Recent and fossil phytoplankton pigments in Lake Baikal as markers for community structure and environmental changes

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ABSTRACT (ENGLISH)

Lake Baikal is the World´s oldest, deepest and largest (by volume) lake and contains many endemic species. Since 1996, after becoming a UNESCO World Heritage Area, the effects of global warming and local anthropogenic eutrophication on its unique ecosystem become a subject of international discussion. Recent and fossil phytoplankton pigments are being increasingly used to monitor recent and past changes of the phytoplankton composition and productivity that indicate changes of climatic and other environmental conditions in marine and freshwater systems. However, phytoplankton pigments were not yet investigated in the water column of Lake Baikal and only little in its sediment. The objective of this thesis was to assess whether and to which extent phytoplankton pigments of the water column and sediments in Lake Baikal can indicate recent and past phytoplankton community structure changes as well as climatic and other environmental changes.

The first task was to assess the phytoplankton pigment distribution in the water column. A three year-long intense phytoplankton monitoring programme was carried out from 2001 to 2003 as part of the EU-funded CONTINENT project in conjunction with a much longer-term monitoring programme (over 60 years) by the Irkutsk State University. HPLC-aided pigment analyses were combined with microscopic counts. Significant changes of the total chlorophyll *a* (ubiquitous in phytoplankton) as well as of characteristic marker pigments were found between near-shore regions, river inflow sites and open basins. The marker pigments allowed estimating phytoplankton chemotaxonomic group composition at all investigated sites. In situ fluorescence horizontal and depth profiles and satellite image analyses complemented the pigment-based monitoring. Canonical correlation analyses indicated a major influence of temperature and stratification on the phytoplankton composition even for the regional distribution. Phytoplankton pigments were shown to be useful proxies to determine the recent phytoplankton assemblage and its variations induced by environmental changes.

The second aim of this thesis was to determine the pigment flux through the water column and how the main phytoplankton groups were represented in the deposited material. It was assumed that strong degradation by grazing and oxidation affects the phytoplankton pigments during their sedimentation. In contrast to most other deep lakes, Lake Baikal is oxygen saturated throughout the water column even within the water-sediment interface. To study the pigment flux to the surface sediment, sediment traps were moored in the South and North basins. Heavy, non-edible Bacillariophyceae formed the main contribution to the settling material. Strong degradation processes controlled the sedimentation of small, light and edible phytoplankton. In the South, these processes took place within the upper 300 m of the water column (two-exponential

regression models). In the North, strong degradation occurred down to the lake bottom (linear regression models). The pigment loss during settling through the water column was much higher in the North than in the South. Further strong degradation occurred within the oxidised surface sediment. The degradation was strongest in the North and lowest at the river inflows. The sedimentation out of the euphotic zone can be projected backward using regression models given in the present thesis.

A third task of this thesis was to examine whether phytoplankton pigments can be used to assess the phytoplankton response to natural climate changes in the pristine lake. To this end, the sedimentary phytoplankton pigments were analysed in cores covering the Holocene (last 10,000 years). The cores were taken from three main regions of Lake Baikal: South, North and Selenga Delta. Differential sequences were found for these regions with significantly the lowest chlorophyll *a* versus organic carbon ratios (indicating lowest production), but highest variability with time (indicating strongest climatic oscillations) in the North. Highest phytoplankton production was found during the early Holocene at approximately 9 kyr BP at the time of climate amelioration following the Younger Dryas (Boreal). Short phytoplankton production maxima occurred also during the late Atlantic and at the Subboreal/Subatlantic transition. Chlorophyll *b* plus its degradation products provided important additional information on the past development of Chlorophyceae, but most other sedimentary phytoplankton pigments were found to be unsuitable to determine past phytoplankton community structures in Lake Baikal, because their degradation products could not be definitely related to the parent pigments. Furthermore, the sedimentary pigment and organic carbon sequence of the Kazantsevo Interglacial (European Eemian, Marine Isotopic Stage 5e) was investigated. Higher production indicating warming at the time of the Kazantsevo was found when compared to the glacial periods. Strong climate oscillations occurred during the Kazantsevo and phytoplankton abundance was halved or doubled within centennial time scales. Sedimentary chlorophyll *a* in Lake Baikal was shown to be a reliable indicator of phytoplantonic response to published climate changes and may serve for validation of future climate models in continental regions.

Taken together, pigment-based analyses were shown to accurately reflect phytoplankton variation caused by environmental changes of natural or human origin in Lake Baikal. In conjunction with the EU project CONTINENT and the long-term monitoring in Irkutsk, the phytoplankton development determined from the last interglacial up until the early 21st century will be used for future research of climate changes as well as for the Lake Baikal's protection.

ZUSAMMENFASSUNG (DEUTSCH)

Der Baikalsee ist der älteste, tiefste und größte (gemessen am Volumen) See der Welt, mit vielen endemischen Arten. Er wurde 1996 zum UNESCO Weltnaturerbe deklariert. Doch auch dieses einzigartige Ökosystem könnte in Zukunft durch anthropogen bedingte Klimaänderungen und Nährstoff-Einträge gefährdet sein. Rezente und fossile Phytoplankton-Pigmente werden immer häufiger in Monitorings genutzt, um aktuelle und historische Änderungen der Phytoplankton-Produktivität und –Zusammensetzung zu bestimmen, welche Änderungen von klimatischen und anderen Umweltbedingungen anzeigen. Dennoch wurden im Baikal bislang keine rezenten und nur in wenigen Studien fossile Phytoplankton-Pigmente untersucht. Daher sollte geprüft werden, ob Phytoplankton-Pigmente im Wasser und Sediment des Baikals herangezogen werden können, um rezente und historische Änderungen der Phytoplankton-Gemeinschaft sowie von klimatischen und anderen Umweltbedingungen zu bestimmen.

Zunächst wurde die Phytoplankton-Pigment Verteilung in der Wassersäule bestimmt. Von 2001 bis 2003 wurde im Rahmen des CONTINENT Projektes und des Langzeit-Monitorings der Staatlichen Universität Irkutsk (Rußland) ein intensives Phytoplankton-Monitoring-Programm durchgeführt. Signifikante Änderungen des Chlorophylls *a* (welches allen Phytoplanktern gemein ist) und charakteristischer, gruppenspezifischer Pigmente wurden zwischen allen untersuchten Gebieten (2 Flussmündungen, 3 offene Becken) gefunden. Anhand der Marker-Pigmente konnte die Zusammensetzung der Phytoplankton-Gemeinschaft bestimmt werden. Der Eindruck der extremen Heterogenität der Phytoplankton-Abundanz und -Zusammensetzung, welcher in diesem Ausmaß einzigartig für einen See ist, wurde durch Fluoreszenz-Profile und Satelliten-Bild-Auswertung verstärkt. Temperatur und Schichtung waren von besonderer Bedeutung für die saisonale, aber auch regionale Entwicklung des Phytoplanktons. Es konnte gezeigt werden, dass Phytoplankton Pigmente als verlässliche Indikatoren angesehen werden können, um die rezenten Änderungen der Phytoplankton-Abundanz und -Zusammensetzung sowie den Einfluss von Umweltvariablen im Baikal zu bestimmen.

Des Weiteren wurden die Sedimentation und Degradierung der Phytoplankton-Pigmente im Wasser bestimmt. Es wurde angenommen, dass die Pigmente während ihrer Sedimentation über die bis zu 1,6 km tiefe, durchgehend oxische Wassersäule starken Degradierungs-Prozessen unterlagen. Analysen von Sedimentfallen-Material aus dem Nord- und Südbecken ergaben, dass sich im Baikal das sedimentierende Material v.a. aus schweren, nicht-fressbaren Kieselalgen zusammensetzte. Die Sedimentation der kleinen, leichten und fressbaren Phytoplankter wurde durch variable Degradierungs-Prozesse kontrolliert. Im Südbecken erfolgten diese Prozesse (Zooplanktonfraß und Oxidation)

v.a. innerhalb der obersten 300 m der Wassersäule, der winddurchmischten Schicht im Baikal. Im Norden erfolgte starke Degradierung bis zum Seeboden in 900 m Wassertiefe. Eine weitere Degradierung erfolgte im oxidierten Oberflächen-Sediment. Die Pigment-Sedimentation kann in retrospektiven Analysen fossiler Pigmente anhand der hier dargelegten Regressions-Modelle berechnet werden.

Zuletzt wurde bestimmt, ob Phytoplankton-Pigmente genutzt werden können, um historische klimabedingte Änderungen des Phytoplanktons im Baikal zu rekonstruieren. Hierfür wurden die Änderungen der fossilen Pigmente während des Holozäns (seit ca. 10.000 Jahren) in drei Regionen des Baikals untersucht: Südbecken, Nordbecken und Selenga Delta. Im Norden wurde das niedrigste mittlere Verhältnis von Chlorophyll *a* pro organischen Kohlenstoff (welches niedrige Produktion andeutet) gefunden, aber die höchste Variabilität mit der Zeit (welche ausgeprägte Klima-Oszillationen andeutet). Höchste Produktion wurde während des frühen Holozäns (vor ca. 9000 Jahren) nach dem Gletscher-Rückzug bestimmt. Chlorophyll *b* (inklusive Degradierungsprodukte) lieferte wichtige Informationen zu Änderungen der Chlorophyta (Grünalgen), während die meisten anderen fossilen Pigmente nicht geeignet waren, historische Änderungen der Phytoplankton-Gemeinschaft zu erfassen, da die Degradierungsprodukte dieser Pigmente nicht definitiv ihren Ausgangs-Pigmenten zugeordnet werden konnten. Die fossilen Pigmente wurden des Weiteren während der letzten Warmzeit (Kazantsevo, beginnend vor ca. 129.000 Jahren) untersucht. Ausgeprägte Klima-Oszillationen erfolgten während des Kazantsevos, wobei die Phytoplankton-Produktion sich innerhalb weniger hundert Jahre halbierte oder verdoppelte. Fossiles Chlorophyll *a* ist daher ein geeigneter Indikator für die klimabedingte Änderung der Phytoplankton-Produktion im Baikal.

Schlussfolgernd läßt sich sagen, dass Pigment-basierte Analysen im Baikal verlässliche Aussagen über rezente und historische Phytoplankton-Variationen ermöglichen, welche durch Umwelteinflüsse (natürlichen oder menschlichen Ursprungs) induziert werden. Im Rahmen des EU-Projekts CONTINENT und des Langzeit-Monitorings der Staatlichen Universität Irkutsk werden die Ergebnisse zur Phytoplankton-Entwicklung seit der letzten Warmzeit bis zum Beginn des 21. Jahrhunderts den lokalen Naturschutz und globale Klimastudien unterstützen.

ABSTRACT (RUSSIAN)

Основной целью диссертационной работы являлась проверка возможности использования данных о пигментном составе фитопланктона в водном столбе и в осадках оз. Байкал для оценки характера структурных изменений в сообществах фитопланктона, а также их связи с климатическими и другие изменения характеристик окружающей среды, происходящих в недавнем прошлом.

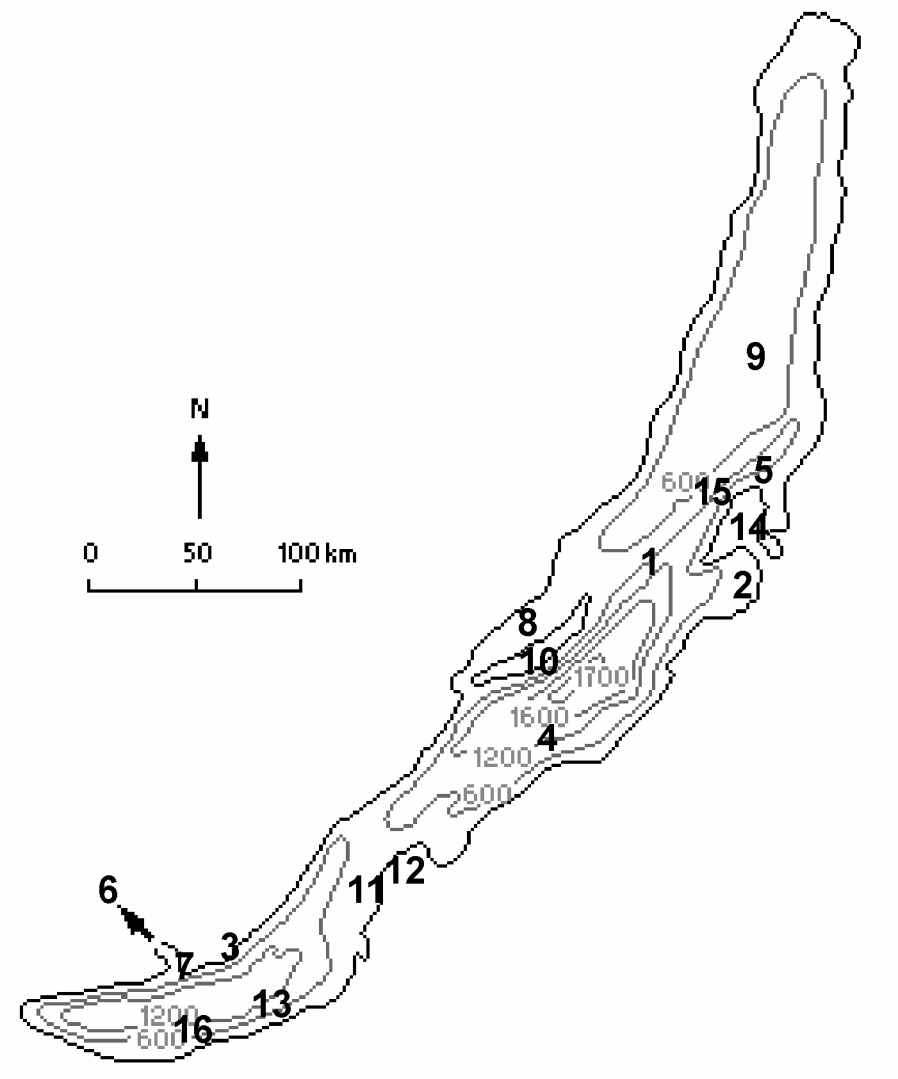
В течение трехлетнего периода (2001-2003 гг.) была проведена программа интенсивного мониторинга фитопланктонных сообществ на Байкале. Проводимые исследования являлись частью проекта "КОНТИНЕНТ" финансируемого ЕС. Мониторинг был проведен в связке с программой длительной многолетней мониторинговой программы (более 60 лет) проводимой Научно-исследовательским институтом биологии при Иркутском Государственном Университете. В ходе работы современные методы анализа пигментов с использованием высокоэффективной жидкостной хроматографии были скомбинированы с традиционным микроскопическим подсчетом, флюометрией и дистанционным зондированием. Данный комплексный подход, базирующийся на пигментной оценке, зарекомендовал себя в качестве наиболее подходящего метода при мониторинге временных и сезонных изменений численности и структуры фитопланктонных сообществ, и их связи с характеристиками среды. Анализ пигментов из осадочных ловушек показал, что длительные пигмент-зависимые процессы разложения регулируют осаждение пигментов через всю толщу воды. Дальнейшее и наиболее сильное разложение связано с окисленными поверхностными осадками. Процессы седиментации за пределами эвтрофической зоны могут быть описаны с помощью регрессионной модели, представленной автором в данной диссертационной работе.Дополнительно к пигментам из фитопланктонных осадков были проанализированы Голоценовые слои (последние 10,000 лет), взятые из Южного и Северного районов Байкала, а также из дельты реки Селенга. Также были проанализированы осадковые слои, относящиеся к последнему ледниковому периоду (р-н Казанцево).

Хлорофил а из осадков, проявивший себя как наиболее подходящий индикатор, отражающий реакции фитопланктонных сообществ на известные климатические изменения, предложен для использования при дальнейшей оценке и построении климатических моделей континентальных регионов. Обобщенные результаты пигментного анализа показали изменения структур фитопланктонных сообществ на Байкале, вызванные причинами естественной или антропогенной природы.

LIST OF FREQUENTLY USED ABBREVIATIONS

APP	Autotrophic Picoplankton
BP	Before Present
CCA	Canonical Correlation Analysis
Chl*a*	Chlorophyll *a*
Chl*a*s	Chlorophyll *a* plus its degradation products (chlorophyllide, pheophorbide, pyropheophorbide, pheophytin, and pyropheophytin; plus steryl chlorin esters in the interglacial core segement)
Chl*b*	Chlorophyll *b*
Chl*b*s	Chlorophyll *b* plus its degradation products (same as for ´Chl*a*s´)
Chl*c*	Chlorophyll *c*
CI	Confidence Interval
DM	Dry Matter
HPLC	High Performance Liquid Chromatography
SCE	Steryl Chlorin Ester
TOC	Total Organic Carbon
TN	Total Nitrogen
vs.	versus
yrs	years

LIST OF THE REGIONS MENTIONED IN THIS THESIS



1 - Academician Ridge
2 - Barguzin Bay
3 - Bolshye Koti
4 - Central basin
5 - Continent Ridge
6 - Irkutsk
7 - Listvianka (harbour)
8 - Maloe More
9 - North basin
10 - Olkhon Island
11 - Posolski Bank
12 - Selenga Delta
13 - South basin
14 - Svyatoi Nos Peninsula
15 - Ushkanin Islands
16 - Vidrino Shoulder

PREFACE

This thesis is based on the following articles:

Recent phytoplankton pigments:

- S. **FIETZ** and Nicklisch A. 2004. An HPLC analysis of the summer phytoplankton assemblage in Lake Baikal. *Freshwater Biology* 49, 332-345.
  → Appendix A

- S. **FIETZ**, Bleiß W, Hepperle D, Koppitz H, Krienitz L, and Nicklisch A. (awaiting editor's decisions after revision). First record of *Nannochloropsis limnetica* (Eustigmatophyceae) in the autotrophic picoplankton of Lake Baikal. *Journal of Phycology*.
  → Appendix B

- S. **FIETZ**, Kobanova G, Izmest'eva LR, and Nicklisch A. (in review). Recent spatial and seasonal phytoplankton and photosynthetic pigment distribution in Lake Baikal. *Journal of Plankton Research*
  → Main text

- B. HEIM, Oberhänsli H, **Fietz** S, and Kaufmann H. 2005. Variation in Lake Baikal´s phytoplankton distribution and fluvial input assessed by SeaWiFs Satellite Data. *Global and Planetary Change*, in press (online available).
  → Discussion

- V. STRAŠKRÁBOVÁ, Izmest'yeva LR, Maksimova EA, **Fietz** S, Nedoma J, Borovec J, Kobanova GI, Shchetinina EV, and Pislegina EV. 2005. Primary production and microbial activity in the euphotic zone of Lake Baikal (Southern Basin) during late winter. *Global and Planetary Change*, in press (online available).
  → Discussion

Transfer through the water column and preservation in the surface sediment:

- S. **FIETZ**, Sturm M, and Nicklisch A. 2005. Flux of lipophilic photosynthetic pigments to the surface sediments of Lake Baikal. *Global and Planetary Change*, in press (online available).
  → Main text

- S. **FIETZ**, Sturm M, Müller B, and Nicklisch A. (in preparation). Phytoplankton pigment sedimentation through the water column and preservation in the surface sediment in open basins and river inflow sites of Lake Baikal.
  → Main text

Fossil phytoplankton pigments:

- S. **FIETZ,** Nicklisch A., and Oberhänsli H. (submitted). High-resolution analysis of photosynthetic pigments and organic carbon during Holocene and last Interglacial (Kazantsevo) in Lake Baikal. *Journal of Paleolimnology*
  → Main text

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1 INTRODUCTION

1.1 Phytoplankton pigments as markers for community structure and environmental changes

Recent phytoplankton pigments as markers for community structure: Phytoplankton pigments capture solar energy, mediate its conversion to chemical energy, and ultimately control primary production by regulating the supply of organic carbon to the pelagic food web (cf. Fig. 1). In contrast to higher plants, which all contain a rather similar pigmentation, algae and cyanobacteria have group-specific pigment compositions (Tab. 1). All algae and cyanobacteria contain chlorophyll *a* (Chl*a*), however other chlorophylls and most of the carotenoids are found in only some taxonomic groups (Tab. 1), thus making them ideal marker pigments. Such marker pigments can be used to quantify the potential contribution of different chemotaxonomic groups making up the phytoplankton community (Weber and Wettern 1981, Gieskes et al. 1988, Everitt et al. 1990, Wilhelm et al. 1991, Mackey et al. 1996, Wright et al. 1996, and others). For instance, lutein is often used as marker pigment for Chlorophyta (´green algae´), alloxanthin for Cryptophyta, fucoxanthin for Bacillariophyceae (´diatoms´) and Chrysophyceae, and zeaxanthin for cyanobacterial picoplankton (cf. Tab. 1).

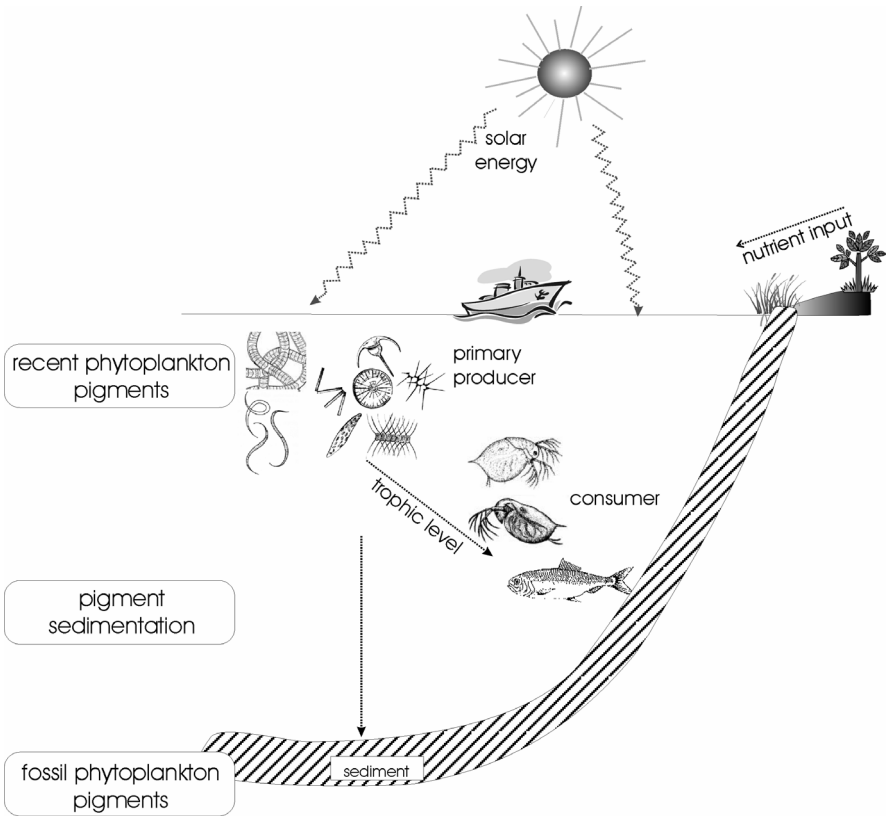

Fig. 1. Phytoplankton pigment production in relation to energy capture, grazing, sedimentation, and burial.

Tab. 1. Overview of phytoplankton classes and higher plants along with selected photosynthetic pigments indicating the much greater pigment composition variability in phytoplankton compared to higher plants (after Kohl and Nicklisch 1988, Leavitt et al. 1993, Mackey et al. 1996).

	chlorophylls			carotenes		xanthophylls						
	a	*b*	*c*	α	β	alloxanthin	diadinoxanth..	fucoxanthin	lutein	peridinin	violaxanthin	zeaxanthin
Higher plants	x	x	-	-	x	-	-	-	x	-	x	(x)
Cyanobacteria	x	-	-	-	x	-	-	-	-	-	-	x
Chlorophyceae	x	x	-	-	x	-	-	-	x	-	x	(x)
Bacillariophyceae	x	-	x	-	x	-	x	x	-	-	-	-
Chrysophyceae	x	-	x	-	x	-	x	x	-	-	-	-
Pyrrophyceae	x	-	-	-	x	-	-	-	-	x	-	-
Cryptophyta	x	-	-	x	x	x	-	-	-	-	-	-
Eustigmatophyceae	x	-	-	-	x	-	-	-	-	-	x	-

High Performance Liquid Chromatography (HPLC) is central to the study of phytoplankton pigments, since it allows semi-automated and rapid analysis of lipophilic photosynthetic pigments (Gieskes et al. 1988, Wilhelm et al. 1991, Millie et al. 1993, Jeffrey et al. 1997, -1999). Using HPLC the separation and quantification of all chlorophylls and carotenoids as well as their degradation products can be performed, even at extremely low concentration levels. Phycobilins (phycoerythrin and phycocyanin), however, which occur in cyanobacteria mainly, cannot be detected together with chlorophylls and carotenoids using HPLC due to their water-soluble nature.

The contribution of specific phytoplankton groups to the total phytoplankton community have been estimated for marine systems (Gieskes et al. 1988, Everitt et al. 1990, Letelier et al. 1993, Andersen et al. 1996, Bidigare and Ondrusek 1996, Wright et al. 1996, Latasa et al. 1997, Jeffrey et al. 1997, Rodriguez et al. 2002) and freshwater bodies (Wilhelm et al. 1991, Lami et al. 1992, Soma et al. 1993, -1995, Quiblier et al. 1994, Descy and Métens 1996, Woitke et al. 1996) based on marker pigment analyses using HPLC. In the case of marine systems, Jeffrey et al. (1999) suggested that a HPLC-aided pigment study should be complemented by underway fluorometry and remote sensing that allow *in situ* and large-scale monitoring (Fig. 2). However, although standardisations and software program for the use of pigments in regular monitorings have been developed for marine systems (Mackey et al. 1996, Jeffrey et al. 1997, -1999), this is not yet the case for freshwater systems.

The advantages of a pigment-based monitoring compared to a microscopic count-based approach are three-fold: (1) it is much less time consuming, and therefore, a larger

sample set may be analysed, which is particularly important in large lakes or marine systems; (2) it can also detect picophytoplankton and fragile cells that may be missed using the microscopic counting approach (Gieskes and Kraay 1983, Everitt et al. 1990, Millie et al. 1993); and (3) Chl*a* is closely related to primary production (Gervais and Behrendt 2003), and in comparison to biovolume, Chl*a* is the better parameter to allow primary production estimation because it indicates the photosynthetically active phytoplankton (Wilhelm et al. 1995).

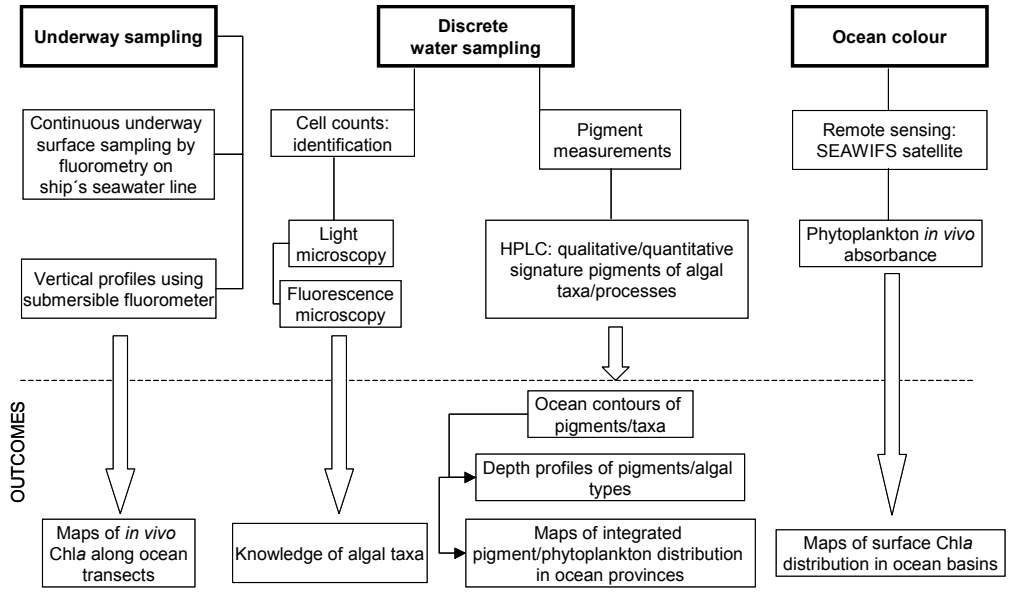

Fig. 2. Methods used for investigating phytoplankton and their pigments in marine systems; adapted from Jeffrey et al. (1999).

Recent phytoplankton pigments as markers for environmental changes: Different phytoplankton groups have distinct environmental preferences, e.g. light, nutrient and temperature requirements, which affect their growth. Thus, marker pigments that allow the phytoplankton composition to be estimated thereby help to monitor environmental changes. In an early study, Chl*a* and marker pigments were successfully used to monitor the phytoplankton response to environmental changes by monsoon-induced upwelling or downwelling in the Indonesian Sea (Gieskes et al. 1988). In other studies, Chl*a* and marker pigments were also successfully used to study the development and composition of phytoplankton forming deep chlorophyll maximum layers in the North Pacific gyre (Letelier et al. 1993) or blooms in the North Atlantic (Barlow et al. 1993). Furthermore, marker pigments were also analysed in conjunction with physical, chemical and nutrient measurements, in order to describe how El Niño conditions affect phytoplankton populations in the central equatorial Pacific (Bidigare and Ondrusek 1996, Latasa et al. 1997). Phytoplankton pigment distribution was used to document the trophic conditions

from coastal to open basin regions of the Mediterranean (Barlow et al. 1997) and in various German lakes (Wilhelm et al. 1995), as well as to describe climate and catchment-related conditions in Canadian shallow mountain lakes and ponds (Vinebrooke and Leavitt 1999). Thus, phytoplankton pigment composition is taken as a measure of the response of phytoplankton to environmental changes in various marine and freshwater systems, and hence is nowadays regularly monitored.

Fossil phytoplankton pigments as markers for community structure and environmental changes: Reconstructions of long-term climatic and other environmental changes have been based on several different biogenic proxies such as pollen, macrofossils, diatom valves, stable isotopes, biomarkers and lipophilic photosynthetic pigments that are preserved in the sediments (cf. Smol et al. 2001). Thereby, the use of photosynthetic pigments for reconstructions of the phytoplankton standing crop has been attempted for many years (e.g. Watts and Maxwell 1977, Züllig 1981, Sanger 1988). Multiproxy approaches that included fossil phytoplankton pigments have successfully tracked climatic and other environmental changes in lakes (Hall et al. 1997, Bianchi et al. 1999, Leavitt et al. 1999, Verschuren et al. 1999, Pienitz et al. 2000, Bennett et al. 2001, Ariztegui et al. 2001, Francis 2001, Lotter 2001, Rusak et al. 2004) and seas (Chondrogianni et al. 2004). In these studies, fossil phytoplankton pigments were established to be able to further complement the information one can extract from the sediment, allowing estimates of the composition of the sedimented phytoplankton and of the total autochthonous primary productivity.

Several single parameter studies have described pigment deposits in lake sediments, which were, nonetheless, also thought to be proxies of changing climate (Vinebrooke et al. 1998, Kowalewska 2001) or physical properties, such as stratification and, thereby, changing redox conditions (Sanger and Crowl 1979, Hodgson et al. 1998, Squier et al. 2002). Similarly, fossil pigments have also been suggested as proxies of changing UV radiation (Leavitt et al. 1997, -2003), changing trophic state (Gorham et al. 1974, Adams and Prentki 1986, Lami et al. 1994), lake acidification (Guilizzoni et al. 1992), food-web manipulations (Leavitt et al. 1993), or anthropogenic influence such as sewage enrichment, land use or dam building (Griffith et al. 1969, Soma et al. 1995). Moreover fossil pigments were used to model the variability and predictability of phytoplankton assemblages after anthropogenic fertilisation (Cottingham et al. 2000).

Traces of carotenoids, chlorophylls and their degradation products were shown to persist long after the disappearance of morphologically distinguishable remains of the

organisms that produced them (Brown 1969) and are often the sole remnants of non-siliceous algae (Leavitt 1993). However, degradation and diagenesis affect all biogenic proxies during sinking and subsequently deposition, and therefore make direct reconstructions difficult. However, despite this, Guilizzoni et al. (1983) found significant correlations between the primary production and total pigment concentration of surface sediments in 12 Italian lakes. Additionally, Gorham et al. (1974), Swain (1985), and Brenner and Binford (1988) obtained similar results in several European and American lakes.

Several studies have also identified pigment-specific correlations between fossil pigments and historical data of the standing crop (Griffiths et al. 1969, Leavitt et al. 1989, Leavitt and Findlay 1994, Hall et al. 1999, Bianchi et al. 2002). For instance, Griffiths et al. (1969) showed in an early sedimentary pigment study, a strong correlation between the fossil oscillaxanthin content and the historical occurrence of *Oscillatoria* (cyanobacteria). Later, Leavitt and Findlay (1994) established that the ubiquitous pigments ß-carotene and pheophytin *a* were correlated to total biomass ($r = 0.56$-0.65) and that the marker pigments lutein+zeaxanthin and pheophytin *b* were correlated to the biomass of Chlorophyta ($r = 0.53$-0.55). However, in contrast, these authors also found that the marker pigments α-carotene and alloxanthin were only weakly correlated to Cryptophyta. Moreover, fucoxanthin and Chl*c* were uncorrelated to Chrysophyceae or Bacillariophyceae and peridinin to Pyrrophyta. These three pigments were strongly degraded. Generally, the correlations between fossil pigments and historical data of biomass were highest when fossil pigments were calculated as units per organic matter (Leavitt and Findlay 1994). Pigment concentrations relative to total organic carbon (TOC) are suggested to remain similar over time, so that TOC-specific pigment plots reduce the problem of differential degradation and allow an interpretation based on changing primary productivity in a lake (Vallentyne 1960, Daley and Brown 1973, Sanger 1988).

The correlations between the sedimentary pigments and the phytoplankton standing crop vary strongly because of differential degradation during sedimentation before permanent burial. Depending on the type of degradation process, chlorophyll can, for example, degrade to chlorophyllide, pheophorbide, pheophytin or steryl chlorin esters (SCE), or ultimately to colourless compounds (Fig. 3). Carotenoids degrade more slowly than chlorophylls, but faster than some chlorophyll degradation products (Sanger 1988). Therefore, the ratios of carotenoids to Chl*a* (including degradation products) often decrease from the euphotic zone to the sediment (Repeta and Gagosian 1984). Moreover,

the different carotenoids degrade with different rates. Generally, within the carotenoids, xanthophylls (such as fucoxanthin) degrade faster than carotenes (such as ß-carotene; Vallentyne 1960). An example of xanthophyll degradation towards non-carotenoid products is given for fucoxanthin in Fig. 4.

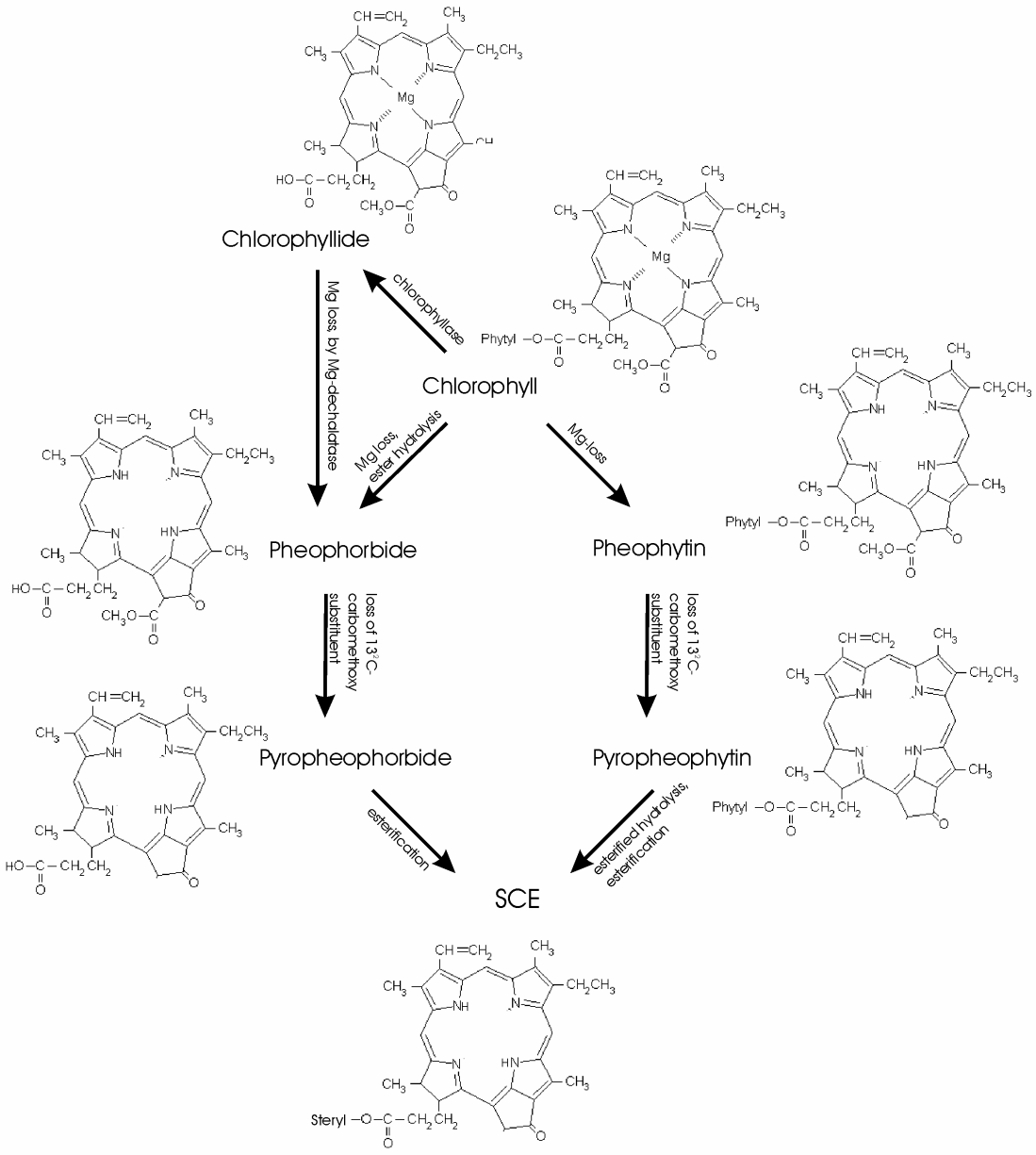

Fig. 3. Simplified scheme of Chl*a* degradation. In most of the chlorophyll degradation products, the tetrapyrrol macrocycle remains intact. Magnesium is removed from chlorophylls in the presence of dilute acids (gut passage) and high-light intensities (photooxidation). One of these degradation products is, for instance, pheophytin, where the central Mg-atom is replaced by two H^+. Chlorophyllide arises by dephytylation of Chl*a* and Chl*b* by the ubiquitous catabolic enzyme, chlorophyllase. Chl*c* is already chlorophyllide-like and does not undergo this process. Pheophorbide arises by removing the central Mg-atom from a chlorophyllide (Llewellyn et al. 1990, Leavitt 1993, Matile et al. 1999). Steryl chlorin esters (SCE) are formed by esterification from chlorophyll degradation products during zooplankton gut passage, and are relatively stable compared to chlorophylls and other degradation products; however their formation and sedimentation processes are not clear at present (King and Repeta 1991, Prowse and Maxwell 1991, Talbot et al. 1999, Soma et al. 2001b).

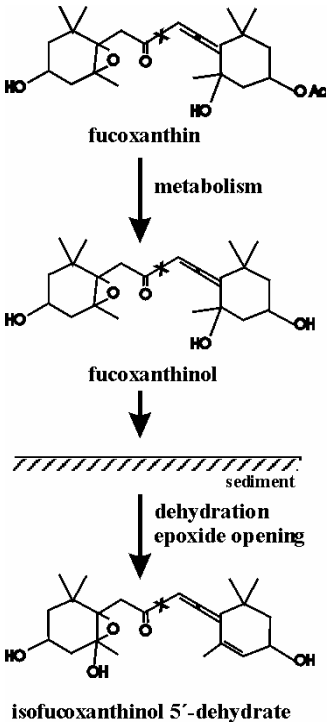

Fig. 4. Example of carotenoid (fucoxanthin) degradation by herbivore grazers (metabolism) and after sedimentation: Zooplankton herbivores and other heterotrophs hydrolyse carotenoid esters to free alcohols (fucoxanthin to fucoxanthinol) in the water column. Dehydration and epoxide rearrangement occur (fucoxanthinol to isofucoxanthinol 5´-dehydrate) in the surface sediment after burial (Repeta and Gagosian 1982, -1984).

Because pigment degradation is a very complex issue, the degradation processes within the water column and in the surface sediment have to be investigated specifically for each lake and pigment (Cuddington and Leavitt 1999). Differential pigment degradation and losses during deposition in marine and fresh water depend mainly on (1) selective meso- and microzooplankton grazing as well as the different digestibility of cells, (2) light and oxygen availability during and after sedimentation, and (3) sinking rates that differ between species as well as between living and dead cells and faecal pellets (Leavitt 1993, Cuddington and Leavitt 1999, Leavitt and Hodgson 2001, and references therein; Fig. 5).

Pigment destruction by zooplankton grazing depends on various factors such as gut passage time, edibility and even on food quality. Large Bacillariophyceae, for instance, are less edible than small Chlorophyta or even picoplankton. On the other hand, the extent of the degradation also depends on the grazer size and type (Carpenter and Bergquist 1985, Carpenter et al. 1988). Small protozoa, for example, degrade more efficiently compared to large protozoa (Strom et al. 1998). Also, filter feeders feed on other phytoplankton cells compared to raptorial feeders. Therefore, transformation products that are produced by herbivorous grazing (e.g. pheophorbide and SCE, cf. Fig. 3) were also used to monitor predation in a lake (Leavitt et al. 1993).

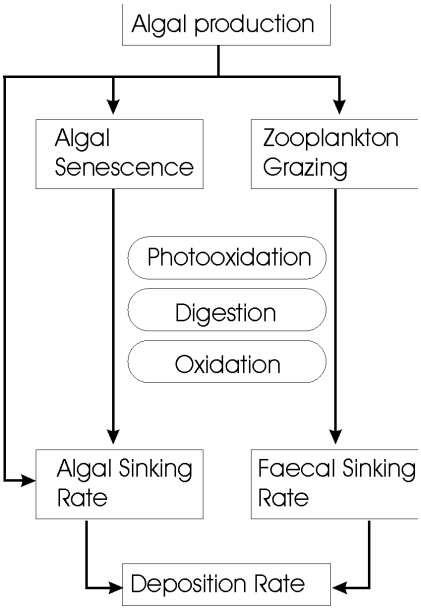

Fig. 5. Pathway of pigment production, transformation and degradation within the water column of a lake; scheme adapted from Leavitt and Hudgson (2001).

Oxygen enhances degradation in dead or moribound cells by direct oxidation of the conjugated chromophores or by stimulation of the microbial activity (Leavitt 1993). The fast oxidative degradation in the photic layer is due to photooxidation, whereas in the deeper water, this is caused by chemical oxidation. Further degradation occurs, however, after burial in the surface sediment, especially when the water to sediment interface is oxic (Leavitt 1993). Therefore, only those pigments that reach the deeper sediment layers below the redox zone are well preserved over hundreds of years.

Sinking rates determine the exposure time to light and oxygen. Factors that reduce the length of light exposure, e.g. high cell sinking rate or faecal packaging, will increase pigment deposition (Cuddington and Leavitt 1999). The incorporation of phytoplankton into zooplankton faecal pellets, for example, enhances the sinking velocity by up to 1000-fold (Welschmeyer und Lorenzen 1985a, -b).

Whether changes in fossil pigment concentrations arose from changes in phytoplankton standing crop or degradation has been a matter of discussion for a long time (Brown 1969, Swain 1985, Sanger 1988, Leavitt 1993, Cuddington and Leavitt 1999). Based on previous studies, an attempt has recently been made to model the extent and rate of lake-specific degradations (Cuddington and Leavitt 1999); however, data to test this model are scarce, especially for deep lakes. Hence, investigating phytoplankton pigments in the photic zone as well as its sedimentation and preservation is still a prerequisite for the interpretation of fossil phytoplankton pigments.

1.2 Phytoplankton and pigments in Lake Baikal

Recent phytoplankton and its pigments: Regular monitoring of a few specific parameters of phytoplankton in Lake Baikal has been conducted by the local institutions for several decades (e.g. Limnological Institute Irkutsk and University of Irkutsk, Fig. 6). Gradients of temperature, insolation, and nutrients are caused in Lake Baikal by its great length over five degrees of latitude, its rift-generated morphometry as well as its large tributaries and bays (Kozhov 1963, Galazii 1993, Kozhova and Izmest'eva 1998). Temperature and stratification regime, as well as ice cover duration and snow cover thickness, are important parameters for phytoplankton development in Lake Baikal, as concluded from recent monitoring (Shimaraev et al. 1994, Kozhov 1963, Kozhova and Izmest'eva 1998) and models based on sedimentary proxies (Mackay et al. 1998, -2003, Semovski 1998) or published data (Verkhozina et al. 2000). However, the regional variation of nutrient supply is also a critical factor (Goldman et al. 1996, Genkai-Kato et al. 2002).

The extreme intracontinental location of the lake creates highly contrasting seasonal changes, i.e. very cold and dry winters and very warm, cloudy and wet summers (Kozhov 1963, Kozhova and Izmest'eva 1998). In addition to the temperature and wind-induced mixing, ice and snow cover also strongly influence the seasonal succession of the phytoplankton (Mackay et al. 2003). So-called "*Melosira*" years, which occur every three or four years (at least in the South basin), are characteristic for Lake Baikal. During such years, blooms of endemic Bacillariophyceae, e.g. *Aulacoseira baicalensis* (its former name was *Melosira*), develop in the convective layer under the snow-free ice (Kozhov 1963, Kelley 1997, Kozhova and Izmest'eva 1998, Granin et al. 1991, -1999) and these years have been estimated to have a biovolume 10- to 100-fold more than that of "non-*Melosira*" years (Popovskaya 2000).

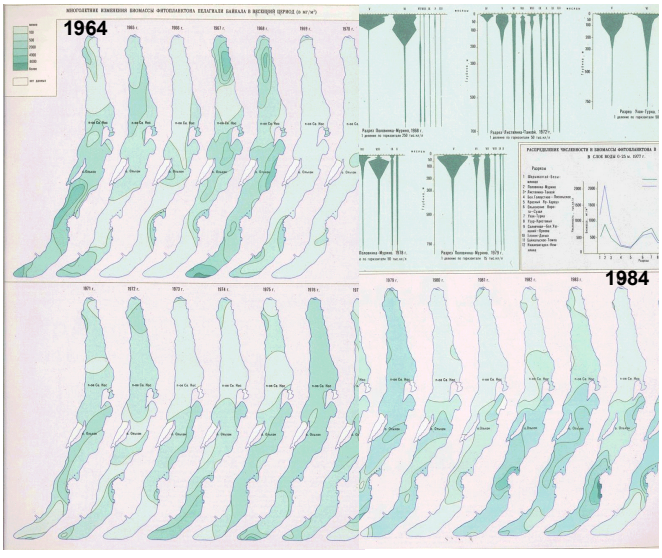

Fig. 6. Regular phytoplankton monitoring in Lake Baikal (scan from Galazii 1993).

Moreover, vertical gradients of temperature and insolation influence the distribution of total phytoplankton abundance and composition in the extremely deep Lake Baikal, where the euphotic zone and the wind-induced overturn can reach up to 50 and 300 m water depth, respectively. For example, during periods of overturn, living phytoplankton was found down to over 200 m (Popovskaya 2000) and even during stratification photosynthetically active cells sinking out from the euphotic zone were found down to more than 500 m water depth (Genkai-Kato et al. 2003).

These previous phytoplankton studies have therefore highlighted the need to investigate three gradients in Lake Baikal: region, depth and season. Additionally, due to the high interannual variability, subsequent years should also be examined for the three gradients. Finally, for a comprehensive study of this lake, all phytoplankton size classes (from large Bacillariophyceae to small picocyanobacteria) should be studied.

Thus far, single phytoplankton studies in Lake Baikal have usually considered only one parameter, e.g. biomass, Chl*a* or primary production. Moreover, conclusions on environmental impact were generally drawn from a series of different studies conducted over several decades and at different sites and seldom supported by statistical analyses (Kozhov 1963, Kozhova and Izmest'eva 1998, and others). Additionally, most studies have used the traditional method of microscopic measurement and counting, which primarily records nano- and microphytoplankton. Autotrophic picoplankton (APP, < 3µm), believed to contribute significantly to the summer assemblage (Popovskaya 2000, Belykh and Sorokovikova 2004, Popovskaya and Belykh 2004), have not been extensively included in the studies until now, partly due to technical difficulties (Boraas et al. 1991, Nagata et al. 1994).

To date, phytoplankton pigments other than chlorophylls have not yet been investigated in the water column of Lake Baikal. Hence, no information about phytoplankton pigment distribution and its driving forces is currently available; thereby hampering also accurate interpretation of sedimentary pigment composition.

Previously, *in situ* fluorescence measurements had already indicated the applicability of pigment-based approaches for phytoplankton and environmental surveys in Lake Baikal; however, up until now only total Chl*a* was determined using single-wavelength fluoroprobes (Granin et al. 1991). As yet, multi-wavelength fluoroprobes that allow the estimation of the relative importance of phytoplankton groups (Beutler et al. 2001, -2002a, -2002b) have not been used in Lake Baikal.

Sedimentation through the water column and preservation within the surface sediment: Lake Baikal's depth, fully oxic water column and low temperatures distinguish it from most freshwater lakes, and its oxic water to sediment interface also sets it apart from marine systems. Hence, this makes Lake Baikal an interesting water mass to study. Three different zones can be distinguished in the water column of Lake Baikal: (1) the euphotic zone, which extends up to 40-50 m; (2) the aphotic zone down to 250 m, which is mixed by wind during homothermy; and (3) the stable aphotic, but oxic deep water zone from approximately 250 m to the lake bottom, which is in the open pelagic regions more than 1 km deep. Deep-water ventilation explains the permanent high content of oxygen in the near-bottom layer and throughout the water body of Lake Baikal (Weiss et al. 1991, Dobretsov 2000). Even up to 2 cm of sediment surface are oxic (Müller et al. 2005) and up to 20 cm are oxidised (Vologina et al. 2000). Ferromanganese (Fe-Mn) crusts indicate redox boundaries in many regions of Lake Baikal (Vologina et al. 2003, Granina 2004).

Strong degradation was, therefore, assumed for biogenic proxies, such as phytoplankton pigments, diatom valves or pollen. For diatom-valve studies, species-specific correction factors have been recently established that allow the composition of the source populations to be reconstituted (Battarbee et al. 2005). Only approximately 1 % of the diatom valves from the phytoplankton crop are preserved in the sediment and some valves are more affected than others (Battarbee et al. 2005). However, as yet such studies were not conducted for pollen or phytoplankton pigments.

Surface sediment distribution of photosynthetic pigments has been investigated across Lake Baikal, and an attempt has been made to estimate the relevant factors for the sedimentation; although no correlation to the degradation processes in the water column has been undertaken (Soma et al. 2001a). The concentrations of phytoplankton pigments preserved in the surface sediment have been established to be high in the South basin and minimum in the Central basin, while TOC was distributed rather evenly (Soma et al. 2001a). Soma et al. (2001a) hypothesised that the oxidising conditions in the surface sediments and low sedimentation rates in certain regions of Lake Baikal caused intense decomposition of pigments. However, no analysis of the oxidised layers has been undertaken to study such decomposition. Furthermore, this research group also supposed that the river Selenga significantly disturbs sedimentation in the South basin causing uneven spatial pigment distribution; diverse carotenoids were detected in this basin that indicated the former presence of different algal classes although no correlation to the pigments of the standing crop was established (Soma et al. 2001a). Thus, despite this accurate study on the regional pigment distribution in Lake Baikal's surface sediment

the degradation processes of phytoplankton pigments through the water column and within the surface sediment have not been investigated to date. Hence, no information is available on either the pigment distribution in the euphotic zone or their sedimentation in the hypolimnion or their degradation in the surface sediment layers.

Fossil phytoplankton pigments: Lake Baikal is particularly well suited for studies of the natural environment and climate because this lake is believed to have never been glaciated, although glaciers reached the surrounding mountains during the glacial periods. Consequently, sediments have accumulated continuously for 25 million years and today form an up to 7.5 km thick layer. During the past 130,000 years, the Baikal region was subjected to several major glacial and interglacial periods. An alternating deposition of diatom-rich and compact, diatom-barren clayey material reflects the climatic changes in the sediment.

Several biologic parameters, such as diatom valves, biogenic silica and pollen, have been intensively studied in Lake Baikal sediments and the results demonstrate that they act as indicators of climatic and other environmental change (Bezrukova et al. 1991, Qiu et al. 1993, Mackay et al. 1998, Edlund and Stoermer 2000, Horiuchi et al. 2000, Karabanov et al. 2000a, -b, Minoura 2000, Khursevich et al. 2001, BDP Members 2004, and others). Despite important work has been conducted based on the determination of diatom valves or biogenic silica, this traditional method of fossil phytoplankton determination may be insufficient in Lake Baikal as recent reports suggest that (1) in summer more than 50 % of the Chl*a* in Lake Baikal results from APP (autotrophic picoplankton) (Popovskaya 2000), (2) high contributions of the APP to the total primary productivity occur even under ice cover (Straškrábová et al. 2005) and (3) APP were found to be the main chain of the trophic link of Lake Baikal (Popovskaya and Belykh 2004). Hence, to establish the composition of algal populations other than diatoms, chlorophylls, carotenoids and their degradation products should also be determined.

Due to the oligotrophic, marine-like phytoplankton abundances in Lake Baikal, the microfossils are preserved in very low amounts. However, modern HPLC systems equipped with fluorescence detectors can identify the remaining lipophilic pigments with high sensitivity. In the first ever pigment study at Lake Baikal, Soma et al. (1996) showed that degradation products of chlorophylls were present even in the deepest layers of short cores (41 cm) taken from the South basin. The major chlorophyll degradation product was pheophytin, with pheophorbide occurring only in low amounts. Because pheophorbide has been proposed as a grazing biomarker, the authors considered the

effect of grazing in Lake Baikal to be small. No degradation processes were identified either for the water column or for the surface sediment. Moreover, no xanthophylls with epoxide groups (such as fucoxanthin) were detected in this preliminary study, while ß-carotene, alloxanthin, lutein, diatoxanthin and canthaxanthin were found (Soma et al. 1996). The concentrations of the carotenoids varied at intervals of 6-10 cm, while the content of TOC was rather stable through the whole core length (Soma et al. 1996). The authors suggested that phytoplankton changes were manifested in an amplified way in the depth profiles of the pigments in the sediment.

Tani et al. (2001, -2002) continued these preliminary studies by investigating the phytoplankton pigments in two longer and ^{14}C-dated cores from the South basin. In both cores, the transitions from the last glacial period to the Holocene were successfully shown (Tani et al. 2001, -2002). Additionally, Tani et al. (2002) provided initial data on how the phytoplankton pigments could be used as a climatic indicator, in this case for a major cooling event (the Younger Dryas); however these analyses were performed at low resolution (2-5 cm, which in Lake Baikal correspond to c. 100-400 yrs). Also, one of the cores was taken at a site close to the southern coast with rather a steep slope and it was uncertain whether the core was representative of pelagic conditions in the lake. It therefore remains to be determined whether the observation in these two cores can be generally applied to all the basins of the 600 km long Lake Baikal (Tani et al. 2002).

Nonetheless, these studies along with that of Naylor and Keely (1998) revealed that SCEs (steryl chlorin esters, cf. Fig. 3) were well preserved within Lake Baikal´s sediments. Soma et al. (2001b) could reconstruct global climate changes that occurred during the last 2.8 million years using these SCEs as phytoplankton markers. SCEs accounted for 90 % of the total chlorophyll degradation products in sediment layers deeper than 10 m. Soma et al. (2001b) concluded that although records of phytoplankton preserved in long cores of lake sediments, spanning millions of years, have so far been confined to fossil diatoms, their investigation on fossil pigments suggested that SCEs were useful indicators of phytoplankton communities as a whole, including diatoms. However, investigating a 100 m long core, the resolution was low (every 10 cm corresponding to c. every 2400 yrs), and therefore it remains to be proven whether fossil pigments can also be used to track climate changes with accuracy at higher resolutions.

1.3 International interest in paleoclimate and paleolimnologic research in Lake Baikal

Approximately 150 years ago, a global warming phase began and reconstructions of climate data for the past 1000 years indicate that this warming is unusual and also unlikely to be entirely the result of natural causes (IPCC 2001). Unfortunately, most models predict further worsening (IPCC 2001). Although confidence in the ability of models to accurately predict general future climatic change has increased, there are still a large number of areas for which uncertainties for global extrapolations remain (IPCC 2001). One reason for this is that most models were based on Atlantic studies and may be valid for regions under oceanic influence, but they struggle to explain several events in continental regions. Hence, there is an important gap in our knowledge of how large-scale climate processes affect continental regions (Oberhänsli and Mackay 2005).

Climate models are usually validated by comparing predicted scenarios with measured changes in the past. Traditionally, climatic changes in areas with ocean influence are assessed with, for instance, analysis of ice cores from Greenland or the Antarctic. In continental areas, climatic changes are known from the lake's sedimentary archives. Thus, for further improvement of climate models one needs the analysis of the biologic record contained in sediment cores in lakes far remote from marine influence. For example, in the northern hemisphere, only few lakes located intracontinentally fit this criterion due to large parts of the northern hemisphere being periodically glaciated. However, one of the lakes which was unaffected by glaciation, and therefore having the advantage of an uninterrupted archive, is the Siberian Lake Baikal.

Lake Baikal is located far from marine influence at the boundaries of major global weather systems such as the North Atlantic Oscillation and Asian Monsoon. Therefore, knowledge on the changes in Lake Baikal and comparison with well-studied European climatic oscillations can considerably aid understanding of the extent of climatic changes and the ecological consequences in continental regions. Thus, the multiproxy analysis of sediment cores from Lake Baikal within the EU framework 5 project CONTINENT (EVK2-CT-2000-0057; http://continent.gfz-potsdam.de; cf. Oberhänsli and Mackay 2005), which besides phytoplankton pigments, also includes plant microfossils, e.g. pollen and diatom valves, as well as techniques such as sediment geochemistry, site survey, and dating, represents a useful tool for climate scenario validation in continental areas.

However, the biological record contained in Lake Baikal's sediment is not only central to better understand the aforementioned climate variability and to improve climate models, but it is also pivotal to understand the evolution of the specific fauna and flora of the lake and to the impacts of recent environmental change and pollution. Yet the effect of global warming and local nutrient enrichment on the ecology of the World´s largest lakes, including Lake Baikal, is poorly known.

In 1996, Lake Baikal was granted World Heritage Status by the UNESCO. Since then, the lake's protection and conservation for the future generations has shifted from a solely local, Russian affair to an international one. This unique ecosystem has changed very little since regular research began in the early 20th century (Kozhova and Izmest'eva 1998), although an increase in air and water temperature as well as precipitation and a decline of the ice cover duration have been reported recently (Magnuson et al. 2000, Shimaraev et al. 2002, Hulme et al. 2003). Additionally, pollution in the river Selenga and South basin due to both industrial and domestic discharge has also been discussed (Galazii 1982, -1991, Martin 1994, Kozhova and Silow 1998, Mackay et al. 1998, Beeton 2002). Spreading of small cosmopolitan species at the expense of the many large endemic Bacillariophyceae was also suggested to have occurred (Popovskaya 1991, Kozhova and Izmest'eva 1998). However, an alternative view is that some of the variations attributed to human impact were within the range of natural changes; hence, the 'ecological alarm' was overestimated (Grachev et al. 1989, Grachev 1994, cf. Zumbrunnen 1974, cf. Flower 1998). This controversy has not yet been resolved. However, there is agreement that only changes over and above the ´norms´ can be used to decouple natural from anthropogenic impacts. Therefore, rate and extent of natural changes must be studied to precise the norms. Regular monitoring can assess the recent variations, and the historical variability can be taken from sedimentary records. The CONTINENT project's overriding aim, and hence under its auspices the present thesis', was to contribute to the local and international effort to understand the processes of Lake Baikal, and thereby also to its protection.

1.4 Outline of the thesis

The objective of this thesis was to investigate whether and to which extent recent and fossil phytoplankton pigments in Lake Baikal are potential markers for phytoplankton community structure and environmental changes. Moreover, in conjunction with the paleoclimate project CONTINENT and the long-term monitoring programme of the State University Irkutsk, the information gathered by the phytoplankton pigments should be used to complement our knowledge on the current and historical productivity variations in Lake Baikal. Three main aspects were investigated: (1) the distribution of phytoplankton and phytoplankton pigments in the euphotic zone, (2) its sedimentation through the water column and preservation within the oxidised surface sediment, and (3) variation of fossil phytoplankton pigments.

Distribution of phytoplankton and its pigments in the euphotic zone: Considering the enormous size of Lake Baikal, monitoring the phytoplankton response to anthropogenic and climatic influences requires a less time-consuming method than traditional microscopic cell counts that, however, includes all phytoplankton size classes. I hypothesised that a pigment-based approach would enable regular monitoring to answer the question previously posed by Reynolds (1984) for ecological research on phytoplankton: ´what lives where – and why?´. To test this hypothesis, the present thesis combined pigment-based methods (HPLC and fluorometry) in conjunction with traditional microscopic spot checks.

