

Phytoplankton succession and diversity- productivity relation in German and Brazilian shallow lakes

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Dedicated to Maria Elisa and Lian

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Statutory declaration

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which has been accepted for the award of any other degree or diploma of the university or other institute. Quotations and other direct or indirect information have been clearly marked and noted.

Melissa Guimarães Baptista

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Table of Contents

Acknowledgments.....	2
Statutory declaration.....	3
List of figures.....	6
List of tables.....	8
Summary.....	9
<u>Chapter 1</u> Introduction.....	10
1.1 Background.....	11
1.2 Objectives.....	14
1.3 Methodology.....	15
1.4 Structure of the thesis.....	16
1.5 References.....	16
<u>Chapter 2</u> Succession determines productivity and diversity at non-equilibrium/steady state conditions in two very shallow lakes.....	19
2.1 Abstract.....	20
2.2 Introduction.....	21
2.3 Hypothesis.....	23
2.4 Study sites.....	23
2.5 Methodology.....	25
2.6 Results.....	26
2.6.1 Abiotic parameters.....	26
2.6.2 Succession of phytoplankton groups and RUE.....	31
2.6.3 Steady state conditions.....	35
2.6.4 Diversity.....	39
2.7 Discussion.....	46
2.8 References.....	49
<u>Chapter 3</u> Low disturbances favor steady state: Case of cyanobacterial monodominance in Brazilian coastal lagoon.....	53
3.1 Abstract.....	54
3.2 Introduction.....	55
3.3 Hypothesis.....	56
3.4 Study site.....	57

3.4.1 Local area.....	57
3.4.2 Climatic influences.....	59
3.5 Methodology.....	60
3.6 Results.....	60
3.6.1 Abiotic variables.....	60
3.6.2 Phytoplankton composition and morphology of <i>C. raciborsii</i>	63
3.6.2 Diversity at steady-state.....	64
3.7 Discussion.....	67
3.7.1 Abiotic Parameters.....	67
3.7.2 <i>C. raciborskii</i> and functional groups of phytoplankton.....	68
3.7.3 Relationship between disturbances and equilibrium.....	70
3.8 References.....	71
<u>Chapter 4</u> Role of conditional differentiation on diversity and succession in Brazilian and German shallow lakes dominated by cyanobacteria.....	76
4.1 Abstract.....	77
4.2 Introduction.....	78
4.3 Hypothesis.....	81
4.4 Sites description.....	82
4.4.1 German lakes.....	82
4.4.2 Brazilian lakes.....	83
4.5 Methodology.....	86
4.6 Results.....	86
4.6.1 Abiotic parameters.....	86
4.6.2 Phytoplankton succession associated with temperature.....	91
4.6.3 Diversity and its relation with biovolume.....	100
4.7 Discussion.....	102
4.8 References.....	106
<u>Chapter 5</u> Conclusion.....	111

List of figures

Fig. 2.1: Location of PET and MEL and morphometric parameters.....	24
Fig. 2.2: Dissolved nitrogen and ammonium concentration of PET and MEL.....	28
Fig. 2.3: Dissolved inorganic phosphorus and silica concentration of PET and MEL.....	29
Fig. 2.4: chlorophyll a concentration, total phosphorus, Imix and Secchi depth.....	31
Fig. 2.5: Succession of phytoplankton groups in MEL associated with RUE.....	32
Fig. 2.6: Succession of phytoplankton groups in PET, associated with RUE.....	35
Fig 2.7: Biovolume proportion (%) of the 3 most dominant species, represented by algal groups in MEL.....	35
Fig 2.8: Biovolume proportion (%) of the 3 most dominant species, represented by algal groups in PET.....	37
Fig. 2.9: Course of the 3 most dominant species associated with richness, Shannon Wiener index and complement of Simpson index.....	40
Fig. 2.10: Differences between two types of Shannon Wiener index (abundance and biovolume) and cell proportion.....	42
Fig. 2.11: Different performances of richness versus evenness of Shannon Wiener index.....	43
Fig. 2.12: Relation between richness and biovolume.....	44
Fig. 2.13: Mean values of RUE, Imix and richness along the year.....	45
Fig. 2.14: Schema of the variation of diversity (richness), productivity and biovolume, cell proportion, associated with Imix, dominance of algal groups, and equilibrium and non-equilibrium along the seasons.....	46
Fig. 3.1: Location of Peri coastal lagoon.....	59
Fig. 3.2: Picture of Peri coastal lagoon.....	59
Fig. 3.3: Chlorophyll a, total and dissolved inorganic phosphorus concentration, and Secchi depth.....	62
Fig. 3.4: Depth-time isopleths of water temperature (°C).....	62
Fig. 3.5: Portion of phytoplankton groups as biovolume and abundance.....	63
Fig. 3.6: Morphology of <i>Cylindrospermopsis raciborskii</i> in Peri coastal lagoon.....	64
Fig. 3.7: Diversity indices and richness during the cold and rainy periods in Peri.....	65
Fig. 3.8: Portion of biovolume (%) of the 3 most dominant species in Peri.....	65
Fig. 4.1: Trait distributions of communities exemplified by the optimal temperature for growth in temperate and tropical regions.....	79

Fig. 4.2: An envelope function for temperature-dependent growth rates in phytoplankton and examples of single species replacement responses to temperature.....	81
Fig. 4.3: Location of 4 shallow lakes in Scharmützelsee region.....	82
Fig. 4.4: Location of Ingazeira reservoir together with Ingazeira monthly precipitation.....	83
Fig. 4.5: Map of Manacás lake showing the sampling station, besides of monthly precipitation and mean air temperature.....	84
Fig. 4.6: Map of Santa Catarina state, showing the Peri coastal lagoon, monthly precipitation and mean air temperature.....	84
Fig.4.7: Location of Billing reservoir, monthly precipitation and water temperature.....	85
Fig. 4.8 Depth-time isopleths of water temperature of Peri coastal lagoon, Manacás lake and Ingazeira reservoir.....	89
Fig. 4.9: Seasonal variation of algal groups and water temperature of 4 polymictic shallow lakes in Brandenburg region.....	93
Fig 4.10: Biovolume variation of algal groups along the temperature in 4 German polymictic shallow lakes in Brandenburg region.....	96
Fig. 4.11: Seasonal variation of algal groups and annual water temperature variation of 4 Brazilian lakes.....	97
Fig. 4.12: Proportion (%) of species in Brazilian lakes in terms of biovolum.....	100
Fig. 4.13: Relation of annual richness and annual mean of biovolume in tropical and temperate shallow lakes.....	101

List of tables

<i>Table 1.1: Phytoplankton groups proposed by Reynolds (1997).....</i>	<i>13</i>
<i>Table 2.1: Abiotic parameters in PET and MEL.....</i>	<i>27</i>
<i>Table 2.2: Species at equilibrium conditions according to Sommer et al. (1993) and its functional groups, biovolume ($\text{mm}^3 \text{ l}^{-1}$ and %), abundance (cell ml^{-1}) and total monthly biovolume ($\text{mm}^3 \text{ l}^{-1}$) in MEL from 2008 to 2010.....</i>	<i>36</i>
<i>Table 2.3: Species at equilibrium conditions according to Sommer et al. (1993) and its functional groups, biovolume (BV in $\text{mm}^3 \text{ l}^{-1}$ and %), abundance (cell ml^{-1}) and total monthly biovolume ($\text{mm}^3 \text{ l}^{-1}$) in PET from 2008 to 2010.....</i>	<i>38</i>
<i>Table 3.1: Air temperature, wind speed and precipitation in Santa Catarina airport.....</i>	<i>59</i>
<i>Table 3.2: Abiotic parameters during hot-rainy and cold-dry periods in Peri.....</i>	<i>61</i>
<i>Table 3.3: Species and its functional groups in Peri.....</i>	<i>66</i>
<i>Table 4.1: Morphometric parameters of studied German lakes.....</i>	<i>83</i>
<i>Table 4.2: Morphometric parameters of studied Brazilian lakes.....</i>	<i>85</i>
<i>Table 4.3: Means and limnological variables of 4 temperate shallow lakes.....</i>	<i>87</i>
<i>Table 4.4: Mean, minimum and maximum of abiotic parameters in 4 Brazilian lakes.....</i>	<i>88</i>
<i>Table 4.5: Diversity of 5 shallow polymictic lakes in Brandenburg and 11 Brazilian lakes.....</i>	<i>101</i>

Summary

Phytoplankton succession linked to productivity-diversity relationship at steady-state/non steady state conditions, mixing events as predominant disturbance in sense of Connell (1978) and influence of conditional differentiation (temperature) on phytoplankton diversity were investigated. Water samples were taken two times a week in 4 German shallow lakes in Brandenburg region (Melangsee, Petersdorfer See, Wolziger See, and Langer See) from 2007 to 2010 and in 2009/2010 during cold and rainy season in a Brazilian coastal lagoon Peri. A comparison between literature data from 4 Brazilian lakes, in order to investigate the influence of temperature on diversity and dynamic of phytoplankton species was also done. The cyanobacterial species dominated all studied lakes and the mixing had a positive effect on the supremacy of this group in tropical lakes. The high biovolume of cyanobacteria contributed to the achievement of steady state conditions in sense of Sommer et al. (1993) during consecutive periods in Petersdorfer See and in Peri lagoon practically during all phases. The monodominance of *Cylindrospermopsis raciborskii* was observed in warm water, under no stratification regime. Oscillatoriales of group S1 (Reynolds 2002), represented by *Limnothrix redekei* and *Pseudanabaena limnetica*, typical in turbid mixed layers and with high nitrogen affinity, were typical in Petersdorfer See. In Melangsee, steady state was observed during colder periods under dominance of Bacillariophyceae and Chrysophyceae. Lower diversity coincided with steady state conditions and higher values of resource use efficiency (RUE), while higher diversity occurred mainly at transitional state during the spring in temperate lakes, supporting the non-equilibrium concept (Hutchinson 1961) at lower RUE values. Higher biovolume occurred mainly during the late summer in temperate lakes under dominance of cyanobacteria, and/or at steady state. Concerning the temporal variation of phytoplankton, the highest peak of species richness preceded the resource use efficiency, suggesting the productivity as consequence of diversity. The richness was much higher in temperate shallow lakes, which were more similar to each other in terms of seasonality, species number and biovolume. A positive correlation between richness and biovolume of temperate lakes was found and the opposite was observed in tropical lakes. The biovolume and richness in tropical lakes were more variable and in temperate lakes presented higher richness at intermediate level of biovolume (annual mean from 10 to 18 mm³/l). Low level of biodiversity allows an ecosystem to function under constant conditions, but a greater biodiversity occurred in fluctuating environments.

Chapter

1

1 Introduction

1.1 Background

Biodiversity is a quintessential ecological phenomenon because it represents the net result of a complex set of interacting ecological, evolutionary, and physical processes (Huston 1997). Equilibrium/steady-state and non-equilibrium hypothesis have often been used to explain community ecology and emerged in phytoplankton studies when discussing the diversity-disturbance relationship. Some theories have been proposing different processes to explain the coexistence of a large number of species under limited resources. Non-equilibrium concepts are linked to the paradox of phytoplankton, which argues that equilibrium states were unlikely to form in planktonic systems (Hutchinson 1961). Originally, compelling experimental evidence for the predictability of interspecific interactions determine a steady-state outcome wherein one or relative few species dominance thought competitive exclusion (Hardin 1960) and, on the other, a wealth of observational data pointing to the apparent co-existence of several species under limited resources (Hutchinson 1961). The equilibrium/steady state concept describes a situation of little variability of species dominance and total biomass across time (Naselli-Flores et al. 2003), and may represent a situation where a maximum of three species dominate the assemblage for, at least, three weeks without considerable change in total biomass (Sommer et al. 1993).

Connell (1978) proposed the Intermediate Disturbance Hypothesis (IDH) to explain the community's responses to environmental disturbances and its relation with diversity. The Intermediate Disturbance Hypothesis arguments that non-disturbed or highly disturbed communities develop low diversity; and those disturbances of intermediate frequency and intensity are needed to maintain diversity (*i.e.* the number of species is at its highest when disturbance frequency and intensity are intermediate). Disturbances are mainly stochastic abiotic events that result in distinct abrupt changes in the community taxonomic composition, directing its internal organization and ecological equilibrium. Such events include the time scale and the frequency of the algal generation time (Reynolds 1993). Disturbance can also be defined as any sudden change in the aquatic environment is also responsible for determining the high degree of diversity in phytoplankton communities (Roxburgh et al. 2004). Examples of these disturbances are temperature changes, influx of nutrients, wind, and chemical fluctuations (Padisák 1993). The onset and break down of thermal stratification represent the

most important disturbances affecting the phytoplankton species composition in a lake (Morabito et al. 2003). Measuring the disturbance is somewhat problematic since phytoplankton under natural conditions is subjected to different types of disturbances that are difficult to quantify. There is no universal common scale for estimating changes in physical features, nutrient availability or grazing pressure. However, disturbance impact can be evaluated by the responses obtained from biological variables (Sommer 1993). The species diversity index is the most used biological response for evaluation of IDH in the phytoplankton community (Rojo & Alvarez-Cobelas 1993, Flöder & Sommer 1999). IDH is an attempt to reconcile the equilibrium and non-equilibrium argument because the scales of disturbance determine the state of community organization and diversity Reynolds (1993).

The contrast between the historical and contemporary perspectives on diversity-productivity relationships has engendered a lively debate about whether species richness is a cause or consequence of ecosystem productivity (Loreau et al. 2001, Schmid 2002). Recent experiments have provided evidence of the functional importance of biodiversity to ecosystem processes in microcosmos experiments with terrestrial environments (Kinzig et al. 2001, Schmid et al. 2002). Compared to terrestrial systems, aquatic ecosystems are characterized by greater propagule and material exchange, often steeper physical and chemical gradients, as well as rapid biological processes. These characteristics limit potential to transfer conclusions derived from terrestrial experiments to aquatic ecosystems whilst at the same time provide opportunities for testing the general validity of hypotheses about effects of biodiversity on ecosystem functioning (Giller et al. 2004). Some studies highlighting the potential for bi-directionality in this relation, in which productivity stands as both a cause and a consequence of biodiversity patterns (Gross & Cardinale 2007, Cardinale et al. 2009), since species are known to be dependent on nutrient availability for growth, and diversity can allow for the more efficient conversion of nutrients into biomass, for example through niche differentiation processes. While biodiversity has historically been seen as a response variable that is affected by climate, nutrient availability and disturbance, 'Biodiversity-Ecosystem Function Paradigm' sees the environment primarily as a function of diversity, underlining the active role of the biota in governing environmental conditions. There are obvious conflicts with published evidence from work on natural rather than synthesized ecosystems (Loreau et al. 2002).

Considering the study of the structure of phytoplankton community capable to adapt and colonize the same habitat under similar conditions, the strategy to apply the functional group

classification provides important information on the causes of species selection in the pelagic community (Reynolds 1997, Reynolds et al. 2002). The table 1 shows a general description of functional groups by Reynolds (1997):

Table 1.1: *Phytoplankton groups according to Reynolds (1997), taken from Knopf et al. (2000).*

Group	Trophie	Typical representatives	Designation
A	oligotrophic	<i>Urosolenia, Cyclotella comensis</i>	Diatoms in clear well mixed lakes
B	oligotrophic	<i>Asterionella, Aulacoseira italica</i>	Spring diatoms in small-medium lakes
C	eutrophic	<i>Asterionella, Stephanodiscus rotula, Aulacoseira ambigua</i>	Spring diatoms in small-medium lakes
D	hypertrophic	<i>Stephanodiscus hantzschii</i>	Enriched turbid water diatoms
E	mesotrophic	<i>Dinobryon, Chrysosphaerella</i>	Chrysophyceae
F	oligotrophic	<i>Sphaerocystis, Botryococcus</i>	Chlorococcales in clear epilimnia
G	eutrophic	<i>Eudorina, Pandorina</i>	Chlorophyceae
H	eutrophic	<i>Anabaena</i>	N-fixing, colonial cyanobacteria
I	eutrophic	<i>Pediastrum, Scenedesmus, Oocystis borgei</i>	Chlorophyceae
K		<i>Aphanocapsa, Aphanothece</i>	Small colonial cyanobacteria
L _O	oligo- bis mesotrophic	<i>Ceratium, Peridinium inconspicuum, Gomposphaeria</i>	Dinoflagellates
L _M	meso- bis eutrophic	<i>Ceratium, Microcystis</i>	Summer dinoflagellate
M		<i>Microcystis</i>	Cyanobacteria <i>Microcystis</i>
N	oligo- bis mesotrophic	<i>Cosmarium, Tabellaria</i>	Desmidiaceae-diatoms
P	eutrophic	<i>Staurastrum, Fragilaria</i>	
R		<i>Planktothrix rubescens, P. ? mougeotii</i>	Cyanobacteria in metalimnia of mesotrophic stratified lakes
S	eutrophic	<i>Planktothrix agardhii, Limnothrix redekei</i>	Turbid water filamentous cyanobacteria
S _N	eutrophic	<i>Cylindrospermopsis</i>	N-fixing filamentous cyanobacteria 'warm mixed layers'
T		<i>Geminella, Binuclearia, Tribonema</i>	Filamentous plankton in deep, well-mixed epilimnia
U		<i>Uroglena</i>	earlier summer plankton
V	eutrophic	Photo (trophic) bacteria	Bacterioplankton in metalimnia of stratified lakes
W		<i>Euglena, Synura, Gonium</i>	Small organic ponds
X1	eutrophic	<i>Chlorella, Ankyra, Monoraphidium</i>	Nanoplankton in shallow mixed layers
X2	meso-eutrophic	<i>Rhodomonas, Chrysochromulina</i>	Nanoplankton in clear mixed layers
X3	oligotrophic	<i>Koliella, Chrysococcus</i>	Nanoplankton in shallow clear mixed layers
Y	meso-eutrophic	<i>Cryptomonas</i>	Cryptomonads in small enriched lakes
Z	oligotrophic	<i>Synechococcus, Chlorella minutissima</i>	Picoplankton in clear-mixed layers

Functional groups consist of species with similar morphology and environmental requirements, but they do not necessarily belong to the same phylogenetic group. In contrast to long species lists or usage of dominant taxonomical groups, functional groups make it much easier to examine and compare the seasonal changes in various lake types and to evaluate the responses to environmental conditions and changes (Kruk et al. 2002, Weithoff et al. 2001). Reynolds (1997) called phytoplankton associations as ‘evolutionary development’, supplemented by further investigations, as happened in the case of S_N association (Padisák & Reynolds 1998). Reynolds (2002) advocated for the separation of phytoplankton into functional groups based on their traits, differentiating groups of algae according to habitat type and tolerances to key environmental variables like light, phosphorus, and nitrogen.

Species may also occupy a different niche, which tends to reduce competition through different patterns of resource use, which can arise as an evolutionary effect of competition (Harris 1986). Conditional differentiation is a type of niche differentiation, which occurs when two competing species differ in their abilities to use a resource based on varying environmental conditions. One species may be more competitive in one set of environmental conditions, but another species is more competitive in another set of conditions. Therefore, in a varying environment, each species is sometimes a better competitor and they can coexist. Indeed, Hutchinson’s suggestion, namely the continuous variation in environmental conditions, due to the seasonal cycle and less predictable factors like the change in weather, is the most obvious explanation (Hutchinson 1961, Richerson et al. 1970). Changes of temperature in tropical and temperate lakes are factors capable to influence strongly the structure and diversity of the phytoplankton community (Norbert 2004, Becker et al. 2008). The succession driver in tropical lakes may also to be linked to precipitation and stratification pattern (Dantas et al. 2008). The composition of phytoplankton communities at the level of genus and species varies little between temperate and tropical systems, showing broad overlap in species composition and little endemism in tropical latitudes (Lewis 1996, Kalff & Watson 1986).

1.2 Objectives

The aim of this study is to investigate and to compare the relation between diversity and productivity in temperate and tropical shallow polymictic lakes, besides of the succession and diversity of phytoplankton at equilibrium/non equilibrium conditions.

1.3 Methodology

The samples were taken biweekly from 2007 to 2009 in Melangsee, Wolziger See, Langer See and Petersdorfer See, and monthly during 2010 in Petersdorfer See and Melangsee. In Peri coastal lagoon (Brazil), the samples were taken twice a week from 02th June to 03th July (cold-dry period) 2009 and from 02th March to 03th April (hot-rainy period) 2010. The water was taken each 0.5 meter with a 2.3 L-LIMNOS sampler and analysed as mixed samples. Sampling stations were above the deepest points, where Secchi depth was also recorded. Depth profiles of physical and chemical parameters were measured with a HYDROLAB H20 probe connected to a field computer (HUSKY Hunter). Total phosphorus, dissolved inorganic phosphorus, total nitrogen and inorganic dissolved nitrogen, dissolved silica, as well as chlorophyll *a* concentration were determined according to standard methods (DEV 2011). Phytoplankton was counted after fixation with Lugol's solution according to Utermöhl (1958). Biovolume was calculated by measuring the corresponding dimensions using the geometric formulas given by Rott (1981) and Willén (1976). For the Brazilian lake, water temperature, conductivity, pH and dissolved oxygen were measured *in situ* with specific probes (WTW – Multi350i). Nitrite (Golterman et al. 1978), nitrate (Mackereth et al. 1978), ammonium (Koroleff 1976), soluble reactive phosphorus (Strickland & Parsons 1960), total phosphorus and nitrogen (Valderrama 1981), and silica (Strickland & Parsons 1968) were determined. Chlorophyll *a* concentration was done according to Nusch (1980), using equations described by Lorenzen (1967). RUE as resource use efficiency indicating productivity was calculated by converting unit (μg) Chl *a* per unit (μg) TP (Ptacnik et al. 2008, Nixdorf et al. 2009). The mean of cell proportion ($\mu\text{m}^3 \text{ cell}^{-1}$) was obtained by division of biovolume/abundance ($\mu\text{m}^3 \text{ ml}^{-1}/\text{cell ml}^{-1}$). The criteria to identify an equilibrium phases according to Sommer et al. (1993), which phytoplankton is dominated more than 80% of biovolume by maximum 3 species for more than 2 weeks, and the functional groups proposed by Reynolds et al. (2002) were tested. The vertical attenuation coefficient K_d was calculated according to Kirk (1994), mean PAR in the mixed water column (I_{mix}) was calculated according to Riley (1957) and the fraction of the total global radiation comprising the PAR and the reflection at the surface of the water were calculated using a correction factor of 0.445, as proposed by Behrendt & Nixdorf (1993). Richness (number of species), Shannon Wiener index, evenness, and complement of Simpson Index were used as diversity measures as followed:

Shannon-Wiener index: $H' = -\sum_{i=1}^s p_i \log p_i$ where p_i = biovolume belonging to the i^{th} of S species/ total biovolume.

Evenness = $H'/H_{\text{max}} = H'/\log S$

Comp. Simpson index: $1 - C = \sum_{i=1}^s p_i^2$ where p_i = number of individuals belonging to the i^{th} of S species/ total number of individuals.

1.4 Structure of the thesis

In Chapter 2, ecological conditions in two very shallow polymictic lakes (Petersdorfer See and Melangsee) were investigated, in order to associate diversity and productivity with steady state/non-equilibrium situations. The focus of this chapter was the association between diversity and productivity as resource use efficiency (RUE) in the course of ecological succession. In Chapter 3, mixing events as disturbance in sense of Connell (1978) capable to control diversity of phytoplankton were studied a Brazilian shallow coastal lagoon Peri, strongly dominated by the toxic cyanobacteria *Cylindrospermopsis raciborskii*. Uninterrupted steady state conditions in sense of Sommer et al. (1993) occurred under monodominance of this toxic cyanobacterium. In Chapter 4, a comparison of data between 4 German and 4 Brazilian lakes was done, in order to investigate the influence of conditional differentiation on diversity and dynamic of the phytoplankton species, as well as the relation between richness and productivity (biovolume) in both types of ecosystems.

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Chapter

2

2 Phytoplankton succession determines productivity and diversity at non-equilibrium /steady state conditions in two very shallow lakes

2.1 Abstract

Ecological conditions and phytoplankton succession in two very shallow polymictic lakes (Petersdorfer See and Melangsee) in a lake chain in Eastern Germany were analyzed from 2008 to 2010 in order to associate the diversity and productivity with steady state/non-equilibrium situations. The dominance of Chlorophyceae occurred during the spring under higher diversity (richness, Shannon-Wiener index, Simpson index), lower levels of biovolume and productivity as resource use efficiency. Higher productivity occurred mainly during the late summer under dominance of cyanobacteria, and/or at steady state. Higher diversity supported non-equilibrium conditions at transitional states, while lower diversity coincided with steady state conditions. Petersdorfer See was dominated by cyanobacteria practically during all phases, achieving the steady state during consecutive periods. Oscillatoriales of group S1 (Reynolds 2002), represented by *Limnothrix redekei* and *Pseudanabaena limnetica*, typical in turbid mixed layers with light deficient conditions and nitrogen affinity, were typical in this lake. The equilibrium situations were not common in Melangsee, which occurred only during colder periods. The dominance of Bacillariophyceae group as *Cyclotella radiosa* and *Rhizosolenia longiseta* (A), *Fragilaria ulna* (P), together with Chrysophyceae as *Dinobryon sociale*, *Mallomonopsis* sp. and *Synura* sp (E), common in shallow lakes with very low nutrients concentration, composed the steady state in Melangsee. Both lakes were colonized by *Cylindrospermopsis raciborskii* (S_N) and *Aphanizomenon gracile* (H1), which contributed to the achievement of steady state conditions in Petersdorfer See. These two species had similar performance, although *C. raciborskii* was more common during late summer and *A. gracile* extended its dominance until autumn. A positive relation between richness and biovolume was found, more accentuated in Melangsee. A negative relation was observed in regards to richness versus evenness. The Shannon-Wiener Index if using biovolume values was highest in Melangsee, while this diversity indice using abundance values was lowest in Petersdorfer See. The individual cell proportion was between 30 and 70 $\mu\text{m}^3 \text{cell}^{-1}$ at higher diversity, suggesting that the cell size plays a major role in the variation of diversity. Concerning the temporal variation of phytoplankton, the highest peak of species

richness preceded the resource use efficiency, suggesting the productivity as consequence of diversity.

2.2 Introduction

The structure and functional relationships of lake-phytoplankton exhibit many puzzling phenomena (Richerson et al. 1970). Investigations linked to biodiversity and population dynamic of phytoplankton are often accompanied by questions involving equilibrium and non-equilibrium theories and its causes. The ecological consequences of biodiversity loss have aroused considerable interest and controversy during the past decade. There is, however, uncertainty as to how results obtained in recent experiments scale up to landscape and regional levels and generalize across ecosystem types and processes (Loreau 2001). A comprehensive synthesis of evidence linking changes in biodiversity to ecosystem functioning and the mechanisms underlying the relationships is not attempted, since assessing the ecosystem-level consequences of species loss has just begun in aquatic systems and pertinent information is still limited at present (Gessner et al. 2004).

The relationship between species diversity and the productivity of ecosystems is one of the most fundamentally important and widely studied relationships in biology (Cardinale 2009). The contrast between the historical and contemporary perspectives on diversity-productivity relationships has engendered a lively debate about whether species richness is a cause or consequence of ecosystem productivity (Loreau et al. 2001, Schmid 2002, Worm & Duffy 2003). Investigations into relations between biodiversity and ecosystem functioning have led to the general consensus that species functional characteristics have a strong influence over ecosystem properties (reviewed in Hooper et al. 2005). Ecological experiments show that ecosystem properties depend greatly on biodiversity (Hector et al. 1999). Resource supply can affect species richness and richness can affect productivity simultaneously at a single spatial scale highlighting the potential for bi-directionality in this relation (Gross & Cardinale 2007). The recent advances led to a new synthetic ecological framework, which has even been denoted as a new paradigm of ecology. This new emerging paradigm called 'Biodiversity-Ecosystem Function Paradigm' (Naeem 2002, Schmid et al. 2002) sees the environment primarily as a function of diversity, underlining the active role of the biota in governing environmental conditions.

Phytoplankton research on small lakes has been controversial, since many of them exhibit large and complex habitat diversity; therefore, they are very important in conservation biology. Some theories have been proposing different processes to explain the coexistence of a large number of species under limited resources, trying to solve the paradox of phytoplankton (Hutchinson 1961) over more than four decades. The paradox argues that equilibrium states were unlikely to form in planktonic systems, where currents and a lack of spatial structure might prevent any stable, long-term interaction among species. Since conditions change quite rapidly in the plankton habitat, perhaps one, and then another, organism is the superior competitor, but in such rapid succession, no one organism has the advantage long enough to cause the extinction of the others (Richerson et al. 1970). Hutchinson himself already suggested that the explanation could be that plankton communities are not in equilibrium at all due to weather-driven fluctuations (Scheffer et al. 2003). This phenomenon occurs mainly at transitional states in temperate lakes, defined as the period in spring/early summer, when abiotic conditions change and the diversity increases, without dominance of Cyanophyceae.

The equilibrium/steady state concept describes a situation of little variability of species dominance and total biomass across time (Naselli-Flores et al. 2003). Equilibria may occur during the spring phytoplankton peak (usually dominated by Bacillariophyceae), in clear-water phases (dominated by one or several species of Chrysophyceae and Cryptophyceae), during winter stagnation, when species are largely selected according to their tolerance of stress conditions (cold temperatures, mixing, low light) and most prominently during summers when the stagnation period allows the development of competition (Padisák et al. 2003). During the late summer period in eutrophic lakes, equilibrium may be characterized by self-induced habitats where phototrophic competitors fail because of low-light conditions, combined with effective exploitation of nutrients (high resource use efficiency) by the dominant Cyanophyceae (Nixdorf et al. 2003). This concept may also represent a situation where a maximum of three species dominate the assemblage for, at least, three weeks without considerable change in total biomass (Sommer et al. 1993). In many observational studies of steady state have been resulted in a decrease of biodiversity (Reynolds 1991, Morabito et al. 2003, Padisák et al. 2003, Mischke & Nixdorf 2003).

Steady state conditions are expected to be more likely in deep lakes than in shallow mixed ones (Mischke & Nixdorf 2003). On the other hand, very shallow lakes are more efficient in converting available phosphorus into phytoplankton biomass because of the constant and

sufficient underwater light climate due to the favorable relation of z_{eu} (euphotic depth) and z_{mix} (mixing depth). The generally accepted definition of a "shallow lake or pond" is that class of shallow standing water in which light penetrates to the bottom sediments to potentially support rooted plant growth throughout the water body (Sheffer 2004). The phytoplankton biomass in this special group of shallow lakes may be about twice higher as the medium shallow or deeper lakes at the same range of nutrients concentration. Stratification in very shallow lakes is generally rare since they have water mixing throughout their water column due to wind energy input. They are associated with a probably high intensity of polymixis, with Z_{max} (maximum depth) much smaller than the predicted area-related Z_{epi} (theoretical epilimnion depth) value. These lakes have a differentiated morphometry and topography with similar loading characteristics for the following properties: limited morphological variability, more mixing intensity, more regular light-dark rhythms, higher productivity, and frequently dominated by cyanobacteria. The chlorophyll *a* concentration of very shallow lakes may exceed the content in the medium shallow waters by 10 up to 40 $\mu\text{g/l}$ at the same nutrient load (Nixdorf & Deneke 1997).

In contrast to the trophic assessment of water bodies by trophic indices on annual or vegetation average, the resource use efficiency (RUE) indicates how efficient phosphorus will be converted into phytoplankton biomass. This parameter allows the assessment changes in productivity and is therefore consistent with the diversity – productivity approach (Ptacnik et al. 2008, Nixdorf et al. 2009). Mouillot et al. (2005) pointed out that functional diversity can be decomposed into functional evenness and functional richness. An important aspect is that richness and evenness are orthogonal to each other (i.e. vary independently of each other).

2.3 Hypothesis

The seasonal succession as driver of productivity is suggested, as well the productivity as consequence of species richness. The variation of productivity as RUE and individual cell proportion are useful to determine the temporal composition of phytoplankton groups and its diversity, as well as the tendency of non-equilibrium/steady state conditions. Higher diversity occurs mainly at transitional state during the spring and seems to support the non-equilibrium concept, while steady state conditions are found under lower diversity.

