate (Tozzi *et al.*, 2004). The storage vacuole allows diatoms to exploit pulses of inorganic nutrients, which can deprive competing taxa of these resources, overcome light-dependent nutrient uptake in mixing systems, or both. Two to three cell divisions can be performed thanks to this storage capacity without the need for nutrient uptake from the environment. Consequently, planktonic diatoms thrive best in regions where nutrients are supplied with high pulse frequencies (Katz *et al.*, 2006). On the other hand, in benthic diatoms living attached to sediments / mud (epipelic) motility is a key feature; in fact the motility allows these diatoms to access nutrients that may not be available in the immediate surroundings. Several diatoms are also able to fix nitrogen, e.g. *Epithemia* spp. and *Rhopalodia gibba*, not independently, but due to their cyanobacterial endosymbionts (Prechtl *et al.*, 2004); others are themselves endosymbionts in dinoflagellates and foraminifers (Round *et al.*, 1990). Facultative heterotrophy is another way by which diatoms uptake nutrients, especially when light availability is low in the aquatic environment (Tuchman *et al.*, 2006). Planktonic diatoms, analogously to, e.g. dinofagellates, can form resting stage cells (Hargraves and French 1983; Garrison 1984).

Like other algae, the Bacillariophyta respond directly to growth stimulants (nutrients) and/or stressors such as toxic compounds, as well as to physical factors and therefore are extensiviely used in biomonitoring. Diatoms are essential in environmental diagnostics because they show a broad range of tolerance along a gradient of aquatic productivity and they are sensitive to changes in nutrient concentrations, supply rates and silica/phosphate ratios; having an extremely short generation time (Round, 1991) they can be used as early signals to detect important ecological changes such as the degradation of water quality (De la Rey *et al.*, 2004). The assessment of the ecological status of freshwater bodies such as rivers (Kelly *et al.*, 2008; Yallop *et al.*, 2009; Omar, 2010), lakes (Reavie *et al.*, 2006; Bennion *et al.*, 2014), wetlands (Harding *et al.*, 2005; Salomoni *et al.*, 2006; Weilhoefer *et al.*, 2008) and ditches (Yallop, 2008) relies increasingly on diatoms. Changes in diatom assemblages can be studied alongside shifts in other biotic assemblages such as other algae, zooplankton and fish in order to comprehensively assess aquatic ecosystems' health (Harding *et al.*, 2005).

Diatoms are the most species-rich group of microbial eukaryotes and have global to narrow endemic geographic distribution (Vanormelingen *et al.*, 2008). Despite most of the >900 known genera (Fourtanier and Kociolek, 1999) and morphospecies (Krammer and Lange-Bertalot, 1986–1991) being cosmopolitan, numerous examples of endemic species (Potapova and Charles, 2002) exist, suggesting an underestimation of

geographical factors influencing their distribution (Kociolek and Spaulding, 2000). Different authors estimate the number of existing species of diatoms; from 10,000 - 12,000 species (Round *et al.*, 1990; Norton *et al.*, 1996), to 20,000 (Guiry, 2012) or 200,000 species according to Mann and Dropp (1996). Andersen (1992) suggests that as many as 10 million species of Bacillariophyta may exist. Thus diatoms may be the most diverse algal phyla, followed by green algae, though many species are yet to be described in all phyla.

Chlorophyta (green algae)

Green algae are photosynthetic eukaryotes with double membrane-bound plastids containing Chlorophyll *a* and *b*, ß-carotene and xanthophylls (Lee, 2008). They have nine pairs of microtubules in the flagellar base arranged in a stellate structure (Kenrick and Crane, 1997). Starch is stored inside the plastid and cell walls which are usually composed of cellulose (Graham and Wilcox, 2000). Green algae do not produce the algal blooms typical of diatoms, blue-green algae, and dinoflagellates, but they tend to become dominant or co-dominant in the early summer; large mats of periphyton, i.e. attached algae may form under high nutrient concentrations (Bellinger and Sigee, 2010). Reproduction can be asexual via fragmentation or formation of spores (non-flagellated aplanospores or autospores, e.g. in *Chlorella*) similar to the mother cell (Lee, 2008) or sexual via conjugation, for example in Zygnematiinae such as *Mougeotia*, for which genus species identification requires the observation of reproductive stages (Bellinger and Sigee, 2010). Chlorophyta are well adapted to high light availability, with desmids being even better adapted to high light than other green algae (Schwaderer *et al.*, 2011).

The morphology of green algae ranges from flagellate and nonflagellate unicells (e.g. *Monoraphidium*) to colonial forms (e.g. *Volvox*), coenobia (e.g. *Pediastrum*, *Oocystis*) and unbranched (e.g. *Oedogonium*, *Mougeotia* and *Zygnema*) and branched filaments (order Charales). John *et al.* (2002) grouped microscopic green algae into these most important orders:

1. Volvocales: motile vegetative cells with 2-4 flagella, sexual reproduction (most commonly isogamous) or asexual reproduction by simple division or via zoospores; common genera are colonial *Volvox* and unicellular *Chlamydomonas*.

2. Chlorococcales: coccoid unicells and non-motile coenoibia; Hoek *et al.* (1995) broadened the group to include all green algae in which the daughter cells stay in the parental wall to make of Chlorococcales one of the largest chlorophyte orders.

Examples of genera are *Chlorella*, *Monoraphidium* and *Oocsystis*, *Pediastrum*, *Scenedesmus*.

3. Oedogoniales: branched (*Bubochaete*) and unbranched (*Oedogonium*), filamentous algae with a specialised sexual reproduction important for species determination, based on features of organs, gametes and spores.

4. Zygnematales: three large sub-orders: i) Zygnematiinae, including the Zygnemataceae family, such as the widely distributed *Mougeotia, Spirogyra* and *Zygnema* and the Mesotaeniaceae, saccoderm desmids having simple cells with circular cross-section and no median constriction, pores or ornamentations (e.g. *Cylindrocystis*, *Mesotaenium*, *Netrium* and *Spirotaenia*) (John *et al.*, 2002); ii) Closteriineae, with elongated cells without median constriction (cylindrical or with extended conical curved ends) and with one plane of symmetry (e.g., *Closterium*, *Gonatozygon* and *Penium*) and iii) Desmidiineae ("true" or placoderm desmids), with laterally compressed cells (with three planes of symmetry), walls with one constriction called isthmus where adjacent segments overlap. Many species have ornamented walls with pores; unicellular genera include *Cosmarium*, *Euastrum*, *Haplotenium*, *Micrasterias*, *Staurastrum*, *Staurodesmus* and *Xanthidium* while examples of filamentous forms are *Teilingia*, *Onychonema* (with *Cosmarium*-like cells) and *Bambusina* and *Desmidium* (cells more similar to *Staurastrum*) (see also Lind and Brook, 1981).

Chlorophyta have high growth and loss rates so that their nutrient demand is high (C-strategist, *sensu* Reynolds, 1988) to the point that, with very high P and N concentrations in shallow non stratified lakes, green algae can compete with nitrogen-fixing Cyanophyta (Jensen *et al.*, 1994). Green algae have been widely used in ecological studies as indicators of environmental change such as water pollution (e.g. Foster, 1982, del Giorgio *et al.*, 1991) or oligotrophy, i.e. better water quality due to lower nutrient levels indicated by desmids (Coesel, 1983; 2001). Desmids live in "*stabilized environments rich in ecological niches*" and are susceptible to environmental disturbance; this makes them good early indicators of environmental change (Coesel, 1977). In particular, Desmidiinae and Mesotaeniaceae represent a significant part of the algal biomass in nutrient poor / slightly acidic ecosystems, but they may also live in more alkaline environments (Borics *et al.*, 2003). They rely on clear, relatively nutrient poor water, are most abundant in environments with spatial (habitat) and temporal (niche) differentiations (Coesel, 1983) and they reach high species diversity in shallow wetlands (Bellinger and Sigee, 2010). Chlorophyta mostly reproduce vegetatively, with sexual reproduction being infrequent, but present in

genera such as *Cylindrocystis* (www.desmids.nl) and *Closterium* (Sekimoto *et al.*, 2012). The majority of desmid taxa are regarded as K-strategists as they place high demands on environmental conditions (Spijkerman *et al.*, 2004). These, like other green algae, are thought to have a terrestrial origin (Stebbins and Hill, 1980) and hence are often most abundant in areas dominated by macrophytes, i.e. most desmids are benthic, e.g. epiphytic forms (e.g. Borics *et al.*, 2003). Stable water supply and presence of macrophytes have been shown to allow the development of a rich algal flora in numerous microhabitats, for example in bog lakes (e.g. Borics *et al.*, 2003). Desmids are of particular interest in the Okavango Delta due to the fact that they are thought to have evolved in the tropics for the following reasons: i) they are more diversified in tropical regions as compared to that in (sub)polar areas; ii) their share of total algal biomass and abundance tends to be higher in tropical aquatic systems than in cold-temperate ones; iii) the optimal growth temperature for several desmid strains ranges from 25 to 30 °C (Coesel, 1996), and they are well adapted to high light intensities, typical of shallow water bodies, but also low latitudes (Stamenković and Hanelt, 2011). These algae are used in environmental monitoring, for example, Coesel (2001) proposed a method to assess the intrinsic nature conservation value of different environments on the basis of desmid species richness, rarity and presence of taxa indicating ecosystem maturity, e.g., *Micrasterias*, *Tetmemorus* and *Actinotaenium*.

