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Patterns of the Kara Sea primary production in autumn: biotic and abiotic forcing of subsurface layer

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ABSTRACT. Primary production and fundamental environmental factors were measured during September–October 1993, 2007 and 2011 in the Kara Sea. Relationships between the depth-integrated primary production (PP_{int}), the surface chlorophyll *a* (Chl_0) concentration and the maximum chlorophyll specific carbon rate within water column (P^b_{opt}) had shown that only 12% of PP_{int} variability were determined by Chl_0 and there were strong correlations between PP_{int} and P^b_{opt} (R^2 = 0.64). Thus, in the autumn PP_{int} values were largely influenced by the phytoplankton assimilation activity. At the end of a vegetative season high (close or above 1 mg m^{-3}) values of Chl_0 were not an index of phytoplankton productivity within photosynthetic layer where the organic matter synthesis rate was low which testifies the lack of correlation between Chl_0 and PP_{int} (R^2 = 0.12) and between Chl_0 and depth-integrated chlorophyll *a* (chl *a*) (R^2 = 0.22). This conclusion is based on the low assimilation activity within water column and small thickness of the photosynthetic layer. The latter corresponds to low insolation and water transparency. The lack of correlation between surface and depth-integrated productivity parameters is the challenge for satellite PP_{int} estimations. In turn PP_{int} and P^b_{opt} depended mainly on photosynthetically available radiation (PAR) and weakly related to the nitrogen and phosphorus concentrations. At the end of a vegetative season PAR level, apparently, should be considered as the main factor for primary production in the Kara Sea. Comparison between the integrated primary production from shipboard in September and the simulated evaluations of productivity (PP models) suggests that PP models overestimate the *in situ* PP_{int} by a factor of 3–7 in the different Kara Sea regions. Improving of Kara Sea primary production estimations imply the development of regional satellite chl *a* algorithm and local primary production model considering specific features of PP in this Arctic Ocean region.

KEY WORDS: Primary production; Chlorophyll *a*; Chlorophyll specific carbon rate; Phytoplankton; Photosynthetically available radiation; Nutrients

1. Introduction

The Kara Sea has the considerable differences from another Arctic seas owing to particular processes of organic matter synthesis. Ob and Yenisey runoff averages nearly 1100 $km^3 y^{-1}$ (Stein 2000) that is approximately 55% of the general river flow in the Russian Arctic Seas and more than 1/3 of overall freshwater runoff in the Arctic Ocean (Hanzlick and Aagaard, 1980). Interaction of fresh and salty waters with sharp halocline development promotes spatial and vertical differentiation of composition and functional characteristics of plankton communities (Gordeev, 1998; Makarevich et al., 2003; Nöthig et al., 2003; Hirche et al., 2006; Sukhanova et al., 2010; Flint et al., 2010). The shoal is another unique feature of the Kara Sea which determines peculiarity of the photosynthetic zone nutrient supply. The average depth of the Kara Sea is equal to 110 m (Carmack et al., 2006). Shelf (<200 m) underlays 15% of the water area, average depth of the shelf is equal to 56 m (Jakobsson et al., 2004).

Specific environmental factors (abiotic and biotic) influenced on the primary productivity depend on sharp physical and chemical gradients of the water properties such as salinity, particular (POM) and dissolved (DOM) organic matter concentrations. Such features are cause of high turbidity, small (M = 22 m) depth of the photosynthetic layer and high (M > 1 mg m^{-3}) chlorophyll content above pycnocline (Vedernikov et al., 1994; Mosharov, 2010). At the end of a vegetative season (September–October) low subsurface concentrations of dissolved nitrogen and phosphorus and low incident surface irradiance are the limiting factors for the PP in the Kara Sea (symbols and abbreviation are presented in Table 1). Previously, it has been shown that the fundamental environmental factors limited primary production in the Kara Sea at least since the end of August (Vedernikov et al., 1994).

The studies performed previously have shown low PP_{int} (<100 mg C m^{-2} d^{-1}) on a considerable part of the Kara Sea in August and September, and high PP_{int} in the Yenisey estuary and Southwestern area where PP_{int} values exceeded 100 mg C m^{-2} d^{-1} and reached 200–360 mg C m^{-2} d^{-1} (Bobrov et al., 1989; Vedernikov et al., 1994, Mosharov, 2010). At the same time, remote sensing estimations appear to be several times more than *in situ* Kara Sea PP (Pabi et al., 2008; Arrigo and van Dijken, 2011; Vetrov and Romankevich, 2011; Hill et al., 2013). It is possible that discrepancy between these estimations are caused by the calculation errors for the surface chl *a* concentration as one of the main model parameter because of the high allochthonous DOM and POM concentrations (Dittmar and Kattner, 2003; Amon, 2004; Rachold et al., 2004; Vetrov and Romankevich, 2004), and imperfection of PP algorithms (Pabi et al., 2008; Hill and Zimmerman, 2010; Hill et al., 2013; Matrai et al., 2013). The low PP_{int} and high chl *a* concentration (>1 mg m^{-3}) in UML as a bloom characteristic (Sullivan et al., 1993) in the Kara Sea in September is paradoxical if the phytoplankton biomass have been considered as basis of the primary production.

The main purpose of this work was to explain the reasons for low water column primary production in the autumn despite high chlorophyll *a* values in terms of environmental factors. Our working hypothesis is that at the end of growth season the level of assimilation activity may be the prevalence factor influenced on Kara Sea PP_{int}. A second objective was to determine the main abiotic factor influenced on PP_{int}. Determination of principal environmental factors controlling Kara Sea primary productivity allows parameterizing PP_{int} models.

Here we studied dependence of the phytoplankton production characteristics on variability of subsurface layer parameters and vertical chl *a* distribution, underwater irradiance and nutrients. Represented problem is actual in the context of the Arctic climate changes in the last decades determining variations of productivity in this region (Arrigo et al., 2008; Pabi et al., 2008; Arrigo and van Dijken, 2011). The importance of improving of the Kara Sea productivity estimation is obvious, so need to develop specific PP and chl algorithms with regional data sets and analysis of primary production patterns.

2. Materials and methods

2.1. Data sources and Kara Sea sub-regions

The database analysed in this article has been developed based on three Kara Sea expeditions: 49th cruise R/V "Dmitry Mendeleev" (August–September 1993), 54th and 59th cruises R/V "Academik Mstislav Keldysh" (September 2007 and September–October 2011, respectively) (Fig. 1). The chl *a* concentrations were measured at 113 stations and primary production – at 85 stations.

The Kara Sea could be divided into water areas with various hydrophysical and biogeochemical conditions, that caused by different influence of Ob and Yenisey river runoff at a short and long distance. The main indices of river runoff are surface salinity and silica content. The various water areas defined as water masses of Kara Sea (WM) were classified using these parameters. Apparently, phytoplankton of various Kara Sea WM should be different with respect to productivity characteristics.

Based on the classification of WM developed early (Pivovarov et al., 2003), we have allocated Southwestern outflow area (Southwestern WM) (I), Ob estuary (II), Yenisey estuary (III), Ob-Yenisey area of river runoff (primarily shelf < 200 m) (IV) and Northern WM (areas of eastern and western slopes of St. Anna's trough) (V) (Fig. 1). The areas I, IV and V were demarcated using a mean annual surface 25 psu isohaline (Pivovarov et al., 2003). The Ob and Yenisey estuaries were studied separately because of differences in environmental conditions and primary production reported previously (Vedernikov et al., 1994). The northern estuaries boundary was defined as average position of 10 psu isohaline. Salinity of 2–10 psu is typical for river mouths and estuaries so-called mixohaline zones according to the Venice system (1958). The Northern WM and Southwestern WM are characterized relatively high salinity (30–32 psu and 28–32, respectively) and low dissolved silicon concentration (<10 μM and <5 μM, respectively) (Pivovarov et al., 2003).

2.2. Sampling

Sampling was conducted in various Kara Sea areas which were differed in hydrophysical and optical characteristics. The layout of the stations was determined by the results of continuous measurement using the scanning multiparametrical probe "Rybka" and flow fluorometer developed in P.P. Shirshov Institute of Oceanology RAS. Sampling depths were defined after preliminary sounding of temperature, conductivity and chlorophyll fluorescence by CTD probe Seabird Electronics (SBE-19 and SBE-32). At the stations Niskin bottles were deployed to obtain water samples from discrete depths within upper 100-m layer. At these stations the surface sample was taken by a plastic bucket simultaneously with bottles closing at 0 m depth. Trace-metal clean procedures (e. g. Teflon coated covers and springs of the Niskin bottles) were used in all cruises.

During August–September 1993 **(**49th cruise R/V "Dmitry Mendeleev") at three stations the water samples were collected from the different depths of upper 100-m layer for *in situ* primary production determination. At another stations only the surface sample was used (see below). During October 2007 (54th cruise R/V "Academik Mstislav Keldysh") the water samples for determination of primary production were collected from the depths corresponding to 100%, 75%, 50%, 25%, 10%, 5% and 2% of surface PAR (Mosharov, 2010). During October–November 2011 (59th cruise R/V "Academik Mstislav Keldysh") the water samples were collected from the depths corresponding to 100%, 79%, 64%, 49%, 24%, 6%, 3%, 2% of surface PAR where light conditions approximately agree with nominal transparency of flasks with neutral filters included into the complete set of ICES incubator.

2.3. Primary production and light measurements

Primary production was estimated onboard using radiocarbon method (Steemann Nielsen 1952). During August–September 1993 (49th cruise R/V "Dmitry Mendeleev") samples were exposed *in situ* into acid-cleaned 275-ml bottles after addition of 0.05 µCi per 1 ml of the sample (two light and one dark bottles on each depth) during half of a lightday. At the end of incubation the samples were filtered onto 0.3 or 0.6-µ "Synpor" membrane (Czechia). After filtration samples were treated with 0.1 N HCl and filtered seawater. After overnight evaporation each filter was placed in scintillation vial with 10 ml of scintillation cocktails (we used the different cocktails during cruises: Lipoluma, Aqualuma, Ecoluma). Radioactivity in the samples was determined using liquid scintillation counter (RLS-05, Russia). Depth-integrated PP was calculated from the surface to the base of the photosynthetic zone using trapezoidal integration of the discrete depth values. Indirect calculations of PP_{int} were performed according to Ryther and Yentsch (1957) modified method. Surface samples were exposed in the deck incubator with temperature maintained *in situ* conditions. Primary production was calculated using PP_0, vertical distribution of chl *a*, underwater PAR and vertical *in situ* assimilation number (AN) distribution (Vedernikov et al., 1994).

During September 2007 (54th cruise R/V "Academik Mstislav Keldysh") primary production was determined by simulated *in situ* approach. After addition $NaH^{14}CO_3$ into acid-cleaned experimental bottles (140 ml) samples were exposed in the deck pool with flowing sea water from midday to sunset. The transparency of neutral lighting filters was chosen based on the light exposure conditions at the sampling depths. After exposition samples were filtered through 0.45 µ "Vladipore" membrane (Russia). Radioactivity of the samples were counted using RackBeta (LKB, Sweden) liquid scintillation counter.

During September–October 2011 (59th cruise R/V "Academik Mstislav Keldysh") PP was determined using the simulation of light conditions at constant artificial illumination. Water samples collected at each depth were spilt into 50 ml experimental flasks with neutral lighting filters of 100–2% of I_0 transparency. Exposition was carried out in ICES photosynthetron (Hydro-Bios, Germany) during 3 hours (Colijn and Edler, 2002). Water temperature in the tank was equal to T_0. Maintenance of constant T was achieved by aquarium chiller HAILEA (China). After incubation flasks were filtered onto 0.45 µ "Vladipore" membrane (Russia). Radioactivity of the samples was determined using Triathler (Hidex, Finland) liquid scintillation counter.

Intensity of surface irradiance was measured by pyranometer (Vedernikov et al., 1994) or using LI-190SA (LI-COR) sensor (Mosharov et al., 2014, in print). Results of the measurements were automatically integrated in LI-1400 module for five-minute intervals (mol quanta м$^{-2}$) during the day and saved in the internal memory. Subsequently, these data were used for calculation of integrated PAR values during an exposition of experimental bottles under the primary production determination and for all lightday. Diffused attenuation coefficient (k_d) was measured by alphameter (Vedernikov et al., 1994). In the absence of underwater hydrooptical measurements, k_d has been calculated based on k_d Z_s versus Z_s empirical dependence (Fig. 2).

2.4. Chlorophyll a and nutrients determination

All of sampling treatment was performed onboard during the cruises. In August–September 1993 chl *a* concentration was determined using the spectrophotometric method (SCOR–UNESCO, 1966). Seawater samples (5–6 l) were filtered through a Vladipore membrane with 0.6 µ pore size. Chlorophyll was extracted in 90% aqua acetone solution twice during an hour. The extracts were clarified twice by centrifugations (8000 rpm). Chl *a* concentration was measured using spectrophotometer SF-46 (Russia) and calculated according to Jeffrey and Humphrey equation for mixed phytoplankton (Jeffrey and Humphrey, 1975).

In September–October 2007 and 2011 the chl *a* concentration was measured fluorometrically (JGOFS, 1994). Seawater samples (500 ml) were filtered onto Whatman GF/F glass fiber filters with low vacuum (~0.3 atm) and extracted in 90% acetone (at 5ºC, in the dark, 24 h). The fluorescence of extracts was measured with a Turner Designs fluorometer (Trilogy Fluorometer) before and after acidification with 1 N HCl. Fluorometer was calibrated before and after each cruise using pure chl *a* (Sigma) as a standard. The concentration of chl *a* and phaeophytin *a* was calculated according to Holm-Hansen and Riemann (1978).

Previous comparisons have shown a good agreement between various methods of chl *a* determination (Neveux et al., 1990; Mantoura et al., 1997). However these comparisons did not concern experiments designs, conditions of filtration, filters type, phaeopigments and instrument corrections. Therefore, in various applications of different chl *a* techniques comparison of the results should be carried out. Comparison of mentioned above methods and approaches had been made in the southwestern part of Atlantic and the central areas of the Drake Passage during October–November 2008 (Demidov et al., 2011). Despite the large scatter of compared values, the data obtained using different techniques and experimental approaches can be applied for estimation of spatial and temporal variability of chl *a* (Yunev et al., 2002).

Fixation of dissolved oxygen and NH_4 in the samples was performed directly after sampling. Samples to determine pH, nutrients (silicates, phosphates, nitrogen forms) and alkalinity were selected in 0.5 l plastic bottles without preservation and were treated immediately after sampling. At works in the areas with a considerable quantity of POM (bays and river-sea interface) the water samples were preliminary filtered through the nuclearpore 1 μ filter (Dubna, Russia). PO_4, NO_3, NO_2, NH_4 and $Si(OH)_4$ concentrations were measured by coulometric titration method according to DOE (1994).

Determination of total alkalinity (Alk) was carried out using direct titration method. Calculation of dissolved CO_2 and concentration of various forms of the dissolved inorganic carbon was performed by pH-Alk method using thermodynamic equations of carbon balance with constants of carbonic acid dissociation (Millero, 1995; Hansen and Koroleff, 1999) and corrections for low salinity and DOM reached waters (Makkaveev, 1998).

2.5. Calculations and statistical analysis

Before calculations data were log transformed to achieve normal distribution (Fig. 3a,b and 4a,b) and for use the parametrical statistics methods. Then data were checked for normality using the Kolmogorov–Smirnov test. The null hypothesis for the fundamental investigated characteristics was accepted at the $p > 0.20$.

Relationships between parameters were tested using linear and exponential regression analysis. Correspondences between variables were estimated using coefficient of determination (R^2), standard error of regression (m) and factor F ($F = 10^{2m}$) (Croxton, 1959; Berthelot and Deschamps, 1994; Vinogradov et al., 1999). Factor F and standard error of regression show the greatest possible deviation (on Y axis) experimental points relative to the regression line so being a scattering indicator.

3. Results

Analysis of the data for the phytoplankton productivity parameters in the Kara Sea in September–October as a result of three expeditions has allowed us to study its spatial variability (Fig. 5). In the most productive Yenisey estuary average PP_{int} was 145 mg C m^{-2} d^{-1} (Table 2) and 2–5 fold higher than in the other Kara Sea sub-regions. The same result was achieved for PP_0 values. Mean value for the depth-integrated chl *a* in the Yenisey estuary was 2–3 fold higher than in the other Kara Sea sub-regions. In contrast, Chl_0 concentration in the Ob estuary was 1.4 fold higher than in the Yenisey estuary and 4–7 fold higher than in the other sub-regions. P^b_{opt} defined as the maximum values within euthotic layer were highly variable between sub-regions. Maximum regional value of this parameter was observed in the Southwestern area and minimum in the areas of western and eastern slopes of St. Anna's trough, corresponding to region average values of 1.81 and 0.57 mg C (mg chl *a*)$^{-1}$ h^{-1}, respectively (Table 2). It should be noted high variability of the phytoplankton productivity characteristics in various Kara Sea areas. Coefficient of variation was > 32% and sometimes exceeded 100%.