2.4 Study sites

The study was carried out in two polymictic-polytrophic very shallow lakes in the eastern part of Brandenburg region in Germany: Melangsee and Petersdorfer See. In the catchment area of the river Dahme in Scharmützelsee region locate shallow and highly eutrophicated lakes, regularly are dominated by blooms of Cyanophyceae in summer (Rücker et al. 1997, Wiedner et al. 2002, Rücker et al. 2009, Grüneberg et al. 2011). In Melangsee, *Limnothrix* species as *L. amphigranulata* were the most common components of phytoplankton, accompanied by *Pseudanabaena limnetica* and *Planktothrix agardhii* during the summer (Nixdorf & Mischke 2003). Since 2003, the general algal composition has been changed significantly and the population of toxic cyanobacteria *Cylindrospermopsis raciborskii* has been increased in this lake (Rücker & Nixdorf 2004). Dissolved inorganic phosphorus is a scarce resource in the lakes of Scharmützelsee region but sufficient to maintain the growth of cyanobacteria, which outcompete other algal groups under poor underwater light climate. A decrease of annual total phosphorus concentration from 70 $\mu\text{g/l}$ to 40 $\mu\text{g/l}$ in both lakes has been noted (Rücker et al. 1997, Grüneberg et al. 2011).

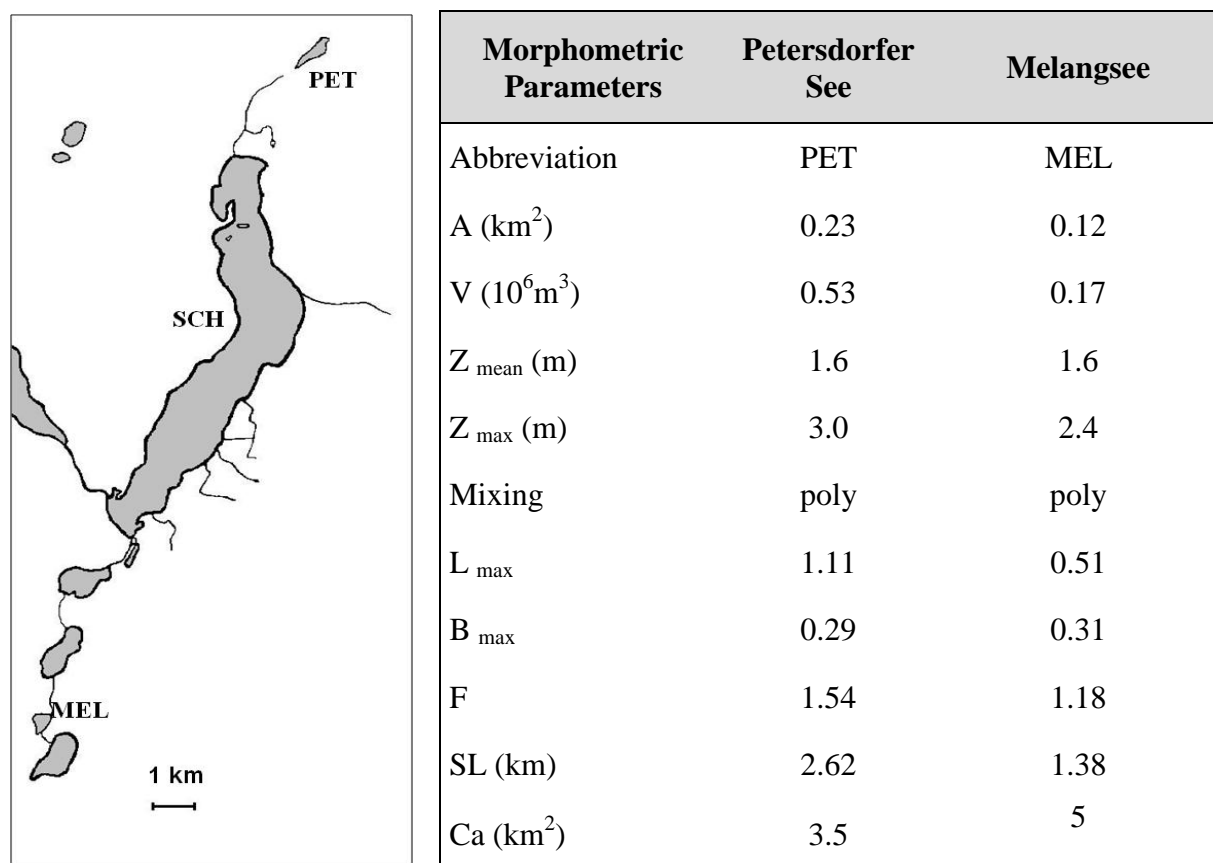


Fig. 2.1: Right: Part of the Scharmützelsee region, showing the very shallow lakes Petersdorfer See and Melangsee, divided by the large Scharmützelsee (SCH) in the middle. **Left:** Morphometric parameters: (A: total lake area, V: total lake volume, L_{max} : maximum length, B_{max} : maximum width, F: shore development, Ca: catchment area, l: shoreline length.

2.5 Methodology

The samples were taken biweekly from 2008 to 2010 in Petersdorfer See and Melangsee. The water was taken each 0.5 meter with a 2.3 L-LIMNOS sampler and analysed as mixed samples. Sampling stations were above the deepest points, where Secchi depth was also recorded. Depth profiles of physical and chemical parameters were measured with a Hydrolab H20 probe connected to a field computer (HUSKY Hunter). Secchi depth (SD), concentration of total phosphorus (TP), dissolved inorganic phosphorus (DIP), total nitrogen (TN) and inorganic dissolved nitrogen (DIN), dissolved silica (DSi) as well as chlorophyll *a* (Chl *a*) were determined according to standard methods (DEV 2011). Phytoplankton was counted after fixation with Lugol's solution according to Utermöhl (1958). Biovolume was calculated by measuring the corresponding dimensions using the geometric formulas given by Rott (1981) and Willén (1976). Shannon-Index ($H' = -\sum (P_i \log P_i)$ P_i = biovolume of the i^{th} of S species/total biovolume or abundance of the i^{th} of S species/total abundance), evenness ($H'/\log S$ S = number of species), richness (number of species), and complement of Simpson Index (the probability that two randomly picked individuals in a community belong to different species), calculated by $1-C = \sum_{i=1}^s p_i^2$ (abundance of the i^{th} of S species/total abundance) were used as diversity measures. RUE as resource use efficiency indicating productivity was calculated by converting unit (μg) chl *a* per unit (μg) TP (Ptacnik et al. 2008, Nixdorf et al. 2009). The mean cell proportion ($\mu\text{m}^3 \text{ cell}^{-1}$) was obtained by division of biovolume/abundance ($\mu\text{m}^3 \text{ ml}^{-1}/\text{cell ml}^{-1}$). The equilibrium phases were tested according to Sommer et al. (1993), using the functional groups proposed by Reynolds et al. (2002). Global radiation ($\text{J cm}^{-2}\text{d}^{-1}$) was provided by the meteorological station in Lindenberg located 15–30 km from the two lakes and was converted into photon flux ($\text{E m}^{-2} \text{ d}^{-2}$) by a factor of 0.445 as photosynthetic active radiation (PAR) at water body surface (I_0). Photosynthetically active radiation (PAR) was measured at half-meter intervals along the water column using two spherical quantum sensors (SA 193, Li-Cor, Lincoln, NE, USA). In order to estimate the mean PAR in the mixed water column (I_{mix}), the vertical attenuation coefficient K_d was calculated according to Kirk (1994) as follows:

(1)

$$K_d = \frac{\ln I_1 - \ln I_2}{z_1 - z_2}$$

Whereby I_1 is the PAR at depth Z_1 and I_2 is the PAR at depth Z_2 . The turbid lakes in different trophic states were calculated as follows:

$$\text{Melangsee: } K_d = 1.2534 \cdot 1/Z_{SD} + 0.3109 \quad (R^2 = 0.84; n = 112) \quad (2)$$

$$\text{Petersdorfer See: } K_d = 0.7215 \cdot 1/Z_{SD} + 0.6675 \quad (R^2 = 0.65; n = 46)$$

Mean PAR in the mixed water column (I_{mix}) was calculated according to Riley (1957):

$$I_{mix} = 0.445 \cdot I_0 \left(\frac{1 - e^{-K_d \cdot Z_{mix}}}{K_d \cdot Z_{mix}} \right) \quad (3)$$

Where Z_{mix} is the depth of the mixed water column, which was assumed to be equal to the mean depth of the lake. Daily K_d values were interpolated linearly between sampling dates. The fraction of the total global radiation comprising the PAR and the reflection at the surface of the water were calculated using a correction factor of 0.445, as proposed by Behrendt and Nixdorf (1993).

2.6 Results

2.6.1) Abiotic Parameters:

The very shallow lakes PET and MEL have similar values of pH, temperature, and concentration of dissolved inorganic phosphorus. The mean of total nitrogen concentration was two times higher in PET (1,631 $\mu\text{g/l}$) than in MEL (828 $\mu\text{g/l}$) and $\text{SiO}_2\text{-Si}$ concentration was almost six times higher in MEL (4,169 $\mu\text{g/l}$) than in PET (725 $\mu\text{g/l}$). The values of Secchi depth were lower in PET (minimum = 0.3 meter in September, mean = 0.75 m) than in MEL (minimum = 0.4 meter in August, mean = 1.0 meter). The concentration of dissolved inorganic phosphorus was low at the two shallow lakes, slightly higher in PET. The annual mean of TP concentration was slightly higher in MEL, with more irregular peaks and tendency to increase the phosphorus availability along the years. The highest values of TP concentration were observed during August (57 $\mu\text{g/l}$ in PET) and (137 $\mu\text{g/l}$ in MEL) and during the winter (48 $\mu\text{g/l}$ in PET and 95 $\mu\text{g/l}$ in MEL). In January, the parameters were measured under 10 cm ice cover in MEL and in PET under 24 cm. During this period in 2010, the oxygen concentration was lowest in PET (7.5 mg/l and 61% saturation in January), and in MEL the lowest concentration was detected in May (58% and 6.1 mg/l). The opposite was noted in relation to conductivity values, higher in MEL than in PET all studied period, with peaks during January in PET (420 $\mu\text{S/cm}$) and in MEL during May (555 $\mu\text{S/cm}$). The pH

values of both lakes were similar, slightly lower in MEL. The mean of I_{mix} presented lower values in PET during 2008 and 2009, but not during 2010 (see table 2.1).

Table 2.1: *Abiotic parameters of PET and MEL (mean, minimum and maximum respectively) from January until December 2008 (n=22) to 2009 (n=22) and during 2010 (n=12).*

PARAMETERS	PET 2008	PET 2009	PET 2010	MEL 2008	MEL 2009	MEL 2010
I_{mix} (μ mol photons $m^{-2} s^{-1}$)	86(7.0-165)	75(6.7-175)	79(4.5-218)	114(4.0-241)	83(7.0-188)	74(4.0-190)
Secchi Depth (m)	0.7(0.3-1.2)	0.7(0.35-1.2)	1.0(0.5-1.5)	1.0(0.5-1.4)	0.9(0.6-1.6)	1.2(0.4-1.7)
pH	8.0-8.9	7-9-8.9	7.9-8.9	7.6-8.6	7.7-8.6	7.4-8.8
Water Temp. ($^{\circ}C$)	12(1.5-23)	12(2.0-23)	11(1.0-24)	15(2.2-22)	12(2.1-23)	12(1.7-26)
Conductivity ($\mu S/cm$)	360 (331-381)	373(342-420)	372(343-428)	519 (506-555)	524 (498-567)	518 (377-595)
O ₂ (%)	109(89-143)	103(61-144)	97(56-114)	104(59-143)	100(73-117)	107(74-140)
O ₂ (mg/l)	12(8.7-14)	11(8.2-14)	11(7.5-14)	10(6.1-15)	11(7.2-15)	11(8.0-14)
TP ($\mu g/l$)	35(20-51)	35(18-55)	39(26-50)	31(15-44)	49(25-137)	52(12-96)
TN ($\mu g/l$)	1533 (1191-1832)	1841 (999-2757)	1519 (1265-2073)	782 (550-1056)	845 (643-1094)	856 (355-1118)
DIP ($\mu g/l$)	14(7.1-19)	12(5.0-28)	13(5.0-34)	7.2(4.6-13)	8(4.3-12)	12(2.7-34)
NH ₄ -N ($\mu g/l$)	172(5.8-608)	459(39-1489)	447(67-1622)	96(31-359)	103(34-503)	165(10-513)
NO _x -N ($\mu g/l$)	39(1.7-179)	45(3.2-117)	33(13-62)	21(1.2-88)	20(2.0-93)	24(3.0-45)
SiO ₂ -Si ($\mu g/l$)	645(169-1370)	689(208-1085)	840(406-1230)	6495(132-11845)	3352(79-6111)	2660(519-4278)
Chla ($\mu g/l$)	53(19-95)	47(18-85)	48(9-83)	40(25-75)	40(17-61)	39(8-94)

The course of distribution of dissolved nitrogen concentration is shown in figure 2.2. The NH₄-N concentration in PET was much higher than in MEL and the highest values in both lakes were observed during 2010. The lowest levels of NH₄-N concentration in PET were detected during September-October (5.8 $\mu g/l$ in 2008) and the highest from February (1,622 $\mu g/l$ in 2010) until April. In MEL, the highest peak was recorded in February 2010 (674 $\mu g/l$) and the lowest in April 2010 (10.2 $\mu g/l$). In this lake, the highest concentration was noted during the winter and fast consume of this nutrient during the spring was observed. The distribution of dissolved nitrogen concentration showed more seasonal regularity in PET. The highest availability of NO_x-N was measured in April in PET (179 $\mu g/l$) and in MEL during the winter

(maximum= 93 $\mu\text{g/l}$ during February 2009), and also during the summer 2010 (72 $\mu\text{g/l}$ in July), showing lower seasonality for this parameter in MEL.

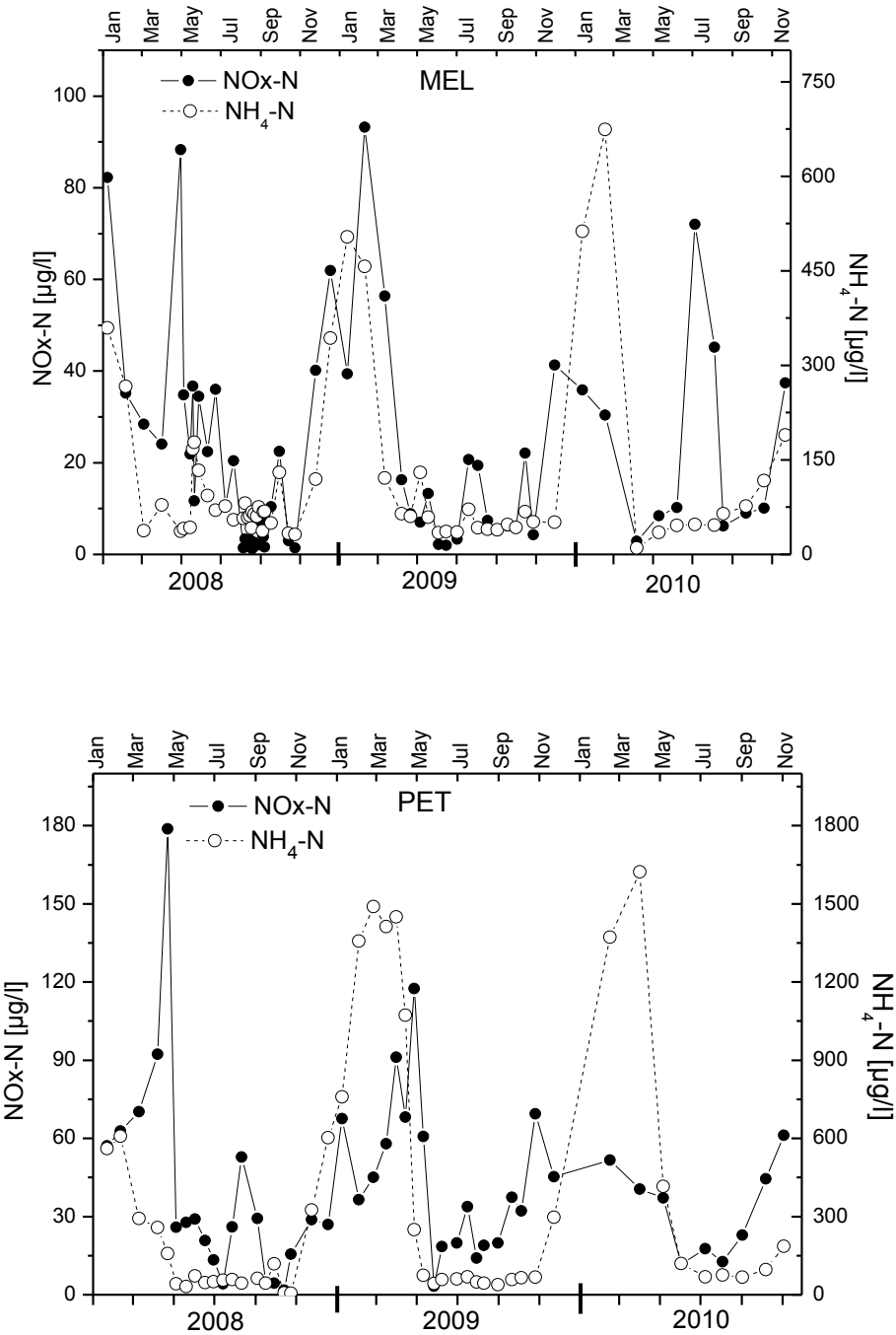


Fig. 2.2: Dissolved inorganic nitrogen ($\text{NO}_x\text{-N}$) and $\text{NH}_4\text{-N}$ concentration in MEL and PET during the studied period.

The dynamic of dissolved inorganic phosphorus concentration in MEL presented higher peaks during the winter, but a highest one was during the summer 2010, year considered atypical for this nutrient. The DIP concentration was generally lower in MEL, close to detection levels

during spring and summer, while in PET it presented more peaks during autumn and spring. Silica concentration was much higher in MEL, with the highest peaks during August (10,815 $\mu\text{g/l}$) and September (11,846 $\mu\text{g/l}$), declining during the spring bloom periods (minimum = 79 $\mu\text{g/l}$ in May). In PET, the highest levels were detected during colder periods, from September (1,370 $\mu\text{g/l}$) until February (1,830 $\mu\text{g/l}$) (see fig 2.3).

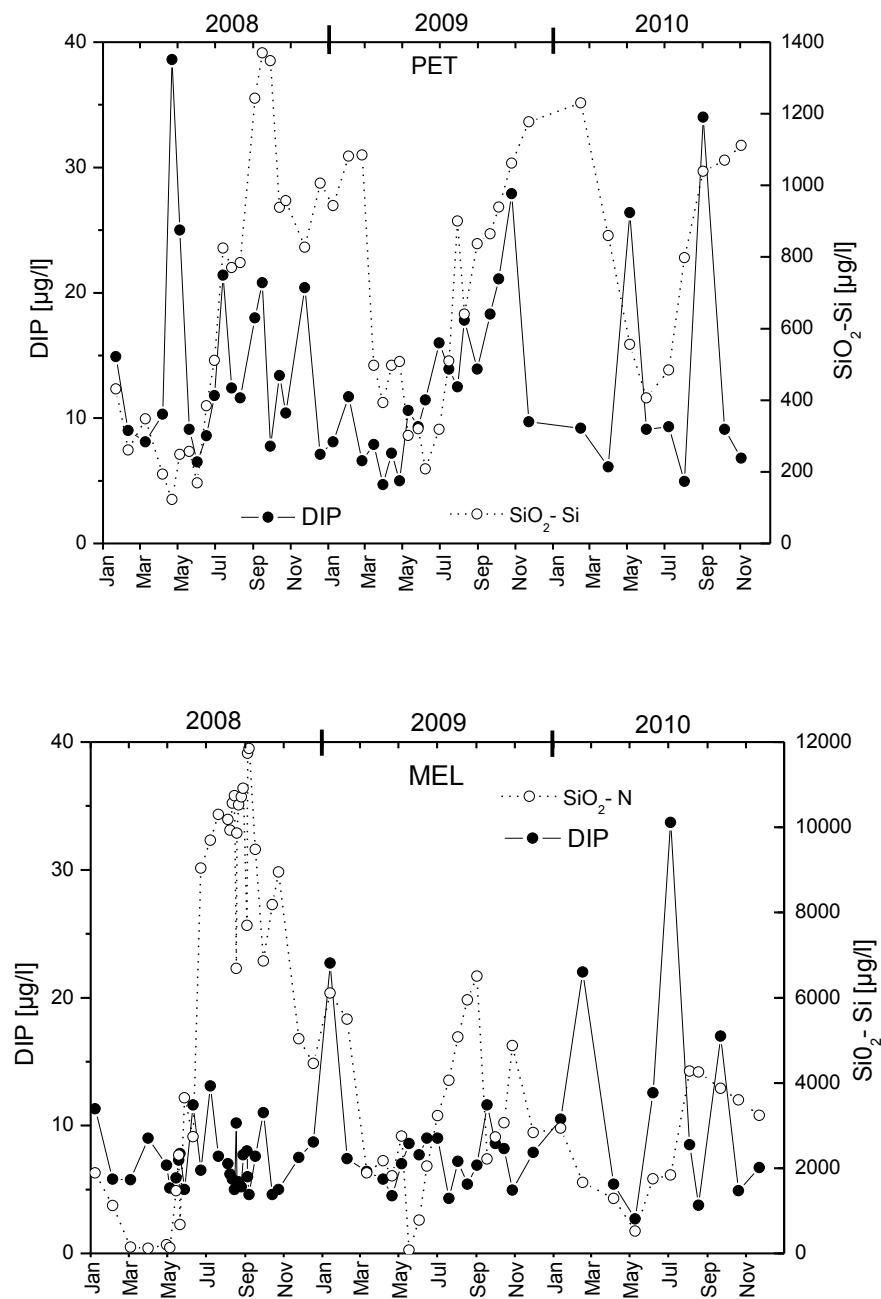
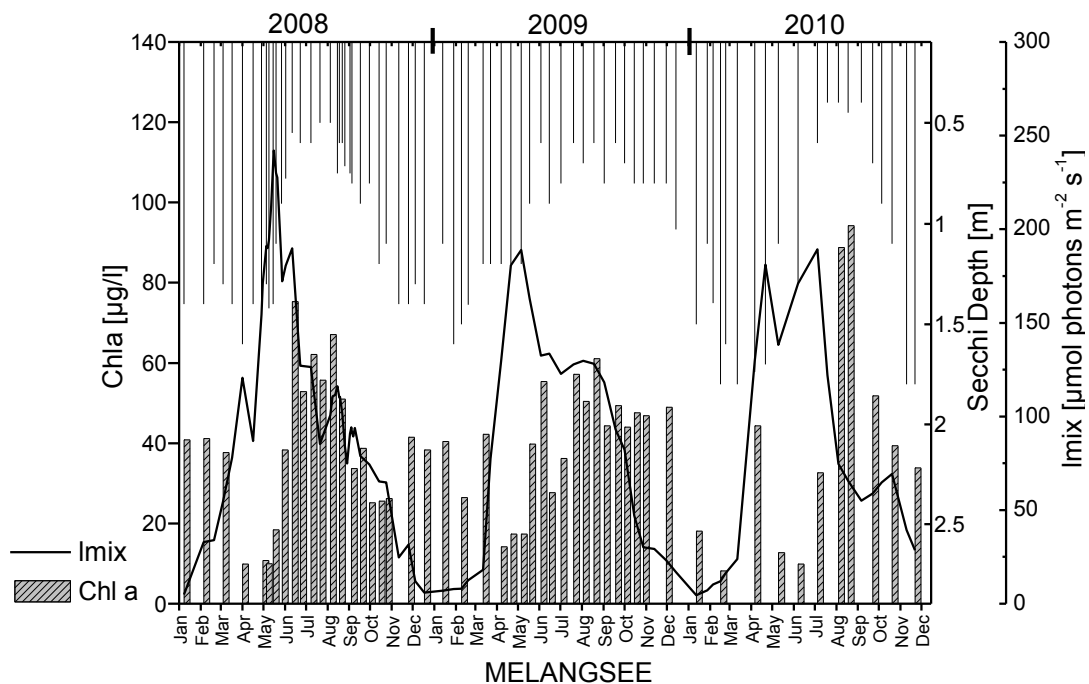


Fig. 2.3: Annual course of dissolved inorganic phosphorus (DIP) and silica concentration in PET and MEL from 2008 to 2010.

In Figure 2.4, the development of total phosphorus, Imix, Chl *a* concentration and Secchi depth are illustrated. Chlorophyll *a* concentration was normally higher in PET (maximum = 96 µg/l in August 2008, mean = 47 µg/l) than in MEL (maximum = 94 µg/l in August 2010, mean = 39 µg/l). In PET, the chlorophyll *a* concentration was also higher in autumn (about 85 µg/l), and in MEL during the winter (20 µg/l in PET and 40 µg/l in MEL during January). The Secchi depth of PET had its minimum (0.3 m) in August 2008 and was generally lower than in MEL (minimum = 0.4 m in July 2010). A clear water phase, defined as the highest Secchi disk reading after the spring algal bloom (Scheffer et al. 2001) together with considerable changes of phytoplankton composition, could not be observed. In early May 2008, the Secchi depth increased in MEL from 1.3 to 1.6 meter and the end of the month fell to 0.9 meter. In the spring 2009 and 2010, a sudden decline of the Secchi depth could not be observed (variation of 0.2 meter during May). The underwater irradiation in MEL (mean of Imix = 97.0 µmol photons m⁻² s⁻¹) was higher than in PET (mean = 78.8 µmol photons m⁻² s⁻¹), with a maximum of 227 µmol photons m⁻² s⁻¹ in May 2008 and in PET 218 µmol photons m⁻² s⁻¹ in July 2010. The higher values were found in PET and in MEL from spring and summer. The highest peaks were observed during July 2010 in PET (218 µmol photons m⁻² s⁻¹) and during May 2008 in MEL (230 µmol photons m⁻² s⁻¹). The lowest values for this parameter were measured during January 2010 (4.0 µmol photons m⁻² s⁻¹) at both lakes.



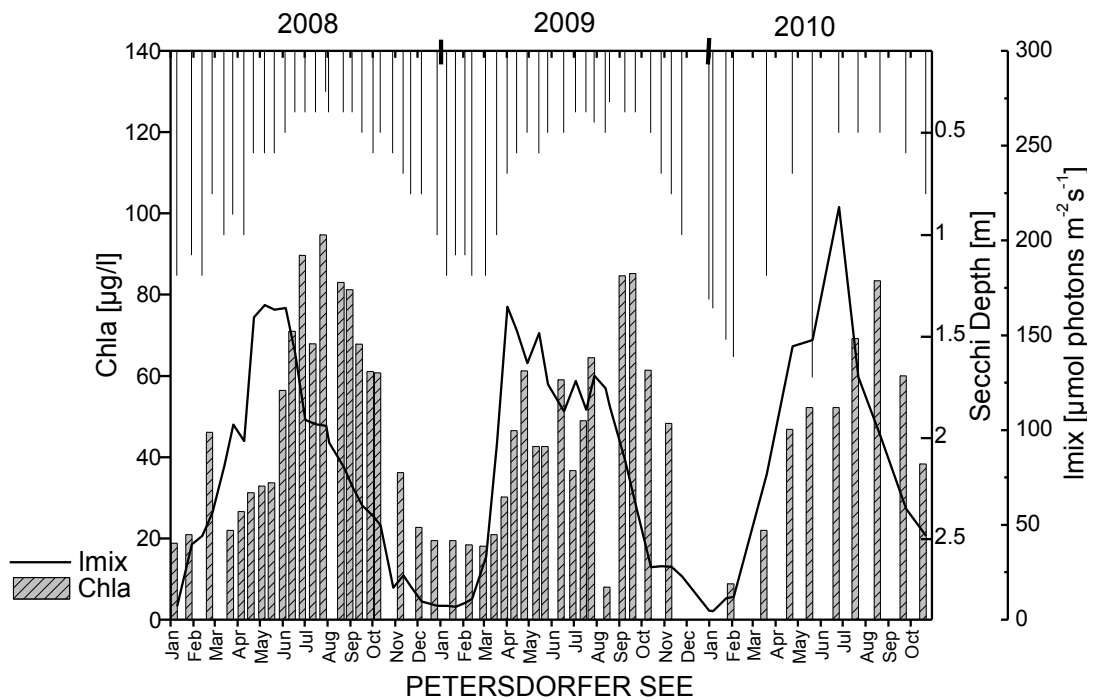


Fig. 2.4: Concentration of chlorophyll a, total phosphorus, Imix and corresponded values of Secchi depth from 2008 to 2010 in PET ($n=60$) and MEL ($n=55$).

2.6.2) Succession of phytoplankton groups and Resource use efficiency (RUE)

The annual pattern of phytoplankton showed a relative regularity in both lakes. In Melangsee, the group of Cryptomonadae and Bacillatoriales dominated in winter, following by Chrysophyceae, Chlorophyceae and Peridinales in spring and summer, and cyanobacterial group in later summer (fig. 2.5). A peculiar succession in 2008, characterized by higher peak of cyanobacterial dominance and resource use efficiency was observed in MEL. The RUE values in MEL tended to decrease along the years. The highest peaks of RUE were under dominance of cyanobacteria in both lakes, but considerable high in MEL in the presence of Bacillatoriales. In the beginning of spring, when the other groups of phytoplankton increased because of availability light and use of nutrients recourses, RUE decreases to minimum values in both lakes. The mean of efficiency to convert TP into biomass determined by resource use efficiency was higher in PET (1.5) if compared with MEL (1.0). This values show tendency to decrease along the years in both lakes.

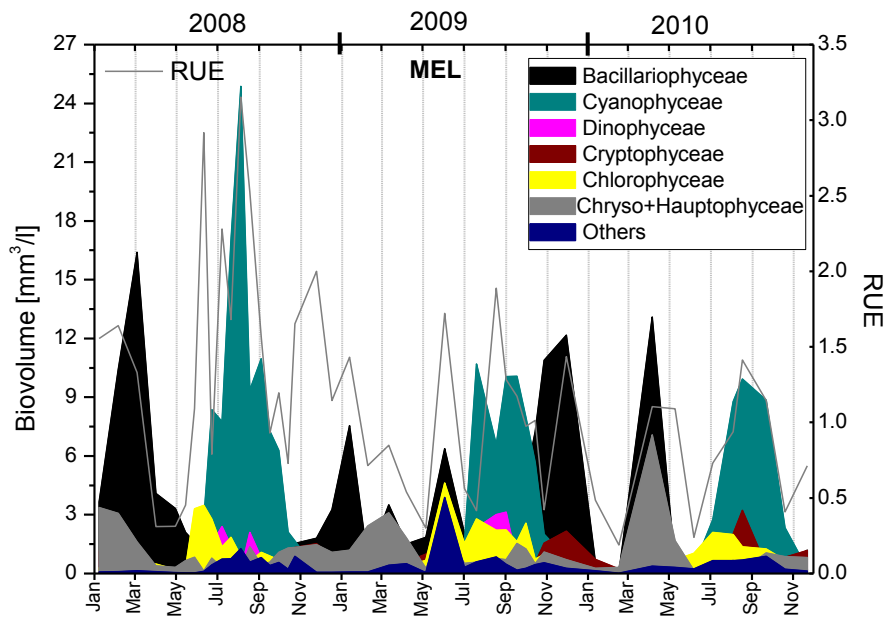


Fig. 2.5: Succession of phytoplankton groups associated with RUE in MEL from 2008 to 2010.

The Bacillariophyceae was a very important group in MEL, dominant from November until end April. The specie *Cyclotella radiosa* (association C), was the most common species of this group from February until June ($5.2 \text{ mm}^3/\text{l}$ in 2009). *Fragilaria ulna* (P) was more common during colder periods ($15.6 \text{ mm}^3/\text{l}$ in March 2008), decreasing its dominance during 2009 ($6.7 \text{ mm}^3/\text{l}$ in January). In 2010, *C. radiosa* was practically absent and *Fragilaria ulna* was the most dominant Bacillatoriales during April ($12.8 \text{ mm}^3/\text{l}$). After May during all 3 years, the specie *Fragilaria capucina* and *Aulacoseira granulata* (B) have substituted the winter species, but always under $1.0 \text{ mm}^3/\text{l}$. Other components of the group as genera *Nitzschia* and *Stephanodiscus* were present during all periods under low biovolume. A total of 32 species of Bacillariophyceae were found in MEL.