Chlorophyta (green algae) are one of the most diverse groups of algae, with about 16,000 - 17,000 recognized extant species (Andersen, 1992; Graham and Wilcox, 2000) and up to 100,000 species that may remain to be described (Andersen, 1992). Zygnematales and Desmidiales are the most species-rich group, with approximately 25% (4,000) of the total green algal species (Gerrath, 2003). Chlorophyta are mostly (90%) freshwater, with about 10% of green algae living in marine environments (Smith, 1955) and tend to be cosmopolitan (Fritsch, 1953; Lee, 2008). Reproduction or genetic experiments have been rarely used to test the reality of cosmopolitanism among algae (Tyler, 1996) and endemic species of algae (genera *Scenedesmus* and *Chlorella*) were recorded in Brazil, Europe, North America and Java (e.g. desmid species of *Euastrum* and *Staurastrum*) (Tyler, 1996). The Australian algal flora is characterised by high endemism. Indeed some species have been likely overlooked due to force-fitting of European names to Australian species (Tyler, 1996). In general, rarity, e.g. due to insufficient investigation, can be mistaken for endemism; very small algae can be more easily overlooked (Tyler, 1996).

Chrysophyta (golden brown algae)

These algae are golden-brown coloured mixotrophic algae containing fucoxanthin, a golden-brown pigment, also found in diatoms. They are equipped with unequal flagella, one long and hairy and the other short and smooth. They form resting stages named stomacysts that have silicified wall with a pore. Some species are provided with siliceous scales, e.g. the flagellate *Mallomonas*, whereas the cells of another common genus, *Dinobryon*, are not covered by siliceous structures, but live in vase-like cases composed of cellulose. Chrysophytes have a fragile cell construction and do not disperse that well due to desiccation problems (Kristiansen, 2008), but they are as widely distributed as, e.g., cyanobacteria and desmids, which have cells better adapted for dispersal (Hoffman, 1996; Coesel, 1996). These mainly freshwater algae are difficult to identify to species level without SEM microscopy; however their cysts (statospores) are used in palaeoecological studies to reconstruct past environmental conditions, e.g., lake acidification and eutrophication (Smol, 1988). There are about 1,000 species of Chrysophyta, mostly unicellular and colonial flagellates, mainly living in freshwater environments. Previously deemed to be restricted to temperate waters, Chrysophytes have been found to have a tropical flora of about 20 taxa, some endemic and others widely distributed across the tropics, e.g. Australia, Papua New Guinea and tropical East Asia (Cronberg, 1989 in Vyverman and Cronberg, 1993).

Cryptophyta (cryptomonads)

Cryptophyta are small to medium sized algae with high cell surface:volume ratios forming a relative minor part of the phytoplankton, they are similar to Euglenophyta for structure (section 1.3.6), but they do not form part of the benthos. Most cryptomonad species swim following a spiralling path with the flagella directed forwards, but the cell also revolves about its longitudinal axis (John *et al.*, 2002). These algae have chlorophyll *a* and *c2* as well as carotene and diatoxanthin (Lee, 2008). Cryptophyta are very sensitive to light, often living at high depths in oligotrophic lakes (Nauwerck, 1968); they migrate vertically by less than 5 metres and they are mixotrophic, being able to ingest bacteria (phagotrophy) or synthetise organic compounds from inorganic nutrients (phototrophy) (Lee, 2008). These algae difficult to identify by means of light microscopy alone due to the absence of distinctive characteristics, their significant phenotypic variability and constant developments in their taxonomy and systematics. Cryptophyta are typical of temperate waters and abound in colder seasons. 200 species

have been described, about 100 in freshwater environments. *Cryptomonas*, *Chroomonas* and *Rhodomonas* are the most important genera of this phylum.

Cyanophyta (Cyanobacteria)

The Cyanophyta are unicellular and colonial prokaryotic algae with their cell contents not differentiated into organelles surrounded by membranes such as chloroplasts and mitochondria. Colonies may be filamentous, sheets or hollow balls (John *et al.*, 2002). They contain chlorophyll *a* and *b*, but also the blue pigment phycocyanin; hence the name Cyanophyta. Some bacteriologists group these algae under the name Cyanobacteria according to the conventions of the International Code for Bacteriological Nomenclature; others classify them as per the International Code for Botanical Nomenclature.

Cell dimensions vary from 0.6 μm to over 30 μm, but multicellular filaments can be a few millimiters long. Some species of Cyanophyta (e.g. *Nostocales*) are able to fix nitrogen by means of specialized organelles (heterocysts); a number of species possess gas vacuoles to help buoyancy (e.g. *Oscillatoria*). Some filamentous colonies form akinetes (e.g. *Nostoc*), i.e. spores resistant to difficult climatic conditions (e.g. low temperature), phosphate deficiency, carbon limitation and reduced light energy (Li *et al.*, 1997). Blue-green algae have a thick, gelatinous cell wall / sheath, they lack flagella, but filamentous forms like *Oscillatoria* are capable of a waving motion.

Cyanophyta may form summer blooms because of their optimum growth at high temperatures, they tolerate low light due to high efficiency in using it (Schwaderer *et al.*, 2011), prefer low N/P ratios and high pH/low CO_2 concentrations. These prokaryotic algae can regulate their position in the water column by buoyancy, they resist zooplankton grazing and form symbioses with aerobic bacteria (Bellinger and Sigee, 2010). Cyanophyta evolved over 3.5 billion years ago and have contributed decisively to the transformation of the Earth's atmosphere enriching it with oxygen (Schopf, 1993).

The orders of Cyanophyta and their distinctive features are:

1. Chroococcales: never form true filaments;
2. Oscillatoriales: filaments, but not forming heterocysts;
3. Nostocales: unbranched filaments forming heterocysts;
4. Stigonematales: branched filaments forming heterocysts.

Cyanophyta may be considered prokaryotic bacteria (Cyanobacteria) rather than algae, but they occupy the same niche as most algae, given that they are planktonic autotrophs preferring more turbid waters than green algae do (Scheffer and Nes, 2007). Whereas these microorganisms can stabilize their dominance in turbid waters, their maximum growth is lower than that of most other algae; therefore in clear waters other primary producers like green algae are more competitive and can become dominant over Cyanophyta (Scheffer and Nes, 2007). These prokaryotes tend to be S-strategists (*sensu* Reynolds, 1988) with lower growth and loss rates than Chlorophyta; in deep lakes (but not in shallow ones) they are able to outcompete green algae (Jensen *et al.*, 1994). Both cosmopolitan and holarctic or pantropical taxa of Cyanophyta exist and there may be endemic species (Hoffmann, 1996). In the tropics habitat diversity is high, with environments found only there, such as rainforests and lateritic soils. This may have allowed morphological types of Cyanophyta to evolve adapting to these special biotopes (Komarek, 1985), thus explaining the latitudinal distribution patterns of many species (Hoffmann, 1996).

Euglenophyta

The Euglenophyta are unicellular, flagellated or able to move changing body shape (metaboly); they normally live in environments with decaying material and many of them are heterotrophic (they used to be classified as *Protozoa*). The outer part of the cell consists of a pellicle formed by a plasma membrane, units of proteins, subtending microtubules and tubular cisternae of endoplasmic reticulum (Leander and Farmer, 2000); some euglenoids contain chloroplasts, others are heterotrophic and can ingest or absorb their food (stored as a polysaccharide, paramylon). When present, cells have several chloroplasts of dark green colour with different shapes and contain both chlorophyll *a* and *b*; the storage product is paramylon (John *et al.*, 2002). The cells have one or more active contractile vacuoles and usually have two flagella, one reduced and not emergent, while the emergent one forms the photosensory transduction system with the photoreceptor and red-orange eyespot. These algae move by swimming in a rotational fashion with a variable wobbling motion in different species and they reproduce asexually by longitudinal division. This phylum includes about 800 species (belonging to over 40 genera). Most are colourless and have phagotrophic or heterotrophic nutrition, but one third are green and phototrophic (John *et al.*, 2002). Common genera are *Euglena*, *Phacus* and *Trachelomonas,* the last is typically surrounded by a lorica, or hard surrounding cell. These algae live in a wide range of

water bodies with varying organic matter content and pH and in aerobic or anaerobic conditions. From a biogeographic viewpoint, over 200 species are restricted to South America, with more than 100 belonging to the genus *Trachelomonas* (Tell, 1998). A few *Euglena* species are found exclusively in North America and central Europe (Tyler, 1996).

Eumastigophyta

The Eumastigophyta are yellow-green unicellular algae occurring in freshwater, brackish and seawater and in the soil, with cells similar to those of the Xanthophyta. Their name stems from a large orange-red eyespot in the flagellated forms (two flagella present), placed outside rather than inside the chloroplast, as in the Xanthophyta. The choroplasts have chlorophyll *a*, ß-carotene and two xanthophylls (Lee, 2008).

Glaucophyta

The Glaucophyta are a very old group of algae with endosymbiotic Cyanophyta called cyanelles in place of chloroplasts in the cytoplasm, deemed to be an intermediate stage in the evolution of the chloroplast. The pigments of the Glaucophyta are chlorophyll *a* and phycobiliproteins. The main genera are *Glaucocystis* and *Cyanophora*, both living in freshwater ecosystems (Lee, 2008).

Haptophyta

These algae also known as Prymnesiophyta, are flagellates with two flagella. Their chloroplasts contain chlorophylls *a*, *c1/c2* and sometimes *c3* but their green colour is masked by accessory pigments, so that the chloroplasts appear golden or yellow-brown. Small calcified scales (coccoliths) are present in species of coccolithophorids. The large majority of the 300 described species of Haptophyta are marine, with about a dozen freshwater species (John *et al.*, 2002).

