Biogeosciences Discuss., 10, 2305–2344, 2013
www.biogeosciences-discuss.net/10/2305/2013/
doi:10.5194/bgd-10-2305-2013

Biogeosciences Discussions
Open Access

Phytoplankton community structure in the Lena Delta (Siberia, Russia) in relation to hydrography

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Received: 27 October 2012 – Accepted: 19 November 2012 – Published: 11 February 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

The Lena Delta in Northern Siberia is one of the largest river deltas in the world. During peak discharge, after the ice melt in spring, it delivers between 60–8000 $m^3 s^{-1}$ of water and sediment into the Arctic Ocean. The Lena Delta and the Laptev Sea coast also constitute a continuous permafrost region. Ongoing climate change, which is particularly pronounced in the Arctic, is leading to increased rates of permafrost thaw. This is likely to profoundly change the discharge rates of the Lena River and the chemistry of the river waters which are discharged into the coastal Laptev Sea, e.g. by increasing concentrations of inorganic nutrients, DOC and importantly methane. These physical and chemical changes will also affect the composition of and interactions between phytoplankton and zooplankton communities, forming the basis of the food web. However, before potential consequences of climate change for coastal arctic plankton communities can be judged, the inherent status of the diversity and linked foodweb interactions within the delta need to be established. As part of the AWI Lena Delta Programme in 2010 the phyto- and microzooplankton community in three river channels as well as four coastal transects were investigated to capture the typical river phytoplankton communities and the transitional zone of brackish/marine conditions. Most CTD profiles from 23 coastal stations showed very strong stratification. The only exception to this was a small a shallow and mixed area running from the outflow of Bykovskaya channel in a northerly direction parallel to the shore (transect 3). Of the five stations in this area three had a salinity of close to zero. Two further stations had salinities of around 2 and 5 throughout the water column. In the remaining transects on the other hand salinities varied between 5–30 with depth. Phytoplankton counts from the outflow from the Lena were dominated by diatoms (*Aulacoseira* species) cyanobacteria (*Aphanizomenon*, *Pseudanabaena*) and chlorophytes, in those stations characterized by river outflow (stations in the Lena itself and in coastal transect 3). In contrast in the stratified stations the plankton was mostly dominated by dinoflagellates, ciliates and nanoflagellates, with only an insignificant diatom component from the genera *Chaetoceros* and

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Thalassiosira (brackish as opposed to freshwater species). Ciliate abundance was significantly coupled with the abundance of total flagellates. A pronounced partitioning in the phytoplankton community was also discernible with depth, with a different community composition and abundance above and below the thermocline in the stratified sites. This work represents the first attempt at analyzing the phytoplankton structure of the region of freshwater influence at confluence Lena–Laptev sea.

1 Introduction

The Lena River is one of the largest rivers in the world. It alone is responsible for the discharge of 20 % of the total freshwater volume into the Arctic Ocean, namely the Laptev Sea (Cauwet and Sidorov, 1996). Discharge rates into the Laptev Sea are extremely variable. They are low in the winter period, but just after the snow and ice melt in spring peak discharge rates surge, reaching 60–80 000 $m^3 s^{-1}$ in June (Yang et al., 2002). The coastal Laptev Sea is therefore characterized by a complex hydrography resulting from the varying extent of the so-called region of freshwater influence (ROFI) and advection of Arctic Ocean water from the North (Gordeev, 2000). As a result of ongoing climate change, rates of permafrost thaw are also increasing, which is expected to lead to an increased discharge to the Arctic ocean (Lyon and Destouni, 2010). This is likely to have a major impact on coastal hydrography. Changed discharge patterns and general rise in air and ocean temperature could in the long run lead to stronger stratification of coastal waters (Doney, 2006) and a changed positioning and greater stability of fronts in the transitional zone between the region of freshwater influence and the open sea. Paleoecological studies using palynomorphs and diatoms as proxies have shown that considerable fluctuations in discharge from the Lena river have occurred several times during the Holocene (Polyakova et al., 2006).

The Lena is considered to be the major source of organic matter entering the Laptev Sea (Gordeev et al., 1996; Kassens et al., 1998, 1999; Lobbes et al., 2000). But while coastal erosion and fluvial transports of particulate as well as dissolved organic carbon

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into the Buor Khaya Gulf are normal processes (Charkin et al., 2011), the expected increase in discharge resulting from permafrost thaw is also likely to lead to a considerable increase in delivery of inorganic nutrients (Nowinski et al., 2008), terrigeneous DOC and POC as well as methane to coastal waters (Finlay et al., 2006). Changes in these parameters could also have profound consequences for the resident phytoplankton communities.

More pronounced stratification, keeping cells in the better illuminated surface waters could have considerable effects on local food webs via bottom-up effects, where inorganic nutrients fuel increased primary production which is then available for higher trophic levels in the water column (Doney, 2006). Increasing methane release from the permafrost could also form a substrate for methanotrophic bacteria which in turn are a food source for the microzooplankton supporting the microbial loop (Azam et al., 1983). The formation of frontal systems for instance is already known to be associated with the triggering of algal blooms and particularly in communities likely to be light limited, such as in the Arctic Ocean (Taylor and Ferrari, 2011). Moreover, increased stratification could lead to changes in production patterns, favouring the slow-growing cyanobacteria over diatoms (Oliver and Ganf, 2000; Thompson et al., 2003; Paerl, 1996).

However, in order to assess potential effects of future climate change effects such as changes in coastal water chemistry and hydrography on biological communities in the Lena Delta we first need to understand the dynamics in the present day system. In neighbouring rivers, e.g. the Yenisei diatom community composition is known to some extent and was dominated by centric taxa such as several species of the genus *Aulacoseira*, *Stephanodiscus* and *Cyclotella* species (Genkal et al., 2010). The overall diversity seemed high with more than 300 species (*chlorophyceae*, cyanobacteria, diatoms, dinoflagellates) recorded, in e.g. the Taz river in Western Siberia (Yarushina, 2008). Microzooplankton community data are also available for the Ob river (Kopylov and Kosolapov, 2011). However, no comprehensive data are yet available for the Lena Delta except a study by Tuschling (2000) in the Southern Laptev Sea and Sorokin and

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Sorokin (1996), which, however, did not refer in detail to the freshwater component of the coastal plankton (with the exception of a small number of cyanobacterial species), although this could make a significant contribution to local primary production and of course serve as a food source for coastal zooplankton.

The aim of this study was therefore not only to establish the diversity of coastal phytoplankton communities, but to also examine community composition in relation to salinity and water chemistry to identify potential links to observed patterns, which will allow us to gauge future effects of permafrost thaw on the algal community.

2 Material and methods

2.1 Sampling area

Since the major focus of our analyses was to establish the differences between biological communities in different hydrographic regimes 4 coastal transect were established (see Fig. 1, Table 1) to capture these different conditions. Two transects ran in a north-southerly direction (transects 3 and 4) while two further transects ran in an easterly (transect 1) and south-easterly direction (transect 2). Transects 3 and 4 were chosen to capture the region of freshwater input running north from the mouth of Bykovskaya channel, while transects 1 and 2 traversed the ROFI and represented the transitional zone from brackish to marine waters (see Table 1 for start and end co-ordinates of each transect). While transect 3 was very shallow (average depth 3.9 m) all other transects had an average depth exceeding 10 m (Table 1).

Additional samples were also collected from the major river channels (those that were accessible by ship): 1. Olenowskaya Channel (western delta), 2. Trofimofskaya Channel (central delta) and 3. Bykovskaya channel (eastern delta, and the main source of freshwater discharge to Buor Khaya Bay). For the purpose of this work, Sampling stations in the Lena channels will be referred to as "in the delta or delta stations",

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whereas transects 1–4 and the stations they comprise, will be referred to as the "coastal transects" or "coastal stations".