The group of Chlorophyceae had the highest richness in MEL, with a total of 70 different species at all studies periods (54 in 2008, 49 in 2009 and 56 in 2010). This group was more common during spring/early summer (transitional state) and has preceded the cyanobacterial dominance. A maximum of monthly richness was in June 2010 (34 species), with relative uniform distribution. The biovolume of each specie was generally low ($< 0.1 \text{ mm}^3/\text{l}$), with exception of genera *Coelastrum* (J) and *Oocystis* ($0.4 \text{ mm}^3/\text{l}$ and $1.2 \text{ mm}^3/\text{l}$ respectively) in June. The genus *Scenedesmus* was found under higher richness (14 species).

The group of Cyanophyceae in MEL had a total of 46 species. Generally, S1 species were more successful during September-October, as *Pseudanabaena limnetica* (from 2.0 to 5.0 mm³/l, with exception of 2008, when this specie achieved 15.8 mm³/l) and *Limnothrix redekei* (0.3 to 2.2 mm³/l). The cyanobacterial growth was more pronounced during the summer 2008, through the presence of *Cylindrospermopsis raciborskii* (maximum = 3.3 mm³/l), *Aphanizomenon gracile* (2.4 mm³/l), *Pseudanabaena limnetica* (15.8 mm³/l), and *Limnothrix redekei* (2.2 mm³/l). There was a slightly decrease of the maximum of Notocales represented by *Cylindrospermopsis raciborskii* (S_N) during August from 2008 to 2010 (3.3, 0.8 and 0.7 mm³/l respectively). *Aphanizomenon gracile* doubled its population from 2008 (2.5 mm³/l) to 2009 (5.0 mm³/l) during August-September and maintained this last performance in 2010. Other important component of the group was the Chlorococcales *Microcystis aeruginosa* (group M), present all months and stronger from spring until autumn (maximum 3.9 mm³/l in September 2009).

The Chrysophyceae was mainly represented by *Mallomonas* sp. (E) (except during the summer with a maximum = 1.3 mm³/l in March 2009) and *Mallomonopsis* sp. during the winter (maximum 1.9 mm³/l in January 2008). The specie *Dinobryon sociale* (E) achieved high density (5.6 mm³/l and 20,133 cell/ml) in April 2010, supplying the highest peak of all periods. The Haptophyceae *Chrysochromulina parva* (X2) was present during all months, mainly in October (about 1.0 mm³/l) and at the beginning of spring (maximum 1.5 mm³/l during May 2010). The Cryptophyceae was well represented by *Cryptomonas erosa* (S1) mainly during the summer and autumn (maximum = 1.1 mm³/l, 1.4 mm³/l, and 2.8 mm³/l) from 2008 to 2010 respectively. The Peridinales *Ceratium hirundinella* (L_M) (1.75 mm³/l) and *Peridinium willei* (L_o) had more density during June (1.0 mm³/l) until September (1.5 mm³/l), while *Gymnodinium lantzschii* was notable during colder periods (< 0.5 mm³/l) (see fig. 2.5).

The mean of RUE were generally higher in PET (1.5 in 2008, 1.6 in 2009, and 1.4 in 2010) than in MEL (1.5 in 2008, 1.0 in 2009, and 0.7 in 2010) and tended to decrease along the years. In summer 2008, a peak of RUE as observed in MEL (3.2) under significant dominance of cyanobacteria. The maximum of RUE in PET was in July during 2008 and 2009 (2.5 and 3.9 respectively) and during 2010, a more irregular profile could be noted, with a maximum of RUE in November (2.0). There were some peaks under dominance of Bacillatoriales, group more common in MEL, but in general, the progress of RUE tended to accompany the

cyanobacterial performance. The minimum of RUE (0.2) was detected during the winter in PET and during the spring in MEL.

The algal succession in PET exhibited a distinct pattern, if compared to Melangsee. The Cyanobacteria was the most significant group, composed to 41 different species, more concentrated during the summer and autumn; the colonization of other algal groups was weaker. The toxic Nostocales *Cylindrospermopsis raciborskii* (Sn) began to increase in May and had its climax in August and September (1.2 mm³/l in 2008, 1.3 mm³/l in 2009, and 2.0 mm³/l in 2010) when its population began to decline, taking place to increase of *Limnothrix redekei*. *Aphanizomenon gracile* (H1) was also present in PET during consecutive periods, more dominant during September. A regular presence of *Anabaena bergii* (H1) from June until October was registered, which obtained its highest point in late summer (mean of 3 years = 0.4 mm³/l). During this period in 2008, the biovolume of this specie was 2.3 mm³/l, decreased to 1.0 mm³/l in 2009, and fell dramatically to 0.07 mm³/l in 2010. *Limnothrix redekei* (S1) was very important, obtaining more success generally at the end of the year (10.0 mm³/l in November) during all periods, with exception of May 2009 (13.7 mm³/l). The mean of annual population of the Oscillatoriales *Limnothrix redekei* increased during 2010 from 2.3 to 3.9 mm³/l, when its biovolume was also relevant during July (7.2 mm³/l). *Pseudanabaena limnetica* (S1) was the most predominant cyanobacteria in PET. The persistence of this specie showed great seasonal regularity along the years. Its population began to rise in May, had its climax in August (highest in 2010 = 39 mm³/l), decreased gradually until October (mean = 11 mm³/l of all years), and then abruptly until December (1.0 mm³/l).

The group of Dinophyceae was well represented by several species of genus *Peridinium* as *P. umbonatum*, with more than 1000 cell/ml at the highest phases, mainly in May (maximum = 2.0 mm³/l in 2009) and July (2.7 mm³/l in 2010), together with *Gymnodinium lantzschii* (about 1.0 mm³/l). The richness and biovolume of the Chlorophyceae was lower in PET (56 species during all periods), with special attention to genera *Coelastrum* (annual sum < 5.0 mm³/l.) and *Oocystis* (annual sum < 0.8 mm³/l.). The Cryptophyceae was characterized primarily by the presence of *Cryptomonas erosa* during consecutive periods. Cryptophyceae and Haptophyceae were no common in PET. The group of Bacillariophyceae was lower in PET and presented an irregular pattern, with the presence of *Fragilaria ulna* (around 1.0 mm³/l) (fig. 2.6).

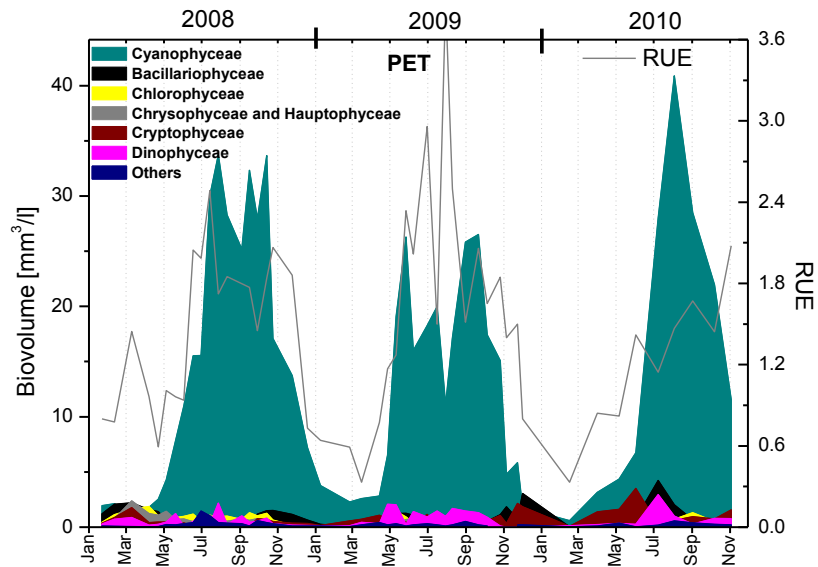


Fig. 2.6: Succession of phytoplankton groups in PET, associated with RUE variation from 2008 to 2010.

2.6.3 Steady state conditions

Steady-state conditions in MEL occurred during the winter and in April, period dominated by Bacillariophyceae and Chrysophyceae during four alternated periods (fig. 2.7 and table 2.2).

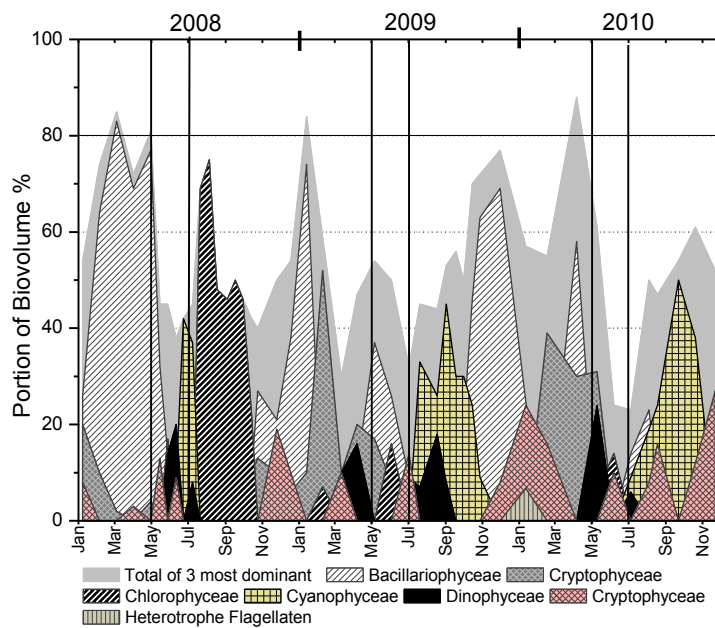


Fig. 2.7: Biovolume proportion (%) of the 3 most dominant species, represented by algal groups in MEL. The vertical lines represent transitional states.

Steady state conditions were not common in Melangsee, in opposite of PET. In MEL, the equilibrium through the dominance of Cyanophyceae (Nixdorf et al. 2003) could not be achieved. The performance of the 3 weightiest components of phytoplankton was more multifaceted in MEL, with discontinuous and dynamic substitution of species along the time. Equilibrium conditions (steady state) according to Sommer et al. (1993) just occurred at the beginning of the year, when Bacillariophyceae species dominated. The Cryptophyceae group at the steady state was represented by *Pseudopeninella erkensis* in April 2008. The species *Cyclotella radiosa* (A), *Fragilaria ulna* (P), and *Rhizosolenia longiseta* represented the Bacillariophyceae group. The Chrysophyceae as *Uroglena* sp. (U), *Mallomonopsis* sp. (E), *Synura* sp. (E), and *Dinobryon sociale* (E), contributed also to achievement of steady state conditions in MEL.

Table 2.2: Species at equilibrium conditions according to Sommer et al. (1993) and its functional groups (FG) according to Reynolds (2002), biovolume (BV in $\text{mm}^3 \text{l}^{-1}$ and %), abundance (cell ml^{-1}) and total monthly biovolume ($\text{mm}^3 \text{l}^{-1}$) in MEL from 2008 to 2010.

Date	Species	FG	BV $\text{mm}^3 \text{l}^{-1}$	BV %	Cell ml^{-1}	Total $\text{mm}^3 \text{l}^{-1}$
04.03.2008	<i>Fragilaria ulna</i>	P	15.6	80.3	10,138	19.4
30.04.2008	<i>Cyclotella radiosa</i>	A	3.2	76.7	3,322	
	<i>Pseudopedinella erkensis</i>		0.1	2.3	308	
	<i>Uroglena</i> sp.	U	0.1	2.2	1,099	4.2
13.01.2009	<i>Fragilaria ulna acus</i>	P	6.7	67.6	3,873	
	<i>Mallomonopsis</i> sp.	E	1.0	10.5	623	
	<i>Rhizosolenia longiseta</i>	A	0.7	6.6	13,086	9.9
06.04.2010	<i>Dinobryon sociale</i>	E	5.6	59.2	20,132	
	<i>Fragilaria ulna acus</i>	P	12.8	26.1	14,045	

Steady state conditions were very frequent in PET during consecutive periods, mostly through the strong dominance of Cyanophyceae. For the period of June 2008 and February 2009, the equilibrium was observed throughout 8 consecutive months. From August 2009 until November 2010, an incessantly steady state for 4 uninterrupted months was also registered (fig. 2.8).

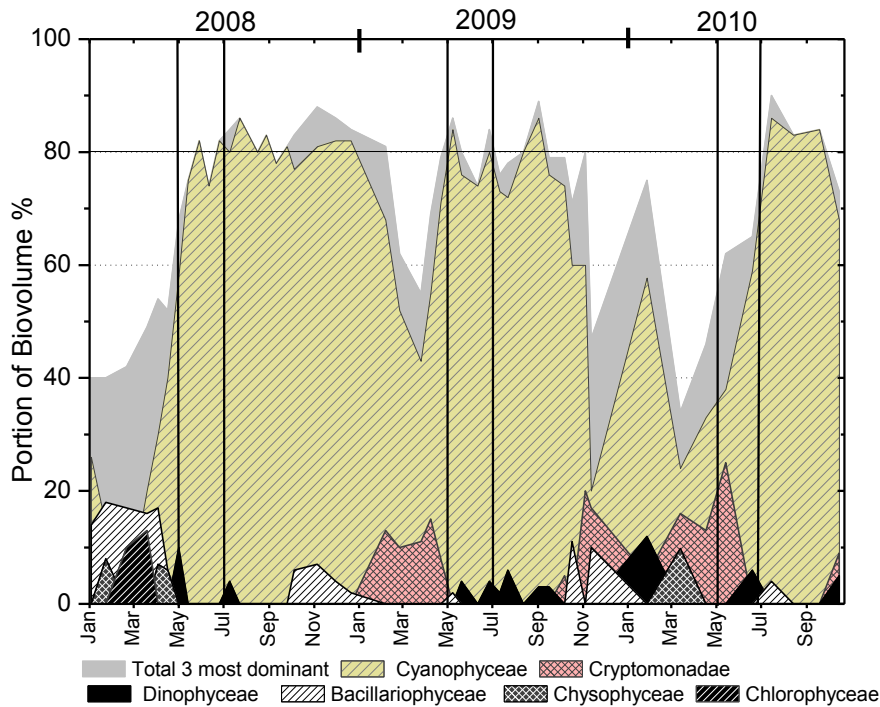


Fig. 2.8: Biovolume proportion (%) of the 3 most dominant species, represented by algal groups in PET. The vertical lines represent transitional states.

Pseudanabaena limnetica (S1) was the most common specie, stronger during warmer periods (about 70% in August), followed by *Limnothrix redekei* (principally from October until January). The occurrence of *Cylindrospermopsis raciborskii* was more evident from July to September together with *Aphanizomenon gracile*, which prolonged its presence until October. Colder periods were dominated by Bacillariophyceae and Cryptophyceae, under lower biovolume. *Fragilaria ulna acus* was notable from October until December 2008 and during August 2010 (around 5%), *Cyclotella radiosa* during January 2009 (0.1 mm³/l), and *Cryptomonas erosa* from November to April. The group of Dinophyceae was represented by *Peridinium umbonatum* (Lo) (4.0%) and *Gymnodinium uberrinum* (3.4%) during the summer, besides of *Gymnodinium helveticum*, more relevant during cold periods (5.0%). In opposite of MEL, there were during transitional states in PET two peaks at steady state conditions, both under high biovolume of *P. limnetica* (table 2.3).

Table 2.3: Species at equilibrium conditions according to Sommer et al. (1993) and its functional groups (FG) according to Reynolds (2002), biovolume (BV in $\text{mm}^3 \text{ l}^{-1}$ and %), abundance (cell ml^{-1}) and total monthly biovolume ($\text{mm}^3 \text{ l}^{-1}$) in PET from 2008 to 2010.

Date	Species at steady state	FG	BV $\text{mm}^3 \text{ l}^{-1}$	BV %	Cell ml^{-1}	Total $\text{mm}^3 \text{ l}^{-1}$
17.06.08	<i>Pseudanabaena limnetica</i>	S1	7.1	38.0	560,841	18.7
	<i>Limnothrix redekei</i>	S1	7.0	37.1	378,687	
	<i>Aphanizomenon gracile</i>	H1	1.3	6.8	26,450	
14.07.08	<i>Pseudanabaena limnetica</i>	S1	26.8	77.3	2,108,196	34.6
	<i>Aphanizomenon gracile</i>	H1	1.2	3.4	24,345	
28.07.08	<i>Pseudanabaena limnetica</i>	S1	30	78.0	2,358,407	38.4
	<i>Gymnodinium uberrimum</i>	Lo	1.3	3.4	80	
11.08.08	<i>Pseudanabaena limnetica</i>	S1	24.7	80.4	1,946,165	30.7
04.09.08	<i>Pseudanabaena limnetica</i>	S1	19.9	69.5	1,566,519	28.6
	<i>Limnothrix redekei</i>	S1	2.0	7.1	128,466	
	<i>C. raciborskii</i>	S _N	1.0	3.6	20,261	
16.09.08	<i>Pseudanabaena limnetica</i>	S1	30	70.5	1,967,256	35.5
	<i>Aphanizomenon gracile</i>	H1	2.3	6.6	49,213	
	<i>Limnothrix redekei</i>	S1	2.0	5.6	124,631	
14.10.08	<i>Pseudanabaena limnetica</i>	S1	19.6	49.9	1,541,593	39.2
	<i>Limnothrix redekei</i>	S1	11	28.2	696,017	
	<i>Aphanizomenon gracile</i>	H1	1.3	3.2	23,249	
24.10.08	<i>Limnothrix redekei</i>	S1	12.6	61.4	686,431	20.5
	<i>Pseudanabaena limnetica</i>	S1	3.2	15.8	255,014	
	<i>Fragilaria ulna acus</i>	P	1.2	5.7	1,534	
24.11.08	<i>Limnothrix redekei</i>	S1	12	75.8	630,825	15.8
	<i>Fragilaria ulna acus</i>	P	1.0	6.6	1,342	
19.12.08	<i>Limnothrix redekei</i>	S1	6.2	72	328,355	8.6
	<i>Pseudanabaena limnetica</i>	S1	0.9	10	70,944	
	<i>Fragilaria ulna acus</i>	P	0.4	4.5	504	
09.01.09	<i>Limnothrix redekei</i>	S1	3.6	78.1	186,467	4.6
	<i>Pseudanabaena limnetica</i>	S1	0.2	4.2	15,099	
25.02.09	<i>Limnothrix redekei</i>	S1	1.1	34.5	59,440	3.3
	<i>Pseudanabaena limnetica</i>	S1	1.1	33.7	87,481	
	<i>Cryptomonas erosa/ovata</i>	Y	0.4	12.8	491	
27.05.09	<i>Pseudanabaena limnetica</i>	S1	22	73.3	1,729,498	29.9
	<i>Limnothrix redekei</i>	S1	3.2	10.6	166,814	
16.07.09	<i>Pseudanabaena limnetica</i>	S1	17	74.6	1,335,472	22.7
	<i>Limnothrix redekei</i>	S1	1.2	5.4	73,820	
31.08.09	<i>Pseudanabaena limnetica</i>	S1	21.2	72.9	1,670,059	29.0
	<i>C. raciborskii</i>	S _N	1.2	4.2	26,076	
	<i>Aphanizomenon gracile</i>	H1	1.0	3.4	21,139	
21.09.09	<i>Pseudanabaena limnetica</i>	S1	21.6	74.0	1,696,903	29.1

Date	Species at steady state	FG	BV mm ³ l ⁻¹	BV %	cell/ml	Total mm ³ l ⁻¹
23.11.09	<i>Aphanizomenon gracile</i>	H1	3.5	12.0	32,500	9.4
	<i>Limnothrix redekei</i>	S1	4.6	49.0	261,726	
	<i>Cryptomonas erosa/ovata</i>	Y	2.0	21.1	2,300	
03.08.10	<i>Pseudanabaena limnetica</i>	S1	1.0	10.5	77,655	46.4
	<i>Pseudanabaena limnetica</i>	S1	39	84.0	3,069,323	
02.09.10	<i>Pseudanabaena limnetica</i>	S1	22.8	69.8	1,796,540	32.7
	<i>C. raciborskii</i>	S _N	2.0	6.2	41,064	
07.10.10	<i>Limnothrix redekei</i>	S1	2.1	6.7	137,032	25.0
	<i>Pseudanabaena limnetica</i>	S1	6.0	23.8	467,799	
	<i>Limnothrix redekei</i>	S1	15.0	60.3	852,435	
03.11.10	<i>Cryptomonas erosa/ovata</i>	Y	0.5	2.0	582	15.5
	<i>Limnothrix redekei</i>	S1	10.6	68.4	554,744	
	<i>Gymnodinium helveticum</i>	Lo	0.8	5.0	144	
	<i>Cryptomonas erosa/ovata</i>	Y	1.4	8.8	1,582	

2.6.4 Diversity

Usually, diversity was higher in MEL than in PET. A total of 248 different species were identified in MEL and 131 in PET. The highest monthly richness in MEL was observed during May 2010 and beginning of July (92 species) and in PET from July until the beginning of September (74 species). During this period, a larger discrepancy between richness and diversity indices was observed in PET and it coincided with the higher dominance of *P. limnetica*, which contributed to decline the indices. Normally, the lowest diversity in PET was noted from October until December, when *Limnothrix redekei* dominated. In MEL, the richness was frequently correlated with Shannon-Wiener index (biovolume), both presenting lower from December until March, at the dominance of Bacillariophyceae (steady state). Higher cells proportion of this group during colder periods contributed to decrease the Shannon Wiener index (biovolume), but did not affect the Simpson index (based on abundance values). A maximum of non-equilibrium in MEL (transitional states) coincided more precisely with highest diversity indices occurred in May until beginning of July. In PET, there was a tendency to increase the diversity earlier, at the beginning of March, showing less regularity than in MEL. The diversity was lower at steady state conditions in both very shallow lakes (figure 2.9).

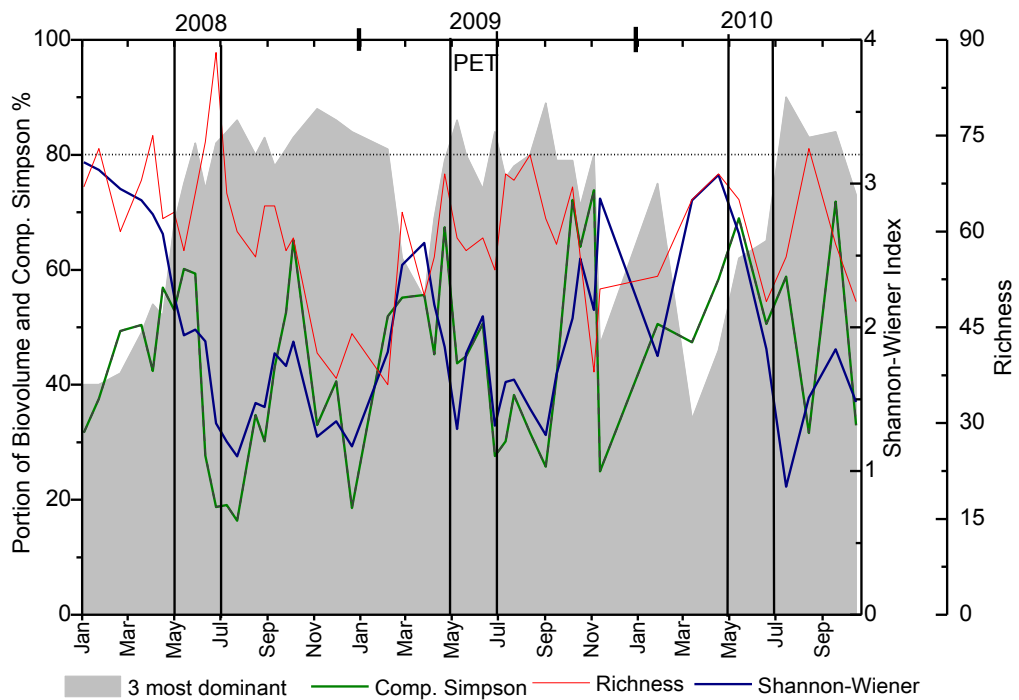
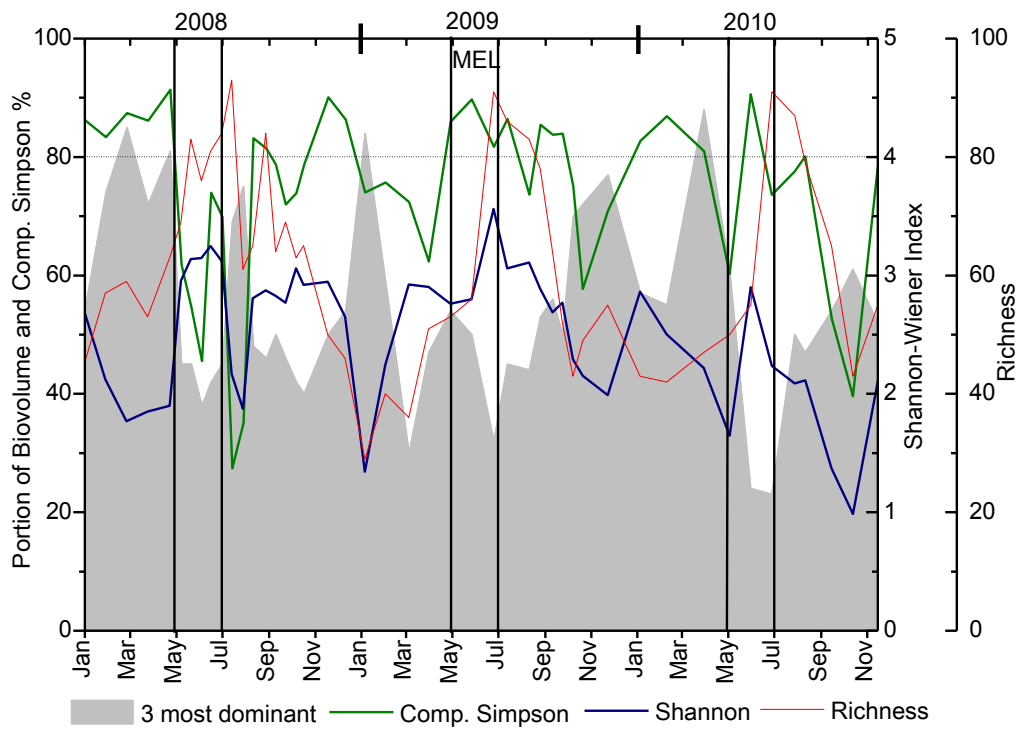


Fig. 2.9: Course of the 3 most dominant species associated with richness, Shannon Wiener index (biovolume) and complement of Simpson index from 2008 to 2010 in MEL and PET. The vertical bands represent transitional states.

The species composition with their singular cells proportion, course differentially along the time and define the differentiation between Shannon-Wiener indices. The individual cell proportion was much higher in MEL (maximum = 374 $\mu\text{m}^3/\text{cell}$ and mean = 101 $\mu\text{m}^3/\text{cell}$) than in PET (maximum = 53 $\mu\text{m}^3/\text{cell}$ and mean = 19 $\mu\text{m}^3/\text{cell}$). In Peterdorfer See, lake dominated by cyanobacteria practically all periods, the two Shannon-Wiener indices were lower, especially that using abundance, due the large number of cyanobacterial filaments. The discrepancy between the two Shannon-Wiener indices was more accentuated in this lake, mainly from January until May. During this phase, the presence of more species with larger cells, for example *Fragilaria* sp. and *Cryptomonas erosa*, contributed to the more uniformity of monthly biovolume, increasing the Shannon Wiener index (biovolume). It may be confirmed through the increase of cell proportion during colder periods and somewhat before the transitional states, which coincided with the highest diversity in PET (figure 2.10).

In MEL, the highest cell proportion phases did not coincided with the transitional states and with the peak of diversity, as occurred in PET. The lowest values of Shannon-Wiener index (biovolume) in MEL coincided evidently with the high individual cell proportion during colder periods, dominated by Bacillariophyceae. Lower cell proportion values were registered at transitional state in MEL during the spring (under dominance of Chlorophyceae), and during the summer (dominance of filamentous cyanobacteria). The abrupt presence of small cells with high abundance values (790,929 cell/ml) and low biovolume (0.55 mm^3/l) as *Aphanothece clathrata* (group K) decreased the Shannon Wiener index (abundance) in June 2008 in MEL. The maximum of Shannon (3.7) biovolume and Shannon Wiener index using abundance (3.0) was registered at transitional state in June. The highest diversity of both lakes was observed under cell proportion < 100 $\mu\text{m}^3/\text{cell}$.

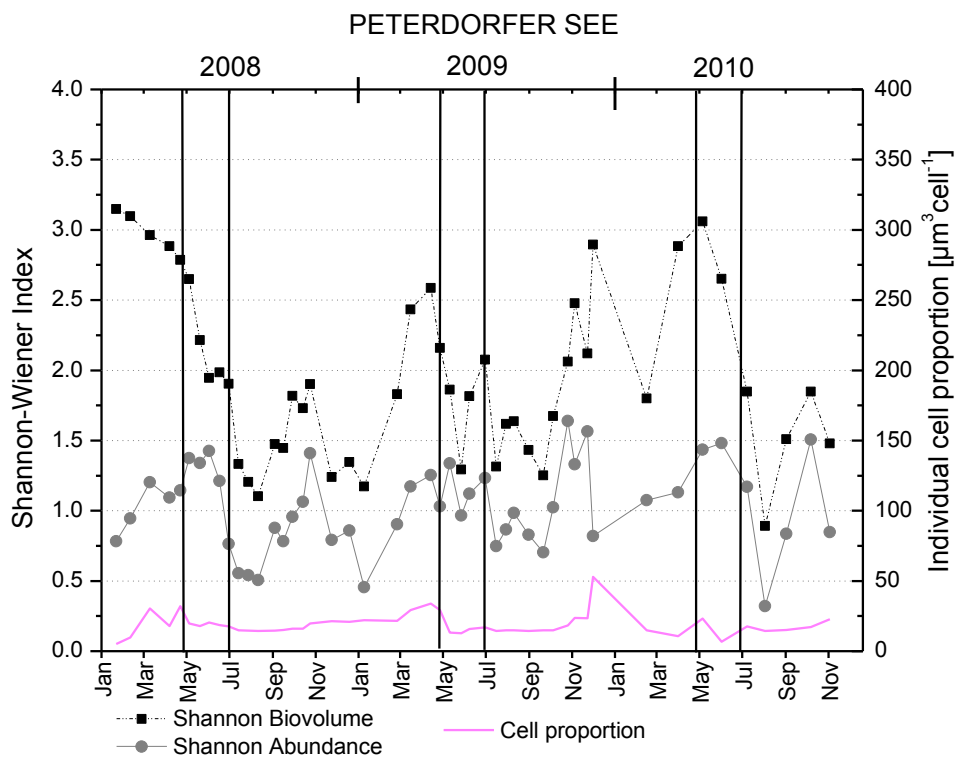
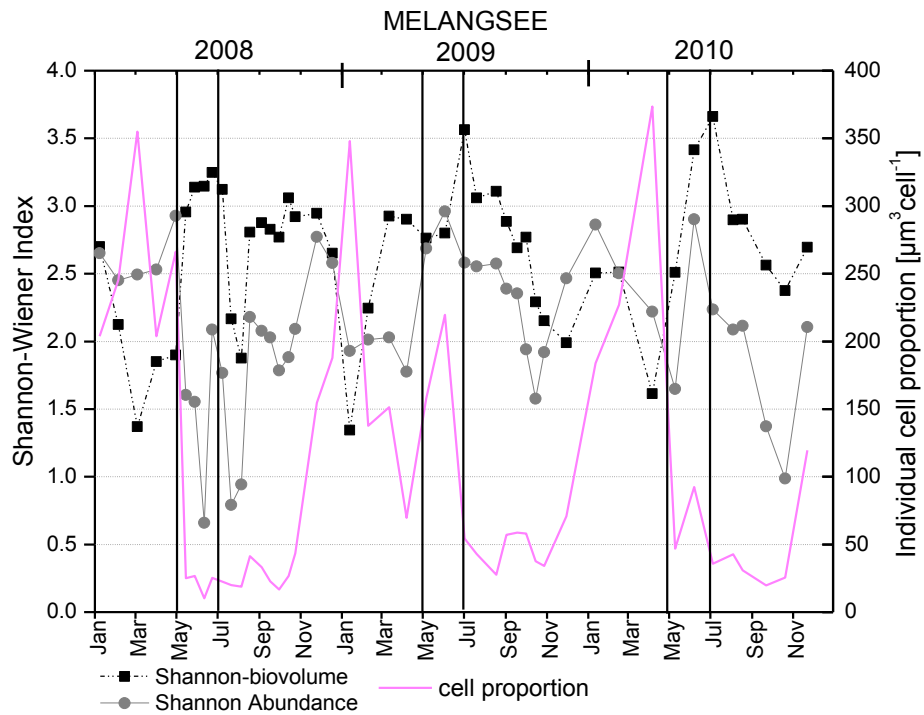


Fig. 2.10: Differences between two types of Shannon-Wiener index (abundance and biovolume) and cell proportion of the two very shallow lakes. The vertical bands represent the transitional phases.