Phaeophyta

This group of algae is mostly composed of benthic macroscopic seaweeds, with 1% of species being microscopic freshwater filamentous species. A total of 2,000 species is estimated to exist worldwide; these algae are usually brown (they are also called brown algae) or yellow in colour (John *et al.*, 2002).

Prasinophyta

This phylum represents the oldest group of green algae from which all other phyla may have evolved; it is deemed to include about 100 species. They are mostly flagellate algae, characterised by yellowish-green colour and by organic scales on the cell walls (John *et al.*, 2002).

Pyrrophyta (dinoflagellates)

Pyrrophyta are unicellular motile algae, naked or with an organic cell wall composed of a set of plates. The plates can be thick in the armoured forms with ornamentations or they can be less reinforced; the plate pattern of the latter helps distinguish between genera. The cell is divided into two halves by a broad horizontal groove; each half has a flagellum and the cell moves by waving the flagella in a characteristic whirling motion from which the name dinoflagellate comes. The colour of the chloroplasts (*a* and *c2*) is different gradations of brown and peridinin and neoperidinin are the main carotenoids. These algae are common in fresh waters, particularly in small water bodies, but their greatest diversity is in the sea. The rate of division is low, typical of K-strategists; dinoflagellates may use facultative heterotrophy as an alternative to photosynthesis (Gaines and Elbrachter, 1987). During summer some species perform diurnal vertical migrations along the water column to follow nutrient concentrations, i.e. moving towards the light by day and to phosphate-rich bottom waters at night (e.g. bloom-forming *Glenodinium sanguineum*; Flaim *et al.*, 2003). Dinoflagellate blooms are usually unpredictable, ephemeral phenomena. They have multiple life-forms adapted to diverse habitats but tend to be represented just by one or a few species at a given location (Smayda and Reynolds, 2003). About 3,000 species are known to science; common genera are *Peridinium*, *Ceratium*, *Gymnodinium* and *Amphidinium* (John *et al.*, 2002); endemism has been recorded in Australia and Tasmania (Tyler, 1996).

Raphidophyta

The Raphidophyta are a small group of unicellular bi-flagellated algae. Some genera have chlorophylls *a* and *c* and several xanthophylls. Both marine and freshwater species exist, the latter in acid waters of ponds and pools (John *et al.*, 2002).

Rhodophyta (red algae)

The Rhodophyta, or red algae, have eukaryotic cells with no flagella; they contain the accessory photosynthetic pigments phycoerythrin, phycocyanin and allophycocyanins

arranged in phycobilisomes, and do not have flagella and centriole (Woelkerling, 1990). These algae are found mostly in marine environments, e.g. as carbonate-secreting autotrophs in coral reefs, with only 3% of the over 5,000 species living in freshwater habitats (Sheath, 1984).

Xanthophyta (yellow-green algae)

Xanthophyta are characterized by having disc-like carotenoids-rich yellow-green plastids (useful to discriminate them from green algae) and by accumulating oil and leucosin rather than starch (John *et al.*, 2002). Reproduction is by and large asexual, but sexual reproduction has been found in three genera: *Botrydium*, *Tribonema* and *Vaucheria* (Lee, 2008). These algae are distinguished from the Chlorophyta by yellow-brown chloroplasts, absence of pyrenoids and starch and presence of carhohydrate granules as storage product, and walls of pectin or pectic acid. They do not contain chlorophyll b, but have chlorophyll *a*, *c1* and *c2* as well as carotenoids and three or more xanthophylls (John *et al.*, 2002). 600 species (100 genera) are deemed to exist globally (mostly non-motile cells or colonies), living mostly in small water bodies, particularly in hard and humic waters in spring, but sometimes also found in subaerial habitats (John *et al.*, 2002).

APPENDIX B. ***Full list of the algal species observed in the Okavango Delta (main source of authorities: www.algaebase.org).***

BACILLARIOPHYTA

Species	**Authority**
Achnanthidium minutissimum	(Kützing) Czarnecki 1994
Amphora libyca	Ehrenberg 1840
Amphora ovalis	Kützing 1844
Amphora pediculus	(Kützing) Grunow in Schmidt 1875
Asterionella formosa	Hassall (1850)
Aulacoseira ambigua	(Grunow) Simonsen 1979
Aulacoseira granulata	(Ehrenberg) Simonsen 1979
Caloneis bacillum	(Grunow) Cleve 1894
Caloneis tenuis	(W.Gregory) Krammer
Caloneis undulata	(W.Gregory) Krammer
Craticula cuspidata	(Kützing) Mann 1990
Cymatopleura solea	(Brébisson and Godey) W. Smith (1851)
Cymbella cuspidata	Kützing 1844
Cymbella naviculiformis	(Auerswald) Cleve (1894)
Epithemia adnata	(Kützing) Brébisson 1838
Eunotia alpina	(Nägeli) Hustedt in Schmidt *et al.* 1913
Eunotia arcus	Ehrenberg 1837
Eunotia asterionelloides	Hustedt 1952
Eunotia bilunaris	(Ehrenberg) Schaarschmidt 1880
Eunotia exigua	(Brébisson ex Kützing) Rabenhorst 1864
Eunotia faba	(Ehrenberg) Grunow in van Heurck 1881
Eunotia flexuosa	(Brébisson ex Kützing) Kützing 1849
Eunotia incisa	W.Smith ex W.Gregory 1854
Eunotia intermedia	(Krasske) Nörpel and Lange-Bertalot in Lange-Bertalot 1993 1993
Eunotia minor	(Kützing) Grunow in van Heurck 1881
Eunotia muscicola	Krasske 1939
Eunotia naegellii	Migula 1907
Eunotia okawangoi	Cholnoky
Eunotia pectinalis	(Kützing) Rabenhorst 1864
Eunotia praerupta	Ehrenberg 1843
Eunotia rhomboidea	Hustedt 1950
Eunotia serra	Ehrenberg 1837
Eunotia soleirolii	(Kützing) Rabenhorst 1864
Fragilaria africana	Hustedt
Fragilaria crotonensis	Kitton 1869
Frustulia rhomboides	(Ehrenberg) De Toni 1891
Frustulia saxonica	Rabenhorst 1853
Gomphonema angustum	C. Agardh 1831

Species (Bacillariophyta)	Authority
Gomphonema augur	Ehrenberg 1840
Gomphonema clevei	Fricke in Schmitd *et al.* 1902
Gomphonema globiferum	Meister 1913
Gomphonema gracile	Ehrenberg 1838
Gomphonema hebridense	W.Gregory 1854
Gomphonema lanceolatum	Kützing 1844
Gomphonema olivaceum	(Hornemann) Brébisson 1838
Gomphonema parvulum	(Kützing) Kützing 1849
Gomphonema pfannkucheae	Cholnoky
Gomphonema resendei	Moura
Gomphonema subtile	Ehrenberg 1843
Gomphonema truncatum	Ehrenberg 1832
Gyrosigma spencerii	(W.Smith) Griffith and Henfrey 1856
Hantzschia amphyoxis	(Ehrenberg) Grunow in Cleve & Grunow 1880
Meridion circulare	(Greville) C.Agardh 1831
Navicula cryptocephala	Kützing 1844
Navicula cryptotenella	Lange-Bertalot in Krammer and Lange-Bertalot 1985
Navicula halophila	(Grunow) Cleve 1894
Navicula laevissima	Kützing 1844
Navicula menisculus	Schumann 1867
Navicula pupula	Kützing 1844
Navicula radiosa	Kützing 1844
Navicula veneta	Kützing 1844
Neidium ampliatum	(Ehrenberg) Krammer in Krammer and Lange-Bertalot 1985
Neidium productum	(W.Smith) Cleve 1894
Nitzschia acicularis	(Kützing) W.Smith 1853
Nitzschia linearis	(C.Agardh) W.Smith 1853
Nitzschia pellucida	Grunow 1880
Nitzschia perminuta	(Grunow) M.Peragallo 1903
Nitzschia recta	Hantzsch ex Rabenhorst 1862
Nitzschia scalaris	(Ehrenberg) W.Smith 1853
Nitzschia sigma	(Kützing) W.Smith 1853
Nitzschia sigmoidea	(Nitzsch) W.Smith 1853
Nitzschia subacicularis	Hustedt
Nitzschia vermicularis	(Kützing) Hantzsch in Rabenhorst 1860
Pinnularia abaujensis	(Pantocsek) R.Ross 1947
Pinnularia braunii	(Grunow) Mills 1934
Pinnularia divergentissima	(Grunow) Cleve 1895
Pinnularia gibba	Ehrenberg 1843
Pinnularia interrupta	W.Smith 1853

Species (Bacillariophyta)	Authority
Pinnularia lundii	Hustedt 1954
Pinnularia maior	Kutzing (Rabenhorst) 1997
Pinnularia mesolepta	(Ehrenberg) W.Smith 1853
Pinnularia nobilis	(Ehrenberg) Ehrenberg 1843
Pinnularia subcapitata	W.Gregory 1856
Pinnularia subrostrata	(A.Cleve) Cleve-Euler 1955
Pinnularia viridis	(Nitzsch) Ehrenberg 1843
Rhopalodia gibba	(Ehrenberg) O. Müller (1895)
Sellaphora bacillum	(Ehrenberg) D.G.Mann 1989
Sellaphora pupula	(Kützing) Mereschkovsky 1902
Stauroneis anceps	Ehrenberg 1843
Stauroneis phoenicenteron	(Nitzsch) Ehrenberg 1843
Stauroneis producta	Grunow in van Heurck 1880
Surirella capronii	Brébisson ex F.Kitton
Surirella elegans	Ehrenberg
Surirella linearis	W.Smith 1853
Synedra acus	Kützing 1844
Synedra amphicephala	Kützing 1844
Synedra capitata	Ehrenberg (1836)
Synedra nana	F.Meister 1912
Synedra rumpens	Kützing 1844
Synedra ulna	Ehrenberg 1832
Tabellaria fenestrata	(Lyngbie) Kützing 1844