A preliminary study established the applicability of an HPLC-based approach to determine accurately the summer phytoplankton assemblage in Lake Baikal (Fietz and Nicklisch 2004, Appendix A). This study also demonstrated the need for microscopic spot checks to aid accurate interpretation of the pigment results. This preliminary study of pigments in the Baikal water samples even induced us to revise the autotrophic eukaryotic picoplankton composition, because, due to unusual pigment ratios, one would expect Eustigmatophyceae to be present in the phytoplankton (Fietz and Nicklisch 2004, Appendix A), although none have as yet been described (Kozhova 1987, Bondarenko 1995, Kozhova and Izmest'eva 1998). Three new strains, isolated from Lake Baikal water samples, were identified as *Nannochloropsis limnetica* Krienitz, Hepperle, Stich & Weiler and were shown to be common members of the Baikalian picoplankton (Fietz et al., submitted, Appendix B).

The recommended remote sensing (Jeffrey 1997, Fig. 2) was studied by Birgit Heim from GeoForschungsZentrum (GFZ) Potsdam, Germany, based on the pigment data reported in the present thesis (Heim et al. 2005, Heim, in prep.). Furthermore, the monitoring was complemented by size fractionated primary production and nutrient availability determinations by Vera Straškrábová and Jakub Borovec from Hydrobiological Institute, Ceské Budejovice, Czech Republic (Straškrábová et al. 2005).

This suite of methods allowed the phytoplankton to be studied below the water surface as well as from space. Three gradients, region, depth and season, were studied during three consecutive years (2001 to 2003) within or additionally to the long-term monitoring of the Scientific Research Institute of Biology (SRIB) at the Irkutsk State University (Russia). An attempt was made to predict Lake Baikal's phytoplankton response to further global warming and possible local nutrient enrichment. The knowledge on the phytoplankton pigment distribution also helped interpretation of the sedimentary pigment sequences, as no information about phytoplankton pigment distribution other than Chl*a* has been available until now.

Sedimentation and preservation through the water column and within the oxidised surface sediment: The second task was to determine transfer fluxes of phytoplankton pigments through the water column and to to determine the type and extent of the degradation occurring after burial in the surface sediment. I hypothesised that the phytoplankton standing crop can be projected backward from recently buried pigments or its degradation products. To test this hypothesis sediment traps were moored for two consecutive years in the southern and northern basins of Lake Baikal, and the sedimentary pigments were also analysed in the oxidised surface sediments from open basin and river inflow sites. It was to be determined how the main phytoplankton groups were represented in the deposited material. The potentials and limits of retrospective studies from sedimentary pigments were also documented.

Variation of fossil phytoplankton pigments: The final task was to reconstruct the phytoplankton development during glacial and interglacial periods. It was hypothesised that climate induced changes of total primary production can be tracked based on fossil Chl*a* and that marker pigments tracked changes of phytoplankton composition. For this purpose, the variation of photosynthetic pigment concentrations and organic carbon contents during the Holocene was analysed at three sites within Lake Baikal (South, Selenga Delta, and North). Furthermore, the first continuous photosynthetic pigment

sequence of the Kazantsevo Interglacial (European Eemian, Marine Isotopic Stage MIS 5e) at a resolution of c. 150 yr was established. Coring sites were carefully chosen to obtain uninterrupted sequences of sediments and to avoid impacts by secondary processes such as turbidity currents (cf. Vologina et al. 2003) and tectonic activity (Charlet et al. 2005). Age models were specifically established for each site and for the most recent as well as for the up to 200 kyr old segments (Piotrowska et al. 2004, Demory et al. 2005). Diatom, pollen, and for some core sections also biogenic silica and oxygen isotopes analyses have been performed on these cores within the CONTINENT project (Boës et al. 2005, Demske et al. 2005, Granoszweski et al. 2005, Morley et al. 2005, Rioual and Mackay 2005). Both Holocene and Interglacial pigment sequences were compared to the diatom and pollen sequences and to published climate changes.

2 MATERIALS, METHODS AND SITE DESCRIPTIONS

2.1 Lake Baikal

Lake Baikal is located in the southeastern Siberia between 51° and 56° North latitude and between 104° and 110° East longitude (Fig. 7); it lies at 486 m elevation and is surrounded by mountain ridges that rise northward to the altitudes of 2500 - 3000 m (Galazii 1993). Lake Baikal is 23 million years old and is the oldest lake of the world (Kozhov 1963). It measures more than 600 km long by 80 km wide and the deepest point is over 1.6 km (Kozhov 1963). It holds 23,000 km³ of water and 20 % of the World´s fresh surface water. Lake Baikal has an exceptional clarity, which allows 40-50 m of visibility (Kozhova and Imest´eva 1998).

Lake Baikal can be divided into three basins (Fig. 7). The North basin is separated from the Central basin by the Academician Ridge, and the Central basin is separated from the South basin by the more than 20 km wide Selenga Delta. All basins exhibit an asymmetric, half-graben morphology, with steep margins on the northwestern side and more gradual, though still faulted margins on the southeastern side (Colman et al. 2003, Fig. 8).

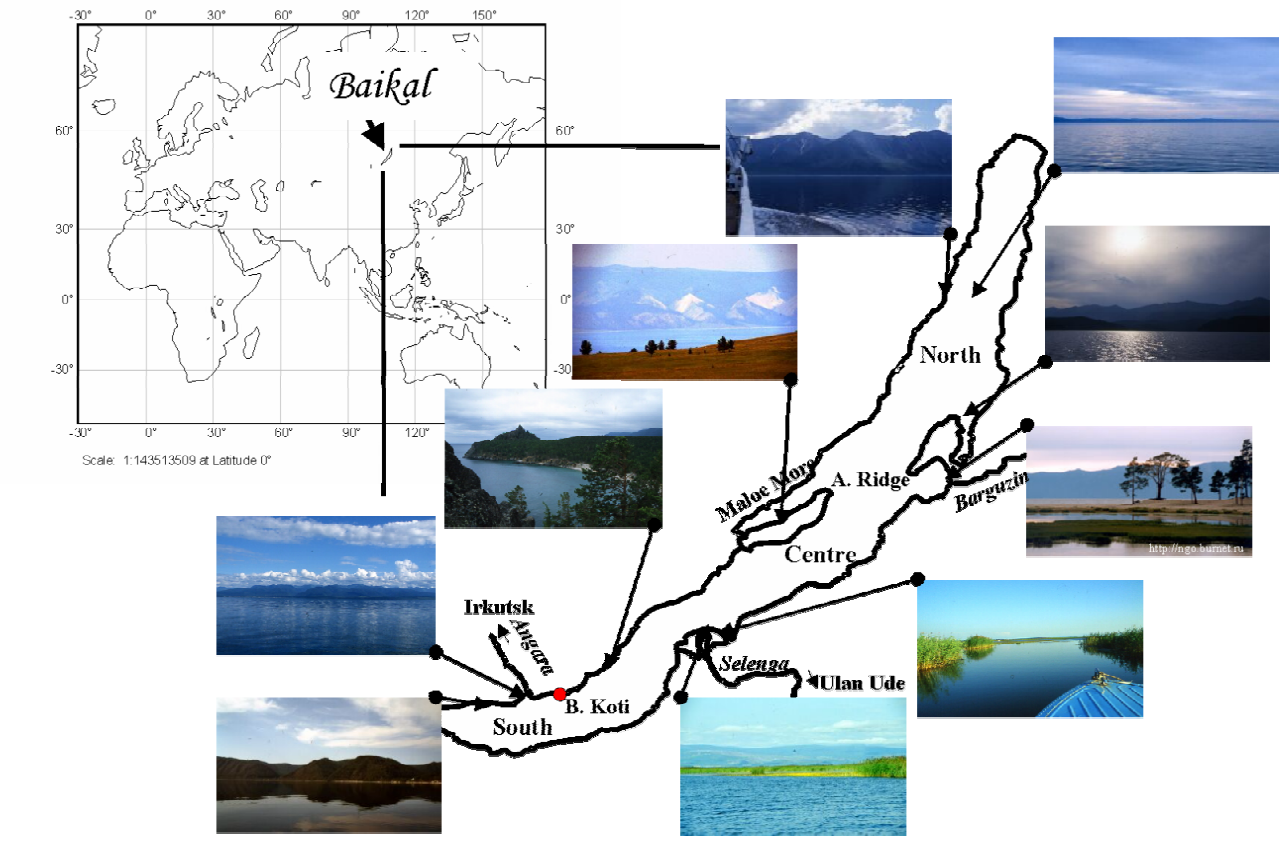

Fig. 7. Map of Lake Baikal locating relevant regions for the present study and impressions of the respective surrounding regions.

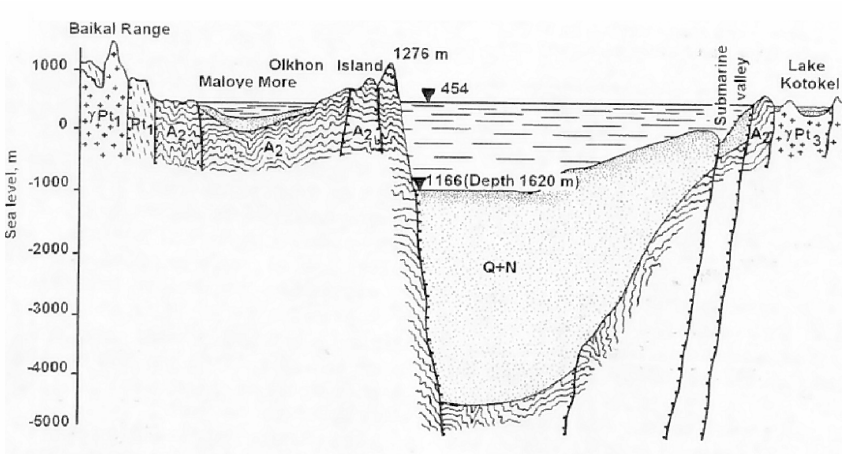

Fig. 8. Half-graben morphology from West to East: Maloe More, Olkhon Island, Central basin; from Kozhova and Izmest'eva 1998.

While approximately 365 inflows enter the Baikal, from which the river Selenga is the largest one, only one effluent is known, the river Angara at the western shore of the South basin (Fig. 7). The lake´s catchment area encompasses c. 540.000 km^2 of forest and desert environments. Most of the watershed area is surfaced with rocks so that water inflow has little mineral or chemical content. The chemical composition is constant through the water column. Budgets of nitrogen and phosphorus compounds have been poorly investigated reporting contradictory results (Granina 1997). Recent studies on nutrient availability indicated, that, although Lake Baikal is a freshwater lake, the nutrient status of the pelagial is ocean-like, and the only nutrient-rich regions of the lake are the deltas of the main river inflows (Genkai-Kato 2002).

Lake Baikal is a dimictic lake. However, even during homothermy the wind-induced overturn is limited to the upper 250-300 m; the water masses below the wind-induced mixed layer are homothermal (c. 4° C; Granin et al. 1991, Shimaraev et al. 1994). Deep water ventilations occur regularly (Weiss et al. 1991, Shimaraev et al. 1994). The lake freezes by December or January, depending from latitude. Ice thickness often exceeds one meter and holds mostly only a thin snow cover. Melting starts from April to May.

The climate is continental. The winters are influenced by the Siberian high pressure system, which brings cold Arctic air into the region (clockwise circulation). In spring the central pressure of the Siberian High decreases and the air masses shift west towards Europe (Bradbury et al. 1994). During this transitional period the Siberian High becomes weaker, but more variable in the Lake Baikal region and this variability affect timing and rate of ice thaw and consequently the extent and rate of the characteristic spring phytoplankton development (Bradbury et al. 1994). In summer the low-pressure system of the Asiatic Low extends towards the Baikal region and brings moisture from the Indian Ocean (counterclockwise winds; Bradbury et al. 1994).

2.2 Water samples

2.2.1 Sample collection

CONTINENT summer cruises: Sampling for the study of regional distribution was conducted in July 2001, 2002 and 2003 during the CONTINENT cruises CON 01-4, CON 01-5, CON 02-8, CON 03-9 with the research vessel "Vereshchagin" (Fig. 9). In 2001 samples for pigment analyses were taken from 0.5, 5, 10 and 30 m water depth. Samples for phytoplankton counting were taken from 5, 10 and 30 m water depth. In 2002 samples for pigment and phytoplankton analyses were taken from 5, 10 and 30 m and/or in the deep Chl*a* maxima determined with a submersible fluorimeter (FluoroProbe, bbe Moldaenke GmbH, Kiel, Germany). In 2003 only samples for pigment analyses were taken (same depths as in 2002). Due to the differences in sampling depth, samples were grouped into "0.5 m", "5 m", "10 – 20 m" and "20 – 30 m" and "45 – 85 m". In 2001 temperature was directly measured in the samples. Temperature in 2002 and 2003 was provided by the fluorimeter and by CTD (Conductivity, Temperature, and Depth) profiles (R. Gnatovsky and N. Granin, Limnological Institute of Irkutsk, Russia).

Fig. 9. Research vessel "Vereshchagin" (left) and on board of the research vessel "M.M. Kozhov" (Bolshye Koti in the background) (right).

Seasonal monitoring at Bolshye Koti: For the study of seasonal dynamics, weekly sampling from May 2002 to June 2003 was carried out at the long-term sampling site of the Scientific Research Institute of Biology (SRIB, State University Irkutsk, Russia), located 2.8 km offshore from Bolshye Koti (51°54´ N 105° 04´E, Fig. 7, Fig. 9). Water depth at that site was 800 m. Samples from this latter station were taken with the research vessel "M.M. Kozhov" in summer or from the ice in winter and processed at the Biological Station Bolshye Koti (G. Kobanova, L. Kraschuk, E. Pislegina, and L. Izmest'eva, SRIB).

2.2.2 Phytoplankton qualitative and quantitative determination

Samples for autotrophic picoplankton (APP, 0.2 – 3 μm; 50 mL) were preserved with formaldehyde (0.7 % final concentration) and filtered through black Nuclepore© polycarbonate filters (0.2 μm pore size). The filter was placed on a microscope slide, quickly dried and covered with a drop of fluorescence-free immersion-oil and a coverslip. Once frozen, preparations were stable for months. APP were counted at 1000-x magnification using a Zeiss Axioskop epifluorescence microscope equipped with filters for green (546 nm excitation filter, 580 nm splitter and 590 nm barrier filter) and blue (450-490 nm excitation filter, 510 nm splitter and 520 nm barrier filter) excitation. Eukaryotic APP fluoresced deep red (>665 nm) when excited with blue or green light, whereas cyanobacterial APP fluoresced light-red (<665 nm) when excited with green light (Phycobilins). Phycoerythrin and phycocyanin containing cyanobacteria were distinguished by their respective yellow or extreme weak emission at blue light excitation, but this difference was not definite in all stored preparations. Cell counts were converted to biovolume according to their size and geometric form (Fietz and Nicklisch 2004, Appendix A). During the seasonal monitoring APP was counted with a light microscope, whereby colonies were easily identified, but single cells could be overlooked.

In both years of phytoplankton counts (2001 and 2002) samples (1-2 L) were enriched by filtering through Nuclepore© polycarbonate filters (2 μm pore size), fixed with some drops of Lugol´s solution and stored at room temperature. Counting and identification was done according to the settling technique (Utermöhl 1958). In 2001 the algae were classified in accordance with Ettl et al. (1986) (H. Täuscher, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany). In 2002 the taxonomic composition of algae was established more in detail (G. Kobanova, SRIB) in accordance with "The Keys of Freshwater Algae of the USSR" (see Kozhova and Izmest'eva 1998, p. 325 for references), with monographs (references in Kozhova and Izmest'eva 1998, Bourrelly 1957), and additional keys (references in Kozhova and Izmest'eva 1998, Topachevsky and Masyuk 1984, Wasser et al. 1989, Gleser et al. 1992), and supplemented by articles (references in Kozhova and Izmest'eva 1998, Edlund et al. 1996). *Gymnodinium coeruleum* (Pyrrophyta) is often cited within Lake Baikal phytoplankton assemblages (Kozhova 1987, Kozhova and Izmest'eva 1998, Genkai-Kato et al. 2003), but has been omitted from the phytoplankton counts in the present study because it did not contain chloroplasts and, therefore, was counted as protozoan. All species were tentatively grouped into functional associations according to the scheme proposed by Reynolds et

al. (2002). We consulted with its authors over the classification of the species we have encountered.

In this study we also used chemotaxonomic groups, which may be classes or families, according to the respective pigment compositions. In that way we used "Bacillariophyceae+Chrysophyceae", because both families contain the marker pigments fucoxanthin and Chl*c* but other families of their class "Heterokontophyta" contain other marker pigments. Also, we used "Chlorophyta", because all phytoplankton families of this class contain the same pigment composition, but we used "cyanobacterial picoplankton" that clearly dominate the Baikalian cyanobacteria, because of their marker pigments zeaxanthin and caloxanthin, not prominent in filamentous cyanobacteria. Eustigmatophyceae were considered to be a common member of the Baikalian eukaryotic picoplankton, although they were not considered in previous phytoplankton studies (Kozhov 1963, Kozhova and Izmest'eva 1998, Popovskaya 2000), because their presence was suggested from peculiar pigment ratios (Fietz and Nicklisch 2004, Appendix A); furthermore, three new strains of *Nannochloropsis limnetica* (Eustigmatophyceae) were isolated from Lake Baikal recently (Fietz et al., submitted, Appendix B).

2.2.3 HPLC-aided pigment analysis in water samples

Duplicate samples for HPLC-aided pigment determination (1–2.5 L), were filtered through Whatman GF/F-filters with 25 mm diameter, put in 2 mL reaction vessels, immediately freeze-dried and stored frozen in the dark. Chlorophylls, carotenoids, and their derivatives were extracted in 2001 with 1 mL of a mixture of acetone, methanol and water (80:15:5 by volume, Leavitt et al. 1989) and in 2002 and 2003 with 1 mL of dimethylformamide under dim light at 4° C. No significant difference was found between both solvents. The extraction was done by vibration shaking at a frequency of 2000 min^{-1} with a supplement of glass beads (0.75-1 mm) over 1.5 h. An ionpairing reagent solution (15 g L^{-1} tetrabutyl ammonium acetate and 77 g L^{-1} ammonium acetate) was added 10:1. The extract was centrifuged for 20 min at 4° C at 2500 *g* in a cooled centrifuge (Biofuge Fresco Heraeus Instruments, Hanau, Germany). The separation, identification and quantification of pigments were performed according to Woitke et al. (1994) with a Waters HPLC system described by Fietz and Nicklisch (2004, Appendix A).

2.2.4 Spectrophotometric data from long-term monitoring

HPLC-aided pigment analysis was provided for the three summer cruises as well as for the intensive monitoring from May 2002 to June 2003. Additional weekly Chl*a* data were provided from January 2001 to December 2003 by the long-term monitoring programme conducted by the SRIB. For these analyses water samples were taken at the aforementioned Bolshye Koti station, filtered through 0.7 mm pore size Nuclepore® polycarbonate filters, dried in cold, dark conditions and stored frozen. Extraction was done with 96 % acetone. Extracts were centrifuged and the absorbance of the supernatant was measured with a spectrophotometer at 750, 665, 645 and 630 nm. Chl*a* was calculated according to guidelines given by the SCOR-UNESCO workgroup (1966).

2.2.5 Fluorescence measurements

During the CONTINENT summer cruises 2002 and 2003 as well as during the regular August cruise 2003 of the SRIB a series of fluorescence depth profiles were taken across the lake with a submersible fluorimeter (FluoroProbe, bbe Moldaenke, Kiel, Germany, Fig. 10) provided by the GFZ Potsdam (H. Oberhänsli). The FluoroProbe uses five excitation wavelengths and allows discriminating the contribution of the dominant groups (http://www.chlorophyll.de/; Beutler et al. 2001, -2002a, -2002b). Because the calibration at factory was not satisfying for Lake Baikal, the FluoroProbe was newly calibrated based on the HPLC and microscopic results (A. Nicklisch, Humboldt University, Berlin, Germany). Additionally to the depth profiles, which were taken at high resolution (c. 1 m) down to a depth of 120 m, a series of horizontal transects (resolution of 100 - 1000 m) were taken during the same cruises. The FluoroProbe was then connected to a drinking water pump on board, which pumped continuously water from c. 3 m water depth into the FluoroProbe.

Fig. 10. FluoroProbe vertical measurements.

2.3 Sediment traps

2.3.1 Mooring and sampling

Four moorings were deployed within the project (M. Sturm, EAWAG, Switzerland): During 16 months from March 12, 2001 to July 5, 2002, a sediment trap mooring, comprising 15 integrating traps (Fig. 11), was deployed in the centre of the South basin (51°42 N / 105°01 E), where water depth reached 1400 m. The traps were deployed at 40, 100, 255, 350, 445, 540, 635, 730, 825, 922, 1015, 1113, 1210, 1305, and 1396 m (cf. Müller et al. 2005). The same mooring string was deployed at the same site during the ensuing 12 months from July 6, 2002 to July 5, 2003. Another sediment trap mooring, comprising 9 integrating traps was deployed in the centre of the North basin (54°27 N/ 109°04 E) from July 9, 2001 to July 8, 2002 at 50, 255, 335, 445, 555, 720, 775, 885, and 903 m. Due to technical disturbances material from the uppermost two traps were lost in 2001-2002. The same mooring string was deployed at the same site during the ensuing 12 months from July 9, 2002 to July 9, 2003.

The integrating traps were two acrylic cylinders with each an active area of 65 cm^2 and an aspect ratio of 1:8 (EAWAG-130, Ohlendorf and Sturm 2001). After recovery of the traps, the overlaying water was siphoned off and the sampling cups were covered with aluminium foil to avoid photo-degradation of the pigments. Duplicate subsamples of the suspended sediment trap material were filtered within two hours upon recovery through GF/F-filters (Whatman, Kent, UK) and immediately frozen. The filters were freeze-dried within 24 h upon recovery and stored frozen at -20° C in the dark until analysis.

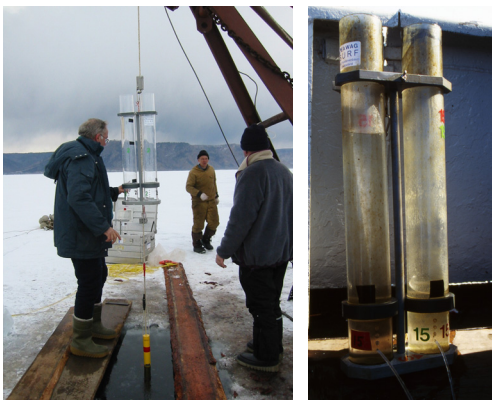

Fig. 11. Sediment trap deployment (left) and top traps after recovery (right)

2.3.2 HPLC-aided pigment analysis in sediment trap materials

Chlorophylls, carotenoids, and their derivatives were extracted with 1.25 mL of dimethylformamide under dim light at 4° C. The extraction was done by vibration

shaking with a frequency of 2000 min^{-1} over 3 hours. 125 µL of the aforementioned ion-pairing reagent solution (cf. chapter 2.2.3) were added. The extract was centrifuged for 20 min at 4° C at 5000 *g* in a cooled centrifuge (Biofuge Fresco, Heraeus Instruments, Hanau, Germany) and the supernatant was transferred in vials for HPLC-analysis. The separation, identification and quantification of pigments of all samples were done similarly to the water samples. The eluting peaks were monitored at 440 nm using a Waters 996 photodiode array detector and at 410/670 nm (excitation/detection wavelength) using a Waters 474 fluorescence detector.

Unialgal cultures, acidified cultures, cultures of *Dunaliella tertiolecta* (with high chlorophyllase activity), standards, and literature data were used for identification of chlorophylls and various degradation products. The distinction between Chl*a* degradation products and Chl*b* degradation products was performed using the ratio of the fluorescence at 410/670 vs. 430/650 nm. According to Soma et al. (2001b) and Soma et al. (2003), the concentration of SCE*a* and *b* was determined assuming that their fluorescence at 410/670 nm and 430/650 nm (excitation/detection wavelength) was identical to their respective pheophorbides.

The terms Chl*a*s or Chl*b*s mean the sum of all respective chlorophylls, epi- and allomers and degradation products. Chl*c* degradation products were not identified definitely. The same was true for carotenoids. Most carotenoid degradation products could not definitely be attributed to their parent carotenoid and thus, the description of the sedimentary carotenoids in the following will be limited to the intact carotenoids.

2.3.3 C/N –analysis

The total organic carbon (TOC) and total nitrogen (TN) contents of the sediment trap samples 2001-2002 were determined with a EURO-EA® CNS-analyser at EAWAG (M. Sturm, Switzerland). The TOC and TN contents of moorings 2002-2003 were determined with a Vario EL CHNOS elemental analyser (Elementar Analysesysteme GmbH, Germany) after acidification with 0.2 N HCL.

2.4 Sediment

2.4.1 Description of CONTINENT coring sites

The main CONTINENT coring sites were chosen after intensive side scan sonar studies above preselected regions. High-resolution seismic data (M. De Batist and F. Charlet,

Renard Centre of Marine Geology, Belgium), long core description (N. Fagel and F. Hauregard, University of Liège, Belgium) and physical property measurements (H. Oberhänsli, J. Klump, F. Démory, and P. Sorel, GFZ Potsdam, Germany) were performed to characterise the sedimentary environment of these main coring sites.

The three coring sites were located on elevated plateaus: Vidrino Shoulder, Posolski Bank, and Continent Ridge (Fig. 12). The Vidrino Shoulder, in the eastern part of the South basin, is composed of a series of elevated ridges, perpendicular to the coast, and separated by deeply incised channels (Charlet et al. 2005). The main material is medium to fine-grained sediment (Charlet et al. op. cit.). The core was taken on a flat crest of one of the ridges, where seismic data suggest a stable depositional environment (Charlet et al. op. cit.). The upper meter of the sediment was laminated and was composed of diatom-rich biogenic sediments. The uppermost 10 cm were oxidised. There were no visible signs of bioturbation. According to Martin et al. (2005) bioturbation was low in the three investigated recent sediments (Vidrino, Posolski, and Continent Ridge), but a possible disturbance should not be dismissed. The effect of biological mixing by oligochaeta was less important in the deepest stations (Continent Ridge and Vidrino) than in the shallower regions (Posolski).

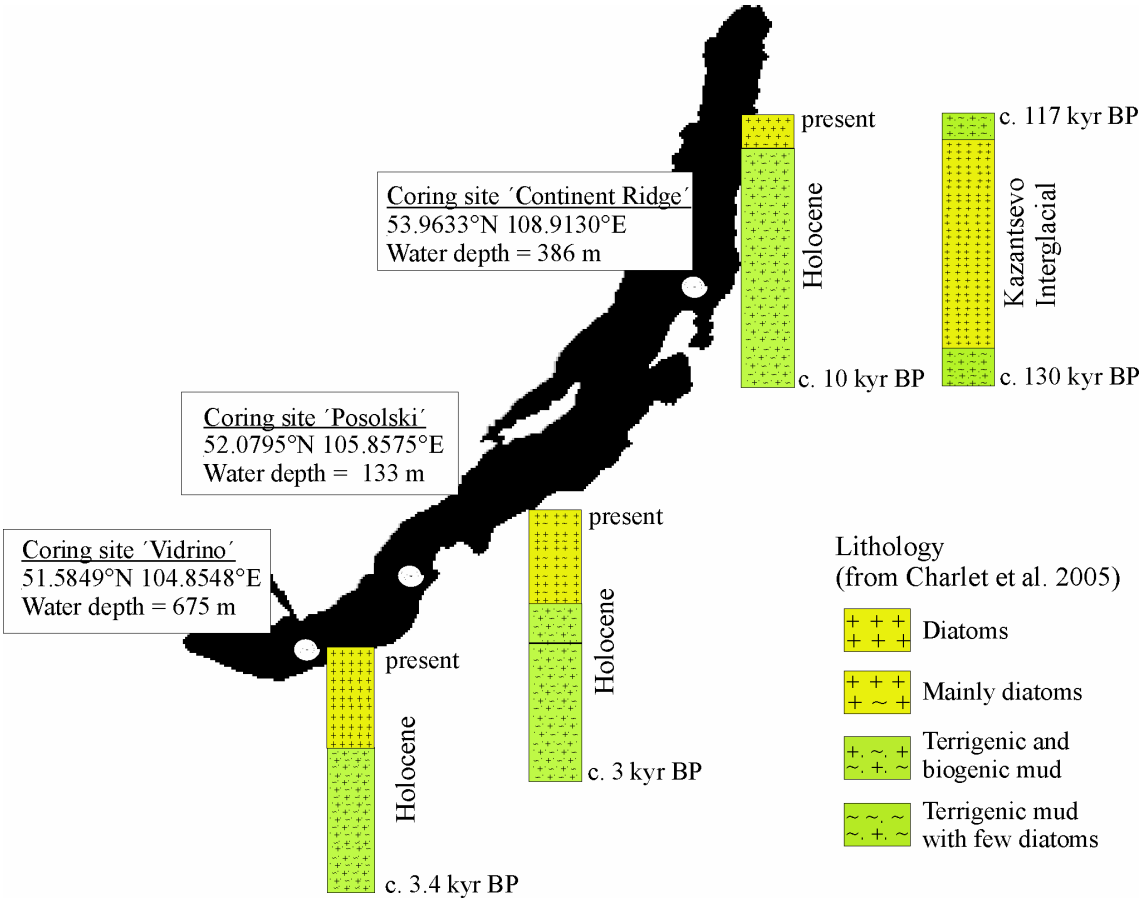

Fig. 12. Map locating the coring sites with lithological descriptions of the analysed segments.

The Posolski Bank is a shallow plateau within the Selenga Delta Accommodation Zone. The core was taken from the central part that is characterised by undisturbed sedimentation and predominance of fine-grained sediments (Charlet et al. op. cit.). The upper 25 cm of the sediment is homogeneous and composed of biogenic muds. Below, the sediment is composed of a mixture of biogenic and terrigenic muds (Charlet et al. op. cit.). The sedimentation is predominantly hemipelagic; the terrigeneous input is low (< 30 %) at Posolski, despite the input from the Selenga River at that site (Charlet et al. op. cit.).

The Continent Ridge is located in the North of the Svyatoi Nos Peninsula near the eastern coast of the North basin. Within the Continent Ridge, the core was taken at a flat crest with featureless morphology, thought to represent undisturbed sedimentation (despite the tectonic activity of the rift system; Charlet et al. op. cit.). Fine-grained sediments prevailed (Charlet et al. op. cit.). The upper 10 cm were oxidised and were dominated by diatoms. Below, the sediment was composed of a mixture of biogenic and terrigenic muds (Charlet et al. op. cit.). The sedimentation is, like at Posolski, predominantly hemipelagic and the terrigeneous input is < 30 %. The sediment of the Kazantsevo Interglacial, which was taken from the Continent Ridge site only, was laminated, biogenic and diatom-rich (Charlet et al. op. cit.). The transitions between glacial and interglacial phases were clearly marked by the transition from grey to brownish (diatom-rich) colour of the sediment (Fig. 13).

Fig. 13. Core CON01-603-3, segment 458-590 cm: shift from grey terrigenic material (glacial periods) towards brownish diatom-rich material (warm period).

2.4.2 Short and piston core sampling

Short cores: During the coring campaigns in July 2001 and July 2002, a series of short (gravity) cores (60 – 70 cm long, covering all or parts of the Holocene) were taken using a gravity corer (EAWAG-63) with a PVC-liner (Ø 63 mm) (M. Sturm, EAWAG, Switzerland; E. Vologina, Institute of Earth Crust, State University Irkutsk, Russia). Cores were collected with intact water to sediment interfaces. For pigment analyses cores from ´Vidrino´, ´Posolski´, and ´Continent Ridge´ coring sites were sliced on ship under dim light in contiguous samples 0.5 cm thick for the upper 20 cm and 1 cm thick below.

Six additional short cores taken from the South basin, Selenga Delta, Barguzin Bay, and North basin, were dedicated to the study of the pigment degradation processes within the oxidised surface sediment. From these additional cores only the oxidised layers (up to 20 cm) were sliced into contiguous 1 cm thick samples. All short cores slices were freeze-dried on ship within 24 h upon slicing and stored frozen at -20° C until analysis.

Piston cores: Several piston cores were taken during the CONTINENT cruise in July 2001 using aluminium liners (Ø 120 mm; Fig. 14; D. Meischner, University of Göttingen, Germany). The piston cores had length of approximately 11 m. The piston cores were sealed, eliminating at a maximum headspace for gases, stored in the liner at ambient temperature during transport and at 4° C in the laboratory at GFZ Potsdam (Germany). For pigment analysis samples from piston core number CON01-603-3 (Continent Ridge) were taken from the centre of the liner, which should not have been affected by light or oxygen. From this piston core the segments W0006 and W0005 (corresponding to cm 428 – 578), covering the Kazantsevo and its transitions to the glacial periods, were sliced at each centimetre. All subsamples (0.4-1.5 g dry weight) were immediately frozen, freeze-dried within 7 days and stored frozen at –20° C until analysis.

Fig. 14. Recovery of the c. 11 m long piston cores. Fotos from J. Klump (http://continent.gfz-potsdam.de/html/gallery).

2.4.3 Pigment and C/N-analyses in sediment samples

The analyses of pigments (HPLC) and TOC and TN in the sediment samples were performed according to the methods described in chapter 2.3.2 and 2.3.3 for sediment trap samples.

2.4.4 Chronography

Surface sediment: The recent mass accumulation rates of the short cores were determined based on excess-activity of ^{210}Pb, measured with a CANBERRA well-type γ-detector (M.

Sturm, EAWAG, Switzerland). These rates are valid for the uppermost layer (approximately 150 years), but are difficult to be extrapolated into longer-term sedimentation rates, valid for depositional time scales of thousands years.

Holocene: According to AMS radiocarbon dating of pollen, the average sedimentation during the Holocene was 17.29 ± 0.39 cm kyr^{-1} at Vidrino, 11.6 ± 2.3 cm kyr^{-1} at Posolski, and 6.86 ± 0.21 cm kyr^{-1} at Continent Ride (Piotrowska et al. 2004). The ^{14}C sedimentation rates were also confirmed by determinations of the magnetostratigraphy on parallel piston cores (Demory et al. 2005). Subsequent dates (gathered by AMS radiocarbon dating or magnetostratigraphy) are quoted as kyr before present (kyr BP) and refer to calibrated ages. However, as dating in Lake Baikal is a complex issue for a number of reasons (cf. Colman et al. 1996, Karabanov et al. 2000a) dating of the most recent Holocene periods should be considered as indicative rather than exact.

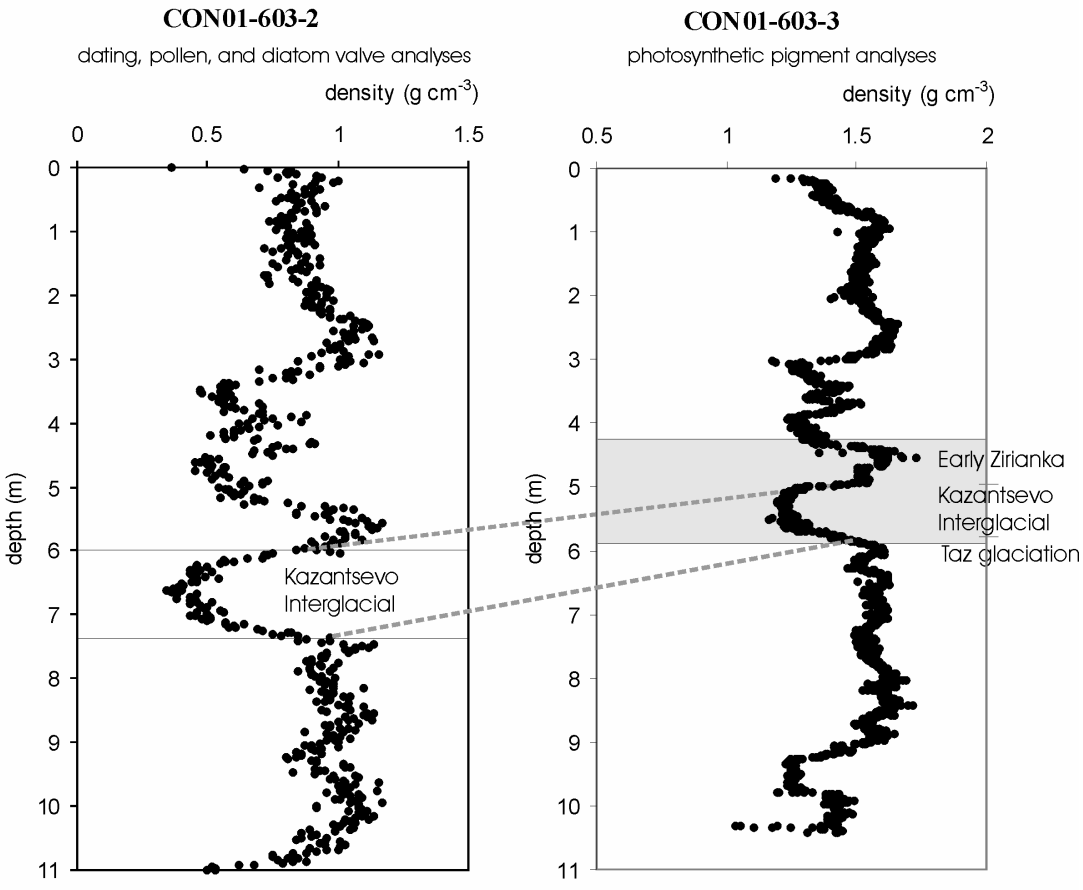

Fig. 15. Density along core CON01-603-2 used for dating, for pollen and for diatom analyses and along core CON01-603-3 used for pigment analyses. Both cores were taken from the same site (Continent Ridge) in the North basin. The highlighted rectangle marks the segment where photosynthetic pigments were analysed. Pollen and diatom analyses showed that the Kazantsevo Interglacial in core CON01-603-2 was between 6.10 m to 7.20 m (Granoszewski et al. 2005, Rioual and Mackay 2005). According to the density, this section corresponded to the section between 4.80 m and 5.60 m in core CON01-603-3.

Last Interglacial (Kazantsevo): The Kazantsevo segment has been determined within the 11 m long piston core based on the dating by magnetostratigraphy (Demory et al. 2005), on the lithology (Charlet et al. 2005), as well as on the high-resolution pollen and diatom records (Granoszewski et al. 2005, Rioual and Mackay 2005). These analyses have been carried out on a parallel core (CON01-603-2), whereas for pigment analyses core CON01-603-3 was used, because analyses of photosynthetic pigments required that the sediment had not previously been exposed to light or oxygen. Both cores were taken from the same site (Continent Ridge). High-resolution density analysis of both cores allowed locating the Kazantsevo Interglacial within the core CON01-603-3 (Fig. 15). Density was measured with a GEOTEK Multi-Sensor Core Logger at an interval of 0.5 cm with a counting time of 5 sec (P. Sorel, GFZ Potsdam, Germany). According to the diatom analysis the Kazantsevo spanned from 127.5 to 117 kyr BP (Rioual and Mackay 2005). According to the pollen analysis, the Kazantsevo spanned from 129 to 117.4 kyr BP (Granoszewski et al. 2005).

2.5 Statistics used

Variance analyses, Spearman-Rho and Pearson correlations, linear regressions, principal components analysis (PCA) and discriminance analysis were calculated with SPSS© (SPSS Inc., Chicago, IL, USA) statistical package. Canonical correlation analysis (CCA) was calculated with Statistica© (StatSoft Inc., Tulsa, OK, USA). Nearest neighbouring interpolation was performed using ArcMap© (ESRI Geoinformatik GmbH, Kranzberg, Germany). The Simpson index and Shannon-Wiener index were calculated with BioDap© (New Brunswick, Canada, cf. Magurran 2003) using cell abundances. Curve fittings were performed with TableCurve 2D® (Systat Software Inc., Point Richmond, CA, USA).

3 RESULTS

3.1 Recent spatial and seasonal phytoplankton and pigment distribution

3.1.1 Regional distribution

The phytoplankton in Lake Baikal included autotrophic picoplankton (APP), nano- and microphytoplankton. The phytoplankton biovolume, the Chl*a* and other phytoplankton pigments were distributed very heterogeneously in Lake Baikal, thereby indicating variations of both phytoplankton abundance and composition. Differences were found between the open basins (South, Centre, and North) as well as between the near-shore (Maloe More) and river-inflow (Selenga Delta, Barguzin Bay) sites.

Regional distribution of APP, nano- and microphytoplankton: The whole lake median of the total phytoplankton biovolume was 0.61 $mm^3\ L^{-1}$, of which 78 % was nano- and microphytoplankton and 22 % APP. The median APP biovolume over the whole lake was 0.097 $mm^3\ L^{-1}$ and significant differences for the total APP biovolume were found in the following order: Selenga Delta > South, Centre > North (Fig. 16). Thus, the APP comprised only 11 % of the total phytoplankton biovolume in the North, but 61 % in the Selenga Delta (Fig. 16). Eukaryotic APP dominated in the South, whereas cyanobacterial APP dominated in the Centre, North and Selenga Delta (Tab. 2).

The median nano- and microphytoplankton biovolume was 0.4 $mm^3\ L^{-1}$ (Fig. 16). No significant differences were found between individual regions, either based on biovolumes (Fig. 16) or cell numbers. Bacillariophyceae dominated the nano- and microphytoplankton assemblage all over the lake in both years with 70 – 90 % by volume (Tab. 2), while all other groups contributed less than 10 %.

In 2002, nano- and microphytoplankton species were investigated in greater detail than in 2001. Therefore, the results presented here will be limited to 2002. On average 53 % of the nano- and microphytoplankton biovolume resulted from endemic species (see Appendix C - Tab. 1 for endemic species). Between 9 and 14 nano- and microphyto-plankton species were identified at the different sites and depths. The mean reciprocal Simpson diversity index for the whole lake was 3.96 (Shannon-Wiener 1.92) ranging at individual sites from 2.1 to 3.6 (Tab. 2), but no significant differences or trends between the regions, stations and depths could be found for the diversity indices.

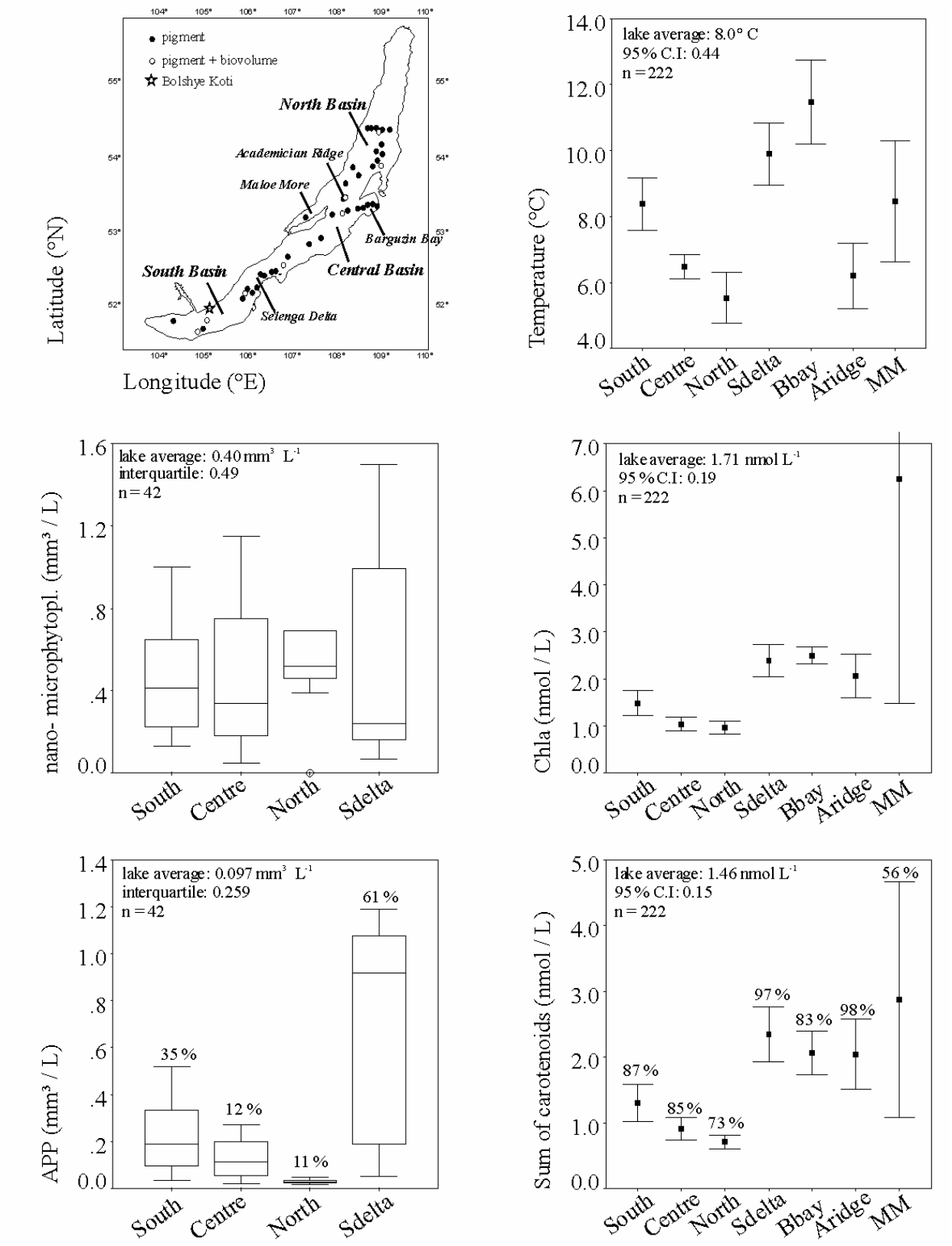

Fig. 16. Regional variability of temperature, Chl*a*, carotenoids, and biovolumes; bars represent means with 95 % C.I. and boxes medians with interquartile ranges (25-75 %). A map of Lake Baikal showing the sampling sites is given for orientation. The APP biovolume vs. total phytoplankton biovolume ratios as well as the sum of carotenoids vs. Chl*a* are given as percentages. The number of samples (n) for temperature and pigments was 43 - 52 in each of the three open basins and at Selenga Delta (Sdelta), 22 at Barguzin Bay (Bbay) and 6 at Academician Ridge (Aridge) and Maloe More (MM). The number of samples (n) for biovolumes was 9 - 12 in each of the three open basins and Selenga Delta.

All species were tentatively grouped into functional groups (Tab. 2) according to the scheme of Reynolds et al. (2002). The dominant functional group (by biovolume) was that of vernal bacillariophycean blooms typical of oligotrophic lakes (A), due to the dominance of *Cyclotella* species (Tab. 2). At a few sites the dominances changed. In the South (5 m) the dominant functional group was that usually found at the start of summer stratification in oligotrophic conditions (E) (Tab. 2). This group indicated slightly higher nutrient availability than the functional group (A). Also the groups (S1) and (Z) were found in the Selenga Delta, which indicated summer stratification (Tab. 2).

Tab. 2. Regional variation of diversity, functional groups and of the contribution to total biovolume. Only those species were listed here, which contributed more than 1 % at any of the sites.

			South (C)			South (E)				Centre (N)			North (E)			North (C)			A Ridge			S Delta (N)			S Delta (S)		
Regions[a]																											
Depth (m)			5	10	30	5	10	20	85	5	10	16	5	10	30	5	10	30	5	10	45	5	10	16	5	10	30
Diversity Index[b]			3.11	3.48	2.17	3.91	3.54	1.68	4.98	3.68	4.26	3.56	3.35	1.39	2.51	2.32	3.74	4.06	4.68	3.89	2.28	3.82	1.02	1.74	3.40	1.17	1.57
Dominant FG[c]			A	A	A	E	A	A	B	A	A	C	A	A	A	A	A	A	A	A	A	A	S_1	Z	A	A	B
Group	**Species**[d]	***FG***[c]	**Percentage contribution to total biovolume**																								
Bacillariophyceae	S. meyerii	*B*																									
	C. dubius	*B/C*																									
	A. baicalensis	*B*																									
	S. acus	*D*																									
	C. baicalensis	*A*																									
	C. ornata and minuta	*A*																									
	N. acicularis	*C*																									
Chlorophyta	K. longiseta f. tenuis	X_3																									
	K. longiseta f. longis.	X_3																									
	K. longiseta f. variab.	X_3																									
	Koliella sp.	X_3																									
	M. pseudomirabile	X_1																									
	E. genevensis	*F*																									
Pyrr.	Glenodinium sp.1	X_2																									
	Glenodinium sp.2	X_2																									
Crypto.	Cryptomonas sp.	*Y*																									
	R. pusilla	X_2																									
	R. lens	X_2																									
	Rhodomonas sp.	X_2																									
Chrysoph.	Flagellata, small	*E*																									
	Chrysidalis sp.	-																									
	Chrysococcus sp.	X_3																									
	D. cylindricum	*E*																									
Cyano.	Aulosira sp.	*H*																									
	eukaryotic APP	X_3																									
	cyanobacterial APP	*Z*																									

..... **<1%**
——— **1-10 %**
——— **10-30 %**
——— **30-50 %**
——— **50-80 %**
═══ **> 80 %**

[a] - Abbreviations: C- Central, E - Eastern, N- Northern, S- Southern.

[b] - Reciprocal Simpson diversity index

[c] - Rough interpretation of the functional groups (FG;details in Reynolds *et al.* (2002); the classification of endemic species base on their description in the literature and classification of related species): A,B,C+D: vernal diatom blooms in mixed oligotrophic (A) to eutrophic (D) lakes; E, F, H: start of summer stratification, E: able to mixotrophy, F: oligotrophic Chlorococcales, H: dinitrogen-fixing Nostocaleans; L_M: summer epilimnia in eutrophic lakes, sensitives to mixing; S_1, X_1, X_2+X_3: tolerant to stratification, sensitive to mixis, filamentous cyanobacteria (S_1) or eukaryotic pico- and smaller nanoplankton (X) in shallow mixed turbid (S_1) or clear (X) layers from eu- (X_1) to oligotrophic (X_3). Y is represented by larger cryptomonad species in enriched conditions; Z is represented by cyanobacterial APP.

[d] - All species are listed with their full name in Table 2.

Besides *Cyclotella* species, flagellata, most of them belonging to Chrysophyceae, were numerous across the whole of the lake (Tab. 2). The contribution to the total biovolume of these flagellates was nonetheless higher in the South and Selenga Delta than in the North (Tab. 2). A high number of *Koliella longiseta* (Chlorophyta) was found besides *Cyclotella* in the South and Centre, as well as a high number of *Nitzschia acicularis* in the Centre (Bacillariophyceae; Tab. 2). In the North *Cryptomonas* spp. (Cryptophyta) were found among the flagellates in high concentrations as well as *Rhodomonas pusilla* (Cryptophyta), which dominated the cryptophycean species at all other sites (Tab. 2). Furthermore, in the North the contribution of *Cyclotella* species to the total biovolume was higher than at all other sites unless Academician Ridge (Tab. 2). At Academician Ridge, *Cyclotella* cells were very numerous and the biovolume per *Cyclotella* cell was much higher than at the other sites. Their diameter reached 150 µm. The number of *Aulosira* sp. (cyanobacteria) cells was the highest at both sample sites within the large Selenga Delta, but they were much less abundant (> 5 times) at 5 m than at 10 m and 30 m (Tab. 2). Potential grazers of these filamentous cyanobacteria (the ciliophora *Strombidium* sp.) were numerous at 5 m but not in the deeper layers. The respective *Aulosira* species differed morphologically from *A. implexa* and *A. laxa*, which up until now were the only *Aulosira* species described for Lake Baikal (Bondarenko 1995) and has thus not yet been described for Lake Baikal. The description will be done elsewhere.

*Regional differences of temperature and Chl*a*:* The mean July temperature across the whole lake (including all sampled depths) during the three expeditions was 8° C (Fig. 16, Fig. 17). A significant decline in temperature was found along the transect South > Centre > North (Fig. 16), with the difference between Centre and North only given at 90 % C.I. The Selenga Delta and Barguzin Bay had the highest temperatures (Fig. 16, Fig. 17). Nonetheless, the surface water (upper 5 m) in the Maloe More was also warmer compared to the open basins (Fig. 17).

The Chl*a* concentration was significantly correlated to temperature. The whole lake average Chl*a* concentration (2001-2003, including all sample depths) was 1.71 ± 0.19 nmol L^{-1} (95 % C.I., n=222; Fig. 16). The Chl*a* concentrations in the three open basins (South, Centre and North) were significantly lower compared to those at the river inflows (Selenga and Barguzin) and within the open basins the North had a significantly lower Chl*a* concentration than the South (Fig. 16). The warm surface waters of the shallow Maloe More were Chl*a*-rich compared to the open basins (Fig. 17). The

interpolation of the Chl*a* results showed furthermore the transition from Chl*a*-rich near-shore regions to Chl*a*-poor open basin regions (Fig. 17).

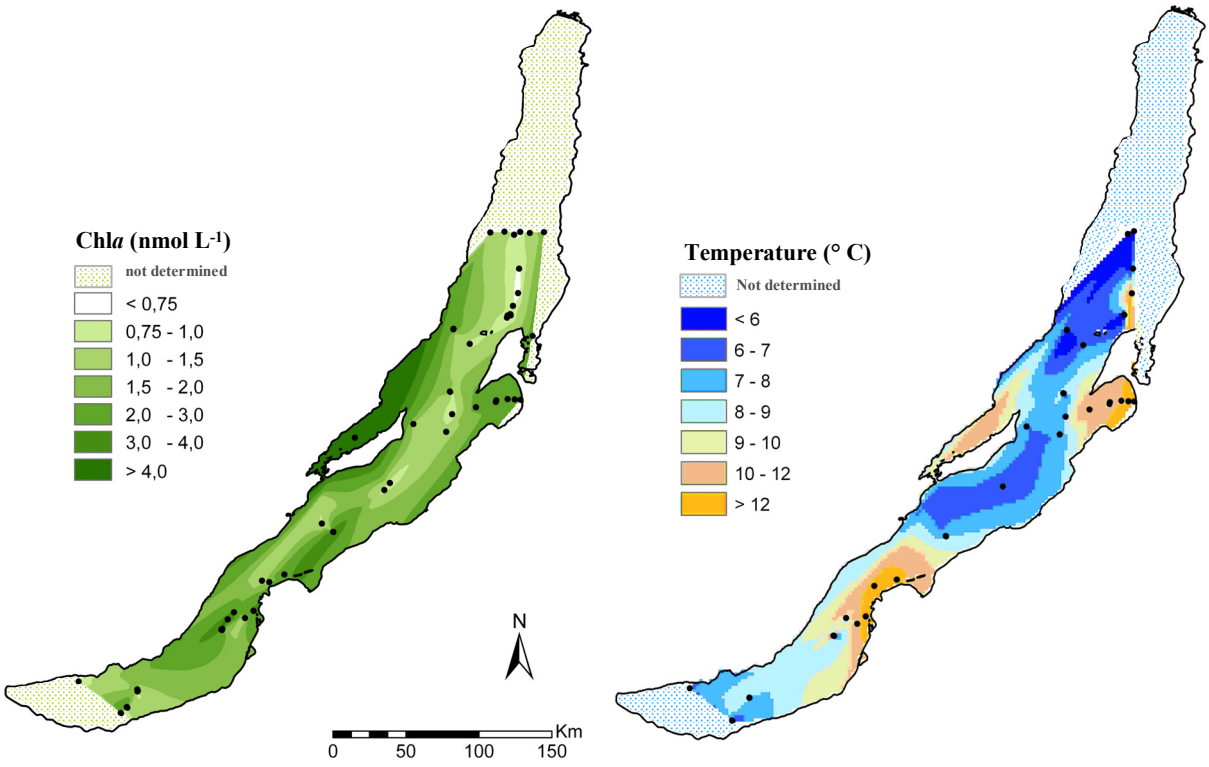

Fig. 17. Map of Chl*a* (left) and temperature (right) by nearest neighbouring interpolation from direct water samples taken from surface waters (0.5-5 m).

Fluorescence horizontal transects (c. 3 m water depth) performed in July 2002 and July 2003 during ship travel confirmed the interpolation of the Chl*a* and temperature distribution (Fig. 18). From those transects the changes within the basins and towards the river inflows and near-shore regions could be continuously tracked and these transects confirmed the extremely heterogeneous Chl*a* distribution and temperature gradients along the lake (Fig. 18). From the Ushkanin Islands (in front of the west coast of the Svyatoi Nos peninsula) along the west coast of Svyatoi Nos towards the Barguzin inflow, for example, the temperature increased from 10° to 15° C and the Chl*a* concentrations doubled at the same time from 1.6 to 3.2 µmol L^{-1} (Fig. 18-1). From the North of Svyatoi Nos along the east coast of Olkhon Island the profiles indicated a clear shift from higher temperatures and Chl*a* concentrations near Svyatoi Nos to low temperatures and Chl*a* concentrations in the open water of the Central basin; and temperature and Chl*a* concentration increased again nearing the southern end of Olkhon Island (Fig. 18-2). A profile from the harbour of Listvianka (South basin) to the North of

the Selenga Delta showed furthermore the increase of temperature and Chl*a* concentration nearing the Selenga Delta (Fig. 18-5).

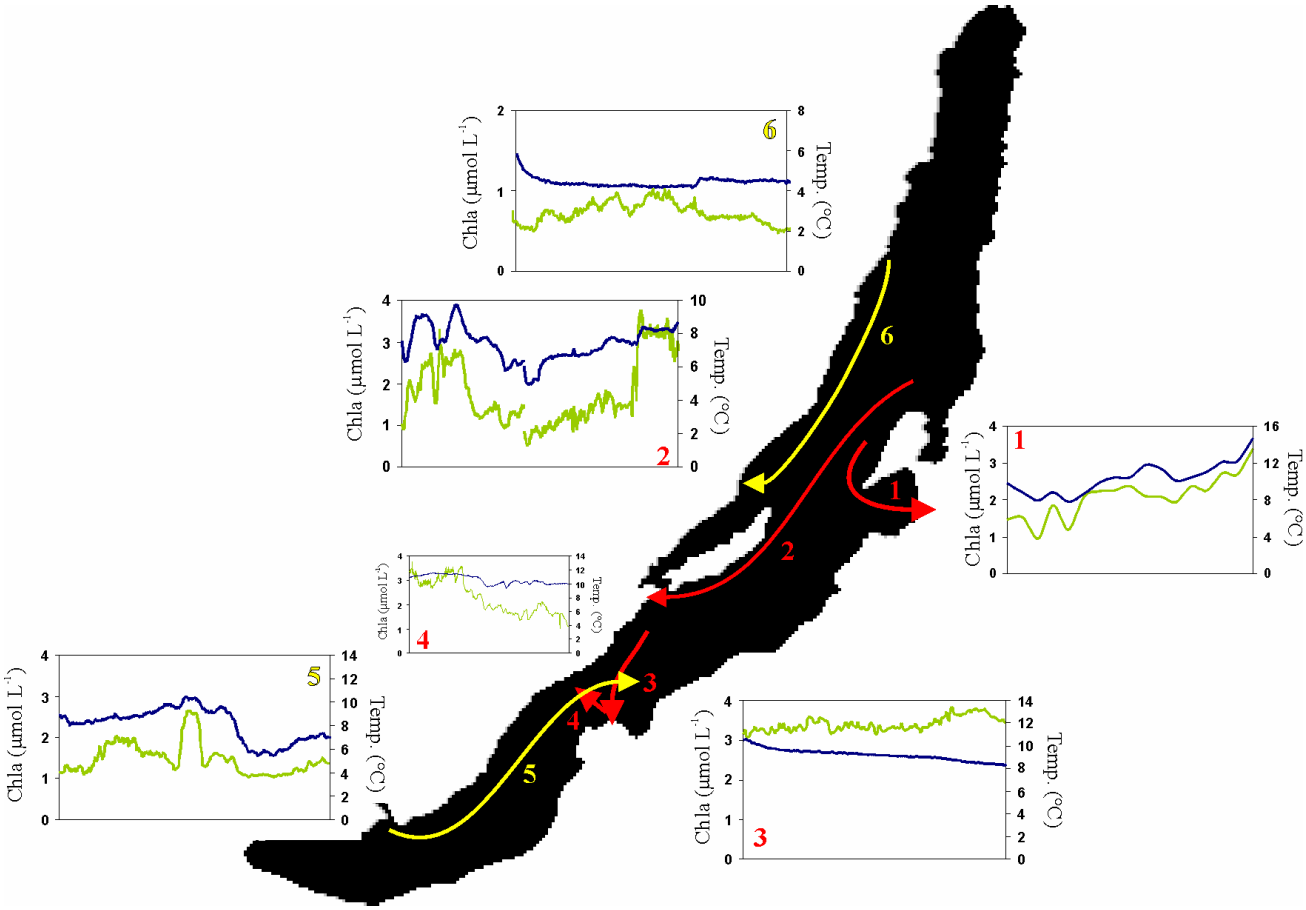

Fig. 18. Horizontal Chl*a* (green) and temperature (blue) profiles by underway measurements (c. 3 m water depth) in July 2002 (red) and July 2003 (yellow).