The trophic status of the Kara Sea sub-regions was determined from regional average values of primary production and chl *a*. Based on surface chl *a* (Antoine et al., 1996) the Ob and Yenisey estuaries, as well as the river runoff area in the autumn, were identified as an eutrophic waters (Chl_0 > 1 mg m^{-3}). The Southwestern area and waters of St. Anna's trough (Northern WM) are identified as typically mesotrothic (0.1–1 mg chl m^{-3}). However, according to PP_{int}, only the Yenisey estuary may be identified as intermediated between mesotrothic and oligotrophic waters (M = 145 mg C m^{-2} d^{-1}), and other Kara Sea areas are typically oligotrophic with water column primary production < 100 mg C m^{-2} d^{-1}.

The data used in this paper had been obtained during different years. Thereby, the question is how the average long-term values characterize a spatial variability of productivity parameters in different years. Table 3 illustrates the average values of the productivity parameters in the Kara Sea sub-regions in 1993, 2007 and 2011. As a whole, the spatial variability of PP, chl *a* and AN in the different years are close to a patterns based on averaged long-term values. According to PP_{int} and PP_0 data the Yenisey estuary in 1993 and 2011 was more productive than other areas. The least values of these parameters were observed in the northern St. Anna's trough. In the Yenisey estuary in 2011 Chl_{ph} was 3–4 fold higher than in the other studied areas while in 1993 maximal value of this parameter was observed in the Ob estuary. It should be noted that there were no studies in the Yenisey estuary in 2007 and in the Ob estuary in 2011, therefore impossible to compare the productivity of these regions at that time (Table 3). In 1993 Chl_0 values in the Ob estuary were higher than in the Yenisey estuary, the Ob–Yenisey river plume WM and the Southwestern area by the factors of 3, 6 and 19, respectively. Such distribution was achieved for averaged long-term data. In 2007 various Kara Sea sub-regions were not distinguished by average Chl_0 values. In 2011 average Chl_0 values in the Yenisey estuary were 3–5 fold higher than in the other studied areas of the sea (Table 3).

Table 4 represents the equations of linear regression for relationships between productivity parameters and environmental factors in the Kara Sea. There is a weak correlation between the surface chl *a* and water column primary production (R^2 = 0.12) (Table 4, Fig. 6a). In contrast, PP_{int} were strongly correlated with P^b_{opt} and Chl_{ph} (R^2 = 0.64 and 0.34, respectively) (Table 4, Fig. 7a, b). Similar positive correlations existed between surface primary production and chl *a*, as well as P^b_0 (R^2 = 0.49 and 0.58, respectively) (Table 4, Fig. 8a,b). It is interesting to note that very close to our results relationship between PP and chl *a* (R^2 = 0.46) was quantified with pan-arctic approach for all depths (Matrai et al., 2013).

Regarding PP_{int} and environmental variables relations noteworthy the lack of dependence on T_0 and week positive correlations with PO_4 and NO_2+NO_3 (R^2 = 0.22 and 0.13, respectively). More close link marked with $Si(OH_4)$ (R^2 = 0.35) (Table 4). It should be noted that the most strong correspondence was between PP_{int} and I_0 (R^2 = 0.57) (Fig. 9a) that may be indicates dominating role of incident solar irradiance in limitation of the integrated primary production during the autumn. The similar output was achieved as a result of correlation analysis of P^b_{opt} and environmental variables relationships. P^b_{opt} depended on level of incident surface PAR (R^2 = 0.56) (Fig. 9b) and poor correlated with nutrients and surface temperature (Table 4).

The exponential relationships were marked between PP_{int} and Chl_0 as dependent variables and surface salinity and stratification index ($\Delta\sigma_t$). The last parameter is a residual between the water density on 20 and 0 m (Tremblay et al., 2009) (Fig. 10a,b and 11). Depth of 20 m was chosen based on analysis of vertical σ_t distribution as the depth which set directly under the maximum density gradients horizon.

It should be noted the high values of standard error of function (m) and factor F as an indicator of data scattering which suggest that strong spatiotemporal variability of phytoplankton productivity characteristics and environmental parameters is the pattern of the Kara Sea ecosystem (Table 4). At the same time another source of the scatter is the methodical uncertainties with application of different field approaches.

4. Discussion

4.1. Spatial variability of primary production and chlorophyll

Surface chl *a* distribution in the Kara Sea depends on river input. There is negative correlation between S_0 and Chl_0 (Fig. 11). The Southwestern and Northern WM with average salinity ~ 25–30 psu were characterized by relatively low Chl_0 (<1 mg m^{-3}). Chl_0 content in the Ob and Yenisey estuaries, as well as river runoff area (S_0 ~ 3–20 psu) exceeded 1 mg m^{-3}. On the contrary, there is no well expressed relationship between PP_{int} and S_0. In the Ob estuary minimum average salinity (2.90 psu) and very low values of integrated primary production (M = 38 mg C m^{-2} d^{-1}) are registered. On the other hand, the Southwestern area with intermediate PP_{int} values (82 mg C m^{-2} d^{-1}) was characterized by relatively high average S_0 (24.93 psu). Apparently, some differences in defined links between, PP and S_0 at the end of vegetative season arise due to predominant role of incident and underwater irradiance in water column primary production. In the Southwestern region relatively high PP_{int} may be cause by increasing water transparency and, as consequence, depth of photosynthetic zone (M = 47 m) which was 2–8 fold deeper than that in the other areas (Table 2). In contrast, in the Ob estuary low PP_{int} values were depended on low water transparency and incident irradiance level. It is shown that in the sunny weather the PP_{int} values could be higher by a factor of 2 (Vedernikov et al., 1994). High phytoplankton biomass in the estuaries was often related to maximum of turbidity in fresh water streams and not related to local increase of growth rate and photosynthesis (Lapierre and Frenette, 2008).

Negative correlations between the phytoplankton productivity characteristics and salinity are a prominent feature of the Siberian seas at the end of summer and in the autumn (Bobrov et al., 1989; Sorokin and Sorokin, 1996; Vedernikov et al., 1994; Nöthig et al., 2003; Mosharov, 2010; Mosharov et al., 2014, in print). It should be noted that this is indirect relation, and increase of PP and chl *a* in a brackish waters should be caused by other reasons. Those factors are the concentrations of PO_{4av} and $Si(OH)_{4av}$ which exceed limitation values (Fisher et al., 1992) in the Ob and Yenisey estuaries, as well as on the adjacent shelf, which are influenced by rivers discharge (Table 5). Regarding to sum of nitrite and nitrate this conclusion is not evident. Above limitation NO_2+NO_{3av} values are measured only in the Ob estuary. Spatial distribution of NH_{4av} was similar to the PO_{4av} and $Si(OH)_{4av}$.

Transfer of phytoplankton with river runoff to the Ob-Yenisey shoal and transport with river origin lenses to the western part of the sea are another reasons of productivity increase in water with low salinity (Zatsepin et al., 2010; Makkaveev et al., 2010). Such explanation based on "outwelling" hypothesis involving that the considerable part of synthesized organic matter is not used in estuaries ecosystems and can be transported to the adjacent areas of the sea enhancing their productivity (Dame et al., 1986; Small et al., 1990; Winter et al., 1996).

4.2. Relationships between primary production, chl a and phytoplankton assimilation activity

Surface chl *a* concentration strongly varied in the Kara Sea in autumn (Table 3). The maximum Chl_0 concentration was registered in the Ob and Yenisey estuaries (> 3 mg m^{-3}). On the shelf and in the Southwestern area its concentration varied from 1 to 3 mg m^{-3} and from 0.2 to 1 mg m^{-3}, respectively. Relatively low average Chl_0 was in the St. Anna's trough, Northern WM (0.5–0.7 mg m^{-3}) (Bobrov et al., 1989; Vedernikov et al., 1994; Nöthig et al., 2003;Vetrov, 2008; Mosharov, 2010; Mosharov et al., 2014, in print). Calculations of Chl_0 concentration which are presented on the modern satellite Kara Sea maps need correction, especially for river discharge areas. However, these maps well describe a relative chl *a* distribution patterns (Vetrov, 2008; Pabi et al., 2008).

Surface chl *a* is considered in some empirical algorithms as a single variable which allows to estimate the integrated ocean primary production (Smith and Baker, 1978; Eppley et al., 1985; Vinogradov et al., 1996; Vinogradov et al., 2000; Carr et al., 2006; Tilstone et al., 2009; Hill and Zimmerman, 2010; Matrai et al., 2013; Hill et al., 2013). Therefore, it is important to estimate influence of Chl_0 on water column primary production. Regression analysis of Chl_0 and PP_{int} links reveals that only 12% variability of integrated PP in the Kara Sea depends on the surface chl *a* ($R^2 = 0.12$). It is accepted that in the World Ocean Chl_0 defines <50% of integrated primary production (Banse and Yong, 1990; Balch et al., 1992; Behrenfeld and Falkowski, 1997a). Fig. 6a represents results of comparison between Chl_0–PP_{int} relationships in the Kara Sea and the regions of the World Ocean with comparable environmental conditions (Vedernikov and Gagarin, 1998; Vinogradov et al., 1999; Vedernikov et al., 2001; Pabi et al., 2008). The Kara Sea Chl_0–PP_{int} database is different from other Arctic regions and cold-water areas of the World Ocean (Fig 6). The difference was that PP_{int} values in the Kara Sea were less than in the other regions with the same Chl_0 concentrations. Depth-integrated Kara Sea primary production was 2–3 fold less than in the Barents and Pechora Seas (Vedernikov and Gagarin, 1998; Vedernikov et al., 2001) and 8–12 fold less than in the Chukchi and Beaufort Seas (Pabi et al., 2008), as well as in the World Ocean areas located polarward 40º (Vinogradov et al., 1999).

At present chlorophyll specific photosynthetic rate under optimum light conditions (optimum assimilation number) is considered as the key parameter in the primary production models. Accuracy of P^b_{opt} estimations determines a models performance (Behrenfeld and Falkowski, 1997b; Carr et al., 2006). The regression analysis shown a close relationship between PP_{int} and P^b_{opt} in the Kara Sea ($R^2 = 0.64$) (Fig. 7a). Previously it was noted that variability of integrated ocean primary production mainly depends on Chl_{ph} and spatial variability of P^b_{opt} (Behrenfeld and Falkowski, 1997b).

Thus, in autumn in the Kara Sea the water column primary production were mainly determined by phytoplankton photophysiology expressed in terms of assimilation activity rather than chlorophyll biomass. On the other hand, surface primary production depended on both Chl_0 and P^b_0 closed to P^b_{opt} ($R^2 = 0.49$ and 0.58, respectively). Hence, at the end of a vegetative season high (≥ 1 mg m^{-3}) surface chl *a* was not an indicator of phytoplankton activity within photosynthetic layer where carbon assimilation was low. Maximum of PP and P^b_{opt} values usually were registered within subsurface layer (upper 5 m). PP values sharply decline with depth as indicated by Z_{ph} thickness in the different Kara Sea regions (Table 2, see also section 4.4).

4.3. Relationships between productivity parameters and surface environmental characteristics

It is known that the fundamental environmental factors limiting Arctic Ocean primary production in the second half of a vegetative season are the low nutrients concentration, low water temperature and incident and underwater PAR (Sakshaug, 2004). However, it is not clear what factor mainly limits PP_{int} (Popova et al., 2012).

4.3.1. Influence of incident PAR on primary production and phytoplankton assimilation activity

It had been shown that in the global scale incident solar radiation insignificantly influence on water column PP due to photoacclimation mechanisms to low light level and photoinhibition at high I_0, as well as impact of co-limiting factors, first of all nutrients (Behrenfeld and Falkowski, 1997b). *A priori* it is possible to assume that light conditions in the Arctic Ocean significantly influence on primary production, especially at the end of vegetative season due to low daily PAR related to decreasing day length and solar elevation angle (Smith and Sakshaug, 1990; Sakshaug, 2004). In the areas of river discharge PP_{int} can be limited by underwater PAR because of low water transparency besides incident surface irradiance (Vedernikov et al., 1994; Sorokin and Sorokin, 1996).

Since the end of August to October I_0 values varied from 1.56 to 32.07 mol quanta m^{-2} d^{-1} (Fig. 12). Wide range of variability allows to estimate a significant relationship between integrated primary production, maximum water column assimilation number and incident PAR (Table 4). It is shown that log-based PP_{int} and P^b_{opt} strongly correlated with I_0 (R^2 = 0.57 and 0.56, respectively) (Fig. 9a,b). Linear relationship between AN and I_0 was noted in some areas of the Canadian Arctic during the summer (Platt et al., 1987). Low irradiance mainly defined low (<100 mg C м$^{-2}$ d^{-1}) PP_{int} in many Kara Sea areas.

In some studies light conditions are considered as a key factor in limiting Arctic Ocean primary production in spring and summer (Lee and Whitledge, 2005; Hill and Cota, 2005; Ardyna et al., 2011). During the autumn at the end of a growth season PAR becomes the main factor for primary productivity (Platt et al., 1987; Hegseth, 1997; Brugel et al., 2009; Yun et al., 2012). In September 1993 low irradiance (Vedernikov et al., 1994) limited PP_{int} in the Ob estuary. In the second half of September and at first of October 2011 I_0 did not exceed 12 mol quanta m^{-2} d^{-1}, and the lowest (2–7 mol quanta m^{-2} d^{-1}) values of incident solar radiation was registered in St. Anna's trough area and in vicinity of Novaya Zemlya (Mosharov et al., 2014, in print). These values are close to compensation irradiance of diatom communities in the Arctic (1.3–1.9 mol quanta m^{-2} d^{-1}) (Tremblay et al., 2006). Such extremely low values of I_0 with a low water transparency (Secchi depth on average 10 m) decreased of photosynthetic layer and led to

PP_{int} decline. This process was confirmed by reliable positive correlation between log-transformed values of I_0 and Z_{ph} ($R = 0.38$, $p = 0.002$, $N = 69$).

It is interesting to analyse variability of water column photosynthetic efficiency index (ψ) (Falkowski, 1981) which is used in primary production models (Behrenfeld and Falkowski, 1997b). In September and at first of October average ψ values varied from 0.56 to 2.14 g C (g chl *a*)$^{-1}$ mol quanta^{-1} d^{-1}. The minimum value of this index was calculated in the Southwestern and Northern areas, and maximum was obtained in the Ob estuary (Table 2). The average ψ = 0.77 g C (g chl *a*)$^{-1}$ mol quanta^{-1} d^{-1} registered at the end of a vegetative season in the Kara Sea was 2 fold higher than calculated earlier in summer in the other Arctic Ocean areas (0.33–0.36 g C (g chl *a*)$^{-1}$ mol quanta^{-1} d^{-1}) (Harrison et al., 1982; Platt et al., 1987). Our results is close to the values calculated for Norwegian Sea in July (0.79 g C (g chl *a*)$^{-1}$ mol quanta^{-1} d^{-1}) (Vedernikov and Demidov, 1997). The dependence between ψ and I_0 was not found that inconsistent with previous results where the reliable inverse relationship between these parameters was noted (Vedernikov and Demidov, 1999). Such contradictory results suggest that the further studies of ψ spatiotemporal variability and relations of this parameter with environmental variables are important.

4.3.2. Influence of nutrients on Kara Sea primary production and phytoplankton assimilation activity

In the present work we studied relationships between phytoplankton productivity characteristics and content of nutrients (PO_4, NO_2+NO_3, NH_4 and $Si(OH)_4$), which were integrated and averaged within photosynthetic layer. The correlation analysis suggests that these variables more related with PP_{int} and P^b_{opt}, than the surface nutrients (data not shown).

During the autumn in the Kara Sea, PO_{4av} changed from 0.04 to 2.08 µM, concentration of NO_2+NO_{3av} varied within 0.04–7.79 µM, values of $Si(OH)_{4av}$ varied from 0.38 to 112.62 µM, and NH_{4av} ranged from 0.09 to 4.37 µM (Fig. 12). Means nutrient concentrations shown that phytoplankton growth and photosynthesis were limited by NO_2+NO_3 in September and at the first of October almost the entire sea except the Ob estuary (Table 5). Phosphates concentration in photosynthetic layer slightly exceeded limiting values in the Southwestern area (0.23 µM) and was 2–6 fold higher in the Ob and Yenisey estuaries and in the river discharge area. Northern WM was characterized by a little below limiting concentrations of PO_4 (0.18 µM). $Si(OH)_4$ could be the limitation factor of phytoplankton development in the Southwestern and Northern WM despite exceeding limit (2.74–4.77 µM) (Fisher et al., 1992). It is known that under low water temperatures in Arctic and Antarctic the low rates of dissolution and silicon regeneration can limit photosynthesis even at raised $Si(OH)_4$ (Treguer et al., 1989; Harrison and Cota, 1991).

N/P was less than Redfield-ratio (Redfield et al., 1963) in entire Kara Sea (Table 5). This result corresponds with representations about a prominent role of nitrogen in the Arctic Ocean (Tremblay et al., 2006; Tremblay and Gagnon, 2009). Variability of Si/N ratio shown the depletion of dissolved nitrogen in comparison with silicon within subsurface layer in the autumn (Si/N> 1.44).