2.2 Sampling methodology

All samples were taken using small Russian vessels (RV). The four coastal transects were sampled from onboard the RV TB-0012 (29 July 2010–2 August 2010) and the delta transects on the RV P405 (4 August 2010–9 August 2010). At all stations water samples were taken from the surface water, water just above the bottom and intermediate discrete water depths ("subsurface samples"). All subsurface sampling depths were determined on the basis of CTD casts (Sea and Sun Technology GmbH) made for all coastal transect stations (T1–T4). In the delta transects, temperature, pH and dissolved oxygen were measured only manually with a pH meter and oxygen probe (WTW, multi 350i). Where stratification could be detected, samples were then taken from above and below the thermocline (see examples in Fig. 3). In total, 66 samples were collected. From the CTD casts vertical profiles for temperature, salinity and oxygen distribution were constructed using the open source Ocean Data View (ODV) software version 4.

At all sites the same basic variables were measured: Niskin bottle samples were taken to sample for CHN, chlorophyll, inorganic nutrients and biological plankton samples for manual counts. To sample the micro- and mesoplankton community more efficiently vertical hauls using plankton nets (Hydrobios, Kiel) of different mesh sizes (20 µm, 80 µm, 125 µm and 500 µm, Hydrobios – Kiel) were also carried out at all stations (mesozooplankton is examined in more detail by Abramova et al., 2012 in this issue). The nets, with the exception of the 20 µm net, were fitted with a flow meter so that the distance towed and thereby the volume filtered could be calculated, facilitating quantitative assessments of the zooplankton community. Here we will present only the phytoplankton, nutrient and physical measurements.

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2.3 Satellite imagery

Optical satellite data may provide additional information in space and time, visualizing optical quantities and hydrodynamic structures of surface waters such as fronts and eddies. The optical Ocean Colour sensor MERIS onboard the ENVISAT satellite collected cloud-free satellite data of the Buor-Khaya Bay within the timeframe of the ship expeditions on 3, 4 and 5 August 2010. The top-of-atmosphere data were processed towards bio- and geo-optical parameters using BEAM-VISAT4.9© with the MERIS Case-2 Regional Processor for coastal application (C2R) (Doerffer and Schiller, 2008, 2007). The diffuse attenuation coefficient, K is a robust calculated optical C2R parameter. The vertical attenuation of sun light with depth can be described by an exponential equation, where the coefficient K is measured within the Photosynthetically Active Radiation, (PAR), wave length region in m^{-1}. The euphotic depth, Z_{Eu}, down to which significant phytoplankton photosynthesis can occur, is the depth where the downwelling light is reduced to 1 %. and is calculated from K:

$$Z_{Eu}(\lambda) = \frac{4.6}{K(\lambda)} \mathrm{m}, \quad (1)$$

The MERIS C2R processing of the Laptev Sea region is in more detail described in Heim et al. (2012).

2.4 Chemical analyses

For chlorophyll analyses raw water samples were filtered over a Watman 0.45 µm Nylon filter. Filters were placed in 15 ml plastic Falcon tubes to which 2 ml of HPLC grade acetone was added. The filtrate was used for inorganic nutrient analyses. It was transferred to 200 ml white Nalgene vessels. Both chlorophyll filters and the water for nutrient analyses were then frozen at −20 °C and delivered to Germany in a frozen state. Upon return to the laboratory water samples for nutrients were analyzed following the method by Grasshoff (1976). Chlorophyll analyses was carried out by HPLC using the

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methods of Wiltshire (1998) and Knefelkamp et al (2007. Analyses were carried out in duplicate for both nutrient and chlorophyll samples. Not all samples could be recovered in the freight from Siberia. The actual number of samples used will be indicated in the numerical analyses.

2.5 Phytoplankton counts

250 ml of raw sample were transferred to brown glass bottles and fixed with 2 ml of neutral Lugols iodine solution. A further 250 ml of each sample was fixed with 2 ml alkaline buffered formaldehyde. The bottles were stored in the cool and dark until further analysis. For counting, samples were transferred to 25 ml Utermöhl chambers and left to settle for at least 24 h (Utermöhl, 1931; Lund et al., 1958). They were counted at ×400 magnification to also efficiently enumerate the smaller phytoplankton. This also facilitated more reliable counts of small organisms in very sediment-rich samples. Counts were carried out with a Zeiss Axiovert 135 inverted microscope with phase contrast or brightfield illumination. As most samples were extremely dense with plankton only half a slide was counted per sample in most cases. Taxa were identified at species level where possible using standard reference works by (Wehr and Sheath, 2003; Cremer, 1998; Tomas, 1997; John et al. 2011). However, many taxa could not be identified reliably to species or easily be assigned to a higher taxon. As they were nevertheless distinct, they were therefore grouped into unidentified size categories (e.g. Gymnodinaceae < 20 µm length) or on the basis of morphological characteristics such as spines. However, the aim of this work was not the construction of a complete species list. Additional taxa were only added to the species list, if they were categorically seen for the first time in a particular sample. Taxa that were identified to species level during the course of the study, but had initially only been recorded as size class, were not included in the taxa list used for the final analyses. This was to avoid bias in the calculation of diversity indices (see Sect. 2.6.2 for further information on index calculations). The species data as well as physic-chemical data have been archived in the online data repository Pangaea (http://pangaea.de). Supplementary image material from the

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taxon image catalogue has also been archived online in the online plankton information repository PLANKTON*NET (http://planktonnet.awi.de//index.php?thematicid=2076).

2.6 Numerical analyses

Multivariate community analyses were carried out using Primer V6. As a first explorative technique, to establish patterns in the phytoplankton communities, data were subjected to a non-parametric multidimensional scaling analysis. Prior to commencing the analyses the data were first log-transformed ($\log(x+1)$), to account for the strongly zero-inflation in the data set (Clarke and Gorley, 2006). Based on the log-transformed data a similarity matrix was constructed using Bray-Curtis similarities. Multidimensional scaling analysis was then carried out with the following settings: 25 restarts, a minimum stress of 0.01 and Kruskal fit scheme 1. The resulting configuration plots indicate distance between samples in terms of the similarity of their underlying species composition, i.e. samples clustered together closely on the plot have a similar composition. The lines in the plot in Fig. 10 delineate the 60 % similarity contours. These were obtained from a classification analysis on the same similarity matrix also used for the nMDS. The clusters found in the nMDS procedure were also used to subdivide the physic-chemical data into groups for significance tests of differences in individual parameters (see Results 3.1 and 3.3.1).

Univariate pairwise or group comparisons of parameters (diversity, species counts in surface vs subsurface samples), were also analyzed using non-parametric methods: Kruskal-Wallace median tests for tests between several independent groups and Mann-Whitney statistic for tests between two groups (Statistica v10, Statsoft). Non-parametric methods were appropriate in the context of the present study as the unavoidable differences in lengths and depth of transects meant that a balanced number of samples per group was not a given. Regression analyses for the relationship between the two microzooplankton groups ciliates and dinoflagellates and different potential phytoplankton preys were conducted using the software “SigmaPlot 10.0” (SYSTAT Software) under a linear model. The statistical significance of the linear regressions were tested by

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analysis of variance at a significance level of $p = 0.05$. The data points for ciliates in brackets result from a bloom (109 200 cells l^{-1}) of the mixotrophic/phototrophic ciliate *Myrionecta rubra* (*Mesodinium rubrum*) and were excluded from the regression analyses (see Figs. 9a, c, e. g).

2.6.1 Species – environment relationships

To relate the species data set to the available environmental parameters and to establish the variables with the most explanatory power, a Redundancy analysis was performed using CANOCO 4.5 software. The decision to carry out a Redundancy analysis, was taken after a preliminary detrended correspondence analysis (DCA), which determined a gradient length of 0.852 for the first ordination axis had been carried out. Such a short gradient length indicates a linear relationship between response (i.e. species) and explanatory variables (environmental factors) (Leps and Smilauer, 2007), in which case a linear method such as PCA or Redundancy analysis are the most appropriate techniques. The data were log+1 transformed prior to the analysis. To further test which physico-chemical factors are most relevant in determining the multivariate species patterns, a further Primer routine was also performed. BEST finds the best match between multivariate patterns in the sample matrix and the matrix of environmental parameters by matching sites in the data sets using a Spearman rank correlation method. Nine environmental variables and the complete species similarity matrix were included in the analysis. The similarity matrices were constructed using Bray-Curtis similarity for the species data set and Euclidean Distance for the environmental data set. Of the two analysis tools available the BIOENV tool was chosen for the present analysis. This carries out a full analysis of all possible variable combinations as opposed to stepwise tests (Clarke and Gorley, 2006).

