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Fluorescence Parameters of Marine Plankton Algae at the Assimilation of Organic Nitrogen

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Abstract—fluorescence parameters of marine plankton algae *Pseudo-nitzschis delicatissima, Thalassiosira weissflogii*, and *Tetraselmis viridis* were estimated after the addition of organic (urea and glycine) and inorganic (nitrate and ammonia) nitrogen to nitrogen-limited cultures acclimated to limited and saturated irradiance. The photochemical efficiency of photosystem 2, the maximum relative electron transport, and the light saturation index increased in the algae assimilating organic nitrogen. The dynamics of parameters depended species specifically on the nitrogen source and irradiance. The ecological role of organic nitrogen in the seasonal dynamics and vertical distribution of phytoplankton is discussed.

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The primary production in most regions of the World Ocean is controlled by shortage of nitrogen (Glibert, 1988). Nitrogen deficiency leads to the decrease in the efficiency of light reactions of photosynthesis, in the rate of photosynthetic fixation of carbon, and of populational growth of algae (Flakowski and Raven, 1997). Under conditions of the shortage of mineral nitrogen, the significance of consumption of dissolved organic nitrogen (N_{org}) by planktonic algae increases. There is vast information on the capacity of various algae to assimilate organic substrata containing organic nitrogen (see, e.g., Antia et al., 1991) but no data on the dynamics of photosynthetic activity, in particular on light reactions of photosynthesis, at consumption of N_{org}.

A widely used approach for determination of the efficiency of light reactions of photosynthesis is the estimation of fluorescent parameters of photoautotophs. In particular, the relative output of alternating fluorescence reflects the efficiency of photochemical transformation of energy in reaction centers of photosystem 2 (Falkowski and Raven, 1997). This parameter is used as a characteristic of the physiological state of phytoplankton and of its photosynthetic activity (Matorin and Venediktov, 1990; Falkowski and Raven, 1997).

In natural ecosystems the concentration of N_{org} is significantly changing both in time and in space. A significant part in N_{org} consists of substances which can be assimilated by planktonic algae. For example, in the summer the part of nitrogen of urea in the total content of N_{org} may attain 48% and the part of nitrogen of free amino acids—over 25% (Flynn and Butler, 1986). Phytoplankton in natural ecosystems in the surficial layer experiences photoinhibition stress. At the intermediate depths of the photic zone, the illumination is close to the saturation level for photosynthesis. At the lower boundary of the photic zone, the illumination limits photosynthesis. Different light energy resources of phytoplankton and the dependence of the rate of consumption of urea and amino acids by algae on illumination (Bonin et al., 1982; Wallen and Allan, 1987) indicate the investigation of the dynamics of photosynthetic activity in algae assimilating N_{org} at various illumination levels as an urgent problem. This approach acquires special urgency in the aspect of annual increase of organic nitrogen discharged to aquatic ecosystem from anthropogenic sources (Seitzinger and Sanders, 1999).

The present study is aimed at elucidation of special traits of the dynamics of fluorescence parameters of marine planktonic algae *Tetraselmis viridis, Thalassiosira weissflogii*, and *Pseudo-nitzschia delicatissima* at assimilation of urea and glycine under conditions of illumination limiting and saturating photosynthesis.

MATERIAL AND METHODS

The material for the study was algological pure cultures of marine planktonic algae *Pseudo-nitzschia delicatissima* (Cleve) Heiden (Bacillariiphyta), *Thalassisira weissflogii* (Grunow) Freyxell et Hasle (Bacillariophyta), and *Tetraselmis viridis* (Rouch.) Morris (Prasinophyta).

Experimental scheme. The algae were cultivated at illumination 115 (I_1) and 38 (I_2) μE/(m^2s), duration of the light period was 14 h a day, and the temperature was 20 ± 1°C in media prepared with artificial sea water (Shubravyi, 1983) diluted to salinity 17‰. In the experiments the nitrogen-limited cultures of algae were used, acclimated to I_1 or to I_2. Such cultures were obtained by exposition of algae at a certain illumination during 2–3 weeks in the "nitrogen-free" medium. For prepara-

tion of the latter, all ingredients were introduced to water except for nitrogen according to the recipe of medium f/2 (Guilliard and Ryther, 1962). In the nitrogen-limited algae acclimated to a certain level of illumination, the response to the addition of organic (urea and glycine) and mineral (nitrate and ammonia) nitrogen was estimated by fluorescent parameters. The additives were introduced at the concentration 0.18 or 0.89 mmol of nitrogen which corresponds to the content of this element in media f/10 and f/2. The cultures without additives were used as a control. The additives were introduced in the beginning of the light period. In a separate series of experiments, the additives were introduced in the beginning of the dark period to solve the question of if the algae are able to assimilate urea and glycine in darkness.