While richness is increasing, the evenness of Shannon Wiener index (abundance) is decreasing, in both very shallow lakes, more accentuated in MEL (figure 2.11). The increase of equitability in terms of abundance did not coincide with the increase of richness. In PET, lake characterized by the dominance of cyanobacterial filaments with large abundance values (cell/ml), had lower evenness throughout the years. Generally, the data from 2008 to 2010 showed no greater correlation between these two measurements of diversity (low R^2 values).

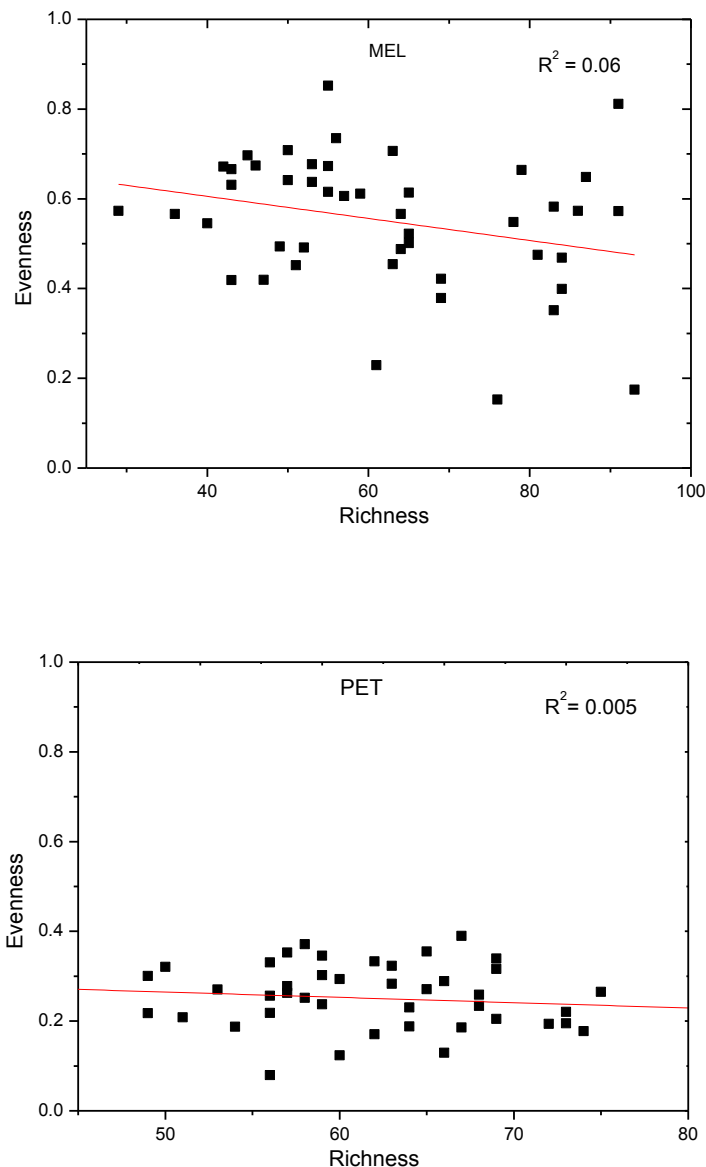


Fig. 2.11: Different performances of richness versus evenness of Shannon-Wiener index (using abundance) from PET and MEL.

The two very shallow lakes have a different relation between richness and biovolume. In PET, changes of total biovolume had a weaker influence of richness, and the linear fit appeared more or less constant. In MEL, increase of phytoplankton biovolume seems to influence more positively the richness (fig 2.12).

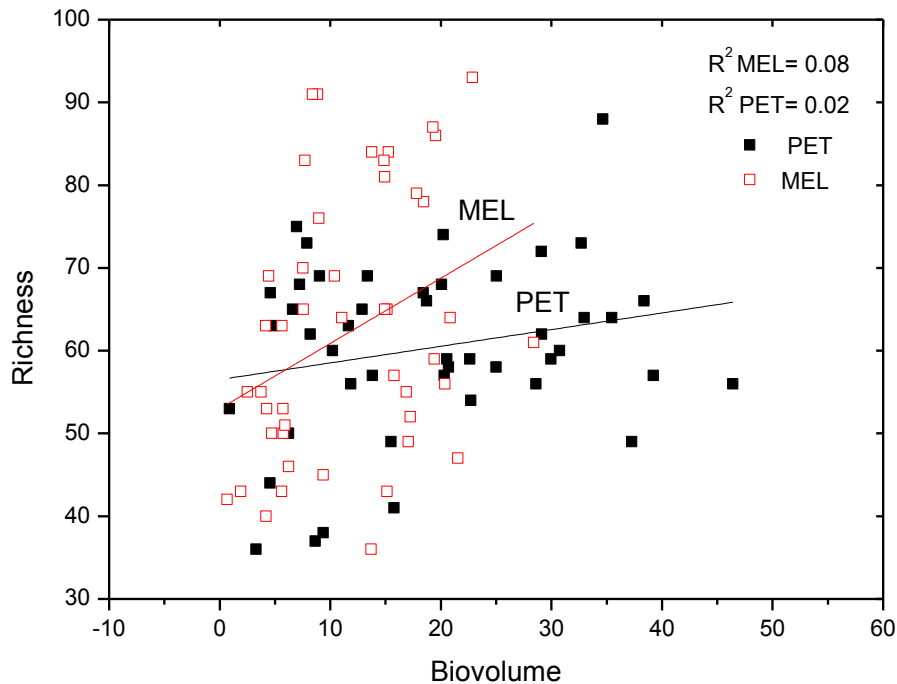


Fig. 2.12: Relation between richness and biovolume of MEL and PET.

The debate about whether species richness is a cause or consequence of ecosystem productivity was investigated as temporal variability of richness and RUE along the seasons. Concerning the combination of all data, the temporal changes of richness preceded the increase of productivity as resource use efficiency (RUE, fig. 2.13). Richness began to increase during the spring and had its maximum at the end of the transitional phase. RUE was highest during the late summer at low values of cell proportion, due the dominance of filamentous cells. A second higher peak began from the end October until December, because of the stronger presence of S1 species in PET and Bacillariophyceae in MEL. The single cell proportion peaked during colder periods, characterized by the presence of large cells of Bacillariophyceae. Imix achieved its maximum from April until the end of June.

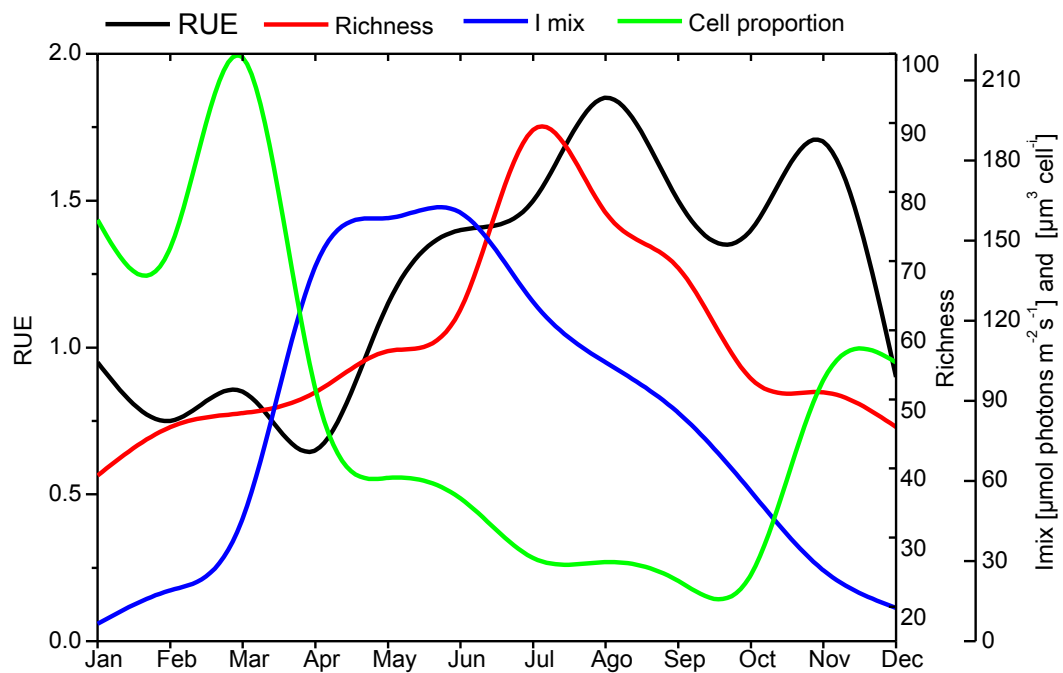


Fig. 2.13: Monthly mean of RUE, richness, Imix and cell proportion of PET and MEL from all studied data.

A scheme of a temporal development of productivity (RUE) together with biovolume, richness, cell proportion, and propensity to steady state/ non-equilibrium conditions along the seasons is represented in figure 2.14. During winter periods (steady state), the RUE values had a little peak, more observed in MEL. The productivity decreases gradually by the substitution of Bacillariophyceae in winter to the Chlorophyceae in spring, achieving the minimum values (non-equilibrium), whereas richness increases (start of transition state). Richness has its maximum during this phase and precedes the highest peak of RUE, found during the late summer (steady state). Imix has its greatest phase during the spring, decreasing during the summer because of higher algal biomass. The single cell proportion decreases during the spring (70 to $30 \mu\text{m}^3 \text{cell}^{-1}$), is the lowest during the late summer (20 to $30 \mu\text{m}^3 \text{cell}^{-1}$), and achieves its maximum in February-March ($220 \mu\text{m}^3 \text{cell}^{-1}$).

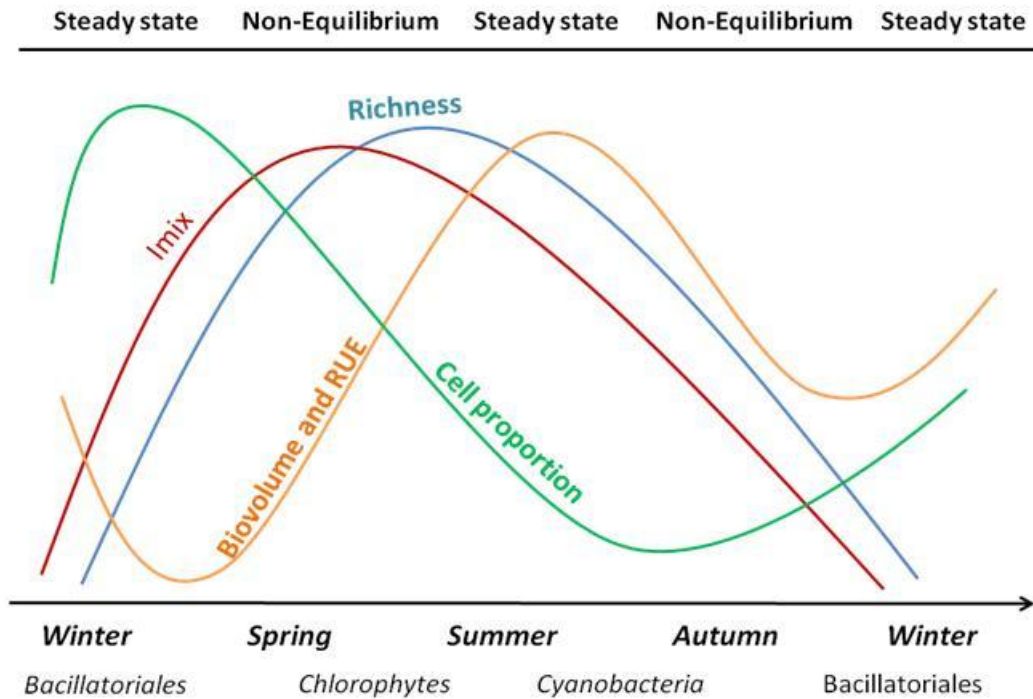


Fig. 2.14: Proposed scheme about the variation of diversity (richness), productivity as resource use efficiency (RUE) and biovolume, cell proportion, associated with the Imix, dominance of algal groups, and equilibrium and non-equilibrium tendency along the seasons.

2.7 Discussion

The two shallow lakes are considered turbid, because of Secchi depth during summer below 0.5 m, and annual average about 1 m (Nixdorf et al. 2003). Pelagial of shallow lakes receives nutrients pulse-wise due to resuspension of the lake sediment during mixing events (Wiedner 1999). A wind protected lake such as Melangsee (Mischke & Nixdorf 2003) is less susceptible to complete mixing than the wind exposed Peterdorfer See. The more propensity to mixing, lower underwater irradiation and higher nitrogen availability in PET may have influenced positively the dominance of the Oscillatoriales S1 group *L. redekei*, mainly from September until the end of the year ($10.0 \text{ mm}^3/\text{l}$ in November). The annual dominance phases of filamentous Oscillatoriales in a shallow German lake have been attributed to light-deficient conditions caused by high shading effects (Mischke & Nixdorf 2003). The specific abilities of the species, especially photoadaptation (Reynolds et al. 2002), may have contributed considerably to their development. In terms of low TP and DIP concentrations, the both lakes were relatively comparable, but the dynamic and concentration of nitrogen in both lakes are dissimilar, with higher concentration in PET. More intensive consume of dissolved nitrogen

occurred during the spring in MEL and during autumn in PET. The nitrogen concentration in PET and its light climate influenced strongly the phytoplankton dynamic of this lake. The main species found in PET have high affinity to ammonium, and are good competitors when this nutrient concentration increases. For example, the earlier increase of $\text{NH}_4\text{-N}$ in February 2009 (1,367 $\mu\text{g/l}$) coincided with the steady state composed by *P. limnetica* and *Limnothrix redekei*. The lowest levels of $\text{NH}_4\text{-N}$ concentration in PET were detected during September-October (5.8 $\mu\text{g/l}$ in 2008) under stronger dominance of *L. redekei*. In Melangsee, the lowest peak of this nutrient concentration was recorded in April 2010 (10.2 $\mu\text{g/l}$), during the spring bloom. The *Pseudanabaena limnetica* (S1) was the most dominant specie in PET, occurring preferentially during the summer, but also survives in lower underwater irradiation and lower temperatures. This specie is often able to persist throughout the year under greater seasonal regularity. The two very shallow lakes offered favorable conditions to colonization of warm mixed layer species as *Cylindrospermopsis raciborskii* (S_N) and *Aphanizomenon gracile* during the summer, which had their climax in August-September, under favorable abiotic conditions as availability of light and temperature. According to Nixdorf & Mischke (2003), the Nostocales *Aphanizomenon gracile* (H1) seems to be more tolerant of light deficiency, and mixing conditions, performing as members of S1 and S_N groups.

The lake Melangsee has changed along the years. The very thin *Limnothrix* species *L. amphigranulata* (Van Goor) Meffert was the most common species for the years 1999 and 2001, dominating between 3 and 7 weeks, accompanied by *Pseudanabaena limnetica* and *Planktothrix agardhii* (see Mischke & Nixdorf 2003), but did not dominate during this study. Melangsee showed more likely to receive higher diversity of phytoplankton species at lower nutrients concentration, as supported the non-equilibrium concept (Hutchinson 1961). Steady state conditions seem to be rare in this lake, occurring at the beginning of the year through the Bacillatoriales and E group. The good availability of SiO_2 concentration in MEL explained the higher increase of biovolume and diversity of A-D species. According to Reynolds (1998), genus *Cyclotella* (A) is frequently associated with clearer mixed small lakes during March and April. The appearance of eutrophic Chlorophyceae species like genera *Pediastrum* and *Scenedesmus*, together with other biomass conserving canopy species as *Peridinium* were common in MEL, when free nutrients had been exhausted. *Peridinium umbonatum* was present together with *C. raciborskii* (Borics et al. 2005, 2000). The presence of nanoplanktonic fast-growing invasive persistent genera as *Monoraphidium*, *Chlamydomonas*, and *Chrysochromulina* were notable during several different periods.

Higher RUE values may be an indicator to the achievement of steady state conditions and diversity along the ecological succession, and showed to decrease along the years in both lakes. This type of productivity measurement coincided with higher values at steady state, in MEL during the winter and in PET during consecutive periods. Lower RUE values represented the non equilibrium conditions with high diversity at transitional states. In MEL, this phase coincided with the higher presence of Chlorophyceae with low cell proportion (30 to 70 $\mu\text{m}^3 \text{ cell}^{-1}$). RUE values tended to accompany the dominance of Cyanophyceae at both lakes, more pronounced in PET. Organisms adapted to convert phosphorus into biomass use the resources more efficiently in very shallow lakes. Although the steady state conditions are expected to be more likely in deep lakes than in shallow mixed ones, very shallow as Peterdorfer See was more efficient in converting available phosphorus into phytoplankton, maintaining high productivity. The steady state period as a self-induced habitat, in which competitors fail, combined with effective exploitation of nutrient resources by the dominant Cyanophyceae, could not be achieved in MEL, but was confirmed in PET. The more complex succession in MEL, characterized by several types of algal groups, made possible the higher richness and diversity indices, found in this lake.

Although the higher number of species and more dynamic successional pattern found in MEL (replacement of more diverse functional groups), the repetitive phytoplankton assemblages occurring in shallow lakes (as appointed by Mischke & Nixdorf 2003) could also be observed in very shallow lakes. The discussion, whether this phenomenon of regular succession in shallow polymictic lakes is caused by adaptation to a resilient and an extreme environment or by the pool of species that can live or survive in that environment is suggested by Nixdorf et al. (2003). Considering the low level of dissolved nutrients, the resilience of a more composite species pool is very adapted to recolonize and maintain its diversity during the years, particularly in MEL. The ecological consequences of biodiversity loss have aroused considerable interest and controversy during the past decade. The question if species richness drive community production or vice-versa has been investigated over the past 20 years and have led to the general consensus that species functional characteristics have a strong influence over ecosystem properties (reviewed in Hooper et al. 2005). Several controlled experiments have now established that species diversity influences ecosystem-level processes such as primary production (Kinzig et al. 2001, Loreau & Hector 2001, Tilman et al. 2001). There is, however, uncertainty how to scale up results obtained in recent experiments to landscape and to generalize across ecosystem types (Loreau et al. 2001). The ecological

succession, represented by the dynamic more or less predictable and orderly changes in the composition of a community, shows which direction the productivity should take. Concerning the temporal changes of productivity and diversity, this study suggests that the productivity is a consequence of diversity, since the increase of species number creates potential force to enhance the biomass of the more adapted species in the pool. This information is complemented by the negative correlation between richness and evenness, showing a possible increase of biomass by some species when richness decreases. A positive relation between richness and biovolume was observed, and seems to be less pronounced in lakes dominated by S1 species. The cell proportion as additional measurement is useful, since it may influence the diversity indices and gives signs about which type of specie is present in the course of succession. The actual needs for a better differentiation between medium shallow lakes and very shallow lakes in terms of nutrient cycles and succession of communities are suggested to more comprehension of their ecological aspects, and great efforts are therefore being put into the understanding of these ecosystems. Additionally, studies linked to diversity-productivity of these special types of lakes is necessary, in order to clarify the enigma about the relation between diversity and ecosystem functioning.

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Chapter

3

3 Low disturbances favour steady state: Case of cyanobacterial monodominance in Brazilian coastal lagoon

3.1 Abstract

Mixing events as predominant disturbance in sense of Connell (1978), capable to control diversity of phytoplankton were investigated. Water samples were taken twice a week during cold-dry and hot-rainy periods 2009/2010 in a Brazilian shallow coastal lagoon Peri (Santa Catarina state, Brazil). Uninterrupted steady state conditions in sense of Sommer et al. (1993) occurred under monodominance of *Cylindrospermopsis raciborskii*. Morphologically, the filaments of *C. raciborskii* in Peri lagoon were short (length mean = 70 μm), with rare terminal heterocysts (8%), absence of akinetes forms, and presence of coiled forms (9%), more evident during the cold-dry phase. The diversity measurements (Shannon Wiener index, evenness Shannon Wiener, complement of Simpson index, and richness) were considered low during all phases. This cyanobacterial specie belongs to S_N association in terms of life strategies (Reynolds 2002), and has been dominated under no nitrogen deficiency, low availability of dissolved nutrients (DIP and NO_x = about 5.0 $\mu\text{g/l}$, and NH_4 = 20 $\mu\text{g/l}$), and no stratification regime. Models of competition as of Tilman (1999) that predict greater diversity, leading to greater levels of primary productivity under complete utilization of limiting resources were not confirmed in this study. The results showed no direct correspondence between diversity indices and biomass, suggesting that primary production is not proportionally linked to diversity. Nutrient availability seems to play a weak force capable to drive the variation of phytoplankton in Peri lagoon, more controlled by environmental attributes as temperature. The functional groups were represented by associations common in shallow, mixed, turbid, meso-eutrophic, with phosphorus deficiency ecosystems. A new association between best adapted Lo species as *Peridinium umbonatum* and *C. raciborskii* is proposed. Constant mixing was not sufficient to interrupt the species dominance and to change significantly the diversity and species composition. Although competitive exclusion would be the primary mechanism that selects species towards equilibrium, higher adaptability by few species under selective conditions seemed to be a more important factor to explain the occurrence of steady states at low disturbance level.

3.2 Introduction

Equilibrium/steady-state and non-equilibrium hypotheses have often been used to explain community ecology and emerged in phytoplankton studies when discussing the diversity disturbance relationship. Biodiversity should be added to species composition, disturbance, nutrient supply, and climate as a major controller of population and ecosystem dynamics and structure (Tilman 1999). The equilibrium concept is a term selected from the diverse terminology; the ultimate goal is to describe a situation of little variability of species dominance and total biomass across time (Naselli-Flores et al. 2003). The concept may represent a hypothetical situation where a maximum of three species dominate the assemblage for, at least, three weeks without considerable change in total biomass (Sommer et al. 1993). The constant mixing tendency due to wind would be a convenient biotope for the emergence and susceptibility of steady-state (Rott 2002) and it may fit the characteristic dominance (Komáková & Tavera 2003).

The diversity is directly related to the community's responses to environmental disturbances. The Intermediate Disturbance Hypothesis (IDH) states that non-disturbed or highly disturbed communities may develop low diversity; and disturbances of intermediate frequency and intensity are necessary to maintain high levels of diversity (Connell 1978). Disturbances are mainly stochastic abiotic events that result in distinct abrupt changes in the community taxonomical composition, directing its internal organization and ecological equilibrium. Such events include the time scale and the frequency of the algal generation time (Reynolds et al. 1993). Examples of these disturbances are temperature changes, influx of nutrients, salinity, wind, and chemical fluctuations (Padisak 1997).

Measuring the disturbance is somewhat problematic since phytoplankton under natural conditions is subjected to different types of disturbances that are difficult to quantify. However, disturbance impact can be evaluated by the responses obtained from biological variables (Sommer 1993). The onset and break down of thermal stratification represent the most important disturbances affecting the phytoplankton species composition in dimictic lakes (Morabito et al. 2003). These irregularly occurring mixing events are the predominant disturbance to the succession of phytoplankton in shallow lakes (Mischke & Nixdorf 2003). Thus, application of the IDH may contribute to the understanding of complex structural changes in the community, mainly in the tropical region where they are not yet well understood (Lopes et al. 2009). The species diversity index is the most used biological response for

evaluation of IDH in the phytoplankton community (Rojo & Alvarez-Cobelas 1993, Flöder & Sommer 1999). Models of competition predict that greater diversity leads to greater primary productivity, causing more complete utilization of limiting resources (Tilman 1999).

Cylindrospermopsis raciborskii (Woloszynska) Seenayya & Subba Raju is a bloom forming cyanobacteria (order Nostocales) with high potential toxicity and remarkable negative consequences for human health (Chorus & Bartram 1999, Backer 2002). Because of its potential toxicity and tendency to form dense blooms that interfere with different types of water use, *C. raciborskii* has become one of the most notorious blue-green algal specie. Its ecological success is attributable to many factors like buoyancy regulation, tolerance of low light, high affinity for phosphorus and ammonia, N₂ fixation ability and resistance to grazing by zooplankton (Padisák 1997). Its presence may also modify the general structure of other planktonic components (Bouvy 2000) or a substantial decrease in phytoplankton diversity (Dobberfuhl 2003, Borics et al. 2000, Mischke & Nixdorf 2003). Less sharp seasonality linked to higher temperatures in the tropics may lead to a higher probability for existence of long-lasting blue-green stages (Huszar et al. 2000), which are highly resilient (Dokulil & Mayer 1996). The high temperature demand and the inability of *C. raciborskii* to adapt to temperature fluctuations indicate that it evolved in tropical lakes (Padisák 1997). The occurrence of cyanobacteria in Brazil has caused several problems of the water quality mainly in warm, shallow and frequently mixed water bodies (Tucci & Sant'anna 2006, Huszar et al. 2000).

The functional groups of phytoplankton capture much of its ecology and are useful to verifiable quantitative method of describing community structure and changes (Reynolds et al. 2002, Kruk et al. 2002). The investigation during short generation time of algae provides a useful model for a better understanding of community types and of ecosystems in general (Reynolds 1997, Harris 1986).

3.3 Hypothesis

Steady state occurs mainly under less pronounced abiotic changes (i. e. nutrients concentration, temperature), frequently leading to low diversity, and common in tropical shallow lagoons. The longer certain conditions persist, the poorer is the survival of the sensitive groups and the better the survival of the tolerant ones. The dominance of cyanobacteria decreases diversity of other species as a consequence of its more effective

exploitation of resources. Mixing events at dominance of cyanobacterial species do not represent disturbances in the sense of Connell (1978), since they do not interrupt the species performance and do not change the diversity. A low disturbance status, created by permanent circulation, decreases the diversity at the dominance of this type of algae. Since disturbances didn't change significantly the species composition, the phytoplankton community in this case may present a non-successional change.

3.4 Study site

3.4.1 Local area

The samples were taken at a tropical riverine Peri coastal lagoon in Brazil (27°44'S and 48°32'W), a shallow lake in the southwest of the island of Santa Catarina State (Area = 5.07 km²; Z_{max} = 11m; Z_{mean} = 4.18m; Volume = 21.2 x 10⁶ m³, and Catchment area = 20.1 km²). The climate is characteristically subtropical, with rainfall concentrated in spring and summer months (October-March). The lagoon is enclosed and slightly above the sea level, located in a preservation area (Parque Municipal da Lagoa do Peri) with a restricted human occupation and surrounded by Atlantic Forest. Its fresh water is a result of 2 rivers inflow (Ribeirao Grande and Cachoeira Grande) and rainfall.

Coastal lagoon is defined as an inland water body, usually oriented parallel to the coast, separated from the ocean by a barrier, connected to the ocean by one or more restricted inlets, and having depths which seldom exceed a couple of meters. A lagoon may or may not be subject to tidal mixing, and salinity can vary from that of a coastal completely fresh-water (such as Peri) to a hypersaline lagoon, depending on the hydrologic balance. Lagoons are formed as a result of rising sea level during the Holocene or Pleistocene and through the formation of coastal barriers such sand transport by marine processes (Kjerfve 1994). The coastal lagoons of Brazil are generally shallow, with no thermal stratification due the strong influence of wind (Esteves 1984). Some studies about phytoplankton diversity in Brazilian coastal lagoons are carried out in southeastern region of the country and data for southern region are scarce (Huszar 1992). A low diversity associated with monospecific blooms is common in coastal lagoons and is considered characteristic of immature communities (Margalef 1977). The cyanobacteria *C. raciborskii* in Peri have been showing most dominant throughout year (Laudares Silva 1999, Monardo et al. 2006), and toxin analyses have revealed the presence of saxitoxin at lower concentrations (0.2 µg/L) (Grellmann 2006). Currently, in

addition to practices such as tourism, research and recreation, the Peri lagoon has been used as a source of water treatment (Catarina Water and Sanitation - CASAN), which supply drinking water to the local community of the east and south of the Santa Catarina island.

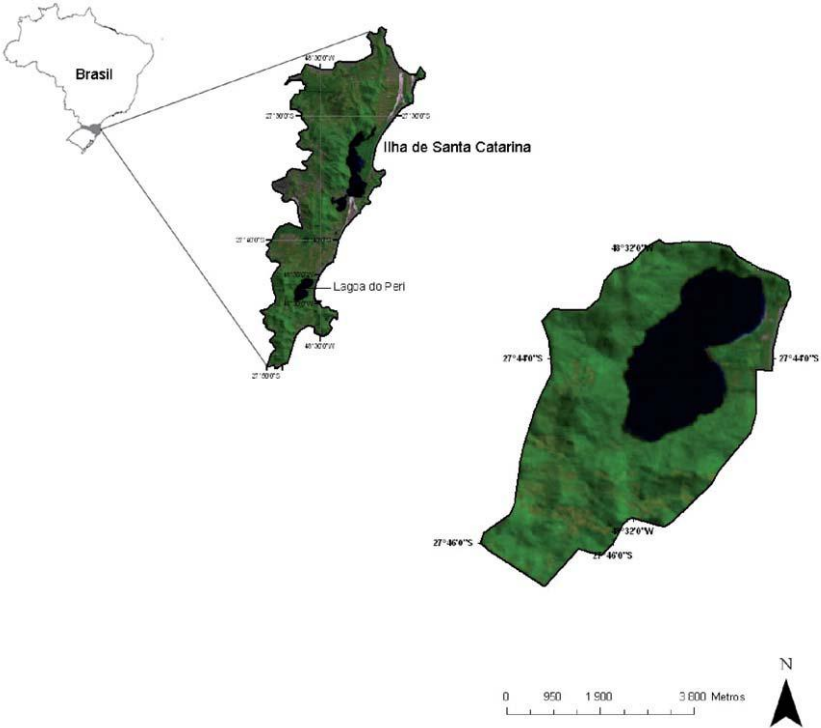


Fig. 3.1: Location of Peri coastal lagoon.



Fig. 3.2: Picture of Peri coastal lagoon (June 2009).

3.4.2 Climatic influences

The Santa Catarina Island is influenced by two air masses: Tropical Atlantic and Polar Atlantic. The influence of tropical Atlantic, predominantly during the year (80%), reaches the region raising local temperature. The Polar Atlantic is less active (20%), often reaching the island mainly in winter (see table 3.1). The cold mass from the south causes sudden and abrupt changes in weather in any season. The temperatures on the island of Santa Catarina are under marine influence, giving low-amplitude (annual temperature variation around 8.8% and daily 4.2% (Monteiro 1992).

According to Nimer (1989), the mean of winter temperature varies between 15° C and 17° C and between 24° C and 26 °C during the summer. The hottest month is February and the coldest is July. The average of annual relative humidity is high 82%. Precipitation is relatively well distributed throughout the year, most abundant during the summer and the average rainfall is around 1,500 mm annually. Freyslebem (1979) described that northerly winds are more frequent in summer, while the southern is more frequent during colder periods. The southerly winds have speeds and more intense than those in the north, reaching up to 80 km/h.