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2.6.2 Further relationships

As a means of estimating the strength of stratification at a given station a simple stratification index was devised whereby the difference in temperature and salinity between the surface and deepest samples were calculated as:

$$\text{Stratification Strength} = (T_{\text{surface}} - T_{\text{bottom}})/D, \quad (2)$$

where T is the temperature and D the depth. For a completely mixed water column this results in an index value of zero. This is of course an oversimplification as the true relationship between temperature change and depth is not linear. The aim was simply to indicate the degree of change in temperature and salinity and therefore strength of stratification between top and bottom layer of water.

Moreover the Shannon diversity was calculated for the complete species data set at each station. Shannon diversity (H) was calculated as:

$$H = \sum_{i=1}^{R} p_i \log p_i, \quad (3)$$

where p_i is the proportion of individuals belonging to the ith species in the data set.

3 Results

3.1 Hydrography of the coastal region

The surface plots of temperature, salinity, oxygen and pH (Fig. 2a–d) provide a first indication of the complexity of the coastal hydrography in the Lena region of freshwater influence. Salinity, pH and temperature showed a separation into two zones, a near coastal region characterized by the outflow from two of the river channels (Bykovskaya and Trofimovskaya, see black arrows in Fig. 2a) and a further zone further offshore. The

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near-shore hydrographic region (particularly transect 3) had a salinity close to zero and a slightly lower pH than the region further offshore (coastal transects 1, 2 and 4). An exception was the region just north of Bykovskaya peninsula (corresponding to stations T4-1004 and T3-1002), where salinity was approximately 2. Oxygen concentrations on the other hand were rather uniform in the surface waters with percentages in excess of 90 % at all stations.

The two regions discernible in the surface plots showed striking differences in their "vertical" hydrography. Transect 1, with the exception of the station closest to the shore (T1-1001) was strongly stratified throughout (Fig. 3a, b). The same was true for transect 2. The thermocline in these two transects was located at a depth of between 4–6 m and 5–7 m, respectively. The transition was often very sharp with decreases in temperature of up to 4 degrees within 1 m of the water column (see also stratification index in Fig. 4a). In all of the shallow stations (< 5 m depth), bottom temperatures did not sink below 10 °C, while in the deep sites depth greater than 9 m, displayed temperatures below 0 °C (Fig. 3a, c, g). Although the CTD profiles of the stations in transect 3 appeared well-mixed, the top 50 cm were approximately 1.5 degrees colder than the underlying water column in three of the stations. These stations, had therefore a negative stratification index. The northern-most station in transect 3 was colder and more saline throughout indicating a transition to different water masses (Fig. 3e, f). The vertical changes in temperature and salinity are summarized in the plots of the stratification index (Fig. 4a, b).

Lastly transect 4 was strongly stratified with an abrupt transition from surface waters (6–10 degrees) to the waters below the thermocline which had temperatures at or even slightly below zero. The different water masses in transect 4 were demonstrated even more clearly by the salinity profile, which indicated the extent of the Lena river plume (freshwater) northwards and at the same time the intrusion of saline bottom waters in the northernmost station (bottom salinity 21.68 at Station T4-1005). The heterogeneity of the sampling area was also evident in the supporting satellite imagery, which indicated euphotic depths of less than 5 m for the stations in transect 3 (approximately

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corresponding to the depth of the water) and approximately 10 m in transects 1 and 2 (approximate depth of thermocline) (Fig. 5).

The physico-chemical parameters were grouped into a delta and a coast group as well as into transect groups and were tested for significant differences using Mann-Whitney U-tests and Kruskal-Wallis tests, respectively. For the physical parameters temperature and salinity and the derived stratification indices tests were significant at the 5 % level for both the Mann-Whitney test based on the two larger regions (temperature stratification: $Z = -4.981$, $p < 0.005$, salinity stratification: $Z = -6.144$, $p < 0.005$, temperature: $Z = 5.23$, $p < 0.005$, salinity: $Z = -5.38$, $p < 0.005$) and for the more detailed analysis based on transects (Kruskal-Wallis analyses: Temperature stratification: $H_{(6,N=58)} = 38.022$, $p < 0.005$, salinity stratification: $H_{(6,N=61)} = 40.43$, $p < 0.005$, temperature: $H_{(6,N=60)} = 24.98$, $p = 0.003$, salinity: $H_{(6,N=62)} = 30.001$, $p < 0.005$). The relationships between these physical conditions and the biological community will be described in Sect. 3.3.1.

3.2 Nutrient dynamics

Nutrient concentrations were examined for both, the Lena Delta proper, and the coastal region. Concentrations of nitrate and phosphate concentrations were low in both the delta and coastal stations. Significant differences only occurred in the concentrations of silicate. Silicate concentrations appeared to be generally lower in the coastal transects (varying between average values of 21.5 µmol l^{-1} in transect 1 and 24.5 µmol l^{-1} for transect 4, values averaged across all stations per transect) but the difference was only significant on the basis of delta vs coastal sites as defined by the multivariate analyses (Mann-Whitney U-test: $Z = 1.9$ $p = 0.048$). No significant differences were found when differences between transects were compared. However, despite the differences between coastal and Lena stations, the regression analysis, pooling data from all stations and depths, revealed no significant relationship between silicate concentrations and salinity (Regression analysis: $F_{1,72} = 0.31$, $p = 0.57$). There was however, a significant increase in phosphate concentration ($F_{1,57} = 22.958$, $y = 0.536x + 0.26$, $p < 0.005$)

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and nitrate concentration ($F_{1,57}$ = 71.872, y = 0.747x+0.198, $p < 0.005$) in combination with salinity, although this was also related to the often higher nutrient concentrations in the more saline deep waters.

In the delta transects (transects 5 to 8) concentrations of silicate were not only significantly higher than in the coastal transects but also exhibited considerable differences between the different channels. The highest average concentrations occurred in Bykovskaya Channel (transect 8, 48.5 µmol l^{-1} on average) and in Trofimovskaya Channel (transect 6, average silicate concentration of 37.4 µmol l^{-1}) both of which discharge into coastal waters within the sampling area (transect 3) (Fig. 6a, b).

3.3 Plankton community composition and diversity

Overall 133 distinct taxa or taxon groups from six broader groups were recorded: three autotrophic groups (diatoms, cyanobacteria and chlorophytes) and three groups containing both heterotrophic and autotrophic/mixotrophic components (dinoflagellates, ciliates and flagellates). Flagellates were grouped as such on the basis of morphology. They contained cryptophytes and crysophytes, but also prasinophytes, which taxonomically also belong to the chlorophytes. However, for the analyses they were grouped with the total flagellates due to their potential role as food for microzooplankton grazers. Taking a broad view, comparing overall differences between delta and coastal transects, the most striking difference was the shift from diatom and chlorophyte dominance in the delta to dinoflagellate, ciliate and flagellate dominance in the coastal transects, with the exception of transect 3, which captured the outflow from the Bykovskaya and Trofimovskaya channels going North and therefore resembled the delta communities very closely (Fig. 7a, b). The highest number of autotrophic organisms occurred in transects 3, 5 and 8 reflecting the river plume flowing northwards. Transect 2 on the other hand was dominated by mixotrophic and heterotrophic taxa particularly dinoflagellates and ciliates such as *Myrionecta rubra*. This transect was also characterized by large populations of flagellates, particularly crypotpytes and prasinophytes less than 10 µm in length. This essentially separates the community spatially into predominantly

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autotrophic and heterotrophic components, respectively. Ordering the sites in Fig. 7 by decreasing diatom abundance, gave rise to two groups of sites, with freshwater sites (delta transects and T3) on one hand and the coastal communities on the other. The most abundant taxa of the different groups are given in Table 2. The most abundant diatom taxa included typical freshwater diatom taxa such as *Aulacoseira* spp. and *Asterionella formosa*. These species dominated in the delta sites and transect 3, but were replaced by *Chaetoceros and Thalassiosira* species (the 3. most abundant diatom taxon overall) in transect 1 and transect 2. Cyanobacteria were represented mainly by *Aphanizomenon*, *Anabaena* and *Pseudanabaena* species, although their abundance was usually at least an order of magnitude lower than the diatom abundance. The *chlorophyceae* were diverse with taxa in the family *Selenastraceae* numerically most abundant and having the broadest distribution. The diatom : dinoflagellate ratio, which had also been calculated for all samples showed a significant decrease with increasing calculated stratification strength (Fig. 8, $F_{(1,58)} = 184.32$, $p < 0.0001$, $y = -0.88x + 1.25$). It was also significantly negatively correlated with salinity and temperature as well as positively correlated with silicate concentration ($F_{(1,56)} = 10.613$, $p < 0.0001$, $y = 0.399x + 23.75$) but was not affected by other inorganic nutrients.