It has been shown that the river runoff into the Arctic Ocean is enriched by the dissolved forms of nitrogen and silicon compared with phosphates (Macdonald et al., 1987; Gordeev et al., 1996). Therefore, it is possible to assume PO_4 limitation of phytoplankton growth and photosynthesis in the vicinity of Kara Sea estuaries (Sakshaug, 2004). On the other hand, it is noticed that the dissolved phosphorus presents at a surface in sufficient quantity for phytoplankton growth even in summer at its minimum annual concentrations (Harrison and Cota 1991). The analysis of the nutrient database allows to conclude that PO_4 in photosynthetic layer less influenced on phytoplankton development than NO_2+NO_3 concentrations.

Interestingly to consider the $NH_4/\Sigma N$ ratio variability as an indicator of possible compensation of nutrient supply by regenerated nitrogen. $NH_4/\Sigma N$ ratio varied on average by 2 times from 0.39 in the Ob estuary to 0.61 in the Southwestern area (Table 5). High values of $NH_4/\Sigma N$ ratio and relatively high NH_4 (M = 0.54–2.11 µM) suggest the considerable role of regenerated nitrogen during the autumn (Eppley et al., 1969; MacIsaac and Dugdale, 1969). Previously the importance of regenerated N for the nutrient supply has been repeatedly noted in other areas of the Arctic Ocean (e. g. Harrison et al., 1982; Kristiansen and Lund, 1989).

It was shown a slight correlation between PP_{int} and PO_4, as well as between P^b_{opt} and PO_4 in the photosynthetic layer (R^2 = 0.22 and 0.17, respectively). Weak relationships between PP_{int} and NO_2+NO_3, as well as between P^b_{opt} and NO_2+NO_3, is noted also (R^2 = 0.15 and 0.08, respectively). It is known, that direct relation between parameters of productivity and nutrients in the Arctic Ocean is often hard to determine (Harrison and Platt, 1986; Harrison and Cota, 1991, Cota et al., 1996). The explanations of the lack of correlation are in mismatch in time of nutrients enrichment of the photosynthetic zone and intensification of productivity processes, use the recycled nutrients, and also succession changes of phytoplankton community structure. The close relationships was obtained between PP_{int}, P^b_{opt} and $Si(OH)_4$ (R^2 = 0.35 and 0.21, respectively) that revealed the significance of diatoms in the Kara Sea phytoplankton community on the most sites (Nöthig et al., 2003; Sukhanova et al., 2010).

The problem of the main factor in limitation of Arctic Ocean phytoplankton primary production continues to be the focus of attention (Carmack et al., 2006; Popova et al., 2012;

Matrai et al. 2013). The principal role of the dissolved nitrogen is noted (Carmack et al., 2004; Lee and Whitledge, 2005; Tremblay and Gagnon, 2009). Light conditions are considered to be the key of environmental factor reducing PP_{int}, especially at the end of the vegetative season (Platt et al., 1987; Hegseth, 1997; Hill and Cota, 2005; Brugel et al., 2009; Bélanger et al., 2012; Yun et al., 2012). Comparison of coefficients of correlations between PP_{int}, P^b_{opt} and incident PAR, as well as the these parameters and nutrients, has shown that in September and in the beginning of October phytoplankton primary production in the Kara Sea (Table 4) was depended mainly on I_0 (Table 4). Weak relations with concentrations of PO_4 and NO_2+NO_3 are caused by low phytoplankton assimilation activity at the end of the growth season. In this period a possible additional flux of nutrients into the photosynthetic layer owing to local upwelling and vertical mixing does not lead to the increase of primary production (Codispoti et al., 2013).

Annual PP in the Arctic Ocean depends on intensity of the spring, and sometimes fall blooms, and length of the growth season. Currently, remains unclear what more have more control annual PP and timing of the growth season: available nutrients or incident radiation. Based on available data including only autumn studies we can conclude that incident PAR controls the time of the end of the vegetative season as previously was shown by Tremblay and Gagnon (2009).

4.4. Influence of vertical distribution of productivity parameters on integral values of primary production

Vertical chl *a* distribution features in the Arctic Ocean can significantly impact on primary production due to subsurface chlorophyll maximum (SCM). SCM forms mainly in summer and occasionally promotes of deep primary production maximum or smoothing PP profiles (Martin et al., 2010; Arrigo et al., 2011; Ardyna et al., 2013). Detailed description of vertical PP and chl *a* distribution in the Kara Sea and estimation of environmental influence on peculiarities of profiles of these parameters evidently will be a subject of special study.

The typical profiles of vertical PP and chl *a* distribution and some abiotic factors in the different Kara Sea productivity regions chosen based on surface chl *a* shown in Fig. 13. Earlier was shown that the surface chlorophyll concentration is related to water column integrated chl *a* and shape of the phytoplankton vertical distribution (Morel, Berthon, 1989; Uitz et al., 2006). These findings were obtained using database from Case I waters where optical properties depended on mainly phytoplankton (Jerlov, 1968; Gordon, Morel, 1983). Kara Sea is the basin with Case II waters sensitive to the significant impact of allochthonous organic and mineral matter. Based on available data vertical PP and chl *a* profiles were separated according to the trophic categories with Chl_0 0.1 – 0.5 (I), 0.5 – 1.0 (II), 1.0 – 2.0 (III) and >2 (IV) mg m^{-3}.

As seen in the Fig. 13 and in Table 6 SCM and deep PP maximum in the autumn was marked substantially in the waters of I trophic category (Chl_0 = 0.1 – 0.5 mg m^{-3}) although there are some exceptions to this rule. Relation $Chl_{max}/Chl_0 \geq 1.15$ was accepted as an indicator of well pronounced SCM (Uitz et al., 2006). Apparently, SCM formation in the Kara Sea was similar to the Arctic Seas (Tremblay et al. 2008, Ardyna et al., 2011, Ferland et al. 2011) and other regions of the World Ocean (e. g. Cullen, 1987; Huisman et al., 2006). Its vertical position links with nitracline and near compensation depth where PAR ~ 1% I_0. According to our observations upper boundary of nitracline located within photosynthetic layer or near its lower limit (Fig. 13). It should be noted, that NO_2+NO_3 concentration in the nitracline at some stations was lower than limiting values (< 2 μM) (Fisher et al., 1992) that could prevent from SCM formation. Number of stations with well pronounced Chl_{max} and degree of SCM manifestation (Chl_{max}/Chl_0) decreased with increasing of water productivity. In the previous works the similar patterns were marked in the tropics and moderate waters (Morel, Berthon, 1989; Uitz et al., 2006) and in the Arctic Ocean (Ardyna et al., 2013). As shown in the Table 6 depth of SCM decreased with Chl_0 rising while Chl_{max} values, on the contrary, increased.

To clarify conditions of PP_{int} development we proposed the average chl *a* and PP vertical distribution in the waters of different productivity (Fig. 14) and some statistic parameters (Table 7). Average chl *a* and PP values were calculated for each trophic categories within 5 meters layers. As follows from Fig. 14, SCM in the Kara Sea in the autumn was weakly marked. According to average profiles insignificant SCM (Chl_{max}/Chl_0 = 1.25) was registered in the waters of I trophic type (Chl_0 = 0.1 – 0.5 mg m^{-3}) within 20–25 m close to the 1% PAR (Fig. 14). In the waters of II – IV categories the average chl *a* values gradually decreased with depth. PP maximum was registered on the surface and there are no deep maximum in all trophic categories. Average boundaries of photosynthetic layer were located close to the 0.1% PAR (Fig. 14). Vertical distribution of assimilation number was similar to PP (data not shown). P^b_{opt} was registered in the upper 5 m layer. Obviously, average profiles do not always describe a vertical distribution on the particular station. As shown in the Table 6 SCM was registered in the waters of I category on fairly large number of the stations (65%). Weak degree of SCM manifestation corresponds with various Chl_{max} position within water column and large standard deviations, which reflects significant variability in the shape of vertical chl *a* profiles (Ardyna et al., 2013) (Table 7).

Results of calculations presented in the Table 6 demonstrate the potential role of SCM in PP_{int} in the waters of different productivity. Such estimation is actual in terms of using chl *a* profiles in the Arctic Seas PP models (Arrigo et al., 2011; Ardyna et al., 2013). To calculate width of SCM we use the Gaussian function which parameterize chl *a* profiles (e. g. Platt et al., 1988)

$$H = h / \sigma \sqrt{2\pi} \text{ , where}$$

H – maximum water column chl *a* concentration; h – investigated layer integrated chl *a*; σ – width of SCM. Transforming this equation we obtain

$$\sigma = h / H \sqrt{2\pi}$$

Calculations showed that contribution of the SCM to depth-integrated PP in the different trophic categories ranged from 1 to 27% (Table 7). Our results are close to the previously estimations obtained in September for the Baffin Bay (5.1 – 15.8%) and also for the Beaufort Sea (20.4%) and Greenland Sea (16.6%) (Arrigo et al., 2011).

Peculiarities of vertical chl *a* distribution can be reflected by the relationship between Chl_0 and Chl_{ph} (Fig. 6b). Lack of correlation (R^2 = 0.22) evidence that surface chl *a* poorly predict the water column values. As was shown in case of PP_{int} (Fig. 6a), Kara Sea Chl_{ph} values were less than in the other regions with the same Chl_0 concentrations (Morel, Berthon, 1989; Uitz et al., 2006). As has been recently noted by Ardyna with coauthors (2013), correlation between Chl_0 and Chl_{ph} decreases through the year and reach the minimum during the post-bloom period.

In conclusion it should be noted that presence of SCM at some sites could lead to the decrease of correlation between PP_{int} and Chl_{ph} versus Chl_0 (Fig. 6; Table 4). Generally, pattern of the chl *a* vertical distribution in the Kara Sea at the end of the growth season proves the weak SCM development and influence on PP allocation within water column (Fig. 14). Nevertheless, we consider the low assimilation activity and small Z_{ph} linked to low insolation and water transparency as the main factors decreased relation between surface and water column productivity parameters in the Kara Sea.

4.5. Estimation of Kara sea primary production in September

Estimation of annual and seasonal Arctic Ocean primary production is the most difficult among the World Ocean. Difficulties are associated with sparse of satellite and field data and the absence of local PP and chl *a* algorithms considering Arctic Ocean ecosystem features (Pabi et al., 2008; Arrigo et al., 2011). These problems arise especially for Kara Sea. Thus, ARCSS-PP database recently used for modeling and Arctic Ocean PP estimation (Matrai et al., 2013; Hill et al., 2013) includes only ~ 3 % of Kara Sea chl *a* field measurements.

Comparison of the Kara Sea field and simulated PP data never has been done before. Table 6 represents the results of comparison of model PP_{int} and the shipboard data summarized in the present article. Calculation of water column primary production was made using the C-based model developed for the Southern Ocean (Arrigo et al., 1998; 2008) and modified by Pabi et al. (2008), regression link between PP_{int} and Chl_0 which was performed for the Russian Arctic seas (Vinogradov et al., 2000; Vetrov and Romankevich, 2011), as well as the model developed based on the pan-Arctic PP and chl *a* data (Hill et al., 2013). Information about seasonal variability of PP_{int} in the Kara Sea in September has been obtained from work of Arrigo and van Dijken (2011) who used algorithm of Arrigo et al. (2008). It should be noted that in the model estimates satellite data of chl *a* within the penetration depth ($1/k_d$) were used. Regression analysis suggested that in the Kara Sea average chl *a* within the penetration depth strong correlated with surface chlorophyll (R^2 = 0.99; slope = 0.98; N = 104).

As seen in Table 6 PP_{int} estimations realized using models overestimate *in situ* PP by a factor of 3–7 in estuaries, by a factor of 3–4 in the shelf and by a factor of 3–5 in Northern WM. PP_{int} calculations averaged for the entire sea were 3-fold (Hill et al., 2013) and 7-fold higher (Arrigo and van Dijken, 2011) than field measurements. It should be noted that according to V.Hill with co-authors (2013) annual and monthly PP was integrated to the shallower of UML or Z_{ph} (Table 6).

Differences between measured and estimated values of Kara Sea integrated primary production turned out to be higher than obtained before for the entire Arctic Ocean according to Hill and Zimmerman (Hill and Zimmerman, 2010). These authors found out that models regardless of the complexity and seasonal adaptation overestimate or underestimate the Arctic Ocean PP_{int} by a factor of 2. On the basis of these results the conclusion about well prediction of integrated PP without PAR and photoadaptive parameters input was made. This conclusion can be confirmed by results of researches in Beaufort Sea where it was not possible to establish the reliable relation between primary production and phytoplankton assimilation activity (Hill and Cota, 2005). On the contrary, in the Kara Sea in autumn the correlation analysis revealed a strong relationship between primary production and assimilation activity level, indicating a close link between PP_{int} and P^b_{opt}. Thus, magnitude of chlorophyll specific carbon fixation is an essential PP_{int} models parameter.

In spite of the imprecision of such comparisons (the different time of averaging, spatiotemporal discrepancies), nevertheless, is certain that model calculations of Kara Sea water column primary production by the several times overestimate the proper value of this parameter, at least, in autumn.

5. Conclusions

In the present work the question about influence of integrated and average biotic and environmental values of subsurface layer on primary production in a water column was considered. Also we considered in general how vertical PP and chl *a* distribution features can be reflected in integrated primary production.

The analysis of the database formed by the results of three expeditions during the autumn allows to pay attention to the so called "Kara Sea primary production paradox" which consists in mismatch high surface chlorophyll biomass and low values of water column primary production which feature to the oligotrophic conditions, at least at the end of a vegetative season. Thus, surface chl *a* inaccurately defines the phytoplankton productivity throughout the entire photosynthetic layer. This conclusion, possible, is applicable to the both shipboard and satellite Chl_0. The reason of it is the low transparency of Kara Sea shelf waters because of high allochthoneous POM and DOM that leads to abnormal reduction of a photosynthetic depth, decrease of underwater PAR and, hence, decline PP_{int}. Other reason of the Kara Sea oligotrophy is the low phytoplankton activity caused by PAR limitation at the end of the growth season. Based on available data including just autumn studies we achieved the good agreement with other researchers who concluded that at the end of the growing season the level of incident PAR and phytoplankton photophysiology are the main factors in Arctic Ocean PP (see references in Tremblay et al., 2008).

Low values of Kara Sea primary production at the end of growth season are caused by the general reduction of incident solar radiation in September–October in high latitudes. Apparently, low PAR limits integrated primary production more than the low nutrients in the photosynthetic layer. The results presented here revealed that integrated primary production is closer related with average nutrients concentration in the photosynthetic layer than with their surface values.

The lack of correlation between water column primary production and surface chl *a*, as well as the close relationship between PP_{int} and P^b_{opt}, indicates the main role of photophysiological adaptive processes in Kara Sea primary production during the study period. On the other hand, values of a chlorophyll biomass cannot be an indicator of Kara Sea primary production. It is known also that models of water column primary production based on only surface chl *a* overestimate primary production at low PAR and extremely low temperatures especially in high latitudes (Carr et al., 2006).

To summarize the article should conclude that estimations of Kara Sea primary production performed using algorithms based on solely surface chl *a* are extremely inaccurate.

Other not region specific primary production models are also rough. Improving of Kara Sea primary production estimations imply the development of regional satellite chl *a* algorithm and local primary production model considering specific features of PP in this Arctic Ocean region.

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Fig. 1. Location of the sampling sites in the different regions and water masses of the Kara Sea during August–September 1993 (49 cruise R/V "Dmitry Mendeleev"), September 2007 and September–October 2011 (54 and 59 cruises R/V "Akademik Mstislav Keldysh", respectively). I – Southwestern WM; II – Ob estuary; III – Enisey estuary; IV – River runoff WM; V – Northern WM (St. Anna's trough). Surface 25 psu isohaline is shown (see text of article).

Fig. 2. Relationship between diffuse attenuation coefficient for downwelling irradiance (k_d) and Secchi disk depth (Z_s) obtained in September 1993.

Fig. 3. Frequency distributions of log transformed surface chlorophyll *a* concentration (A) and depth-integrated primary production (B). Solid line is the curve of expected normal distribution.

Fig. 4. Frequency distributions of log transformed surface temperature (A) and concentration of NO_2+NO_3 within euphotic layer (B). Solid line is the curve of expected normal distribution.

Fig. 5. Average values of phytoplankton productivity characteristics in the different regions of the Kara Sea. (A) – depth-integrated primary production (PP_{int}); (B) – surface primary production (PP_0); (C) – surface chl *a* (Chl_0); (D) – chl *a* integrated within photosynthetic layer (Chl_{ph}); (E) – maximum chlorophyll specific carbon fixation rate within a water column (P^b_{opt}). Vertical bars represent the limits of magnitude variability.

Fig. 6. (A) – depth-integrated primary production (PP_{int}) vs. surface chl *a* concentration (Chl_0) in the Kara Sea – closed circles (1); in the Barents and Pechora Seas (Vedernikov and Gagarin, 1998) – triangles (2); in the Chukchi and Beaufort Seas (Pabi et al., 2008) – open circles (3) and in the cold and temperate (polarward 40º) waters (Vinogradov et al., 1999) – (4). Regression parameters of (1) see in Table 4. (B) – photosynthetic layer integrated chl *a* (Chl_{ph}) vs. surface chl *a* concentration (Chl_0) – points and regression line. Relationships between these parameters based on World Ocean datasets are presented (Morel and Berthon, 1989; Uitz et al., 2006).