Estimation of fluorescent parameters. The intensity of fluorescence at the level F_0 (permanent fluorescence) was measured by means of a one-ray fluorometer (Matorin et al., 1992). The intensity of fluorescence at closed reaction centers of photosystem 2 (F_m, maximum fluorescence) was measured similarly in presence of 10^{-5} mol of diuron. The relative output of variable fluorescence $F_v/F_m = (F_m - F_0)/F_m$ is a measure of quantum efficiency of the work of reaction centers of photosystem 2 (RC PS 2) and characterizes the photosynthetic activity of algae (Matorin and Venediktov, 1990; Falkowski and Raven, 1997).

Estimation of parameters describing dependence of photosynthetic activity on illumination (P/E curves). For the nitrogen-limited cultures of *T. viridis* and *T. weissflogii* grown at illuminations I_1 and I_2 and for the cultures of these algae in a day after the introduction of additives of urea, glycine, and nitrate at the concentration 0.18 mmol of nitrogen, the dependence of the photosynthetic activity on illumination was estimated (P/E curves). P/E curves were obtained on the basis of values of relative rate of electrons by the electron transport chain according to methods described by Lippemeier et al. (1999) with some modifications. Up to 10 ml of each variant of cultures were exposed for 30 minutes in test tubes at illuminations 43, 82, 122, 151, and 197 μE/(m^{2}s). Within 30 minutes in each variant of cultures, the quantum efficiency of the work of RC PS 2 was measured directly at exposition illumination (Φ_{P_i}) using a fluorometer RAM-2000 (Walz, Germany). For each variant of cultures, Φ_{P_i} was measured in three replications. The relative rate of electron transport was calculated by the following equation (Lippemeier et al., 1999): $J_i = \Phi_{P_i} \cdot E_i$. According to recommendations (Van Liere and Walsby, 1982), E_i was calculated by the following equation: $E_1 = (E_0 - E_z)/(\ln E_0 - \ln E_z)$, μE/(m^{2}S), where E_0 is illumination in front of the test tube with culture and E_z is illumination behind the test tube.

With consideration of the obtained *P/E* curves, the coefficient of maximum utilization of light energy (the angle of the slope of the *P/E* curve, α), the maximum rate or electrons by the electron transport chain (J_{max}), and saturating light intensity (E_s) were calculated. α was calculated as the coefficient of linear regression plotted by points on the light-limited stretch of the *P/E* curve, J_{max}—as an average by the values of J_i situated on the light saturating stretch (Jassby and Platt, 1976). E_s was calculated by the equation (Platt et al., 1977) $E_s = J_{max}/\alpha$.

In the nitrogen-limited cultures acclimated to illumination I_2, the satiating light intensity was for *T. viridis* 105 μE/(m^{2}s); for *T. weissflogii* it was 90 μE/(m^{2}s). Consequently, I_2 is the illumination limiting photosynthesis. In the nitrogen-limited cultures acclimated to illumination I_1, E_s was for T. viridis 97 μE/(m^{2}s), and for *T. weissflogii* it was 95 μE/(m^{2}s). At the illumination 122 μE/(m^{2}s), there was a decrease in J_{max}. Accordingly, I_1 is the illumination exceeding E_s and may partially inhibit the rate of electronic transport. The values of E_s in pennate diatoms provided with components of mineral nutrition are within 42–150 μE/(m^{2}s) (Geider et al., 1985; Willemoës and Monas, 1991). With consideration of published data and of the fact that in the nitrogen-limited algae E_s are lower than those in the algae provided with biogenous elements (Kolber et al., 1988), it may be assumed that, for the diatom *P. delicatissima*, I_2 is the illumination limiting photosynthesis and I_1 exceeds E_s and may partly inhibit the rate of electronic transport.