Regional distribution of carotenoids: The total carotenoid concentration was significantly correlated to Chl*a* (r^2= 0.94, p< 0.001, n= 222) and was 85 % of the Chl*a* concentration considering molar ratio (60 % considering weight ratios; Fig. 16). As was shown for the Chl*a* variations, the total carotenoid concentrations were significantly lower in the open basins than at the river inflow sites and the North also showed significantly lower carotenoid concentrations than the South (Fig. 16). The ratios of carotenoids that collected light (such as fucoxanthin) to carotenoids that protected cells against high light (such as diadinoxanthin) was not correlated to the total carotenoid vs. Chl*a* ratio (data not shown). Only at Maloe More the very low carotenoid vs. Chl*a* ratio clearly resulted from lowering protecting carotenoids, indicating thus low light acclimation of the phytoplankton at that site.

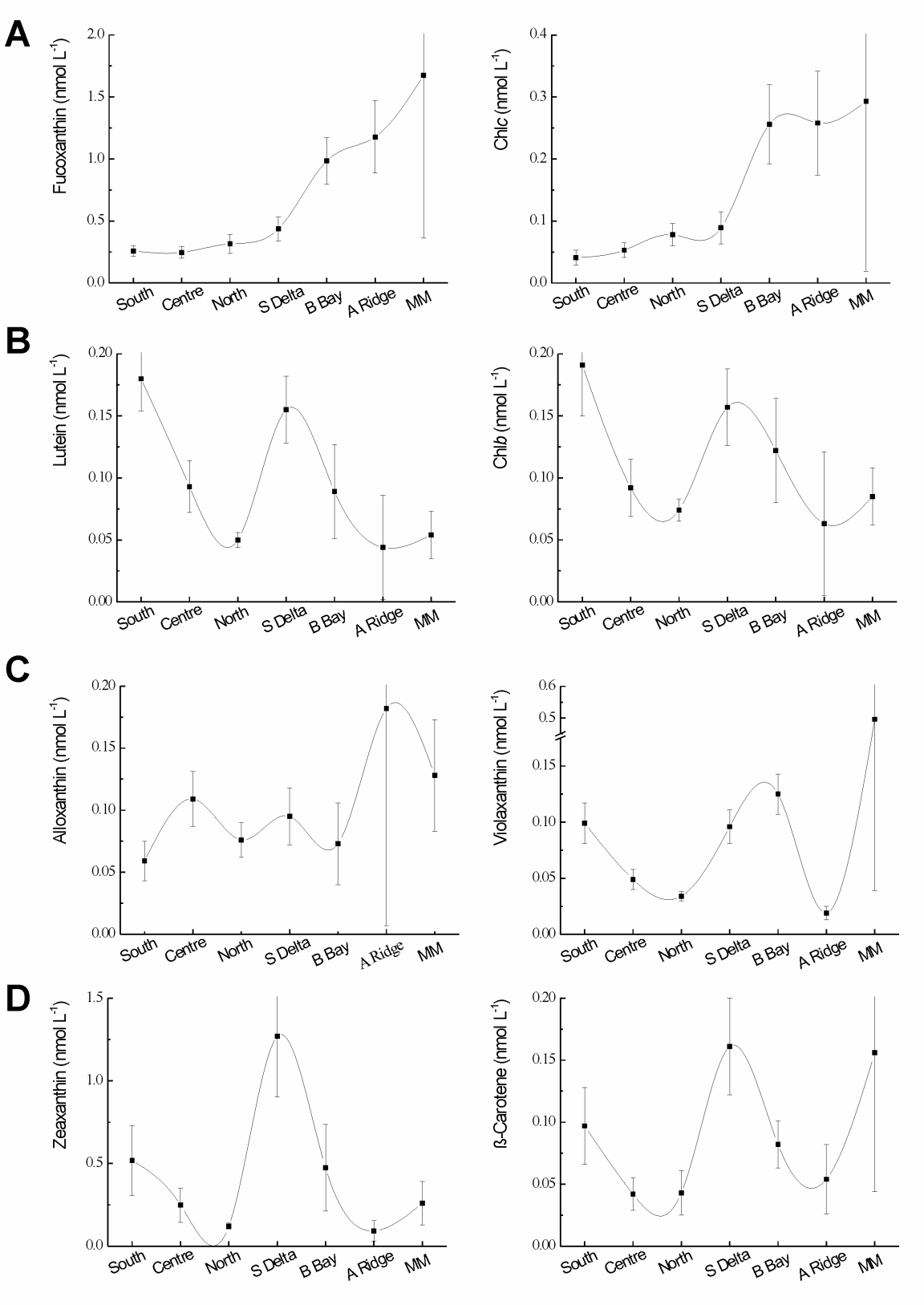

Fig. 19. Regional variability of the marker pigment concentrations for (A) Bacillariophyceae+ Chrysophyceae (fucoxanthin and Chl*c*), (B) for Chlorophyta (lutein and Chl*b*), (C) for Cryptophyta (alloxanthin) and for Eustigmatophyceae (violaxanthin), and (D) for cyanobacterial APP (zeaxanthin and ß-carotene). Combined data set 2001-2003 (July) was used for the calculations. Error bars represent a 95 % C.I. Abbreviations: SDelta – Selenga Delta, BBay – Barguzin Bay, ARidge – Academician Ridge, MM – Maloe More. Lines do not indicate trends between two neighboured points, but serve to visualise regional differences.

Taking a lake average (July 2001, 2002 and 2003), the dominant carotenoids were zeaxanthin, fucoxanthin and lutein. Fucoxanthin (Fig. 19A), Chl*c* (Fig. 19A), diadinoxanthin and diatoxanthin concentrations showed no significant differences between the open basins, but significantly higher values were found at Barguzin Bay and at Academician Ridge. Chl*b* and lutein showed significantly higher concentrations in the South than in the Centre and North, as well as at Academician Ridge and Maloe More (Fig. 19B). Alloxanthin (Fig. 19C) and peridinin did not show significant variations between the open basins and the remaining regions. Violaxanthin concentrations showed significant decreases in the order South > Centre > North (Fig. 19C). Zeaxanthin and ß-carotene were significantly highest in the Selenga Delta, and the South showed significantly higher concentrations than the North (Fig. 19D).

A discriminant analysis (Wilk´s Lamba=0.08, $p<0.001$; Fig. 20) indicated, that considering the pigment composition, Academician Ridge and Barguzin Bay (root 1, $p<0.001$) as well as Maloe More (root 2, $p<0.001$) were most distinct from all other regions. The major pigment within root 1 was fucoxanthin (standardised canonical coefficient = 0.89) and the major pigment, influencing root 2, was violaxanthin (standardised canonical coefficient = -1.17), indicating major influence of Bacillariophyceae+Chrysophyceae at Academician Ridge and Barguzin Bay and of Eustigmatophyceae at Maloe More.

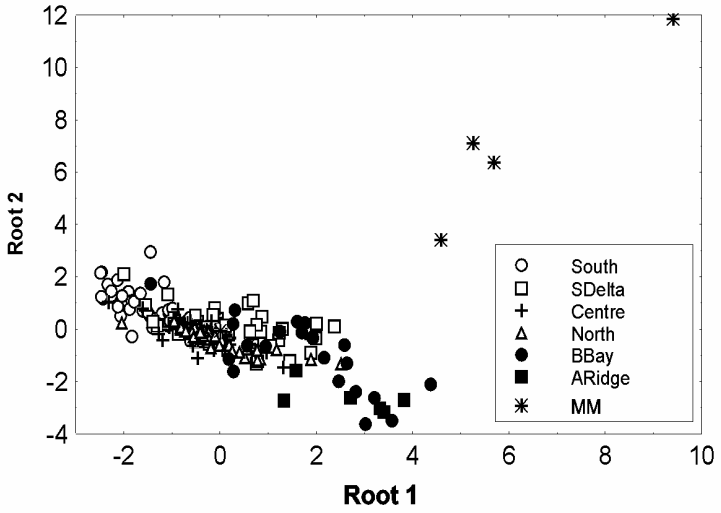

Fig. 20. Discriminance analysis separating the seven regions according to the pigment distribution. See Fig. 19 for abbreviations.

Estimation of phytoplankton composition using marker pigments: Accessory pigments can be used to estimate the composition of the phytoplankton assemblage (cf. Fietz and Nicklisch 2004, Appendix A). Based on the whole data set of 2001 to 2003 (n= 222)

significant molar Chl*a*/marker pigment ratios were calculated using multiple linear regression. This resulted in the following equation:

Chl*a* = 1.26 ·Fuco + 1.62 ·Allo + 3.0 ·Chl*b* + 0.61 ·Zea` + 6.49 ·Viola` (Tab. 3A), whereby Chl*a* was the total Chl*a* from the five phytoplankton groups, "Fuco" (fucoxanthin) was the marker for Bacillariophyceae+Chrysophyceae, "Allo" (alloxanthin) was the marker for Cryptophyta, "Chl*b*" was the marker for Chlorophyta, "Zea´" was the marker for cyanobacterial APP and "Viola´" was the marker for Eustigmatophyceae. Zea´ was the cyanobacterial zeaxanthin and Viola´ was the eustigmatophycean violaxanthin only (cf. Fietz and Nicklisch 2004, Appendix A for calculations; cf. Fietz et al., submitted, Appendix B for having considered Eustigmatophyceae to be a common member of the Baikalian phytoplankton). The coefficient of determination (r^2) was high (0.97; Tab. 3A) and the calculated Chl*a* matched the measured Chl*a* with a mean error of 6 % and a maximum error of 24 % in all regions and years.

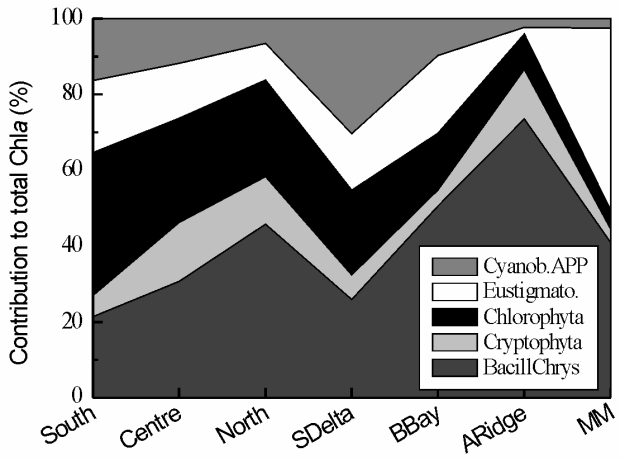

Fig. 21. Contribution of main chemotaxonomic phytoplankton groups to total Chl*a*. Abbreviations: ARidge – Academician Ridge, Bacill.Chrys. – Bacillariophyceae+Chrysophyceae, BBay – Barguzin Bay, Cyanob. – cyanobacterial, Eustigmato. – Eustigmatophyceae, SDelta – Selenga Delta.

The contributions to total Chl*a* of the chemotaxonomic groups varied between the regions (Fig. 21). Whereas Bacillariophyceae+Chrysophyceae contributed only 20 % to the total Chl*a* in the South and Selenga Delta, its contribution was higher (45-50 %) in the North and Barguzin Bay and highest (70 %) at Academician Ridge. The contribution of Cryptophyta was small (< 15 %) all over the lake. The contribution of Chlorophyta to the total Chl*a* was highest in the South (40 %) and lowest at Academician Ridge and Maloe More (< 10 %). The contribution of Eustigmatophyceae was about 20 % in the South and Selenga Delta and was highest at Maloe More (45 %). Possibly several Chrysophyceae contributed to the total violaxanthin at Maloe More so that the eustigmatophycean violaxanthin was overestimated at that site. The contribution of the cyanobacterial APP was highest in the Selenga Delta (30 %) and lowest in the North, Academician Ridge and Maloe More (<5 %).

Tab. 3. Molar ratios of Chl*a* vs. marker pigments and their respective statistics calculated by multiple linear regression (A) for the complete data set (July 2001, July 2002 and July 2003) and (B) regionally differentiated.

A) Whole lake	**molar ratio**	**P**	**partial c.**	**95 % C.I.**	**P**	**r²**
Chl*a* / Fucoxanthin	1.26	< 0.001	0.81	0.12		
Chl*a* / Chlb	3.00	< 0.001	0.69	0.42		
Chl*a* / Alloxanthin***	1.62	< 0.001	0.37	0.54	< 0.001	0.98
Chl*a* / Zeaxanthin*	0.61	< 0.001	0.82	0.06		
Chl*a* / Violaxanthin**	6.49	< 0.001	0.84	0.57		
B) Regions	**molar ratio**	**P**	**partial c.**	**95 % C.I.**	**P**	**r²**
South						
Chl*a* / Fucoxanthin	1.17	< 0.001	0.77	0.33		
Chl*a* / Chl*b*	3.28	< 0.001	0.95	0.37		
Chl*a* / Alloxanthin***	1.55	< 0.05	0.33	1.50	< 0.001	0.99
Chl*a* / Zeaxanthin*	0.79	< 0.001	0.96	0.07		
Chl*a* / Violaxanthin**	1.64	<0.005	0.45	1.10		
Centre						
Chl*a* / Fucoxanthin	1.57	< 0.001	0.94	0.18		
Chl*a* / Chl*b*	3.18	< 0.001	0.87	0.57		
Chl*a* / Alloxanthin***	1.17	< 0.001	0.55	0.57	< 0.001	0.99
Chl*a* / Zeaxanthin*	0.57	< 0.001	0.77	0.15		
Chl*a* / Violaxanthin**	3.35	< 0.001	0.52	1.76		
North						
Chl*a* / Fucoxanthin	1.12	< 0.001	0.64	0.38	< 0.001	0.94
Chl*a* / Chl*b*	7.36	< 0.001	0.73	1.96		
Selenga Delta						
Chl*a* / Fucoxanthin	1.39	< 0.001	0.69	0.45		
Chl*a* / Chl*b*	3.87	< 0.001	0.70	1.24		
Chl*a* / Alloxanthin***	1.48	0.08	0.26	1.69	< 0.001	0.98
Chl*a* / Zeaxanthin*	0.66	< 0.001	0.86	0.12		
Chl*a* / Violaxanthin**	3.45	< 0.05	0.32	3.16		
Barguzin Bay						
Chl*a* / Fucoxanthin	0.79	< 0.001	0.68	0.41		
Chl*a* / Chl*b*	5.77	< 0.001	0.85	1.71	< 0.001	0.97
Chl*a* / Violaxanthin**	9.75	< 0.001	0.79	3.61		

* cyanobacterial zeaxanthin only (see text)
** eustigmatophycean violaxanthin only (see text; see Fietz et al., submitted, Appendix B for Eustigmatophyceae)
*** In a preliminary study (Fietz and Nicklisch 2004, Appendix A) it was mentioned that caloxanthin, a zeaxanthin transformation product, possibly coeluted with alloxanthin in some samples. In the present study, the correlation between α-carotene and alloxanthin, both contained in Cryptophyta, was significant. Therefore we assumed that alloxanthin in almost all samples did not coelute with caloxanthin. Few outliers from the significant alloxanthin/α-carotene relationships were omitted in the multiple linear regression calculations of the present study.

The factors calculated for the whole lake do not account for the variances of differential phytoplankton compositions in the individual regions of the lake (as indicated by the regional variations of the species and marker pigments, Fig. 19). Therefore, individual Chl*a*/marker pigment ratios were calculated for each region (Tab. 3B). The

splitting of the data set, however, limited the calculation of significant factors in the North and also in Barguzin Bay (Tab. 3B). In most cases the regionally differentiated factors did not differ significantly from those calculated for the whole lake data set (Tab. 3A,B) and, therefore, the use of the whole lake factors can be recommended.

Interannual variability: Significant differences in the Chl*a* concentrations were found in each basin when the three years were compared, particularly in the North (Fig. 22A). In 2001 the Centre had significantly the lowest Chl*a* concentrations, while in 2002 concentrations were lowest in the North (Fig. 22A). Similarly, significant interannual differences were found for each of the carotenoids, for Chl*b* (Fig. 22B), for Chl*c* (Fig. 22C), for the sum of carotenoids and for the carotenoids vs. Chl*a* ratios (data not shown), particularly in the North and Centre.

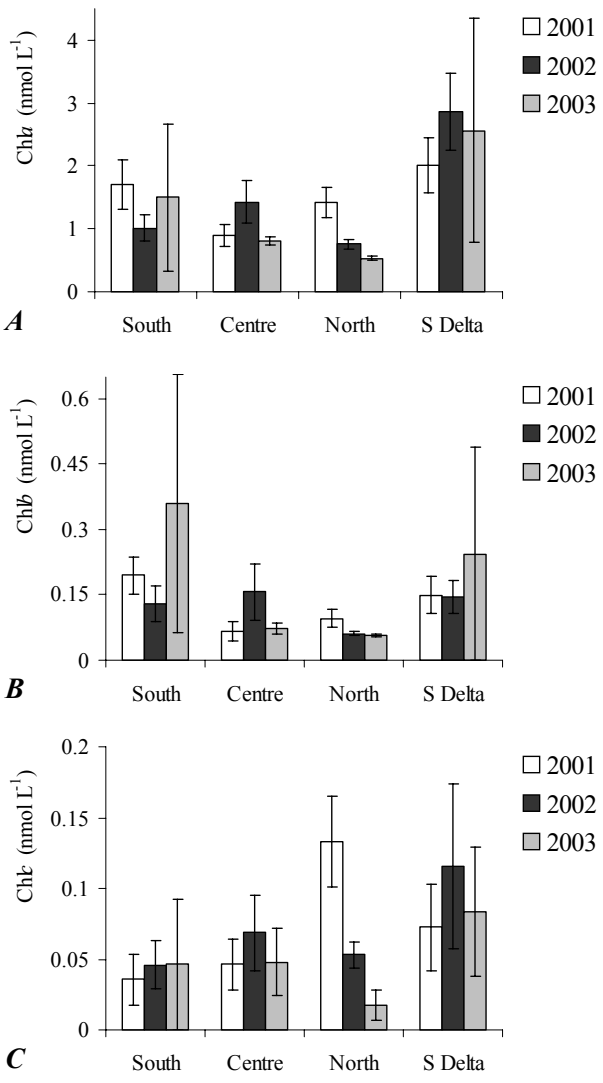

Fig. 22. Interannual variability of Chlorophylls: (A) Chl*a*; (B) Chl*b*, and (C) Chl*c*. Error bars represent a 95 % C.I. Abbreviation: S Delta – Selenga Delta.

High interannual variability was also found for the cyanobacterial and eukaryotic APP biovolume, particularly in the South and Centre (Fig. 23A). Nevertheless, the North had lowest APP biovolumes in both years and the Selenga Delta the highest (Fig. 23A). Additionally, high interannual variability was found for the nano- and microphytoplankton biovolume, particularly in the North, where a much lower biovolume was determined in July 2002 compared to July 2001 (Fig. 23B). This change in biovolume was mainly due to shifts in the species composition that means shifts in the biovolume/cell ratio (mainly of Bacillariophyceae, data not shown). As has been shown for the biovolumes (Fig. 23A,B) and for chlorophylls and carotenoids (Fig. 22), the estimated contributions of the distinct chemotaxonomic groups differed also between the three investigated years (Fig. 23C).

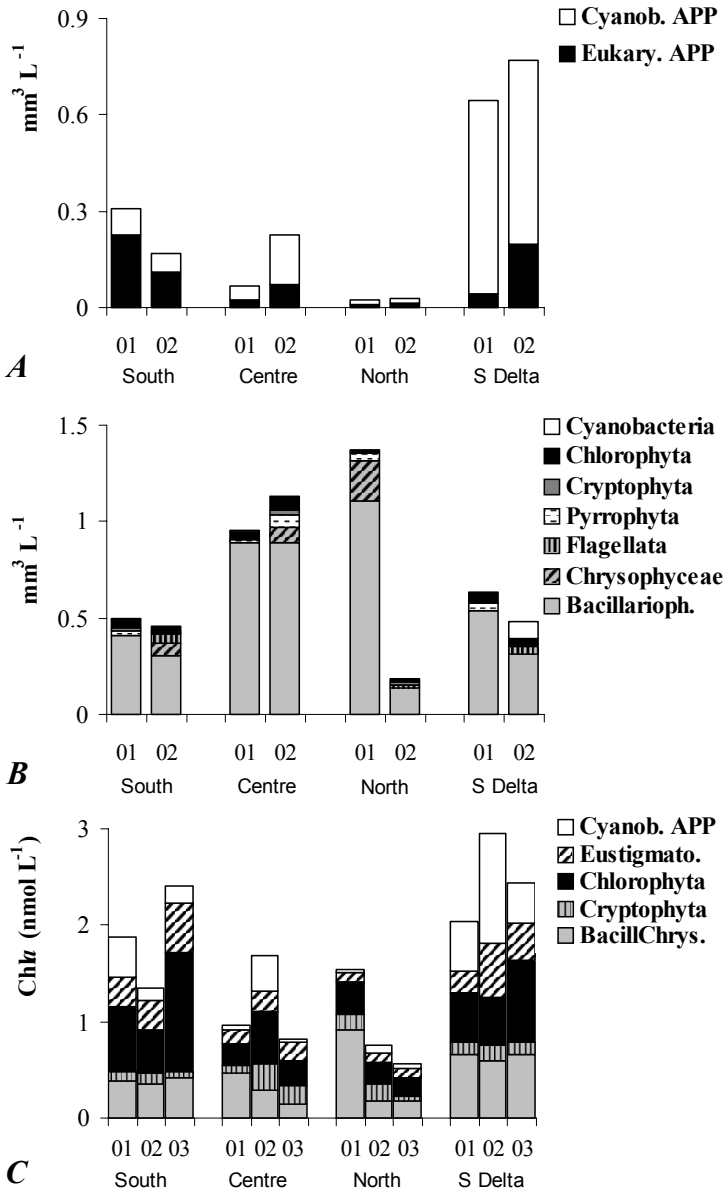

Fig. 23. Interannual variability of (A) eukaryotic and cyanobacterial APP biovolume; (B) nano- and microphytoplankton biovolume; (C) contribution of chemotaxonomic groups to total Chl*a* (see text for calculation); Abbreviations: Bacillarioph. – Bacillariophyceae, BacillChrys – Bacillariophyceae+Chrysophycea, Cyanob. APP – cyanobacterial APP, Eukary APP – eukaryotic APP, Eustigmato. – Eustigmatophyceae, S Delta – Selenga Delta.

Note: see Appendix B for having considered Eustigmatophyceae to be a common member of the Baikalian phytoplankton.

3.1.2 Vertical distribution

Temperature and chlorophyll depth profiles from January 2001 to December 2003 near Bolshye Koti (see Fig. 16 for location) are plotted in Fig. 24. A thin convective layer occurred under the ice in February, where temperatures below 0.5° C were found down to 25 m (Fig. 24). The temperature increased to 3° C between 50 m and 100 m, and remained between 3 and 4° C from 250 m down to the lake bottom (Fig. 24). Therefore, this period showed an inverse stratification, with mixing restricted to a shallow layer under the ice. Every year wind-induced mixing spanning over the upper 250 m occurred from May to June, after ice-break up, and another in November (Fig. 24). During spring overturn in 2001 Chl*a* concentrations up to 0.5 nmol L^{-1} were found down to 100 m and up to 0.25 nmol L^{-1} down to 250 m (Fig. 24). During the spring overturn in 2002 Chl*a* concentrations over 2 nmol L^{-1} were found down to 100 m and up to 0.5 nmol L^{-1} down to 250 m, while during summer stratification the Chl*a* concentration was low (<0.2 nmol L^{-1}) below 50 m (Fig. 24).

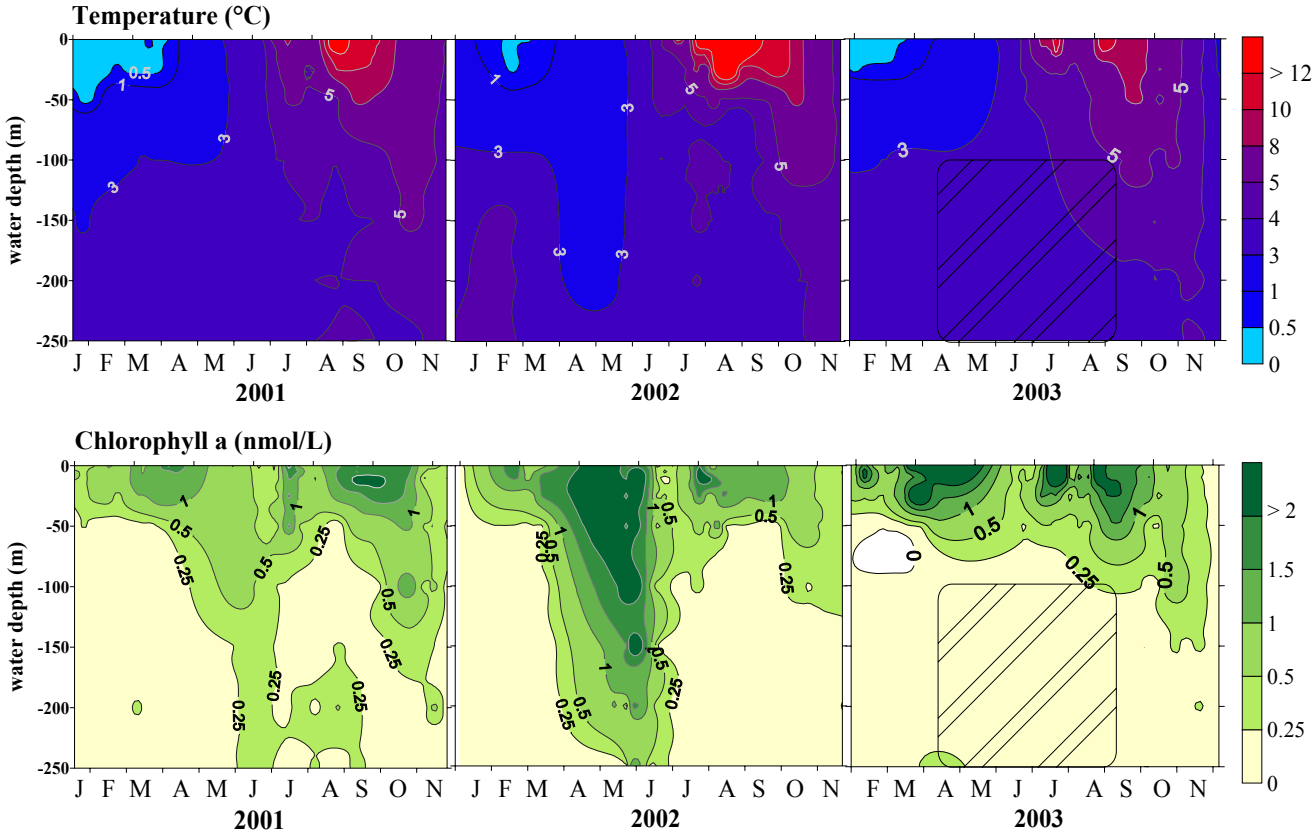

Fig. 24. Temperature and Chl*a* depth profiles (0-250 m) from January 2001 to December 2003 showing mixing and stratification over the season and regions. Values at the time of ice break-up (April) have been interpolated. From Mid-April to end of August 2003 data below 50 m were not available (hatched rectangle).

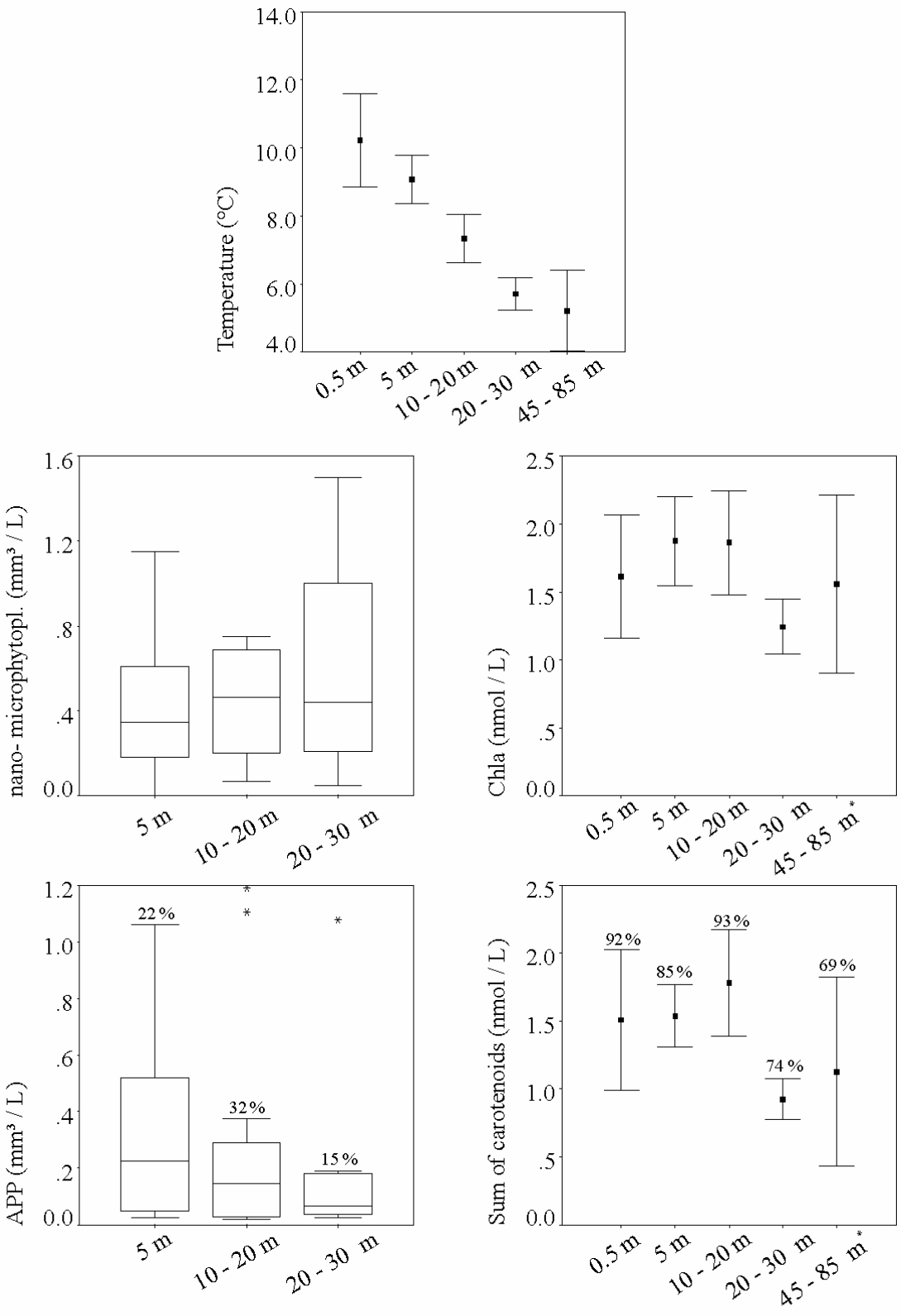

Fig. 25. Vertical variability of temperature, pigments (see Fig. 16 for bars and boxes). The APP biovolume vs. total phytoplankton biovolume ratios as well as the sum of carotenoids vs. Chl*a* are given as percentages. The number of samples (n) for temperature and pigments was 21 at 0.5 m, 110 at 5 m, 43 at 10-20 m, 36 at 20-30 m and 6 at 45-85 m. The number of samples (n) for biovolumes was 10 - 18 at each depth.

The average July temperatures of the lake (2001-2003) decreased significantly with the depth in the order: 0.5 m, 5m > 10-20 m > 20 – 30 m, 45 – 85 m (Fig. 25). Stratification and mixing might also result from conductivity in oceanic and also some freshwater systems, but in Lake Baikal conductivity varied only between 100 to 110 µS cm^{-1} (corrected to 20° C) between the individual regions as well as with the depth (Fig. 26). Mixing conditions varied among the different basins and regions. High-resolution temperature and conductivity depth profiles showed that in the North mixed conditions prevailed, while a weak stratification developed in the South and Selenga Delta. Stable stratification with a broad epilimnion developed in Barguzin Bay (Fig. 26). There, the conductivity showed a second maximum at 20-25 m, probably indicating the influence of subsurface water currents induced by the river (Fig. 26). The Chl*a* concentration in July showed a maximum at 16 m in the South, whereas it was rather homogeneously distributed in the North and Centre. It decreased with depth in the Barguzin Bay and most prominently in the Maloe More (Fig. 26).

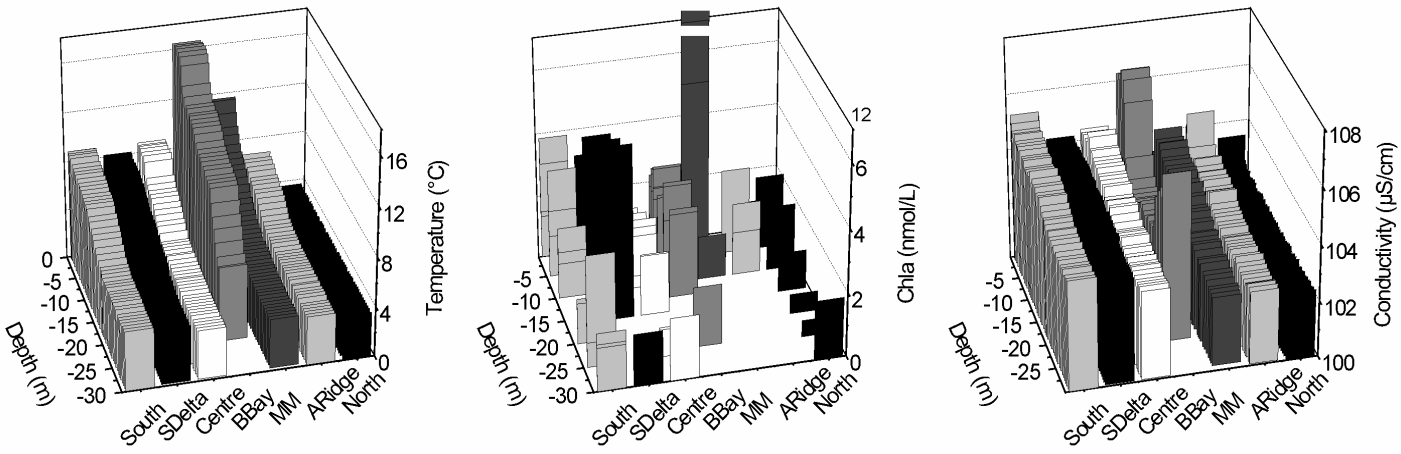

Fig. 26. Depth profiles (0-30 m) of (A) temperature, (B) Chl*a*, and (C) conductivity.

The combined data set of all samples collected during the July expeditions 2001 and 2003 revealed a significant decrease of the Chl*a* concentration and the sum of carotenoids below 20 m compared to the 5 m and 10 – 20 m samples (Fig. 25). The percentage sum of carotenoids compared to the Chl*a* was also lowest (74 % molar ratio) in the 20 – 30 m layers (Fig. 25). At several stations, deep Chl*a* maxima were found in depths of 45 m, 50 m and 85 m. Within these deep maxima the Chl*a* concentrations were as high as above 20 m (Fig. 25). The sum of carotenoids was lower in these deep layers than above 20 m and the percentage molar ratio was only 69 % (Fig. 25). At 45 – 85 m the ratio of ´light-collecting´ vs. ´protecting´ carotenoids was highest (data not shown),

indicating that the lower total carotenoid vs. Chl*a* ratio in greater depths resulted from reduced protecting carotenoids. Thus, as expected low-light conditions prevailed at the great depths, but high light conditions down to 10 – 20 m.

The total APP also decreased in the 20 – 30 m samples compared to the 5 m samples, whereas no significant changes could be found for the nano- and microphytoplankton (Fig. 25). There were some tendencies in both years that biovolumes differed with depths within the individual regions. The relatively shallow Selenga Delta for example showed a maximum of the APP biovolume at 16 m depth and of the nano- and microphytoplankton at 5 m (Tab. 2). Several species showed also distinct relationships with depth. *Aulacoseira baicalensis* for example formed a deep maximum in 85 m water depth in the South (Tab. 2).

Tab. 4. Canonical correlation analysis of set one comprising the environmental variables, and set two comprising total calculated Chl*a* and the respective percentage contribution of each phytoplankton group to the total calculated Chl*a*. See text for calculation of the contributions.

	Regional distribution				**Seasonal distrib.**	
	Canonical loadings				**Canon. loadings**	
	Root 1	**Root 2**	**Root 3**	**Root 4**	**Root 1**	**Root 2**
Set 1, environmental variables						
Latitude	-0.52	-0.67*	0.10	0.52	-	-
Water Depth	-0.51	0.44	-0.71*	0.20	-	-
Stratification	0.99*	-0.05	-0.15	-0.05	-0.73*	-0.68
Temperature	0.53	-0.47	-0.20	-0.68*	-0.74*	0.67
Set 2, phytoplankton group contribution						
Total Chl*a*	0.87*	-0.40	-0.01	0.08	-0.51	-0.57*
Bacillario.+Chrysophyceae	-0.28	-0.44	0.74*	0.16	0.39	-0.57*
Chlorophyta	-0.06	0.92*	0.09	0.14	0.44*	-0.22
Cyanobacterial APP	0.46*	-0.02	-0.29	-0.07	-0.91*	0.07
Eustimatophyceae	0.16	-0.12	-0.30	-0.84*	-0.33	0.38*
Cryptophyta	-0.62*	-0.10	-0.50	-0.02	0.16*	-0.04
	Root 1	**Root 2**	**Root 3**	**Root 4**	**Root 1**	**Root 2**
Eigenvalue	0.51	0.27	0.10	0.03	0.75	0.20
Canonical Correlation (r)	0.72	0.52	0.31	0.18	0.86	0.45
Significance (p)	0.00	0.00	0.00	0.06	0.00	0.30
Percentage variance, set 1	0.45	0.22	0.14	0.19	0.54	0.46
Percentage variance, set 2	0.24	0.20	0.16	0.13	0.26	0.14
Redundancy, set 1	0.23	0.06	0.01	0.01	0.40	0.09
Redundancy, set 2	0.13	0.05	0.02	0.00	0.19	0.03

* Highest values within a set for each canonical variate.

Note: The stratification was determined as 0=mixed and 1=stratified according to the temperature profiles carried out with the CTD-probe and/or submersible FluoroProbe.

Driving factors for phytoplankton distribution: Canonical correlation analysis (CCA; Tab. 4) indicated that total Chl*a* as well as the percentage contributions of cyanobacterial APP and Cryptophyta to the total Chl*a* were correlated with the first canonical variate, which explained 24.5 % of the variance. The percentage contribution of Cryptophyta to the total Chl*a* was negatively correlated to the first canonical variate. Considering the environmental data the first canonical variate showed the strongest correlation to the stratification (Tab. 4). The second canonical variate was related to the contribution of Chlorophyta and to latitude. The third canonical variate was related to the contribution of Bacillariophyceae+ Chrysophyceae and to the water depth. The fourth variate was not significant. Although CCA does not provide direct covariation between the two sets of variables, we may state for example, that cyanobacterial APP showed highest contributions where the water column was stratified, whereby the temperature was secondary. Chlorophyta dominated in the low latitude regions, probably related to the insolation, as temperature was not of great importance. Bacillariophyceae+ Chrysophyceae dominated, where the water depth was high, that means rather in the open basins than in the near-shore or river inflow regions.

Fluorescence depth profiles: As has been suggested from the CCA, mixing and stratification were very important factors for the differential phytoplankton group distribution. Thus, *in situ* fluorescence depth profiles, showing the mixing/stratification regime of the water body by recording the temperature and the total Chl*a* were analysed in July 2002 and July 2003 (Fig. 27, Fig. 28) and August 2002 (Fig. 29). Basically these profiles strengthened two trends: The first one was a trend from near-shore to offshore, well visible for example from the Barguzin transect where the regime changed from a stratified one to a mixed one with the increasing distance from the shore towards the open Central basin (Fig. 27). Another trend in July was the one from the South to the North. While in the South the water body was almost always stratified, the water body of the North was mixed (Fig. 28). Nonetheless, this trend was much less expressed in August. Then, almost all stations were stratified, even those of the North (Fig. 29).

The August depth profiles exhibited great heterogeneity for the Chl*a* maxima even between neighbouring sites, which in Lake Baikal are, however, still a few kilometres away from each other (Fig. 29). In the South, the epilimnion spanned up to 50 m and the Chl*a* maxima mostly occurred up to that depth (Fig. 29). Only in the central part of the South basin, where water depth reached up to 1400 m, the epilimnion was limited to 20 m (Fig. 29). Then, the Chl*a* maximum was found between 10 and 20 m within the

thermocline and the maximum Chl*a* concentration was much higher than at all the near-shore stations. In the North several Chl*a* maxima were also found in depths varying from 10 to 50 m (Fig. 29). The Chl*a* maxima occurred often within the thermocline, as has been shown for the deep-water stations in the South (Fig. 29). Some of these trends were already indicated by the direct water samples (Fig. 26), but using continuous measurements, the resolution was strongly increased. Using direct samples, the risk persist to overlook deep Chl*a* maxima.

However, it is worth to be mentioned here, that these data are uncorrected for humic substances and not calibrated including all dominant phytoplankton groups. Nonetheless, preliminary correlation analyses of A. Nicklisch (HU Berlin, Germany, pers. comm.) indicated that total Chl*a* concentrations measured with the FluoroProbe fitted well to the total Chl*a* determined by HPLC ($r^2 = 0.96$).

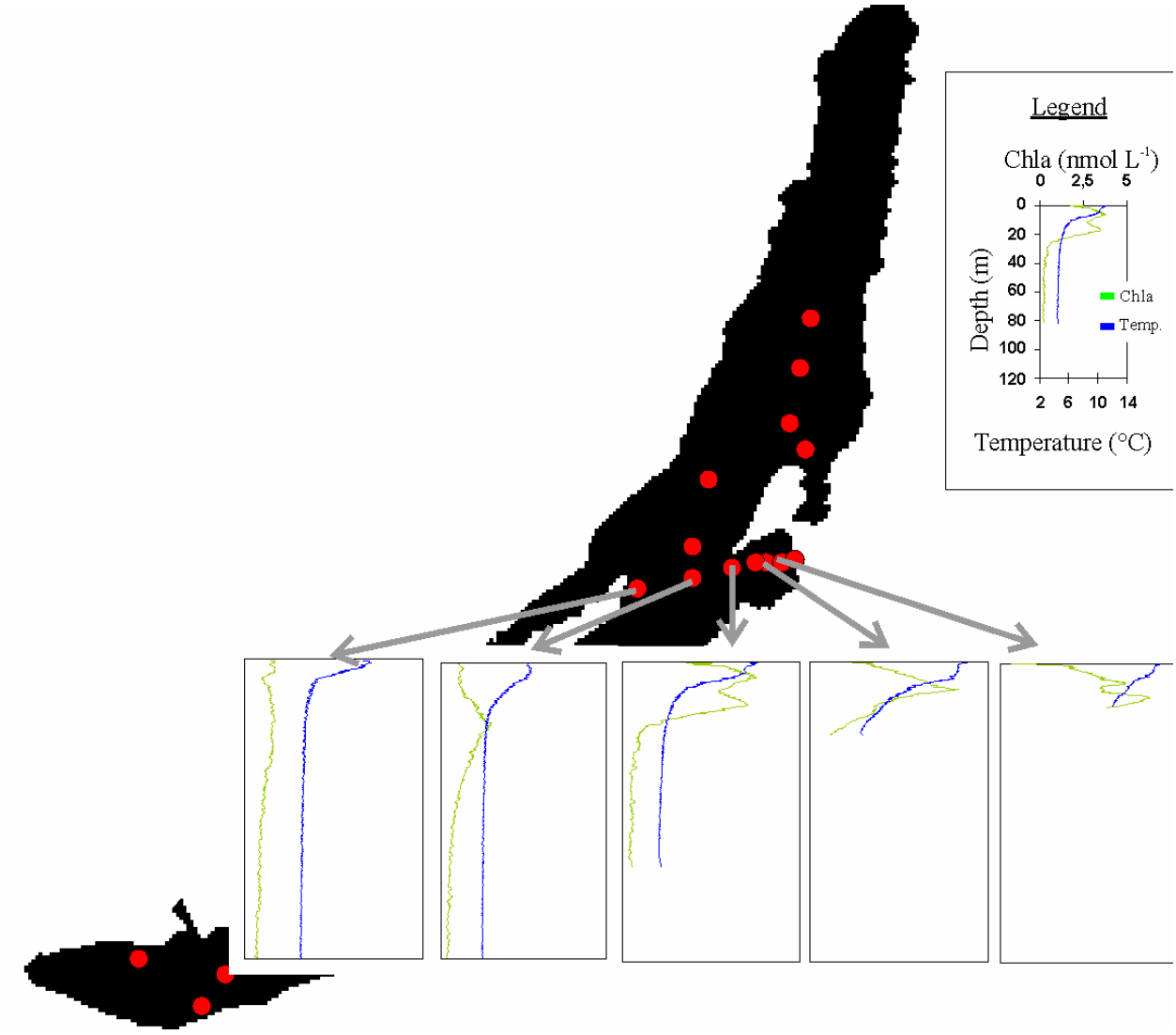

Fig. 27. Chl*a* and temperature depth profiles assessed with the submersible fluorimeter in July 2002. Transect from near-shore to off-shore (from Barguzin Bay to eastern shore of Olkhon Island).

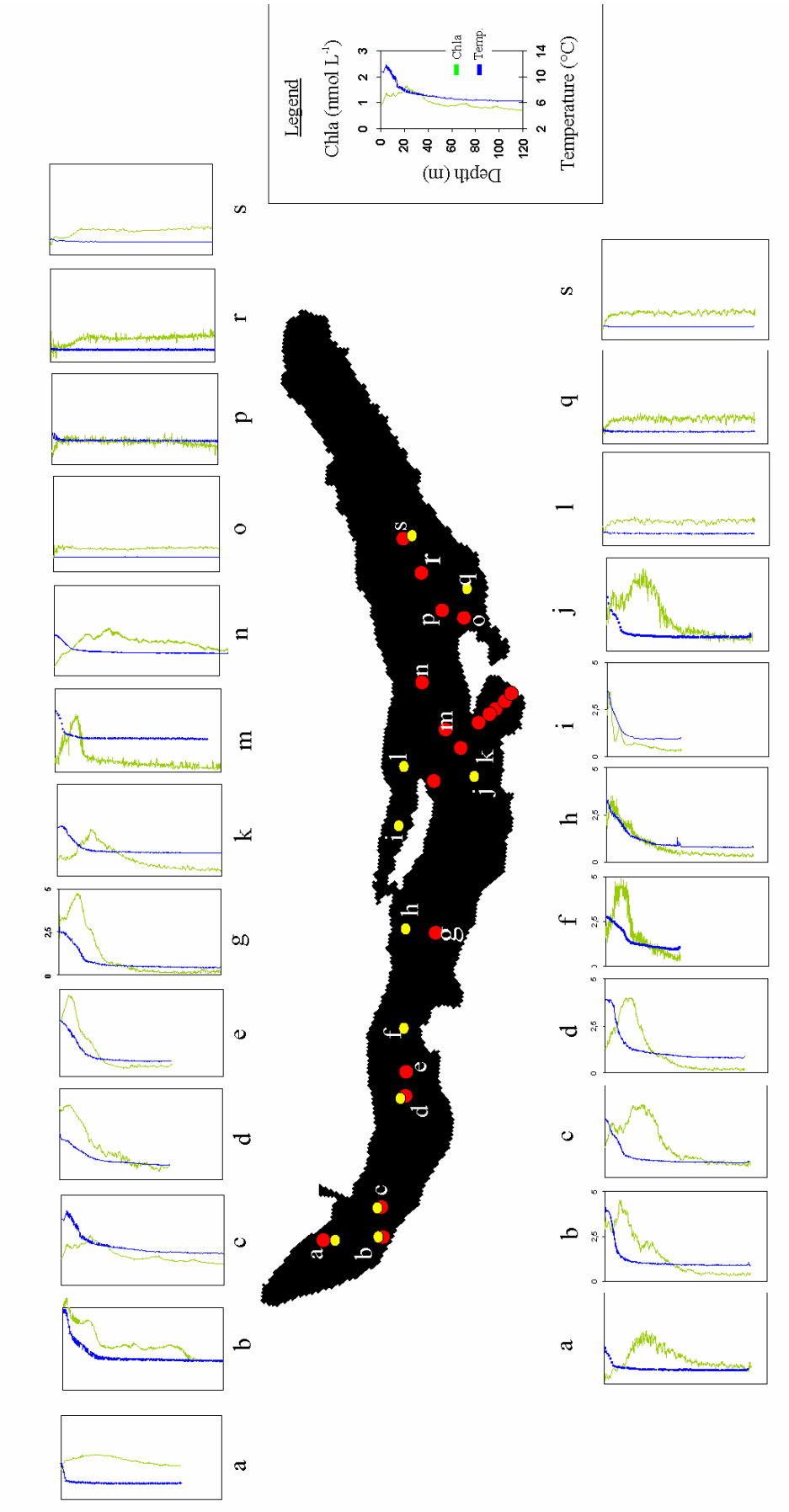

Fig. 28. South to North transsects of Chl*a* and temperature depth profiles in July 2002 (red circles, profiles on left side) and July 2003 (yellow circles, profiles on right side).

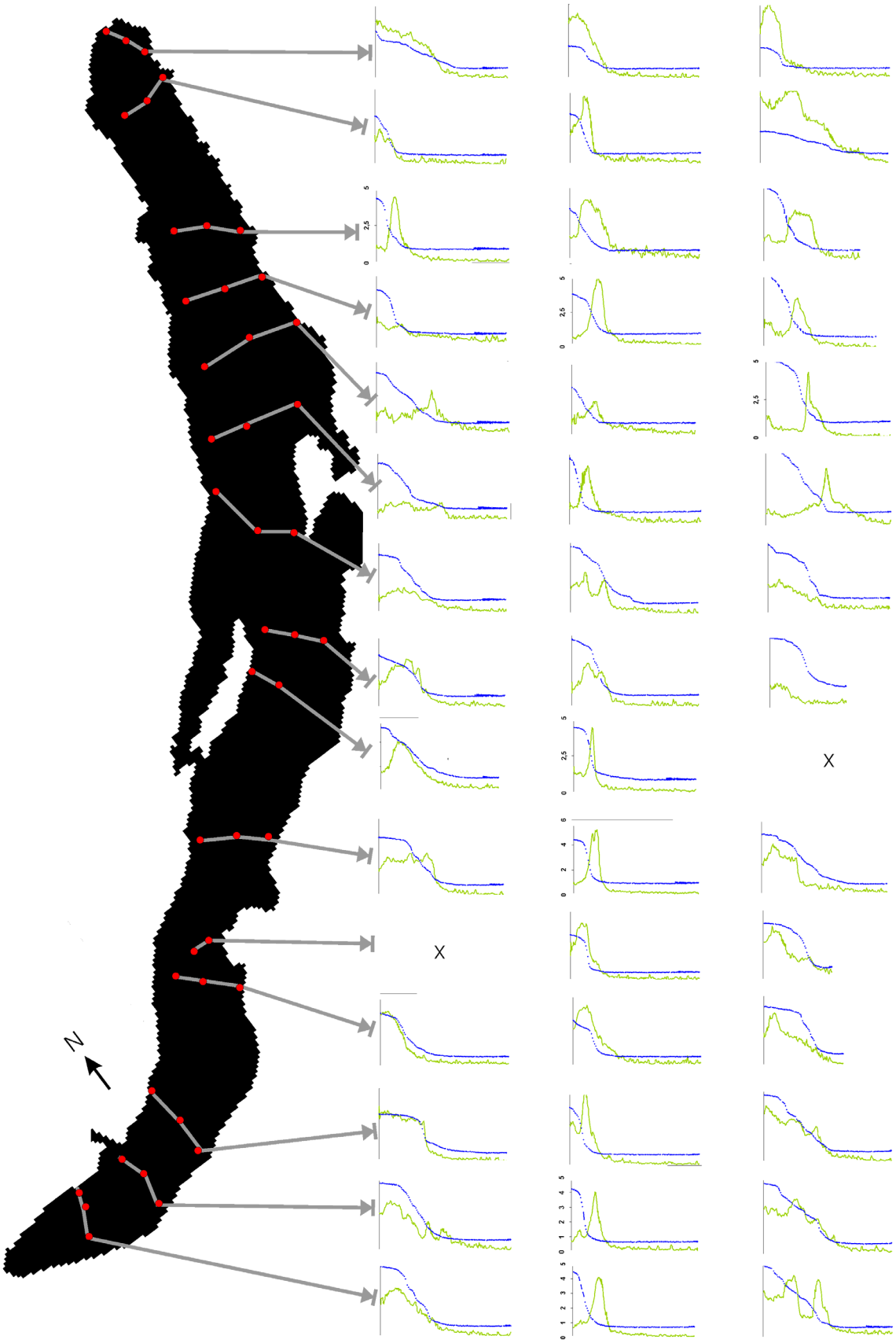

Fig. 29. Depth profiles of Chl*a* (green lines) and temperature (blue lines) in August 2002. See Fig. 28 for legend, whereby in August maximum measured depth was 100 m and maximum temperatures were 18°, 16° and 14° C in the South (including Selenga Delta), Centre and North, respectively.

3.1.3 Seasonal dynamics

Intense monitoring was conducted from May 2002 to June 2003. Variations from January 2001 to December 2003 are plo than 2001 and 2003 with a mean summer (July-September) temperature at 5 m water depth of 12° C, compared to 8.5° C in 2001 and 8° C in 2003. Peak temperatures reached 17.4° C in 2002 compared to 15.4° C in 2001 and 11.6° C in 2003. The ice cover lasted shortest in 2002 (1 month) relative to 2001 (2.5 months) and 2003 (2 months). In every year the integrated Chl*a* below the ice was as high as in summer. Generally four peaks could be discerned (around March, June, July and September), but their intensities varied interannually. The spring peak 2001 was probably missed due to the inaccessibility of the sampling station. The spring peak 2002 was by far the highest within the three investigated years.

Seasonal dynamics of APP, nano- and microphytoplankton: During the intense monitoring 2002-2003, only spot samples could be counted with the epifluorescence microscope for APP. The amount of APP was high in July (about 0.7 $mm^3 L^{-1}$) and decreased towards autumn (less than 0.2 $mm^3 L^{-1}$; Fig. 30B). The APP started to increase again by the end of March (Fig. 30B). Nevertheless, the presence of APP in February and March (about 0.1 $mm^3 L^{-1}$), when the lake was covered with ice, indicated an important APP formation under the ice. Light microscopic estimations of the total APP during the whole season supported the conclusions drawn from epifluorescence spot checks (Fig. 30B).

The median annual nano- and microphytoplankton biovolume was 0.07 $mm^3 L^{-1}$. In spring the nano- and microphytoplankton biovolume and the cell number were high, while the diversity was low (Fig. 30B). This spring bloom (2002) was dominated by *Stephanodiscus meyerii* and *Aulacoseira baicalensis* (Bacillariophyceae) that belong to the indicators of vernal blooms usually found in mixed, mesotrophic conditions (B; Tab. 5). At the end of May to the beginning of June the nano- and microphytoplankton biovolume and cell number decreased, while the diversity increased to a maximum in Mid-June (Fig. 30B). The diversity was, therefore, highest at the time of the minimum biovolume and cell abundance.

The nano- and microphytoplankton biovolume was then low during summer and autumn, but the cell number, in contrast, was in summer as high as during spring (Fig. 30B). Towards the beginning of July (2002), the contribution of Bacillariophyceae decreased and Chlorophyta (*Koliella* sp. and *Monoraphidium* sp.) became important (Fig. 30B; Tab. 5). The dominant functional groups changed to mixed, oligotrophic (E) or mesotrophic conditions (X_2; Tab. 5). In July the assemblage comprised mainly *Koliella*

longiseta (Chlorophyta) and *Rhodomonas pusilla* (Cryptophyta) (Tab. 5). According to the functional groups the large number of chrysophycean flagellates indicated the start of summer stratification (E) (Tab. 5). Bacillariophyceae were rather rare at that time of the year (Fig. 30B; Tab. 5). Small algae such as *R. pusilla* and Chrysophyceae (chrysophycean flagellates as well as *Chrysidalis* sp. and *Dinobryon* spp.) predominated also during the whole August and September (Tab. 5). *Asterionella formosa* (Bacillariophyceae) reached a mass development (10-fold increase within one week) in autumn that was unusual for the Bolshye Koti site (Tab. 5).

Under the ice of the next year (2003) the biovolume and cell number were low, but the diversity was as high as in summer (Fig. 30B). The assemblage was dominated by species preferring cold, mixed and enriched conditions (C), such as *A. formosa* (Bacillariophyceae) (Tab. 5). Shortly before ice-break-up *Synedra acus* (Bacillariophyceae) and *Gymnodinium baicalensis* (Pyrrophyta) became dominant (Tab. 5). The former prevail in vernal mixed conditions (D), but, in contrast to larger Bacillariophyceae, such as *Cyclotella*, they might not be sensitive to stratification. *Gymnodinium* species are mostly sensitive to mixing and dominated in stratified epilimnia (L_M; Tab. 5). Both groups indicate conditions of nutrient availability. The bacillariophycean maximum expected after ice-break up 2003 was probably missed, because sampling had to be stopped during ice-break up until a time when conditions permitted ship access to the sampling location.

Seasonal dynamics of phytoplankton pigments: The biovolume maximum did not correspond to the chlorophyll and carotenoid one (Fig. 30B). Shifts towards Chl*a*-rich phytoplankton groups prevailed in summer, while large and Chl*a*-poor cells dominated in winter and spring. Thus, the Chl*a* vs. nano- and microphytoplankton biovolume ratios were < 6 nmol mm^{-3} in spring (May-June) but 22 nmol mm^{-3} on average in summer (July-September) and 8.5 nmol mm^{-3} on average under the ice (February-April).

After the ice break-up at the end of April 2002, Chl*a* showed a first maximum in Mid-May (2 nmol L^{-1}), decreasing strongly from the end of May to the beginning of June (0.9 nmol L^{-1}; Fig. 30B). The sum of carotenoids was about 90 % of Chl*a* (based on molar ratios and 60 % based on weight ratios) during the time of spring mixing. Secchi depth was low (10 m) at the Chl*a* maximum but increased while chlorophylls and carotenoids decreased (Fig. 30B).

Tab. 5. As Tab. 2, but for seasonal variation.

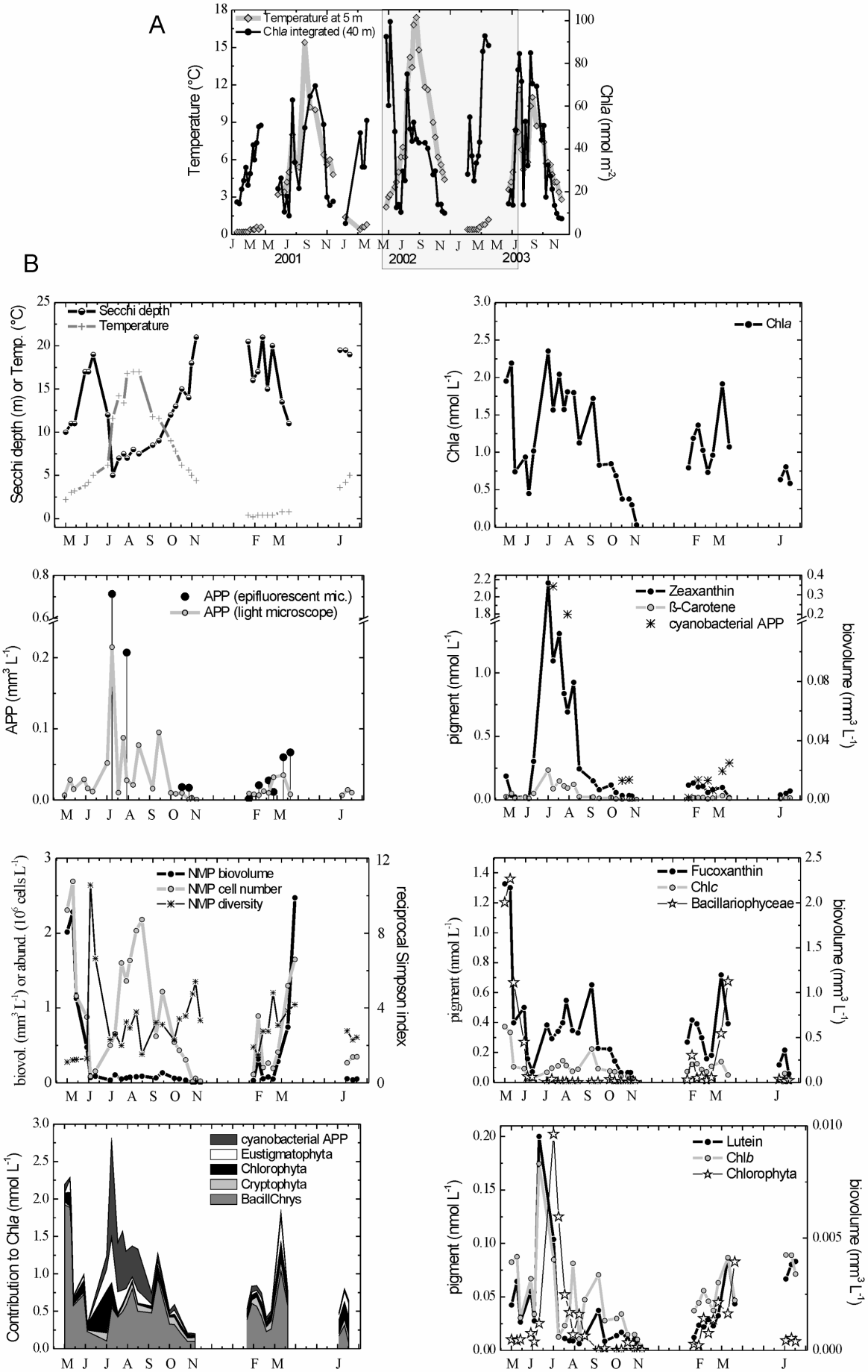
A
Temperature at 5 m
Chla integrated (40 m)
Temperature (°C)
Chla (mmol m-2)
2001
2002
2003
B
Secchi depth
Temperature
Secchi depth (m) or Temp. (°C)
Chla
Chla (nmol L-1)
APP (epifluorescent mic.)
APP (light microscope)
APP (mm3 L-1)
Zeaxanthin
ß-Carotene
cyanobacterial APP
pigment (nmol L-1)
biovolume (mm3 L-1)
NMP biovolume
NMP cell number
NMP diversity
biovol. (mm3 L-1) or abund. (10^6 cells L-1)
reciprocal Simpson index
Fucoxanthin
Chlc
Bacillariophyceae
cyanobacterial APP
Eustigmatophyta
Chlorophyta
Cryptophyta
BacillChrys
Contribution to Chla (nmol L-1)
Lutein
Chlb
Chlorophyta
M J J A S O N F M J

Fig. 30. Seasonal monitoring during May 2002 to June 2003 (at the long-term monitoring station of SRIB 2.8 offshore from Bolshye Koti, South Basin) of temperature, Secchi depth, biovolumes and selected pigments.(A) temperature at 5 m water depth and Chl*a* integrated over 40 m water depth (the suggested euphotic zone) from January 2001 to December 2003. The highlighted area designate the period of the intensive monitoring, detailed in section (B): Intensive monitoring from May 2002 to June 2003. On the left side: Secchi depth, temperature, total APP biovolume (epifluorescence microscopic spot counts + light microscopic estimation), total nano- and microphytoplankton (NMP biovolume and cell abundance), reciprocal Shannon-Wiener diversity index, and composition of the phytoplankton community based on their share to total Chl*a* (see text for calculations). On the right side: total Chl*a* as well as marker pigments and biovolumes of the respective phytoplankton groups.