Fig. 7. Relationships between depth-integrated primary production (PP_{int}) and: (A) – maximum chlorophyll specific carbon fixation rate within a water column (P^b_{opt}); (B) – photosynthetic layer integrated chl *a* (Chl_{ph}).

Fig. 8. Relationships between surface primary production (PP_0) and: (A) – surface chl *a* concentration (Chl_0); (B) – surface chlorophyll specific carbon fixation rate (P^b_0).

Fig. 9. Relationships between depth-integrated primary production (PP_{int}) and: (A) – maximum chlorophyll specific carbon fixation rate within a water column (P^b_{opt}); (B) – subsurface PAR (I_0).

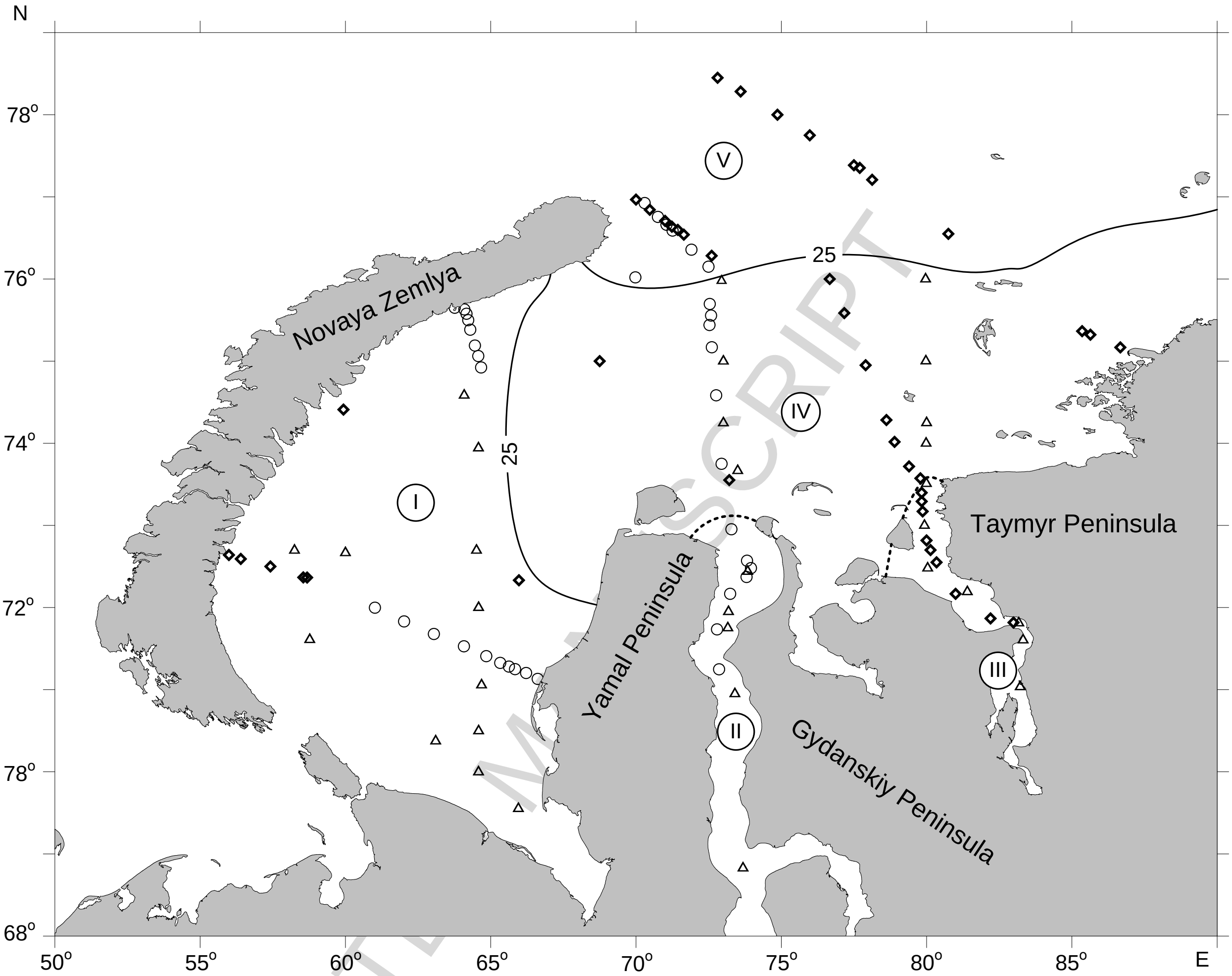
Fig. 10. Depth-integrated primary production (PP_{int}) vs. surface salinity (S_0) (A) and values of stratification index ($\Delta\sigma_t$) (B).

Fig. 11. Correspondence of chl *a* concentration (Chl_0) and surface salinity (S_0) in the Kara Sea.

Fig. 12. Mean values of environmental variables in the different Kara Sea regions. (A) – underwater PAR (I_0); (B) – average content of nitrite and nitrate nitrogen within photosynthetic layer (NO_2+NO_{3av}); (C) – average phosphate content within photosynthetic layer (PO_{4av}); (D) – surface temperature (*T*); (E) – surface salinity (S_0). Vertical bars represent the limits of magnitude variability.

Fig. 13. Typical vertical distribution of primary production (PP), chlorophyll *a* (Chl *a*), sum of nitrite and nitrate (NO_2+NO_3) and water density (σ_t) in the waters of different trophic status determined according to Chl_0 (see text): I – 0.1–0.5 mg m^{-3}; II – 0.5–1.0 mg m^{-3}; III – 1.0–2.0 mg m^{-3}; IV – ≥ 2.0 mg m^{-3}. Sampling was performed: 17.09.2011 at 74.28 N 78.62 E (I); 15.09.2011 at 72.33 N 65.97 E (II); 29.09.2011 at 76.60 N 71.44 E (III); 19.09.2011 at 72.17 N 81.00 E (IV).

Fig. 14. Average profiles of vertical primary production (PP) and chlorophyll *a* (Chl *a*) distribution in the waters of different trophic status determined according to Chl_0 (see text): I – 0.1–0.5 mg m^{-3}; II – 0.5–1.0 mg m^{-3}; III – 1.0–2.0 mg m^{-3}; IV – ≥ 2.0 mg m^{-3}. Horizontal solid bars represent the upper boundary of UML and average depth of photosynthetic layer ($\overline{Z_{ph}}$). Dashed lines represent 10%, 1% and 0.1% levels of underwater PAR (I_0).



△ 49th cruise R/V *Dm. Mendeleev*

○ 54th cruise R/V *Akademik Mstislav Keldysh*

◇ 59th cruise R/V *Akademik Mstislav Keldysh*

Figure 1

ACCEPTED MANUSCRIPT

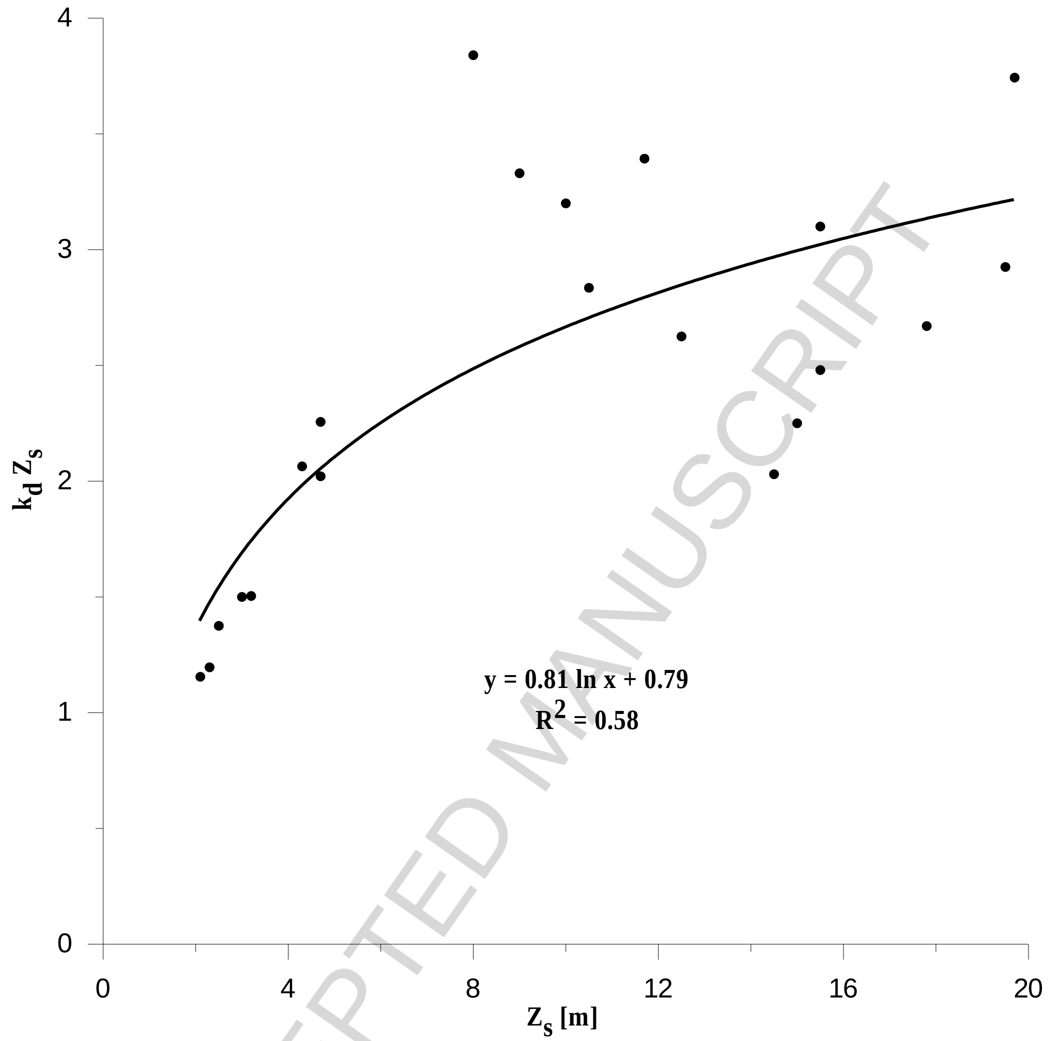


Figure 2

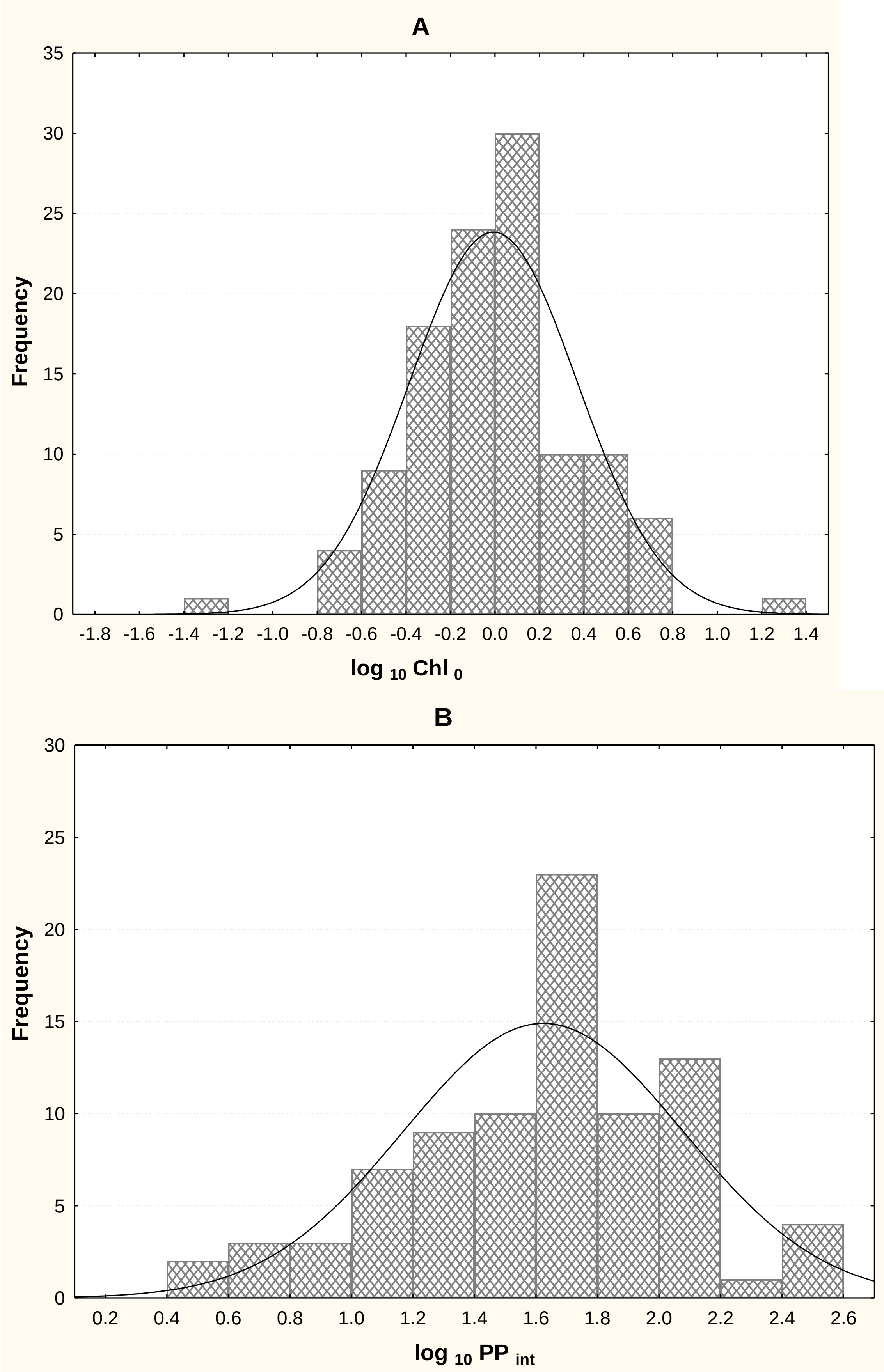

A
Frequency
35
30
25
20
15
10
5
0
-1.8 -1.6 -1.4 -1.2 -1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
log 10 Chl 0
B
Frequency
30
25
20
15
10
5
0
0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6
log 10 PP int