RESULTS AND DISCUSSION

Dynamics of the relative output of alternating fluorescence in the algae assimilating organic and mineral nitrogen. In the nitrogen-limited algae, the values F_v/F_m were 0.2 and less. Low values of F_v/F_m correspond to the general pattern of disturbance of action of the photosynthetic apparatus (PA) at limitation of nitrogen revealed earlier both in marine and freshwater algae of various taxonomic positions (Chemeris et al., 1989; Kolber et al., 1988; Geider et al., 1993; Falkowski and Raven, 1997; etc). After addition of both urea and glycine in all three algae, F_v/F_m increased. This indicates that the assimilated N_{org} was used for restoration of PA. Duration of the period before the increase of F_v/F_m (T_{inc}) at assimilation of N_{org} in most cases does not differ significantly from T_{inc} at assimilation of mineral nitrogen (N_{min}) (Table 1). The exceptions are higher values of T_{inc} at growth with additions of urea and glycine than at growth with additions of nitrate in the alga *P. delicatissima* at I_2 and lesser values of T_{inc} at assimilation of urea and glycine than at assimilation of nitrate in *T. weissflogii* at I_1. For the increase of F_v/F_m in all three algae when the substrata are used with the same level of reduction of nitrogen (urea, glycine, and ammonium), approximately identical time is required. In a similar way, the values T_{inc} in the case of assimilation of reduced organic nitrogen did not differ significantly from those in the case of assimilation of

Table 1. Duration of the period from the moment of introduction of additives of urea, glycine, nitrate, and ammonium at the concentration 0.89 mmol of nitrogen to the beginning of the increase of the quantum efficiency of photosystem 2 (T_{inc}) and the highest values attained by the quantum efficiency of photosystem 2 $(F_v/F_m)_{max}$ in the algae *Tetraselmis viridis* (*Tv*), *Thalassiosira weissflogii* (*Tw*), and *Pseudo-nitzschia delicatissima* (*Pd*) at the growth under conditions of illumination 115 (I_1) and 38 (I_2) μE/(m^2 s)

Algae	Nitrogen source	I_1		I_2	
		T_{inc}, h	$(F_v/F_m)_{max}$	T_{inc}, h	$(F_v/F_m)_{max}$
Tv	Urea	3.7 (2.1)	0.42 (0.08)	1.8 (1.5)	0.52 (0.09)
	Glycine	4.2 (2.5)	0.39 (0.04)	2.6 (2.0)	0.48 (0.01)
	Nitrate	1.8 (0.9)	0.44 (0.10)	1.0 (0.8)	0.46 (0.03)
	Ammonium	3.0 (2.7)	0.48 (0.06)	4.0 (0.7)	0.49 (0.01)
Tw	Urea	4.5 (2.6)	0.38 (0.07)	3.5 (2.8)	0.52 (0.09)
	Glycine	4.0 (2.3)	0.51 (0.06)	2.5 (1.9)	0.48 (0.01)
	Nitrate	>11.5	0.41 (0.02)	3.0 (2.4)	0.54 (0.03)
	Ammonium	5.5 (4.8)	0.40 (0.05)	4.0 (0.6)	0.54 (0.01)
Pd	Urea	>10	0.25 (0.05)	>12	0.43 (0.07)
	Glycine	>10	0.32 (0.04)	3.5 (2.0)	0.56 (0.01)
	Nitrate	8.0 (2.0)	0.39 (0.08)	1.5 (0.8)	0.60 (0.03)
	Ammonium	>10	0.30 (0.04)	>12	0.63 (0.01)

Note: In parentheses the value of standard deviation is indicated.

oxidized nitrate nitrogen, but only in algae at limiting illumination. The only exception was *P. delicatissima* in which restoration of F_v/F_m in the case of assimilation of urea required more time than in the case of assimilation of nitrate. At I_1 the species specificity of algae manifests itself in the response to additives of N_{org} and nitrate. Thus, in *T. viridis*, T_{inc} does not differ significantly at assimilation of N_{org} and nitrate. In *T. weissflogii* the value F_v/F_m began to increase the earliest at growth with assimilation of urea, and in *P. delicatissima*—with assimilation of nitrate.

The species specificity of algae also manifests itself in the highest value of the relative output of alternating fluorescence $(F_v/F_m)_{max}$ attained in the first three days of growth on various forms of nitrogen. The ratio of values $(F_v/F_m)_{max}$ at assimilation of N_{org} and N_{mnr} depends on illumination (Table 1). Thus, in *T. viridis* and *T. weissflogii*, the values $(F_v/F_m)_{max}$ at assimilation of urea and N_{mnr} did not differ significantly from each other at two levels of illumination. In *P. delicatissima* the values of $(F_v/F_m)_{max}$ at assimilation of urea were lower than those at assimilation of N_{mnr}. At assimilation of glycine, the highest values of F_v/F_m did not differ significantly from those at assimilation of N_{mnr} in *T. viridis* and *P. delicatissima* at both illuminations. The highest values of F_v/F_m in the cultures of *T. weissflogii* assimilating glycine at I_1 were higher than $(F_v/F_m)_{max}$ at the assimilation of N_{mnr}. In addition, in *P. delicatissima* at both illuminations and in *T. weissflogii* at I_1, the values $(F_v/F_m)_{max}$ at assimilation of glycine were higher than at the assimilation of urea. The latter might depend on direct incorporation of glycine in protein without previous transformation in *P. delicatissima* and *T. weissflogii*, as this occurs, e.g., in the dinoflagellate *Gymnodinium breve* (Baden and Mende, 1979) and in the green alga *Chlamydomonas reinhardtii* (Kirk and Kirk, 1978).