CHLOROPHYTA	
Species	**Authority**
Actinastrum hantzschii	Lagerheim 1882
Actinotaenium cucurbitum	Teiling
Ankistrodesmus falcatus	(Corda) Ralfs 1848
Ankistrodesmus spiralis	(W.B.Turner) Lemmermann 1908
Bambusina borreri	(Ralfs) Cleve 1864
Bambusina brebissonii	Kützing ex Kützing 1849
Chlamydomonas mirabilis	Pascher 1927
Chlorobion braunii	(Nägeli) Komàrek 1979
Closteriopsis acicularis	(Chodat) J.H.Belcher and Swale 1962
Closterium acerosum	Ehrenberg ex Ralfs 1848
Closterium aciculare	West 1860
Closterium acutum	Brébisson in Ralfs 1848
Closterium attenuatum	Ralfs 1848
Closterium closterioides	(Ralfs) A.Louis and F.Peeters 1967
Closterium cornu	Ehrenberg ex Ralfs 1848
Closterium dianae	Ehrenberg ex Ralfs 1848
Closterium directum	W.Archer 1862
Closterium ehrenbergii	Meneghini ex Ralfs 1848

Species (Chlorophyta)	Authority
Closterium gracile	Brébisson ex Ralfs 1848
Closterium idiosporum	West and G.S.West 1900
Closterium incurvum	Brébisson 1856
Closterium jenneri	Ralfs 1848
Closterium juncidum	Ralfs 1848
Closterium kuetzingii	Brébisson 1856
Closterium leiblenii	Kutzing ex Ralfs 1848
Closterium littorale	F.Gay 1884
Closterium lunula	Ehrenberg and Hemprich ex Ralfs 1848
Closterium monoliferum	(Bory) Ehrenberg ex Ralfs 1848
Closterium navicula	(Brebisson) Lutkemuller 1902
Closterium parvulum	Nägeli 1849
Closterium ralfsii	Brébisson ex Ralfs 1848
Closterium setaceum	Ehrenberg ex Ralfs 1848
Closterium subfusiforme	Messikommer
Closterium venus	Kutzing ex Ralfs 1848
Coelastrum microporum	Nägeli 1855
Coelastrum pseudomicroporum	Korshikov 1953
Coelastrum sphaericum	Nägeli 1849
Cosmarium regnellii	Wille 1884
Cosmarium annulatum	(Nägeli) de Bary 1849
Cosmarium australe	Raciborski (Lütkemüller)
Cosmarium binum	Nordstedt in Wittrock and Nordstedt 1880
Cosmarium bioculatum	Brébisson ex Ralfs 1848
Cosmarium biretum	Ralfs, J. (1848)
Cosmarium blythii	Wille 1880
Cosmarium botrytis	Meneghini ex Ralfs 1848
Cosmarium brebissonii	Meneghini ex Ralfs 1848
Cosmarium caelatum	Ralfs 1848
Cosmarium connatum	Brébisson in Ralfs 1848
Cosmarium contractum	Kirchner 1878
Cosmarium cucumis	Corda ex Ralfs 1848
Cosmarium depressum	(Nägeli) P.Lundell 1871
Cosmarium difficile	Lütkemüller 1892
Cosmarium elegantissimum	P.Lundell 1871
Cosmarium formulosum	Hoff in Nordstedt 1888
Cosmarium geminatum	P.Lundell 1871
Cosmarium granatum	Brébisson in Ralfs 1848
Cosmarium haynaldii	Schaarschmidt 1883
Cosmarium impressulum	Elfving 1881
Cosmarium margaritatum	(P.Lundell) J.Roy and Bisset 1886
Cosmarium meneghinii	Brébisson ex Ralfs 1848
Cosmarium moniliforme	Ralfs 1848
Cosmarium monomazum	P.Lundell 1871

Species (Chlorophyta)	Authority
Cosmarium obsoletum	(Hantzsch) Reinsch 1867
Cosmarium okavangicum	Coesel and van Geest 2009
Cosmarium ornatum	Ralfs ex Ralfs 1848
Cosmarium portianum	Archer 1860
Cosmarium pseudoconnatum	Nordstedt 1870
Cosmarium pseudoprotuberans	O.Kirchner 1878
Cosmarium pseudopyramidatum	P.Lundell 1871
Cosmarium pseudosulcatum	Rich in F.E.Fritsch & Rich 1937
Cosmarium pseudotus	Coesel and Van Geest 2009
Cosmarium pygmaeum	W.Archer 1864
Cosmarium pyramidatum	Brébisson ex Ralfs 1848
Cosmarium quadratulum	(F.Gay) De Toni 1889
Cosmarium ralfsii	Brébisson ex Ralfs 1848
Cosmarium regnesii	Reinsch 1867
Cosmarium reniforme	(Ralfs) W. Archer 1874
Cosmarium richianum	Compère 1987
Cosmarium taxichondrum	P.Lundell 1871
Cosmarium trilobulatum	Reinsch 1866
Cosmarium turpinii	Brebisson 1856
Cosmarium undulatum	Corda ex Ralfs 1848
Cosmarium zonatum	P.Lundell 1871
Crucigenia tetrapedia	(Kirchner) West et G.S. West 1902
Crucigeniella crucifera	(Wolle) Komarek 1974
Crucigeniella rectangularis	(Nägeli) Komàrek 1974
Desmidium grevillei	(Ralfs) De Bary 185
Desmodesmus communis	Hegewald 2000
Docidium baculum	Brébisson ex Ralfs 1848
Eremosphaera gigas	(W.Archer) Fott and Kalina 1962
Eremosphaera viridis	De Bary 1858
Euastrum africanum	(Bourrelly) Coesel and Van Geest 2008
Euastrum ansatum	Ralfs 1848
Euastrum attenuatum	Wolle
Euastrum bidentatum	Nägeli 1849
Euastrum binale	(Turpin) Ehnrenberg ex Ralfs 1848
Euastrum denticulatum	F. Gay 1884
Euastrum divergens	Joshua 1886
Euastrum dubium	Nageli 1849
Euastrum elegans	(Brebisson) Kützing ex Ralfs 1848
Euastrum mononcylum	(Nordstedt) Raciborski 1885
Euastrum pectinatum	Brebisson ex Brebisson in Ralfs 1848
Euastrum sphyroides	Nordstedt 1888
Euastrum spinulosum	Delponte 1876
Euastrum truncatiforme	G.S. West 1907
Euastrum verrucosum	Ehrenberg ex Ralfs 1848

Species (Chlorophyta)	Authority
Golenkinia paucispina	(J.W.G.Lund) Fott 1981
Golenkiniopsis chlorelloides	West and G.S.West 1902
Gonatozygon aculeatum	Hastings 1892
Gonatozygon brebissonii	De Bary 1858
Gonatozygon kinahanii	(Archer) Rabenhorst 1868
Gonatozygon monotaenium	De Bary 1856
Gonatozygon pilosum	Wolle 1882
Groenbladia undulata	(Nordstedt) Kurt Förster 1973
Haplotaenium minutum	(Ralfs) T.Bando 1988
Haplotaenium rectum	(Delponte) Bando 1988
Hyalotheca dissiliens	Brébisson ex Ralfs 1848
Kirchneriella irregulare	(G.M.Smith) Korshikov 1953
Kirchneriella obesa	(G.S.West) West and G.S.West 1894
Koliella spiculiformis	(Vischer) Hindák 1963
Korshikoviella michailovskoensis	(Elenkin) P.C.Silva 1959
Micrasterias americana	Ehrenberg ex Ralfs 1848
Micrasterias crux-melitensis	(Ehrenberg) Trevisan 1842
Micrasterias foliacea	Bailey ex Ralfs 1848
Micrasterias mahabaleshwarensis	Brühl and Biswas
Micrasterias oscitans	Ralfs 1848
Micrasterias pinnatifida	Ralfs 1848
Micrasterias pusilla	G.C.Wallich
Micrasterias rotata	Ralfs 1848
Micrasterias tropica	Nordstedt 1870
Micrasterias truncata	Ralfs 1848
Monoraphidium arcuatum	(Korshikov) Hindák 1970
Monoraphidium contortum	(Thuret) Komàrková-Legnerová 1969
Monoraphidium convolutum	(Corda) Komárková-Legnerová 1969
Monoraphidium griffithii	(Berkeley) Komárková-Legnerová 1969
Monoraphidium irregulare	(G.M.Smith) Komárková-Legnerová
Monoraphidium komarkovae	Nygaard 1979
Monoraphidium minutum	(Nägeli) Komárková-Legnerová 1969
Monoraphidium obtusum	(Korshikov) Komárková-Legnerová 1969
Monoraphidium pusillum	(Printz) Komárková-Legnorová 1969
Monoraphidium tortile	(West and G.S.West) Komárková-Legnerová 1969
Netrium digitus	(Brébisson ex Ralfs) Itzigsohn and Rothe in Rabenhorst 1856
Netrium interruptum	(Brébisson ex Ralfs) Lütkemüller 1902
Onychonema filiforme	(Ehrenberg ex Ralfs) J.Roy and Bisset 1886
Oocystis natans	(Lemmermann) Lemmermann 1908
Oocystis solitaria	Wittrock 1879
Pediastrum angulosum	Ehrenberg ex Meneghini 1840
Pediastrum boryanum	(Turpin) Meneghini 1840
Pediastrum duplex	Meyen 1829