Table 3.1: *Variation of air temperature, wind speed, and precipitation at meteorological station in the airport of Santa Catarina State (Laudares Silva 1999).*

Months	Temperature (°C)			Wind (m.s ⁻¹)			(mm)
	Min.	Mean	Max.	Direction	Speed mean	Speed max.	Precip. mean
Jan	20	25	34	S	3	9	640
Feb	21	25	35	N	2.5	8	273
Mar	16	24	30	S	2.5	10	284
Apr	10	23	32	S / N	3	13	17
May	12	20	29	S	2	8	34
Jun	7	16	28	S	3	13	110
Jul	4	14	23	N	2.1	11	55
Aug	8	14	25	N	3.2	8	117
Sep	9	18	26	N	3	9	252
Oct	13	21	29	N	3	10	96
Nov	16	22	31	S / N	3	11	34
Dec	18	25	34	S	3	12	124

3.5 Methodology

The study was carried out from 02th June to 03th July (cold-dry period) 2009 and from 02th March to 03th April (hot-rainy period) 2010, twice a week. The samples were taken from each 0.5 meter until 8 meter depth at the deepest point of the lake and analyzed as mixed sample. Water temperature, conductivity, pH and dissolved oxygen were measured *in situ* with specific probes (WTW – Multi350i). Nitrite (N-NO₂ - Golterman et al. 1978), nitrate (N-NO₃ - Mackereth et al. 1978), ammonium (N-NH₄ - Koroleff 1976), soluble reactive phosphorus (SRP - Strickland and Parsons 1960), total phosphorus and nitrogen (TP and TN - Valderrama 1981), and silica (Strickland & Parsons, 1968) were determined. Chlorophyll-*a* concentration was obtained according to Nusch (1980), using equations described by Lorenzen (1967). Aliquots for phytoplankton analyses were fixed with Lugol solution and investigated according to Utermöhl (1958). Biovolume was calculated by measuring the corresponding dimensions using the geometric formulas given by Rott (1981) and Willén (1976). Diversity measurements Shannon Wiener index ($H' = -\sum P_i \log P_i$, $P_i = \text{biovolume of the } i^{\text{th}} \text{ of } S \text{ species} / \text{total biovolume}$), evenness ($H / \log(S)$ $S = \text{number of species}$), richness (number of species), and complement of Simpson index as probability that two individuals belong to different species ($1 - C = \sum_{i=1}^S p_i^2$, $P_i = \text{abundance of the } i^{\text{th}} \text{ of } S \text{ species} / \text{total abundance}$) were calculated. Resource use efficiency (RUE) as measure of productivity converting unit (μg) Chl *a* per unit (μg) TP (Ptacnik et al. 2008, Nixdorf et al. 2009) was calculated. Criteria to identify an equilibrium phase according to Sommer et al. (1993), with the functional groups proposed by Reynolds et al. (2002) were used.

3.6 Results

3.6.1 Abiotic variables

The abiotic parameters of Peri lagoon (table 3.2) presented certain constancy during the sampled periods. The pH and alkalinity were higher during warm periods (maximum = 7.6 and 9.1 mg/l CaCO₃ respectively). The variation and concentration of dissolved inorganic phosphorus (from 4.2 $\mu\text{g/l}$ to 13.0 $\mu\text{g/l}$) and nitrate (from 3.0 $\mu\text{g/l}$ to 11.0 $\mu\text{g/l}$) were very low at both periods. Higher availability of total nitrogen was observed during colder periods (747 $\mu\text{g/l}$) if compared to warmer periods (517 $\mu\text{g/l}$). The ammonium concentration was also considered low, more available during the colder period (maximum = 53 $\mu\text{g/l}$) than during warmer periods (maximum = 33 $\mu\text{g/l}$). The silica concentration showed similar during both

periods, more available during the colder period (mean = 2.4 µg/l) than during the warmer period (mean = 2.0 µg/l).

Table 3.2: *Abiotic parameters (mean, minimum and maximum respectively) during the hot-rainy and cold-dry periods (10 samples per period) in Peri coastal lagoon.*

Parameters	Hot-rainy period March	Cold-dry period June
Dissolved oxygen (mg/l)	8.0 (7.4-8.8)	7.6 (7.3-8.4)
pH	7.0-7.6	6.1-7.0
Conductivity (µS/cm)	74 (73-75)	72 (68-76)
Water temperature (°C)	26.8 (26.0-28.0)	18.0 (17.0-21.0)
Secchi depth (m)	1.3 (1.1-1.3)	0.9 (0.9-1.0)
Alkalinity (mg/l CaCO ₃)	7.8 (7.6-9.1)	7.5 (7.2-8.3)
Dissolved inorganic phosphorus (µg/l)	4.2 (4-13)	5.5 (2-12)
Total phosphorus (µg/l)	19 (15-23)	17 (12-18)
Nitrate (µg/l)	4 (3-6)	9 (8-11)
Total nitrogen (µg/l)	517 (412-613)	747 (623-883)
Ammonium (µg/l)	27 (22-33)	33 (22-53)
Chlorophyll <i>a</i> (µg/l)	25 (23-26)	18 (16-19)
Silica (mg/L)	2.0 (1.5-2.6)	2.4 (2.0-2.9)
TN:TP Molar	23	37
Resource use efficiency (RUE)	1.3 (0.9-1.6)	1.2 (0.9-1.5)

The resource use efficiency (RUE) had its maximum (1.6) during the hot-rainy period, if compared to the cold-dry period (1.5), and presented the same minimum values (0.9). The water temperature presented a variation of 11°C, if comparing the both seasons. At the beginning of June, the mean of water temperature was 18°C, while during the warm period was around 27°C during all days of this phase.

The chlorophyll *a* concentration was higher during the hot-rainy period (mean = 25 µg/l) than during cold-dry period (mean = 18 µg/l). This value had its maximum at the end of February (26 µg/l) and had its minimum in the beginning July (16.0 µg/l), at lower water temperatures (see figure 3.3). The increase of chlorophyll *a* was accompanied by the enhancement of dissolved oxygen, noted during the hot-rainy period (mean = 8.3 mg/l), if compared to the cold-dry (mean = 7.6 mg/l). The Secchi depth was higher and more variable during the summer (1.1 to 1.3 m) than during the colder period (0.9 to 1.0 m). The photic zone was larger during the summer (mean of Secchi depth= 1.3 m) than during the cold-dry period (0.9

m), showing that the increase of chlorophyll *a* during the summer was not sufficient to decrease notably the Secchi depth values.

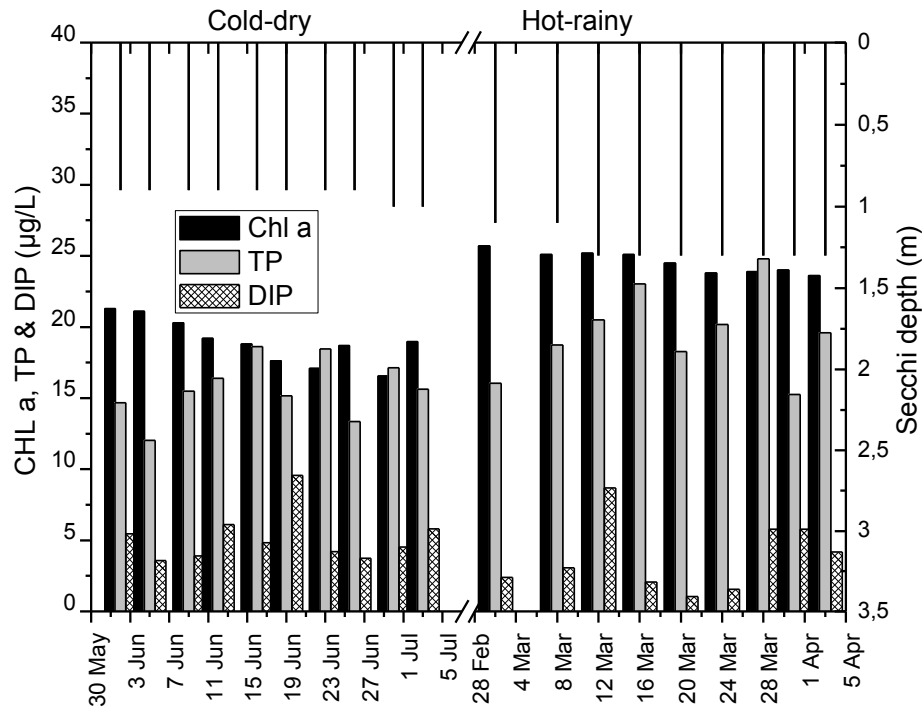


Fig. 3.3: Chlorophyll *a*, total and dissolved inorganic phosphorus (TP and DIP) concentration, associated with Secchi depth values in Peri lagoon during cold-dry and hot-rainy periods.

The depth-time isopleths of water temperature is shown in figure 3.4.

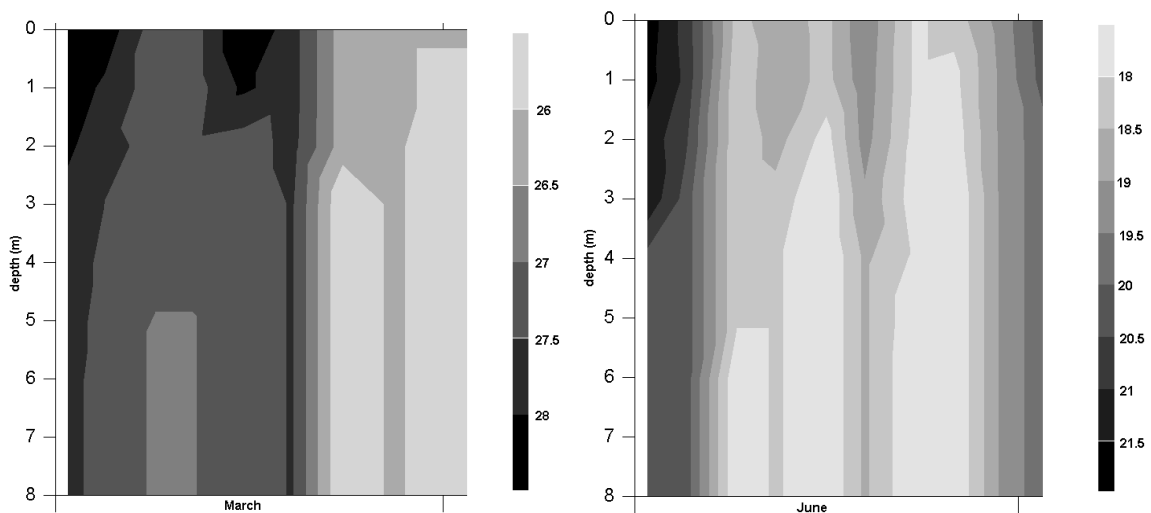


Fig. 3.4: Depth-time isopleths of water temperature (°C) during the summer and winter respectively.

The variation of oxygen availability in the surface and bottom was 2 mg/l (mean of saturation 97% at 1 meter and 74% at 8 meters). The depth-time isopleths showed a relative homogeneity of the water column during the both periods (fig. 3.4). Generally, there was a difference of 0.5 °C between bottom and surface. The tendency of homogeneity and no oxygen deficiency along the depth were also recorded by previous studies of Peri (Simonassi 2001, Laudares Silva 1999).

3.6.2 Phytoplankton composition and morphology of *Cylindrospermopsis raciborskii*

The group of Nostocales represented by *C. raciborskii* was the most dominant at both seasons, with higher biovolume during the hot-rainy period (22.7 mm³/l) than during the cold-dry period (18.6 mm³/l) (fig. 3.5). The greater presence of Oscillatoriales, represented by *Pseudanabaena galeata* and *Oscillatoria* sp. in terms of abundance (305,093 cell/ml), was observed during the cold-dry period, if compared to hot-rainy (52,874 cell/ml). Other groups of phytoplankton were not relevant and represented 2.4 mm³/l of total biovolume during the cold period and 1.5 mm³/l during the hot period.

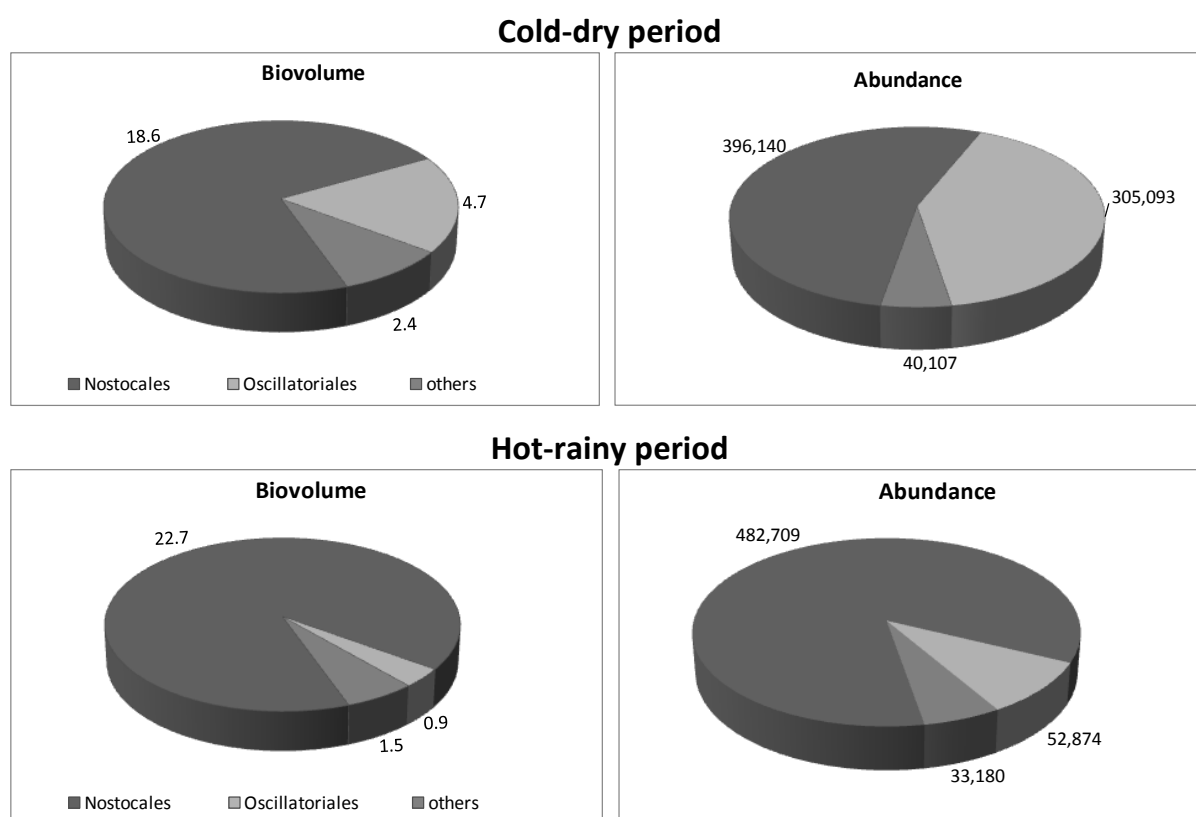


Fig. 3.5: Portion of phytoplankton groups as biovolume (mm³/l) and abundance (cell/ml) during the studied period.

Morphologically, the filaments of *C. raciborskii* presented diverse lengths, between 9 μm and 150 μm (mean = 70 μm), and width of 2.9 μm , with shorter and more abundant trichomes during the hot rainy period. Terminal heterocysts in Peri (8% of all filaments) were positioned at the end of longer filaments. Coiled forms were more evident during the cold-dry period (9% of biovolume), than during the hot-rainy period (< 1%). Akinetic forms were not found in Peri (fig.3.6).

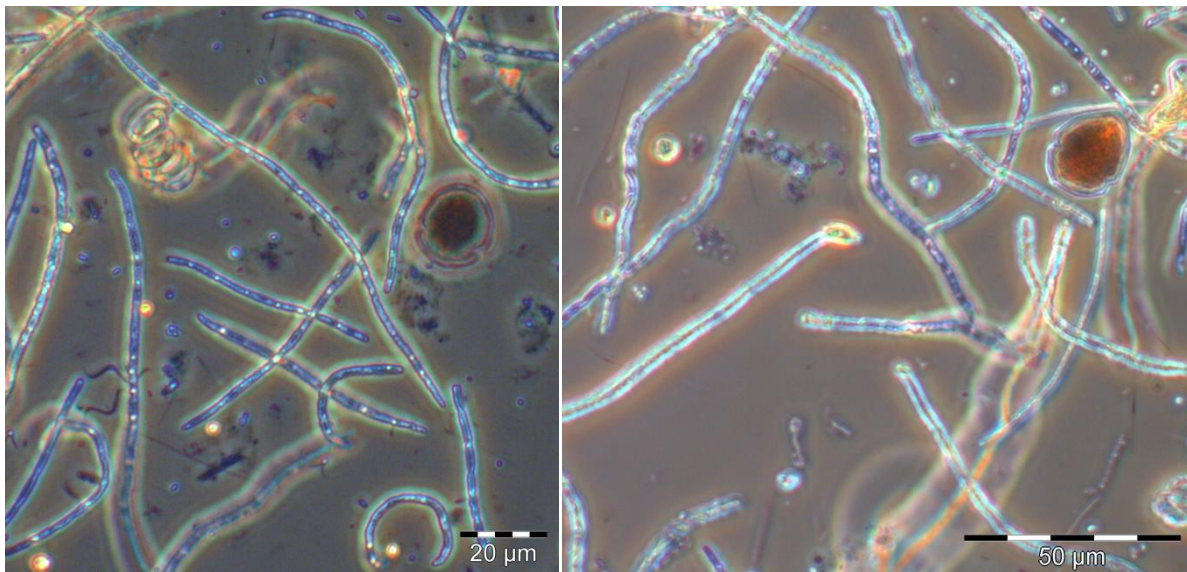


Fig. 3.6: Morphology of *Cylandrospermopsis raciborskii* in Peri lagoon, showing different filaments length and presence of coiled form (left), besides of rare heterocysts on a terminal cell (right).

3.6.3 Diversity at steady state

The diversity indices and richness during the cold and rainy periods are illustrated in figure 3.7. Generally, the diversity was low at both periods. The probability that two randomly picked individuals belong to different species defined by complement of Simpson index was lower during the summer, because of the increase of *C. raciborskii*. The mean of diversity indices during the hot period was lower (Shannon Wiener = 0.48, evenness = 0.15, and comp. Simpson index = 31.6%) than during the cold period (Shannon Wiener index = 0.56, evenness = 0.18, and comp. Simpson index = 54.6%). Although the richness during the warmer period was more variable, the mean of both periods was the same (23 species). A total of 42 different species were found, with different species at both periods, represented by 15 Chlorophyceae, 11 Cyanophyceae, 5 Dinophyceae, 3 Bacillariophyceae, 4 Zygnematales, 2 Chrysophyceae, and 2 Euglenophyceae.

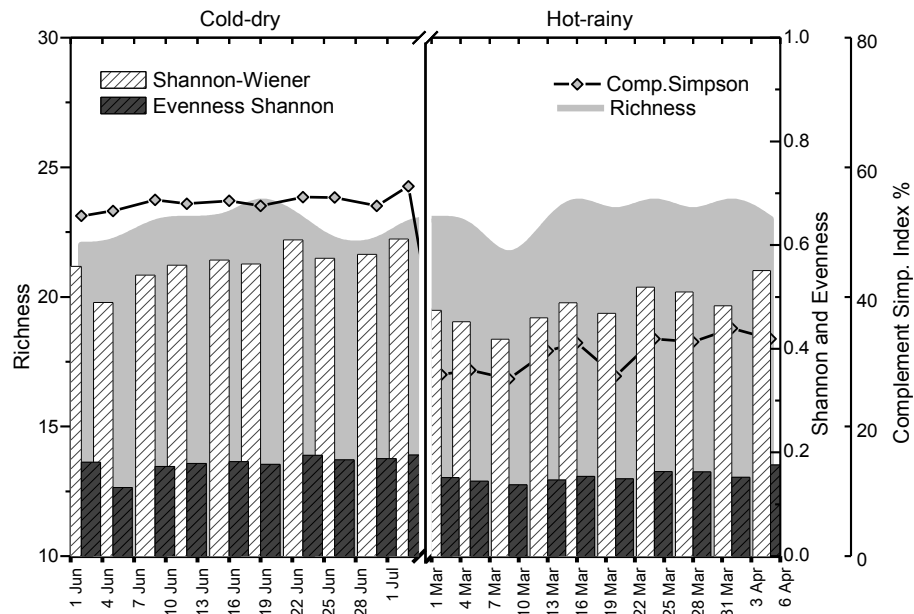


Fig. 3.7: Shannon Wiener index, evenness of Shannon Wiener, complement of Simpson index and richness during the cold and rainy periods respectively.

The share of three most dominant species represented by *C. raciborskii*, *Pseudanabaena galeata* and *Aulacoseira* sp. supported the equilibrium conditions according to Sommer et al. (1993) during all periods (Figure 3.8).

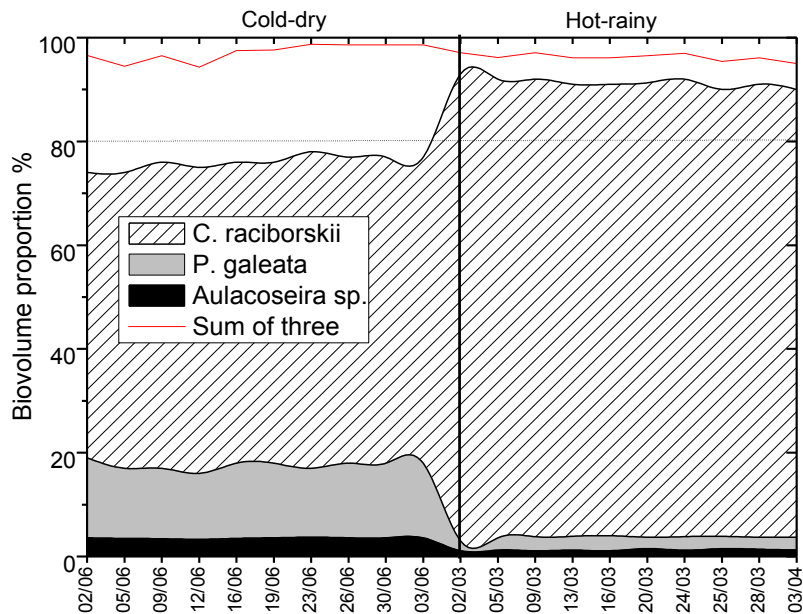


Fig. 3.8: Portion of biovolume (%) of the 3 most dominant species in Peri during the studied periods.

The portion of biovolume occupied by *C. raciborskii* shows clearly its monodominance, since this specie alone represents more than 90% of total biovolume during March. The lower biovolume of this specie during colder period was offset by the increase of *P. galeata*, which contributed to maintain the steady state during June. The information about the species found in Peri lagoon is illustrated in the table 3.3. The *C. raciborskii* (S_N group) achieved the highest biovolume, abundance and biovolume proportion at both seasons. The Oscillatoriales *Pseudanabaena galeata* (S1) occupied the second place of dominance, stronger during the cold period (4.6 mm³/l) than during the hot period (0.9 mm³/l). Both groups together suppressed other species in more than 92% of total biovolume. The Chlorophyceae was the group with more different species, found with very low abundance, except the specie *Monoraphidium irregulare* (group X1), relatively common in Peri lagoon. The Dinophyceae, represented by genera *Peridinium* and *Gymnodinium* (L_O), occupied the fourth place of biovolume. *Peridinium umbonatum* was found preferentially during the cold period (0.2 mm³/l), while *Gymnodinium lantzschii* was present only during the summer (0.1 mm³/l). *Gymnodinium uberrimum* and *Peridinium gatunense* were not observed during hot periods. The genus *Aulacoseira* (P) was the most important Bacillariophyceae of Peri lagoon, present at both seasons but more abundant during the cold period (440 cell/ml). The group X2 represented by *Chrysochromulina parva* and *Chlamydomonas* sp. obtained more advantages during the warmer season. Other phytoplankton species were not considerable, in terms of biovolume.

Table 3.3: Species with its functional groups, biomass proportion (%), mean of abundance (cell/ml) and biovolume (mm³/l) at cold-dry and hot-rainy periods.

Species	Functional group	Season	Biomass %	Abund. cel/ml	Biovol. mm ³ /l
<i>Cylindrospermopsis raciborskii</i>	Sn	cold-dry	75.5	396,140	18.6
		hot-rainy	92	482,709	22.7
<i>Pseudanabaena galeata</i>	S1	cold-dry	18.9	231,308	4.6
		hot-rainy	3.7	45,256	0.9
<i>Aulacoseira</i> sp.	P	cold-dry	3.6	440	0.8
		hot-rainy	1.2	147	0.3
<i>Peridinium umbonatum</i>	Lo	cold-dry	1.0	84	0.2
		hot-rainy	0.64	68	0.1
<i>Oscillatoria (Phormidium) sp.</i>	R	cold-dry	0.72	73,785	0.1
		hot-rainy	0.06	7618	0.014
<i>Planktolyngbya limnetica</i>	S	cold-dry	0.60	33,136	0.1
		hot-rainy	0.40	23,131	0.07
<i>Gymnodinium lantzschii</i>	Lo	cold-dry	-	-	-
		hot-rainy	0.51	79	0.1
<i>Gymnodinium uberrimum</i>	Lo	cold-dry	0.29	8	0.05

		hot-rainy	-	-	-
<i>Monoraphidium irregulare</i>	X1	cold-dry	0.29	4,330	0.05
		hot-rainy	0.21	4,782	0.05
<i>Gymnodinium sp.</i>	Lo	cold-dry	0.27	48	0.05
		hot-rainy	0.06	16	0.01
<i>Chrysochromulina parva</i>	X2	cold-dry	0.04	89	0.007
		hot-rainy	0.25	1,855	0.06
<i>Staurastrum tetracerum</i>	P	cold-dry	0.05	24	0.008
		hot-rainy	0.2	164	0.05
<i>Tetraedron minimum</i>	J	cold-dry	0.14	111	0.02
		hot-rainy	0.11	621	0.02
<i>Chlamydomonas sp.</i>	X2	cold-dry	0.05	79	0.008
		hot-rainy	0.11	257	0.03
<i>Phacus sp.</i>	W1	cold-dry	0.10	5	0.02
		hot-rainy	0.11	5	0.03
<i>Peridinium gatunense</i>	Lo	cold-dry	0.09	6	0.02
		hot-rainy	-	-	-
<i>Cyclotella sp.</i>	A	cold-dry	0.03	24	0.005
		hot-rainy	0.08	77	0.02
<i>Actinastrum aciculare</i>	X1	cold-dry	0.03	119	0.005
		hot-rainy	0.07	249	0.02
<i>Dictyosphaerium ehrenbergianum</i>	K	cold-dry	-	-	-
		hot-rainy	0.06	105	0.01
<i>Kirchneriella rosellata</i>	F	cold-dry	0.05	30	0.009
		hot-rainy	0.05	38	0.01
<i>Closterium pronum</i>	P	cold-dry	0.04	12	0.006
		hot-rainy	0.05	44	0.01
<i>Tetraedron caudatum</i>	D	cold-dry	0.01	11	0.002
		hot-rainy	0.05	96	0.01
<i>Others (14)</i>		cold-dry	0.2	1,551	0.03
<i>Others (17)</i>		hot-rainy	0.1	1,570	0.07

3.7 Discussion

3.7.1 Abiotic Parameters

The variation of dissolved nutrients was low, and a slightly increase during cold periods was noted. Laudares Silva (1999) also found a negative correlation between inorganic concentration and temperature, which was explained by more optimal use of resources during hot periods. The decrease of photic zone due the enhancement of phytoplankton biomass, typical during the summer, was not observed in this study. The increase of Secchi depth during the hot-rainy period may be associated with the solid suspended and organic matter in water column. The higher resource use efficiency (RUE) during the hot-rainy period

coincided with the increase of biovolume of *C. raciborskii*, suggesting its capacity to assimilate phosphorus and convert it into biomass.

The pH oscillation of Peri lagoon was recorded by previous studies (Laudares Silva 1999, Simonassi 2001). Branco & Senna (1994) described high annual pH variation (6.0-10.0) in a Brazilian lake (Paranoá) when *C. raciborskii* was strongly present. This specie seems to support large pH range. According to Padisák (1997), the most favourable pH to the occurrence of *C. raciborskii* is from 8.0 to 8.7, and its dominance in acidic water seems to be rare. Higher pH (> 8.0) inducing dominance of *C. raciborskii* was not confirmed in Peri, where pH around 7.0 has influenced positively the dominance of this toxic Nostocales. The highest pH was observed during the summer (7.6), and was probably due to the increase of primary production of phytoplankton.

This cyanobacterial specie was favored at TN:TP Molar lower than 29 (N:P molar in Peri = 23 during the summer), as supported by Smith (1983). Guildford and Hecky (2000) proposed TN:TP molar ratios to determine if lakes are N-limited (TN:TP <20) or P-limited (TN:TP >50). At intermediate TN:TP ratios, either N or P can become deficient. TP alone would be a also better predictor to regulate cyanobacterial biomass than TN or TN:TP relation, as supported by Pick & Lean (1987). The results of TN:TP relation and nutrient concentration in Peri indicate P-limitation. The rarity of other phytoplankton groups as Chlorophyceae, Euglenophyceae, and Bacillariophyceae at the dominance of *Cylindrospermopsis raciborskii* was also recorded by Bouvy et al. (1999) in Northeast of the country. According to Huszar et al. (2000), most of *Cylindrospermopsis* populations in Brazilian reservoirs were dominant in non-N-deficient conditions (with only 10% of the filaments possessed heterocytes), so enhancing the similarity of these versatile species to non-heterocytic filamentous blue-greens (Oscillatoriales), found secondly in this lake.

No thermal stratification and good availability of dissolved oxygen in Brazilian coastal lagoons were recorded by various studies of the country. According to Petrúcio (1998), water column homogeneity is often recorded in tropical coastal lagoons, because of lower depth and exposure to winds, which allow greater movement and water oxygenation. The same pattern of vertical distribution was recorded by Leite & Fonseca (2002) in lakes located in Rio Grande do Sul State and by Soares et al. (2009) in Minas Gerais State.

3.7.2 Characteristics of *C. raciborskii* and functional groups of phytoplankton

The morphology of the *C. raciborskii* filaments in Peri is considered anomalous (Laudares-Silva 1999). Since heterocytes are not present at all filaments and the akinetes forms are absent, the field populations of Peri are difficult to identify, as described in Paranoá Lake (Branco & Senna 1991). In a review about the genus *Cylindrospermopsis* Komárková (1998) confirmed that *C. raciborskii* is a common species in freshwater plankton but in the form of straight trichomes. The presence of coiled forms of filaments in natural populations seems to be present mainly in turbulent ecosystems, under limited dissolved nutrients. Akinete formation may be triggered by cold temperatures or large temperature fluctuations and requires high levels of reactive phosphorus (Moore et al. 2005). The coiled form of filaments was recorded by Bouvy (1999) in Northeast Brazil, together with scarce akinetes and heterocytes. The production of akinete seems to be rare in tropical lakes, not found in Peri coastal lagoon. It shows that the nitrogen in Peri seems not to be scarce to *C. raciborskii*. The adaptive advantages of *C. raciborskii* in Peri lagoon may be maintained by constant availability of light under high temperatures, no thermal stratification together with low phosphorus and inorganic carbon concentration. According to Reynolds (2002), *C. raciborskii* belongs to S_N association in terms of life strategies (warm mixed layers) and may represent shallow, turbid, and nutrient limited water. The variation of phytoplankton biovolume, especially *C. raciborskii*, during the seasons may be more controlled by environmental abiotic attributes as temperature.

The Group S represented by the genera *Pseudanabaena* (S1) and *Planktolyngbya* (S), which can live on a minimal income of light and temperature, was more benefited during the cold period. The widespread diatom *Aulacoseira* (P), which dominates under turbid conditions (Hutchinson 1967), also related in tropical lakes to turbulent environments (Huszar et al. 1998), was the most abundant diatom in Peri, despite their low abundance. The silica concentration (2.0 mg/L) showed not to limit potentially the biomass of diatoms, so the low diversity of this group may be explained by higher temperatures. The colonial Chlorophyceae species (group F) as genera *Botryococcus* and *Dictyosphaerium*, which tolerate low nutrients and high turbidity, were found with low biomass in Peri lagoon.