The increase in F_v/F_m started during the light period; in the first hours of it, the additives were introduced (except *T. weissflogii* assimilating nitrate at I_1). If the additives of nitrogen were introduced in the dark period, then, in the beginning of the next light period, the higher values of F_v/F_m were noted in algae exposed with additives in comparison with the control cultures (Table 2). This points to assimilation by the algae *T. viridis, T. weissflogii*, and *P. delicatissima* of additives in the dark as the exposition of the algae at light before measurements did not exceed the values T_{inc} recorded at the introduction of additives in the beginning of the light period.

The ability of N_{mnr} to assimilate in the dark increases with the increase of the nitrogen deficiency in the cells (Clark and Flynn, 2002). The dark assimilation occurs at the expense of energy and of the reducer formed in the mitochondrial electron transport chain (Van Lerberghe et al., 1992). As a substrata of the tricarbonic acid cycle in the dark, the products of glycolytic decomposition of reserve carbohydrates are used (Granum and Myklestad, 2001). If the reserve carbohydrates are the energy source at assimilation of mineral nitrogen in the dark, it may be assumed that the mito-

Table 2. The relative (in relation to the control) values of the quantum efficieny of photosystem 2 in the algae *Tetraselmis viridis* (*Tv*), *Thalassiosira weissflogii* (*Tw*), and *Pseudo-nitzschia delicatissima* (*Pd*) acclimated to illumination 115 (I_1) and 38 (I_2) μE/(m^2 s) at the introduction of additives of urea, glycine, nitrate, and ammonium at the concentration 0.89 mmol of nitrogen in the beginning of the dark period

Nitrogen source	*Tv*		*Tw*		*Pd*	
	I_1	I_2	I_1	I_2	I_1	I_2
Urea	1.52	2.32	1.36	1.67	1.11	1.28
Glycine	1.45	1.90	1.91	1.83	1.21	1.45
Nitrate	1.13	1.47	1.55	1.88	1.68	1.45
Ammonium	1.52	1.84	1.59	1.79	1.00	1.27

Note: Duration of the period from introduction of the additives was 10–11 hour, of which, in the latter 2–3 h, the algae were exposed to light.

Table 3. Parameters describing the dependence of the photosynthetic activity on illumination in the algae *Tetraselmis viridis* and *Thalassiosira weissflogii* acclimated to illumination 38 (I_2) and 115 (I_1) μE/(m^2 s) in the 24 h after introduction of additives of urea, glycine, and nitrate at the concentration 0.18 mmol to the nitrogen-limited cultures (control)

	Additives	α, rel. units	J_{max}, rel. units	E_s, μE/(m^2 s)
		Tetraselmis viridis		
I_2	Control	0.17 (0.03)	18 (2.7)	105 (12)
	Urea	0.26 (0.03)	37 (5.6)	142 (33)
	Glycine	0.32 (0.03)	43 (5.6)	134 (42)
	Nitrate	0.38 (0.04)	44 (6.1)	116 (49)
I_1	Control	0.17 (0.02)	16 (1.5)	97 (4)
	Urea	0.19 (0.03)	37 (3.5)	195 (44)
	Glycine	0.23 (0.06)	35 (3.5)	152 (58)
	Nitrate	0.22 (0.08)	39 (4.1)	177 (98)
		Thalassiosira weissflogii		
I_2	Control	0.30 (0.14)	27 (9.3)	90 (13)
	Urea	0.34 (0.10)	57 (5.1)	168 (23)
	Glycine	0.36 (0.09)	62 (7.0)	172 (22)
	Nitrate	0.56 (0.10)	88 (15.0)	157 (39)
I_1	Control	0.20 (0.07)	19 (1.4)	95 (14)
	Urea	0.33 (0.06)	40 (8.0)	114 (33)
	Glycine	0.35 (0.07)	42 (4.0)	120 (26)
	Nitrate	0.34 (0.06)	43 (10.1)	126 (43)

Note: α is the cioefficient of maximum utilization of light energy, J_{max} is the maximum relative rate of electrons via the electron transport chain, and E_s is the satiating light intensity. In parentheses the value of standard deviation is indicated.

chondrial NADP · H and ATP are used for assimilation in the dark of urea and glycine too.