The clear-water phase gave way to another Chl*a* maximum in Mid-July (2 nmol L^{-1}; Fig. 30B) and the sum of carotenoids increased up to 160 % of Chl*a*. The Chl*a* concentration was high during summer, when temperatures rose to a maximum of 16° C and Secchi depth was less than 10 m (Fig. 30B). The carotenoids were about 100 % of Chl*a* during the summer stratification. From the end of summer to autumn the temperature and Chl*a* concentration and percentage carotenoids decreased while the Secchi depth increased (Fig. 30B). From February to March 2003 the Chl*a* concentration increased under the ice and Secchi depth was decreased (Fig. 30B). The sum of carotenoids was low (70 % of Chl*a*) under the ice.

The distinct pigment changes likely reflected the variations in the phytoplankton groups. Similar to the biovolume of the Bacillariophyceae, all related pigments, such as fucoxanthin, Chl*c* and diadinoxanthin showed maxima in May after ice-break up (Fig. 30B). In summer, Bacillariophyceae biovolume decreased while the related pigments decreased to a lesser extent, marking shifts towards smaller, pigment-rich Bacillariophyceae or towards Chrysophyceae (which also contain those pigments). Microscopic counts confirmed the shift towards Chrysophyceae (flagellates, Tab. 5).

Chlorophyta and its related pigments also showed some discrepancies (Fig. 30B). While the Chlorophyta biovolume was low in spring 2002 and 2003, lutein and Chl*b* were high (Fig. 30B). In summer, both pigments increased faster than the biovolume, suggesting the influence of chlorophycean APP with high pigment vs. biovolume ratios (Fig. 30B). The summer maxima and the winter decrease of zeaxanthin and ß-carotene correspond to the course of the cyanobacterial APP (Fig. 30B). Except cyanobacterial ones, pigment concentrations were also high under the ice and pigments of Cryptophyta (alloxanthin) and Pyrrophyta (peridinin) even showed maxima.

Estimation of phytoplankton composition using marker pigments: As has been shown for the regional variability, the contributions of distinct chemotaxonomic groups to the total

Chl*a* can be calculated using the marker pigments. Based on the factors listed in Tab. 3A for the whole lake average, contributions have been calculated for the period of the intense monitoring (Fig. 30B): Bacillariophyceae+Chrysophyceae had highest (up to 90 %) proportions of total Chl*a* in spring, autumn and winter, Chlorophyta and Eustigmatophyceae in early summer, and cyanobacterial APP in summer; Cryptophyta contributed low proportions to total Chl*a* throughout the year.

The calculated Chl*a* matched the measured one with a median error of 2 % in spring (May-June), of 13 % in summer (July-September), but of 38 % in fall (October-December) and of 31 % under the ice (February-March). It matched the measured Chl*a* in June 2003 again with an error of only 5 %. As the applicability of the factors differ with the phytoplankton composition, the regional factors, accounting for these heterogeneities (Tab. 3B), were also tested. The best fit for the summer community was reached using the Selenga Delta factors (Tab. 3B) with a median error of only 10 % between calculated and measured Chl*a*. Best fits for autumn (Selenga Delta factor) and under ice (Centre factor) communities, in contrast, implied errors greater than 25 % and thus, these communities were different from all others.

Driving factors for seasonal succession: Canonical correlation analysis (CCA) showed that stratification and temperature dominated the first canonical variate (Tab. 4). The percentage contribution of Chlorophyta and cyanobacterial APP to total Chl*a* were highly correlated to this first variate, as well as, although negatively, Cryptophyta. The second variate was not significant. Taken together the CCA for regional and seasonal variations indicated that temperature and stratification were of major importance for the phytoplankton development in Lake Baikal and potentially influence predominantly small cells such as cyanobacterial picoplankton.

3.2 Pigment transfer through the water column and preservation in the surface sediment

3.2.1 Transfer fluxes and composition of settling material (South 2001-2002)

Through the upper water column (water samples), the deeper water column (sediment traps) and also within the water to sediment interface (top sediment slice) major lipophilic photosynthetic pigments known from freshwater samples were detected by the HPLC-aided analysis (Tab. 6). Characteristic fluorescence and absorption chromatograms are shown in Fig. 31 for the water samples (Fig. 31A), the 40 m trap (Fig. 31B), the 1400 m trap (Fig. 31C) and the top sediment slice (Fig. 31D).

N°	Pigment	40 m trap	1400 m trap
		(μmol m^{-2} $month^{-1}$)	
1	Chlorophyll *a*	12.1	2.89
2	Chlorophyll *b*	0.53	0.11
3	Chlorophyll *c*	2.63	0.41
4	Chlorophyllide *a*	2.13	0.68
5	Pheophorbide *a*	40.8	6.74
6	Pheophytin *a*	6.5	
7	Pheophytin *b*	0.075	
8	Pyropheophytin *a*	0.32	
9	Fucoxanthin	11.6	1.55
10	Violaxanthin	0.05	-
11	Diadinoxanthin	0.57	0.26
12	Diatoxanthin	1.44	2.00
13	Alloxanthin	0.84	0.04
14	Lutein	0.40	0.06
15	Zeaxanthin	1.38	0.1
16	ß-Carotene	0.39	0.007

Tab. 6. Major lipophilic photosynthetic pigment fluxes into the 40 m trap and into the trap at the lake bottom. Values for the lake bottom (1400 m) were extrapolated from the curve fittings shown in Fig. 32 and Fig. 33 for all pigments with exponential decrease. For pheophytin *a*, pyropheophytin *a* and pheophytin *b*, which did not show a significant decrease with depth, 40 m and lake bottom values were calculated as averages of all traps. Chl*a* included allo-, epimers and other derivates; pheophorbide *a* included all pheophorbide *a* derivates and pheophytin *a* all pheophytin *a* derivates.

Pheopigments, degradation products of chlorophylls, were found only in sedimented material (Fig. 31, Tab. 6). Four different pheophorpide *a* -like pigments were found (Fig. 31). The occurrence of those pheophorpide and pyropheophorbide derivates was not correlated with the depth. Thus, all of them are grouped as "pheophorpide *a*" in the following text. All pheophytin *a* -like pigments were also grouped to "pheophytin *a*" in the text below. Pyropheophytin *a* could be clearly differentiated from pheophytin *a* and is discussed separately (Fig. 31, Tab. 6). The chromatograms of pigment extracts of the sediment traps and sediment slices also contained several unidentifiable components (unnumbered peaks in Fig. 31). They were strongly degraded pigments, which were not included in our quantitative comparisons.

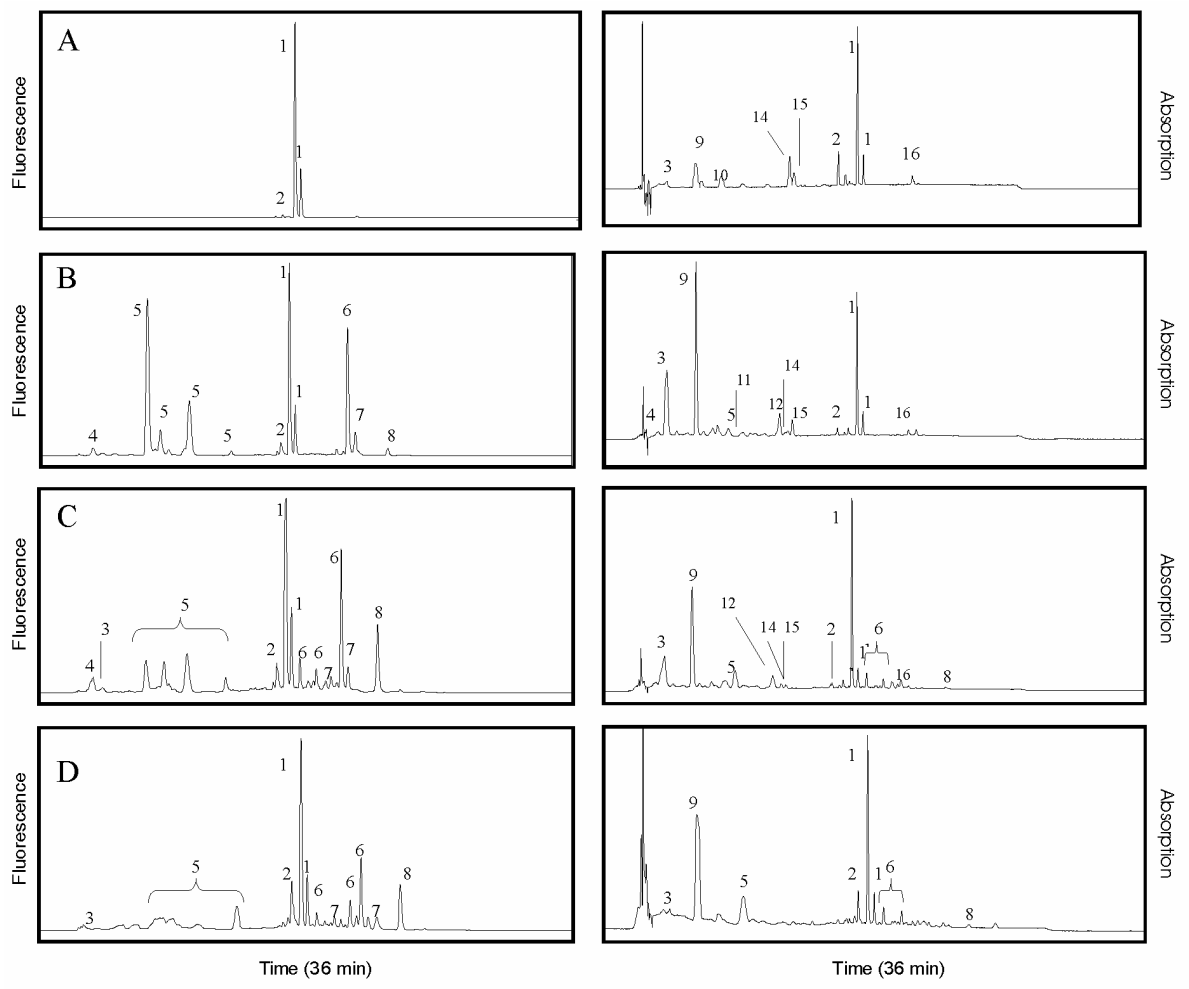

Fig. 31. Typical fluorescence (410 nm / 670 nm excitation / detection wavelength, left side) and absorption (440 nm) chromatograms (right side) of (A) the water column, (B) the 40 m trap, (C) the 1400 m trap and (D) the top sediment slice below the mooring. Numbering of the peaks confers to pigments listed in Tab 6.

Transfer fluxes: During 16 months of deployment 239 g m^{-2} dry matter (DM) settled in the 40 m trap, with an average flux of 14.9 g m^{-2} $month^{-1}$ (Tab. 7, Fig. 32). The content of total organic carbon (TOC) was 21.9 % at that depth and that of total nitrogen (TN) 1.6 % (Tab. 7, Fig. 32). The resulting atomic ratio of TOC vs. TN (C/N) of 15 indicated that the sedimented material resulted from the autochthonous production by suspended phytoplankton and that terrigenous input is likely to be negligible at that site. The amount of pigments gathered during the 16 months deployment in the 40 m trap was 193.1 µmol m^{-2} for Chl*a* and 797 µmol m^{-2} for chlorophyllide *a*+pheopigment *a* (Tab. 6). It is worth noting that the replicate samples of the 40 m trap deviated strongly (coefficient of variation: 60.5%), whereas the coefficients of variation for the replicate samples in the traps below varied from 2.5% to 15.5%. Pheophorbide *a* was the most

prominent degradation product in the 40 m trap (Tab. 6, Fig. 32). With respect to TOC (total organic carbon) only 3.9 μmol g^{-1} Chl*a* but 9.47 μmol g^{-1} pheophorbide *a* were found (Tab. 8). The lowest ratio was found for pyropheophytin *a*/ TOC (Tab. 8).

	40 m trap	**1400 m trap**
dry weight (g m^{-2} $month^{-1}$)	14.9	9.49
TOC (%)	21.87	7.14
TN (%)	1.60	0.76
C/N (mol mol^{-1})	14.80	9.91

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Tab. 7. Sedimentation and accumulation rates of the dry matter, total nitrogen and atomic C/N ratio in the 40 m trap and at the lake bottom. Values for the lake bottom (1400 m) were extrapolated from the curve fittings shown in Fig. 32 (see also Appendix C - Tab. 2.).

	40 m trap	**1400 m trap**
	μmol g^{-1}	
chlorophyll *a*/ TOC	4.1	4.38
chlorophyllide *a*/ TOC	1.14	
pheopheorbide *a*/ TOC	9.87	
pheophytin *a*/ TOC	2.25	8.12
pyropheophytin *a*/ TOC	0.08	0.42

Tab. 8. Ratios of Chl*a* and its degradation products per organic carbon in the 40 m trap and at the lake bottom. Values for the lake bottom were extrapolated from the curve fittings (Fig. 34, Appendix C - Tab. 4.). Data for chlorophyllide *a*/ TOC and pheophorbide *a*/ TOC, which did not show significant depth trends, were calculated as averages of all traps.

In the 40 m trap fucoxanthin was the dominant carotenoid (Tab. 6, Fig. 33). Other pigments of Bacillariophyceae+Chrysophyceae (Chl*c,* diadinoxanthin and diatoxanthin) as well as the cyanobacterial zeaxanthin also showed high sedimentation rates, whereas the chlorophyte Chl*b* and lutein as well as the cryptophyte alloxanthin, sedimented only in low amounts (Tab. 6, Fig. 33).

A principal component analysis (PCA) including the dry matter, TOC and TN as well as all pigments revealed that three components controlled 90.7 % of the variance. The first component (65.5 %) included the depth and controlled dry matter, TOC and TN. The first component controlled also the labile pigments Chl*a*, *b* and *c* as well as chlorophyllide *a* and pheophorbide *a* and also all carotenoids. The second and third components comprised the more stable pigments pheophytin *a*, pyropheophytin *a* and pheophytin *b*.

The sedimentation to the lake bottom showed a power regression for dry matter, but two-exponential or two first order independent decay regressions were apparent for TOC, TN, Chl*a*, *b*, *c*, chlorophyllide *a*, pheophorbide *a* and most carotenoids (Fig. 32,

Fig. 33, Appendix C - Tab. 2, Appendix C - Tab. 3). In contrast, for the more stable chlorophyll degradation products, pheophytin *a*, pyropheophytin *a* and pheophytin *b*, none of those regression models fitted accurately (Fig. 32). The composite character of the regressions (Appendix C - Tab. 2, Appendix C - Tab. 3) indicated that the degradation passed through two different phases, triggered by different factors.

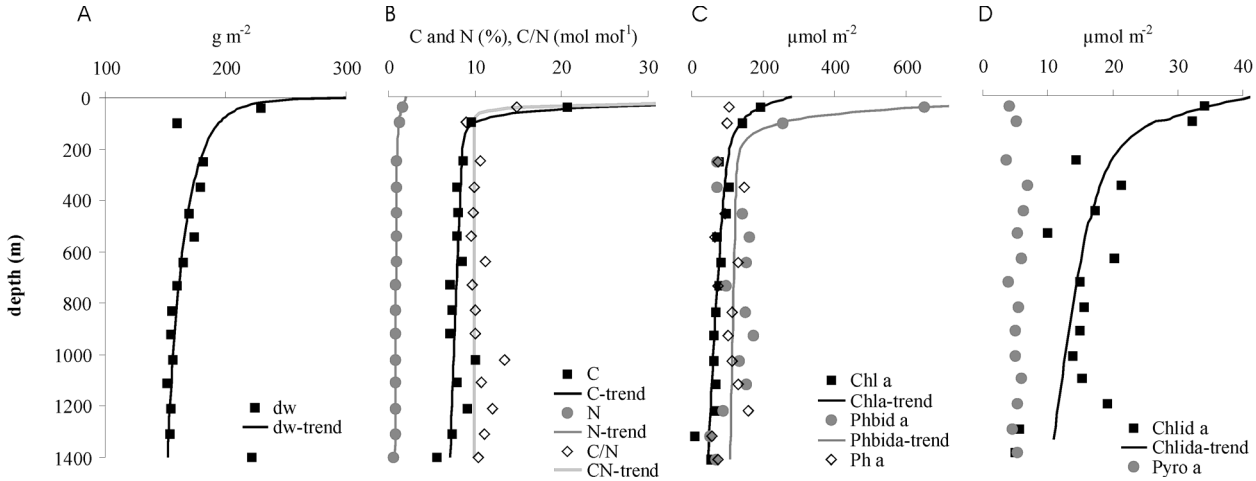

Fig. 32. Vertical profiles of settling particles in the water column, showing (A) total mass fluxes (dw, g m^{-2}), (B) organic carbon (C %), (C) total nitrogen (N %) and (D) atomic C/N ratios as well as vertical profiles of Chl*a*, and its degradation products (µmol m^{-2}). The traps were deployed for about 16 months. The respective regression equation and their coefficient of determinations (r^2) are reported in Appendix C - Tab. 2, and Appendix C - Tab. 3. Abbreviations: Chlid*a* – chlorophyllid *a*, Phbid*a* – pheophorbide *a*, Ph*a* – pheophytin *a*, PyroPh*a* – pyropheophytin *a*.

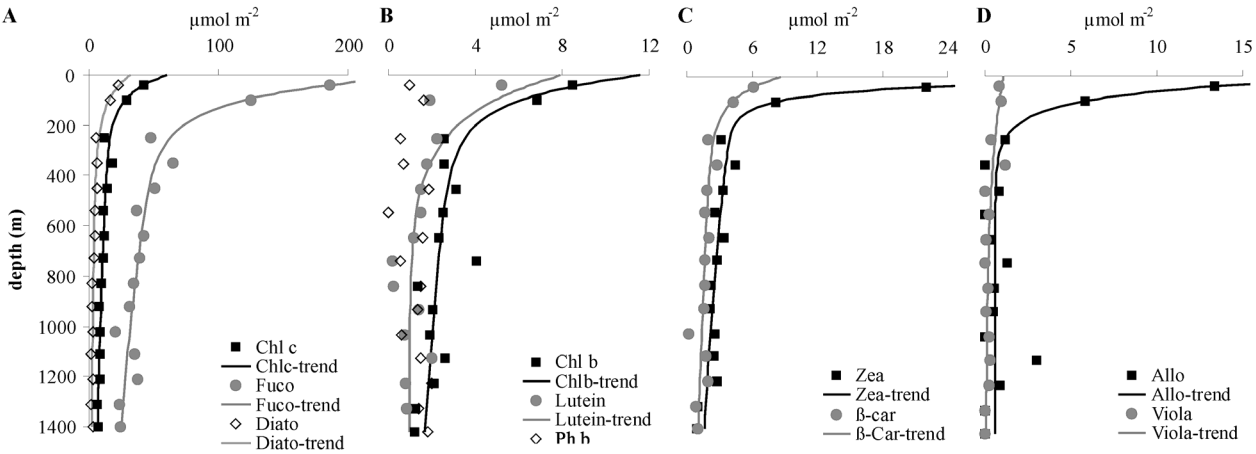

Fig. 33. Depth profiles of marker pigments from Bacillariophyceae+Chrysophyceae (A), Chlorophyta (B), cyanobacterial picoplankton (C), Eustigmatophyceae and Cryptophyta (D). The traps were deployed for about 16 months. The respective regression equations and their coefficients of determination (r^2) are reported in Appendix C - Tab. 3. Abbreviations: Allo – alloxanthin, ß-car – ß-carotene, Diato – diatoxanthin, Fuco – fucoxanthin, Ph*b* – pheophytin *b*, Viola – violaxanthin, Zea – zeaxanthin.

The first degradation phase occurred within the upper 250 m and was much stronger than the second. Below 250 – 300 m the degradation became visibly lowered. Calculations of simple exponential or decay models for those pigments resulted in much lower coefficients of determinations or insignificant models. Therefore, one simple phase cannot describe the pigment degradation with depth. The functions (Appendix C - Tab. 2 and Appendix C - Tab. 3) should allow reconstructions of initially settled pigments from trap or sediment data in further investigations. The models are nevertheless preliminary, as they do not take into account different degradation extents within the traps.

Different degradation patterns were revealed when chlorophylls and its degradation products were referred to TOC (Fig. 34) instead of area references (Fig. 32). The Chl*a*/ TOC ratio decreased with depth, indicating that organic carbon is more slowly degraded than Chl*a* (Fig. 34, Appendix C - Tab. 4), whereas the pheophytin *a*/ TOC ratio and the pyropheophytin *a*/ TOC ratio increased with the depth, indicating the formation of pheophytin and pyropheophytin with depth (Fig. 34, Appendix C - Tab. 4). Best fits for the chlorophyllide *a*/ TOC ratio and pheophorbide *a*/ TOC ratio vs. depth were also linear regression models, but they were not significant (Fig. 34).

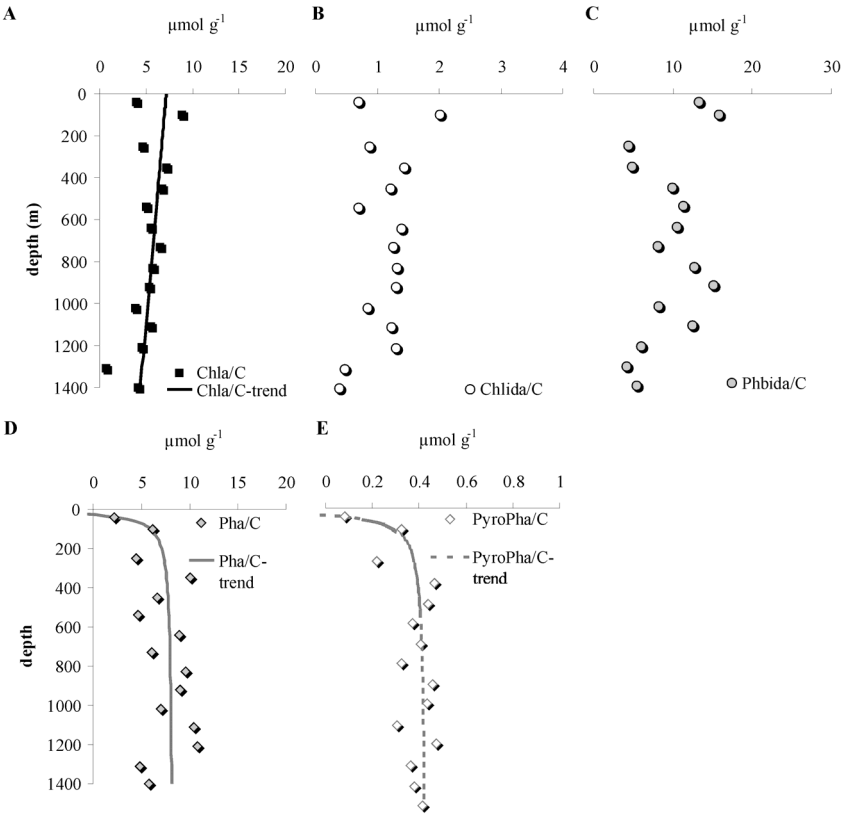

Fig. 34. Depth profiles of Chl*a*/ TOC ratio (Chl*a*/C), chlorophyllide *a*/ TOC ratio (Chlid*a*/C), pheophorbide *a*/ TOC ratio (Phbid*a*/C), pheophytin *a*/ TOC ratio (Ph*a*/C) and pyropheophytin *a*/ TOC (PyroPh*a*/C). The respective regression equations and their coefficient of determination (r^2) are reported in Appendix C - Tab. 4.

Considering that the 40 m trap was collecting 100 % of the particles that settled out of the euphotic zone, 100 % dry matter would be 14.9 mg m^{-2} $month^{-1}$. At 100 m 10 mg m^{-2} $month^{-1}$ dry matter were collected which accounts for 67 %. At the lake bottom an estimate of 64 % of dry matter settled down. The estimated percentages of TOC and TN that reached the lake bottom were, in contrast, only 33 % and 48 %, respectively (Tab. 7, Fig. 32). The organic compounds were obviously more strongly degraded than the non-organic fraction (mainly siliceous valves of diatoms) of the settled material. The loss during the sedimentation was, however, even stronger for most of the pigments. Only 24 % of Chl*a* reached the lake bottom and 21 % of Chl*b* (Tab. 6, Fig. 33). The distinct degradation products of Chl*a* showed different losses. About 100 % of the pheophytin *a* reached the lake bottom, but only 16 % of pheophorbide *a*.

Composition of the settling material: Fucoxanthin, Chl*b* and zeaxanthin were used to estimate the contribution of Bacillariophyceae+Chrysophyceae, Chlorophyta and cyanobacterial picoplankton to total Chl*a*. According to the factors established in Fietz and Nicklisch (2004, Appendix A-Table 3), the Chl*a* content in the 40 m trap was composed of 87 % Bacillariophyceae+Chrysophyceae, 11 % Chlorophyta and 2 % cyanobacterial picoplankton (Fig. 35). The percentage contribution did not change with the water depth, as the same composition was found in the deepest traps (Fig. 35).

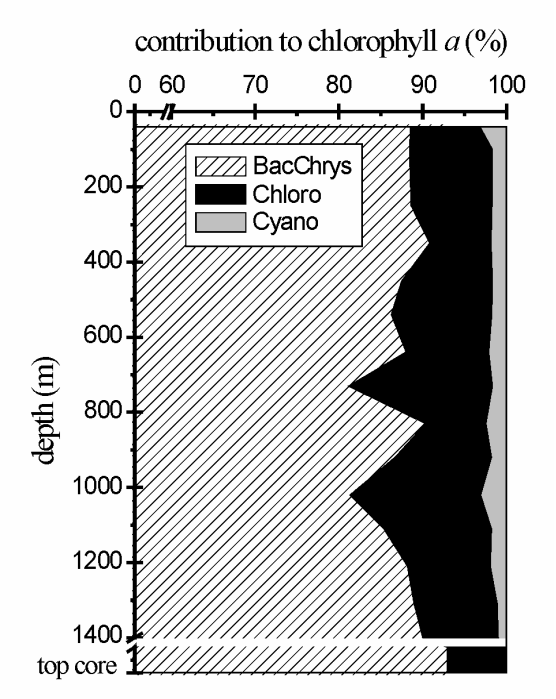

Fig. 35. Contribution to total Chl*a* of the dominant phytoplankton groups in the sediment traps and in the surface sediment. Estimates based on the marker pigment vs. Chl*a* ratios calculated by multiple linear regession (cf. Fietz and Nicklisch 2004, Appendix A for calculations). Abbreviations: BacChrys – Bacillariophyceae+Chrysophyceae, Chloro – Chlorophyceae, Cyano – cyanobacterial picoplankton.

In all traps the calculated Chl*a* concentration – based on the marker pigments – was much higher compared to the measured Chl*a* concentration. On average the calculated value of the Chl*a* concentration was 157 % of the measured value. Pheopigment *a*, which results from grazing and photooxidation, were not added to Chl*a* because carotenoid degradation products, resulting from the same processes, were also not added to the marker pigments. Adding chlorophyllide *a* that occurs in senescent cells due to enzymatic lyses, which does not affect carotenoids (Jeffrey et al. 1997), the average calculated Chl*a*+chlorophyllide *a* concentration was 121 % the measured value. This overestimation could result from an unusual high carotenoid or Chl*b*/Chl*a* ratio of specific settling taxa or from a higher degradation rate of Chl*a* than carotenoids or Chl*b*. The second assumption is likely.

A conclusion concerning the source of pheopigment *a*, as has been shown for Chl*a*, is limited, because marker pigments which underwent a similar degradation then pheopigments are missed. The only share which can be calculated is for Chlorophyta assuming that the ratio of pheophytin *a* to pheophytin *b* represents the former ratio of Chl*a* to Chl*b* in the settling material. Then, the factor for the Chl*a*/Chl*b* relationship (cf. Fietz and Nicklisch 2004, Appendix A-Table 3), can be adopted for the pheophytin *a*/ pheophytin *b* relationship. According to this approach 2.6 % of pheophytin *a* should originate from Chlorophyta.

3.2.2 Regional and interannual differences of pigment sedimentation

Fluxes and ratios in the top traps: Two mooring strings, containing 9 traps in the North and 15 in the South, were deployed during two ensuing periods (2001-2002 and 2002-2003). Annual fluxes to the uppermost trap varied strongly between both investigated deployment periods (2001-2002 and 2002-2003) and between the two investigated sites (South and North; Tab. 9A). At both sites (South and North) the Chl*a*s (Chl*a* + chlorophyllide *a* + pheopigment *a*) flux was much lower during 2002-2003 than during 2001-2002 (Tab. 9A). The dry matter (DM) and TOC fluxes were lower during the second period as well (Tab. 9A). The Chl*a*s and TOC fluxes as well as the Chl*a*s/TOC ratio were higher in the South than in the North in 2001-2002, but lower in 2002-2003 (Tab. 9A).

The fluxes of Chl*b*s, Chl*c*, fucoxanthin (Tab. 9A) and other carotenoids were lower during the second deployment period in both basins similar to the Chl*a*s flux (whereby for the North the 300 m trap has to be considered when comparing both years, because the 50 m trap was lost during the first deployment). The Chl*b*s/Chl*a*s ratio was much lower (1-3 %), than the Chl*c*/Chl*a*s and fucoxanthin/Chl*a*s ratios (42-48 % and 18.5-20 %, respectively) in the South and similar results were found for the North (cf. Tab. 9A). These ratios indicated a much greater proportion of the Bacillariophyceae+ Chrysophyceae (indicated by Chl*c* and fucoxanthin) flux into the top traps than of Chlorophyta (indicated by Chl*b*) in both years and at both sites.

Fluxes and ratios in the bottom traps: At both sites the Chl*a*s fluxes were significantly lower during the second deployment than during the first (Tab. 9B). Furthermore, the Chl*a*s fluxes, which reached the lake bottom, were significantly higher in the South than in the North. Compared to the top traps, the Chl*a*s fluxes which reached the lake bottom were 80-95 % lower for the South mooring 2001-2002, and both North moorings, but higher in the South mooring 2002-2003 (cf. Tab. 9A,B).

The fluxes of Chl*b*s, Chl*c*, fucoxanthin (Tab. 9B) and other carotenoids as well as of dry matter and TOC (Tab. 9B) were (similar to the Chl*a*s fluxes) also significantly higher in the South than in the North. No significant differences were found for the C/N ratios (Tab. 9A,B).

Tab. 9. Fluxes and ratios of dry matter, organic carbon and Chl*a*s in (A) the top traps and (B) the bottom traps of the four investigated moorings, and (C) in the top of cores from below the moorings.

site		**South**		**North**	
period		**2001-2002**	**2002-2003**	**2001-2002**	**2002-2003**
A) top traps	**at depth**	**40 m**	**40 m**	**300 m**	**50 m (300 m)**
DM	(g m^{-2} yr^{-1})	174.5	39.9	127.4	30.7 (19.7)
TOC	(g m^{-2} yr^{-1})	38.2	5.0	10.0	9.0 (2.5)
C/N	atomic ratio	14.8	12.4	11.8	9.9 (12.3)
Chl*a*s	(µmol m^{-2} yr^{-1})	752.0	43.8	179.6	146.3 (70.8)
Chl*a*s/DM	(µmol g^{-1})	4.3	1.1	1.4	4.7 (3.0)
Chl*a*s/TOC	(µmol g^{-1})	21.0	8.7	18.0	16.2 (28.3)
Chl*b*s	(µmol m^{-2} yr^{-1})	7.2	1.4	2.0	0.77 (1.0)
Chl*c*	(µmol m^{-2} yr^{-1})	31.5	2.1	1.9	6.1 (0.03)
Fucoxanthin	(µmol m^{-2} yr^{-1})	139.2	8.7	12.9	22.3 (0.28)
B) bottom traps	**at depth**	**1.1 - 1.4 km**	**1.1 - 1.4 km**	**0.68 - 0.9 km**	**0.68 - 0.9 km**
DM	(g m^{-2} yr^{-1})	117.8 ^{N2}	141.0 $^{N1, N2}$	109.3 $^{S2, N2}$	18.7 $^{S1, S2, N1}$
TOC	(g m^{-2} yr^{-1})	9.2 $^{N1, N2}$	12.1 $^{N1, N2}$	5.3 $^{S1, S2, N2}$	1.7 $^{S1, S2, N1}$
C/N	atomic ratio	11.2	13.0	11.0	11.2
Chl*a*s	(µmol m^{-2} yr^{-1})	203.9 $^{S2, N1, N2}$	81.2 $^{S1, N1, N2}$	30.2 $^{S1, S2, N2}$	6.3 $^{S1, S2, N1}$
Chl*a*s/DM	(µmol g^{-1})	1.55 $^{S2, N1, N2}$	0.64 $^{S1, N1, N2}$	0.26 $^{S1, S2}$	0.32 $^{S1, S2}$
Chl*a*s/TOC	(µmol g^{-1})	20.4 $^{S2, N1, N2}$	6.5 $^{S1, N2}$	5.5 ^{S1}	3.9 $^{S1, S2}$
Chl*b*s	(µmol m^{-2} yr^{-1})	2.6 $^{N1, N2}$	2.5 $^{N1, N2}$	0.82 $^{S1, S2, N2}$	0.40 $^{S1, S2, N1}$
Chl*c*	(µmol m^{-2} yr^{-1})	5.8 $^{N1, N2}$	0.93 $^{N1, N2}$	0.26 $^{S1, S2, N2}$	0.03 $^{S1, S2, N1}$
Fucoxanthin	(µmol m^{-2} yr^{-1})	22.3 $^{N1, N2}$	5.6 $^{N1, N2}$	0.37 $^{S1, S2, N2}$	0.17 $^{S1, S2, N1}$
C) core tops	**section**	**0-1 cm**		**0-1 cm**	
time span	yr	~7*		~7**	
DM	(g m^{-2} yr^{-1})	89*		90**	
TOC	(g m^{-2} yr^{-1})	3.4		3.5	
C/N	atomic ratio	8.5		9.1	
Chl*a*s	(µmol m^{-2} yr^{-1})	9.9		2.3	
Chl*a*s/DM	(µmol g^{-1})	0.11		0.03	
Chl*a*s/TOC	(µmol g^{-1})	2.92		0.66	
Chl*b*s	(µmol m^{-2} yr^{-1})	0.54		0.21	
Chl*c*	(µmol m^{-2} yr^{-1})	0.17		0.06	
Fucoxanthin	(µmol m^{-2} yr^{-1})	1.14		-	

* Müller et al.(2005); ** Mackay et al. (1998), core ´baik29´

Note: In the South during both deployments the top trap was exposed at 40 m. In the North the top trap was exposed at 300 m water depth in 2001-2002 and at 50 m in 2002-2003. Therefore, in the North (second deployment) the fluxes and ratios at 50 m were given and those found in 300 m were added in parenthesis. As the fluxes and ratios in the deepest traps varied only little, the lowest four traps were combined as "bottom traps" and median was calculated. They were deployed between 1100 and 1400 m in the South and between 650 and 900 m in the North. Within the bottom traps superscript S1, S2, N1, and N2 indicate significant differences (at 90 %, Mann-Whitney-U-test) to South 2001-2002 (S1), South 2002-2003 (S2), North 2001-2002 (N1), and North 2002-2003 (N2).

Regression models: The dry matter and Chl*a*s fluxes through the water column decreased with the water depth in the South first deployment and North second deployment, while the flux increased in the South second deployment (cf. Tab. 9A,B). However, the flux of original Chl*a* and other labile pigments as well as TOC and generally the ratios of organic compounds (e.g. TOC and Chl*a*s) vs. dry matter, significantly decreased with depth at both sites and deployment periods (Fig. 36, Appendix C - Tab. 5). These results indicated that although unusual high settling material was trapped in the bottom traps of the South basin in 2002-2003, the degradation of the organic compounds was strong in the water column during that period as well.

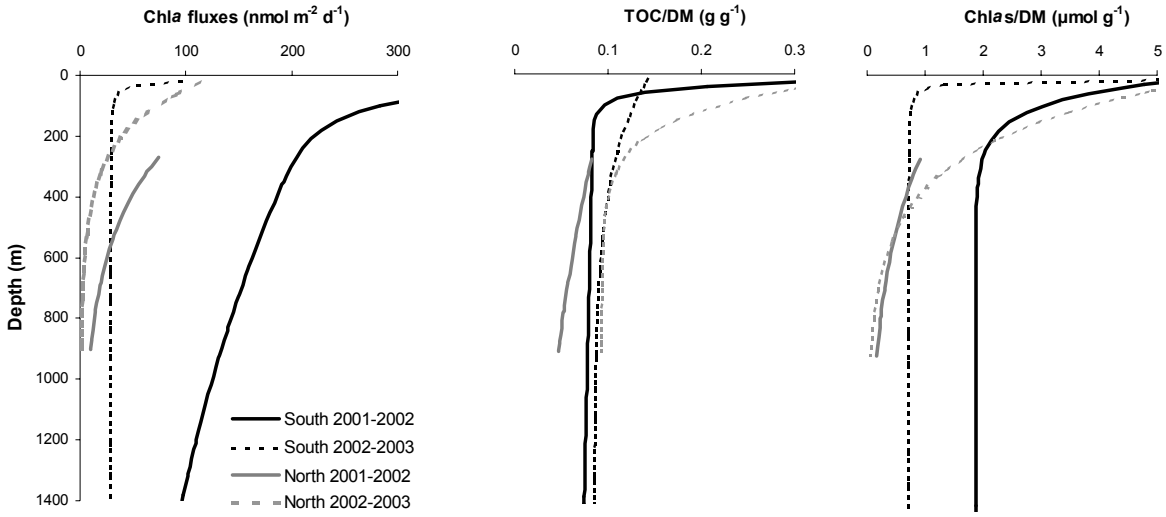

Fig. 36. Chl*a* fluxes as as well as TOC/DM and Chl*a*s/DM ratios for both sites and both investigated deployment periods. The respective regression equations and their coefficient of determination (r^2) are reported in Appendix C - Tab. 5. The water depth at the mooring site in the North and South basins were c. 900 m and 1400 m, respectively; the upper traps of the North mooring 2001-2002 were lost due to technical disturbances.

In the South, the Chl*a*/TOC, Chl*a* degradation products/TOC and Chl*a*s/TOC ratios did not decrease significantly with the water depth and the pheophytin *a*/TOC ratio even showed significant formation with depth (Fig. 37A, Appendix C - Tab. 6). In the North, in contrast, the Chl*a*/TOC and pheopigments/TOC ratios decreased linearly with depth; only the pheophytin *a*/TOC ratio did not vary significantly (Fig. 37B, Appendix C - Tab. 6). These differences of the transfer through the water column caused that the decrease of Chl*a*s/TOC ratios were significantly stronger in the bottom traps of the North than of the South (Tab. 9B).

The Chl*b* or Chl*b*s/TOC ratios did not show significant decreases with water depth either in the South or in the North, while the Chl*c*/TOC ratio significantly decreased at both sites (Fig. 37A,B, Appendix C - Tab. 6). Chl*c* degradation products were not

detected. Most carotenoids/TOC ratios showed exponential decreases with water depth in the South, while in the North significant regressions were calculated only for fucoxanthin and diatoxanthin (Fig. 37A,B, Appendix C - Tab. 6). The pigment/TOC ratios decay with water depth was therefore pigment- and site-specific.

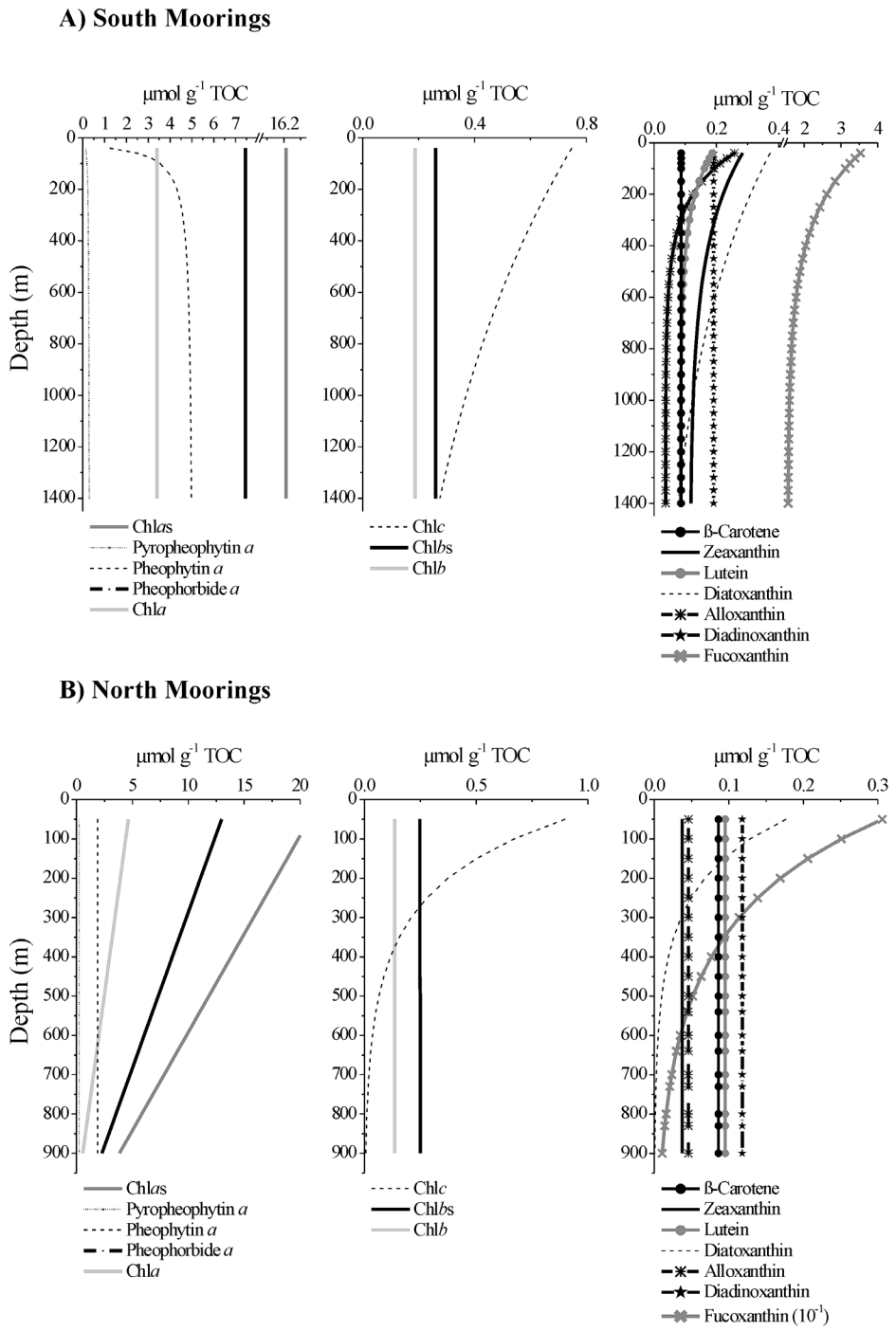

Fig. 37. Pigment/TOC ratios vs. depth through the water column of the South (A) and North (B) basins (see Fig.1 for locations). Curve calculations were based on mean values of the two deployment periods (2001-2002 and 2002-2003). The regression functions are given in Appendix C - Tab. 6. Mean values over the 15 (South) or 9 (North) traps were plotted for pigment/TOC ratios, where no significant decay or formation was found.

3.2.3 Degradation and preservation within the surface sediment

Comparison between core tops and bottom traps: The trap material in almost all traps was thought to be anoxic because of the dark grey colour, dead *Gammarus*, the smell of hydrogen sulphide (H_2S) and a lack of oxidised ferric iron (Fe(III)), whereas the topmost centimetre of the surface sediment was oxic (Müller et al. 2005). High degradation could therefore be expected. In both South and North the Chl*a*s/DM and Chl*a*s/TOC ratios diminished strongly in the core tops compared to the bottom traps (Tab. 9B,C). Thereby the Chl*a*s/DM ratios diminished stronger (about 90 %) than the Chl*a*s/TOC ratios (70-80 %). Furthermore, whereas the Chl*a*/DM ratio decreased similarly at both mooring sites, the Chl*a*s/TOC ratio decreased much stronger in the North (~90 %) than in the South (70-80 %; Tab. 9B,C). However, the residence time of the settled material within the upper centimetre was similar at both sites (Tab. 9C). Regional variations in the pigment preservation within these core tops were therefore likely.

Tab. 10. Dry matter (DM) and TOC fluxes, C/N ratios, and Chl*a*s fluxes and ratios in the core top (0-1 cm) of nine short cores. Medians from triplicate samples were calculated. The Chl*a* concentrations in the respective regions in summer and the sedimentation rates are given to describe the sites. Abbreviations: B Bay - Barguzin Bay, S Delta - Selenga Delta. See Fig. 38 for locations, numbering refers to sites from South to North within a region.

	South (1)	**South (2)**	**North (1)**	**North (2)**	**North (3)**	**North (4)**	**S Delta (1)**	**S Delta (2)**	**B Bay**
summer Chl*a*[a] (nmol L^{-1} ± 95 % CI)	1.43 ±0.26	1.43 ±0.26	0.97 ±0.13	0.97 ±0.13	0.97 ±0.13	0.97 ±0.13	2.39 ±0.34	2.39 ±0.34	2.49 ±0.18
sedim. rate (mm yr^{-1})	0.75[b]	0.47[b]	0.57[b]	0.52[c]	0.52[c]	0.52[c]	1.49[b]	0.91[e]	nd
time span yr	4[d]	7[b]	nd	7[d]	7[d]	7[d]	nd	nd	nd
DM (g m^{-2} yr^{-1})	143[b]	89[b]	68[b]	90[d]	90[d]	90[d]	266[b]	340[e]	nd
TOC (g m^{-2} yr^{-1})	5.9	3.4	2.2	3.5	3.5	3.5	7.7	11.7	2%
C/N atomic ratio	9.9	8.5	7.9	9.1	9.4	7.2	8.6	8.6	7.7
Chl*a*s (µmol m^{-2} yr^{-1})	69.5	9.9	1.7	2.3	2.7	2.1	14.9	51.0	nd
Chl*a*s/DM (µmol g^{-1})	0.490	0.111	0.024	0.026	0.027	0.023	0.056	0.15	0.037
Chl*a*s/TOC (µmol g^{-1})	11.79	2.92	0.74	0.66	0.85	0.69	2.11	5.06	1.87

[a] cf. Fig. 16, chapter 3.1.1
[b] Müller et al. (2005)
[c] M. Sturm (EAWAG, Switzerland) pers. comm.
[d] Mackay et al. (1998), core ´baik29´ and ´baik38´
[e] Edgington et al. (1991), core ´station 4´

Regional differences of DM, TOC and pigments at the sediment surface: The top centimetres of seven additional short cores taken across the lake, one in the South, three in the North, two in the Selenga Delta and one in the Barguzin Bay were therefore analysed. The sedimentation rate was highest in the Selenga Delta; however, because the C/N ratio was not higher in the Selenga Delta (Tab. 10) most of the settling organic material likely results from autochthonous production rather than from allochthonous material transported by the river. The Chl*a*s flux into the surface sediment was highest in the eastern South, much lower in southern Selenga Delta and in the central South, and lowest in the North. The Chl*a*s/DM and Chl*a*s/TOC ratios in the surface sediments varied in the order South, Selenga Delta > Barguzin Bay > North (Tab. 10).

Undegraded Chl*a* contributed less than 6 % to the total Chl*a*s in the North and Barguzin Bay and less than 13 % in the South; it was best preserved (19 %) in the western Selenga Delta (Fig. 38A). That intact Chl*a* was found in the surface sediment marked the importance of the sedimentation of living or at least moribund cells. The share of pheophytin was much greater in the North than in the South and Selenga Delta. Lutein and canthaxanthin were the only pigments detected in all North cores, while in the South and at both river inflow sites fucoxanthin and diadinoxanthin were the dominant carotenoids (Fig. 38B). Highest pigment diversity was found in the southern Selenga Delta (Fig. 38B).

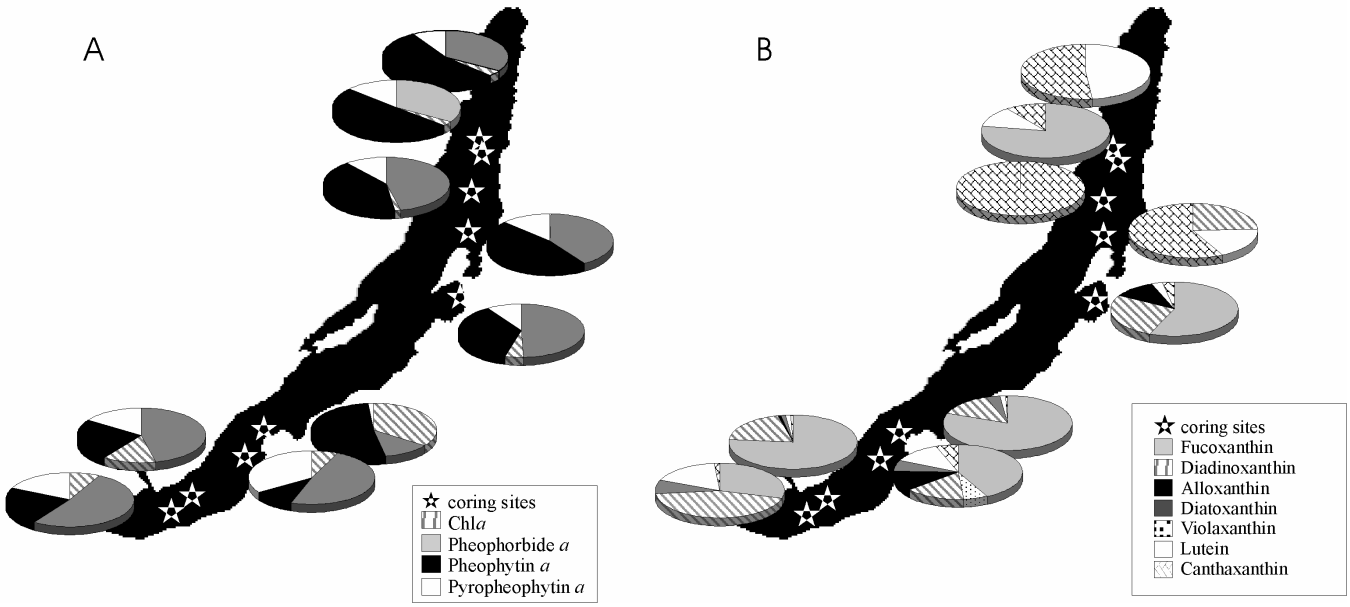

Fig. 38. Composition of (A) Chl*a*s and (B) carotenoids within the uppermost centimetre of the surface sediment gathered from nine coring sites across Lake Baikal in July 2001 and July 2002. Stars mark the coring sites of the associated composition diagrams.

Degradation within the oxidised surface layers: Oxidised layers could be well discerned in the short cores due to sharp changes between the upper orange-brownish layer and the greyish layer below (reduced layer; Fig. 39). Strong degradations of the organic compounds occurred within the upper oxidised layers, which spanned 4 to 15 cm. The thinnest oxidised layer was found in the Barguzin Bay and thickest in the cores from the North.

Fig. 39. Transition from upper oxydised layer (brownish) to the lower reduced layer (grey) of a short core from Continent Ridge (North basin). Core section span from core top (0 cm) to 25 cm depth.

Degradation for the surface sediments is shown exemplarily for the sites below the moorings and for southern Selenga Delta (Fig. 40, Appendix C - Tab. 7). The TOC/DM ratio, the Chl*a*/TOC ratio, pheopigments/TOC ratio and Chl*a*s/TOC decreased in all three cores (Fig. 40) with the sediment depth. The degradation of TOC (when referred to dry matter) was linear in all cores (Fig. 40, Tab. 11). Thereby, higher decay slopes were found in the core from North and lowest decay slopes were found in the Selenga Delta and in the central South (Tab. 11). The decay of the Chl*a*s/TOC ratios was exponential in all short cores (Tab. 11). Hence, the decay with depth was constant and proportional to the ratio left. Again higher decay slopes were found in the North and lowest decay slopes were found in the central South and in the Selenga Delta (Tab. 11) indicating stronger degradation in the North than in the central South and Selenga Delta.

Chl*a*/TOC, pheophorbide *a*/TOC and Chl*a*s/TOC decreased exponentially in the South and Selenga Delta, while pheophytin *a*/TOC and pyropheophytin *a*/TOC decreased linearly (Fig. 40, Appendix C - Tab. 7). In the North, in contrast, all ratios of chlorophylls and its degradation products to TOC decreased exponentially with sediment depth (Fig. 40, Appendix C - Tab. 7, Tab. 11). Chl*b*s/TOC and Chl*c*/TOC also decreased exponentially (except Chl*c* in the southern Selenga Delta, which was not detected at the bottom of the core; Fig. 40, Appendix C - Tab. 7, Tab. 11).

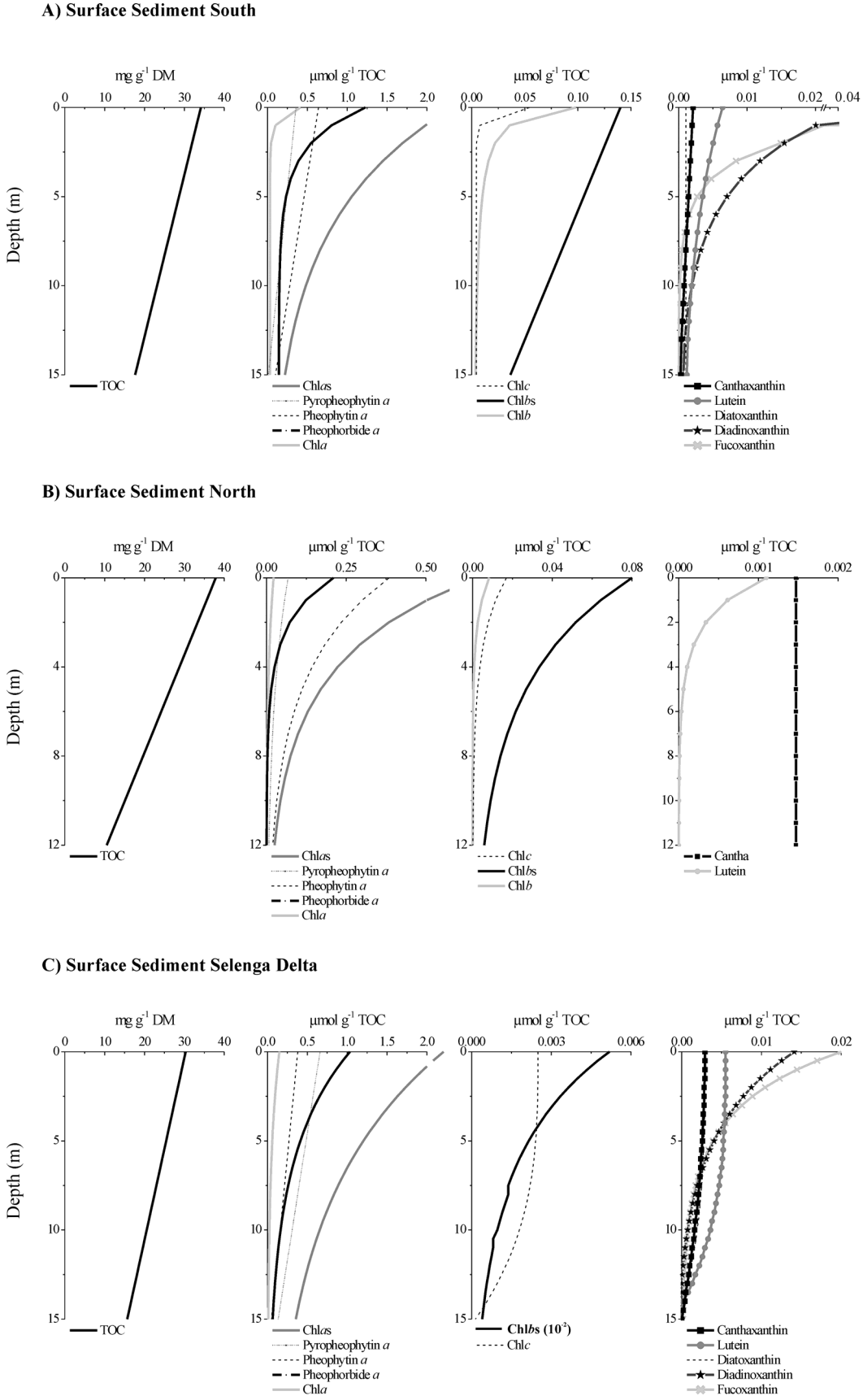

Fig. 40. TOC/DM ratio and pigment/TOC ratios vs. depth in the surface sediments of the (A) South basin, (B) North basin and (C) Selenga Delta. The regression functions are given in Appendix C - Tab. 7. Mean values over the 15 (South, Selenga Delta) or 12 (North) surface sediment slices were plotted for pigment/TOC ratios, where no significant decay or formation was found.

Tab. 11. Regression models for the decay of TOC/DM and pigments/TOC ratios within the upper, oxidised part of short cores.

	TOC/DM		**Chl*a*s/TOC**		**Chl*a***	**Ph-bide*a***	**Ph-tin*a***	**Pyro-ph*a***	**Chl*bs***	**Chl*c***
	mg g^{-1}		**µmol g^{-1}**		**µmol g^{-1}**					
	model	**slope <95 %CI>**	**model**	**slope <95 %CI>**	**model**					
South (E)	linear	-1.32 <-1.70; -0.94>	exp	0.33 <0.10; 0.56>	exp	exp	exp	exp	exp	exp
South (C)	linear	-1.10 <-1.47; -0.73>	exp	6.36 <3.87; 8.84>	exp	exp	linear	linear	linear	exp
North (E)	linear	-1.69 <-1.87; -1.50>	exp	3.54 <2.34; 4.75>	exp	exp	exp	exp	exp	exp
North (C1)	linear	-2.28 <-2.67; -1.88>	exp	3.69 <2.84; 4.55>	exp	exp	exp	exp	exp	exp
North (C2)	linear	-1.24 <-1.45; -1.04>	exp	3.04 <1.88; 4.20>	exp	exp	exp	exp	exp	-
North (C3)	linear	-2.58 <-2.90; -2.27>	exp	1.07 <0.62; 1.52>	exp	exp	exp	exp	exp	exp
Selenga Delta (S)	linear	-0.98 <-1.02; -0.91>	exp	8.22 <6.01; 10.42>	exp	exp	linear	linear	exp	$a+bx^3$

Note: All models were significant at a level of $P< 0.01$ and the coefficient of determination (r^2) was >0.5.
´Linear´ designate y=a+bx models and ´exp´ y=a+exp(-x/b). Examples of the models are shown in Fig. 40 and Appendix C - Tab. 7.
Abbreviations: C – central, E- eastern, exp – exponential, Phbide – pheophorbide, Phtin – pheophytin, Pyroph – pyropheophytin, S – southern.

The composition of total carotenoids did also change with the core depth (Fig. 40, Appendix C - Tab. 7). In the South and Selenga Delta, the dominant carotenoids in the core top were fucoxanthin (77 %) and diadinoxanthin. Other carotenoids contributed less than 2 % to the total carotenoids. However, at 10 cm core depth, fucoxanthin could no more be identified and most prominent carotenoids were diadinoxanthin and lutein. However, in the North, lutein and canthaxanthin were the only carotenoids identified already in the core top and only canthaxanthin was identified in the sediment below. These findings strengthened the assumption of a much stronger degradation in the North compared to the South before final deposition below the redox layer. Thus, as has been shown for the water column processes, the degradation in the surface sediment was also pigment- and site-specific.