L₀ association refers originally to the *Peridinium–Woronichinia*, which has tried to accommodate more acidic assemblages involving *P. inconspicuum* and such cyanobacteria. The biomass conserving canopy dinoflagellates genera with its high biovolume and lower

growth, are common in mesotrophic ecosystems when free nutrients have been exhausted (Reynolds 1997). The presence of several species of genera *Peridinium* were reported together with *C. raciborskii* in warm, mesotrophic systems, under nutrient limitation (Borics et al. 2005, Ramberg 1987). Several species of Dinophyceae are motile species, able also to migrate between the well illuminated epilimnion and nutrient rich hypolimnion when the nutrients became scarce. This physiological adaptation is similar to the buoyancy regulation of *C. raciborskii*, as an advantage to store phosphorus. This specie has been reported together with several species of genera *Peridinium* mainly in warm, mesotrophic systems under nutrient limitation (Borics et al. 2005, 2000). The new association between best adapted k-selected species with lower S/V ratio such as L_O group *Peridinium umbonatum* and *C. raciborskii* is here proposed to represent warm, mesotrophic, and nutrient limited lakes. Concerning to the concept of Reynolds (1988), C species (colonist-invasive) represented by small cells of Chlorophyceae, susceptible to zooplankton grazing, and dominant under low intensity of disturbance, were not representative in Peri coastal lagoon. Reynolds (1993) also appoints that a continuous disturbance represent a form of environmental constancy, where successive generations build up populations in the analogous manner to the colonists of habitats. The mainly functional groups found in Peri were represented by species association common in shallow, mixed, turbid, meso-eutrophic, and phosphorus deficient lakes.

3.7.3 Relationship between disturbances and equilibrium

Steady state conditions are more probable and longer lasting in tropical regions because of the smaller ranges in physical changes. Constant mixing events, representing disturbances in the sense of Connell (1978) were here not sufficient to interrupt the species dominance and the steady state. Since this disturbance is not strongly conducive to maintenance of high species diversity (eternal steady state), the dominance by a pioneer superior competitors may lead to the competitive exclusion and reduces species diversity. An important point is if that in real world the homogeneous well-mixed conditions assumed in the competitive exclusion principle hardly exist (Scheffer 2003). Although competitive exclusion would be the primary mechanism that selects species towards equilibrium, higher adaptability by few species under selective conditions seemed to be a more important factor to explain the occurrence steady states (Soares et al. 2009, Reynolds 1993). According to Chorus & Schlag (1993), a permanent circulation can create low disturbance status. It would be complemented by the little variation of abiotic conditions. It is possible to state that the phytoplankton community

in this case presented a non-successional change, since disturbances didn't change significantly the species composition.

The more adapted species like *C. raciborskii* under such abiotic conditions influenced the diversity as showed by low Simpson index during the summer (oriented by abundance) and Shannon (biovolume). Its dominance affects the biomass of other species more significantly than the richness, similar at the both seasons. Results showed no direct correspondence between the diversity indices and biovolume, suggesting that primary production is not proportionally linked to diversity. Nutrient availability seems to play a weak force driving the variation of total biomass on Peri. The higher primary production (biovolume) during the hot-rainy period is not explained by a considerable variation of dissolved nutrients and total phosphorus. This study does not support models, which associate greater diversity with greater primary productivity under utilization of limiting resources (Tilman 1999).

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Chapter

4

4 Role of conditional differentiation on diversity and succession in Brazilian and German shallow lakes dominated by Cyanobacteria

4.1 Abstract

Water samples were taken in four temperate shallow lakes in Brandenburg region (Germany) during 2007 and compared with data from four Brazilian lakes, in order to investigate the influence of temperature on diversity and dynamic of the phytoplankton species. The richness was much higher in the temperate shallow lakes, which were more similar to each other in terms of seasonality, species number and productivity. The cyanobacterial group dominated all studied lakes. The mixing events had a positive effect on the dominance of this group in tropical lakes. *Cylindrospermopsis raciborskii* and *Anabaena* sp. (S_N) were more common at temperature above 20°C, while S1 group (Reynolds et al. 2002) as the genus *Limnothrix* was more successful at temperatures between 6.0°C and 20°C. *Aphanizomenon gracile* and *Pseudanabaena limnetica* were frequent at higher temperatures, but persisted until autumn, in opposite to other species of the genus *Aphanizomenon*. The group of Bacillariophyceae was adapted in temperate lakes under lower temperatures, with the exception of *Aulacoseira* sp., recurrent in tropical not stratified lakes. The richness of Chlorophyceae was high in temperate lakes, mainly during the spring (>15°C) and in tropical lakes was more frequent before and after cyanobacterial blooms. Lo species as *Peridinium* sp. was favored by higher temperatures (>19°C) and low level of dissolved nutrients. A positive correlation between richness and biovolume of temperate lakes was found and the opposite was observed in tropical ones, lakes under higher dominance of few phytoplankton species. The biovolume and richness in tropical lakes was more variable, while in temperate lakes presented higher richness at intermediate level of biovolume (annual mean from 10.0 to 18.0 mm³/l). Low level of biodiversity allows an ecosystem to function under constant conditions, but a greater biodiversity occurred in fluctuating environments. Niche differentiation based on variation of environmental conditions is indeed a plausible explanation to explain changes in plankton groups and its diversity. Climate changes can influence the phytoplankton community in continental waters and drives modifications in their dynamics, since the effect of global warming may enhance toxic cyanobacterial blooms.

4.2 Introduction

The decrease of biodiversity related to the phenomena of global climate change is stimulating the scientific community towards a better understanding of the relationships between biodiversity and ecosystem functioning. The climate change could lead to gradual losses of species as abiotic conditions begin to exceed species tolerance limits. Specific knowledge of functional types may be critical to predict ecosystem responses under different global change scenarios (Loreau 2001). The phytoplankton composition in tropical lakes is not more complex and diverse than in temperate ones (Lewis 1996, Serruya & Pollinger 1983). The composition of phytoplankton communities at the level of genus, and even at the level of species, varies little between temperate and tropical latitudes, showing broad overlap in species composition and little endemism (Lewis 1978, Kalff & Watson 1986).

The ability to grow in different types of environments is one of main characteristics of cyanobacteria. The availability of light and temperature (15°C to 30°C) are more important factors for the bloom formation than concentration of nutrients, particularly for nitrogen fixers, besides of the stability of the water column (Reynolds 2002). Global warming may stimulate the increase of cyanobacterial biomass (Wiedner 2006) and consequently decrease the diversity of other algal groups (Frizzo et al. 2004).

Lake warming is indeed a plausible explanation for the observed changes in plankton dynamics. Simulations with a seasonally forced plankton model confirm that temperature raise rules phytoplankton changes (Scheffer et al. 2001). At temperate latitudes, there is typically a successional pattern in the development of phytoplankton communities. Frequently this succession involves first a predominance of diatoms, often accompanied by cryptomonads, followed by chlorophytes, and finally bluegreen algae and dinoflagellates (Sommer et al. 1986, Reynolds 1989). In tropical lakes, the season of minimum temperature in deep lakes is usually the season of complete mixing, except for shallow lakes, which present a irregular thermal stratification throughout the year (Hutchinson & Löffler 1956) or even daily (Lopes et al. 2009). Some investigations indicate that the existence of non-seasonal variations in their phytoplankton communities in tropical lakes is more frequent than in temperate ones (Hutchinson & Löffler 1956, Melack 1979).

Studies linked to seasonality and diversity of tropical water bodies can reveal not only unexpected characteristics but may also contribute to a better comprehension of the

functioning of tropical aquatic ecosystems. The temporal sequences of species in tropical lakes superficially appear irregularly, disappear, and then reappear, failing to stratify seasonally, resulting on more successional episodes (Dokulil et al. 1983). Esteves (1998) argued that phytoplankton composition in tropical lakes is strongly influenced by local factors, leading specific temporal variations instead of seasonal variations. The succession driver in tropical lakes is also supposed to be linked to precipitation and stratification pattern as perturbation factors (Chellappa et al. 2008, Dantas et al. 2008), specially when seasonal thermal differences are small. The water temperature controls directly vital processes as primary productivity and decomposition of organic matter. The more constant abiotic conditions in tropical lakes, for example high temperatures are considerate the main “motor” of the dynamic of these lakes, which contribute to maintain the algal biomass throughout the year (Esteves 1998). In subtropical ecosystems, seasonal changes in temperature are more related to the succession dynamics of phytoplankton than in equatorial regions, acting directly or indirectly in mechanisms as nutrients and light underwater (Becker et al. 2008).

The particular traits of phytoplankton may have a wider distribution in temperate areas compared to tropical ones because the environmental temperature is more variable (Norbert 2004). Even though the relation between diversity and latitude is unclear for phytoplankton, one might speculate that the range of temperature optima found in the tropics is far lower due to a very stable temperature regime, while temperate areas may have a much larger range in temperature optima represented by species in the community (Fig. 4.1).

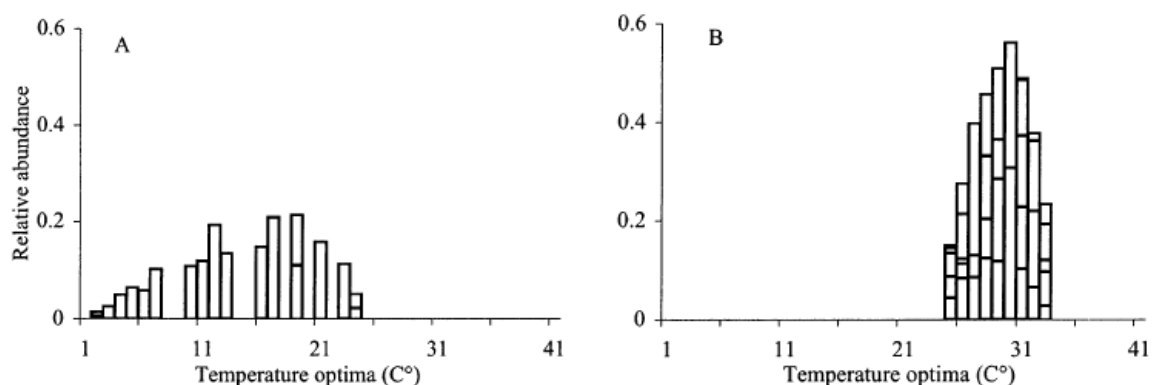


Fig. 4.1: An illustration of how distributions of traits in communities, here exemplified by the optimal temperature for growth, may result from different environments such as (A) temperate and (B) tropical regions (Norbert 2004).

Biodiversity is a key factor in ecology, directly linked with the regulation and functioning of the ecosystems. Ecosystem functioning are activities, processes or properties of ecosystems that are influenced by its biota (Scherer-Lorenzen 2005) and is determined by the state of the environmental factors as well as the aggregated properties of the community (Norbert 2004). Conditional differentiation is a type of niche complementarity, which occurs when two competing species differ in their abilities based on varying environmental condition. The principle of niche complementarity constitutes a possible mechanism linking diversity and ecosystem functioning (Tilman 1999, Kinzig et al. 2001). The impact of biodiversity on productivity has been explained by an effect generated by niche differentiation and a selection effect that can cause dominance of the most productive species (Loreau 1998, Loreau & Hector 2001).

Hutchinson (1967) also discusses additional mechanisms as niche diversification, and believes that the phytoplanktonic species are just opportunistic, suitable for growth for restricted periods. It appears that a low level of biodiversity allows an ecosystem to function under constant conditions, but that a greater biodiversity is called for in fluctuating environments (Humbert & Dorigo 2005). The planktonic communities are subject to environmental fluctuations in the real world, and the effects of environmental variability are magnified rather than damped by the species interactions (Scheffer et al. 2003). Depending on their intensity and on their frequency, this principle supports the paradox of phytoplankton (non-equilibrium dynamics) and would enhance the species diversity of the ecosystem (Huchinson 1961, Margalef 1958, Harris 1986). The paradox (Huchinson 1961) argues that equilibrium states were unlikely to form in planktonic systems, where currents and a lack of spatial structure might prevent any stable, long-term interaction among species. The changes in abiotic conditions avoid the possibility of competition and enhance diversity, since the conditions of competition would change frequently enough to invert competitive hierarchies before exclusion occurs. High growth rates at one temperature trade off with growth rates at other temperatures, so that species are predicted to replace each other (Fig 4.2).

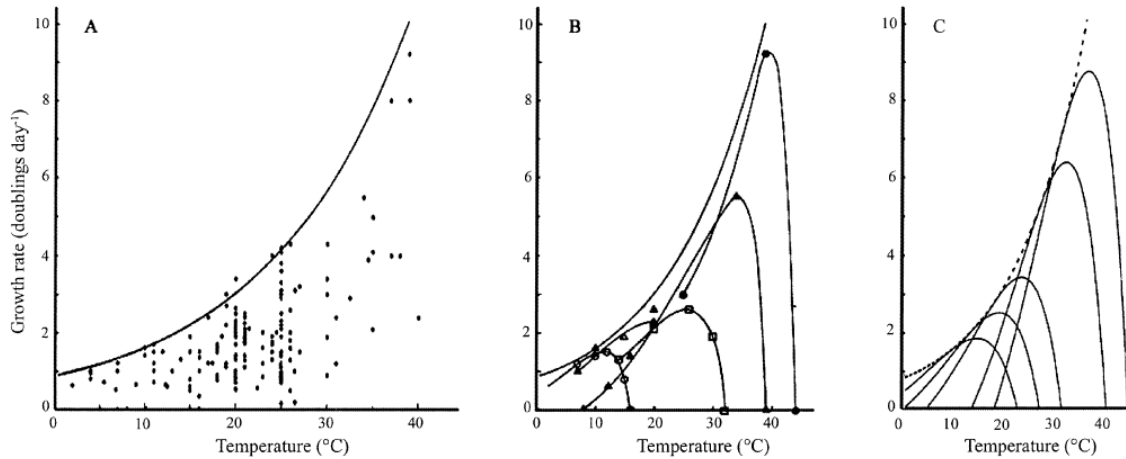


Fig. 4.2: (A) An envelope function for temperature-dependent growth rates in phytoplankton. (B) Examples of single species replacement responses to temperature (redrawn from Eppley 1972). (C) A mathematical formulation of an interspecific temperature response function (Norbert 2004).

4.3 Hypothesis

The different types of environments (tropical and temperate) show the possibility of coexistence of the same phytoplankton species and recursive functional groups. The presence of same genera occur during the spring and summer in temperate lakes comparing to cold-dry and hot-rainy periods in tropical lakes. It appears that a lower level of biodiversity allows an ecosystem to function under constant conditions, but that a greater biodiversity is called for in fluctuating environments at intermediate level of biovolume. There is no causal dependence of biodiversity on phytoplankton biomass in tropical lakes. In these systems, patterns of algal biomass are more variable and weak evolutionary forces drive phytoplankton speciation. There is a tendency of dominance of few species, which contributes to decrease the diversity. The form of niche complementarity that often occurs in temperate lakes is the conditional differentiation, which occurs when two competing species differ in their abilities to use a resource based on varying abiotic conditions (temperature). This phenomenon allows higher annual richness in temperate lakes. In tropical lakes, more constant abiotic conditions lead to low niche complementarity. No stratification pattern seems to favour the dominance of cyanobacteria in tropical lakes.

4.4 Sites description

The samples were taken biweekly during 2007 at 4 German lakes in Brandenburg State (Germany). In order to compare with the lakes from tropical regions, literature data were taken from 4 Brazilian lakes, located in several parts of the country as followed:

4.4.1 German lakes

In the catchment area of the river Dahme in Scharmützelsee region locate shallow polymictic lakes, regularly dominated by blooms of Cyanophyceae in summer, which outcompete other algal groups under poor underwater light climate. The concentration of dissolved inorganic phosphorus is a scarce resource in the lakes of Scharmützelsee region but sufficient to maintain the growth of this algal group at relatively higher level (Rücker et al. 1997, Grüneberg et al. 2011).

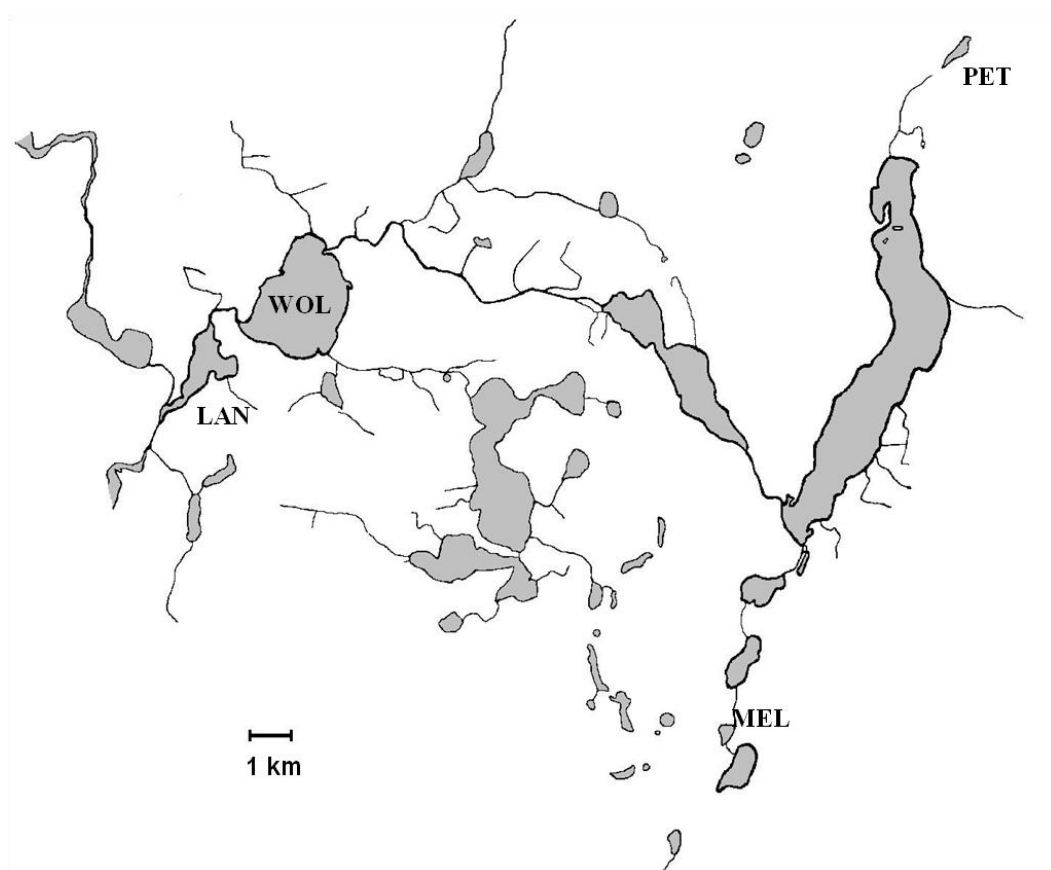


Fig. 4.3: Location of shallow lakes in Scharmützelsee region (Germany): Petersdorfer See (PET), Wolziger See (WOL), Langer See (LAN), and Melangsee (MEL).

Table 4.1: Morphometric parameters of studied German lakes

Parameters	Petersdorfer See	Langer See	Melangsee	Wolziger See
Abbreviation	PET	LAN	MEL	WOL
Area (km ²)	0.23	1.6	0.12	5.2
Volume (10 ⁶ m ³)	0.53	3.3	0.17	32.0
Mean depth (m)	1.6	2.1	1.6	5.5
Max. depth (m)	3.0	3.5	2.4	13.0

4.4.2 Brazilian lakes

The study of the literature data was carried out in Ingazeira reservoir during 1997 /1998 by Bouvy et al. (1999), in Manacás lake during 1999/2000 by Soares et al. (2009), in Peri coastal lagoon during 1996/1997 by Laudares Silva (1999), and in Billings reservoir during 2002/2003 by Gemelgo et al. (2009).

a) Ingazeira Reservoir (Northeast region): The Ingazeira reservoir is situated in Pernambuco state, 250 km from the Atlantic Ocean. It was built in 1986 to retain water for irrigation and drinking purposes. The hydrological balance in this Brazilian region is characterized by an annual precipitation range between 400 and 800 m (Cadier 1993). The irregularities in precipitation are observed in the entire Brazilian semi-arid region, as a direct consequence of the El Niño event (Bouvy et al. 1999).

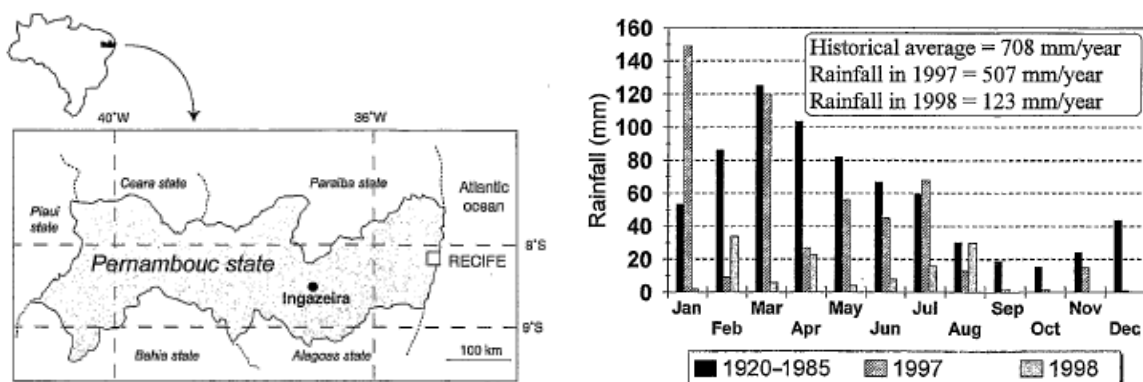


Fig. 4.4: Left: Map of Pernambuco State (Brazil) and location of the Ingazeira reservoir. Right: Ingazeira Monthly average precipitation for 1920 to 1985 period and for studied period 1997/1998 (Bouvy et al. 1999).

b) Manacás lake (Southeast region): Manacás lake is a small and shallow reservoir surrounded by a remnant of the Atlantic Forest, in southeast Brazil. It is located on the campus of the Federal University of Juiz de Fora in Minas Gerais state. The regional climate is tropical at altitude, with a cold dry season and a warm wet season. The total annual precipitation is 1500 mm, and the annual mean temperature is 19 °C (Soares et al. 2009).

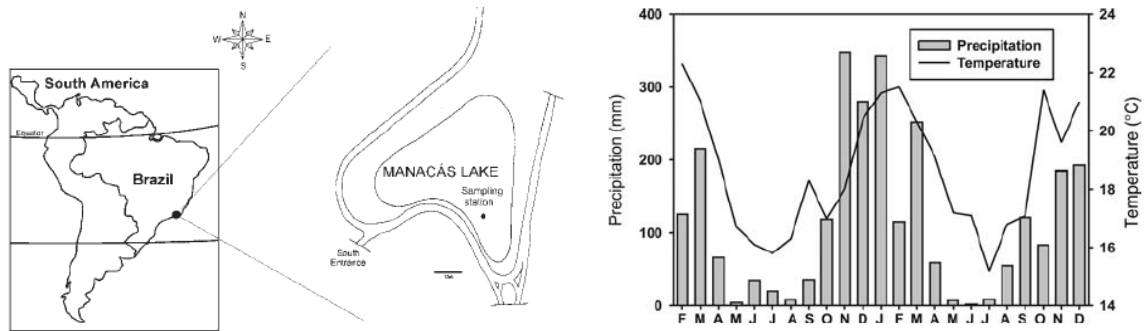


Fig. 4.5: Left: Map of Manacás lake showing the geographical location and the sampling station. Right: Monthly precipitation and mean air temperature of the region (Soares et al. 2009).

3) Peri coastal lagoon (South region): Peri is a tropical riverine coastal lagoon, a shallow lake in the southwest of the island of Santa Catarina State. The climate is subtropical, with rainfall concentrated in spring and summer months (October-March). The lagoon is enclosed and slightly above the sea level, located in a preservation area (Parque Municipal da Lagoa do Peri) with a restricted human occupation and surrounded by Atlantic Forest. Its fresh water is a result of 2 rivers inflow (Ribeirao Grande and Cachoeira Grande) and rainfall (Laudares Silva 1999).

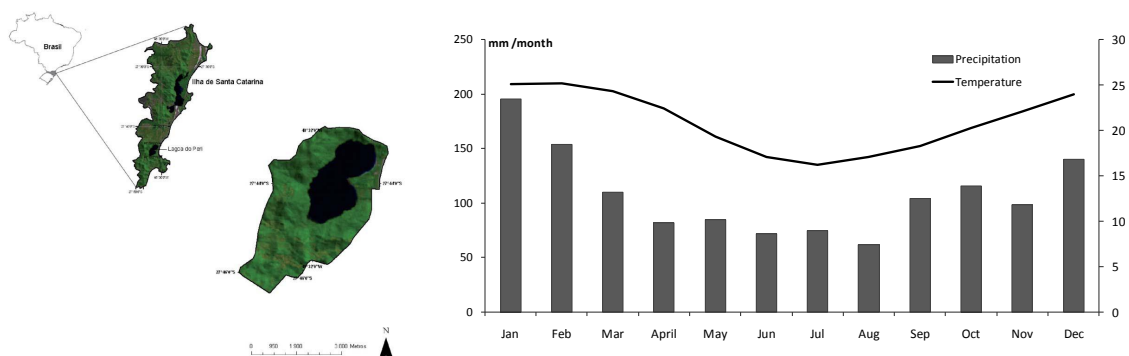


Fig. 4.6: Left: Map of Santa Catarina state, showing the geographical location of Peri coastal lagoon. Right: Monthly precipitation and mean air temperature of the region (Laudares Silva 1999)

4) Billings Reservoir (Southeast region): The Billings reservoir is located in the city of São Paulo Metropolitan area, and has been submitted to intense human influence, especially in relation to the discharge of domestic, industrial and agricultural wastes, along with the removal of the surrounding vegetation. This reservoir is used for the public water supply and recreation of three million people and supply hundreds of industries with water (Gemelgo et al. 2009).

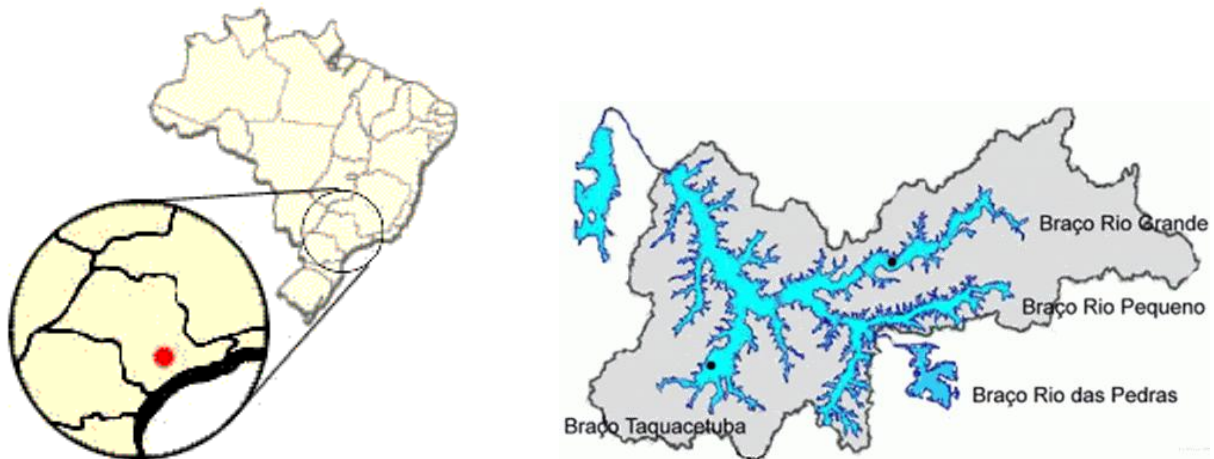


Fig. 4.7: Left: Location of Billing reservoir in São Paulo state. Right: Catchment area.

Table 4.2: Morphometric parameters of studied Brazilian lakes

Parameters	Peri lagoon	Manacás lake	Ingazeira reservoir	Billings reservoir
Main uses	Water supply	Recreation	Irrigation/drinking	Water supply
Latitude	27°43' S 48°32' W	21° 84' S 43° 82' W	8° 34' S 36° 52' W	23° 47' S 46° 40' W
Volume (10 ⁶ m ³)	21.2	0.2	4.6	995
Area (km ²)	5.07	0.02	1.3	127
Mean Depth (m)	4.2	0.83	5.0	-
Max. Depth (m)	11.0	5.0	13.0	18.0
CA (km ²)	20.1	392	326	560

4.5 Methodology (German Lakes)

The water was taken each 0.5 meter with a 2.3 L-Limnos sampler and analyzed as mixed samples. Sampling stations were above the deepest points, where Secchi depth was also recorded. Depth profiles of physical and chemical parameters were measured with a Hydrolab H20 probe connected to a field computer (HUSKY Hunter). Secchi depth (SD), total phosphorus (TP), dissolved inorganic phosphorus (DIP), total nitrogen (TN) and different inorganic dissolved nitrogen fraction (DIN), dissolved silica (DSi) as well as chlorophyll *a* (Chl *a*) were determined according to standard methods (DEV 1986–1998). Chl *a* concentrations were corrected for phaeophytin. Phytoplankton was counted after fixation with Lugol solution according to Utermöhl (1958). Biovolume was calculated by measuring the corresponding dimensions using the geometric formulas given by Rott (1981) and Willén (1976). Richness (number of species), Shannon Wiener index, evenness of Shannon Wiener index (H'/H_{max}), and complement of Simpson index (probability that two individuals drawn randomly from the sample belong to different species) were used as diversity measurements as followed:

Shannon-Wiener index: $H' = -\sum_{i=1}^s p_i \log p_i$ where p_i = biovolume belonging to the i^{th} of S species/ total biovolume.

Comp. Simpson index: $1 - C = \sum_{i=1}^s p_i^2$ where p_i = number of individuals belonging to the i^{th} of S species/ total number of individuals.

4.6 Results

4.6.1 Abiotic parameters:

a) Lakes in Brandenburg region (Germany)

The limnological variables of the shallow temperate lakes are shown in the table 4.3. The Secchi depth values of PET, LAN and MEL were comparable, higher during the winter (maximum = 1.8 m) and lower during the summer (minimum = 0.4 m). This parameter achieved its maximum in WOL (4.6 meter). The pH and water temperature were similar in all Brandenburg lakes, and had its minimum and maximum in LAN (1.7 °C in December and 25 °C in June). The conductivity had the highest values in LAN (mean = 518 $\mu\text{S}/\text{cm}$) and the lowest in PET (mean = 356 $\mu\text{S}/\text{cm}$). The concentration of dissolved oxygen had a mean about 11.0 mg/l and was around 100% saturation in all 4 lakes. The total phosphorus concentration varied from 40 to 64 $\mu\text{g}/\text{l}$, presenting its minimum in MEL (24 $\mu\text{g}/\text{l}$) and its maximum in WOL (95 $\mu\text{g}/\text{l}$). The ammonium concentration was variable, more pronounced in WOL (8.4 $\mu\text{g}/\text{l}$ in April and 655 $\mu\text{g}/\text{l}$ in November). The variation of dissolved inorganic nitrogen was

lower in MEL (from 4.3 to 66 µg/l) and PET (2.4 to 99 µg/l), and was higher in WOL (8.7-924 µg/l) and LAN (0.7-339 µg/l). The minimum of chlorophyll *a* concentration was observed in MEL and WOL (9.4 and 6.4 µg/l respectively), and the maximum was noted in PET and LAN (133 and 138 µg/l respectively). The mean of silica concentration was similar in LAN (2,584 µg/l), MEL (2,580 µg/l) and WOL (2,266 µg/l), and lower in PET (595 µg/l).

Table 4.3: Means and intervals of limnological variables of 4 German temperate lakes during 2007.