The major plankton groups were also investigated in relation to potential predator-prey relationships. Figure 9 shows the results of regression analyses of the microzooplankton groups with potential prey groups. These analyses revealed highly significant positive relationships between total ciliate and flagellate abundance on one hand (Fig. 9a) and dinoflagellates and flagellates on the other. Both microzooplankton groups were also significantly associated with diatoms (Fig. 9g, f) although in this case it was an inverse relationship, while no significant relationship was found between the two grazer group and chlorophytes (Fig. 9c, d).

Overall, cell numbers and number of taxa were highest in the surface samples. Shannon diversity of the community on the other hand was significantly higher in sub-surface than in surface samples (Table 3, Mann-Whitney U test, $p = 0.005$). This was mainly due to the more even distribution of cell numbers across taxa, despite a significantly

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lower total number of taxa. However no significant differences in diversity were found when separating data into individual transects (including all depths) (Kruskal-Wallace test, df = 6, $p = 0.11$) or on the basis of the delta vs coast sites (Mann-Whitney test, $p = 0.86$). However, the number of species were significantly higher in the Delta than in the coastal stations (Mann-Whitney test: $Z = 5.944$, $p < 0.005$) and also significantly different between transects (Kruskal-Wallis test, $H_{(1,N=66)} = 35.41158$, $p < 0.01$).

3.3.1 Multivariate phytoplankton community analyses

The different hydrographic characteristics of the 4 transects were also reflected in the multivariate analyses considering the whole phytoplankton community. The delta cluster was clearly separated from all other stations and contained all of the delta stations, transect 3 and in addition 3 samples from transect 1 (stations T1-1001, T1-1002) (Fig. 10). The latter were located close to the outflow of the Bykovskaya channel into the bay. They were characterized by higher concentrations of freshwater diatoms and chlorophytes than other transect 1 stations and the remainder of coastal stations in Buor Khaya Bay. They therefore grouped with the delta cluster in the nMDS analysis. The remainder of the sites formed a heterogeneous group of small clusters. Six stations were exceptional in that they did not cluster with any larger group. Their species composition was more than 60 % different from all other clusters and from each other. These samples represented the deepest samples from several of the coastal stations, all of which had a salinity of above 20 and a temperature below 1 degree. The BEST analysis indicated that a combination of several factors including stratification strength and absolute temperatures could best describe these observed multivariate patterns (Spearman rank correlation 0.528). But interestingly salinity as absolute values rather than as part of the stratification index had little explanatory power in the analysis.

The second multivariate analysis, the redundancy analysis, related the biological communities to the environmental factors. The first two ordination axes explained 36.2 % of the overall variation. This analysis showed the most important factors (denoted by the length of the arrow, Leps and Smilauer, 2007) to be the two calculated

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indices of stratification strength. Of the nutrients phosphate and nitrate were the most important factors and they were closely correlated with salinity. Silicate concentration on the other hand, as in the regression analyses of individual physic-chemical parameters, was only weakly correlated with salinity (Fig. 11). This setting of physico-chemical parameters gave rise to three distinct communities: 1. The true freshwater communities, rich in chlorophyte taxa and cyanobacteria. The driving factors here were higher temperatures in the riverine sites and to a lesser extent silicate concentrations. This cluster contained the delta cluster already identified in the nMDS analysis but also included stations from transect 4. A second cluster was formed by those sites containing marine taxa such as *Dinophysis*. This patterns was driven by lower temperatures and increasing salinity. The third and largest cluster contained stations from several transects and was dominated by the sub surface samples (Fig. 11).

4 Discussion

4.1 Hydrography

The principal aim of this study was to establish a baseline for biodiversity and structure of the microplankton community and to relate these to hydrographic conditions in the Lena Delta and coastal Laptev Sea. The salinity patterns of the Lena Delta and adjacent areas proved very complex and were partitioned clearly into the actual region of freshwater influence which was shallow and mixed or only weakly stratified, located on the near-cost shallow sill around the delta (transect 3), and the "offshore" deeper coastal waters which were clearly stratified with respect to salinity and temperature with the deep stratification leading to de-oxygenation near the benthos in several stations (oxygen data not shown). The location of the thermo- and haloclines at depths between 5–10 m were in agreement with a study by Sorokin and Sorokin (1996) carried out in 1991.

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The two regions could also be distinguished by satellite imagery, which showed considerable differences in euphotic depth between the river channels themselves and the coastal regions directly influenced by river discharge and re-suspension on the shallow delta sill around the Lena Delta on one hand and the coastal Laptev Sea region with deeper bathymetry on the other. The turbid waters of the river channels and on the shallow sill around the Lena Delta were limited to euphotic depths above 5 m in contrast to the more transparent deeper coastal waters with euphotic depths considerably deeper down to 8 to10 m depth and considerably different nutrient concentrations measured particularly of silicate (Cauwet and Sidorov, 1996).

Stratification patterns in this region are known to be highly variable and to weaken/break up completely during peak discharge after ice-off in spring (May/June), which can result in considerable variability in the size of the coastal area still under freshwater influence and therefore the degree to which riverine, terrigeneous material can be exported to the open sea. Importantly the satellite imagery also revealed the presence of a large meander indicating a high degree of instability between the principal hydrographic zones on smaller than seasonal scales (Heim et al., 2012, in this special issue), making the interpretation of biological signals in the area even more difficult, as the extent of these meanders is also related to the discharge magnitude from the major river branches. Long-term changes in discharge/run-off patterns from the Lena Delta including Trofimovskaya and Bykovskaya channels have already been shown, probably due to recent climate warming (Yang et al., 2002; Berezovskaya et al., 2004). These expected changes concomitant with the already high inherent variability of the system are likely to affect the biological communities in the area.

4.2 Biological communities: transition from freshwater to marine conditions

The multivariate community analyses here have shown the biological communities to mimic the salinity features thus showing the strong influence of riverine input on the coastal ecosystem with significant differences in species numbers between the delta cluster and the coastal sites. All coastal areas directly influenced by the freshwater

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inputs had surface waters dominated by assemblages of freshwater phytoplankton, although in these areas the abundance of cyanophytes was markedly lower than in the river channels, which could have been a consequence of the slightly increasing salinities in the coastal waters, which cyanobacteria are thought not to be able to tolerate. But Moisander et al. (2002) have shown that for cyanobacteria in brackish conditions, abundance is not necessarily determined by salinity. Light and nutrient conditions as well as stratification patterns are likely to be more important drivers. Particularly stratification patterns as the result of continued climate warming might be expected to significantly alter dominance patterns in the major phytoplankton groups in future (Taranu et al., 2012). At any rate, differences in surface salinities in the present study would also appear to be too small to explain the decline in abundance of cyanobacteria in the coastal phytoplankton community (Paerl, 1996). This was also confirmed by the results of the multivariate analyses where salinity alone was not an important driving factor in the BEST analysis. Salinity was a more important factor in the redundancy analysis but was also closely correlated with nutrient concentrations.