Species (Chlorophyta)	Authority
Pediastrum simplex	Meyen 1829
Pediastrum tetras	(Ehrenberg) Ralfs 1844
Penium cylindrus	Brébisson ex Ralfs 1848
Penium gonatozygiforme	Claassen
Penium margaritaceum	Brébisson in Ralfs 1848
Pleurotaenium coronatum	Rabenhorst 1868
Pleurotaenium ehrenbergii	(Brébisson ex Ralfs) Delponte 1878
Pleurotaenium trabecula	(Ehrenberg) Nägeli 1849
Scenedesmus acuminatus	(Lagerheim) Chodat 1902
Scenedesmus acutus	Meyen 1829
Scenedesmus alternans	Reinsch
Scenedesmus arcuatus	Lemmermann 1899
Scenedesmus armatus	(Chodat) R.Chodat 1913
Scenedesmus brasiliensis	Bohlin 1897
Scenedesmus communis	Hegewald 1977
Scenedesmus ellipsoideus	Chodat
Scenedesmus ellipticus	Corda 1835
Scenedesmus falcatus	Chodat 1894
Scenedesmus longispina	Chodat 1913
Scenedesmus magnus	Meyen 1829
Scenedesmus maximus	(West and G.S.West) Chodat 1913
Scenedesmus obtusus	Meyen 1829
Scenedesmus planctonicus	(Korshikov) Fott 1973
Scenedesmus protuberans	F.E. Fritsch and M.F. Rich 1929
Scenedesmus quadricauda	(Turpin) Brébisson in Brébisson & Godey 1835
Scenedesmus serratus	(Corda) Bohlin 1901
Scenedesmus verrucosus	Roll 1925
Schroederia robusta	Korshikov 1953
Selenastrum bibraianum	Reinsch 1866
Selenastrum gracile	Reinsch 1866
Sorastrum americanum	(Bohlin) Schmidle 1900
Spirotaenia condensata	Brébisson in Ralfs 1848
Staurastrum arachne	Ralfs ex Ralfs 1848
Staurastrum arctiscon	(Ehrenberg ex Ralfs) P.Lundell 1871
Staurastrum armigerum	Brébisson 1856
Staurastrum avicula	Brébisson in Ralfs 1848
Staurastrum cerastes	P.Lundell 1871
Staurastrum chaetoceras	(Schröder) G.M.Smith 1924
Staurastrum convergens	(Ehrenberg) Meneghini
Staurastrum denticulatum	(Nägeli) W.Archer 1861
Staurastrum excavatum	West and G.S.West 1895
Staurastrum fuelleborniforme	Coesel and Van Geest 2009
Staurastrum furcatum	Brébisson 1856
Staurastrum gemelliparum	Nordstedt 1870

Species (Chlorophyta)	Authority
Staurastrum gracile	Ralfs ex Ralfs 1848
Staurastrum hagmannii	Grönblad
Staurastrum hexacerum	Ehrenberg ex Wittrock 1872
Staurastrum hirsutum	Ehrenberg ex Ralfs 1848
Staurastrum hystrix	Ralfs 1848
Staurastrum johnsonii	West and G.S.West 1896
Staurastrum leptocladum	Nordstedt, 1869
Staurastrum longispinum	(Bailey) Archer 1861
Staurastrum margaritaceum	Meneghini ex Ralfs 1848
Staurastrum muticum	Brébisson ex Ralfs 1848
Staurastrum paradoxum	Meyen ex Ralfs 1848
Staurastrum planctonicum	Teiling 1946
Staurastrum proboscideum	(Brébisson) Archer in Prichard 1861
Staurastrum productum	(West and G.S.West) Coesel 1996
Staurastrum quadrangulare	Brébisson in Ralfs 1848
Staurastrum rzoskae	Grönblad and Scott 1958
Staurastrum sebaldi	Reinsch 1866
Staurastrum tetracerum	Ralfs ex Ralfs 1848
Staurastrum volans	West & G.S.West 1895
Staurastrum wildemanii	Gutwinski 1902
Staurodesmus aversus	(P.Lundell) S.Lillieroth 1950
Staurodesmus brevispina	(Brébisson) Croasdale 1957
Staurodesmus convergens	(Ehrenberg ex Ralfs) S.Lilleroth 1950
Staurodesmus crassus	(West and G.S.West) M.-B.Florin 1957
Staurodesmus cuspidatus	(Brébisson) Teiling 1967
Staurodesmus dejectus	(Brébisson) Teiling 1967
Staurodesmus dickiei	(Ralfs) S.Lillieroth 1950
Staurodesmus extensus	(Borge) Teiling 1948
Staurodesmus glaber	(Ralfs) Teiling 1948
Staurodesmus mamillatus	(Nordstedt) Teiling 1967
Staurodesmus megacanthus	(P.Lundell) Thunmark 1948
Staurodesmus mucronatus	(Ralfs ex Ralfs) Croasdale 1957
Staurodesmus sellatus	(Teiling) Teiling 1948
Staurodesmus subulatus	(Kützing) Thomasson 1963
Teilingia excavata	(Ralfs ex Ralfs) Bourrelly 1964
Teilingia granulata	(J.Roy and Bisset) Bourrelly 1964
Tetmemorus euastroides	A.M.Scott and Prescott
Tetraedron caudatum	(Corda) Hansgirg 1888
Tetraedron incus	G.M.Smith 1926
Tetraedron minimum	(A.Braun) Hansgirg 1888
Tetraedron regulare	Kutzing 1845
Tetraedron triangulare	Korshikov 1953
Tetrastrum elegans	Playfair 1917
Tetrastrum triangulare	(Chodat) Komárek 1974

Species (Chlorophyta)	Authority
Triploceras gracile	J.W.Bailey 1851
Trochiscia hirta	Hansgirg 1888
Ulothrix zonata	(Weber and Mohr) Kützing 1843
Xanthidium antilopaeum	(Brébisson) Kützing 1849
Xanthidium bifidum	(Brébisson) Deflandre 1929
Xanthidium cristatum	Brébisson ex Ralfs 1848
Xanthidium fascicolatum	Ehrenberg ex Ralfs 1848
Xanthidium octocorne	Ehrenberg ex Ralfs 1848
Xanthidium subhastiferum	West 1892
Xanthidium subtrilobum	West and G.S.West 1897

CHRYSOPHYTA	
Species	**Authority**
Bitrichia chodatii	(Reverdin) Chodat 1926
Mallomonas caudata	Iwanoff 1899
Mallomonas insignis	Penard 1919

CRYPTOPHYTA	
Species	**Authority**
Chroomonas acuta	Utermöhl 1925
Chroomonas baltica	(J.Büttner) N.Carter 1937
Chroomonas coerulea	(Geitler) Skuja 1948
Cryptomonas acuta	Butcher 1952
Cryptomonas anomala	Fritsch 1914
Cryptomonas curvata	Ehrenberg 1831
Cryptomonas erosa	Ehrenberg, 1832
Cryptomonas marssonii	Skuja 1948
Cryptomonas ovata	Ehrenberg 1832
Cryptomonas platyuris	Skuja 1948
Rhodomonas lacustris	Pascher and Ruttner 1913

CYANOPHYTA	
Species	**Authority**
Anabaena circinalis	Rabenhorst ex Bornet and Flahault 1886
Anabaena cylindrica	Lemmermann 1896
Chroococcus limneticus	Lemmermann 1898
Lyngbya contorta	Lemmermann 1898
Merismopedia elegans	Braun ex Kützing 1849
Nostoc coeruleum	Lyngbye 1819
Oscillatoria limnetica	Lemmermann 1900
Oscillatoria limosa	C.Agardh ex Gomont 1892
Oscillatoria redekei	Van Goor
Oscillatoria rubescens	De Candolle 1826

Species (Cyanophyta)	Authority
Oscillatoria tenuis	Agardh 1813
Phormidium lucidum	(C.Agardh) Kützing 1843
Phormidium luridum	(Kützing) Gomont 1892
Snowella lacustris	(Chodat) Komárek and Hindák 1988
Spirulina maior	Kützing ex Gomont 1892
Woronichinia naegeliana	(Unger) Elenkin 1933

EUGLENOPHYTA	
Species	**Authority**
Euglena acus	(O.F.Müller) Ehrenberg 1830
Euglena ehrenbergii	Klebs 1883
Euglena elongata	Schewiakoff 1891
Euglena geniculata	F.Schmitz 1884
Euglena granulata	(Klebs) F.Schmitz 1884
Euglena limnophila	Lemmermann 1898
Euglena mutabilis	F.Schmitz 1884
Euglena oblonga	F.Schmitz 1884
Euglena oxyuris	Schmarda 1846
Euglena proxima	P.A. Dangeard 1901
Euglena repulsans	J. Schiller 1952
Euglena sociabilis	P.A.Dangeard 1901
Euglena spirogyra	Ehrenberg 1832
Euglena splendens	P.A.Dangeard 1901
Euglena texta	(Dujardin) Hubner 1886
Lepocinclis caudata	A.M. Cunha 1913
Lepocinclis fusiformis	(H.J.Carter) Lemmermann 1901
Lepocinclis playfairiana	Deflandre 1932
Lepocinclis steinii	Lemmermann 1901
Phacus acutus	Pochmann 1941
Phacus alatus	G.A.Klebs 1886
Phacus anomalus	F.E.Fritsch and M.F.Rich 1929
Phacus caudatus	Hübner 1886
Phacus circumflexus	Pochmann 1941
Phacus curvicauda	Svirenko 1915
Phacus elegans	Pochmann 1942
Phacus helicoides	Pochmann 1942
Phacus longicauda	(Ehrenberg) Dujardin 1841
Phacus nordstedtii	Lemmermann 1904
Phacus orbicularis	K.Hübner 1886
Phacus pusillus	Lemmermann 1910
Phacus suecicus	Lemmermann
Phacus triqueter	(Ehrenberg) Perty 1852
Strombomonas deflandrei	(Y.V.Roll) Deflandre 1930