Parameters	Petersdorfer See	Langer See	Melangsee	Wolziger See
Secchi Depth (m)	0.9 (0.4-2.0)	0.8 (0.4-1.6)	1.1 (0.4-1.8)	1.8 (0.8-4.6)
pH	8.0-9.0	7.9-9.0	7.5-8.5	7.8-9.0
Water Temp. (°C)	13 (3.1-23)	12 (1.7-25)	14 (2.4-24)	12 (3.3-22)
Conductivity (µS/cm)	356 (327-406)	518 (483-547)	486 (447-521)	490 (468-504)
O ₂ %	101 (82-131)	106 (87-133)	104 (74-138)	95 (73-125)
O ₂ (mg/l)	11 (7.1-13.5)	12 (7.5-18.5)	11 (6.9-12.8)	11 (7.1-15.2)
TP (µg/l)	40 (32-54)	57 (40-79)	45 (24-63)	64 (31-95)
TN (µg/l)	1581 (1313-2205)	945 (584-1401)	912 (440-1421)	1044 (687-1315)
DIP (µg/l)	12 (3.5-31)	8.0 (3.6-29)	8.0 (4.7-14.3)	27 (3.5-70)
NH ₄ -N (µg/l)	215 (24-806)	102 (31-283)	81 (14-394)	197 (8.4-655)
NO _x -N (µg/l)	40 (2.4-99)	93 (0.7-339)	29 (4.3-66)	179 (8.7-924)
SiO ₂ -Si (µg/l)	595 (50-1168)	2584 (54-3894)	2580 (490-4868)	2266 (44-6757)
Chla (µg/l)	64 (11-133)	75 (44-138)	52 (9.4-89)	34 (6.4-81)

b) Brazilian lakes

The water temperature varied from 16.2 °C during the cold-dry period to 29.5 C during hot-rainy period in Manacás lake. Dissolved oxygen was lower during warmer periods (minimum 52% saturation in April) and higher during colder periods (150% saturation in July). The pH presented large variation from 4.2 in August to 7.8 in September. The Secchi depth presented large range, varied from 0.1 meter in March to 1.5 meter in November. Conductivity was considered low (30 µS/cm). Great variability was observed in relation to dissolved forms of nitrogen, from below the detection level during colder periods and higher during warmer periods (N-NO₃ = 1,300 µg/l and N-NH₄ = 270 µg/l).

In the Billings reservoir, the mean of water temperature ranged from 19 to 29 °C. The Secchi depth showed little variation, around 0.4 m. The pH and concentration of dissolved oxygen were higher in June and October. The concentration of N-NH₄ (550 µg/l) presented highest values more pronounced during September. The dissolved inorganic nitrogen was highest during May (560 µg/l), and total phosphorus varied around 100 µg/l, more pronounced during January (220 µg/l).

In Ingazeira, variations of conductivity were large, showing an inverse pattern of total volume fluctuations of the reservoir. The Secchi depth showed high values in January (close to 2.5 m) and the lowest in the middle of the year (53 cm in June). The water temperatures were always high during the survey with minima registered in June and August (24 to 25 °C) at 0.5 m (subsurface). The pH values were always above 8.1 and reached up to 9.4 in March. The high pH values corresponded to high oxygen concentrations in March and April 1998 (10 mg/l). The dissolved inorganic phosphorus concentrations were very variable, with high values observed in February 1997 (544 µg/l) to low values in September 1998 (6.0 µg/l). Nitrite and nitrate had the lowest values in November and December 1998 and the highest values in May. The highest chlorophyll a concentration was observed between May and September 1998.

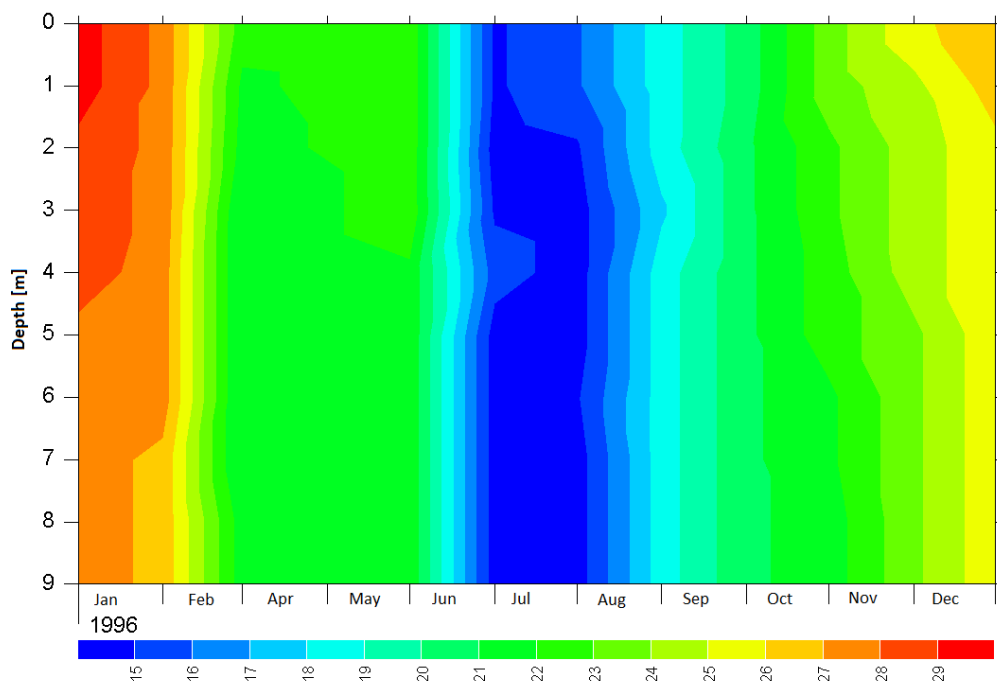
Table 4.4: Mean, minimum, and maximum of abiotic parameters in 4 Brazilian lakes. The data were taken from: (1): *Laudares Silva (1999) during 1996*; (2): *Soares et al. (2009) during 1999/2000*; (3): *Bouvy et al. (1999) during 1997/1998*; (4): *Gemelgo et al. (2009) during 2002*.

	Peri (1)	Manacás (2)	Ingazeira (3)	Billings (4)
Secchi Depth (m)	1.1 (0.9-1.5)	0.6 (0.1-1.5)	0.5-2.5	0.5 (0.4-1.0)
pH	6.1-7.3	4.2-7.8	6.8-9.4	7.0-9.0
O₂ (mg/l)	7.2 (5.6-8.3)	-	6.0 (2.0-10)	8.0 (6.0-15)
O₂ (%)	85 (65-96)	83 (62-150)	-	-
Water temp. (°C)	22 (14.5-28.5)	20 (16-29.5)	26 (24-29)	24 (20-29)
Conductivity (µS/cm)	105 (70-205)	30 (21-36)	(700-1700)	200 (170-220)
DIP (µg/l)	7.0 (2.7-21)	23 (35-58)	75 (6.0-544)	-
DIN (µg/l)	7 (1.8-14)	310 (186-1300)	2.0-92	270 (4.0-560)
TN (µg/l)	546 (97-828)	-	-	-
NH₄-N (µg/l)	16 (1.7-56)	54 (16-270)	41 (8.0-98)	240 (5.0-550)
Chl a (µg/l)	14 (2.7-34)	-	75 (26-135)	-
TP (µg/l)	15 (10-32)	-	-	100 (80-220)

According to Laudares Silva (1999), the Secchi depth of Peri coastal lagoon varied from 0.9 in October to 1.5 in July. The conductivity values varied from 70 $\mu\text{S}/\text{cm}$ in September to 205 $\mu\text{S}/\text{cm}$ in May. The dissolved oxygen concentration varied from 5.6 in February to 8.3 mg/l observed in August. The lowest values of oxygen saturation were detected in March and the highest in July. The annual variation of oxygen concentration and saturation were 9.0 mg/l and 8% respectively. The pH varied from 6.0 to 6.7 and the alkalinity from 0.12 to 0.18 mEq/l, higher during peak of precipitation. The solid suspended varied from 0.67 to 140 mg/l, lower during the rainy season, with predominance of organic matter. The total nitrogen presented great variation (97 to 828 $\mu\text{g}/\text{l}$), higher during December and lower during May. The nitrite concentration ranged around the detection level (from < 0.01 $\mu\text{g}/\text{l}$ to 1.17 $\mu\text{g}/\text{l}$). The nitrate concentration was also very low (1.82 to 14 $\mu\text{g}/\text{l}$), highest during cold periods (August) and lowest during warmer periods (February). The lowest concentration of ammonium, total and dissolved phosphorus occurred also during July (2.0 $\mu\text{g}/\text{l}$ $\text{NH}_4\text{-N}$, 10.0 $\mu\text{g}/\text{l}$ TP and 3.0 $\mu\text{g}/\text{l}$ DIP). The silica concentration varied from 3.0 to 3.6 mg/l.

The isopleths of water temperature of Brazilian lakes showed the presence of no stable thermal stratification, which occurred during different periods of the year (figure 4.8).

Peri Coastal Lagoon



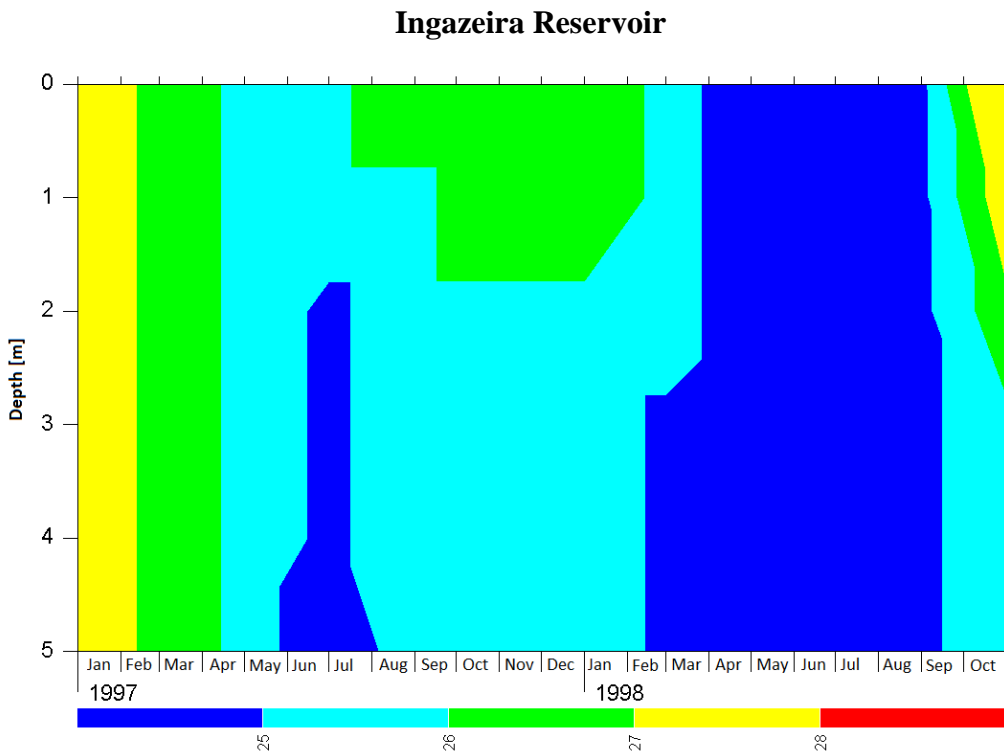
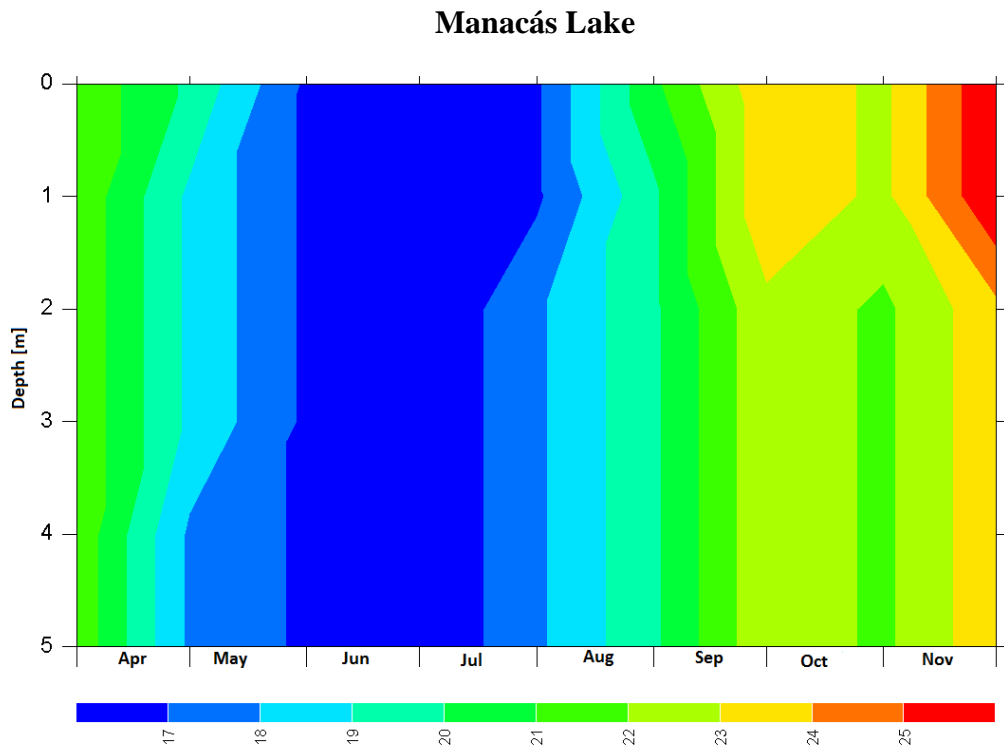


Fig. 4.8: Depth-time isopleths of water temperature from Peri coastal lagoon (1996), Manacás lake (mean data from 1999/2000), and from Ingazeira reservoir (1997/1998).

In Peri, the largest differences of temperature between surface and bottom were 2 °C, observed during warmer periods. Generally, the water temperature in Peri was lower from May until August and higher from September until April, which indicates the presence of seasonal aspects. A similar pattern was observed in Manacá lake, where a thermal stratification was established in October, and the overturn succeeded from April to September, during the colder period. A different example was noted in Ingazeira reservoir, where the temperature variation did not show considerable seasonal differences (4 °C along the years). During October to December, water temperatures in the upper column were slightly higher. In 1998, the vertical profiles showed a great homogeneity of the water column, compared with those observed in 1997.

4.6.2 Phytoplankton succession associated with temperature

1) German lakes

The succession of algal groups of 4 German polymictic lakes along the annual variation of water temperature is illustrated in figure 4.9. Regarding the Cyanophyceae, the dominance of this group in terms of biovolume was noted in all studied German lakes. In Langer See, 45 species of Cyanophyceae was identified, well represented by the S1 association *Planktothrix agardhii* from June and October (8.5 mm³/l), with a peak at the end of August (12.4 mm³/l) together with *Pseudanabaena limnetica* (10 mm³/l). This other S1 specie maintained its biovolume until October (8.0 mm³/l) taking place to the increase of *Limnothrix redekei* in November (1.5 mm³/l). *Cylindrospermopsis raciborskii* had considerable biovolume in LAN only during the summer (maximum = 1.0 mm³/l in July), accompanied by *Aphanizomenon issatschenkoi* and *Aphanizomenon gracile* (maximum in June = 6.7 mm³/l and 3.7 mm³/l respectively). The specie *Aphanizomenon issatschenkoi* (2.2 mm³/l in September and 0.5 mm³/l in October) decreased its population earlier than *A. gracile*, which maintained its biomass up to 1.4 mm³/l until November, when began to decline.

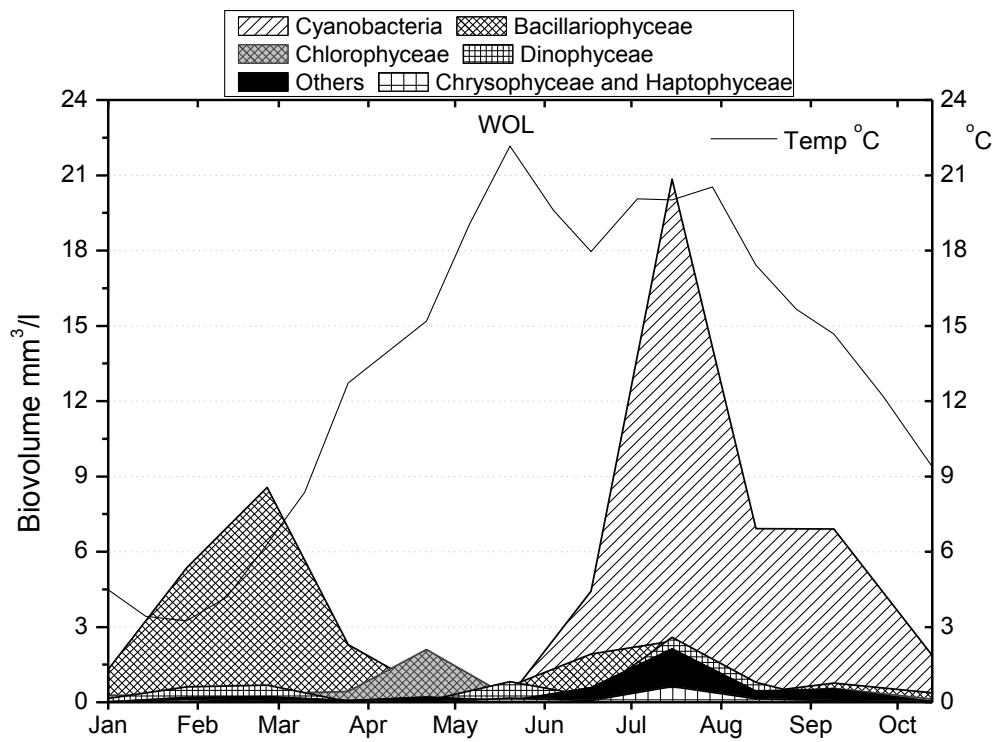
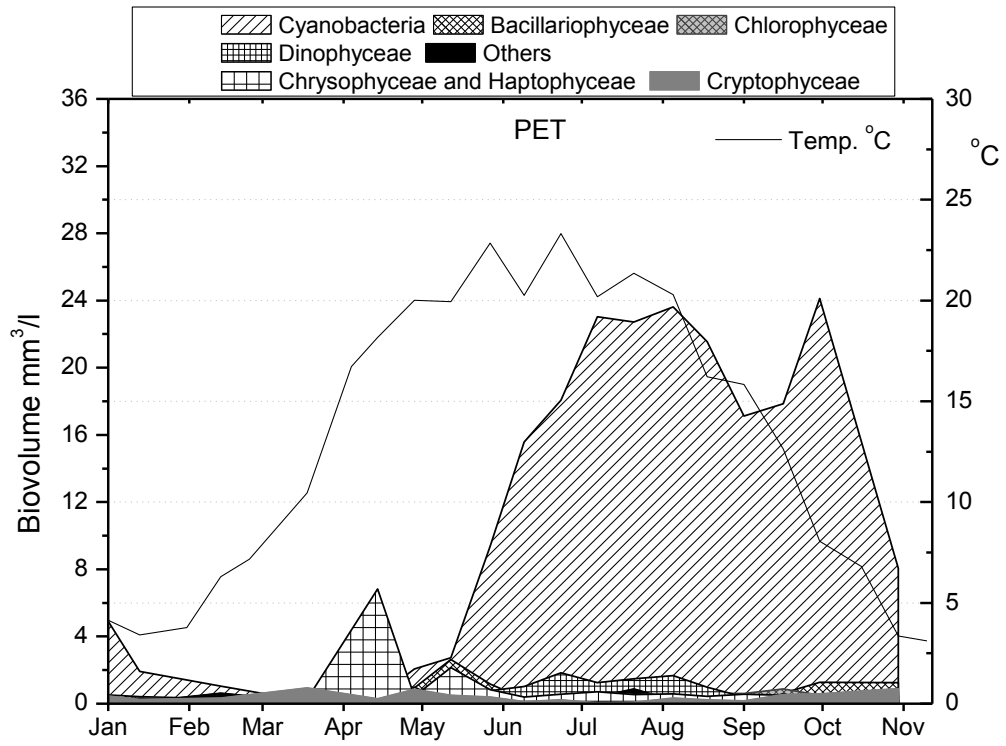
A similar situation was observed in Wolziger See. *Aphanizomenon issatschenkoi* had its maximum in August (2.7 mm³/l) until September (0.2 mm³/l), while the population of *A. gracile* was preserved until October (0.3 mm³/l). A notable presence of *Aphanizomenon flos-aquae* was detected in July (2.6 mm³/l). A total of 32 species of Cyanobacteria was identified in WOL, including 7 species of genus *Anabaena*, mainly during August (*Anabaena flos-aquae* = 3.6 mm³/l, *A. solitaria* = 2.0 mm³/l, and *A. circinales* = 0.8 mm³/l). During colder

periods, a presence of *Limnothrix redekei* was noted, mainly during March (0.4 mm³/l) and April (0.3 mm³/l). *Planktothrix agardhii* maintained its performance from late summer until autumn (5.0 mm³/l in August, 4.0 mm³/l in October, and 1.5 mm³/l November), together with *Pseudanabaena limnetica* (2.4 mm³/l in August and 1.7 mm³/l in October).

In Peterdorfer See, as well as in Wolziger See, the cyanobacterial biomass was more pronounced from the late summer until autumn, with 30 different species of the group. The S1 specie *P. limnetica* dominated in PET, achieving two high peaks, during August (21.0 mm³/l) and October (22.0 mm³/l). High biovolume of *L. redekei* was noted in January (8.0 mm³/l). *A. gracile* and *C. raciborskii* were more relevant during the summer (about 2.5 mm³/l), but *A. gracile* maintained its population until October (1.5 mm³/l).

In Melangsee, 44 species of cyanobacteria were identified. *L. redekei* (1.7 mm³/l in February and 1.3 mm³/l in October) and *P. limnetica* (3.4 mm³/l in September and 2.1 mm³/l in November) also dominated during colder periods. *A. gracile* peaked during August (4.5 mm³/l and 92,610 cell/ml), with considerable biovolume until October (2.1 mm³/l). *Mycrocystis aeruginosa* was important from July until October (about 1.5 mm³/l) and *Anabaena macrospora* during July (5.0 mm³/l).

The group of Bacillariophyceae was well represented by *Aulacoseira granulata* during hot periods in WOL (0.8 in July mm³/l and 1.4 in August mm³/l) and PET (maximum in June = 2.1 mm³/l). In WOL and LAN, centric diatoms during colder periods as *Cyclotella radiosa* (1.8 mm³/l in April in WOL and 4.0 mm³/l in LAN) and *Stephanodiscus* sp. (4.4 mm³/l in February in WOL and 2.0 mm³/l in LAN; 6.4 mm³/l in March in LAN) were observed. A low biomass of this group was observed in PET, with 25 species. *Fragilaria ulna* was important in the beginning of the year in LAN (3.6 mm³/l in February) and MEL. This specie was also relevant at the end of the year in MEL as well as *Asterionella formosa* in LAN (1.4 mm³/l in December).



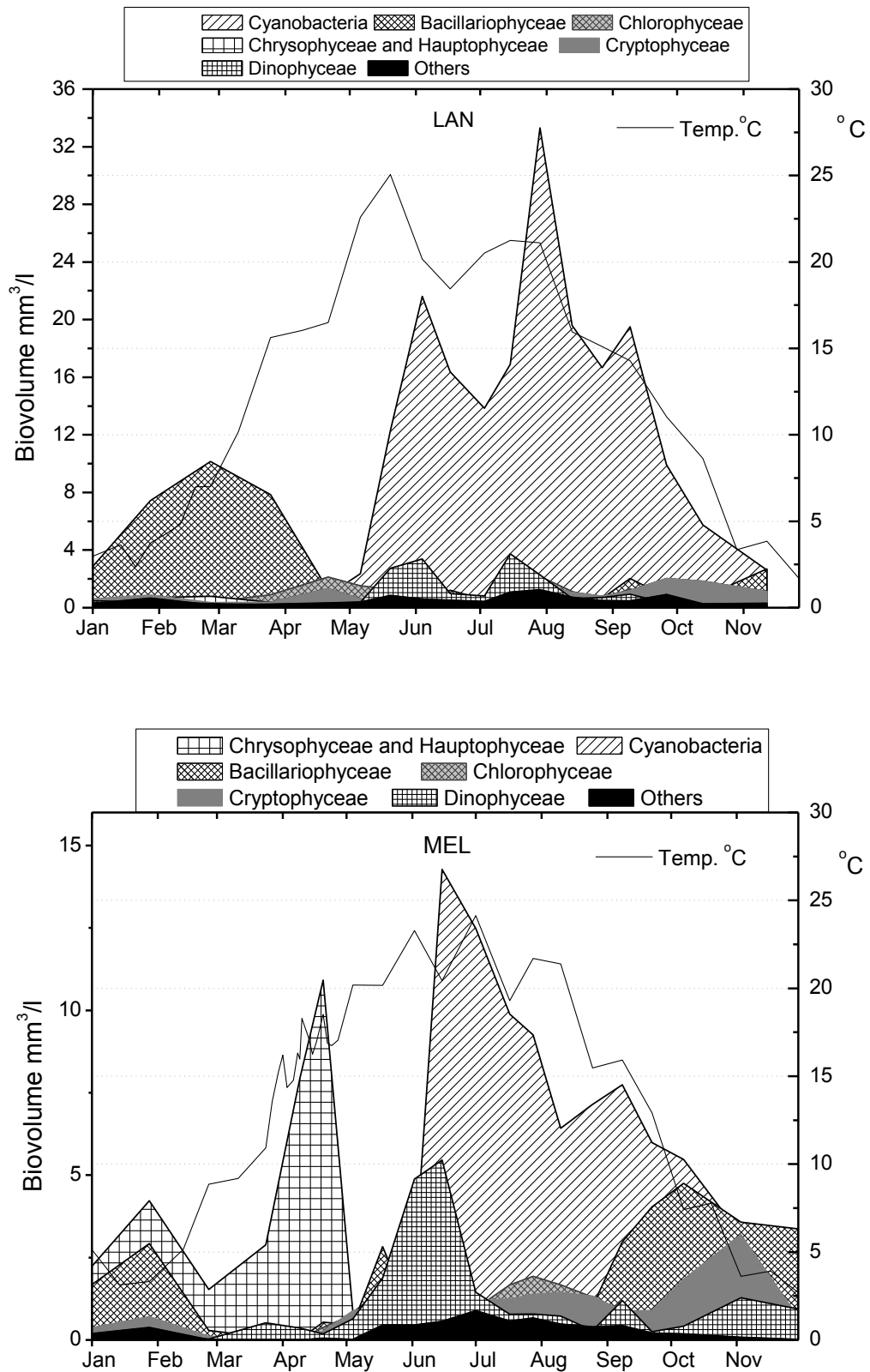


Fig. 4.9: Seasonal variation of the algal groups and the water temperature variation of 4 polymictic shallow lakes in Brandenburg region during 2007.

Although the group of Chlorophyceae in LAN, WOL and PET presented low biovolume, the richness of this group was high (63 species in LAN, 48 in PET and 45 in WOL and 53 in MEL). *Oocystis*. sp was relevant during the spring in WOL (1.6 mm³/l) and PET (0.3 mm³/l) during May. The genus *Coelastrum* was noted during the late summer in WOL (0.9 mm³/l). Generally, the species were well distributed (biovolume of a single specie < 1.0 mm³/l), concentrated during spring and summer. The appearance of the Dinophyceae was also more pronounced during warmer periods, higher in MEL. In this lake, *Peridinium willei* was common during June and July with 4.0 mm³/l (160 cell/ml) and was the most representative of the 7 species of genus *Peridinium*. In WOL and LAN, the genus *Ceratium* contributed to the increase of biovolume of this group. *C. hirundinella* was more present in May until June (0.8 mm³/l in WOL and 2.4 in LAN) and *C. furcoides* during August (0.6 mm³/l in WOL and 3.3 in LAN). The specie *Gymnodinium lantzschii* was most abundant during colder periods in LAN (639 cell/ml in October) and in WOL (February and March with 388 cell/ml), and also during August (439 cell/ml in LAN and 517 cell/ml in WOL). The Chrysophyceae was well represented in PET by *Dinobryon sociale* (6.7 mm³/l) in May and *Uroglena* (2.0 mm³/l) in June. In MEL, *Uroglena notabilis* achieved high biovolume during the spring (10.8 mm³/l in May). The Cryptophyceae group was represented by *Cryptomonas erosa* in LAN and MEL, more pronounced from August until November (max = 1.6 mm³/l in LAN and 2.3 mm³/l in MEL).

In figure 4.10, the relation of algal groups and temperature of the studied shallow German lakes is illustrated. Usually, the cyanobacterial species were more common at temperatures between 16 to 26 °C. The group S₁ as *Limnothrix redekei* and *Pseudanabaena limnetica* were more successful at lower temperatures, while S_N group as *Cylindrospermopsis raciborskii*, together with genera *Aphanizomenon* and *Anabaena* were more frequent at higher temperatures. The Dinophyceae group was benefited by temperatures up to 19 °C, mainly during the summer, and the Chlorophyceae at up to 15 °C, relevant during the spring. On the other hand, the group of Bacillariophyceae became more visible at lower temperatures (<15 °C), with the exception of *Aulacoseira granulata*, common at higher temperatures. Chrysophyceae occurred preferentially at colder periods (<12 °C) under lower biovolume, and had 2 peaks due the larger biovolume of *Dynobryum sociale* and *Uroglena notabilis* at 19 °C. The group of Cryptophyceae was widespread at high and low temperatures.

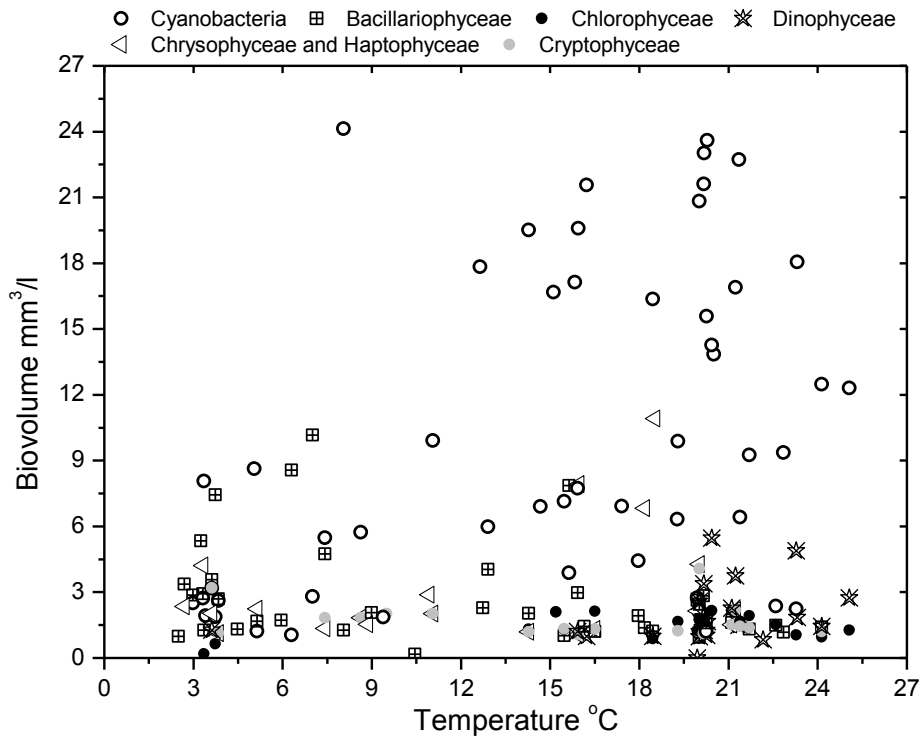


Fig. 4.10: Biovolume of algal groups per sample along the temperature in 4 German polymictic shallow lakes in Brandenburg region. Groups with biovolume $< 1.0 \text{ mm}^3$ and heterotrophic species were excluded.