Nevertheless the presence of all major taxonomic groups and particularly the persistence of chlorophytes in transect 3 and around the outflow of Bykovskaya channel into Buor Khaya Bay indicates the transitional nature of the coastal phytoplankton community between freshwater and marine conditions and it seems conceivable that in the only slightly increased salinities, and colder temperatures of the western part of Buor Khaya Bay *chlorophyceae* still actively contribute to primary production. It was particularly members of the family *Selenastraceae* that remained abundant in the bay (e.g. *Monoraphidium*, *Selenastrum*, *Ankistrodesmus*), which appear to have the broadest environmental tolerances of all investigated taxa. They were also 1 of only 4 *chlorophyceae* taxa identified in a previous study by Tuschling (2000) in one of their transects that was located just east of our transect 4 and seems to have captured only remnants of the freshwater plankton community.

The low concentrations of microzooplankton and thus probably low grazing pressure in the coastal areas of Buor Khaya Bay (see Abramova et al. submitted in this volume)

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will, at least in theory, facilitate transport of phytoplankton cells to greater depth by sinking out and to the open Laptev Sea. While no sediment studies were carried out in the present study, a previous study by Cremer (1999) showed that horizontal transport (judging by the extent to which typical freshwater diatom frustules were found in the sediment) might actually be relatively limited and this also seems to be corroborated by the plankton diversity data, which showed a replacement of the freshwater diatoms by brackish/marine taxa, e.g. *Thalassiosira* and *Chaetoceros* and the appearance of marine dinoflagellates such *Dinophysis* spp. (but see Rachold et al., 2000). Sinking of phytoplankton particles within the bay would then become available for bacterial degradation and re-mineralization of nutrients within Buor Khaya Bay fuelling the microbial loop (Azam et al., 1983). Earlier studies have shown that bacterial production/distribution is closely linked to chlorophyll concentrations, as they utilize phytoplankton derived carbon, in the form of DOC (Fuhrman et al., 1980, Teeling et al., 2012). The bacterial production in turn serves as a food source for heterotrophic flagellates. In this way carbon and nitrogen are returned to the foodweb via respiration and excretion. Bacterial abundance was not directly quantified in the present study, but considerable flagellate cell numbers occurred even at greater depths (app. 10 m), below the estimated euphotic zone, suggesting a heterotrophic mode of life. Feeding relationships between microzooplankton and flagellates have previously been observed for numerous dinoflagellate and ciliate species including *Myrionecta rubra* (= *Mesodinium rubrum*) (Yih et al., 2004; Johnson et al., 2007), which was also an abundant ciliate in the present study. Total abundance of ciliates (and to a lesser extent that of dinoflagellates) was also linked to that of the total flagellates suggesting a predator-prey relationship. However, only concurrent counts of bacterial and phytoplankton abundances and the exact determination of proportions of autotrophic and heterotrophic nanoflagellates coupled with grazing experiments *in situ* will reveal the true nature and strength of these relationships. Limited horizontal transport and efficient recycling of nutrients in the Buor Khay system would, if conclusively proven, be a possible explanation for the

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relatively high productivity of the coastal system (see Doerffer et al., 2012; Tuschling, 2000; Sorokin and Sorokin, 1996).

A marked feature of the coastal region was the low species richness in the dinoflagellate group. While, this group also contained the highest number of unidentified species and only detailed studies using techniques such as Scanning electron microscopy can reveal their true diversity, previous studies have also shown dinoflagellate diversity in the East Siberian and Laptev sea to be low compared to other Arctic Regions (Okolodkov and Dodge, 1996). Considering that only 10 % of extant dinoflagellate species are thought to occur in freshwater (Taylor et al., 2008), it is possible that this apparently low diversity is a consequence of greater freshwater influence in the coastal Laptev Sea as opposed to other regions of the Arctic Ocean. Even easily identifiable marine species found in previous studies such as *Neoceratium arcticum* and *N. longipes* or *Protoperidinium* species such as *P. depressum* (Tuschling, 2000) were never found in the present study. Other taxa representative of more oceanic conditions, such as *Dinophysis* also only occurred in stations further offshore is a further pointer to the entire sampling area still being transitional between fully marine and freshwater conditions.

Due to their sensitivity to different environmental conditions dinoflagellates have also received attention as indicator species, i.e. species that due to their set of environmental tolerances, only occur in particular areas and can therefore be used as sensitive tools for the management of the marine environment (Birk et al., 2012; Rovira et al., 2012). One of the simplest indicator systems currently in use is the diatom:dinoflagellate ratio. A decreasing ratio has often been interpreted as a sign of excessive nutrient inputs (Ninčević et al., 2010). In the present study however, the ratio is not linked significantly to any inorganic nutrients, other than silicate, which is not surprising. It was on the other hand correlated with stratification strength on the basis of both salinity and temperature. While this could potentially present a simple indicator (without a need of taxonomic knowledge) of the extent of freshwater influence in the coastal Laptev Sea, whether this index is reliable could only be determined on the basis of long-term observations covering a range of environmental settings, but it

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seems unlikely that it will be able to discriminate between a series of co-varying factors (e.g. salinity, phosphate and nitrate) as in the present study.

The data shown here are still only a snapshot of the environmental conditions and several years of data will be required to understand the natural variability in hydrography and its effects on the biological communities in the Lena Delta and southern Laptev Sea. Importantly, for an assessment of potential climate change effects future studies should also include laboratory investigations of the environmental tolerances of key Arctic phytoplankton species (particularly *cyano-* and *chlorophyceae*). Only if these physiological parameters are known, can the potential responses of these taxon groups to future environmental conditions be judged. At present such data are still largely lacking and they should be investigated as part of well co-ordinated interdisciplinary investigations of the physics, chemistry and biology of the Lena Delta and coastal Laptev Sea.

Acknowledgement. Thanks are due to the ship crews and the organizers of the Lena Delta expedition in 2010. We are also grateful to Tamar Zohary and Alla Alster for help with the identification of some of the phytoplankton species, particularly the *chlorophyceae* and *cyanophyceae*. Particular thanks are also due to Kristine Carstens for carrying out the nutrient and chlorophyll analyses. We are also grateful to our Russian collaborators at AARI St. Petersburg and at the Lena Delta Reserve in Tiksi. Without their help and logistics support our work would not have been possible.

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Table 1. Geographical co-ordinates of the sampled transects. Average depth was estimated based on the depth of the individual transect stations.

Transect	Start latitude	Start longitude	End latitude	End longitude	Stations/ samples	Transect length (km)	Average depth (m)
1	71.686	132.423	72.335	129.734	7/21	119.5	13.0
2	71.5656	129.734	71.686	132.081	6/13	60.0	12.0
3	71.832	129.472	72.701	130.267	5/5	101.5	3.9
4	72.746	130.453	71.768	130.500	5/15	102.0	14.4
5	72.473	125.291	72.425	126.654	3/4	34.7	10
6	72.425	126.654	72.626	127.268	3/5	31.0	16.3
8	72.415	126.867	72.029	128.518	3/3	70.8	10.7

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Table 2. Summary of the most abundant taxa in the different taxon groups together with their abundance averaged over all sites. Supplementary material of individual taxa is available at http://planktonnet.awi.de.

Taxon groups	Mean (cells l^{-1})	Peak abundance (cells l^{-1})	Site of peak abundance
Diatoms			
Aulacoseira spp.	194 580	1 796 240	T5-1003
Asterionella formosa	48 141	292 920	T3-1004
Chaetoceros spp.	3144	102 480	T1-1007-3
Aulacoseira granulate var angustissima	3444	26 080	T5-1001-6
Aulacoseira granulata	3342	33 120	T5-1002-18
Dinoflagellata			
Gymnodiniaceae < 20 µm	5295	40 680	T4-1003
Unidentified thecate aff *Heterocapsa*	1635	11 920	T4-1004
Amphidinium cf. *extensum*	953	15 600	T2-1004
Gymnodiniaceae 20–50 µm	811	11 280	T1-1003
Gymnodiniaceae > 50 µm	234	12 400	T1-1005-15
Chlorophyta			
Monoraphidium spp./*Koliella* spp./ *Ankistrodesmus* spp.	3498	18 200	T1-1005
Actinastrum hantzschii	909	5600	T1-1002-4
Desmodesmus spp.	743	3680	T3-1003
Other *Selenastraceae*	664	4650	T2-1005
Monorhaphidium contortum	591	1920	T1-1004-4
Colonial chlorophytes (excl. *Dictyospharium*)	269	640	T3-1003, T5-1002-18
Cyanobacteria			
Aphanizomenon spp.	1286	8480	T5-1001
Anabaena spp. (irregular coils)	321	2240	T5-1003
Pseudanabaena spp.	1279	8400	T8-1002-14
Unidentified filaments < 3 µm	463	2880	T5-1001
Planktothrix spp.	179	1360	T5-1001

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Table 3. Summary of the differences between key community parameters in the subsurface and subsurface samples. The subsurface samples were not further subdivided into different depth for the analysis, N = 66 (surface = 23, subsurface = 43).