Species (Euglenophyta)	Authority
Trachelomonas caudata	(Ehrenberg) Stein 1878
Trachelomonas planctonica	Svirenko 1914

PRASINOPHYTA	
Tetraselmis cordiformis	(Carter) Stein 1878

PYRROPHYTA	
Species	**Authority**
Gymnodinium cnecoides	T.M.Harris 1940
Gymnodinium triceratium	Skuja 1939

XANTHOPHYTA	
Species	**Authority**
Goniochloris fallax	Fott 1960
Goniochloris mutica	(Braun) Fott 1960
Goniochloris smithii	(Bourrelly) Fott 1960
Ophiocytium capitatum	Wolle 1887
Ophiocytium parvulum	(Perty) A.Braun 1855
Pseudostaurastrum enorme	(Ralfs) R.Chodat 1921

APPENDIX C. ***List of algal genera observed not included in the species list (main source of authorities: www.algaebase.org).***

BACILLARIOPHYTA	
Genus	**Authority**
Achnanthes	Bory de Saint-Vincent, 1822
Actinella	Lewis 1864
Anomoeoneis	E.Pfitzer, 1871
Cocconeis	Ehrenberg 1837
Cyclotella	Brebisson 1838
Diatoma	Bory de St-Vincent (1824)
Diploneis	(Ehrenberg) Cleve 1894
Encyonema	Kützing 1833
Melosira	Agardh 1824
Placoneis	Mereschkovsky, 1903
Staurosira	Ehrenberg, 1843
Stenopterobia	Brebisson ex Van Heurck, 1896

CHLOROPHYTA	
Genus	**Authority**
Actinochloris	Korschikov, 1953
Ankyra	Fott, 1957
Botryococcus	Kutzing 1849
Bulbochaete	Agardh 1817
Calothrix	Agardh 1824
Carteria	Diesing, 1866
Centritractus	Lemmermann 1900
Chilomonas	Ehrenberg ex Ralfs 1831
Chlamydocapsa	Fott 1972
Chlorella	Beijerinck 1890
Chlorococcum	Meneghini 1842
Chromulina	Cienkowsky 1870
Cladophora	Kutzing 1843
Coccomixa	Schmidle 1901
Cylindrocapsa	Reinsch, 1867
Cylindrocistis	Meneghini ex De Bary, 1858
Cystodinium	Klebs 1912
Dictyosphaerium	Nageli 1849
Didymogenes	Schmidle, 1905
Dimorphococcus	Braun 1855
Elakatothrix	Wille 1898
Eudorina	Ehrenberg 1832

Genus (Chlorophyta)	Authority
Gonium	O.F. Muller, 1873
Haematococcus	Flotow, 1844
Hydrodictyon	Roth, 1797
Microspora	Thuret 1850
Mougeotia	C. Agardh, 1824
Nephrocytium	Nageli, 1849
Oedogonium	Link ex Hirn, 1900
Phacotus	Perty, 1852
Pteromonas	Seligo, 1887
Radiofilum	Schmidle, 1894
Sphaerozosma	Corda ex Ralfs, 1848
Spirogyra	Link, 1820
Spondylosium	Brebisson ex Kutzing, 1849
Stigeoclonium	Kutzing, 1843
Volvox	Linnaeus, 1758
Zygnema	Agardh 1817

CHRYSOPHYTA	
Genus	**Authority**
Dinobryon	Ehrenberg 1834
Kephryon	Pascher 1911
Synura	Ehrenberg 1834
Uroglena	Ehrenberg 1834

CYANOPHYTA	
Genus	**Authority**
Coelosphaerium	Nageli 1849
Gloeocapsa	Kutzing 1843
Gomphosphaeria	Kutzing 1836
Hapalosiphon	Nageli ex Bornet et Flahault, 1886
Microcystis	Lemmermann 1907
Planktosphaeria	G.M.Smith, 1918
Rivularia	C. Agardh ex Bornet et Flahault, 1886
Scytonema	C. Agardh ex Bornet and Flahault, 1886
Sphaerocystis	R. Chodat, 1897
Stigonema	C. Agardh ex Bornet and Flahault, 1886
Synechococcus	Nageli 1849
Tolypothrix	Kutzing ex Bornet and Flahault 1886

EUGLENOPHYTA	
Genus	**Authority**
Peronema	

PYRROPHYTA	
Genus	**Authority**
Amphidinium	Claparède and Lachmann, 1859
Glenodinium	Ehrenberg 1836
Katodinium	Fott 1857
Peridiniopsis	Lemmermann, 1904
Peridinium	Ehrenberg, 1832
Woloszynskia	Thompson 1951

XANTHOPHYTA	
Genus	**Authority**
Tribonema	Derbès and Solier 1851

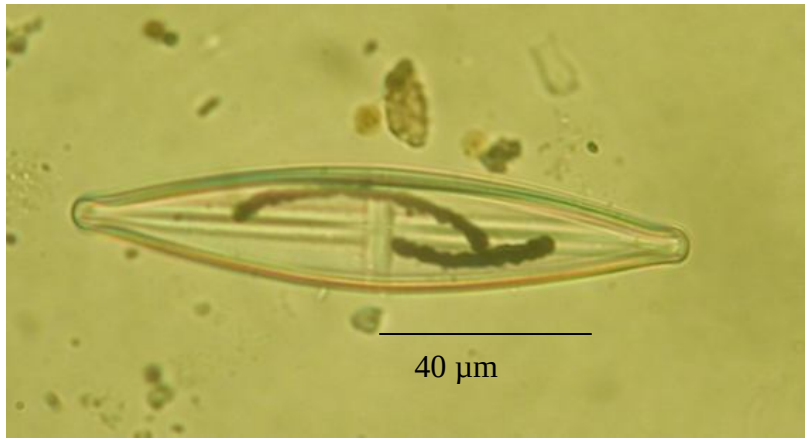
APPENDIX D. ***Site numbers displayed in boxplots in Chapters 4 and 5.***

Sample	N
ALD1-6	1
ALD1-7	2
ALD1-8	3
ALD1-9	4
ALD2-6	5
ALD2-7	6
ALD2-8	7
ALD2-9	8
ALD3-7	9
ALD3-8	10
ALD3-9	11
BOR10A-3	12
BOR10A-4	13
BOR14-4	14
BOR15-3	15
BOR17A-4	16
BOR19A-4	17
BOR19B-4	18
BOR2-3	19
BOR2-4	20
BOR8-4	21
BOR8A-3	22
BOR8A-4	23
BOR9A-4	24
BUF1-6	25
BUF1-7	26
BUF1-8	27
BUF1-9	28
BUF2-9	29
BUF3-6	30
BUF3-7	31
BUF3-8	32
BUF3-9	33
DAU1-6	34
DAU1-7	35
DAU1-8	36
DAU1-9	37
DAU3-6	38
DAU3-7	39
DAU3-8	40
DAU3-9	41
HIP1-6	42
HIP1-8	43
HIP1-9	44
HIP2-6	45
HIP2-7	46

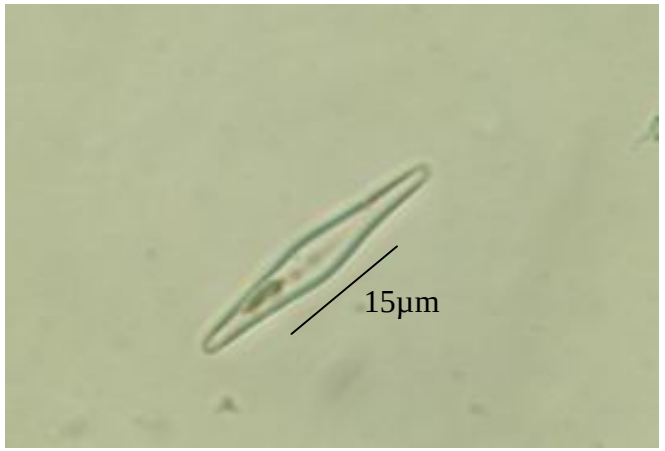
Sample	N
HIP2-8	47
HIP2-9	48
HIP3-6	49
HIP3-7	50
HIP3-8	51
HIP3-9	52
LEC2-6	53
LEC2-7	54
LEC2-8	55
LEC3-6	56
LEC3-7	57
LEC3-8	58
LEC3-9	59
LPH1-1	60
LPH3-1	61
LPH3A-4	62
LPH4A-1	63
LPH4B-1	64
LPH4B-4	65
LPH5B-4	66
LPH6-4	67
LPH8A-4	68
LPH9A-4	69
POC1-6	70
POC1-7	71
POC1-8	72
POC1-9	73
POC2-6	74
POC2-7	75
POC2-8	76
POC2-9	77
POC3-6	78
POC3-8	79
POC3-9	80
SAN1A-1	81
SAN2-1	82
SAN3A-1	83
SAN3B-1	84
SAN4A-1	85
SAN4B-1	86
SAN5A-1	87
SAN5B-1	88
SAN6A-1	89
SAN6B-1	90
UPH1A-1	91
UPH1B-1	92