3.3 High-resolution analysis of fossil phytoplankton pigments

3.3.1 Holocene

In all three investigated short cores (´Vidrino´, ´Posolski´, and ´Contintent Ridge´, located in the South basin, Selenga Delta, and North basin, respectively) a strong decrease of pigment and TOC contents was found within the upper 10 cm (Fig. 41, Fig. 42, and Fig. 43). Those decreases cannot be related only to an increase in the phytoplankton standing crop from former to present time, but with high certainty to strong degradation within the oxic or oxidised layers (cf. chapter 3.2.3). The upper 10 cm will, therefore, not be discussed further in this Holocene study. In all three Holocene cores, original, undegraded Chl*a* that indicated the presence of living algae occurred within the uppermost centimetres, but was not detected below.

Tab. 12. Comparisons of mean C/N ratios, TOC contents and Chl*a*s/TOC and Chl*b*s/TOC ratios and their variation within the Holocene until c. 5.1 kyr BP (the maximum reached at Vidrino, cf. Fig. 41). The upper 10 cm (oxidised layer) were excluded. Abbreviations: SD – standard deviation, CV – coefficient of variation.

	Vidrino				**Posolski**				**Continent Ridge**			
Time	Holocene (c. 5.1 kyr)				Holocene (c. 5.1 kyr)				Holocene (c. 5.1 kyr)			
Depth	10 - 60 cm				10 - 61 cm				10 - 27 cm			
	C/N	TOC	Chl*a*s/ TOC	Chl*b*s/ TOC	C/N	TOC	Chl*a*s/ TOC	Chl*b*s/ TOC	C/N	TOC	Chl*a*s/ TOC	Chl*b*s/ TOC
	atomic	(%)	μmol g^{-1}		atomic	(%)	μmol g^{-1}		atomic	(%)	μmol g^{-1}	
mean	10.48 P,C	1.50 P,C	0.33 C	0.033 P,C	9.84 V,C	1.87 V,C	0.42 C	0.069 V,C	7.71 V,P	1.26V,P	0.09 V,P	0.012 V,P
SD	0.93	0.03	0.14	0.021	0.64	0.02	0.17	0.039	1.17	0.72	0.06	0.017
CV (%)	8.9	2.2	41.6	62.4	6.5	1.3	41.2	56.9	15.2	5.7	71.3	150.0

V - significant at 95 % C.I. to Vidrino
P - significant at 95 % C.I. to Posolski
C - significant at 95 % C.I. to Continent Ridge

Vidrino (South basin): The average atomic C/N ratio was 10.5 and varied little along the core (8.9 % variation from 9 to 12; Tab. 12 and Fig. 41). The average TOC content over the core was 1.5 % and the average Chl*a*s/TOC ratio over the core was 0.3 μmol g^{-1} (Tab. 12). Both the TOC content and the Chl*a*s/TOC ratio increased from 40 to 60 cm sediment depth (Fig. 41).

The proportion of the distinct Chl*a* degradation products varied only slightly with depth and the contribution of pheophorbide *a* was low throughout the core (Fig. 41).

The Chl*b*s/Chl*a*s ratio varied without any depth trend (Fig. 41). The mean Chl*b*s/TOC ratio was 0.03 μmol g^{-1} with a higher coefficient of variation than that of Chl*a*s/TOC (62 %; Tab. 12). Chl*c* was not detected in all core depths. Several Chl*c*/Chl*a*s ratio peaks were found within the upper 15 cm as well as below 40 cm, only one peak was found in between (Fig. 41). The carotenoid/Chl*a*s ratios showed a similar trend to the Chl*a*s/TOC ratio with lowest occurrence between 10 to 30 cm, but towards the bottom of the core greatly increased carotenoid/Chl*a*s ratios were found.

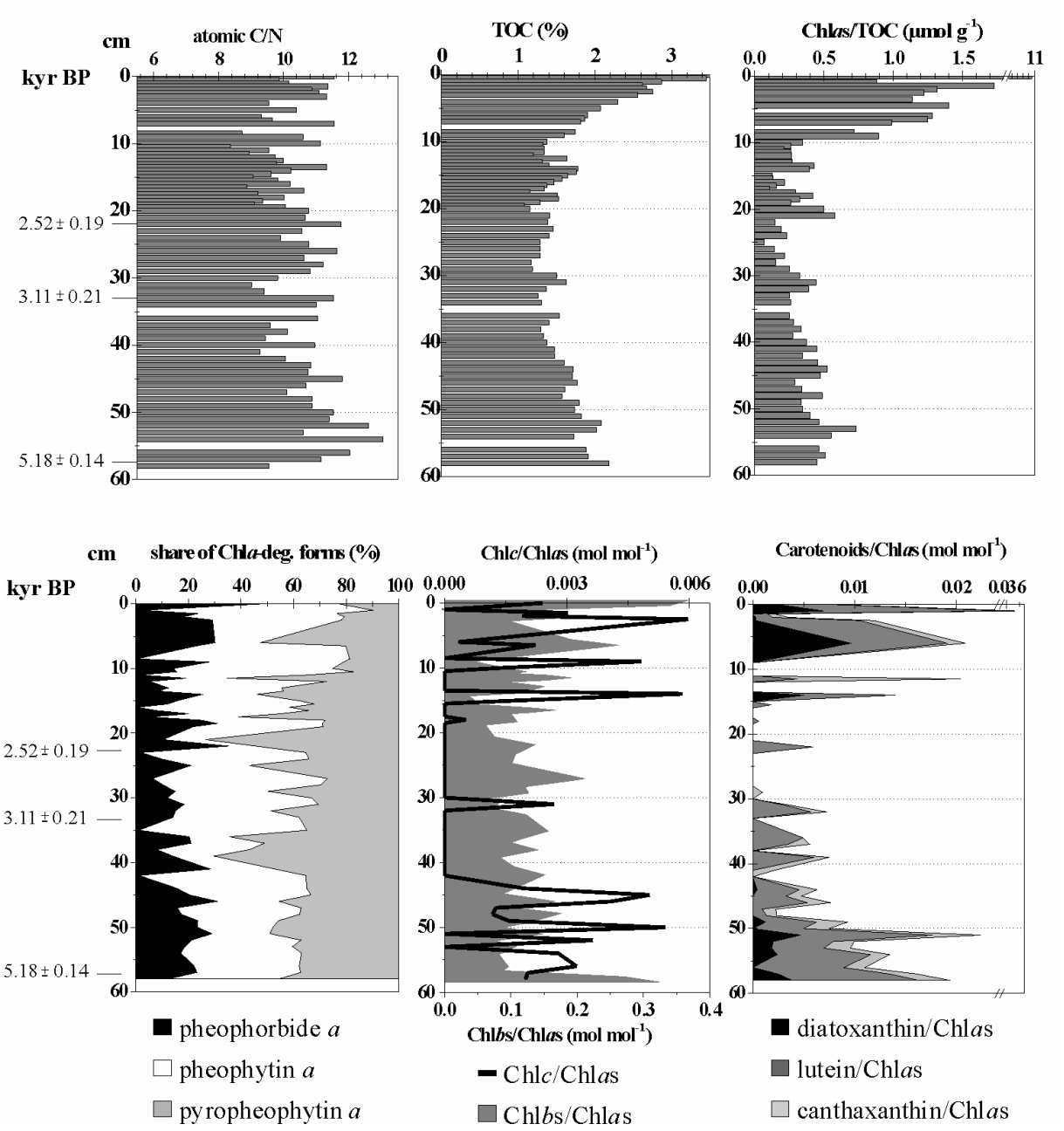

Fig. 41. Holocene high-resolution analysis of lipophilic photosynthetic pigments and organic carbon at ´Vidrino´ coring site (South basin). Abbreviations: BP – before present, Chl*a*s – sum of all forms of all chlorophyll *a* degradation products (same for Chl*b*s), TOC – total organic carbon.

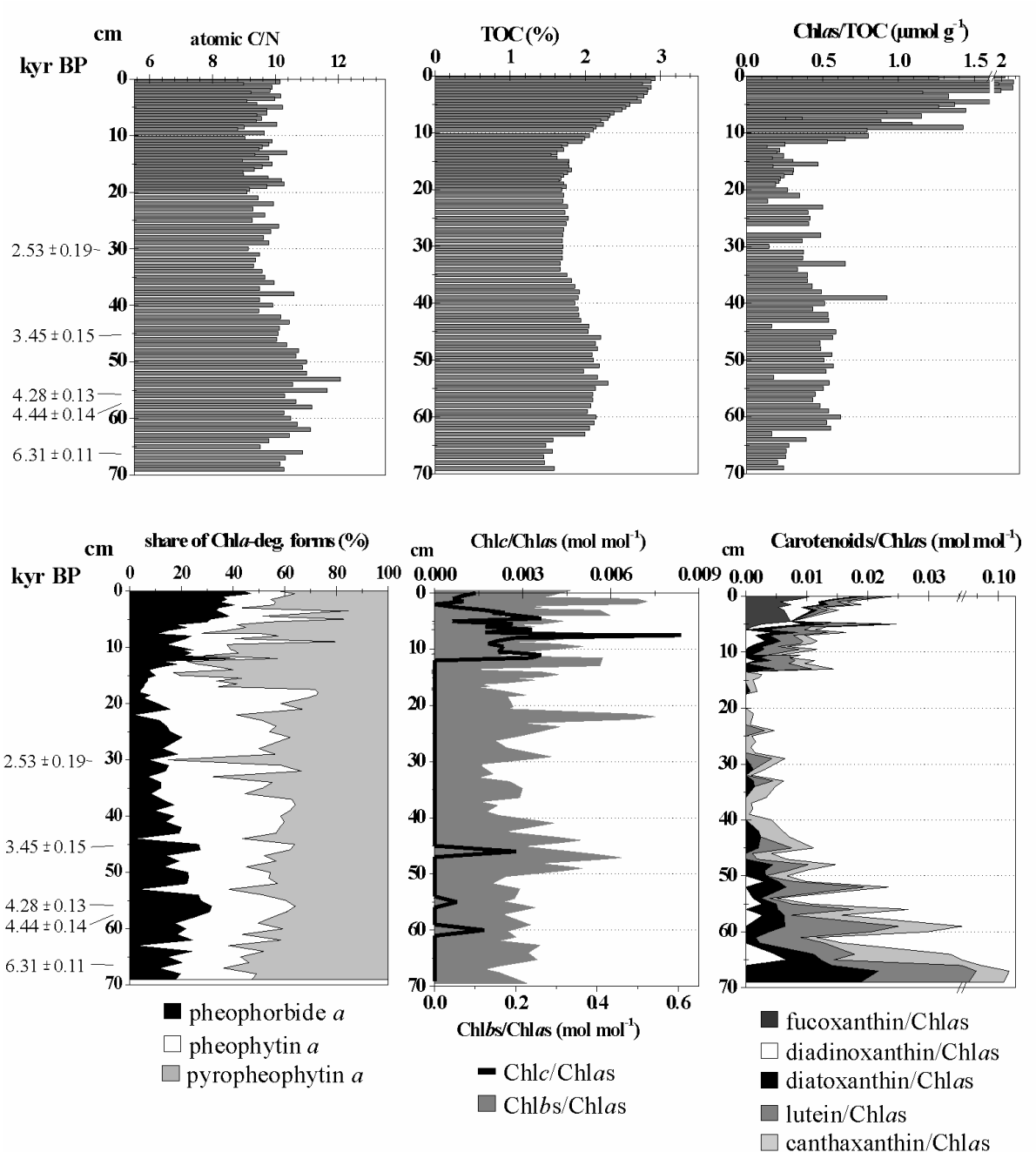

Fig. 42. Holocene high-resolution analysis of photosynthetic pigments and organic carbon at ´Posolski´ coring site (Selenga Delta). See Fig. 41 for abbreviations.

Posolski (Selenga Delta): The average atomic C/N ratio was 9.8 and varied little along the core (6.5 % of variation from 9 to 11; Tab. 12, Fig. 42). The average TOC content and the Chl*a*s/TOC ratio over the core were 1.87 % and 0.4 µmol g^{-1}, respectively, with a coefficient of variation of 1.3 % for TOC and 41.2 % for the Chl*a*s/TOC ratio (Tab. 12). Both the TOC content and the Chl*a*s/TOC ratio showed a long lasting maximum from 35 to 65 cm and were lowest at the bottom of the core (65-70 cm; Fig. 42).

The proportion of the distinct Chl*a* degradation products varied along the core (Fig. 42). The proportion of pyropheophytin *a*, for example, was higher than that of pheophytin *a* in the upper 15 cm, but similar on average between 20 and 40 cm and increased again at the bottom of the core (Fig. 42).

The Chl*b*s/Chl*a*s varied along the core without any depth trend (Fig. 42). However, the Chl*b*s/TOC ratio was significantly higher at Posolski than at Vidrino. The Chl*c*/Chl*a*s ratio showed several maxima within the upper 10 cm and another at 47 cm similar to the Chl*b*s/Chl*a*s-peaks (Fig. 42). The number of detected carotenoids was highest at Posolski compared to the other two sites. The carotenoids/Chl*a*s ratios showed were lowest between 15 and 40 cm and showed then a strong increase from 40 cm towards the bottom of the core (Fig. 42). They did not show similar trends to Chl*a*s/TOC, Chl*b*s/Chl*a*s, or Chl*c*/Chl*a*s ratios (Fig. 42).

Continent Ridge (North basin): The average atomic C/N ratio was 7.7 and was significantly lower than that at Vidrino and Posolski (Tab. 12). Two pervasive C/N maxima were found between 20 and 42 cm, and between 46 and 65 cm (Fig. 43). The average TOC content was 1.26 % and was like the average Chl*a*s/TOC ratio (0.1 μmol g^{-1}) significantly lower at Continent Ridge than at Vidrino or Posolski (Tab. 12). The variability, in contrast, was highest for both TOC content (5.7 %) and Chl*a*s/TOC ratio (71.3 %) at Continent Ridge (Tab. 12). The TOC content showed similar trends to the C/N ratio (Fig. 43). Strong maxima of the Chl*a*s/TOC ratio were found at around 50 and 60 cm (Fig. 43).

The distinct Chl*a*s degradation products showed distinct trends with the core depth (Fig. 43). In the 5-20 cm section (during TOC and Chl*a*s/TOC minimum), the share of pheophorbide *a* was low, but the share of pyropheophytin was high, although not constantly. Below 20 cm, pheophytin was the dominant degradation product, and only at the bottom of the core, did the proportion of pyropheophytin increase.

The Chl*b*s/TOC ratio was lower at Continent Ridge than at Vidrino and Posolski, like the Chl*a*s/TOC ratio, but the variability was much higher (Tab. 12). The Chl*b*s/Chl*a*s and the Chl*c*/Chl*a*s ratios showed several maxima along the core, which did not correspond to the Chl*a*s/TOC maxima (Fig. 43). Canthaxanthin was detected within the uppermost centimetres, at 14 cm depth and below 20 cm, but lutein was detected only in a few samples between 56 and 62 cm (Fig. 43). The carotenoid/Chl*a*s peaks did not correspond to C/N, TOC, Chl*a*s, Chl*b*s or Chl*c* versus TOC peaks.

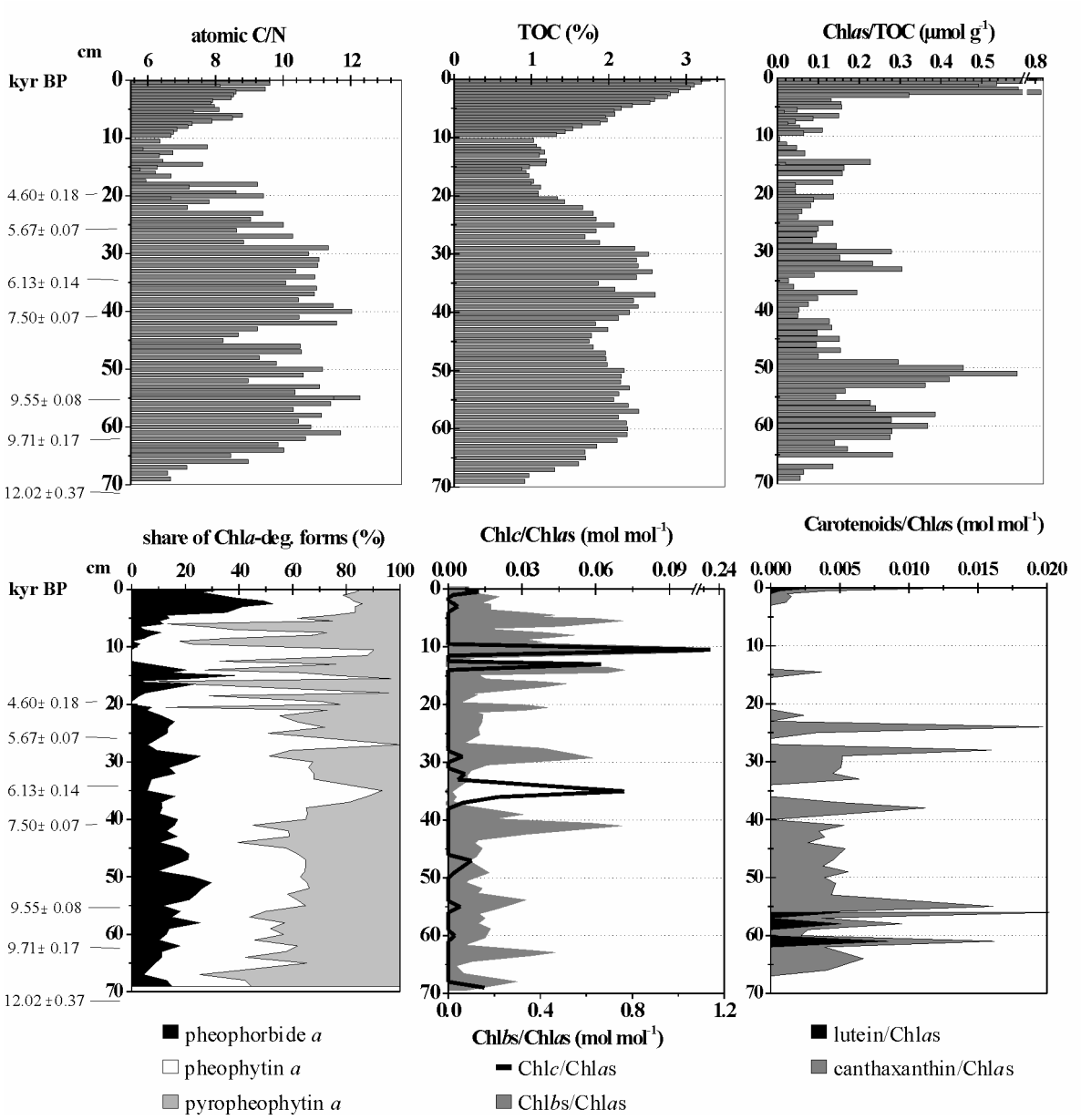

Fig. 43. Holocene high resolution analysis of photosynthetic pigments and organic carbon at ´Continent Ridge´ coring site (North basin). See Fig. 41 for dating and abbreviations.

Comparison of temporal changes at the three coring sites: At Continent Ridge, TOC and Chl*a*s/TOC increased strongly from c. 11 to 9 kyr BP (Fig. 44). The Chl*a*s/TOC ratio then decreased strongly from 9 to 8 kyr BP, was then low up to c. 6.5 kyr BP, and had a clear peak at c. 6 kyr BP. Shortly after 6 kyr BP, TOC and Chl*a*s/TOC ratio decreased towards c. 4 kyr BP. For TOC this minimum lasted up to c. 2 kyr BP. Meanwhile the Chl*a*s/TOC ratio showed a peak at c. 3.5 kyr BP. At Vidrino the TOC and Chl*a*s/TOC ratio decreased from c. 4.5 kyr BP on and this trend lasted for c. 3 kyr. At Posolski the TOC and Chl*a*s/TOC ratio decreased from 3 kyr BP on and this trend lasted for c. 1.5

kyr. All cores showed highest TOC contents and Chl*a*s/TOC ratios from c. 1.5 kyr to present, which are however within the oxidised layer characterised by strong degradation processes (cf. chapter 3.2.3).

At Continent Ridge the Chl*b*s/Chl*a*s ratio and the Chl*c*/Chl*a*s ratio varied only slightly during the early Holocene (c. 11 to 8 kyr BP; Fig. 44). From c. 8 to 7 kyr BP the Chl*b*s/Chl*a*s ratio showed a peak, while the Chl*c*/Chl*a*s ratio was low. Then at c. 6.5 kyr BP the Chl*b*s/Chl*a*s was at a minimum and the Chl*c*/Chl*a*s ratio exhibited a strong peak. Thereafter, the Chl*b*s/Chl*a*s ratio increased strongly, while the Chl*c*/Chl*a*s ratio tended again towards zero. Both the Chl*b*s/Chl*a*s and Chl*c*/Chl*a*s ratios increased at Continent Ridge sharply again between c. 3 and 2 kyr BP, but both peaks were not detected at Vidrino and at Posolski. At Vidrino a considerable increase of the Chl*c*/Chl*a*s ratio was noted from 5 to 4 kyr BP, which was, however, not found at Continent Ridge and at Posolski.

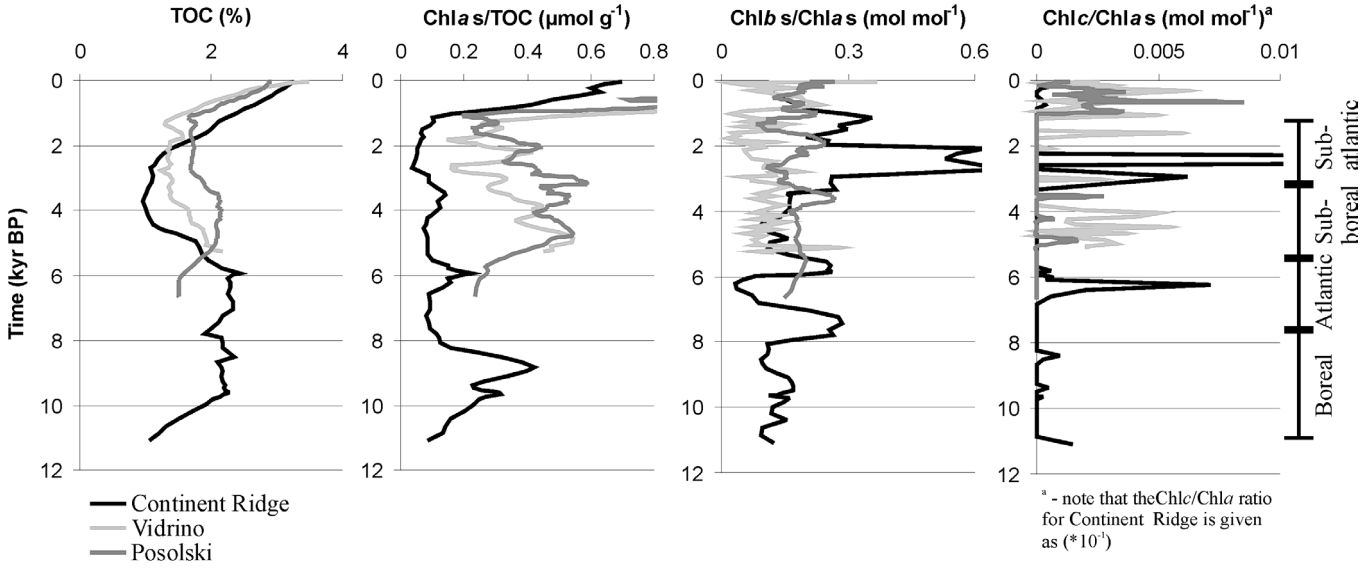

Fig. 44. Comparison of temporal changes at three coring sites ´Vidrino´, ´Posolski´, and ´Continent Ridge´ for TOC content, Chl*a*s/TOC ratio, Chl*b*s/Chl*a*s ratio, and Chl*c*/Chl*a*s ratio. See Fig. 41, Fig. 42, and Fig. 43 for dated data points and abbreviations. The periods between the dated depths were linearly interpolated. For TOC content, Chl*a*s/TOC ratio, and Chl*b*s/Chl*a*s ratio averages of two contiguous data points were plotted in order to minimise a possible analytical error; each peak was then supported by several data points. Single peaks for high-resolution contexts can be found in Fig. 41, Fig. 42, and Fig. 43. For Chl*c*/Chl*a*s ratio data were not averaged because most peaks were detached (cf. Fig. 41-Fig. 43).

3.3.2 Last Interglacial (Kazantsevo)

Pigments detected in deep sediments: A typical fluorescence chromatogram of the Kazantsevo optimum is shown in Fig. 45 (refer to Fig. 3 for degradation pathway). The terms Chl*a*s or Chl*b*s mean the sum of all respective chlorophylls, epi- and allomers and degradation products. Steryl chlorin esters (SCE) were also analysed and added to the Chl*a*s or Chl*b*s.

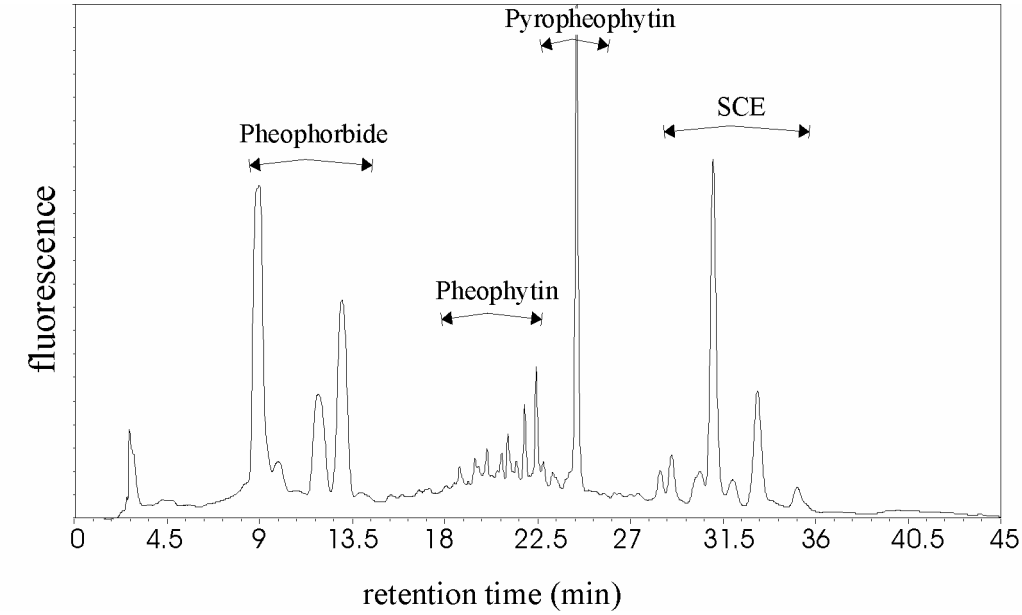

Fig. 45. Typical HPLC-chromatogram of the Kazantsevo Interglacial showing the retention times of the main chlorophyll degradation products pheophorbide, pheophytin, pyropheophytin and steryl chlorin ester (SCE; refer to Fig. 3 for degradation pathway).

High resolution analysis: The TOC content and the Chl*a*s/TOC ratios was much higher between 560 and 480 cm of this core than in the section below (580 – 560 cm) and the section above (480 – 420 cm), clearly indicating a warm phase during that period (Fig. 46). Assuming a sedimentation rate of 6.4 cm kyr^{-1} (Demory et al. 2005) this Kazantsevo Interglacial lasted for c. 12.5 kyr (this time is approximate, as the dating was performed on a parallel core).

The C/N ratio was only slightly higher during the Interglacial than in the glacial periods (Fig. 46), and was significantly lower than during the Holocene (Tab. 13). The TOC content increased from the Tazovsky Glaciation to the Kazantsevo Interglacial from 0.3 % to 1.5 %, but was also significantly lower than that preserved during the Holocene (Tab. 13).

Tab. 13. Comparison of mean C/N ratios, TOC contents and Chl*a*s/TOC ratio and Chl*b*s/TOC ratio and their variation during the Holocene and Kazantsevo Interglacial at Continent Ridge (North basin). Abbreviations: SD – standard deviation, CV – coefficient of variation.

Site	**Continent Ridge**				**Continent Ridge**			
Time	Holocene (c. 11 kyr)				Kazantsevo (c. 12 kyr)			
Depth	10 - 70 cm				480 - 560 cm			
	C/N	TOC	Chl*a*s/ TOC	Chl*b*s/ TOC	C/N	TOC	Chl*a*s/ TOC	Chl*b*s/ TOC
	atomic	(%)	μmol g^{-1}		atomic	(%)	μmol g^{-1}	
mean	8.98 K	1.79K	0.16 K	0.021 K	7.87 H	1.35H	0.26 H	0.024 H
SD	1.77	0.07	0.12	0.020	0.86	0.02	0.09	0.012
CV (%)	19.7	3.7	76.3	93.5	11.0	1.3	35.1	50.1

K - significant at 95 % C.I. to Kazantsevo

H - significant at 95 % C.I. to Holocene

The average (centennial) Chl*a*s accumulation rate during the Kazantsevo Interglacial was 2.3 nmol cm^{-2} 100 yr^{-1}. The Chl*a*s accumulation rates showed similar trends to the Chl*a*s/TOC ratios and the TOC content, but the difference between the glacial and interglacial phases was even more pronounced for the Chl*a*s accumulation rates and Chl*a*s/TOC ratios than for the TOC content.

During the preceding (Tazovsky) glacial period negligible amounts of Chl*a*s and Chl*b*s were detected (<0.1 μmol g^{-1} TOC), however, during the Kazantsevo Interglacial a strong increase occurred. The Chl*a*s accumulation rates and the Chl*a*s/TOC ratios showed three maxima, one at 535 cm (c. 125 kyr BP), one at 515 cm (c. 122 kyr BP) and one at 505 cm (c. 120.5 kyr BP) (Fig. 46). Even during the ensuing Early Zirianski Glaciation, the Chl*a*s accumulation rates and the Chl*a*s/TOC ratios were not homogenous; both first sharply decreased, but then increased again showing two small peaks (cut-out, Fig. 46). These events clearly indicate that during the glacial phases short and slight warmings occurred.

The Chl*b*s/TOC ratios were significantly lower during the Kazantsevo interglacial than during the Holocene (Tab. 13). However, the Chl*b*s/Chl*a*s ratios increased strongly from the Kazantsevo Interglacial towards the Early Zirianski glacial period, indicating increasing importance of Chlorophyta (Fig. 46).

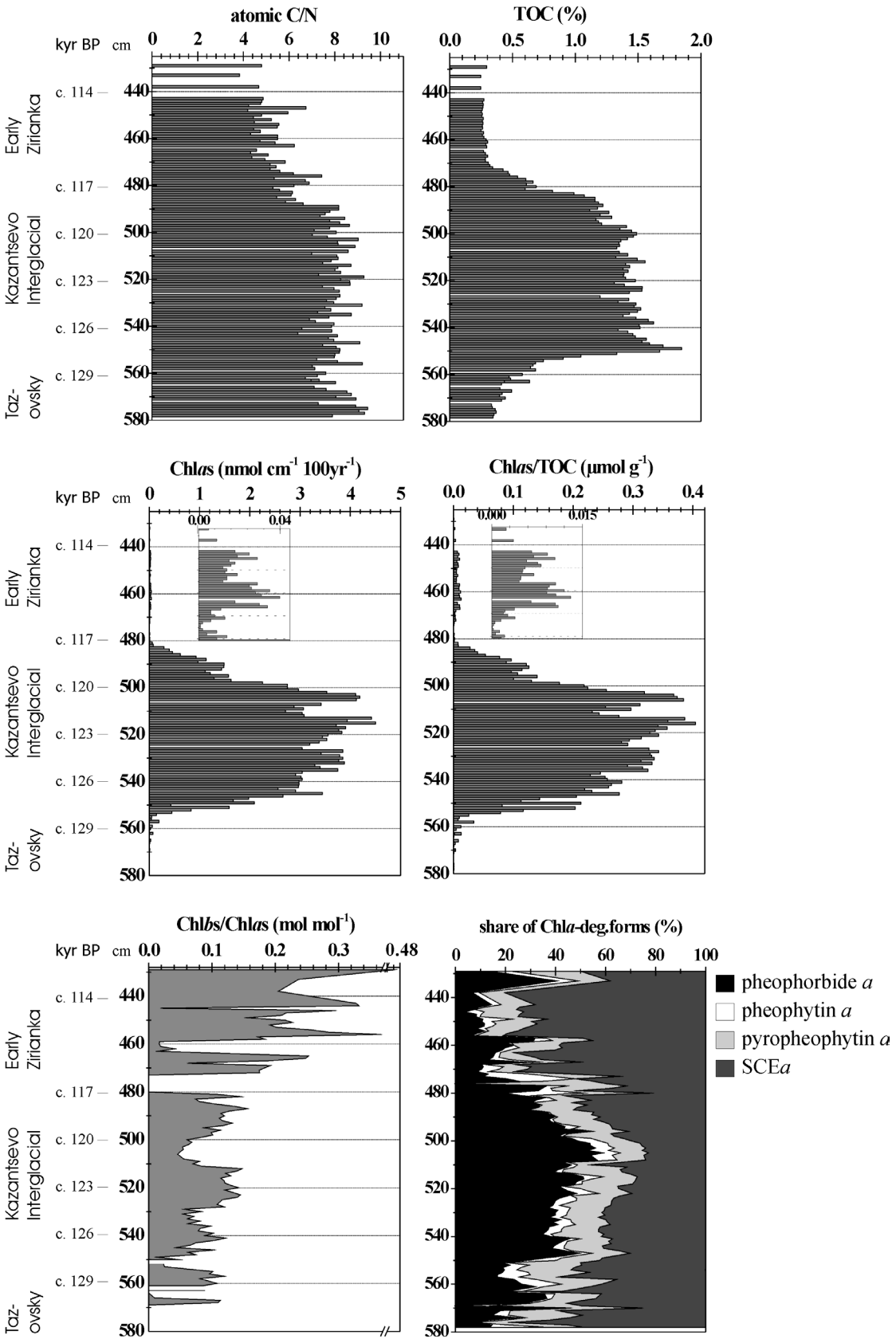

Fig. 46. High resolution analysis of lipophilic photosynthetic pigments and organic carbon during the Kazantsevo Interglacial at ´Continent Ridge´ (North basin). See Method section for dating, and Fig. 41 for abbreviations. SCEs (steryl chlorin esters) were included within the term ´Chl*a*s´ and ´Chl*b*s´.

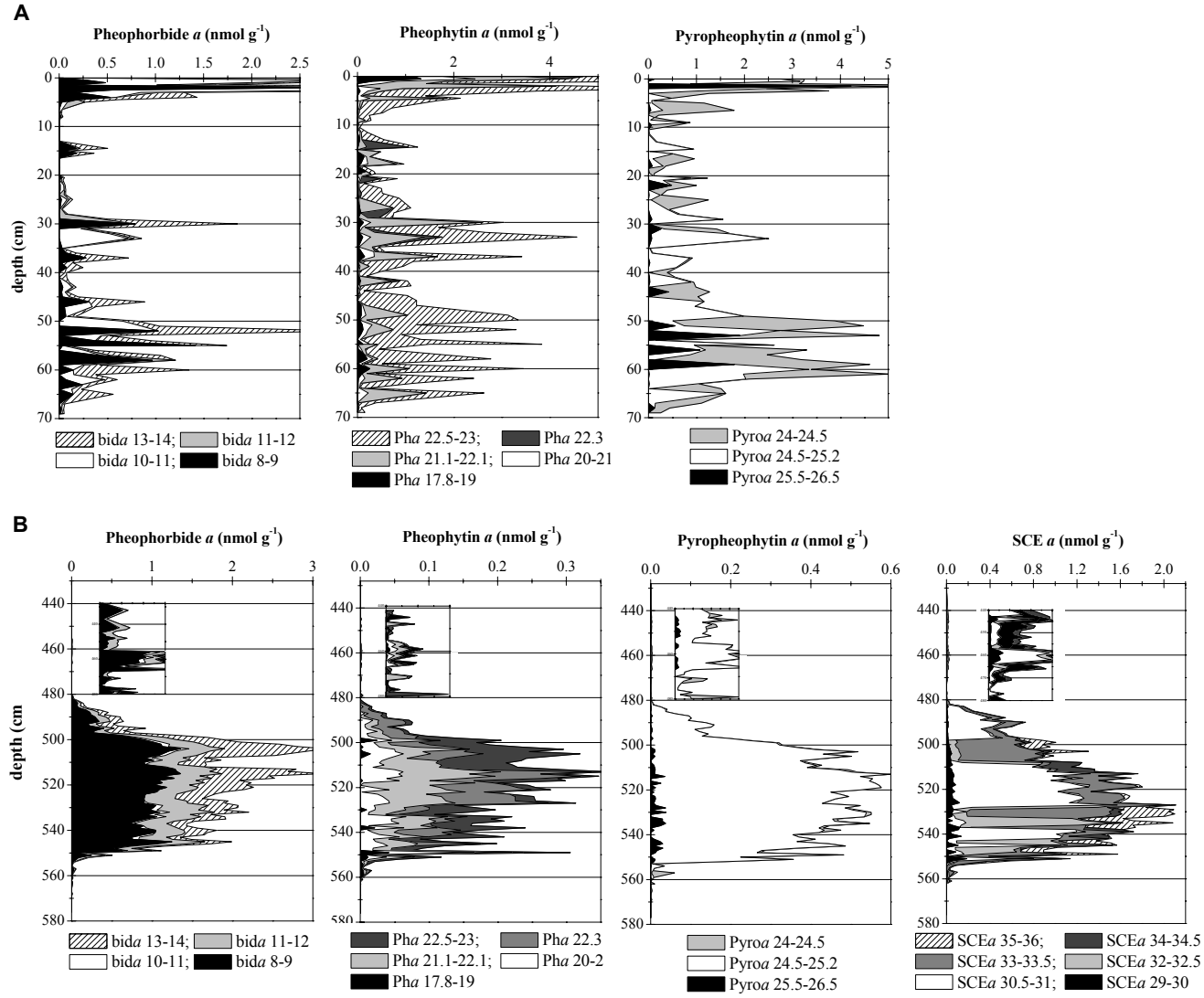

Fig. 47. High resolution analysis of different forms of pheopigments and SCEs (steryl chlorin esters) eluting at different retention times during (A) the Holocene (0-70 cm sediment depth) and (B) Kazantsevo plus transitions (440-580 cm sediment depth) at Continent Ridge (North basin). The numbers reflect the eluting time of the respective pheopigment or SCE form. Abbreviations: bid*a* – pheophorbide *a*, Ph*a* – pheophytin *a*, Pyro*a* – pyropheophytin *a*.

During the late Tazovsky Glaciation pheophorbide *a* contributed only 20 - 40 % to the total Chl*a*s, while SCE*a* contributed up to 60 %. During the early Interglacial, pheophorbide *a* and SCE*a* showed similar contributions, but during the late Interglacial the pheophorbide *a* contributed more than 50 % to the total Chl*a*s. During the Early Zirianski Glaciation the SCE*a* clearly dominated again.

Several forms of pheophorbides, pheophytins, pyropheophytins and SCEs were found whereby some occurred also during the Holocene (Fig. 47). Depth trends were found during the Kazantsevo and clear distinctions between the Kazantsevo and the surrounding cold phases. Similar to the Holocene (Continent Ridge core), the dominant

pheophorbide *a* was pheophorbide *a*8+9 during the Kazantsevo, but pheophorbide *a*11-12 and *a*13-14 were also found in considerable amounts. They were scarce, in contrast, during the cold periods. Pheophytin *a*20-21 occurred at the top of the Holocene core as well as during the warm Kazantsevo but also during the Chl*a*s maximum of the Early Zirianski Glaciation. In contrast, pheophytin *a*21.1-22.1 was found during the Kazantsevo optimum, but only in low amounts during the glacial periods. The distinct pyropheophytin *a* forms did not show depth trends during the Holocene, but during the complete Kazantsevo and its transitions pyropheophytin *a*24.5-25.2 dominated with more than 95 %. The SCE*a* forms identified in the Kazantsevo segment, showed periodicities, which were, however, not related to Chl*a*s maxima or to warm and cold periods.

Perylene: Perylene was detected in the three Holocene cores and also in the Kazantsevo segment (Fig. 48). At Vidrino and at Posolski perylene peaked at around 0.5 kyr BP. In the North (Continent Ridge), in contrast, perylene was not detected or only in traces since 4 kyr BP. Major peaks in the North were found before 7 kyr BP. No significant correlation of perylene with any of the photosynthetic pigments or with TOC was found. Furthermore, perylene was not detected during the Tazovsky Glaciation, peaked during the early Kazantsevo Interglacial, was again not detected during the late Kazantsevo Interglacial, but peaked again during the Early Zirianski Glaciation. Therefore, the occurrence of perylene in Lake Baikal could not be attributed to any region or to climatic changes.

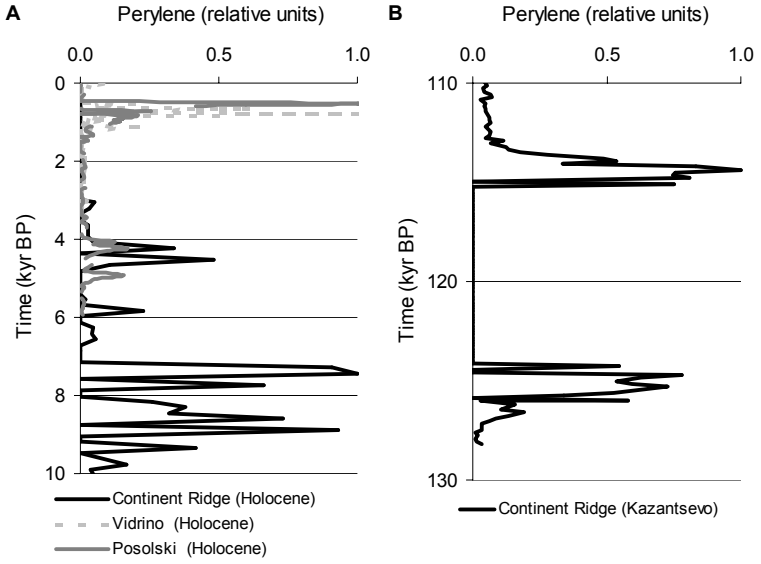

Fig. 48. Temporal changes in perylene concentrations in the (A) Holocene (three sites) and (B) in the Kazantsevo Interglacial (one site). Perylene (in relative units) was normalised to one, whereby one is the highest content of perylene found within the respective core. The highest content of perylene in the Vidrino core was 25 fold higher than that of the Continent Ridge core and three fold higher than that of the Posolski core.

4 DISCUSSION

Lake Baikal is known for a list of superlatives such as the World's oldest, deepest and largest (by water volume held) lake, with a high number of endemic species. Shortly resumed, Lake Baikal represents an extreme in the global spectrum of freshwater types (Flower 1998). This lake is therefore object of major interest to biologists and paleoenvironmental scientists alike (Flower 1998). The understanding of the biological record contained in Baikal's sediments is central to understanding not only past climate variability in the region but also impacts of recent environmental change and pollution (Flower 1998).

The main objective of the present thesis was to study the phytoplankton pigments as a tool for tracking environmental changes in Lake Baikal. Three main tasks were performed for this purpose: (1) the recent phytoplankton and photosynthetic pigments were analysed to improve the knowledge on their occurrence and formation in the euphotic zone; (2) the transfer of the pigments through the water column and the incorporation into the sediment were analysed to investigate degradation processes in the aphotic, but oxic water column and oxic or oxidised surface sediment; and finally (3) sedimentary pigments were analysed to prove their potential to record environmental changes that happened long ago.

4.1 Recent phytoplankton pigments in Lake Baikal as markers for community structure and environmental changes

Phytoplankton responds quickly to environmental changes and thus can be very useful for assessing changes in aquatic ecosystems. This is especially the case for Lake Baikal where monitoring has been carried out for more than 60 years (Kozhov 1963, Galazii 1993, Kozhova and Izmest'eva 1998, Popovskaya 2000, Goldman and Jassby 2001 and references therein). However, up until now, few multiparameter studies have been conducted in parallel of regional, vertical and seasonal variability. Also, studies conducted in different decades have had to be used to estimate the varying importance of the autotrophic picoplankton (APP; cf. Kozhova and Izmest'eva 1998, Popovskaya and Belykh 2004). Phytoplankton pigments other than Chl*a* were not yet investigated. Here, a pigment-based approach complemented with traditional microscopic counts was used to determine phytoplankton spatial and seasonal distribution patterns over a three year-long period (2001-2003).

4.1.1 Regional phytoplankton and pigment distribution and driving factors

Autotrophic picoplankton: Former studies already indicated the importance of cyanobacterial and eukaryotic APP in the South (Votintsev et al. 1972, Nagata et al. 1994) and Centre (Nakano et al. 2003) as well as at near-shore or river delta stations (Boraas et al. 1991), but only few studies compared the APP distribution in the different regions (cf. Popovskaya and Belykh 2004). Most of these former studies used light and a few used epifluorescence microscopy (cf. Popovskaya and Belykh 2004). The broadest study on APP was recently performed by Belykh and Sorokovikova (2003) using scanning electron microscopy. They reported an APP abundance that varied by 2 to 10 times in different parts of the lake. Based on light-microscopic long-term data from spring 1964 to 1990, Popovskaya and Belykh (2004) reported dominance of cyanbacterial APP (*Synechocystis limnetica*) in the North, which was not confirmed in our study in summers 2001-2003 as the APP contribution to total biovolume was 3-6 times lower in the North than in the South and Selenga Delta. However, Popovskaya and Belykh (2004) reported furthermore that during late summer 2000, using scanning electron microscopy highest numbers of cyanobacterial APP were registered in the South.

The marker pigment zeaxanthin allowed the contribution of cyanobacterial APP to the total Chl*a* to be calculated and the results showed that the contribution to total Chl*a* was also 4-6 times lower in the North than in the South and Selenga Delta. Based on the contribution to total Chl*a* data and environmental data, canonical correlation analysis (CCA) could be calculated to define the environmental conditions that most probably impact the phytoplankton composition. This CCA showed that latitude is negatively correlated to the cyanobacterial APP contribution. Both the APP contribution to total biovolume and the contribution to total Chl*a* contrasted, therefore, suggestions of Popovskaya (2000) that APP is generally most prominent in the North.

In most marine and freshwater systems the contribution of APP to the total biovolume and production was inversely correlated to increasing trophy (Stockner 1991, Callieri and Stockner 2002). This general concept might not be adopted for Lake Baikal, assuming higher trophy in the deltas and oligotrophic conditions in the pelagic regions of the lake (Callender and Granina 1997, Genkai-Kato et al. 2002). The CCA indicated that water depth (and thus the distance to the shore, which may be indicative for the trophic state of the regions) was of minor influence for the cyanobacterial APP contribution. In growth experiments with *Synechocystis limnetica*, it was concluded that temperature is the major driving force (Richardson et al. 2000). We now can specify that stratification was the dominant factor for increasing cyanobacterial APP contribution.

Nano- and microphytoplankton: The nano- and microphytoplankton biovolume varied between the basins and also between years, but not significantly. A general increase of the biovolume from North to South, as reviewed by Goldman and Jassby (2001), could not be confirmed in 2001 and 2002. It could also not be confirmed that the regions with shallow waters and with river water input, such as the Selenga Delta showed highest biovolumes (even including the APP), as mentioned in former comparative studies (Bondarenko et al. 1996, Popovskaya 2000). Therefore, if eutrophication occurs in the Selenga Delta due to anthropogenic impacts (Popovskaya 2000) it might affect the phytoplankton composition rather than the total biovolume.

Kozhova (1987) noted for river-estuary regions enrichment by the flora of the tributaries. These species might not persist as a diversity increase could not be found in the delta. However, one sign of changing phytoplankton community was the mass development of the N_2-fixing *Aulosira* sp., which indicated a possible N-limitation in the Selenga Delta. Low N/P ratios (14) were found in the Selenga Delta in preliminary nutrient measurements in July 2003, whereas the ratios in the open basins varied between 25 and 36 (V. Straškrábová and J. Borovec, HBI Ceske Budejovice, Czech Republic, personal comm.). Increasing P-load with the tributaries (Callender and Granina 1997) was supposed to create the N-limitation (Goldman and Jassby 2001).

Phytoplankton pigments: As has been pointed out by Kozhova et al. (1985), it is impossible to delineate a region within the pelagic basins characterised from year to year by constant higher or lower Chl*a*. In fact, in the North for example, each year showed significantly different Chl*a* concentrations. While lowest Chl*a* concentrations in 2001 were found in the Centre, they were found in the North in 2002 and 2003. Nevertheless, the combined data set (July 2001+2002+2003) showed significant differences for Chl*a* and the sum of carotenoids, as well as for several marker pigments. For example, significantly higher Chl*a* concentrations in the South compared to the Centre and North were found.

Besides variations among the open basins, significantly higher Chl*a* concentrations were found at the river inflows. Nutrient enrichment could be assumed to trigger Chl*a* increase, but the CCA suggested instead a higher correlation with stratification. Stratification was enhanced in the delta because of the warm river water inflow and because the shallow water zone warmed up faster than the deep water basins. The role of eutrophication might, therefore, be secondary up to now for total phytoplankton

abundance. The development of the N_2-fixing *Aulosira* sp. (as aforementioned) indicated, however, enhanced P-loading from the Selenga River and thus a possible change in species composition might be expected if nutrient loading further increases.

Marker pigment analysis showed significant changes of the phytoplankton community within the open basins that could not be stated as statistically significant using the limited capacity of phytoplankton counts, showing the benefit of fast techniques for large sample sets. For example, marker pigments of the Chlorophyta, cyanobacteria and Eustigmatophyceae decreased significantly from South to North, while those of Bacillariophyceae+Chrysophyceae remained relatively constant among the three open basins. Marker pigments are also potential indicators of varying environmental conditions in regions where total biovolume, Chl*a* and sum of carotenoids did not show significant differences. For example, Chl*a* and total carotenoids were both high in the Selenga Delta and Barguzin Bay suggesting similar environmental conditions. Nevertheless, the marker pigments of Bacillariophyceae+Chrysophyceae fucoxanthin and Chl*c* were significantly higher in the Barguzin Bay than in the Selenga Delta, whereas the marker pigments of cyanobacterial APP zeaxanthin and ß-carotene were significantly lower. Therefore, different environmental conditions are likely at the two sites. Discriminance analysis enhanced the assumption of particular phytoplankton composition at some sites such as Barguzin Bay, Academician Ridge, and Maloe More.

Estimation of chemotaxonomic group contribution: In a previous, preliminary study based on the data set gathered in July 2001, it was shown that the share of selected chemotaxonomic groups could be estimated in Lake Baikal using conversion factors determined by multiple linear regression and by the CHEMTAX matrix factorisation program (Fietz and Nicklisch 2004, Appendix A). New factors calculated from the whole data set 2001–2003 could add a fifth group, i.e. Bacillariophyceae+Chrysophyceae, Cryptophyta, Chlorophyta, Eustigmatophyceae and cyanobacterial APP. The presence of Eustigmatophyceae was proven in another study (Fietz et al. submitted, Appendix B).

The estimation of the relative compositions and distributions of the distinct chemotaxonomic groups done in the preliminary study (Fietz and Nicklisch 2004, Appendix A) could be confirmed now with the more extensive dataset. However, although the factors calculated in the present study for Chlorophyta (Chl*b*, lutein) and Eustigmatophyceae (violaxanthin) did not differ significantly from those reported for 2001 (Fietz and Nicklisch 2004, Appendix A), the factors for Bacillariophyceae+ Chrysophyceae (fucoxanthin, Chl*c*) as well as for cyanobacterial APP (zeaxanthin) were

significantly lower than those reported for 2001. Hence, the Bacillariophyceae+ Chrysophyceae community and the cyanobacterial APP changed in 2002 and 2003 towards cells with higher amounts of accessory pigments (fucoxanthin and Chl*c*) per Chl*a*. Most of the ratios fitted also well to those of isolated Baikalian strains (Fietz and Nicklisch 2004, Appendix A).

High-resolution analysis of phytoplankton community structure changes using fluorometry: Horizontal fluorescence transects confirmed the great variability of phytoplankton abundance (given here by the total Chl*a* concentration). Previous continuous fluorescence records were performed in spring 1990 (Granin et al. 1991). Nonetheless, the probe measured Chl*a* only and the authors were therefore unable to relate Chl*a* maxima to specific phytoplankton groups. The Moldaenke FluoroProbe used in this study detected the emitted fluorescence at five wavelengths and allowed calculating the contribution of preselected phytoplankton groups to the total Chl*a*. However, information on dominant phytoplankton groups and their pigment characteristics was required to calibrate the FluoroProbe accurately. Today calibration has been performed for three dominant groups (A. Nicklisch, HU Berlin, Germany): Bacillariophyceae+ Chrysophyceae+Pyrrophyta (with similar fluorescence characteristics), Chlorophyta and phycoerythrin-containing cyanobacteria.

The respective transects enhanced the assumption of great heterogeneity in the phytoplankton composition. For instance, within a transect from Ushkanin Islands along the coast of Svyatoi Nos Peninsula into the Barguzin Bay, the contribution of Chlorophyta increased strongly, while those of Bacillariophyceae+Chrysophyceae+ Pyrrophyta and cyanobacteria decreased (Fig. 49). Another transect from the port of Listvianka (west coast of South basin) to the North of Selenga Delta showed how distinct phytoplankton groups were responsible for small scale (few kilometres wide) peaks (Fig. 49). This latter transect also indicated the changing phytoplankton composition from dominances of Chlorophyta and Bacillariophyceae+Chrysophyceae+ Pyrrophyta to cyanobacteria in the Selenga Delta region (Fig. 49), as has been assumed from discrete water sample analyses (A. Nicklisch, HU Berlin, Germany, pers. comm.). These profiles indicated the potential of *in situ* fluorescence measurements that, in regular monitoring, may complement laboratory studies of microscopic counts and HPLC-aided pigment analyses.

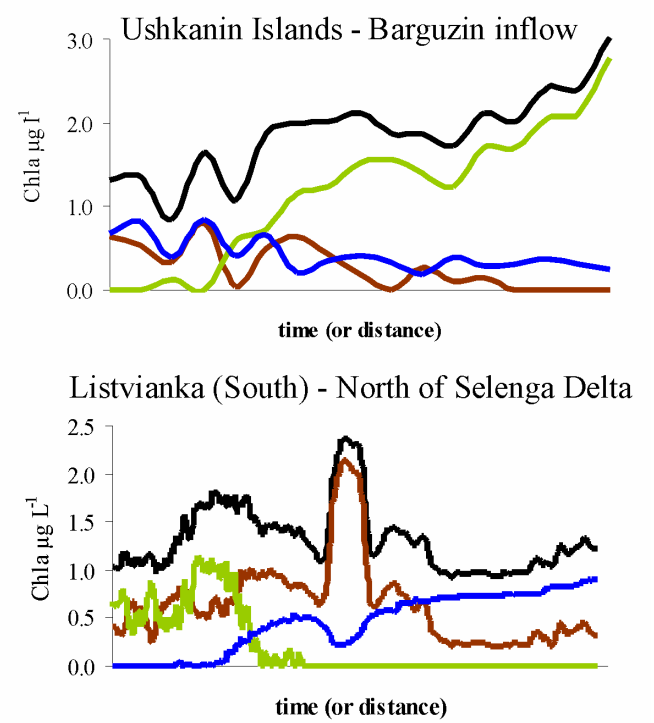

Fig. 49. Horizontal fluorescence transects showing total Chl*a* (black), contribution of Bacillariophyceae+ Chrysophyceae+Pyrrophyta (brown), Chlorophyta (green) and cyanobacteria (blue). Data provided by A. Nicklisch (HU Berlin, Germany) from unpublished data sets.

4.1.2 Pigments as markers for vertical changes during stratification and homothermy

Regional and daily varying wind, insolation, and stratification have been shown to strongly influence the phytoplankton vertical distribution (Bondarenko et al. 1996, Kartushinsky 1997). Below the ice, the homogeneous layer was due to convective flow-fields (Kelley 1997, Granin et al. 1999). This layer, which may vary between 10 m (Popovskaya 2000) and 50 m (Zavoruyev et al. 1992), was restricted to the upper 25 m in 2001-2003 (Fig. 24). The euphotic zone under the clear, snow-free ice in Lake Baikal in 2003 was 1.7 Secchi depth (Straškrábová et al. 2005) and therefore a 15-35 m thick euphotic zone can be assumed. The convective layer under the ice was then not deeper than the euphotic zone. In spring 2001, 2002 and 2003 Chl*a* concentrations up to 0.5 nmol L^{-1} reached 250 m and concentrations over 2 nmol L^{-1} reached 100 m. Thus, cells were obviously transported out of the zone of maximal productivity (euphotic zone).

In summer, the phytoplankton is concentrated in the upper 25 m but even during stratification Chl*a* was found down to 100 m in 2001 and 2002 (Fig. 24). Genkai-Kato et al. (2003) found that cells collected during mixing as well as during stratification in the deep water of Lake Baikal (500 m) were able to photosynthesis when exposed to surface levels of irradiance. They suggested that live Bacillariophyceae, remnants from the spring

community, sank out to greater depths during stratification, which was supported by unpublished taxon depth profiles of our long-term monitoring.

However, even during homothermy the Baikalian pelagial is not homogenous. The South is ice-free many weeks before the North and thus is stratified earlier. Warm water inflows from rivers, such as the Selenga and Barguzin, also enhanced the stratification locally (Fig. 26). Primary productivity and biomass increased strongly at stratified stations in summer 1990 (Goldman et al. 1996). According to the present data, the higher production was due to Chlorophyta and APP, both highly correlated to stratification.

As aforementioned, the Moldaenke FluoroProbe used in this thesis allowed estimating the contribution of selected phytoplankton groups to the total Chl*a*. These profiles clearly showed that in the South the Chl*a* maxima were formed mainly by Chlorophyta, while those in the Selenga Delta were formed mainly by cyanobacteria (Fig. 50; A. Nicklisch, HU Berlin, Germany, pers. comm.). At Academician Ridge the Chl*a* maximum was formed in the upper layer by cyanobacteria, while the lower part was formed by Chlorophyta and Bacillariophyceae+Chrysophyceae+Pyrrophyta (Fig. 50; A. Nicklisch, pers. comm.). According to Granin et al. (1991) early summer warming of the water induce two phytoplankton maxima: one near the photic zone and the other in greater depths, due to the formation of two "convective cells" each with high internal turbulent exchange. The phytoplankton in the upper "convective cell" will develop, while the phytoplankton population in the deeper "convective cell" will decline, getting light insufficiency. The authors assumed that smaller phytoplankton is likely to form the upper maximum, while larger ones (such as *Aulacoseira*) are more likely to form the deeper one. With further warming the larger ones will decline. Such convective cells may have developed at Academician Ridge. However, because calibration is not yet accomplished discussion about would be rather speculative. Nonetheless the preliminary high-resolution depth profiles of phytoplankton community structure highlight the usefulness of multiwavelength fluorometric measurements in such large and deep lakes, where dramatic changes of the regional and vertical phytoplankton distribution occur.

Taken together, the present data of regional differences in the depth profiles confirmed Granin's (Granin et al. 1991) conclusion that mesodifferences of the hydrological-climatic conditions determine the meso-inhomogeneities in the spatial distribution of water temperature, depth of convection development at a certain time, chlorophyll content, phytoplankton productivity and distribution of the physical transparency of the water.