Site factor	Surface	Subsurface	Mann Whitney U-test, p-value
No of taxa	42.9	33.9	$p = 0.03$
Average abundance per site (N l^{-1})	1 050 000	345 007	$p < 0.00001$
Shannon diversity index	1194	1.631	$p = 0.007$

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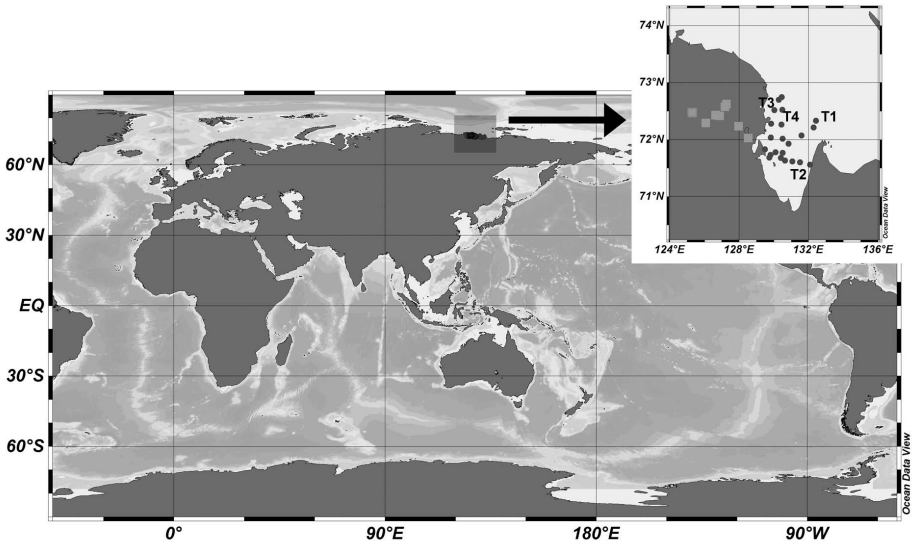

Fig. 1. Map of the Lena Delta and coastal Laptev Sea, the insert is showing the Delta (light grey marks) and coastal (dark grey marks) stations stations sampled in 2010, plots were generated in Ocean Data View software, v4.The transect numbers are indicated in the insert map

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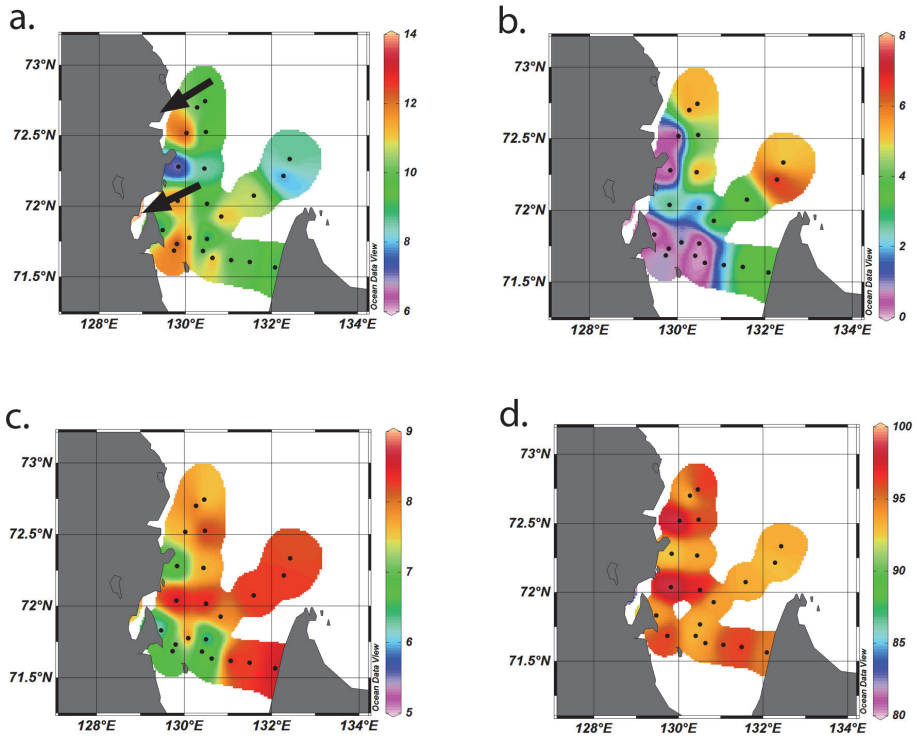

Fig. 2. ODV surface plots for **(a)** temperature (°C), **(b)** salinity, **(c)** pH and **(d)** oxygen (%) for the area covered by the 4 coastal transects, as obtained from CTD casts, the arrows in a. are pointing to the outflows of Bykovskaya (bottom) and Trofimovskaya (top) channels respectively

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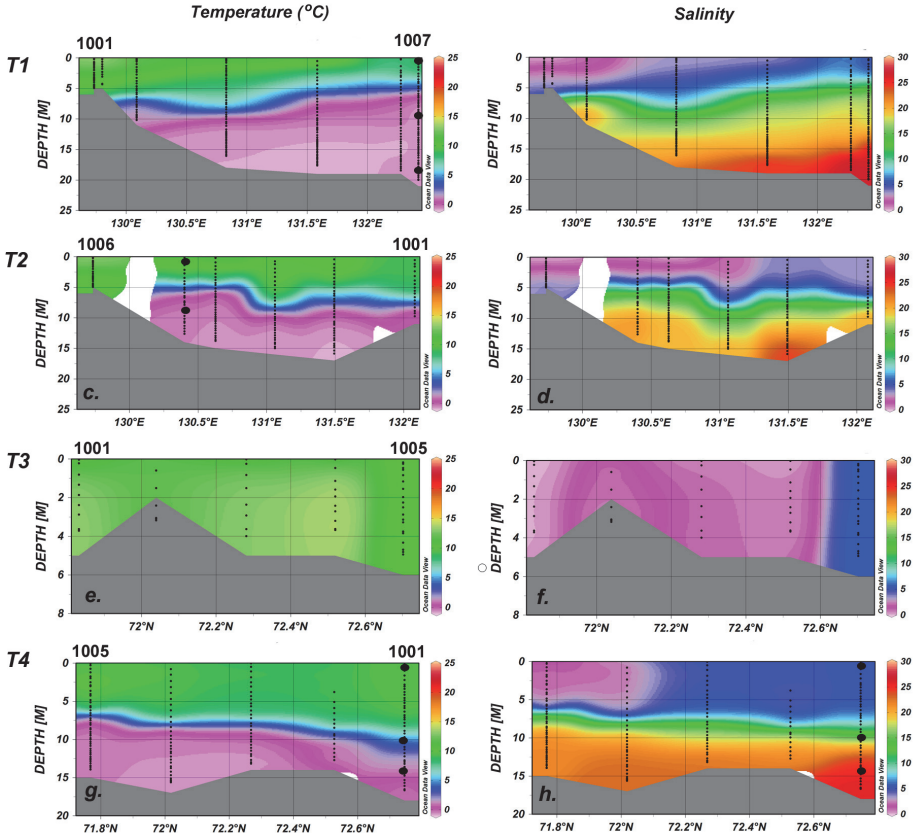

Fig. 3. Salinity and temperature profiles for the four coastal transects: a = transect 1, b = transect 2, c = transect 3, d = transect 4. The larger circles indicate examples of sampling locations in relation to the thermocline in stratified water columns. Samples were taken from surface waters and above/below the thermocline.