Parameters describing the dependence of the photosynthetic activity on illumination (P/E curves) in the algae T. viridis and T. weissflogii assimilating organic and mineral nitrogen. In the day after the introduction of both additives, N_{org} and N_{mnr} parameters describing *P/E* curves differed from those in the nitrogen-limited cultures (Table 3). This points to the change at assimilation of N_{org} of the intensity and direction of biophysical, biochemical, and metabolic processes regulating photosynthesis.

In both algae growing with assimilation of N_{org} at illumination I_1 and in *T. viridis* at I_2, the increase in α and J_{max}, in comparison with the values of these parameters in the nitrogen-limited cultures, corresponded to the level of the increase at N_{mnr} assimilation. At illumination I_2 in *T. weissflogii*, the greatest increase of α and J_{max} occurred in the cultures which grew with the assimilation of nitrate. The algae manifested a species-specific response of the parameter α to additives of N_{org} depending on illumination. Thus, in *T. weissflogii* the values of α increased more at I_1, while in *T. viridis*—at I_2. On the contrary, J_{max} increased approximately equally at two illuminations both in *T. viridis* and in *T. weissflogii.* In the alga *T. weissflogii* assimilating N_{org} during 24 h, the values α and J_{max} corresponded to the values of parameters in the cultures of this alga provided with components of mineral nutrition and growing at 600 μE/(m^{2}s) (Lippemeier et al., 1999).

In both species of algae in the 24 h after the introduction of additives, the satiating light intensity increased too (Table 3). Inhibition of the relative rate of electron transport at illumination up to 150 μE/(m^{2}s) was not observed. The values E_s in *T. viridis* increased more at I_1, and in *T. weissflogii* it increased at I_2.

CONCLUSIONS

The marine planktonic algae *Pseudo-nitzschia delicatissima, Thalassisira weissflogii*, and *Tetraselmis viridis* are able to grow using urea and glycine as a sole source of nitrogen. These algae assimilate urea and glycine in the dark too. In this case the energy and substrate expenditures for consumption and intracellular transformation of the substrata are covered, obviously, by the oxidation of reserve polysaccharides as is the case at the dark assimilation of mineral nitrogen.

In all three species of algae at a high level of cellular nitrogen deficiency, the assimilation of urea and glycine contributes to the increase of the relative output of alternating fluorescence, maximum relative rate of electrons via the electron transport chain, and the value of satiating light intensity. This indicated the use of the assimilating N_{org} for restoration of the normal action of the photosynthetic apparatus. The algae are characterized by the species-specific dependence of the dynamics of F_v/F_m on illumination. They are also character-

ized by the species-specificity in the ratio F_v/F_m at N_{org} and N_{mnr}. In many cases the dynamics of F_v/F_m at assimilation of urea and glycine did not differ from that at the assimilation of N_{mnr}.

In natural ecosystems the mineral and organic resources of phytoplankton and the source of light energy vary in time and space. For example, in the seas with the expressed seasonal dynamics of abiotic factors, the development of phytoplankton in spring lead to a complete depletion of mineral nitrogen in the photic layer. The relative part of N_{mnr} in the total content of dissolved nitrogen decreases and the part of N_{org} increases (Mantoura et al., 1988). In the summer, the part of urea–nitrogen may attain 48% in the total content of dissolved nitrogen and the part of nitrogen of free amino acids may attain over 25% (Flynn and Butler, 1986). Under such conditions, in some cases, phytoplankton develops intensively. It is represented, as was shown, e.g., for the White Sea (Ilyash et al., 2003), principally by mixotrophic diatoms and flagellates. We revealed for the algal cultures the efficient restoration of the photosynthetic apparatus at the expense of assimilation of urea and glycine. It pointed to formation of the summer "bloom" of diatoms, and the mass development of flagellates may depend on their capacity for the assimilation of nitrogen-containing organic substrata and for support from resources of N_{org} of normal functioning of the photosynthetic apparatus and populational growth.

The quantity of N_{org} of anthropogenous origin released to aquatic ecosystems increases every year (Seitzinger and Sanders, 1999). The increase in the abundance of organic resources available to algae may change the productivity of ecosystems. For example, during the recent decade, the biomass of the diatom *Skeletonema costatum* increased by more than an order of magnitude in the coastal waters of the White Sea. It may be attributed to greater discharge to the sea of organic nitrogen predominantly of anthropogenous origin (Ilyash et al., 2003).

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