Sample	N
UPH1B-3	93
UPH1C-4	94
UPH3-1	95
UPH3A-3	96
UPH4A-1	97
UPH4A-3	98
UPH4B-1	99
UPH5A-4	100
UPH6-3	101
UPH7A-3	102
UPH7A-4	103
UPH8-3	104
UPH9A-3	105
WBE2-6	106
WBE2-8	107
WBE2-9	108
WBE3-6	109
WBE3-8	110
WBE3-9	111
WLI2-6	112
WLI2-7	113
WLI3-6	114
WLI3-7	115
WLI3-8	116
WLI3-9	117
XAK12-3	118
XAK12-4	119
XAK13-4	120
XAK14-3	121
XAK15-3	122
XAK16-3	123
XAK18-4	124
XAK19-4	125
XAK4A-3	126
XAK5A-4	127
XAK7a-4	128
XAK7b-4	129
XAK9-4	130

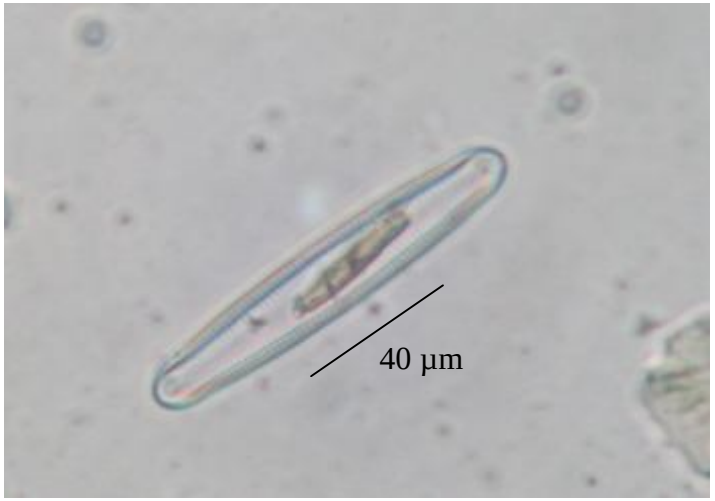
APPENDIX E1. ***Micrographs of diatom species observed in the Okavango Delta.***



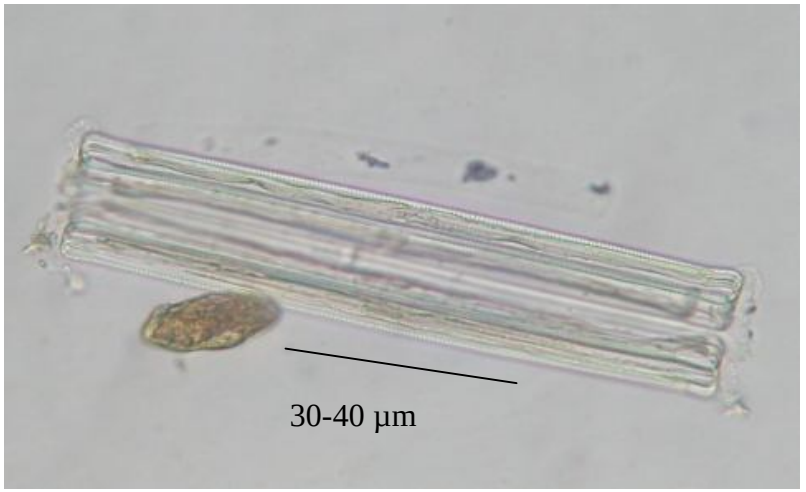
Stauroneis phoenicenteron



Gomphonema gracile

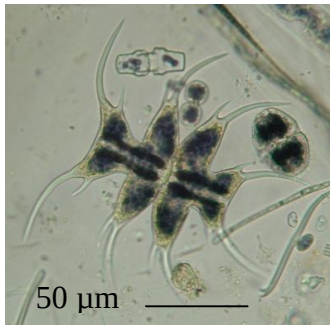


Pinnularia subcapitata

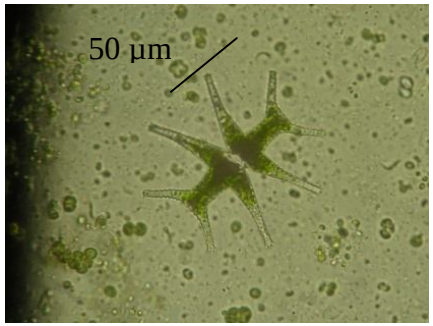


Fragilaria crotonensis

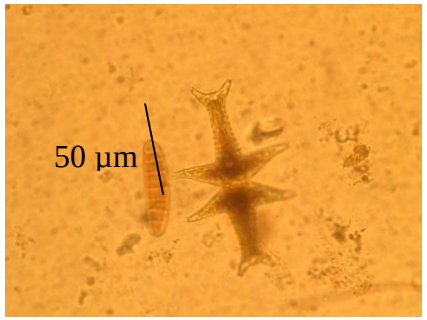
APPENDIX E2. ***Micrographs of desmid species observed in the Okavango Delta (Micrasterias sudanensis was found in a BOR sample used for trial).***



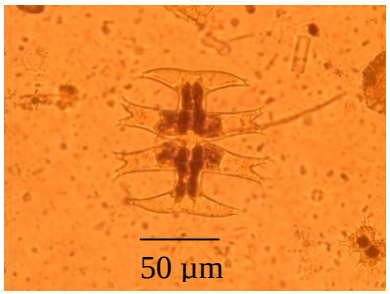
Micrasterias sudanensis



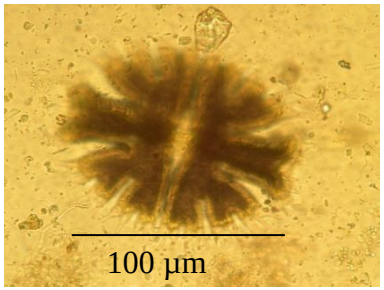
M. tropica (var. elegans)



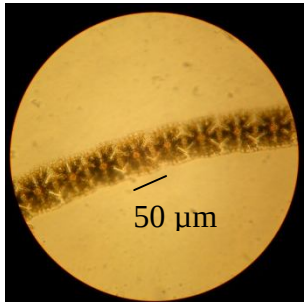
M. tropica (var. elongata)



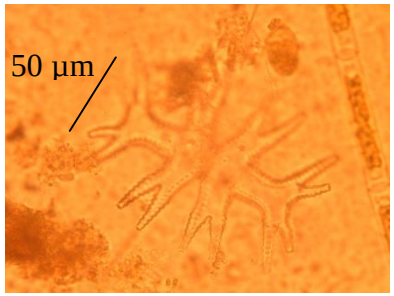
M. pinnatifida



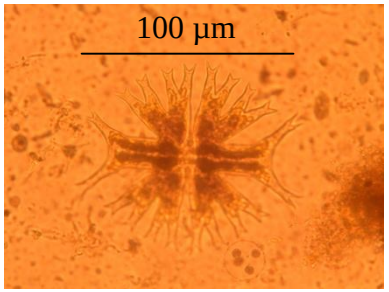
M. rotata



M. foliacea



M. mahabuleshwarensis



M. americana

APPENDIX F. List of common taxa to different algal studies in the Okavango Delta.				
Taxon	**Marazzi, 2014**	**Cholnoky, 1966**	**Cronberg *et al.*, 1996a/b**	**Mackay *et al.*, 2012**
Achnanthidium minutissimum (Bac)	x	x		
Actinastrum hantzschii (Chl)	x		x	
Amphora libyca (Bac)	x			x
Amphora ovalis (Bac)	x	x		x
Amphora pediculus (Bac)	x			x
Anabaena spp. (Cya)	x		x	
Ankistrodesmus falcatus (Chl)	x		x	
Asterionella spp. (Bac)	x		x	
Aulacoseira ambigua (Bac)	x			x
Aulacoseira granulata (Bac)	x		x	x
Bambusina brebissonii (Chl)	x		x	
Botryococcus spp. (Chl)	x		x	
Caloneis bacillum (Bac)	x	x		x
Chlamydocapsa spp. (Chl)	x		x	
Chlamydomonas spp. (Chl)	x		x	
Chroococcus limneticus (Cya)	x		x	
Closterium aciculare (Chl)	x		x	
Closterium acutum (Chl)	x		x	
Closterium gracile (Chl)	x		x	
Closterium incurvum (Chl)	x		x	
Closterium kuetzingii (Chl)	x		x	
Coelastrum microporum (Chl)	x		x	
Coelastrum sphaericum (Chl)	x		x	
Cosmarium spp. (Chl)	x		x	
Cosmarium spp. (Chl)	x		x	
Craticula cuspidata (Bac)	x			x
Crucigenia tetrapedia (Chl)	x		x	
Crucigeniella rectangularis (Chl)	x		x	
Cryptomonas spp. (Cry)	x		x	
Cyclotella spp. (Bac)	x		x	
Cymbella naviculiformis (Bac)	x	x		