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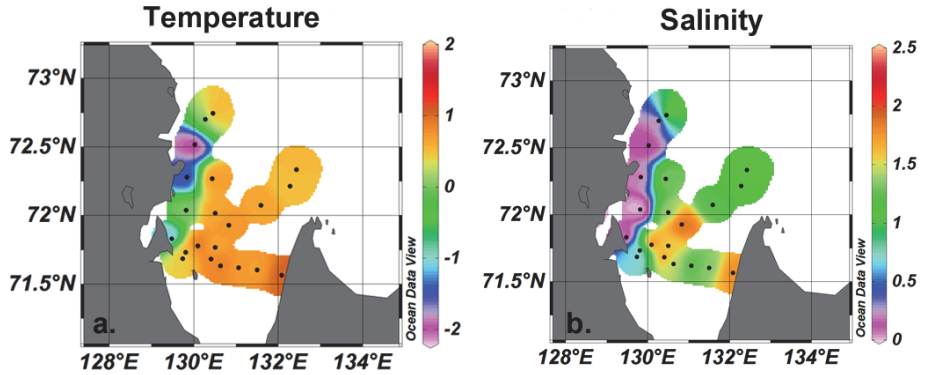

Fig. 4. ODV surface plots summarizing the stratification strength with respect to **(a)** temperature and **(b)** salinity at each station in the coastal transects (T1–T4). The figure is based on the stratification indices calculated for temperature and salinity.

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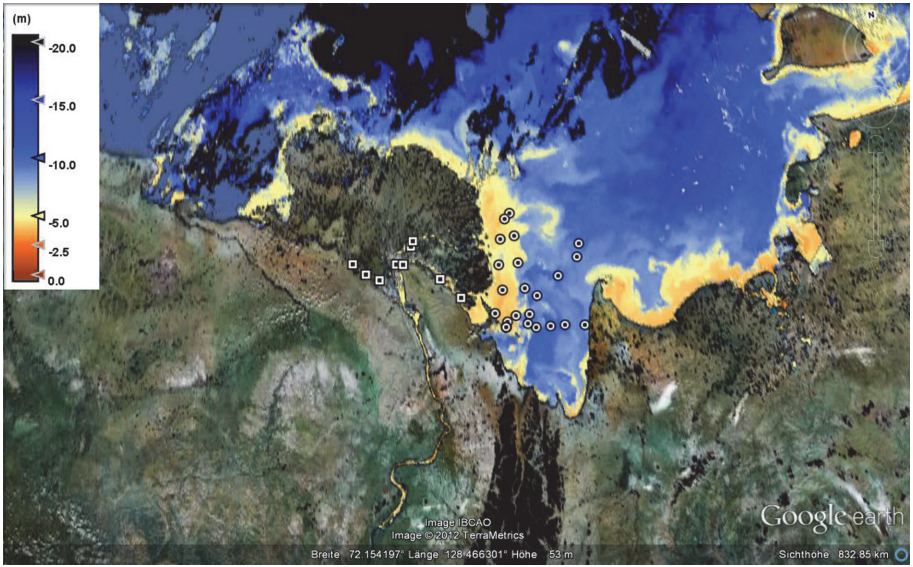

Fig. 5. Satellite image of 3 August 2012, from the Ocean Colour sensor MERIS indicating euphotic depth calculated as $Z_{Eu}\ (\lambda) = \frac{4.6}{K(\lambda)}$ m, where k is the diffuse attenuation coefficient in the PAR spectrum.

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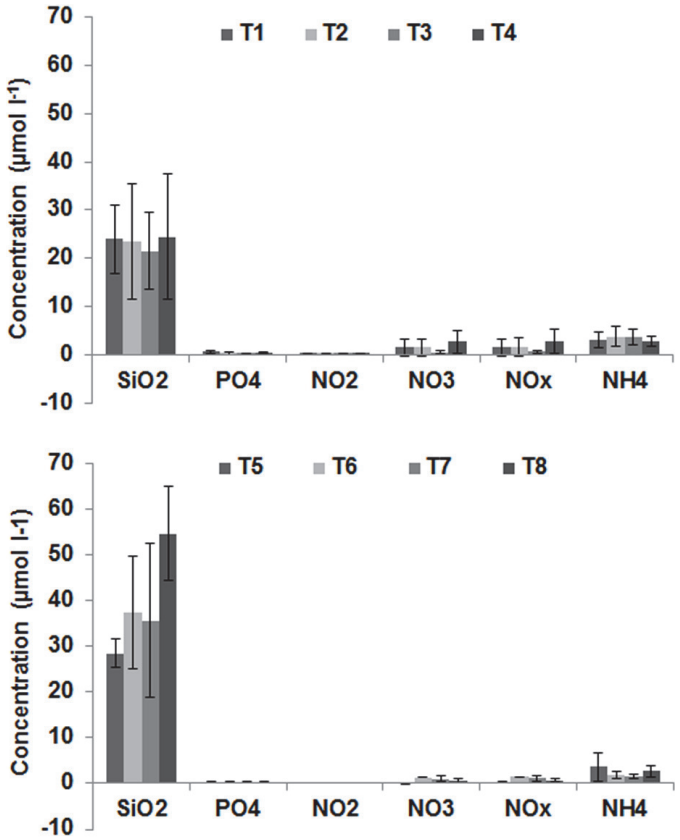

Fig. 6. Concentrations of inorganic nutrients mol/L, in **(a)** the Delta transects (T5 = Oleynovskaya channel, T6 = Trofimofskaya channel, T8 = Bykovskaya channel), **(b)** the coastal transects T1-T4. Values were pooled across the stations in each transect. Error bars indicate the standard deviation for the stations per transect.

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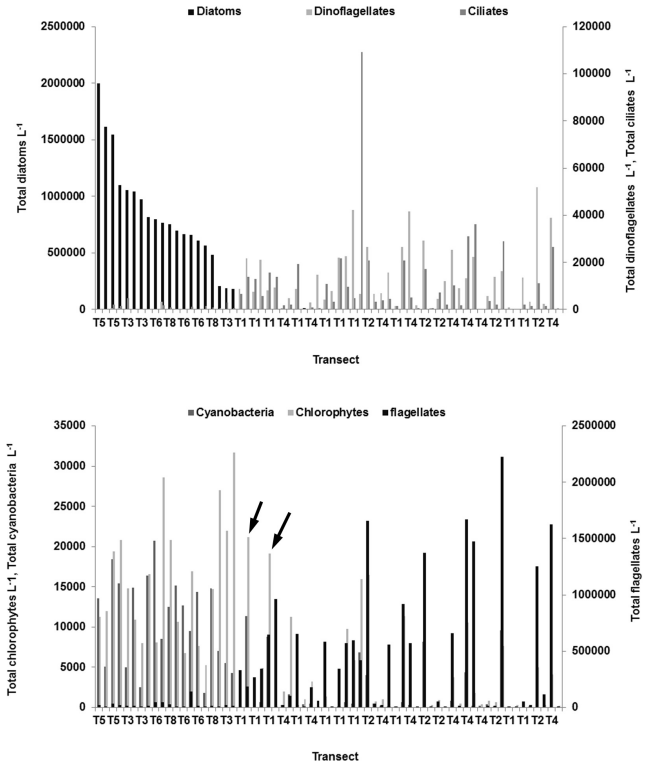

Fig. 7. Abundance of the principal plankton groups at all stations and transects: **(a)** diatoms (black bars), dinoflagellates (light grey bars), ciliates dark (grey bars); **(b)** flagellates (black bars), cyanobacteria (dark grey bars) and chlorophytes (dark grey bars). Stations were sorted along decreasing diatom abundance, which gave rise to a grouping of the Delta sites followed followed by the coastal sites. Data are shown across the whole dataset, i.e. including both surface and subsurface samples, $n = 66$. Arrows are pointing to coastal stations on T1 with particularly high numbers of chlorophytes.