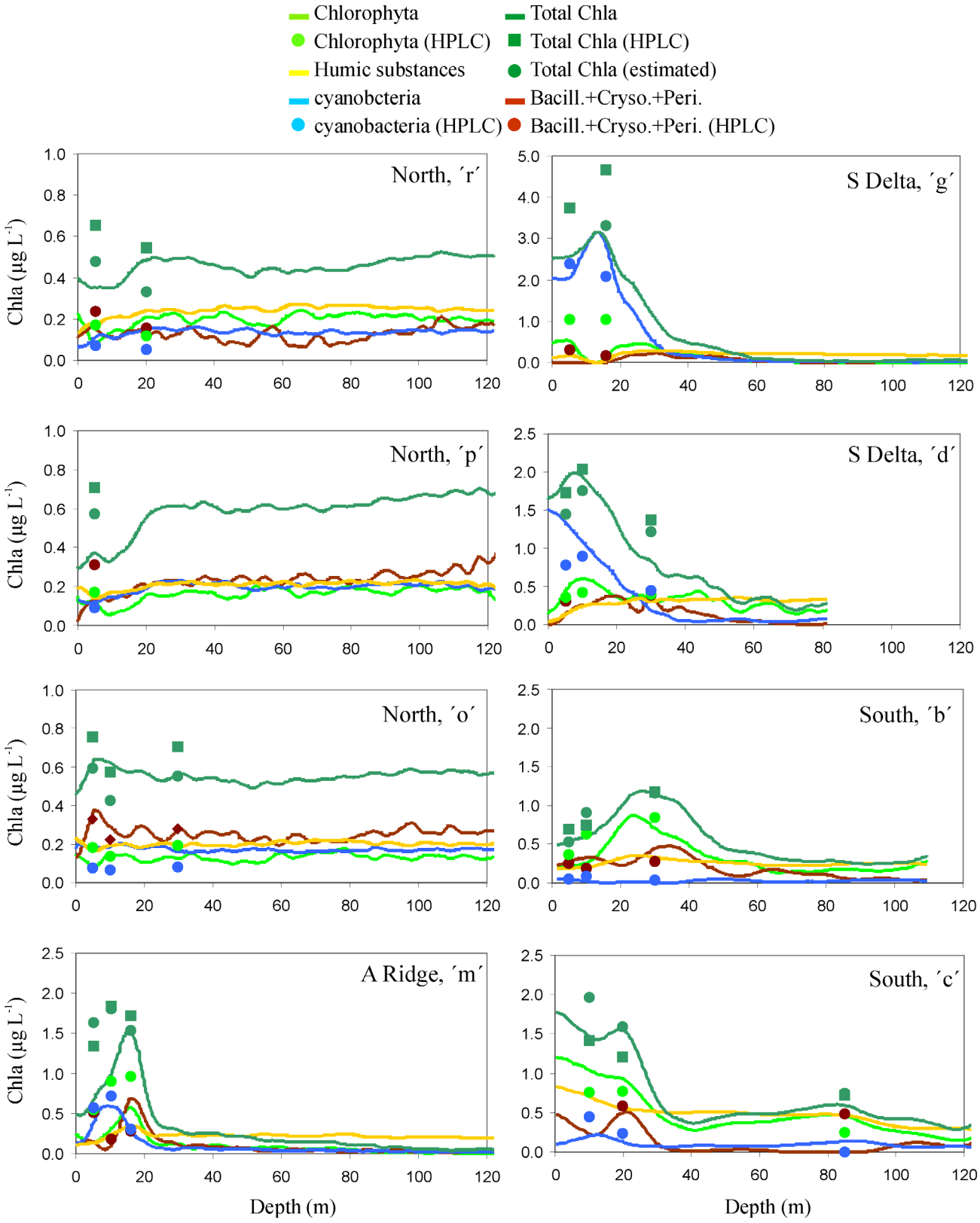

Fig. 50. FluoroProbe depth profiles (lines) showing total Chl*a* as well as contributions of selected phytoplankton groups to the total Chl*a*. Measured (by HPLC) total Chl*a* and contributions are given as well as the estimated total Chl*a* based on marker pigments (see Appendix A and chapter 3.1 for marker pigment based calculations). Letters in quotations refer to Fig. 18. Data provided by A. Nicklisch (HU Berlin, Germany; from unpublished data set).

4.1.3 Seasonal dynamics of phytoplankton and pigments and driving factors

The bacillariophycean spring development began beneath the ice. The spring bloom 2002 was founded on *Aulacoseira baicalensis* and *Stephanodiscus meyerii*. Thus, although the spring peak 2002 did not reach the biovolume of real "*Melosira*"-years, it was based on two formerly called "*Melosira*" species (Kozhova and Kobanova 2000). The dominance of large Bacillariophyceae in spring is not conform with the generally agreed PEG-model for freshwater lakes, which would assume a spring crop of small, fast growing algae such as Cryptophyta and small centric Bacillariophyceae (Sommer et al. 1986). Such dominance of large Bacillariophyceae was found in only five out of 18 compared lakes, and four of these five were stratifying, temperate, eutrophic lakes or reservoirs not deeper than 34 m (references in Sommer et al. 1986). The CCA illustrated that Bacillariophyceae+Chrysophyceae in Lake Baikal were negatively correlated to temperature for seasonal succession as has been suggested from culture experiments with *Aulacoseira baicalensis* (Richardson et al. 2000). In summer *A. baicalensis* was found in greater depths only. This species sank out through the summer stratified water column to cooler waters, probably to avoid hotter summer temperatures. Nonetheless, in this study we cannot definitely determine whether *A. baicalensis* was limited by temperature or by competition with other phytoplankton groups.

The decline of biovolume and Chl*a* (the ´clear-water´ phase) in June might be due to intense grazing. Consistent with the PEG-model, edible Cryptophyta became dominant, as well as small Chrysophyceae. In summer the ratios of pigments vs. biovolume of the Bacillariophyceae and Chlorophyta decreased indicating a shift towards smaller, pigment-rich cells with increasing temperatures. During summer, functional groups indicated summer stratification in oligo- to mesotrophic conditions (E+X, Reynolds 2002). Contrary to the PEG-model, which predicts growth of non-edible algae, an explosive growth of edible algae, such as eukaryotic and cyanobacterial APP took place in Lake Baikal.

The importance of APP varied with the season with a maximum in summer and a minimum under the ice in former years (Moskalenko 1971, Goman 1973, Belykh and Sorokovikova 2003, Popovskaya and Belykh 2004). APP epifluorescence and light microscopic estimations supported these trends for 2002-2003. Belykh and Sorokovikova (2003) noted a small APP peak in April of each year from 1997 to 2000, which could in fact be found again in 2003. According to the CCA the seasonal cyanobacterial APP development might be triggered by temperature and stratification. Light limitation due to mixing (>100 m) much below the euphotic zone (<40 m) might depress the APP

formation at the time of maximal homothermy after ice-break up and in autumn. However, during inverse stratification under the ice APP contributed surprisingly large amounts to the total Chl*a* (c. 9 %) as well as to the total primary production (up to 40 %, Straškrábová et al. 2005).

High fucoxanthin/biovolume and Chl*c*/biocolume ratios (Fig. 30) indicated a summer development of small pigment-rich Bacillariophyceae or Chrysophyceae cells besides the development of picoplanktonic cells. This summer development of small cosmopolitans at Bolshye Koti enhanced the suggestion of the shift within the phytoplankton community attributed to global warming (Popovskaya 1991, -2000, Mackay et al. 1998, Bondarenko 1999). However, the summer communities in the open basins were still dominated by endemics (*Cyclotella baicalensis, ornata,* and *minuta*) and therefore, we may claim that fortunately, until now, the warming or eutrophication possibly affects the nearshore regions, such as Bolshye Koti (where the seasonal monitoring was conducted), but that the open basins still remain unaffected, due to the huge water masses.

Those APP were replaced by large Bacillariophyceae only towards autumn. A regular autumn maximum has been described for Lake Baikal (Popovskaya 2000), which was found in 2001 and 2003 (Fig. 30A). Its absence in 2002 might be due to strong winds, which were noted in this year and which induced a transport into the deeper, aphotic layers. Consistent with the PEG-model was a reduction of light energy input, which caused a decline of the total biovolume in early winter.

The maximum of the nano- and microphytoplankton biovolume found in February/March 2003, when ice cover was 0.8 m thick and almost free from snow, could be due to convection under the ice when solar radiation warmed the near-surface water. Then voluminous, non-motile Bacillariophyceae can be maintained days or even months near the surface providing cells with enough light for growth (Kelley 1997, Granin et al. 1999). Those under-ice blooms are often related to *Aulacoseira*, *Gymnodinium* or recently *Nitzschia acicularis* (Popovskaya 2000, Bondarenko 1999), but in 2002 the dominant species were *Asterionella formosa* and *Synedra acus.*

Aulacoseira baicalensis, the classic example of a diatom able to bloom under spring clear ice (Kozhova and Izmest'eva 1998), was surprisingly insignificant before ice-break up in 2003. That could be due to the snow cover and the consequent stopping of light penetration, which could have inhibited the building of the convective layer, essential for its maintenance in the euphotic zone. *A. formosa* dominated this site for the first time since the beginning of the long-term monitoring at Bolshye Koti. According to the

regional distribution *A. formosa* was localised at Bolshye Koti, as it wasn't found in abundance elsewhere. It may be that this species is an opportunistic taxa filling a niche where available but never dominating the whole lake. Its mass development at Bolshye Koti was probably a result of multiple asexual reproductions (Kobanova and Izmest'eva 2003).

4.1.4 Remote sensing

Optical remote sensing analyses base on the light leaving the water surface (differential absorption and backscatter of irradiance inside the water), corrected for atmospheric and surface effects (e.g. caused by air molecules, aerosols, and the lake surface itself; Heim et al. 2005). Jeffrey et al. (1997) predicted that because pigments are the only biological parameter measurable from space, pigments will serve as basic or proxy parameter for global mapping of components of the ocean carbon cycle. However, the Ocean Colour research is well developed for the World's oceans, but is still in development for coastal zones and today, investigations on large oligotrophic inland water bodies have rarely been carried out (e.g. EEGLE – Episodic Events-Great Lakes Experiment Understanding the Historical Magnitude of Spring Turbidity Plumes in Southern Lake Michigan, and KITES – Keweenaw Interdisciplinary Transport Experiment in Superior) in the North American Great Lakes (e.g. Bergmann et al. 2004). For Lake Baikal, there was another chance to conduct an optical remote sensing study by using the interdisciplinary CONTINENT field data set, of which the most important has been the pigment data set presented in this thesis (Heim et al. 2005; Heim, in prep.).

Semovski (1999) first conducted preliminary remote sensing studies of Lake Baikal's water constituents with AVHRR satellite data in the visible wavelength range, which did, however, not result in an applicable Chl*a* algorithm. Within the CONTINENT framework global Chl*a* algorithms, and Chl*a* algorithms for oligotrophic systems (e.g. Iluz et al. 2003) were evaluated using the here presented pigment data set (cf. Heim et al. op. cit., Heim op. cit.). In addition, blue-green ratio Chl*a* algorithms were calculated by linear regression using the Chl*a* pigment data sets 2001 and 2002 (cf. Heim et al. op. cit., Heim op. cit.). However, the most robust performing algorithm for the SeaWiFS acquisitions in 2001 and 2002 was found with the Ocean Colour "OC2" Chl*a* algorithm (O'Reilly et al. 1998) that represents a blue-green ratio algorithm based on a global pigment data set (830 cases); by evaluating the present pigment data set, accuracies below

35 % for pelagic waters covering all bio-optical provinces were achieved (cf. Heim et al. op. cit., Heim op. cit.) meeting NASA quality standards (O'Reilly et al. 1998).

The remotely sensed data provided continuous records of the Chl*a* concentration in the upper photic zone (as a measure of the productivity) at nearly each point of the cloud free parts of satellite image (cf. Heim et al. op. cit., Heim op. cit.). The images provided important information of the formation of eddies and patches, as well as of the differential formation of phytoplankton abundance and community structure within the different basins (Fig. 51). For example, the North is shown to be more oligotrophic than the South in summers 2001 and 2002 (Fig. 51), but small, pigment-rich eddies were also revealed in the North, which can easily be overlooked even with hundreds of water samples in a 600 km long lake.

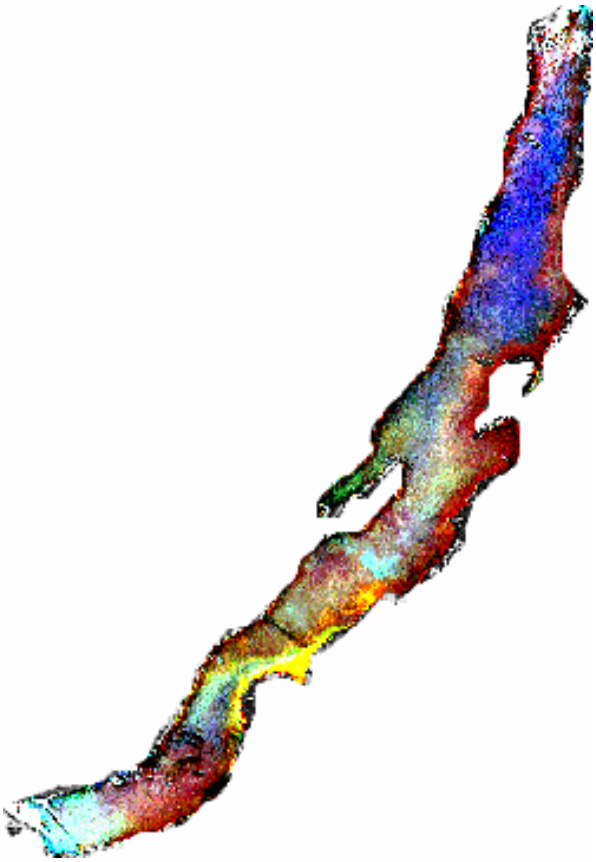

Fig. 51. Quasi-true colour SeaWifs for 6 August 2001 (Heim pers. comm.). The blue colour indicate more oligotrophic water; turquoise colouring indicate cyanobacterial picoplankton-rich water; yellow and brownish colours indicate terrigenous and more productive regions.

Based on these satellite images the differential seasonal phytoplankton variation, represented by the total Chl*a*, could be established (Fig. 52). The results of which showed a much higher summer maximum in the South than in the North and Centre for example. This difference should be kept in mind when seasonal data from the Bolshye

Koti site are extrapolated to other areas of the lake. However, it has to be admitted here, that these data are still preliminary, because in regions, which are optically influenced by terrigeneous matter, e.g. in the Selenga Delta, there is considerable Chl*a* overestimation (3 to 5 fold) due to additional absorption processes compared to the measured Chl*a* in July. These areas had to be masked and were excluded from the remote sensing Chl*a* data set. Nonetheless, available SeaWiFS satellite images combined the regional and the seasonal monitoring, which was not possible by direct sampling or measurements due to the extreme size of the lake. These results prove the usefulness of phytoplankton pigment detection from space for regular monitoring in large lakes.

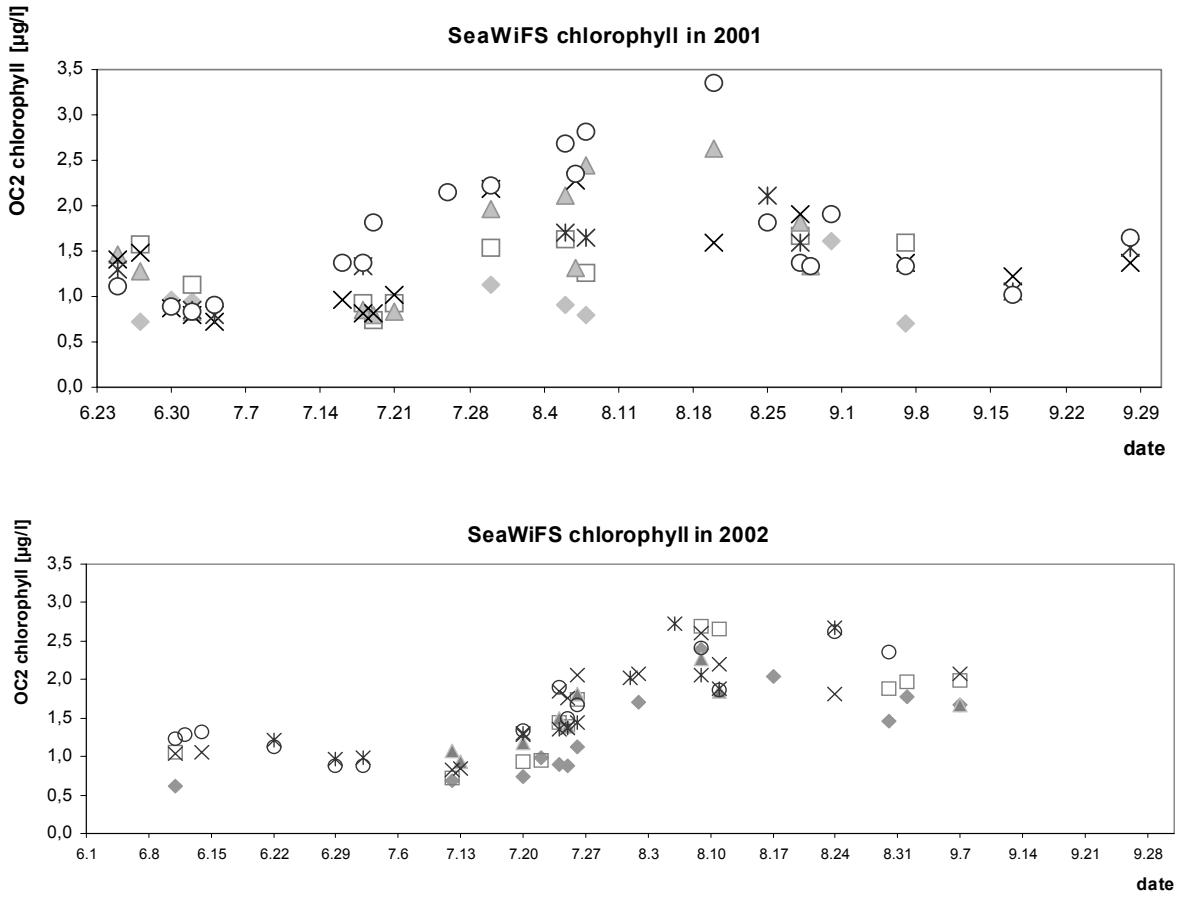

Fig. 52. SeaWiFS Chl*a* time series (June-September 2001and 2002). Diamonds represent the ultra-oligotriophic gyre in which the northern mooring was situated; rectangles represent the Continent Ridge coring site; triangles represent Academician Ridge; crosses represent the Central basin; stars represent the Posolski area (Selenga Delta); circles represent the central South basin in which the southern mooring was situated. (B. Heim pers. comm.)

4.1.5 Does a pigment-based approach accurately monitor phytoplankton community and environmental changes in Lake Baikal's euphotic zone?

Using a combined methods approach of pigment-based analyses and measurements complemented with traditional microscopic counts, this investigation of regional, vertical, and seasonal distribution patterns has provided a broad overview of the recent phytoplankton community structure of Lake Baikal. A for freshwater exceptional broad range of natural changes of the total phytoplankton abundance and composition could be proven. While the total biovolume did not show significant changes, total Chl*a*, which is closely related to primary production, revealed impacts of the river inflow and shallow strait regions. Marker pigment changes revealed differences between regions, where biovolumes and Chl*a* were not significantly different, e.g. between Selenga Delta and Barguzin Bay. Thus, phytoplankton pigments reflected the variability of primary productivity (measured as total Chl*a*) and phytoplankton community composition (via marker pigments) in Lake Baikal's euphotic zone.

Factorisation and ordination of the broad pigment sample set and environmental variables provided further insights into the driving forces. Temperature and stratification were shown to have major impact on the composition of the phytoplankton community structure. Different stratification regimes within a lake are rather unusual and set Lake Baikal apart from other freshwater systems. We can expect that a possible long-term warming that affect the peculiar stratification regime, would lead to significant changes in the phytoplankton group and species composition towards smaller, pigment-rich cells such as small diatoms up to picocyanobacteria at the expense of the large endemic diatom flora that prevailed up until now.

Recently, palaeoecological analysis of preserved markers such as diatom valves or photosynthetic pigments is increasingly used to monitor environmental change in response to climate and human activities. Insights into the driving forces will aid interpretation of sediment formation in this ancient lake.

4.2 Phytoplankton pigment transfer through the water column and preservation within the surface sediment

The aim of the second task within this thesis was to determine transfer functions for the organic matter, especially lipophilic photosynthetic pigments, to determine the degradation processes within the water column and surface sediment and to infer how the main phytoplankton groups were represented in the deposited material.

4.2.1 Fluxes in Lake Baikal compared to marine and freshwater systems

The mass fluxes of dry matter as well as of Chl*a,* pheopigments *a* and carotenoids in Lake Baikal corresponded well to those found in different oceanic regions (Welschmeyer and Lorenzen 1985a, -b, Landry et al. 1995, Barlow et al. 1995, Nodder and Gall 1998). Fluxes in the moderatively productive marine Dabob Bay, in contrast, were much higher (Welschmeyer and Lorenzen 1985a). Organic carbon fluxes at the bottom of Lake Baikal (0.9-1.4 km) were within the highest ranges or higher than those reported for deep moorings (0.5-4 km) in open ocean areas (Ittekott 1996, Lampitt and Antia 1997). Due to its extreme depth and extension of the euphotic zone, organic matter fluxes in Lake Baikal should be compared with marine rather than with freshwater systems. Nonetheless, mass and pigment fluxes corresponded also to different oligo- to mesotrophic lakes; eutrophic lakes, in contrast, showed higher rates, but the depths of those lakes varied from 3 to 36 m only (Baines and Pace 1994, Poister et al. 1999, Hurley and Armstrong 1991). Little is known about the pigment or organic matter flux in deep lakes, because the study is limited to few lakes, such as Lake Tanganyika (~1450 m) or Caspian Sea (~1000 m), whereby the latter is not a freshwater system. Lake Baikal differs also from lakes such as Lake Tanganyika by its oxic bottom water and surface sediment, its heterogeneous stratification and low temperatures (<15° C in the pelagial). Anyway, no transfer functions are known for organic material or photosynthetic pigments in these comparable deep lakes.

4.2.2 Degradation processes in the water column of the South basin

The permanent temperature of 3-4° C below 250 m and the higher temperatures of 12-15° C during summer stratification in the epilimnion (Kozhova and Izmest'eva 1998) bring Lake Baikal closer to oceanic systems. The low temperatures might depress the

degradation rates relative to shallower and warmer aquatic systems, because most degradation processes (photooxidation, grazing etc.) are temperature dependent (Leavitt 1993). On the other hand, Lake Baikal is oxygenated down to the maximal depth due to lake overturn, convections and deep-water currents (Weiss et al. 1991) and enhanced oxidation might occur across the whole water column.

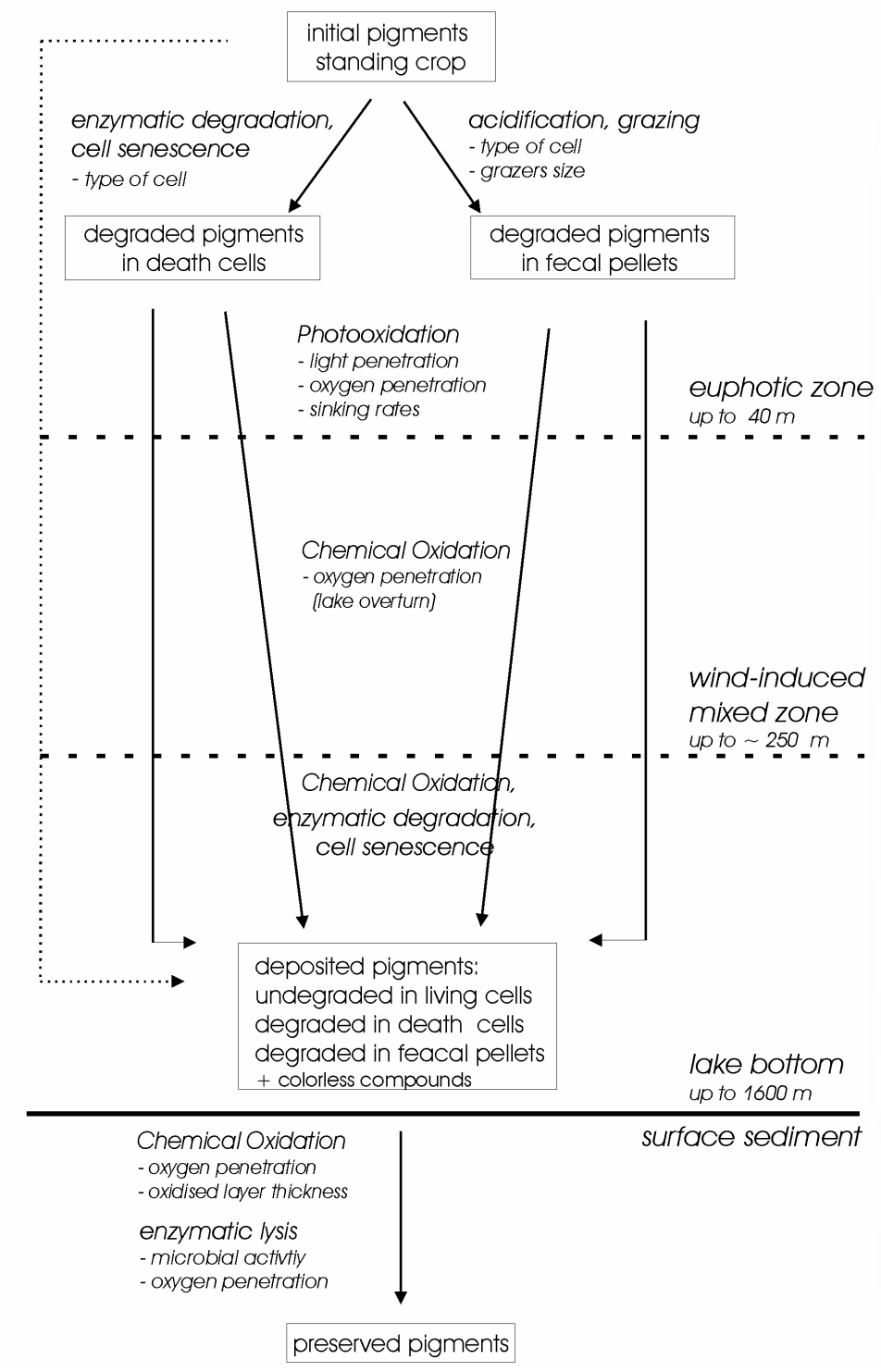

Fig. 53. Schematic diagram of degradation in the water column from the euphotic zone to the sediment surface.

In southern Lake Baikal, the most prominent degradation of the settling material occurs within the upper 250 m water column, which is the wind-mixed depth during overturn, where particles are suspended (Müller et al. 2005). The degradation below 250 m was very low for most pigments. The biphasic character of the flux curves (Appendix C - Tab. 2. Appendix C - Tab. 3, Fig. 32, Fig. 33) clearly highlights that the degradation is divided into a stronger and weaker degradation phases. Only 24 % of the trapped Chl*a* at 40 m settled deeper than 250 m. These low rates indicated that the initially settling Chl*a* was transformed into pheopigments or colourless compounds. Possible causes could be (1) photooxidation due to extended residence in the euphotic zone during mixing, (2) death of living or moribund settling cells in the dark during stratification or (3) zooplankton grazing and further bacterial destruction.

Photooxidation due to extended residence in the euphotic zone by wind induced turbulence might explain the losses between the suspended and the settled matter, but it can only affect the uppermost trap, as the euphotic zone is limited to approximately 40 m (Kozhova and Ismest'eva 1998). Thus, the loss of Chl*a* between 40 and 250 m should be caused by the death of settling cells in the dark or grazing. The loss of chlorophyllide *a* (which may represent moribund cells) may be caused by autolysis, bacterial destruction or also grazing. The much stronger decrease of pheophorbide *a* between 40 and 250 m almost certainly results from mesozooplankton faecal pellets being destroyed.

Death of living or moribund cells in the dark might be less common in Lake Baikal than in other aquatic systems. For the Dabob Bay and Central Pacific Gyres (Welschmeyer and Lorenzen 1985a, -b) as well as for a marine convergence zone (Head and Horne 1993) an over 10-fold higher average pheopigment *a* than Chl*a* flux was found. As Chl*a* is associated to the flux of intact cells, sinking of intact cells is an insignificant loss term in those areas. In southern Lake Baikal, in contrast, the pheopigment *a* flux was only three times the Chl*a* flux, and it can therefore be assumed that sinking of living cells is important. The importance of the sinking of living cells can be explained by the high inherent sinking rates of "heavy" Bacillariophyceae as bacillariophycean sinking rates of 60-100 m d^{-1} have been reported in Lake Baikal (Ryves et al. 2003).

Pigment destruction by zooplankton grazing is a complex issue: rates of transformation and degradation depend on gut passage time, and hence of edible cell concentration and even on food quality. It has been shown that micro- and mesozooplankton can degrade Chl*a* in part or even entirely into non-fluorescent breakdown products (Klein et al. 1986, Burkill et al. 1987, Barlow et al. 1988, Head and

Harris 1992). Grazer size implies differences of faecal packaging and sinking rates. Faecal pellets of mesozooplankton, such as cladocerans, have high sinking rates, whereas faecal debris of microzooplankton, such as protozoa, has negligible sinking rates (Welschmeyer and Lorenzen 1985a). High sinking rates tend to prevent photooxidation, while low sinking rates lead to long permanence within the euphotic zone and therefore to a conversion into colourless products. Pheopigments found in the traps may originate from mesozooplankton rather than from microzooplankton, since they were found in the traps but not in the water samples, and hence they may originate from fast sinking faecal pellets (Welschmeyer and Lorenzen 1985a).

4.2.3 Composition of the settling material in the South basin

The relative contribution of the various accessory pigments can be used to infer various algal groups as sources of sinking material. The contributions of dominant phytoplankton groups could be determined with appropriate factors for the respective marker pigments. However, these calculations showed several limits, when applied to the traps.

On the one hand, the total Chl*a* concentrations in the sediment traps could not be accurately estimated based on the factors determined for the water samples. It has been suggested that the overestimation of Chl*a* resulted from a stronger degradation of carotenoids or Chl*b* than Chl*a*. Carotenoids are more stable than chlorophylls in the presence of light and oxygen (Leavitt and Findlay 1994) and in the presence of grazers (Strom et al. 1998), but in oxic surface sediments of Lake Baikal carotenoids were more susceptible to decomposition than chlorophylls (Soma et al. 2001a). Further, fucoxanthin, the predominant carotenoid, easily decomposes and only zeaxanthin, which contributes only a small amount to the total Chl*a*, is known to be stable (Leavitt and Findlay 1994). The differential chlorophyll and carotenoid degradations might therefore not be applied from one aquatic system to another.

On the other hand, Bacillariophyceae+Chrysophyceae dominated the sinking material at 90 % and Chlorophyta and cyanobacterial picoplankton made only minor contributions. However, Chlorophyta and the cyanobacterial picoplankton were also important contributors to the standing crop at least in summer (cf. Fietz and Nicklisch 2004, Appendix A, and chapter 3.1) and a dominance of 90 % is also not common during most of the year and hence, even the rough comparison with long-term studies (Kozhova and Ismest'eva 1998, Popovskaya 2000, chapter 3.1.3), indicate that a 90 %

dominance of Bacillariophyceae+Chrysophyceae marks a group-specific sedimentation. This overestimation may be caused by the fact that fucoxanthin and Chl*c* originated sometimes from very large Bacillariophyceae (cf. Fietz and Nicklisch 2004, Appendix A, and chapter 3.1) which have very fast sinking rates (60-100 m d^{-1}, Ryves et al. 2003) so that its pigments suffered less from light induced degradation processes than pigments of the smaller Chlorophyta and the cyanobacterial picoplankton. Selective grazing might also be an important factor, as it can also be assumed that autotrophic picoplankton is preferentially grazed by microzooplankton and mesozooplankton, whereas large siliceous Bacillariophyceae suffered less from zooplankton grazing (Hurley and Armstrong 1990).

Hence, the record of the phytoplankton standing crop by trapped pigments in southern Lake Baikal was group-specific. Some carotenoids are more preserved than others, and they cannot record whole algal assemblages, unlike differential degradation rates be taken into account. This has been found also for several shallow lakes in surface sediment studies (Leavitt and Carpenter 1990, Leavitt and Findlay 1994, Leavitt 1993). Similar problems are also well known from established methods such as bacillariophycean valve based analyses. Battarbee et al. (2005) also warn that differential dissolution of diatom species occurs mainly at the water to sediment interface.

4.2.4 Comparison of the sedimentation and degradation between South and North

Since the southern and northern mooring sites were located about 400 km away from each other and were characterised by different morphometry, ice cover, length of vegetation period, temperatures (Shimaraev et al. 1994) and productivity (Kozhov 1963, Kozhova and Izmest'eva 1998), differences of the pigment fluxes and of the pigment degradation were expected.

The Chl*a*s fluxes recorded in the top traps were greater in the South than in the North in the first year, but lower in the second year. The fact that the first South mooring was deployed during 16 months, instead of 12 months, because of the inaccessibility of the site (thin ice in 2002), and, therefore, recorded two spring diatom peaks (M. Sturm, EAWAG, Switzerland, unpublished results from sequential traps), could have caused the higher fluxes therein. However, also in the North the flux was twice as high in the first year than in the second. Thus, the interannual variability of pigment deposition in the upper traps overlay the regional impact.

In contrast to the top traps, significantly lower Chl*a*s fluxes into the bottom traps in the North than in the South were found. Within same traps much lower sterol and fatty acid fluxes were found at the lake bottom in the North than in the South as well (Russell and Rosell-Mélé 2005). As there was no definite regional impact found for Chl*a* or Chl*a*s fluxes in the upper traps, the regional impact might act during settling below 40-50 m water depth.

The pigment flux in the South decreased in two phases (two-exponential regression model) with a strong degradation in the upper hundred meters and a much weaker below, while the decrease in the North occurred with a constant degradation rate throughout the whole water column (one-exponential regression model). Processes within the upper wind-induced mixed layer, as they were described in Fietz et al. (2005, chapter 4.2.2) were obviously particularly important in the South, but not in the North. An important cause for the regional variances can be higher summer temperatures in the upper layer of the South compared to the North (Shimaraev et al. 1994), because in the South, ice break-up, warming and stratification begins earlier than in the North, where the water column is homogeneous during most time of the year and increases rarely above 10° C (Shimaraev et al. 1994). These higher temperatures may result in higher degradation rates within the upper layer in the South (Cuddington and Leavitt 1999).

Chl*b* and its degradation products showed similar degradation to TOC at both sites, while Chl*c* was degraded significantly stronger in the North than in the South (decay slope significantly higher in the North, Appendix C - Tab. 6). Fucoxanthin was the major carotenoid in the top traps at both sites. This fucoxanthin likely resulted from large Bacillariophyceae, which rapidly sink out of the euphotic zone, being then protected against photooxidation (Fietz et al. 2005, chapter 4.2.3). However, fucoxanthin is known to be a very labile pigment (Repeta and Gagosian 1984, Leavitt and Findlay 1994) and it was in fact subject to stronger degradation compared to other carotenoids within the water column. However, despite the strong degradation, the contribution of fucoxanthin to total carotenoids (and also the estimated contribution of Bacillariophyceae+ Chrysophyceae to total Chl*a*, Fietz et al. 2005, chapter 4.2.3) was high at the lake bottom in the South, due to the very high initial fucoxanthin fluxes trapped in the 40 m traps, while other carotenoids, such as lutein, ß-carotene and diadinoxanthin, dominated at the lake bottom in the North (cf. Fig. 37).

Taken together, the main contribution to the initial settling material was formed by heavy, non-edible Bacillariophyceae in both basins. However, the degradation processes during sedimentation varied between both basins. While major degradation occurred in

the uppermost wind-induced mixed layer in the South, strong degradation was found down to the lake bottom in the North. As a result higher losses of organic matter and in particular of photosynthetic pigments were found in the North compared to the South. Additionally, pigment-specific degradations were found to differ between both sites. The regionally varying extent and manner of the degradation must be considered for further interpretation of fossil biologic proxies recovered from different sites within a lake.

4.2.5 Degradation within the surface sediment

Oxic water-sediment interface: Another extensive degradation before permanent burial occurred at the water to sediment interface. Most pigments occurred in much lower concentrations in the core top, than even in the deepest sediment traps (Tab. 9). Several previous studies in other freshwater sediments indicated that fossil pigment concentration directly reflects the standing crop abundance in the euphotic zone, while others indicated that up to 99 % of the autochthonous pigments are lost during sinking (see review in Leavitt 1993). In this study we found a loss of up to 75 % during sinking towards the bottom trap but up to 98 % loss after settling at the sediment surface. Similar high losses were found for the major lipid biomarker classes (Russell and Rosell-Mélé 2005) and for diatom valves (Battarbee et al. 2005), thus the figures here are likely to be a reliable dimension for the losses in a deep oxygenated lake.

The oxygen penetration into the sediment varies from 5 mm in the Selenga Delta to 50 mm in the North basin and Academician Ridge (Martin et al. 1993, Mackay et al. 1998, Granina et al. 2000, Vologina et al. 2000). Hence, buried pigments in Lake Baikal remain up to a few decades in an oxygen-saturated zone. The anoxic sediment trap material, in contrast, remained relatively protected from oxidation after burial into the traps. Thus, strong degradation affected those pigments or pigment degradation products that reached the sediment surface. Thereby, the degradation of chlorophyll, pheophorbide and pheophytin was much stronger than that of organic carbon. Typical Chl*a*/TOC ratios in phytoplankton are 6-28 μmol g^{-1} (Sterner and Elser 2002) and whereas the Chl*a*s/TOC ratios found in the top traps were within that range, the ratios found in the surface sediment were much lower except in the eastern South (Tab. 10).

The Chl*a*s/DM and Chl*a*s/TOC ratios varied about one order of magnitude among the distinct regions (South, Selenga Delta, North and Barguzin Bay). Similar high variation was already found for Chl*a*s/DM in a previous study in Lake Baikal (Soma et al. 2001a). In both studies the Chl*a*s/DM ratios were much higher in the South and Selenga

Delta than in the North. Therefore, it may correspond to the significantly higher Chl*a* concentration indicating higher primary production in the euphotic zone of the South and Selenga Delta compared to the North in summer (cf. chapter 3.1.1). Seasonal monitoring in the high latitude is required for further comparisons. However, one would expect also higher ratios in the Barguzin Bay, where the river inflow caused higher Chl*a* concentrations in the euphotic zone, but the Chl*a*s/DM ratio in the core top was much lower than in the South and Selenga Delta. Dilution with terrigeneous anorganic material is likely as the TOC content was also low. Referring pigments as units per TOC avoid the problem of dilution with terrigeneous anorganic material in studies of fossil pigments.

The differential degradation patterns at the investigated regions (South, North, Selenga Delta and Barguzin Bay) were also obvious from the share of Chl*a* degradation products to total Chl*a*s. For instance, only less than 10 % of the original Chl*a* that reached the lake bottom traps was preserved in the surface sediment in the South, but less than 5 % in the North. Chl*a* was best preserved in the northern Selenga Delta. Also, the share of the stable pheophytin to total Chl*a*s was greater and that of the labile pheophorbide was lower in the North compared to the South. Pyropheophytin *a*, in contrast, that occurred only in traces in the trap material was well preserved at both sites. A conversion from pheophytin *a* to pyropheophytin *a*, where pheophytin *a* looses its methylcarboxylated group, could also be possible (cf. Fig. 3). Finally, the differential degradation was also obvious from share of carotenoids to total carotenoids: the labile fucoxanthin and diadinoxanthin (Leavitt and Findlay 1994, Leavitt and Hodgson 2001), both from Bacillariophyceae+ Chrysophyceae, were dominant carotenoids in the core tops from South, Selenga Delta and Barguzin Bay, whereas the only detected carotenoids in the North, in contrast, were the stable lutein and canthaxanthin.

Oxidised layer: Further degradation occurred below the water to sediment interface within the oxidised layer, which can be up to 30 cm thick in Lake Baikal (Granina et al. 2000). The redox boundary is indicated by Mn and Fe accumulation, forming crusts in some regions of Lake Baikal (Vologina et al. 2003, Granina et al. 2004). Thus, buried pigments remain several centuries within the oxidised environment. Cuddington and Leavitt (1999) predicted that rates of pigment deposition were inversely related to the thickness of the oxic conditions, because the degradation within the surface sediment results predominantly from chemical oxidation and enzymatic lysis by microbial activity (Fig. 53). In Lake Baikal both processes were suggested to have higher effect in the North, as the decay was significantly higher there than in the South or Selenga Delta.

Sharp decreases of the total Chl*a*s and carotenoids were found within these oxidised layers in all short cores (cf. Fig. 40). A sharp decrease of chlorophylls within the upper 20 cm was also found in 12 Italian lakes (Guillizoni et al. 1983). It has been attributed to recent eutrophication. Although eutrophication has been suggested from diatom valve studies for the past 150 years in Lake Baikal (Mackay et al. 1998), it is not sufficient to explain the strong increase of Chl*a* (from the historical point of view) within the upper 10 cm in all cores. This sharp increase of Chl*a* with time or decrease with depth certainly resulted from degradation processes within the sediment rather than from production changes in the euphotic zone.

One indication of strong degradation was the high pheophytin/pheophorbide (lipophilic/water soluble) ratios in the surface sediments. Another indicator was the strong decay of the Chl*a*s/TOC ratios with depth of the surface sediment. Diagenetic processes, such as canthaxanthin formation also indicated that changes resulted from processes within the surface sediment rather than from processes in the euphotic zone.

Hence, other than diatom valves (Mackay et al. 1998), the photosynthetic pigments may not be suited to reconstruct recent, i.e. during past 150 years, short-term variations in Lake Baikal. That does, however, not exclude that photosynthetic pigments can be useful tools for reconstructing long-term relative variations (in contrast to absolute abundance) before the time spanned by the oxidised layer.

4.2.6 Do recently buried pigments reflect the phytoplankton standing crop?

The record of the phytoplankton standing crop by trapped pigments in Lake Baikal was group-specific. Some carotenoids were more preserved than others, and they cannot record whole algal assemblages, unlike differential degradation rates be taken into account. The main contribution to the settling material was formed by heavy, non-edible Bacillariophyceae. Strong and variable degradation processes controlled the sedimentation of small, light and edible phytoplankton. Basically, in the South these processes took place within the upper 250 m of the water column, while the processes extended over the whole water column in the North. The pigment preservation was much better in the South than in the North, although the water column is deeper. The sedimentation out of the euphotic zone can be projected backward using the preliminary regression models given in the present study.

A second degradation took place within the oxydised surface sediment. Rough estimates were given to calculate initial Chl*a* concentrations from sedimentary pigments

below the oxidised layers. Nonetheless, oxygen penetration may have varied in the past, and therefore the Chl*a*s/TOC ratios or Chl*a*s/DM ratios are potentially unsuitable to determine total phytoplankton abundance but preferably to estimate relative changes. That has been concluded already for smaller or shallower lakes (Leavitt 1993), but seems to be particularly important in the deep, oxidised rift system of Lake Baikal.

In as much as the paleoecological analysis of preserved markers such as photosynthetic pigments is increasingly used to monitor environmental change in response to climate and human activities, the complexity and variability of the degradation, revealed in this study, should improve our understanding of the limits of such retrospective analyses. Because Lake Baikal is unusual in terms of size and depth, it represents an interesting end-member in investigations of pigment biogeochemistry. The conclusions are difficult to apply to other mainly shallower freshwater systems, but can considerably contribute to the understanding on the manner in which organic molecules are incorporated into the sediments in cold, deep, oxygenated lakes and in marine systems.

4.3 Reconstruction of past phytoplankton variations

The aim of this part of the thesis was to determine the potential of fossil photosynthetic pigments for the reconstruction of past relative abundance and community structure of phytoplankton in Lake Baikal. The studies on the vertical transfer and preservation of photosynthetic pigments in Lake Baikal showed, that the decomposition within the water column and the surface sediment is strong and that pigments were likely unsuitable to reconstruct changes of the past hundreds of years (chapter 4.2). However, the present study showed that major paleoclimatological changes of the past 130,000 years were assessed and we may presume that the Chl*a*s/TOC ratio in Lake Baikal is a useful indicator for past relative changes of the phytoplankton abundance. This was demonstrated in all three Holocene cores (´Vidrino´, ´Posolski´ and ´Continent Ridge´) and in the deep core section from the Continent Ridge that encompassed the last glacial and interglacial periods.

4.3.1 Holocene

Regional differences of the Holocene record: Comparison between the Holocene cores from the three coring sites (´Vidrino´, ´Posolski´ and ´Continent Ridge´, located in the South basin, Selenga Delta and North basin, respectively) indicated lowest productivity (lower average Chl*a*s/TOC ratio), and thereby lower temperatures, but frequent climate oscillations (higher coefficient of variation, cf. Tab. 12) at Continent Ridge. Temporal changes varied also regionally, and today we are not able to discern whether these differences resulted from different phytoplankton production or pigment preservation. Oxygen isotope analyses (Morley et al. 2005) have indicated south-northwards shifts of the weather systems influences, for example of the North Atlantic Westerlies and Siberian High, during Holocene. Such shifts may explain differential records in the North and South and by their impact on the catchments area also differential records in the Selenga Delta.

The C/N ratios (< 12 atomic ratio) proved the essentially autochthonous nature of the organic compounds buried at these three sites (even at river inflow) that has also been demonstrated for a series of other sites previously (Qiu et al. 1993). Typical phytoplankton C/N ratios in suspended and settling material are around 6 (Redfield ratio), while those of higher plant leaves are much higher (c. 45, Hutchinson 1975, Sterner and Elser 2002) and those of littoral macrophytes about 15 (Likens 1985).

Holocene climate records: Before 9 kyr BP (Boreal), the very low amounts of TOC, and very low ratios of Chl*a*s/TOC and Chl*b*s/TOC, found in the Continent Ridge core, may be a late consequence of a cooling known as the Younger Dryas in European sites, which interrupted the warming in the Lake Baikal region (Colman 1995). Grey scale density in thin sections as well as pollen and sporomorph analyses (conducted on parallel kasten cores, Boës et al. 2005, Demske et al. 2005), indicated the Younger Dryas was represented at c. 12 kyr BP. This event has also been imprinted in the sedimentary photosynthetic pigment record of a core in the South basin (Tani et al. 2002).

During the Boreal, the TOC content and the Chl*a*s/TOC ratios increased markedly. At c. 9 kyr BP, the Chl*a*s/TOC ratios indicated a maximum of phytoplankton abundance, which may even have exceeded the current abundance. Pollen analyses indicated that high temperatures and favourable moisture favoured an optimum development of dark-coniferous taiga at Continent Ridge at that time (Demske et al. op. cit.). A maximum of diatom valve abundance was also found at that time in the Selenga Delta, which was related to high temperature and humidity in western Siberia (Karabanov et al. 2000a).

The strong Chl*a*s/TOC decline between 8-7 kyr BP corresponded to a mid-Holocene cooling event reported from pollen analyses (Demske et al. op. cit.). A Chl*a*s/TOC maximum occurred between 6.5-5.7 kyr BP during the following Atlantic, which was, however, less expressed than the Boreal maximum. At that time, an Atlantic maximum was also found for diatoms (Karabanov et al. op. cit.) and pollen (Horiuchi et al. 2000). Maximum distribution of Scots pine forests marked the Holocene thermal optimum at that time (Demske et al. op. cit.), and, therefore, although from phytoplankton records (pigments + diatom valves) the Holocene optimum occurred during Boreal, the pollen record indicated the Holocene optimum during Atlantic.

Subsequently, a cooling period at the Atlantic-Subboreal transition (5.7-4.5 kyr BP) was indicated by TOC content and Chl*a*s/TOC ratio, diatom abundance (Karabanov et al. op. cit.) and pollen data (Demske et al. op. cit.). During that time, the southern cores showed increasing temperatures (increased Chl*a*s/TOC ratio), probably indicating the aforementioned shifts of the major weather systems. From c. 4.5 to 3 kyr BP the Chl*a*s/TOC ratios increased, indicating a Subboreal optimum, which was also indicated by grey scale density and pollen data (Boës et al. op. cit., Demske et al. op. cit.). This period has previously also been shown to be one of high diatom productivity and biogenic silica accumulation (Qiu et al. 1993, Karabanov et al. op. cit.). However, the widely accepted opinion that the warmest period of the Holocene in the Baikal region

was the Subboreal (Karabanov et al. op. cit.) could not be confirmed here for the Continent Ridge site, as the Boreal optimum was higher than that of the Subboreal. The cores at Vidrino and Posolski did not reach the Boreal period and hence no comparison with the Subboreal optimum could be made.

Subsequently, between 3 and 1 kyr BP a cooling period may be assumed at all three sites as we recorded lowest TOC content, Chl*a*s/TOC and Chl*b*s/TOC ratios, and carotenoids/Chl*a*s ratios during that time. In a previous pigment study (Tani et al. 2001) lowest total Chl*a*s and carotenoid concentrations were also found during approximately the same period in a core from the South basin. From 1 kyr BP to present an increase of the Chl*a*s/TOC ratio indicated an increase of the phytoplankton productivity, but as aforementioned (chapter 4.2.5) this increase was related to strong degradation within the oxidised layer rather than to productivity changes.

Variation of phytoplankton composition during Holocene: During the Boreal Chl*a*s/TOC maximum, the Chl*b*s/Chl*a*s ratios slightly increased, while Chl*c* was not detected; we assume, therefore, that during this Boreal optimum Chlorophyta occurred in higher amounts than Bacillariophyceae. Since today Chlorophyta occur mainly during early summer and in the South basin, while Bacillariophyceae occur mainly in the cooler waters (Kozhova and Izmest'eva 1998; chapter 3.1), the Boreal increase of the Chl*b*s/Chl*a*s strengthened the assumption of a Holocene temperature optimum at that time. During the subsequent Chl*a*s/TOC minimum (c. 8-7 kyr BP), the Chl*b*s/Chlas ratio was also high, however, so that evidently some cold-adapted Chlorophyta occurred during cold periods of the Holocene. Varying Chl*b*s/lutein ratios throughout the cores also indicated changes of the chlorophycean species composition.

At the time of the Atlantic temperature optimum (c. 6.5 to 5.5 kyr BP) the Bacillariophyceae started enhanced growth before the Chlorophyta (as the Chl*c*/Chl*a*s peaked at the early optimum (c. 6.2 kyr BP) and the Chl*b*s/Chl*a*s thereafter (c. 5.8 kyr BP)). Nonetheless, Chl*c* peaks were not correlated to those of diatom valve abundance (Rioual and Mackay 2005), which could be due high Chl*a*/Chl*c* ratios in Bacillariophyceae, as has been suggested in previous studies (cf. Squier et al. 2002) or to strong degradation of Chl*c*. Chl*c* is, alike pheophorbide, missing the phytol ester group and is therefore more water soluble than Chl*a*, Chl*b* or its pheophytins. Moreover, Chlc cannot degrade to pheophytins and therefore no degradation products were detected.

Pigments from cyanobacteria were not detected in the cores, because cyanobacteria either do not or only negligibly settle into Lake Baikal's sediment due to their small size,

lightness and edibility (cf. chapter 4.2). Thus, unfortunately, tracking the development of the cyanobacterial picoplankton cannot be accomplished directly by tracking the marker pigments in Lake Baikal. Fossil canthaxanthin has previously been used to track cyanobacterial development in freshwater lakes, including Lake Baikal (Soma et al 1996, Tani et al. 2002). However, canthaxanthin could not be detected or was present only in trace amounts in more than 300 water samples from Lake Baikal (although the presence of cyanobacterial picoplankton was demonstrated by other marker pigments and epifluorescence counts therein) and in isolated Baikalian cyanobacterial strains (cf. chapter 3.1 and Fietz et al., submitted, Appendix B). We assume that the canthaxanthin detected in Lake Baikal's sediment comes not directly from phytoplankton (especially cyanobacteria), but from crustaceans that feed on phytoplankton. The crustacean carapace contains protein-bound astaxanthin. Within the sediment these carapaces are destroyed and astaxanthin is liberated. Under reducing conditions, astaxanthin is then transformed to canthaxanthin. With that assumption, the canthaxanthin detected in Lake Baikal's sediment indicated enhanced zooplankton abundance.

Most of the detected carotenoid degradation products were not attributable to their parent pigments. The use of HPLC-MS (connexion of HPLC and mass spectrometry) based methods will presumably provide further information on the degradation products in future studies conducted in similar oligotrophic and deep lakes with oxic hypolimnia. Mass spectrometry identifies the nature of molecular modifications because it confirms the molar mass of a pigment or degradation product as well as characteristic fragmentation patterns (Leavitt and Hodgson 2001) and has been successfully used in a few marine and freshwater systems (e.g. Squier et al. 2002). However, mass spectrometric techniques require pure compounds in high concentrations for the analysis of pigment characteristics (Leavitt and Hodgson 2001). For the Lake Baikal sediment samples detailed structural information about phospholipid mixtures were gathered by the use of HPLC-ESI-MS-MS that allowed deeper insights into the compositions of microbial communities and the influence of environmental conditions (Zink and Mangelsdorf 2004). The use of similar techniques for the sedimentary pigments of these Baikal sediment samples can be hypothesised from preliminary measurements (unpublished data).

4.3.2 Last Interglacial (Kazantsevo)

Kazantsevo climate record: The TOC content and the Chl*a*/TOC ratio were much higher during the Kazantsevo Interglacial compared to the preceding (Tazovsky, equivalent to European Saalian) and subsequent (Zirianski, equivalent to European Weichselian and MIS 5d; Karabanov et al. 1998) Glaciations. Hence, although strong degradation my have occurred during cold and warm periods, the relative changes in the TOC content and the Chl*a*/TOC ratio delivered important information about paleoclimatic changes.

The strong increase in the Chl*a*s/TOC ratio we observed at c. 128 kyr BP was in good agreement with the simultaneous increase of the total sporomorph concentrations (particularly of *Pteridinium aquilinium* spores), indicative of a considerable rise in temperature (Granoszwski et al. 2005). Study of diatom valves also indicated a strong increase in productivity at c. 128 kyr BP, as biovolume accumulation rate increased by an order of magnitude (Rioual and Mackay 2005). At that time insolation was maximal in the Baikal region (Prokopenko et al. 2002). According to pollen, diatoms, and biogenic silica the Kazantsevo Interglacial lasted for 11-12 kyr BP (Edlund and Stoermer 2000, Prokopenko et al. 2002, Granoszewski et al. op. cit., Rioual and Mackay op. cit.). Assuming a sedimentation rate of 6.4 cm kyr^{-1} (Demory et al. 2005), the TOC and chlorophylls in our study indicated approximately the same time span. Studies of the corresponding European Eemian pointed to duration of 11 to 13 kyr (Tzedakis et al. 2003).

The Chlas/TOC ratio was highest between c. 126 and 121 kyr BP. This period corresponded to the maximum diatom abundance (Rioual and Mackay op. cit.). The pollen fossils indicated a short-lived rise of temperature and moisture at c. 126.4 kyr BP (Granoszewski et al. op. cit.), and the TOC content we recorded was highest around that date. However, neither the Chlas/TOC ratio (Fig. 8) nor the diatom abundance (Rioual and Mackay op. cit.) exhibited a peak at that time. A change of phytoplankton composition towards cells with low pigment content, and diatoms with high dissolution, was likely.

During the Kazantsevo, the Chl*a*s accumulation rate and the Chl*a*s/TOC ratio indicated short cooling events at c. 125.5, 123.5 and 122 kyr BP and temperature optima in between at c. 124.5, 122.5, and 121 kyr BP. These short-lived events did not all correspond to the pollen and diatom variations (Granoszewski et al. op. cit., Rioual and Mackay op. cit.). This apparent mismatch could be due to the fact that the measurements were done on parallel cores and, although they were dated and correlated accurately, short peaks were possibly attributed to slightly varying dates. Overall, pollen, diatom and

pigment data indicated a suite of strong, short-lived, oscillations of the weather conditions during the Kazantsevo Interglacial. Phytoplankton abundance was halved or doubled within centennial time scales only.

Within the late Kazantsevo, a first drop of the TOC, Chl*a*s accumulation rate and Chl*a*s/TOC occurred at c. 119.5 kyr BP, which was even more expressed by the diatom abundance (Rioual and Mackay op. cit.). This drop has also been found in previous studies on biogenic silica and diatom valve abundance in other regions of Lake Baikal (Karabanov et al. 2000b, Prokopenko et al. 2002).

Lithology and photosynthetic pigments indicated an abrupt end of the Kazantsevo Interglacial that closely followed a sharp decrease of the insolation towards 116 kyr BP (Prokopenko et al. 2002). At c. 116 kyr BP the insolation turned and increased again during the Early Zirianski (Prokopenko et al. 2002). However, even during the Early Zirianski Glaciation, the Chl*a*s/TOC ratio we observed pointed to considerable oscillations of the paleoclimatic conditions, which were not observed in the TOC content or lithologically nor were they revealed within the diatom and pollen studies (Prokopenko et al. 2002, Granoszewski et al. op. cit., Rioual and Mackay op. cit.). The short-term changes may have been caused by fast responses of phytoplankton other than diatoms, such as Chlorophyta.

Phytoplankton composition: Three Chlbs/Chlas maxima were found during the Interglacial: around 126, 123, and 118 kyr BP, indicative of three temperature optima. The Chlbs/Chlas peaks during the glacial periods may be explained by the occurrence of so-called "snow algae", which today are formed by Chlorophyta (e.g. Chlamydomonas, Hoham and Duval 2001). These algae could have developed on the ice and snow that likely covered the lake during most of the year during the cold periods. The Chlbs/Chlas ratios during the Early Zirianski exceeded 20 % (Fig. 46). Chlb/Chla ratios within the euphotic zone as well as in isolated Chlorophyta were found to be 30 to 40 % (Fietz and Nicklisch 2004, Appendix A; Fietz et al., submitted, Appendix B). Hence, the Chlas during the Early Zirianski Glaciation was formed nearly completely by Chlorophyta. Different Chlorophyta species obviously developed under very different climatic conditions.

*Occurrence of Chl*a *derivatives*: Tani et al. (2002) suggested from a core spanning c. 24 kyr BP, that pyropheophytin and SCE are the dominant Chl*a* derivatives in Lake Baikal sediments whose ages exceed 10-15 kyr BP. In our study, pyropheophytin and even

SCEs, which may be of greatest stability (Prowse and Maxwell 1991, Talbot et al. 1999), were not the dominant Chl*a* derivatives during the Kazantsevo Interglacial; pheophorbide *a*, in contrast, contributed up to 50 % of the total Chl*a*s during the Kazantsevo Interglacial. The high contribution of pheophorbide *a* to the total Chl*a*s indicated high grazing activity, because pheophorbide is a degradation product of chlorophyll following passage through zooplankton gut. Enhanced zooplankton growth strengthened the assumption of warm conditions during that period. In a 2.8 million years old sediment SCEs were the only preserved chlorophyll derivatives and were thought to be proxies of global planetary changes in Lake Baikal (Soma et al. 2001b). They were also thought to be formed by passage through zooplankton guts (Soma et al. 2001b). However, as SCEs are only trace components within the surface sediments (unpublished), a conversion from pheophorbide after burial should be considered too.

Interestingly, the distinct forms of pheophorbide, pheophytin, and pyropheophytin showed greater variability during the Holocene than during the Kazantsevo Interglacial (Fig. 9). Different forms resulted from either different phytoplankton species or from differential sedimentation. Thus, it might be assumed that either phytoplankton compositions or the sedimentation conditions were more variable during the Holocene than during the Kazantsevo Interglacial. Further analysis and experiments on the origin of the distinct degradation forms will provide further insights into past environmental conditions and degradation processes.

Perylene: Perylene occurred during the Holocene and Kazantsevo Interglacial without correlation to chlorophylls or carotenoids. Sillimann et al. (1998) did also not found significant correlation in Lake Ontario, but Soma et al. (1996) and Tani et al. (2001), in contrast, found significant correlations between perylene and photosynthetic pigments in cores from the South basin of Lake Baikal. Perylene has been found in lakes and seas evenly in recent (except oxic surface) and ancient sediments (Aizenshtat 1973, Louda and Baker 1984, Silliman et al. 1998, Jiang et al. 2000, and references therein). The organic precursor of perylene was suggested to be phytoplankton or its photosynthetic pigments (Aizenshtat 1973, Laflamme and Hites 1978), but many studies indicated also a potential terrestrial precursor even in aquatic sediments (Jiang et al. 2000, and references therein), and in situ formation from non-specific precursors is although likely. All studies agreed, however, that only anoxic conditions allow the formation of perylene and that therefore perylene is an indicator of depositional conditions rather than of organic matter (Silliman et al. 1998). With that assumption, changing redox conditions may be tracked in Lake

Baikal. However, as far as neither the precursor, nor the formation processes, nor the preservation are definite, interpretations based on perylene variations are rather speculative. Nonetheless, the differential occurrence of perylene within the regions and periods in Lake Baikal may incite further detailed studies.

Reconstruction of the past phytoplankton abundance: Pollen data indicated that in Lake Baikal more favourable climatic conditions prevailed during the Kazantsevo Interglacial than during the Holocene (Granoszewski et al. 2005), which was confirmed for phytoplankton by the significantly higher mean Chl*a*s/TOC ratios we observed during the Kazantsevo (Tab. 13). However, the predominance of large-celled diatoms during the Kazantsevo maximum dampens this assumption, as these indicate deep-mixing events and clear ice cover that preferentially occur at low temperatures (Edlund and Stoermer 2000). An alternative to higher temperatures is that higher productivity (higher mean Chl*a*s/TOC ratios) resulted from a higher nutrient availability. The significantly lower C/N-ratios (Tab. 13) found during the Kazantsevo compared to the Holocene indicated higher nitrogen availability (increase of N) or lower productivity (decrease of C) during the Kazantsevo. Lower productivity was unlikely because the Chl*a*s/TOC ratios (as aforementioned) were significantly higher; thus, higher nitrogen availability was likely. Phosphorus-enrichment in Lake Baikal do not serve as a direct marker for paleoproductivity, but is controlled by porewater chemistry and sedimentation rates (Fagel et al. 2005). However, the sedimentary phosphorus-content (measured as P_2O_5) was 35 % higher during several thousands years before the onset of the Kazantsevo compared to several thousands years before the onset of the Holocene (Fagel, pers. comm. from unpublished data on the parallel core CON01-603-2). We therefore assume that possible limiting nutrients (nitrogen and phosphorus) were more available for the phytoplankton development during the Kazantsevo than for the phytoplankton development during the Holocene. That could explain the long lasting high Chl*a*s/TOC ratios found during the Kazantsevo, which are unlikely to be caused by temperature changes only. Another possible factor is that increasing productivity reduced the thickness of the oxidised layer at the sediment surface and thus reduced the degradation and increasde the preservation.