Figure 3

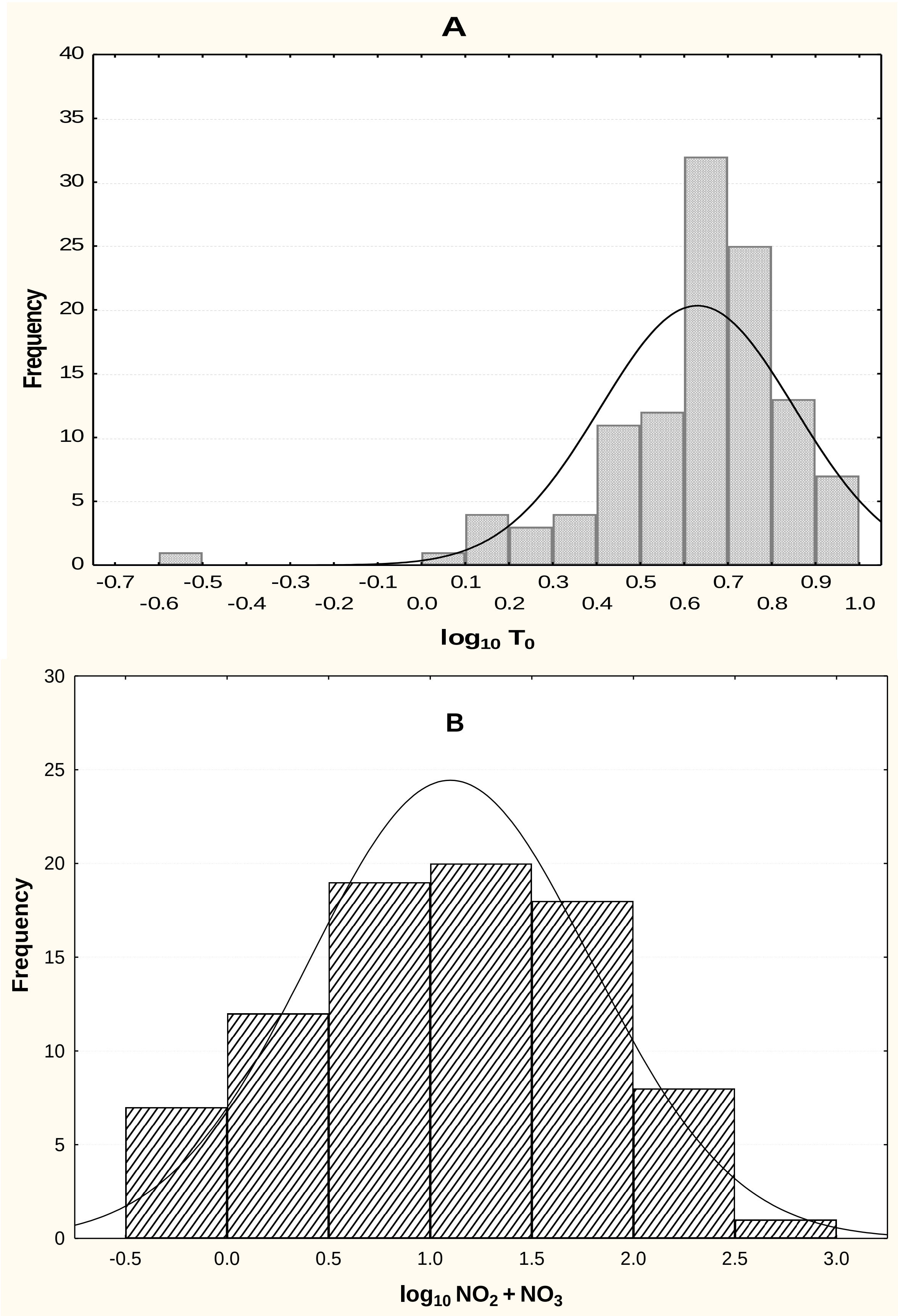
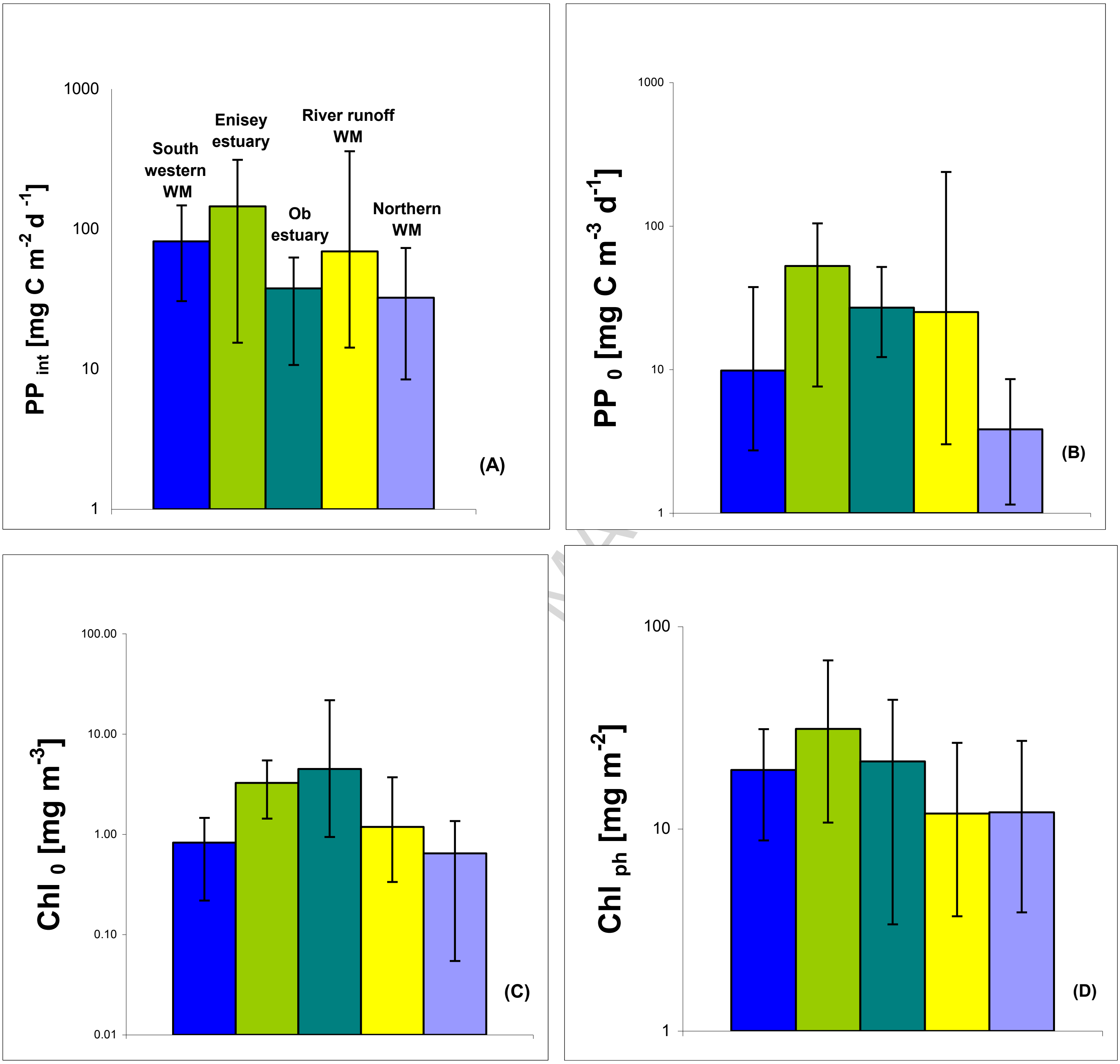

A
Frequency
40
35
30
25
20
15
10
5
0
-0.7 -0.5 -0.3 -0.1 0.1 0.3 0.5 0.7 0.9
-0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
log10 T0
B
Frequency
30
25
20
15
10
5
0
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
log10 NO2 + NO3

Figure 4


1000
100
10
1
PP int [mg C m-2 d-1]
South western WM
Enisey estuary
Ob estuary
River runoff WM
Northern WM
(A)
PP 0 [mg C m-3 d-1]
(B)
100.00
10.00
1.00
0.10
0.01
Chl 0 [mg m-3]
(C)
Chl ph [mg m-2]
(D)

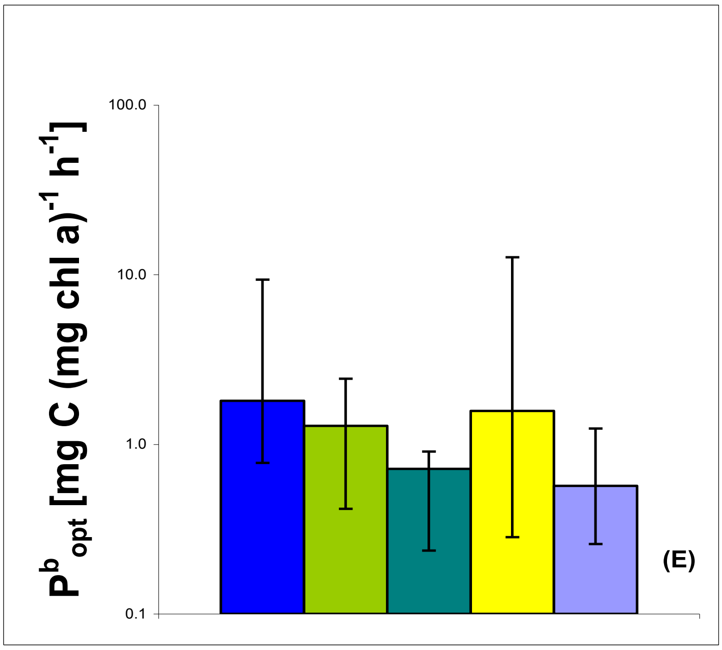
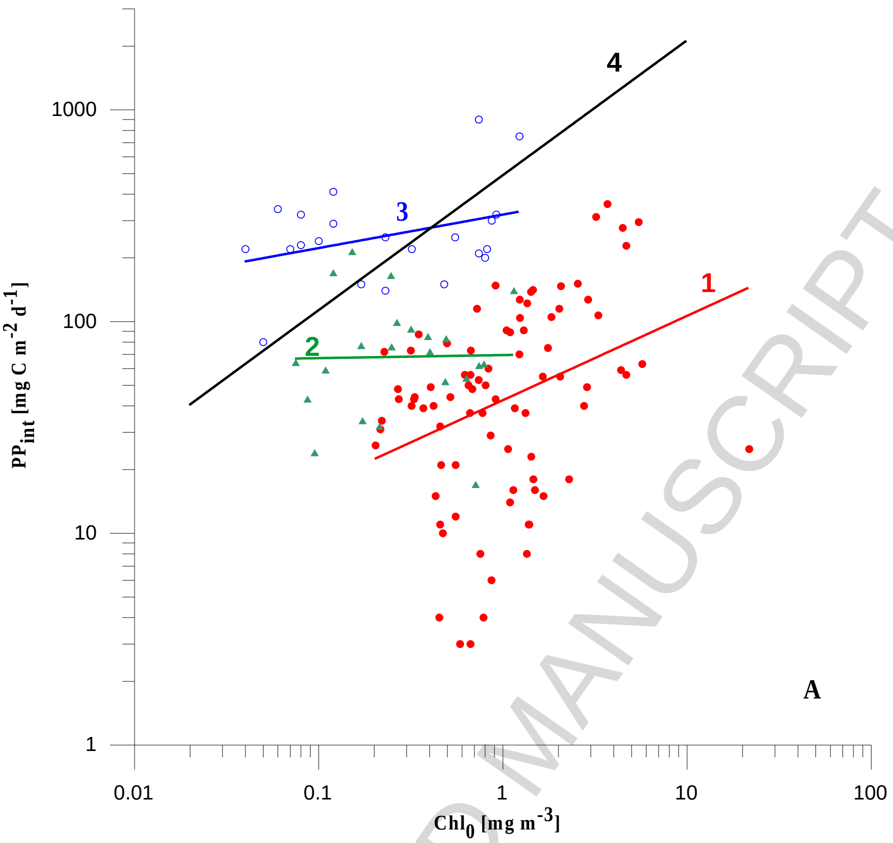
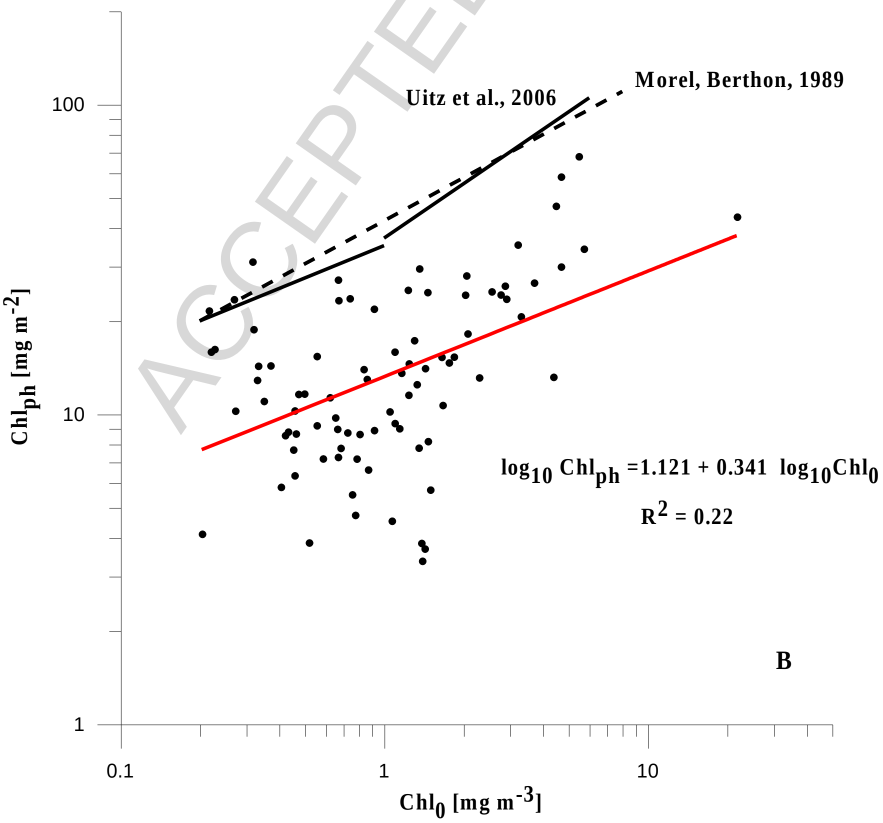


Figure 5



1000
100
10
1
0.01
0.1
1
10
100
PPint [mg C m-2 d-1]
Chl0 [mg m-3]
4
3
2
1
A



100
10
1
0.1
1
10
Chlph [mg m-2]
Chl0 [mg m-3]
Uitz et al., 2006
Morel, Berthon, 1989
log10 Chlph =1.121 + 0.341 log10Chl0
R2 = 0.22
B

Figure 6

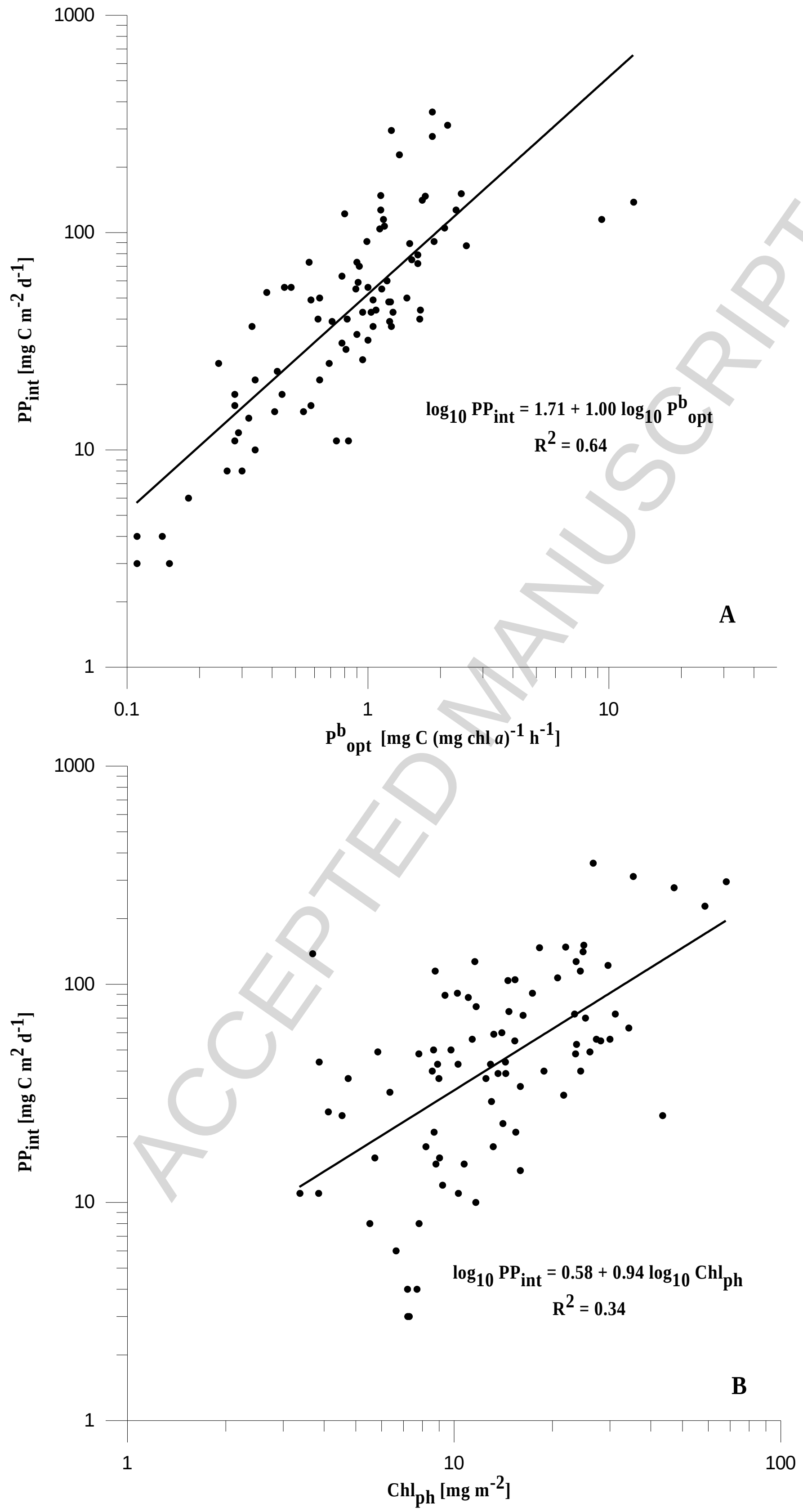
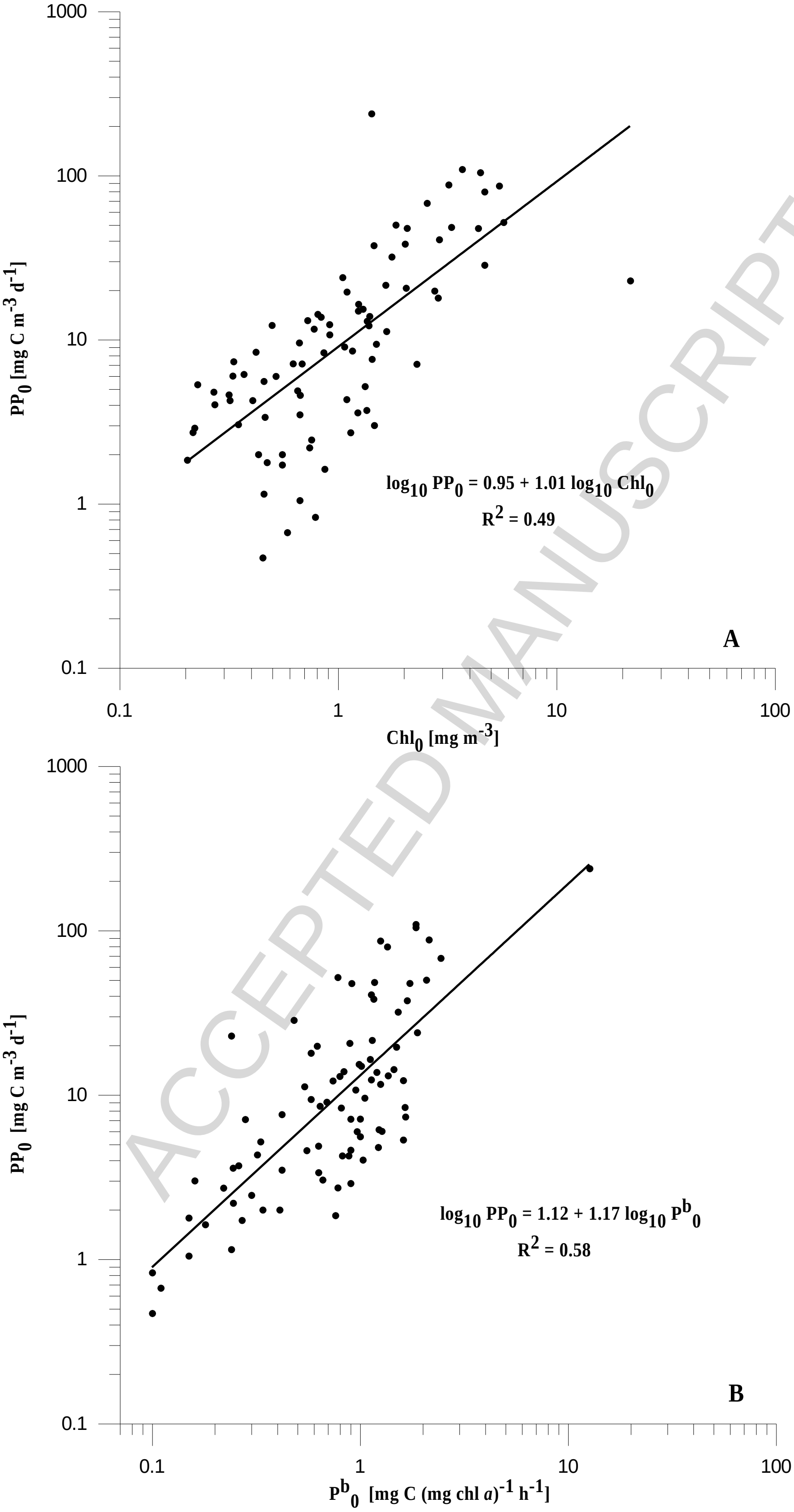