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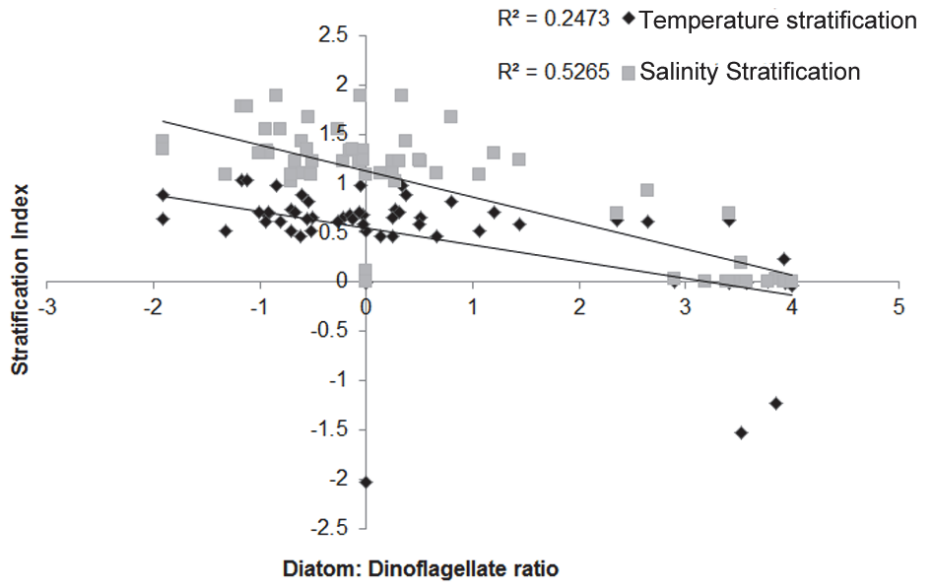

Fig. 8. The relationship between stratification index and diatom to dinoflagellate. A value of zero in the stratification index means no stratification at all. Positive values show successively stronger stratification. Negative values indicate inverse stratification: dark marks = temperature stratification, grey marks = salinity stratification, n = 61.

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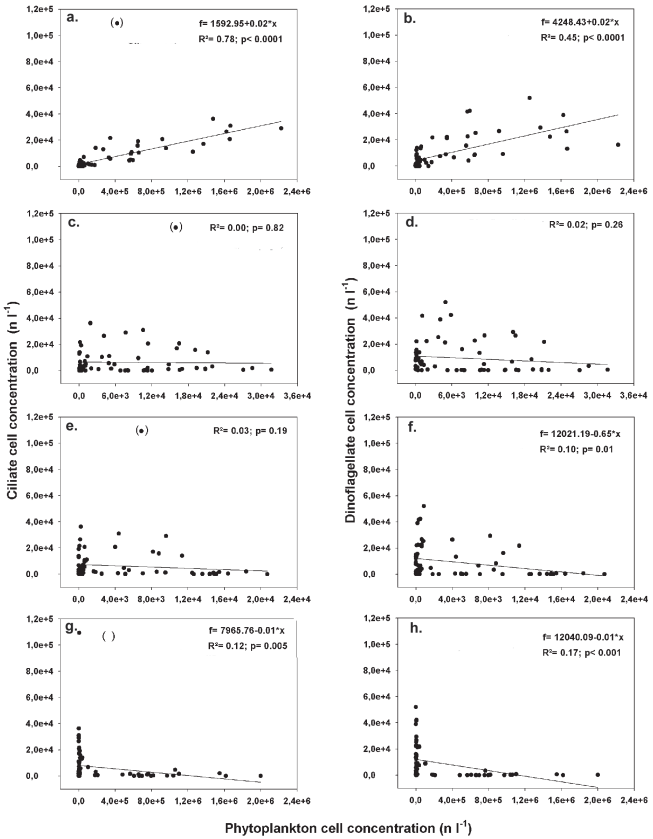

Fig. 9. Patterns of co-occurrence ciliates (graphs on the left) and dinoflagellates (on the right), with their potential food sources: total flagellates **(a–b)**, chlorophytes **(c–d)**, cyanobacteria **(e–g)**, diatoms **(g–h)**. The significance of the relationships was analyzed by linear regression analysis. Regression equations for relationships significant at the 5 % level are given in the relevant plots. All Delta and coastal sites were included in the analysis, $n = 66$.

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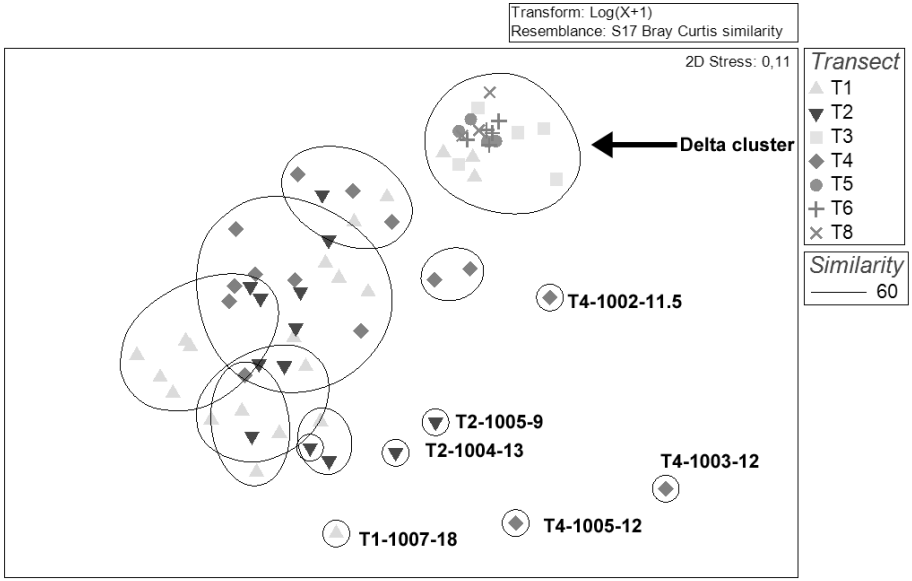

Fig. 10. Multidimensional scaling plot, showing the distances (in terms of similarities) between the sites in the Delta and coastal regions. All depths were included in the analysis. Black lines indicate 60 % similarity contours. The arrow is pointing to the cluster containing all Delta sites, T3 and three samples from stations 1 and 2 in transect 1 (the two stations closest to the coast).

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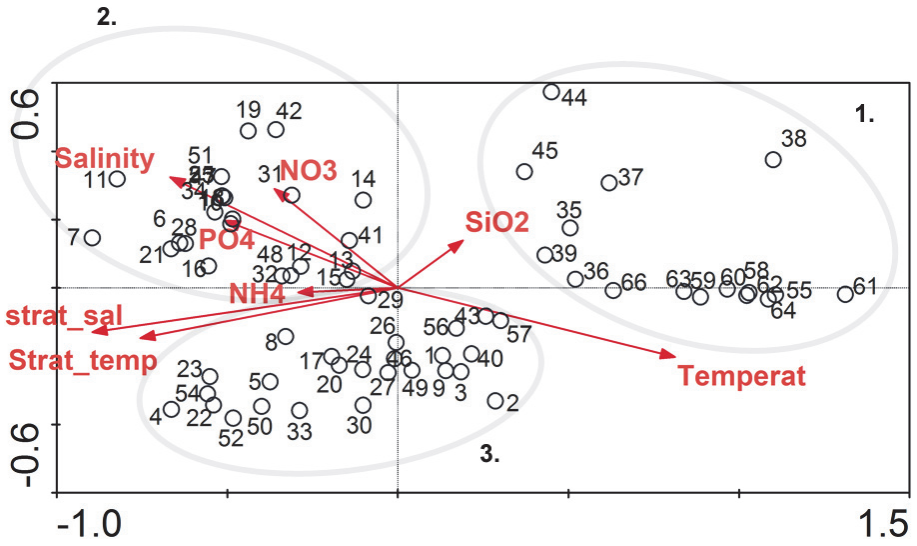

Fig. 11. Sample-environment biplot of the Redundancy analysis carried out on all counted samples. For the calculation of the influence environmental factors only those samples also used for the analysis of biological trends were included: site numbers: 1–22 = T1, 23–35 = T2, 36–40 = T3, 41–55 = T4, 56–59 = T5, 60–64 = T6, 65–67 = T8.

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