2) Brazilian lakes

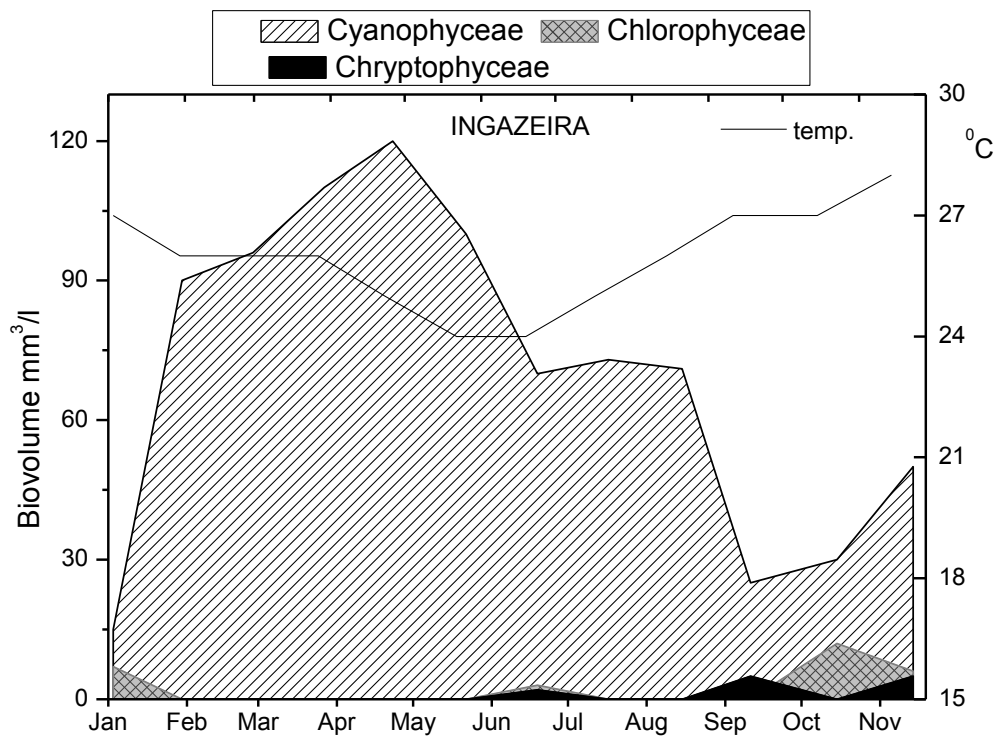
In Ingazeira reservoir, the low water temperature variation (24 to 28 °C) illustrated the typical pattern found in the semi-arid region of Northeast Brazil. According to Bouvy et al. (1999), the Cyanophyceae group had the highest biovolume, with the permanent presence of *Cylindrospermopsis raciborskii* throughout the year, with almost 100% dominance. The largest number of species belonged to Chlorophyceae, mainly represented by *Closterium acutum* and *Oocystis lacustris*, before and after the cyanobacterial bloom. Organisms belonging to Cryptophyceae, Dinophyceae and Bacillariophyceae are not very important members of the phytoplankton community.

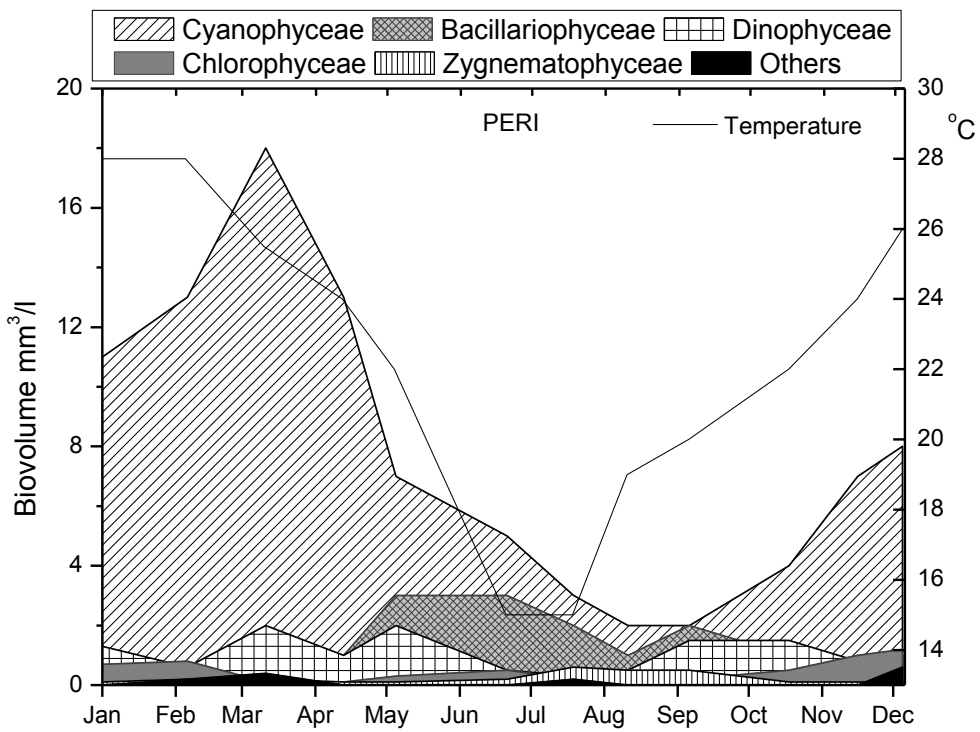
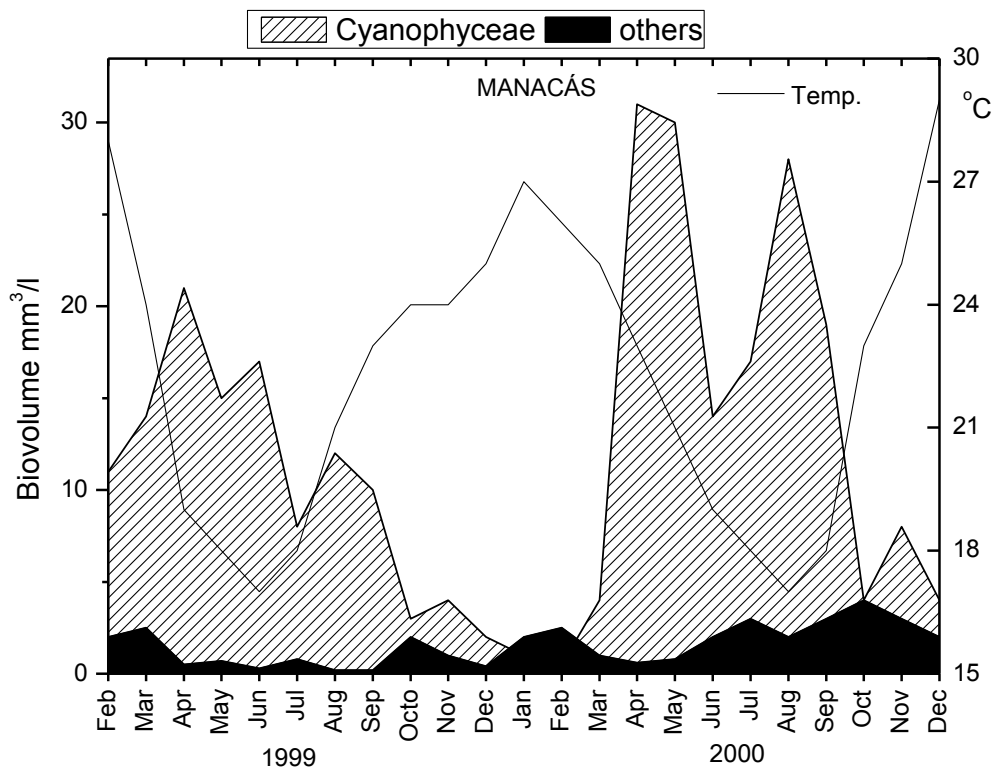
In Manacá lake, the periods of stronger dominance of *Lymnothrix bicudoii* (group S1) consisted of two distinct phases with contribution of annual biomass around 80%. There was one peak per year, noted during colder periods. Other periods with lower biovolume were especially related to water temperature above 20 °C and a stratified water column. An increase in the biomass of other algae, especially the flagellate *Erkenia* sp. (Chrysophyceae) and a

small desmid (*Cosmarium* sp.), was responsible for the biomass portion of other species in Manacás.

The Peri lagoon was strongly dominated by *Cylindrospermopsis raciborskii* throughout the year, more pronounced during the summer. The second place of the cyanobacterial group was occupied during the colder periods by *Pseudanabaena galeata*. Bacillariophyceae was also more abundant during the cold-dry periods, mainly characterized by *Aulacoseira ambigua* (C). Dinophyceae peaked during warmer periods, represented by *Peridiniopsis* sp. during the spring and *Peridinium gatunense* and *P. volzii* at the beginning of the cold period. Chlorophyceae was not relevant to the total biovolume in Peri. The specie *Monoraphidium irregulare* dominated in terms of abundance during the summer and a tenuous presence *Botryococcus* sp. during colder periods was noted.

In Billings reservoir, the group of Cyanophyceae began to increase from September until the summer, well represented by *Microcystis panniformis*, *Microcystis aeruginosa*, and *Planktothrix agardhii*. Chlorophyceae occupied considerably the phytoplankton biomass from March until July (colder periods), mainly represented by *Mougeotia* sp. (see figure 4.11).





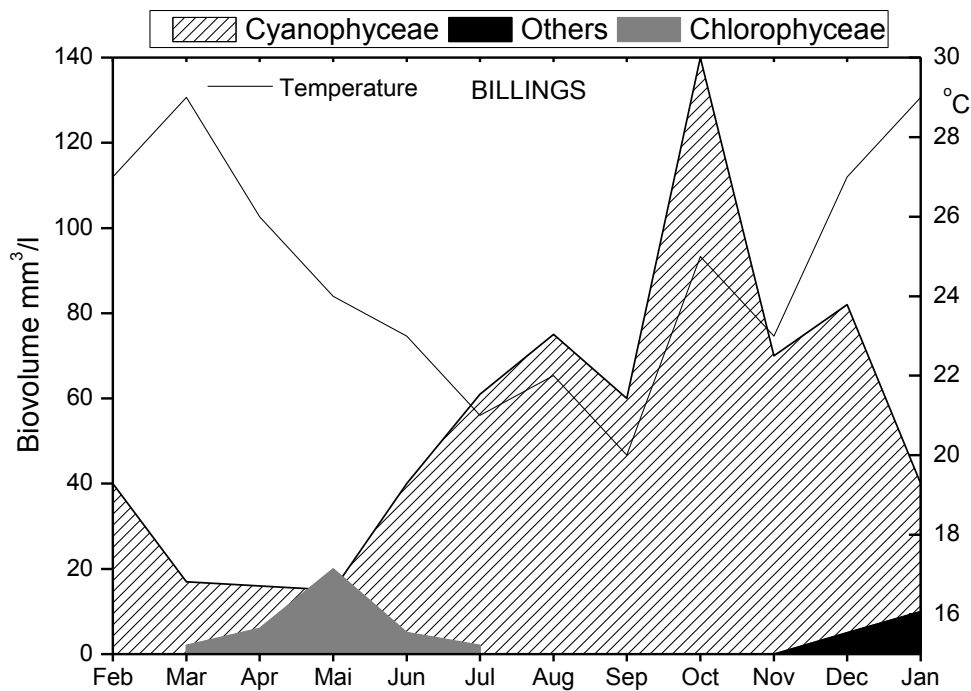


Fig. 4.11: Seasonal variation of algal groups associated to water temperature of 4 studied Brazilian lakes.

The portion of phytoplankton species in terms of biovolume of Brazilian lakes is shown in figure 4.12. Cyanobacteria dominated the phytoplankton community with the permanent presence of the Nostocales specie *Cylindrospermopsis raciborskii* in Ingazeira reservoir. In Peri lagoon, this specie was also the most dominant, and the cyanobacterial group presented a mean of 71% of total biovolume. The Bacillariophyceae *Aulacoseira ambigua* achieved 20% of total biovolume. Other species were mainly represented by *Staurastrum tetracerum*, *Cosmarium bioculatum*, *Peridiniopsis* sp. and *Monoraphidium irregulare*. In Manacá lake, the Oscillatoriales specie *Lymnothrix bicudoii* was the most important component of the phytoplankton, with a mean of 87% of total biovolume. In Billings reservoir, the specie *Planktothrix agardhii* was the most dominant species in terms of biovolume, higher during warmer periods (from September until January), followed by the genus *Microcystis* with 25% (*Microcystis aeruginosa* and *M. panniformis*) and *Cylindrospermopsis raciborskii* with 7%.

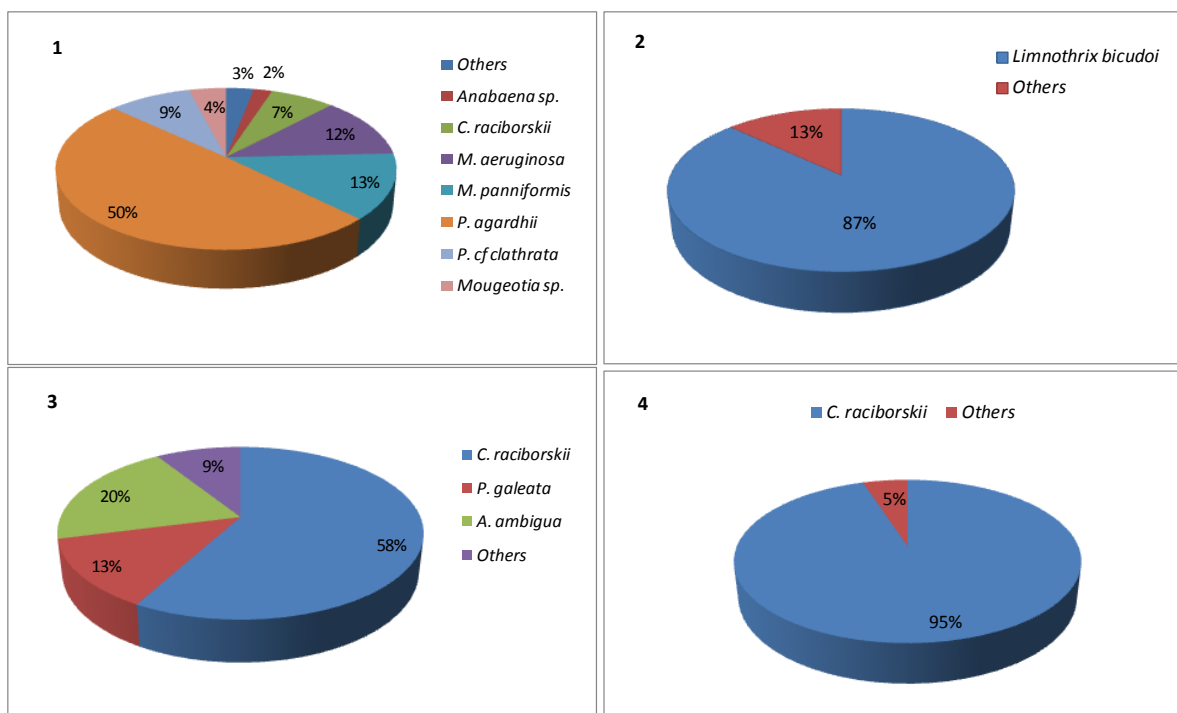


Fig. 4.12: Proportion mean (%) of phytoplankton species in Brazilian lakes in terms of biovolume: 1) in Billings reservoir; 2) Manacás lake (cold-dry period); 3) Peri lagoon; 4) Ingazeira reservoir.

4.6.3 Diversity and its relation with biovolume

Temperate shallow lakes presented higher annual richness, if compared to the tropical ones. The Peri lagoon showed higher diversity during the winter (Shannon Wiener = 2.7 and evenness = 0.66) and the lower during the hot-rainy period with the presence of *C. raciborskii* (Shannon Wiener = 1.2 and evenness = 0.3). Generally, the Shannon Wiener index of the temperate lakes was higher during the spring (LAN = 3.5, PET = 3.4, WOL = 3.3, and MEL = 3.6). Concerning the 4 temperate studied lakes, LAN presented the highest species richness (225) and the WOL the lowest (185). In Ingazeira reservoir, the Shannon Wiener and evenness showed low values, with a mean of 0.33 and 0.28 respectively. A relevant relationship between Shannon Wiener index and algal groups were observed, with negative correlations for Cyanophyceae and positive correlations for Chlorophyceae. In Manacá lake, the Shannon Wiener varied from 0.1 at the massive presence of *Limnothrix bicudoii* to 3.0 (January 2000) when the biomass of *L. bicudoii* was the lowest. Generally, the difference between the richness of the two types of lakes was more pronounced than the mean of diversity indices itself (see table 4.5).

Table 4.5: Annual richness, mean of Shannon-Wiener index and evenness from 5 shallow polymictic lakes in Brandenburg region (PET, LAN, MEL, WOL and Scharmützel See Institut, INS), together with 11 Brazilian lakes. Additional Brazilian data were taken from Souza & Fernandes (2009), Nascimento (2010), Huszar et al. (1998), Loverde-Oliveira & Huszar (2007), Rodrigues (2008), and Cardoso (2009).

Lakes	Richness	Shannon-Wiener	Evenness Shannon
PET	187	2.7	0.7
LAN	223	2.8	0.8
MEL	198	2.7	0.7
WOL	185	2.7	0.6
INS	167	2.8	0.6
Manacás	22	1.1	-
Ingazeira	30	0.3	0.3
Peri	76	2.1	0.5
Billings	68	-	-
Mae-Bá	138	2.7	0.5
Pantanal	20	1.6	-
Imboassica	12	2.2	0.5
Barra lagoon	72	2.4	-
Monte Alegre	118	3.1	-
Jucazinho	47	2.3	0.6
Sapucúa	10	2.2	0.5

As additional data, the relation between biovolume and richness of 5 temperate shallow lakes and 11 Brazilian lakes is illustrated in figure 4.13.

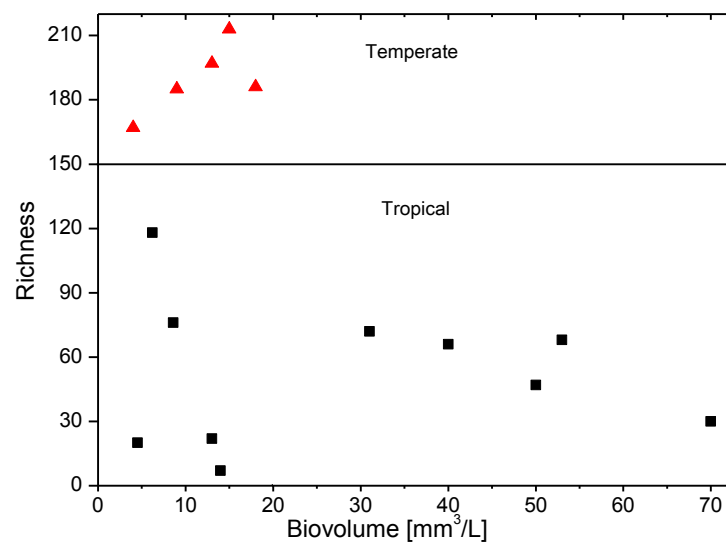


Fig. 4.13: Relation of annual richness and annual mean of biovolume in tropical (below) and temperate (above) shallow lakes ($n=14$). Additional data were taken from Rodrigues

(2008), Huszar et al. (1998), Loverde-Oliveira & Huszar (2007), Dantas et al. (2008); Cardoso (2009), and Nascimento (2010).

The temperate lakes presented higher richness at lower level of productivity (annual mean of biovolume from 9.0 to 18 mm³/l), if compared to tropical lakes. The data of temperate lakes suggested a positive relation between richness and increase of biovolume. In tropical lakes, the richness tended to decrease when biovolume increases. The biovolume and richness in tropical lakes was more variable, if compared to temperate ones.

4.7 Discussion

The group of Cyanophyceae dominated in terms of biovolume in all studied lakes, during the summer in temperate lakes and in tropical lakes during consecutive periods. The S1 specie *Planktothrix agardhii* was well represented in LAN and WOL, with a peak during August (12.4 mm³/l in LAN and 5.0 mm³/l in WOL). This specie was also important in Billings reservoir during the hot-rainy season, associated with high concentration of dissolved inorganic nitrogen by Gemeldo et al. (2009). This nutrient achieved higher concentration in WOL (924 µg/l) and in LAN (339 µg/l). Nascimento (2009) associated the success of *Planktothrix agardhii* with pH around 8.0 and high conductivity. *P. agardhii* seems to be cosmopolitan, with persistent presence in shallow lakes (Chorus & Bartram 1999, Pouličková et al. 2004). Nixdorf et al. (2003) attributed the success of *Planktothrix agardhii* to very shallowness in wind-exposed lakes, with intense sediment water interactions inducing short term nutrient pulses. This specie was often accompanied by *Pseudanabaena limnetica* during the same periods, which had higher peaks during August (LAN = 10.0 mm³/l, Wol = 2.4 mm³/l and PET = 21.0 mm³/l) and during October (LAN = 8.0 mm³/l, WOL = 1.7 mm³/l, PET = 22 mm³/l, and MEL = 2.4 mm³/l). Laudaes Silva (1999) recorded the presence of *Pseudanabaena galeata* in Peri lagoon, especially during colder periods. Other main S1 specie was *Limnothrix redekei*, more common before and after the winter in the German shallow lakes (LAN = 1.5 mm³/l in November, WOL = 0.4 mm³/l in March, PET = 8.0 mm³/l in January, and in MEL = 1.7 mm³/l in February). According to Soares et al. (2009), high biomass of *Limnothrix bicudo* (S1) in Manacás lake was especially related to cold-dry (< 20 °C) and mixing periods, because nutrient availability did not change significantly during the year, and significant correlations between nutrients and *L. bicudo* were not found. The main characteristics distinguishing the periods of highest biomass were lower temperature and the consequent overturn of the water column, from the end of March until September. Low light

availability was also observed, especially during the *L. bicudoi* bloom. The specific abilities of the species, especially photoadaptation (Reynolds et al. 2002), may have contributed considerably to their development. The annual dominance phases of filamentous Oscillatoriales in a German lake have been attributed to light-deficient conditions caused by high shading effects, induced by high biomass, suppressing other phytoplankton associations (Mischke and Nixdorf 2003).

The important group S_N, typical in warm mixed layers, was well represented by the N-fixing specie *Cylindrospermopsis raciborskii*, which dominated massively in Ingazeira Reservoir during all periods of the year and in Peri coastal lagoon, principally during the summer. According to Bouvy et al. (1999), favorable temperature conditions occurred in Ingazeira reservoir during the survey, with values always higher than 24°C, and no thermal stratification of the water column during consecutive periods were observed at dominance of *C. raciborskii*. This Nostocales specie achieved considerable biovolume in the German shallow lakes only during the summer at temperature greater than 20 °C (1.0 mm³/l in LAN, 2.5 mm³/l in PET, and 1.2 mm³/l in MEL during July). *C. raciborskii* population grows and increases only in warm (> 25°C) water. Consequently, it can maintain large populations in permanently warm water, and more restrict during summer periods towards higher latitudes (Padisák 1997). *C. raciborskii* represents good indication related to global warming and climate change, which may be explained by its expansion in temperate latitudes (Briand et al. 2004, Wiedner et al. 2007). *C. raciborskii* blooms appear to be controlled by water temperature and not by nutrients (Hamilton et al. 2005), achieving high population under high and low nutrient concentrations. Présing et al. (1996) reported blooms under very low SRP (4.0 µg/l), as well as taking up phosphorus at low concentrations (Shafik et al. 2001). Concomitantly, increase this specie has been observed under excessive nutrient conditions, for example in the case which occurs eutrophication. Azevedo et al. (1994) reported the increase of *C. raciborskii* blooms close to urban regions, where the nutrient input of organic material originating from drains and chemical products are more accentuated. Additionally, its success in Peri was associated to the ability to store phosphorus and possible grazing rejection by zooplankton (Laudares Silva 1999). *C. raciborskii* is responsive to meteorological conditions, as stronger winds and thunderstorms (Padisák 1997). It was confirmed in Peri lagoon, where *C. raciborskii* was more present during higher precipitation. Is not clear if *C. raciborskii* is greatly influenced by stratification regime or not. Studies as of Padisák (1997), suggested the positive relation between stratification and dominance of *C. raciborskii*, since this species has

the capacity to buoyancy regulation. Moreover, this specie is a strong competitor for light in destratified lakes (Antenucci et al. 2005) and artificially mixed reservoirs (Burford et al. 2006). Poor light underwater conditions due to the lack of precipitation from August 1997 and the high evaporation rate in Northeast Brazil, favored eutrophic status and represented for them ecologically good conditions (Bouvy et al. 1999). Well-mixed waters seemed to be favorable to the colonization of *C. raciborskii* in Peri lagoon and in Ingazeira reservoir. High pH values (> 8.0) may facilitate the occurrence of *C. raciborskii* (Padisák 1997), which was confirmed in the temperate lakes. Conversely, this specie has also been dominated under lower pH in Peri (pH < 7), and under large pH range between 6.8 and 9.4 during the bloom in Brazilian lakes (Bouvy et al. 1999). *C. raciborskii* was also dominant at large range of conductivity in Ingazeira reservoir (70 to 1700 $\mu\text{S}/\text{cm}$).

The toxic Nostocales more common in Brazilian waters is mainly represented by the genera *Anabaena*, *Aphanizomenon* and *Cylindrospermopsis* (Azevedo et al. 2002, Huszar et al. 2000). *Aphanizomenon flos-aquae* and *A. gracile* were the most abundant Nostocales in Northeast Germany, but few specific studies on the ecology of this genus are published (Stüken et al. 2006). In the present study, *A. gracile* were more related to summer periods (2.5 mm^3/l in PET, and 4.5 mm^3/l in MEL during August), but maintained its population until November. *Aphanizomenon issatschenkoi* and *Aphanizomenon flos-aquae* decreased its population earlier than *A. gracile*, showing an adaptative divergence between these species of the same genus. *A. gracile* seems to be most resistant to temperature decrease, which shows to persist until the end of autumn.

According to Sant'Anna and Azevedo (2000), records showed the occurrence of at least 20 species of cyanobacteria including 14 genera, with a toxic potential in several Brazilian aquatic ecosystems. Moreover, species of *Microcystis aeruginosa* represent the largest distribution in Brazil and *Anabaena* is the genus with the most number of species potentially toxics (*A. circinalis*, *A. flos-aquae*, *A. planctonica*, *A. solitaria*, *A. spiroides*). This observation was confirmed in Billings reservoir through the presence of *Microcystis panniformis*, *M. aeruginosa* and *Anabaena* sp. The genus *Anabaena* was found during the late summer in WOL (August), represented by *Anabaena flos-aquae* (3.6 mm^3/l), *A. solitaria* (2.0 mm^3/l), *A. circinales* (0.8 mm^3/l), and *A. macrospora* (5.0 mm^3/l) was also found in MEL during July, confirming that this specie is more abundant under higher temperatures.

The group of Bacillariophyceae was well represented by the genus *Aulacoseira* in temperate lakes like *A. granulata* (P) in WOL, PET, and MEL, as well as in Peri by *A. ambigua* (C), both typical in mixed small-medium lakes. *Aulacoseira granulata* is the most adapted species found in tropical not stratified lakes (Reynolds 1999). *Cyclotella radiosa* (A), *Stephanodiscus* sp. (D), *Fragilaria ulna* and *Asterionella formosa* (C) were more common during colder periods in temperate lakes. *Stephanodiscus hantzschii* and *Nitzschia* sp. (D), sensitive under low nutrients concentration, were more pronounced under lower temperatures. High temperatures may explain the low diversity of Bacillariophyceae observed in tropical lakes.

Although the group of Chlorophyceae in LAN, WOL and PET presented low biovolume, the richness of this group was high, mainly during the spring and summer in temperate lakes and in tropical lakes during consecutive periods. *Oocystis* sp. was common during the spring in WOL (1.6 mm³/l) and PET (0.3 mm³/l). The largest number of species belonged to Chlorophyceae, mostly represented by *Closterium acutum* and *Oocystis lacustris*, were found before and after the cyanobacterial bloom in Ingazeira reservoir. The genus *Oocystis* is widespread around the world, with high species number in Brazilian lakes (Nogueira & Oliveira 2009).

The group Lo is adapted to survive under low concentration of dissolved nutrients and higher temperatures (Reynolds 2002). The biovolume and diversity of the genus *Peridinium* were more pronounced during warmer periods, with special attention to *Peridinium willei* (4.0 mm³/l) in MEL. The highest biovolume of *P. umbonatum* occurred at the beginning of the rainy season and the lowest during dry months under nutrient poor conditions in a Brazilian small-size lake (Gomes et al. 2010). The species *Gymnodinium lantzschii* was most abundant during colder periods, in October and March in LAN and WOL.

Longer periods dominated by cyanobacteria in tropical regions may be influenced the negative relation between richness and biovolume. The richness in temperate shallow lakes was much higher than in tropical lakes. The difference of species number between the both types of lakes was more pronounced than the diversity indices. In relation to seasonality in tropical lakes, the influence of local factors may play an important role (use of catchment area, type of sediment, input of nutrients), since the difference in terms of biovolume and richness between the tropical lakes was very large. The temperate studied lakes were more similar to each other in terms of seasonality, richness and biovolume values. Niche differentiation based on environmental conditions may explain the difference of diversity in tropical and temperate lakes. A close relationship between temperature changes and dynamic

of phytoplankton species was observed in this study. In a varying environment, each species is sometimes a better competitor and they can coexist. Global climate changes may influence phytoplankton community dynamics and drive modifications its diversity, with the example of a warming affecting the frequency of the *C. raciborskii* blooms.

4.6 References

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Chapter

5

5 Conclusions

Higher adaptability by few phytoplankton species to convert phosphorus into biomass under selective conditions seemed to be a more important factor to explain the occurrence steady states. At low disturbance status (permanent circulation), phytoplankton community may in this case present a non-successional change, since disturbances didn't change significantly the species composition. Steady state conditions are more probable and longer lasting in tropical regions. Constant mixing events, representing disturbances in the sense of Connell (1978) were here not sufficient to interrupt the species dominance and the steady state. Low level of biodiversity allows an ecosystem to function effectively under constant conditions. This situation leads commonly to steady state, mainly under high productivity and low diversity. In opposite of temperate lakes, the study in Peri lagoon does not support models, which associate greater diversity with greater primary productivity under utilization of limiting resources (Tilman 1999). Generally, lower variation of abiotic conditions may sustain the phytoplankton biomass status in tropical lakes. Mixing and temperature determined dominance of cyanobacterial species in tropical lakes, with the example of *L. bicudo* at lower temperatures and *C. raciborskii* at higher temperatures. In temperate lakes, equilibria occurred in clear-water phases (dominated by chrysophytes), during winter stagnation (species selected by tolerance of stress conditions under low temperature, low light), and most prominently during the summer, when the period allows the development of competitively stronger species. The variation of productivity as RUE is useful to determine the temporal composition of phytoplankton groups and its diversity, as well as the tendency of non-equilibrium/steady state conditions. The cell proportion as additional measurement is valuable, since it may influence the diversity indices and gives signs about which type of specie is present in the course of succession.

The biovolume and richness in tropical lakes was more variable than in temperate lakes, which presented higher richness at intermediate level of biovolume. The question, if the mean of annual productivity in tropical lakes is equivalent or superior to temperate lakes is here suggested. The same species and its functional groups tended to occur under similar abiotic condition, with strong presence of local factors and little endemism in tropical latitudes. There is no causal dependence of biodiversity on productivity in tropical lakes. The results showed no direct correspondence between the diversity and biovolume, suggesting that primary production is not proportionally linked to diversity in tropical lakes.

Niche differentiation based on changes in temperature seems to avoid competition processes, since the phytoplankton species occurs during shorter periods, supporting the non-equilibrium concept. It occurs mainly at transitional states and supports high diversity, which may explain the higher diversity found in temperate lakes. Global climate changes can influence phytoplankton population dynamics in continental waters and drive modifications in the dynamics of with the example of a warming affecting the frequency of the *C. raciborskii* blooms. Since assessing the ecosystem-level consequences of species loss has just begun in aquatic systems, more studies are necessary to characterize the relationships between diversity, particular functional groups, and various ecosystem functions in these ecosystems, with special attention to very shallow lakes. We suggest the seasonal succession as driver of productivity, as well the productivity as consequence of species richness, concerning the temporal variation of phytoplankton. It suggests that ecosystem properties depend greatly on biodiversity. While biodiversity experiments are not intended to provide justification for protecting particular species or ecosystems, they are important to conservation because they provide information needed to protect and maintain viable communities.