Transfer models for the degradation within the surface sediment (oxidised layers) and within the water column have been calculated based on a series of short cores and two series of sediment trap moorings previously (cf. chapter 3.2). The degradation within the surface sediment (oxidised layer) at Continent Ridge was exponential: y=F*exp(-x/3.69),

whereby y was the Chl*a*s/TOC ratio (in μmol g^{-1}) at the depth x (in cm) and F the estimated ratio at the sediment surface (in μmol g^{-1})(Appendix C - Tab. 7). The maximal Chl*a*s/TOC ratio at the Kazantsevo optimum was 0.38 μmol g^{-1}. The degradation below the oxidised layer can be neglected, and therefore, x is set as the approximate thickness of the oxidised layer. Assuming an at least 5 cm thick oxidised zone at the Kazantsevo maximum, a Chl*a*s/TOC ratio of 1.5 μmol g^{-1} resulted [F=0.38/exp(-5/3.69)]. The recent ratio in the core top at Continent Ridge is 0.73 μmol g^{-1}. Assuming thicker oxidised layer even increased the reconstructed Chl*a*s/TOC ratio. Hence, the reconstructed Chl*a*s/TOC ratio for the Kazantsevo maximum was twice as high as that preserved recently.

The results from sediment trap moorings were used to reconstruct the Chl*a*s/TOC ratio of the euphotic zone during the Kazantsevo (cf. chapter 3.2). Strong degradation occurred at the water to sediment interface: from the Chl*a*s/TOC that reached the lake bottom only c. 13.5 % were preserved in the surface sediment of the North, and therefore, the reconstructed ratio in the bottom trap during Kazantsevo optimum was 11 μmol g^{-1}. Furthermore, the decrease of the Chl*a*s/TOC ratio within the water column (from top trap at 50 m to bottom trap at c. 900 m) in the North basin was linear: y=F-0.019*x (Appendix C - Tab. 6). Therefore, in 50 m water depth, which is the lower boundary of the euphotic zone in Lake Baikal (Kozov 1963, Kozhova and Izmest'eva 1998), a Chl*a*s/TOC ratio of 27 μmol g^{-1} was estimated at the Kazantsevo optimum [F=11+0.019*850].

Thus, the reconstructed Chl*a*s/TOC ratio for the Kazantsevo maximum was higher than the Chl*a*s/TOC ratio determined in the 50 trap of the North mooring (2002-2003), which was 16 μmol g^{-1} (cf. chapter 3.2.2). However, analyses of ocean colour satellite data (using appropriate bio-optical modelling), indicated that the Continent Ridge site differed from the site of the mooring in phytoplankton abundance and terrigeneous input (Heim et al. 2005). Hence, interpretation must be drawn carefully. However, apparently the reconstructed Chl*a*s/TOC ratio, which indicated the phytoplankton productivity, suggested more favourable conditions during the Kazantsevo optimum than today.

4.3.3 Do fossil pigments track past phytoplankton community structure and environmental changes?

It could be shown that fossil Chl*a*s serve in Lake Baikal as reliable indicators for global climatic changes. Moreover, fossil Chl*b*s tracked the development of Chlorophyta. However, other pigments, such as Chl*c* or carotenoids, were not suitable to track changes of the phytoplankton community structure as their degradation products were not detected or could not be related definitely to their parent pigments. Yet a few major trends can be stated from sedimentary phytoplankton pigments for Lake Baikal: (1) Higher Chl*a*s/TOC ratios indicated higher phytoplankton production and thereby higher water temperatures during the Kazantsevo Interglacial compared to the glacial periods. Strong climate oscillations occurred during the Interglacial and phytoplankton was halved or doubled within centennial time scales. (2) Highest phytoplankton production during the Holocene occurred at c. 9 kyr BP at the time of climate amelioration following the Younger Dryas (Boreal). (3) Short maxima occurred during the late Atlantic and at the Subboreal/Subatlantic transition. The comparison of the sedimentary pigments with published diatom records indicated that phytoplankton other than diatoms contributed to the buried organic material.

5 CONCLUSION

The objective of this thesis was to assess whether and to which extent phytoplankton pigments in Lake Baikal can indicate changes of the recent and past phytoplankton community structure as well as climatic and other environmental changes. Moreover, the information gathered by the phytoplankton pigments should be used to complement our knowledge on the current and historical productivity variations in Lake Baikal in conjunction with the paleoclimate project CONTINENT and the long-term monitoring programme of the State University Irkutsk.

Here, I show that the analysis of recent phytoplankton pigments in the water column of Lake Baikal was a useful approach to characterise the recent phytoplankton assemblage and its variations induced by environmental changes. Pigment-based studies were demonstrated to greatly aid our understanding of the ecology of large lakes as well as to be a considerably improvement on traditional monitoring by microscopic counts. Even planktonic groups, e.g. the picoplanktonic Eustigmatophyceae, which cannot be distinguished by light or epifluorescence microscopy, could be traced by this method. Chl*a* concentrations, as a measure of potential productivity, strongly differed between the regions, years and seasons. However, the community structure varied more than the total productivity with changing environmental conditions, with temperature and stratification being the main driving forces. Therefore, we can expect that predicted future warming in the lake would lead to significant changes in the phytoplankton composition. Moreover, this change would be towards small phytoplankton species at the expense of the characteristic large endemic diatoms.

The use of fossil phytoplankton pigments to determine past community structural changes and environmental influences was more complex than the use of recent phytoplankton pigments to determine the recent community composition. During sedimentation out of the euphotic zone and even at the surface sediment, Chl*a* or phytoplankton pigments in general were considerably affected by degradation processes. The degradation was mainly caused by oxidation and grazing. The manner and extent of the degradation processes varied regionally even among the open basins, indicating the limits of extrapolations within the lake. Transfer functions were provided in this thesis for different regions in order to further improve reconstructions based on fossil phytoplankton pigments.

However, although the degradation of the phytoplankton pigments before permanent burial in the sediment was strong, the ratio of fossil Chl*a* plus its degradation

products vs. organic carbon accurately tracked published past climate changes, even those that occurred more than 100,000 years ago. Hence, sedimentary Chl*a* in Lake Baikal was shown to be a reliable indicator of phytoplanktonic response to published climate changes and may serve for validation of future climate models in continental regions. Chl*b* plus its degradation products provided important additional information on the past development of Chlorophyta. Most other sedimentary phytoplankton pigments were found to be unsuitable to determine past phytoplankton community structures in Lake Baikal, because their degradation products could not be definitely related to the parent pigments.

The ratio of fossil Chl*a* plus its degradation products vs. organic carbon (as a measure of the productivity) indicated that strong oscillations of the productivity occurred during the Holocene (from c. 10,000 years BP to present day) and the last interglacial (from c. 129,000 to 117,000 BP). These results highlighted the great natural variability at times before any human impact on a pristine lake. Productivity optima were found that even surpassed the present productivity.

Taken together, pigment-based analyses were shown to accurately reflect phytoplankton variation caused by environmental changes of natural or human origin in Lake Baikal. In conjunction with the EU project CONTINENT and long-term monitoring by the State University Irkutsk, the phytoplankton development determined from the last interglacial up to the early 21st century presented in this thesis will be a useful basis for future research and modelling of climate changes as well as for the protection of Lake Baikal.

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APPENDIX A

Fietz and Nicklisch (2004)

Freshwater Biology 49 (2004): 332-345

An HPLC analysis of the summer phytoplankton assemblage in Lake Baikal

Susanne Fietz and Andreas Nicklisch

ABSTRACT

1. Lake Baikal is one of the largest freshwater lakes in the world, whose enormous size and spatial heterogeneity require rapid methods for large sample sets. We therefore tested the applicability of a novel, HPLC-based, combination of methods for analysing phytoplankton. In July 2001, samples were collected in a transect across the lake at various depths down to 30 m. Phytoplankton (>3 μm) and autotrophic picoplankton (APP) were counted under light and epifluorescence microscopes, respectively. Pigments were analysed with HPLC.
2. The pigment data allowed the contributions of the dominant phytoplankton groups to the total chlorophyll a in the lake to be estimated by multiple linear regression and by the CHEMTAX matrix factorisation program. Three marker pigments fucoxanthin, lutein and zeaxanthin were shown to be useful indicators of the abundance and spatial distribution of certain phytoplankton groups. The relative contributions of the various phytoplankton groups to the total chlorophyll a in the lake determined using these marker pigments were similar but not identical to those determined by cell counts.
3. Pigment analyses of isolated strains from Lake Baikal and some European lakes confirmed that phycoerythrin-containing Cyanobacteria with very high amounts of zeaxanthin were responsible for the low Chla/zeaxanthin ratios of the water samples. A picoplanktonic species of Eustigmatophyceae was isolated from the lake. Its high violaxanthin content, responsible for very low Chla/violaxanthin ratios of some water samples, can be used to estimate the contribution of this group to total chlorophyll a.

INTRODUCTION

Lake Baikal is one of the largest freshwater bodies in the world and is a unique ecosystem with many endemic species (Martin 1994, Timoshkin 1997). It extends over five degrees of latitude, is more than 600 km long and more than 1.6 km deep. Although Lake Baikal is a freshwater lake, the nutrient status of the pelagial is ocean-like, and the only nutrient-rich regions of the lake are the deltas of the main river inflows (Genkai-Kato 2002).

Seasonal, horizontal and vertical changes in the phytoplankton biomass have been well investigated in Lake Baikal (Kozhova & Izmest'eva 1998, Popovskaya 2000). Most studies have used the traditional method of microscopic measurement and counting, which primarily records nano- and microphyto-plankton. Autotrophic picoplankton (APP), believed to contribute significantly to the summer assemblage (Kozhova & Izmest'eva 1998, Popovskaya 2000), is little known, in part due to technical difficulties (Boraas, Bolgrien & Holen 1991, Nagata et al. 1994).

Considering the enormous size of the lake, monitoring the phytoplankton response to anthropogenic and climatic influences requires a less time-consuming method that includes all phytoplankton size classes. One suitable approach might be the determination of chlorophylls and carotenoids as measures of the biomass of the dominant groups. This approach allows no differentiation at the species level, but most former studies of Lake Baikal have drawn their main conclusions based only on algal groups and not on single species (Popovskaya 2000). A rapid quantitative pigment analysis, supplemented by qualitative microscopic taxonomic analysis, would provide a sufficiently comprehensive record of phytoplankton in Lake Baikal.

High-Performance Liquid Chromatography (HPLC) allows semi-automated and rapid analysis of lipophilic photosynthetic pigments (Gieskes et al. 1988, Wilhelm, Rudolphi & Renner 1991, Millie, Paerl & Hurley 1993, Jeffrey, Mantoura & Wright 1997, Jeffrey, Wright & Zapata 1999). With HPLC all chlorophylls and carotenoids, plus their degradation products, can be separated and quantified at extremely low detection levels. Marker pigments allow the identification of most phytoplankton classes, including different groups of APP and fragile cells which can be overlooked during microscopic counting (Gieskes & Kraay 1983, Everitt et al. 1990).

Marker pigments permit the quantitative contribution from different groups to total chlorophyll a (Chla) to be calculated by multiple linear regression (MLR) (Gieskes & Kraay 1983, Gieskes et al. 1988, Woitke et al. 1996) or to total biovolume by simple linear regression. Such calculations have been successfully applied to marine systems (Gieskes et al. 1988, Everitt et al. 1990, Letelier et al. 1993, Andersen et al. 1996, Bidigare & Ondrusek 1996, Wright et al. 1996, Latasa et al. 1997, Jeffrey et al. 1997, Rodriguez, Varela & Zapata 2002) and to freshwater bodies (Wilhelm et al. 1991, Lami et al. 1992, Soma et al. 1993 & 1995, Quiblier et al. 1994, Descy & Métens 1996, Woitke et al. 1996).

However, although these calculations have been standardised and software such as the CHEMTAX matrix factorisation program have been developed for marine systems (Mackey et al. 1996 & 1998, Jeffrey et al. 1997), this is not yet the case for freshwater systems. Since the pigment content and the Chla to marker pigment ratio vary between species and are influenced by light and nutrient availability (Kohl & Nicklisch 1988, Gieskes et al. 1988, Wilhelm & Manns 1991, Wright et al. 1996, Millie et al. 1993, Nicklisch & Woitke 1999), marker pigments must be chosen carefully, taking into account the taxonomic composition of the phytoplankton.

The present study investigated the applicability of an approach utilising MLR and the CHEMTAX program for phytoplankton from Lake Baikal collected during a 3-week cruise by the research vessel "Vereshchagin" in summer 2001. Counts of phytoplankton (including APP) and pigment analysis were carried out. Additionally, a comparison was made between Chla to marker pigment ratios estimated by MLR and those found in cultures of algal and cyanobacterial strains isolated from European lakes and from Lake Baikal.

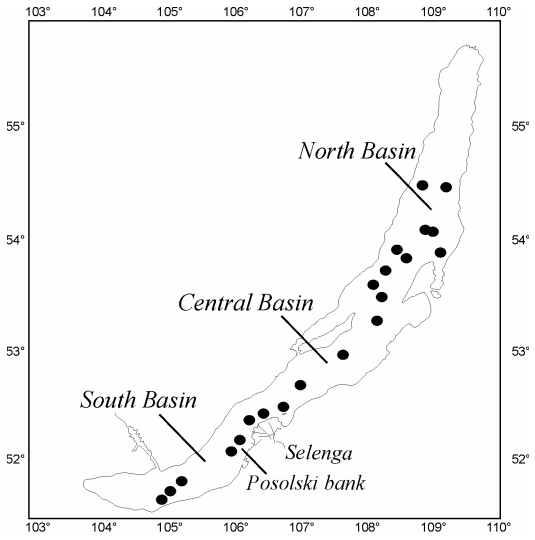

Figure 1. Diagram of Lake Baikal locating the sample stations for pigment analyses.

METHODS

Lake Baikal can be divided into three basins (Fig. 1). The north basin is separated from the central basin by Academician Ridge, and the central basin is separated from the south basin by the more than 20 km long Selenga Delta. The so-called Posolski bank is located in the southern part of the delta (Fig. 1). In July 2001 samples were collected during the CONTINENT cruises CON 01-4 and CON 01-5 in a seven-station transect over the lake (Table 1). At all stations, samples were collected within the euphotic layer at 5 m, 10 m and 30 m depths. For the pigment analysis, additional samples were taken at 5 m depth (21 stations) and just below the water surface at 0.5 m depth (11 stations). Samples were processed on board for further analyses as follows.

Phytoplankton samples (1-2 l) were concentrated by filtering through Nuclepore© polycarbonate filters (2 µm pore size). The overlaying water (1/10 of the original sample) was fixed with some drops of Lugol´s solution (Utermöhl 1958) and stored at room temperature.

Table 1 Details of the seven main sample stations in Lake Baikal, where micro-, nano- and picoplankton were counted. Chlorophylls and carotenoids were analysed at these seven and from 21 additional stations.

						water temperature [°C] at		
station	date	basin	latitude [°N]	longitude [°E]	water depth [m]	5m	10m	30m
CON01-501	16.7.01	Central	52.66	107.00	-1250	7	7	5
CON01-504	16.7.01	Central	53.,50	108.,25	-1069	6	5	4
CON01-505	17.7.01	North	53.,96	108.91	-390	6	5	4.5
CON01-510	18.7.01	North	53.,88	108.31	-888	4	4	4
CON01-525	21.7.01	Posolski	52.08	105.86	-30	12	9	7
CON01-526	22.7.01	South	51.72	105.02	-1431	12	9	7
CON01-527	23.7.01	South	51.56	104.85	-625	11	8	6

Samples for cyanobacterial and eucaryotic APP (50 ml) were fixed with formaldehyde (0.7% final concentration) and filtered through black Nuclepore© polycarbonate filters (0.2 µm pore size) according to well-established methods (Søndergaard 1991, Stockner & Shortreed 1991, Nagata et al. 1994). The filter was placed on a microscope slide, dried briefly and covered with a drop of fluorescence-free immersion oil and a cover slide. Slides were stored frozen. The preparations were stable for at least six months. Duplicate samples for HPLC-aided pigment determination (1–2.5 l) were filtered through 25 mm Whatman GF/F-filters, the filters put in 2 ml test-tubes, immediately freeze-dried and stored frozen in the dark. The further analyses were conducted at the laboratory in Berlin.

Phytoplankton counts and taxonomic identification were made under the microscope according to Utermöhl (1958). The algae were classified in accordance with Ettl et al. (1986). Cells were counted at 100-x magnification. 40-x magnification was used to count less abundant species. The whole chamber of 25 - 50 ml was then examined. APP (0.2 – 3 µm) were counted at 1000-x magnification using a Zeiss Axioskop epifluorescence microscope equipped with filters for green (546 nm excitation filter, 580 nm splitter and 590 nm barrier filter) and blue (450-490 nm excitation filter, 510 nm splitter and 520 nm barrier filter) excitation. Eucaryotic APP fluoresced deep red (>665 nm) when excited with blue or green light due to the dominance of chlorophyll. Phycobilin-containing procaryotic APP was identified by its light-red autofluorescence (<665 nm) when excited with green light (Fahnenstiel et al. 1991). Phycoerythrin (PE) and phycocyanin (PC) containing cyanobacteria could be distinguished by their yellow or extreme weak emission at blue light excitation, respectively, but the difference was not

definite in all stored preparations. The different taxonomic groups of APP were further divided into size classes: 1 µm spherical, 1x2 µm oblong, 2x2 µm spherical and 2x3 µm oblong. Cell counts were converted to biovolume according to their size and geometric form.

Chlorophylls, carotenoids and their derivatives were extracted with 1 ml of a mixture of acetone, methanol and water (80:15:5 by volume; Leavitt, Carpenter & Kitchell 1989) under dim light at 4 °C. The extraction was carried out by vibration shaking for 1.5 hours at 2000 rpm with a supplement of glass beads (0.75-1 mm). An IPR solution (ion-pairing reagent, 15 g l-1 tetrabutyl ammonium acetate and 77 g l-1 ammonium acetate) was added 10:1. The extract was centrifuged for 20 min at 2500 g and at 4 °C in a cooled centrifuge (Biofuge Fresco, Heraeus Instruments). The separation, identification and quantification of pigments were performed according to Woitke et al. (1994).

The HPLC system (Waters, USA) comprised a Waters 717 autosampler, a Waters 616 pump and a Waters 600S controller. Pigments were separated at a flow rate of 1.0 ml min-1 at 30 °C through a non-endcapped Waters Resolve C18 column (30 cm),protected with an appropriate precolumn, with an optimised gradient from eluent A to eluent B. Eluent A consisted of methanol, acetonitril and IPR (45:45:10) and eluent B consisted of acetonitril and acetone (45:55). Peaks were detected by a Waters 996 photodiode array detector. The system was controlled by Millenium© software. Pigments were identified by their relative retention times and by their absorption spectra.

Unialgal cultures, standards and literature data were used for comparison. Peak area integration allowed quantification with factors determined by Woitke et al. (1994, 1996) and checked from time to time with standards supplied by Sigma, Hoffmann-La Roche AG (Grenzach, Germany) or Carbon 14 Centralen (Hørsholm, Denmark).

If not specifically mentioned, strains from the culture collection of our institute (Leibniz-Institute of Freshwater Ecology and Inland Fisheries) were grown under saturating nutrient and light conditions at 15 °C in semi-continous culture (Nicklisch 1992). Statistical tests were performed using the SPSS© statistical package (SPSS Inc., USA).

RESULTS

The micro- and nanophytoplankton biovolumes in the basins of Lake Baikal varied from 0.5 to 1.4 mm3 l-1 (Fig. 2a). The mean biovolume was 0.89 mm3 l-1 and the median 0.52 mm3 l-1. Although the biovolume appeared to be highest in the north basin (Fig. 2a), differences between the basins were not significant. Nor were differences in depth significant but, the biovolume decreased from 1.8 to 0.16 mm3 l-1 with depth (5 m to 30 m) at Posolski bank, which is influenced by the Selenga River. The share of the algal groups did not differ significantly either over the transect (Fig. 3a) or over the vertical profile. Bacillariophyceae dominated all over the lake. Dinophyceae and Chlorophyceae were present in all basins and at all depths. Chrysophyceae were absent at Posolski bank. Except at 10 m depth in the south basin, where some *Planktothrix cf. suspensa* were present, micro- and nanoplanktonic Cyanobacteria were absent.

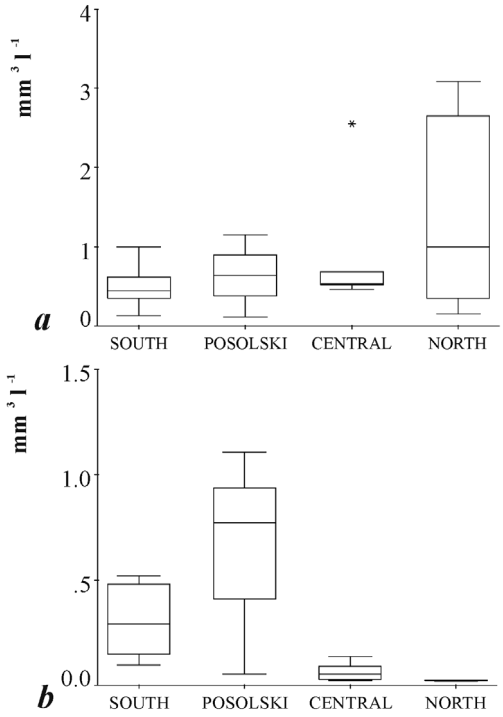

Figure 2. Boxplots of the biovolume of (a) total phytoplankton (>3µm) and (b) total APP. Boxes represent the median with interquartile ranges (25% to 75%), minima and maxima and extremes (asterisk). Variances aroused from combining different depths and and stations within each basin.

In contrast to the algal groups, the species composition did show differences. In the south basin and at Posolski bank microplanktonic centric Bacillariophyceae (15-50 µm) dominated. The main contribution to biovolume in the central basin was from pennate Bacillariophyceae. In the north basin, the main contribution to Bacillariophyceae biovolume was from a relatively small number of very large centric cells (>80 µm). The main Bacillariophyceae species present were *Cyclotella sp.* (Centrales) and *Fragilaria sp.* (Pennales). *Aulacoseira spp.* occurred only in the north basin. Other important algal species were *Chlorella sp., Monoraphidium spp.* (Chlorophyceae), *Dinobryon sp.* (Chrysophyceae) and *Gymnodinium sp.* (Dinophyceae). *Peridinium sp.* (Dinophyceae), *Rhodomonas sp.* (Cryptophyceae) and *Chrysochromulina sp.* (Haptophyceae) occurred only sporadically. In order to reduce the number of groups in Figures 3 & 5, *Chrysochromulina sp.* (Haptophyceae, containing fucoxanthin) was included with the Chrysophyceae.

The mean APP biovolume was 0.21 mm3 l-1 (median 0.08 mm3 l-1). The total amount of APP decreased significantly from south to north (Fig.

2b). The highest amount was found at Posolski bank, where cyanobacterial APP dominated. In the south basin, eucaryotic APP was dominant. In the north and central basins, the contribution of cyanobacterial APP and eucaryotic APP was nearly equal (Fig. 3b). The ratio of PC-containing cells to PE-containing cells gradually diminished from the south to the north. Generally, cyanobacterial APP cells were smaller (1-2 µm) than those of eucaryotic APP (2-3.5 µm). All over the lake, but most prominently at Posolski bank, colonies or aggregates of cyanobacterial APP with up to 40 cells for the 1 µm spherical size class and 15 cells for the 1x2 µm oblong size class were found, but these were not frequent. The vertical profiles did not show a significant difference in total APP content. However, at Posolski bank the APP decreased dramatically with increasing depth, as did the phytoplankton. At all depths throughout the lake, the mean amount of cyanobacterial APP was higher than that of eucaryotic APP and the contributions of PC-containing and PE-containing cells were nearly equal.

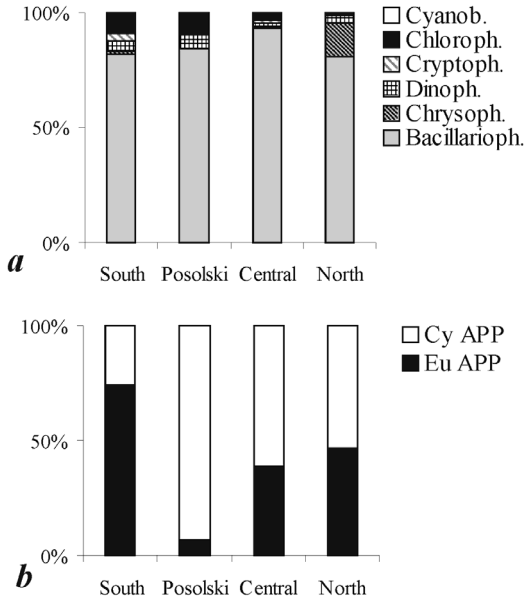

Figure. 3. Relative algal class distribution determined by light- and epifluorescence microscopy: (a) phytoplankton (>3µm) and (b) APP. Abbreviations: Bacillarioph. = Bacillariophyceae, Chrysoph. = Chrysophyceae, Dinoph. = Dinophyceae, Cryptoph. = Cryptophyceae, Chloroph. = Chlorophyceae, Cyanob. = Cyanobacteria, Cy APP = cyanobacterial APP, Eu APP = eucaryotic APP

The HPLC method effectively separated out distinct lipophilic photosynthetic pigments, except for the co-eluting pigments alloxanthin and caloxanthin. Eighteen pigments were resolved (Table 2). Pigment degradation products were negligible. Mean Chla concentration in Lake Baikal in July 2001 was 1.35 µg l^{-1}. The Chla concentration was significantly lower in the central basin than in all other basins (Fig. 4). The Chla concentration in the north basin was significantly lower than at Posolski bank, but not significantly different from that found in the south basin (Fig. 4). Mean Chla concentrations did not, in general, vary significantly with depth. The only exception was at Posolski bank, where the Chla concentration decreased dramatically at 30 m depth. All over the lake, the sum of the carotenoids was about 60% of the Chla.

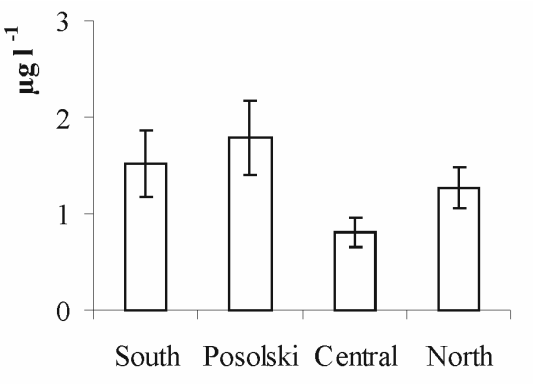

Figure 4. Chla concentration in Lake Baikal in July 2001. Error bars represent a 95% C.I., n=92.

In order to calculate the contribution of different taxonomic groups of phytoplankton to Chla, a multiple linear regression (MLR) of pigment data was performed using the following model:
Chla=a(fucoxanthin) + b(lutein) + c(zeaxanthin)
where a is the Chla/fucoxanthin ratio of Bacillariophyceae plus Chrysophyceae, b is the Chla/lutein ratio of Chlorophyceae and c is the Chla/zeaxanthin ratio of Cyanobacteria (cyanobacterial APP). An iterative process was used to check whether these or other marker pigments were suitable for a correct description using the coefficient of determination (r^2) and the correct prediction of Chla in each basin as criteria. For a right interpretation of pigment data the knowledge of the occurring species and its carotenoids, as known from literature and cultures, was very important.

Fucoxanthin was more suitable than Chlc as a marker pigment for Bacillariophyceae and Chrysophyceae and lutein was more suitable than Chlb for Chlorophyceae (Table 3a). The only possible marker pigments for cyanobacterial APP were zeaxanthin and caloxanthin, but caloxanthin was not clearly separated from alloxanthin. Therefore, zeaxanthin was chosen as a marker, although Chlorophyceae also contain small amounts of zeaxanthin. The amount of zeaxanthin derived from Chlorophyceae was calculated from lutein using a zeaxanthin/lutein ratio of 5.3 (Nicklisch & Woitke 1999). Zeaxanthin/lutein ratios of isolated strains from Lake Baikal were similar to this suggested ratio.

The calculated proportion of zeaxanthin attributed to the Chlorophyceae was subtracted from the total zeaxanthin of each sample so that the zeaxanthin used in the final MLR (zea*) included only the cyanobacterial part of zeaxanthin,

Table 2. List of pigments detected by HPLC in Lake Baikal in July 2001. Abundances were described by "trace", "minor" and "major" indicating means of <0.01 µg l^{-1}, 0.01 - 0.03 µg l^{-1} and >0.03 µg l^{-1} respectively. Superscripts "m" indicate marker pigments of the respective algal classes.

	abundance	occurence
Peridinin	trace	Dinophyceae^{m}
19´-Butanoyloxyfucoxanthin	trace	some Chrysophyceae
Fucoxanthin	major	Bacillariophyceae^{m}, Chrysophyceae^{m}
Neoxanthin	minor	Chlorophyceae
Violaxanthin	major	Chlorophyceae, Eustigmatophyceae^{m}, some Chrysophyceae
Diadinoxanthin	major	Chrysophyceae, Dinophyceae
Antheraxanthin	trace	Chlorophyceae
Diatoxanthin	minor	Chrysophyceae, Dinophyceae
Lutein	major	Chlorophyceae^{m}, Eustigmatophyceae, Xanthophyceae
Zeaxanthin	major	Cyanobacteria^{m}, Chlorophyceae, Eustigmatophyceae
Canthaxanthin	trace	Cyanobacteria, Eustigmatophyceae
Vaucheriaxanthin	trace	Eustigmatophyceae^{m}
Echinenone	trace	Cyanobacteria, Eustigmatophyceae
a-Carotene	trace	Cryptophyceae^{m}, Chlorophyceae
b-Carotene	major	all classes
Chlorophyll a	major	all classes
Chlorophyll b	major	Chlorophyceae^{m}, Euglenophyceae
Chlorophyll c	major	Bacillariophyceae^{m}, Chrysophyceae^{m}, Cryptophyceae, Dinophyceae

which was at least 94 % of the total zeaxanthin. The contribution to the total Chla was calculated for every dominant algal group from the significant factors listed in Table 3a, considering all samples which were also microscopically analysed. In all basins and at all depths the estimated Chla (Fig. 5a) was then very close to the measured Chla (Fig. 4).

The pigment data were also processed using the CHEMTAX software – a matrix factorisation program for estimating class abundances in marine systems (Mackey et al. 1996). The same phytoplankton groups as mentioned for the MLR were included. Fucoxanthin, Chlc, lutein, Chlb, zea* and ß-carotene were chosen as marker pigments. The factors calculated by MLR were used as estimates of the initial pigment-ratios that are crucial for good CHEMTAX results. Suggestions given in the accompanying paper of Mackey et al. (1996) were used as initial factors for ß-carotene. The final pigment ratios differed greatly from the initial factors and the coefficient of determination (r^2) was lower (Table 3a).

Nevertheless, the estimated percentage contributions of the phytoplankton groups to Chla (Fig. 5b) fitted well to the figure assessed via MLR (Fig. 5a). Only at Posolski bank were Chlorophyceae overestimated at the expense of Bacillariophyceae and Cyanobacteria. A splitting of the Bacillariophyceae and Chrysophyceae was not successful with our data set, due to the lack of precise initial Chla vs. fucoxanthin or Chlc ratio of Lake Baikal Chrysophyceae. Unreliable results were also obtained when less abundant groups, such as Cryptophyceae, Dinophyceae and Haptophyceae, were included. Causes could be that α-carotene (Cryptophyceae), peridinin (Dinophyceae) and butanoyloxyfucoxanthin (Haptophyceae) were detected in too low concentrations.

The contributions to the total biovolume of the main groups were also calculated based on the marker pigments (Fig. 5c). For this purpose marker pigment vs. biovolume ratios calculated by simple linear regression were used (Table 3b). Contributions of the Bacillariophyceae and Chrysophyceae could be divided by calculating their respective fucoxanthin/biovolume ratios via MLR. However, the result was not significant (Table 3b).

Altogether, the correspondence between the models (Fig. 5a,b&c) and the microscopic counts of micro-, nano- and picoplankton (Fig. 5d) was good. Dominances were clearly distinguishable by all models (Fig. 5a,b,c&d). In contrast, they differed strongly from dominances deduced from the simple micro- and nanoplankton data (Fig. 3a).

In order to evaluate the accuracy of the determined Chla vs. marker pigment ratios in the Baikal water they were compared to mean ratios of strains from European lakes and isolated strains from Lake Baikal. The relationship of fucoxanthin and Chlc fitted very well to these reference values, whereas we found some discrepancies for Chlorophyceae and Cyanobacteria. The Chla/zea* ratio in the Baikal samples was one quarter of that of European Cyanobacteria (Fig. 6a). While the Chla/zea* ratio of PC containing cells of Lake Baikal was similar than that of European strains, the Chla/zea* ratio of PE containing cells was only half (Fig. 6a). Grown under nutrient limitation the Chla/zea* ratio of this latter group was nearly the same than that of the Baikal samples (Fig. 6a).

The Chla/Chlb ratio of the Baikal samples was slightly lower than that of European strains, but this difference was minimal when the Baikal samples were compared to Baikal strains (Fig. 6b). The Chla/lutein ratio was higher in Baikal samples compared to the mean of 15 European and one Chlorophyceae APP strain from Lake Baikal, but was nearly the same as the ratio of an isolate of *Monoraphidium sp.* from Lake Baikal (Fig. 6b). Nevertheless, whereas in the south and central basin and at Posolski bank the lutein/Chlb ratio was about 0.44 mol mol^{-1} it was only 0.26 mol mol^{-1} in the north basin which is an unusually low ratio for Chlorophyceae.

The extreme Chla/violaxanthin ratio of lake samples indicates an abundant presence of Eustigmatophyceae since their Chla/ violaxanthin ratio was even lower (Fig. 6b).

Table 3. (a) Chla vs. marker pigment ratios calculated by multiple linear regression through the origin and with the CHEMTAX program (n=89). Zea is the cyanobacterial zeaxanthin only (see text). (b) Marker pigment vs. biovolume ratios calculated by simple linear regression through the origin. The contributions of the Bacillariophyceae plus Chrysophyceae (BacillChrys.) were divided by multiple linear regression based on the amount of total fucoxanthin and the biovolumes of Bacillariophyceae (Bacill.) and Chrysophyceae (Chrys.). (c) Chla vs. marker pigment ratios calculated by multiple linear regression and with the CHEMTAX program including Eustigmatophyceae as fourth group (n=89). Viola* is the eustigmatophycean violaxanthin only (see text).*

	MLR			limits of 95% CI			CHEMTAX	
	µg µg^{-1}	r^2	significance	lower	upper	partial corr.	µg µg^{-1}	r^2
a)								
Chla/Fuco	2.61		p<0.01	2.43	2.80	.948	1.99	
Chla/Lutein	6.33	.983	p<0.01	5.30	7.36	.793	9.26	.952
Chla/Zea*	.931		p<0.01	.811	1.05	.855	.989	
Chla/Chlc	9.77	.915	p<0.01	7.42	12.1	.564	11.9	.884
Chla/Chlb	3.84		p<0.01	2.65	5.03	.661	6.86	
b)								
BacilChrys./Fuco	2.69	.672	p<0.01	1.82	3.56	.829		
Chloro/Lutein	1.88	.672	p<0.01	1.27	2.49	.830		
Cyano/Zea*	.524	.907	p<0.01	.446	.603	.955		
Bacill./Fuco$_{Bacill}$	.147	.702	.088	-.027	.322	.567		
Chrys./Fuco$_{Chrys}$	1.16		.063	-.081	2.40	.606		
c)								
Chla/Fuco	2.43		p<0.01	2.19	2.67	.908	2.23	
Chla/Chlb	2.52	.979	p<0.01	1.95	3.10	.683	3.74	.964
Chla/Zea*	1.11		p<0.01	.992	1.23	.897	1.02	
Chla/Viola*	5.57		p<0.01	3.30	7.85	.683	4.67	
Chla/Chlc	8.49	.932	p<0.01	6.37	10.6	.648	13.88	.904

The presence of Eustigmatophyceae is also suggested by the record of vaucheriaxanthin traces, their marker pigment (Table 2). Finally, the presence of this easily overlooked group could be demonstrated by their isolation from Lake Baikal water samples. The isolated strains belong to the group of eucaryotic APP and resemble *Nannochloropsis limnetica* described first by Krienitz et al. (2000). Since in the south the violaxanthin content was highest, vaucheria-xanthin was detected and the eucaryotic APP was most abundant, a higher contribution of Eustigmatophyceae in this part of the lake could be assumed.

The Eustigmatophyceae were therefore included in the contribution to the Chla-model considering the eustigmatophycean part of violaxanthin as difference between the total violaxanthin and the chlorophycean part (Table 3c). The chlorophycean part of violaxanthin was estimated as being 15% of Chlb (Nicklisch and Woitke 1999). For this model Chlb should be used as marker for Chlorophyceae instead of lutein since Eustigmatophyceae do not contain Chlb, but stressed cells can contain lutein. Additionally we cannot exclude that a derivative of vaucheriaxanthin co-eluted in HPLC with lutein. Although the coefficient of determination (r^2) of this model was high, the prediction of the total Chla was slightly less accurate. Again, the factors calculated with the CHEMTAX program differed from those calculated by MLR (Table 3c), but the estimated contributions to Chla were similar in both calculations.

DISCUSSION

The average phytoplankton biovolume of nearly 0.9 mm^3 l^{-1}, exceeded values of biovolume or fresh weight (equal to biovolume) reported in former studies (Bondarenko et al. 1996, Popovskaya 2000, Goldman & Jassby 2001). The most prominent difference was the much higher biomass in the north basin observed in July 2001, although biovolume in the different regions is known to vary greatly from year to year (Popovskaya 2000).

The latitudinal differences of the species composition and of cell sizes found in July 2001 reflected seasonal patterns: the southern part of the lake showed a summer community, whereas the northern part showed components of the usual spring community. Popovskaya (2000) stated in her review that after Chrysophyceae and cysts, the Baikal summer phytoplankton was usually dominated by small centric Bacillariophyceae, similar to our findings in the south basin. In contrast, the north basin was dominated by very large centric Bacillariophyceae, notably *Aulacoseira baicalensis*. This species and the other relatively common *Aulacoseira* species, *A. skvortzowii*, generally formed large blooms in spring but gradually

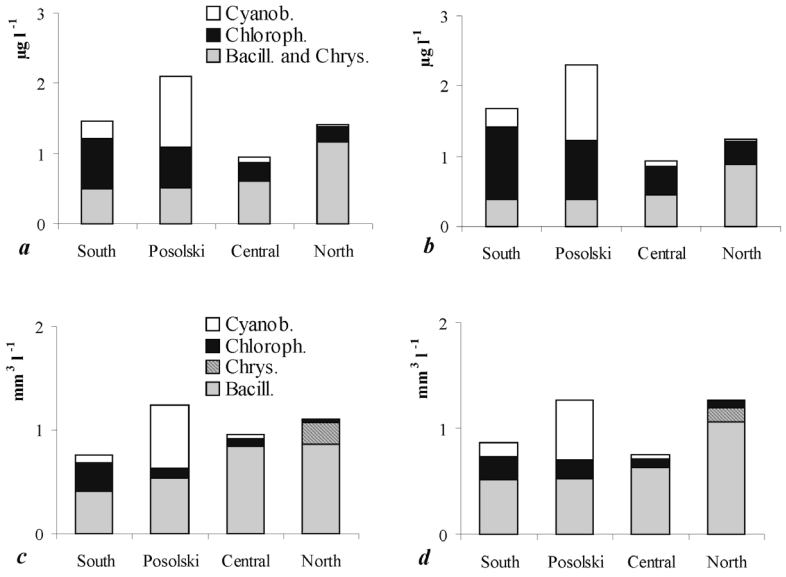

Figure 5. Contribution of the different phytoplankton groups - considering all samples, which were also microscopi-cally analysed – (a) to the total Chla, based on fac-tors calculated by MLR (shown in Table 3a), (b) to the total Chla, based on factors calculated by CHEMTAX (shown in Table 3a), (c) to the total biovolume based on fac-tors calculated by simple linear regres-sion (shown in Table 3b), (d) to the total biovolume based on cell counts ta-king into account the phytoplankton (>3µm) and the APP (see also Fig. 2 & 3). Abbreviations: Bacill. = Ba-cillariophyceae, Chrys. = Chrysophy-ceae, Chloroph. = Chlorophyceae, Cyanob. = Cyanobacteria.

disappeared in summer (Kobanova 2000, Richardson, Gibson & Heaney 2000).

The APP reached nearly 20% of the total biovolume. The high contribution of APP in the south and at Posolski bank confirmed findings of Boraas et al. (1991) that about half of the Chla in the south basin, including the Selenga delta, originated from cells smaller than 5 µm. The contribution of APP to the primary production was probably even more important (Votintsev, Meshcheryakov & Popovskaya 1972). Neglecting the contribution of APP would clearly lead to a false interpretation of the summer community in Lake Baikal.

Similar to reviews for marine and freshwater systems (Søndergaard 1991) the relative importance of APP in Lake Baikal is highest in summer (Votintsev et al. 1972, Popovskaya 2000). Therefore, the assumption that latitudinal variations reflected seasonal patterns was emphasized by the decrease of APP from south to north in July 2001. Nevertheless, this decrease of APP from south to north contradicted findings of Popovskaya (2000) that the maximum APP growth is typical for the north basin. The cell number of cyanobacterial APP in July 2001 (1.9*105 cells ml-1) was higher than mean values reviewed by Popovskaya (2000) as lake average (2-80*103 cells ml-1) but similar to the maximum abundance of 1.2*105 cells ml-1 reported by an early study of Votintsev et al. (1972).

Only rough indications such as "abundant" could be found in the recent literature about APP of the north and central basin (Bondarenko et al. 1996), but few studies were available for the south. Considering only the southern part of the lake, including Posolski bank, the cell numbers of cyanobacterial and eucaryotic APP ($3.8*10^5$ and $0.08*10^5$ cells ml^{-1}, respectively) in July 2001 were similar to those found by Goman (1971), Boraas et al. (1991), Nagata et al. (1994) and Bondarenko et al. (1996). Direct comparisons with these data were difficult because of different cell sizes, and because some of the former studies made no reference to group or size specification at all.

Traditional measurements like Chla determination can be made with improved precision using HPLC (Jeffrey et al. 1999). The mean Chla concentration (1.35 µg l^{-1}) was high in July 2001. Usually mean summer Chla concentration in the 0-50 m layer of Lake Baikal was below 1 µg l^{-1} (Kozhova et al. 1985, Kozhova 1987, Kozhova & Izmest'eva 1998), although higher concentrations have been reported, particularly in those areas influenced by river inputs, such as the Selenga shallow waters, where Chla concentrations up to 5 µg l^{-1} were found (Kozhova et al. 1985, Boraas et al. 1991, Kozhova & Izmest'eva 1998). In our study this region also showed highest Chla concentrations. Probably, nutrients carried by the Selenga River as well as the longer growth period mentioned by Popovskaya (2000) influenced the Chla concentration at these stations. Summer Chla concentrations are therefore strongly dependent on sample location in Lake Baikal.

According to Rodriguez et al. (2002) HPLC is especially useful when APP contribute a large proportion of the phytoplankton community. The phytoplankton assemblage was described very accurately based on marker pigments. In general, the estimated contribution to Chla and biovolume by multiple or simple linear regression showed good correspondence to the results of microscopic counts. The contribution to Chla-model was processed with a correlation value (r^2) of 0.98 and the calculated Chla in each basin deviated from the measured Chla by less than 7%. Therefore, it can be assumed that environmental changes had only little effect on the marker pigment vs. Chla relationships and that the species within a taxonomic group had very similar marker pigment vs. Chla relationships.

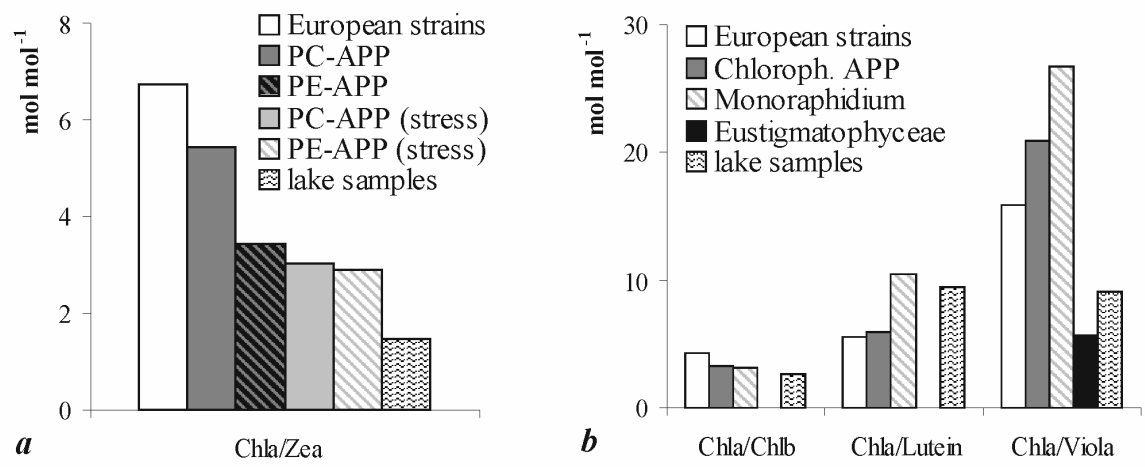

Figure 6. Comparison of Chla vs. marker pigment ratios from European strains, Baikal strains and Baikal water samples: (a) Chla vs. zeaxanthin: Comparison of 5 cyanobacterial APP strains from European lakes, new isolated cyanobacterial APP strains from Lake Baikal and Baikal water. The cyanobacterial APP of Lake Baikal were differentiated into Phycocyanin (PC) and Phycoerythrin (PE) containing cells. Baikal cultures that experienced nutrient deficiency or high light stress during growth were reported too. (b) Chla vs. marker pigments for Chlorophyceae: Comparison of 15 Chlorophyceae strains from European lakes, new isolated Chlorophyceae strains of Lake Baikal (chlorophycean APP and Monoraphidium sp.), new isolated Eustigmatophyceae and Baikal water samples.

Estimates of the contribution of different phytoplankton groups were also accurate, although slightly less exact than the MLR model, when processed by the CHEMTAX factor analysis (r^2=0.95). Since it was launched in 1997 this program has been applied successfully to different oceanic regions (Mackey et al. 1996 & 1998, Wright et al. 1996, Rodriguez et al. 2002) and also to Wisconsin lakes (Descy et al. 2000) and is now confirmed to be applicable to Lake Baikal.

However, there were some discrepancies. The MLR and the CHEMTAX models assume that all algal groups identified in the samples were included into the calculations. However, only the CHEMTAX model was improved including Eustigmatophyceae as a fourth group, whereas the MLR model , was then less exact. Groups or pigments that occurred only in very low concentrations were not usefully included in both analyses. Hence the contribution of the less abundant groups could only be estimated directly from marker pigments or by cell identification and quantification. An advantage of the CHEMTAX program in previous studies was that it could separate algal groups with the same marker pigments, such as Bacillariophyceae and Chrysophyceae, based on differences of the initial ratios between both groups (Mackey et al. 1996 & 1998, Wright et al. 1996, Rodriguez et al. 2002). However, an exact knowledge of initial ratios of the local species is a prerequisite for reliable results. Initial ratios reported for oceanic species (Mackey et al. 1996) were obviously not suitable here. Pigment analyses of isolated Chrysophyceae and other species will be necessary in future to improve the CHEMTAX calibration.

The contribution to the biovolume-model was less exact than the contribution to Chla-model, and correlation values (r^2) of only 0.67 were reached. But from the present data set it cannot be deduced if changes within the species or within the species composition were the cause. The shape of the contribution to the Chla plot and that of the contribution to biovolume will only be the same when the Chla content per unit biovolume is constant.

Comparing the contribution to Chla and to biovolume models results in an apparent overestimation of the Chlorophyceae and an underestimation of the Bacillariophyceae since the mean Chla content of the former group is higher due to the chlorophyll a/b antennae (Reynolds 1984, Wilhelm et al. 1991). According to the CHEMTAX results, the ratio of the total Chla vs. chlorophycean Chla was lowest compared to the ratios of Bacillariophyceae and Cyanobacteria. These findings confirmed the results of Soma et al. (1993) where measured Chla could be explained by the Chla calculated from carotenoids except for those samples in which green algae were dominant. In these cases total Chla was overestimated.

Bacillariophyceae and Chrysophyceae showed an inverse relationship: they were apparently underestimated by the pigment-based MLR model compared to the counts and to the pigment-based simple linear regression model. Woitke et al. (1996) found the same discrepancies for similar models and concluded that they were caused by different Chla contents of the Chlorophyceae and Bacillariophyceae. Compared to the Chlorophyceae, the ratio of the total Chla vs. bacillariophycean Chla was higher when calculated by the CHEMTAX software. Nevertheless, an overestimation of the bacillariophycean biovolume is also possible when calculating the biovolume from the cell number because of the variable thickness vs. diameter ratio

of the silica valves. Rodriguez et al. (2002) also found discrepancies for the Bacillariophyceae contribution derived from CHEMTAX calculations compared to cell counts, suggesting changes of in situ pigment ratios in Bacillariophyceae with different cell sizes. Cyanobacteria were assumed to be overestimated as their Chla content is low and the ratio of the total Chla vs. cyanobacterial Chla was high. But this overestimation could not be confirmed by comparing the contribution to Chla and contribution to biovolume models.

Calculated Chla vs. marker pigment and biovolume vs. marker pigment ratios for fucoxanthin, Chlc, lutein and Chlb fitted well to those found in Bacillariophyceae, Chrysophyceae and Chlorophyceae cultures reported in this paper and by Wood (1979), Wilhelm et al. (1991), Woitke et al.(1996) and Nicklisch & Woitke (1999). For calculations of the contribution of Cyanobacteria to Chla the choice of the right marker pigment is species-specific. It could be oscillaxanthin or myxoxanthophyll in lakes with a dominance of *Planktothrix* sp. (Quiblier et al. 1994), echinenone for a community with different nano- and microplanktonic species (Woitke et al. 1996) or zeaxanthin at a dominance of cyanobacterial APP, as in this paper.

Discrepancies between cultures and lake samples were found for the Chla/zeaxanthin ratio. The high zeaxanthin content of Lake Baikal´s water could be explained by the presence of PE-containing APP, especially as the zeaxanthin concentration increased in cells suffering from nutrient or light stress (Fig. 6a). As Lake Baikal is oligotrophic and therefore certainly sometimes nutrient limited, and had a secchi depth of up to 30 m, both conditions could be important in the upper 30 m of the water column.

The unusual violaxanthin concentration could be explained by the presence of other violaxanthin containing groups besides Chlorophyceae. Chrysophyceae can also reach Chla/violaxanthin ratios of 5.8 (Mackey et al. 1996), but none of the Chrysophyceae isolated from Lake Baikal had violaxanthin, so no comparison was possible. Xanthophyceae have also Chla/violaxanthin ratios of up to 4.8 (Krasnovská, Masarovicová & Hindák 1994). According to Kozhova & Izmest'eva (1998) five Xanthophycae species have been described from Lake Baikal (living in river mouths) but they were not found microscopically in our samples. A very high violaxanthin content could be found in the green (eucaryotic) picoplanktonic Eustigmatophyceae isolated from Lake Baikal in March 2002 in the south basin and in July 2002 in the north basin. The taxonomic identification of this group that had not been described in Lake Baikal until now was done by comparison of the pigment composition with that of *Nannochloropsis limnetica* published by Krienitz (2000).

The models presented offer a useful approach to quantitative determinations of the summer assemblage of Lake Baikal, but the importance of microscopic checks for a right interpretation of a broad pigment sample set was also demonstrated. Pigment analysis can also contribute to the knowledge of groups such as Eustigmatophyceae, which cannot be reliably identified microscopically. The disadvantage of pigment analysis that they cannot distinguish between genera or even species should be less important since most former studies of phytoplankton have drawn its main conclusions based only on algal groups (cf. Popovskaya 2000). In comparison with the microscopic determination of the biovolume, the HPLC based pigment determination has the strength that Chla is closer related to primary production than biovolume (Kiefer & Mitchel 1983), and that the total Chla was successfully used as a measure of biomass in many limnological studies.

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APPENDIX B

Fietz et al. (submitted)

Journal of Phycology (awaiting editor´s decision after revision)

First record of *Nannochloropsis limnetica* (Eustigmatophyceae) in the autotrophic picoplankton from Lake Baikal

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ABSTRACT

Three new strains of eukaryotic picoplankton, isolated from Lake Baikal, were identified as *Nannochloropsis limnetica* Krienitz, Hepperle, Stich & Weiler. To date, *N. limnetica* had only been detected in small German and North American inland water bodies. On determination of the 18S rDNA sequence, the three new strains were found to be identical to each other as well as to the type strain KR 1998/3 (GenBank Acc. No. AF251496). RAPD-PCR revealed that the genotypes were different, although the Baikalian eustigmatophycean strains were more similar to each other compared to the type strain KR 1998/3 from Germany. Ecophysiological differences were also evident between the new strains from Lake Baikal and the type strain from growth rate determinations. The morphological characteristics were similar to that of a previous description of the species. However, while the cells of Eustigmatophyceae usually propagate by autosporulation, in these newly detected species germination of single daughter cells from thick-walled cells were observed for the first time. Based on pigment analysis, the occurrence of Eustigmatophyceae in Lake Baikal was estimated. Eustigmatophyceae were established to be a common member of the phytoplankton community of this large oligotrophic Siberian lake and occurred throughout the year, even under the ice cover during winter. Moreover, they peaked during early summer and in the South Basin. Hence, the widely accepted opinion that Chlorophyceae solely comprise the eukaryotic picoplankton should be changed and consider the Eustigmatophyceae.

INTRODUCTION

The widespread occurrence of eukaryotic, autotrophic picoplankton in Lake Baikal was previously established using light and epifluorescence microscopy (Boraas et al. 1991, Nagata et al. 1994, Belykh and Sorokovikova 2003, Fietz and Nicklisch 2004). However, to date, identification of Baikalian eukaryotic picoplanktonic species is still very rare (Belykh et al. 2000) and the Chlorophyceae were suggested to dominate the eukaryotic picoplankton of Lake Baikal (Nagata et al. 1994, Semenova and Kuznedelov 1998, Belykh et al. 2000). A chlorophycean strain from Lake Baikal was identified as *Choricystis minor* (Skuja) Fott by 18S rDNA sequencing. (Belykh et al. 2000). Moreover, due to a high violaxanthin content and a very low Chla/violaxanthin ratio in Lake Baikal, one would expect Eustigmatophyceae to be present in the phytoplankton (Fietz and Nicklisch 2004), although none have as yet been described (Kozhova 1987, Bondarenko 1995, Kozhova and Izmest'eva 1998).

Eustigmatophycean picoplankters exhibit a simple morphology, but they have unique ultrastructural features and photosynthetic pigments (Andersen et al. 1998, Krienitz et al. 2000). To accurately determine the composition of eukaryotic picoplankton communities, Hooks et al. (1988) suggested that microscopic observations should generally be complemented by HPLC-aided pigment analysis. Eustigmatophyceae are well known from marine systems (Volkman et al. 1993, Gladu et al. 1995, Andersen et al. 1998, Lubián and Montero 1998, and others), but only a few studies have been carried out in freshwater (Krienitz et al. 2000, Phillips and Fawley 2000, Fawley et al. 2004). However, Krienitz et al. (2000) described a new species, *Nannochloropsis limnetica* Krienitz, Hepperle, Stich and Weiler, from a hypertrophic freshwater pond, which was also found in a polytrophic lake in Germany.

Here, we characterize three new eustigmatophycean strains isolated from Lake Baikal in regard to their morphology, growth rates, pigment composition, fluorescence and absorption characteristics. Genetic similarities of these strains were established by RAPD-PCR and nuclear encoded 18S rDNA sequence analyses. Finally, we estimated the regional and seasonal occurrence of eustigmatophycean picoplankton in Lake Baikal from pigment data.

METHODS

Sampling. Water samples were collected in the main basins of Lake Baikal (South, Centre and North) and in the Selenga Delta during cruises within the framework of the CONTINENT project in July 2001, March 2002, July 2002 and July 2003 (EVK2-CT-2000-0057). Water samples were collected from 0.5 m, 5 m, 10-20 m, 20-30 m and/or 45-85 m water depths at all three sites and on all aforementioned dates. Samples were also collected biweekly by members of the Scientific Research Institute of Biology, State University Irkutsk from May 2002 to June 2003 at 5 m depth, 2.8 km offshore from Bolshy Koti near the western shore of the South Basin.

Isolation of algae. Diluted subsamples (containing 50 particles with chlorophyll fluorescence per 50 µL) from water samples taken in March and July 2002 were streaked on 0.8 % agar plates containing mineral nutrient solution complemented with vitamins. Agar Noble (Difco Lab., Detroit, Michigan, USA) was rinsed twice with supra pure water. Then, a 4 % agar solution was prepared in supra pure water, autoclaved and combined with either MIIIKS or M99F nutrient solution at a ratio of 1:5. Both solutions are modifications of M III (Nicklisch 1992) and contained 0.5 mmol·L^{-1} $CaSO_4$, 0.5 mmol·L^{-1} $CaCl_2$, 0.25 mmol·L^{-1} $MgSO_4$, 0.1 mmol·L^{-1} KCl, 0.75 mmol·L^{-1} HCl, 2 mmol·L^{-1} $NaHCO_3$ as well as a trace element solution (Nicklisch 1999) added at a dilution of 1:1000. Additionally, MIIIKS contained 0.4 mmol·L^{-1} Na_2SiO_3, 0.5 mmol·L^{-1} $NaNO_3$, 0.05 mmol·L^{-1} KH_2PO_4, 0.01 mmol·L^{-1} $FeCl_3$ and 0.02 mmol·L^{-1} Na_2EDTA, whereas M99F contained 0.3 mmol·L^{-1} Na_2SiO_3, 0.2 mmol·L^{-1} $NaNO_3$, 0.01 mmol·L^{-1} KH_2PO_4, 0.002 mmol·L^{-1} $FeCl_3$ and 0.004 mmol·L^{-1} Na_2EDTA. In equilibrium with air, the pH was 8.3 ± 0.2. Finally, the vitamins cobalamin (1 µg·L^{-1}), biotin (1 µg·L^{-1}) and thiamine (100 µg·L^{-1}) were added to both solutions.

Twenty-five phytoplankton strains were isolated and stored in the culture collection of the Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany. Strains were grown under saturating nutrient (i.e. in the aforementioned solutions) and light conditions at 15° C in semi-continuous cultures (cf. Nicklisch 1992). From those strains, the three eustigmatophycean ones will be discussed here in detail: (1) strain baik03 was isolated in March 2002 from a sample collected in the South basin (104.41 °E, 51.76 °N); (2) strain baik43 from a sample collected in July 2002 in the North basin (109.00 °E, 54.08 °N); and (3) strain baik85 from a sample collected in July 2002 in the South Basin.

Light and electron microscopy. Living and formaldehyde-fixed (0.5 %) samples of cultures were investigated under a Jenalumar Contrast light microscope (Carl Zeiss AG, Oberkochen, Germany) by means of bright field illumination, epifluorescence and differential interference contrast. Staining was performed with DAPI (4',6-diamidino-2-phenyl-indol, Sigma-Aldrich Co., St. Louis, MO, USA) and Fluorescent Brightener 28 (Sigma-Aldrich Co., St. Louis, MO, USA). The Fluorescent Brightener, also named Calcofluor White (M2R powder from Polysciences or Blankophor BA from Bayer), is used as whitening agent and selectively binds to cellulose and chitin.

For transmission electron microscopy (TEM), ca. 1 mL cell suspensions were concentrated by centrifugation (10 min, 600 x g, laboratory centrifuge 203, Sigma-Aldrich Co., St. Louis, MO, USA) in 1.5 mL microcentrifuge tubes. Pellets were resuspended and fixed in freshly prepared primary fixative containing 2.5 % glutaraldehyde, 2.0 % paraformaldehyde and 3 mM $CaCl_2$ in 0.1 M Na-cacodylate buffer, pH 7.4 for 2 h at room temperature. The samples were centrifuged and the pellets were mixed with a small volume of melted 2.5 % agarose (Carl Roth GmbH & Co., Karlsruhe, Germany) in 0.1 M Na-cacodylate buffer and immediately chilled on ice. The solidified agarose was cut into ca. 1 mm^3 blocks. These were rinsed three times for 20 min each with 4° C cold 0.1 M Na-cacodylate buffer, and subsequently fixed in Karnovsky's mixture of 1 % osmium tetroxide and 1.5% potassium hexacyanoferrate (II) in double distilled water for 2 h (Karnovsky 1971). The samples were then rinsed in cold Na-cacodylate buffer solution, post-stained with 1 % uranyl acetate in 0.05 M sodium maleate buffer solution, pH 5.2 for 1 h at 4° C, dehydrated in a graded ethanol series, infiltrated, and finally embedded in Spurr's epoxy resin and polymerized for 24 h at 70° C (Spurr 1969). Ultrathin sections were cut with a diamond knife using an Ultracut S microtome (Leica, Vienna, Austria). The sections were sampled on uncoated 300 mesh grids and post-stained with uranyl acetate and Reynold's lead citrate. They were viewed in a Zeiss EM 900 electron microscope (Carl Zeiss AG, Oberkochen, Germany).