1000
100
10
1
PP_{int} [mg C m^{-2} d^{-1}]
0.1
1
10
P^b_{opt} [mg C (mg chl *a*)$^{-1}$ h^{-1}]
$\log_{10} PP_{int} = 1.71 + 1.00 \log_{10} P^b_{opt}$
$R^2 = 0.64$
A
1000
100
10
1
PP_{int} [mg C m^2 d^{-1}]
1
10
100
Chl_{ph} [mg m^{-2}]
$\log_{10} PP_{int} = 0.58 + 0.94 \log_{10} Chl_{ph}$
$R^2 = 0.34$
B

Figure 7



1000
100
10
1
0.1
PP0 [mg C m-3 d-1]
0.1
1
10
100
Chl0 [mg m-3]
log10 PP0 = 0.95 + 1.01 log10 Chl0
R2 = 0.49
A
PP0 [mg C m-3 d-1]
Pb0 [mg C (mg chl a)-1 h-1]
log10 PP0 = 1.12 + 1.17 log10 Pb0
R2 = 0.58
B

Figure 8

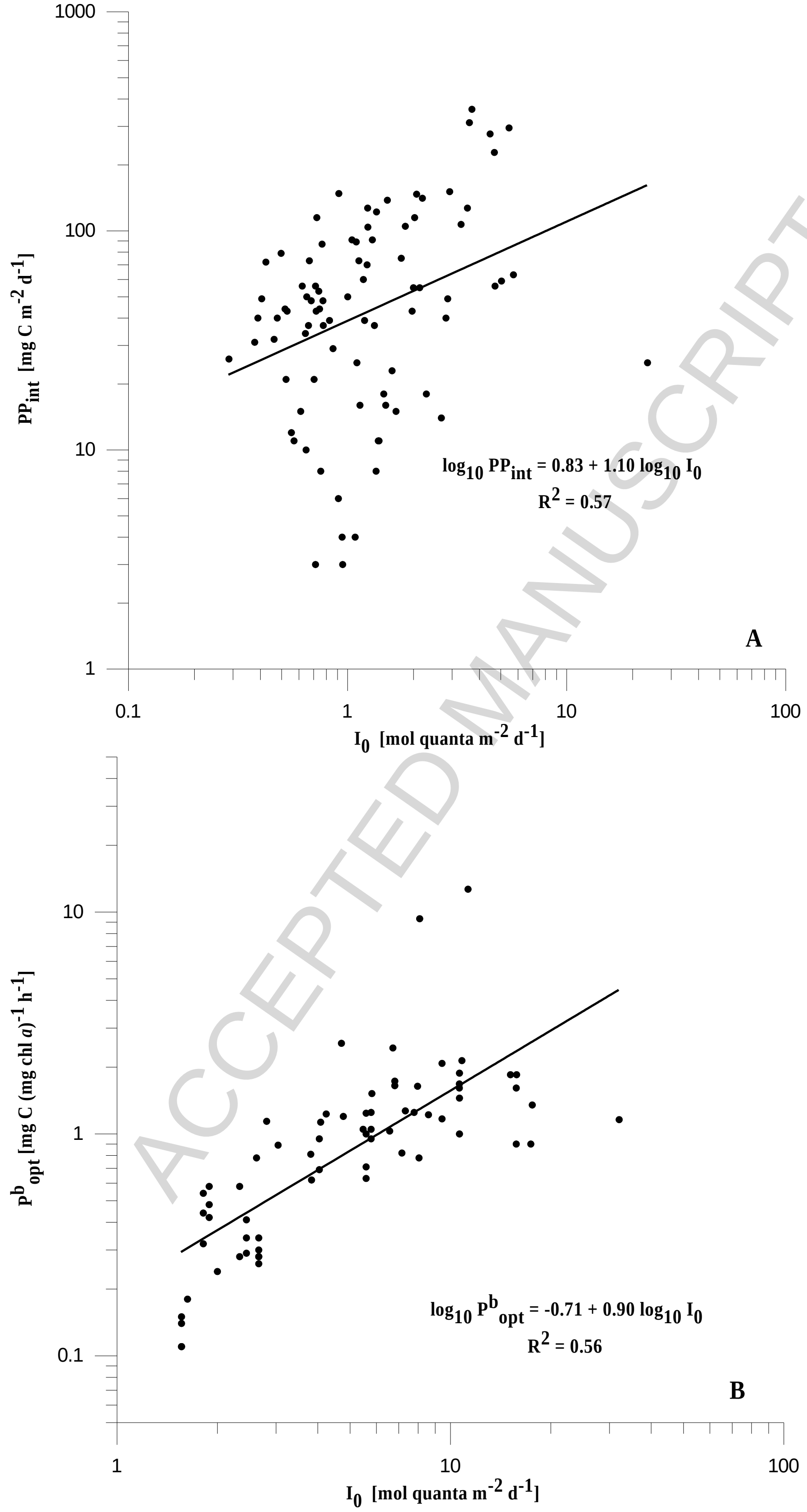
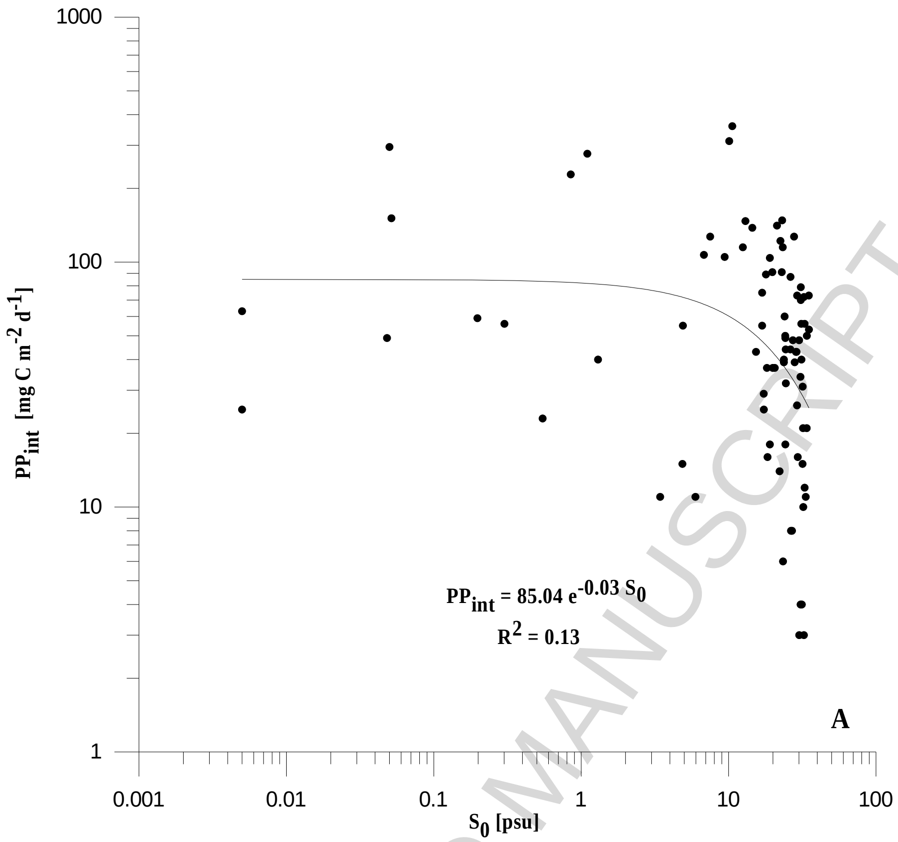
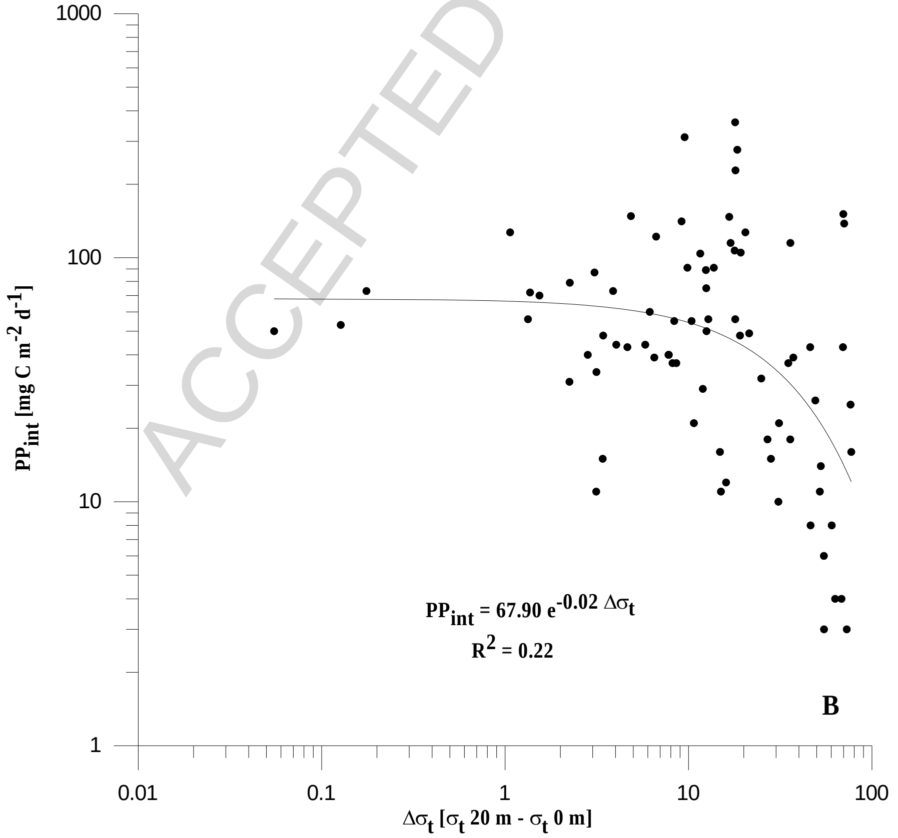

1000
100
10
1
PP_{int} [mg C m^{-2} d^{-1}]
0.1
1
10
100
I_0 [mol quanta m^{-2} d^{-1}]
$\log_{10} PP_{int} = 0.83 + 1.10 \log_{10} I_0$
$R^2 = 0.57$
A
10
1
0.1
P^b_{opt} [mg C (mg chl *a*)$^{-1}$ h^{-1}]
1
10
100
I_0 [mol quanta m^{-2} d^{-1}]
$\log_{10} P^b_{opt} = -0.71 + 0.90 \log_{10} I_0$
$R^2 = 0.56$
B

Figure 9

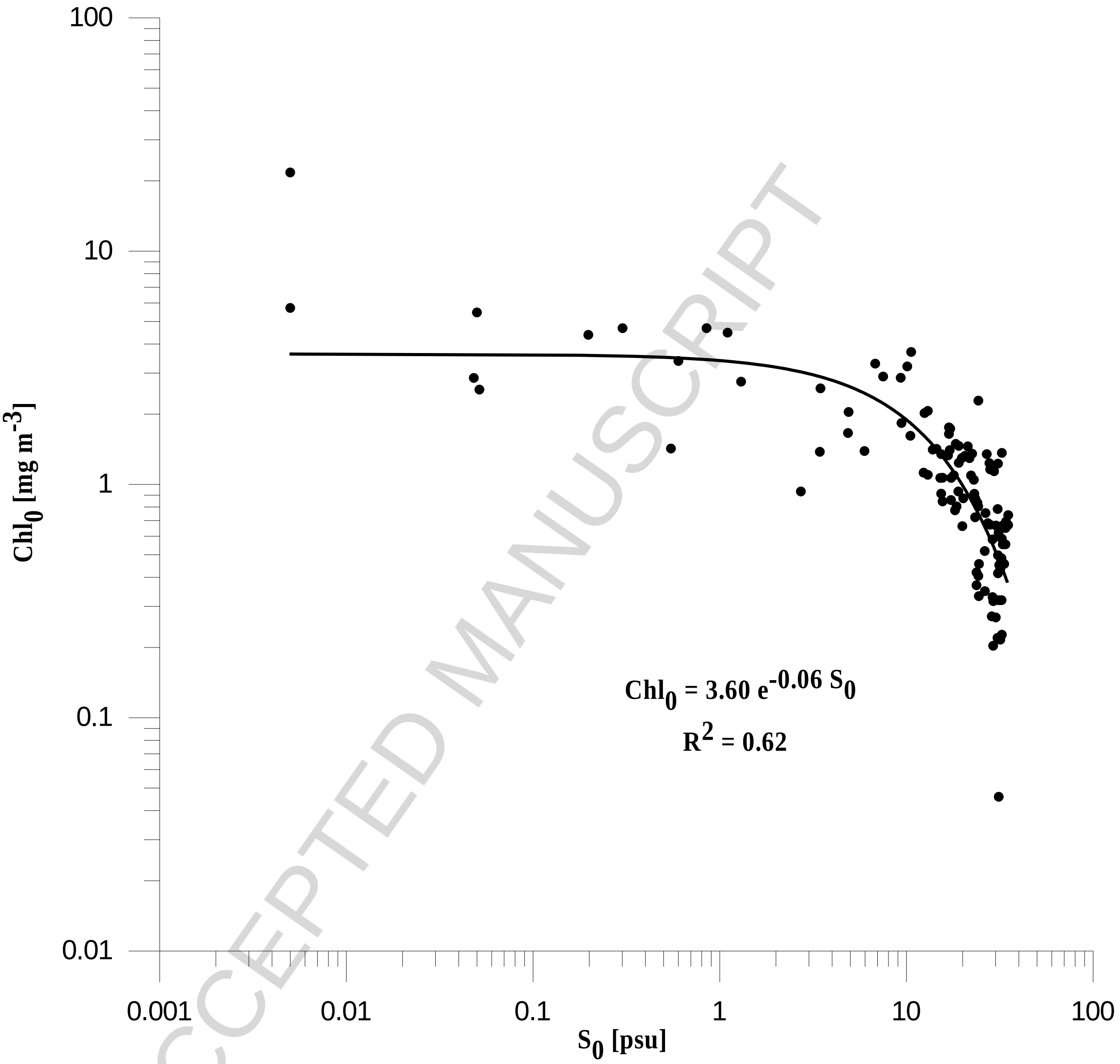


1000
100
10
1
PPint [mg C m-2 d-1]
PPint = 85.04 e-0.03 S0
R2 = 0.13
A
0.001
0.01
0.1
1
10
100
S0 [psu]