APPENDIX F (*continued*).				
Taxon	**Marazzi, 2014**	**Cholnoky, 1966**	**Cronberg *et al.*, 1996a/b**	**Mackay *et al.*, 2012**
Desmidium grevillei (Chl)	x		x	
Dictyosphaerium spp. (Chl)	x		x	
Dimorphococcus spp. (Chl)	x		x	
Dinobryon spp. (Chr)	x		x	
Elakatothrix spp. (Chl)	x		x	
Euastrum africanum (Chl)	x		x	
Euastrum elegans (Chl)	x		x	
Eudorina spp. (Chl)	x		x	
Euglena spp. (Eug)	x		x	
Eunotia alpina (Bac)	x	x		
Eunotia asterionelloides (Bac)	x	x		x
Eunotia bilunaris (Bac)	x			x
Eunotia faba (Bac)	x			x
Eunotia flexuosa (Bac)	x	x		x
Eunotia incisa (Bac)	x			x
Eunotia naegelii (Bac)	x			x
Eunotia okawangoi (Bac)	x	x		x
Eunotia pectinalis (Bac)	x	x		x
Eunotia praerupta (Bac)	x	x		x
Eunotia rhomboidea (Bac)	x	x		x
Eunotia soleirolii (Bac)	x			x
Fragilaria africana (Bac)	x	x		x
Fragilaria crotonensis (Bac)	x		x	x
Frustulia rhomboides (Bac)	x	x		
Frustulia saxonica (Bac)	x	x		
Gomphonema augur (Bac)	x	x		x
Gomphonema clevei (Bac)	x	x		
Gomphonema globiferum (Bac)	x			x
Gomphonema gracile (Bac)	x	x		x
Gomphonema lanceolatum (Bac)	x	x		
Gomphonema olivaceum (Bac)	x			x

APPENDIX F (*continued*).				
Taxon	**Marazzi, 2014**	**Cholnoky, 1966**	**Cronberg *et al.*, 1996a/b**	**Mackay *et al.*, 2012**
Gomphonema parvulum (Bac)	x	x		x
Gomphonema pfannkucheae (Bac)	x	x		
Gomphonema resendei (Bac)	x	x		x
Gomphonema subtile (Bac)	x	x		x
Gonatozygon aculeatum (Chl)	x		x	
Goniochloris smithii (Xan)	x		x	
Gonium spp. (Chl)	x		x	
Hantzschia amphioxys (Bac)	x	x		x
Hyalotheca dissiliens (Chl)	x		x	
Kirchneriella obesa (Chl)	x		x	
Mallomonas spp. (Chr)	x		x	
Merismopedia (Cya)	x		x	
Micrasterias americana (Chl)	x		x	
Micrasterias crux-melitensis (Chl)	x		x	
Micrasterias foliacea (Chl)	x		x	
Micrasterias mahabuleshwarensis (Chl)	x		x	
Micrasterias pinnatifida (Chl)	x		x	
Micrasterias tropica (Chl)	x		x	
Microcystis (Cya)	x		x	
Monoraphidium contortum (Chl)	x		x	
Mougeotia spp. (Chl)	x		x	
Navicula cryptocephala (Bac)	x	x		x
Navicula cryptotenella (Bac)	x			x
Navicula halophila (Bac)	x	x		
Navicula menisculus (Bac)	x	x		
Navicula pupula (Bac)	x	x		
Navicula radiosa (Bac)	x	x		x
Neidium affine (Bac)	x	x		
Neidium ampliatum (Bac)	x			x
Neidium productum (Bac)	x	x		x
Nephrocytium spp. (Chl)	x		x	

APPENDIX F (*continued*).				
Taxon	**Marazzi, 2014**	**Cholnoky, 1966**	**Cronberg *et al.*, 1996a/b**	**Mackay *et al.*, 2012**
Nitzschia acicularis (Bac)	x	x		x
Nitzschia linearis (Bac)	x	x		
Nitzschia perminuta (Bac)	x	x		x
Nitzschia subacicularis (Bac)	x	x		
Oocystis solitaria (Chl)	x		x	
Oscillatoria spp. (Cya)	x		x	
Pediastrum angulosum (Chl)	x		x	
Pediastrum boryanum (Chl)	x		x	
Pediastrum duplex (Chl)	x		x	
Pediastrum tetras (Chl)	x		x	
Peridiniopsis spp. (Pyr)	x		x	
Peridinium spp. (Pyr)	x		x	
Phacus caudatus (Eug)	x		x	
Phacus longicauda (Eug)	x		x	
Phacus suecicus (Eug)	x		x	
Pinnularia braunii (Bac)	x	x		
Pinnularia gibba (Bac)	x	x		x
Pinnularia interrupta (Bac)	x	x		
Pinnularia maior (Bac)	x	x		x
Pinnularia mesolepta (Bac)	x	x		
Pinnularia nobilis (Bac)	x			x
Pinnularia subcapitata (Bac)	x	x		
Pinnularia viridis (Bac)	x	x		x
Rhodomonas (Cry)	x		x	
Rhopalodia gibba (Bac)	x	x		x
Scenedesmus acuminatus (Chl)	x		x	
Scenedesmus arcuatus (Chl)	x		x	
Scenedesmus armatus (Chl)	x		x	
Scytonema spp. (Cya)	x		x	
Selenastrum spp. (Chl)	x		x	
Sellaphora bacillum (Bac)	x			x

APPENDIX F (*continued*).				
Taxon	**Marazzi, 2014**	**Cholnoky, 1966**	**Cronberg *et al.*, 1996a/b**	**Mackay *et al.*, 2012**
Sellaphora pupula (Bac)	x			x
Snowella lacustris (Cya)	x		x	
Sphaerozosma spp. (Chl)	x		x	
Spirogyra spp. (Chl)	x		x	
Spirulina spp. (Cya)	x		x	
Spondylosium spp. (Chl)	x		x	
Staurastrum leptocladum (Chl)	x		x	
Staurastrum paradoxum (Chl)	x		x	
Staurastrum tetracerum (Chl)	x		x	
Staurastrum wildemannii (Chl)	x		x	
Staurodesmus extensus (Chl)	x		x	
Staurodesmus subulatus (Chl)	x		x	
Stauroneis anceps (Bac)	x	x		x
Stauroneis phoenicenteron (Bac)	x	x		x
Strombomonas spp. (Eug)	x		x	
Surirella linearis (Bac)	x	x		
Synedra acus (Bac)	x	x		x
Synedra amphicephala (Bac)	x	x		
Synedra nana (Bac)	x	x		
Synedra rumpens (Bac)	x	x		x
Synedra spp. (Bac)	x		x	
Synedra ulna (Bac)	x	x		x
Synura spp. (Chr)	x		x	
Teilingia granulata (Chl)	x		x	
Tetraedron caudatum (Chl)	x		x	
Tetraedron minimum (Chl)	x		x	
Trachelomonas spp. (Eug)	x		x	
Triploceras gracile (Chl)	x		x	
Volvox spp. (Chl)	x		x	
Woronichinia spp. (Cya)	x		x	
Xanthidium subtrilobum (Chl)	x		x	

APPENDIX G. ***List of additional species and varieties identified by David Williamson in a subset of samples from Campaign 2 (ALD2-7; ALD2-8; BUF3-7; HIP1-8; HIP3-7; LEC2-7; LEC2-8; POC3-8; WBE2-7; WBE2-8; WLI2-7).***

Species / variety	**Species / variety (cont'ed)**
Actinotaenium elongatum var. africanum	*Euastrum hieronymusii*
Closterium lineatum var. elongatum	*Euastrum luetkemuelleri var. carniolicum*
Closterium monoliferum	*Euastrum osmondii*
Closterium turgidum var. borgei	*Euastrum prox. subcrassum var. elaboratum*
Closterium prox. calosporum var. brasiliense	*Euastrum subhypochondrum var. croasdaleae*
Cosmarium prox. bituberculatum	*Micrasterias ambadiensis*
Cosmarium prox. capense var. nyassae	*Micrasterias apiculata prox. var. lacerata*
Cosmarium cunningtonii	*Micrasterias decemdentata*
Cosmarium decoratum	*Micrasterias prox. divisa*
Cosmarium prox. dorsitruncatum	*Micrasterias radians var. evoluta*
Cosmarium fuelleborniforme	*Micrasterias schmidleana*
Cosmarium mamilliferum var. madagascariense	*Phymatodocis irregulare*
Cosmarium pachydermum	*Pleurotaenium cylindricum var. stuhlmannii*
Cosmarium permaculatum var. tuberculatum	*Pleurotaenium engleri*
Cosmarium porteanum with zygospore	*Pleurotaenium ovatum*
Cosmarium prox. pseudoarmatum	*Pleurotaenium subcoronulatum*
Cosmarium pseudobroomei	*Staurastrum bidentulum*
Cosmarium pseudodecoratum	*Staurastrum prox. cyclacanthum*
Cosmarium pseudotaxichondrum var. pentachondrum	*Staurastrum distentum*
Cosmarium quadrum	*Staurastrum fuellebornei*
Cosmarium salisburii	*Staurastrum prox. novae-terrae*
Cosmarium stappersii	*Staurastrum orbiculare var. depressum*
Cosmarium striolatum var. nordstedtii	*Staurastrum rotula*
Cosmarium trachypleurum	*Staurastrum setigerum var. villosum*
Cosmarium prox. transvaalense	*Staurastrum tohopekaligense var. trifurcatum*
Desmidium aptogonum var. acutius	*Staurodesmus corniculatus prox. fa. latus*
Desmidium gracilliceps	*Staurodesmus leptodermus var. ikapoae*
Euastrum compereanum	*Staurodesmus mucronulatus*
Euastrum corpulentum	*Staurodesmus prox. validus*
Euastrum fritschii	*Xanthidium prox. trilobum var. africanum*