Growth rates. Cultures were grown in 500 mL Erlenmeyer flasks filled with 100 mL suspension and sealed with aluminium foil caps and mixed by circular shaking (60 ± 10 rpm) in a thermostat-controlled water bath (± 0.5° C). Illumination was supplied from the bottom by "cool white" fluorescent tubes on a 12/12 hours light/dark cycle and with a scalar irradiance of 100 ± 5 µmol quanta·m^{-2}·s^{-1}. M99F medium with or without vitamins was used as nutrient solution.

Determination of growth rates was performed in semi-continuous cultures according to the turbidostat-principle (Nicklisch 1992). First, the cultures were acclimated to the preselected conditions of temperature and light for three generation times. Biomass was measured and the culture was diluted to a constant starting concentration every two to three days. Specific growth rates were calculated from dilution rates during several weeks (Nicklisch 1999). The reported specific growth rate (µ) is the natural logarithm of biomass increase (start biomass / end biomass) normalized to time (day^{-1}).

Before the dilutions, the absorbance was determined with a photometer (type1101M, Eppendorf Inc., Hamburg, Germany) at 436 nm in a cuvette of 5 cm path-length as an optical measure of biomass concentration. Furthermore, the fluorescence signs F_o and F_m (Krause and Weis 1991) were determined with a pulse amplitude modulated fluorometer (Xenon-PAM, Heinz Walz GmbH, Effeltrich, Germany) as measures of the physiological state. By maintaining the maximum biomass below 100 µg·L^{-1} Chl*a* during cultivation,

self-shading and nutrient limitation could be excluded.

Pigment composition. 30 – 50 mL of algal cultures were filtered through 25 mm Whatman GF/F-filters. The filters were frozen at – 80° C and then freeze-dried. Pigments were extracted with dimethylformamide by vibration shaking at a frequency of 2000 min^{-1} for 1.5 h with a supplement of glass beads (0.75 – 1 mm). The extract was centrifuged for 20 min at 2500 g in a cooled centrifuge at 4° C (Biofuge Fresco, Heraeus Instruments, Hanau, Germany). The separation, identification and quantification of pigments were carried out according to Woitke et al. (1994) with a Waters HPLC system (Waters, Millford, MA, USA) as described previously by Fietz and Nicklisch (2004).

Fluorescence and absorption characteristics. Fluorescence of dark-adapted cells (F_o-value) was measured with a Phyto-PAM (Phytoplankton Analyzer, Heinz Walz GmbH, Effeltrich, Germany) using a diode array emitting light at four different wavelengths (470, 535, 620 and 650 nm). In vivo absorption spectra were measured with a spectrophotometer (UV-2101 PC, Shimadzu Corp., Kyoto, Japan) equipped with an integrating sphere from 400 to 750 nm.

Genetic analyses. RAPDs: About 1 mg freeze-dried (vacuum evaporator Christ, Osterode, Germany, at –20° C) algae were homogenized for 3 min in liquid nitrogen at a frequency of 1500 min^{-1} (swing–mill MM 2000, Retsch, Haan, Germany). Total DNA was extracted using the CTAB method described by Rogers and Bendich (1985). After adding 600 µL of pre-warmed (60° C) 2 x CTAB buffer and vortexing, the solution was incubated at 60° C for 30 min, then 1 volume chloroform / isoamylalcohol (24:1) was added, and the sample centrifuged at 10000 rpm for 10 min at room temperature. The upper phase was removed and the DNA was precipitated with cold isopropanol. After 10 min centrifuging at 10000 rpm at 4° C and washing with 70 % ethanol the pellet was resuspended in distilled water.

RAPD-PCR was carried out as described by Koppitz et al. (1999) in 50 µL volumes containing approximately 25 ng genomic DNA, 1 x Taq DNA polymerase buffer (Boehringer Mannheim GmbH, Mannheim, Germany), 3 mM magnesium acetate, 0.2 mM each of dATP, dCTP, dGTP and dTTP (Boehringer Mannheim GmbH, Mannheim, Germany), 20 ng primer ($[GACA]_4$ or M13: 5'-GAGGGTGGCGGTTCT) and 2.5 units of Taq DNA polymerase (Boehringer Mannheim GmbH, Mannheim, Germany). PCR amplifications were performed in a MJ Research-Multicycler PTC 200 for 40 cycles of 20 s denaturation at 93° C, 60 s annealing at 50° C and 20 s extension at 72° C, and a final extension step at 72° C for 6 min. Amplification products were separated in 1.4 % agarose gels using 1 x TAE buffer and detected by staining with ethidium bromide.

For data evaluation, band positions on the gels were determined visually and the fingerprint pattern were transformed into a binary character matrix with 1 for presence or 0 for absence of a band at a particular position in a lane. Genetic similarity (GS) was estimated according to Nei and Li (1979) as $GS = 2n_{xy} / (n_x+n_y)$ in which n_x and n_y are the total numbers of bands in the lanes of the sample x and y, respectively, and n_{xy} is the number of bands shared by the two samples.

Sequencing: Genomic DNA was extracted from small algal pellets derived from liquid cultures using DynaBeads (Deutsche Dynal GmbH, Hamburg, Germany) following the manufacturer's protocol for plant species. The genomic 18S rDNA - ITS 1 - 5.8S rDNA - ITS 2 region was amplified in 25 µL PCR reactions using primers 18S-PCR-5'F (5'-CCGAATTCGTCGACAACCTGGTTGATCCT GCCAGT-3', Hepperle unpubl.) and ITS-PCR-3'R (5'-CCCGGGGGGATCCATATGCTTAAGTTC AGCGGGT -3', Coleman et al. 1994) and puReTaq™ Ready-to-Go™PCR Beads (Amersham Biosciences, Freiburg, Germany) in a standard PCR protocol. At least two PCR reactions were pooled and DNA purified on GFX columns (Amersham Biosciences, Freiburg, Germany). Before sequencing on an ABI3100 prism sequencer (Applied Biosystems, Darmstadt, Germany), about 40 ng purified PCR product, 2 µL 0.8 pmol µL sequencing primer, and Big Dye Terminator™ Version 3.1 (Applied Biosystems, Darmstadt, Germany) were cycle-sequenced in final volumes of 10 µL using a standard cycle sequencing protocol.

Sequencing reactions were purified by ethanol precipitation using a final concentration of 66 % EtOH, rinsed in 70 % EtOH and air-dried. The pellet was resuspended in 20 µL HiDi-formamid™ (Applied Biosystems, Darmstadt, Germany) and run on a 50 cm capillary using standard settings. Partial sequences were assembled and subjected to proof-reading using SeqAssem© Version 01/2004 (Hepperle 2004a).

The obtained 18S rRNA gene sequences were compared with the *Nannochloropsis limnetica* 18S rDNA sequence (GenBank Acc. no. AF251496, Krienitz et al. 2000) using Align Version 01/2004 (Hepperle 2004b).

Occurrence in Lake Baikal. The determination of total phytoplankton and autotrophic picoplankton biomass was described in Fietz and Nicklisch (2004). Total nano- and microphytoplankton were counted according to the settling technique (Utermöhl 1958). Samples for cyanobacterial and eukaryotic autotrophic picoplankton (50 mL) were fixed with formaldehyde (0.7 % final concentration) and filtered through black Nuclepore© polycarbonate filters (0.2 µm pore size). The filters were placed on a microscope slide, briefly dried and covered with a drop of

fluorescence-free immersion oil and a coverslip. Nano- and microphytoplankton were enumerated using a light microscope and autotrophic picoplankton were counted using an epifluorescence microscope. Eukaryotic autotrophic picoplankton fluoresced deep red (>665 nm) when excited with blue or green light. Phycobilin-containing procaryotic autotrophic picoplankton were identified by their light-red autofluorescence (<665 nm) when excited with green light. Cell counts were converted to biovolume according to their size and geometric form.

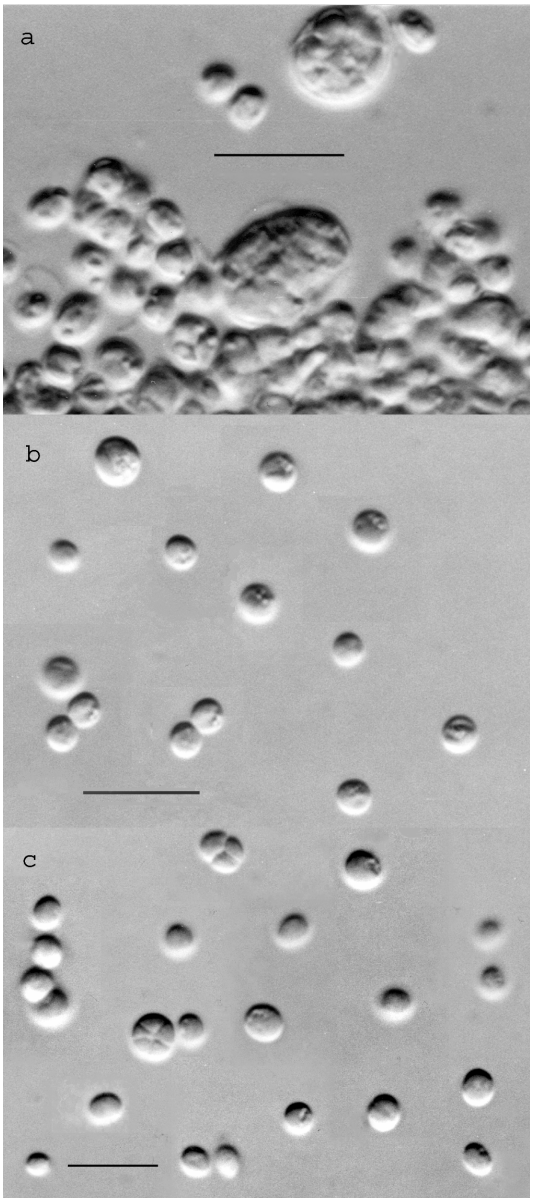

Figure 1. Light microscopic pictures (interference contrast) of new strains of Nannochloropsis *and a chlorophycean picoplankton strain (baik90) isolated from Lake Baikal. (a) baik03 with giant cells, (b) baik85, (c) baik90. Scale bar, 10 µm.*

Based on the pigment data set (n=89) of water samples collected in Lake Baikal in July 2001, Chl*a*/marker pigment ratios were calculated by multiple linear regressions as described by Fietz and Nicklisch (2004). The ratios were checked by the CHEMTAX matrix factorisation program. These Chl*a*/marker pigment ratios allow us to calculate the contribution of the distinct chemotaxonomic groups to the total Chl*a*, and thereby to estimate the phytoplankton composition of the standing crop. The final regression equation was: total Chl*a* = 2.43 ·Fuco+2.52 ·Chl*b*+ 1.11 ·Zea*+5.57 ·Viola*, where Fuco (fucoxanthin) was the marker pigment of Bacillariophyceae and Chrysophyceae, Chl*b* was the marker pigment of the Chlorophyceae, Zea* was the marker pigment of cyanobacterial picoplankton, and Viola* was the marker pigment of Eustigmatophyceae. Zea* included only the cyanobacterial part of zeaxanthin, which was at least 94 % of the total zeaxanthin. Chlorophyceae might also contain low amounts of zeaxanthin (5.3 % of lutein, Nicklisch and Woitke 1999). Therefore, the calculated proportion of zeaxanthin attributed to the Chlorophyceae was subtracted from the total zeaxanthin of each sample. Similarly, the eustigmatophycean part of violaxanthin (Viola*) was calculated as the difference between the total violaxanthin and the chlorophycean part. The chlorophycean part of violaxanthin was estimated as being 15 % of Chl*b* (Nicklisch and Woitke 1999).

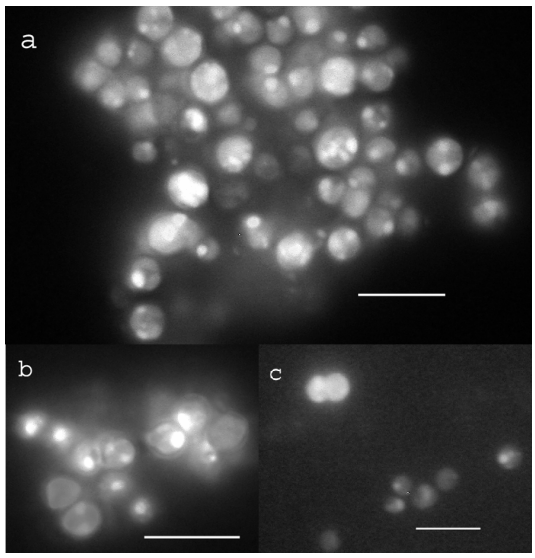

Figure 2. Epifluorescent microscopic pictures of (a) autofluorescence of chloroplasts, (b) DAPI-staining and (c) staining with Fluorescent Brightner 28 (Calcofluor White) – two cells show a stained cell wall and the others the red autofluorescence of chloroplasts. Scale bar, 10 µm

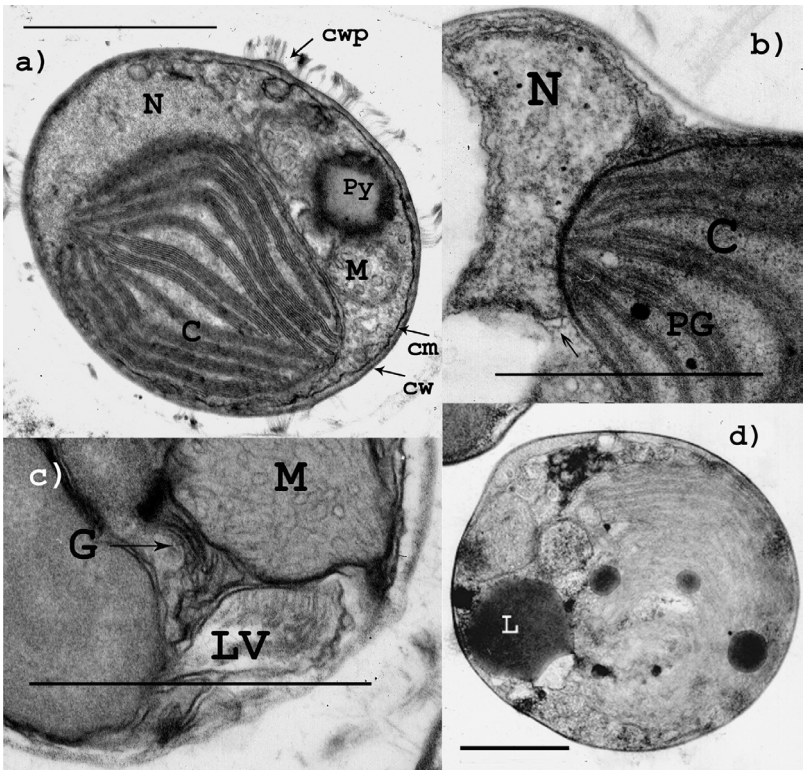

Figure 3. Ultrastructure of the Nannochloropsis strains isolated from Lake Baikal. (a) TEM images of strain baik03, (b) strain baik03 with the chloroplast endoplasmatic reticulum connected to the nuclear envelope (arrow), (c) strain baik43 with a lamellate vesicle, (d) a cell with lipid droplets. Abbreviations: C – chloroplast, G – Golgi body, LV – lamellate vesicle, L – lipid droplets, M – mitochondrium, N – nucleus, PG – plastoglobulus, PY – pyrenoid-like bodies , cm – cell membrane, cw – cell wall, cwp – cell wall papilla. Scale bar, 1 µm.

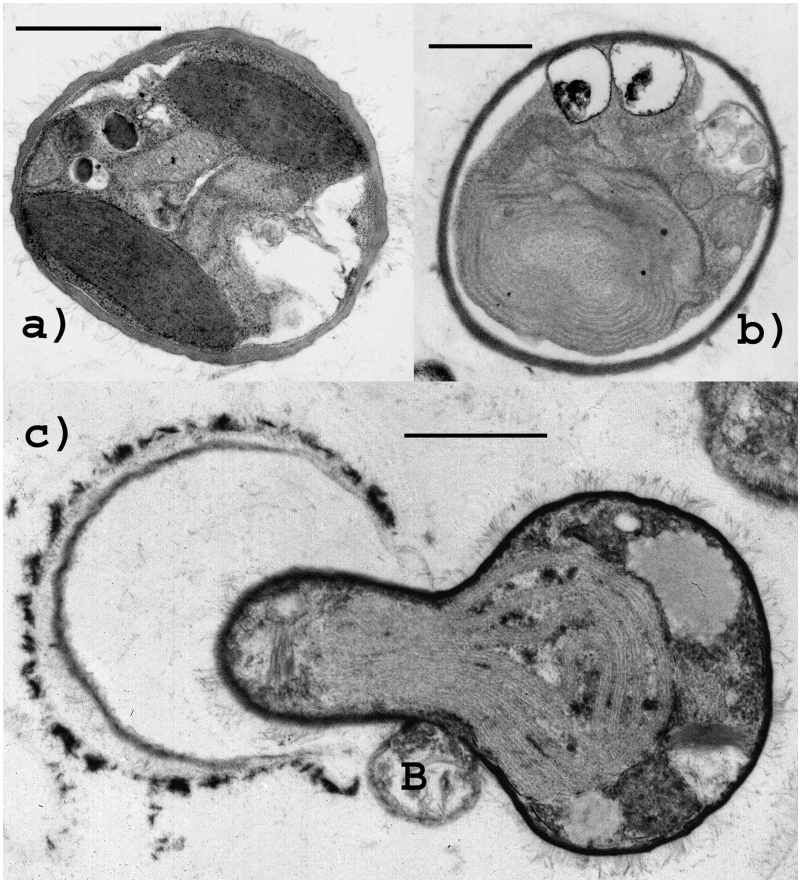

Figure 4. Strain baik43 cells with badly fixed thick cell walls (a and b) and with a germinating (assumed resting) cell (c). Abbreviations: B – bacteria cell. Scale bar, 1 µm

RESULTS

Morphology and ultrastructure. The eustigmatophycean cells in exponential growing cultures were spherical to oval with diameters of 1.5 – 6 µm (Fig. 1, a and b). Using autofluorescence and DAPIstaining, the cells were determined to contain 1 to 8 chloroplasts and 1 to 8 nuclei with numbers of nuclei correlating to cell volume (Fig. 2, a and b). Larger cells with a diameter of up to 10 µm were found, although seldom, which contained many chloroplasts and nuclei (Fig. 1a). In contrast to the chlorophycean picoplankter (baik90, Fig. 1c) small refractive, rod-like bodies were frequently visible in the eustigmatophycean cells (Fig. 1, a and b). All typical morphological characteristics of *Nannochloropsis* were found in the TEM preparations of the eustigmatophycean strains isolated from Lake Baikal: chloroplasts with up to four thylakoid double layers (Fig 3a), plastoglobuli (Fig. 3b), a chloroplast endoplasmatic reticulum connected to the nucleus envelope (Fig. 3b), lamellate vesicles and Golgi bodies (Fig. 3c), pyrenoid-like structures (Fig. 3a), lipid droplets (Fig. 3d) and cell wall papilla (Fig. 3a). A cell membrane was also well visible along with a cell wall of variable thickness (Fig. 3a). Additionally, filament-like structures were found on the outside of cell wall (Fig. 3, a and e).

Some cells were not stainable with DAPI after formaldehyde fixation, indicating a less permeable cell wall. Less permeable cell walls were also observed in TEM preparations in which the fine structures were badly preserved in some cells, indicating insufficient fixing (Fig. 4, a and b). These small cells with thick, less permeable walls were considered as resting stages, because single cells – instead of several autospores – germinated from them (Fig. 4c). The special characteristics of the cell wall of these cells was also demonstrated with the fluorochrome Fluorescence Brightener 28, which selectively binds to cellulose. Although cellulose is unique to the cell walls of Chlorophyta and Dinophyta, some cells (assumed resting stages) of our cultures were also stained by this fluorochrome (Fig. 2c). Additionally, some cell walls of chlorophycean picoplankton cultures (baik90), which should contain cellulose, were not stained by this fluorochrome. Taken together, it was therefore impossible to distinguish cells of chlorophycean from eustigmatophycean picoplankton using this staining technique.

Growth rates. The specific growth rates of the new isolated strains from Lake Baikal were 0.3 – 0.7 d^{-1} at 10° or 15° C under conditions of nutrient and light saturation (Fig. 5). However, the Baikal strains (including the chlorophycean one) had these high rates only when the nutrient solution was supplemented with vitamins, whereas the strain KR1998/3 exhibited no difference in growth whether vitamins were supplied or not. At 15° C the strain KR1998/3 grew with a significantly higher rate than all Baikal strains (Fig. 5). The differences among the Baikalian eustigmatophycean strains as well as between the Baikalian eustigmatophycean strains and the chlorophycean one were not significant at 15° C (Fig. 5). The coefficient of variation was relatively high for the strain baik43 (25 % in contrast to 8-20 % for all other strains and growing temperatures). On the one hand, this was caused by variable amounts of assumed resting stages, with Fluorescence Brightener 28; on the other hand, the growth rate determination was also influenced by a variable tendency to form small aggregates, which influenced the optical biomass measurement.

At 10° C the strain baik03 had the highest growth rate compared to the other Baikalian eustigmatopyhcean strains and the chlorophycean picoplankter (baik90) (Fig. 5). The difference between baik03 and KR 1998/3 was not significant (Fig. 5). The changing growth abilities at both different applied temperatures (10° and 15° C) were well reflected by the Q10 (Fig. 5), which was calculated based on a linear extrapolation of growth rates to a difference of 10° C. The Q10 was very high for KR 1998/3, the German strain, and very low for the Baikalian baik03, which was isolated from the water under the ice in March.

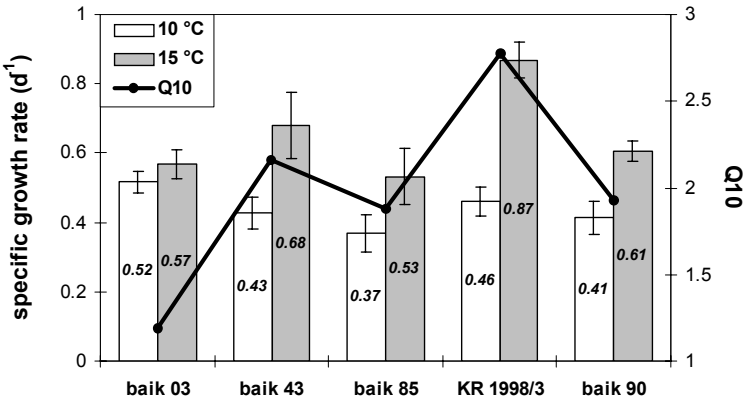

Figure 5. Specific growth rates of the new strains of Nannochloropsis limnetica *at 10 and 15° in comparison to the reference strain KR 1998/3 and a chlorophycean picoplankter (baik90). C.I.: confidence interval*

Pigment composition. The pigment composition clearly demonstrated that the eustigmatopyhcean strains differed greatly from the other phytoplankton groups (Table 1). Eustigmatophyceae lack chlorophylls other than Chl*a* and were therefore clearly distinguishable from Bacillariophyceae and Chlorophyceae. Also, Eustigmatophyceae were characterized by a very high violaxanthin content (Table 1), a pigment that is often related only to the Chlorophyceae. The vaucheriaxanthin content, including vaucheriaxanthin-like (esterified) pigments, was much lower than that of violaxanthin in Eustigmatophyceae (Table 1). Vaucheriaxanthin is characteristic for Eustigmatophyceae but occur also in Xanthophyceae (Table 1). However, Eustigmatophyceae were also easily distinguishable from Xanthophyceae by the high Chl*a*/violaxanthin ratio and absence of diadinoxanthin in Eustigmatophyceae (Table 1)

Fluorescence and absorption spectra: Fluorescence (Fig. 6, a and b) and absorption (Fig. 6, c and d) characteristics confirmed that the eustigmatophycean photosynthetic system differed from that of Chlorophyceae and Bacillariophyceae. However, both characteristics were similar for Eustigmatophyceae and Xanthophyceae. The fluorescence excitation of the Eustigmatophyceae is characterized by its maximum at 470 nm (Fig. 6a). The fluorescence at 535 nm was also high and decreased strongly towards 620 nm and 650 nm (Fig. 6a). The shape of the absorption cross-section was similar to that of the Chlorophyceae but differed in the region around 475 nm and 630 nm (Fig. 6c). Hence, Eustigmatophyceae can be distinguished from other phytoplankton groups, such as Chlorophyceae, Bacillariophyceae and also cyanobacteria (including phycobilin containing picoplankton), by use of fluorescence probes or spectral measurements.

Genetic analyses. RAPD-PCR determined that the eustigmatophycean strains (baik03, baik43, baik85) from Lake Baikal differed among one another and from the reference strain *Nannochloropsis limnetica* (German strain KR 1998/3) as well as from a macrophyte sample (*Phragmites australis* (Cav.) Trin. ex Steud.) from NE Germany (Fig. 7). The genetic similarities among the three new eustigmatophycean strains were about 55 % (Table 2), but a lower similarity of about 35 % was found between these Baikal strains and the German KR 1998/3 strain (Table 2).

The determined 18S rDNA - ITS1 - 5.8S rDNA - ITS2 sequences for the three eustigmatophycean strains from Lake Baikal were identical to each other as well as to the 18S rDNA of the type strain *Nannochloropsis limnetica* (GenBank Acc. no. AF251496, Krienitz et al. 2000). Phylogenetic

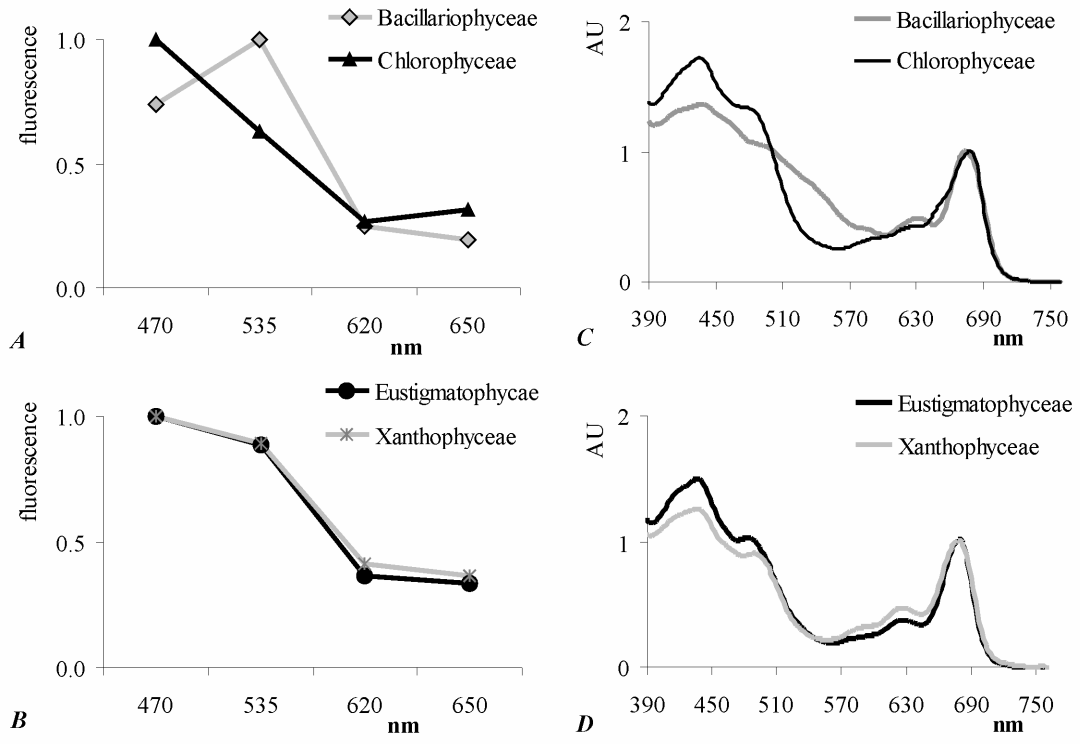

Figure 6. Fluorescence and in vivo absorption cross section of different strains isolated from Lake Baikal; (A) Fluorescence of Bacillariophyceae (strains baik03, baik43 and baik85) and Chlorophyceae, (B) Fluorescence of Eustigmatophyceae and Xanthophyceae. (C) Absorption of (strains baik03, baik43 and baik85) Bacillariophyceae and Chlorophyceae, (D) Absorption of Eustigmatophyceae and Xanthophyceae. Results are means for 5 to 20 samples taken at different times during culturing.

Table 1. Pigment content as % per Chla of selected strains isolated from Lake Baikal in July and March 2002. For the Eustigmatophyceae pigment contents in exponential growing cultures are given as well as in batch cultures with high biomasses in parenthesis. Abbrev.: Ant – antheraxanthin, ß-C – ß-carotene, Can – canthaxanthin, Ddx – diadinoxanthin, Dia – diatoxanthin, Ech – echinenon, Fuc – fucoxanthin, Lut – lutein, Neo – neoxanthin, Vau – vaucheriaxanthin, Vio – violaxanthin, Zea – zeaxanthin.

% Chl*a*	Chl*c*	Fuc	Neo	Vio	Ddx	Ant	Cal	Dia	Lut	Zea	Vau	Can	Chl*b*	Ech	ß-C
Bacillariophyceae															
Pennate[a]	14.4	64.9	-	-	8.8	-	-	-	-	-	-	-	-	-	1.5
Centric[b]	10.7	53.3	-	-	8.7	-	-	-	-	-	-	-	-	-	1.5
Chlorophyceae															
Nano.[c]	-	-	5.6	5.6	-	0.1	-	-	22.1	2.0	-	-	41.2	-	1.7
Pico.[d]	-	-	5.5	8.8	-	1.0	-	-	33.8	3.4	-	-	31.3	-	3.6
Xanthophyceae															
Heteroth.[e]	-	-	-	4.8	13.5	-	-	1.9	-	0.2	3.8	0.1	-	0.3	1.6
Eustigmatophyceae															
baik03	-	-	-	16.6 (32.1)	-	-	-	-	-	- (1.8)	5.0 (10.2)	- (0.1)	-	0.22 (6.7)	2.6 (2.4)
baik43	-	-	-	14.7 (32.5)	-	-	-	-	-	- (1.3)	4.9 (8.5)	- (0.04)	-	0.27 (0.7)	2.2 (1.4)
baik85	-	-	-	15.1 (26.2)	-	-	-	-	-	- (2.0)	4.7 (9.9)	- (0.3)	-	0.29 (1.3)	2.3 (1.8)

[a] *Fragilaria ulna* f. *acus*, *Nitzschia acicularis*

[b] *Aulacoseira* sp., *Cyclotella* sp.

[c] Nanoplankton: *Koliella* sp., *Kirchneriella* sp., *Elakatothrix* sp., *Monoraphidium* sp.

[d] Picoplankton (<3µm)

[e] *Heterothrix* cf. *solida*

analyses were therefore not performed as resulting phylogenetic tree reconstructions from 18S rDNA data would be identical to those published by Krienitz et al. (2000). No comparable analysis of the ITS1 and ITS2 sequences with other Eustigmatophyceae was possible as no ITS sequences are currently deposited in GenBank.

Occurrence. The *contribution* of eukaryotic picoplankton biomass, which included Eustigmatophyceae, to the total phytoplankton, was highest in the South compared to the Centre, North and Selenga Delta (Table 3). Eustigmatophyceae also had significantly higher contribution to total Chl*a* in samples taken from the South (15 %) compared to the North and Selenga Delta (9-10 %; Table 3). The contribution of eukaryotic picoplankton to total biomass or of Eustigmatophyceae to total Chl*a* did not show significant differences in connection with depth within the upper 30 m (Table 3). At several sites, deep Chl*a* maxima (45-85 m) were detected with a fluorescence probe. At those depths, the contribution of Eustigmatophyceae to the total Chl*a* was very low (<5 %, Table 3).

These regional and vertical differences relate to the summer communities only, since samples were collected in July 2001, July 2002 and July 2003. From May 2002 to April 2003, weekly samples were taken 2.8 km offshore from Bolshye Koti, located at the western shore of the South basin. Here, the contribution of the Eustigmatophyceae to the total Chl*a* was highest in summer (14 % from mid-July to August) and much lower in all other seasons (Table 3). The percentage contribution of eukaryotic picoplankton, studied as spot checks, appeared also to be highest from mid-July to August (Table 3). However, even under the ice, Eustigmatophyceae were present and contributed about 3 % to the total biomass and 2.5 % to the total Chl*a* (Table 3). Nevertheless, considering the regional and seasonal data, the occurrence of the Eustigmatophyceae (here, its contribution to total Chl*a*) was weakly, but significantly correlated to the temperature ($r = 0.276$, $P < 0.01$, $n = 214$, Spearman-Rho correlation).

	baik 03	baik 43	baik 85	KR1998/3	*Phragmites*
baik 03	1	0.553	0.554	0.342	0.182
baik 43		1	0.593	0.351	0.293
baik 85			1	0.346	0.244
KR1998/3				1	0.267
Phragmites					1

Table 2. Matrix of similarity coefficients of three Nannochloropsis strains (baik03, baik43, baik85) from Lake Baikal, Nannochloropsis limnetica KR1998/3 from Germany and a sample of Phragmites australis from Germany derived from PCR fingerprinting analysis with primer (GACA)4 and M13 (see Figure 7).

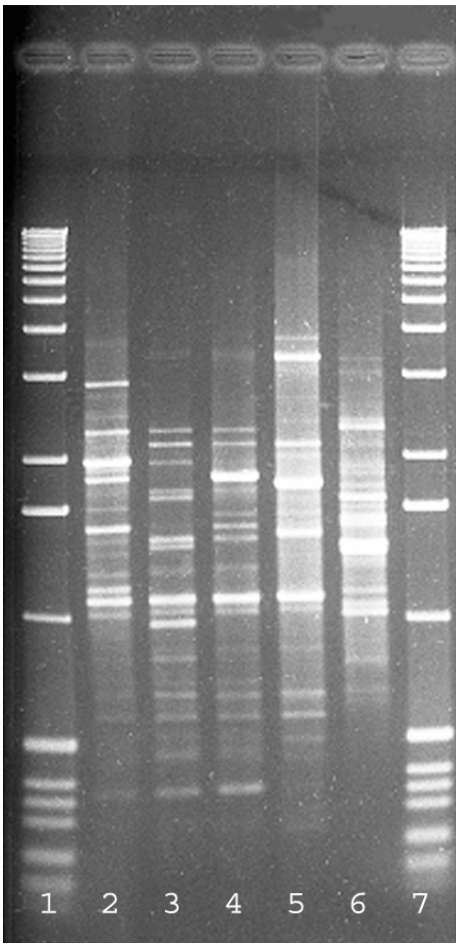

Figure 7. PCR fingerprints of Nanochloropsis *strains, primed with (GACA)$_4$. Lane1 and 7: 1 kb DNA-ladder, lane 2-4 from the left to the right: strains baik03, baik43 and baik85, lane5: KR1998/3, lane 6:* Phragmites australis.

DISCUSSION

The determined 18S rDNA sequences were identical for all three Baikalian eustigmatophycean strains as well as to the previously published *Nannochloropsis limnetica* sequence (Krienitz et al. 2002). Therefore, we conclude that the Baikalian eustigmatophycean strains belong to the species *Nannochloropsis limnetica* Krienitz et al. (2001). However, the PCR clearly showed that the genotypes of these strains were not identical either among the strains isolated from Lake Baikal or between these strains and the German strain KR 1998/3. Nevertheless, the genotypes of the Baikalian eustigmatophycean strains were more similar to each other than to the reference strain KR 1998/3.

Interestingly, *Nannochloropsis limnetica* was identified in a hypertrophic pond and a polytrophic lake in Germany (Krienitz et al. 2000), in different lakes of North America (Fawley and Fawley 2004, Fawley et al. 2004) and in the oligotrophic to mesotrophic regions of Lake Baikal. However, analyses of the genotypic and ecophysiological differences between the strains established that distinct ecotypes exist. ´Ecotypes´ describe genetically determined differences between populations within a species that reflect local matches between the organisms and their environments (Turesson (1922) in Begon, Harper and Townsend 1996).

Fawley and Fawley (2004) and Fawley et al. (2004) detected seven different genotypes of *Nannochloropsis* in lakes of Arrowwood National Wildlife Refuge, North Dakota and Itasca State

	Region	**South Basin**	**Central Basin**	**North Basin**	**S Delta**
A	Temperature (°C)	8.4	6.5	5.5	9.9
	95 % C.I.	*<7.6; 9.2>*	*<6.1; 6.9>*	*<4.8; 6.3>*	*<9.0; 10.8>*
B	% of total biomass	21.3	2.9	3.9	7.8
	<min; max>	*<5.7; 68.3>*	*<1.2; 11.3>*	*<0.4; 15.0>*	*<2.2; 28.7>*
C	% of total Chl*a*	15.3	13.5	8.6	10.0
	95 % C.I.	*<11.8; 18.8>*	*<10.2; 16.7>*	*<7.1; 10.1>*	*<8.3; 11.7>*
	Depth	**0.5 m**	**5 m**	**10-30 m**	**>45 m**
A	Temperature (°C)	10.2	9.1	6.6	5.2
	95 % C.I.	*<8.9; 11.6>*	*<8.4; 9.8>*	*<6.1; 7.1>*	*<4.0; 6.4>*
B	% of total biomass	n.d.	5.8	7.1	n.d.
	<min; max>	-	*<0.1; 68.2>*	*<0.1; 29.4>*	-
C	% of total Chl*a*	10.3	13.3	10.9	4.2
	95 % C.I.	*<5.8; 14.8>*	*<11.5; 15.1>*	*<9.1; 12.8>*	*<0.5; 7.9>*
	Season	**May - June**	**July-Aug.**	**Aug.-Nov.**	**Feb. – Apr.**
A	Temperature (°C)	3.5	11.6	10.3	0.4
	<min; max>	*<2.2; 5.0>*	*<6.2; 14.2>*	*<4.4; 17.0>*	*<0.2; 0.8>*
B	% of total biomass	n.d.	45.2	10	3.4
	<min; max>	-	*n=1*	*<1.2; 19.1>*	*<1.2; 10.0>*
C	% of total Chl*a*	2.1	13.9	4.3	2.5
	<min; max>	*<0.4; 5.0>*	*<12.7; 14.8>*	*<1.7; 12.7>*	*<0; 12.0>*

Table 3. Regional and vertical (July 2001, July 2002 and July 2003) as well as seasonal variation (2002/ 2003) of A) temperature, B) contribution of eukaryotic autotrophic picoplankton, which included Eustigmatophyceae, to the total phytoplankton biomass (in %) and C) contribution of Eustigmatophyceae to total Chla (in %). Mean values with 95 % C.I. are listed where normal distributed data sets were considered, and otherwise median values with minimum and maximum were given.

Park, Minnesota; one of them possessed 18S rDNA and rbcL sequences identical to those of *N. limnetica* from Europe and the other belong to new taxa. The new types varied in both 18S rDNA and rbcL sequences and some morphological characters that distinguish them from *N. limnetica*. No type could be further differentiated by the rbcL sequence alone. These findings support the phenomenon that even though eukaryotic picoplankton exhibit a uniformed coccoid morphology, i.e. 'green balls', an extraordinarily high genetic diversity is hidden both in marine (Potter et al. 1997) and in freshwater (Krienitz et al. 1999) ecosystems. One explanation for this, is an adaptative advantage of the coccoid morphology in the ecosystem (Potter et al. 1997).

The ecophysiological difference between the genotypes of *N. limnetica* was demonstrated by different (1) growth rates, (2) Q10 values and (3) vitamin demand. The growth rate at 15° C, for example, was significantly highest for the German strain KR 1998/3 which also did not require vitamins. The Q10 was also highest for KR 1998/3, whereas it was lowest for the strain baik03. The unusual low Q10 of baik03, which was isolated from below the ice in March, could mean that its temperature optimum is between 10° and 15° C. This is nearing that of *Synechocystis limnetica* Popovskaya, a widespread cyanobacterial picoplankter in Lake Baikal, which was determined to be 8° C (Richardson et al. 2000).

The existence of distinct ecotypes may explain the occurrence of the same Eustigmatophyceae species (*Nannochloropsis limnetica*) in all seasons and regions including the cold waters in the North basin and under the ice (Table 3). Nevertheless, the most important development occurred in the warmer South basin and during the early summer. This is in contrast to observations in North America where *Nannochloropsis* are more common during cold water periods (Fawley and Fawley 2004, Fawley et al. 2004).

The morphological characteristics of the new strains of *Nannochloropsis limnetica* correspond to former descriptions concerning form, size of cells and inclusions of refractive bodies (Krienitz et al. 2000). Additionally, giant cells with diameters of up to 10 µm were found in exponential growing cultures (Fig. 1a) as well as cells with thick cell walls (Fig. 4, a and b), which were stainable with Calcofluor White (Fig. 2c), but badly stainable with DAPI and badly preserved by fixation for electron microscopy. They were considered as resting stages since the germination of single cells were observed and a higher number of such cells was found during depressed growth. The ultrastructural analyses identified lamellate vesicles in the cytoplasma (Fig. 3c) and that the chloroplast endoplasmatic reticulum was connected to the nuclear envelope (Fig. 3b); both are common characteristics in all eustigmatophycean species (Santos and Leedale 1995, Krienitz et al. 2000, Suda et al. 2002). The chloroplasts contained up to four stacked thylakoids and plastoglobuli (Fig. 3) as described by Krienitz et al. (2000), and pyrenoid-like structures and cell wall papilla (Fig. 3a) were also found as reported for *Nannochloropsis oceanica* by Suda et al. (2002). The interpretation of the pyrenoid-like structure in our material is difficult because this structure is located outside of the chloroplast and exhibits similarities to some of the 'electron-dense bodies' found in *N. granulata* Karlson & Potter (Karlson et al. 1996). We identified filament-like structures on the outside of the cell wall (Fig. 3, a and e) that, to our knowledge, have never been previously described. Their function is not yet defined. They could be involved in the formation of cell aggregates as observed in our cultures or could serve for moving of cells out of its old envelopes (Fig. 4c). Assumed resting stages and germination of single daughter cells were observed for the first time in *Nannochloropsis* as well as generally for the Eustigmatophyceae. These stages are comparable with the aplanospores of the closely related Xanthophyceae (Ettl 1978) and the germination stages of the green alga *Marvania geminata* Hindák (Hindák 1976, Sluiman and Reymond 1987).

Although distinction between chlorophycean and eustigmatophycean picoplankton using the epifluorescence microscope is not possible, more sophisticated measurements which profit from differences in absorption and fluorescence spectra can determine this (Fig. 5). Additionally, due to exceptional high violaxanthin/Chl*a* ratio and the occurrence of vaucheriaxanthin and its esters, pigment analysis also allows eustigmatophycean and chlorophycean cells to be distinguished from each other.

However, besides the Eustigmatophyceae, also Chlorophyceae, Xanthophyceae (Table 2) and a few Chrysophyceae (Mackay et al. 1996) contain violaxanthin, and Xanthophyceae also contain vaucheriaxanthin. Software algorithms, as used in the CHEMTAX matrix factorization, can also help to discriminate between chemotaxonomic groups, which contain the same marker pigment in different amounts (Mackey et al. 1996), but detailed knowledge of the phytoplankton composition and its pigmentation is essential (Fietz and Nicklisch 2004). In this study, we did not identify violaxanthin-containing Chrysophyceae, and thus, these violaxanthin-containing Chrysophyceae species might be of lesser importance in Lake Baikal. Additionally, Xanthophyceae were not detected in earlier microscopic analyses (Fietz and Nicklisch 2004). However, they are known to occur in Lake Baikal, but only in sors (locally "lagoon") and river mouths (Kozhova 1987, Kozhova and Izmest'eva 1998). Thus, the estimation of the Eustigmatophyceae occurrence, which is based on the violaxanthin/Chl*a* ratio, seems reasonable.

The most common prokaryotic autotrophic picoplankters in Lake Baikal belong to *Synechocystis limnetica* (Popovskaya 2000) and *Synechococcus* spp. (Belykh and Sorokovikova 2003), and the most

common eukaryotic picoplankters belong to *Choricystis minor* (Belykh et al. 2000). Although abundant in marine systems (Andersen et al. 1998), *Nannochloropsis* has only been rarely found in freshwater systems (Krienitz et al. 2000); however, this could be because identification might need a combination of microscopic, HPLC-aided and preferably molecular analyses (Fawley et al. 2004). The wide range of habituation of picoplankton was already demonstrated for the chlorophyte *Choricystis minor*, which is common in Lake Baikal and also found in different German inland waters along a nutrient gradient from oligotrophic to hypertrophic state (Hepperle and Krienitz 2001). However, now, it is evident that eustigmatophycean picoplankton may also be commonly found in freshwaters.

The marine *Nannochloropsis* is grown as a food source because of its high content of polyunsaturated fatty acids, particularly eicosapentaenoic acid (Sukenik et al. 1993). The German type strain (Krienitz et al. 2000) as well as the Baikalian strains (unpublished data) of the freshwater *Nannochloropsis limnetica* are also rich in polyunsaturated fatty acids (about 25 % of total fatty acids). Nevertheless, the content of eicosapentaenoic acid was much lower for Baikalian strain baik03 (1.6 %, unpublished data) than in the German type strain (24 %, Krienitz et al. 2000); however, it was similarly high as reported for marine strains (Sukenik et al. 1993). In contrast to the German type strain (Krienitz et al. 2000, Wacker et al. 2002), docosahexaenoic acid was found in the Baikalian strain baik03 in similar high amounts as eicosapentaenoic acid (1.3 %, unpublished data). *Nannochloropsis limnetica* is therefore very important for the food-web quality and should be included in the phytoplankton community surveys of Lake Baikal

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APPENDIX C

SUPPLEMENTARY MATERIAL

Appendix C - Tab. 1. List of nano- and microphytoplankton species found in July 2002 and at 2.8 km offshore of Bolshye Koti from May 2002 to April 2003.

Bacillariophyceae
Asterionella formosa Hass.
[e]*Aulacoseira baicalensis* (K. Meyer) Simonsen (=*Melosira baicalensis* (K. Meyer) Wisl.)
[e]*Aulacoseira skvortzowii* Edlund, Stoermer, Taylor (=*Melosira (Aulacoseira) islandica* O. Müll.)
[e]*Cyclotella baicalensis* (K. Meyer) Skv.
[e]*Cyclotella minuta* Antip.
[e]*Cyclotella ornata* (Skv.) Flower
Cyclostephanus dubius (Fricke) Round.
Navicula sp.
Nitzschia acicularis W. Sm.
[e]*Stephanodiscus meyerii* Genkal *et* Popovskaya (=*S. binderanus* var. *baicalensis* Popovskaya et Genkal)
Synedra acus Kütz. var. *acus; Synedra acus* Kütz. var. *radians* (Kütz.) Hust.
Synedra ulna (Nitzsch.) Ehr.

Chrysophyceae
Chromulina sp. Cienk (calculated in the group of "small flagellata")
Chrysidalis sp. Schiller (in this paper *Chrysidalis sp.* unites some species including *Chrysochromulina sp.)*
Chrysococcus spp. Klebs
Dinobryon cylindricum var. *cylindricum* Imh.; *Dinobryon cylindricum* var. *alpinum* Imh.
Dinobryon sociale Imh.
Dinobryon elegantissimum (Kors.) Bourr.
Mallomonas vannigera Asmund
Pseudopedinella sp. Carter

Pyrrophyta
Ceratium hirundinella (O.F.M.) Bergh.
Gymnodinium baicalense Antip.
Glenodinium spp. Ehr.
[e]*Peridinium baicalensis* I. Kiss. et Zwetkow

Cryptophyta
Cryptomonas gracilis Skuja
Cryptomonas reflexa Marsson
Cryptomonas ovata Ehr.
Rhodomonas pusilla (Bachm.) Javorn. (=*Chroomonas acuta* Uterm.)
Rhodomonas lens Pasch. et Ruttner (=*Chroomonas sp.*)

Chlorophyta
Coelastrum sp. Nägeli
Coenochloris polycocca (Korsch.) Hindák, 1984 (=*Sphaerocystis polycocca* Korsch., *Sphaerocystis schroeteri* Chod.)
Elakatothrix genevensis (Reverd.) Hind. (=*E. lacustris* Korschik.)
Didymocystis sp. Koschikoff
Kephyrion sp. Pasch.
Koliella longiseta (Vischer) Hind. *f. longiseta; K. l. f. tenuis* Nygaard; *K .l. f. variabilis* Nygaard
Monoraphidium contortum (Thur.) Komar.-Legner. (=*Ankistrodesmus angustus* Bern.)
Monoraphidium pseudomirabile (Korsch.) Hindák et Zagorenko, 1992 (= *Ankistrodesmus pseudomirabilis* Korsch.)
Monoraphidium longiusculum (Hindák) Hindák
Tetraedron sp. Kütz.

Cyanobacteria
Aphanizomenon flos-aquae (L.) Ralfs
Anabaena lemmermannii P.Richt.
Aulosira sp.[1] Kirchn.
Cyanarcus sp. Pasch.
Lyngbya sp. C. Agardh. ex Gom.
Pseudanabaena sp.

[1] new species not yet described in Lake Baikal.
[e] marks endemic species

Appendix C - Tab. 2. Regression models to Fig. 32: power ($y = a\ x^b$) and two first order independent decay ($y = a*exp(-bx) + c*exp(-dx)$) models of the decrease in the dry matter (y= g m-2) as well as of the TOC and TN percentages (y = %) and the C/N ratio (y=mol mol^{-1}) vs. water column depth; x designates the depth in (m), r^2 the respective squared correlation coefficient and P the significance; the mooring was deployed in the South basin from March 2001 to July 2002.

	Function (y=)	**Factors**		**r²**		**P**	
		a	**b**	**c**	**d**		
dry weight	$a*x^b$	299.7	-0.09	-	-	0.69	<0.01
P=		<0.01	<0.01				
TOC	$a*exp^{(-bx)} + c*exp^{(-dx)}$	76.2	0.04	8.8	$1.5\ 10^{-4}$	0.92	<0.01
P=		0.34	0.11	<0.01	0.238		
TN	$a*exp^{(-bx)} + c*exp^{(-dx)}$	1.09	0.02	1.03	$2.2\ 10^{-4}$	0.95	<0.01
P=		<0.01	<0.05	<0.01	<0.01		
C/N	$a*exp^{(-bx)} + c*exp^{(-dx)}$	223.3	0.09	9.91	$1\ 10^{-12}$	0.50	0.05
P=		0.98	0.94	<0.01	1.00		

Appendix C - Tab. 3. Regression models to Fig. 33: single exponential ($y = a + b * exp(-x/c)$), two exponential ($y = a*exp(-x/b) + c*exp(-x/d)$), two first order independent decay ($y = a*exp(-bx) + c*exp(-dx)$) models of the decrease of the distinct pigments vs. water column depth; y designate the pigment content in (µmol m^{-2}), x the depth in (m), r^2 the respective squared correlation coefficient and P the significance; the mooring was deployed in the South basin from March 2001 to July 2002.

	Function (y=)	**Factors**		**r²**		**P**	
		a	**b**	**c**	**d**		
Chlorophyll *a*	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	115.7	1527	166.5	56.0	0.87	<0.01
P=		<0.01	<0.01	0.082	0.19		
Pheophorbide *a*	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	129.8	7580	1399	40.8	0.93	<0.01
P=		<0.01	0.67	<0.01	<0.01		
Chlorophyllide *a*	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	20.7	2184	22.7	101.2	0.72	<0.01
P=		<0.05	0.24	0.08	0.42		
Chlorophyll *c*	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	17.5	1446	43.4	74.5	0.97	<0.01
P=		<0.01	<0.01	<0.01	<0.01		
Fucoxanthin	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	60.4	1574	204.8	85.4	0.97	<0.01
P=		<0.01	<0.05	<0.01	<0.05		
Diatoxanthin	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	6.7	1179	25.4	99.0	0.98	<0.01
P=		<0.01	<0.05	<0.01	<0.01		
Alloxanthin	$a + b*exp^{(-x/c)}$	0.6	23.5	65.7	-	0.95	<0.01
P=		<0.05	<0.01	<0.01			
Chlorophyll *b*	$a*exp^{(-x/b)} + c*exp^{(-x/d)})$	3.2	2160	8.4	96.9	0.89	<0.01
P=		<0.01	0.2	<0.01	0.08		
Lutein	$a + b*exp^{(-x/c)}$	1.0	7.0	173.7	-	0.92	<0.01
P=		<0.01	<0.01	<0.01			
Violaxanthin	$a + b*exp^{(-x/c)}$	0.04	1.0	392.2	-	0.56	<0.01
P=		0.84	<0.01	0.19			
Zeaxanthin	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	4.6	1358	48. 9	39.1	0.99	<0.01
P=		<0.01	<0.01	<0.01	<0.01		
ß-carotene	$a*exp^{(-x/b)} + c*exp^{(-x/d)}$	2.6	1592	6.2	76.9	0.90	<0.01
P=		<0.01	0.08	<0.01	0.08		

Appendix C - Tab. 4. Regression models to Fig. 34: linear models for the Chl*a*/ TOC, pheophytin *a*/ TOC and pyropheophytin *a*/ TOC ratios vs. depth (y= µmol g^{-1}); x designates the depth in (m), r^2 the respective squared correlation coefficient and P the significance; the mooring was deployed in the South basin from March 2001 to July 2002.

	Function (y=)	**Factors**		**r^2**	**P**
		a	**b**		
Chl*a* / TOC	a + bx	7.2	-0.002	0.30	<0.05
P=		<0.01	<0.05		
pheophytin *a*/ TOC	a + b/x	8.3	-241.4	0.33	<0.05
P=		<0.01	<0.05		
pyropheophytin *a*/ TOC	a + b/x	0.43	-13.5	0.61	<0.01
P=		<0.01	<0.01		

Appendix C - Tab. 5. Regression models to Fig. 36: single exponential and two exponential models of the Chl*a* flux (representative of all labile pigments) and TOC/DM and Chl*a*s/DM ratios at both sites (South and North) and during both deployment periods (2001-2002 and 2002-2003); x designates the depth in (m) and r^2 the respective squared correlation coefficient; superscript asterisks mark the significances with * P<0.05, **P < 0.005, and *** P<0.001.

	Function (y=)	r^2
South mooring 2001-2002		
Chl*a* flux (nmol m^{-2} d^{-1})	241.076*exp(-x/1527)+346.9*exp(-x/56.0)	0.82^{***}
TOC/DM (g g^{-1})	0.085*exp(-x/10166)+0.58*exp(-x/25.5)	0.89^{***}
Chl*a*s/DM (µmol g^{-1})	1.87+4.33*exp(-x/75.2)	0.54^{**}
South mooring 2002-2003		
Chl*a* flux (nmol m^{-2} d^{-1})	29,13+26941/x^2	0.38^{*}
TOC/DM (g g^{-1})	0.085+0.063*exp(-x/277.6)	0.22^{*}
Chl*a*s/DM (µmol g^{-1})	0.72+554.3/x^2	0.20^{*}
North mooring 2001-2002		
Chl*a* flux (nmol m^{-2} d^{-1})	176.4*exp(-x/310.4)	0.43^{*}
TOC/DM (g g^{-1})	0.106*exp(-x/1105)	0.66^{*}
Chl*a*s/DM (µmol g^{-1})	1.89*exp(-x/374.2)	0.29^{*}
North mooring 2002-2003		
Chl*a* flux (nmol m^{-2} d^{-1})	127.8*exp(-x/173.3)	0.92^{***}
TOC/DM (g g^{-1})	0.093+0.32*exp(-x/108.6)	0.93^{***}
Chl*a*s/DM (µmol g^{-1})	6.34*exp(-x/199.2)	0.90^{***}

Appendix C - Tab. 6. Regression models to Fig. 37: linear or exponential models of pigment/TOC ratios (µmol g^{-1}) vs. water depth in the South and North basins. Curve calculations were based on mean values of the two deployment periods to simplify the visualisation; types of models were similar for both deployment periods in the respective (South or North) basin; x designates the depth in (m) and r^2 the respective squared correlation coefficient; superscript asterisks mark the significances with * P<0.01, **P < 0.005, and *** P<0.001; N designate rate constant significantly (at 95 % CI) different to that of the North, idem S to South, and idem SD to Selenga Delta.

	Function (y =)	**r^2**	
South mooring			
Pheophytin *a*/TOC	5.1+(-154.2)/x	0.43*	
Pyropheoph.*a*/TOC	0.28+(-6.42)/x	0.43**	
Chl*c*/TOC	0.77*exp(-x/1363)	0.63***	N
Fucoxanthin/TOC	1.56+2.31*exp(-x/257.4)	0.53*	
Alloxanthin/TOC	0.037+0.28*exp(-x/171.0)	0.78***	
Diatoxanthin/TOC	0.39*exp(-x/864.4)	0.58***	N
Lutein/TOC	0.085+0.12*exp(-x/205.7)	0.60***	
Zeaxanthin/TOC	0.12+0.19*exp(-x/344.8)	0.77***	
North mooring			
Chl*a*/TOC	4.88+(-0.0048)*x	0.56*	
Pheophorbide *a*/TOC	13.6+(-0.013)*x	0.79***	
Chl*a*s/TOC	21.8+(-0.019)*x	0.67*	
Chl*c*/TOC	1.20*exp(-x/171.7)	0.99***	S
Fucoxanthin/TOC	3.73*exp(-x/253.0)	0.98***	
Diatoxanthin/TOC	0.24*exp(-x/156.8)	0.87***	S

Appendix C - Tab. 7. Regression models to Fig. 40: linear and exponential models for TOC/DM ratios (mg g^{-1} DM) and pigment/TOC ratios (µmol g^{-1}) vs. depth of the oxidised layer of the surface sediment; x designates the depth in (m) and r^2 the respective squared correlation coefficient; superscript asterisks mark the significances with * P<0.01, **P < 0.005, and *** P<0.001; N designate rate constant significantly (at 95 % CI) different to that of the North, S to South, and SD to Selenga Delta.

	Function (y =)	**r^2**	
South core			
TOC/DM	34.2+(-1.10)*x	0.76***	N
Chl*a*/TOC	0.033+0.38*exp(-x/0.58)	0.96***	N, SD
Pheophorbide *a*/TOC	0.14+1.09*exp(-x/2.02)	0.80***	SD
Pheophytin *a*/TOC	0.64+(-0.036)*x	0.75***	
Pyropheoph. *a*/TOC	0.36+(-0.023)*x	0.81***	
Chl*a*s/TOC	2.32*exp(-x/6.36)	0.77***	
Chl*b*/TOC	0.098/(1+0.098*17.7*x)	0.77***	
Chl*b*s/TOC	0.14+(-0.0069)*x	0.41***	
Chl*c*/TOC	0.0044+0.050*exp(-x/0.37)	0.92***	N
Fucoxanthin/TOC	0.046*exp(-x/1.76)+0.31*exp(-x/0.26)	0.99***	
Diadinoxanthin/TOC	0.029*exp(-x/3.84)+0.062*exp(-x/0.026)	0.96***	
Lutein/TOC	0.0064*exp(-x/8.28)	0.61***	N
Canthaxanthin/TOC	0.0021+(-0.00013)*x	0.78***	

	Function (y =)	r^2	
North core			
TOC/DM	37.9+(-2.28)*x	0.96***	S, SD
Chl*a*/TOC	0.022*exp(-x/3.73)	0.84***	S
Pheophorbide *a*/TOC	0.21*exp(-x/1.89)	0.95***	SD
Pheophytin *a*/TOC	0.39*exp(x/4.04)	0.96***	
Pyropheoph. *a*/TOC	0.068*exp(-x/5.55)	0.83***	
Chl*a*s/TOC	0.66*exp(-x/3.69)	0.97***	SD
Chl*b*/TOC	0.0083*exp(-x/1.72)	0.95***	
Chl*b*s/TOC	0.080*exp(-x/4.59)	0.71***	
Chl*c*/TOC	0.017*exp(-x/2.61)	0.94***	S
Lutein/TOC	0.0011*exp(-x/1.71)	0.80***	S
Selenga Delta core			
TOC/DM	30.3+(-0.98)*x	0.97***	N
Chl*a*/TOC	0.15*exp(-x/5.56)	0.81***	S
Pheophorbide *a*/TOC	1.03*exp(-x/5.43)	0.83***	S, N
Pheophytin *a*/TOC	0.38+(-0.023)*x	0.28***	
Pyropheoph. *a*/TOC	0.66+(-0.035)*x	0.44***	
Chl*a*s/TOC	2.21*exp(-x/8.22)	0.73***	N
Chl*b*s/TOC	0.52*exp(-x/5.67)	0.48***	
Chl*c*/TOC	0.0025+(-7.5e^{-7})*x^3	0.31**	
Fucoxanthin/TOC	0.02*exp(-x/3.1)	0.86***	
Diadinoxanthin/TOC	(-0.00089)+0.015*exp(-x/4.5)	0.81***	
Diatoxanthin/TOC	0.0029+(-9.6e^{-7})*x^3	0.43**	
Lutein/TOC	0.0055+(-1.9e^{-6})*x^3	0.45***	
Canthaxanthin/TOC	0.0029+(-1.3e^{-5})*x^2	0.61***	

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Berlin, February 14, 2005 .....

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SELBSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, die Dissertation selbständig und nur unter Verwendung der angegebenen Hilfen und Hilfsmittel angefertigt habe.

Ich habe mich anderwärts nicht um einen Doktorgrad beworben und besitze einen entsprechenden Doktorgrad nicht.

Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät I der Humboldt-Universität zu Berlin.

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