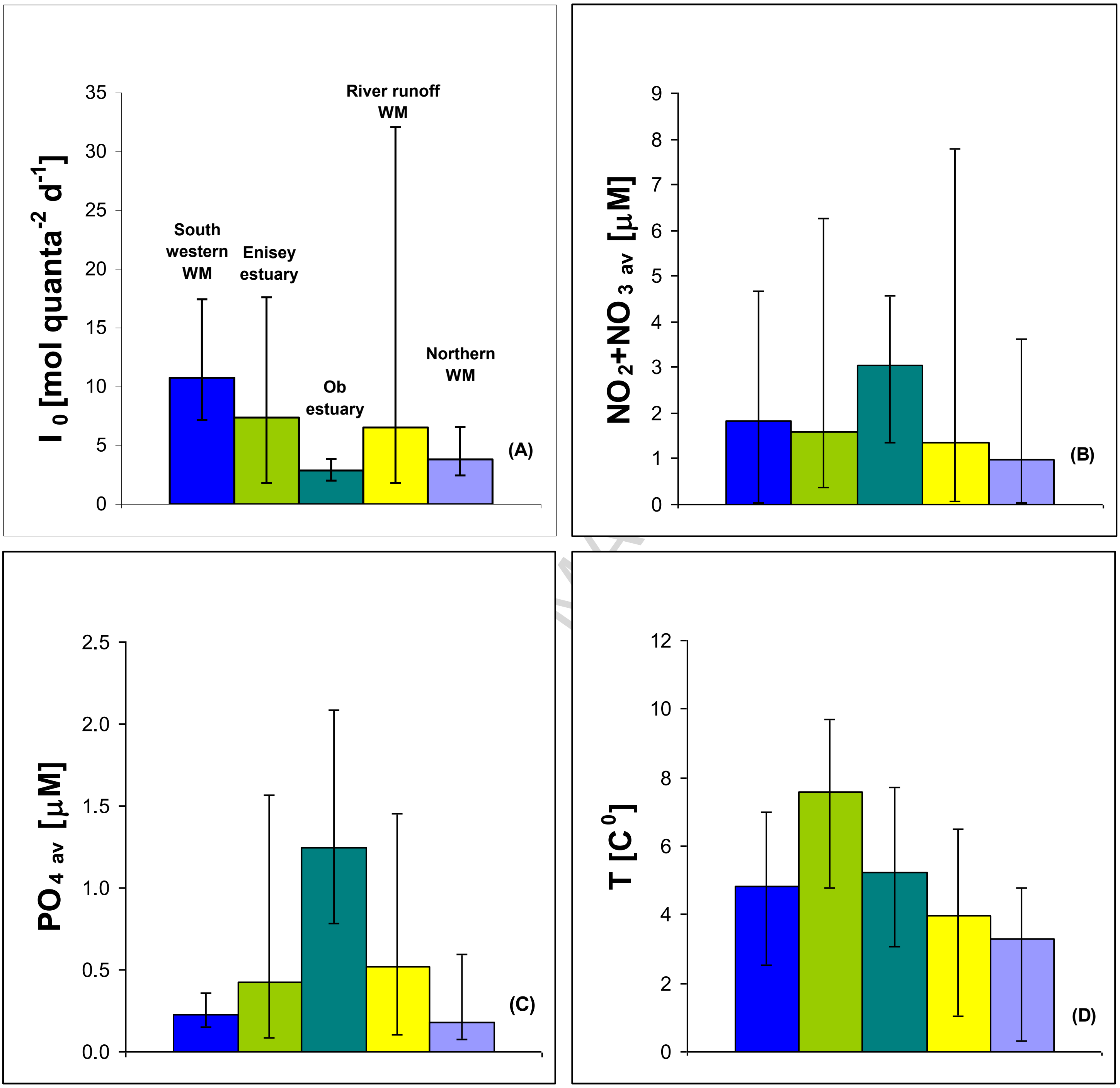
1000
100
10
1
PPint [mg C m-2 d-1]
PPint = 67.90 e-0.02 Δσt
R2 = 0.22
B
0.01
0.1
1
10
100
Δσt [σt 20 m - σt 0 m]

Figure 10



100
10
1
0.1
0.01
Chl0 [mg m-3]
Chl0 = 3.60 e-0.06 S0
R2 = 0.62
0.001
0.01
0.1
1
10
100
S0 [psu]

Figure 11



I 0 [mol quanta-2 d-1]
35
30
25
20
15
10
5
0
South western WM
Enisey estuary
Ob estuary
River runoff WM
Northern WM
(A)
NO2+NO3 av [µM]
9
8
7
6
5
4
3
2
1
0
(B)
PO4 av [µM]
2.5
2.0
1.5
1.0
0.5
0.0
(C)
T [C0]
12
10
8
6
4
2
0
(D)

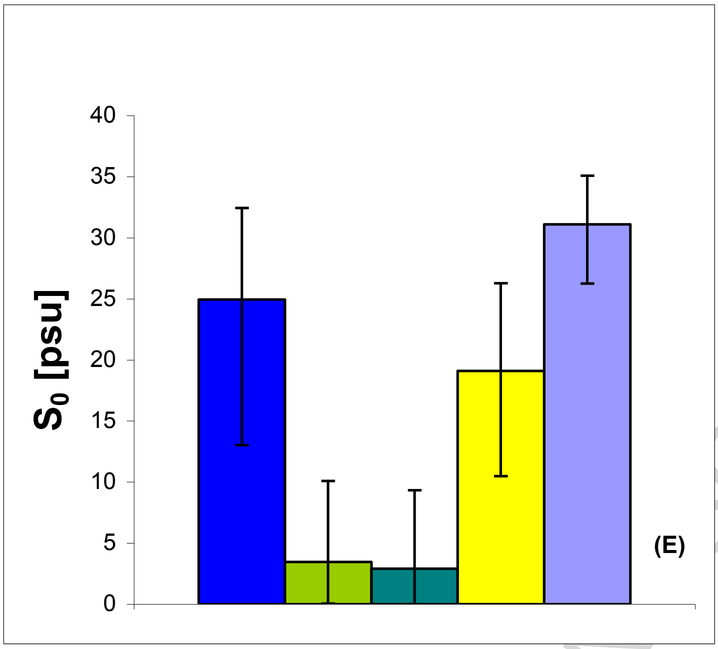
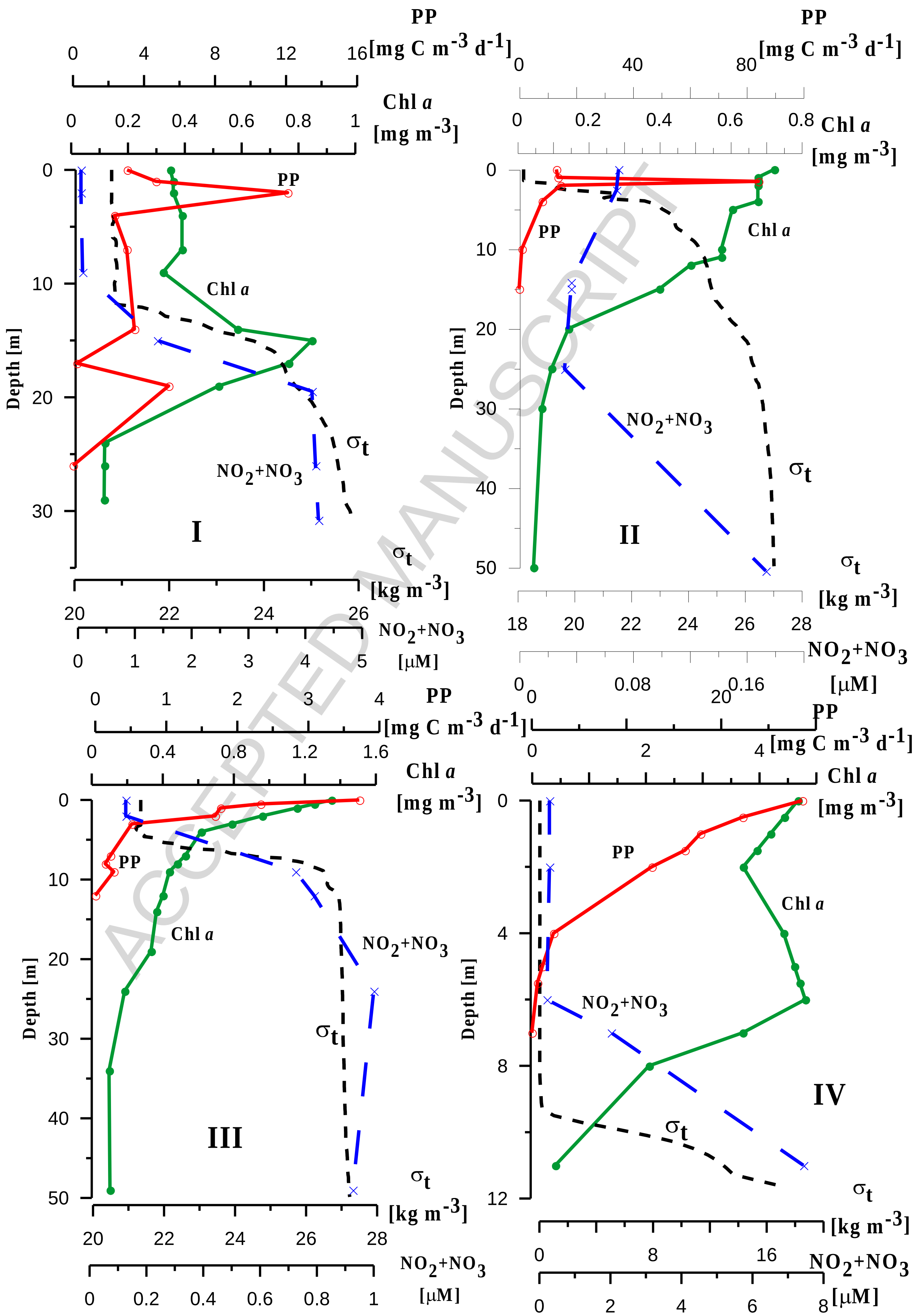
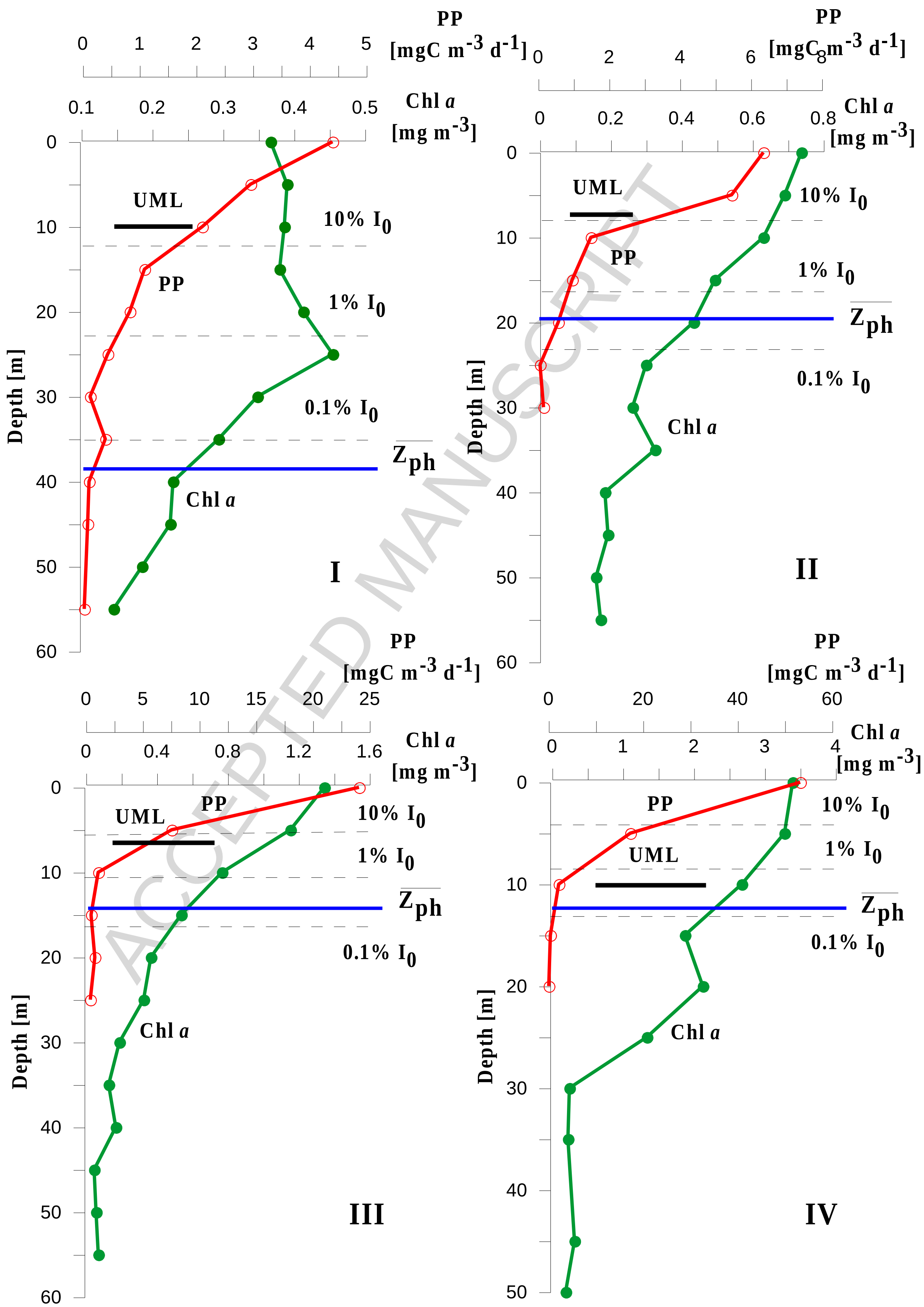


Figure 12



PP
[mg C m-3 d-1]
Chl a
[mg m-3]
Depth [m]
PP
Chl a
NO2+NO3
σt
I
σt
[kg m-3]
NO2+NO3
[μM]
PP
[mg C m-3 d-1]
Chl a
[mg m-3]
Depth [m]
PP
Chl a
NO2+NO3
σt
II
σt
[kg m-3]
NO2+NO3
[μM]
PP
[mg C m-3 d-1]
Chl a
[mg m-3]
Depth [m]
PP
Chl a
NO2+NO3
σt
III
σt
[kg m-3]
NO2+NO3
[μM]
PP
[mg C m-3 d-1]
Chl a
[mg m-3]
Depth [m]
PP
Chl a
NO2+NO3
σt
IV
σt
[kg m-3]
NO2+NO3
[μM]

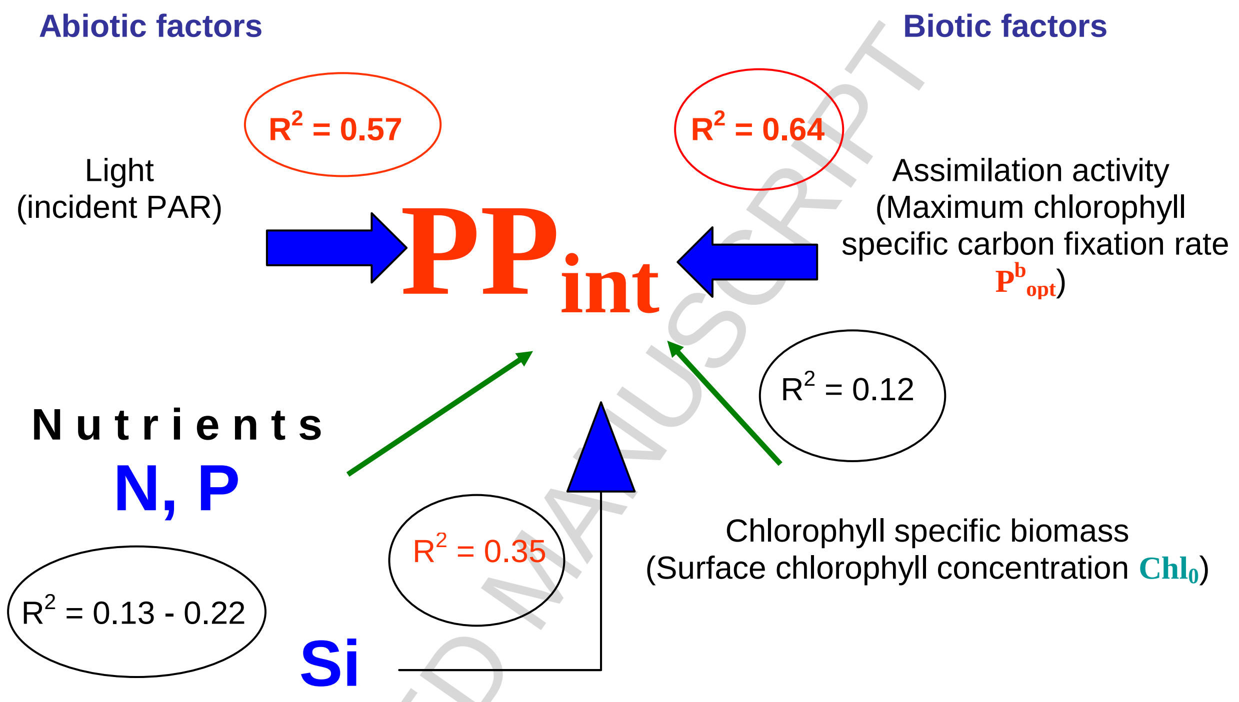
Figure 13



PP [mgC m-3 d-1]
Chl a [mg m-3]
Depth [m]
UML
PP
Chl a
10% I0
1% I0
0.1% I0
Zph
I
II
III
IV

Figure 14

Biotic and abiotic factors controlling Kara Sea water column primary production (PP_{int}) in autumn



Graphical abstract

Table 1 Variables and definitions used in the article

Variable	Units	Definition
PP_{int}	mg C m^{-2} d^{-1}	Depth-integrated primary production
ΣPP_{max}	mg C m^{-2} d^{-1}	Integrated primary production within layer of maximum chl *a* concentration
PP_0	mg C m^{-3} d^{-1}	Surface primary production
Chl_0	mg m^{-3}	Surface chl *a* concentration
Chl_{ph}	mg m^{-2}	Photosynthetic layer integrated chl *a*
Chl_{max}	mg m^{-3}	**M**aximum water column chl *a* concentration
P^b_{opt}	mg C (mg chl *a*)$^{-1}$ h^{-1}	**M**aximum chlorophyll specific carbon fixation rate within a water column
P^b_0	mg C (mg chl *a*)$^{-1}$ h^{-1}	Surface chlorophyll specific carbon fixation rate
ψ	g C (g chl *a*)$^{-1}$ mol quanta^{-1} d^{-1}	Water column efficiency of photosynthesis
I_0 (PAR)	mol quanta m^{-2} d^{-1}	Subsurface photosynthetically available radiation
Z_{ph}	m	Photosynthetic layer up to the compensation depth
Z_s	m	Secchi disk depth
T_0	°C	Surface temperature
σ_t	kg m^{-3}	Water density
$\Delta\sigma_t$ (σ_t 20-σ_t 0)	m	Stratification index
S_0	psu	Surface salinity
$PO_{4\ av}$	µM	Average phosphate content within euphotic layer
NO_2+$NO_{3\ av}$	µM	Average nitrite and nitrate content within euphotic layer
$NH_{4\ av}$	µM	Average ammonium content within euphotic layer
$Si(OH)_{4\ av}$	µM	Average silicic acid concentration within euphotic layer
k_d	m^{-1}	Diffuse attenuation coefficient for downwelling irradiance
Symbols		
PP		Primary production
chl *a*		Chlorophyll *a*
AN		Assimilation number
Abbreviations		
PAR		Photosyntetically available radiation
UML		Upper mixed layer
WM		Water mass
SCM		Subsurface chl *a* maximum

Table 2 Average phytoplankton productivity parameters (M) in the different regions and water masses of the Kara Sea, cv: coefficient of variation (%); N: number of measurements

Variables	Southwestern WM			Ob estuary			Enisey estuary			River runoff WM			Northern WM		
	M	cv	N	M	cv	N	M	cv	N	M	cv	N	M	cv	N
PP_0	9.8	93	14	27.0	60	7	53	62	12	25.2	186	28	3.8	56	18
PP_{int}	82	51	14	38	59	7	145	74	12	69	98	28	32	64	18
Chl_0	0.8	55	29	4.5	132	11	3.3	40	12	1.2	58	34	0.6	47	20
Chl_{ph}	19.6	36	14	21.5	71	7	31.2	58	12	11.9	47	28	12.1	53	18
$P^b{}_0$	1.1	36	14	0.7	32	7	1.3	55	12	1.5	151	28	0.5	58	18
$P^b{}_{opt}$	1.8	122	14	0.7	32	7	1.3	55	12	1.6	142	28	0.6	56	18
ψ	0.6	73	11	2.1	47	4	0.8	33	12	0.8	88	24	0.6	36	13
Z_{ph}	47	51	14	6	77	7	12	27	12	18	40	28	25	38	18

Table 3 Average phytoplankton productivity parametres (M) in the different regions and water masses of the Kara Sea in September–October 1993, 2007 и 2011 гг., cv: coefficient of variation (%); N: number of measurements

Variables	Year	Southwestern WM			Ob estuary			Enisey estuary			River runoff WM			Northern WM		
		M	cv	N	M	cv	N	M	cv	N	M	cv	N	M	cv	N
PP_0	1993	8.9	124	9	28.8	54	4	59.6	42	3	27.5	111	11	-	-	-
	2007	11.0	46	4	24.6	82	3	-	-	-	14.2	44	4	4.2	34	5
	2011	13.1	-	1	-	-	-	50.5	71	9	26.6	241	13	3.7	66	13
PP_{int}	1993	62	55	9	46	37	4	181	63	3	91	106	11	-	-	-
	2007	117	28	4	27	103	3	-	-	-	80	37	4	55	20	5
	2011	115	-	1	-	-	-	133	82	9	48	78	13	24	71	13
Chl_0	1993	0.4	87	10	8.0	115	4	2.7	27	3	1.3	77	11	-	-	-
	2007	1.1	33	18	2.4	52	7	-	-	-	1.1	19	6	0.6	42	7
	2011	0.7	-	1	-	-	-	3.5	42	9	1.1	46	17	0.7	48	13
Chl_{ph}	1993	19.6	32	9	32.6	26	4	24.8	41	3	15.7	36	11	-	-	-
	2007	22.1	35	4	6.8	82	3	-	-	-	13.5	25	4	17.6	58	5
	2011	8.8	-	1	-	-	-	33.4	60	9	8.2	44	13	10.0	26	13
	2007	0.7	35	4	2.3	82	3	-	-	-	0.8	36	4	0.5	52	5
	2011	0.6	-	1	-	-	-	3.0	45	9	0.7	51	13	0.5	35	13
P^b_0	1993	1.2	31	9	0.6	45	4	1.8	32	3	1.4	24	11	-	-	-
	2007	0.8	49	4	0.8	10	3	-	-	-	1.0	49	4	0.6	48	5
	2011	1.4	-	1	-	-	-	1.1	62	9	1.8	189	13	0.5	64	13
P^b_{opt}	1993	1.2	31	9	0.6	45	4	1.8	32	3	1.4	24	11	-	-	-
	2007	1.3	54	4	0.8	10	3	-	-	-	1.0	49	4	0.6	44	5
	2011	9.3	-	1	-	-	-	1.1	62	9	1.9	170	13	0.6	63	13
ψ	1993	0.5	48	10	2.1	47	4	0.7	54	3	0.3	42	11	-	-	-
	2007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	2011	1.6	-	1	-	-	-	0.8	29	9	1.2	62	13	0.6	36	13
Z_{ph}	1993	56	44	9	8	65	4	16	13	3	22	31	11	-	-	-
	2007	33	2	4	3	0	3	-	-	-	19	15	4	36	19	5
	2011	15	-	1	-	-	-	11	25	9	15	47	13	20	28	13

Table 4 Parameters of linear (*y* = *a* + *bx*) regression of log_{10} based phytoplankton production characteristics versus biological and environmental variables, *y* – dependent variable; *x* – independent variable; *a* – intercept; *b* – slope; *N* – number of measurements; R^2 – determination coefficient; *p* value – statistical reliability of regression; *m* – standard error of regression; $F = 10^{2m}$ – index of variability *y* at a defined *x*.

Linear fit								
y	*x*	*a*	*b*	*N*	R^2	*p* value	*m*	*F*
PP_{int}	Chl_0	1.62	0.40	85	0.12	0.001	0.43	7.1
PP_{int}	P^b_{opt}	1.71	1.00	85	0.64	0.000	0.28	3.5
PP_{int}	Chl_{ph}	0.58	0.94	85	0.34	0.000	0.38	5.4
PP_{int}	PP_0	1.01	0.65	85	0.62	0.000	0.28	3.6
PP_{int}	T_0	1.63	-0.01	85	0.000	0.980	0.45	8.1
PP_{int}	I_0	0.83	1.10	69	0.57	0.000	0.31	4.2
PP_{int}	PO_4	1.25	0.53	81	0.22	0.000	0.40	6.3
PP_{int}	$Si(OH)_4$	0.49	0.52	85	0.35	0.000	0.40	6.2
PP_{int}	$NO_2+NO_{3\ av}$	1.36	0.24	85	0.13	0.001	0.42	6.9
PP_{int}	UML	1.49	0.16	85	0.01	0.400	0.45	8.0
PP_{int}	Z_{ph}	1.33	0.24	85	0.03	0.130	0.49	9.5
Chl_0	T_0	-0.48	0.75	113	0.19	0.000	0.34	4.7
PP_0	Chl_0	0.96	1.01	85	0.49	0.000	0.39	6.1
PP_0	P^b_0	1.12	1.17	85	0.58	0.000	0.40	6.2
P^b_{opt}	T_0	-0.01	-0.14	85	0.01	0.460	0.36	5.2
P^b_{opt}	I_0	-0.71	0.90	69	0.56	0.000	0.26	3.2
P^b_{opt}	PO_4	-0.36	0.39	81	0.17	0.000	0.34	4.7
P^b_{opt}	$Si(OH)_4$	-0.79	0.32	85	0.21	0.000	0.32	4.4
P^b_{opt}	$NO_2+NO_{3\ av}$	-0.24	0.14	85	0.07	0.018	0.35	5.0
Z_{ph}	Chl_0	1.24	-0.54	85	0.43	0.000	0.28	3.6

Table 5 Environmental variables in the different regions and water masses of the Kara Sea. M: average value; cv: coefficient of variation (%); N: number of measurements

Variables	Southwestern WM			Ob estuary			Enisey estuary			River runoff WM			Northern WM		
	M	cv	N	M	cv	N	M	cv	N	M	cv	N	M	cv	N
T_0	4.8	19	29	5.3	29	11	7.6	25	12	4.0	44	34	3.3	35	20
S_0	24.9	28	29	2.9	102	11	3.5	115	12	19.1	23	34	31.1	9	20
I_0	10.8	35	11	2.9	27	4	7.4	73	12	6.5	94	28	3.8	43	13
$PO_{4\ av}$	0.2	30	11	1.2	34	7	0.4	95	12	0.5	60	27	0.2	71	18
$NO_2+NO_{3\ av}$	1.8	91	14	3.0	34	7	1.6	104	12	1.4	113	28	1.0	121	18
$NH_{4\ av}$	0.5	56	6	2.1	51	4	1.8	67	12	0.8	57	24	0.7	47	18
$Si(OH)_{4\ av}$	4.8	93	14	36.6	54	7	64.6	61	12	19.8	56	28	2.7	97	18
Si/N	28.9	204	14	15.0	49	7	90.4	101	12	68.9	197	28	8.5	131	18
Si/P	25.5	99	11	33.7	24	7	317	102	12	54.3	123	27	16.9	99	18
N/P	7.0	66	11	3.9	63	7	12.7	92	12	4.4	50	27	9.9	30	18
$NH_4/\Sigma N$	0.6	53	6	0.4	26	4	0.6	47	12	0.5	62	24	0.6	55	18
UML	9	52	29	10	72	11	10	78	12	7	34	34	7	63	20
$\Delta\sigma_t$	6.9	108	29	9.6	53	7	24.4	73	9	23.5	96	30	19.5	101	20

Table 6 Features of chlorophyll *a* maximum in the waters of different trophic status

Trophic status*	Number of the stations with well pronounced SCM	% of the stations with SCM	Width of SCM, m	Chl_{max}, mg m^{-3}	Depth of Chl_{max}, m	SCM manifestation (Chl_{max}/Chl_0)	$\Sigma PP_{max}/PP_{int}$, %	Number of stations where Chl_{max} was below Z_{ph}
0.1 – 0.5	17	68	<u>6–28**</u> 13	<u>0.29–1.26</u> 0.71	<u>9–40</u> 20	<u>1.22–3.56</u> 2.16	<u>5–46</u> 23	1
0.5 – 1.0	5	17	<u>4–6</u> 5	<u>0.71–1.73</u> 1.06	<u>8–30</u> 19	<u>1.22–1.90</u> 1.44	27	3
1.0 – 2.0	2	6	<u>4–5</u> 5	<u>2.20–2.68</u> 2.44	<u>8–15</u> 12	<u>1.51–2.45</u> 1.98	<u>1–13</u> 7	–
>2.0	1	5	5	2.93	9	1.15	1	–

* Waters of different trophic status were separated according to Chl_0, mg m^{-3}.

** The limits of parameters represent above the line and average values below the line.

Table 7 Statistics of vertical distribution of primary production and chlorophyll *a* in the Kara Sea waters of different productivity

Trophic status*	Statistical parameter**	Layer, m																						
		0		0-5		5-10		10-15		15-20		20-25		25-30		30-35		35-40		40-45		45-50	50-55	
		chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*	PP	chl *a*
0.1 -0.5	min	0.20	0.47	0.19	0.47	0.20	0.14	0.08	0.02	0.05	0.00	0.08	0.00	0.03	0.00	0.06	0.34	0.01	0.00	0.12	0.03	0.06	0.07	0.00
	max	0.50	12.26	0.54	12.08	0.65	6.80	0.63	3.46	1.08	5.38	1.13	1.98	1.26	0.51	0.76	0.46	0.47	0.21	0.42	0.20	0.40	0.23	0.10
	M	0.37	4.41	0.39	2.96	0.39	2.11	0.38	1.09	0.41	0.83	0.45	0.44	0.35	0.13	0.29	0.40	0.23	0.11	0.23	0.09	0.19	0.15	0.03
	σ	0.10	2.72	0.08	2.37	0.11	1.28	0.14	0.90	0.24	1.17	0.31	0.52	0.32	0.17	0.22	0.08	0.14	0.08	0.12	0.10	0.15	0.06	0.04
	N	25	21	52	44	45	36	35	24	38	26	23	15	24	13	11	2	12	5	5	3	5	11	7
0.5 -1.0	min	0.52	0.67	0.28	0.31	0.14	0.00	0.07	0.00	0.04	0.00	0.04	0.00	0.03	0.00	0.05	0.00	0.02		0.03		0.02	0.03	
	max	0.93	14.32	1.02	84.23	1.18	3.83	1.09	7.51	1.73	2.60	1.23	0.26	0.71	0.48	0.85	0.00	0.69		0.69		0.33	0.58	
	M	0.74	6.36	0.69	5.46	0.63	1.49	0.49	0.96	0.43	0.57	0.30	0.05	0.26	0.15	0.33	0.00	0.18		0.19		0.16	0.17	
	σ	0.12	4.70	0.15	10.47	0.20	1.26	0.26	1.79	0.35	0.75	0.28	0.09	0.24	0.21	0.28		0.22		0.26		0.15	0.18	
	N	30	23	85	67	54	32	53	29	35	15	30	7	22	7	15	1	8		7		5	9	
1.0 -2.0	min	1.05	2.72	0.39	0.00	0.08	0.00	0.05	0.00	0.03	0.00	0.03	0.00	0.02		0.03		0.05		0.04		0.03	0.07	
	max	1.84	238.7	1.62	66.33	2.20	6.36	2.68	2.68	1.10	1.60	0.94	1.60	1.05		0.25		0.35		0.05		0.12	0.07	
	M	1.35	24.08	1.15	7.56	0.77	1.09	0.54	0.46	0.37	0.79	0.33	0.39	0.19		0.13		0.17		0.05		0.06	0.07	
	σ	0.21	47.18	0.29	9.55	0.42	1.51	0.56	0.80	0.27	0.72	0.24	0.66	0.25		0.09		0.13		0.01		0.03		
	N	36	24	105	84	70	43	47	21	31	6	24	6	18		7		4		2		9	1	
>2	min	2.02	7.11	0.68	0.00	0.56	0.00	0.33	0.00	0.21	0.00	0.15	0.00	0.24		0.13				0.32		0.17		
	max	5.71	109.3	5.70	62.65	5.70	17.39	5.25	1.44	5.25	0.21	5.04	0.00	0.25		0.29				0.32		0.22		
	M	3.39	53.28	3.28	17.32	2.68	2.19	1.88	0.40	2.13	0.07	1.34	0.00	0.25		0.23				0.32		0.19		
	σ	1.13	31.26	1.27	15.46	1.41	3.55	1.56	0.49	1.86	0.12	1.74		0.01		0.07						0.03		
	N	20	17	60	54	36	27	27	19	15	3	15	1	2		4				1		2		

* The trophic categories were separated according to surface chl *a* concentration (mg m^{-3}).

** min и max – limits of values variability; M – averaged value; σ – standard deviation; N – number of data.

Table 8 Average water column daily primary production (mg C m^{-2} d^{-1}) in September in the different regions of the Kara Sea

Regions	Field data (present article)	Mean Kara Sea value (present article)	Models estimates			
			Pabi et al. 2008 (mean Arctic ocean data)	Vetrov & Romankevich 2011	Arrigo & Van Dijken 2011 (range of September data)	Hill et al. 2013** (mean Kara Sea data)
Estuaries*	38–145	72	300	200–1000	280–730	221***
Shelf (<200m)*	69–82		175–300	100–500		
Northern regions (>200m)	32		150	<100		

*The range of average values is presented for Ob and Yenisey regions (Estuaries), River plume WM and Southwestern area (Shelf < 200 m).
**Calculated total monthly primary production is 6.13 Tg C. In daily PP estimating the Kara Sea area is accepted equal to 926 × 10^3 km^2 (Sakshaug 2004).
*** Water column daily primary production was integrated to the shallower of UML or Z_{ph}.

Highlights

- We studied influence of biotic and abiotic factors on Kara Sea primary production in autumn.
- Primary production was largely influenced by the phytoplankton assimilation activity.
- High values of surface chlorophyll were not an index of water column phytoplankton productivity.
- Production characteristics depended mainly on photosynthetically available radiation.
- Models overestimate the *in situ* Kara Sea primary production by a factor of 3–7.